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A TAXONOMIC REVISION OF SAGINA (CARYOPHYLLACEAE) IN NORTH AMERICA[1]

GARRETT E. CROW

Sagina (Pearlwort), a genus of the Caryophyllaceae, consists of about 15 species indigenous to the cool temperature regions of the Northern Hemisphere. The genus is well defined, although it is occasionally confused with superficially similar taxa of *Spergularia* and *Arenaria.* Confusion with taxa of *Colobanthus,* the genus most closely related to *Sagina* (Pax & Hoffman, 1934), seldom occurs because *Colobanthus* is a circumaustral genus.

There has been, however, confusion within the genus regarding delineation of taxa. Wright (1935, p. 1) commented "I find among my friends many who are unwilling to give a definite opinion on Saginas, regarding them difficult to determine. I think such opinion arises from inadequate realisation of the extreme variability of these plants." The extreme variability within the genus has generated nomenclatural recognition of numerous variants, especially in Europe, the primary center of diversity for the genus. Many of these taxa were based on characters which are inconsistent in expression.

Previous work of a revisionary nature in *Sagina* is limited. Works include only a revision of the British species of *Sagina* by Williams (1918) and a treatment of the species of *Sagina* occurring in Japan by Mizushima (1960).

My study was undertaken with the intention of assessing the variability within the genus and attempting to clarify interspecific and intraspecific relationships. Over 6000 herbarium specimens, European and east Asian as well as North American, were ex-

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[1] Published with the approval of the Director of the University of New Hampshire Agricultural Experiment Station as Scientific Contribution No. 875.

amined. Most of the North American taxa have also been studied in the field and in a growth chamber. An analysis of the seed morphology, utilizing scanning electron microscopy, has been helpful in assessing relationships within the genus.

This revision is presented to provide a better understanding of the species in North America, to contribute to the knowledge of the entire genus and to benefit resolution of problems in the classification of other genera of the subfamily Alsinoideae.

HISTORICAL ACCOUNT

Botanical history of *Sagina* begins in the 17th Century with the finding of *S. nodosa* by John Goodyer on August 12, 1626, "on the boggy ground below the red Well of Wellingborough in Northamptonshire" in Great Britain, recorded in Johnston's Herball in 1633 under the name "Saxifraga palustris alsine folia" (Williams, 1918; Druce, 1932). In 1719 Dillenius included the Pearlworts under the generic name *Alsinella* in his *Catalogus Plantus,* a pre-Linnean name perpetuated by Hill (1756) in *The British Herbal* and by Greene (1891) in *Flora Franciscana.*

The generic name *Sagina* first appears in print in Linnaeus' *Systema Naturae* in 1735. His *Genera Plantarum* (1737b) indicates it was based on *S. procumbens.* In *Species Plantarum* (Linnaeus, 1753) the genus included two tetramerous members of the tribe Alsineae, *Sagina procumbens* and *Moenchia erecta,* and a third species, *Bartonia virginica,* now recognized as belonging to the Gentianaceae.

Presl (1826), in his *Flora Sicula,* was the first to include any of the exstipulate Spergulas in the genus *Sagina.* Dumortier (1827), on the other hand, recognized the non-stipulate Spergulas of Linnaeus as a distinct genus, *Phaloe.* Reichenbach (1827) likewise regarded this group as a separate genus, giving it the name *Spergella.* Fenzl's (1833) redefinition of *Sagina* retained only *S. procumbens* of Linnaeus' genus and incorporated Reichenbach's *Spergella.* Koch (1837), in the first edition of *Synopsis Florae Germanicae et Helveticae* retained Reichenbach's *Spergella* in the genus *Spergula* as sect. *Spergella.* In the second edition (Koch, 1843) he transferred sect. *Spergella* to *Sagina,* thus erecting the subdivisions in *Sagina* as sect. *Saginella,* including the 4-merous taxa, and sect. *Spergella,* comprising the 5-merous taxa.

Although this subdivision is sometimes followed in European floristic works, it neither adequately reflects natural relationships, nor provides a practical basis for classification. Not only are there both 4- and 5-merous plants within taxa, but individual plants may have both types of flowers.

Moss (1920), in his treatment of *Sagina* for the *Cambridge British Flora* regarded the species as being too closely allied to be meaningfully subdivided into distinct groups higher than series. Thus, he treated the British Saginas in four series: *Nodosae, Subulatae, Procumbentes,* and *Apetalae.* With the exception of ser. *Apetalae* his groupings are quite natural. However, they deal only with the British species.

Mizushima (1960) likewise concluded that generic subdivision does not merit rank above series level and attempted to apply Moss' series to the east Asian Saginas, but found it necessary to redefine these series. Unfortunately he based these divisions on 4-merous taxa versus 5-merous taxa.

Recently, Löve and Löve (1975) have expressed the viewpoint that *Sagina,* at the generic level, is heterogeneous, and they support recognition of three genera on cytological grounds: *Sagina* L., characterized by a basic chromosome number $x = 11$; *Saginella* Koch (never published at the generic level) with a basic number of $x = 6$; and *Spergella* Reichb., with a basic number of $x = 7$. Unfortunately both taxa which the Löves transferred to *Spergella* (*Sagina caespitosa* and *S. intermedia*) have a basic number of $x = 11$ (not $x = 7$). In my opinion neither cytological nor morphological evidence suggests that *Sagina* should be divided at the generic level.

FLORAL MORPHOLOGY

Inflorescence. The flowers of *Sagina* are borne singly and are terminal and axillary in position. Vivian (1942) has shown in an investigation of phyllotaxy in *S. procumbens* that this apparent floral arrangement is, in actuality, a modification of the typical caryophyllaceous cymose inflorescence, a uniparous scorpioid cyme.

Flowers. The flowers are quite small and generally inconspicuous. Both pentamerous and tetramerous flowers occur. Gynodioecy has been observed in some European populations of *Sagina procumbens, S. saginoides, S. nodosa* and *S. nivalis* (Müller, 1883); however, this state has not been observed in the North American plants.

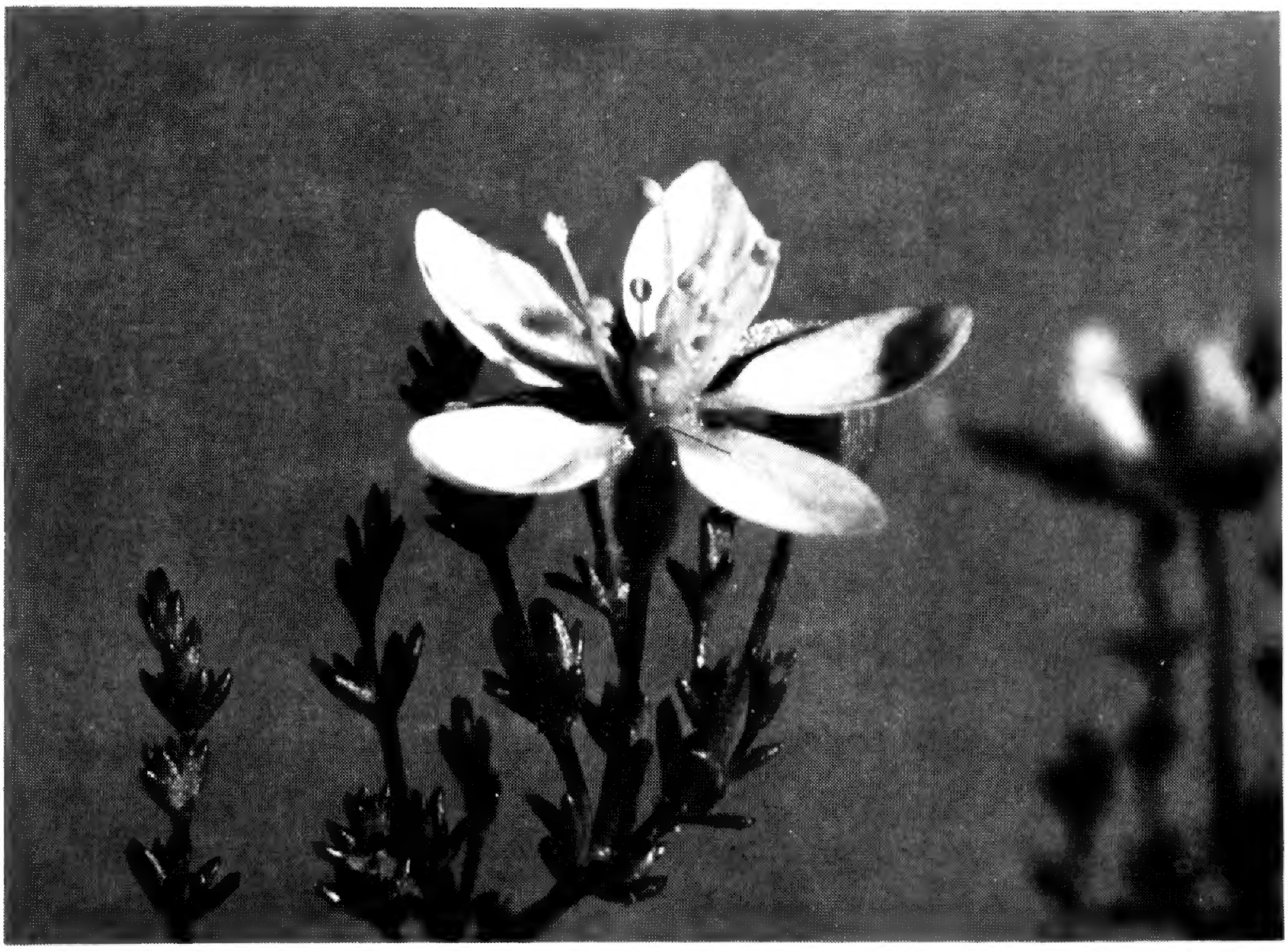

Figure 1. *Sagina nodosa*. Flower showing nectariferous gland at the base of outer whorl of stamens (opposite sepals).

Glandular hairs occur associated with the flowers in several taxa. Most densely concentrated at the calyx base and uppermost portion of the pedicel, the hairs are uniseriate, arising from the ep dermis and consisting of three or four cells with a knobbed gla at the apex (Figure 2).

Calyx. The sepals are separate to the base and elliptical to orbicular and blunt at the apex. Rarely are the sepals acute and this is never characteristic of a taxon. A narrow band of hyaline tissue occurs around the margins of the sepals and is generally whitish. When anthocyanins are abundant in the sepals the whole sepal may take on a purplish cast. More frequently, color is concentrated in the hyaline margin or sometimes only the tip takes on the distinctive purplish tinge. In bud the sepals are imbricate, cupped and frequently cucullate. Sepal size does not increase during capsular maturation.

Corolla. Occasionally emarginate, the petals alternate with the sepals, are thin, white, elliptical to orbicular in shape, have a short claw at the base and are typically blunt at the tip. Development occurs late in the bud stage, and in some taxa the petals remain poorly developed, vestigial, or aborted. In the annual taxa the petals are frequently caducous. In taxa where the petals are shorter than, equal to, or slightly exceeding the sepals, there is very little shrinkage and no withering. Petals which conspicuously exceed the sepals wither considerably following anthesis.

Androecium. The stamens occur in one or two whorls and are the same number as or twice that of the styles. Stamens of the outer whorl, opposite the sepals, are nectariferous at the base (Figure 1). In cases where there is one whorl, it is the outer, nectariferous whorl which is present. Meiosis and pollen grain maturation take place very early in the bud stage, long before stamens take on a mature form. Anther dehiscence is longitudinal and extrorse. Individual cases of aborted stamens are not uncommon in the genus. Anther dehiscence more frequently occurs prior to floral anthesis and stamens are only very slightly exserted beyond the calyx and never exceed the stigmas. Filaments ultimately bend toward the stigmas, effecting self-pollination.

The pollen grains (Figure 3) are spherical, range between 18 μ and 36 μ in size (mean = 27.5 μ), and are periporate. The pores have a distinct annulus, are ca. 30 in number, and are evenly distributed. The tectum has indistinct perforations and is distinctly scabrate (terminology from Faegri & Iversen, 1964).

Gynoecium. The ovary is 4- or 5-carpellate with formation of carpel walls arrested early in development, resulting in free-central placentation (Lister, 1884). Ovules are campylotropous. Coherent styles arise from a disc at the apex of the ovary. Elongation occurs just prior to or at anthesis, the styles separating and their inner surfaces becoming papillate and stigmatic. Styles alternate with the sepals and are opposite the sutures of the capsules.

Fruit. The fruit is a capsule with the number of capsule valves equal to that of the styles and sepals. Sutures run from the apex to the base, dehiscence varying from one-fourth the capsule length to the entire length. The capsule remains green until late in the developmental stage and becomes tan or straw-colored upon maturity. According to the fruit classification of Kaden and Kirpicznikov (1965), the fruit type would be termed a cerastiocarpum.

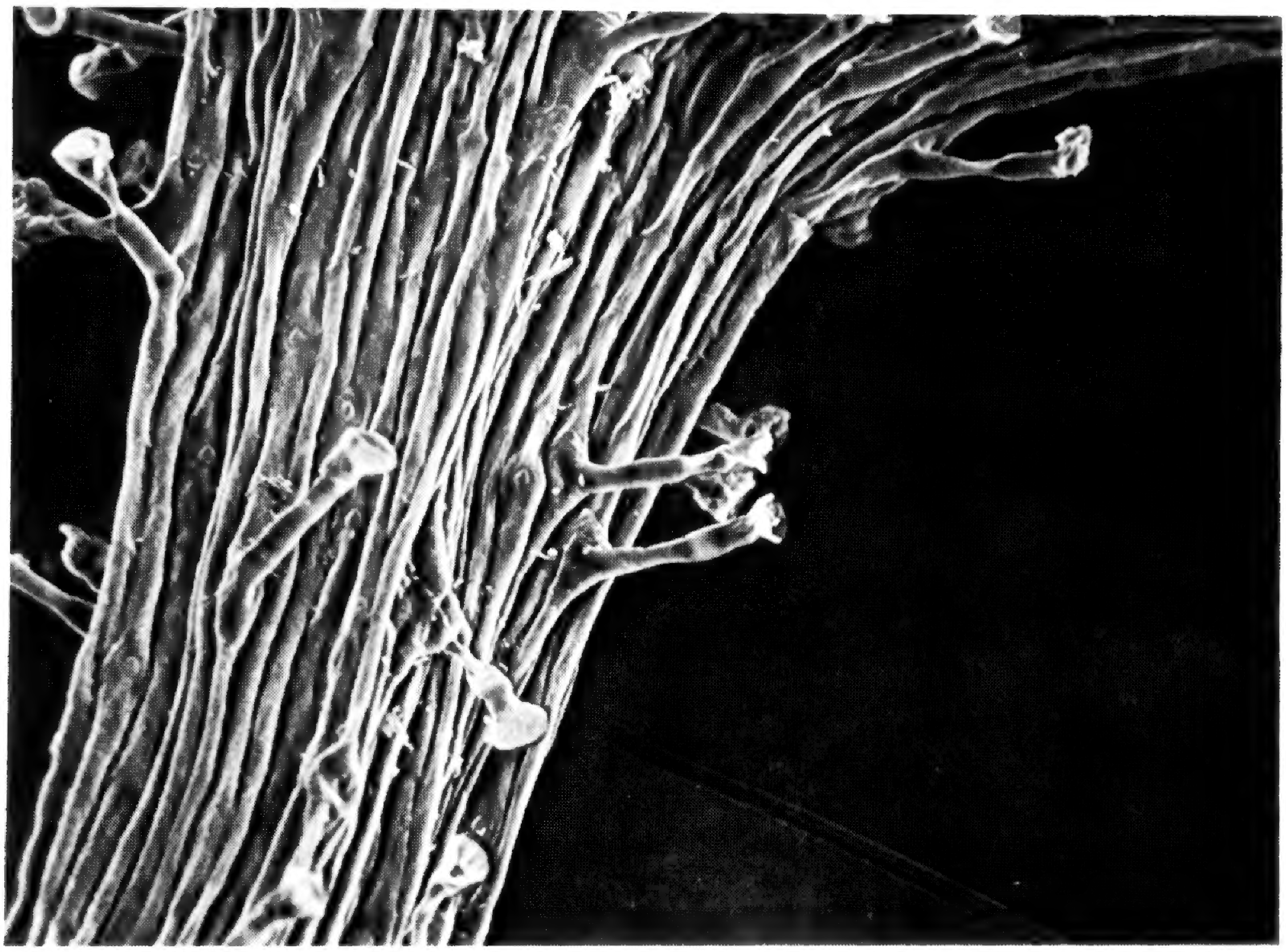

Figure 2. *Sagina nodosa.* SEM micrograph of pedicel showing glandular hairs. × 200.

POLLINATION

The flowers of *Sagina* are all capable of self-fertilization. However, a trend exhibiting a progression from outcrossing to selfing and culminating in cleistogamy can be observed within the genus.

The flowers in *Sagina* open under bright conditions. The stamens of the outer whorl secrete some nectar and insect visitation is thus solicited, though somewhat feebly. Under dull weather conditions the flowers usually remain closed and self-pollination occurs.

There appears to be a strong correlation between petal size and tendency to inbreed, for those plants with the strongest tendency toward selfing and toward cleistogamy are those in which the petals are reduced or lacking.

Sagina nodosa, the strongest outcrosser, is the largest flowered species, with petals being about twice the length of the sepals. The stamens occur in two whorls. The anthers of the outer, nectariferous whorl dehisce at anthesis, while the stigmatic surfaces remain unexposed. Later, the stigmatic surfaces become exposed, receptive and cross-pollination is encouraged. When the sepals close and push the inner whorl of stamens, with its remaining pollen, onto the stigmas, autogamy results (Wright, 1935).

A further step toward self-fertilization can be seen in *Sagina procumbens*. In this species the androecium is generally reduced to one whorl, the outer, nectariferous whorl. At anthesis the stigmas are receptive and curled toward the stamens. The filaments, in turn, are bent toward the stigmas and the anthers shed their pollen directly onto the stigmas. The nectaries are functional and a few small flies and bees have been reported as visitors (Knuth, 1908). However, the tendency is clearly toward self-pollination, for even in favorable weather the flowers frequently remain closed and effectively pollinate themselves.

In *Sagina apetala*, an annual whose petals are lacking or quickly caducous, pollination takes place quite regularly prior to the flower opening, if, indeed, the flower opens at all.

DISPERSAL

The tiny, light seeds of *Sagina* are well adapted to wind dispersal. Under calm weather conditions dispersal is minimal and seeds remain in the vicinity of the parent plant. In species where dehiscence occurs along the entire length of the sutures, capsule dehiscence is somewhat explosive and seeds are scattered several inches. Raindrops appear to be an effective means of scattering seeds in those species where capsule dehiscence is less than half the length of the capsule. Brodie (1951) has observed this splash-cup dispersal mechanism in *Sagina decumbens* ssp. *decumbens* and has measured dispersal distances up to 18 inches.

Although dispersal is minimal on quiet days, when there is a high degree of air turbulence near the ground light seeds can be lifted to sufficient heights for long distance dispersal to take place (Ridley, 1930; Dahl, 1958; D. Löve, 1963). The seeds of *Sagina* are regarded as prime candidates for long distance dispersal (D. Löve, 1963) and are categorized as "dust diaspores" by Van der Pijl (1969).

PHYTOGEOGRAPHY

Native taxa. The modern distribution patterns of boreal and cool temperate species in North America reflect the effect of Pleistocene glaciation. Thus the postglacial distributions of *Sagina* must be evaluated in this light and an attempt be made to determine where

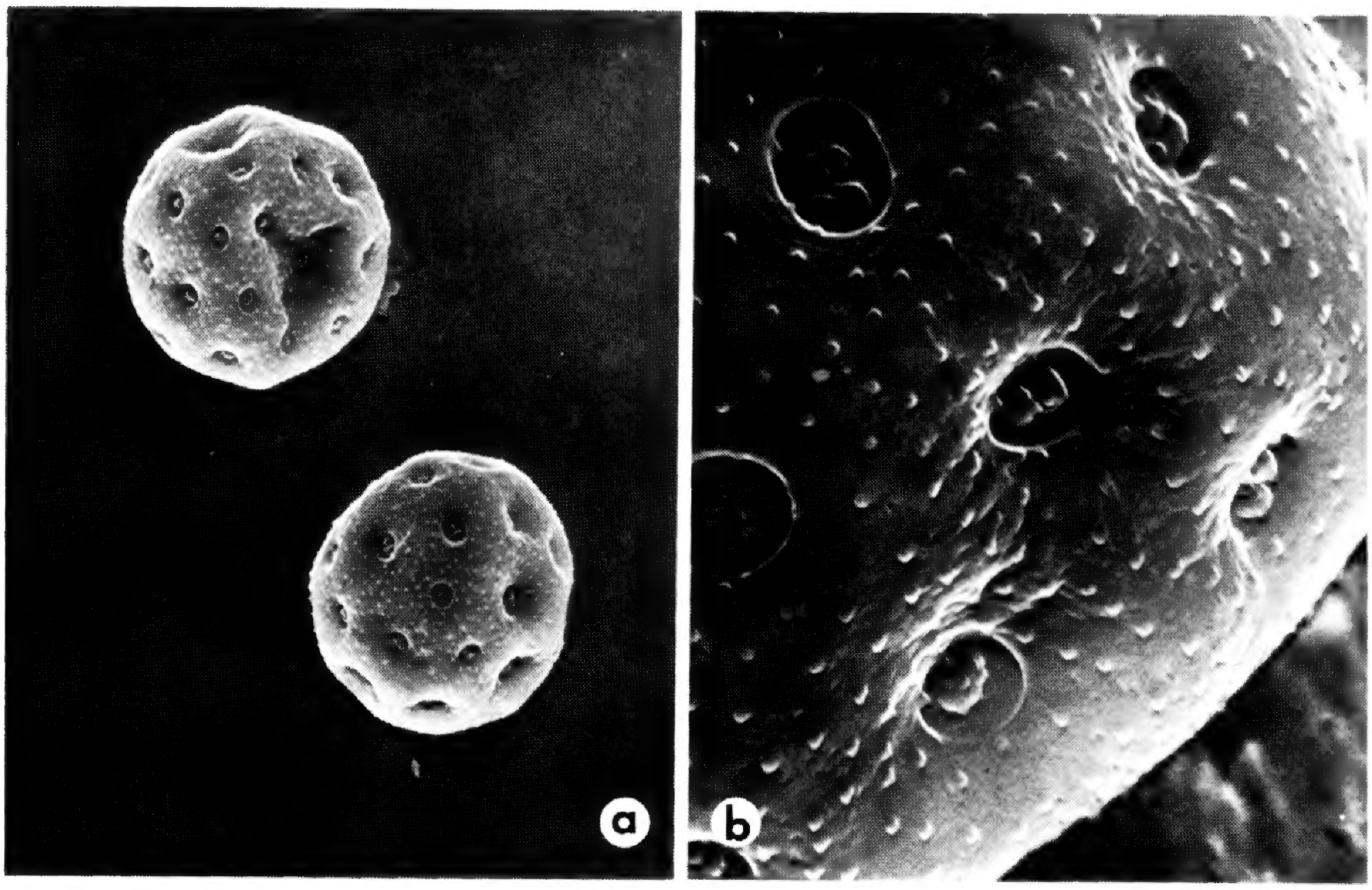

Figure 3. *Sagina nodosa.* Pollen grains. a. × 1000; b. × 5000.

the taxa may have survived the glacial advances.

Circumpolar *Sagina nivalis* is widespread in the North American Arctic and appears to have survived the Pleistocene in the Beringian refugium. A large portion of Alaska, including the Bering Strait region and the North Slope remained ice-free during glacial advances (Péwé *et al.,* 1965; Heusser, 1965) and the geographical distributions of numerous arctic species suggest a "Beringia radiant" pattern (Hultén, 1937).

Although portions of the high Arctic Archipelago do not show signs of glaciation (Flint, 1957; Savile, 1961), this region probably did not serve as a refugium. One would not expect a region like the northwest Elizabeth Islands, with a depauperate flora and stunted plant growth, to function as a survivium (Savile, 1961). Savile is of the opinion that the flora of this region is one recently derived.

Present on Prince Patrick Island and Axel Heiberg Island, but not between, the distribution of *Sagina nivalis* shows a noticeable gap in the region of the northwest Queen Elizabeth Islands. The gap apparently does not reflect lack of collecting, for Savile (1961), who has done much collecting in this region, notes that the distributions of a number of widespread arctic species exhibit this pattern.

Rare disjunct populations of *Sagina nivalis* occur southward in the alpine habitat along the Cordilleran system to Alberta. It is possible that these populations are relictual. Another possible explanation is that these populations are a result of long distance dispersal having become established in suitable niches in newly opened habitats in the glaciated alpine of the Cordilleran range.

Sagina caespitosa, a rare species, exhibits an amphi-Atlantic distribution, occurring as a coastal plant in the eastern Arctic, western and southern Greenland, and as a montane plant on Iceland and in Scandinavia. The existence of coastal mountain refugia, as described by Dahl (1946), provides the most plausible explanation of survival. Dahl notes that nunataks occurring in western Greenland support a relatively rich flora. The populations occurring in the eastern Arctic of North America have distinct affinity with populations of western Greenland, pubescence of pedicel being present in both, while plants in populations of southern Greenland, Iceland, Jan Mayen and Scandinavia are completely glabrous.

The circumpolar distribution of *Sagina saginoides* correlates almost entirely with montane regions of the Northern Hemisphere. Hultén (1958) notes that the Pleistocene fragmented many circumpolar distributions. This seems to be the case here.

In North America this species survived Pleistocene glaciation in the southern portion of the Cordillera. Although mountain glaciation occurred during the Pleistocene, Weber (1965) points out that large areas in Colorado were free of ice. In the Sierra Nevada, glaciers descended to 1300–2200 meters elevation but numerous refugia existed throughout the range (Wahrhaftig & Birman, 1965). Recession of alpine glaciers in the Olympic Mountains occurred during continental expansion of the Cordilleran ice sheet, thus refugia occurred nearby at the time the Puget Sound lobe reached its maximum (Crandell, 1965).

Mount Albert, on the Gaspé Peninsula of Quebec, has a serpentine summit which supports an alpine flora containing a curious Cordilleran element, including *Sagina saginoides.* Fernald (1925b) considered these disjuncts to be relictual, persisting through the glacial period on this unusual nunatak, but his theory has lost much credibility. Marie-Victorin (1938) does not consider this serpentine habitat as a nunatak, but rather regards it simply as a place where arctic plants can survive while others cannot. The presence of *S. saginoides* at one locality on the eastern shore of Hudson Bay, one locality near Schefferville, Quebec, on the Labrador-Quebec Penin-

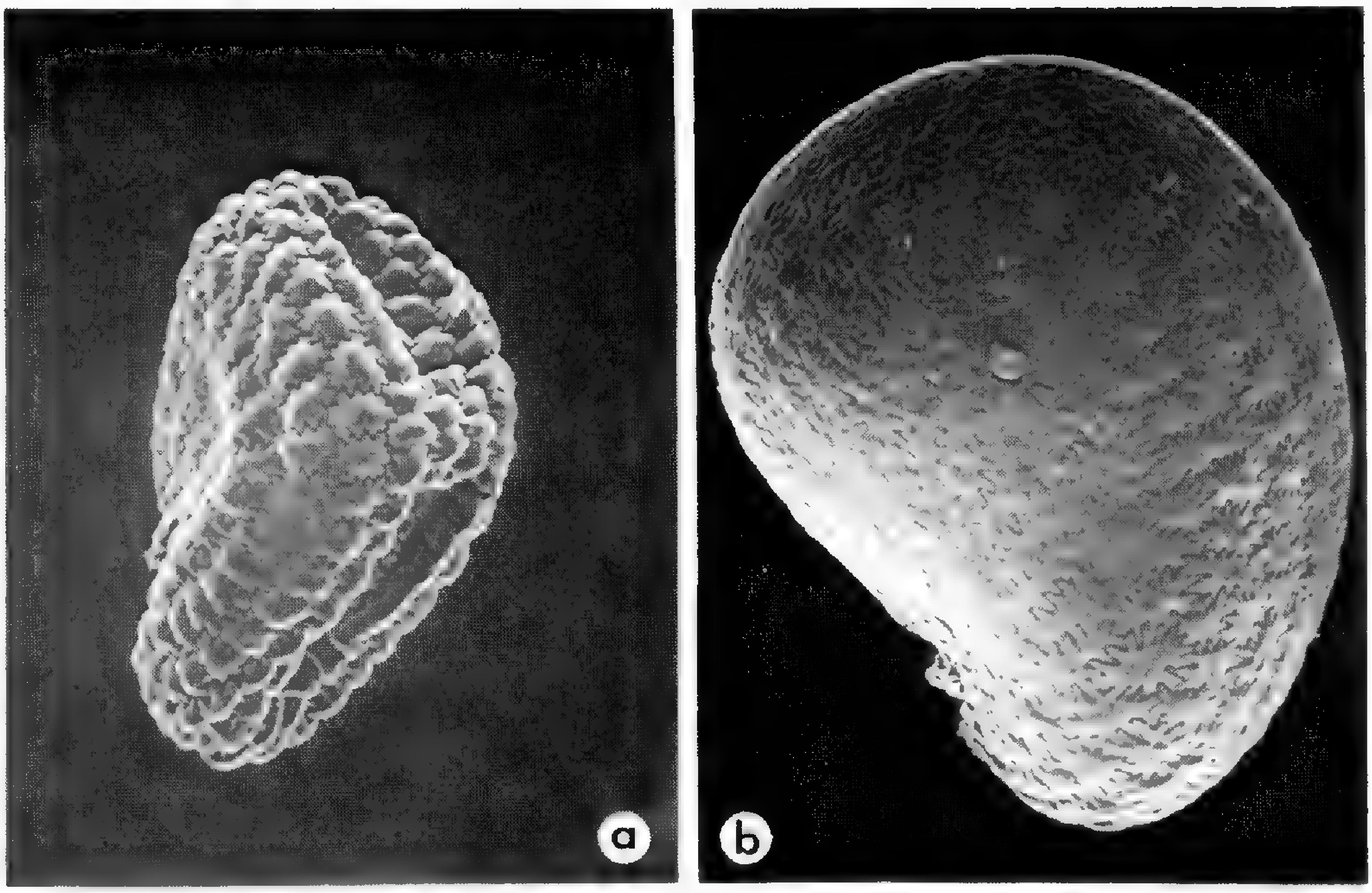

Figure 4. Seed types. a. saginoid seed type, *Sagina apetala*, oblique view showing dorsal groove, × 200; b. crassuloid seed type, *S. maxima* ssp. *crassicaulis*, lateral view, × 200.

sula, and on the Gaspé Peninsula seems better explained as the result of long distance dispersal. The diaspores of the Saginas clearly have properties conducive to long distance dispersal by wind (Löve, D., 1963; Van der Pijl, 1969). These isolated populations illustrate well "a case-in-point" in support of "Baker's Law" regarding long distance dispersal which basically states that for self-compatible taxa a single propagule is sufficient to start a new colony and that establishment is much more likely than establishment of self-incompatible taxa (Baker, 1955, 1967).

Sagina maxima ssp. *crassicaulis*, a strictly coastal taxon, was largely unaffected in the lower and major portion of its range. To the north, however, its range was abruptly truncated by the Cordilleran ice sheet. Hultén (1937) regards the taxon as one of his "Western America Coast Radiants." Migration northward along the coast was likely rapid during the post-Pleistocene as coastal winds may have facilitated rapid dispersal for species with light disseminules (Calder & Savile, 1960; Savile, 1961). Such dispersal would have been enhanced during periods when sea level was lower (Heusser, 1960). Heusser (1960) notes that some diaspores are quite capable of traveling long distances over water, citing as evidence the composition of the flora of Middleton Island, Alaska. *Sagina maxima* ssp. *crassicaulis* (as *S. crassicaulis*) is recorded in this flora (Thomas, 1957). The range of *S. maxima* ssp. *crassicaulis* reaches northward and westward to Attu Island in the Aleutians.

With the retreat of the ice along the Alaskan coast, the Asiatic *Sagina maxima* ssp. *maxima* was also able to extend its range along the newly opened North American Pacific coast.

While the region south of the glacial boundary provided the major source of plants for the revegetation of western North America, nunataks along the coast of British Columbia and Alaska served as refugia during the Pleistocene. One nunatak complex was the Queen Charlotte Islands, which are noted to have both floristic endemics (Calder & Taylor, 1968) and faunal distinctions reflecting separation from mainland relatives (Heusser, 1960). It is entirely possible that *Sagina maxima* ssp. *maxima* or perhaps even both ssp. *maxima* and ssp. *crassicaulis* could have existed as refugees on this nunatak complex. However, Hultén (1937) considered *Sagina maxima* ssp. *maxima* (as *S. litoralis* Hult.) as a Beringia radiant.

Locating a survivium for *Sagina nodosa* ssp. *borealis* presents a problem, as it occurs entirely within the glacial boundaries of eastern North America. A number of northern species display this distribution pattern, perhaps reflecting a periglacial element (Crow, 1969). Some southward migration of northern species was made possible in part by slightly cooler climatic conditions and in part by lack of competition on the newly exposed coastal terraces and alluvial deposits during withdrawal of the sea (Braun, 1947). *Sagina nodosa* would be well adapted to the periglacial situation, for it is a successful pioneer plant on rocky shores and gravelly beaches. Its capacity for vegetative reproduction through the production of numerous bulbils in the leaf axils increases its effectiveness for rapid migration. Inability to compete well with later successional vegetation might explain its absence from unglaciated regions south of the glacial boundary.

In Europe *Sagina nodosa* ssp. *borealis* is restricted to the northern glaciated regions, apparently having migrated from North America following the retreat of glaciers. Subspecies *nodosa*, having survived the Pleistocene in southern Europe occurs more widely in the southern regions of that continent and where the ranges of the two taxa come together intermediates are not infrequent.

Sagina decumbens ssp. *occidentalis*, a plant of somewhat disturbed habitats at lower elevations of the coastal mountains of the Northwest and of the Great Valley of California, occurs almost entirely within non-glaciated territory and reaches its northern limits at the southern border of British Columbia. The coastal mountains were free from ice, with the exception of a few high peaks in the northern portion (Crandell, 1965; Wahrhaftig & Birman, 1965). In the Great Valley there occurred depositions of large amounts of alluvial soil derived from erosional activity in surrounding mountain systems (Wahrhaftig & Birman, 1965). This disturbance probably provided numerous sites suitable for this taxon.

Hultén (1937) considered the taxon as a "Western America Coast Radiant." However, specimens from his area identified as *Sagina occidentalis* (*S. decumbens* ssp. *occidentalis*) were misdeterminations of plants belonging to the *Sagina maxima* complex.

The present distribution of *Sagina decumbens* ssp. *decumbens* does not readily reflect events of the Pleistocene as its distribution in eastern United States, primarily the Coastal Plain and Piedmont, is within unglaciated territory.

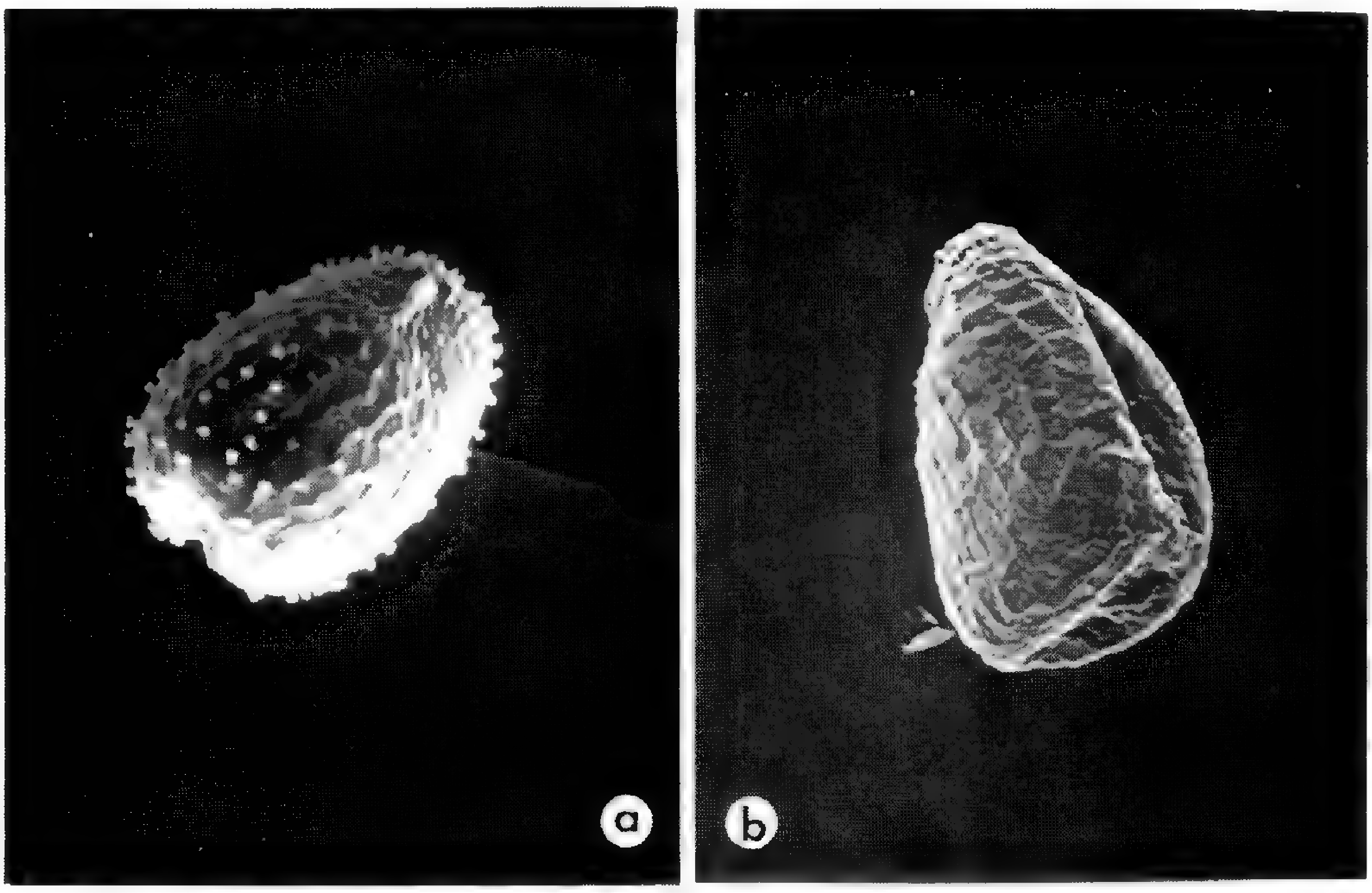

Figure 5. *Sagina decumbens* ssp. *decumbens*. a. seed showing tuberculae borne on ridges, × 200; b. non-tuberculate surface with ridges forming reticulate pattern, × 200.

Introduced taxa. The presence of *Sagina procumbens* in North America as a native of the flora is a matter open to speculation. In the Northeast the plant occurs frequently on coastal rocks and sands and sea cliffs, along stream banks, stream beds and rocks in streams and in springy places. Occurrence in such habitats might lead one to include it as a native species. However, it appears to be equally frequent along roadsides, disturbed ground and around gardens, lawns and dwellings, and in cracks between bricks of sidewalks and pavement.

Torrey and Gray (1838) questioned the status of the species as a native of North America, but subsequently Gray (1895–97), and later Fernald (1950), regarded the species as native. Hultén (1958) includes the species among his "amphi-Atlantic plants," but, in a questioning tone, he notes that the species is anthropochorous to a large extent and attributes a great portion of its Eurasian range and possibly its presence in North America to this type of dispersal. It is noteworthy that in North America the species is most widely established in areas of early settlement, New England and the Maritime Provinces, and is especially prevalent in Massachusetts.

Man is certainly responsible for the species' occurrence in the Southern Hemisphere. Hooker (1847) observed *Sagina procumbens* to be abundant near the sea in the Falkland Islands and considered it most certainly native. However, he also noted that it was indistinguishable from European material. Is it any wonder? Port Louis had been settled in Berkeley Sound by Bougainville in 1763 (Godley, 1965), and ships from Europe regularly visited the island during the 79 years prior to Hooker's visit to this locale. He searched carefully for the plant in Fuegia but did not encounter it. He also indicated he knew no other locality for the plant in the subantarctic region.

Subsequent to Hooker's explorations in Fuegia, an Anglican mission and settlement of Ushuaia was established along the Beagle Channel on Isla Grande, Tierra del Fuego. On an expedition to this region in the austral spring of 1971 I found *Sagina procumbens* to be very abundant in such disturbed sites as roadsides and grassy meadows of logged and burned sites in the *Nothofagus pumilio* forest region; it also appeared very natural growing in a gravelly stream bed at the east end of Lago Fagnano. This latter site is along a gravel highway (the southern extent of the Pan American Highway). In contrast, the plant was not found on the uninhabited eastern tip of the island, Peninsula Mitre, nor on uninhabited Isla de los Estados, even though "weedy" species native to Fuegia were present (Crow, 1975).

Sagina procumbens has become frequent throughout the subantarctic where man has been active. Although the species was not encountered by Hooker on either the Campbell or Kuerguelen Islands, R. C. Harris (personal communication) reports that he found the plant to be frequent at both localities and that growth was so lush in places on Kuerguelen that, on occasion, reindeer (also introduced) feed on it.

Man's activities are most certainly responsible for the occurrence of the species in central and western North America. By the time of the writing of Part 1 of *A Flora of North America* (Torrey & Gray, 1838) *Sagina procumbens* had appeared in the iron mining regions of the south shore of Lake Superior, presumably introduced from eastern North America.

Introduction into the Pacific Northwest probably took place in the latter part of the 1800's. The earliest collections I am aware of include one specimen from Oregon, collected by Elihu Hall in 1871 and one specimen from Vancouver Island, collected by John Macoun, May 9, 1875. As of 1894 the species had apparently not reached San Francisco, where it is now quite common, for it was not included in Greene's *Manual of the Botany of the Region of the San Francisco Bay*.

I am of the opinion that *Sagina procumbens* became introduced into northeastern North America shortly after settlement and soon became naturalized. Introduction into the Northwest most likely came by way of ships sailing around Cape Horn and could have originated from plants from eastern North America or Europe. The early collections in the Northwest are associated with coastal civilization while more recent collections indicate the plant is becoming naturalized in more remote areas of this region.

Sagina apetala is an alien which probably appeared in California during the rapid influx of civilization in the mid-1800's. The earliest recorded specimen I have seen is that of Congdon, collected in April, 1883, in Mariposa Co., California, where the species was probably a well established weed by that time. California collections prior to 1900 include: Mariposa, Tuolumne, Tehama, Plumas, and San Joaquin Counties. As early as 1892 the species had reached southern Jackson Co., Oregon. Greene (1891) described the plant as a new species (*Alsinella ciliata*) in his *Flora Franciscana.*

Gray (1895–97) indicated the presence of the species in the Middle Atlantic States region, especially near the coast. The specimens he cited, however, belong to *Sagina decumbens* ssp. *decumbens.* I have seen four herbarium specimens from eastern North America referable to *S. apetala.*

Sagina nodosa ssp. *nodosa* appears to have been introduced from Europe prior to the mid-1800's. The earliest collections known were made by J. Blake at Cape Elizabeth, Maine in 1857, and collections prior to 1900 included localities from Massachusetts to Nova Scotia. Several introductions may have occurred, and the taxon appears to be especially well established along the coast in Lincoln Co., Maine and in the region of Digby, Nova Scotia. The taxon is not weedy, and Seymour (1969) notes in *The Flora of New England* that the plant is "uncommon."

The normal range of *Sagina maxima* ssp. *maxima* extends into North America by way of the Aleutian Islands down along the Pacific coast. However, this chiefly northeast Asian taxon also occurs in eastern North America. Here it is of incidental introduction, occurring sporadically and does not appear aggressive or spreading. Known localities include Toronto, Montreal and Quebec, Canada and Amherst, Massachusetts, where plants were found growing in damp places around buildings and along footpaths.

The east Asian *Sagina japonica* has appeared at only three localities, all seaports, in western North America. As early as 1889 Macoun collected the plant at Nanaimo, Vancouver Island. Suksdorf made collections of the species at Portland, Oregon in 1899 and 1900. In 1939 the plant was found growing along a railway bed at Prince Rupert, British Columbia. A single collection, found as a weed in a botanical garden in Ottawa, Ontario, is known from eastern North America.

TAXONOMIC CRITERIA

Taxa within species complexes of *Sagina* native to North America are largely allopatric. While sterility barriers are believed to be poor between taxa, isolation is effective due to habitat preference and/or flowering time, combined with an inbreeding reproductive system. Generic subdivision is based chiefly on seed morphology correlated with floral and vegetative morphology and geographical distribution. Because none of the species can be discriminated by

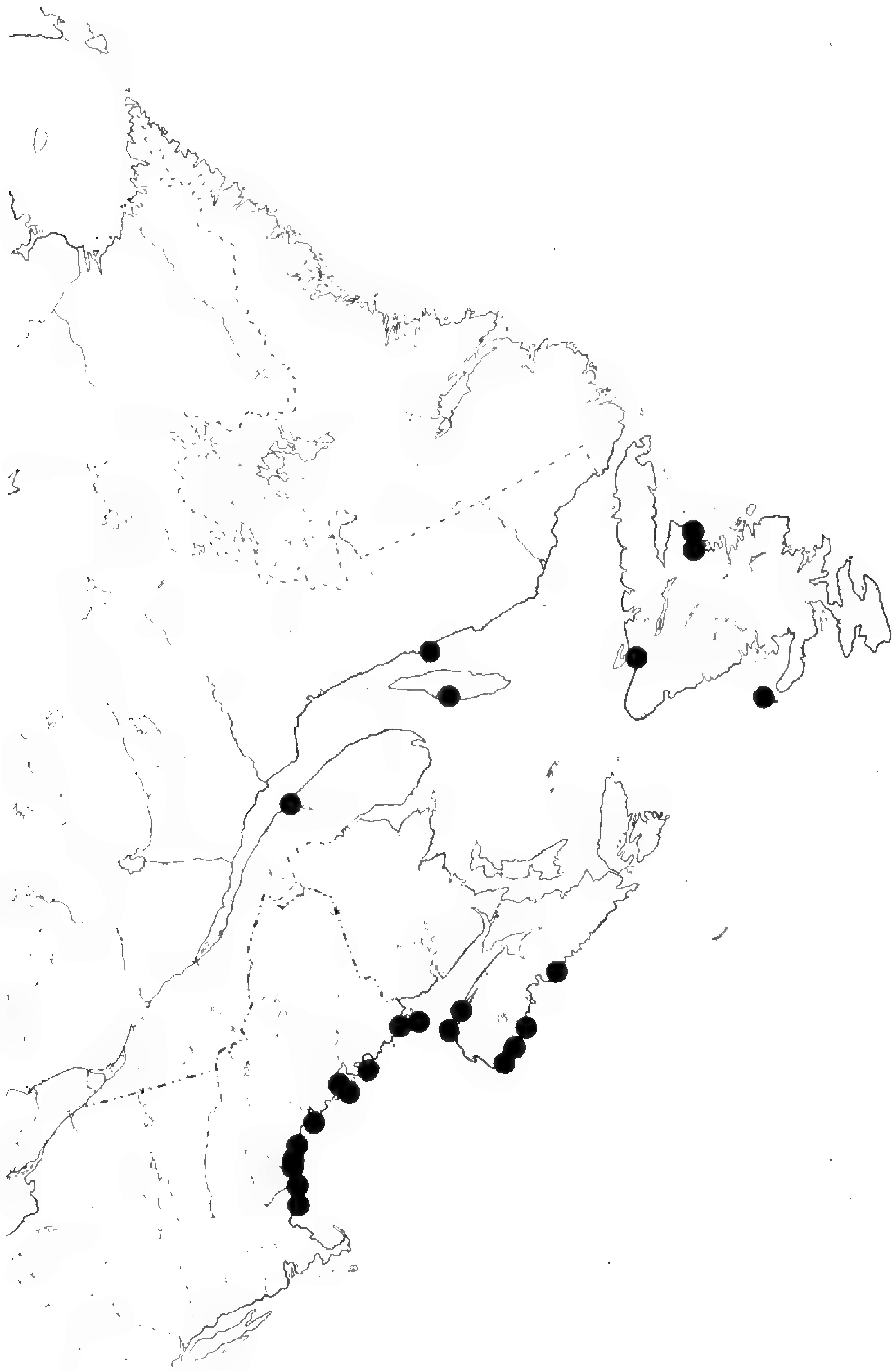

Figure 6. Geographical distribution of *Sagina nodosa* ssp. *nodosa* in North America.

use of any single character, they have been recognized on the basis of combinations of various characters. Taxa reflecting less distinction are treated at the subspecific level. These subspecies are geographically well defined and include considerable morphological variation. Intergradation occurs in regions of geographic overlap. While plasticity in the American taxa is generally too great to permit meaningful varietal distinctions, the varietal rank might be appropriate to accommodate some of the diversity within certain subspecies in Europe.

The constancy of characters expressed in the taxa of *Sagina* is important in determining the reliability of characteristics for delineating taxa. As the taxa of *Sagina* are highly variable, presence of a particular characteristic or a combination of characters must be regarded as more reliable and indicative of a taxon than absence. The following characters are particularly noteworthy.

Two types of seeds occur and I have found them to be diagnostic of sectional subdivisions of the genus. The saginoid seed type, characteristic of sect. *Sagina,* is obliquely triangular, possesses a dorsal groove, and its sides are drawn inward (Figure 4a). The crassuloid seed type, characteristic of sect. *Maxima,* is more nearly reniform or globose, lacks a dorsal groove, and its sides remain full and plump (Figure 4b). I regard the crassuloid seed type as primitive in the genus, and only two species in the genus, *Sagina nodosa* and *S. abyssinica,* express intermediacy in this character.

Leaf succulence is likewise sufficiently stable to be used as a character state for distinguishing sect. *Maxima* from sect. *Sagina.*

Presence or absence of pubescence at the base of the calyx and upper portion of the pedicel is reliable in some species. However, in *Sagina nodosa* and in *S. decumbens* ssp. *decumbens* and ssp. *occidentalis,* presence of pubescence is not consistent within populations or even on a single plant. In the North American populations of *S. caespitosa* glandular pubescence is sometimes only a weakly expressed character.

One character frequently used as distinctive in *Sagina saginoides, S. procumbens* and *S. subulata* is the reflexed nature of the pedicel on fruiting specimens. Actually, the pedicels are recurved only during capsular development and become erect at the time of capsular dehiscence. Often this character is not visible in herbarium specimens, but when it is present the character is reliable.

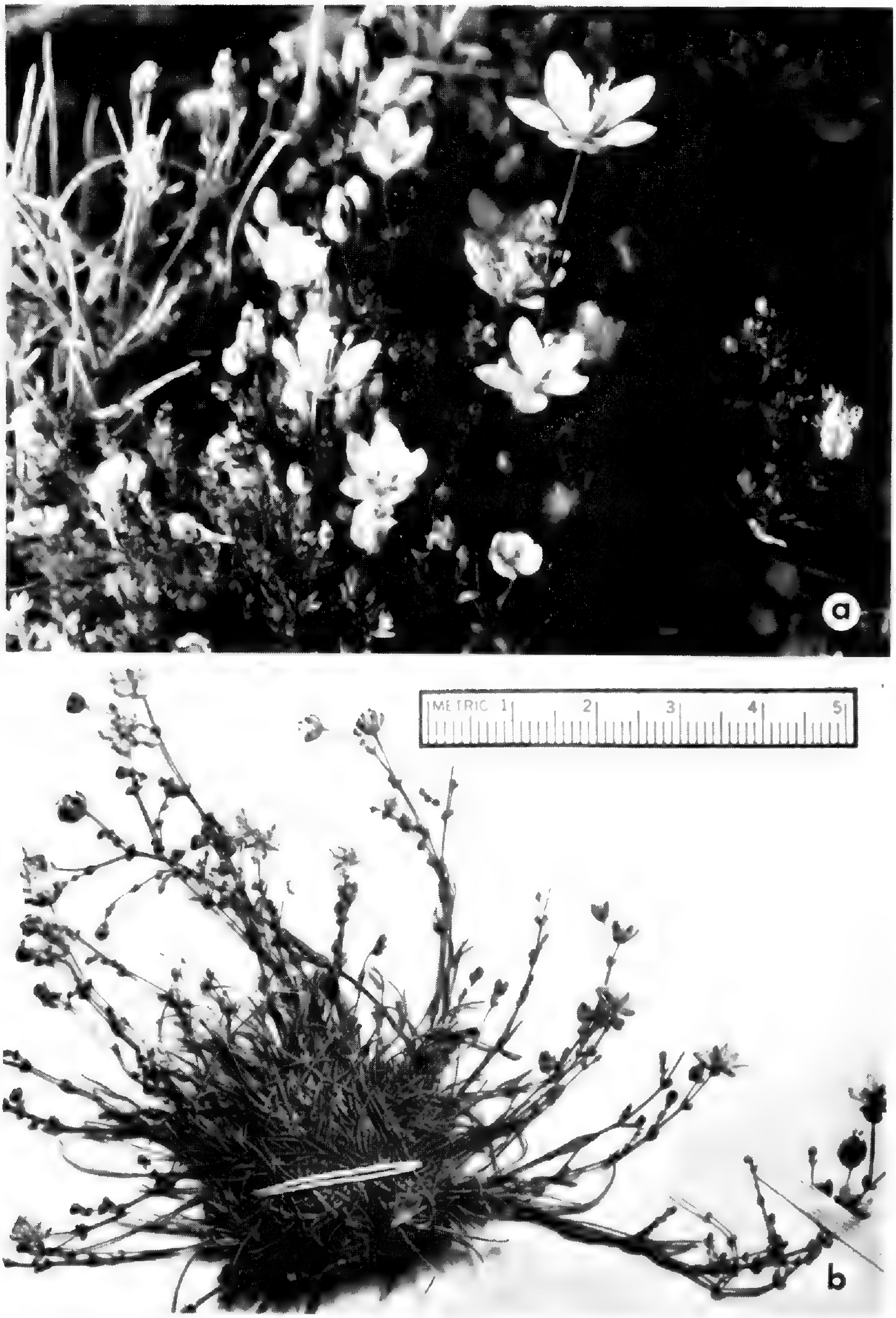

Figure 7. *Sagina nodosa* ssp. *borealis*. a. living specimen, Lake Superior, Ontario; b. herbarium specimen, Lake Superior, Ontario (*Voss 11319*, MICH).

The character state of tetramerous versus pentamerous flowers has previously been regarded as very important not only in the delineation of taxa, but especially in characterizing infrageneric categories. In several taxa, however, both tetramerous and pentamerous flowers may occur on a single plant. In each case, one of the flower forms will predominate, and caution must be exercised regarding the use of this as a key character. The character state of tetramerous versus pentamerous flowers is not useful at all for distinguishing the infrageneric categories recognized in this study.

ACKNOWLEDGMENTS

This study is based in part upon a dissertation submitted in partial fulfillment of the Ph.D. degree at Michigan State University. I wish to express my sincere appreciation to my major professor, Dr. John H. Beaman, for his guidance and encouragement during this study. Drs. A. T. Cross, J. Harman, S. N. Stephenson and W. Tai provided helpful comments and criticism concerning the manuscript. Special thanks are also expressed to Dr. John H. Thomas who introduced me to the taxonomic problems in *Sagina* and provided the Stanford University specimens for a preliminary investigation. He has been a source of encouragement to me throughout the study.

During my field work several persons took time to guide me to collecting sites: Drs. E. K. Longpre and H. Barclay in Colorado, Dr. J. H. Thomas in California and Dr. E. G. Voss in Ontario. Mr. Robert L. Watson accompanied me in the field. Special thanks are extended to Dr. H. Z. Snyder who provided travel support for field work through the Snyder Foundation.

Dr. J. K. Morton graciously provided me with his unpublished chromosome counts of North American material of *Sagina*. Dr. William T. Stearn kindly provided assistance in the typification of Linnaean species. Financial support from Sigma Xi to study type specimens in England is acknowledged.

I also wish to thank the curators of the herbaria from which specimens were borrowed for this study. These herbaria are listed below with other pertinent information concerning measurements.

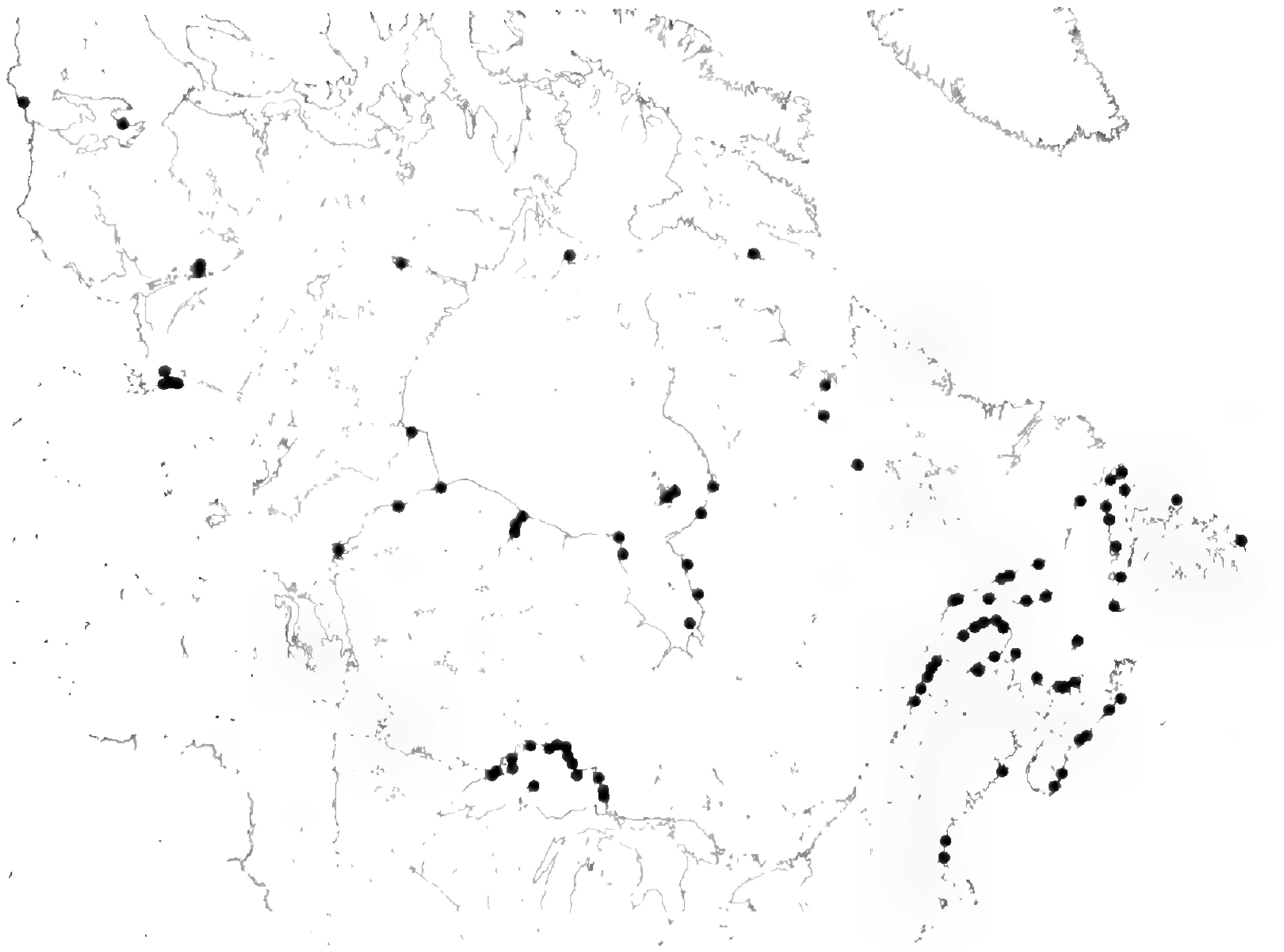

Figure 8. Geographical distribution of *Sagina nodosa* ssp. *borealis* in North America.

SPECIMENS EXAMINED

In this study measurements are based on dried material using a millimeter rule. Measurements of seeds and stamens were made under 30× magnification.

In the citation of herbarium specimens abbreviations of institutions follow those of *Index Herbariorum* 6th edition (Holmgren & Keuken, 1974). Specimens from the following herbaria were examined: BM, C, CAN, CAS, COLO, DAO, DS, F, E, ENCB, GH, JEPS, K, LE, LINN, MICH, MIN, MO, MONTU, MSC, NA, NFBC, NHA, NY, OSC, P, RM, S, TI, UC, US, WAT (University of Waterloo; abbreviation not listed in *Index Herbariorum*), WIS, WS, WTU.

TAXONOMIC TREATMENT

Sagina Linnaeus, Sp. Pl. **1:** 128. 1753.

Alsinella Dillen. ex Hill, Brit. Herb. 225. 1756, in part.
Phaloe Dumortier, Fl. Belg., p. 110. 1827.
Spergella Reichenbach in Moessler, Handb. d. Gewachsk, ed. 2, **1:** 65. 1827.

Low annual or perennial herbs; tufted, caespitose or matted. Stems ascending, decumbent or procumbent, horizontal stems becoming slightly woody in mat-forming species. Basal rosette or basal tuft of leaves present in perennial species, absent or early deciduous in annuals, rarely persisting. Secondary rosettes present in mat-forming species. Stems glabrous or glandular pubescent. Cauline leaves opposite, linear to subulate, scarious-connate at base; non-stipulate. Flowers small, whitish, terminal or axillary, 4- or 5-merous. Calyx base and upper pedicel glabrous or glandular pubescent. Sepals obtuse with scarious margins and obscure veins, cupped and frequently cucullate in bud. Petals undivided, frequently absent or caducous in annual species. Stamens equal to or twice the number of stigmas, in one or two whorls, outer whorl with nectaries at base. Styles the same number as the sepals and alternate with them, recurved at anthesis, inner surface stigmatic, papillose. Capsule many seeded (ca. 125), 4- or 5-valved, sutures running to base, valves opposite the sepals. Seeds (0.25–) 0.3 mm-0.5 (–0.6) mm long, obliquely triangular with dorsal groove or reniform to nearly globose with dorsal groove lacking, smooth, pebbled, papillate or tuberculate.

TYPE SPECIES: *Sagina procumbens* L.; lectotype designated by Britton and Brown (1913) and also adopted by Britton (1918), Hitchcock and Green (1929), and Phillips (1951).

About 15 species, chiefly of the cold temperate Northern Hemisphere. Primary center of diversity, Europe; secondary center of diversity, eastern Asia.

Table 1. **Comparative Features of Sagina Sections Sagina and Maxima**

Character	Sect. *Sagina*	Sect. *Maxima*
Center of diversity	Europe	eastern Asia
Seed type	saginoid	crassuloid
Leaves	not fleshy (sometimes only slightly fleshy)	distinctly fleshy
Flowers	4- or 5-merous; morphology tends to favor inbreeding	5-merous; morphology tends to encourage outbreeding
Sepal length	1.5–2.5 (–3.0) mm	2.0–3.5 mm
Capsule length	1.5–3.0 (–4.0) mm	2.0–4.5 mm

KEY TO NORTH AMERICAN SPECIES AND INFRASPECIFIC TAXA OF SAGINA

a. Flowers with petals nearly twice the length of sepals, 3.0–4.5 mm long; leaves of upper main stem and lateral branches usually bearing axillary fascicles of minute, succulent leaves, giving a "knotted" appearance. (Sect. *Sagina,* in part; see Table 1.) . . . . b.

  b. Stems glabrous, occasionally weakly pubescent at the nodes, pedicels and calyx bases glandular pubescent or glabrous. . . . 1b. *S. nodosa* ssp. *borealis.*

  b. Stems, pedicels, calyx bases and frequently leaf margins glandular pubescent. . . . . 1a. *S. nodosa* ssp. *nodosa.*

a. Flowers with petals shorter than, equal to, or barely exceeding sepals, up to 2.5 mm long or absent; cauline leaves lacking axillary fascicles of minute succulent leaves. . . . . c.

  c. Flowers 5-merous; leaves succulent; seeds reniform or nearly globose, plump, lacking a dorsal groove. (Sect. *Maxima;* see Table 1.) . . . . d.

    d. Seeds dark brown, distinctly tuberculate. . . . . 10. *S. japonica.*

    d. Seeds reddish-brown, smooth or slightly pebbled. . . . . .e.

      e. Calyx bases and upper portion of pedicels glandular pubescent . . . . 9a. *S. maxima* ssp. *maxima.*

      e. Plants entirely glabrous. . . . . 9b. *S. maxima* ssp. *crassicaulis.*

  c. Flowers 4- or 5-merous; leaves not succulent, or if slightly succulent, then flowers predominantly 4-merous; seeds obliquely triangular, dorsal groove present. (Sect. *Sagina,* in part; see Table 1.) . . . . f.

    f. Plants annual; stems capillary; upper cauline leaves subulate, becoming shorter toward apex of stem. . . . . g.

      g. Flowers 4-merous; hyaline portion of leaf bases distinctly ciliate, especially of the upper cauline leaves; capsules equaling or barely exceeding sepals. . . . . .8. *S. apetala.*

      g. Flowers 5-merous, rarely 4-merous; leaf bases never ciliate; capsules exceeding the sepals. . . . . h.

        h. Seeds light tan, with delicate reticulate ridge pattern; surface smooth or tuberculate (Figure 5). . . . . . 7a. *S. decumbens* ssp. *decumbens.*

        h. Seeds light brown, never with reticulate ridge pattern; surface smooth to slightly pebbled. . . . 7b. *S. decumbens* ssp. *occidentalis.*

    f. Plants perennial; stems not capillary, upper cauline leaves linear, linear-subulate or if subulate, then plants caespitose. . . . . i.

      i. Plants caespitose, forming low cushions, cauline leaves subulate; sepal margins purple. . . . . j.

        j. Petals exceeding or rarely equaling sepals, 2.5–3.0 mm long; flowers 5-merous, sometimes accompanied by 4-merous flowers; primary basal rosette lacking, several secondary rosettes of linear leaves often present. . . . . 6. *S. caespitosa.*

        j. Petals less than or equaling sepals, 1.5–2.0 mm long; flowers 4-merous, sometimes accompanied by 5-merous flowers; primary basal rosette of succulent, subulate leaves present, secondary rosettes absent. . . . . 5. *S. nivalis.*

i. Plants ascending, spreading, procumbent or mat-forming, rarely caespitose in alpine plants; leaves linear; sepal margins green or white. .. k.
  k. Flowers 4-merous, sometimes accompanied by 5-merous flowers; petals minute, 0.75–1.0 mm long, sometimes absent; sepals divergent at time of capsule dehiscence................ 3. *S. procumbens.*
  k. Flowers 5-merous; petals (1.0–) 1.5–2.0 mm long; sepals appressed or at least loosely appressed at time of capsule dehiscence. ..... l.
    l. Plants completely glabrous; leaf tips apiculate. 2. *S. saginoides.*
    l. Plants with leaves, stems, pedicels and calyx bases glandular pubescent; leaf tips aristate, arista long, equaling or exceeding leaf width................................ 4. *S. subulata.*

Sagina L. sect. **Sagina**

Spergella (Reichb.) Koch, Syn. Fl. Germ. et Helv., p. 109. 1835, as section in *Spergula*. *Spergella* (Reichb.) Koch, Syn. Fl. Germ. et Helv., ed. 2, p. 117. 1843, as section in *Sagina*.

Spergella (Reichb.) Williams, Jour. Bot. **34:** 427. 1896, as subgenus in *Sagina*. TYPE: *Sagina nodosa* (L.) Fenzl (lectotype designated herein).

Saginella Koch, Syn. Fl. Germ. et Helv., ed. 2, p. 117. 1843, as section in *Sagina*. TYPE: *Sagina procumbens* L.

Eusagina Williams, Jour. Bot. **34:** 427. 1896, as subgenus in *Sagina*. TYPE: *Sagina procumbens* L.

Procumbentes Williams, Jour. Bot. **34:** 427. 1896, as section in *Sagina*. *Procumbentes* (Williams) Williams, Rep. Bot. Soc. & Exch. Club Br. Isl. **5:** 191. 1918, as subsection in *Sagina*. TYPE: *Sagina procumbens* L.

Maritimae Williams, Jour. Bot. **34:** 427. 1896, as section. *Maritimae* (Williams) Williams, Rep. Bot. Soc. & Exch. Club Br. Isl. **5:** 192. 1918, as subsection in *Sagina*. TYPE: *Sagina maritima* G. Don (lectotype designated herein).

Nodosae Moss, Cambr. Br. Fl. **3:** 24. 1920, as series in *Sagina*. TYPE: *Sagina nodosa* (L.) Fenzl.

Subulatae Moss, Cambr. Br. Fl. **3:** 24. 1920, as series in *Sagina*. TYPE: *Sagina subulata* (Sw.) Presl (lectotype designated herein).

Procumbentes Moss, Cambr. Br. Fl. **3:** 24. 1920, as series in *Sagina*. TYPE: *Sagina procumbens* L.

Apetalae Moss, Cambr. Br. Fl. **3:** 24. 1920, as series in *Sagina*. TYPE: *Sagina apetala* Ard. (lectotype designated herein).

Seeds obliquely triangular, possessing a dorsal groove; leaves not fleshy, or if fleshy, then only slightly so. Temperate regions of the world, chiefly Eurasia and North America. TYPE SPECIES: *Sagina procumbens* L.

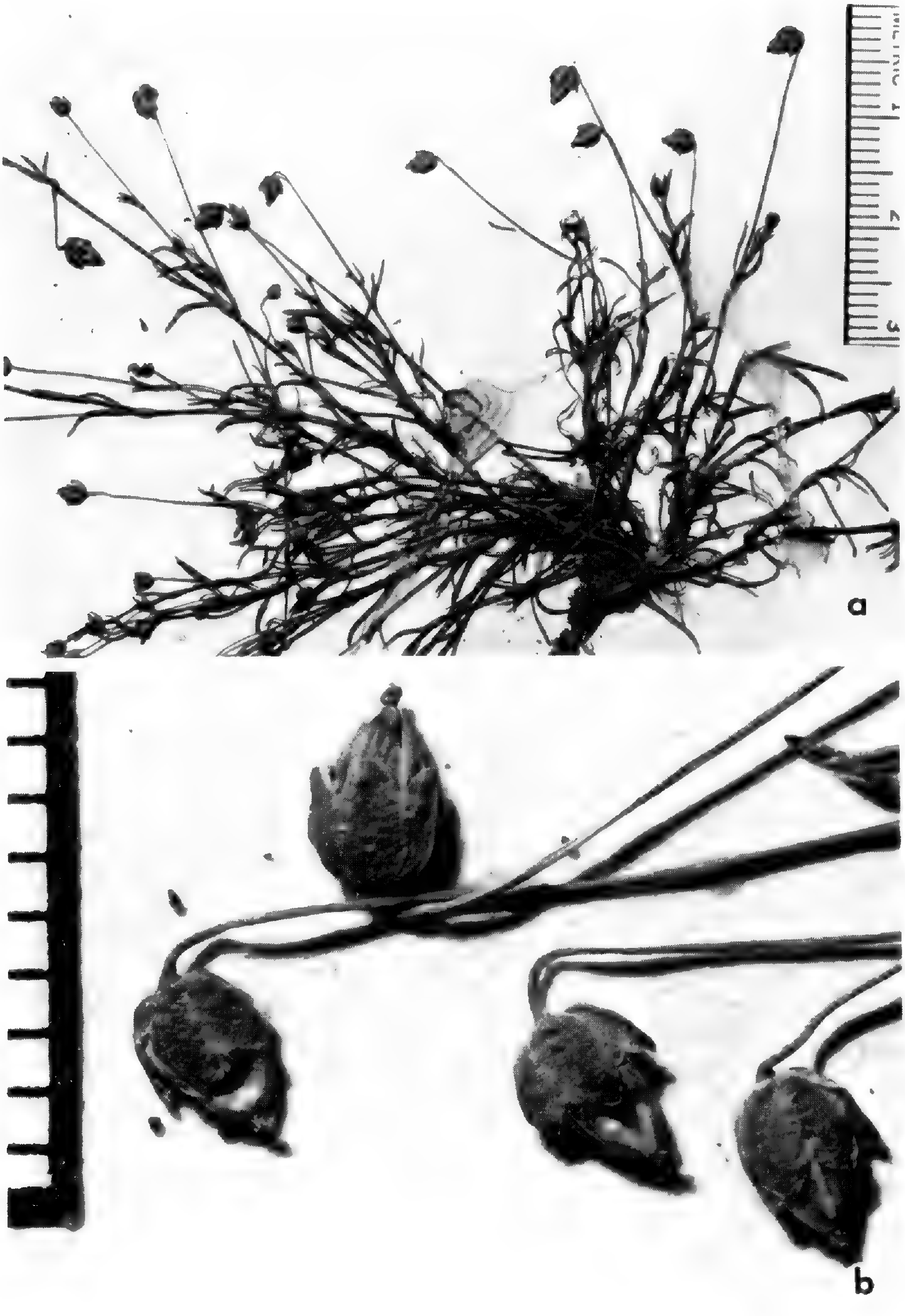

Figure 9. *Sagina saginoides.* a. habit. b. close-up of fruiting material.

1a. **Sagina nodosa** (L.) Fenzl, Ver. Verbr. Alsin, *tab. ad.* p. 18. 1833. ssp. **nodosa**

Spergula nodosa L., Sp. Pl. **1:** 440. 1753. *Alsine nodosa* (L.) Crantz, Inst. **2:** 408. 1766. *Phaloe nodosa* (L.) Dumort., Fl. Belgica, p. 110. 1827. *Spergella nodosa* (L.) Reichb., Fl. Germ. Excurs. p. 795. 1832. *Sagina nodosa* (L.) E. Meyer, Elench. pl. boruss. p. 29. 1835. *Arenaria nodosa* (L.) Wallr., Sched. Crit. 200, in obs. 1822. *Alsine nodosa* (L.) Krause, in Sturms, Fl. Deutschl. 2 ed., **5:** 34. 1901. TYPE: LINN *604.4.* (Lectotype, LINN!).

Spergula glandulosa Bess., Prim. Fl. Galic. **1:** 298. 1807. *Spergula nodosa* var. *pubescens* (Bess.) Mert. & Koch, in Röhling, Deutschl. Fl. ed. 3, **3:** 362. 1831. *Spergella nodosa* var. *glandulosa* (Bess.) Reichb., Fl. Germ. Excurs. p. 795. 1832. *Sagina nodosa* var. *glandulosa* (Bess.) Asherson, Fl. Brandenb. p. 97. 1860. *Spergella nodosa* var. *glandulifera* Schur, Enum. Pl. Transs. p. 109. 1866. TYPE: not seen. ORIGINAL MATERIAL: In sandy sites in wet meadows of hills. Lvov, Ukraine, U.S.S.R.

Perennial. Basal tufts of short compacted non-flowering branches bearing long linear leaves. Basal leaves ca. 15–30 mm long, usually bearing glandular hairs, especially on margins, sometimes glabrous. Rosettes lacking. Main stems ascending to loosely spreading to prostrate, with none, few, or many lateral branches bearing only subulate leaves, 1 mm long. Lower cauline leaves linear to subulate, apiculate to mucronate; axillary fascicles lacking. Upper cauline leaves subulate, 1.0–1.5 mm long, mucronate. Subulate cauline leaves of main stem and lateral branches with axillary fascicles of succulent subulate leaves, giving 'knotted' appearance. Stems pubescent; nodes frequently purplish. Pedicels pubescent on the uppermost portion. Flowers showy, protandrous, ca. 6–10 mm in diameter, 5-merous or 5- and 4-merous. Calyx glandular pubescent at base. Sepals elliptic, 2–3 mm long; tips frequently purplish; hyaline margins rarely purplish. Petals greatly exceeding sepals, rarely equaling or shorter than sepals, (2–) 3.0–4.5 (–5) mm long. Stamens 10 or 8, filaments 2.0–3.0 mm long, anthers 0.5 mm long. Styles long, 1.0–1.5 mm, upper half stigmatic on inner surface. Capsule valves thick, 3.0–4.0 mm long. Sepals remaining appressed after capsule dehiscence. Seeds dark brown; smooth to distinctly pebbled; ovoid to reniform with a distinct notch present at hilum; dorsal groove present or absent, 0.5 mm long. Chromosome number: $2n = 56$.

ECOLOGY AND DISTRIBUTION: Restricted to coasts, growing in moist crevices of rocks along seashore and on sea cliffs and in wet sand flats at river mouths. From Massachusetts to Nova Scotia, rare on Newfoundland and reported once from Anticosti Island and the Mingan Islands. Probably introduced. Europe. Flowering July and August. Figure 6.

REPRESENTATIVE SPECIMENS: **Canada.** NEW BRUNSWICK: Charlotte Co., Herring Cove, Campobello Island, *Malte 944/29* (CAN); east side of Whale Cove, Grand Manan Island, *Weatherby & Weatherby 5607* (US). NEWFOUNDLAND: St. Georges, Bay St. George, *Fernald & Wiegand 3344* (NY, US). New World Island, southern shore Notre Dame Bay, *Fernald & Wiegand 5380* (GH). Tilt Cove, northern shore Notre Dame Bay, *Fernald & Wiegand 5381* (CAN, GH, NY). NOVA SCOTIA: Anapolis Co., Victoria Beach, *Adams s.n.*, 31 July 1937 (DAO). Digby Co., Digby Neck, Bay of Fundy shore, *Cox s.n.*, 28 July 1919 (DAO); Brier Island, *Smith, Roland, Collins, Erskine & Schofield 13* (DAO). Halifax Co., West Lawrencetown, *Bell & Erskine s.n.*, 21 July 1949 (DAO). Queens Co., near mouth of Broad River, *Fernald & Bissell 21195* (CAN, GH). Shelburne Co.: Round Bay, *Prince & Atwood 1295* (WIS). QUEBEC: Anticosti Island Co., peat bog at Salt Lake, *Macoun 24033* (CAN, US). Matane Co., 15 mi. east of Mont Joli, *Bassett & Crompton 4321* (DAO). Saguenay Co., Ile à Charre, Mingan Islands, *St. John 90417* (GH); Ile St. Généviève, Mingan Islands, *St. John 90418* (GH). **France.** ISLES ST. PIERRE ET MIQUELON: Isthme de Langlade, *Arsène 249* (GH).

United States. MAINE: Cumberland Co., Western Brown Cow, Casco Bay, *Chamberlain & Norton 1116* (US); Bailey's Island, Harpswell, *Cushman 3968* (MIN). Hancock Co., Seal Harbor, Mount Desert Island, *Rand s.n.*, 21 July 1903 (UC). Knox Co., Matinicus Island, *McAtee s.n.*, 4 November 1915 (US). Lincoln Co., Thrumcap Island, off Boothbay, *Churchill s.n.*, 10 July 1903 (MIN, MO, NHA); Thread-of-Life Ledges, Bristol, *Fassett 10375* (F, WIS); White Island, *Fassett 2428* (WIS); Southport, *Fernald s.n.*, 4 August 1894 (GH, MIN); Pemaquit Pt., *Hodgdon 5728* (DAO, NHA); Lighthouse Hill, Monhegan Island, *Hodgdon & Hodgdon 16154* (NHA); Monhegan Island, *Jenney, Churchill & Hill s.n.*, 2 July 1919 (MIN, MO). Sagadahoc Co., near Popham Beach, Fox Island, *Hodgdon 6802* (NHA); Griffith Head, Georgetown Island, *Hodgdon 7401* (NHA); Indian Point, Georgetown Island, *Hodgdon 411* (NHA). Washington Co., Joe Dyer's Point, Baldwin Head, *Walder 4054* (US). York Co., Cape Elizabeth, *Blake s.n.*, 25 August 1857 (F, NY); Kennebunk, *Chickering s.n.*, August 1875 (DS, US); Biddeford Pool, *Clark s.n.*, 3 September 1955 (US); York, sea ledges southwest of Bald Head Cliff, *Hodgdon 10594* (NHA); Kennebunkport, *Morong s.n.*, August 1878 (F). MASSACHUSETTS: Essex Co., Manchester, *Chamberlain s.n.*, date unknown (NY); Cape Ann, 1 mi. north of Rockport, *Churchill s.n.*, 8 July 1944 (MSC); Gloucester, near Long Beach, *Williams s.n.*, 14 August 1898 (GH). NEW HAMPSHIRE: Rockingham Co.: Isle of Shoals, *Oakes & Robbins s.n.*, date unknown (GH, NHA, NY, US).

Sagina nodosa was first described by Linnaeus in *Hortus Cliffortianus* (1738). However, the diagnostic polynomial published in *Species Plantarum* (1753) differed significantly by the addition of "foliis subulatis laevibus" which indicates that he took his concept of the species from material he had studied later in the preparation of *Species Plantarum.* The Linnaean Herbarium at the Linnean Society of London contains a specimen, LINN *604.4,* upon which Linnaeus has written "3 nodosa" (3 being the species number in *Species Plantarum*) and which was probably available to him in his preparation of *Species Plantarum.* This specimen, which belongs to the species to which the name *Sagina nodosa* is currently applied, is hereby designated as the lectotype of the basionym, *Spergula nodosa* L.

The presence of only the short, descriptive phrase-name in *Species Plantarum* has led to some confusion in subsequent recognition of infraspecific taxa. The inclusion of "foliis subulatis laevibus" implied a glabrous plant. Besser (1807) later described a new species from the Ukraine, *Spergula glandulosa* (subsequently treated as *Sagina nodosa* var. *pubescens* (Besser) Mert. & Koch), provided a very detailed description and noted that it differed from *Spergula nodosa* L. by the presence of glandular pubescence on the stem and linear leaves. Upon examination of LINN *604.4* I discovered that while the subulate leaves are indeed glabrous, many of the linear basal leaves are glandular pubescent, particularly along the margins and midrib. Likewise the stems bear glandular hairs. Since Besser's taxon does not differ from Linnaeus' the name *Sagina nodosa* var. *pubescens* (Besser) Mert. & Koch is relegated to the ranks of synonomy. This leaves the taxon previously known as var. *nodosa* as an unnamed taxon and thus it is described as a new subspecies in this paper.

In addition to the characteristic stem pubescence and frequent leaf pubescence of *Sagina nodosa* ssp. *nodosa* there is a tendency in this taxon for basal leaves to appear more rigid and the midveins more prominent in herbarium material. The wrinkled texture of these leaves suggests they are slightly more succulent than those of ssp. *borealis.*

Some variation occurs in the amount and distribution of pubescence on the leaf surface in *Sagina nodosa* ssp. *nodosa.* In plants with a lesser amount of pubescence the glandular hairs are restricted chiefly to the leaf margins. In more pubescent plants the trichomes are more frequent along the veins on the abaxial surface as well as the leaf margins. The leaves may be glabrous.

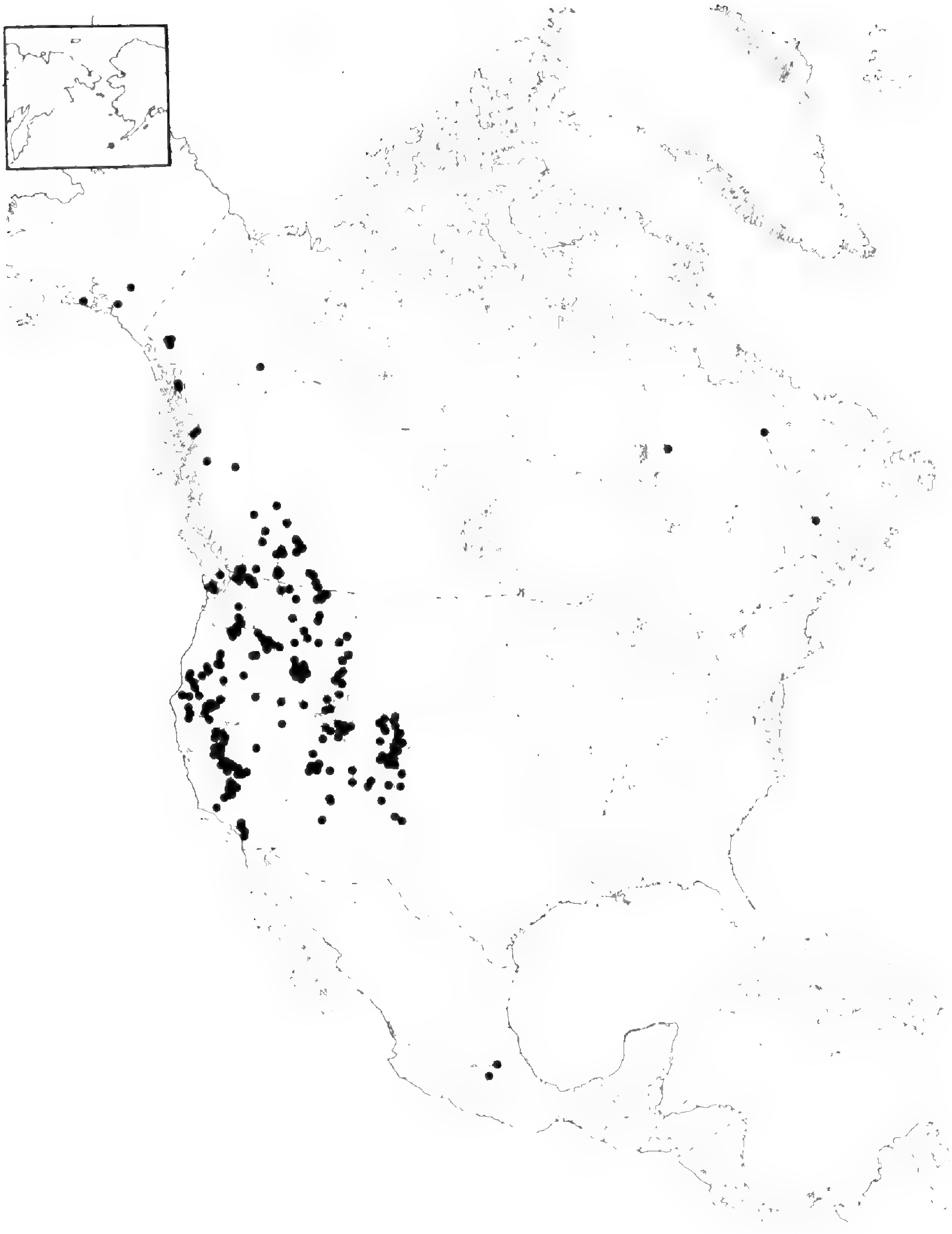

Figure 10. Geographical distribution of *Sagina saginoides* in North America.

1b. **Sagina nodosa** (L.) Fenzl ssp. **borealis** Crow, ssp. nov. TYPE: *J. F. Collins & M. L. Fernald 75.* **Canada.** QUEBEC: Gaspé County, Ste. Anne Des Monts. Brackish shores, covered at high tide. 19 August 1905. (Holotype, MSC-33878; isotypes, CAN, GH, MIN, NY, UC, US).

Sagina nodosa f. *bulbillosa* Polunin, Bull. Nat. Mus. Can. **92:** 205. 1940. TYPE: *Polunin 2312* (cited as *Polunin 2315* in original publication). Lake Harbour, Baffin Island. August 27, 1936. (Holotype! CAN; isotypes, GH!, BM, OXF).

Caulis glaber, raro sparsim glandulose pubescens ad basim nodorum; pars distalissima pedicelli et basis calycis glandulose pubescens vel glabra.

Perennial. Basal tufts of short compacted non-flowering branches bearing long linear leaves, ca. 15–30 mm long. Rosettes lacking. Main stems ascending to loosely spreading to prostrate, with none or few to many lateral branches bearing only subulate leaves, 1 mm long. Lower cauline leaves short-linear to subulate, apiculate to mucronate; axillary fascicles lacking. Upper cauline leaves subulate, 1.0–1.5 mm long; mucronate. Subulate cauline leaves of main stem and lateral branches with axillary fascicles of succulent subulate leaves, giving 'knotted' appearance. Stems glabrous or rarely weakly pubescent at nodes; nodes frequently purplish. Pedicels glabrous or pubescent on the uppermost portion. Flowers showy, protandrous, ca. 6–10 mm in diameter, 5-merous or 5- and 4-merous. Calyx glabrous or glandular pubescent at base. Sepals elliptic, 2–3 mm long; tips frequently purplish; hyaline margins rarely purplish. Petals greatly exceeding sepals, rarely equaling or shorter than sepals; (2–) 3.0–4.5 (–5) mm long. Stamens 10 or 8, filaments 2.0–3.0 mm long, anthers 0.5 mm long. Styles long, 1.0–1.5 mm, upper half stigmatic on inner surface. Capsule valves thick, 3.0–4.0 mm long. Sepals remaining appressed after capsule dehiscence. Seeds dark brown, 0.5 mm, ovoid to reniform, a distinct notch present at hilum, dorsal groove present or absent, smooth to distinctly pebbled. Chromosome number: $2n = 44, 56$. Figure 7.

ECOLOGY AND DISTRIBUTION: A shoreline plant occurring in rock crevices, wet gravels and sands and in tufts of moss along rocky coasts from New England north to Newfoundland and infrequently to Baffin Island, along the St. Lawrence Seaway, on the shores of Hudson and James Bays and Lake Superior and occasionally on lake shores westward to Lake Athabaska and Great Slave Lake. The taxon appears to be absent in the region of the Clay-belt of Ontario between James Bay and Lake Superior (Soper, 1963). Amphi-Atlantic. Flowering July and August. Figure 8.

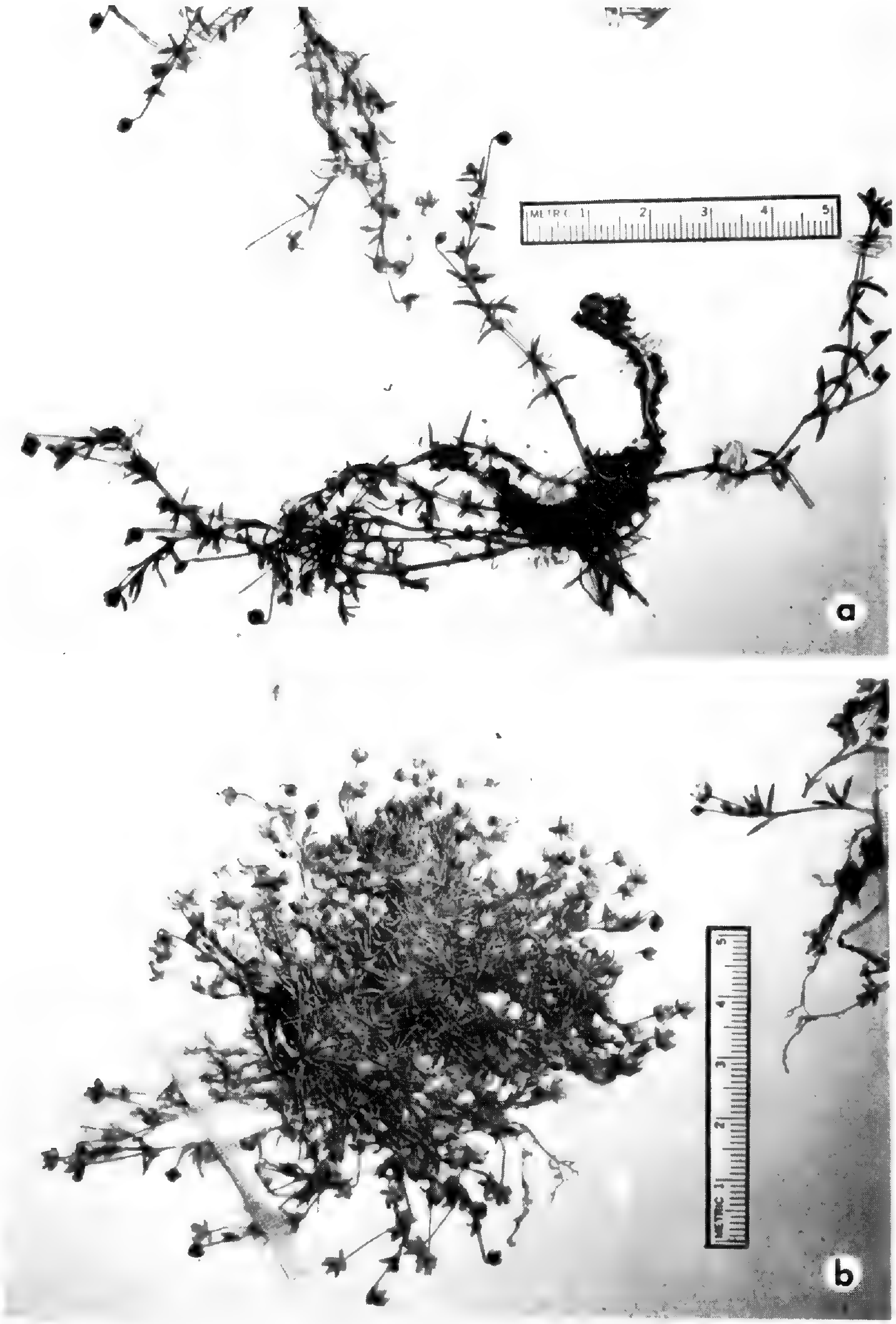

Figure 11. *Sagina procumbens.* a. habit, Quebec, (*Marie-Victorin, Rolland-Germaine, Raymond & Rouleau 56363,* GH); b. habit, Newfoundland (*Bassett 541,* DAO).

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: Sand Point, north shore of Lake Athabaska, 58°51′N., 110°50′W., *Raup 701* (GH). MANITOBA: Cochran River, 58°02′ N., 101°23′W., *Baldwin 2118* (CAN). Muskey Island, Lake Winnipeg, *Macoun s.n.*, 4 August 1884 (CAN). Vicinity of Churchill, 58°46′N., 94°10′W., *Schofield & Crum 6896* (DS, MIN, WTU). Gillman, Churchill District, *Schofield 1209* (WS). Pipestone Lake, 35 mi. north of Lake Winnipeg at entrance of Nelson River, *Scoggan 3379* (CAN). York Factory, *Scoggan 6165* (CAN, GH, MIN). NEW BRUNSWICK: Charlotte Co., Whale Cove, Grand Manan Island, *Weatherby & Weatherby 5581* (GH). Gloucester Co., Miscou Point, Miscou Island, *Dore, Senn & Gorham 45.621* (DAO); Younghall, *Fletcher 784* (CAN, DAO). Restigouche Co., Eel River, *Chalmers s.n.*, September 1875 (CAN). NEWFOUNDLAND: Bonne Bay, near Winterhouse Brook, *Fernald, Long & Fogg 1666* (GH, US). Cow Head, region north of St. Paul's Bay, *Fernald & Wiegand 3341* (CAN). Flower Cove, Straits of Belle Isle, *Fernald, Long & Dunbar 26650* (NY). Port Saunders Harbor, region of Ingornachoix Bay, *Fernald & Wiegand 3343* (GH). Near Frenchman's Cove, Bay of Islands, *Griscom s.n.*, 8 August 1920 (GH). Stephenville Crossing, *Kennedy 438* (GH). Daniel's Harbour, *Rouleau 5115* (CAN, DAO, US). Englee, *Savile 2664* (DAO). St. Anthony, Cremaillère Bay, *Savile & Vaillancourt 2381* (DAO). Fogo Island, *Sornborger s.n.*, 7 August 1903 (CAS, GH, NY, US). NOVA SCOTIA: Guysborough Co., Canso, *Fowler s.n.*, 7 August 1901 (US). Halifax Co., Halibut Cove, near Halifax, *Dore, Senn & Gorham 45.513* (DAO). Queens Co., Port Mouton, *Graves, Long & Linder 21198* (GH). Shelburne Co., Villagedale, *Fernald, Long & Linder 21197* (GH). NORTHWEST TERRITORIES: District of Franklin, Lake Harbour, Baffin Island, *Polunin 2312* (CAN, GH). District of Keewatin, Coral Harbour, Southampton Island, 64°13′N., *Beckett 404* (MIN). Baker Lake, south shore, ca. 64°07′N, 97°W., *Porsild 6119* (CAN, US). District of MacKenzie, Indian Lake, 64°17′N., 115°12′W., *Cody & McCanse 3395* (DAO). Norman Wells, *Cody & Gutteridge 7469* (CAS, DAO, F, MICH, MIN, NY, US). Mackenzie River, opposite Ft. Simpson, *Crickmay 39* (CAN). McTavish Arm, Great Bear Lake, ca. 66°20′N., 119°30′W., *Porsild & Porsild 5175* (CAN). Fairchild Pt., Great Slave Lake, 62°43′N., 109°10′W., *Raup 705* (GH). ONTARIO: Lake River, James Bay, 54°20′N., *Dutilly & Lepage 16784* (CAN, GH). Between Limestone and White Seal Rapids, Severn River, *Moir 1196* (CAN, MIN). Vicinity of mouth of the Severn River, *Moir 1359* (CAN, MIN). Severn River at mouth of the Beaver River, *Moir 266* (MIN). Algoma District, Vrooman Island, in Lake Superior, *Cowell 25* (DAO); 3 mi. southwest of Mica Bay, Lake Superior, *Parmelee & Savile 3674* (DAO); Old Woman Bay, Lake Superior, ca. 16 mi. southwest of Wawa, *Voss 11319* (MICH). Thunder Bay District, Rossport, Lake Superior, *Crow 1297* (MSC); Michipicotin Island, Lake Superior, *Macoun s.n.*, 24 July 1869 (CAN); shore of Lake Superior at Heron Bay, ca. 6 mi. southeast of Marathon, *Voss 10441* (MICH). PRINCE EDWARD ISLAND: Kings Co., between South Lake and the Gulf, near Bothwell, *Fernald, Long & St. John 7446* (CAN, GH, NY, US). Prince Co., Lower Sea Cow Pond, *Fernald, Long & St. John 7443* (CAN, GH, WS). Queens Co., Dalvay, National Park, *Erskine 1532* (DAO, NY). QUEBEC: Great Whale River, near mouth, east coast of Hudson Bay, *Abbe & Abbe 3929* (CAN, MIN, US). Fort George, east coast of James Bay, 53°53′N., *Dutilly & Lepage 12706* (GH). Koksoak River, Ungava basin, 57°40′–58°05′N., 68°25′ 69°35′W., *Dutilly & Lepage 14731* (GH). Near Lake Otelnuc, 56°01′N., 68°09′W., *Dutilly & Lepage 39233* (DAO). Anticosti Island Co., Cape Henry, *Adams s.n.*, 6 August 1936 (DAO); Salt Lake, *Macoun 24033* (NY). Bonaventure Co., Carleton

Point, Carleton, *Collins & Fernald 66025* (CAN, GH, MICH, NY, US). Gaspé-Est Co., Grand Vallés, *Clausen & Trapido 3054* (MIN, US). Bay of Gaspé, Riviere York, *Marie-Victorin, Brunel, Rolland-Germain & Rousseau 17726* (GH). Gaspé-Ouest Co., Ste-Anne-des-Monts, *Collins & Fernald 75* (CAN, GH, MIN, MSC, NY, UC, US). Magdalen Islands Co., Alright Island, *Fernald, Long & St. John 7445* (CAN, GH, NY, US). Matane Co., Matane, mouth of Matane River, *Forbes s.n.*, 3 August 1904 (CAN, GH). Rimouski Co., Cape Enragé, Bic, *Fernald & Collins 1019* (GH). Riviere-De-Loup Co., Trois-Pistoles, *Mulligan & Beales 3209* (DAO). Saguenay Co., Wolf Bay, *Lewis 131997* (CAN); Seven Islands, *Robinson 674* (CAN, GH, NY). SASKATCHEWAN: Small island at base of Charlot Pt., Lake Athabaska, ca. 59° 36′N., 109° 13′W., *Raup 6379* (CAN, DAO, GH, NY).

United States. MAINE: York Co., Kennebunk, *J. W. C., Jr.* [Chickering] *s.n.*, 25 July 1877 (UC). Washington Co., Cutler, *Fernald s.n.*, 28 August 1902 (GH); Rogue Bluff, *Knowlton s.n.*, 31 July 1916 (MO). MICHIGAN: Keweenaw Co., Rock Harbor, Isle Royale, *Cooper 65* (MIN, US). MINNESOTA: Cook Co., Clark Bay, Pigeon Point, *Butters, Abbe & Abbe 385* (F, MIN, US). NEW HAMPSHIRE: Rockingham Co., Isle of Shoals, *Oakes & Robbins s.n.*, date unknown (NY).

Sagina nodosa is the most clearly defined species of the genus and its floral morphology apparently most nearly represents that of the ancestral type.

The glandular and glabrous pedicel characteristics in *Sagina nodosa* ssp. *borealis* are frequent throughout the greater portion of the geographical range and are often found within a single population. The glandular condition is slightly predominant and populations occurring in the interior region of Canada are almost entirely of the glandular pedicel type.

In populations along the shores of Lake Superior plants sometimes occur with glandular hairs sparsely distributed on the stems, chiefly or solely at the base of the nodes, as well as on the pedicels and calyx.

Polunin (1940) described a form from Baffin Island, *Sagina nodosa* f. *bulbillosa*, which occurs totally without flowers and produces bulbils in the axils of the cauline leaves. The disarticulation of these tiny fascicles of leaves in late autumn is a normal mechanism of vegetative dispersal which occurs with greatest frequency in higher latitudes. The mechanism is not restricted to sterile plants and nomenclatural recognition of this condition is meaningless.

It appears that a typographical error was made in the citation of the holotype of *Sagina nodosa* f. *bulbillosa* in the original publication. The type specimen designated was *Polunin 2315*, but no specimen bearing this collection number can be found at the National Museum of Canada, depository designated for the holotype, or at

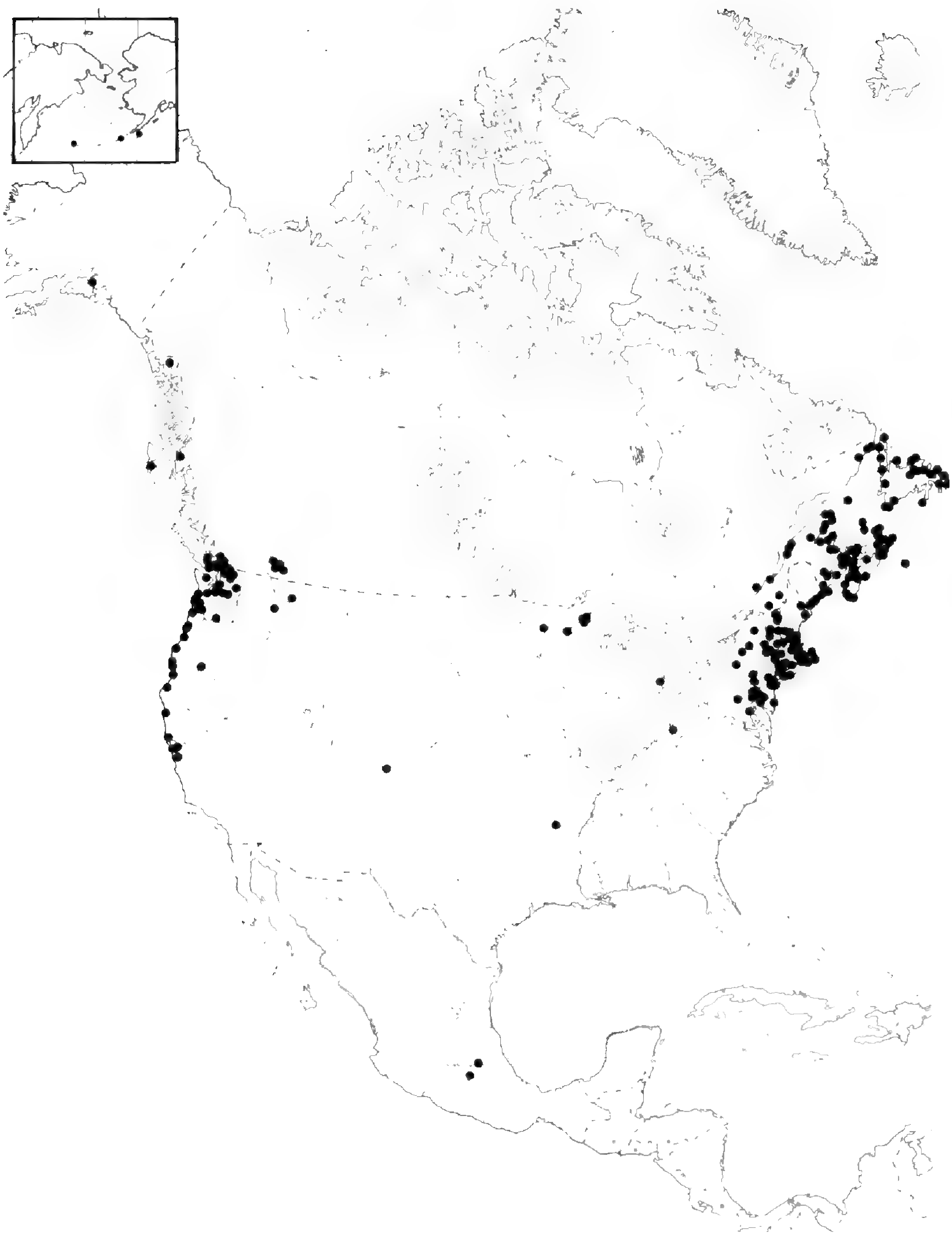

Figure 12. Geographical distribution of *Sagina procumbens* in North America.

the Gray Herbarium, depository designated for an isotype. The only specimens at either institution collected on Baffin Island bear the collection number *Polunin 2312*. With the exception of the last digit of the collection number, the label data for these two sheets are identical to the data published for the type.

2. **Sagina saginoides** (L.) Karst., Deutsch. Fl. p. 539. 1882.

Spergula saginoides L., Sp. Pl. **1:** 441. 1753. *Alsine saginoides* (L.) Crantz, Inst. **2:** 408. 1766. *Phaloe saginoides* (L.) Dumort., Fl. Belgica, p. 110. 1827. *Sagina Linnaei* Presl, Rel. Haenk **2:** 14. 1831. *Nom. superfl.* for *Spergula saginoides* L. *Spergella saginoides* (L.) Reichb., Fl. Germ. Excurs., p. 794. 1832. *Sagina spergella* Fenzl, Ver. Verbr. Alsin., tab. ad. p. 18. 1833. *Nom. illeg. Alsinella saginoides* (L.) Greene, Fl. Fran. p. 125. 1891. *Alsine Linnaei* (Presl) Krause, in Sturms, Fl. Deutschl. 2 ed., **5:** 35. 1901. *Nom. illeg.* TYPE: LINN *604.6.* "Habitat in Sibiria". (Lectotype, LINN!)

Sagina saginoides var. *hesperia* Fern., Rhodora **27:** 131. 1925. TYPE: *Crandall 89*, 9500 ft., Chambers Lake, Colorado. (Holotype, GH!)

Spergula micrantha Bunge, in Ledeb, Fl. Alt. **2:** 183. 1830. *Sagina micrantha* (Bunge) Fern., Rhodora **27:** 131. 1925. TYPE: pr. Barnaul, Tomskoi Sawod. (Lectotype, LF!).

Spergula saxatilis Wimm., Fl. Schles. p. 193. 1832. *Sagina saxatilis* (Wimm.) Wimm. Fl. Schles. p. 75. 1841. *Spergella saxatilis* (Wimm.) Schur, Enum. Pl. Transs. p. 109. 1866. TYPE: not seen. ORIGINAL MATERIAL: grass-covered rocky sites in mountains, near Waldenburg and Einsiedel, Silesia (Germany).

Spergella macrocarpa Reichb., Ic. Fl. Germ. **5:** 26. 1841. *Sagina macrocarpa* (Reichb.) Maly, Enum. Pl. Phan. p. 292. 1848. *Sagina Linnaei* var. *macrocarpa* (Reichb.) Beck, Fl. Nied.-Öst. p. 358. 1890. *Nom. illeg. Sagina saginoides* var. *macrocarpa* (Reichb.) Moss, in Jour. Bot. **52:** 60. 1914. *Sagina saginoides* ssp. *macrocarpa* (Reichb.) Soó, in Acta Bot. Acad. Sci. Hung. **18:** 177. 1973. TYPE: destroyed.

Sagina Baumgarteni Simonkai, Enum. Fl. Transs. p. 144. 1886. TYPE: not seen.

Perennial. Plants tufted, branches ascending or sometimes procumbent, becoming caespitose in alpine habitats. Entire plant glabrous. Rosettes of linear leaves frequently present, 9–45 mm in diameter, or replaced by a tuft of ascending linear leaves. Cauline leaves linear, sometimes linear-subulate in caespitose plants. Connate leaf bases not conspicuous, rarely appearing inflated and then so only in caespitose plants. Axillary fascicles of linear leaves frequently on procumbent stems. Flowers axillary or terminal. Pedicels generally long, filiform, mean length 14.5 mm, recurved during capsular development, becoming erect at maturity. Flowers 5-merous, very rarely 4-merous. Sepals elliptical, hyaline margins white, rarely purple in alpine specimens, 2.0–2.5 mm long. Petals elliptical, (1.0–) 1.5–2.0 mm long, shorter than or equaling the sepals. Stamens 10, or less frequently 5, filaments 1.0–1.5 mm long, anthers 0.25 mm long. Capsules 1.5–2 times the length of the sepals; capsule valves thin, 2.5–3.0 (–3.5) mm long, dehiscing to base. Sepals remaining appressed following capsule dehiscence. Seeds brown, obliquely triangular, with distinct dorsal groove, surface

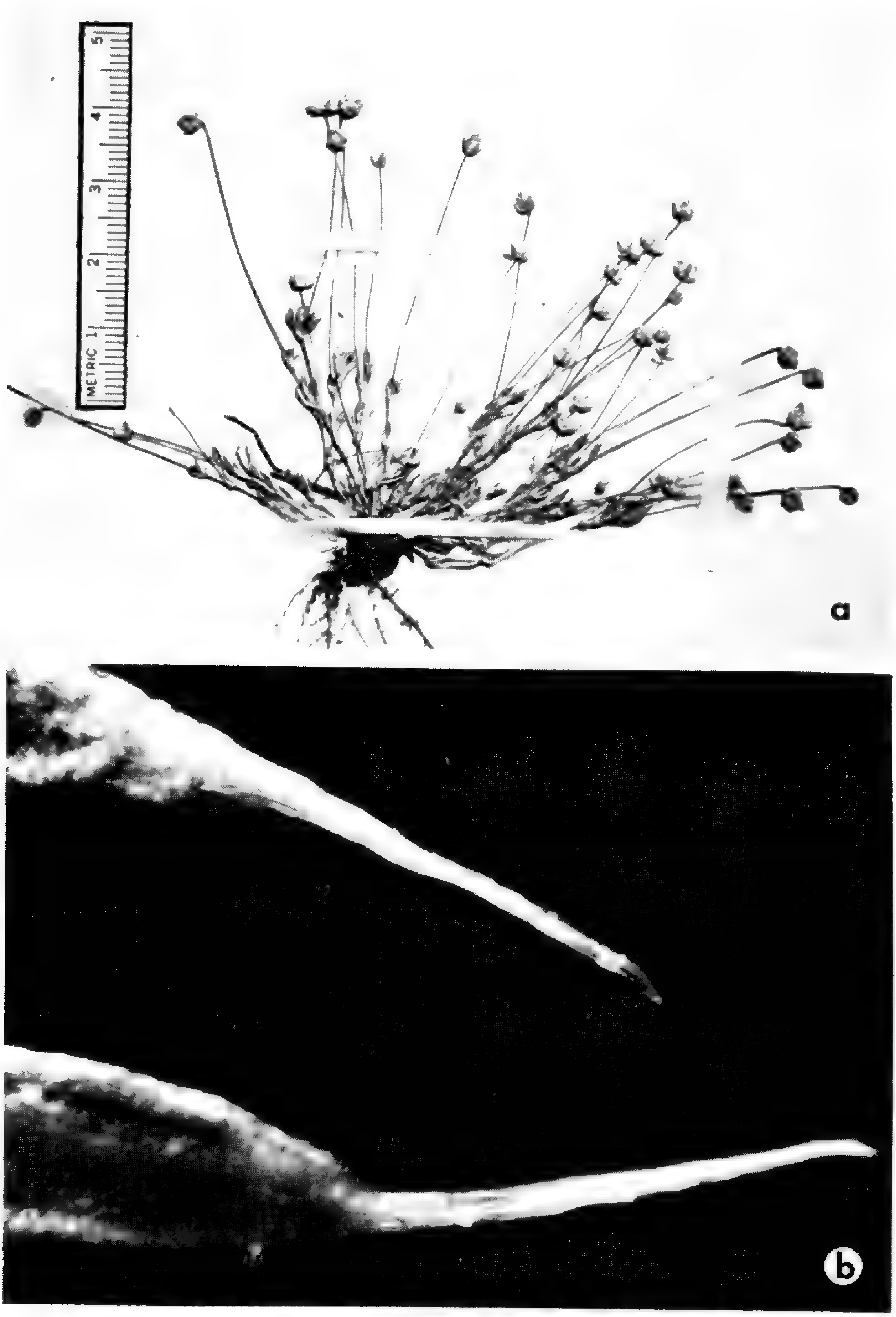

Figure 13. *Sagina subulata.* a. habit, Sweden (*Särnquist s.n.*, 20 June 1948, DAO); b. close-up of aristae, photographed under epi-illumination, Sweden (*Bagge s.n.*, 16 June 1890, UC).

smooth to slightly pebbled, 0.3 0.4 mm long. Chromosome number: $2n = 22$. Figure 9.

ECOLOGY AND DISTRIBUTION: A montane species growing in the open or in light shade in wet places on lake margins, along streams and seepages in rock ledges and roadcuts, often in subalpine and alpine zones. From Alaska, south to Arizona and New Mexico. Its occurrence is rare in eastern North America. I have seen collections only from Richmond Gulf on Hudson Bay, the Schefferville area of the Labrador-Quebec Peninsula and on the Gaspé Peninsula, Quebec. Circumpolar. Flowering June to August. Figure 10.

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: Bertha Lake, Waterton Lakes National Park, elev. 6000 ft., *Breitung 16239* (NY). Malique Lake, near headwaters of the Saskatchewan and Athabasca Rivers, *Brown 1176* (GH, MO, NY). Little Beehive Mt., vicinity of Lake Louise, *Hunnewell 3529* (MIN). About 5 mi. east northeast of Bow Peak, Banff National Park, *Hitchcock & Martin 7756* (COLO, DS, GH, MO, NY, OSC, RM, UC, WS, WTU). Crow's Nest Pass, summit of Turtle Mt., *Macoun 18290* (CAN). Mt. Edith Cavell, Jasper National Park, *Scamman 3189* (GH). BRITISH COLUMBIA: Asulkan Valley, Glacier, Selkirk Mts., *Brown 581* (GH, MO, US). About 8 mi. southeast of Barkerville, elev. 5500 ft., *Calder, Savile & Ferguson 14237* (DAO). North of Ft. St. James, Wolverine Lake, 55°41′N., 124°26′W., *Calder, Savile, & Ferguson 13645* (DAO). Between Baldy Mt. and Dunn Peak, ca. 7½ mi. east northeast of Littlefort, ca. 51°27′N., 120°03′W., elev. 7100 ft., *Calder, Parmelle, & Taylor 19908* (DAO, UC). 8 mi. southeast of Nelson along road to Copper Mt., elev. 5400 5700 ft., *Calder & Savile 10993* (DAO). Mt. Apex, southwest of Penticton, elev. 6800 ft., *Calder & Savile 11731* (DAO). Mt. Thornhill, near Terrace, elev. 3800 ft., *Calder, Savile & Ferguson 14871* (DAO). Near Rogers Pass, Selkirk Mts., *Heacock 4400* (GH, MIN, MO, NY, US). Victoria Lake, ca. 11 mi. west of Revelstoke, elev. 1785 ft., *Hitchcock & Martin 7592* (DS, WTU). Battle Mt., Wells Gray Park, 50°N., 120°W., *Ahti & Ahti 7003* (WTU). Chilliwack River, *Macoun 34034* (CAN). Lake House, Skagit River, *Macoun 79583* (CAN, NY). Upper Canyon Creek, Golden, *Taylor 6727* (MICH). Sheep Mt., Elk River Valley, 34 mi. north of Natal, *Weber 2347* (COLO, GH, UC, WS). Vancouver Island, below Mt. Burman, near Burman Lake, 49°37′N., 125°44′W., elev. 5000 ft., *Calder & MacKay 32567* (DAO). Along Elk River, Strathcona Provincial Park, 49°46′N., 125°51′W., elev. 2800 ft., *Calder & MacKay 31643* (DAO). Mt. Arrowsmith, *Anderson & Fletcher s.n.*, 7 August 1901 (DAO). Vicinity of Victoria, *Macoun s.n.*, 23 May 1893 (MSC). DISTRICT OF MACKENZIE: Vicinity of Brintnell Lake, ca. 62°05′N., 127°35′W., *Raup & Soper 9159* (GH). YUKON TERRITORY: Canol Rd., upper south fork of MacMillan River, opposite mile 280, *Porsild & Breitung 11300* (CAN). Canol Rd., Rose-Lapie River Pass, mile 98 99, elev. 4000 ft., *Porsild & Breitung 11900* (GH, UC, US). Canol Rd., slopes of Mt. Sheldon, opposite mile 222, elev. 6000 ft., *Porsild & Breitung 11742* (CAN). Vicinity of Mackintosh, mile 1022 Alaska Highway, slopes of Mt. Decoeli, elev. 4000 ft., *Schofield & Crum 8049* (CAN). QUEBEC: Fishing Lake Creek, Richmond Gulf, east coast of Hudson Bay, ca. 56°N., 76°W., *Abbe, Abbe & Marr 4396* (CAN, DAO, MIN, US).

Knob Lake, Schefferville area, Quebec-Labrador Peninsula, ca. 54°45′N., 66°40′W., *Hustich & Kallio 752* (CAN). Gaspé Co., Mt. Albert, elev. 950 m, *Collins & Fernald 74* (CAN, GH, MIN, MSC, NY, UC); 1 mi. above Marten River, River Ste-Anne-des-Monts, *Collins & Fernald s.n.*, 3 17 August 1905 (GH).

Mexico. BAJA CALIFORNIA: La Grulla, Sierra San Pedro Mártir, elev. 2100 m, *Moran 19173* (ENCB); Yerba Buena, Sierra San Pedro Mártir, elev. 2500 m, *Moran & Thorne 14173* (ENCB). HIDALGO: Cerro de las Ventanas, 6 km al N de Pachuca, elev. 2900 m, *Rzedowski 23010* (ENCB). MEXICO: Ameyalco, 73 km de la carretera Amecameca-Tlamacas, elev. 3100 m. *Rzedowski 21864* (ENCB); 12 km al E de Amecameca, sobre la carretera a Tlamacas, elev. 3000 m, *Rzedowski 26720* (ENCB).

United States. ALASKA: Thompson Pass, Richardson Highway, *Anderson 2777* (CAN). Unalaska, *Anderson 4117* (GH). Falls Creek Mine, near Kenai Lake, Kenai Peninsula, 60°26′N., 149°17′W., *Calder 6088* (CAS, DAO). Head of Resurrection Bay, Seward, Kenai Peninsula, 60°07′N., 149°25′W., *Calder 7018* (DAO). Isabel Pass, mile 199 Richardson Highway, 63°32′N., 145°52′W., *Cody & Webster 5824* (DAO). Tangle Lakes area, mountain east of Landmark Gap, Alaska Range, *Gjaerevoll 1293* (CAN). Smith's Dry Lake, Attu Island, Aleutian Islands, *Hardy 385* (GH). Juneau Ice Field, *Heusser 212* (OSC). Mountains southeast of Texas Lake, 20 mi. northwest of Hyder, elev. 4600 ft., *McCabe 8428* (UC). About 15 mi. due east of Berners Bay at Vaughan Lewis glacier, 25 mi. north of Juneau, Alaska, elev. 2800 ft., *Miller 1745* (MSC). Peaceful Valley, Attu Island, Aleutian Islands, *Soule 185* (WTU). Along Salmon River road 3 mi. north of Hyder, *Whited 1208½* (MO, WS). ARIZONA: Coconino Co., San Francisco Mts., elev. 11500 ft., *Knowlton 134* (US); Kaibab Basin, elev. 8200 ft., *Merkle 586* (CAS); Little Park, North Rim Grand Canyon, elev. 8800 ft., *Merkle 601* (CAS). CALIFORNIA: Alpine Co., Carson Pass, elev. 8200 ft., *Jepson 8116* (UC). Amador Co., Silver Lake, elev. 8000 ft., *Newell s.n.*, 24 August 1929 (CAS). Butte Co., Butte Meadows, *Heller 14688* (DS, MO, US). Calaveras Co., Big Meadows, Stanislaus National Forest, *Crow 1175* (MSC, NHA). Del Norte Co., High Prairie Creek, *Jepson 9346* (JEPS). Fresno Co., Pine Ridge, elev. 5300 ft., *Hall & Chandler 135* (MIN, NY, UC, US). Glenn Co., Sheetiron Mt., elev. 5950 ft., *Bacigalupi 4677* (UC). Humboldt Co., Trinity Summit, near Box Camp, elev. 5500 ft., *Tracy 17918* (UC, US, WTU). Inyo Co., Lone Pine Creek Canyon, east slope of Sierra Nevada, elev. 6950 ft., *Alexander & Kellogg 2907* (DS, UC, US). Kern Co., about ½ mi. northeast of Evans Flat, Greenhorn Mts., elev. 5925-2950 ft., *Smith 652* (UC). Lassen Co., Lassen Butte, *Eastwood 1772* (CAS). Madera Co., Long Meadow, elev. 6800 ft., *Hawkes 5204* (UC). Mariposa Co., Yosemite Valley, elev. 3900 ft., *Hall 8879* (DS, US). Modoc Co., 15 mi. southeast of Alturas, elev. 5500 ft., *Hitchcock 6708* (NY, UC, WTU). Mono Co., along California Rt. 120, 5½ mi. west of Ranger Station, Inyo National Forest, elev. 8500 ft., *Crow 1161* (MSC, NHA). Nevada Co., Lytton Creek, Norden, *Jorgesen 501* (DS, WTU). Place Co., Summit Valley, *Howell 18582* (CAS). Plumas Co., slopes across from the Devils Kitchen, Lassen Volcanic National Park, *Gillett 846* (UC). Riverside Co., Deer Springs, San Jacinto Mts., elev. 9000 ft., *Meyer 541* (UC). San Bernardino Co., Big Bear Lake, San Bernardino Mts., *Breitung 15504* (DAO). Shasta Co., Brokeoff Meadows, Lassen Volcanic National Park, elev. 6300 ft., *Gillett 112* (UC). Siskiyou Co., Horse Camp Springs, Mt. Shasta, elev. 8250 ft., *Cooke 11474* (UC); Wagon Camp, Mt. Shasta, elev. 6000 ft., *Crow 1206* (MSC, NHA). Tehama Co., north slope of North Yollow Bolly Peak, *Munz 16679* (CAS, DS, NY). Trinity Co., South Fork Mt., *Tracy 19055* (UC). Tulare Co., headwaters of Freeman Creek, north slope of The Needles, Sequoia National Forest, *Bacigalupi, Wiggins & Ferris 2569* (DS, WTU). Tuolumne Co., Mather, *Keck 5318* (CAS, DS, US). Ventura Co., Seymour Creek, *Pierson s.n.*, in 1922(?) (US). COLORADO: Boulder Co., Green Lakes Valley, north of Kiowa Peak, elev. 11500–12000 ft., *Weber & Dahl 8589* (COLO). Clear Creek Co., mountains about the headwaters of Clear Creek, valley near Empire, *Patterson 173* (COLO, F, MICH, MIN, MO, MSC, UC, US). Conejos Co., just south of Platoro, elev. 9900 ft., *Weber 7864* (CAS, COLO, DAO, MIN, RM, WS, WTU). Costilla Co., slope of old Baldy Peak, 8 mi. from Fort Garland, elev. 9700 ft., *Mattoon 179* (COLO). Freemont Co., Lake Creek, 3 mi. west of Hillside, Sangre de Cristo Mts., *Erlanson 1416* (MICH). Gilpin Co., Eldora to Baltimore, elev. 8500–9500 ft., *Tweedy 5535* (RM, NY). Grand Co., East St. Louis Creek, Fraser Experimental Forest, southwest of Fraser, elev. 9500 ft., *Weber 8616* (COLO, DAO, WTU). Gunnison Co., just west of Schofield Pass in Elko Park, 6 mi. northwest of Gothic, *Crow 1147* (MSC, NHA). Lake Co., Twin Lakes, *Clements 421* (NY). La Plata Co., near La Plata, elev. 9000 ft., *Baker, Earle & Tracy 675* (F, MIN, MO, NY, RM, US). Larimer Co., Chamber's Lake, elev. 9500 ft., *Crandall 79* (GH, NY); trail from Platte Gulch to Wheeler Lake, ca. 5 mi. northwest of Alma, elev. 11500 ft., *Weber 8747* (COLO, DAO, MIN, WTU). Routt Co., trail from Columbine to summit of Hahn's Peak, elev. 8400–10800 ft., *Weber 6913* (COLO). San Juan Co., Needle Mt., Tenmile Basin, ca. 18 mi. southeast of Silverton, elev. 12800 ft., *Michener 830* (COLO). Summit Co., near Breckenridge, elev. 9800 ft., *Mackenzie 234* (MO, NY, RM, WIS). IDAHO: Blaine Co., 14 mi. north of Ketchum, Wood River, *Christ 15818* (NY). Boise Co., headwaters of S. Fork Payette River above Sacajawea Hot Springs, 3 mi. north of Elk Lake, Sawtooth Primitive Area, *Hitchcock & Muhlick 9861* (NY, WTU). Boundary Co., north slope of Mt. Rootnaah, *Daubenmire 44379* (WS). Custer Co., on banks of Yankee Fork, near Custer, *Christ 11345* (NY). Franklin Co., Bear River Range, Franklin Basin, *Maguire 21627* (NY). Freemont Co., Red Rock Pass, *Christ 5767* (NY). Idaho Co., west side of Seven Devils Divide, Seven Devils Mts., *Christ 12493* (NY, US). Lemhi Co., South Fork Camas Creek near Sleeping Deer Mt., 4 mi. northwest of Challis, *Hitchcock & Muhlick 11345* (WTU). Shoshone Co., near Sohons Pass, region of the Coeur D'Alene Mts., elev. 1500 m, *Leiberg 1425* (GH, NY, US). Teton Co., Victor, *Merrill & Wilcox 893* (GH, NY, RM, US). Valley Co., valley of Monumental Creek, near old town of Roosevelt, 21 mi. east of Stibnite, *Christ & Ward 1464* (NY). MONTANA: Deer Lodge Co., 4 mi. west of Storm Lake, Anaconda Mts., *Hitchcock & Muhlick 14868* (NY, WIS, WS, WTU). Flathead Co., near Whitefish Divide on Yakinikak Creek, *Mooar 10736* (MSC). Missoula Co., near Lagoon Lake, above Glacier Lake, Mission Mts. Primitive Area, elev. 6500 ft., *Crow 918* (MSC). Gallatin Co., Spanish Basin, elev. 6500 ft., *Rydberg & Bessey 4034* (CAN, NY). Glacier Co., Many Glacier, Glacier National Park, *Jones 5329* (GH). Lincoln Co., Big Cherry Creek, east of Libby, *Harvey 2703* (MONTU). Park Co., Cooke Guard Station, about 2 mi. east of Cooke City, elev. 8000 ft., *Witt 1780* (CAS, COLO, DAO, MIN, NY, UC, WIS, WS, WTU). Ravalli Co., Watchtower Creek Trail, Bitterroot Mts., elev. 5600 ft., *Lackschewitz & Fageraas 633* (MONTU). Sweet Grass Co., Sweet Grass Canyon, Crazy Mts., elev. 6000–7000 ft., *Flodman 447* (MO, NY). NEVADA: Douglas Co., 2 mi. east of junction of Kingsbury & Clear Creek Grades, *Train 3178* (UC). Elko Co., Jarbidge River, 2 mi. south of Jarbidge, *Baker 8636A* (WTU). Esmerald Co., Chiatovitch Creek, *Duran 2801* (UC). Humboldt Co., valley of Lawance Creek, Santa Rosa Mts., elev. 6000 ft., *Archer 246* (MICH). Nye Co., North Twin River, Toyabe Mts., *Linsdale & Linsdale 658* (CAS). Ormsby Co., head of Fall Creek, elev. 2460 m, *Baker 1332* (GH, MO, MSC, NY, UC, US). Washoe Co., Third Creek, near Mt. Rose, elev. 8500 ft., *Howell 14055* (CAS, WTU). NEW MEXICO: Rio Arriba Co., vicinity of Brazos Canyon, *Standley & Bollman 11043* (US). San Miguel Co., Winsor's Ranch, Pecos River National Forest, elev. 8400 ft., *Standley 4170* (GH, MO, NY, US). Santa Fe Co., Santa Clara Canyon, *Marcelline 1911* (F). OREGON: Baker Co., Hudson Creek, R44E, T6S, sec. 9., *Head 1594* (OSC). Crook Co., vicinity of Laidlaw, *Whited 3216½* (US). Deschutes Co., Diller Glacier, Three Sisters Mts. elev. 7500 ft., *VanVechten 248* (WTU). Grant Co., Strawberry Mt., Blue Mts., elev. 8000 ft., *Maguire & Holmgren 26843* (GH, NY). Harney Co., White Horse Mts., *Griffiths & Morris 464* (US). Hood River Co., White River, S. Mt. Hood; 10 mi. southeast of Mt. Hood, *Lloyd s.n.*, July 1894 (NY). Jackson Co., northern slopes of Mt. Asland, *Rossbach 599* (DS). Josephine Co., near Bolan Lake, Siskiyou Mts., *Hitchcock & Martin 5238* (DS, NY, UC, WS, WTU). Klamath Co., 15 mi. north of Fort Klamath, *Peck 9367* (DS, GH, MO, NY). Lake Co., Cogswell Creek, 8 mi. south of Lakeview, *Peck 15564* (DS, WTU). Lane Co., Scott Lake, McKenzie Pass, *Jones 5769* (WTU). Umatilla Co., 2 mi. north of Tollgate, Blue Mts., elev. 5000 ft., *Crow 1235* (MSC, NHA). Union Co., Indian Creek, Blue Mts., *Darlington 146* (CAS). Wallowa Co., Imnaha Canyon, 24 mi. above Imnaha, *Peck 18379* (DS, NY, WTU). Wasco Co., 15 Mile Meadow, Mt. Hood National Forest, elev. 4500 ft., *Jones 4135* (GH, UC, WTU). UTAH: Beaver Co., vicinity of Big John Flats, Beaver River headwaters, elev. 9000–10000 ft., *Maguire 19834* (GH, WTU). Box Elder Co., Dunn Canyon, Raft River Range, elev. 6500 ft., *Maguire & Holmgren 22176* (GH, NY, UC, US). Cache Co., mountains near Logan, *Shear s.n.*, 9 August 1895 (NY). Daggett Co., Green Lakes, elev. 7500 ft., *Hermann 4824* (MO). Duchesne Co., Moon Lake, Ashley Forest, elev. 8100 ft., *Harrison & Larsen 7704* (MO). Elko Co., Verdi Lake, Ruby Mts., elev. 10450 ft., *Mills & Beach 1575* (UC). Grand Co., north base of Haystack Mt., La Sal Mts., elev. 9300 ft., *Maguire, Richards, Maguire & Hammond 17965* (CAN, WTU). Juab Co., Granite Creek, Deep Creek Range, elev. 7000 ft., *Maguire & Holmgren 21865* (GH, NY, UC, US, WTU). Piute Co., Tate Mine, near Maryville, *Jones 5855* (MSC, NY, RM, UC). Rich Co., Laketown, elev. 6300 ft., *Harrison & Larsen 7956* (MO). Salt Lake Co., Silver Lake, Big Cottonwood Canyon, *Clemens s.n.*, 30 September 1909 (RM, UC). San Juan Co., southeast part of La Sal Mts., elev. 10000 ft., *Goldman & Hitchcock 1473* (MO). Sanpete Co., vicinity of Clayton Peak, Wasatch Mts., elev. 9000 ft., *Stokes s.n.*, 12–26 August 1903 (MO). Sevier Co., Fish Creek Canyon, *Garrett 2596* (NY). Summit Co., Mill Creek, southwest base of Mt. Elizabeth, Uinta Mts., elev. 8500 ft., *Hermann 5897* (MO, RM). Uintah Co., Paradise Park, Uinta Basin, elev. 10000 ft., *Graham 10056* (GH, MO). Utah Co., American Fork Canyon, elev. 8000 ft., *Jones 1362* (CAS, F, MICH, MSC, NY, UC, US, WS, WTU). Wayne Co., Blind Lake, Aquarius Plateau, elev. 10000 ft., *Dixon 758* (F). WASHINGTON: Asotin Co., Blue Mts., *Jones 1876* (WS). Clallam Co., east face of Obstruction Point, elev. 5600 ft., *Meyer 1258* (MO). Chelan Co., northeast side of Snow Lake, Stuart Range, Wenatchee Mts., southwest of Leavenworth elev. 5000 ft., *Crow 1108* (MSC, NHA). Columbia Co., Indian Corral, Blue Mts., *Carlington 146* (WS). Jefferson Co., Mt. Olympus, elev. 5000 ft., *Flett 3043* (WTU). Klickitat Co., Bingen, *Suksdorf s.n.* 18 April 1895 (WS). Okanogan Co., head of Middle Fork of Pasayten River, north of Harts Pass, *Ownbey & Meyer 2312* (DS, MO, NY, UC, WS, WTU). Pend

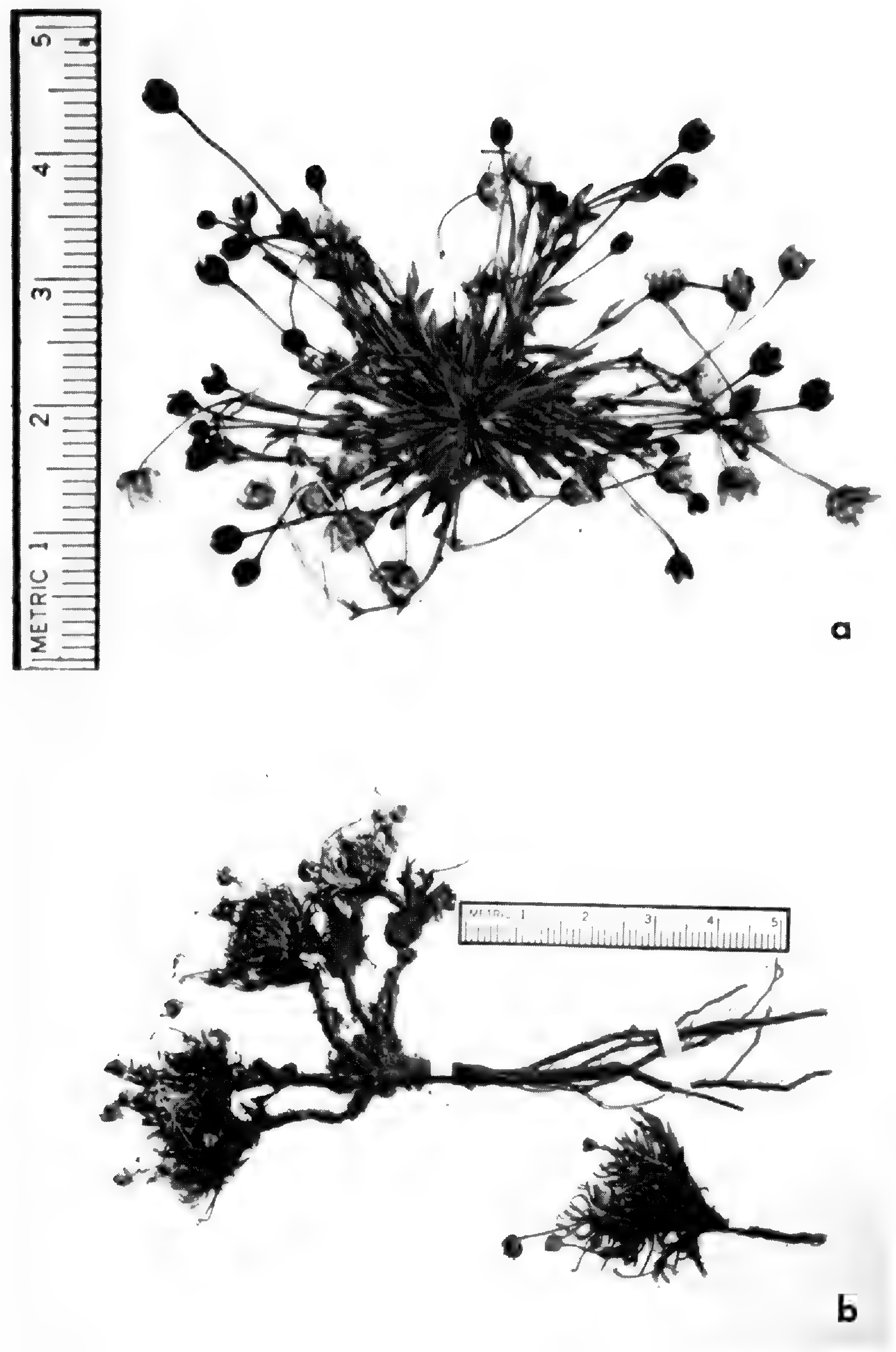

Figure 14. *Sagina nivalis.* a. habit, Axel Heiberg Is., N. W. T. (*Hegg & Beschel 10857*, GH); b. habit, Attu Is., Aleutians (*Jordal & Miller 3077-A*, MICH).

Oreille Co., near Gypsy Meadow, elev. 4800 ft., *Layser 918* (WS). Pierce Co., road to Sunrise glacier, Mt. Rainier, *Crow 1236* (MSC). Whatcom Co., Bagley Lake, near Mt. Baker Lodge, elev. 4300 ft., *Thompson 5700* (DS, MO, WTU). Yakima Co., Wodan's Vale, Mt. Adams, elev. 2000 m, *Suksdorf 6829* (COLO, DS, NY, UC, WS, WTU). WYOMING: Albany Co., Centennial, *Nelson 7728* (GH, MIN, MO, NY, RM, US). Carbon Co., South Spring Creek, Hayden Forest, *Eggleston 11277* (US). Fremont Co., Brooks Lake, near Dubois, *Churchill s.n.*, 18 July 1958 (MSC). Lincoln Co., near junction of Box Canyon Creek and Grey's River, elev. 7800 ft., *Goodman 5133* (RM). Park Co., Beartooth Pass, Beartooth Range, elev. 9200 ft., *Porsild, Johnson & Darling 22753* (CAN). Teton Co., vicinity of Holback Canyon, elev. 7500 ft., *Williams & Pierson 735* (CAS, GH, MO, NY, RM).

The binomial *Spergula saginoides* was published by Linnaeus (1753) in *Species Plantarum*. Although he refers to a Vaillant and Sauvages synonym, his knowledge of the species was certainly based on a Siberian specimen received from Johnn George Gmelin. This species is represented by a specimen at the Linnean Society of London, LINN *604.6*, which bears a note in Linnaeus' handwriting on the back of the sheet stating "Spergula foliis linearibus oppositis . . . Gmel." (W. T. Stearn, 1974, personal communication). The specimen is also annotated by Linnaeus as "5 saginoides," thus relating it to *Species Plantarum*. I feel this specimen is the lectotype.

The combination *Sagina saginoides* Karsten is accepted in *Flora Europea* as having priority, dated at 1882, although Dalla Torre made the same combination in Hartinger's *Atlas der Alpinflora* (1882). I have not been able to confirm the dates of publication.

In reorganizing the specimens of *Sagina* in the Gray Herbarium, Fernald (1925a) noted that the typical phase of *S. saginoides* of the Arctic and Eurasia occurred locally throughout the North American range of the species, but that most of the material of western America had sepals and capsules shorter than those of the typical phase. This American extreme he described as var. *hesperia*.

The Eurasian specimens exhibit considerable variability, the range for sepal and capsule length being continuous (sepals 2.0–3.0 mm long; capsules 2.5–5.0 mm long). Frequently plants of lower elevations tend to be more robust, producing slightly larger flowers, while plants of higher elevations are generally smaller. The more robust, larger flowered plants, with capsules up to 5.0 mm long were first recognized at the specific level as *Spergella macrocarpa* Reichb., and later at the varietal level as *Sagina saginoides* var. *macrocarpa* (Reichb.) Moss. Moss (1914) admits that the discontinuity between the two varieties is trifling, but continues to recognize two varieties in *S. saginoides* (Moss, 1920). The treatment in *Flora Europaea* (Clapham & Jardin, 1964) notes that the larger flowered plants cannot be clearly separated from typical *S. saginoides* as a distinct taxon.

In this variable species discontinuity appears to be lacking in the characters used to delineate *Sagina saginoides* var. *macrocarpa* and var. *hesperia.* Therefore, I am not recognizing infraspecific categories in this species.

Earlier collections of Reichenbach, which were housed at the Zwinger Museum in Dresden, Germany, were destroyed by fire in May 1849 (Stafleu, 1967). However, the original plates of his *Icones Florae Germanicae et Helveticae* are preserved at Vienna (W).

Another taxon which cannot be regarded as distinct is *Sagina micrantha.* While arranging the specimens of *Sagina* in the Gray Herbarium, Fernald (1925) found it desirable to make the combination *Sagina micrantha* (Bunge) Fern. based on five specimens from the Aleutians and St. Paul Island. These specimens annotated by Fernald belong to *Sagina nivalis.* The original description for the taxon is not descriptive of *S. nivalis.* After study of Bunge's original material preserved at the Komarov Botanical Institute in Leningrad, the specimen representing *Spergula micrantha* Bunge is clearly seen as *Sagina saginoides,* and I herein designate Bunge's specimen "pr. Barnaul, Tomskoi Sawod" as the lectotype for *Spergula micrantha* Bunge.

3. **Sagina procumbens** L., Sp. Pl. **1:** 128. 1753.

Alsine procumbens (L.) Crantz, Inst. **2:** 404. 1766. TYPE: unknown. "Habitat in Europae, pascuis sterilibus uliginosis aridis."

Sagina procumbens var. *compacta* Lange, Meddel. Groenl. **3:** 242. 1887. TYPE: unknown. ORIGINAL MATERIAL: Igaliko, Greenland. Collected by Vahl. (Not at C).

Sagina muscosa Jord., Pugill. Pl. Nov. p. 32. 1852. TYPE: "C. Martin, Pl. de ENV. de LYON, 1851. Bords des chemin an Mt. Pilat (Loire). 20 Juil." (Lectotype, P!, designated herein)

Sagina corsica Jordan, Obs. Pl. Crit. **7:** 15. 1849. TYPE: "Corse, Cagnone, juillet 1840. Jordan." (Lectotype, P!, designated herein)

Perennial. Plants totally glabrous. Stems ascending or, more frequently, procumbent. Rosettes of linear leaves frequent in younger plants, 9–35 (–55) mm in diameter. Procumbent stems with axillary fascicles giving rise to secondary tufts or, less frequently, secondary rosettes, rooting at the nodes. Cauline leaves

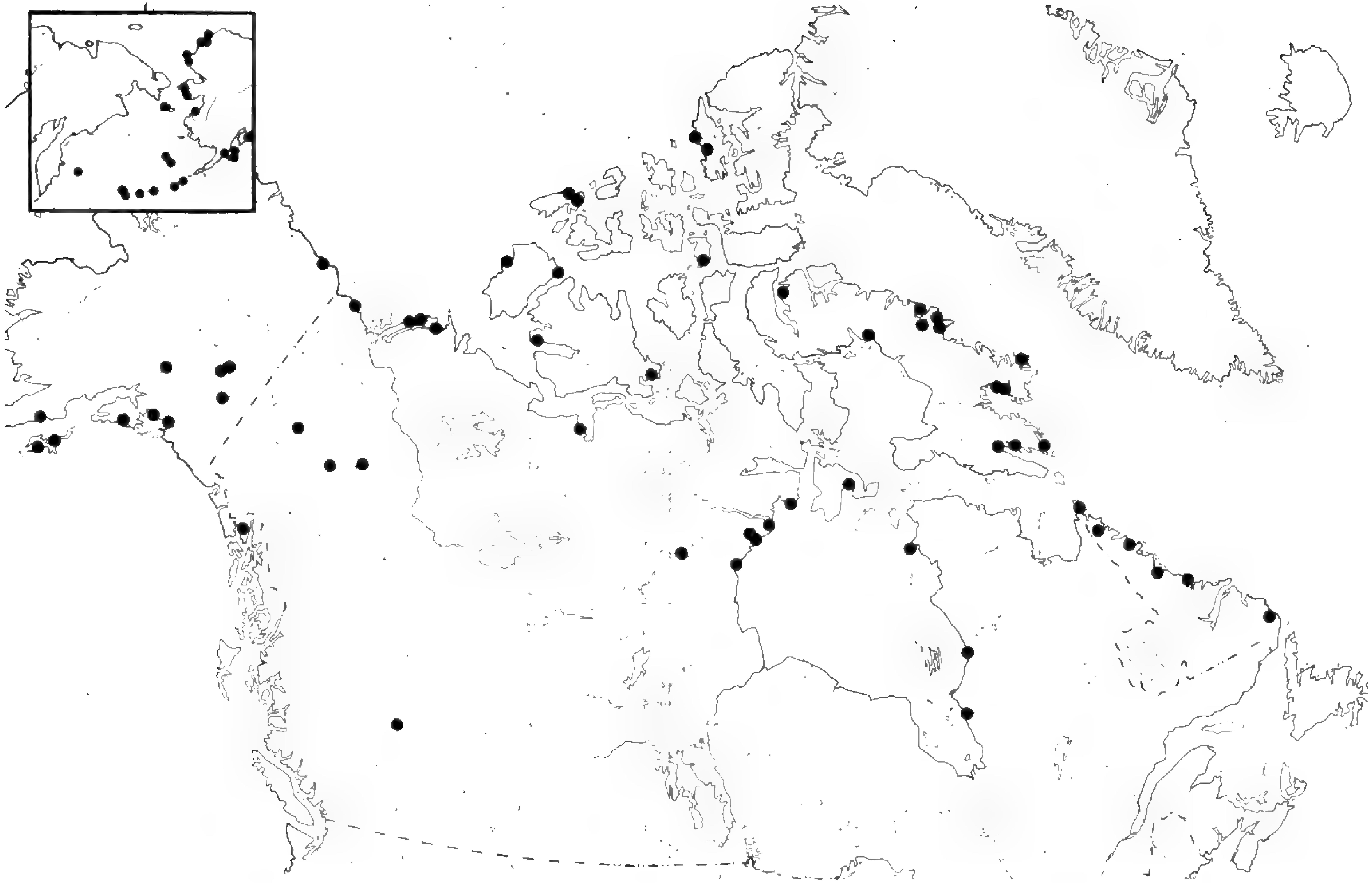

Figure 15. Geographical distribution of *Sagina nivalis* in North America.

linear, lower leaves 4–15 mm long, becoming shorter toward the apex, upper leaves 2.5–6.0 mm long. Leaf margins entire, rarely with minute glandular cilia. Leaves apiculate to aristate. Connate leaf bases not conspicuous, never forming an inflated cup. Pedicels generally long, filiform, recurved during capsule development, becoming erect at maturity. Flowers 4-merous, occasionally 4- and 5-merous. Pedicels long, filiform. Sepals elliptical to orbicular, 1.5–2.0 (–2.5) mm long, hyaline margins white, never purple tinged. Petals equal to or fewer than number of sepals, sometimes absent; 0.75–1.0 (–1.5) mm long, orbicular to elliptical. Stamens 4, occasionally 8, filaments 1.0–1.5 mm long, anthers 0.25 mm long. Capsules slightly exceeding sepals. Capsule valves thin, (1.5–) 2.0–2.5 (–3.0) mm long. Sepals appressed during capsular development, divergent following dehiscence. Seeds brown, obliquely triangular, with a distinct dorsal groove, (0.3–) 0.4 (–0.5) mm long. Chromosome number: $2n = 22$. Figure 11.

ECOLOGY AND DISTRIBUTION: A weedy species, growing in wet or damp gravelly or sandy soils along roadsides, sidewalk cracks, and margins of paths or lawns. Also frequent along pond and lake margins, coastal rocks and sands and sea cliffs. The species is sometimes cultivated as a ground cover. In eastern North America from Newfoundland, west to New York and eastern Pennsylvania, and the southwest shore of Lake Superior. In western North America, from the San Francisco area north to Washington and infrequently northward to the Queen Charlotte and Aleutian Islands. Single collections are known from Detroit, Michigan; Columbus, Ohio; Pulaski Co., Arkansas; Missouri (no specific locality cited); and Marysvale, Utah. Occasionally at high elevations in Mexico and Central America. Also introduced in eastern Asia and the Southern Hemisphere. Native to Eurasia. Flowering May to September. Figure 12.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA: Between Prince Rupert and Galloway Rapids, *Calder, Savile & Ferguson 13208* (DAO). Near east end of Summit Lake on road from Nakusp to New Denver, *Calder & Savile 10010* (DAO, NY). Vancouver, *Eastham 9906* (UC). New Westminster, *Henry 9139* (RM). Hecate Island, *McCabe 7134* (UC). East shore of Kootnay Lake, 15 mi. south of Boswell, *Senn & Frankton 5868* (DAO). Queen Charlotte Islands, Summit, between Gillatt Arm of Cumshewa Inlet and Peel Inlet, Moresby Island, *Calder & Taylor 35173* (DAO). Vancouver Island, Duncans-Cowichan Lake road, *Rosendahl 1758* (GH, NY, UC, US). NEW BRUNSWICK: Charlotte Co., Mill Cove, Campobello Island, *Malte*

Figure 16. *Sagina caespitosa.* a. habit; b. close-up showing pubescence on calyx base and pedicel. Both Baralzon Lake, Manitoba (*Scoggan & Baldwin 8206*, CAN).

971/29 (CAN, GH). Gloucester Co., Grande Anse, *Blake 5533* (CAS, GH, NY, US, WTU). Kent Co., Bass River, *Fowler s.n.*, August 1875 (WIS). Kings Co., Sussex, *Svenson & Fassett 2000* (GH). Northumberland Co., Little Branch, Miramichi, *Fowler s.n.*, 24 August 1894 (F, US, WIS). Restigouche Co., Eel River, near Dalhousie, *Malte 456* (CAN). Sunbury Co., Oromocho River at Fredericton Junction, *Roberts & Bateman 64 2069* (DAO). Westmorland Co., about 15 mi. northeast of Sackville, *Scoggan 12243* (CAN). York Co., Fredericton, *Scoggan 11867* (CAN). LABRADOR: Perquet Island, 51°26′N., *Allen 66* (GH, NY). Red Islands, near Turnavik, 53°48′N., 56°46′W., *Bishop 285* (CAN, US). Forteau, on Strait of Belle Isle, *Donly s.n.*, ca. 20 August 1964 (DAO). NEWFOUNDLAND: Gander, *Bassett 483* (DAO, MO). Birchy Cove, Curling, Bay of Islands, *Fernald & Wiegand 3334* (CAN, GH, NY). Cow Head, north of St. Paul's Bay, *Fernald & Wiegand 3335* (GH). Dildo Run, southern shores of Notre Dame Bay, *Fernald & Wiegand 5378* (F, GH, MO). Grand Bruit, district of Burgeo and La Poile, *Fernald, Long & Fogg 247* (GH). Port Saunders, region of Ingorachoix Bay, *Fernald & Wiegand 3336* (GH). Ship Cove, Sacred Bay, *Fernald, Wiegand & Long 28152* (GH). Tilt Cove, northern shores of Notre Dame Bay, *Fernald & Wiegand 5379* (NY, RM, UC). Bell Island, near Topsail, Conception Bay, *Howe & Long 1308* (NY). St. John's, *Robinson & Schrenk 218* (CAN, DAO, F, GH, MIN, MO, NY, US). Hughes Brook, Humber District, *Rouleau 1662* (CAN, DAO, NY, US). Fogo Island, *Sornborger s.n.*, 7 August 1903 (CAN, GH, NY, US). NOVA SCOTIA: Cape Breton Co., Sydney, Cape Breton Island, *Barnhart 832* (NY). Colchester Co., Lynn, *Dore 45.1095* (DAO). Cumberland Co., cliffs near Moose River, about 8 mi. east of Parrsboro, *Scoggan 13820* (CAN). Digby Co., Brier Island, *Smith, Roland, Collins, Erskine & Schofield 126* (DAO). Guysborough Co., Boyleston, *Hamilton 18294* (CAN, US). Halifax Co., Halibut Cove, near Halifax, *Dore, Senn & Gorham 45.521* (DAO). Inverness Co., near Pleasant Bay, Cape Breton Island, *Pease 26634* (GH). Kings Co., Hall Harbor, *Fassett 19049* (WIS). Lunenburg Co., Chester, *Pease 26655* (GH). Pictou Co., Pictou, *Robinson 209* (NY). Shelburne Co., on the island, Barrington Passage, *Macoun 80869* (CAN, MO). Victoria Co., Money Rocks, St. Paul Island, *Perry & Roscoe 194* (CAN, GH, MO, NY, US). Yarmouth Co., Jassy Lake, Lake Annis, *Bean, White & Linden 21193* (GH, NY, US). Sable Island, 43°59′N., 59°47′W., *St. John 1226* (CAN, GH, NY, US). PRINCE EDWARD ISLAND: Near Bonshaw, *Erskine & Dore 1105* (DAO, NY). QUEBEC: Anticosti Island Co., Pointe de l'est, *Marie-Victorin, Rolland-Germain & Louis-Marie 21 642* (GH). Bonaventure Co., Port Daniel,*Lepage 13542* (DAO). Brome Co., Bolton Pass, *Marie-Victorin, Rolland-Germain, Raymond & Rouleau 56363* (GH). Gaspé-Est Co., Perce, *Marie-Victorin & Rolland-Germain 49 462* (DAO, MICH). Levis Co., Point Garneau, *Cing-Mars & Cayouette s.n.*, 15 September 1954 (DAO). Magdaline Islands Co., Grindstone, Grindstone Island, *Fernald, Bartram, Long & St. John 7439* (GH). Matane Co., Riviere Blanche, *Forbes 1494* (CAN, DS, GH). Rimouski Co., Cap a'l'Original, Bic, *Clausen & Trapido 2827* (MIN, UC). Riviere-De-Loup Co., Trois-Pistoles, *Lepage 15325* (DAO). Saguenay Co., Blanc Sablon, Straits of Belle Isle, *Fernald, Wiegand & Long 28156* (GH). Temiscouata Co., Saint-Hongré, *Blouin, Carrier, Lemiaux & Richard 7373* (DAO). Wolfe Co., Notre-Dame de Ham, Canton d'Ham Nord, *Hamel & Brisson 15399* (CAN). **France.** ILES SAINT-PIERRE: Savoyard, *Le Hors s.n.*, 16 August 1950 (DAO).

Mexico. FEDERAL: Llano do la Cieneguilla, cerca del Cerro de la Palma, Sierra de las Cruces, elev. 3500 m, *Rzedowski 23849* (FNCB); 3 km al SW de Ajusco, elev. 3050 m, *Cruz Cisneros 1343* (ENCB); Puerto de Las Cruces, delagación de Cuajimalpa, elev. 3000 m, *Rzedowski 30804* (ENCB); Cerca del Puerto de Las Cruces, Sierra de Las Cruces, elev. 3000 m. *Rzedowski 21733* (ENCB). HIDALGO: Cerro de las Ventanas, 6 km al N de Pachuca, elev. 2900 m, *Rzedowski 28003* (ENCB). MEXICO: Vertiente NW del Ixtaccíhuatl, en la región de Peñas Cuatas, La Ciénega, *Rzedowski 21813* (ENCB, MICH); Vertiente SW del Ixtaccíhuatl, La Joya, elev. 3850 m, *Rzedowski 21813* (ENCB, MICH); Cerca del Paso de Cortés, entre Popocatépetl e Ixtaccíhuatl, elev. 3550 m, *Rzedowski 21847* (ENCB); Canón al E de Santiago Cuautenco, municipio de Amecameca, elev. 2650 m, *Rzedowski 26711a* (ENCB).

United States. ALASKA: Haines (Chilkoot Inlet, Lynn Canal, N of Juneau), *Anderson 6047* (CAN). Unalaska (Aleutian Islands), *Eyerdam 2273* (CAN, CAS, DS, NY, UC, US). Girdwood (Cook Inlet, Turnagain Arm, SE of Anchorage), *Hultén s.n.*, 1 July 1961 (US). Sand Point, Shumagin Islands, *Riggs s.n.*, 31 July 1913 (US). Vicinity of Massacre Bay, Peaceful Valley, Attu Island (Aleutian Islands), *Van-Schaack 499a* (US). ARKANSAS: Pulaski Co., without definite locality, *Hasse s.n.*, May 1886 (MONTU). CALIFORNIA: Amanda Co., weed in University of California Botanical Garden, Berkeley, *Crow 1179* (MSC, NHA). Del Norte Co., along road in redwoods north of Crescent City, *Eastwood 12299* (CAS). Humboldt Co., Freshwater Creek near Wrangletown, *Tracy 5338* (CAS, UC, WTU). Marin Co., Shell Beach, *Howell 20929* (CAS). Mendocino Co., Highway 1, Caspar, *Nobs & Smith 1149* (CAS). San Francisco Co., Golden Gate Park on cross park boulevard, San Francisco, *Howell 32571* (CAS, MSC). San Mateo Co., ravine north of Seal Cove, *Dudley s.n.*, 16 March 1900 (DS). Santa Clara Co., weed in Stanford Experimental Garden, Stanford University, Stanford, *Thomas 8725* (DS). CONNECTICUT: Fairfield Co., Fairfield, *Johnson s.n.*, 30 June 1890 (NY). Hartford Co., South Glastonbury, *Wilson 75* (RM). Litchfield Co., Norfolk, *Redfield 13062* (MO). New Haven Co., Milford, *Eames 1494* (MIN). New London Co., Franklin, *Woodward s.n.*, 30 August 1914 (GH). Tolland Co., Hop River, Andover, *Seymour 17643* (WIS). Windham Co., Connecticut River, Westminster, *Blanchard 70* (GH). DELAWARE: New Castle Co., Wilmington, *Tatnall s.n.*, 21 May 1930 (GH). IDAHO: Kootenai Co., Hayden Lake, *Baker 14882* (WTU). MAINE: Cumberland Co., Portland, *Garber s.n.*, 29 August 1874 (F). Franklin Co., South Chesterville, *Eaton 17001* (WIS). Hancock Co., vicinity of Blue Hill, *Maxon 11036* (US). Kennebec Co., South Litchfield, *Fassett 18292* (WIS). Knox Co., Union, *Cole 973* (US). Lincoln Co., Ocean Point, *Fassett 15442* (WIS). Sagadahoc Co., Bowdoinham, *Fassett 2850* (WIS). York Co., South Berwick, *True 1141* (US). Washington Co., *Cutler, Kennedy, Williams, Collins & Fernald s.n.*, 2 July 1902 (GH). MARYLAND: Baltimore Co., Baltimore, *Jones s.n.*, 25 May 1904 (F). MASSACHUSETTS: Barnstable Co., Woods Hole, *Bacon 95* (MSC). Berkshire Co., Great Barrington, *Leavenworth s.n.*, in 1820 (MSC). Bristol Co., New Bedford, *Greene s.n.*, date unknown (WIS). Dukes Co., Gay Head, Martha's Vineyard, *Seymour 1201* (GH, NY, US). Essex Co., Newburyport, *Fernald s.n.*, 2 October 1902 (GH). Franklin Co., Charlemont, *Hunnewell 10659* (GH). Hampden Co., Granville, *Seymour 121* (GH, MO). Hampshire Co., Huntington, *Robinson 776* (GH). Middlesex Co., Waltham, *Seymour & Seymour s.n.*, 4 July 1911 (CAS, MSC, WIS). Nantucket Co., Brant Point Road, Nantucket Island, *Bicknell s.n.*, 20 June 1908 (NY). Plymouth Co., Middleboro, *Murdoch 596* (F). Suffolk Co., Revere, *Clark s.n.*, in 1873 (MSC). Worcester Co., Lancaster, *Seymour s.n.*, 5 July 1944 (WIS). MICHIGAN: Houghton Co., Otter Lake, *Hyypio 409* (MSC). Keweenaw Co., Allouez, *Hermann 7797* (DS, F, MICH, MO, NY, US, WS). Marquette Co., Champion, *Hill s.n.*, 10 July 1889 (GH, NY). Wayne Co., golf links, Detroit, *Piper s.n.* 8 June 1922 (US). MINNESOTA: St. Louis Co., Duluth, *Lakela 2561* (MIN, NY, UC, WS). MONTANA: Lincoln Co., Stanley Creek, base of Stanley Mt., elev. 760 m, *Harvey 5492* (MONTU). NEW HAMPSHIRE: Carroll Co., Wakefield, *Sargent s.n.*, 2 August 1912 (NHA). Cheshire Co., Hinsdale, *Batchelder 5305* (NHA); Walpole, *Eaton & Griscom 17163* (NHA). Grafton Co., road near confluence of Batchelders Brook and Bakers River, Warren, *Churchill s.n.*, 11 July 1939 (MSC). Hillsborough Co., Peterborough, *Batchelder s.n.*, 3 September 1928 (MO). Rockingham Co., Isle of Shoals, *Canby s.n.*, August 1866 (WS); Windham, *Harris 436* (NHA). Strafford Co., banks of Bellamy River, Madbury, *Moulton & Hodgdon 9047* (NHA). NEW JERSEY: Ocean Co., Beach Haven Terrace, Long Beach Island, *Long 3798* (GH). Passaic Co., Hewitt, *Mackenzie 2850* (MO). NEW YORK: Albany Co., Albany, *House 28498* (NY). Bronx Co., Bronx, *Moldenke 20157* (CAN). Franklin Co., Adirondack Hatchery, Saranac Inn, *Muenscher & Maguire 1113* (F, MO). Fulton Co., Nick Stone Golf Course, Caroga Lake, *Fassett 10374* (WIS). Onadaga Co., near Jamesville, *House s.n.*, 1 August 1903 (NY). Oneida Co., Utica, *Harberer 129* (GH, NY). Rensselaer Co., Troy, *Hall s.n.*, 1828–1834 (F). Richmond Co., Richmond Valley, Staten Island, *E. G. Britton s.n.*, 24 June 1894 (GH, NY). Rockland Co., Clarkestown Twp., *Lehr 1020* (NY). Saratoga Co., Satatoga Springs, *House 27928* (GH, NY). Suffolk Co., Wading River, Long Island, *Miller 327* (UC). Tompkins Co., Ithaca, *Eames 9870* (GH, MO). Westchester Co., Tarrytown, *Barnhart 1446* (NY). OHIO: Pickaway Co., Tarlton, *Bartley 1526* (NY, US). OREGON: Clatsop Co., Cannon Beach, *Thompson 12746* (MO, NY, WS, WTU). Coos Co., Fossil Point, Coos Bay, *Abrams & Benson 10577* (DS). Curry Co., The Heads, Port Orford, *Peck 9062* (GH, MO, NY). Klamath Co., north end of Lake-of-the-Woods, *Peck 16598* (DS). Land Co., just south of Heceta Head lighthouse, *Cronquist 6112* (GH, NY, UC, WTU). Lincoln Co., Yachats, *Cooke 10717* (OSC). Multnomah Co., Albina, *Suksdorf 1744* (WS). Tillamook Co., Garibaldi, *Erickson s.n.*, 15 July 1954 (OSC). PENNSYLVANIA: Berks Co., Reading, *Fisher s.n.*, 23 August 1905 (MICH). Cumberland Co., Newville, *Wahl, Wherry, Hammond, Stafford & Tanger 6624* (GH). Lackawana Co., Scranton, *Glowenke 6861* (GH). Lehigh Co., Allentown, *Schaeffer 56239* (US). Monroe Co., Pocono Manor, *Wherry s.n.*, 18 June 1945 (DAO). Montgomery Co., Philadelphia, *Witte s.n.*, 7 July 1934 (RM, NY). RHODE ISLAND: Newport Co., Newport, *Tweedy s.n.*, June 1881 (DS). Providence Co., Providence, *Collins s.n.*, 30 May 1891 (US). Washington Co., Block Island, *Watson s.n.*, June 1885 (GH). UTAH: Piute Co., Tate Mine, Marysvale, elev. 9000 ft., *Jones 5855* (MO). VERMONT: Caldonia Co., Groton, *Seymour 18328* (WIS). Orange Co., Newbury, *Jesup & Sargent s.n.*, 29 July 1891 (GH). Washington Co., Walden and Cabot, *Burbank, Grout & Eggleston s.n.*, 4 July 1894 (NY). Windham Co., Newfane, *Grout s.n.*, 2 July 1895 (F). Windsor Co., Rochester, *Dutton s.n.*, 10 July 1914 (GH, MICH, MO). WASHINGTON: Clallam Co., Elcoha River, Olympic Peninsula, *Jones 3522* (WTU). Chelan Co., head of Poison Creek, north side of Lake Chelan, *Ward 700* (CAS, WS, WTU). Clatsop Co., Cornet Bay, Whidbey Island, *Smith 1720* (UC). King Co., Kirkland Lake, *Eyerdam 1686* (DAO). Kittitas Co., Snoqualmie Pass, *Wiegand 840* (F). Kitsap Co., Colby, *Warren 276* (WS, WTU). Klickitat Co., Bingen, *Suksdorf 5013* (WS). Pacific Co., Ilwaco, *Abrams 11272* (DS). San Juan Co., Long Island, *Muenscher & Muenscher 15979* (MIN). Skagit Co., Bear Creek, T36N, R8E, sec. 10, Mt. Baker National Forest, *Crow 1241* (MSC, NHA). Snohomish Co., Everett, *Minch s.n.*, 23 July 1928 (WS). Wahkiakum Co., Cathlamet, *Foster s.n.*, 10 May 1907

(WS). Whatcom Co., Little Sandy Creek, Baker Lake, T37N, R8E, sec. 12, *Crow 1238* (MSC, NHA). WISCONSIN: Iron Co., Hurley, *Fassett 9541* (WIS).

Typification of *Sagina procumbens* presents a difficult problem which I have discussed at length with W. T. Stearn of the British Museum (Natural History). Using the diagnostic phrase *ramis procumbentibus,* Linnaeus (1737a), placed his *Sagina procumbens* in "Octandria Tetragynia" in his *Flora Lapponica* and clearly intended the name to apply to a Lapland plant with flowers parts in fours and procumbent shoots. In *Species Plantarum* Linnaeus (1753) utilized the same phrase name, unaltered from *Flora Lapponica,* but placed *S. procumbens* in "Tetrandria Tetragynia" and recognized two additional varieties. This suggests that his concept of the species at the time of the writing of *Species Plantarum* was based on material he had seen since writing *Flora Lapponica.* I have studied the specimen labelled *Sagina procumbens* in the Linnaean Herbarium at the Linnean Society of London, LINN *177.1.* It is clearly *S. subulata* (a pentamerous species), as annotated by Smith. A specimen supposedly representing Linnaeus' *Flora Lapponica* no. 157 is in the Linnaean Lapland herbarium at the Institute de France, Paris. In an account of this herbarium by Th. M. Fries (1861), it is stated that the specimen representing *Flora Lapponica* no. 157 was not the accepted *S. procumbens* but was *S. saxatilis* Wimmer (now considered conspecific with *S. saginoides*), a pentamerous taxon. I have studied a photograph of this specimen and agree it cannot be taken to represent Linnaeus' concept of *S. procumbens.* In the absence of a *S. procumbens* specimen which can be indubitably accepted as the type I choose to allow Linnaeus' protologue to represent the name.

A few specimens from the coast of Labrador and of the St. Lawrence seaway have been considered as *Sagina procumbens* var. *compacta* Lange. These plants appear to be depauperate, environmentally induced growth forms. Dr. J. K. Morton (personal communication, 1973) has also questioned the validity of this taxon. His field observations in a dune situation indicate that there seemed to be a cline from the very compact form ("good" var. *compacta*) growing away from the shore and becoming more normal toward the shore. Morton collected seed and vouchers from both extremes and grew the plants under cool greenhouse conditions. Because plants grown from the compact form appear as normal *S. procum-*

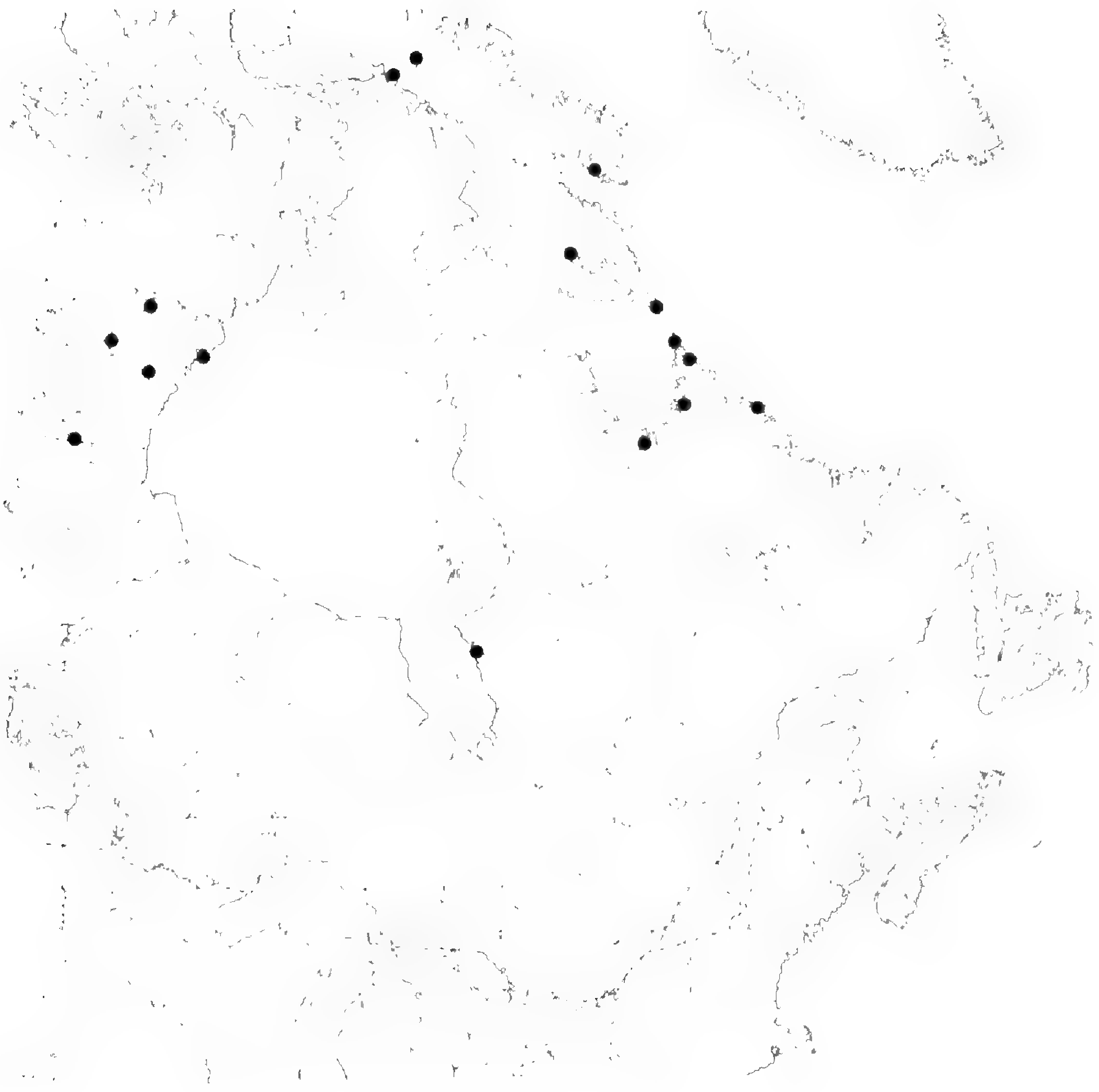

Figure 17. Geographical distribution of *Sagina caespitosa* in North America.

bens, we agree that var. *compacta* should be considered no more than a growth form.

I have studied J. Vahl's specimens of *Sagina procumbens* from Greenland on deposit at Copenhagen (C) and none of these can be taken as type material. The two specimens labelled Igaliko, Greenland, the type locality, do not fit Lange's concept of var. *compacta.*

4. **Sagina subulata** (Sw.) Presl, Fl. Sic. 158. 1826.

Spergula subulata Sw., Sven. Vet. Acad. Handl. Stockh. p. 45. 1789. *Phaloe* *subulata* (Sw.) Dumort., Fl. Belgica p. 110. 1827. *Spergella subulata* (Sw.) Reichb., Fl. Germ. Excurs. p. 794. 1832. *Alsine subulata* (Sw.) Krause, in Sturms, Fl. Deutschl. 2 ed. **5**: 34. 1901. TYPE: "Halland, Doct. Osbeck". (Lectotype, BM!)

Sagina revelieria Jord. & Fourr., Brev. Pl. Nov. fasc. i. p. 11. 1866. TYPE: not seen. ORIGINAL MATERIAL: Corsica Mountains, Quenza, Corsica, France.

Perennial. Plants tufted, caespitose, frequently forming dense mats. Horizontal stems becoming slightly woody with extensive mat formation. Branches short, with short internodes, ascending or decumbent, often not exceeding basal leaves. Stems densely glandular pubescent or less frequently glabrous. Leaves densely glandular pubescent or with glandular hairs restricted to the margins, and then often minutely glandular ciliate, rarely glabrous. Leaves with long aristae, 0.5–0.75 mm long. Basal tufts of leaves linear, 3.0–12 mm long, curled inward. Cauline leaves linear-subulate, 3.0–10 mm long. Connate leaf bases scarious, forming a conspicuous cup. Flowers axillary or terminal, usually solitary. Pedicels long, filiform, mean length 22.5 mm, erect during capsular development. Pedicels densely to weakly pubescent. Flowers 5-merous, rarely 4- and 5-merous. Sepals elliptical, 1.5–2.0 mm long, the hyaline margins white. Petals elliptical, 1.5–2.0 mm long, shorter than or equaling sepals. Stamens 10, filaments (1.0–) 1.5 mm long, anthers 0.25 mm long. Capsules slightly exceeding sepals. Capsule valves thin, 2.0–3.0 (–3.5) mm long, dehiscing to base. Sepals remaining appressed following capsule dehiscence. Seeds brown, obliquely triangular, with dorsal groove, a distinct notch at hilum, surface smooth, 0.4 (–0.5) mm long. Chromosome number: $2n = 18, 22$. Figure 13.

ECOLOGY AND DISTRIBUTION: In wet gravelly sands of stream margins. Introduced from Europe and known only from Harney Co., Oregon, Bedford Co., Virginia and La Laguna, Baja California.

Flowering June to August.

REPRESENTATIVE SPECIMENS: **Mexico.** BAJA CALIFORNIA: Sierra de la Laguna, *Brandegee s.n.*, 22 January 1890 (UC). Sierra de la Laguna, *Brandegee s.n.*, 27 March 1892 (GH, UC). Sierra de la Laguna, *Brandegee s.n.*, 4 October 1899 (GH, NY, UC). Cape Region, La Laguna, elev. 6000 ft., *Thomas 7885* (CAS, DS, GH, MICH, US).

United States. OREGON: Harney Co., Steens Mt., *Faegri s.n.*, 25 July 1965 (OSC); Dino Creek, Steens Mt., *Train s.n.*, 30 July 1935 (US) and 31 July 1935 (MIN). VIRGINIA: Bedford Co., specific locality unknown, *Curtiss s.n.*, 20 May 1872 (MO).

Figure 18. *Sagina decumbens* ssp. *decumbens*. a. habit; b. close-up showing glandular pubescence. Both South Carolina (*Weatherby & Griscom 16524*, US).

Sagina subulata is an extremely variable, wide ranging European species. *Sagina glabra* and *S. pilifera,* two closely allied European montane taxa of restricted distribution, overlap in numerous characteristics with *S. subulata* and appear to be divergent expressions of this variable species. Further study of these taxa may reveal that this complex should be considered a single species with three infraspecific taxa.

I have seen a single specimen from eastern North America which is referable to *Sagina subulata.* Plants treated by Torrey and Gray as *S. subulata* belong to *S. decumbens* ssp. *decumbens* (see discussion under that taxon).

In the Northwest, three specimens (*Train s.n.,* July 30, 1935 and July 31, 1935; *Faegri s.n.,* July 25, 1965) collected in the alpine zone of Steens Mt., Harney Co., Oregon exhibit glandular pubescence. The Train specimens are extremely pubescent while the Faegri specimen is weakly glandular, with foliar pubescence restricted to leaf margins. Introduction of this population of *Sagina subulata* into this remote area is without explanation.

Another isolated population of *Sagina subulata* occurs at the tip of Baja California. Specimens collected by T. S. Brandegee during the period 1890–1899 and by J. H. Thomas in 1959 in the mountains at La Laguna (ca. 5,500 ft. elevation) occurred in the region of an abandoned ranch which had been operated in the 1800's (Goldman, 1951). Introduction of this population probably took place when the ranch was functioning.

A mat-producing form of this taxon is widely used as a ground cover and is available from nurserymen under the names "Scottish Moss" and "Corsican Pearlwort." Living plants observed in the W. J. Beal Botanical Garden, Michigan State University, were noted to flower profusely but with no subsequent capsular development; and herbarium specimens from several localities in the western United States show little capsular development. The cultivar propagates easily by vegetative means, but is not found readily escaping cultivation. The cultivar differs from the native European mat-producing form by being glabrous, except for the minutely glandular-ciliate leaf margins. The cultivated form originated in the Corse Mountains, Corsica, France (Vilmorin, 1894).

5. **Sagina nivalis** (Lindbl.) Fries, Nov. Fl. Suec. Mant. **3:** 31. 1842.
Spergula saginoides var. *nivalis* Lindbl., in Physiogr. Sällsk. Tidskr. p. 328. 1838.

Type: not seen. Original material: region of Kongsvold near Doores, Norway, 24 September 1837.

Sagina intermedia Fenzl, in Ledeb., Fl. Ross. **1:** 339. 1842. *Spergella intermedia* (Fenzl) Löve & Löve, Bot. Notiser 128: 508. 1975. Type: Unknown. Original material: region of Tschuktschorum along bays of St. Laurent, Russia.

Perennial. Caespitose, forming low cushions. Basal rosette of succulent, subulate leaves, tips apiculate. Flowering stems numerous, radiating from axils of basal rosette leaves. Stems slender, sometimes purple tinged. Cauline leaves subulate, with connate leaf bases forming shallow scarious cup, often purplish, becoming shorter toward stem apex. Pedicels long, filiform, glabrous. Flowers 4-merous or 4- and 5-merous. Sepals 1.5–2.0 mm long, nearly orbicular to elliptical, rounded at tip, glabrous, frequently purplish, hyaline margins nearly always purple, sometimes only at tip. Petals equaling to slightly shorter than sepals, 1.5–2.0 mm long. Stamens 8 or 10, filaments 1.5 mm long, anthers 0.25 mm long. Capsules 4- or 5-valved, 2.0–3.0 mm long, dehiscing to base. Capsule valves thick. Sepals remaining appressed following capsule dehiscence. Seeds brown, obliquely triangular, with dorsal groove, distinctly notched at hilum, lateral surfaces frequently with elongate ridges, dorsal surface appearing smooth to pebbled, 0.5 mm long. Chromosome number: $2n = 84, 88$. Figure 14.

Ecology and Distribution: Growing on sandy or gravelly beaches, coastal rocks, alluvial plains, fresh glacial moraines and low, swampy tundra and in alpine areas. Widely distributed in the Arctic Archipelago, Alaska, Hudson-James Bay region and the coast of Labrador. Disjunct population in Alberta. Flowering July and August. Figure 15.

Representative specimens: **Canada.** Alberta: Medicine Lake, Jasper National Park, *Scamman 2527* (GH). Mt. Edith Cavell, Angel Glacier, Jasper National Park, *Scamman 2446* (GH), mixed collection. Labrador: Chateau, 51°49′N. *Allen s.n.*, 8 August 1882 (F, NY). Nunaksuk Island, *Bishop 285b* (GH). Crater Lake vicinity, ca. 52 mi. west southwest of Hebron, 58°02′N., 64°02′W., *Gillett 8938* (DAO, US). Makkovik, 55°N., *Hustick 68* (CAN). Cutthroat Harbour, south of Cape Mugford, 57°30′N., 62°W., *Porsild 189* (CAN). Battle Harbour, *Waghorne 4901* (CAN). Okkak, near Cutthroat Tickle, 57°40′N., 62°W., *Wynn-Edwards 7476* (CAN). Northwest Territories: District of Franklin, Northwest Middle Fiord, Axel Heiberg Island, *Beschel 13118* (CAN). Mould Bay, Prince Patrick Island, 76°14′N., 118°59′W., *Bruggemann 361* (DAO, NY, UC). Frobisher Bay, Baffin Island, 63°45′N., 68°32′W., *Calder 2085* (DAO, US). Erik Harbour, Baffin Island, 72°40′N., 76°30′W., *Coombs 31* (DAO). Head of Inugsuin Fiord, Baffin Island, *Hainault 3634* (CAN). Ferguson

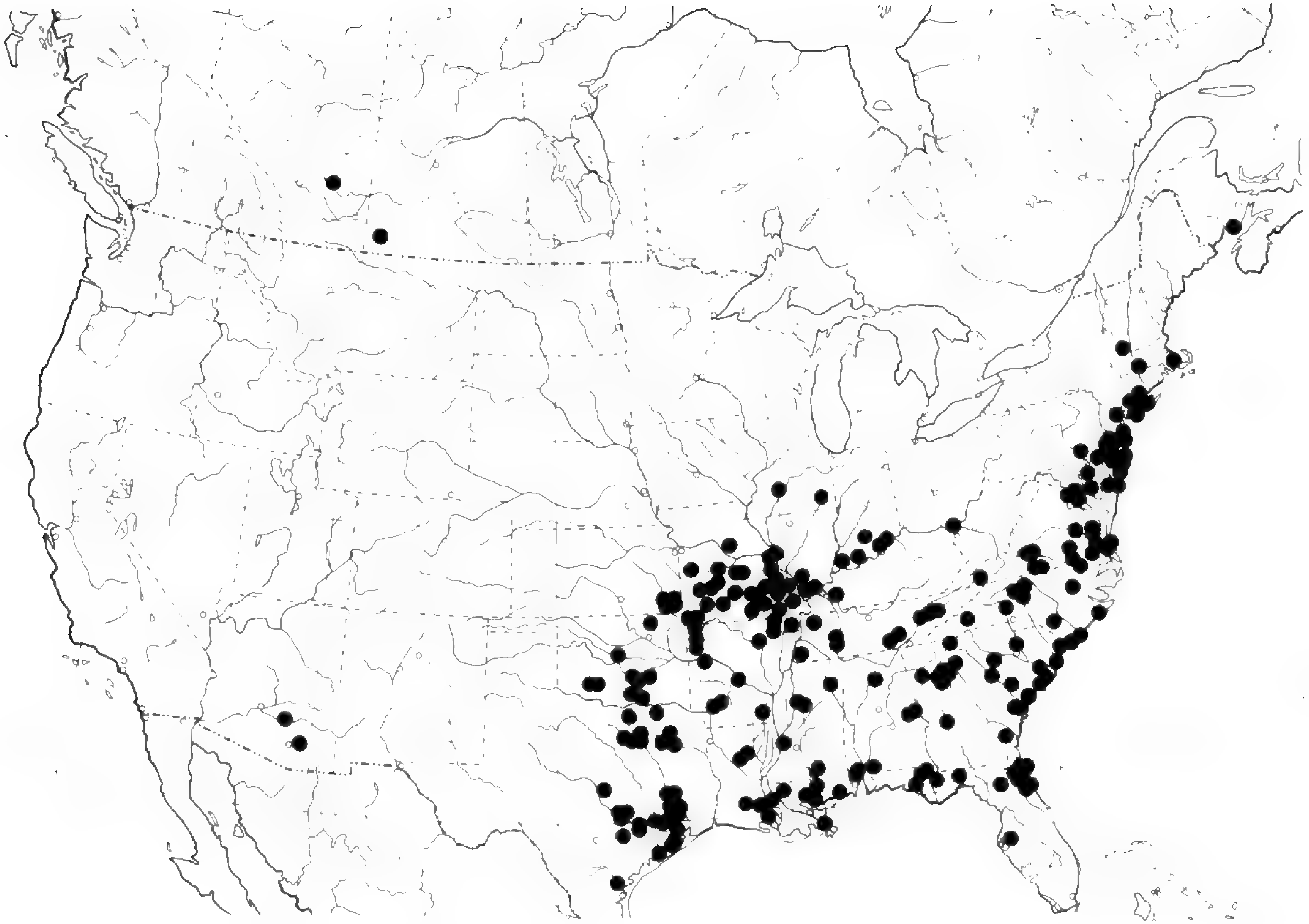

Figure 19. Geographical distribution of *Sagina decumbens* ssp. *decumbens*.

Lake, Victoria Island, 69°25′N., 105°15′W., *Jones 29a* (DAO). Pangnirtung, Baffin Island, *Polunin 1168* (US). Arctic Bay, Baffin Island, *Polunin 2555* (CAN). Banks Island, near northeast corner, ca. 73°24′N., 117°W., *Porsild 17677* (CAN). Bernard Island on northwest coast of Banks Island, *Porsild 17747* (CAN). Resolute Bay, Cornwallis Island, *Porsild 21672* (CAN). Head of Minto Inlet, Victoria Island, *Porsild 17388* (CAN). Botany Bay, Kangerdluak Fiord, Ekalugad Fiord region, Baffin Island, *Webber 1302* (CAN). Cape Searle, Padloping, ca. 67°10′N., 62°30′W., *Wynne-Edwards 9147* (CAN). District of Keewatin, Cape Jones, *Baldwin, Hustich, Kucyniak & Tuomikoski 664* (CAN). Smith Island, east coast of Hudson Bay, *Baldwin 1824* (CAN, GH). Coral Harbour, South Hampton Island, *Calder, Savile & Kukkonen 24228* (DAO). Fullerton, Hudson Bay, 63°57′N., *Macoun 79091* (CAN, GH). Port Burwell, Hudson Strait, 60°22′N., 64°54′W., *Malte s.n.*, 25–28 July 1928 (CAN, GH). Mistake Bay, 62°05N., 93°06W., *Prosild 5664* (CAN). Yathkyed or Hikolikdjuak Lake on the Kazan River, 62°30′–63°N., 97° 98°30′W., *Porsild 5795* (CAN). Chesterfield Inlet, 1 mi. north of settlement, 63°21′N., 90°42′W., *Savile & Watts 1266* (DAO, MO, WTU). District of Mackenzie, O'Grady Lake, Mackenzie Mts., 63°00′N., 129°02′W., *Cody 16416* (DAO). Bathurst Inlet, west side, *Keisall & McEwen 190* (CAN). Cape Dalhousie, Arctic Coast, ca. 70°20′N., 129°55′W., *Porsild & Porsild 2747* (CAN). Shingle Point, Arctic Coast, ca. 69°N., 137°30′W., *Porsild 7099* (CAN). QUEBEC: Richmond Gulf, Cairn Island, east coast of Hudson Bay, ca. 56°15′N., 76°30′W., *Abbe, Abbe & Marr 4399* (MIN). Stromness Harbor, Fort George, James Bay, 53°56′N., *Dutilly & Lepage 12740* (GH). YUKON TERRITORY: Mayo Landing, *Broadfoot 5* (DAO). Canol Rd., Mile 95, upper Rose River valley, *Porsild & Breitung 10368* (CAN).

United States: ALASKA: Mendenhall, *Anderson 434* (NY). Wainwright, *Anderson 4364* (UC). Snow River delta, Kenai Lake, Kenai Peninsula, 60°19′N., 149°21′W., *Calder 6573* (DAO). Head of Katmai River, Katmai National Monument, *Cahalane 518* (US). Ca. 40 mi. east of Cape Lisburne, 4 mi. inland along Pitmegea River, *Cantlon & Gillis 57-2453* (MSC). Okpilak River, 69°23′N., 144°04′W., *Cantlon & Gillis 57-2287* (MSC, US). Glacier Bay, *Cooper 222* (US). Columbia Bay, Prince William Sound, *Cooper 315* (F, MIN). Port Vita, Raspberry Island, Kodiak group, *Eyerdam 5137* (CAS, DAO, MIN). Sable Pass, Mt. McKinley National Park, *Frohne 54-256* (DS). Tangle Lakes area, east of Landmark Gap, Alaska Range, *Gjaerevoil 1324* (CAN). Mead River village, Northern Coastal Plain, *Hultén s.n.*, 5–8 August 1960 (US). Dexter Creek, Nome, Seward Peninsula, *Porsild & Porsild 1340* (CAN). Pastolik, Norton Sound, *Porsild & Porsild 985* (GH). Unalaklet, Norton Sound, *Porsild & Porsild 1148* (CAN). Point Hope, *Scamman 6390* (GH). Columbia Glacier, Heather Island, 60°N., 147°W., *Viereck & Viereck 2312* (COLO). Naivak, 7 mi. southwest of Point Barrow, *Wiggins 12604* (DS, GH, UC, US, WTU). Point Barrow, *Wiggins 12946* (DS, GH, UC, WTU). Cape Thompson, 68°05′N, 165°40′W., *Wood & Wood 511* (CAN). ALEUTIAN ISLANDS: Amchitka Island, *Erdman 578* (COLO). Amlia Island, *Eyerdam 1244* (CAS, DS, GH). Nunivak Island, *Haley s.n.*, 1 July 1927 (CAS). Attu Island, *Hardy 385* (GH, MIN, WTU). Umnak Island, Nikolski, *Hultén 7041* (CAS). Unalaska, *Hultén 6708b* (US). Adak Island, *Jordal 2621-A* (MICH, US). Atka Island, *Oliver & Oliver 55* (MICH, US). BERING SEA: Pribilof Islands, St. George Island, *Johnston s.n.*, 5 May 1920 (CAS). Pribilof Islands, St. Paul Island, *Macoun s.n.*, 28 July 1891 (GH, MO, NY, US). St. Lawrence Island, Gambell, *Anderson 5185* (CAN).

Despite the widely used name *Sagina intermedia* Fenzl, *S. nivalis* (Lindbl.) Fries is adopted as the correct name for the taxon. No type material of either name appears to exist. However, Lindblom's description in 1838 and the even more detailed description by Fries in 1842, given when he elevated the taxon to specific rank, clearly refers to the same taxon published as *S. intermedia* by Fenzl in 1842.

Sagina nivalis, which is otherwise an Arctic species, occurs as a disjunct population in Alberta. Plants on Mt. Edith Cavell, Jasper National Park, representing morphologically good *S. nivalis* (confirmed by chromosome count of $2n = 88$ by J. K. Morton) occur mixed with *S. saginoides.* Specimens appearing intermediate between the two taxa are present here and occur occasionally elsewhere in Jasper and Banff National Parks.

There are several specimens from alpine habitats in Colorado, Utah and Wyoming which are suggestive of *Sagina nivalis.* Although these 5-merous specimens are densely caespitose and the sepal margins are distinctly purple, they belong to *S. saginoides.* However, a few 4- and 5-merous specimens from Colorado do appear to be truly intermediate between the two taxa. J. K. Morton (personal communication, 1976) has obtained an intermediate chromosome count of $2n =$ c. 64 for one such specimen (*S. saginoides,* $2n = 22$; *S. nivalis,* $2n = 88$). I have seen no specimens from Colorado which are clearly *S. nivalis.*

6. **Sagina caespitosa** (J. Vahl) Lange in Rink, Grønl. Geogra. Stat. Beskr. **2**(6): 133. 1857.

Arenaria caespitosa J. Vahl, Icon. Fl. Danica **18:** 4. 1840. *Sagina nivalis* var. *caespitosa* (J. Vahl) Boivin, Nat. Can. **93:** 583–646. 1966. *Spergella caespitosa* (J. Vahl) Löve & Löve, Bot. Notiser **128:** 508. 1975. Type: Groenlandica. (Lectotype, c!)

Perennial. Caespitose, forming small mats or cushions. Basal rosette of leaves lacking; secondary rosettes usually present, leaves linear to linear-subulate. Flowering stems numerous, ascending to radiating, frequently purple tinged. Cauline leaves subulate, becoming shorter toward apex, midvein frequently conspicuous; connate leaf bases forming shallow scarious cup, often purplish. Pedicels long, filiform, glandular pubescent, rarely glabrous (in North American plants). Flowers 5-merous or 5- and 4-merous. Sepals 2.0–2.5 mm long, broadly ovate to lanceolate, obtuse to somewhat

Figure 20. *Sagina decumbens* ssp. *occidentalis*. a. habit; b. close-up. Both Santa Cruz Is., California (*Howell 6356*, CAS).

acute, hyaline margins usually purple tinged, at least at the tip. Calyx base glandular pubescent or glabrous. Petals 2.5–3.0 mm long, exceeding, seldom equaling, sepals. Stamens 10 or 8, filaments 1.5–2.0 mm long, anthers 0.25–0.3 mm long. Capsules 5- or 4-valved, 3.0–3.5 mm long, dehiscing to base. Capsule valves thick. Sepals remaining appressed following capsule dehiscence. Seeds brown, obliquely triangular, with dorsal groove, distinctly notched at hilum, lateral surfaces frequently with elongate ridges, dorsal surface appearing smooth to pebbled, 0.5 mm long. Chromosome number: $2n = 88$, 100 (higher than). Figure 16.

ECOLOGY AND DISTRIBUTION: In wet sands and gravels of shorelines and stream margins, wet mossy places, and dry rocky barrens and gravelly hillocks. Northeast Arctic, south to northern Manitoba, James Bay and northern Labrador. Amphi-Atlantic. Flowering July and August. Figure 17.

REPRESENTATIVE SPECIMENS: **Canada.** LABRADOR: Cape Mugford Peninsula, Kaumajet Mts., 57°50′N., 62°50′W., *Abbe 269* (GH). East Bay, Ikordlearsuk, Torngate region, 59°57′N., 64°24′W., *Abbe & Odell 270* (GH). MANITOBA: Baralzon Lake, 60°00′N., 98°10′W., *Scoggan & Baldwin 8206* (CAN, MIN). NORTHWEST TERRITORIES: District of Franklin, Inugsuin Fiord, Baffin Island, ca. 70°N., 68°30′W., *Hainault 3836* (CAN). Beekman Peninsula, southeast Baffin Island, ca. 63°20′N., 64°50′W., *McLaren 142* (CAN). Pangnirtung, Baffin Island, *Polunin 1568* (WIS). Point Brewster, Frobisher Bay, Baffin Island, *Potter 8237* (GH). Resolution Island, Frobisher Bay, Baffin Island, *Potter 8238* (GH). Tolnes Road, Baffin Island, 66°27′N., *Seidenfaden 1281* (NY). Isortoq Fiord, Baffin Island, ca. 70°N., 77°W., *Webber 407* (CAN). District of Keewatin, Cape Jones, *Baldwin, Hustich, Kucyniak & Tuomikoski 681a* (CAN). Kaminak Lake, 62°N., 95°W., *Güssow 114a* (DAO). Port Burwell, Hudson Strait, 60°22′N., 64°50′W., *Malte s.n.,* 25–28 July 1928 (CAN, GH). Baker Lake, north shore, 64°30′N., 97°W., *Porsild 6094* (CAN). Kazan River, 62°30′–63°N., 97°–98°30′W., *Porsild 5798* (CAN). QUEBEC: Fort Chimo area, 58°07′N., 68°23′W., *Calder 2662* (DAO). Fort George, James Bay, 53°53′N., *Dutilly & Ernest 12500* (GH). Korok River, east side of Ungava Bay, 42 mi. inland from Korok Bay, 58° 35′N., 64°15′–66°W., *Rousseau 1111* (DAO).

This species can be typified by Vahl's specimen in the type collection at Copenhagen (C) in the folder marked "Flora danica, TAB 2289" and labelled "Spergula sp. n., Groenlandia". I have chosen this specimen which is similar, though not identical, to the illustration accompanying the original description to serve as the lectotype. Vahl regarded the plant as having close affinities with *Spergula* (*Sagina*) *saginoides* and thus labelled his specimens *Spergula,* but at the time of publication he used the combination *Arenaria caespitosa* rather than placing his taxon in *Spergula.*

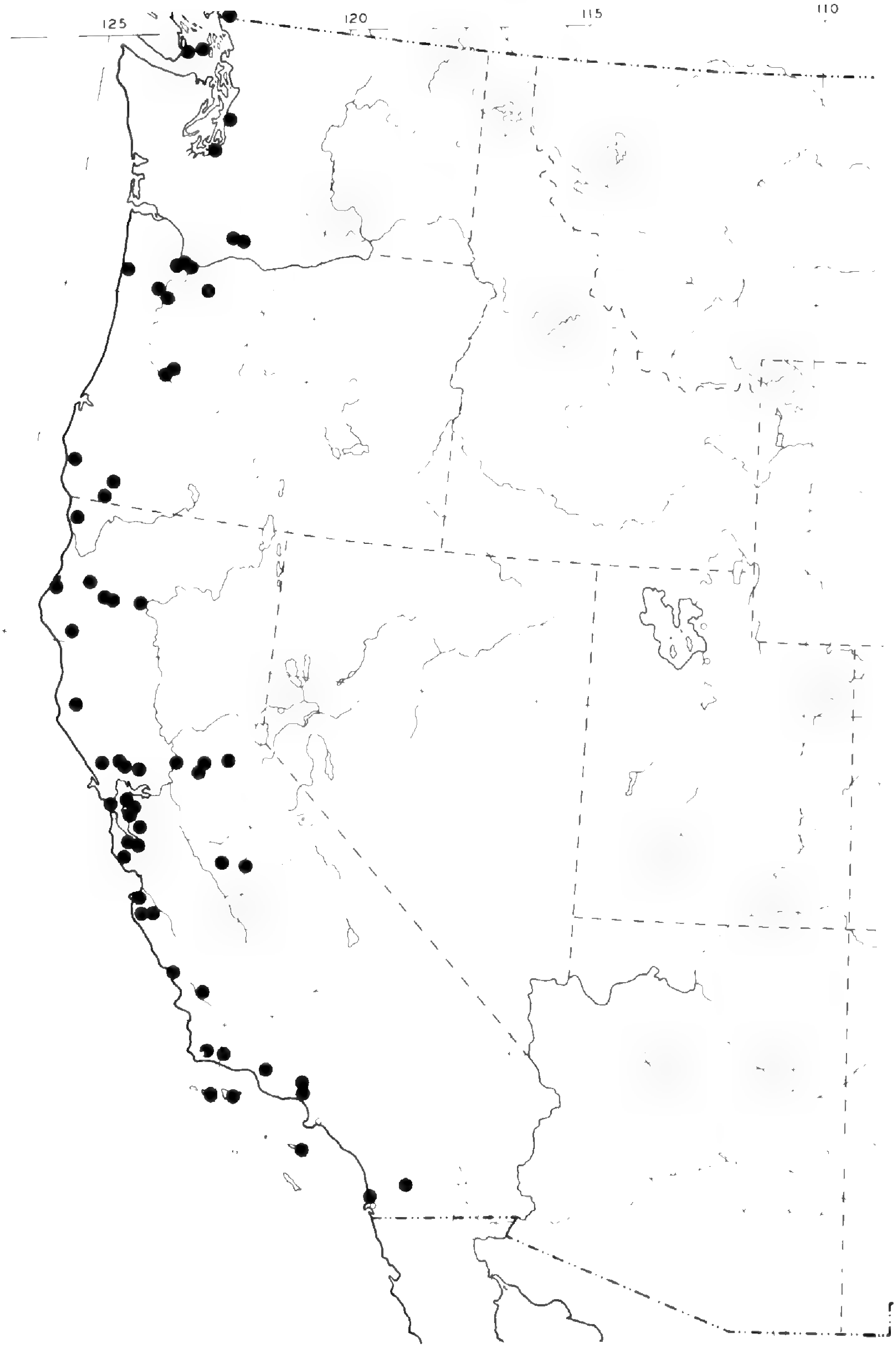

Figure 21. Geographical distribution of *Sagina decumbens* ssp. *occidentalis*.

The material from North America and western Greenland differs from European plants of this taxon in having glandular trichomes on the upper portion of the pedicels and on the calyx bases. While European plants are totally glabrous, the amount of glandular pubescence in the North American material is variable. Weakly glandular plants are frequent and occasionally glabrous specimens are encountered. Among glandular pubescent plants examined, an average of 70% of the flowers exhibited glandular pubescence while 30% of the flowers of these same plants were glabrous. Separate nomenclatural recognition of European and North American material seems unnecessary.

7a. **Sagina decumbens** (Ell.) T. & G., Fl. N. Am. **1:** 77. 1838. ssp. **decumbens**

Spergula decumbens Ell., Sketch **1:** 523. 1821. Type: unknown.

Sagina subulata var. *Smithii* Gray, Manual 5 ed. p. 95. 1867. *Sagina decumbens* var. *Smithii* (Gray) Watson, Manual 6 ed. p. 89. 1889. Type: *C. E. Smith s.n.*, June 1865, sandy road in the pine woods, at the mouth of Great Harbor, New Jersey (Lectotype, GH!).

Annual with slender taproot. Branches slender, ascending or decumbent. Basal rosette of leaves lacking or early deciduous. Lower cauline leaves linear, 4–22 mm long, leaf bases connate, typically with conspicuous hyaline margins, connate portion not generally appearing inflated, apices apiculate. Stems and connate leaf bases frequently purple tinged. Upper cauline leaves becoming subulate toward apex, 1.5–5 mm long at tip, apiculate. Pedicels filiform, glabrous or glandular pubescent. Flowers 5-merous, rarely 4-merous. Calyx base glabrous or glandular pubescent, often sparsely so. Sepals ovate, hyaline margin conspicuous, margins or apex frequently purple. Sepals (1.0–) 1.5–2.0 (–3.0) mm long. Petals elliptical, slightly exceeding sepals at anthesis, equal or shorter than sepals during capsule development, (0.75–) 1.0–2.0 (–2.25) mm long. Stamens 10 or fewer, filaments (1.0–) 1.5 mm long, anthers 0.25 mm long. Capsule valves thin, 2.0–3.0 (–3.5) mm long, dehiscing less than half the length of the capsule. Sepals remaining appressed after capsule dehiscence. Seeds light tan, obliquely triangular, with dorsal groove, surface smooth or tuberculate, with delicate reticulate ridge pattern (sometimes obscure), (0.25–) 0.3–1.4 mm long. Chromosome number $2n = 36$. Figure 18.

ECOLOGY AND DISTRIBUTION: In moist or dryish sandy places, frequently at field margins, open pine woods, paths, roadsides, sidewalk cracks and lawns. Southeastern half of the United States, from Massachusetts, Connecticut, and southern New Jersey, southern Ohio, southern Indiana, Illinois, Missouri and southeastern Kansas, south to northern Florida and eastern Texas. Disjunct populations in Arizona, Alberta, New Brunswick and Vermont. Only those in Arizona are verified by specimens collected this century. *Sagina decumbens* ssp. *decumbens* is chiefly a Coastal Plain and Piedmont taxon. It appears to have extended its range westward with civilization, particularly into Kansas, Oklahoma, northeast Texas, Arizona, Alberta and Saskatchewan. Flowering April to June. Figure 19.

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: east of Hand Hills, *Macoun s.n.*, 8 August 1879 (CAN, DAO). Buffalo Plains, *Macoun s.n.*, 10 August 1879 (US). NEW BRUNSWICK: St. John, *Fowler s.n.*, 30 June 1877 (DAO). SASKATCHEWAN: Hillsides, Farewell Creek, Cypress Hills, *Macoun s.n.*, 27 June 1895 (CAN).

United States. ALABAMA: Cullman Co., Cullman, *Mohr s.n.*, 1 April 1884 (US). Escambia Co., Atmore, *Blanton 201* (DAO, F, GH, MICH). Lee Co., Auburn, *Earle & Baker s.n.*, 18 April 1898 (F, NY, RM, US). Mobile Co., Mobile, *Mohr s.n.*, 24 March 1861 (US). ARIZONA: mountains between Miami and Superior (border of Pinal and Gila Counties), *Nelson & Nelson 1907* (CAS, GH, MO, NY, RM, UC, US). Pima Co., Rincon Range Station, *Darrow s.n.*, 11 April 1937 (CAS). ARKANSAS: Brenton Co., Decatur, *Plank s.n.*, April 1899 (NY). Bradley Co., Warren, *Demaree 21484* (GH). Clay Co., Corning, *Letterman s.n.*, May 1884 (MO). Franklin Co., Mulberry River, Cass, *Fassett 17439* (WIS). Greene Co., specific locality unknown, *Eggert s.n.*, 29 April 1893 (MO). Hempstead Co., Fulton, *Bush 2434* (MO). Independence Co., Newark, *Eggert s.n.*, 23 April 1896 (MO). Nevada Co., Prescott, *Bush 533* (MO). Pulaski Co., Little Rock, *Demaree 22725* (MO). Washington Co., Savoy, *Fassett 17440* (WIS). CONNECTICUT: Fairfield Co., Fairfield, *Eames s.n.*, 19 June 1898 (GH, NEBC). New Haven Co., Milford, *Eames s.n..*, 7 June 1898 (GH). Middlesex Co., Gildersleeve, *Blewitt 644* (NEBC). DELAWARE: Kent Co., Choptank Mills, *Tatnall 2130* (GH). Sussex Co., Bethany Beach, *Tatnall 3321* (GH). DISTRICT OF COLUMBIA: Washington, *Morong s.n.*, 22 May 1877 (NY). FLORIDA: Alachua Co., Gainsville, *Wiggins 19394* (NY). Bay Co., Lynn Haven, *Banker 3671* (NY). Duval Co., near Jacksonville, *Curtiss 6353* (DS, GH, MIN, MO, NY, UC, US). Gilchrist Co., 9 mi. south of Bell, *Wiggins 19493* (DS). Hillsborough Co., no specific locality, *Fredholm 6314* (GH, MIN). Jackson Co., Marianna Caverns State Park, *Godfrey 55331* (GH, NY). Leon Co., near Tallahassee, *Rugel s.n.*, April 1843 (MO). Liberty Co., Apalachicola River swamp south of Bristol, *Small, DeWinkeler & Mosier 11263* (NY). St. Johns Co., St. Augustine, *Leeds s.n.*, 4 March 1893 (F). GEORGIA:

Figure 22. *Sagina apetala.* a. living specimen; b. close-up showing glandular trichomes on pedicel and cilia of leaf base (photographed under epi-illumination). Both California (*Crow 1176*, MSC).

Bartow Co., 2¼ mi. northwest of Acworth, 7½ mi. southeast of Centerville, *Duncan 8041* (MO). Calhoun Co., Edison, *Collom s.n.,* 18 April 1953 (MO). Chatham Co., Tybee Island, *Harper 2175* (GH, MO, US). Clarke Co., 3 mi. west of Winterville, *Cronquist 4237* (GH, NY, US). Dekalb Co., Stone Mountain State Park, *Crow 1919* (MSC). Glynn Co., 5 mi. west of Brunswick, *Cronquist 4913* (US). Gwinnett Co., Yellow River near McGuire's Mill, *Small s.n.,* 7 May 1895 (F, NY). Macon Co., near Macon, *Mohr s.n.,* April 1915 (US). Rabun Co., canyon at Tallulah Falls, *Small s.n.,* 20 April 1893 (F). Richmond Co., Augusta, *Crow 1926* (MSC, NHA). Wilkes Co., just east of Dry Fork of Long Creek, between Washington and Lexington, *Cronquist 4229* (GH, MICH, MO, NY, UC, US). ILLINOIS: Champaign Co., Urbana, *Jones 19605* (DAO). Jackson Co., Giant City State Park, *Fassett 21467* (WIS). Johnson Co., Vienna, *Winterringer 6281* (F). Peoria Co., Peoria, *Chase 10374* (F). Pulaski Co., Wetang, *Vasey s.n.,* no date (F, NY). Union Co., Cobden, *Earle 693* (NY). INDIANA: Brown Co., Nashville, *Lyon s.n.,* 22 May 1930 (MICH). Clark Co., Charlestown, *Baird s.n.,* 2 June 1877 (MICH). Jefferson Co., Hanover, *Barnes 17* (WIS). Posey Co., Mt. Vernon, *Deam 56156* (GH). Spencer Co., Rockport, collector and date unknown (GH). KANSAS: Cherokee Co., 2 mi. northwest of Baster Springs, *McGregor 15337* (US). KENTUCKY: Lyon Co., Kuttawa, *Eggleston 4641* (MIN, NY). LOUISIANA: East Baton Rouge Parish: Baton Rouge, *Brown 860* (NY). Iberia Parish: Weeks Island, *Thieret 16999* (US). Iberville Parish: Plaquemine, *Barnhart 2822* (NY). Lafayette Parish: Lafayette, *Thieret 10333* (DAO). La Salle Parish: Catahoula Lake, 3 mi. southeast of Nebo, *Ewan 19066* (GH). Plaquemines Parish: Point la Hache, *Langlois s.n.,* April 1883 (NY, UC). Rapides Parish: Bluffs of Red River, vicinity of Alexandria, *Ball 411* (MO, NY, US). St. Martin Parish: St. Martinville, *Langlois s.n.,* 15 March 1892 (MICH, MIN). St. Tammany Parish: vicinity of Covington, *Arsène 11978* (US). MARYLAND: Talbot Co., 2¼ mi. southwest of Longwoods, *Earle 4062* (GH). Worcester Co., 10 mi. southeast of Salisbury, *Tatnall 1773* (WS). MASSACHUSETTS: Hampden Co., West Springfield, *Owen s.n.,* June 1884 (NEBC). Hampshire Co., Hadley, no collector, July 1875 (NEBC). Norfolk Co., Braintree, Cranberry Pond, *Kidder s.n.,* 12 June 1886 (NEBC). MISSISSIPPI: Carroll Co., North Carrollton, *Clute 35* (F, NY). Forrest Co., southeast of Hattiesburg, *Cooley, Pease & Ray 3243* (GH). Jackson Co., Biloxi, *Tracy 5040* (F, MICH, MO, MSC, NY). Lee Co., Natchez Trace Parkway, *McDougall 1804* (US). Pearl River Co., 3 mi. north of Picayune, *Rose 8046* (CAS). Warren Co., Snyder's Bluff, *Cooley 3336* (GH). MISSOURI: Barry Co., Eagle Rock, *Bush 507* (MO). Bollinger Co., 5 mi. west of Grassy, *Steyermark 18982* (MO). Boone Co., 4 mi. southeast of Ashland, *Drones 1910* (CAS, GH). Butler Co., Neelyville, *Bush 36* (MIN); 5 mi. southwest of Qulin, *Steyermark 26655* (F). Carter Co., Grandin, *Bush 340* (MO). Cedar Co., 3 mi. north of Stockton, *Steyermark 18655* (MO). Christian Co., Chadwick, *Bush 4441A* (MO). Dallas Co., between Plad and Buffalo, *Steyermark 18691* (MO). Douglas Co., along north fork of White River between Roosevelt and Richville, *Steyermark 19156* (MO). Dunkin Co., about 5 mi. northwest of Campbell, *Steyermark 398* (MO). Franklin Co., Pacific, *Eggert s.n.,* 23 May 1882 (MO, NY, US). Greene Co., specific locality unknown, *Blankinship s.n.,* 23 April 1888 (MO). Henry Co., 3 mi. northeast of Finey, *Steyermark 18774* (MO). Jefferson Co., *Hasse s.n.,* 24 May 1887 (MO). Laclede Co., north of Hazel Green, *Steyermark 8075* (MIN). Lawrence Co., east of Chesapeak, *Steyermark 4519* (MO). MacDonald Co., specific locality unknown, *Bush s.n.,* 24 April 1891 (MO). Miller Co., 4 mi. south of Bogville Dam, *Steyermark*

18798 (MO). Oregon Co., 4 mi. south of Koshkonong, *Steyermark 18970* (MO). Osage Co., east of Linn, *Steyermark 18709* (MO). Phelps Co., 4 mi. southeast of St. James, *Steyermark 22188* (F). Polk Co., north of Burns, *Steyermark 18655* (MO). Pulaski Co., 1 mi. west of Jerome, *Steyermark 4600* (MO). Reynolds Co., south of Ellington, *Steyermark 7944* (MO). St. Francois Co., Bismark, *Russell s.n.*, 15 April 1898 (MO). St. Louis Co., Forest Park (in St. Louis), *Steyermark 1728* (F). Scott Co., 2 mi. south of Benton, *Steyermark 10256* (MO). Shannon Co., Montier, *Bush 54* (MO). Texas Co., along Jack's Fork of Current River, 3 mi. south of Arroll, *Steyermark 18588* (MO). Wayne Co., south of Greenville, *Anderson s.n.*, 31 May 1939 (MO). NEW JERSEY: Atlantic Co., Somer's Pt., *Smith s.n.*, June 1865 (MO, NY). Bergen Co., near Hewitts, *Britton s.n.*, 29 June 1886 (NY). Burlington Co., Atsion, *Canby s.n.*, August 1863 (NY). Camden Co., Camden, *Parker s.n.*, 4 July 1866 (MO). Cape May Co., Cold Springs, *Brown 5236* (GH). Ocean Co., Forked River, *Churchill s.n.*, 27 May 1891 (GH); Surf City, *Long 3821* (GH). NEW YORK: Nassau Co., Rockaway, *Schrenk s.n.*, 30 May 1879 (MICH). Suffolk Co., Wading River, *Miller s.n.*, 22 May 1874 (F). NORTH CAROLINA: Buncombe Co., Asheville, *Hayne 2766* (F). Carteret Co., Beaufort, *Morton 2198* (US). Brunswick Co., Smith Island, *Morton 2118* (US). New Hanover Co., near Wilmington, *Canby s.n.*, May 1867 (MICH, NY). Northampton Co., Garysburg, *Ahles 38345* (DAO). Orange Co., Chapel Hill, *Carlton 38* (MIN). Pitt Co., Gardnerville, *Radford 32534* (NY). Robeson Co., Lumberton, *Knowlton s.n.*, 9 April 1924 (GH). Rowan Co., vicinity of Heilio's Mill, *Small & Heller s.n.*, 4–9 June 1891 (WTU). Wake Co., Raleigh, *Godfrey s.n.*, 8 April 1937 (GH). OHIO: Lawrence Co., Ironton, *Werner s.n.*, 27 May 1892. OKLAHOMA: Carter Co., 6 mi. northwest of Ardmore, *Nelson, Nelson, Goodman & Waterfall 5696* (RM). Comanche Co., vicinity of Fort Sill, *Clemens 11576* (MO). Craig Co., Vinita, Indian Territory, *Carleton 12* (NY, US). Cleveland Co., 2 mi. east of Norman, *Bruner s.n.*, 15 April 1924 (MO, RM). Marshall Co., near Lake Texoma, *Goodman 5806* (GH, US). Murray Co., Crusher Spur, *Stevens 52* (DS, MIN, MO, NY, US). Pontotoc Co., 4–5 mi. east of Ada, *Robbins 2339* (UC). PENNSYLVANIA: Bucks Co., Doylestown, *Pond s.n.*, 27 May 1885 (US). Lancaster Co., Safe Harbor, *Porter s.n.*, 15 May 1861 (NY). Philadelphia Co., ballast ground, Philadelphia, *Parker s.n.*, 30 May 1865 (NY). SOUTH CAROLINA: Allendale Co., Fairfax, *Ahles 10616* (COLO). Beaufort Co., Beaufort, *Churchill 379* (MO). Charleston Co., Charleston, *Smith s.n.*, April 1865 (GH). Dorchester Co., Summerville, *Hunnewell 8139* (MIN). Edgefield Co., north of Edgefield, *Steyermark 63373* (F). Horry Co., Longwood Landing, *Weatherby & Griscom 16524* (NY, US). Kershaw Co., Lynches River, 7 mi. south of Jefferson, *Redford 9068* (WTU). TENNESSEE: Decatur Co., specific locality unknown, *Ames s.n.*, July 1865 (MICH). Franklin Co., north of Estill Springs, *Svenson 9993* (GH). Grundy Co., Goose Pond, near Pelham, *Svenson 7618* (GH). Knox Co., Knoxville, *Ruth 4310* (MO). Obion Co., near Samburg, *Eyles 7801* (GH). Roan Co., Harriman, *McMorine s.n.*, 22 April 1893 (DAO). Shelby Co., near Memphis, *Palmer 17447* (MO). TEXAS: Bastrop Co., Alum Creek, south of Bastrop State Pines Park, *Tharp, Warnock & Barkley 16T011* (F, UC). Bell Co., near Belton, *Wolff 374* (US). Burnet Co., 3 mi. south of Bertram, *Johnson 6158* (DS). Colorado Co., Columbia, *Bush 96* (MIN). Dallas Co., Dallas, *Reverchon s.n.*, April 1876 (MO, NY). Denton Co., 4½ mi. north of Grapevine, *Whitehouse 17970* (MICH). Fayette Co., specific locality unknown, *Wurzlow s.n.*, in 1891 (F). Fannin Co., Bonham, *Milligan s.n.*, April 1892 (US). Galveston Co., Galveston, *Lindheimer s.n.*, April 1863 (MO). Gonzales Co., Ottine Swamp, *Cory 18133* (GH). Harris Co., Houston, *Bush 27* (MO). Kleberg Co., Kingsville, *Rees 37* (NY). Liberty Co., Liberty, *Palmer 7733* (MIN). Matagorda Co., Matagorda, *Palmer 4253* (MO). Montgomery Co., near Conroe, *Palmer 33339* (GH). Tarrant Co., near Handley, *Ruth 452* (F, NY, US, WIS). Travis Co., Austin, *Tharp s.n.,* 19 March 1932 (CAS, GH, MICH, NY, UC, WTU). Van Zandt Co., west of Canton, *Correll & Correll 35679* (UC). Walker Co., specific locality unknown, *Warner 64* (GH, US). Woods Co., Mineola, *Reverchon s.n.,* 22 April, no year (MO). VERMONT: Windham Co., Brattleboro, *Grout s.n.,* 25 July 1895 (GH, NEBC). VIRGINIA: Bedford Co., specific locality unknown, *Curtiss s.n.,* 20 May 1872 (F, MO). Dinwidde Co., near Burgess Station, *Fernald & Long 9917* (GH). Greensville Co., 1 mi. south of Emporia, *Fernald & Long 7016* (NY, US). Hampton Co., Hampton, *Chickering s.n.,* 15 May 1877 (NY). Nansemond Co., Norfolk, *Earll s.n.,* 14 May 1880 (US). Princess Anne Co., False Cape, *Fernald, Griscom & Long 4636* (NY). Pittsylvania Co., Danville, *Small & Heller 230* (DAO, F, GH, MIN, MO, US). Henrico Co., Richmond, *Churchill s.n.,* 11 May 1894 (GH). Smyth Co., south fork of Holston River near Add Wolf, *Small s.n.,* 15 June 1902 (F). York Co., Yorktown, *Thomas 2694* (DS). Southampton Co., Franklin, collector unknown, May 1867 (GH).

There is considerable pubescence variation in this taxon. Pubescent forms predominate three to one over glabrous forms with no geographical segregation of the character. Within the pubescent forms there is a complete range from just a few flowers with glandular hairs to all flowers on a single plant bearing glandular trichomes.

Presence of the tuberculate seed character is likewise variable and without geographical segregation. While only smooth seeds or tuberculate seeds may be present in a single population, frequent occurrences of mixtures of the two seed types are encountered. The frequency of the tuberculate seed type is about 60 percent.

The nomenclature has been somewhat confusing in *Sagina decumbens* ssp. *decumbens.* In *A Flora of North America* Torrey and Gray (1838) correctly transferred *Spergula decumbens* Ell. to *Sagina.* In the same work they included *Sagina subulata,* based on a collection cited as "Rocky Mountains, Drummond" (p. 178), and simultaneously made the transfer of *Spergula subulata* Swartz to *Sagina.* The description provided for this taxon more nearly applies to *Sagina decumbens* ssp. *decumbens* and is not descriptive of any of the Saginas native to the Rocky Mountains.

In Gray's *Manual of the Botany of the Northeastern United States* ed. 2 (1856) the name *Sagina decumbens* is replaced by the name *Sagina Elliottii* Fenzl with *Spergula decumbens* Ell. indicated as the synonym. The binomial *Sagina Elliottii* was never

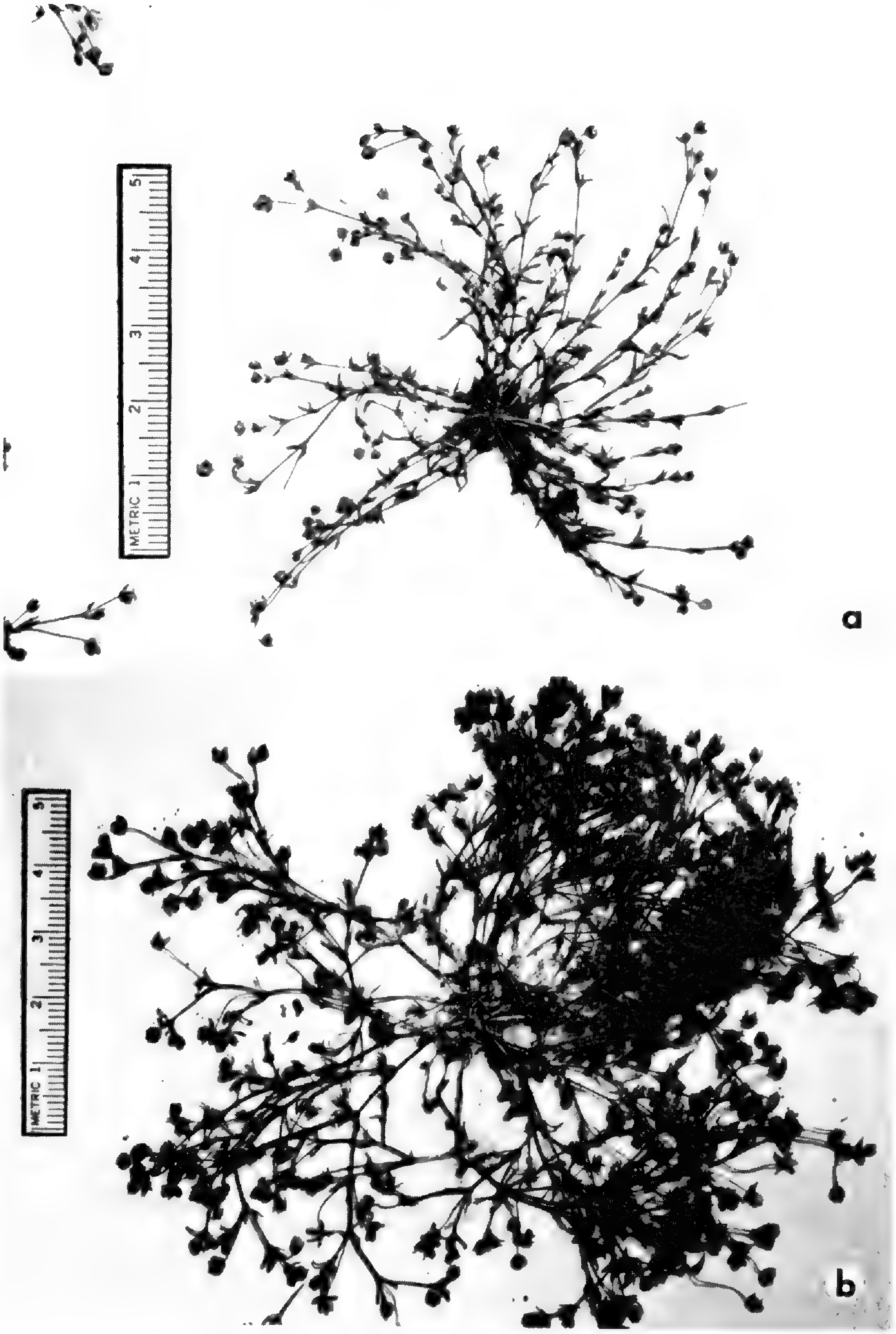

Figure 23. *Sagina apetala*. a. habit, California (*Howell 24202*, CAS); b. habit, California (*Raven & Johnson 21233*, DS).

validly published by Fenzl or Gray.

In the fifth edition of Gray's *Manual* (1867) *Sagina decumbens* is treated as *S. subulata,* Wimmer being recognized as the author of the transfer, and *Sagina Elliottii* is cited in synonymy. Gray also described a new variety of the taxon, *Sagina subulata* var. *Smithii* in that edition.

In Gray's *Manual* ed. 6 (1889, revised by Watson & Coulter), the binomial *Sagina decumbens* is correctly used for the taxon, and a nomenclatural transfer of var. *Smithii* to *Sagina decumbens* was made by Watson.

This slender, nearly apetalous variety described by Gray does not warrant recognition as a distinct taxon. Gray's variety represents an extreme in the range of variability of *Sagina decumbens* ssp. *decumbens* exhibiting a tendency toward a habit which is more slender, with much branched filiform stems and a greater frequency of 4-merous flowers which produce fewer-seeded capsules. The range of variability is continuous and it seems best to consider the material a single taxon.

No single specimen was cited with the original description to typify *Sagina subulata* var. *Smithii.* Of the four collections studied by Gray, all glued to a single sheet, only one specimen bears the notation "no petals" in Gray's handwriting. I therefore designate this specimen, *C. E. Smith s.n.,* June 1865, sandy road in the pine woods, at the mouth of Great Egg Harbor, New Jersey (GH), as the lectotype of *Sagina subulata* var. *Smithii.*

7b. **Sagina decumbens** ssp. **occidentalis** (Wats.) Crow, comb. nov. BASIONYM: *Sagina occidentalis* Wats., Proc. Am. Acad. **10:** 344. 1875.

Alsinella occidentalis (Wats.) Greene, Fl. Franc. p. 125. 1891. TYPE: *Bolander 3891,* in the streets of Ukiah, Mendocino Co., California, 1864 (Holotype, GH!; isotypes, UC! MO! K! US!).

Annual with slender taproot. Branches slender, ascending or sometimes decumbent. Basal rosette of leaves lacking. Lower cauline leaves linear, 5.0–23 mm long. Upper cauline leaves becoming subulate toward tip, 1.0–4.5 mm long at apex. Cauline leaves apiculate. Pedicels filiform, weakly glandular pubescent or glabrous. Sepals ovate to orbicular, tips frequently purple, occasionally the entire hyaline margin purple tinged. Sepals (1.5–) 1.75–2.0 (–2.5) mm long. Petals elliptical, nearly equaling the sepals, (1.25–) 1.5–

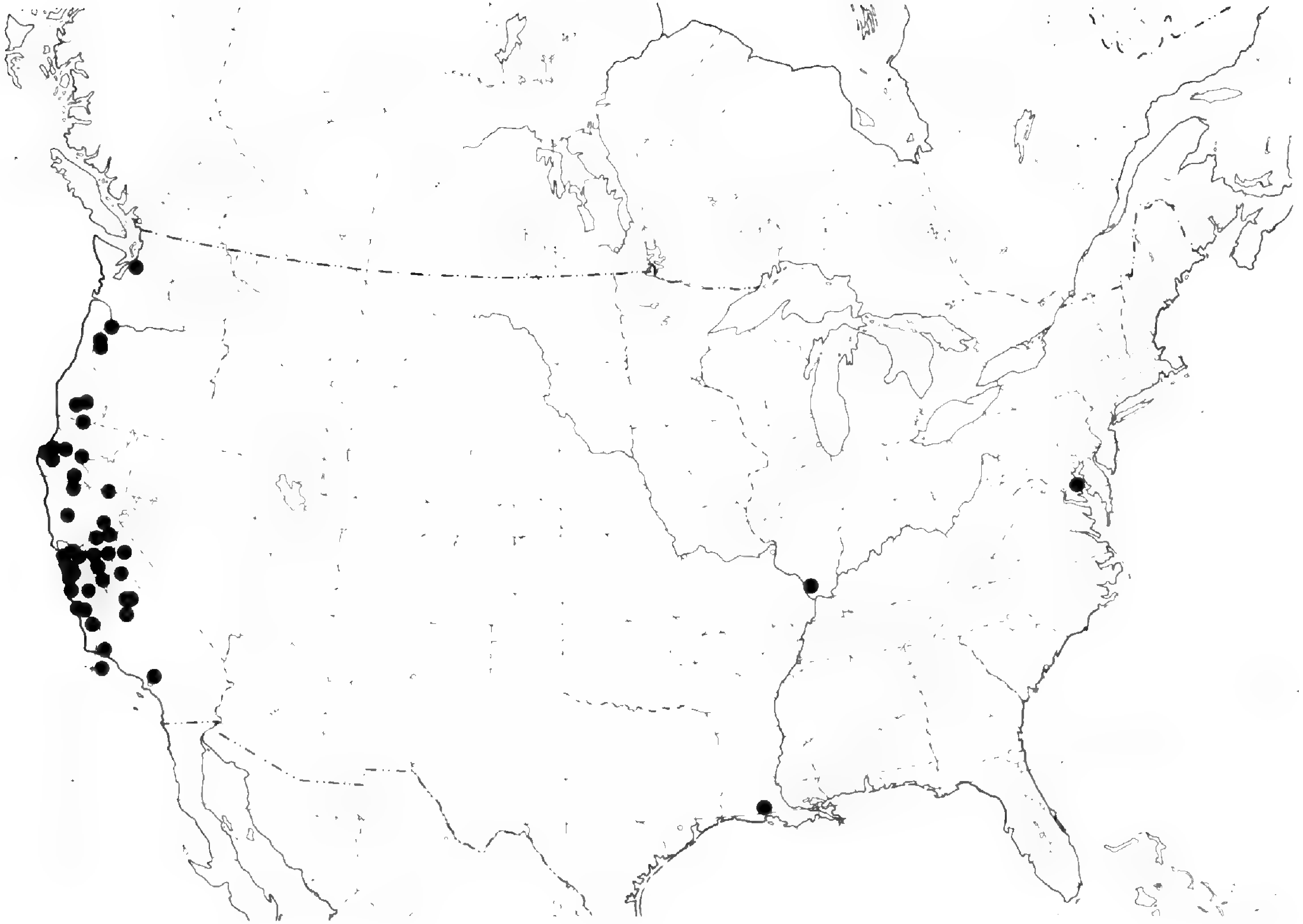

Figure 24. Geographical distribution of *Sagina apetala* in North America.

2.0 mm long. Stamens 5 or 10, filaments (1.0–) 1.5 mm long, anthers 0.25 mm long. Capsules globose prior to dehiscence. Valves thin, (2.0–) 2.5–3.0 (–3.5) mm long, dehiscing to ca. half the capsule length. Sepals remaining appressed following capsule dehiscence. Seeds light brown, obliquely triangular, with dorsal groove, surface smooth to slightly pebbled, rarely with elongate ridges on the lateral surfaces, 0.4 mm long. Figure 20.

ECOLOGY AND DISTRIBUTION: On dryish hillsides, margins of vernal pools, along streams, open spots in redwood and pine woods, along roadsides and around dwellings. Ranging northward from southern California along the Great Valley and Coastal Range to the southern border of British Columbia. Flowering April to June. Figure 21.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA: Gordon Head, Vancouver Island, *Macoun s.n.*, 30 May 1887 (US). Vicinity of Victoria, Vancouver Island, *Macoun s.n.*, 23 May 1893 (F, MICH, MIN).

United States. CALIFORNIA: Alameda Co., vicinity of Oakland, *Holder 2522* (US). Amador Co., New York Falls, elev. 2000 ft., *Hansen 537* (DS, GH). Calaveras Co., Big Meadow, elev. 6600 ft., *Jepson 10084* (JEPS). Contra Costa Co., Rock City Camp, Mont Diablo, *Bowerman 2028* (UC). Del Norte Co., Gasquet to Patricks, *Bacigalupi 8542* (DS). Humboldt Co., Garberville, *Tracy 16212* (UC). Los Angeles Co., Pasadena, *Grant s.n.*, 28 March 1898 (DS); Avalon, Santa Catalina Island, *Trask s.n.*, February 1898 (US). Madera Co., along Fresno-Yosemite road (Calif. 41), 3 mi. north of crossing with Madera Lateral, elev. 750 ft., *Bacigalupi 4876A* (JEPS). Marin Co., McClure Beach, Pt. Reyes National Seashore, *Crow 1180a* (MSC). Mariposa Co., Mariposa, *Congdon s.n.*, 11 April 1897 (MIN). Mendocino Co., Ukiah, *Bolander 3891* (GH, MO, UC, US). Albion Ridge, *McMurphy 31* (DS). Merced Co., 5½ mi. southeast of Planada, north of LeGrand, elev. 245 ft., *Bacigalupi 7339* (JEPS, RM, WTU). Monterey Co., Pacific Grove, *Heller 8502* (DS, F, GH, MIN, MO, NY, WTU). Napa Co., Howell Mountain, 3 4 mi. east of Angwin's, *Tracy 1503* (UC). Riverside Co., Lake Suprise, San Jacinto Mts., *Reed 2442* (UC). Sacramento Co., Elk Grove, *Congdon s.n.*, 31 March 1894 (MIN). San Diego Co., Spencer Valley, near Julian, *Abrams 3797* (DS, NY). San Francisco Co., Point Richmond, *Hall 1663* (GH, MIN). San Luis Obispo Co., Price Canyon, *Hoover 6751* (CAS, UC). San Mateo Co., road from La Honda to Prescadero Creek, *Mason 3685* (UC). Santa Barbara Co., Mission la Purisima, *Jepson 11937* (JEPS); Lady's Cove, East Canyon, Santa Cruz Island, elev. 400 ft., *Wolf s.n.*, 27 March 1932 (DS). Santa Clara Co., Isabel Creek, east base of Mt. Hamilton, elev. 2100 ft., *Sharsmith & Sharsmith 1156* (UC). Santa Cruz Co., near Jamison Creek, *Hesse 2775* (DS). Shasta Co., Olinda, *Blankenship 5* (JEPS, WS). Solano Co., Violet Station, near Vacaville, *Jepson 1205a* (JEPS). Sonoma Co., Santa Rosa, *Eastwood 10329* (CAS). Trinity Co., Junction City, *Tracy 7530* (UC). Tuolumne Co., Mather, elev, 1400 m, *Clausen 1549* (DS). Ventura Co., Kennedy Canyon. Ventura River basin, *Pollard s.n.*, 5 May 1946 (CAS). OREGON: Clackamas Co., Oregon City, *Thompson 687*

(WTU). Clatsop Co., beach near Seaside, *Morrill 89* (WTU). Columbia Co., St. Helens, *Suksdorf s.n.*, 28 May 1895 (WS). Curry Co., Port Orford, *Peck 8454* (GH, MO, NY). Jackson Co., Wimir, *Hammond s.n.*, 21 May 1892 (MO). Josephine Co., Grants Pass, *Piper 5101* (WS). Lane Co., 4 mi. above Takilma on the East Fork of the Illinois River, *Henderson 5892* (CAS, DS, MO, RM). Lincoln Co., Waldo, *Howell s.n.*, June 1887 (MIN). Linn Co., Santiam slough near Lebanon, *Gilkey & Drake s.n.*, June 1934 (OSC). Marion Co., Jefferson, *Nelson 177* (DS). Multnomah Co., Lower Albina, Portland, *Sheldon S. 10328* (F, GH, MIN, MO, NY, US, WS). Polk Co., Nesbit, *Nelson 2073* (GH). Tillamook Co., Sand Lake south of Tillamook, *Thompson 722* (WTU). Wasco Co., Eight Mile Creek, Mt. Hood National Forest, *Jones 4071* (CAS). Washington Co., Forest Grove, *Lloyd s.n.*, 20 April 1893 (GH, NY). Yamhill Co., specific locality unknown, *Summers s.n.*, June 1880 (MONTU). WASHINGTON: King Co., Seattle, *Piper s.n.*, 29 May 1889 (WTU). Klickitat Co., Bingen, *Suksdorf 5014* (WS). Pierce Co., prairies, Tacoma, *Flett s.n.*, 2 October 1897 (WTU). San Juan Co., Cattle Point, San Juan Islands, *Peck 12944* (WS).

As in *Sagina decumbens* ssp. *decumbens,* there is considerable variation in the glandular pubescence character. Although in the original description Watson indicates the taxon as being glabrous, both glabrous plants and plants with sparsely pubescent flowers are present on the type sheet. Few of the flowers of the pubescent form in this collection are glandular. However, the glandular form is predominant in the taxon and relatively few herbarium sheets consist entirely of glabrous specimens.

In the northern portion of its range more robust plants appear very similar to more slender growth forms of *Sagina maxima* ssp. *crassicaulis.* This observation led Piper (1906) to state that species lines in *Sagina* were not well defined and he doubted that the two taxa were really distinct. The saginoid seed type readily distinguishes this taxon from *S. maxima* ssp. *crassicaulis.*

Although not previously recognized nomenclaturally, *Sagina decumbens* ssp. *occidentalis* has long been considered to be the western equivalent of *S. decumbens.* Watson (1875, p. 344) makes a note to this effect in the original description of the taxon and distinguishes it from the eastern taxon by its "laxer and slenderer habit, more elongate pedicels, and in the somewhat less conical base of the calyx." This description falls within the range of variability of both taxa.

Although there is considerable overlap in characteristics, *Sagina decumbens* ssp. *decumbens* can generally be segregated on the reticulate ridge pattern of the seed, a greater tendency to possess purple sepal tips or sepal margins, and anthocyanins frequently

Figure 25. *Sagina maxima* ssp. *maxima*. a. habit; b. close-up showing glandular pubescence. Both Aleutian Islands (*York 44 196*, F).

abundant at the nodes. In ssp. *occidentalis* the sepals tend to be more orbicular and the capsules, prior to dehiscence, are more globose. The seeds lack a reticulate ridge pattern and are never tuberculate.

8. **Sagina apetala** Ard., Animadv. Bot. Spec. alt. **2:** 22. 1764.

Alsinella apetala (Ard.) Krause, in Sturms, Fl. Deutschl. 2 ed., **5:** 38. 1901. TYPE: LINN *177.2.* (Lectotype, LINN!)

Sagina apetala var. *barbata* Fenzl, in Ledeb, Fl. Ross. **1:** 338. 1842. TYPE: Herb. Ledebour 148.1. (Lectotype, LE!)

Sagina filicaulis Jordan, Obs. Pl. Crit. **7:** 16. 1849. TYPE: not seen. ORIGINAL MATERIAL: in sandy places in fields, in the valley of Aspe at Bedous, France, July, 1838. Collected by Jordan.

Sagina quarternella Schloss, in Schloss & Vukot., Fl. Croat. p. 343. 1869. TYPE: Destroyed during World War II. ORIGINAL MATERIAL: in fields and meadows, common in Croatia.

Sagina melitensis Gulia ex Duthie, Jour. Bot. **13:** 37. 1875. TYPE: Dulthie, Insula Melita, Corradino, March 13, 1874. (Lectotype, K!)

Alsinella ciliata Greene, Fl. Franc. p. 126. 1891. *Sagina ciliata* (Greene) Heller, Muhl. **1:** 50. 1904. TYPE: unknown. ORIGINAL MATERIAL: vicinity of Ione, California. Presumably collected by Greene.

Annual with slender taproot. Plants ascending to decumbent, much branched and many flowered. Basal rosette-like whorl of leaves sometimes present, withering early. Stems filiform, glabrous or sometimes glandular pubescent. Lower cauline leaves linear, 4–8 (–12) mm long, upper cauline leaves linear to subulate, 1–3 mm long at apex. Hyaline portion of leaf bases long ciliate; cilia occasionally occurring the length of the leaf, lower cauline leaves sometimes lacking cilia. Leaf tips aristate. Pedicels glandular pubescent (North American plants), short (1.5–) 2.0–5.0 (–13) mm long. Flowers 4-merous, very rarely 4- and 5-merous. Calyx glandular pubescent. Sepals ovoid to elliptical, sometimes lanceolate and somewhat acute, 1.5–2.0 mm long. Petals nearly always lacking, if present then minute. Stamens 4, filaments 0.75–1.0 mm long, anthers 0.2 mm long. Capsules globose, dehiscing to base, valves thin, barely exceeding sepals, 1.5–2.0 (–2.5) mm long. Seeds brown, obliquely triangular, with dorsal groove, distinctly notched at hilum, surface smooth, pebbled or more frequently papillose (papillae distinctly mammillate when viewed under SEM), 0.3–0.4 mm long. Chromosome number: $2n = 12$. Figures 22 and 23.

ECOLOGY AND DISTRIBUTION: Introduced. A weed of open places, frequently in hard packed soils around buildings, along paths, on roadsides, in sidewalk cracks. It occurs less frequently in such places as grassy hillsides and stream banks. California, western Oregon and Seattle, Washington. I have seen four herbarium specimens from eastern North America referable to this taxon, one from Maryland (1933), one from New Jersey (1878), one from Illinois (no date), and one from Louisiana (1883). The species does not appear to have become established in these regions. Native to Europe. Flowering April to June. Figure 24.

REPRESENTATIVE SPECIMENS: **United States.** CALIFORNIA: Alameda Co., Strawberry Canyon, Berkeley Hills, *Howell 11359* (CAS). Amador Co., Jackson, *Hansen 537* (UC). Calaveras Co., Angels Camp, *Eastwood 11580* (CAS). Eldorado Co., Diamond Springs, *Jepson 18632* (UC). Fresno Co., Parlier, *Frazier 101* (DS, WTU). Humboldt Co., ¼ mi. southeast of village of Willow Creek, *Crow 1927* (MSC, NHA). Lake Co., just north of Middletown, *Howell 42249* (CAS). Los Angeles Co., Pasadena, *Grant s.n.*, 15 April 1917 (DS, JEPS, UC). Madera Co., North Fork, *Bacigalupi 2261* (DS). Marin Co., Black Canyon, San Rafael hills, *Howell 17896* (NY). Mariposa Co., Oakvale, *Congdon s.n.*, 27 April 1897 (GH, MIN). Mendocino Co., near Yorkville, *Eastwood & Howell 4570* (CAS). Merced Co., 15 mi. southwest of Merced, *Howell 4112* (CAS). Monterey Co., Jolon, *Howell 39155* (CAS). Plumas Co., Big Meadows *Manstin s.n.*, August 1899 (US). Sacramento Co., Sacramento, *Crampton 7840* (CAS). San Benito Co., 5 mi. north of Pinnacles, *Howell 33016* (CAS). San Francisco Co., McLarsen Park, San Francisco, *Raven 9254* (CAS). San Joaquin Co., Woodland, *Biswell 181* (UC). San Luis Obispo Co., Santa Lucia Mts., ½ mi. west of Paso Robles, *Hardham 4036* (CAS). San Mateo Co., Jasper Ridge Biological Experimental Area, ca. 5 mi. southwest of Palo Alto, *Thomas 9073* (DS). Santa Barbara Co., vicinity of Pelican Bay, Santa Cruz Island, *Abrams & Wiggins s.n.*, 26 April 1930 (DS); Oak Park, Santa Barbara, *Pollard s.n.*, 11 April 1958 (DAO). Santa Clara Co., San Antonio Valley, Mt. Hamilton Range, *Sharsmith & Sharsmith 3272* (UC). Santa Cruz Co., Boulder Creek, *Hesse 397* (CAS). Shasta Co., Anderson, *Smith s.n.*, 21 April 1913 (CAS). Siskiyou Co., Klamath River at Cherry Flat, Siskiyou Mts., *Wheeler 2606* (GH, MO, US). Stanislaus Co., 8 mi. east of Oakdale, "Haystack Hill," *Hoover 3955* (UC, US). Tehama Co., 5 mi. west of Paskenta, *Baker 12542* (UC). Tulare Co., 4 mi. east of Exeter, *Mason 11718* (UC). Tuolumne Co., Columbia, *Jepson 6297* (JEPS); base of Peoria Mt., *Williamson 102* (CAS, DS). ILLINOIS: Union Co., *Forbes s.n.*, no date (MICH). LOUISIANA: no specific locality, *Langlois s.n.*, April 1883 (CAS). MARYLAND: Calvert Co., Plum Point, *Blake 11658* (CAS, NA). NEW JERSEY: Camden Co., Camden, *Martindale s.n.*, June 1878 (NA). OREGON: Jackson Co., Wimer, *Hammond 46* (MO); 2 mi. north of Central Point, *Peck 14966* (DS, WTU). Josephine Co., Grants Pass, *Piper 5072* (WS). Marion Co., Salem, *Peck 9284* (WTU). Multnomah Co., Albina, Portland, *Suksdorf 1345* (GH, WS). WASHINGTON: Fairhaven, *Piper s.n.*, 2 July 1897 (WS).

Our phase of the species has been regarded as *Sagina apetala* var. *barbata* Fenzl, the glandular pubescent phase. However, the species in Europe is extremely variable with regard to cilia of leaves

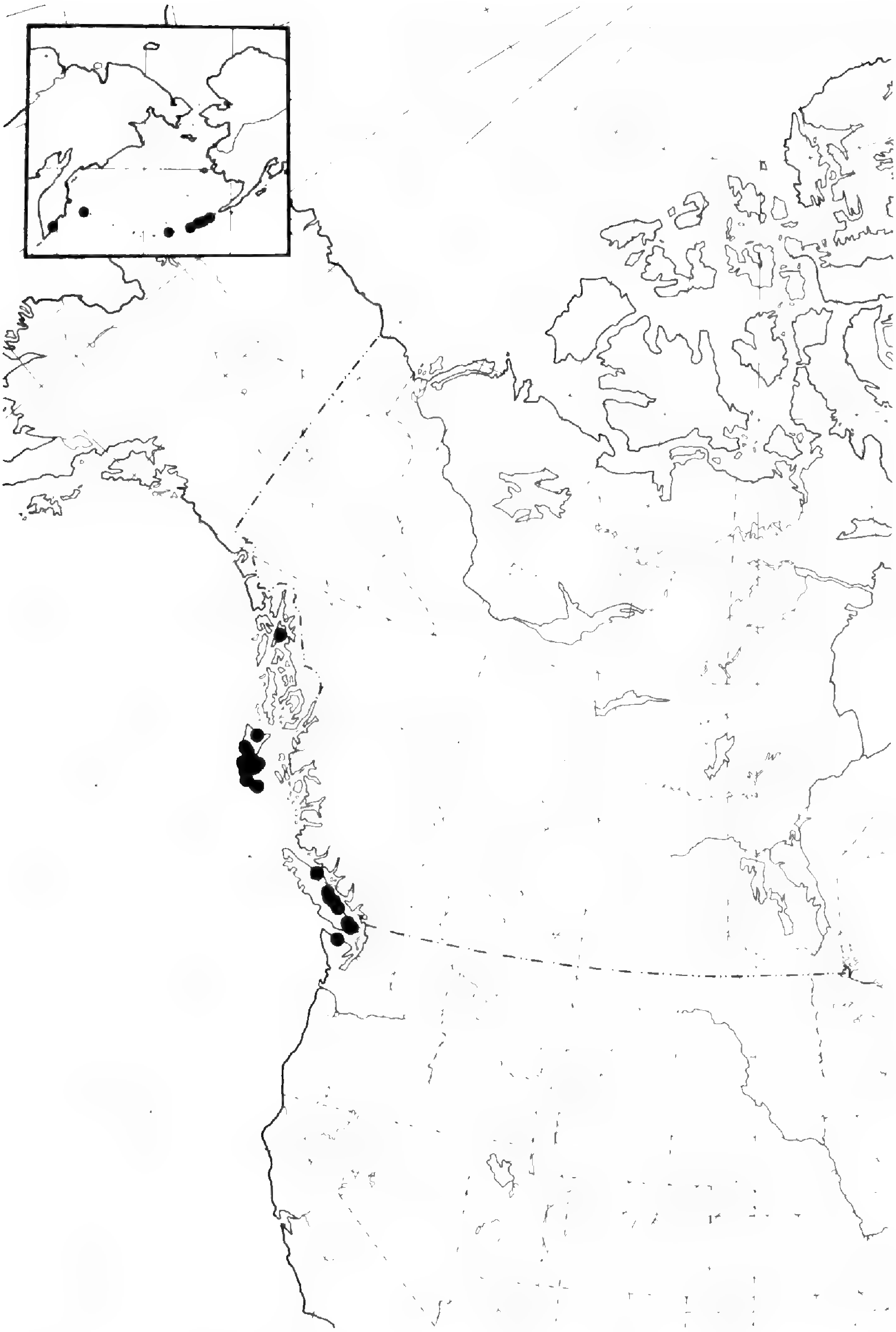

Figure 26. Geographical distribution of *Sagina maxima* ssp. *maxima* in North America.

and pubescence of calyx and pedicels. The character states seem to be without geographical correlation. It thus appears that taxonomic recognition of varieties based on these characters is not valid in this species. The treatment of the species in *Flora Europaea* (Clapham & Jardin, 1964) recognizes two subspecies, ssp. *apetala* and ssp. *erecta.* Our plants do not fit well into either taxon, but do approach ssp. *erecta.* However, the treatment in *Flora Europaea* is regarded by the contributors as tentative. Considering the great variability within the species and that those subspecies recognized in *Flora Europea* are completely sympatric, it does not appear useful to recognize any infraspecific taxa of *S. apetala.*

Linnaeus is often erroneously cited as the author of the name *Sagina apetala.* Following the description of *S. apetala* in *Mantissa Plantarum Altera* Linnaeus (1771) clearly credits Arduino with authorship of the name. The matter is further clarified by reviewing the correspondence between Arduino and Linnaeus preserved in *Linnaeus Correspondence* Vol. I at the Linnean Society of London. Letter no. 164 written by Pietro Arduino in 1763 lists *Sagina apetala* (his no. 59) among specimens he sent to Linnaeus. Linnaeus recorded these plants received and lists this specimen as "Sagina species nova?" Listed in his letter of reply, Linnaeus included "Sagina si careat petalis, ego eam non vidii." The sequence of Linnaeus' list differed from that of Arduino, numbering the only *Sagina* under consideration as no. 39. A pencilled note by Savage in the margin indicates reference to specimen LINN *177.2.* Arduino published *Sagina apetala* as a new species the following year (1764). In the absence of another Arduino specimen of *S. apetala* I have chosen LINN *177.2.* to serve as the lectotype for Arduino's name.

Specimens representing Fenzl's taxa of *Sagina* deposited in Wien (W) were destroyed during World War II (Riedl, personal communication, 1974). Thus I have chosen the *Flora Rossica* specimen at the Komarov Botanical Institute in Leningrad (LE) representing Fenzl's *Sagina apetala* var. *barbata,* HERB. LEDEBOUR *148.1,* to serve as the lectotype.

Sagina sect. **Maxima** Crow, sect. nov.

Semina reniformia vel paene globosa, sine sulco dorsali; folia linearia, succulenta.

Seeds reniform or nearly globose, dorsal groove lacking; leaves linear, fleshy. Eastern Asia, northward, spanning the Aleutian Islands, south on the Pacific coast in North America to California; New Guinea. TYPE SPECIES: *Sagina maxima* A. Gray.

9a. **Sagina maxima** A. Gray, Mem. Am. Acad. N. S. **6:** 382. 1859. ssp. **maxima**

Sagina Linnaei Presl var. *maxima* (Gray) Maximowicz, Bull Acad. St. Pétersb. **18:** 372. 1873. TYPE: *C. Wright s.n.*, Cape Sangar, Hakadadi, Japan. U.S. North Pacific Exploring Expedition under Commanders Ringgold and Rodgers, 1853–1856. (Holotype, GH!; isotype, NY!).

Sagina maxima f. *littorea* Mak., Bot. Mag. Tokyo **25:** 156. 1911. *Sagina crassicaulis* var. *littorea* (Mak.) Hara, Jour. Jap. Bot. **13:** 556. 1937. *Sagina maxima* var. *littorea* (Mak.) Hara, Jour. Jap. Bot. **33:** 147. 1958. TYPE: Not seen. *G. Koidzumi s.n.*, Misaki, Prov. Sagami, Japan. December 27, 1905. (Holotype, TI.)

Sagina litoralis Hult., Svensk Vet. Akad. Handl. ser. III. Bd. 5. **2:** 78. 1928. *Sagina crassicaulis* var. *litoralis* (Hult.) Hult., Arkiv. for Botanik **7:** 147. 1968. TYPE: *Hultén 789*, Sarannaja Bay HN, Toporkof Island, South Kamchatka (Holotype, S!).

Annual or short lived perennial, from slender taproot. Stems stout, rarely filiform, much branched, spreading to decumbent. Upper portion of upper stems frequently pubescent. Usually with basal tuft of ascending linear leaves, secondary fascicles or basal rosette rarely present. Cauline leaves linear, succulent, glabrous, upper pairs rarely minutely glandular ciliate. Lower cauline leaves (6–) 8–15 (–20) mm long, upper cauline leaves linear, becoming shorter toward apex but rarely subulate, (2.5–) 3.5–7 (–9) mm long at apex. Leaf tips apiculate. Connate leaf bases conspicuous, forming a shallow scarious cup. Pedicels usually stout or sometimes slender, densely glandular pubescent at base of calyx, becoming less dense toward the lower portion, lower one-fourth usually glabrous. Flowers 5-merous, protandrous. Calyx glandular pubescent at base. Sepals ovate to orbicular (2–) 2.5–3.5 mm long, sepals with hyaline margins whitish, occasionally purple tinged on margins or tips. Petals elliptical to nearly orbicular, 2.0–2.5 (–3.0) mm long. Stamens 10, filaments 1.5–2.0 mm long, anthers 0.25 mm long. Capsules globose prior to dehiscence. Capsule valves thickish, dehiscing to ca. one-fourth the length of the sutures, (3.0–) 3.5–4.5 mm long. Sepals remaining appressed following capsule dehiscence. Seeds reddish-brown, reniform, dorsal groove lacking, lateral sides plump, surface pebbled or less frequently smooth, 0.5 mm long. Chromosome number $2n = 22$, 42 or 44. Figure 25.

ECOLOGY AND DISTRIBUTION: Coastal, growing on rocky or sandy bluffs, along rocky shores and gravelly beaches. The taxon occurs in eastern Asia, spanning the Aleutian Islands and ranging southward along the coast of North America to northern Washington and intergrading with *Sagina maxima* ssp. *crassicaulis* on the Queen Charlotte Islands and Vancouver Island. Subspecies *maxima* in eastern North America is adventive. The taxon occurs sporadically and does not show signs of aggression or spreading. Known localities include Toronto, Montreal and Quebec, Canada and Amherst, Massachusetts. Flowering June to August. Figure 26.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA: Queen Charlotte Islands, Empire Anchorage, Athlow Bay, Graham Island, *Calder, Savile & Taylor 21443* (DAO); Old Masset, Graham Island, *Calder, Savile & Taylor 21241* (DAO); Hotspring Island, *Calder, Savile & Taylor 22280* (DAO, DS); Limestone Island, *Calder, Savile & Taylor 22424* (DAO); Cumshewa Inlet, Moresby Island, *Calder, Savile & Taylor 21969* (DAO); Fairfax Inlet, Tasu Sound, Moresby Island, *Calder & Taylor 23620A* (DAO); Skedans group off Louise Island, *Calder, Savile & Taylor 22388* (DAO, WS). Vancouver Island, Esquimalt, *Calder & MacKay 29529* (DAO); Seabird Rocks between Cape Beal and Pachena Pt., 48°45′N., 125°10′W., *Calder & MacKay 30253* (NY, OSC); near Port Alberni, *Henry 9059* (GH); Campbell River, *Howell 7712* (CAS); Nanimo, *Macoun 24032* (NY); Oak Bay, vicinity of Victoria, *Macoun 78513* (CAN, F, MO); District of Renfrew, *Rosendahl & Brand 62* (COLO, NY, US). ONTARIO: Toronto, *Clarkston s.n.*, 4 August 1946 (WAT). QUEBEC: Montebello, *Charlebois 5* (DAO).

United States. ALASKA: Mouth of Mahoney Creek, George Inlet, Revillagigedo Island, *Shacklette 4853* (US). ALEUTIAN ISLANDS: Ilak Island (near Adak Island), *Bank 361-A* (MICH, US); Carlisle Island, *Bank 511* (MICH); Adak Island, *Jordal 2623* (CAN, US); Iliulink Unalaska, *Jepson 232* (UC, US); Umnak Island, *Johnson 1052* (WIS); Akutan Island, *Rudd s.n.*, July 1935 (WTU); Attu Island, *Van Shaack 776* (GH, US); Aleutian Island, specific locality unknown, *York 196* (F, MO). MASSACHUSETTS: Hampshire Co., Amherst, *Torrey s.n.*, 25 June 1951 (WTU). WASHINGTON: Clallam Co., Port Crescent, *Lawrence 259* (UC, WS).

In contrast to the east Asian members of this taxon, specimens from the Aleutian Islands and the west coast of North America tend to have slightly larger flowers and smooth seeds. In addition, pubescence is less dense and seldom occurs on the stems. Presence of pubescence was the basis for Hultén's recognition of *Sagina litoralis* Hult. However, characteristics demarking his taxon lie within the range of variability of the east Asian populations.

9b. **Sagina maxima** ssp. **crassicaulis** (Wats.) Crow, comb. nov. BASIONYM: *Sagina crassicaulis* Wats., Proc. Am. Acad. **18:** 191. 1883.

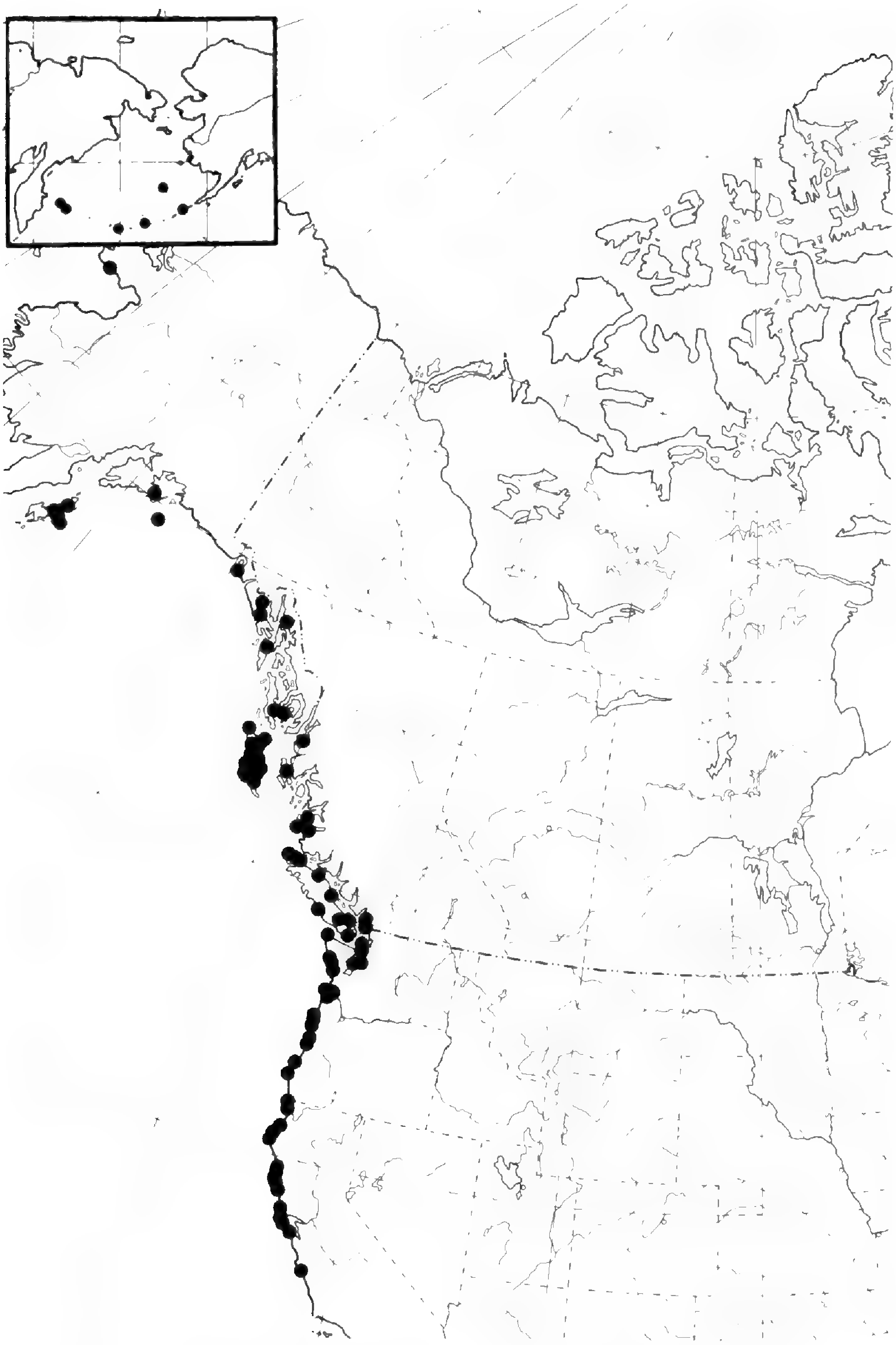

Figure 27. Geographical distribution of *Sagina maxima* ssp. *crassicaulis*.

Alsinella crassicaulis (Wats.) Greene, Fl. Franc. p. 125. 1891. *Sagina maxima* var. *crassicaulis* (Wats.) Hara, Rhodora **41:** 392. 1939. *Sagina maxima* f. *crassicaulis* (Wats.) Mizushima, Jour. Jap. Bot. **35:** 337. 1960. TYPE: *Congdon s.n.*, Dillon's Beach, Marin Co., California, June 6, 1880 (Holotype, GH!; isotype, MIN!).

Perennial. Plants glabrous. Stem stout or rarely filiform, much branched, spreading, decumbent or procumbent. Basal rosette of broadly linear succulent leaves, or if lacking, then primary or secondary tufts of ascending linear basal leaves present; ascending leaves with conspicuous midrib, usually less succulent than rosette leaves (rosettes rarely present in plants occurring north of Washington). Nodes frequently purple tinged. Cauline leaves linear, succulent. Lower cauline leaves 6–15 mm long, upper cauline leaves linear, becoming shorter toward apex but rarely subulate, 3.0–7.0 mm long at apex. Leaf tips apiculate. Connate leaf bases conspicuous, forming shallow scarious cup. Pedicels slender to stout. Flowers 5-merous, protandrous. Sepals ovate to nearly orbicular (2.0–) 2.5–3.0 (–3.5) mm long, hyaline margins whitish, occasionally purple tinged along margins or at sepal tips. Petals conspicuous, elliptical to orbicular (1.5–) 2.0–2.5 (–3.0) mm long, slightly shorter than sepals. Stamens 10, filaments 1.5–2.0 mm long, anthers 0.3–0.5 mm long. Capsules globose prior to dehiscence. Valves thickish, dehiscing to ca. one-fourth the length of the sutures, (3.0–) 3.5–4.0 (–4.5) mm long. Sepals remaining appressed following capsule dehiscence. Seeds reddish-brown, reniform, lateral sides plump, dorsal groove lacking surface smooth to slightly pebbled dorsally, 0.5 mm long. Chromosome number: $2n = 46, 66$.

ECOLOGY AND DISTRIBUTION: Strictly coastal, predominantly on sandy bluffs or crevices of rock cliffs of the Pacific Coast, most frequently at or near the high tide mark. Less often on gravelly-sandy beaches. Monterey Co., California, northward to the Aleutian Islands. Flowering May to September. A few specimens have been collected in flowering condition from California in December and February. Figure 27.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA Fulford Harbour, Saltspring Island (Straight of Georgia), *Ashlee s.n.*, 24 July 1960 (DAO). Duncan Bay, ca. 6 mi. west northwest of Prince Rupert, *Calder, Savile & Ferguson 14956* (DS, WTU). Hope Island, off north end of Vancouver Island, *Calder & MacKay 31180* (DAO). Vancouver, *Greene s.n.*, 19 July 1890 (US). Ann Island, Queen Charlotte Sound, *McCabe 1783* (UC). Calvert Island, head of Kwakshua Inlet, *McCabe 1701*

(UC). Crane Rocks, Gordon Channel, *McCabe 7103* (UC). Hakai Pass, *McCabe 7203* (DS, UC, WTU). Nigei Island, *McCabe 7075* (UC). Porcher Island, Freeman Pass, *McCabe 7345* (UC, WTU). Spider Island, *McCabe 4337* (UC). Queen Charlotte Islands, east side of Naden Harbour, Graham Island, *Calder & Taylor 36872* (DAO); Massett Inlet, Graham Island, *Calder, Savile & Taylor 21642* (DAO); Deena River, Skidegate Inlet, Moresby Island, *Calder & Taylor 23785* (DAO); Louise Island, *Osgood s.n.*, 29 June 1900 (US). Vancouver Island, Fanny Bay, south of Courtnay, *Calder & MacKay 30619* (DAO); Hesquiat Harbour, ca. 49°29′N., 126°24′W., *Calder & MacKay 31107* (DAO); Ivy Green Provincial Park, 2½ mi. northwest of Ladysmith, *Calder & MacKay 28979* (DAO); Kelsey Bay, 50°22′N., 125°57′W., *Calder & MacKay 32454* (DAO); Sarita, 48°53′N., 125°02′W., *Calder & MacKay 30342* (DAO); Port Alberni, *Henry 9060* (GH); vicinity of Ucleulet, *Macoun 78507* (CAN, F); Nanaimo, *Macoun 24032* (CAN); Bould Point, 4 mi. west of Jordan River, *McCabe 5586* (UC).

United States. ALASKA: Beardslee Island, Glacier Bay, *Anderson 1218* (NY). Farragut Bay, *Coville & Kearney 477* (US). Sitka, *Cowles 1085* (US). Port Vita, Raspberry Strait, Raspberry Island, Kodiak group, *Eyerdam 4026* (CAN, GH, MIN, UC, WTU). Washington Bay, Kuiu Island, *Eyerdam 5462* (WTU). Helm Bay, Cleveland Peninsula, *Flett 1981* (US). Attu Island, ½ mi. northeast of Krupa Point, Aleutian Islands, *Hardy 241* (GH). Nome, *Hill 137* (US, WS). Agattu Island, Aleutian Islands, *Hultén 6296* (CAS, DS). Amchitka Island, Aleutian Islands, *Hultén 6467* (US). Atka Island, Aleutian Islands, *Hultén 6968* (CAS). Kenai Peninsula, Seward, *Hultén 7966* (US). Afognak Island, Shelikof Strait off Alaskan Peninsula, *Rich s.n.*, August 1931 (DS). Popof Island, Shumagin Islands, *Saunders 3706* (MO). Revillagigedo Island, George Inlet, *Shacklette 4853* (MICH). Unalga Island, Unalaska, *Steenis 4657* (WIS). Middleton Island, Gulf of Alaska, *Thomas 6394* (CAN, DS, US). Long Island, Kodiak, *Trelease 3695* (US). Yakutat Mission, Yakutat Bay, *Trelease 3701* (MO, US). Prince of Wales Island, *Walker & Walker 913* (GH). Gravina Island, *Went 127* (US). CALIFORNIA: Del Norte Co., Crescent City, *Ripley & Barneby 6759* (CAS, NY). Humboldt Co., Big Lagoon, *Tracy 17927* (DAO, US, WS, WTU). Marin Co., Dillon's Beach, *Crow 1183* (MSC, NHA). Mendocino Co., 2 mi. south of Westport, *Crow 1197* (MSC, NHA). Monterey Co., Asilomar, Monterey Peninsula, *Howell 40368* (CAS). San Francisco Co., Baker's Beach, *Raven 2741* (CAS). Santa Cruz Co., Santa Cruz, *Hesse 986* (DS). OREGON: Clatsop Co., Columbia River, Astoria, *Nelson 3126* (GH). Coos Co., Coos Head, *Abrams & Benson 10589* (DS). Curry Co., Port Orford, *Peck 8435* (CAS, GH, MO, NY). Douglas Co., Winchester Bay, *Pringle s.n.*, 22 October 1881 (CAS, MSC). Lane Co., Heceta Head, *Cronquist 6112* (WS). Lincoln Co., Seal Rocks, *Peck 10595* (WTU). Tillamook Co., Tillamook, *Howell s.n.*, 15 July 1882 (F, MIN, MO, NY, US). WASHINGTON: Clallam Co., Clallam Bay, *Jones 5981* (WTU). Grays Harbor Co., Ocean City, *Jones 3894* (WTU). Island Co., Cornet Bay, Whidbey Island, *Smith 1520* (UC, WTU). Jefferson Co., Ruby Beach, 10 mi. north of Queets, *Meyer 1002* (MO, US). King Co., Seattle, *Piper 470* (US, WS). Kitsap Co., Orchard Point, *Piper 2312* (F, GH, WS). Pacific Co., Ilwaco, *Piper 4996* (US, WS). San Juan Co., Cattle Point, *Peck 12688* (WS). Wahkiakum Co., Altoona, *Suksdorf 6682* (WS).

In the original publication of this taxon, Watson (1883) cites the type specimen as "on Dillon's Beach, Marin County, California (J. W. Congdon, June 1880)." The holotype (GH) is dated June 6, 1880 and is a poorly developed plant. An isotype, acquired by the University of Minnesota (MIN) by the purchase of the herbarium of J. W. Congdon, is much more robust and is more representative of the plants at the type locality and of the taxon as a whole.

Climatic conditions in the higher latitudes sometimes have a dwarfing effect on the growth habit, and several specimens of *Sagina maxima* ssp. *crassicaulis* from Kodiak Island and the Aleutians are somewhat caespitose. These specimens tend to approach *S. nivalis* in general appearance.

Where the ranges of *Sagina maxima* ssp. *maxima* and ssp. *crassicaulis* overlap there is considerable intergradation between the two taxa. Variation of pubescence in populations on Vancouver Island and the Queen Charlotte Islands ranges from completely glabrous specimens to individuals with pedicels and calyx bases weakly pubescent to specimens with densely pubescent pedicels. Several specimens exhibiting a filiform habit and weak glandular pubescence are suggestive of *S. decumbens* ssp. *occidentalis*. However, they may be readily distinguished from the latter by the crassuloid seed.

10. **Sagina japonica** (Sw.) Ohwi, Jour. Jap. Bot. **13:** 438. 1937.

Spergula japonica Sw., Gesellsch. Nat. Freunde Berlin, Neue Schrift **3:** 164. 1801. TYPE: not seen. ORIGINAL MATERIAL: in low, moist regions, Japan.

Sagina japonica f. *glaberrima* Mizushima, Jour. Jap. Bot. **35:** 258. 1960. TYPE: *H. T. Tsai 52295*, in woodlands, 1800 m alt Cheng-hsiung Hsien, Yunnan, China. June 21, 1932. (Holotype, GH!)

Sagina sinensis Hance, Jour. Bot. **6:** 46. 1868. TYPE: *Sampson*, Exsicc. No. 13060. Isl. Kulagsu, across from Amoy, China. May 1866. (Holotype, K!).

Sagina Taquetii Léveillé, Fedde Rep. Sp. Nov. **10:** 350. 1912. TYPE: *Taquet 4125*, littoral zone, southern part of Quelpart, Korea. (Holotype, E!)

Sagina echinosperma Hayata, Icon. Plant. Formos. **2:** 39. 1913. TYPE: *S. Saski s.n.*, 9000 ft. alt., Mt. Morrison, Formosa, 25 October 1909. (Holotype, TAI; isotype, TI!).

Annual, from slender taproot. Stems usually filiform, much branched, ascending to spreading, upper portion of upper stems frequently glandular pubescent. Frequently with basal tuft of ascending linear leaves, secondary fascicle or rosette rarely present. Cauline leaves linear, succulent, glabrous or rarely pubescent. Lower cauline leaves 9–20 mm long, becoming shorter toward the apex, 4.0–7.0 mm long at apex. Leaf tips apiculate. Connate leaf bases conspicuous, forming a shallow scarious cup. Pedicels slen-

Figure 28. *Sagina japonica.* a. habit, Japan (*Ohwi 9142*, UC); b. close-up showing glandular pubescence, Japan (*Ohwi s.n.*, 9 May 1950, MO).

der, densely glandular pubescent at base of calyx, becoming less densely so downward, lower one-fourth of pedicel usually glabrous. Flowers 5-merous. Calyx glandular at base. Sepals elliptical to orbicular, 2.0–2.5 mm long, hyaline margins whitish. Petals ovate to orbicular, 1.0–2.0 mm long, sometimes caducous. Stamens 10 or 5, filaments 1.5 mm long, anthers 0.25–0.3 mm long. Capsules globose prior to dehiscence, the valves thickish, dehiscing to one-fourth the length of the sutures, 2.5–3.0 mm long. Sepals remaining appressed following capsular dehiscence. Seeds dark brown, reniform to nearly globose, dorsal groove lacking, sides plump, the surface densely tuberculate, 0.4–0.5 mm long. Chromosome number: $2n = 42$ or 44. Figure 28.

ECOLOGY AND DISTRIBUTION: Introduced. Growing in dryish sites and waste places. The only North American collections known are from Nanaimo, Vancouver Island and Prince Rupert, British Columbia; Portland, Oregon and Ottawa, Ontario. Native to east Asia. Flowering June to August.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA: Prince Rupert, *Groh 469* (DAO). Nanaimo, Vancouver Island, *Macoun s.n.*, 10 June 1887 (CAN). ONTARIO: Ottawa, Dominion Arboretum, *Groh 1696* (DAO).

United States. OREGON: Albina, Portland, *Suksdorf 2772* (WS) and *2863* (WS).

CHROMOSOME NUMBERS

Very little information is presently available on chromosome numbers in *Sagina*. Publications indicate that two basic chromosome numbers, $x = 6$ and $x = 11$ (Darlington & Wylie, 1956) and perhaps a third, $x = 7$ (Löve & Löve, 1975), occur in the genus.

Table 2 summarizes the chromosome numbers known for the taxa of *Sagina* which occur in North America. A large portion of the published counts is based on European material. Dr. J. K. Morton has graciously provided his previously unpublished counts, all based on North American plants. Voucher specimens for Morton's counts are deposited in the herbarium of the University of Waterloo, Ontario, Canada (WAT).

Table 2. **Chromosome Numbers For Taxa of Sagina Occurring in North America**

Taxon	**2*n*** Number	Reference or Voucher Specimen
S. nodosa	56	Blackburn, in Tischler (1938)
	56	Blackburn & Morton (1957)
	56	Gadella & Kliphuis (1968)
	44	Löve & Löve (1956)
	56	**Canada.** QUEBEC: Bic Island, Gulf of St. Lawrence off the Gaspé Peninsula, *Morton NA 3967.*
	56	**Canada.** QUEBEC: St. Fabien, Gaspé Peninsula, *Morton NA3917.*
	56	**Canada.** ONTARIO: Neys Provincial Park, Lake Superior, *Morton NA3711.*
	56	**Canada.** NEWFOUNDLAND: Cape St. George, *Morton s.n.*
	56	**Canada.** NEWFOUNDLAND: Daniel's Harbour, *Morton, s.n.*
	22-24	Wulff (1937)
S. saginoides	22	Blackburn, in Wright (1938)
	22	Blackburn & Morton (1957)
	22	Löve & Löve (1956)
	22	Packer (1968)
	c. 22	**United States.** MONTANA: Glacier National Park, *Crow 1103.*
	22	**United States.** MONTANA: Bear Tooth Mts., *Morton s.n.* (meiotic and mitotic counts)
	22	**United States.** MONTANA: Cooke City, Yellowstone National Park, *Morton s.n.*
	22	**United States.** WASHINGTON: Mt. Rainier, *Morton NA3324.*
	22	**Canada.** ALBERTA: Cameron Lake, *Morton s.n.*
	22	**Canada.** ALBERTA: Mt. Edith Cavell foot, Jasper National Park, *Morton NA4624a.*

Table 2 (Cont.)

Taxon	2*n* Number	Reference or Voucher Specimen
S. saginoides (cont.)	22	**Canada.** ALBERTA: Mt. Edith Cavell foot, Jasper National Park, *Morton NA4623*.
	c. 22	**Canada.** ALBERTA: Wilcox Mt., Columbia Icefield, Jasper National Park, *Morton NA4635*.
	22	**Canada.** ALBERTA: Waterton Lakes National Park, *Morton NA4731*.
	c. 22	**Canada.** ALBERTA: Highwood Pass, Coleman Hwy., *Morton s.n.*
S. procumbens	22	Blackburn, in Tischler (1938)
	22	Blackburn & Morton (1957)
	22	Calder & Taylor (1968)
	22	Gadella & Kliphuis (1966, 1971)
	22	Rohweder (1937, 1939)
	22	Wulff (1937)
	22	**United States.** VERMONT: White River, *Morton s.n.*
	22	**Canada.** NOVA SCOTIA: Cape Breton, Dingwall, *Morton NA4284a*.
	22	**Canada.** NOVA SCOTIA: Cape Breton, Dingwall,*Morton NA4284b*. (meiotic count)
	22	**Canada.** QUEBEC: St. Louis de Blandford, *Morton NA4313*.
	22	**Canada.** BRITISH COLUMBIA: Vancouver, *Morton NA3353*.
S. subulata	22	Blackburn & Morton (1957)
	22	Findlay & McNeill (1973)
	22	Löve & Löve (1956)
	18	Rohweder (1937, 1939)
S. nivalis	84	Blackburn & Morton (1957)
	88	Löve & Löve (1948, 1956)
	c. 88	**Canada.** ALBERTA: Mt. Edith Cavell foot, Jasper National Park, *Morton NA4624b*.

Table 2 (Cont.)

Taxon	2*n* Number	Reference or Voucher Specimen
S. caespitosa	88	Knaben (1950)
	88	Löve & Löve (1956)
	100 (higher than)	Löve & Löve (1944)
S. decumbens ssp. *decumbens*	36	**United States.** NORTH CAROLINA: Hatteras Seashore, *Morton NA2636.* (meiotic count)
S. apetala	12	Blackburn & Morton (1957)
	12	Diers (1961)
S. maxima ssp. *maxima*	42 or 44	Blackburn, in Wright (1940)
	44	Calder & Taylor (1968)
	22	Taylor (1967)
S. maxima ssp. *crassicaulis*	66	Calder & Taylor (1968)
	46	**United States.** CALIFORNIA: Marin Co., *Crow 1181.* (meiotic count)
S. japonica	42 or 44	Blackburn, in Wright (1940)

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NEW OBSERVATIONS ON THE ROYAL FERN HYBRID OSMUNDA × RUGGII

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The striking hybrid fern, *Osmunda* × *ruggii,* was described in 1940 by Rolla Tryon as the natural cross of *O. regalis* L. var. *spectabilis* (Willd.) Gray and *O. claytoniana* L. A single plant was discovered in Connecticut and grown in the garden of H. G. Rugg of Dartmouth College. Until the population described below was found, no new localities and no known occurrences of this taxon in nature have been reported. It is the only interspecific hybrid known in the Osmundaceae, a family conservatively interpreted as comprising three genera and 16 species (Bobrov, 1967, recognizes five genera and 36 species).

Because the fertile portion of the frond of full-sized hybrid plants exceeds in length those of either *Osmunda regalis* or *O. claytoniana,* F. S. Wagner (1974) suggested that its origin might involve *O. cinnamomea* rather than *O. claytoniana.* Our present interpretation is that the length of the fertile segment in *O.* × *ruggii* results from additive effects of *O. regalis* and *O. claytoniana,* and that *O. cinnamomea* is not involved in the parentage. This conclusion is based upon a number of new observations, herein reported, on *O.* × *ruggii* and its relatives, including data on habitat, morphology, cytology, and chemistry.

Habitat. We know practically nothing about the original collection site of the type specimen. There may have been two different collections, one at Wilton, the other near Hartford, Connecticut (Tryon, 1940). The hybrid proved to be a vigorous garden plant in Rugg's garden in Hanover, New Hampshire, and later in the gardens of Richard Harlow at LaAnna, Pennsylvania, of W. H. and F. S. Wagner at Ann Arbor, Michigan, and of others, where offsets were transplanted.

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For over a quarter of a century we have sought wild populations of this plant in connection with general studies of the role of hybridization in ferns. However, we were unsuccessful although we found the presumed parents growing together in hundreds of localities in the eastern United States and adjacent Canada. Finally, one of us (W. H. W.) encountered a very large colony in Craig County, Virginia, in July, 1974. The plants are scattered over an approximately elliptical area of 16.5 × 6.1 m. at the bottom of a ravine. The slope here is shallow and most of the plants are separated by a meter or more, although some of the crowns are only 10–20 cm. apart, suggesting recent separation. A total of 60 plants was found, so the colony is probably very old. The locality is in the Jefferson National Forest at an altitude of 765 m. on the south slope of Potts Mountain.

The forest type here is primarily montane oak-hickory with numerous ericaceous shrubs present, and the ferns grow in a mostly open understory, where a well developed canopy of tree crowns provides considerable shade. In general the soil is sandy and moist, and the ground is covered with leaf mold composed largely of rotting oak leaves. PH readings under plants of *Osmunda* × *ruggii* gave 6.5.

The forest canopy is dominated by *Acer rubrum, Liriodendron tulipifera,* and *Quercus prinus.* Other woody plants in the habitat include species of *Betula, Castanea, Carya, Cornus, Fraxinus, Lindera, Oxydendron, Quercus, Parthenocissus, Robinia, Rhododendron, Rubus, Sassafras, Smilax, Toxicodendron,* and *Vitis.* The understory is dominated by *Osmunda cinnamomea* L., *O. claytoniana,* and *O. regalis,* which are roughly equal in abundance. The lady-fern, *Athyrium filix-femina,* is also common here. Other herbaceous plants include members of the genera *Amphicarpa, Asplenium, Botrychium, Collinsonia, Chimaphila, Danthonia, Dioscorea, Galax, Goodyera, Habenaria, Lobelia, Hypericum, Panicum, Polystichum, Scutellaria, Smilacina, Solidago, Thelypteris, Veronica,* and *Viola.*

Assuming that the population of *Osmunda* × *ruggii* in the Potts Mountain ravine represents a single clone, it may be the result of hybridization that occurred many centuries ago. In New England, Steeves and Wetmore (1953) estimated that an average annual in-

Figure 1. Frond of *Osmunda* × *ruggii* in middle of photograph with *O. regalis* in the upper background. The photograph was taken at the Virginia locality.

crease in rhizome length in *O. cinnamomea* may be only several millimeters. Klekowski and Berger (1976) gave an approximate growth rate of 0.7 cm. per year for rhizomes of *O. regalis*. Assuming that growth began in the center of the population, and using the latter estimated rate of increase, the age of the *O.* × *ruggii* colony would be greater than 1100 years.

Living plants from Potts Mountain have been introduced at U. S. National Arboretum in Washington, D. C. There is no reason why the fine wild population of *Osmunda* × *ruggii* should not continue to flourish in the future as there is no known threat from natural causes, the habitat is remote, and the District Rangers of the Jefferson National Forest are aware of the interesting nature of the colony and plan to protect its habitat from lumbering operations and vandalism.

Morphology. Growing side-by-side in their native habitat, the four taxa of *Osmunda* are readily distinguishable from distances up to 5–10 m. *Osmunda cinnamomea* differs from the others in July and August in its spreading fronds which are light yellow-green in color and more glossy. Its pinna segments are more conspicuously pointed. *Osmunda regalis* is obvious because of its frond structure, the pinnae with widely separated, large and rounded pinnules and the fronds overlapping each other in dense intergrowth. *Osmunda claytoniana* displays the strictest habit, the fronds of mature individuals nearly upright and parallel. The laminar luster is dull and the color bluish-green. In over-all habit, *O.* × *ruggii* is closest to *O. claytoniana*. The hybrid is like *O. claytoniana* in general shape and appearance, but the pinnae are divided as in *O. regalis* (Figure 1).

For each *Osmunda* taxon in the valley we counted the number of fronds on each of 20 crowns. The average and range for *O. cinnamomea* was 5.3 (3–9), for *O. regalis* 6.8 (4–10), and for *O. claytoniana* 10.0 (6–17). For the hybrid, surprisingly, these values were only 5.0 (3–9). A reason for the absence of intermediacy in frond number per rhizome is unknown. Perhaps it is a peculiarity of this specific genotype and not significant because all of the plants involved, species and hybrid, represent as few as four genetically unique clones.

A disappointing feature of the Potts Mountain *Osmunda* × *ruggii* colony was the total lack of fertile fronds at the time of our

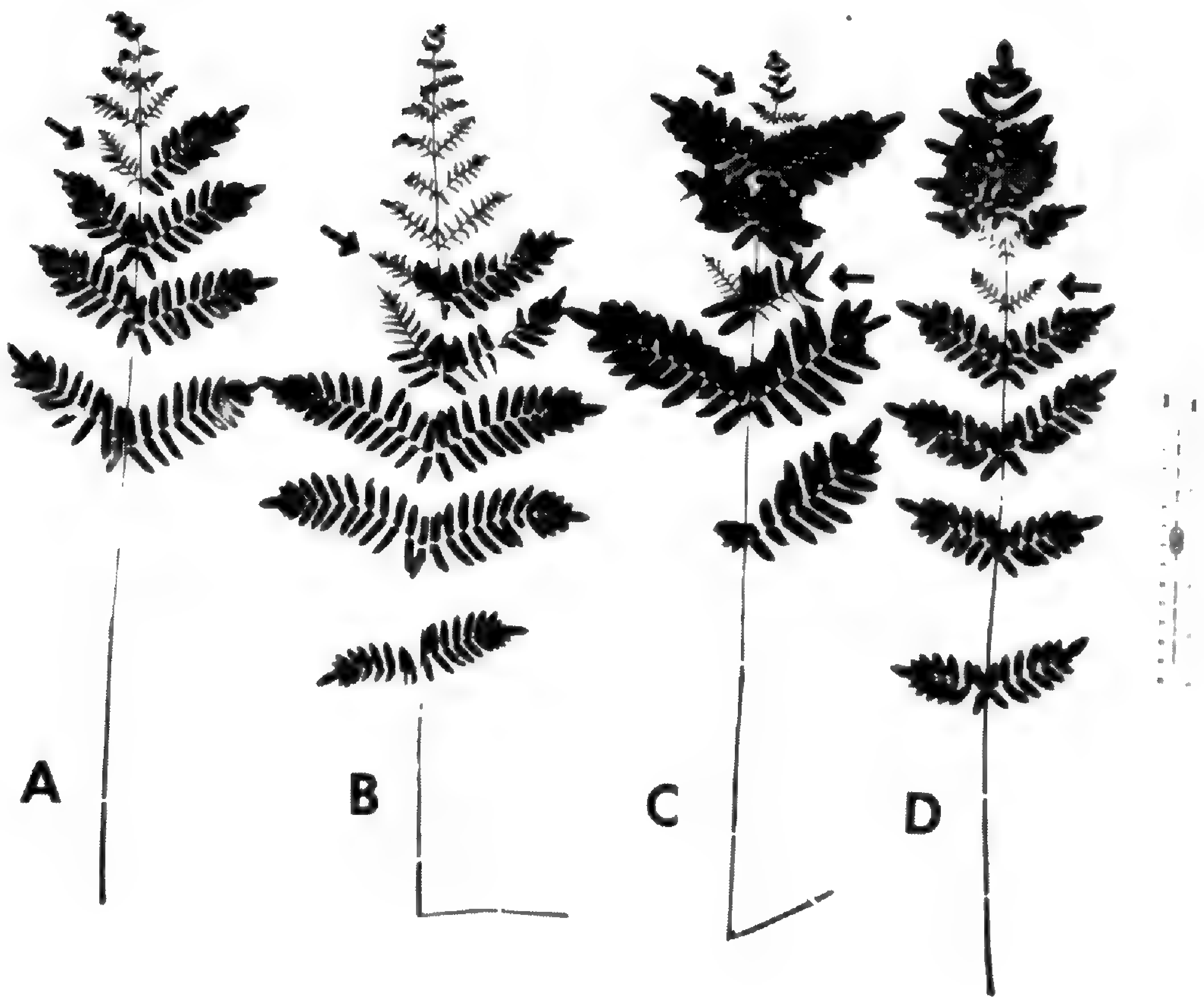

Figure 2 *Osmunda* × *ruggii* fronds transplanted from the Virginia locality to Ann Arbor, with apical (A, B), medial (D), and combined apical and medial fertile pinnae (C).

study in July, 1974. Accordingly, we asked Gerald B. Straley of Eggleston, Virginia, to revisit the spot in the middle of May, 1975, and examine the *Osmunda* populations. He reported as follows: "The *O. claytoniana* fertile fronds were completely developed and the fertile pinnae dark green. The *O. regalis*, on the other hand, had fertile fronds still unfurling and many of the fertile pinnae were still inrolled. There was not one fertile frond to be found on *O. ruggii* and I searched every plant closely."

Fortunately, plants which were transferred to Washington, D. C., and Ann Arbor, Michigan, produced fertile fronds, presumably as a result of transplanting. The fertile fronds displayed beautiful irregularity of expression of pinna dimorphism. In some (Figure 2, A, B) the fertile pinnae were apical, as in *Osmunda regalis.* In others (Figure 2, D) the fertile pinnae were medial, as in *O. claytoniana.* Most interesting were those that showed both conditions on the same frond (Figure 2, C). It should be noted that all of these fronds are fairly small.

The much larger fertile fronds of the cultivated plants growing in the Richard Harlow garden in Pennsylvania show a uniform structure quite different from that in the transplants from the Virginia colony as well as from both parents. On 22 June, 1973, we studied several distinct colonies at the Harlow garden. Among the dozens of fertile fronds observed, all displayed the terminal condition of the fertile pinnae (Figure 3). However, these extended nearly the entire distance to the base of the blade, there being only one to three pairs of sterile pinnae, the remaining 10 15 pinnae being fertile. Indeed, with only a slight change, the conversion of the bottom pinnae into the fertile condition, we would have the situation familiar in the wholly modified sporophyll of *Osmunda cinnamomea.* So unexpected was this condition, in fact, that we wondered whether it was possible that the original Rugg material, from which the Harlow garden specimens were derived, may not have been *O. cinnamomea* × *regalis* rather than *O. claytoniana* × *regalis.* A more likely interpretation of the unusually long fertile segment is that it displays the additive effects of the terminal fertile pinnae of *O. regalis* plus the medial ones of *O. claytoniana.* An explanation such as this would be of special interest as a rare case in which a hybrid fern is not strictly intermediate in all its characters.

In most other respects, however, the hybrid is intermediate between *Osmunda claytoniana* and *O. regalis.* The segments are intermediate in size, although slightly closer to *O. claytoniana* than to *O. regalis.* The segment bases are of special significance in that the parental ones are strongly differentiated. Those of *O.* × *ruggii* are narrowly adnate, whereas those of *O. regalis* are obviously petiolulate in contrast to those of *O. claytoniana,* which are so strongly adnate as to be connate at their bases with the adjacent segments. In the hybrid the segment bases (especially the proximal ones) are sometimes so strongly contracted as to produce a small stalk. The finely dentate margin of *O. regalis* is barely expressed in *O.* × *ruggii,* which is nearly entire, as in *O. claytoniana.*

As R. Tryon (1940) noted, most of the veins of *Osmunda* × *ruggii* segments fork only once, as in *O. claytoniana,* rather than twice,

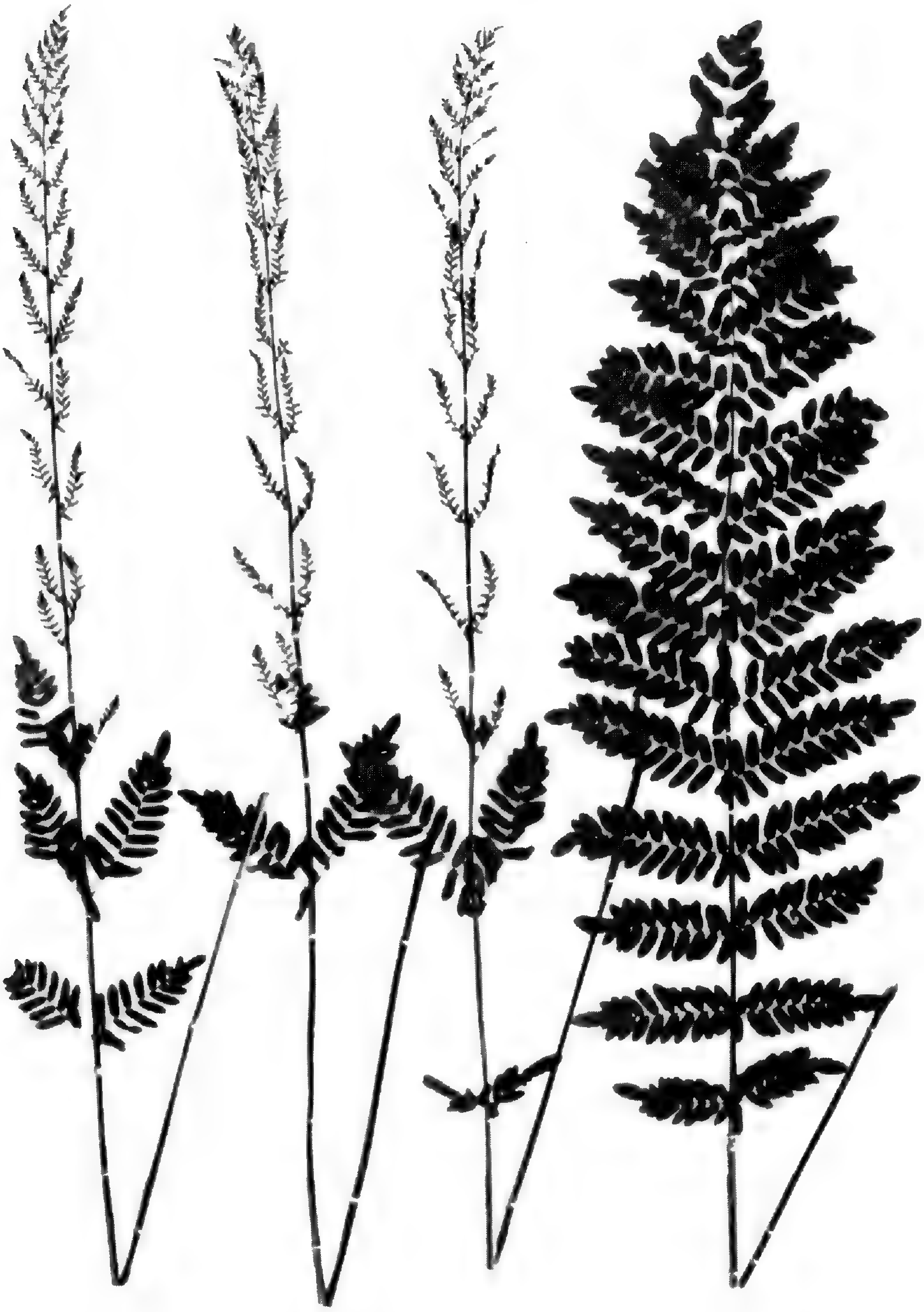

Figure 3. *Osmunda* × *ruggii* full-sized fronds from the Harlow garden in Pennsylvania with unexpectedly long terminal fertile segments; sterile frond at right.

as in *O. regalis* (Figure 5). The positions of the furcations have not previously been contrasted: the branching of the veins in *O. claytoniana* occurs one-fifth to one-third of the distance to the vein tips. In *O. regalis,* most of the veins branch at the base or even in the costa so that the branches come out separately. *Osmunda* × *ruggii* is intermediate in this respect, the branchings occurring anywhere from the base to approximately one-fifth of the distance to the vein tips.

Anatomy. Anatomical features of the species involved in this study have been described by Miller (1967, 1971) and Hewitson (1962). The most significant comparisons of the species with the hybrid involved leaf trace branchings, root number, endodermis, and distribution of sclerenchyma in the stem cortex and leaf base. The first branchings of the leaf trace protoxylem occur in the leaf bases in *Osmunda cinnamomea* and *O. claytoniana.* In *O. regalis* branching is in the inner cortex. Using materials from the Harlow garden, Miller found that *O.* × *ruggii* shows an intermediate branching position in the outer cortex. The number of roots associated with a single leaf trace in *O. cinnamomea* is generally only one, but in *O. claytoniana, O.* × *ruggii,* and *O. regalis,* this number is generally two.

Another distinction of *Osmunda cinnamomea* from the other three taxa is the presence of an internal endodermis. This tissue is unknown in any other recent species of the family Osmundaceae. *Osmunda claytoniana, O.* × *ruggii,* and *O. regalis* conform to the usual condition in the living members of the family in having only an external endodermis. Likewise, *O. cinnamomea* is peculiar in having a nest of thick-walled fibers in the inner cortex of the rhizome adaxial to each leaf trace. Such nests are known only in this species and in *Todea barbara* among extant members of the family. There are no such clusters of fibers present in *O. claytoniana, O.* × *ruggii,* and *O. regalis.* In addition, *O. cinnamomea* is unique in having three groups of thick-walled fibers, one on each side and one abaxial in the outer cortex (sclerenchyma ring) of the leaf base. In *O. claytoniana, O.* × *ruggii,* and *O. regalis* leaf bases the thick-walled fibers form an arch that occupies most of the abaxial semicircle of the sclerenchyma ring.

Thus, of the distinctive anatomical features of *Osmunda cinnamomea,* only one — the first branching of the leaf trace protoxylem

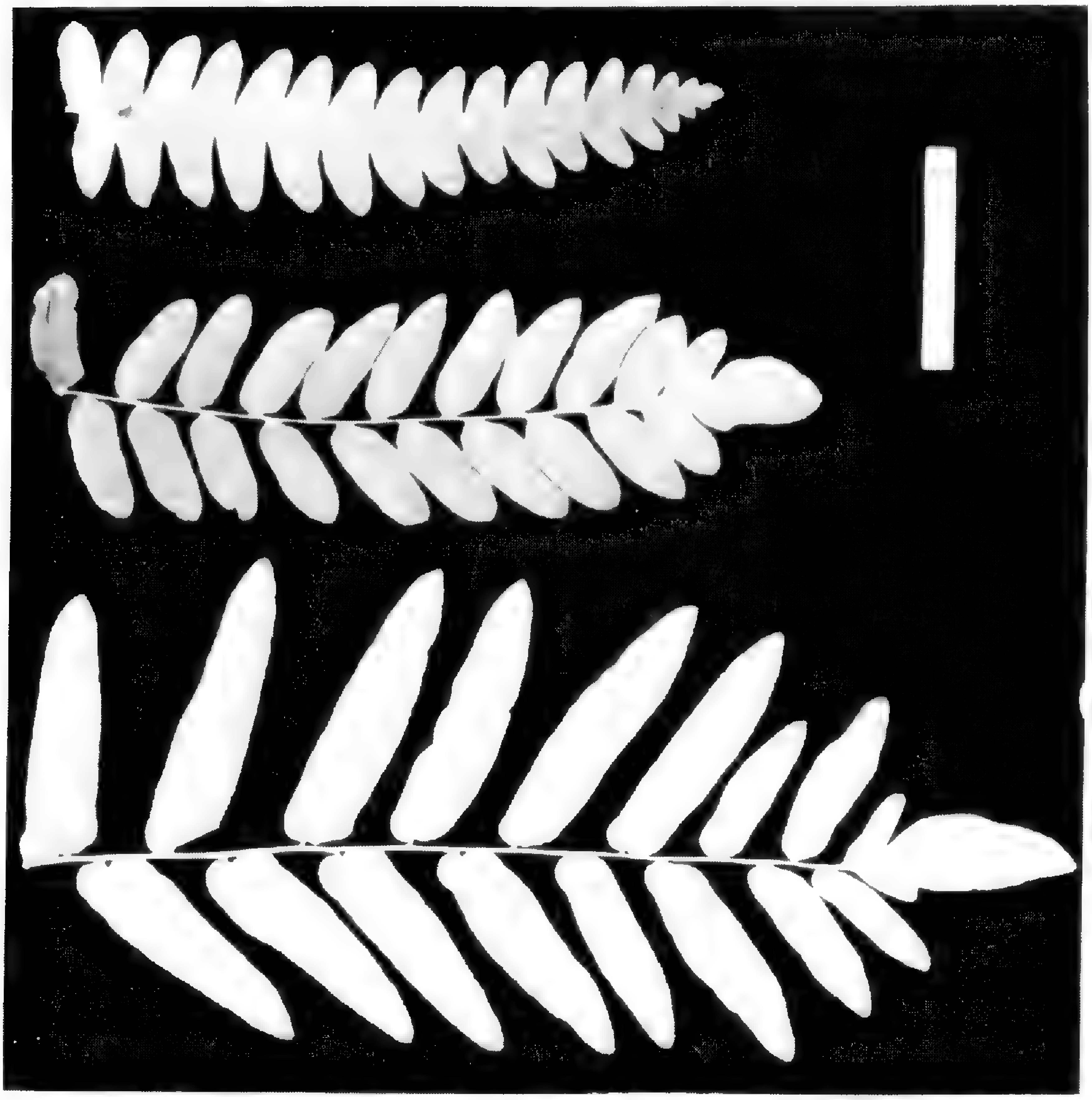

Figure 4. Pinnae of *Osmunda*. Upper, *O. claytoniana*. Middle, *O.* × *ruggii*. Lower, *O. regalis*.

shows evidence of expression in *O.* × *ruggii*. However, since *O. claytoniana* shares this character with *O. cinnamomea*, it has no diagnostic value. All of the anatomical characters of *O.* × *ruggii* are consistent with the original hypothesis of its origin.

Chemistry. Specimens of all four taxa were examined chromatographically by D. H. Wagner for phenolics. Several pinnae from each specimen (vouchers deposited in Marion Ownbey Herbarium, Washington State U., Pullman) were ground in a mortar with grinding sand. The samples were extracted separately with methanol and two-dimensional paper chromatograms prepared according to standard procedures (Mabry, et al., 1970). BAW (4:1:5 n-butanol, gla. acetic acid, water) was used in the first direction and 15% acetic acid for the second direction. Although it was evident that there was no variation in chromatographic patterns within each of the taxa, comparison among them was difficult due to streaking and poor separation of the compounds caused by non-phenolic substances present in the extracts. The extracts from each taxon were pooled and phenolics separated by precipitating with lead (II) acetate (procedure described in D. Wagner, 1976). Chromatograms prepared from the purified extracts are exceptionally clear. Comparison with the first set of chromatograms indicated that few, if any, compounds were lost by the purification.

Diagrams of the chromatograms produced from the pooled extracts are shown in Figure 6. A total of twenty-one compounds can be detected on the chromatograms of *Osmunda* × *ruggii*. These fall into three categories — those shared with none of the species, those shared with only one of the species, and those shared with two of the species.

Four of the compounds in *Osmunda* × *ruggii* can be clearly identified with spots on the chromatograms of any of the three species. Three are shared with both *O. regalis* and *O. claytoniana*. Three are shared with both *O. claytoniana* and *O. cinnamomea*. One is shared with both *O. regalis* and *O. cinnamomea*.

Those compounds of *Osmunda* × *ruggii* that are shared with only one of the species provide evidence regarding origin of the hybrid. Five compounds extracted from *O.* × *ruggii* are shared only with *O. regalis* (Figure 6, ru & re hatchings to the right). Five compounds are shared only with *O. claytoniana* (Figure 6, ru & cl hatching to the left). None of the compounds found in *O.* × *ruggii* is shared only with *O. cinnamomea*. These results support Tryon's original interpretation.

Cytology. Fertile pinnae of a transplant of *Osmunda* × *ruggii* from the Harlow garden were collected during the last two weeks of April, 1973, in Ann Arbor, Michigan. They were fixed in Newcomer's solution after cold pretreatment with paradichloro-benzene aqueous solution. Squashes were made in a mixture of 50% aceto-carmine and 50% Hoyer's solution. The photographs (Figure 7) were made at 500× using Zeiss phase contrast equipment.

We anticipated that meiosis would be abnormal, because abortion of the spores is so extreme. Indeed, we found it impossible

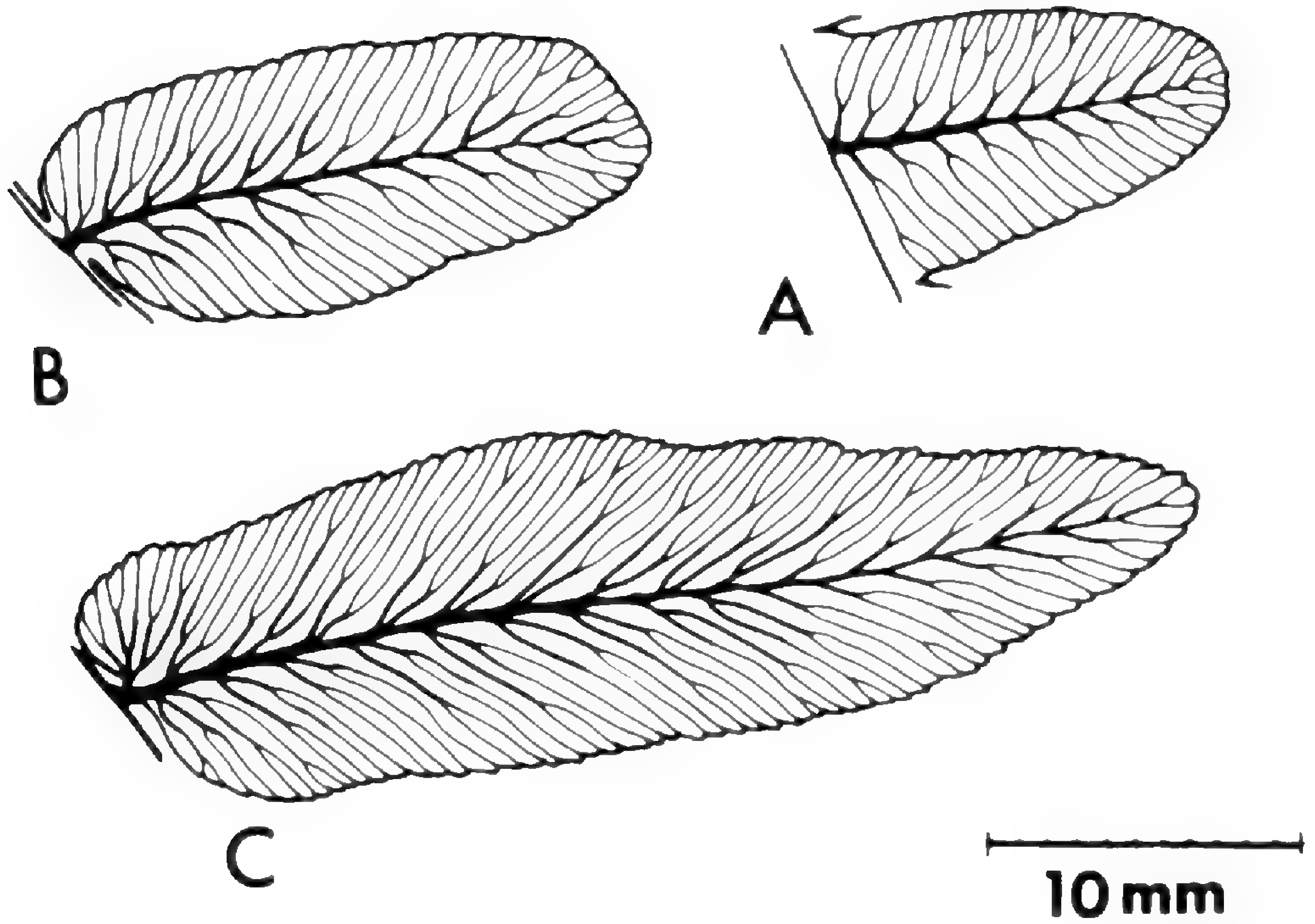

Figure 5. Venation patterns in *Osmunda* pinnae. A, *O. claytoniana*. B, *O.* × *ruggii*. C, *O. regalis*.

to observe individual spores in the sporangia. The capsules contain coalesced masses of thin-walled cells. The sporangial walls themselves do not form normally either, the walls being somewhat fleshy.

In striking contrast to the very uniform conditions thus far reported in the Osmundaceae, with 22 pairs at meiotic metaphase, *Osmunda* × *ruggii* shows 44 units, each unit a single chromosome. The univalents appear as short rods. We found no tendency at all for bivalent groupings, indicating a total lack of pairing factors prior to anaphase. The preliminary report of cytological conditions in *O.* × *ruggii* (F. S. Wagner, 1974) is based on garden specimens derived from the original Rugg plant. Later studies in 1975 of garden transplants from the Potts Mountain colony revealed the same lack of pairing of 44 chromosomes.

Significance. New evidence from a wide variety of sources overwhelmingly supports R. Tryon's hypothesis that *Osmunda* × *ruggii* is the natural hybrid of *O. claytoniana* and *O. regalis*. In spite of the *O. cinnamomea*-like fertile fronds of the large plants of the hybrid growing in the Harlow garden at LaAnna, Pennsylvania, there is little support for regarding *O. cinnamomea* as a possible parent. Most of the fertile fronds from smaller plants of *O.* × *ruggii* show more intermediate conditions, including not only terminal fertile pinnae, but medial, and even both on the same frond.

Osmunda × *ruggii* is now known in a natural population from only one locality in spite of the fact that its parents occur together over a huge area from northeastern Canada to the Appalachians in the south and Minnesota in the west, probably the best explored area botanically in the New World. At maturity the appearance of *O.* × *ruggii* is so splendid and distinctive that an experienced field botanist would recognize it immediately. We can only speculate on causes for its rarity. Perhaps it cannot compete with other plants in its native habitats. At the Potts Mountain locality in Virginia, however, it shows no evidence of inability to compete. Perhaps too, there are strong incompatibility barriers between the parents, and only very rare mutations can hybridize. Experimental investigations in the laboratory may provide some clues.

The hybrid origin of *Osmunda* × *ruggii* bears upon the subgeneric classification of the Osmundaceae. In over-all appearance, *O. claytoniana* and *O. cinnamomea* are so similar that sterile fronds are commonly confused by field workers. *Osmunda regalis,* on the other hand, is very distinctive. Thus, a hybrid between either *O. claytoniana* or *O. cinnamomea* and *O. regalis* would seem to be most unusual. It would be more logical to expect a hybrid between *O. claytoniana* and *O. cinnamomea.*

Of recent taxonomic treatments, those of Bobrov (1967) and Hewitson (1962) place *Osmunda cinnamomea* and *O. claytoniana* together in subg. Osmundastrum, separating them from *O. regalis* in the type subg. Osmunda. In contrast, Miller (1971), although recognizing the two subgenera, places *O. claytoniana* with *O. regalis* in subg. Osmunda. Miller's conclusions are based upon comparative anatomy of fossil and living forms, and they seem to be in conflict with more recent conclusions based upon comparative chemistry. A serological and disc electrophoretic analysis of spore proteins (Petersen & Fairbrothers, 1971) showed that *O. cinnamomea* and *O. claytoniana* have greater protein affinities for each other than either has for *O. regalis.* DNA hybridization techniques were used to estimate the degree of DNA base sequence homology between the three species. Stein and Thompson (1975) concluded that under conditions of extensive reassociation, measurements of

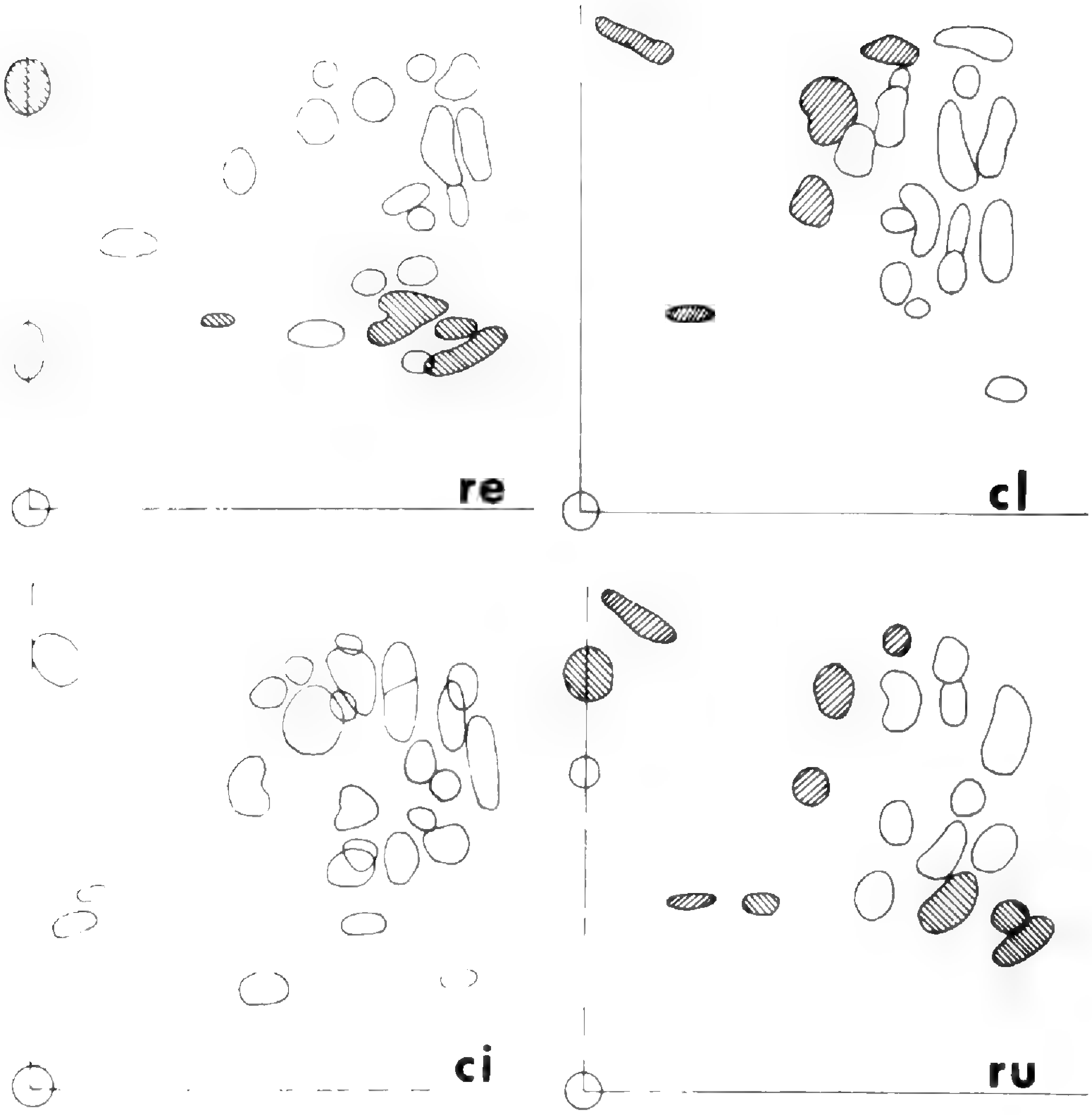

Figure 6. Diagrams of chromatograms of *Osmunda*. Vertical axis = BAW; horizontal axis = 15% acetic acid. Letters refer to specific epithets.

interspecific reaction and thermal stability of hybrid molecules indicated that *O. claytoniana* shares more DNA homology with *O. cinnamomea* than it does with *O. regalis*. The conclusion of both of these chemical studies is that *O. claytoniana* and *O. cinnamomea* should be placed together in subg. Osmundastrum, although Petersen and Fairbrothers (op. cit.) do state that *O. regalis* has, in general, greater protein affinities for *O. claytoniana* than it has for *O. cinnamomea*.

As has been demonstrated again by the study of *Osmunda* × *ruggii*, there is no question that *O. claytoniana* and *O. regalis* are more closely related anatomically to each other than either is to

O. cinnamomea, reaffirming Miller's earlier findings. Indeed, morphologically it is only in characters of leaf cutting and segment structure that *O. claytoniana* and *O. regalis* differ. Although spore protein studies might be difficult to carry out with *O.* × *ruggii* because of the extreme spore abortion, it would be interesting to repeat the DNA hybridization experiments using *O.* × *ruggii* together with its parents and with *O. cinnamomea.*

Hickok and Klekowski (1975) have discussed the possible significance of the absence of chromosome pairing in *Osmunda* × *ruggii.* It has been hypothesized by Klekowski (1973) that the genus *Osmunda* possesses duplicated sets of four chromosomes, but that pairing is restricted to bivalent formation through some sort of physiological control. Lack of structural divergence within the homoeologous sets could be explained through the prevention of structural diploidization by occasional homoeologous pairing within the sets. Accordingly, one might expect in an interspecific hybrid that there would be a level of autosyndetic pairing. The fact that we found no pairing at all, only univalents, in *O.* × *ruggii,* together with the fact that synthetic autopolyploids experimentally produced by Irene Manton (1950) displayed multivalent formation, creates a puzzling situation and casts doubt on Klekowski's hypothesis.

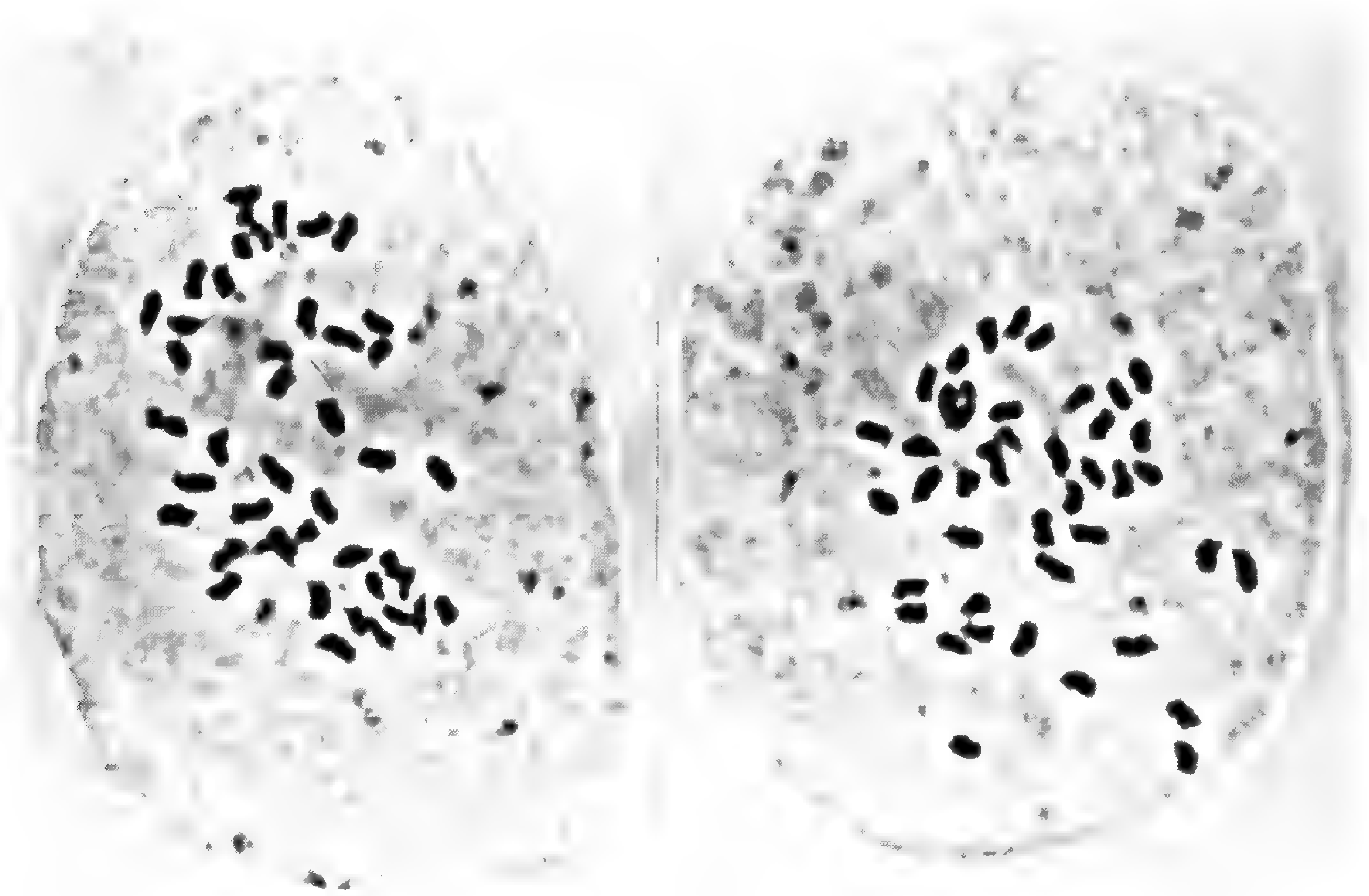

Figure 7. Meiosis in *Osmunda* × *ruggii* with 44 unpaired chromosomes.

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ANALYSIS OF ISOZYME VARIATION IN NATURAL POPULATIONS OF JUNIPERUS ASHEI

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The study of isozymes is now a common part of scientific endeavor, but the recognition of multiple forms of enzymes within an organism is relatively recent, being announced in 1959 by Markert and Moller. Prior to that time, molecular heterogeneity noticed in enzyme preparations was attributed to contaminants or to denatured or degraded enzyme molecules (Markert, 1975). Two decades ago there were suggestions that this enzymatic heterogeneity might not be artifactual but might reflect reality within the cell (Neilands, 1952; Vesell & Bearn, 1957; Weiland & Pfleiderer, 1957). Most of these early investigators used zone electrophoresis to separate enzyme preparations into components; however, these procedures were laborious and had poor resolving power. By coupling the starch gel electrophoresis techniques of Smithies (1955) with histochemical staining procedures to identify separate enzymes, Hunter and Market (1957) developed the zymogram technique, which had greater resolving power for the identification of the isozymes of many enzyme systems. This technique was first applied successfully to esterases and lactate dehydrogenases (Markert & Moller, 1959). The technique was direct, simple, easy to use, and applicable to enzymes in relatively crude homogenates. The development of the zymogram technique allowed recognition of isozymes as a natural and important aspect of cellular biochemistry that is found in nearly all organisms (Markert, 1975). Even greater resolving power was gained when acrylamide gel electrophoresis was introduced by Raymond and Weintraub (1959), and Ornstein and Davis (1959). As a result of the development of these techniques many investigators have focused on isozymes. The study of isozymes is important in order to understand a number of major biological problems, including the evolution of populations, the transformation of one gene into another, and the regulation of gene expression. Isozymes

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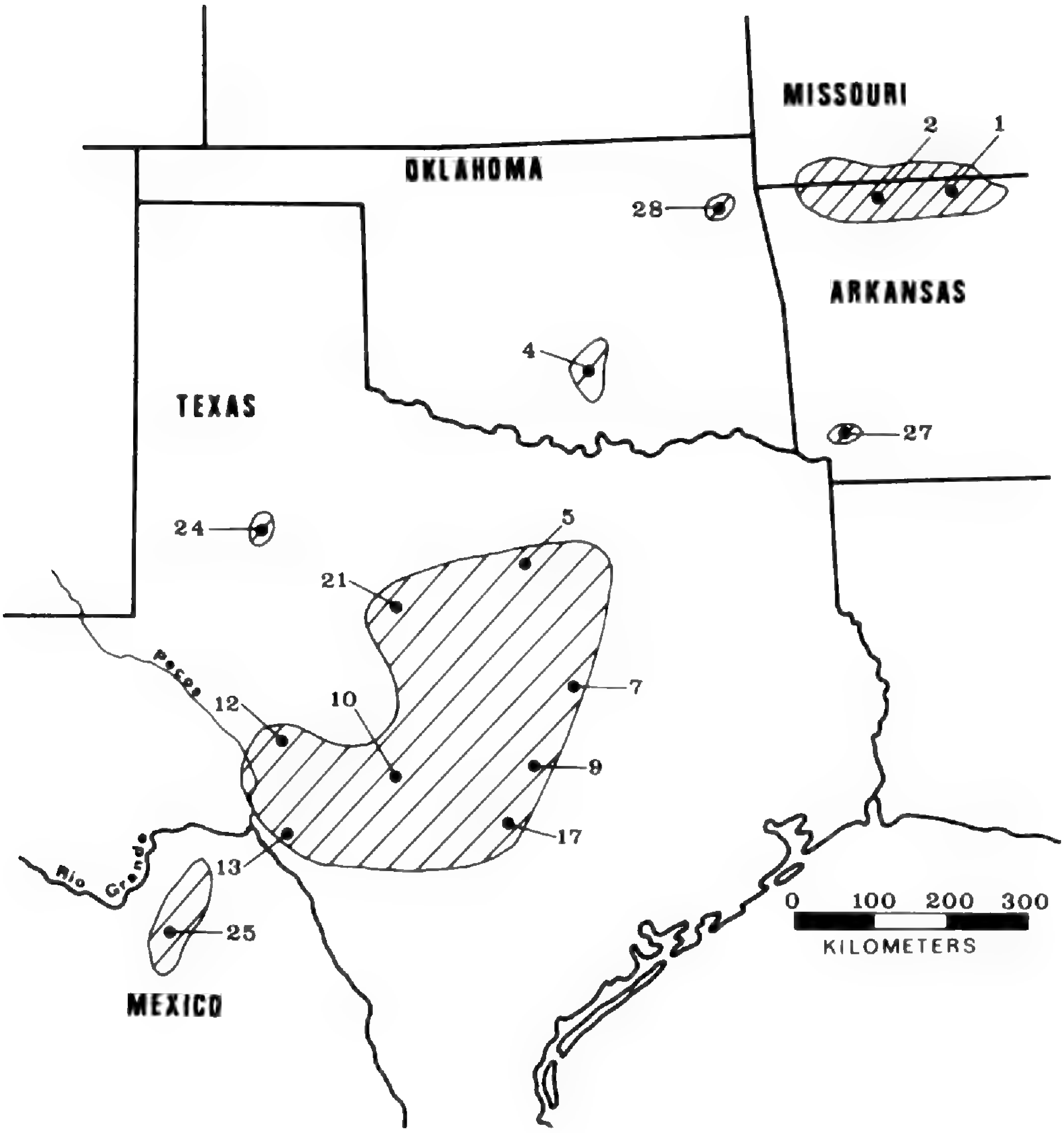


Figure 1. Distribution map of *Juniperus ashei* showing locations of populations samples. Cross-hatched areas show approximate distributional ranges. Population numbers correspond to those used by Adams (1975, 1977).

may also hold the key to the understanding of metabolic regulation and the function of metabolic pathways in differentiated tissues (Horecker, 1975). These initial investigations of isozymes dealt primarily with animal systems. The plant biologists did not become intensely interested in isozymes until ten years ago (Shannon, 1968). At that time the idea that isozyme data might be useful in understanding evolutionary phenomena at the population level in plants was reviewed by Turner (1969) and Gottlieb (1971a).

The first investigations of isozymes in higher plants dealt predominantly with surveys of the various isoenzymatic systems found in plant species (Shannon, 1968). Because of the widespread polymorphisms usually found in isozymes under natural conditions these data were normally more useful at the infraspecific levels than at higher categorical levels and seemed to be especially useful in studying evolutionary problems at the population level (Turner, 1969). There have been a few interesting and notable exceptions to this general principle. Isozymes have been used in interspecific studies on *Nicotiana* (Smith *et al.,* 1970; Sheen, 1970); *Datura* (Conklin & Smith, 1971); *Carthamus* (Efron *et al.,* 1972); *Lycopersicon* (Rich *et al.,* 1973); *Clarkia* (Gottlieb, 1973a, 1974a); *Stephanomeria* (Gottlieb, 1973b). These studies have been taxonomically oriented. On the other hand, infraspecific studies have been chiefly concerned with populational evolution, differentiation and variability. These kinds of studies include those on *Xanthium strumarium* (McMillan, 1975), *Stephanomeria exigua* spp. *coronaria* (Gottlieb, 1973c), *S. exigua* spp. *carotifera* (Gottlieb, 1974b), *Lupinus* and *Hymenopappus* (Babbel & Selander, 1975), *Betula populifolia* (Payne & Fairbrothers, 1973), *Avena barbata* and *A. fatua* (Allard *et al.,* 1972a; Allard & Kahler, 1973; Clegg & Allard, 1972, 1973; Hamrick & Allard, 1972; Marshall & Allard, 1969, 1970a, 1970b), *Bromus mollis* (Brown *et al.,* 1974), *Hordeum vulgare* (Allard *et al.,* 1972b; Clegg *et al.,* 1972; Kahler & Allard, 1970; Weir *et al.,* 1972, 1974), *Picea abies* (Tierstedt, 1973), *Pinus sylvestris* (Rudin, 1975; Rasmuson & Rudin, 1971; Rudin & Rasmuson 1973; Rudin *et al.,* 1974), *Pinus pungens* (Feret, 1974), *Pseudotsuga menziesii* (Muhs, 1974), *Cryptomeria japonica* (Sakai & Park, 1971), and *Thujopsis dolabrata* (Sakai *et al.,* 1971).

The detection of hybridization with the use of isozymes has been investigated in *Phlox* (Levin, 1975) and *Typha* (Lee & Fairbrothers, 1973).

The inheritance of isozymes has been analyzed by many of the aforementioned workers as well as considerable research in the gymnosperm, forest trees such as *Picea abies* (Bartels, 1971; Lundkvist, 1974, 1975), *Pinus attenuate* (Conkle, 1971a,b), *Pinus sylvestris* (Rudin, 1975; Rudin & Rasmuson, 1973; Rudin *et al.,* 1974), and *Pinus nigra* (Bergmann, 1974). The general rule appears to be that most banding patterns are inherited co-dominantly (Allard *et al.,* 1975).

The literature on ontogenetic and seasonal variation has been reviewed by Kelley and Adams (1977) and the reader is referred

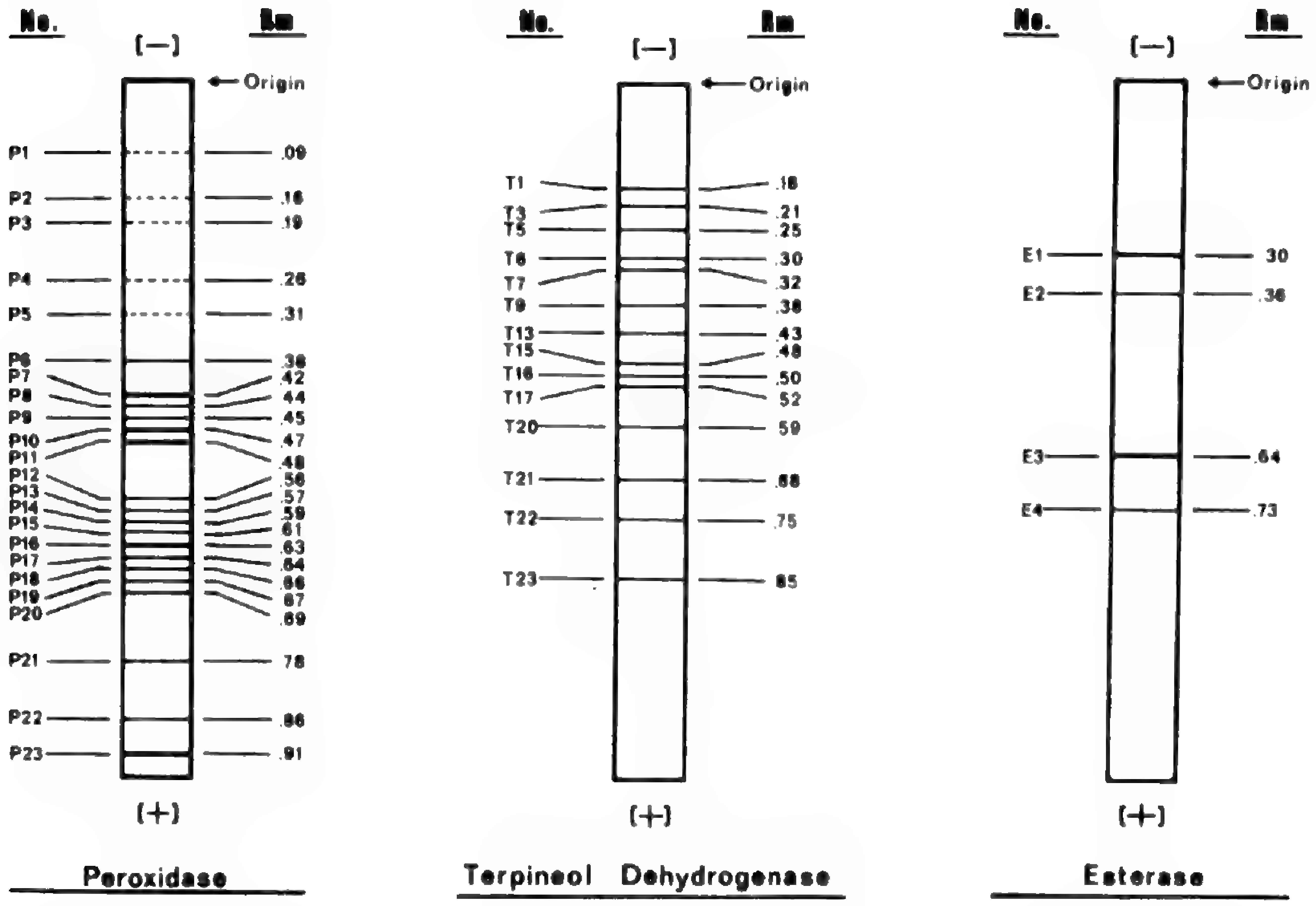


Figure 2. Summary of all possible isozymes observed in the *Juniperus ashei* trees examined. Rm = Relative Migration.

to that paper.

Several hypotheses have been proposed to explain the observed variations seen in the isozymes in these studies of various species. The isoallelic or neutral hypothesis suggests that much of the observed variation is physiologically irrelevant and the alleles are adaptively equivalent and their variation random (Kimura, 1968; Kimura & Crow, 1969; King & Jukes, 1969). In contrast, the selection hypothesis asserts that some form of natural selection is responsible for the maintenance of the variation (Gottlieb, 1971a; Powell, 1975). The disagreement between these two hypotheses is a significant matter, because according to the modern synthetic theory of evolution, natural selection is considered the basic force leading to genetic divergence and adaptation. The neutral hypothesis challenges this position by claiming that some variations at the molecular level are below the levels of selection.

The present isozyme study was undertaken to investigate the amount and nature of genetic variation in natural populations of *Juniperus ashei* Buch. (Cupressaceae). This species has been studied at the populational level by Adams and Turner (1970), and Adams (1975, 1977), using morphological and terpenoid data.

Juniperus ashei is an obligate outcrossing dioecious species that occurs on limestone outcrops and soils in central Texas, northern Mexico and in the Ozark Mountains of southern Missouri and northern Arkansas (Figure 1). Two small isolated populations of *J. ashei* are found in the northeastern portion of the species distribution: one in northeastern Oklahoma (23, Figure 1) and another in southwestern Arkansas (27, Figure 1). Both of these populations are in association with *J. virginiana; J. ashei* occupying the

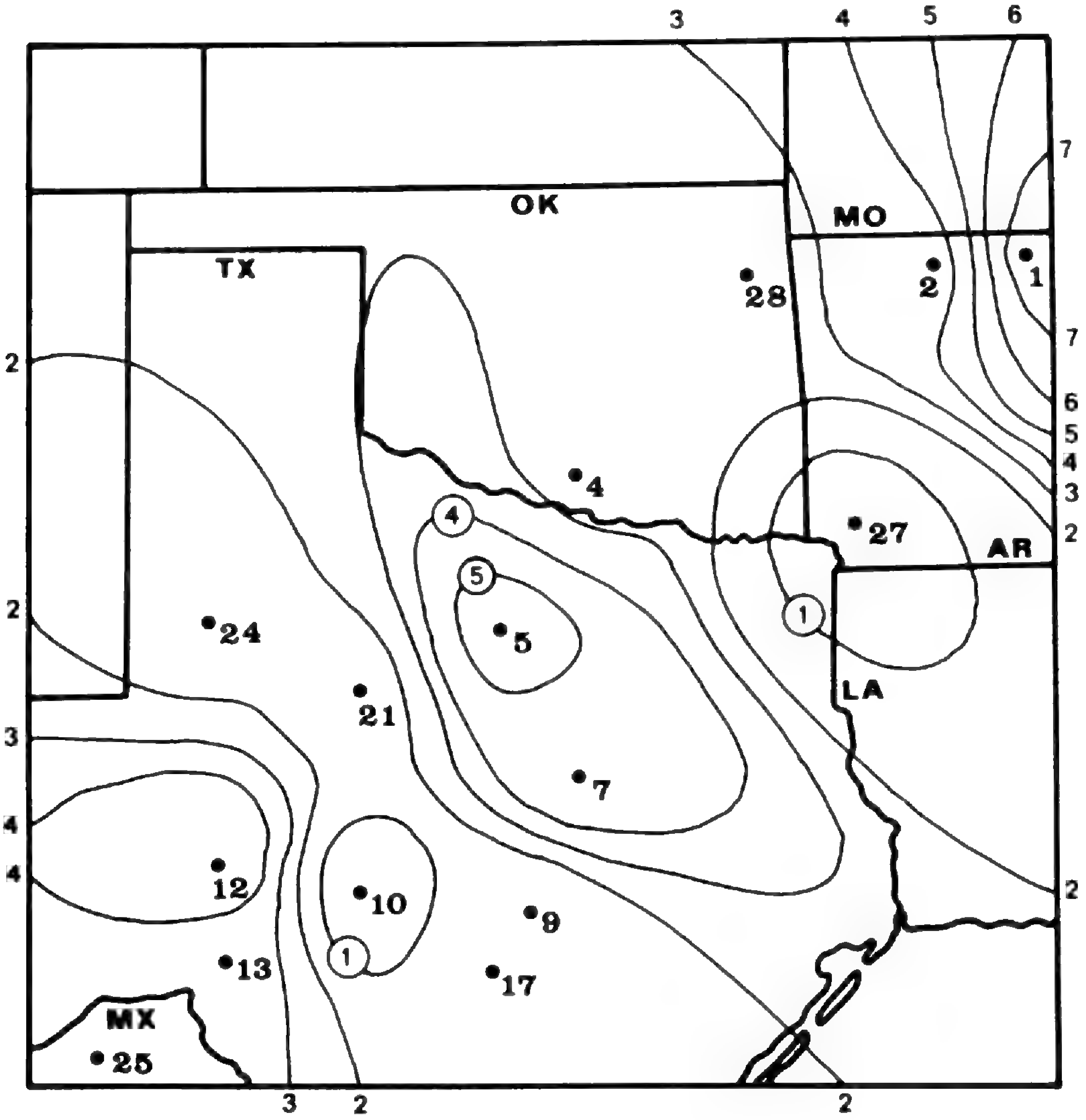


Figure 3. Contour map for average number of isoperoxidases per population of *Juniperus ashei* (Contours: 1 = 5.97; 7 = 10.13). Note the low number of bands at populations 27 and 10.

drier limestone soils at both sites. A small, pure stand of *J. ashei* is found in southcentral Oklahoma in the Arbuckle Mountains (4, Figure 1). The largest expanse of *J. ashei* is on the Edwards Plateau of central Texas. At the eastern edge of the Edwards Plateau, *J. ashei* is mixed with *J. virginiana* (7 & 9, Figure 1) and at the southwestern edge it occurs with *J. pinchotii* Sudw. (10, 12, 13, & 21, Figure 1). On the remaining portions of the Edwards Plateau *J. ashei* grows in relatively pure stands. A small isolated population of *J. ashei* is also found in west central Texas (24, Figure 1) in the more moist canyon floors with *J. pinchotii* occupying the drier sites. In the southwestern limits of its distribution *J. ashei* is found south of the Sierra del Carmen Mountains of Coahuila, Mexico with *J. pinchotii,* and occasionally with *J. flaccida* Schlect. (25, Figure 1).

Thus, by sampling throughout the natural range of *Juniperus ashei,* investigations can be conducted on the nature of isozyme variation in small isolated populations, in large continuous populations, and in populations at the center and the periphery of the species distribution.

MATERIALS AND METHODS

Sample Collection. Populations of *Juniperus ashei* were sampled from throughout its range. Figure 1 shows the locations of the populations sampled and the distribution of *J. ashei.* The population numbers shown in Figure 1 correspond to those used by Adams (1975, 1977) in his studies of this species (for exact locations, see Kelley, 1976). Whenever possible, 30 trees were sampled at random from each population. In populations that did not contain 30 trees, all trees present were sampled. The smallest number of trees sampled at any location was 19 (population 13 and 28).

Fresh foliage samples were collected in plastic bags during a two week period in November and December, 1974, and were stored at -7°C. within one hour from the time of collection. Samples were maintained at -7°C. until all samples were collected and returned to Colorado State University, Fort Collins, Colorado, where they were stored at -20°C. until the enzymes were extracted.

Enzyme Extraction. Populations were selected at random from cold storage and the enzymes of all samples from that population were extracted using the extraction buffer and procedures outlined

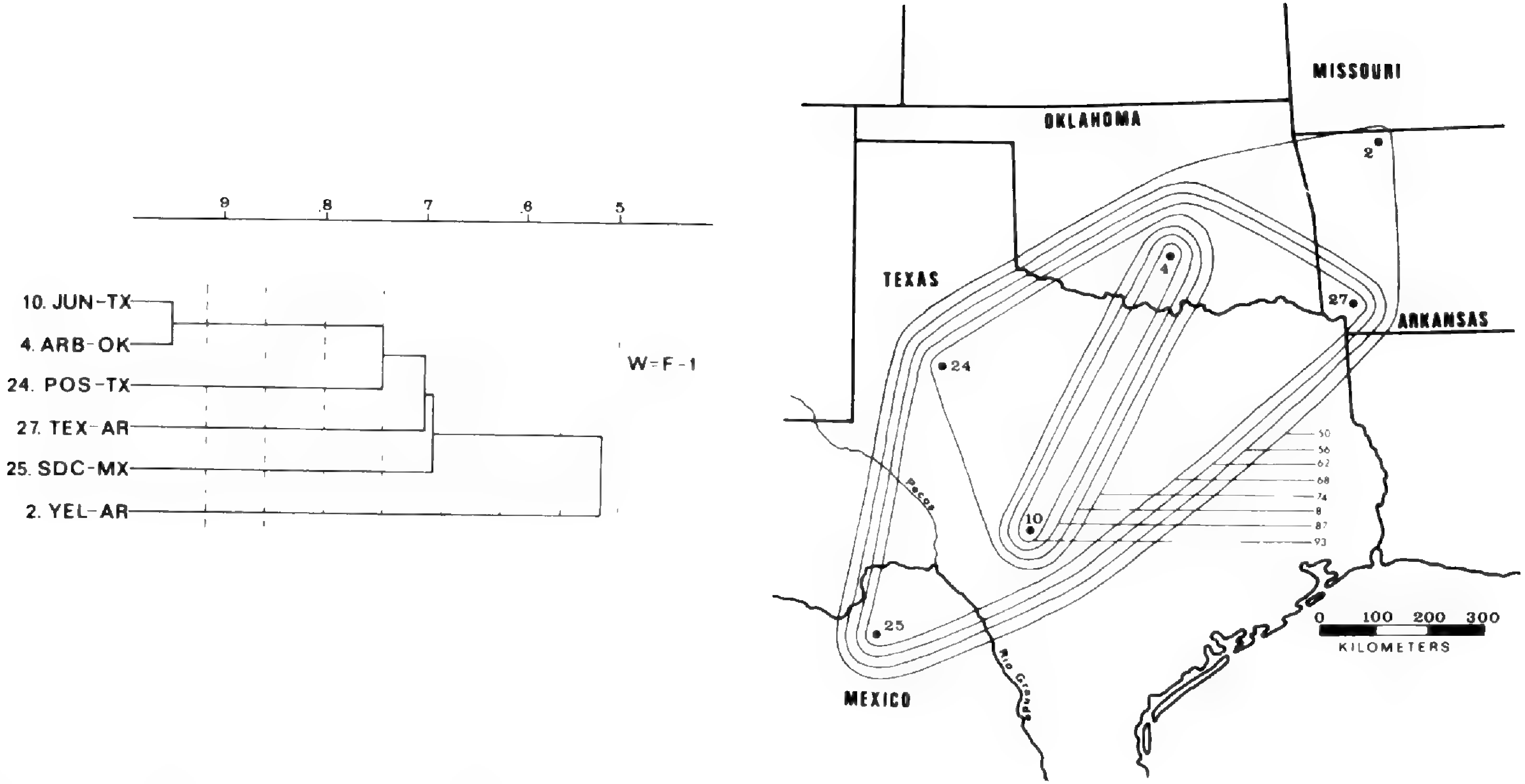


Figure 4. Phenogram and contoured similarity of six populations of *Juniperus ashei* based on four esterases, F-1 weighted. Similarity values are shown on the scale at the top of the phenogram. The dashed lines on the phenogram show the contour levels used on the contoured similarity map.

by Kelley and Adams (1976). Enzyme extracts were stored at -20°C. until electrophoresis.

Samples were subjected to polyacrylamide gel electrophoresis within 96 hours from the time of extraction. Electrophoresis was performed as outlined by Kelley and Adams (1976), with 4½%, 6%, 8% anodic gels being used for peroxidases; 6%, 8% anodic gels being used for esterases and α-terpineol (alcohol) dehydrogenases

Gels were stained for peroxidases, esterases, and α-terpineol (alcohol) dehydrogenases as outlined by Kelley and Adams (1976).

Following electrophoresis and staining, the Relative Migration (Rm) were calculated for all bands, data sheets were scored, and photographs were taken of the gels. DiCamelli and Bryan (1975) define Relative Migration as: Rm = migration of enzyme/migration of bromphenol blue. After all samples of *Juniperus ashei* were run the band numbers for the three enzyme systems were assigned. Assignment numbers started with the band nearest the origin (smallest Rm) and ended with band nearest the anode (largest Rm). Figure 2 shows the locations, band numbers, and Rm values for all bands observed in the *J. ashei* samples.

To eliminate the possibility of error in zymogram band interpretation from one gel to the next, an evaluation of band discreteness was performed. Samples from two or more trees were mixed in various combinations and electrophoresed. These mixed sample gels were run to evaluate all bands that had Rm values differing by 0.05 or less. By running gels with mixed samples in various combinations the discreteness of closely migrating bands for each of the three enzyme systems could be ascertained. Band discreteness was maintained for all peroxidase and esterase bands observed. When in several cases α-terpineol (alcohol) dehydrogenase zymograms of mixed samples showed convergence of bands, the original two bands were counted as one band and the data sheets corrected. This convergence of α-terpineol (alcohol) dehydrogenase bands in mixed samples accounts for the absence of the band T2, T4, T8, T10, T11, T12, T14, T18, and T19 from the data and from Figure 2 (center).

After electrophoresis of all tree samples and band discreteness evaluation, each tree was scored for the presence or absence of each possible band. All 15 populations sampled were analyzed for peroxidases, and in addition six of the 15 populations (2, 4, 10, 24, 25, & 27) were analyzed for esterases and α-terpineol (alcohol) dehydrogenases.

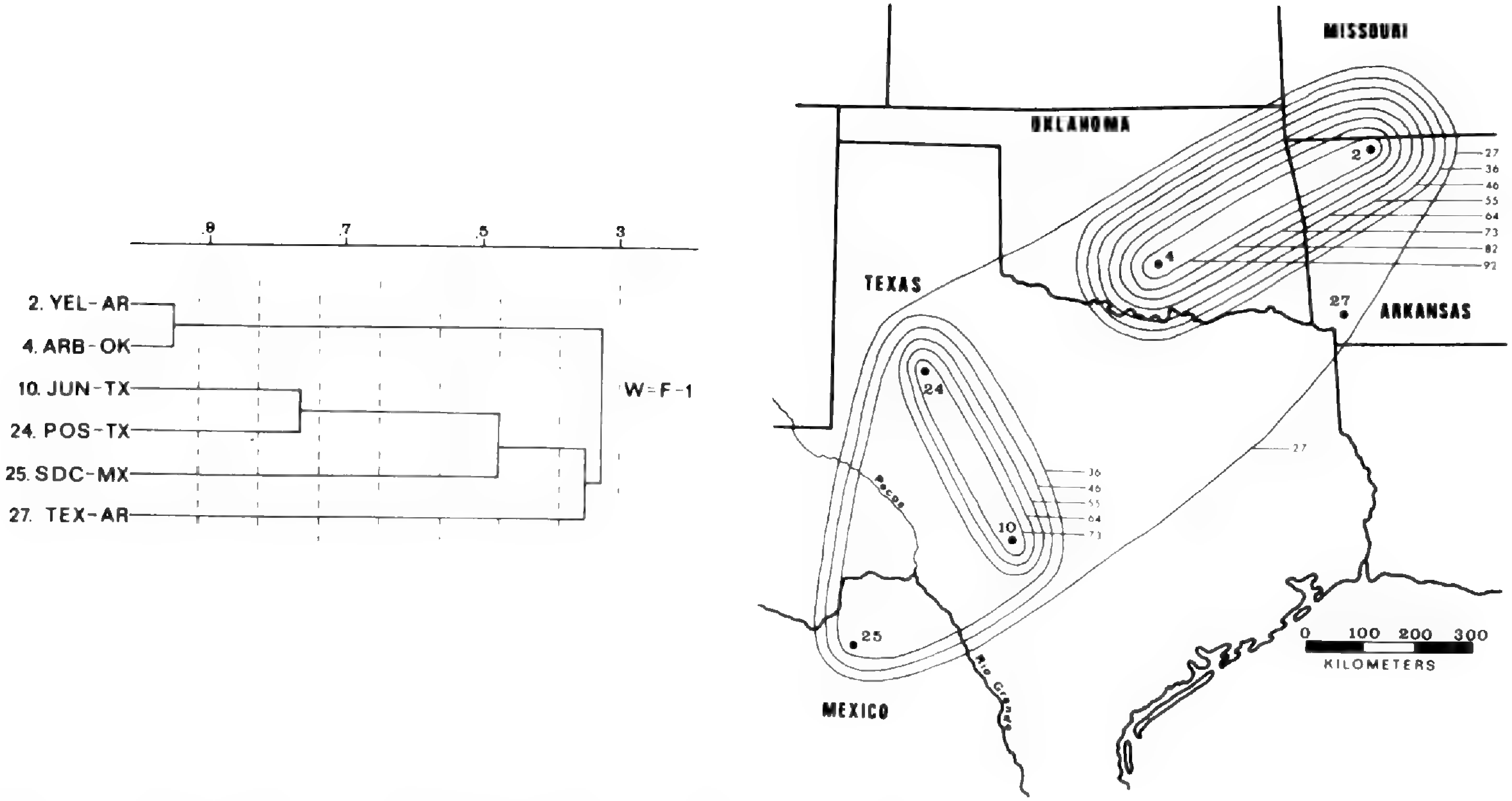


Figure 5. Phenogram and contoured similarity of six populations of *Juniperus ashei* based on 11 α-terpineol dehydrogenases, F-1 weighted. Similarity values are shown on the scale at the top of the phenogram. The dashed lines on the phenogram show the contour levels used on the contoured similarity map.

Data Analysis. As part of preliminary data analysis the average number of bands per population was calculated for peroxidases. Data were subjected to contour mapping following the methods of Adams (1970, 1974).

The raw data were also used to calculate isozyme frequencies in each population. These frequencies are the characters used in the following data analyses. The operational taxonomic units (OTU's) being evaluated are the *Juniperus ashei* populations.

Each character was analyzed to determine the importance of that character relative to the variation observed in the OTU's. Analysis of variance (ANOVA) was performed on each of the 41 band frequencies to detect by the use of the F ratio (variance among OTU's/variance within OTU's) which characters (band frequencies) exhibited statistically significant differences among the OTU's. One should note that ANOVA of qualitative characters may underestimate the F ratios, but these ratios were only used to obtain approximate weights.

A numerical taxonomic method was used to determine similarities among OTU's. The similarity measure utilized was a weighted, mean character difference (MCD) or Manhattan Metric (see Adams, 1972, for formulation).

The first analysis consisted of a combined evaluation of 31 characters (all three enzyme systems) using F-1 for the weight of each character comparison between populations. Similarity measures were also calculated for each enzyme system separately: all OTU's (15 populations) for 16 peroxidases; six OTU's for four esterases; and six OTU's for all α-terpineol (alcohol) dehydrogenases.

The single linkage cluster (SLC) method of Sneath (1957) was used for cluster analysis of the similarity matrices.

Variability within OTU's was evaluated from the raw data by using the coefficient of phenetic variation (CPV) of Gilmartin (1974) and mean similarities ($\bar{S}r$). These values were determined from the combined data set of all characters (41 isozymes; three enzyme systems) and all OTU's, as well as separately for each enzyme system (15 OTU's for 23 peroxidases, six OTU's for four esterases, six OTU's for 14 α-terpineol (alcohol) dehydrogenases).

The $\bar{S}r$'s and CPV's were contour mapped (Adams, 1970, 1974) to aid in the visualization of regional trends.

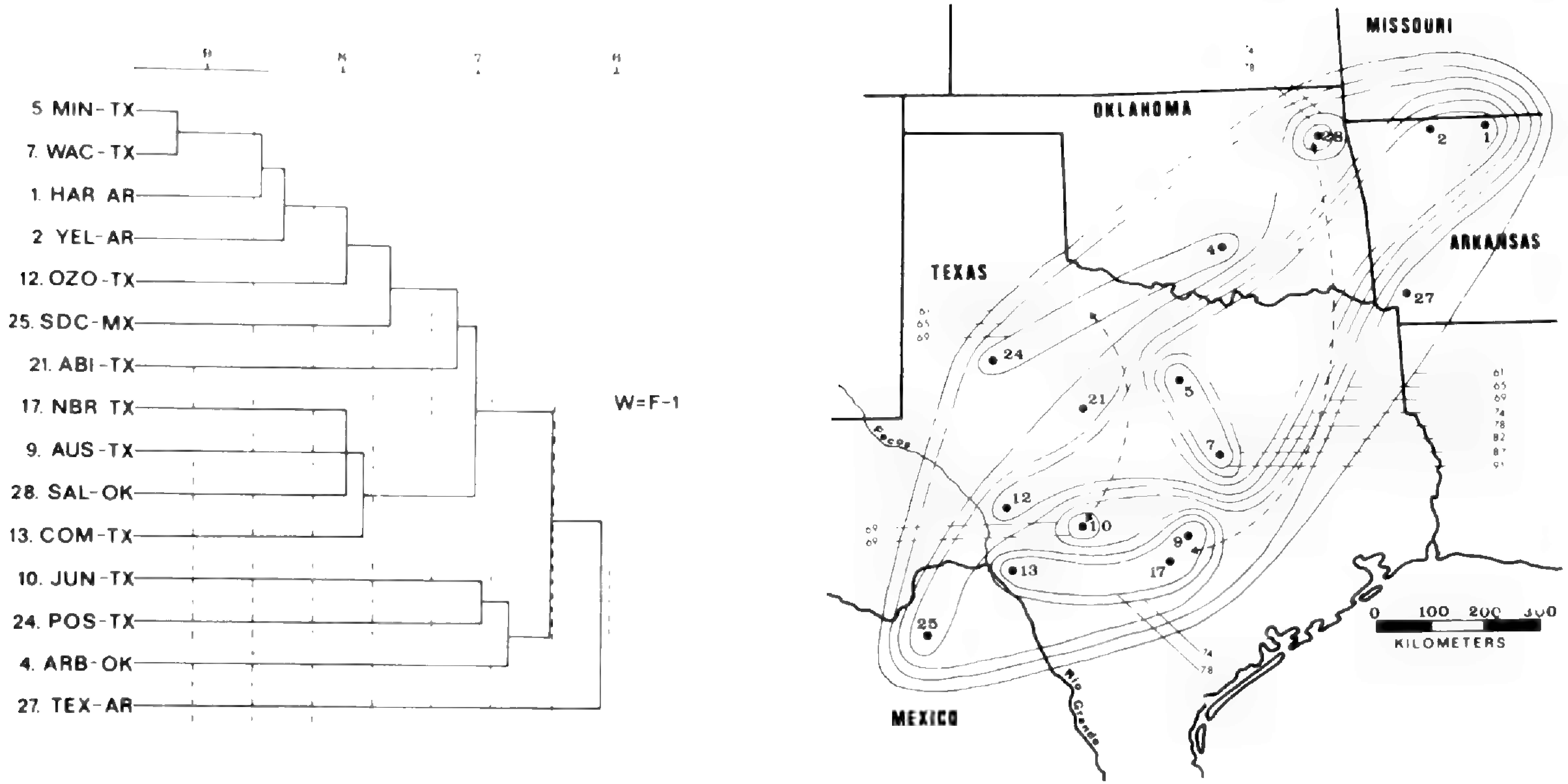


Figure 6. Phenogram and contoured similarity of 15 populations of *Juniperus ashei* based on 16 peroxidases, F-1 weighted. similarity values are shown on the scale at the top of the phenogram. The dashed lines on the phenogram show the contour levels used on the contoured similarity map.

RESULTS

Peroxidases were examined in 415 tree samples (15 populations) and esterases and α-terpineol (alcohol) dehydrogenases in 171 tree samples (six populations). An individual tree had from three to 12 peroxidase bands with an average of 7.4, four to nine α-terpineol (alcohol) dehydrogenases with an average of 5.5, one to four esterases with an average of 1.6. All *Juniperus ashei* trees examined were found to have peroxidase band 23 (P23) and α-terpineol (alcohol) dehydrogenase band 20 (T20); all other bands were variable in expression. Figure 3 shows the contour map for the average number of isoperoxidases per population. No regional trend was detected from the contour maps of the average number of peroxidases per population (Figure 3). The Hardy, Arkansas, population had the highest average number of peroxidases while the lowest average was at Texarkana, Arkansas. Further to the southwest an increase in the average number of peroxidases occurs in populations 5 (Mineral Wells, Tx.) and 7 (Waco, Tx.) on the northeast edge of the Edwards Plateau of Texas. In the central Edwards Plateau area (populations 17 to 24) there is another decrease in the average number of peroxidases. At the southwest extreme of the *J. ashei* distribution there is a slight increase in the average number of peroxidases (populations 12, 13, & 25). One might note that the Texarkana population (27), which has fewest bands, is rather small and isolated; whereas, the Junction population (10), with few bands, is large and centrally located in the *J. ashei* range.

It could be proposed that the large average number of isoperoxidases in the Hardy population (1) may be the result of hybridization between *Juniperus ashei* and *J. virginiana*, both of which occur in this area. Several lines of evidence cast doubt on this proposal. Adams (1975, 1977) and Adams and Turner (1970) could not find any evidence for hybridization between these two species using 59 terpenoids and 15 morphological characters in analyses. When sampling populations it was common to collect both species in mixed populations (populations 1, 2, 7, 9, 27, & 28). Electrophoresis was always performed on both the *J. ashei* and *J. virginiana* samples. These two species could be distinguished by their isoperoxidase zymograms and had only bands P10 and P17 in common. There is thus considerable evidence that hybridization between *J. ashei* and *J. virginiana* is not responsible for the higher number of peroxidases in some populations where their distributions overlapped.

When ANOVA was performed on 41 characters (band frequencies), 31 of the 41 characters had significant F ratios (P = .05). Three bands (P3, T17, T22) had infinite F ratios; these characters had no variance within OTU's. Band P3 was found exclusively in all trees of population 1, T17 exclusively in all trees of population 25, and T22 exclusively in all trees of population 27. Two characters (P23, T20) were found in all samples and therefore had no variation in frequency among OTU's. Five characters (P6, P9, P11, P12, P21) had F ratios less than 2.30 (F.05 = 1.77, df = 14/400, for continuous data). It should be noted that the significance of F is underestimated when using presence or absence data and therefore this statistical test is conservative under these circumstances.

The phenograms and contour maps derived from clustering of similarity values are shown in Figures 4 (four esterase), 5 (11 α-terpineol dehydrogenases), 6 (16 peroxidases), and 7 (all 31 isozymes combined).

Contour maps derived from clustering of similarities present variable results. Each enzyme system examined gave a unique trend. Esterases (Figure 4) cluster population 4 (Arbuckle Mts.) with population 10 (Junction) as being most similar. Populations 24 (Post), 27 (Texarkana), 25 (Sierra del Carmen Mountains, Mexico), and finally population 2 (Yellville, Arkansas) then tail into the cluster (Figure 4).

α-Terpineol (alcohol) dehydrogenases (Figure 5) show a different pattern than seen with the esterases. The α-terpineol dehydrogenases divide the populations studied into two major groupings: a northern group composed of populations 2 (Yellville, Arkansas) and 4 (Arbuckle Mts.) and a southern group composed of populations 24 (Post), 10 (Junction), and 25 (Sierra del Carmen Mts., Mexico) with population 27 (Texarkana) coming in last.

Similarities based on peroxidases show a cluster pattern different from that shown by the other two enzyme systems (Figure 6). A cluster of populations occurs along a line running from population 25 (Sierra del Carmen Mts., Mexico) in the southwest to population 1 (Hardy) in the northeast. Populations 12 (Ozona, Texas), 5 (Mineral Wells, Texas), and 7 (Waco, Texas) lie on this northeast-southwest line and cluster with populations 25 and 1. On either side of this line populations show disjunctions in similarity clustering. One group is composed of populations 13 (Comstock, Texas), 17 (New Braunfels, Texas) and 9 (Austin, Texas) — three populations in the southern portion of the Edwards Plateau along with population 28 (Salina, Oklahoma). A second disjunct clustering is composed of population 10 (Junction) and populations 24 (Post) and 4 (Arbuckle Mts.). The Texarkana population (27) is the last to cluster with the other *Juniperus ashei* populations based on similarity of peroxidases.

Clustering of populations using all isozymes studied (Figure 7) is almost identical to that seen for peroxidases. The only major difference between the contour maps of similarities based on all 31 isozymes and that based on the peroxidases is that population 4 (Arbuckle Mts.), for all isozymes, clustered in with those populations associated with the northeast-southwest cluster, rather than with the population 10 (Junction) population 24 (Post) disjunct cluster. As with the peroxidases, population 27 (Texarkana) clustered at the least similarity to the other *Juniperus ashei* populations.

Contour maps of mean similarity ($\bar{S}r$) and coefficient of phenetic variation (CPV) for esterases (Figure 8) and α-terpineol (alcohol) dehydrogenases (Figure 9) are almost identical. For esterases, the highest $\bar{S}r$ and lowest CPV were in populations 2 (Yellville, Arkansas), 10 (Junction), 24 (Post) and 25 (Sierra del Carmen Mts., Mexico) while Texarkana (27) showed the lowest Sr and highest CPV.

The peroxidases (Figure 10) have the lowest Sr and highest CPV in populations 10 (Junction), 24 (Post) and 14 (Arbuckle Mts.). High $\bar{S}r$ and low CPV were found in populations 7 (Waco, Texas), 9 (Austin, Texas) and 1 (Hardy, Arkansas). All other populations had intermediate $\bar{S}r$'s and CPV's based on peroxidases.

The combined data based on 41 isozymes (Figure 11) showed the lowest $\bar{S}r$ for populations 10 (Junction), 27 (Texarkana), and 4 (Arbuckle Mts.). The highest Sr was seen in population 1 (Hardy). Figure 11 also shows the lowest CPV was in populations 24 (Post), 25 (Sierra del Carmen Mts., Mexico), 7 (Waco, Texas), 1 (Hardy, Arkansas), and 2 (Yellville, Arkansas). High CPV's are seen in populations 24 (Abilene, Texas), 12 (Ozona, Texas), 13 (Comstock, Texas), and (Texarkana), indicating that these populations are not very homogeneous.

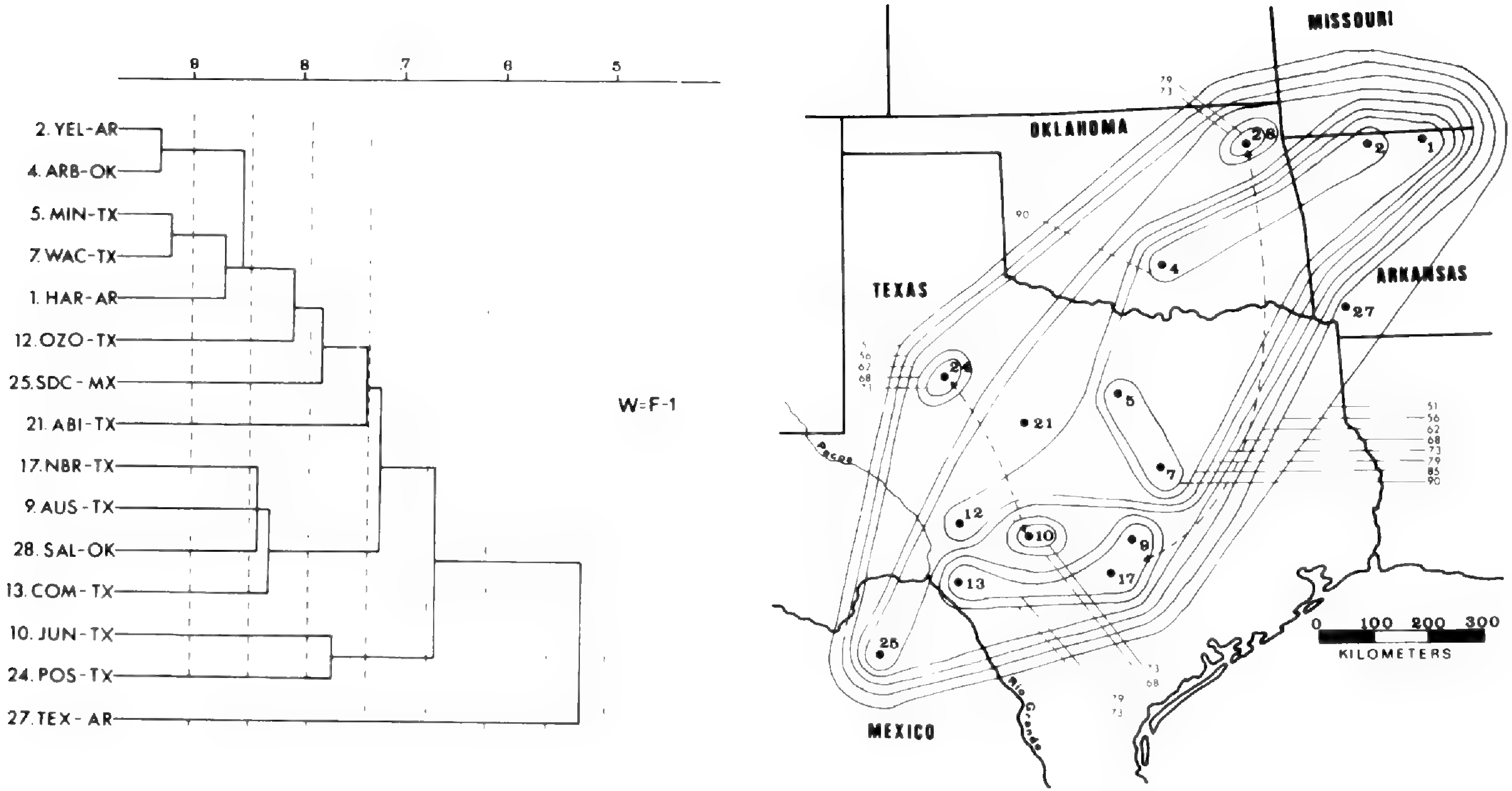
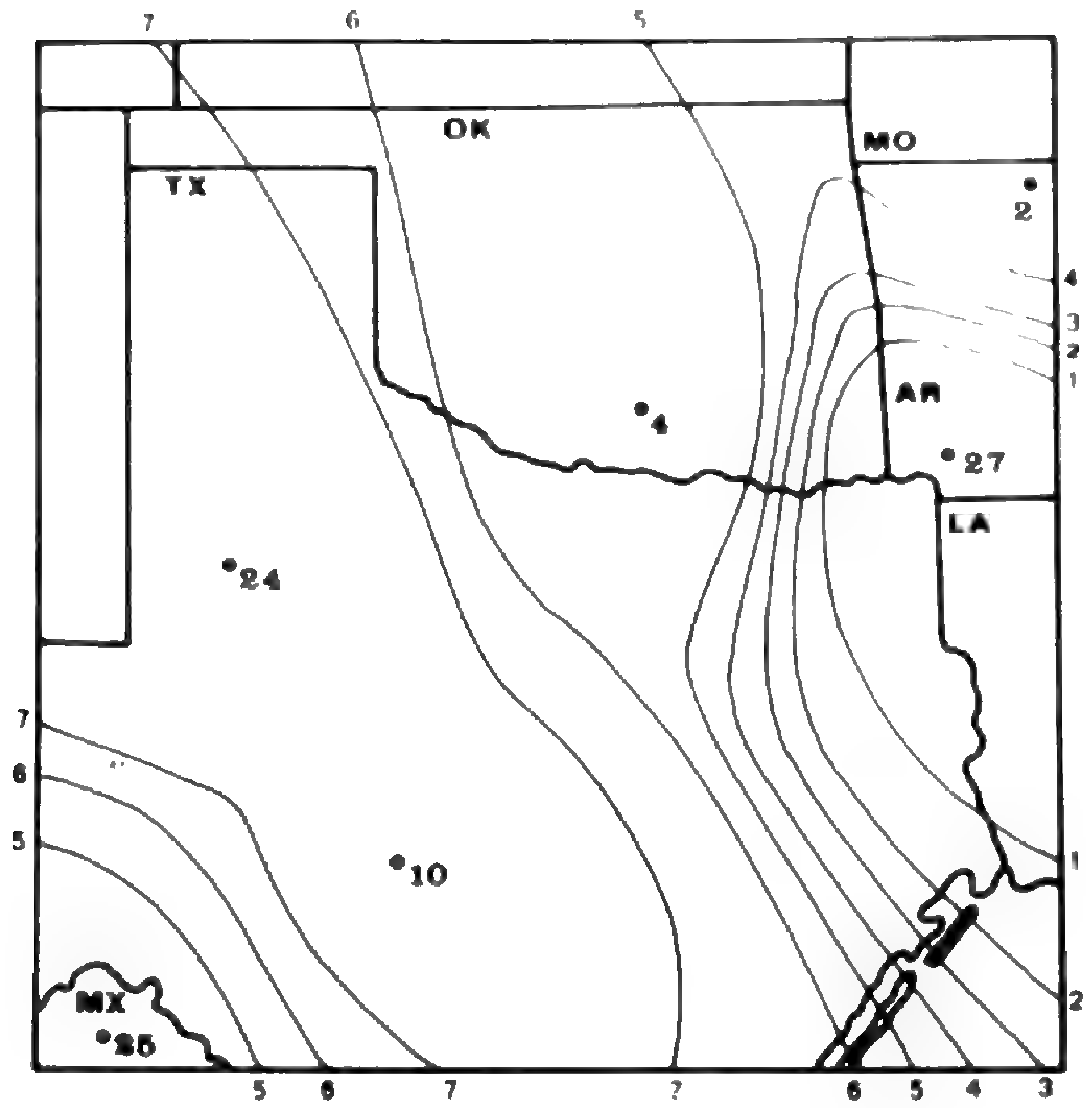
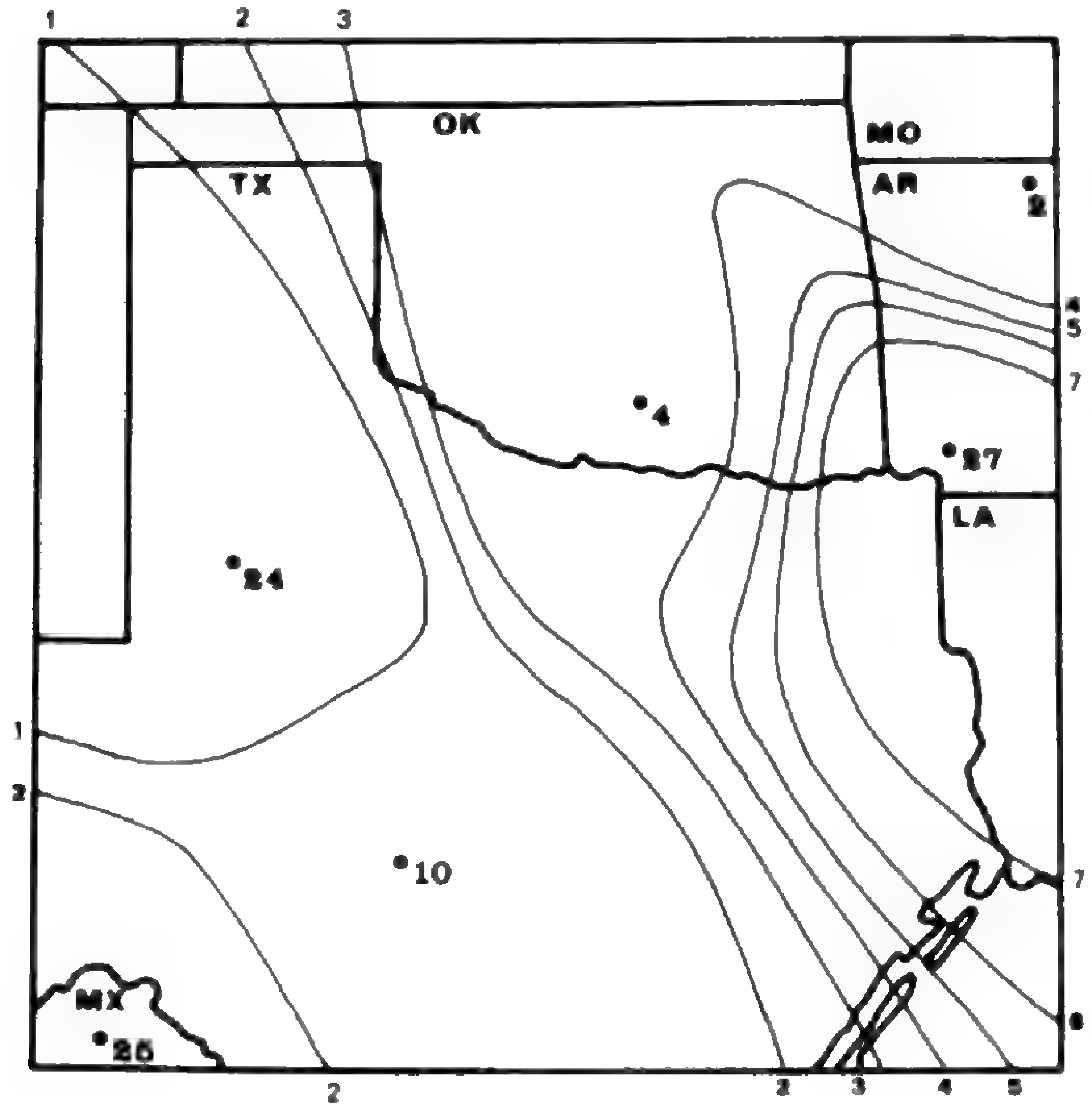


Figure 7. Phenogram and contoured similarity of 15 populations of *Juniperus ashei* based on 31 isozymes, F-1 weighted. Similarity values are shown on the scale at the top of the phenogram. The dashed lines on the phenogram show the contour levels used on the contoured similarity map.



$\bar{S}$r, Esterases



CPV, Esterases

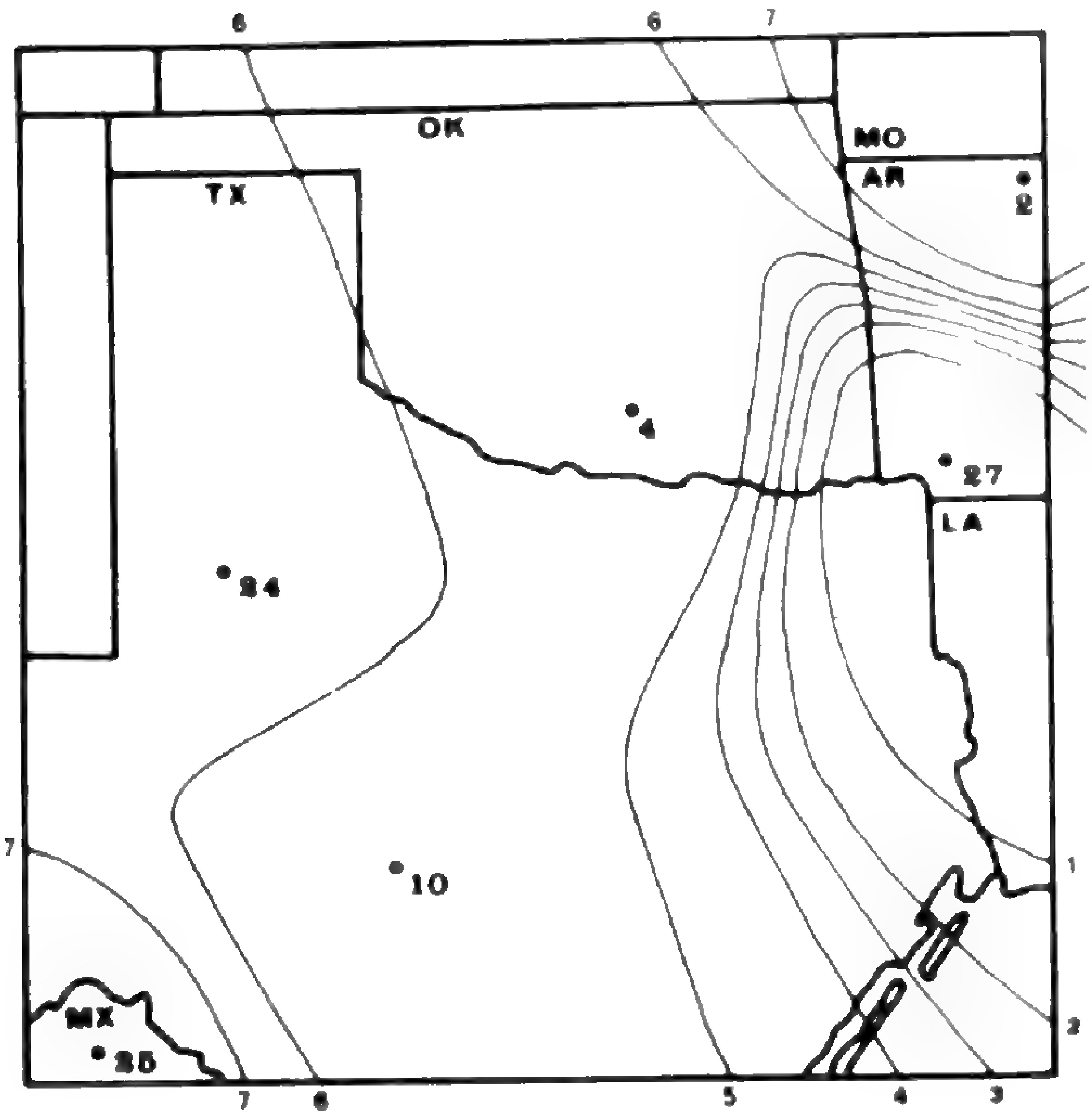
Figure 8. Mean similarity ($\bar{S}$r) and coefficient of phenetic variation (CPV) contour maps for 4 esterases. $\bar{S}$r, Esterases (Contours: 1 = 0.15; 7 = 0.64). CPV, Esterases (Contours: 1 = 40.4; 7 = 92.7).

CONCLUSION

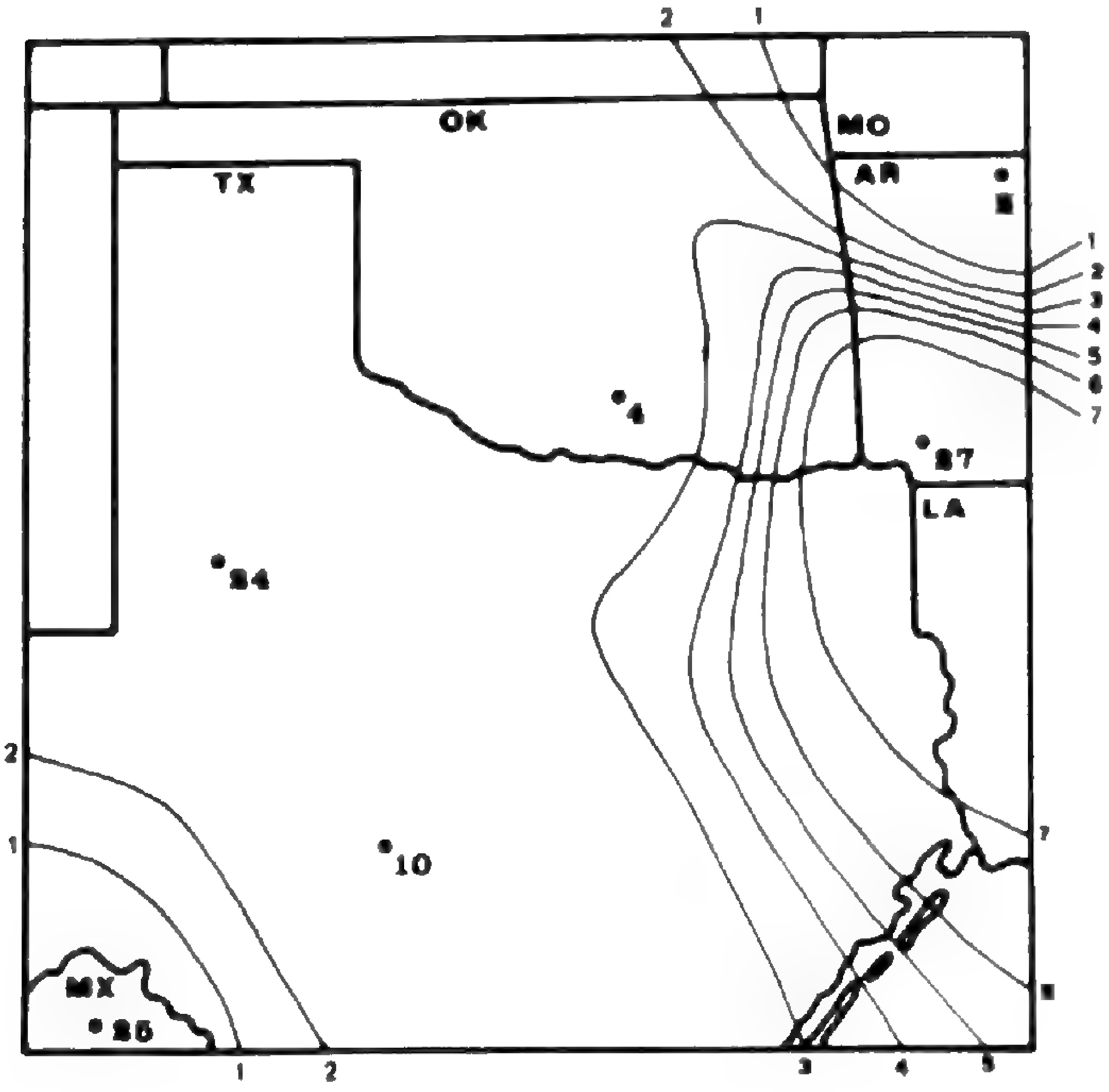
Isozyme analysis in *Juniperus ashei* gives discordant results. Contour mapping of similarity values (Figures 4–7) reflects different trends for each enzyme system studied. The map of similarity values based on all enzyme systems investigated, as well as each enzyme system separately, (Figure 7) is difficult to interpret biologically. The greatest difficulty in understanding lies with the disjunct (mosaic) clustering pattern of populations on the Edwards Plateau of Texas with isolated populations in Texas and Oklahoma. There are several possible explanations for these disjunct clusterings. If selection is acting to control the isozyme patterns seen in each population then parallel (convergent) selection at the microhabitat level may be responsible for these disjunct population clusters. This idea would be compatible with results found in *Avena barbata* (Allard *et al.*, 1972a). Selection was shown to occur at the microhabitat level within distances of several feet but only one or two loci were involved.

It is also possible to explain these mosaic clusterings of populations if many of the isozymes bands are not under selection, but represent random events, responsible for the disjunct similarity of populations. Several investigators have taken this neutralist approach in explaining results similar to those found in *Juniperus ashei*. Differences found in *Cryptomeria japonica* and *Thujopsis dolabrata* could best be explained by random drift followed by geographic isolation since no apparent habitat differences could be detected (Sakai *et al.*, 1971; Sakai & Park, 1971).

These disjunct clusterings of populations of *Juniperus ashei* may have occurred as a result of a lack of homology between isozyme bands having the same relative migration (Rm) values. Although polyacrylamide gel electrophoresis is one of the best methods for separation of isozymes, it is a crude technique at the molecular level. It is highly probable that different amino acid substitutions could result in isozymes with identical overall charges and that these proteins would be of similar size. Thus, two polypeptides with different amino acid composition, and perhaps different biological functions, would migrate to the same location in a gel. An isozyme investigator would then consider these biologically different molecules as homologous since they had the same Rm values. This problem of lack of homology is inherent in electrophoretic studies where



$\overline{\text{Sr}}$. Terpineol DH



CPV. Terpineol DH

Figure 9. Mean similarity (Sr) and coefficient of phenetic variation (CPV) contour maps for 14 α-terpineol dehydrogenases. Sr, α-terpineol dehydrogenases (Contours: 1 = 0.79; 7 = 0.98). CPV, α-terpineol dehydrogenases (Contours: 1 = 2.34; 7 = 30.55).

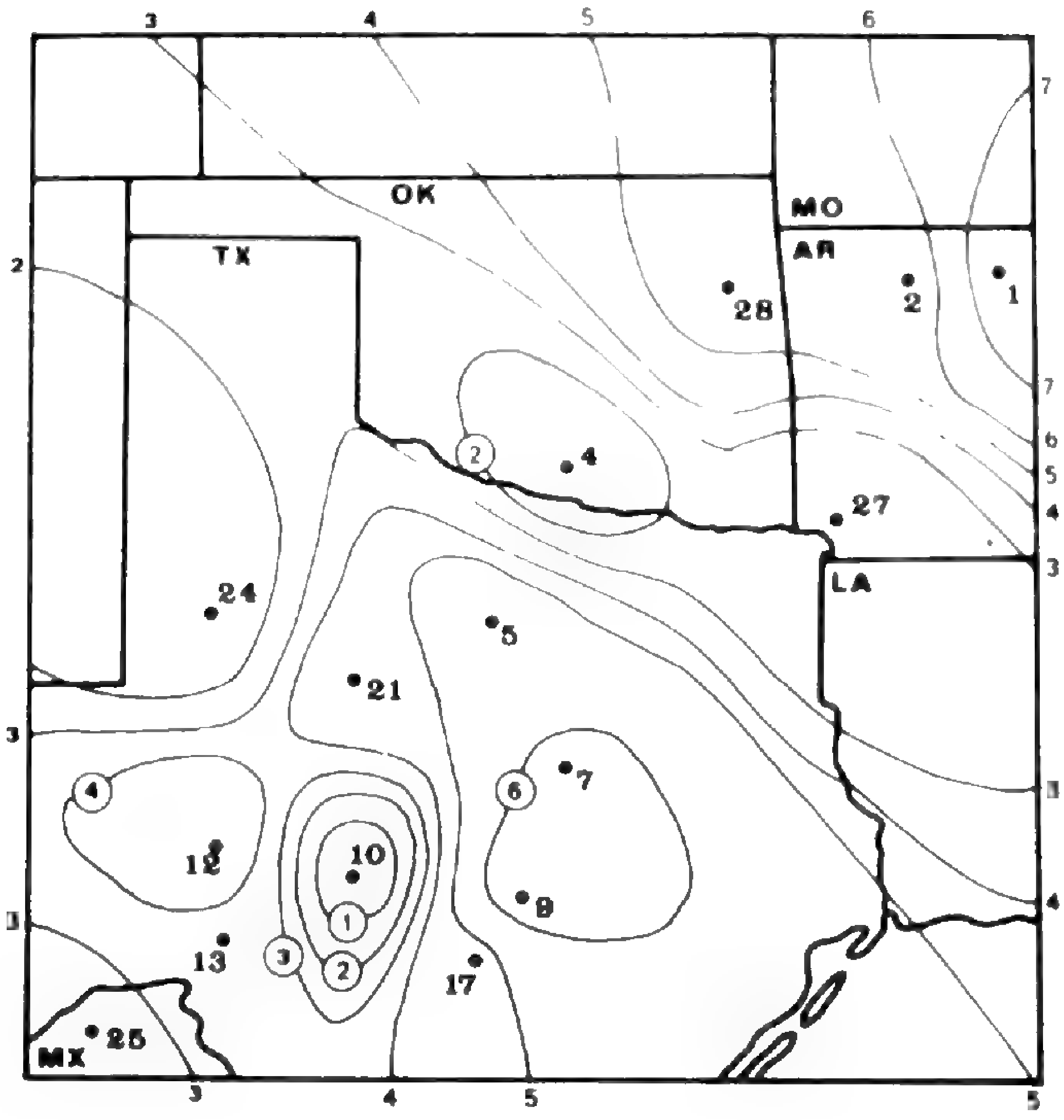
band frequencies are used as the raw data for studies of genetic diversity. In isozyme investigations there is no way, short of amino acid sequencing, to know when this lack of homology is astigmatizing results, although genetic studies will help resolve some of these homologies.

Unfortunately, it appears that genetic analyses would be necessary in many populations of this taxon to resolve this problem.

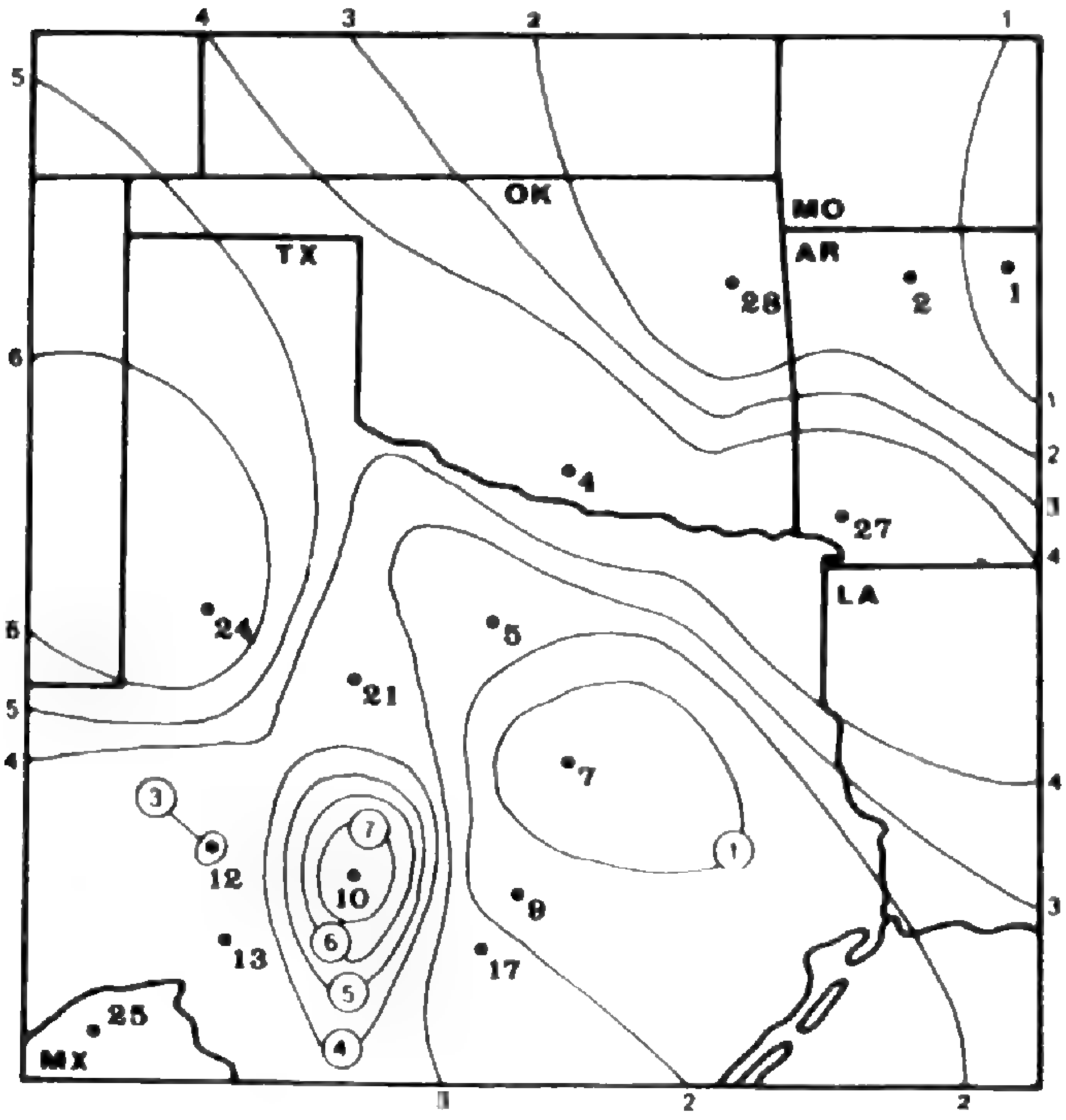
It is not possible at this time to determine which of the above hypotheses best explains these unusual disjunct clusterings of populations. Perhaps no single factor but a combination of all three, to varying degrees, is responsible for the distributional patterns seen in *Juniperus ashei.* Microhabitat selection, random drift followed by geographical isolation, and lack of isozyme band homology may have combined to produce these disjunct clusterings.

These results based on contour maps of similarity in isozymes do not correspond with the patterns seen by Adams and Turner (1970) and Adams (1975, 1977), in investigations of the same populations using morphological and terpenoid data. Using terpenoid data, Adams (1975, 1977) found two major groupings (Figure 12) of *Juniperus ashei* populations; a southwestern group (populations 17, 12, 13, 25, & 26), and a northern cluster (all other populations). This lack of correspondence is comparable to other studies where isozyme, morphological and other data were compared. Gottlieb (1974b) could not divide populations of *Stephanomeria exigua* spp. *carotifera* into coastal and inland ecotypes using isozyme data as was done using morphological characteristics (Gottlieb, 1971b). Muhs (1974) could not find any trends in isozymes which correlated to coastal-interior populations of *Pseudotsuga menziesii* distinguished morphologically (Tusko, 1963).

There did not seem to be any correspondence between population size or distribution and the amount of isozyme variability detected for individual enzyme systems or combined isozyme data. Examination of small isolated populations revealed (Figure 11) a high degree of variability in population 27 (Texarkana, Arkansas) yet very little variability was found in population 24 (Post, Texas). Populations on the Edwards Plateau of Texas are in some cases highly variable (population 21, Abilene, Texas) and in others are very homogeneous (population 7, Waco, Texas). Thus, neither population size nor central versus peripheral location was correlated with the amount of variability seen in these isozymes. Similar



$\overline{Sr}$, Peroxidases



CPV, Peroxidase

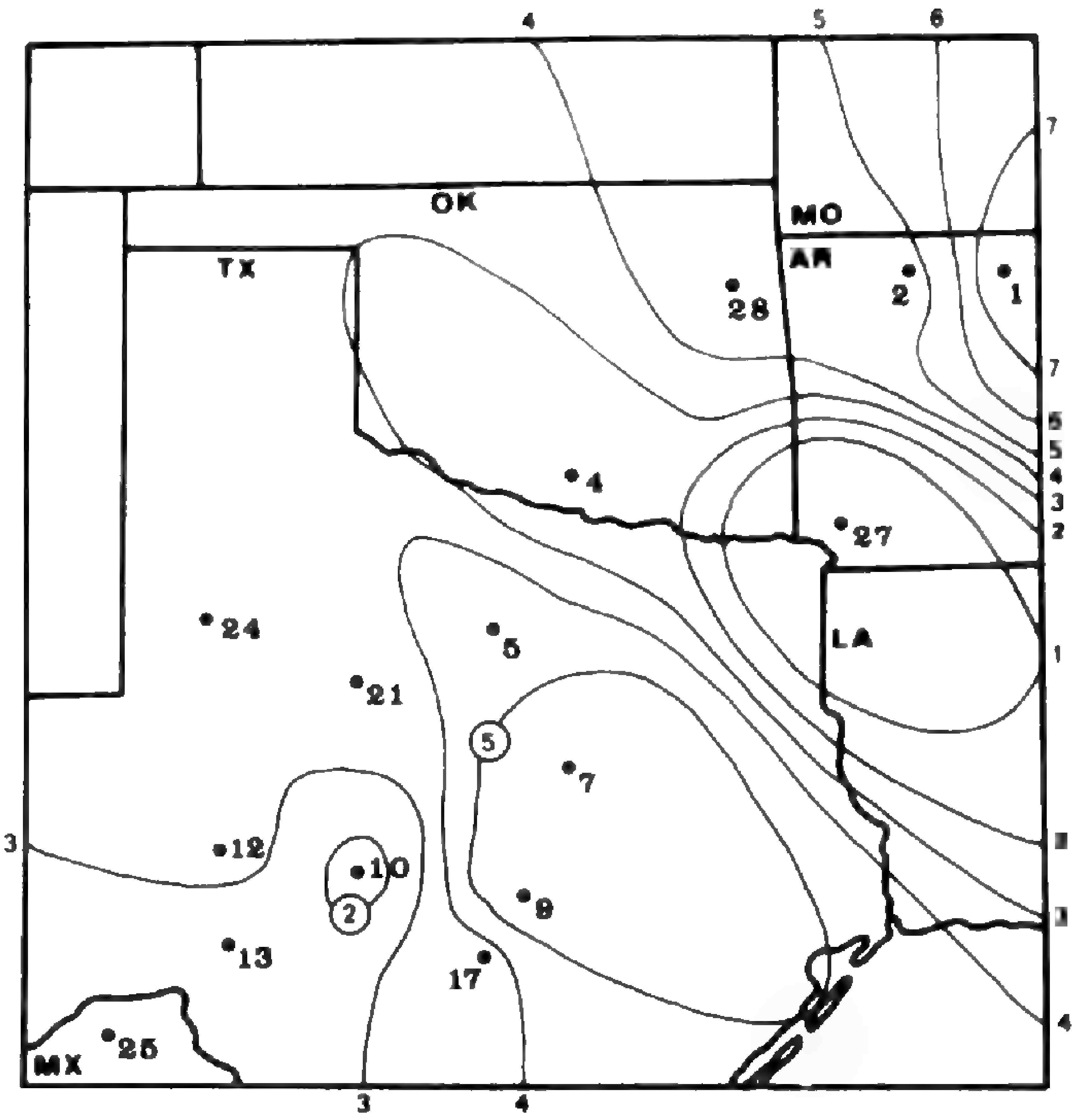
Figure 10. Mean similarity (Sr) and coefficient of phenetic variation (CPV) contour maps for 23 peroxidases. Sr, peroxidases (Contours: 1 = 0.54; 7 = 0.86). CPV, peroxidases (Contours: 1 = 13.45; 7 = 31.50).

results have been reported by Gottlieb (1974b) in *Stephanomeria exigua* spp. *carotifera.* It should also be noted that populations at the northern (1 & 2, Ozark Mts., Arkansas) and southern (25, Mexico) extremes of *Juniperus ashei* distribution are fairly homogeneous (see Figure 11) in most analyses.

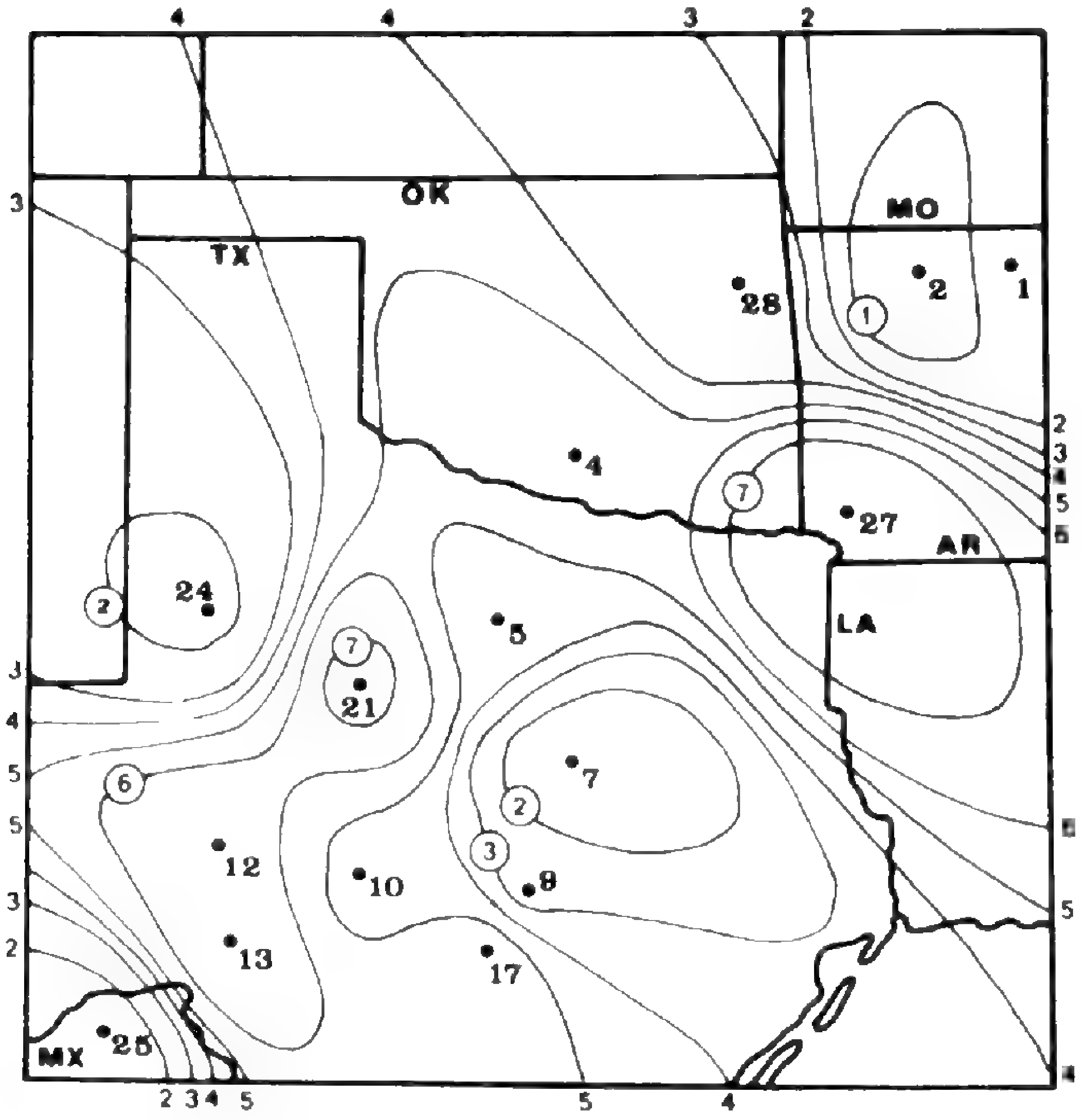
The lack of continuity in the pattern of genetic diversity over short distances can also be seen (Figure 10) for peroxidases. Population 12 (Ozona, Texas) and population 10 (Junction, Texas) occur approximately 160 kilometers apart in the southwestern part of the Edwards Plateau in similar habitats. Population 10 is highly variable and population 12 is intermediate in variability for peroxidases. Approximately 320 kilometers northeast of population 10, the Waco, Texas, population (7) is very homogeneous for peroxidases.

These inconsistencies in *Juniperus ashei* with respect to the amount of variability associated with population size or location and the disjunct clusterings based on similarities raise questions about our concept of breeding population size, gene flow, and natural selection. If selection is the major force responsible for the isozyme patterns seen in *J. ashei,* then the population size upon which selection has acted must be relatively small, while the terpenoids and morphology seem to be under very broad regional selection with ancestral gene pools (see Adams, 1977). Very localized selection is supported by the results obtained in *Avena barbata* (Allard *et al.,* 1972a) where significantly different isozyme patterns were detected within several feet periodically over a geographically continuous distribution of this species. Selection was acting at the microhabitat level producing isozyme patterns which could be correlated with mesic or xeric habitats.

Two factors are important in the size of breeding populations of *Juniperus ashei.* These factors are pollen and seed dispersal distances (Stebbins, 1950). Which factor is of greater importance is not known, but some idea can be obtained from related information. Studies of several wind pollinated species have shown that 95% of the dispersed pollen fell within 60 feet for Douglas fir; 55 feet for pinyon; 1000 feet for elm; and 130 feet for spruce (Faegri & Van der Pijl, 1971; Percival, 1965; Wright, 1953). However, it is estimated that in a related species, most of the seed is dispersed by birds within 17 feet of its source (Phillips, 1910). Birds are of primary importance in the distribution of juniper seeds (Livingston,



$\bar{S}$r, 41 Isozymes



CPV, 41 Isozymes

Figure 11. Mean similarity ($\bar{S}$r) and coefficient of phenetic variation (CPV) contour maps for 41 isozymes. $\bar{S}$r, 41 isozymes (Contours: 1 = 0.64; 7 = 0.87). CPV, 41 isozymes (Contours: 1 = 11.50; 7 = 20.20).

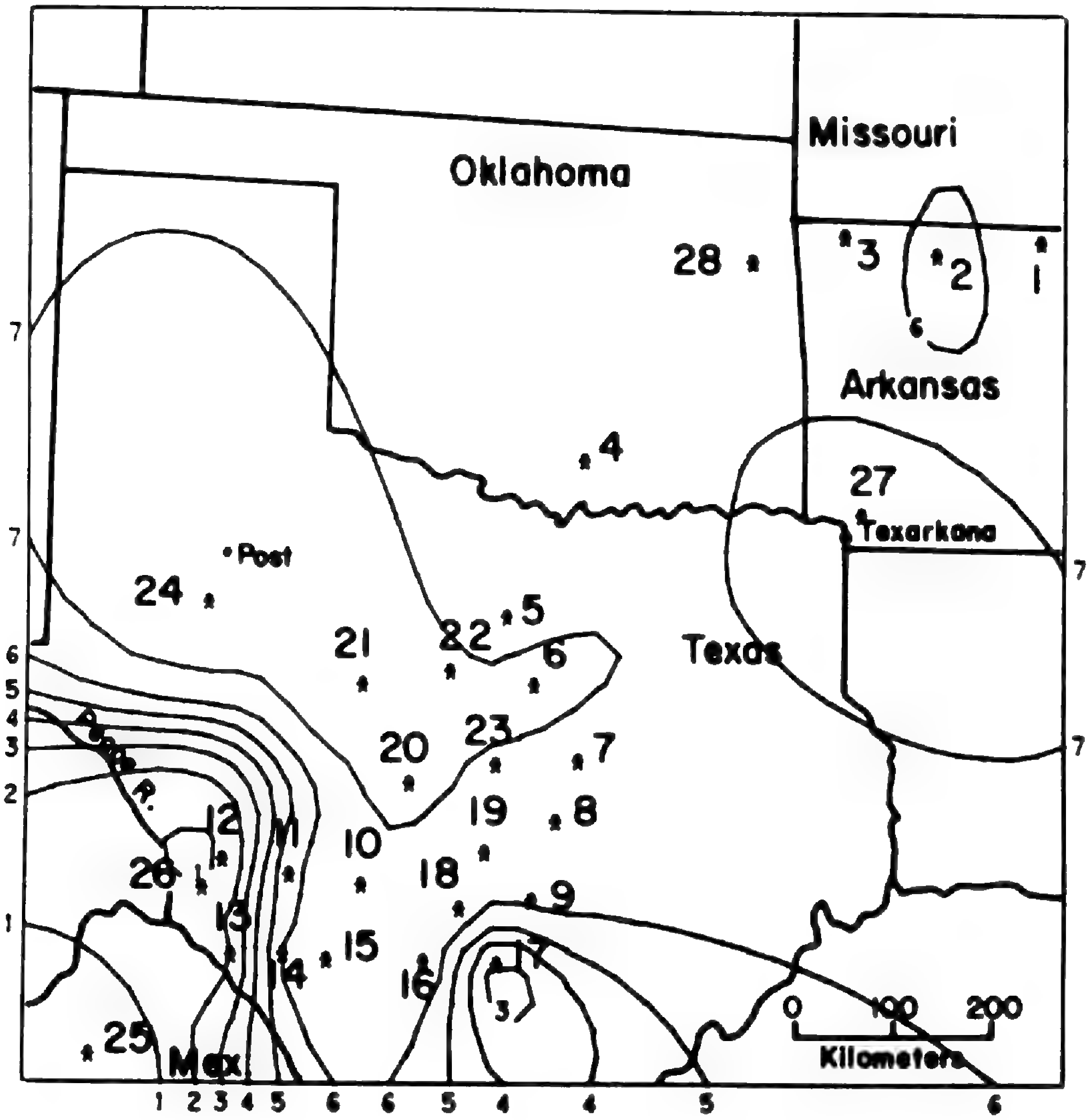


Figure 12. Contoured principal coordinate 1 of similarity measures based on 59 terpenoid characters, F-1 weighted. From Adams (1977). This same pattern was also found in 15 morphological characters, analyzed in like manner.

1972; Phillips, 1910) and arguments could be made that the disjunct similarity clusters of populations seen in Figure 7 could be explained by bird dispersal of seed. Thus, it seems highly improbable to have such large disjunct similarities, especially the southern Texas-northeast Oklahoma disjunction, with no populations showing similar isozyme patterns in between these two locations. This low probablity is also supported by the report that Bohemian waxwings (*Ampelis garrulus*) have been shown to pass more than 900 berries of *J. scopulorum* in four hours (Phillips, 1910). This fact implies that long distance dispersal would be less likely. Definite answers to questions concerning pollen and seed dispersal in *J. ashei* cannot be given here, but these estimates from other juniper species probably approximate the conditions found in this species.

The results of this isozyme investigation of *Juniperus ashei* raise as many, if not more, questions than they answer. This situation is in keeping with results of many current isozyme investigations. Since isozyme investigations in higher plants are relatively new in systematic botany it is not surprising there are many questions at the completion of preliminary studies.

Until the genetic basis of these isozymes in *Juniperus ashei* has been examined, we can only conclude that the use of isozyme banding as a taxonomic character is not feasible and certainly does not agree with the considerable mass of information supplied by the morphological and terpenoid characters previously studied in this taxon.

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REVISION OF PECTIS SECTION PECTIDIUM (COMPOSITAE: TAGETEAE)

DAVID J. KEIL

Pectis L. sect. *Pectidium* (Less.) A. Gray is a small but very wide-ranging group of taxa. The geographic range of this section includes both insular distribution patterns and broad disjunctions. In an effort to clarify the systematic relationships and to provide a possible explanation for the interesting distribution patterns, I undertook an investigation of this section.

TAXONOMIC HISTORY

Pectis linifolia L. was the first representative of *Pectis* to be recognized. Sloane (1707) described and illustrated this species from West Indian material as "Hieracium fruticosum angustissimis gramineis foliis capitulis parvis." Linnaeus (1759) published alternate names for Sloane's plant under both *Pectis* and *Verbesina.*

The history of sect. *Pectidium* is closely intertwined with a long-standing misapplication of the name *Pectis linifolia.* Only a year after Linnaeus described *P. linifolia,* Jacquin (1760) published *Pectis punctata.* Although *P. punctata* is now known to be taxonomically synonymous with *P. linifolia,* this situation was not recognized by early botanists. The name *Pectis punctata* soon gained wide acceptance while *P. linifolia* slipped into obscurity and disuse. In 1831 Lessing described the genus *Pectidium,* based upon *P. punctata.* In the same publication, he misapplied *Pectis linifolia* to a plant now correctly known as *P. leptocephala* (Cass.) Urban. Lessing's misapplication of *P. linifolia* was widely followed, and most 19th century literature mentioning *P. linifolia* actually pertains to *P. leptocephala.*

Gray (1852) reduced *Pectidium* from generic to sectional status. In 1853, Gray described *Pectis imberbis,* and in 1883 he included this species, *P. punctata,* and two species previously assigned to sect. *Heteropectis, P. multiseta* Benth. and *P. coulteri* Harv. & Gray, in a broadened concept of sect. *Pectidium.* Fernald (1897) removed *P. coulteri* and *P. multiseta* from sect. *Pectidium* and raised the section to subgeneric status. Fernald also finally corrected the misapplication of *P. linifolia* and properly relegated *P.*

punctata to synonymy. The present circumscription of sect. *Pectidium* is based upon Fernald's treatment, but the sectional rather than subgeneric rank is used.

SECTIONAL RELATIONSHIPS

The species of sect. *Pectidium* are morphologically distinctive. In most sections of *Pectis*, plants are relatively low-growing and stems are very leafy. In sect. *Pectidium* the plants are usually tall and erect with elongated internodes. Section *Pectidium* does not appear to be closely related to any other section of the genus. The only taxa for which a possible relationship has been suggested probably represent evolutionary convergences in a few characteristics. Gray (1883) suggested a close relationship between the taxa of sects. *Pectidium* and *Heteropectis*. Keil (1975b) indicated that the relationship between these sections is probably remote. Wiggins (1950) proposed a close relationship between *P. linifolia* and his newly-described *P. vollmeri*. On the basis of overall morphology, Keil (1973) placed *P. vollmeri* in sect. *Pectothrix* A. Gray. In the cases of both sect. *Heteropectis* and *P. vollmeri*, undue emphasis has been placed upon similarities in the structure of the pappus, and important dissimilarities in other features have received less attention or have been ignored. At the present time, there do not seem to be any close relatives for sect. *Pectidium*.

CHROMOSOME STUDIES

Prior to this study, a chromosome count of $n = 12$ for *Pectis linifolia* var. *linifolia* was the only published report for a taxon of sect. *Pectidium* (Pinkava & Keil, 1977). This and counts of $n = 12$, from meiotic microsporocytes, reported here for *P. imberbis* (Table 1, Figure 2e), are consistent with the previously established base number for the genus, $x = 12$ (Johnston & Turner, 1962; Keil, 1977). The regular formation of a quadrivalent in meiosis in one plant (*Pinkava & Keil K11006D*) indicates the presence of a heterozygous translocation, a condition not previously reported for any other *Pectis* species.

BIOGEOGRAPHY AND EVOLUTIONARY RELATIONSHIPS

The range of sect. *Pectidium* extends into a variety of different geographical areas (Figure 1), and includes many different vegetational zones. This broad distribution is due almost entirely to the widespread occurrence of a single taxon, *Pectis linifolia* var. *linifolia*. The two remaining taxa occupy only limited ranges. Any explanation that accounts for the broad range of the section must, therefore, concentrate upon the distribution and establishment of *P. linifolia* var. *linifolia*.

Dispersal mechanisms and reproductive biology of *Pectis linifolia* var. *linifolia* are of major importance in its broad distribution. In the establishment of the present range of this taxon, numerous crossings of significant water barriers have occurred. Throughout the West Indies and in the Galapagos Islands, *P. linifolia* var. *linifolia* has become established on many islands. Additionally, its mainland distribution involves disjunctions of thousands of kilometers. The success of this taxon in crossing numerous barriers is indicative of a specialized dispersal mechanism and of reproductive adaptations favoring the establishment of founder populations.

Pectis linifolia var. *linifolia* has adaptations that appear to favor animal dispersal, with birds being the most likely carriers. The achenes of these plants characteristically bear stout, divaricately spreading awns that project from the fruiting heads (Figure 2a). The achenes readily cling to fabrics and presumably equally well to feathers. The plants commonly grow in open rocky coastal sites which in insular situations are favored by sea birds.

Plants of *Pectis linifolia* var. *linifolia* are apparently autogamous. Morphological evidence for autogamy includes the marked reduction in ligule size (only 1 mm. long), the low number of disc florets per head (1–3), and small anthers (less than 1 mm. long) with low pollen production. Other species of *Pectis* with reduced, inconspicuous heads and low pollen production (e.g., *P. cylindrica* (Fern.) Rydb., *P. prostrata* Cav.) are known to be self-fertile (Keil, 1975a). The establishment of the autogamous condition is of primary importance in a colonizing species (Baker, 1955). Such a condition is also a common adaptation to dry habitats (Davis & Heywood, 1965) or coastal situations (Eisikowitch, 1973).

Inland populations among members of sect. *Pectidium* are best developed in North America. The progenitor for sect. *Pectidium* probably developed in the Mexican highlands, a center of diversity for *Pectis* and various other genera of the Tageteae. This original

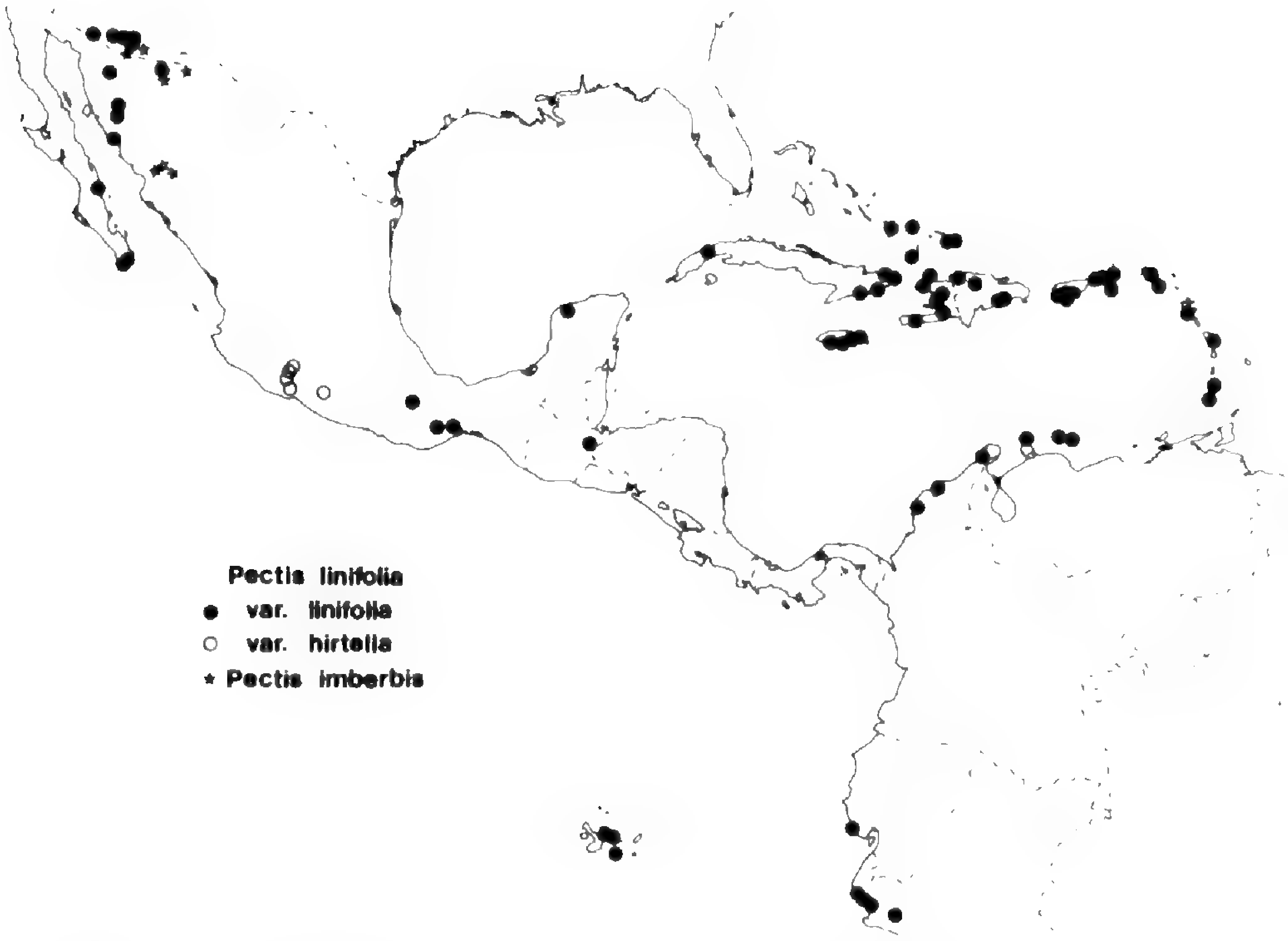

Figure 1. **Geographical distribution of the taxa of Pectis sect. Pectidium.**

Pectidium was probably a perennial and may have been similar to *P. imberbis*. *Pectis linifolia,* an annual, is probably a derived taxon that became adapted to dry lowland conditions and subsequently spread to similar habitats in other areas. With the only significant inland populations restricted to North America, the remaining range is probably attributable to the high dispersibility of achenes of *P. linifolia* var. *linifolia*.

TAXONOMY

Pectis L. sect. **Pectidium** (Less.) A. Gray, Smithsonian Contr. Knowl. 3(5): 83. 1852.

Pectidium Less. Linnaea **6:** 706. 1831. *Pectis* L. subg. *Pectidium* (Less.) A. Gray ex Fern. Proc. Am. Acad. **33:** 85. 1897. TYPE SPECIES: *Pectis punctata* Jacq.

Tetracanthus A. Rich. in Sagra, Hist. Fis. Polit. Nat. Cuba **11:** 60. 1850. TYPE SPECIES: *T. linearifolius* A. Rich.

Annual or perennial, non-aromatic herbs. Stems erect or ascending, 1–12 dm. tall, with internodes usually equalling or longer than the adjacent leaves, usually simple below, much-branched above. Leaves linear to linear-elliptic, punctate on the undersurface with circular glands. Heads solitary or in diffuse cymose clusters, slender-peduncled. Involucre cylindric; bracts 5, linear, very convex, indurate nearly to the apex, strongly glandular-punctate. Ray florets 5; ligules often glandular-punctate. Disc florets 1–7; corollas regular, 5-lobed, some or all of the teeth glandular-punctate just below the apex. Achenes cylindric, puberulent. Pappus of 1–4 stout, spreading, smooth or minutely antrorsely barbed awns, or sometimes reduced to a crown, or absent in some of the achenes. Chromosome base number: $x = 12$.

KEY TO THE TAXA OF PECTIS SECT. PECTIDIUM

1. Annual herbs from a slender to stout taproot; ray corollas 2–4 mm. long. .. 2.
    2. Disc florets 1–3, usually forming achenes; pappus of both ray and disc florets of 1–4 awns; leaves with a single pair of basal setae 1–2 mm. long or lacking setae. . . . . 1a. *P. linifolia* var. *linifolia.*
    2. Disc florets 5–6, usually sterile with shrunken ovaries; pappus of ray florets biaristate, pappus of disc florets coroniform; leaves with 1–3 pairs of basal setae 3–7 mm. long. . . . . 1b. *P. linifolia* var. *hirtella.*
1. Perennial herbs from a slender to stout woody caudex; ray corollas 6–11 mm. long. . . . . 2. *P. imberbis.*

1. **Pectis linifolia** L., Syst. Nat. ed. 10. 1221. 1759.
TYPE: without data (LINN, holotype; IDC microfiche 177: 601: III:4!).

Verbesina linifolia L., Syst. Nat. ed. 10. 1226. 1759, nom superfl.

Pectis punctata Jacq., Enum. Syst. Pl. 28. 1760. LECTOTYPE: Select. Stirp. Am. Hist. *t. 128.* 1763.[1]

Pectidium punctatum (Jacq.) Less., Linnaea **6:** 706. 1831.

Tetracanthus linearifolius A. Rich. in Sagra, Hist. Fis. Polit. Nat. Cuba **11:** 60. 1850. TYPE: **Cuba,** juxta Santiago de Cuba, *Linden 1714* (P, holotype!).

Pectis linifolia L. var. *marginalis* Fern., Proc. Am. Acad. **33:** 85. 1897. SYNTYPES: **United States.** ARIZONA: "Southern Arizona," *Palmer 129* (GH, syntype!; MO, isosyntype!); Tuscan (Tucson?), *Smart 382* (GH!); Santa Catalina, *Lemmon 3031* (GH, snytype!; UC, isosyntype!); Malpais Mts., 31 Aug. 1881, *Pringle s.n.* (GH, syntype!; MICH, MO, US, isosyntypes!). **Mexico.** SONORA: Guaymas, *Palmer 224* (GH, 2 syntypes!; UC, US, isosyntypes!). LECTOTYPE (here designated): *Pringle s.n.* (GH).

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[1] Authentic type specimens have not been located. Stafleu (1967) indicated that few of Jacquin's West Indian material are known to exist, and that Jacquin's 1760 publication represents a prodromus for his larger illustrated work. The illustration of *Pectis punctata* from the latter publication is selected here as the lectotype.

Erect or ascending annual herbs 1–10 dm. tall. Stems solitary or few, pseudodichotomously branched above, sharply 6-angled (at least above), purplish or stramineous. Principal leaves linear to linear-elliptic, 1–6 cm. long, 1–8 mm. wide, apically acute, often revolute-margined, punctate on the undersurface with marginal or scattered glands. Peduncles filiform, 1–3 cm. long, bearing 1–5 scale-like bractlets ca. 1 mm. long. Heads solitary in the axils or forks of the stem, or in diffuse cymose clusters at the ends of the branchlets. Involucre green or more commonly dark purplish-brown; bracts 4.5–7 mm. long, ca. 0.5 mm. wide, apically obtuse or acutish, hyaline-margined, punctate submarginally with one or more rows of linear-elongate to elliptic glands and subapically with one to several elliptic glands. Ray corollas yellow, commonly drying white to purple, 2–4 mm. long, often punctate on the ligule with 1 or 2 small glands, glabrous. Disc florets 1–6; corollas yellow, often drying white to purplish, 2–4 mm. long, 4 or all 5 of the lobes punctate with a solitary round gland, sometimes with a few additional glands on the throat; anthers 0.8 mm. long with tiny emarginate appendages. Achenes of ray and disc similar or disc achenes abortive, 3.5–5.0 mm. long, black or dark brown, strigillose or hirtellous with acute-tipped double hairs. Pappus of 1–4 awns 2–3 mm. long, or sometimes reduced to a low crown.

The range of *Pectis linifolia* (Figure 1) includes several major disjunctions. Populations are found in the Sonoran Desert region of the southwestern United States and adjacent Mexico, southern Mexico, the Caribbean region, the west coast of Ecuador and Peru, and the Galapagos Islands. Flowering time varies greatly depending upon the local seasonal patterns. In drier climates the species is mostly a summer- or fall-flowering ephemeral. In moister regions, the plants apparently flower through much of the year. *Pectis linifolia* is divisible into two varieties.

1a. **Pectis linifolia** L. Syst. Nat. ed. 10. 1221. 1759. var. **linifolia.** Stem glabrous or minutely roughened on the angles. Leaves 2–6 cm. long, 1.0–4.5 mm. wide, with a single pair of basal setae 1–2 mm. long or setae absent on some or all of the leaves, minutely roughened on the margin and midrib beneath, otherwise glabrous. Involucre green to purplish-brown, 4.5–7.5 mm. long, with bracts minutely ciliolate at the apex, otherwise glabrous. Ray florets with the tube 1–2 mm. long, with the ligules ca. 1 mm. long and about as wide. Disc florets 1–3, fertile, with corollas 2–3.5 mm. long, with the ovary turgid. Achenes 3.5–5.0 mm. long. Ray and disc pappus similar, 1–4 aristate, rarely reduced to a crown or absent, the awns 2–3 mm. long, often divaricately spreading in age. Chromosome number: $n = 12$. Figure 2a, b.

Throughout most of its broad range (Figure 1), *Pectis linifolia* var. *linifolia* grows below 200 m., but in southern Arizona and adjacent areas of Sonora, some populations occur at elevations up to 800 m.

Although *Pectis linifolia* var. *linifolia* occurs in many different vegetation zones, it does not appear to be divisible into recognizable subunits. Undoubtedly there are physiological differences among the populations adapted to different areas, but no recognizable morphological features have been found in var. *linifolia* which vary consistently on a geographical basis. Fernald (1897) described var. *marginalis* for the Sonoran Desert populations on the basis of a marginal rather than a scattered position of the foliar oil glands. Additional collections that were unavailable to Fernald, however, do not show this feature consistently.

REPRESENTATIVE SPECIMENS: **Bahamas.** Grand Turk Island, *Millspaugh & Millspaugh 9038* (GH, NY). **Colombia.** BOLIVAR: Tierrabompa Island, *Killip & Smith 14130* (GH, NY, US); MAGDALENA: Santa Marta, *Smith 530* (GH, LL, MICH, MO, NY, TEX, US, USF, WIS). **Cuba.** Farallón, *Wright 1630* (GH, MO). **Dominican Republic.** 3 mi E of Boca Chica, *Liogier 17647* (NY, US). **Ecuador.** GUAYAS: Puntilla, *Svenson 11128* (GH, NY, UC, US); GALAPAGOS ISLANDS: Isla Santa Cruz, *Wiggins & Porter 711* (GH, NY). **Guatemala:** Zacapa, *Standley 73633* (US). **Haiti:** St. Michel de l'Atalaye, *Leonard 7334* (GH, NY, UC, US). **Jamaica:** Hope Grounds, *Harris 12127* (GH, NY, US). **Mexico.** BAJA CALIFORNIA SUR: El Llanito, *Carter & Moran 5283* (MICH, MO, TEX, US); OAXACA: 38 mi W of Tehuantepec, *Cronquist 9682* (MICH, MO, NY, TEX, US); SONORA: between Hermosillo and Tastiota, *Wiggins & Rollins 269* (LL, MICH, MO, UC, US); YUCATÁN, without locality, *Gaumer 887* (F, MO, NY, US). **Netherlands Antilles.** CURAÇAO: Willemstad, *Britton & Shafer 2910* (GH, NY, US). **Peru.** CAJAMARCA: Pucará, *Hutchison & Wright 3578* (GH, MICH, NY, UC, US). **United States.** ARIZONA: Pima Co.: 4 mi W of Havanakya, *Gould & Haskell 3196* (TEX, UC); PUERTO RICO: Ponce, *Heller 6322* (GH, NY, US); VIRGIN ISLANDS: St. Croix, *Ricksecker 12* (GH, NY, UC, US). **Venezuela:** Maracaibo, *Moritz 473* (GH).

1b. **Pectis linifolia** L. var. **hirtella** Blake, Jour. Wash. Acad. Sci. **25:** 322. 1935. TYPE: **Mexico.** GUERRERO: Dist. Coyuca, Tanganhuato, *Hinton 6606* (US, holotype!; F, MO, US, isotypes!).

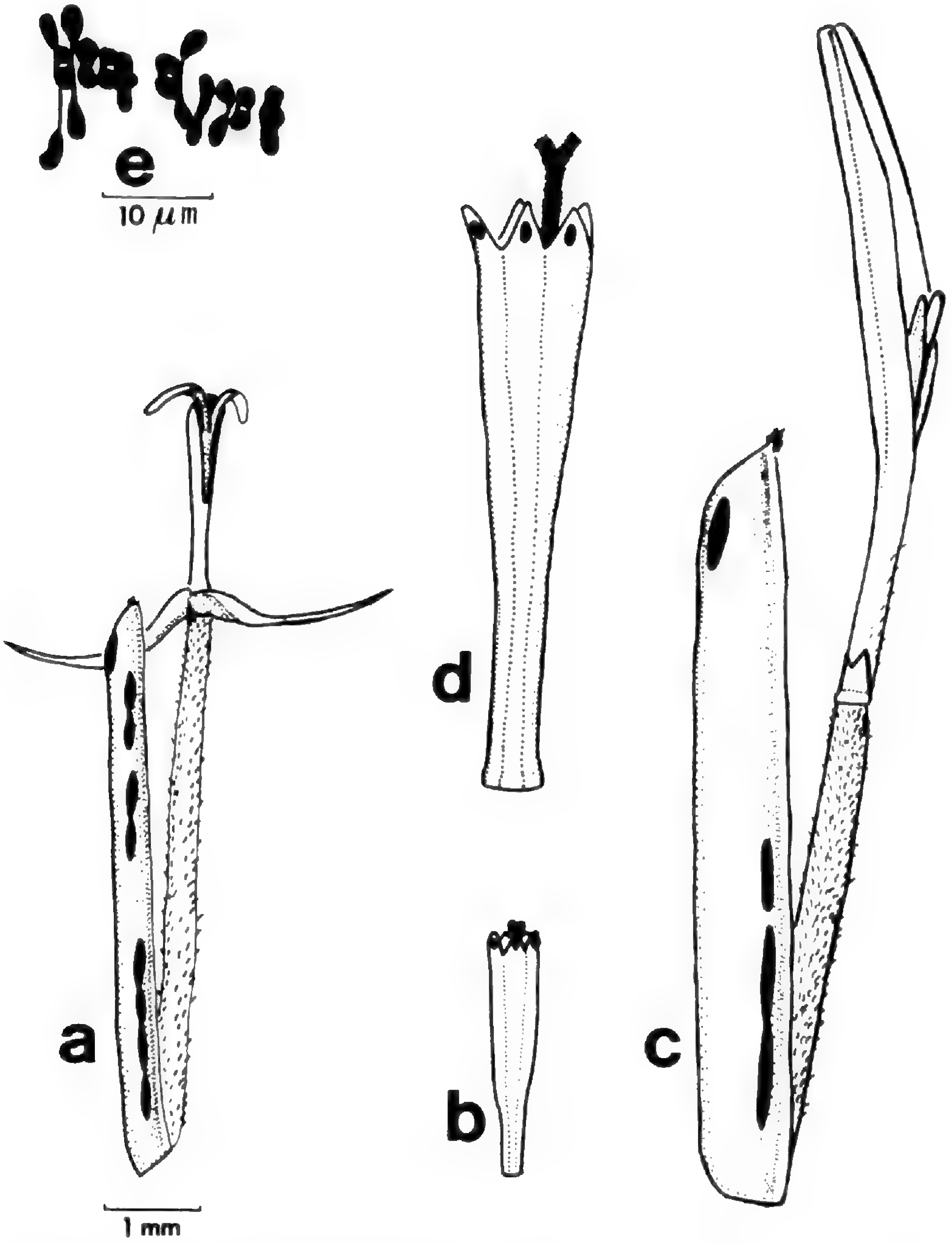

Figure 2. **Pectis linifolia and Pectis imberbis.** a, b, *P. linifolia* var. *linifolia:* a, ray floret with subtending involucral bract; b, disc corolla; a, b, *Nash, Brown, MacIntyre, McGill & Pinkava P9907* (ASU). c, d, e, *P. imberbis:* c, ray floret with subtending involucral bract; d, disc corolla; e, chromosome complement at metaphase I ($2n$ = 12 II); c, d, *Pinkava & Keil K11006A* (ASU); e, *Pinkava & Keil K11006C* (ASU).

Stems glabrous or hirtellous on the angles. Leaves 1.0–5.5 cm. long, 1–8 mm. wide, with 1–3 pairs of basal setae up to 7 mm. long, glabrous or hirtellous on the margins and midrib below. Involucre purple, 5.0–6.5 mm. long, glabrous or hirtellous. Ray florets with the tube 1.5 mm. long and the ligule 2.25–2.50 mm. long. Disc florets 5–6, sterile, with the corollas 3.5–4 mm. long; ovary shrunken, 3 mm. long. Ray achenes 4.5 mm. long. Ray pappus biaristate, 2.5 mm. long; disc pappus coroniform. Chromosome number unknown.

Pectis linifolia var. *hirtella* occupies a limited range in Michoacan and Guerrero, Mexico at 300–600 m. (Figure 1). Plants of var. *hirtella* are known to flower from August to December.

The varietal epithet of this taxon is somewhat of a misnomer. Most collections lack the pubescence of the type. The most easily recognizable characteristic for distinguishing this taxon from var. *linifolia* is the elongate basal setae of the leaves.

REPRESENTATIVE SPECIMENS: **Mexico.** GUERRERO: dist. Coyuca, Chacamerito, *Hinton 6440* (GH, US); MICHOACÁN: below Uruapan, *Lape 26* (MICH); above Apatzingán, *Leavenworth & Hoogstraal 1504* (F, MO); 9 mi SE of Apatzingán, *McVaugh 17987* (MICH, US); Las Juntas, *Rzedowski 26654* (ENCB).

2. **Pectis imberbis** A. Gray, Smithsonian Contr. Knowl. 5(6): 70. 1853. TYPE: "Sonora, on the Sonoita" *Wright 1399* (GH, holotype!; F, GH, MO, US, isotypes!).[2]

Erect perennial herb 3–12 dm. tall, arising from a woody caudex 2–8 mm. diameter. Stems virgate, green, 6-angled above, becoming terete below, much-branched with ascending branches above, glabrous. Leaves narrowly linear, 1–5 cm. long, 1–2 mm. wide, sometimes much-reduced and bractlike above, apically acute, entire or bearing a single pair of basal setae 1–3 mm. long, usually revolute, punctate on the undersurface near each margin with a row of elliptical glands and on the upper surface with a single elongate medial subterminal gland, glabrous except for a minute axillary tuft of hairs. Heads solitary or in open cymose clusters at the tips of the branches. Peduncles 1–8 cm. long, slender, glabrous, bearing 2–4 slender alternate bracteoles 1–2 mm. long. Involucre green or

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[2] Charles Wright collected the type of *Pectis imberbis* prior to the Gadsden Purchase (1853). Although his collection labels list the locality as Sonora, the collection site is now a part of Santa Cruz County, Arizona.

purplish; bracts oblong, 5.0–9.5 mm. long, 1.0–1.5 mm. wide, apically obtuse, narrowly hyaline-margined, punctate with 1–2 swollen subapical glands and a row of 2 or 3 linear submarginal glands on each side of the midrib, minutely ciliolate and bearing an apical tuft of hairs, otherwise glabrous. Ray corollas yellow, often drying pink or purple, 6–11 mm. long, with tubes 2–3 mm. long and ligules 4–8 mm. long and 1.0–2.5 mm. wide, often punctate near the margin with several inconspicuous glands, sparsely puberulent on the tube with multicellular trichomes less than 0.1 mm. long. Disc florets 4–7; corollas yellow, often drying purplish, 3.7–6.0 mm. long, the lobes triangular, ca. 0.5 mm. long, punctate just below the tip with a solitary gland, glabrous or sparsely puberulent; anthers ca. 2.5 mm. long. Achenes black, 3.5–5.0 mm. long, puberulent with ascending blunt-tipped double-hairs 0.1–0.2 mm. long. Pappus of ray and disc achenes similar, aristate with 1–3 stout awns 1–2 mm. long, or reduced to a low crown. Chromosome number: $n = 12$. Figure 2, c-e.

Pectis imberbis occurs over a relatively limited range in southern Arizona, western Chihuahua, and eastern Sonora at elevations of 1100–1700 m. Through most of its range, *P. imberbis* is uncommon. Each of the populations examined in the field during the present study consisted of less than ten individuals. No seedlings were found in these populations. *Pectis imberbis* has been recommended for inclusion on the list of threatened or endangered species (Mrs. Elinor Lehto, pers, comm.).

Fernald (1897) indicated that *Pectis imberbis* has a strong terebinthine odor but did not cite the source of his information. My own observations have indicated that plants from Arizona populations are non-aromatic, and none of the labels from plants of this species that I have examined mention any odor.

REPRESENTATIVE SPECIMENS: **Mexico.** CHIHUAHUA: Guasaremos, *Gentry 1857* (DES, LL, MO, UC, US); Batopillas, *Gentry 2617* (MO, US); **Sonora:** Cañon Saucito, *Gentry 705M* (MICH); Cañon de la Petaquilla, *White 3337* (MEXU, MICH). **United States.** ARIZONA: Cochise Co.: Huachuca Mts, *Lemmon 2783* (US); Ft Huachuca, *Wilcox 390* (US); Santa Cruz Co.: Patagonia Mts, *Kearney & Peebles 14826* (LL, US); Atacosa Mts, *Parker 7399* (UC); Peña Blanca Lake, *Pinkava & Keil K11006* (ASU).

Table 1. **New chromosome counts from Pectis** sect. **Pectidium.**

Pectis imberbis A. Gray

United States. ARIZONA: Santa Cruz Co.: Peña Blanca Lake Recreation Area, *Pinkava & Keil K11006B, C* (Figure 2e), $2n = 12_{II}$; *K11006D*, $2n = 10_{II} + 1_{IV}$. 3.7 mi W of Peña Blanca Lake, *Pinkava & Keil K11076A*, $2n = 12_{II}$.

Vouchers are deposited at ASU.

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WATERCRESS IN FLORIDA

REED C. ROLLINS

Plants of what is loosely called watercress persist in springs, streams and swampy areas for long periods of time without flowering or fruiting and such populations are difficult to handle taxonomically. All too frequently, only leafy specimens from these populations are available and these reflect a tremendous vegetative variation from site to site as well as from one season to another.

In North America, perhaps the most complex and bewildering set of non-flowering populations is in northern Florida. This area abounds in suitable habitats for the persistence of non-flowering plants in spring pools, streams and otherwise permanent watery situations, particularly where there is a flow of some magnitude. In some of the clear mineral springs and their runs, watercress grows on the sandy bottoms, submerged and covered with two to four feet of water. Attempts to positively identify the watercresses of northern Florida have been frustrating for many years, so much so that the present study was undertaken to try to understand and explain the situation. Specimens from this region have been variously interpreted as belonging to *Cardamine* or *Nasturtium* (or sometimes *Rorippa*). Fortunately, Dr. Robert K. Godfrey, recently of Florida State University, has been interested in the problem. He has provided special mass collections that have helped to delineate the variation present at several different sites. I am grateful to him for this important help.

FIELD AND GREENHOUSE OBSERVATIONS

In the early spring of 1973, I made observations at three sites in northern Florida: below Wadesboro Spring, Clay County; at Ichetucknee Spring and run, Ichetucknee State Park, Columbia County; and Alexander Springs, Lake County. Living material was taken from the latter site for further study. The water was cool to cold and swift-running at each of the sites visited.

In all three places, plants growing fully submerged possessed entire, nearly orbicular leaves. In shallower water, where branches became emergent, the leaves were pinnately lobed on the emergent parts of the plants. This dimorphism of leaf form has contributed to taxonomic confusion concerning these plants. Non-flowering plants with entire leaves have usually been referred to the genus *Cardamine* while those showing lobing have been identified as either *Nasturtium* [*Rorippa*] or *Cardamine*.

Fragments of plants, rooting at the nodes, were brought to the greenhouse in Cambridge, Massachusetts. These were grown both deeply submerged and near the surface in the cool circulating water of a large concrete fish tank. True to form, the submerged plants continued for over a year to produce entire leaves. During late spring, 14 months after being transplanted from the wild populations, the emergent parts of the plants grown near the surface produced pinnately lobed leaves and flowers. The deeply submerged plants continued to produce entire leaves (Figures 1 & 2). This is a reversible development and may be, by manipulation, moved in either direction. When the emergent plants with lobed leaves were again wholly submerged to a depth of a foot or more, the new shoots produced entire leaves. When the submerged plants with entire leaves were brought ot the surface, the new emergent shoots produced lobed leaves. These simple manipulations were performed to test the authenticity of the field observations which were critical to an accurate identification of wild populations, and specimens in herbaria. As a result, we can safely associate the entire-leaved plants with the pinnately lobed plants and know in this instance that we were dealing with but a single taxon. No attempt was made to control water temperature, light intensity, or daylength, for our interests were not in the process but rather the nature and amplitude of leaf heterophylly exhibited by the plants.

Several aquatic angiosperms, for example, species of *Ranunculus* (Butcher, 1940; Bostrak & Millington, 1962), *Proserpinaca palustris* (Burns, 1904), *Armoracia* [Neobeckia] *aquatica* (MacDougal, 1914), and a number of others, produce divided leaves under water and either entire or somewhat more entire leaves out of water. In the case of the Florida plants the reverse is true. The entire leaves are the ones growing submerged and the pinnately lobed ones are those growing out of the water. The latter are associated with flowering. These facts alone have tended to mislead and cause a wrong interpretation of specimen material.

CARDAMINE VERSUS NASTURTIUM

Over a century ago there was confusion as to whether the taxa

Figures 1 and 2. *Nasturtium microphyllum* (Boenn.) Reichenb., *Rollins 7311* (GH). Both plants grown for 14 months in a concrete fish tank with circulating cool water. Figure 1, pinnately lobed leaves and inflorescences produced above water from shallowly grown plants. Figure 2, entire leaves and non-flowering shoot grown continuously submerged to a depth of more than one foot.

under consideration belonged to the genus *Cardamine* or to the genus *Nasturtium* and the situation has remained obscure down to the present. A quote from Gray (1880) will illustrate (p. 46), "an imperfect original specimen from Shuttleworth was mixed up with a Florida species, intermediate between *Cardamine* and *Nasturtium,* first received from Leavenworth without fruit, and referred in the Supplement to the first volume of Torrey & Gray's Flora to *N. officinale;* it was afterwards received from Buckley, then from Shuttleworth (Coll. Rugel), first as *Cardamine curvisiliqua* Shuttl., and again as *Nasturtium stylosum,* Shuttl." The specimens with the names on their labels referred to by Gray are in the Gray Herbarium. The name *Cardamine curvisiliqua* was given a description in Chapman's Flora (1887) but the first clear reference I have found to the plants in question from Florida is in the supplement to Torrey and Gray's Flora of North America, published in 1843.

Evidently Watson was uncertain as to the generic position of the plants when he prepared the treatment of *Cardamine* for the Synoptical Flora of North America (1895) because as Robinson (Syn. Fl., p. 156, footnote 3) points out, "This species, although referred by Dr. Watson to *Cardamine,* was not described in his manuscript." While inserting the species into the treatment of *Cardamine,* Robinson placed a question mark between the generic name and the specific epithet *curvisiliqua,* thus indicating his own doubt as to the placing of it in *Cardamine.* Schulz (1903) excluded *C. curvisiliqua* from *Cardamine,* and referred it to *Nasturtium.* He was undoubtedly aware that the specific epithet *curvisiliqua* had already been used in *Nasturtium* by Nuttall (Torrey & Gray, 1838) and a name transfer could not be properly made. Later Schulz (1936) accepted the name *Nasturtium stylosum* Shuttl., dating it from Gray's reference to the name as quoted above. However, there was no description given at that time. The name was not provided with even a few words of descriptive matter until Schulz himself did it (1936, p. 553) in an incidental way. By that time, the epithet *stylosum* was preoccupied by *Nasturtium stylosum* (D.C.) Schulz, based on *Cardamine stylosa* D.C. (1821). *Nasturtium stylosum* Shuttl. ex Schulz is essentially a *nomen nudum* as well as a later homonym.

For some years I have been aware of the unsatisfactory placement in *Cardamine* of what has been called *C. curvisiliqua* and the related *C. gambelli* of southern California and Mexico (Rollins, 1960). These two species are not properly placed in *Cardamine.* As indicated above, this situation was clearly recognized by Schulz, who excluded them from that genus. It is evident from his annotations of specimens in the Gray Herbarium that Fernald (1950) regarded *"Cardamine curvisiliqua"* to be nothing more than *Nasturtium officinale* R. Br., var. *microphyllum* (Boenn.) Thell. However, a more recent clarification of the American representatives of the true watercresses (as *Rorippa*) by Green (1962) did not take into account material filed under *Cardamine curvisiliqua* and this left the question of the Florida watercresses still unresolved.

The true watercresses have been treated as belonging to *Rorippa* when that genus is interpreted to include *Nasturtium.* However, there is a substantial basis for recognizing both *Rorippa* and *Nas-*

turtium. In the most recent treatment of North American *Rorippa,* Stuckey (1972) excluded *Nasturtium* from *Rorippa;* and both *Rorippa* and *Nasturtium* were recognized in Flora Europaea (1964). On the other hand, as indicated above, Green treated the watercresses in the genus *Rorippa.* In many annotations of herbarium material, I have followed Green's treatment. However, it has become increasingly clear that the watercresses form a tightly knit small group of species that are only marginally related to members of the genus *Rorippa.* The true watercresses are *Nasturtium officinale* R. Br. and *N. microphyllum* (Boenn.) Reichenb. These and the gambel watercress, *N. gambelli* (Wats.) Schulz, make up the genus *Nasturtium* as it is presently known in North America.

Nasturtium gambelii and specimens of *N. microphyllum* have repeatedly been referred to *Cardamine* but neither of them possess the elastic valve that is so characteristic of *Cardamine.* Furthermore, in these species, the valve covers the replum and extends to the margin of the silique without intruding into the valvular area. In these respects they differ markedly from *Cardamine* where the valve often opens elastically and even if not, the valve upon discharge leaves a definite extension of the replum into what is the usual valvular area of the silique. It is my conclusion that these species are not properly placed in *Cardamine* and that the Florida material often identified as *Cardamine curvisiliqua* Shuttl. ex Chapm. is in reality *Nasturtium microphyllum* (Boenn.) Reichenb.

There are five taxa (one of which is a hybrid) in Florida that are involved in the various and uncertain interpretations applied to plants loosely called watercress when in the non-flowering condition. Two of these are in fact species of *Cardamine* which can be readily identified if they are in fruit. In flower, identification is more difficult but the anthers of the *Cardamine* species are much shorter and smaller than those of *Nasturtium.* The cardamines are annual and except in the young stages of growth, usually are in flower or fruit during the normal growing season. Insofar as I am aware of it, *Cardamine* does not grow fully submerged for any length of time and neither species forms mats in flowing water. The species tangentially involved in the problem are *C. pensylvanica* (var. *pensylvanica* and var. *brittoniana*) and an as yet unidentified species, probably an introduction from Europe or Asia.

Most of the non-flowering material encountered is *Nasturtium microphyllum* (Boenn.) Reichenb. However, *N. officinale* R. Br.

is found in a number of locations and it is not known whether some entire-leaved non-flowering plants are certainly referrable to the species or not. In fruit, the two species, one a diploid (*N. officinale*), the other a tetraploid (*N. microphyllum*), are easily distinguished from each other. Green (1962) has a full discussion of these closely related species and should be consulted for details.

Nasturtium officinale and *N. microphyllum* do hybridize and the offspring of the cross is a triploid. It is sterile, producing unfilled siliques. Specimens of the hybrid, the fifth of the five taxa mentioned above, have been seen from Florida. The siliques remain undeveloped in hybrid plants but nothing is known about the contribution of the hybrid to the non-flowering populations discussed above. Shaw (1948) has provided the name *Rorippa* × *sterilis* for the hybrid and in *Nasturtium,* it is *N.* × *sterile* (Shaw) Oefel.

Assuming that I am correct in referring what has at times been called *Cardamine curvisiliqua* to *Nasturtium microphyllum,* the question naturally arises as to why a species long treated as being a native of Florida is now considered to be an introduced species. The records show that the diploid *N. officinale* was introduced into the United States at least by the early 1800's and most likely arrived much earlier. Since both *N. officinale* and *N. microphyllum* have been prized as salad plants in Europe for centuries, it is not surprising that either or both of them should have been brought to the United States for the same purposes by the early settlers. The 1840 reference by Gray to plants from Florida now known to be *N. microphyllum,* as mentioned above, is not so surprising when viewed from this perspective.

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GRAY HERBARIUM
HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MA 02138

AN ADDITION TO THE FLORA OF THE GASPE PENINSULA

JAMES P. POOLE

Recently the Curator of Jesup Herbarium has been checking the determination of specimens collected by Mrs. Elizabeth Sherrard in the Gaspe Peninsula in 1946. Among the grasses is a specimen of *Cenchrus longispinus* (Hack.) Fernald collected at Perce July 9–10. Failing to find even the genus *Cenchrus* listed in Frere Marie-Victorin's Flora Laurenienne (1935) or in H. S. Scoggan's Flora of Bic and the Gaspe Peninsula (1950), a specimen was sent to the Canadian National Herbarium, Ottawa, Canada. In his letter of acknowledgment, Dr. John M. Gillett, Curator, Vascular Plant Section, wrote, "As far as I am aware it is a first for the Gaspe. We have a record from Quebec City but that is all for Quebec. I also checked the Agriculture Canada Herbarium (DAO) and they have nothing at all from Quebec." A note from Dr. S. P. vander Kloet, Curator of the Smith Herbarium at Acadia University, Wolfville, N.S. reads, "This genus has not been collected in any of the Maritime Provinces; at least we have no specimen in the herbarium." A number of accounts of botanizing in the Gaspe Peninsula have been published in Rhodora but a search of the Rhodora Indices discloses no listing of even the genus *Cenchrus*.

It seems probable that in 1946 this species was an adventive waif in the area. The fruit is certainly well adapted for distribution on the clothing of tourists, although in 1946 the Gaspe was not the popular tourist region it became later. Also, both the nature of the fruit and the frequent beach habitat of the species make it a likely subject for transport by either the plumage or the feet of shore birds so numerous in the region of Perce. It would be very interesting to learn if the species persisted in the area. The only two specimens collected are deposited in the Canadian National Herbarium and Jesup Herbarium as vouchers.

JESUP HERBARIUM
DARTMOUTH COLLEGE
HANOVER, N.H. 03755

RANGE EXTENSIONS OF TWO NEW HAMPSHIRE TREES

FREDERIC L. STEELE

Thuja occidentalis L. is rather common in swamps north of the Presidential and Franconia Ranges and extends south along the Connecticut River to Orford. There is one small colony along the East Branch of the Pemigewasset River just south of the Franconia Range. Although often planted it has never been observed in natural stands south of the main ranges of the White Mountains.

In December of 1973 I received a report of this species occurrence in the town of Madison and, taking a short trip with some friends, verified the report. In July of 1974, Albion Hodgdon, C. Barre Hellquist and I made a more thorough investigation. We found an extensive stand of *Thuja occidentalis* in a swamp one-half mile east of Whitton Pond in the town of Madison. Access was possible by lumber roads from the Madison Boulder Road and, on the way out, we discovered two trees beside the road itself which had not been previously observed. This *Thuja* stand represents a 50 mile southeastern range extension and is well isolated from any other stand. A collection was made and put in the herbarium of the University of New Hampshire.

Ulmus rubra Muhl is confined to the Connecticut River valley as far north as Haverhill, and in the past was occasionally planted near houses for the supposed medicinal value of its inner bark. In June, 1975 I located a good-sized tree in the town of Rumney on a terrace of the Baker River. This plant was in the woods, not near a house, and appeared to be natural. This represents a considerable eastward range extension. A specimen has been deposited in the herbarium of the New England Botanical Club.

THE WHITE MOUNTAIN SCHOOL
LITTLETON, N.H. 03561

PTERIDOPHYTA OF THE LESSER ANTILLES.[1]

George Proctor of the Institute of Jamaica has been studying the pteridophytes of the Lesser (and Greater) Antilles for many years. His contribution to the *Flora of the Lesser Antilles* reflects his long and close familiarity with the group he treats, especially during his extensive field explorations. The book is excellent and will be welcomed by all interested in the ferns and fern allies, tropical American flora and in plant geography. While there are technical details that pteridologists can disagree with, these do not relate to the overall usefulness of the treatment.

Keys to the families, genera and species are provided, as are an illustration for each genus (one or more species), and full descriptions and synonymy. The general range of each species, and the detailed distribution and ecology in the Lesser Antilles are also included. The taxa recognized include 11 families, 68 genera and 300 species and major geographic varieties. The largest genera are *Thelypteris* (35 species), *Trichomanes*, *Grammitis* and *Polypodium* (22 species each) and *Elaphoglossum* (21 species). The islands with the richest floras are Guadeloupe with 272 species, Martinique with 218 species and Dominica with 194 species.

A brief account of the botanical exploration of the Lesser Antilles indicates the major role that both George Proctor and Richard Howard have played in the field work that forms the basis of our present knowledge of the flora. The author has collected ferns on 15, and Howard on 11, of the 21 islands that have a pteridophyte flora. The third most widely traveled collector in the region was Jacquin who visited the islands in 1759.

The Lesser Antilles do not support a rich pteridophyte flora (Jamaica has almost twice as many species) and the species endemism of 14% is not high. However, they do represent a critical region for tropical American plant geography. They form an arc between the older and floristically richer areas of northern South America and the Greater Antilles. Accordingly the role of the Lesser Antilles as a route of migration is of unusual interest.

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[1] Howard, R. A. Flora of the Lesser Antilles, vol. 2, Pteridophyta by George R. Proctor, pp. 1–414. 1977. Arnold Arboretum, Harvard University, Jamaica Plain, Mass. 02130. (Price $25.00).

The "Pteridophyta of the Lesser Antilles" not only provides for basic needs of classification and identification, but also (for the first time) a basis for biogeographic studies of the whole archipelago.

ROLLA TRYON
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JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

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TAXONOMY OF NERISYRENIA (CRUCIFERAE)[1]

JOHN D. BACON

A small genus of perennial mustards, *Nerisyrenia* is limited, for the most part, to the Chihuahuan Desert. The widest ranging taxon, *N. camporum,* extends into the southern and western edge of the Edwards Plateau and the southern fringe of the Rio Grande Plains of Texas. The remaining species show regional or highly localized distributions, correlated, in the majority of cases, with the occurrence of gypsum ($CaSO_4 . 2H_2O$).

Rollins (1939) studied the genus and treated the three species known to him. Subsequently, two additional species were described (Johnston, 1941; Rollins, 1941b); since that time *Nerisyrenia* has remained unexplored systematically. Therefore, a monograph of the group was undertaken. In addition to field observations and morphological studies, extensive cytological and flavonoid chemical studies were completed on all species. The latter approaches were extremely informative and essential in establishing species limits and relationships. Therefore, this systematic treatment is an amalgam of the total evidence gathered during the study.

TAXONOMIC HISTORY

Events leading to the establishment of *Nerisyrenia* began in 1850 with Asa Gray's description of *Greggia camporum.* He chose the generic name to honor the then recently deceased Dr. Josiah Gregg, even though he was aware that the name, *Greggia,* had been previously applied by Engelmann to the rosaceous genus *Cowania.* Apparently Gray was not aware that the name *Greggia* had been used, even earlier, by Gaertner. In any event, Gray's appellation was rejected.

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[1] This paper is based on a dissertation completed in the Department of Botany, The University of Texas, Austin, Texas, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Greene (1895) attempted to rectify the nomenclatural problem of *Greggia,* now containing an additional species, *G. linearifolia* Watson, by offering the name *Parrasia* for the genus. This name, however, proved equally unsuitable as Greene discovered "soon after the appearance of the third volume of the *Index Kewensis*" that the name *Parrasia* had been previously applied by Rafinesque (Greene, 1900). Greene then proposed the presently accepted name *Nerisyrenia* for the two known species.

The genus remained with two species until the late 1930's and early 1940's. During that period, and as a result of I. M. Johnston's trips into northern Mexico, three species were added to the genus, *Nerisyrenia incana* Rollins, *N. castillonii* Rollins and *N. gracilis* I. M. Johnston.

The above mentioned species constituted the genus when this investigation was initiated. Recent field work in northern Mexico by Drs. M. C. Johnston, B. L. Turner, and their colleagues and students, including myself, has revealed several new taxa referable to *Nerisyrenia.* In this treatment the genus comprises nine species and one variety.

CYTOLOGY

Prior to this study, chromosome numbers had been reported for only two species of *Nerisyrenia.* Rollins (1939) reported a gametic number of $n = 7$ for *N. camporum,* based on a collection from Brewster County, Texas. Subsequently, Rollins (1966) reported two additional counts for the same species: $n = 9$ from material also collected in Brewster County, Texas, and $n = 11$ based on material from Coahuila, Mexico. Material of *N. linearifolia,* from Culberson County, Texas, was also reported for the first time as $n = 9$.

As indicated in Table I, I have obtained counts for the remaining species of the genus. I have also obtained additional counts for the two previously reported taxa. Counts reported here were gathered from over 200 individuals from throughout the range of each species, and it is felt that the survey is a fair portrayal of chromosomal patterns within the genus. In addition, several populations of one species of the closely related genus *Synthlipsis, S. greggii* A. Gray, were examined for chromosome numbers (Table I). Complete voucher citations are available from the author on request.

Materials and Methods

In the field, bud material was collected and put into a modified Carnoy's solution (chloroform : 95% ethanol : glacial acetic acid, 4:3:1, v/v). In the laboratory, the fixed buds were stored under refrigeration until examined. Chromosome numbers were determined from pollen mother cells obtained from suitable anthers squashed in aceto-carmine stain (Smith, 1947). Voucher specimens for all counts are on deposit in The University of Texas Herbarium (TEX).

In most instances, bud material was collected from three to five individual plants per population in order to detect intrapopulational variation, if present. However, this was not possible when buds were scarce in a given population; consequently, several populations are represented by counts for only a single individual.

Results and Discussion

As indicated in Table I, 221 chromosome counts representing 112 populations of the nine species of *Nerisyrenia* were made in the course of this study. The genus as a whole exhibits a rather wide array of chromosome numbers, with diploid, polyploid, aneuploid and, apparently, dysploid numbers represented. With few exceptions, aneuploidy is found in all species. To facilitate the discussion that follows, the species are considered individually.

Nerisyrenia camporum. This taxon consists of two major cytological races (Table I), diploids ($2n = 18$) and tetraploids ($2n = 36$). From presently available data, the diploids appear to be limited to the Chihuahuan Desert of north-central Mexico, entering into the United States in southern Brewster and Presidio Counties, Texas. The tetraploids appear to be distributed peripherally to the diploids. Morphological differences could not be found to distinguish the two cytotypes with their similar variations and forms. Diploid and tetraploid plants were never encountered in the same population; however, populations of one cytotype were collected within a few airline miles of the other. Aneuploidy occurs within both cytotypes. For example, near Lajitas, in southern Brewster County, Texas, predominantly diploid populations are found. However, three plants collected in the area yielded counts of $2n = 21$ (*Bacon 1056b*), $2n = 22$ (*Bacon 1054d*) and $2n = 27$ (*Powell 2191*). The triploid plant usually exhibited two or three trivalents per cell in addition to a few bivalents and several univalents.

Table I. **Summary of Chromosome Numbers for Nerisyrenia and Synthlipsis**

Taxon	*2n =*	*Locality (number of populations examined/total plants counted)*
N. camporum	18	MÉXICO: Coahuila (13/22), Durango (1/5). TEXAS: Brewster Co. (4/7), Presidio Co. (6/9).
	19+	MÉXICO: Coahuila (0/1). TEXAS: Presidio Co. (0/1).
	21+	TEXAS: Presidio Co. (0/1).
	22+	TEXAS: Brewster Co. (0/1).
	27	TEXAS: Presidio Co. (1/1).
	32	MÉXICO: Chihuahua (2/4).
	34+	TEXAS: Reeves Co. (0/1).
	36	MÉXICO: Chihuahua (1/4), Coahuila (5/7). NEW MEXICO: Otero Co. (1/1). TEXAS: Brewster Co. (6/8), Culberson Co. (1/2), Hudspeth Co. (4/6), Jeff Davis Co. (1/1), Loving Co. (1/1), Pecos Co. (1/1), Presidio Co. (2/4), Reeves Co. (3/4), Ward Co. (1/2).
	38*	TEXAS: Culberson Co. (1/1).
	40	TEXAS: Hudspeth Co. (2/3).
	41+	MÉXICO: Coahuila (0/1).
	Ca. 44+	MÉXICO: Coahuila (0/1).
	58*	TEXAS: Culberson Co. (0/1).
N. linearifolia var. *linearifolia*	18	NEW MEXICO: Otero Co. (2/2), Socorro Co. (1/3). TEXAS: Culberson Co. (2/6), Reeves Co. (1/1).
	19	NEW MEXICO: Otero Co. (2/2).
	20+	NEW MEXICO: Otero Co. (0/1).
	34+	TEXAS: Reeves Co. (0/1).
	36	TEXAS: Reeves Co. (3/8), Ward Co. (1/3).
N. linearifolia var. *mexicana*	36	MÉXICO: Nuevo León (1/2).
N. gypsophila	18	MÉXICO: Chihuahua (2/4).
N. gracilis	18	MÉXICO: Nuevo León (1/1).
	34	MÉXICO: Nuevo León (3/6).
	36	MÉXICO: Nuevo León (2/2), San Luis Potosí (5/6).
	38	MÉXICO: Nuevo León (1/1).
N. powellii	38	MÉXICO: Coahuila (1/1).
N. johnstonii	20	MÉXICO: Coahuila (1/1).
N. castillonii	20	MÉXICO: Coahuila (1/2).
	40	MÉXICO: Coahuila (11/21).

Table I — continued

	48	MÉXICO: Coahuila (1/1).
	58	MÉXICO: Coahuila (2/5).
	59+	MÉXICO: Coahuila (0/1).
N. turneri	20	MÉXICO: Nuevo León (2/3).
	32	MÉXICO: San Luis Potosí (5/10).
	33+	MÉXICO: San Luis Potosí (0/1).
	36	MÉXICO: San Luis Potosí (1/1).
	Ca. 38+	MÉXICO: San Luis Potosí (0/1).
N. incana	20	MÉXICO: Coahuila (9/12).
	21	MÉXICO: Coahuila (1/1).
	23	MÉXICO: Coahuila (1/1).
S. greggii	20	MÉXICO: Chihuahua (1/1), Coahuila (8/10), San Luis Potosí (2/3).

+Aneuploid plant in euploid population.
*Plants from same population.

The temptation to recognize the triploid plant as a hybrid between the diploid and tetraploid is great. However, I have found tetraploid populations no closer than 10 airline miles to the east and 25 30 airline miles to the west of the Lajitas site; nevertheless, their presence in the area cannot be ruled out. The triploid might also have arisen from the union of a diploid, unreduced gamete and a reduced diploid gamete. Subsequent outcrossing with diploid plants in the population could then lead to at least a few aneuploid derivatives, as found in this area.

A similar situation was encountered near Torreon, Coahuila. Three plants from this population (*Bacon & Hartman 1344*) were determined as $2n$ = ca. 36, 41 and ca. 44. Approximately three airline miles to the east, diploid populations have been documented. The plant with $2n$ = ca. 44 is suggestive of pentaploidy, possibly derived from an unreduced tetraploid gamete and a reduced diploid gamete. Again, outcrossing to tetraploid neighbors could yield plants with $2n = 41$.

Additional aneuploid plants were encountered sporadically in both diploid and tetraploid populations. Two plants with $2n = 19$ were found in otherwise diploid populations, one west of Cuatro Cienegas, Coahuila (*Bacon & Leverich 1188b*) and one from Presidio County, Texas (*Bacon & Hartman 1423b*). One plant from Reeves County, Texas (*Bacon 1059c*), exhibited a chromosome complement of $2n = 34$. Two populations, separated by about 50 airline miles, were collected in Hudspeth County, Texas, and contained plants with $2n = 40$; one population had two plants with this number (*Bacon 947c,d*) plus a tetraploid individual; the other population (*Bacon 945*) returned chromosomal data from only a single plant. In Culberson County, Texas, two additional chromosomal variants, $2n = 38$ and $2n = 58$, were encountered, both in the same population. With the exception of the $2n = 58$ plant, *all* the above mentioned aneuploids formed the maximum number of bivalents at first meiotic metaphase; the $2n = 58$ plant exhibited univalents, trivalents and quadrivalents at first metaphase.

Evidence for a possible third regional cytotype within *Nerisyrenia camporum* has been found near Aldama, Chihuahua. Three plants from one population (*Bacon & Hartman 1346*) were clearly $2n = 32$. A further count, provided by Dr. A. M. Powell, from material about 20 miles east of the former population was $n =$ ca. 16. Population samples from this region are few, however, and future investigations will undoubtedly show other types to be present.

In spite of several collection trips to the area from which Rollins (1939) obtained the count of $n = 7$ for *Nerisyrenia camporum*, I have been unable to corroborate his report.

Nerisyrenia incana. This taxon gave rather consistent counts of $2n = 20$ (Table I). However, three plants yielded aneuploid numbers of $2n = 21$ (two plants) and 23. Additionally, the count of $n = 11$ reported by Rollins (1966) for *N. camporum* should be referred to this taxon; examination of his voucher specimen (*Rollins & Tryon 58293*, GH!) revealed the plant to have siliques typical of *N. incana.*

Nerisyrenia gypsophila. This species has proven to be consistently diploid with $2n = 18$ (Table I). However, the taxon has been sampled only from the type locality and surrounding area; consequently, further sampling should be undertaken before this number is accepted as characteristic.

Nerisyrenia linearifolia var. **linearifolia.** This taxon consists of two cytological races (Table I), diploids ($2n = 18$) and tetraploids ($2n = 36$); occasional aneuploid plants also occur. Three plants from the White Sands area of New Mexico yielded aneuploid counts; two had $2n = 19$, and one had $2n = 20$ (*Bacon 1046c*). In contrast to two additional plants from the same population with $2n = 36$, a single plant from Reeves County, Texas, was determined as $2n = 34$ (*Bacon 1060c*).

Nerisyrenia linearifolia var. **mexicana.** This taxon is known, at present, from only two counts, both $2n = 36$ (Table I).

Nerisyrenia powellii. This species is known chromosomally from only a single count of $2n = 38$ (Table I). The count came from a "mass bud collection" taken in a population where buds were scarce; therefore, this number should not be taken as characteristic until further sampling can be accomplished.

The chromosome number of this taxon is clearly polyploid and suggestive of amphiploidy via hybridization between some $x = 9$ taxon and an $x = 10$ taxon. However, since those species with $x = 10$ have a distinctive chemistry (with the exception of *N. incana*) as compared to those species with $x = 9$, one might expect the flavonoid chemistry of this taxon to reflect such an origin through an "additive flavonoid profile". The chemical evidence did not support this suggestion. Considering the widespread occurrence of aneuploidy within the genus, this number probably represents aneuploid variation from the tetraploid number of $2n = 36$.

Nerisyrenia gracilis. This species yielded counts of $2n = 18$, 34, 36 and 38, with $2n = 36$ as the predominant number (Table I). One plant with $2n = 34$ (*Bacon 1013b*) provided the only instance other than univalent-multivalent oddities, of meiotic irregularity seen during this study. Lagging chromosomes were seen in some pollen mother cells at first metaphase; micronuclei were present at late second telophase in a number of cells. Other plants with $2n = 34$ had normal meiosis. This taxon proved difficult to count, and many of the determinations reflect only a single plant per locality; therefore, populational chromosome numbers may prove more complex than indicated.

Nerisyrenia johnstonii. A single count of $2n = 20$ (Table I) has been obtained for this rare, extremely localized endemic.

This species and *Nerisyrenia incana* are thought to represent the most "primitive" species in the genus (see PHYLOGENY). The occurrence in both species of the diploid number of $2n = 20$ suggests $x = 10$ as the original basic number for the genus.

Nerisyrenia castillonii. This taxon exhibited chromosome numbers of $2n = 20$, 40, 48, 58 and 59, with the typical number of $2n = 40$ (Table I).

The diploid counts of $2n = 20$ came from two rather depauperate plants, perhaps in their first year of growth.

Those plants with $2n = 58$ were collected during the initial stages of this investigation. After chromosome number determinations, I felt that these collections probably represented amphiploid derivatives of *Nerisyrenia castillonii* and some other taxon in the area. Subsequent attempts, on three different occasions, to re-collect this material from the same locality and surrounding area met with failure. As more chromosome counts were accumulated and the variation in number became apparent, I changed my attitude as to the amphiploid nature of these collections, and thus I include them in this taxon. I was not able to determine the metaphase configurations in these plants, but all countable cells at second division clearly showed 29 chromosomes.

Nerisyrenia turneri. This species yielded counts of $2n = 20$, 32, 33, 36, and ca. 38, with $2n = 32$ predominating (Table I). The counts of $2n = 33$ and 38 came from a population in which three other plants were determined as $2n = 32$ (*Bacon & Hartman 1330*). The count of $2n = 36$ was derived from a single plant (*Bacon & Hartman 1329*), the only material yielding a count from that population.

Counts of $2n = 20$ were derived from two populations. Morphologically, these two populations were somewhat atypical for the species in that they had narrower leaves and more slender siliques than most populations encountered; however, their flavonoid profiles were identical to the bulk of this taxon. Perhaps they represent populations more similar morphologically to ancestral populations of *Nerisyrenia turneri*.

Although the typical chromosome number of this species, $2n = 32$, is unusual for the genus and suggests a base number of $x = 8$, it seems clear that this number has been derived from an original base of $x = 10$. This taxon is most closely related to *Nerisyrenia castillonii*, which has the basic number of $x = 10$. These two species share a similar flavonoid chemistry with *N. johnstonii* (see FLAVONOID CHEMISTRY) which also has a chromosome number of $2n = 20$. These relationships plus the two populations of this taxon with $2n = 20$ suggest that the typical number in this species, $2n = 32$, has been derived through polyploid drop (Grant, 1971,

p. 224) from $2n = 40$. Perhaps the aneuploid counts for this taxon represent "remnants" of the process by which this new number was attained.

Synthlipsis greggii. This taxon exhibited consistently diploid numbers of $2n = 20$ (Table I), confirming the single previous report for this species (Rollins & Rüdenberg, 1969).

The reference to the diploid-polyploid populations noted in some species of *Nerisyrenia* as cytotypes or cytological races reflects the absence of external morphological features differentiating between the ploidy levels. This lack of morphological differentiation suggests that the polyploid populations may be autoploid in origin. The inclusion of diploids and their autopolyploid derivatives within a single species is biologically warranted (Lewis, 1967; Mosquin, 1967). However, as has been shown in some plant groups, most notably in *Gilia* (Day, 1965; Grant, 1964, 1971; see Grant 1964, 1971 for review of other groups), strong reproductive barriers can exist between individuals which are almost indistinguishable morphologically; therefore, in such groups, what is treated as a single taxonomic species consists, in fact, of two or more biological species, termed sibling species (Grant, 1964, 1971). In plants, sibling species are often associated with allopolyploidy (Grant, 1971, p. 30). The inclusion of two biological species within a single taxonomic species, although often the most pragmatic solution for routine identifications, is misleading and obscures the biological relationships within the concerned group (Grant, 1964, 1971). Possibly, sibling species exist within some species of *Nerisyrenia*. The identification and recognition of sibling species, however, requires taxogenetic analysis, and such data were not gathered during this study. Therefore, I have recognized as species those populations with similar morphology, regardless of ploidy level, while noting their chromosomal distinctiveness with the term cytotype. Hopefully, this taxonomic recognition coincides with the biological integrity of the recognized species.

Chromosomal data have been useful in many instances in supporting species delimitation. However, such data have been most helpful in delimiting phyletic groupings. Clearly, two "chromosomal lines" exist, one based on $x = 10$ and the other based on $x = 9$. This dichotomy is further supported by the flavonoid chemistry of the various species (see FLAVONOID CHEMISTRY). *Nerisyrenia incana* is anomalous within the genus in possessing a chromosomal base of $x = 10$ while exhibiting a flavonoid chemistry typical of those species based on $x = 9$; this taxon is thought to be a "primitive" species, the ancestors of which gave rise to the $x = 9$ line.

In those instances of aneuploidy seen in this study, the extra chromosomes are felt to be chromosomes of the "somic" type as opposed to supernumerary or accessory chromosomes; none of the features usually associated with accessory chromosomes, *e.g.*, heterochromaticity or smaller size (Brown, 1972; Swanson, 1958), was observed; also, the general lack of trivalent or multivalent formation on the part of the "extra" chromosomes and their expression as univalents or bivalents is in keeping with the results of numerous reports concerning somic aneuploids, both induced (Rick & Notani, 1961; Dhillon & Garber, 1960; Vasek, 1956) and naturally occurring (W. Lewis, 1962; Lewis, Suda & McBryde, 1967; Lewis, Oliver & Suda, 1967; H. Lewis, 1951, 1953). Indeed, my own observations of meiotic cells in this study suggest the same. In some plants which had consistent bivalent formation at metaphase I, an occasional meiocyte at second prophase was seen to have unequal distribution of chromosomes, which suggests that nondisjunction occurs with at least some frequency throughout the genus.

These observations, plus the fact that *Nerisyrenia linearifolia*, *N. gracilis*, *N. turneri*, *N. powellii* and *N. castillonii*, are strongly rhizomatous, may help explain the array of numbers in these taxa. The remaining taxa, *N. camporum*, *N. incana* and *N. gypsophila*, are tap-rooted. It is perhaps significant that the chromosomal variation within *N. incana* and *N. gypsophila* is either not known (to date) or sporadic and near the diploid level. Within *N. camporum*, if one ignores possible intrapopulational hybridization among cytotypes, the variation in chromosome number is, again, sporadic, and except in one instance, near the euploid level, either diploid or tetraploid.

One must also bear in mind that the presence of agamospermy (Grant, 1971) cannot be eliminated; my attempts to observe embryo sac formation have proved fruitless. Also, the possibility of polyploid complexes (Grant, 1971), especially in *Nerisyrenia castillonii*, must be kept in mind. The resolution of these possibilities must await further chromosome sampling on a more massive level and experimental hybridization among cytotypes.

Table II. **Summary of Populations of Nerisyrenia and Synthlipsis Examined Chromatographically for Flavonoids**

Taxon	*Locality (number populations examined/total plants examined)*
N. camporum	MÉXICO: Chihuahua (3/7), Coahuila (21/34), Durango (1/3). TEXAS: Brewster Co. (13/23), Culberson Co. (2/6), El Paso Co. (1/4), Hudspeth Co. (4/12), Jeff Davis Co. (1/1), Loving Co. (1/1), Presidio Co. (9/20), Reeves Co. (2/4), Ward Co. (2/5).
N. linearifolia var. *linearifolia*	MÉXICO: Coahuila (3/3). NEW MEXICO: Chaves Co. (1/1), Eddy Co. (1/3), Otero Co. (2/2),Socorro Co. (1/4). TEXAS: Culberson Co. (2/7), Reeves Co. (3/13), Ward Co. (3/6).
N. linearifolia var. *mexicana*	MÉXICO: Coahuila (1/1), Nuevo León (5/7).
N. gypsophila	MÉXICO: Chihuahua (2/6).
N. incana	MÉXICO: Coahuila (11/25).
N. johnstonii	MÉXICO: Coahuila (1/2).
N. powellii	MÉXICO: Coahuila (3/8).
N. gracilis	MÉXICO: Nuevo León (11/16), San Luis Potosí (4/8).
N. castillonii	MÉXICO: Coahuila (12/29).
N. turneri	MÉXICO: San Luis Potosí (12/36).
S. greggii	MÉXICO: Chihuahua (1/4), Coahuila (8/15), San Luis Potosí (3/7).

FLAVONOID CHEMISTRY

The utilization of flavonoid chemistry to gain insight into biological relationships within and among plant taxa is becoming a standard systematic approach. Studies of this nature have been used to discern relationships within hybrid swarms (Alston & Turner, 1963; Turner & Alston, 1959), to support taxonomic discrimination (Bierner, 1973; Cruden, 1972; Crawford, 1973; Gardner, 1974) and to suggest or support phyletic relationships within taxonomic groups (Stebbins *et al.*, 1963; Torres & Levin, 1964; Smith

& Levin, 1963; Mabry *et al.*, 1975). In the hope of obtaining insight concerning the relationships of *Nerisyrenia*, a chemical investigation was initiated.

Populations of all taxa of *Nerisyrenia* and one species of the closely related genus *Synthlipsis* were surveyed for their flavonoid components. Populations from throughout the distributional range of each taxon (Table II), representative of the range of morphological variation of each, were examined. Voucher specimens for all populations studied are deposited in The University of Texas Herbarium (TEX). Complete voucher citations are available from the author on request.

METHODS

Chromatographic profiles were established for each collection by extracting a small amount of leaf material overnight with 85% aqueous methanol. The resulting extract was spotted directly on Whatman 3 MM (46 × 57 cm) chromatographic paper. The papers were then developed descendingly in two dimensions; the first, for the long axis of the paper, consisted of tertiary butanol, glacial acetic acid and distilled water (3:1:1; v/v), TBA; the second consisted of glacial acetic acid and distilled water (15:85; v/v), HOAc. The chromatograms were air-dried after each run. To visualize the flavonoid components, the developed chromatograms were viewed over ultraviolet (UV) light (366 nm) in both the presence and absence of ammonia; the color of each spot was noted as was any ammonia induced change in color (Table III).

Isolation of flavonoids for structural analysis was accomplished by a combination of paper and column chromatography (see Bacon & Mabry, 1976 for brief summary of technique). Ultraviolet absorption spectra (Table III) were recorded for each compound isolated, using standard procedures (Mabry, Markham & Thomas, 1970), as well as nuclear magnetic resonance spectra for those compounds isolated in sufficient quantity.

All compounds isolated were glycosides; therefore, each was subjected to acid and enzyme hydrolysis for sugar determination. Sugars were identified by gas-liquid chromatography of their trimethylsilyl ether derivatives (Sweeney *et al.*, 1963; Mabry *et al.*, 1970).

RESULTS AND DISCUSSION

Nerisyrenia elaborates 40 flavonoids of which 31 were isolated and, for the most part, fully characterized. All compounds isolated have been oxygen linked glycosides of the flavonols kaempferol, isorhamnetin and quercetin (Table III). Their distribution among the species is shown in Table IV. A discussion of the significance of the flavonoid pattern within *Nerisyrenia* requires a short digression concerning some aspects of sugars and flavonol glycosides.

The known flavonol glycosides number about 250 (Harborne & Williams, 1975). The most common positions of glycosidic substitution in flavonols are positions 3 and 7 (Figure 1), but flavonols glycosylated in positions 5, 6, 8, 2′, 3′ and 4′ are known (Harborne & Williams, 1975). Sugars may be attached to the flavonol skeleton as single moieties at one position, monoglycosides, as single moieties at two positions or as a disaccharide at one position, diglycosides, and so on through the more highly glycosylated flavonoids.

In disaccharides, two like sugars or two different sugars may be involved. Variations in disaccharides can involve interglycosidic linkages, anomeric forms and ring sizes. Interglycosidic linkages may be between C-1 of one sugar and C-6 of the other, C-1 and C-2, C-1 and C-3 or C-1 and C-4 (see Figure 1). Often, the different linkages are given different names thus identifying the linkage and the sugars involved. For example, the following list indicates the trivial names for the known linkages between disaccharides of β-glucose (Harborne, 1967; Harborne & Williams, 1975; in nature these involve only D-glucose)

(a) 1 → 2 linked — sophorose
(b) 1 → 6 linked — gentiobiose
(c) 1 → 3 linked — laminaribiose
(d) 1 → 4 linked — cellobiose.

When L-rhamnose and D-glucose are involved in disaccharide linkages and rhamnose is the terminal sugar, the sugar moiety is termed as follows, the rhamnose carbon listed first:

(a) 1 → 6 linked — rutinose
(b) 1 → 2 linked — neohesperidose
(c) 1 → 3 linked — rungiose.

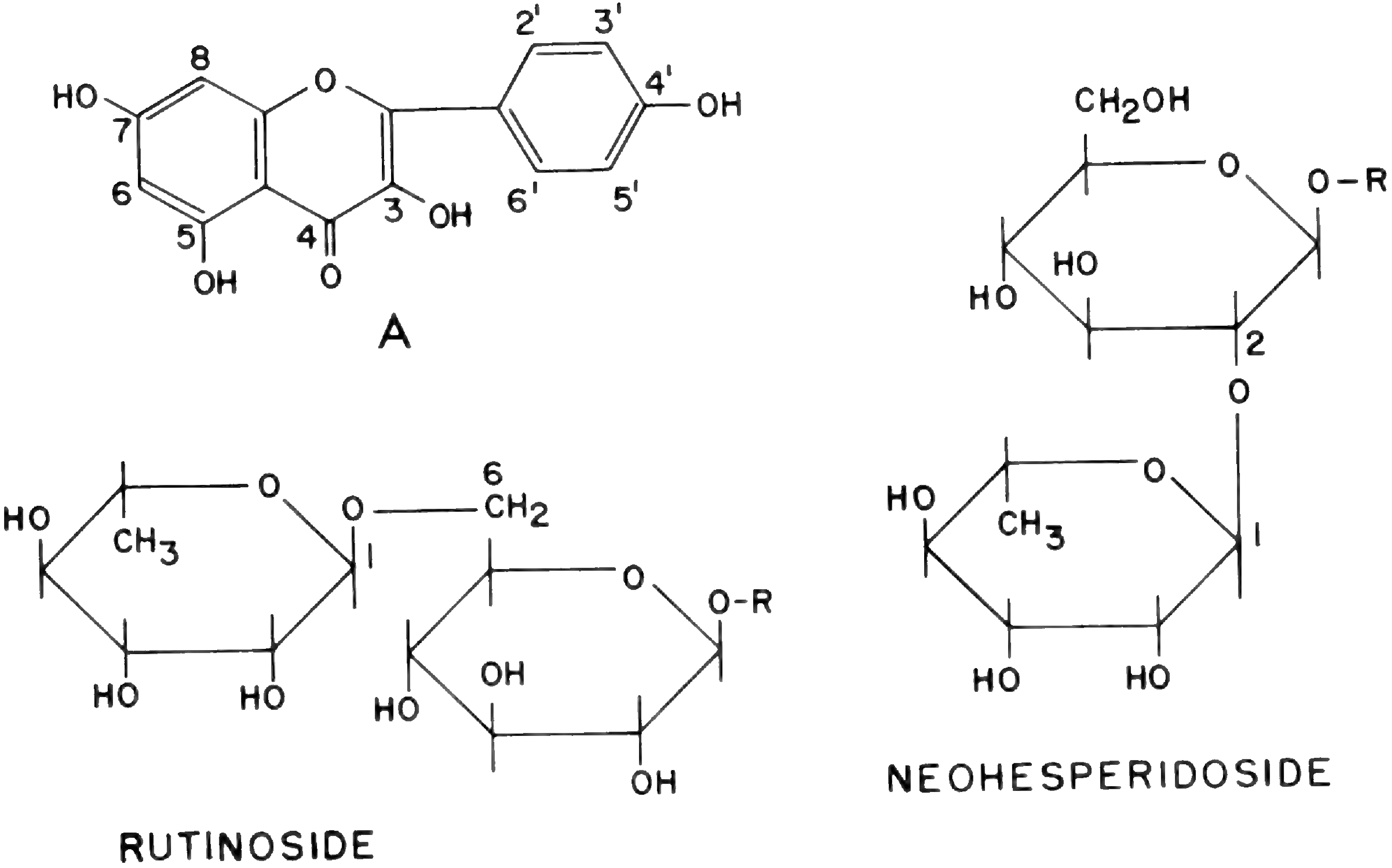

Figure 1. Numbering scheme for flavonoids and representative disaccharides showing different interglycosidic linkages.

While most species of *Nerisyrenia* produce some unique compounds or combinations which suggest species limits (Table IV), the flavonoid data have been most helpful in suggesting species relationships and phyletic groupings.

There is a significant dichotomy within the genus in flavonoid glycosylation patterns. *Nerisyrenia castillonii, N. turneri* and *N. johnstonii* all produce diglycosides (disaccharide types) utilizing glucose and/or galactose with the 1 → 2 linkage between the sugar moieties. The remaining species produce diglycosides containing glucose and/or galactose with the 1 → 6 sugar linkage. Furthermore, the neohesperidosides (1 → 2 linked rhamnoglucosides) are absent in the aforementioned species but are present in the remaining species.

Morphologically, *Nerisyrenia incana* is distinctive within the genus, and most closely resembles *N. johnstonii;* the two species share a base chromosome number of $x = 10$ (see CYTOLOGY). However, these species are very distinctive chemically and fall into opposite glycosylation dichotomies (Table IV). In contrast, *N. camporum*, $x = 9$, is almost identical, chemically, with *N. incana;* furthermore, *N. gypsophila*, although producing fewer compounds than either of the above two species, shares with them, with one exception, all the compounds it produces (Table IV).

Nerisyrenia linearifolia, N. gracilis, and *N. powellii* share several morphological characteristics, such as linear-spathulate leaves with mostly entire margins and a rhizomatous root system, which set these species apart from the species mentioned above. Their chemistry also serves to distinguish these species from the former group (Table IV) and, furthermore, distinguishes *N. linearifolia* from *N. gracilis* and *N. powellii.* Johnston (1941) suggested *N. gracilis* was most closely related to *N. linearifolia* (var. *linearifolia* of this treatment). However, the chemical evidence presented here implies that *N. gracilis* and *N. powellii* are more closely related to each other than either is to *N. linearifolia.*

The distinctive flavonoid chemistry of *Nerisyrenia castillonii, N. turneri* and *N. johnstonii* clearly unites these species as a phyletic unit (Table IV); their chromosomal base of $x = 10$ also separates these species from the bulk of the remaining species (see CYTOLOGY). In addition, their chemistry suggests that they have a phyletic history parallel to, but separate from, the other species within the genus.

Table III.

Compound Number and Identity, Chromatographic Properties and Ultraviolet Absorption Maxima of Nerisyrenia Flavonoids

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm)[a]					
	TBA	HOAc	UV	$+NH_3$	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	NaOAc+H_3BO_3
1. Acyl Iso-3-glucoside	.51	.23	P	Y	354 265s 253	415 330 270	404	400	386 322 274	359
2. Acyl Iso-3-galactoside	.51	.23	P	Y	354 265s 253	415 330 270	404	400	386 322 274	359
3. K-3-glucoside	.68	.53	P	G	348 300s 266	401 325 275	397	394	368 300 272	354
4. Iso-3-glucoside	.66	.43	P	Y	354 300s 266s 254	414 329 270	398	398	382 320 273	354
5. Q-3-glucoside	.55	.41	P	Y	356 290s 264s 254	406 329 270	436	399	400 326 273	378

Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm)[a]					
	TBA	HOAc	UV	$+NH_3$	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	$NaOAc+H_3BO_3$
6. K-3-galactoside	.68	.53	P	G	348 300s 266	401 325 275	397	394	368 300 272	354
7. Iso-3-galactoside	.55	.41	P	Y	357 300s 266s 253	416 331 270	407	401	388 322 274	356
8. Q-3-galactoside	.45	.43	P	Y	359 300s 268s 257	410 328 271	436	404	390 328 271	379
9. K-3-sophoroside	.60	.68	P	G	350 300 266	398 326 275	396	396	396 326 275	350
10. Iso-3-sophoroside	.46	.71	P	Y	354 298s 264s 252	410 320 270	407	402	399 322 273	355

Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm)^a					
	TBA	HOAc	UV	+NH_3	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	NaOAc+H_3BO_3
11. Iso-3-digalactoside	.46	.71	P	Y	354 298s 264s 252	410 320 270	407	402	399 322 273	355
12. K-3-neohesperidoside	.70	.79	P	BG	348 298s 265	394 324 274	398	397	380 306 273	350
13. Iso-3-neohesperidoside	.57	.81	P	BY	350 300s 268s 252	406 326 273	403	400	376 318 274	353
14. Q-3-neohesperidoside	.54	.78	P	BY	354 296s 266s 255	401 325 272	436	401	386 322 272	374

Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm)[a]					
	TBA	HOAc	UV	$+NH_3$	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	NaOAc+H_3BO_3
15. Iso-3-gentiobioside	.60	.50	P	Y	353 300s 264s 252	no data	403	394	380 322 270	358
16. Q-3-gentiobioside	.37	.46	P	Y	362 304s 263s 258	414 322 275	438	402	399 326 274	382
17. K-3, 7-diglucoside	–	–	P	YG	–	–	–	–	–	–
18. Iso-3, 7-diglucoside	.21	.76	P	YO	356 270s 257	404 295s 269 252s	403	400	415 265	360
19. Q-3, 7-diglucoside	.20	.62	P	YO	354 266s 256	397 267	434	403	393 265	377

Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*				Absorption Maxima (nm)[a]			
	TBA	HOAc	UV	+NH_3	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	NaOAc+H_3BO_3
20. Iso-3-glucoside 7-galactoside	.25	.68	P	YO	356 268s 254	408 300s 268	406	404	421 262	360
21. K-3-glucoside 7-gentiobioside	.12	.78	P	YG	348 320s 268	395 360s 300s 275 248	398	395	397 395s 267	351
22. Iso-3-glucoside 7-gentiobioside	.11	.80	P	YO	356 266s 254	416 291s 263	404	400	416 300s 262	360
23. Q-3-glucoside 7-gentiobioside	.10	.69	P	YO	359 269s 257	398 269	427	401	403 266	379

Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm)[a]					
	TBA	HOAc	UV	+NH_3	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	NaOAc+H_3BO_3
24. Iso-3-glucoside 7-glucogalactoside	.09	.81	P	YO	353 264s 253	423 272	406	400	440s 360 263s 253	357
25. Q-3-glucoside 7-glucogalactoside	.06	.72	P	YO	358 266s 255	402 268	441	404	416 263	381
26. K-3-sophoroside 7-glucoside	.22	.75	P	YG	346 263 240	408 365s 300s 274 248	396	396	398 265 260s	350
27. Q-3-neohesperidoside 7-glucoside	.16	.88	P	BY	354 268s 255	399 267	440	404	376 258	375

Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*				Absorption Maxima (nm)[a]			
	TBA	HOAc	UV	$+NH_3$	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	NaOAc+H_3BO_3
28. K-3, 7-digentiobioside	.07	.84	P	YG	350 268	397 292s 266 258	397	395	395 270	350
29. Iso-3, 7-digentiobioside	.06	.78	P	YG	357 262s 254	410 269	408	403	419 262	358
30. K-3-glycoside	.70	.58	P	G	348 262	402 328 272	395	398	372 275	350
31. Iso-3-glycoside	.37	.52	P	Y	356 300s 264s 253	418 330 272	403	400	388 318 271	–
32. Iso-3-glycoside	.27	.70	P	YO	353 300s 267s 254	419 329 272	404	404	–	–

Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*				Absorption Maxima (nm)[a]			
	TBA	HOAc	UV	+NH_3	MeOH	NaOMe	$AlCl_3$	$AlCl_3$+HCl	NaOAc	NaOAc+H_3BO_3
33 Unknown	–	–	P	YG						
34 Unknown	–	–	P	YO						
35 Unknown	–	–	P	YO						
36 Unknown	–	–	P	YO						
37 Unknown	–	–	P	BY						
38 Unknown	–	–	P	Y						
39 Unknown	–	–	P	YO						
40 Unknown	–	–	P	YG						

+Iso=Isorhamnetin, Q=Quercetin, K=Kaempferol.

*P=purple, Y=yellow, G=green, B=brown, O=orange.

[a] only Band I absorption maximum is shown for $AlCl_3$, $AlCl_3$+HCl, NaOAc+H_3BO_3.

Additional support for the phyletic significance of the glycosylation dichotomy within *Nerisyrenia* comes from the flavonoid pattern of *Synthlipsis greggii*. No flavonoids have, as yet, been isolated from this taxon. Nevertheless, the chromatographic profile of this species is very similar to that of *N. turneri* and *N. castillonii;* clearly, this taxon, too, is glycosylating under a 1 → 2 sugar linkage scheme involving glucose and/or galactose. Its chromosomal base is $x = 10$ (see CYTOLOGY).

GENERIC RELATIONSHIPS

Despite some morphological diversity, the taxa composing *Nerisyrenia,* are thought to be more closely related among themselves than any one is to another genus and thus form a natural phyletic unit. Although several genera have been suggested, as direct or indirect relatives of *Nerisyrenia,* I believe only the genus *Synthlipsis* has close affinities.

Although Gray (1850) in his original description of *Nerisyrenia* (as *Greggia*) noted the similarities of *Nerisyrenia* and *Synthlipsis,* subsequent workers such as Bentham and Hooker (1862) and Von Hayek (1911) related *Nerisyrenia* (as *Greggia*) to *Erysimum* and *Syrenia;* indeed, in both the above treatments, *Synthlipsis* and *Nerisyrenia* were placed in different tribes. Bentham and Hooker noted, however, that *Nerisyrenia* had probable affinities with *Synthlipsis*.

In relating *Nerisyrenia* to *Erysimum* and *Syrenia,* Bentham and Hooker emphasized habit, cotyledon position and silique shape; Von Hayek emphasized fruit shape, the presence of branched trichomes, shape of the stigma and characters of the nectaries.

The habit of some species of *Erysimum* is similar to some species of *Nerisyrenia,* but the genera are quite distinct in most respects, as outlined in the following listing:

Erysimum	**Nerisyrenia**
Fruits strongly compressed or somewhat 4-angled.	Fruits rarely compressed, never 4-angled; usually terete to obcompressed.
Trichomes usually coarse and T-shaped, sparsely if at all branched.	Trichomes not coarse, dendritically branched.

Cotyledons accumbent to incumbent.	Cotyledons incumbent.
Sepals erect at anthesis.	Sepals spreading to reflexed at anthesis.
Petals yellow to maroon.	Petals white.

I have not made a thorough survey of the nectaries of *Erysimum*, but Snogerup (1967a) has shown that in *Erysimum* sect. *Cheiranthus* the variation in morphology of these glands renders them virtually useless as taxonomic characters.

Chromosomal evidence is also suggestive of the distinctive nature of the two genera. *Erysimum* is multibasic with $x = 6$, 7 and 8 (Snogerup, 1967b); however, several North American taxa have chromosome numbers of $2n = 36$ (Rollins, 1966, 1970), and Rollins (1966) suggests that these taxa have a base number of $x = 9$. Snogerup (1967b) has proposed that the taxa with $2n = 36$ are hexaploids with a base of $x = 6$; this suggestion is strengthened by the fact that at least one species reported as $2n = 36$, *Erysimum pallasii*, has also been reported as $n = 12$ and $2n = 24$ (Mulligan, 1966); *Nerisyrenia* is essentially dibasic with $x = 9$ and 10.

The flavonoid chemistry of *Erysimum*, as is the case for most Cruciferae, has received only cursory attention. However, the scanty data available for *Erysimum* (Maksyutina, Litvinenko & Kovalev, 1966), when compared to the more completely known chemistry of *Nerisyrenia*, suggest the two taxa are distinct; *Erysimum* utilizes different sugar combinations in its accumulated flavonoid glycosides. In short, considering the above, I can see no justification for relating *Nerisyrenia* closely to *Erysimum*.

The relationship of *Syrenia* to *Nerisyrenia* has yet to be fully studied. I have studied only one specimen of the former taxon. Nevertheless, the distribution of the genus in the Mediterranean region of Europe and its morphological differences, including erect, saccate sepals, erect, yellow petals, and mostly tetragonally-shaped fruits (Vasil'chenko, 1939), clearly delineate this taxon from *Nerisyrenia*. While *Syrenia* is unknown chromosomally, the flavonoids of one species have been investigated (Maksyutina, 1967) and are distinct from those of *Nerisyrenia; Syrenia siliqulosa* accumulates flavonoids glycosylated at the 4′-position, a substitution pattern not found in *Nerisyrenia*, and it also produces disaccharides of glucose and rhamnose in which the glucose moiety is the terminal

Table IV.

Distribution of Flavonoids in Nerisyrenia.

	Compound Number																																							
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
camporum			X	X	X							X			X	X	X	X			X	X						X		X			X							
incana			X	X	X							X			X	X		X			X	X						X	X	X			X							
gypsophila			X	X				X				X									X	X							X											
linearifolia var. *linearifolia*	X	X	X	X	X							X		X		X			X				X				X							X	X	X				
linearifolia var. *mexicana*			X	X	X							X		X				X	X			X	X				X							X						
powellii			X	X		X	X	X				X	X							X		X		X							X	X								
gracilis			X			X	X	X					X							X		X		X	X						X	X					X			
castillonii				X			X		X	X	X															X												X	X	X
turneri				X			X		X	X	X															X												X	X	X
johnstonii							X			X	X																											X		

sugar, a reversal of the condition found in *Nerisyrenia.*

By including them in the same subtribe, Schulz (1936) related *Nerisyrenia* to several genera, including *Capsella, Heidinia, Hornungia, Hutchinsia, Phlegmatospermum, Mancoa, Cibotarium* and *Synthlipsis.* Except for the latter three taxa, all the above genera are native to Europe, Asia, the Mediterranean area, or Australia. Although lack of access to research material of these non-American genera has prevented a thorough assessment of their relationship to *Nerisyrenia,* my preliminary study tends to indicate a more remote relationship to *Nerisyrenia* than that shown by the American genera. *Cibotarium, Mancoa* and *Synthlipsis* are North American in distribution and are found primarily in the Chihuahuan Desert (Rollins, 1941, 1957, 1959). However, on morphological grounds *Cibotarium* and *Mancoa* are distinct from *Nerisyrenia.* Both the former have much smaller flowers and distinctive fruit shapes as compared to *Nerisyrenia,* although the fruits of both are more or less obcompressed. Furthermore, *Cibotarium* has nearly equal, exserted stamens with purplish anthers (Rollins, 1941a), while *Nerisyrenia* has tetradynamous stamens with yellow anthers. Nevertheless, some species of *Cibotarium* have apically notched fruits as found in two species of *Nerisyrenia,* and further study may prove this genus to be more closely related to *Nerisyrenia.* Information as to chromosome number and chemistry of this group is lacking and reflects its sporadic, highly localized occurrence (Rollins, 1957) and relatively rare collection. Until such information can be obtained and studied, its relationship to *Nerisyrenia* is speculative.

Mancoa, through the anomalous species, *M. pubens,* was related by Rollins (1959) to *Synthlipsis* (through its resemblance to *S. elata*). I would agree that *M. pubens* is related to *Synthlipsis* and, therefore, to *Nerisyrenia.* However, in view of the distinctive morphology of *Mancoa,* and in the absence of chromosomal or chemical data for this taxon, speculation as to its direct relationship to *Nerisyrenia* is, at best, tenuous.

In considering the relationship of *Nerisyrenia* and *Synthlipsis,* Rollins (1939) noted the ample technical characters which could be used to distinguish the two genera; these characters included cotyledon position, stigma shape, fruit characters, number of seeds per silique, seed size and presence or absence of dilated petal bases. However, in a later treatment of *Synthlipsis,* Rollins (1959) was less convinced as to the generic distinctness of the two taxa, primarily because of the description of two new species of *Synthlipsis* which was not compatible with some of the previously enumerated differences. For instance, *S. elata* proved to have numerous small seeds with incumbent cotyledons, a state more like *Nerisyrenia* than *Synthlipsis*. Nonetheless, he maintained the taxa at the generic level, noting that merger of the two probably would not be fully warranted even with further study.

I fully concur with Rollins in maintaining the two taxa at the generic level. Even though some characters "overlap" between the two, such as cotyledon position, sepal and petal shape and position at anthesis, and trichome characters, there are many characters which are more or less limited to one or the other of the taxa, and in combination display clear distinction between the two genera. These differences are listed below:

Nerisyrenia	**Synthlipsis**
Perennials.	Annuals (perennials in *S. densiflora*).
Fruit margins never carinate.	Fruit margins carinate.
Fruit apex usually entire, notched only in *N. incana* and *N. johnstonii*.	Fruit apex notched.
Fruits obcompressed or terete.	Fruits obcompressed.
Stigma deltoid-sagittate, rarely cylindrical.	Stigma discoid (rarely deltoid in *S. densiflora*).
Petal base dilated and usually denticulate.	Petal base entire, not dilated.
Species predominantly gypsophilous.	Species not gypsophilous.

It is unfortunate that only one of the three species of *Synthlipsis* has been available for cytological and chemical analysis, but *S. densiflora* and *S. elata* are known only from the type collections (Rollins, 1959). Nevertheless, the occurrence of $n = 10$ in *S. greggii* together with a flavonoid pattern similar to that found in *Nerisyrenia johnstonii*, *N. castillonii* and *N. turneri*, all of which appear to be based on $x = 10$, further emphasizes the close relationship between the two genera. Indeed, it might well be argued that the differences enumerated above are merely "technical", and the two taxa might best be treated as a single genus. But, in a family where generic limits are often "arbitrary" and based "more on tradition than conviction" (Rollins, 1959, 1960, 1962; Rollins & Shaw, 1973), the morphological distinctions presented above would seem sufficient to mark them as genera.

PHYLOGENY

In attempting to reconstruct the phylogeny of *Nerisyrenia,* I have experienced considerable difficulty in determining the ancestral and derived state of morphological characters. This difficulty is, apparently, commonly encountered within the Cruciferae and stems, perhaps, from the fact that many genera, and species within genera, are the "end points of several evolutionary lines" in which intermediate groups are extinct; the "reading" of evolutionary trends is, thus, made difficult (Rollins & Shaw, 1973; Shaw, 1972). Moreover, the "evolutionary stimuli" which have molded the present species of *Nerisyrenia,* primarily extreme aridity and diverse edaphic and topographic settings, are those "stimuli" under which morphological relationships might well be obfuscated, due to relatively rapid divergence with concomitant morphological changes (cf. Stebbins, 1952; Raven, 1964), or misleading, due to parallelisms and associated morphological convergence (cf. Tucker, 1974; Went, 1971). Indeed, I believe that such events have occurred in the history of *Nerisyrenia;* consequently, in constructing the phylogeny of *Nerisyrenia,* I have considered cytological and distributional data and the geological history of the occupied area. I have also relied on the flavonoid data which suggest species relationships and further indicate two evolutionary lines within the genus. In treating the phylogeny of the group, I recognize the two chemical lines as distinct, although no formal taxonomic recognition is accorded them since similar morphological expressions are found in each grouping.

In order to visually express my concept of the relationships of the species of *Nerisyrenia,* I have adopted the "Wagner Divergence Index" (Wagner, 1971; see Hardin, 1957); under this scheme, a numerical value of 0 or 1 is given to those character expressions presumed to be "primitive" or "advanced", respectively. Intermediate character states may be assigned a value of 0.5. The summation of these value assignments for each taxon then represents a numerical expression of the degree of advancement of that taxon from the hypothetical, "primitive" state. These summations may then be plotted on a set of concentric rings to portray a "phyletic tree" for the genus. Listed below are the characters which I feel are useful as phylogenetic indicators and the expressions or state of the characters which I presume to be ancestral or derived; I have based my assumptions on an assessment of the distribution of these character states within *Nerisyrenia* and the related genus *Synthlipsis:*

CHARACTER	STATE	
	Ancestral	*Derived*
1. Fruit shape	obcompressed	terete (compressed)
2. Fruit apex	notched	entire
3. Habit	herbaceous	suffruticose
4. Root	taproot	rhizomatous
5. Leaf shape	broad	linear-spathulate
6. Leaf margin	not entire	entire
7. Vestiture	pubescent	glabrous
8. Base chromosome number	$x = 10$	$x = 9$

The evaluation of these character states for each taxon is given in Table V; the degree of advancement of each taxon is shown in Figure 2.

The relationships illustrated in Figure 2 are based largely upon morphology, although chemical evidence has been utilized in the recognition of this dichotomy. Some minor chemical incongruities exist in the line in which *Nerisyrenia incana* is basal; indeed, a better "chemical phylogeny" would result by assuming that *N. powellii* and *N. castillonii* are the more "primitive" taxa, a reversal of that proposed on morphology. This suggestion arises from the fact that *N. johnstonii, N. castillonii* and *N. turneri* all utilize glucose and galactose as glycosidic constituents. In the other grouping, the species considered "primitive" on morphological grounds do not utilize galactose, whereas galactosides occur sporadically in the more advanced taxa and become quite frequent in the most advanced species. If it is assumed that the original ancestor of

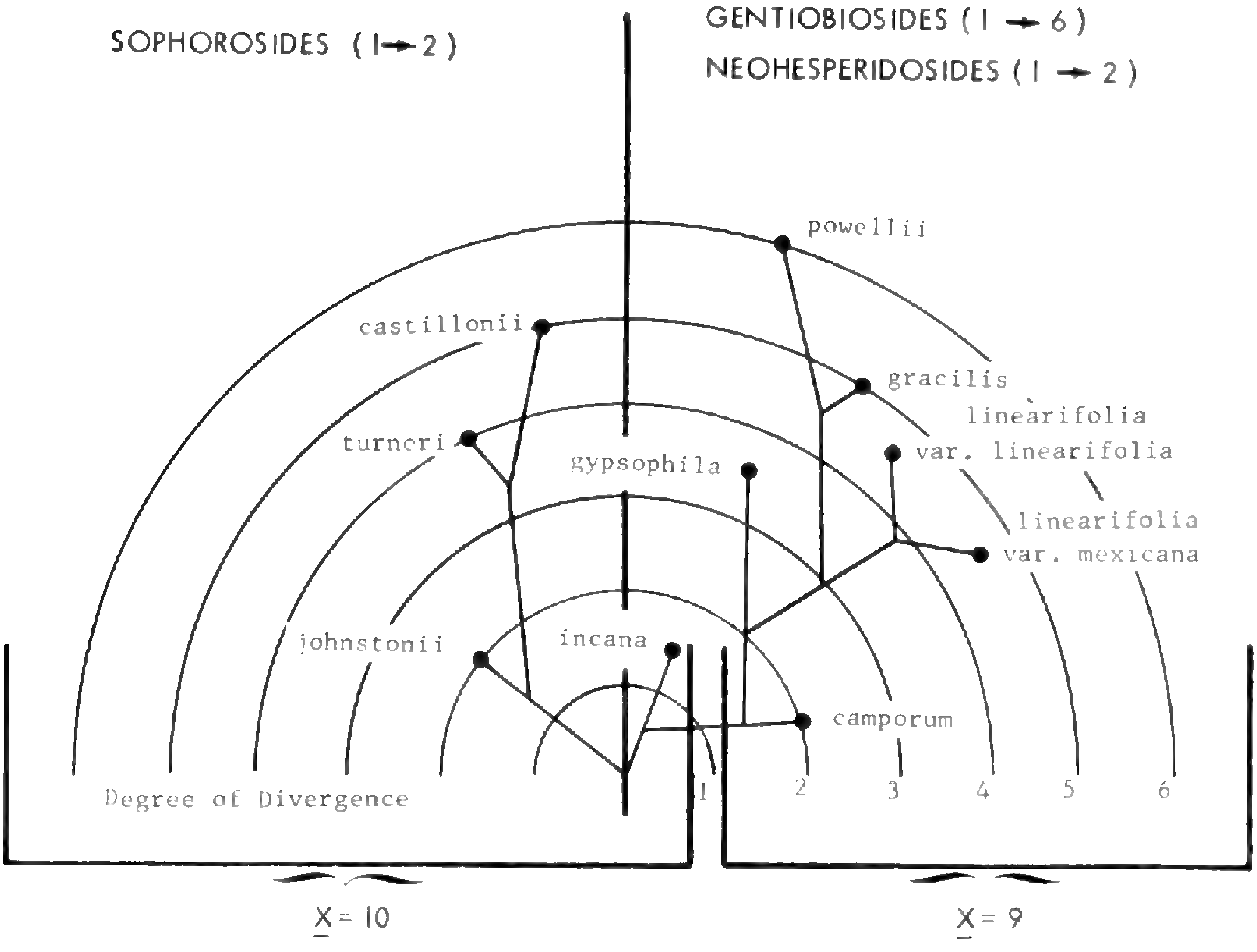

Figure 2. Diagram of species relationships in *Nerisyrenia*.

Nerisyrenia had the ability to produce both types of glycosides, then one might expect this ability to be retained in the more primitive species. This assumption would favor *N. powellii* and *N. castillonii* as the most primitive species. Furthermore, by assuming that the former species are primitive, one finds a progressive decline in the ability to produce galactosides in the "powellii" line, resulting in a decrease in the complexity of the flavonoid profile, while a similar trend is seen in the "castillonii" line, since *N. johnstonii* would then be an advanced taxon, and it lacks the ability to produce the triglycosides characteristic of *N. turneri* and *N. castillonii.* Under this scheme, the trend in flavonoid chemistry would support the generality proposed by Mabry (1973) that within a genus reduction in the complexity of the secondary products chemistry, reflecting a loss of biosynthetic ability, is indicative of evolutionary advancement. Such trends have been noted in several genera of plants including *Vernonia* (Compositae) (Mabry *et al.*, 1975; Abdel-Bassett, 1973), *Linum* (Linaceae) (Gianassi & Rogers, 1970), *Ulmus* (Ulma-

Table V.

Divergence Index Values for Species of Nerisyrenia

	camporum	incana	gypsophila	powellii	gracilis	linearifolia linearifolia	linearifolia mexicana	johnstonii	castillonii	turneri
1. Fruit shape	0.0	0.0	0.0	1.0	1.0	0.5	0.5	0.0	1.0	1.0
2. Fruit apex	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0
3. Habit	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0
4. Root	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0
5. Leaf shape	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0
6. Leaf margin	0.0	0.5	0.5	1.0	1.0	1.0	1.0	1.0	0.0	0.0
7. Vestiture	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
8. Basic chromosome number	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0
TOTAL	2.0	1.5	3.5	7.0	6.0	5.5	5.5	2.0	5.0	4.0

ceae) (Bate-Smith & Richens, 1973), *Geranium* (Geraniaceae) (Bate-Smith, 1973), *Chamaesaracha* (Solanaceae) (Averett, 1970) and *Oenothera* (Onagraceae) (Howard, 1971). However, Harborne (1967) takes a contrasting view and suggests that increasing complexity of glycosylation patterns is indicative of evolutionary advancement; such has been shown to be the case in *Baptisia* Harborne, 1971; Turner, 1969, 1971). Both the above phenomena have occurred in the evolution of the species in *Lasthenia* (Compositae) and *Pyrus* (Rosaceae) (Bohm, Saleh & Ornduff, 1974; Challice & Westwood, 1973). The chemical phylogeny proposed for *Nerisyrenia* flavonoids, on morphological grounds, would fit into the evolutionary scheme proposed by Harborne.

Since the chemical evidence varies somewhat from my interpretation of the morphological trends, I present below the evidence leading to the acceptance of *Nerisyrenia incana* and *N. johnstonii* as the most "primitive" species within the genus.

Both *Nerisyrenia johnstonii* and *N. incana* are localized endemics in south-central Coahuila. The latter occupies the Cuatro Ciénegas Basin and extends further south in the valleys leading away from the central basin; the former is known from only a single locality approximately two kilometers west of the small ejido of Las Delicias, Coahuila, which is approximately 80 miles southwest of Cuatro Ciénegas.

The area occupied by *Nerisyrenia incana* is unusual for the Chihuahuan Desert as it supports several natural streams and ponds; those areas with constant water support aquatic to semi-marsh vegetation (Meyer, 1973; Minckley, 1969; Gilmore, 1947). However, *N. incana* never occurs in the wet areas and is limited to the arid gypseous dunes or saline flats of the area. The single site occupied by *N. johnstonii* appears to be a more mesic habitat, and the species is limited to the area around a natural spring. While the spring has been diverted recently by a concrete aqueduct to supply water to the village of Las Delicias, a deep arroyo, approximately 100 feet deep, attests to the former direction of flow of the spring effluent.

These species share general morphological similarities such as fruit shape, leaf form, a tendency for the fruits to be congested toward the raceme apex, and they also share a diploid chromosome number of $n = 10$. The apical notch of their fruits is found in no other species of *Nerisyrenia* but is present in all species of the related genus *Synthlipsis;* the only species of *Synthlipsis* known chromosomally also has a chromosome number of $n = 10$ (Rollins, 1966; this study). On morphological grounds, both species are somewhat "isolated" from the other members of their respective lines, especially in their fruit morphology, suggesting, perhaps, that they are "old" species, now relict in their distribution (cf. Stebbins & Major, 1965). It is noteworthy that the only perennial species of *Synthlipsis, S. densiflora,* also has a more congested raceme than the other species of *Synthlipsis* and is known only from limestone bluffs on the southwest corner of the Sierra de la Fragua, the same mountain complex in which *N. johnstonii* occurs.

However, the largely polyploid chromosome numbers for *Nerisyrenia castillonii* and *N. powellii*, the diploids either rare or unknown, imply a considerable age for these taxa (cf. Stebbins & Major, 1965). Under such an assumption, *N. johnstonii* and *N. incana* would have to be considered as derived, and then the origin of *N. johnstonii* poses a problem. On morphological grounds, derivation of *N. johnstonii* directly from *N. castillonii* does not seem feasible. An origin for *N. johnstonii* from some now extinct diploid progenitor must be inferred.

No such problem exists as regards *Nerisyrenia incana* since a possible diploid progenitor exists in *N. camporum*. In this case, however, one must assume an aneuploid gain in chromosome number, a possible event (Lewis & Roberts, 1956; see Walker, 1972; Stebbins, 1971, p. 18), although, in plants, not as common as aneuploid loss (see Brown, 1972, for discussion of both types of change); and one must assume the morphological similarities between *N. incana* and *N. johnstonii* are the result of parallel evolution. Clearly, parallelisms in habit, fruit shape and root type have occurred in *Nerisyrenia*, but where these parallelisms have occurred, *e.g.*, between *N. castillonii* and *N. powellii*, and to a lesser extent, between *N. gracilis* and *N. turneri*, the species concerned exist under very similar environmental conditions. The apparent habitat differences between *N. incana* and *N. johnstonii* would seem to negate a strong argument for parallelism, and their similarities seem best considered as indicative of their origin from now extinct, ancestral stocks of *Nerisyrenia*.

The Cuatro Ciénegas Basin has received a relatively large amount of attention from biologists due to its unique permanent water system. The aquatic habitats of the basin harbor a number of endemic fishes and snails, while the terrestrial fauna includes several endemic scorpions and reptiles; many of the endemic species are considered to be relicts (Meyer, 1973; Minckley, 1969; Cole, 1968, p. 476; Miller, 1968; Taylor, 1966; Hubbs & Miller, 1965; Webb, Minckley & Craddock, 1963). The aquatic habitats of the area are inferred to be geologically old and stable; Taylor (1966) has postulated an early to mid-Tertiary isolation for the ancestral stock of the snail fauna and suggests the valley itself, or at least the aquatic habitats, is no younger than Pliocene and may be as old as early Oligocene in age. Miller (1968) suggests an early Pliocene-late Miocene isolation for some of the fishes in the area.

The recent work of Meyer (1973) would also lend support to the suggestion that environmental stability has long characterized the Cuatro Ciénegas Basin. Meyer (1973) has shown, by examination of fossil pollen profiles cored from the valley floor, that the vegetation occupying the basin floor during mid-Wisconsin time, ca. 40,000 years ago, was essentially the same as it is today. There was a vertical lowering of the vegetation now restricted to the higher elevations of the surrounding mountains, suggesting cooler, perhaps moister conditions, as recorded for other areas in the northern Chihuahuan Desert (Martin & Mehringer, 1965; Wells, 1966; Flint, 1971, pp. 503–506), but the descending woodland did not invade the valley floor. Meyer suggests that the unique gypseous-saline edaphic conditions of the basin floor prevented such an invasion. These results, too, render invalid the suggestion by Minckley (1969) and Cole (1968, p. 476) that the basin was covered by a large Pleistocene lake(s). Implicit from these results is the inference that the floor of the Cuatro Ciénegas Basin has been a stable habitat throughout Quaternary time, perhaps longer, and was essentially unaffected by the climatic changes wrought by the glacial periods.

The age of the Cuatro Ciénegas Basin may be estimated as middle Pliocene since the mountains surrounding the basin are part of the Sierra Madre Oriental (Gilmore, 1947; King, 1935) which was uplifted during that period (Garfias & Chapin, 1949; Schuchert, 1935). The area has been available for occupation for a long period of time, and under the stable conditions inferred for the basin, one might expect to find populations not greatly changed from their ancestral state.

The evidence presented above, showing that *Nerisyrenia incana* and *N. johnstonii* share morphological similarities (some of which are also found in the related genus *Synthlipsis*), thought not to be due to parallelism, that they share a diploid chromosome number of $n = 10$ (also found in *Synthlipsis*), and that they occupy a relatively old and stable habitat, strongly suggests that these species are "primitive" as suggested in Figure 2.

The origin of *Nerisyrenia* clearly was in Mexico; the concentration of the diploid populations, the representation of all species in Mexico and the presence of ancestral types in this region make any other origin very unlikely. The age of the taxon is less certain, as it is in any group in which fossil evidence is unavailable. However, the Cruciferae was certainly evolving by Oligocene time since fossil fruits referable to the genus *Thlaspi* have been found in an upper Oligocene flora from the Ruby River Basin in Montana (Becker, 1961). Also, fossil pollen belonging to the family has been reported from Cretaceous deposits in New Zealand (see Rodman, 1974), pointing to an even earlier origin for the family. The evidence previously presented indicates that the area occupied by the "most primitive" species in the genus was available for occupancy by mid-Pliocene time. It is also apparent that *Nerisyrenia* has evolved in response to increasing aridity and edaphic diversity, and arid conditions did not become regional features until late Pliocene (Axelrod, 1950, 1958, 1970). Certainly, the uplifting of the Sierra Madre Oriental accelerated the trend toward aridity in the eastern portions of the Chihuahuan Desert. The distribution of *Nerisyrenia* suggests that it has kept pace with this development of aridity. Considering all this evidence, I would suggest that the genus probably had a Pliocene origin.

The ancestors of *Nerisyrenia* probably were located in the east-central portion of the present Chihuahuan Desert and existed under relatively more mesic conditions. The uplift of the Sierra Madre Oriental brought increasingly arid conditions to the region, resulting in widespread extinction of the ancestral group. Some populations persisted, however, in locally mesic habitats, as represented today by *N. johnstonii.* Other populations expanded under the increasing aridity, perhaps due to their previous occupation of localized "dry spots", therefore, being somewhat pre-adapted to the arid conditions (cf. Axelrod, 1950, 1967, 1972); these populations may have been somewhat divergent from the larger body of the ancestral stock, at least in their flavonoid chemistry, and the net result of this early evolutionary period was the establishment of the two "chemical lines" present today.

In the "incana" line, a reduction of chromosome number from $x = 10$ to $x = 9$ occurred. The more aggressive $x = 9$ stock expanded, and the $x = 10$ populations were restricted in range, as represented today by *Nerisyrenia incana.*

As the $x = 9$ line expanded in range, it encountered numerous localized areas where unique edaphic factors, such as gypsum, were present. In the expanding population, some individuals were predisposed towards this restrictive soil type and became established. These individuals subsequently were isolated due to the withdrawal of the larger body of the progenitor populations in response to local climatic fluctuations such as extended localized drought (cf. Raven, 1964; Lewis, 1966). The derivative populations then diverged, the colonizers themselves being, perhaps, somewhat divergent from the "typical" ancestors, under the combined effects of selection and drift and left *N. gypsophila.* Alternatively, the derivative populations may have diverged under conditions of neighboring sympatry through disruptive selection (cf. Antonovics & Bradshaw, 1970; McNeilly & Antonovics, 1968; Murray, 1972, pp. 87–110; Grant, 1971, pp. 119–122).

The rhizomatous species of the "incana" line are thought to have had their origin in a similar event. *Nerisyrenia linearifolia* is viewed as arising in some localized gypseous area in the central Chihuahuan Desert; it subsequently spread north and south, and regional selection pressures caused the divergence of the two varieties.

The progenitor population(s) of *Nerisyrenia powellii* and *N. gracilis* probably arose as a later offshoot from the "stock" which gave rise to *N. linearifolia.* As these populations diverged from their ancestors, they were able, also, to expand their range, but their emigration was primarily to the south. Again, regional differences in selection pressures resulted in the divergence of the ancestral group into *N. powellii* and *N. gracilis.*

A similar history is envisioned for the "johnstonii" line with similar evolutionary events having occurred. The products of these speciational events were "less successful", however, than those of the "incana" line, and today, only the three species remain.

ACKNOWLEDGMENTS

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TAXONOMY

Nerisyrenia Greene, Pittonia **4:** 225. 1900. *Nom Nov.* Based on *Greggia* A. Gray.

Greggia A. Gray, Smithson. Contrib. Knowl. 3(5): 8. 1850, non Gaertn. 1788, nec. Engelmann, 1848. TYPE: *G. camporum* A. Gray.

Parrasia Greene, Erythea **3:** 75. 1895, non Raf., 1847. *Nom. Nov.* Based on *Greggia* A. Gray.

Suffruticose or herbaceous, often rhizomatous perennials, 0.5 to 6.0 dm tall, pubescent throughout (glabrous in one species), densely to moderately so, with sessile to long-stalked, dendritically branched trichomes. Stems few to many from a usually woody taproot or caudex, upright, ascending to decumbent, branching freely or the branching somewhat restricted. Leaves 10–84 mm long, 1–40 mm broad, terete to flattened, often succulent; linear, oblanceolate, spathulate to elliptic in outline, attenuate-subpetiolate at base, acute to obtuse at apex; margins entire, repand to markedly dentate, weakly revolute in some. Inflorescence racemose, elongating in fruit. Sepals 5–10 mm long, 1–3 mm broad; linear-oblong, lanceolate to oblanceolate in outline, non-saccate, acute to obtuse at apex; margins scarious; spreading at anthesis, reflexing with age. Petals flaring just prior to anthesis, 8–16 mm long, 4.5–9.0 mm broad, white, often fading lavender; the blade obovate, spathulate to broadly elliptic, narrowing rather abruptly to a short claw, the claw dilated and denticulate at base; margins of the blade entire; the midnerve and its branches often yellow in lower 1/3–1/2 of petal. Stamens 5–9 mm long, exserted, divergent; anthers 2–4 mm long, introrse, sagittate, curling with age; filaments 4.0–7.5 mm long, terete to slightly flattened, glandular tissue present, subtending the filaments. Infructescence 4–45 cm long, included to well exserted above the leaves, lax to congested; pedicels 5–20 mm long, expanded at the apex, divaricately ascending to recurved. Siliques 6–40 mm long, 1–9 mm wide, linear-oblong to obovate in outline, terete, compressed or obcompressed, straight, curved to tortuous; valves obtuse-truncate to acute at apex, obtuse at base, with an often obscured single lateral line from base to apex, not carinate. Style persistent, 1.5–6.5 mm long, glabrous. Stigma 0.4–1.5 mm long, sagittate-deltoid, somewhat decurrent on the style. Replum 0.5–3.6 mm broad; septum entire, translucent, with a prominent nerve extending from base to apex. Seeds numerous, 40–100 per fruit; 1.2 mm or less long, less than 1 mm broad; ovate-elliptic to oblong, plump to slightly flattened; wingless; seed coat slightly roughened, yellow to yellow-brown; cotyledons incumbent. TYPE SPECIES: *Nerisyrenia camporum* (A. Gray) Greene.

KEY TO THE SPECIES

1. Broadest leaves 8 mm broad or more. . . . . 2.
2. Plants glabrous, or with a few dendritically branched trichomes along the leaf margin. . . . . 1. *N. johnstonii.*
2. Plants pubescent, the pubescence moderate to dense. . . . . 3.
3. Siliques markedly obcompressed, valves rounded truncate at apex. . . . 4.
4. Siliques 4-9 mm broad, shallowly to deeply notched at apex, valves extending 0.5-1.5 mm past insertion of style; plants woody, pubescence incanous. . . . . 4. *N. incana.*
4. Siliques rarely 4 mm broad, rarely shallowly notched at apex; plants green to gray, never incanous. . . . . 5.
5. Replum 1.1 mm broad or less; pedicels of fruit rather rigidly ascending, never recurved; silique never strongly curved; plants suffruticose. . . . . 6. *N. gypsophila.*
5. Replum 1.0-1.4 mm broad; pedicels ascending to divaricately spreading or recurved; silique straight to strongly curved inward, in conjunction with pedicel, often sigmoid; plants not suffruticose. . . . . 5. *N. camporum.*
3. Siliques terete-subterete or somewhat compressed, valves tapering to the style. . . . . 6.
6. Plants arising from a woody taproot or rhizome, never appearing tufted or caespitose; leaves 7-22 mm broad; styles 3.5 mm long or longer; plants suffruticose. . . . . 3. *N. castillonii.*
6. Plants usually arising from a slender rhizome, usually appearing caespitose; leaves 4-8 mm broad; styles usually less than 3.8 mm long. . . . . 2. *N. turneri.*
1. Broadest leaves less than 8 mm broad. . . . . 7.
7. Plants suffruticose. . . . . 8.
8. Siliques strongly obcompressed, valves rounded truncate at apex, replum 1 mm broad or less. . . . . 6. *N. gypsophila.*
8. Siliques terete to compressed, valves tapering to the style. 9. *N. powellii.*
7. Plants not suffruticose. . . . . 9.
9. Valves of siliques truncate-rounded at apex, or if rarely tapering to the style then plants of the United States. . . . . 7. *N. linearifolia.*
9. Valves of siliques tapering to the style; plants of Mexico. . . . . 10.
10. Infructescence rarely exceeding the leaves but if so then the siliques tortuous and valves papery; fruits slender, valves weakly to strongly constricted between the seeds; leaves usually less than 2.5 mm broad with entire margins. . . . . 8. *N. gracilis.*
10. Infructescence usually exceeding the leaves; fruits not slender, valves rarely constricted between the seeds; leaves mostly over 2.5 mm broad with sinuate to dentate margins. 2. *N. turneri.*

1. **Nerisyrenia johnstonii** Bacon sp. nov. TYPE: **México.** COAHUILA: about 1 km W of Las Delicias at and near spring, top of alluvial fan on side of mountain, 24 Mar 1973, *M. C. Johnston, T. L. Wendt & F. C. Chiang 10388.* (Holotype, TEX!; Isotypes, to be distributed.)

Herbae perennes ad 6 dm altae radice palari radicatae glabrae praeter omnino raro margines foliorum. Caules plures vel multi erecti vel modice effusi. Folia succulenta lanceolata vel oblanceolata subpetiolata apice obtusa vel acuta margine integra vel interdum sinuato-dentata leniter undulata, inferiora 40–60 mm longa 15–25 mm lata. Sepala 4.5–7.0 mm longa 1.5–2.5 mm lata, subulata vel oblanceolata apice acuta vel obtusa demum effusa. Petala 8–11 mm longa 5–8 mm lata, late obovato-spathulata apice obtusa base dilatata. Stamina 6.5–9.0 mm longa, filamenta 4–6 mm longa, antherae 2.5–3.0 mm longae. Infructescentia 15–30 cm longa supra folia plane exserta congesta; pedicelli 9–15 mm longi base admodum recte adscendentes, apicem versus aliquantum effusi, inferiores remoti superiores congesti. Siliquae 10–15 mm longae vel infimae interdum tantum 5 mm longae 5–9 mm latae, ellipticae vel oblongae vel late ovatae obcompressae, apice integrae vel retusae; valvae leviter corrugatae apice rotundatae. Stylus conspicuus 2.5–4.0 mm longus. Stigma deltoideo-sagittatum in stylo leniter decurrens saepe leviter bilobatum. Replum 1.2–1.6 mm latum oblongum. Semina ca. 80 vel in siliquis parvulis pauciora, 0.6–0.8 mm longa 0.4–0.5 mm lata ovata turgida flava. Chromosomatum numerus: $2n = 20$.

DISTRIBUTION: Presently known only from the type locality near Las Delicias, Coahuila (Figure 3).

REPRESENTATIVE SPECIMENS: **México.** COAHUILA: 1 km W of Las Delicias, *Bacon & Dillon 1478* (TEX), *Powell & Turner 2702* (TEX).

Nerisyrenia johnstonii because of its lack of pubescence is the most distinctive taxon in the genus. Its affinities reside with *N. turneri* and *N. castillonii,* as indicated by its chromosomal base ($x = 10$) and flavonoid chemistry. Nevertheless, on morphological grounds the latter species are well differentiated, and this relationship must be viewed as somewhat distant. Indeed, *N. johnstonii* is thought to be among the more "primitive" species of the genus while *N. turneri* and *N. castillonii* are thought to be among the more highly "evolved".

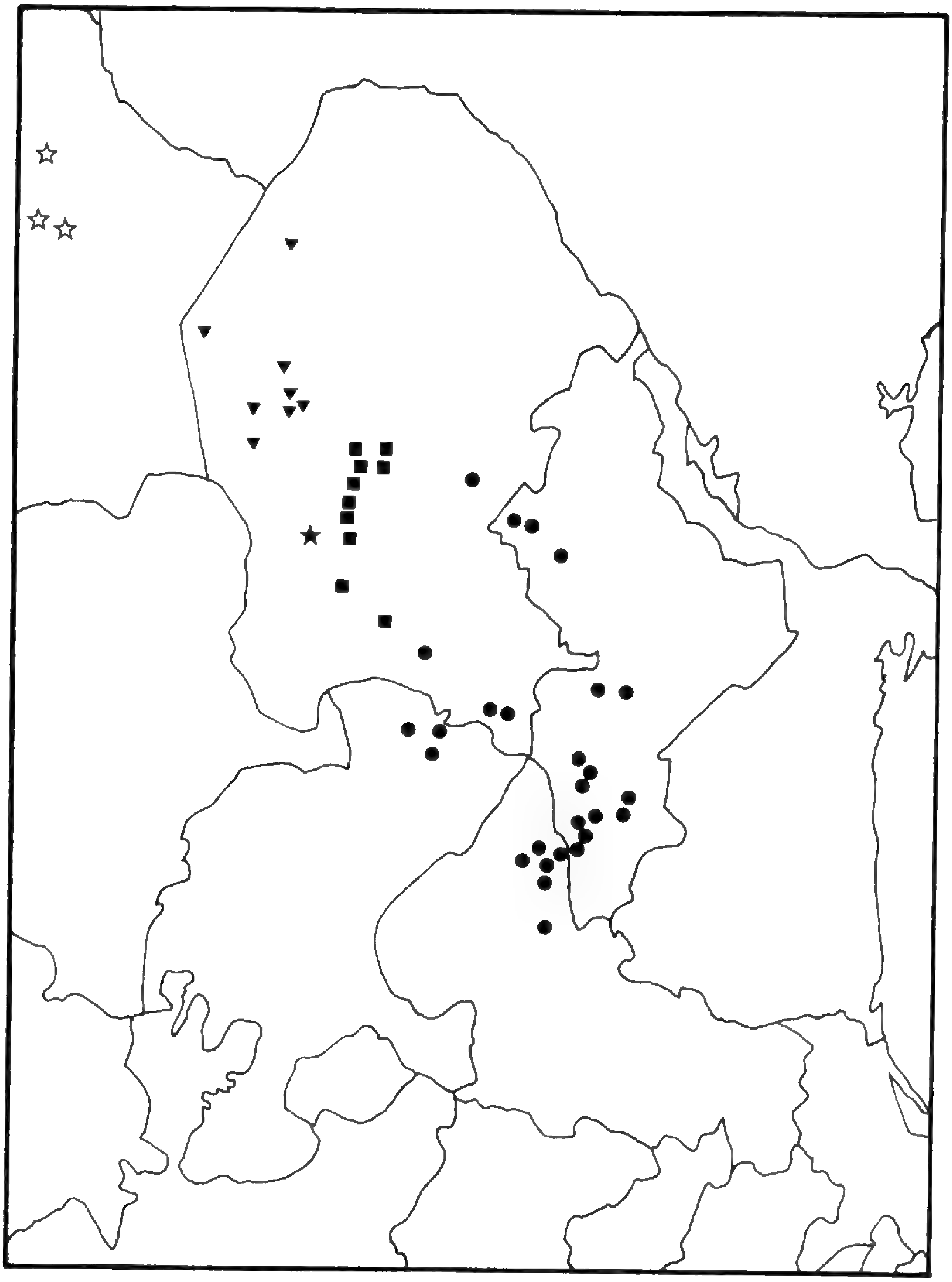

Figure 3. Distribution of species of *Nerisyrenia: N. gracilis,* closed circles; *N. gypsophila,* open stars; *N. johnstonii,* closed star; *N. incana,* closed squares; *N. powellii,* closed triangles.

Morphologically, *Nerisyrenia johnstonii* resembles *N. incana* and they share a base chromosome number of $x = 10$. However, the two are readily distinguished, the former being herbaceous and glabrous while the latter is suffruticose and incanous pubescent. Because the flavonoid chemistry of the two is very distinctive, *N. johnstonii* is clearly allied with *N. turneri* and *N. castillonii*, both of which appear to be based on $x = 10$, and *N. incana* is allied with the remaining taxa in the genus, all of which have $x = 9$. Therefore, the morphological resemblance between the two species is thought to reflect the "primitive" nature of the taxa, their similarities indicating the retention of morphological characters more prevalent in the ancestral stock of the genus.

The name honors Dr. M. C. Johnston, noted student of the Chihuahuan Desert flora, who first brought this remarkable taxon to my notice.

2. **Nerisyrenia turneri** Bacon sp. nov. TYPE: **México.** SAN LUIS POTOSÍ: 5/10 mile west of Jct. Hwy. 101 & 80; along roadside in sandy-loamy, gypseous soil, 24 Jun 1971, *John D. Bacon 983.* (Holotype, TEX!; Isotypes, to be distributed.)

Herbae perennes rhizomatosae 0.5–3.0 dm altae; caules plures erecti vel adscendentes modice pubescentes trichomatibus sessilibus vel brevistipitatis dendriticis. Folia 20–70 mm longa (2–)4–8(–10) mm lata, lineari-oblanceolata raro elliptica, subsucculento-incrassata saepe planata apice acuta vel subacuta basi attenuata margine sinuosa vel dentata raro integra, super dentes elongata angustataque ubi dentata. Sepala 5.0–7.5 mm longa 1.0–2.2 mm lata, oblonga vel lanceolata vel oblanceolata, apice acuta vel obtusa modice vel dense pubescentia trichomatibus sessilibus vel brevistipitatis dendriticus. Petala 6–9 mm longa 5–8 mm lata, laminis obovatis vel anguste ellipticis edentatis, basibus dilatatis denticulatis. Stamina 7–10 mm longa, filamenta 5.5–7.5 mm longa, antherae 2.5–3.5 mm longae. Infructescentia 4–10 cm longa base inter folia inclusa vel non inclusa. Pedicelli 7–15 mm longi divaricate adscendentes vel recurvati. Siliquae 11–26 mm longae 1.2–2.0 mm latae teretes vel raro compressae rectae vel valde arcuatae; valvae aliquantum crassae, raro inter semina constrictae, apicem versus gradatim contractae, apice acutae vel subacutae. Stylus 2.5–3.8 mm longus glaber. Stigma 0.7–1.5 mm latum deltoideo-sagittatum aliquantum super stylum decurrens. Replum 1.0–1.5 mm latum. Semina 50–80, 0.6–1.0 mm longa, 0.5–0.8 mm lata, ovata vel elliptica vel oblonga flavo-brunnea. Chromosomatum numerus: $2n = 20, 32, 33, 36, 38$.

DISTRIBUTION: Plants limited to southern Nuevo León and northern San Luis Potosí (Figure 4), in sandy-gravelly alluvial gypsum soils or crusty, exposed gypsum flats. Flowering from March to September.

REPRESENTATIVE SPECIMENS: **México.** NUEVO LEÓN: 1 mi S of Providencia on Hwy 57, *Bacon & Dillon 1487* (TEX); 14.3 mi N of San Roberto, *Bacon 1017* (TEX); 17 mi S of San Roberto on Hwy 57, *Bacon, Leverich & Turner 1115* (TEX); just W of Hwy 57 on road to Cedral, *Bacon, Leverich & Turner 1127* (TEX). SAN LUIS POTOSÍ: 1/10 mi E of Hwy 57 on road to El Refugio, *Bacon 996* (TEX); 27.6 mi S of Matehuala on Hwy 57, *Bacon & Dillon 1493* (TEX); 42.5 mi S of Matehuala on Hwy 57, *Bacon & Dillon 1494* (TEX); 9 mi NW of Huizache Jct on Hwy 57, *Bacon & Hartman 1333* (TEX); 36.5 mi E of Huizache Jct on Hwy 80, *Bacon & Dillon 1495* (TEX); jct Hwy 101 and 80, *Bacon & Hartman 1330* (TEX); 4.7 mi E of jct Hwy 101 and 80, *Bacon 981* (TEX); 5.3 mi E of jct Hwy 101 and 80, *Bacon & Dillon 1497* (TEX); 10.5 mi E of jct Hwy 101 and 80, *Bacon 982* (TEX); 11 mi E of jct Hwy 101 and 80, *Bacon & Hartman 1329* (TEX).

This species is related to *Nerisyrenia castillonii* (see comments under that taxon) but is easily separated from it.

The distribution of *Nerisyrenia turneri* overlaps, to some extent, with that of *N. gracilis*. While the two species are clearly differentiated, morphologically extreme plants of one taxon may resemble, superficially, plants of the other. In order to alleviate any confusion which might result, the following list of differentiating characters is presented:

N. turneri	**N. gracilis**
Leaves: 4–8 mm broad; margins sinuate-dentate.	0.7–2.5 mm broad; entire.
Siliques: 1.2–2.0 mm broad.	0.7–1.3 mm broad.
Valves: rather "thick", rarely constricted between the seeds.	Thin, commonly constricted between the seeds.

This taxon is named for Dr. B. L. Turner whose encouragement, love of plants and appreciation of living are inspirational.

3. **Nerisyrenia castillonii** Rollins, Contr. Dudley Herb. **3:** 181. TYPE: **México.** COAHUILA: confined to gypsum flats, common

locally; forming depressed, rounded clumps, leaves fleshy, petals white; near corrals of the hacienda Castillon, ca lat. 28° 17′ N, 15 Sep 1940, *I. M. Johnston & C. H. Muller 1264* pro parte. (Holotype, GH! (exclude lower member on sheet = *N. powellii* Bacon); Isotype, TEX!).

Perennial subshrub, 2 4 dm high; stems several to many from a woody taproot or rhizome, erect to subdecumbent, younger stems densely pubescent, canescent to incanous, with sessile and short- to long-stalked, dendritically branched trichomes, the pubescence often appearing tufted; older stems often glabrate. Leaves commonly, somewhat thickened-succulent, rarely thin, 20–60 mm long, 7–20 mm broad, oblanceolate to narrowly oblong-elliptic in outline, attenuate-subpetiolate at base, obtuse to acute at apex; margins rarely entire, usually repand to strongly dentate, often the leaf narrowed and elongated past the final dentations; densely pubescent with sessile or short-stalked dendritically branched trichomes and scattered longer stalked hairs. Petals 9 12 mm long, 5–8 mm wide; obovate-narrowly elliptic, margins entire to somewhat undulate, dilated and denticulate at base, but often the dilation narrow and denticulations absent. Stamens 7–10 mm long; filaments 5.5-7.5 mm long, anthers 2.8–3.5 mm long. Infructescence rather lax, not stout, 7–30 cm long, usually prominent above the leaves; pedicels 6 12 mm long, densely pubescent, ascending, divaricately spreading to declinate, rather uniformly spaced throughout, not densely congested towards apex. Siliques (13–)20 40 mm long, 1–2 mm broad, terete to subterete, commonly somewhat compressed parallel to the replum, straight, more commonly curved, often strongly so, to J-shaped, infrequently tortuous, often somewhat broader at the base than the apex; valves subacute to somewhat rounded at apex (rarely truncate) tapering to the style, not becoming manifestly thinner at maturity. Style manifest, (2.7–) 3.5–6.0(–6.5) mm long, glabrous or rarely with a few scattered trichomes near the apex. Stigma 0.7–1.3 mm long, deltoid-sagittate, somewhat decurrent on the style. Seeds 40 80 (to ca. 100 in longer fruits) per silique, 0.7 1.3 mm long, subelliptic to ovate-oblong, plump to slightly flattened; yellow to tannish-yellow. Chromosome number: $2n = 20, 40, 48, 58, 59$.

DISTRIBUTION: Coahuila, occurring in gypseous clays and sandy alluvial gypsum soils of desert flats (Figure 4). Flowering March to October.

REPRESENTATIVE SPECIMENS: **México.** COAHUILA: 8.7 mi SE of Emiliano Zapata on road to Viesca, *Richardson 1661* (TEX); Sierra de Jimulco and up to 3 km N of Mina San José which is 8 km NE of Estación OTTO, *Chiang, Wendt & Johnston 9532a* (TEX); S end of Cañada Oscuro near Tanque la Luz, *I. M. Johnston 8498* (GH); western base of Picacho del Fuste, NE from Tanque Varionetta, about lat 27°34′ N, *I. M. Johnston 8351* (GH, TEX); Noria, 16 mi S of Estanque, *Shreve 8842* (US); 36.1 mi N of San Pedro de las Colonias on Hwy 30, *Richardson 1658* (TEX); 24.2 mi N of San Pedro de las Colonias on Hwy 30, *Bacon 1023* (TEX); 55.3 mi S of Cuatro Ciénegas on Hwy 30, *Bacon 1036* (TEX); 45 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Dillon 1477* (TEX); ca. 40 mi S of Cuatro Ciénegas on Hwy 30, *Bacon, Leverich & Turner 1095* (TEX); 36 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Dillon 1474* (TEX); ca. 12 mi SW of Cuatro Ciénegas, *Bacon & Leverich 1145* (TEX); 12.4 mi S of Cuatro Ciénegas and 2 mi W, *Richardson 1645* (TEX); 4 mi SW of Cuatro Ciénegas, *Turner 6187* (TEX); 12 mi S of Cuatro Ciénegas, *Bacon 1034* (TEX); 4 mi E of Cuatro Ciénegas, *Leverich & Turner 25* (TEX); San Juan, ca. 18 mi E of Cuatro Ciénegas, *Turner 6206* (TEX); 6.9 mi W of Sacramento, *M. C. Johnston 2582* (GH); several miles NW of Puerto de las Monjas, *I. M. Johnston 8638* (GH, TEX); 33 mi N of Ocampo, *Bacon & Hartman 1278* (TEX); Castillón, *I. M Johnston 8186* (GH); 76.3 mi W of Cuatro Ciénegas, *Bacon & Leverich 1151* (TEX); 20 mi SE of Esmeralda, *Henrickson 6999* (TEX); ca. 3 km S of Puerta de Sardinas, *M. C. Johnston et al. 12174* (TEX); west banks of Laguna del Rey, *Bacon & Leverich 1232* (TEX); Matrimonio Viejo, ca. lat. 27°6′N, *I. M. Johnston 9346* (GH, TEX); ca. 8 mi SSE of Jaco, exactly 8 road mi N of Estación Hormigas, *Henrickson 6933* (TEX); Hermanas, *Bacon & Hartman 1315* (TEX); 0.5 mi S of Estación Hermanas, *Turner & Leverich 26* (TEX); 5/10 mi S of Hermanas on Hwy 57, *Turner 6039* (TEX); just S of Hermanas, *Correll & Johnston 21289* (GH, TEX), *21288* (TEX); ca. 1 mi S of Estación Hermanas, *Powell & Turner 2262* (TEX); 1 mi S of Estación Hermanas, *Turner 6167* (TEX), *Turner 6011* (TEX), *I. M. Johnston 7067* (GH); ca. 1 mi S of Hermanas, *Bacon 1030* (TEX); 2 km S of Estación Hermanas, *Wendt, Chiang & Johnston 10139* (TEX); km 19 on Hwy 57, *Bacon 1027* (TEX).

Nerisyrenia castillonii is most closely related to *N. turneri.* They are similar in many morphological features, differing quantitatively in most, but are easily separated by habit. *Nerisyrenia castillonii* is suffruticose while *N. turneri* is herbaceous.

Rollins (1941b) suggested that this taxon was related to *Nerisyrenia camporum.* He was unaware, however, of the existence of *N. turneri* and did not have the cytological or chemical data utilized in this study. In all respects, *N. castillonii* and *N. camporum* are distinctive and any relationship between the two must be quite distant.

Morphologically, *Nerisyrenia castillonii* resembles *N. powellii.* On the basis of cytological and chemical evidence, however, the two taxa appear to belong to divergent evolutionary lines and are not closely related. Distinguishing characteristics are presented below:

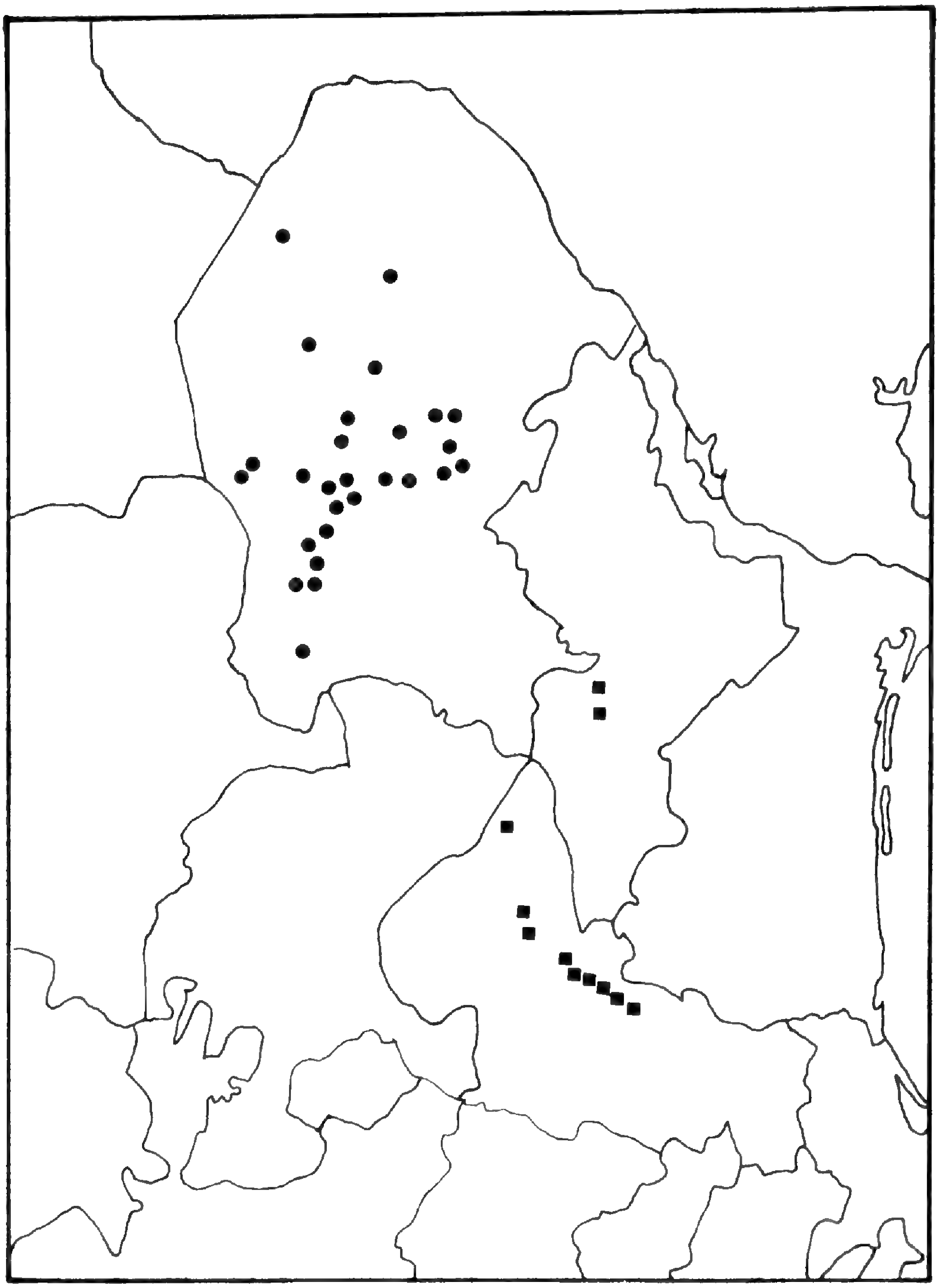

Figure 4. Distribution of species of *Nerisyrenia*: *N. castillonii*, closed circles; *N. turneri*, closed squares.

N. castillonii	**N. powellii**
Leaves: oblanceolate to oblong-elliptic; 7–20 mm broad.	Linear-spathulate; 2–5 mm broad.
Leaf margins: dentate-repand.	Entire.
Style: 3.5–6.0 mm long.	2.3–2.8 mm long.

4. **Nerisyrenia incana** Rollins, Madroño **5:** 132. 1939. TYPE: **México.** COAHUILA: infrequent in alkaline flats, perennial, petals white, associated with *Dondia,* 4 miles west of Cuatro Ciénegas, 24–26 Aug 1938, *I. M. Johnston 7130.* (Holotype, GH!).

Perennial subshrub to 6 dm tall, densely pubescent throughout, incanous, with short- to long-stalked dendritically branched trichomes, pubescence somewhat appressed on younger stems; stems several to many from a woody taproot; erect, somewhat spreading to ascending, branching freely; older stems to 1 cm thick with furrowed and somewhat exfoliating bark, often glabrate below. Leaves succulent-subsucculent, lower 43–84 mm long, 12–30(–40) mm broad, upper 22–42 mm long, 5–13 mm broad, oblanceolate to spathulate, occasionally obovate, obtuse to acute at apex, long to short attenuate at base (subpetiolate); margins entire to, not uncommonly, dentate, usually weakly revolute. Inflorescence elongating greatly in fruit, lower flowers often abortive. Sepals 7–10 mm long, 1.5–3.0 mm broad, linear-lanceolate to oblanceolate, rarely subulate, acute at apex, spreading at anthesis, becoming reflexed with age. Petals 9–16(–19) mm long; 5–8 mm broad, spathulate-obovate, obtuse at apex, margins entire, often weakly undulate, markedly dilated and usually denticulate at base. Stamens 6–9 mm long, filaments 4–7 mm long, anthers 3–4 mm long. Infructescence usually stout, 8–45 cm long, usually well exserted above the leaves; pedicels ascending to spreading at right angles to the axis, stoutish, rather widely spaced on lower 1/3 of axis, moderately to densely crowded on upper portion. Siliques 9–19 mm long, 4–9 mm broad, narrowly obovate to broadly oblong, obcompressed, shallowly to deeply notched at apex, valves extending 0.5–1.5 mm past insertion of the style, rounded-truncate at apex, inner surface of valves often finely pubescent with stalked, dendritically branched hairs. Style prominent, glabrous 2.5–4.7(–5.2) mm long. Stigma 0.8–1.5 mm long, sagittate-deltoid to rather cylindrical, somewhat decurrent on the style. Replum 1.5–3.6 mm broad. Seeds 50–90 per silique, 0.7–1.0 mm long, 0.5–0.7 mm broad, ovate-elliptic-oblong, plump to slightly flattened; brownish-yellow. Chromosome number: $2n = 20, 21, 22, 23$.

DISTRIBUTION: A restricted gypsum endemic found only in the region of Cuatro Ciénegas in south-central Coahuila (Figure 3), occupying areas of pure gypsum sands or highly gypseous alluvial soils. Flowering from March to October.

REPRESENTATIVE SPECIMENS: **México.** COAHUILA: a mile W of Anteojo, W of Cuatro Ciénegas, *I. M. Johnston 8865* (GH, TEX); 3 km SW of Cuatro Ciénegas, *Chiang, Wendt & Johnston 7616* (TEX); 2 mi S of Cuatro Ciénegas, *Bacon, Leverich & Turner 1088* (TEX); ca. 3 mi S of Cuatro Ciénegas, *Bacon & Leverich 1147* (TEX); 4 mi S of Cuatro Ciénegas on Hwy 30, *Bacon 1035* (TEX); 5 mi S and 2 mi E of Cuatro Ciénegas, *Bacon, Leverich & Turner 1084* (TEX); 16 km S of Cuatro Ciénegas, about 2 km SW of Pozo y Balneario La Becerra, *Johnston, Wendt & Chiang 10333* (TEX); 19 km SW of Cuatro Ciénegas, *Chiang, Wendt & Johnston 7644* (TEX); ca. 12 mi S and 5 mi NW of Cuatro Ciénegas, *Bacon, Leverich & Turner 1091* (TEX); W side of gypsum dunes ca. 12 mi SW of Cuatro Ciénegas, *Bacon & Leverich 1144* (TEX), *Bacon & Hartman 1271* (TEX); 14 mi S of Cuatro Ciénegas, then 1.8 mi W, *Turner 6059* (TEX); 15 km SW of Cuatro Ciénegas, *Leverich & Turner 3* (TEX); 38 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Hartman 1320* (TEX); 68 km SW of Cuatro Ciénegas on hwy to Torreon, *Johnston, Wendt & Chiang 10339* (TEX); 45 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Dillon 1476* (TEX); 50 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Hartman 1321* (TEX); 50 mi N of San Pedro de las Colonias on Hwy 30, *Bacon 1025* (TEX); ca. 33 mi N of San Pedro de las Colonias on Hwy 30, *Bacon, Leverich & Turner 1099* (TEX); 42 mi E of Torreon, *Rollins & Tryon 58293* (GH, TEX).

This species shares morphological similarities with *Nerisyrenia johnstonii* (see discussion under that taxon), but on the basis of their flavonoid chemistry and other morphological considerations, the two species are thought to be only distantly related. *Nerisyrenia incana* is closely related to N. camporum (see discussion under the latter) as pointed out by Rollins (1939). The latter two species share broad morphological similarities and an almost identical flavonoid chemistry.

This taxon appears to be rather heavily parasitized by certain insects, since plants of this species often have flower buds on the lower 1/3 of the stem arrested in development, with the sepals remaining closed and the structure persisting as a "dried" remnant on its pedicel; or the lowermost fruits of the raceme are often malformed and produce no seeds. Examination revealed the presence of an insect larva in each of these affected parts.

5. **Nerisyrenia camporum** (A. Gray) Greene, Pittonia **4:** 225. 1900.

Greggia camporum A. Gray, Smithson. Contrib. Knowl. 3(5): 8. 1850. TYPE: **Texas.** VAL VERDE CO.: *Oct. 1849, Charles Wright 11.* (Holotype, GH!; Isotypes, GH! US!).

Parrasia camporum (A. Gray) Greene, Erythea **3:** 75. 1895.

Herbaceous perennial, 1–6 dm tall, densely pubescent throughout, the pubescence of short- to long-stalked dendritically branched trichomes, pubescence often canescent-pannose. Stems erect to ascending from an often woody taproot or caudex, branching rather sparsely throughout; older stems to 5 mm thick and often glabrate. Leaves 10–50 mm long, 7–30 mm broad, oblanceolate, obovate, spathulate or, infrequently, elliptic, attenuate to subpetiolate at base, acute to obtuse at apex; margins entire, repand to strongly dentate. Sepals 5–9 mm long, 1–2 mm broad, oblong-oblanceolate in outline, obtuse-subacute at apex; spreading at anthesis, becoming reflexed with age. Petals 8–14 mm long, 5–9 mm broad, obovate, infrequently elliptic; blade margins entire or rarely undulate; dilated and denticulate at base, often the dilation narrow and obscure. Stamens 6.5–9.0 mm long; filaments 4.5–7.5 mm long; anthers 2.0–3.5 mm long. Infructescence 8–35 cm long, lax, usually well exserted above the leaves; pedicels 7–20 mm long, densely pubescent, ascending to divaricately spreading, rarely recurved. Siliques 15–40 mm long, 1.5–4.0 mm broad, linear-oblong to, rarely, somewhat elliptic in outline, strongly obcompressed, straight to strongly curved inward; valves truncate-rounded at apex; pubescence often appearing tufted, the branches of the longer-stalked trichomes ascending; fruit and pedicel, in conjunction, often sigmoid. Style (1.5–)2.0–3.8(–4.3) mm long. Stigma deltoid-sagittate, 0.5–1.5 mm long, somewhat decurrent on the style. Replum 1.0–1.4 mm broad. Seeds 40–100 per silique, 0.8–1.1 mm long, 0.5–0.7 mm broad, elliptic-ovate to oblong; yellow to yellow-brown. Chromosome number: $2n$ = 18, 19, 21, 22, 27, 32, 34, 36, 40, 41, 58.

DISTRIBUTION: Southeastern New Mexico, western and southern Texas, south into Mexico into the states of Chihuahua, Coahuila, Durango and Nuevo León (Figure 5); occurring on gravelly knolls, clay flats, sandy washes and hills, occasionally on gypseous clays in the Big Bend area of Texas and adjacent Mexico. Flowering sporadically throughout the year, primarily February-September.

REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: 33 mi N of Jiménez, towards Camargo, *White 2182* (GH, US); 5 mi S of Jiménez, *Johnston 7845* (GH); 1 mi NW of Escalón, *Correll & Johnston 21454* (GH, TEX); ca. 35 mi S of Ahumada, *Bacon & Hartman 1351* (TEX); 8 mi S of Ahumada, *Shreve 9037* (GH); 8 mi W of Hwy 45 along Chihuahua Hwy 2 towards Nuevo Casas Grandes, ca. 12 mi SW of Cd Juárez, *Henrickson 5668* (TEX); ca. 32 mi S of Cd Juárez, 1½ mi E of Samalayuca, *Henrickson 5765* (TEX); Colonia Diaz, *Nelson 6442* (GH, US); ca. 24 mi NE of Julimes, ca. 5 mi S of Rancho El Recuerdo, *Henrickson 13024* (TEX); 8 km N of Progresso, *Stewart 2336* (GH); 5 mi SE from San Carlos, *Johnston & Muller 86* (GH, TEX); 10 mi E of Chapo, *Johnston & Muller 16* (GH, TEX); ca. 28°35′15″ N-105°34′17″ W at San Diego Hot Springs on Rio Chuvisca, *Hewitt 101* (GH); 18.5 mi E of Hwy 16, *Powell, Turner & McGill 2041* (TEX); 23.1 mi SW of Coyame at El Pastor, *Henrickson 6744* (TEX); intersection of Hwy 16 and road to Placer de Guadalupe, *Powell, Turner & McGill 2061* (TEX); 7.5 mi S of Ojinaga, *Powell et al. 2085* (TEX).

COAHUILA: near Rancho Santa Teresa, S of Castanos, *Wynd & Mueller 180* (GH, US); Ojo Caliente, ca. 50 km SW of Monterrey, *Johnson & Barkley 16274m* (GH, TEX); 10 mi E of Saltillo on route 60, *Correll & Johnston 21398* (GH, TEX); 20 mi S of Monclova, *Rinehart 247* (GH); vicinity of Saltillo, *Palmer 324* (GH, US); 33 mi W of Saltillo on Hwy 40, *Bacon 1019* (TEX); 4 mi SW of Hipólito, *Muller 3020* (GH, TEX); 12 mi N of Hipólito, on road to Monclova, *White 1688* (GH); 62 mi W of Saltillo on Hwy 40, *Bacon & Hartman 1344* (TEX); 72 mi E of Torreon, *Rollins & Tryon 58301* (GH); 94 mi W of Saltillo on Hwy 40, *Bacon & Hartman 1345* (TEX); 44 mi E of Torreón, *Rollins & Tryon 58298* (GH, TEX); Puerto Ventanillas, *Stewart 2970* (GH); 12 km E of Tanque Toribio, *Stewart 2981* (GH); 2–3 mi N of San Antonio (ca. lat 27°30′N), *Johnston 8232* (GH, TEX); Paila, *Hinton 16552* (US); Viesca, *Purpus 496* (US); San Lorenzo de Laguna, *Palmer 27* (GH, US); Hermanas, *Marsh 1622* (GH, TEX); 12 mi N of Sabinas Hidalgo, *Heard & Barkley 14541* (TEX); 16 mi N of Nueva Rosita on Hwy 57, *Mahler & Thieret 5645* (SMU); Santa Anna Canyon, near Músquiz, *Marsh 464* (GH, TEX); ca. 120 mi N of Ocampo, *Bacon & Hartman 1291* (TEX); 52 mi N of Ocampo, *Bacon & Hartman 1280* (TEX); 3.7 mi N of Ocampo, *Bacon & Hartman 1272* (TEX); 9 mi E of Cuatro Ciénegas, *Johnston 7104* (GH); "Monte de San Vicente", western base of the Sierra de San Vicente, ca. 20 km ESE of Cuatro Ciénegas, *Schroeder 68* (GH); Cuatro Ciénegas, *Marsh 2064* (GH, SMU, TEX); ca. 35 mi SSW of Cuatro Ciénegas, Sierra de los Alamitos, *Henrickson 13663* (TEX); 4 km W of San Juan, *Stewart 809* (GH); 10 mi E of Los Americanos, 11.5 mi W of La Víbora along Esmeralda-Cuatro Ciénegas RR, *Henrickson 7852* (TEX); 78 mi W of Cuatro Ciénegas, *Bacon & Leverich 1172* (TEX); 115 mi W of Cuatro Ciénegas, *Bacon & Leverich 1188* (TEX); southern end of Laguna de Jaco, *Johnston & Muller 1093* (GH, TEX); La Noria, between Laguna de la Leche and Magueyal, *Johnston 8633A* (GH); Llano de Guaje, 7 mi NE of Penquitas, *Johnston & Muller 350* (GH, TEX); Llano de Guaje, 15 mi E of La India, *Stewart 1182* (GH); 5 km E of Guimbalete, *Stewart 2644* (GH); 8 km E of San José, *Stewart 2647* (GH); base of mtns along the eastern margin of the Valle de Acatita, Rancho Parritas, *Stewart 2775* (GH); Portrero del Cuervo Chico, ca. 3 mi S of Tanque La Ley, *Johnston 8574* (GH); E side of Picacho San José, *Johnston 9406* (GH); vicinity of Santa Elena mines, *Stewart 1929* (GH); 8 km S of Progresso, *Stewart 2299* (GH); vicinity of Castillón, *Stewart 391* (GH); arid plain near Boquillas, *Shreve 8448* (US); Mariscal Canyon of Rio Grande, 11 km downstream from entrance, *Johnston*

12381 (TEX); 6 km E of Mesillas toward Santa Cruz, *Johnston, Wendt & Chiang 11624* (TEX); 5 mi N of Matamoros, *Correll & Johnston 21417* (TEX); 8 mi NW of La Rosa, route 60, *Correll & Johnston 21406* (GH, TEX).

DURANGO: 37.5 mi SW of Gomez Palacios on Hwy 40, *Bacon & Hartman 1323* (TEX); 54 mi SW of Torreon, NE of Cuencame, *Rollins & Tryon 58288* (TEX); 20 km NW of Cuencame, *McVaugh 23630* (GH); 7 mi SE of Conejos, *Correll & Johnston 21439* (GH, TEX); 2 mi W of Bermejillo, *Johnston 7753* (GH); 2 mi NW of Bermejillo on rt 49, *Stuessy 933* (TEX); 14 mi W of Mapimi at Cadena Pass, *Johnston 7758* (GH, US); desert just SW of Pedriceña on Hwy 40, *Mick & Roe 38* (GH).

NUEVO LEÓN: ca. 38 mi SW of Nuevo Laredo, *Webster et al. 11169* (GH); 50 mi S of Nuevo Laredo, *Rivas, Ostos & McCart 8139* (SMU, TEX); 32 mi NNE of Sabinas Hidalgo on 85, *Powell & Turner 2346* (TEX); 17 mi NW of Sabinas on Hwy 85, *Rodriguez 67* (SMU); 12 mi N of Sabinas Hidalgo, *Heard & Barkley 14541* (TEX); 34 mi N of Monterrey on road to Nuevo Laredo, *Frye & Frye 2462* (GH); Monterrey, *Palmer 47* (GH, US); 5 mi N of Espinoza, WNW of Monterrey, *Powell & Turner 2318* (TEX); 5 mi SW of Hidalgo at Parque de Portrero, *Turner & Crutchfield 6266* (TEX).

TAMAULIPAS: 65 km S of Nuevo Laredo, Monterrey hwy, *Dominguez & McCart 8344* (SMU, TEX).

ZACATECAS: northern Zacatecas, *Lloyd & Kirkwood 121* (GH); Cedros, *Lloyd 53* (US); near and at Sierra del Yeso, almost due west of La Presa de Los Ángeles, *Johnston, Wendt & Chiang 11528A* (TEX); 7 km NW of San Juan de Ulúa (Primero de Mayo), *Johnston, Wendt & Chiang 10432C* (TEX).

United States. NEW MEXICO: w/o locality, *Wright 1316* (GH); w/o locality, *Wright 1312* (US); plains NE of Parkers Well, 18 Jun 1899, *Wooton s. n.* (US); Doña Ana Co.: foot of Little Mtn, 1 May 1900, *Cockerell s. n.* (US); on and near Tortugas Mtn, *Standley 6434* (US); Tortugas Mtn, SE of Las Cruces, 25 Jul 1895, *Wooton s. n.* (US); Tortugas Mtn, 1 Sep 1908, *Wooton & Standley s. n.* (US); 27 mi NE of Las Cruces, *Shinners 33101* (SMU). Eddy Co.: Malaga, 4 Sep 1946, *Albers 46277* (TEX). Lincoln Co.: Plains S of Lunas Well, 15 Jul 1895, *Wooton s. n.* (GH, US); White Mtns, *Wooton 176* (GH, US). Otero Co.: 2 mi NE of entrance to White Sands Nat'l Monument, *Waterfall 10580* (SMU, TEX); base of Sacramento Mts, Alamogordo, 14 Apr 1902, *Rehn & Viereck s. n.* (GH).

TEXAS: w/o locality, May 1881, *Havard s. n.* (US). Brewster Co.: 4 mi SW Adobe Wall Spring, *Turner, Warnock & Parks 1149* (SMU, GH); Del Norte Mtns., *Tharp 3438* (US); Altuda Point, *Warnock 20901* (GH), *21212* (TEX); ca. 15 mi S of Longfellow, *Powell 2130* (TEX); ca. 4 mi S of Marathon on US 385, *Powell 2125* (TEX); 23 mi S of Marathon, *Goodman & Waterfall 4575* (GH, TEX); Texas state road 2627 to La Linda, 9 mi SE of US 285, *Rollins & Correll 6635* (GH, TEX); Frog tank, Black Gap Wildlife Management Area, *Mahler 6313* (SMU); Big Bend Nat'l Park, *Brenckle & Brenckle 51072* (SMU); Juniper Canyon, Chisos Mtns, *Marsh 269* (GH, TEX); ca. 3 mi S of Persimmon Gap, *McVaugh 7834* (SMU, TEX); Dog Canyon Flats, Big Bend Nat'l Park, *Warnock 47063* (SMU, TEX); ca. 8–10 mi S of Dagger Flat, Big Bend Nat'l Park, *Miller & Miller 1276* (SMU); Oak Creek, Big Bend Nat'l Park, *Rollins & Correll 61810* (GH, TEX); mouth of Terlingua Creek, Big Bend Nat'l Park, *Correll & Johnston 18352* (GH, TEX); Castolon Ranger Station, Big Bend Nat'l Park, *Bacon & Hartman 1437* (TEX); Rio Grande river bottom at mouth of Santa Elena Canyon, *Shinners 8796* (SMU); ca. 1 mi SW of jct of road from Santa Elena Canyon and cutoff to Terlingua, *Webster 4395* (SMU); arroyo W of Johnson Ranch, Chisos Mtns, *Marsh 49* (TEX); desert between Alpine and Terlingua, *Nelson & Nelson 5024* (GH, TEX); 36 mi S of Alpine, *Rose-Innes & Warnock 21597* (TEX); 3 mi below Study Butte, *Moore & Steyermark 3247* (GH, US); 4 mi N of Terlingua, *Warnock 47016* (SMU, TEX); ca. 17 mi SW of jct 118 and FM 170, *Bacon 1054* (TEX); between Terlingua and the Rio Grande, *Nelson & Nelson 5046* (GH); Chinatis region, *Nealley 476* (US). Culberson Co.: 17 mi N of Daugherty, *Waterfall 4480* (GH); Van Horn, 6 Jun 1905, *Reverchon s. n.* (SMU); Balch Mtn, 5 mi N of Van Horn, *Waterfall 4450* (GH), *4448* (GH, TEX); 43 mi N of Van Horn on Hwy 54, *Shinners 33145* (SMU); 18¾ mi SW of Van Horn, *Cory 44066* (TEX); 30 mi E of Van Horn, *Waterfall 4192* (GH); Hurd's Draw, *Janszen 48* (TEX). Dimmitt Co.: Carrizo Springs, 6 Apr 1930, *Hoglund s. n.* (TEX). Duval Co.: 4 mi N of Realitos on Hwy 359, *Cabrera 51* (SMU, TEX). El Paso Co.: 8 mi E of Fabens on state Hwy 20, *Bacon & Hartman 1411* (TEX); W edge of El Paso, *Correll 22602B* (TEX); El Paso, *Rose 4908* (US), *Jones 3761* (GH, US); Corralitos-El Paso, *Thurber 745* (GH); island in Rio Grande near El Paso, *Lemmon 113* (GH); on trail to Cottonwood Springs, E of Canutillo, W side of Franklin Mtns, *Correll & Johnston 21786* (GH, TEX); McKelligon Canyon, Franklin Mtns, *Warnock 7670* (SMU, TEX). Hudspeth Co.: S end of Quitman Mtns, 5½ mi NE of Indian Hot Springs, *Waterfall 4845* (GH); Hwy 80, 8 mi W of Allamore, *Cory 52888* (SMU, US); Panther Hill-Fox Hill area of central Malone Mtns, *Waterfall 5818* (GH); E of Finley, *Waterfall 5029* (GH); foothills S of Guadalupe Peak, 14 Sep 1916, *Young s. n.* (TEX); 12 mi W of Sierra Blanca, *Waterfall 4576* (GH); 15 mi E of Sierra, *Turner & Warnock 330* (SMU, TEX); Ft. Hancock exit on IH 10, *Bacon 945* (TEX); near Ft. Quitman ruins, *Correll 13778* (SMU, TEX); Jeff Davis Co.: ca. 7 mi from US 90, along road leading from FM 2017 to Candelaria, *Powell 2189* (TEX); 11 mi NW of Chispa, *Rose-Innes & Warnock 487* (GH, TEX); Kent, *Jones 88074* (US). Jim Hogg Co.: Hebbronville, *Moran 9* (TEX). Jim Wells Co.: Amargosa Ranch, 15 mi NW of Alice, *Castillo 15* (SMU, TEX). La Salle Co.: Cotulla, *Palmer 11304* (GH, US); Encinal, *Cavazos 84* (TEX). Loving Co.: between Wink and Mentone, *Warnock 10631* (SMU, TEX); 3 mi W of Orla, *Rollins & Correll 6644* (GH); E shore of Red Bluff Lake, *Powell 2141* (TEX). Maverick Co.: Carrizo Springs-Eagle Pass, *Hogland 8838* (US); hills near Eagle Pass, *Pringle 9038* (GH, US). Pecos Co.: 20 to 35 mi S of Ft. Stockton along Sanderson Hwy, *Warnock 13358* (TEX); Presidio Co.: ca. 3 mi W of Lajitas on Hwy 170 along Rio Grande, *Mahler 6233* (SMU); 3 mi W of Lajitas, *Powell 2191* (TEX); Presidio, 28 Apr 1881, *Harvard s. n.* (US); 8 mi N of Presidio along Hwy 67, *Lundell & Lundell 14291* (TEX, US); 7.5 mi N of Candelaria, *McVaugh 7980* (SMU, TEX); 1 mi S of Ruidosa, *Tucker 2992* (GH); 4 mi SE of Ruidosa, *Muller 8439* (SMU, TEX); 8 mi N of Ruidosa, *Muller 8425* (SMU, TEX); S end of Van Horn Mtns near Porvenir, *Waterfall 4749* (GH); ca. 45 mi from Presidio, off Hwy 67, *Lundell & Lundell 14267* (TEX); near Shafter, *Garrett 504* (SMU); Thomas Ranch, 28 mi S of Marfa, *Ingram 2465* (US); ca. 20 mi S of Marfa along FM 169, *Powell 2129* (TEX); 11 mi S of Marfa, *Rollins & Correll 6196* (TEX). Reeves Co.: vicinity of Pecos, *Gillespie 5251* (GH); 22 mi N of Pecos on Hwy 285, *Nelson & Nelson 4986* (GH, TEX); route 302, 29 mi N of Pecos, *Correll & Johnston 19073* (GH). Starr Co.: 5 mi N of Rio Grande City, *Crutchfield 1151* (TEX); off US 283 E of Rio Grande City, *Lundell & Lundell 9934* (SMU, TEX, US). Terrell Co.: Morton Canyon, about 25 mi S of Dryden, *McVaugh 7752* (SMU); ca. 11 mi W of Sanderson on US 90, *Averett 272* (TEX); 42 mi E of Sanderson on route 90, *Gentry & Barclay 18452*

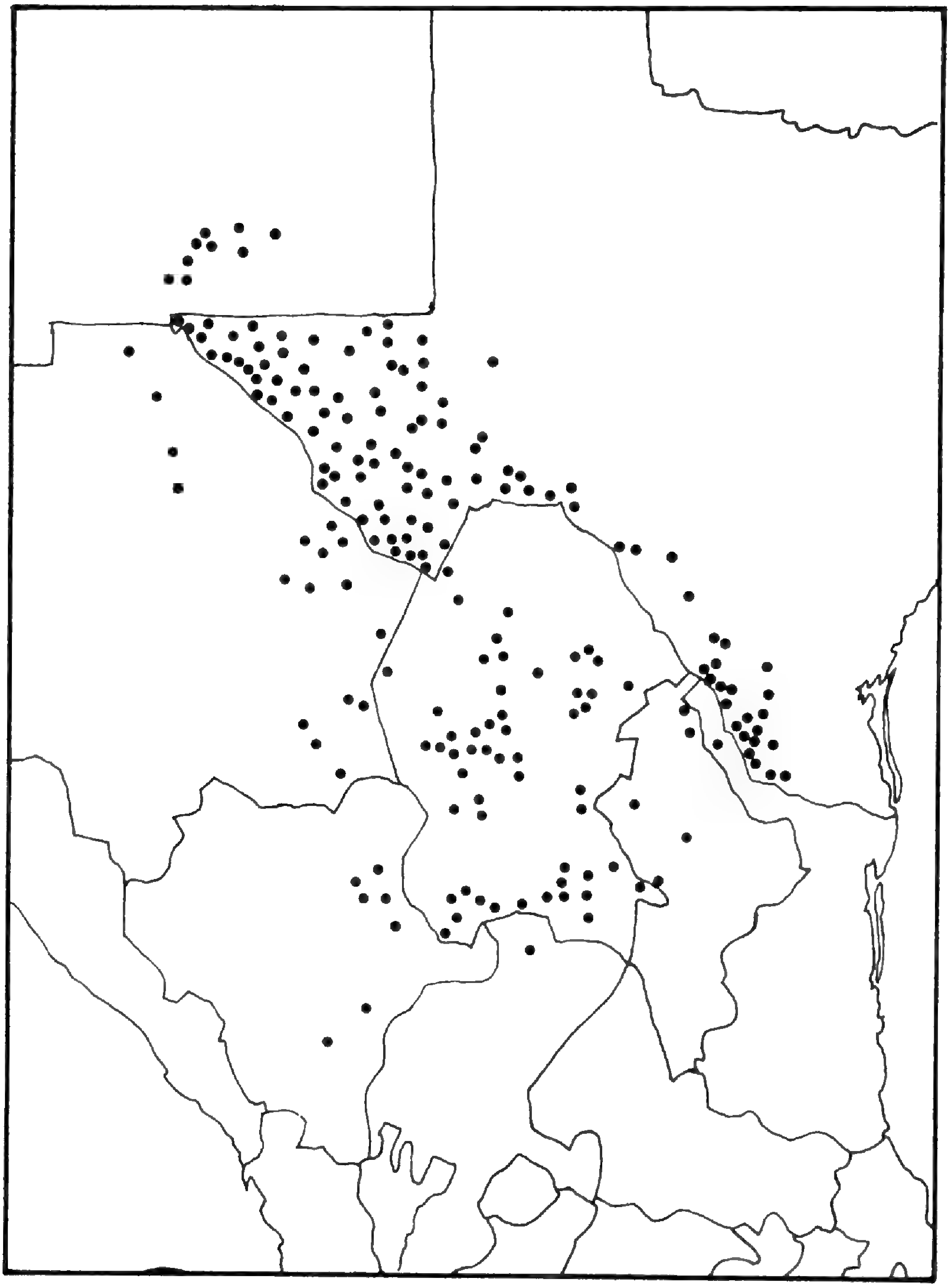

Figure 5. Distribution of *Nerisyrenia camporum.*

(GH, TEX, US); 26 mi W of Langtry, *Wiggins 13362* (US). Val Verde Co.: Soop Road at Del Rio, *Cory 21025* (GH); 3 mi E of Shumla, *Warnock & Cameron 9922* (SMU, TEX); 6 mi E of Langtry, *Rollins & Correll 6157* (GH, TEX). Ward Co.: 5 mi E of Barstow, *Cory 45094* (TEX); Barstow, *Tracy & Earle 25* (GH, TEX, US); 6.4 mi S of Pyote on FM 1927, *Powell 2145* (TEX). Webb Co.: 42 mi N of Laredo, *Rollins & Correll 5943* (GH, TEX); FM 1472, 10 mi N of Laredo, *Paez 125* (SMU, TEX); Lake Casa Blanca, 6 mi NE of Laredo, *Novoa & Cantu 12* (TEX); 10 mi SE of Laredo, *Dickey 123* (TEX). Zapata Co.: S of Laredo, *Rollins 4199* (GH); 13 mi N of San Ignacio, *Shinners 17654* (SMU); Ramireno Ranch, 5 mi S of San Ignacio, *Martinez 31* (TEX); 10 mi N of Zapata, *Cabrera 75* (SMU, TEX); 3 mi S of Zapata on Hwy 83, *Bruno 29* (SMU, TEX). Zavala Co.: Crystal City, 6 Apr 1930, *Hoglund s. n.* (TEX), *Gonzalez 35* (TEX).

Nerisyrenia camporum is the most widespread and most variable species in the genus. Plants referred to this species show considerable variation as to plant height, leaf shape and silique length and width. However, I am unable to correlate these morphological expressions with any geographical, cytological or chemical parameters and am, at present, unable to remove any of the variation by taxonomic recognition of regional variants.

This species is closely related to both *Nerisyrenia gypsophila* and *N. incana.* On morphological grounds, *N. camporum* is more like *N. gypsophila,* but chemically it is almost indistinguishable from *N. incana.* These three species are thought to have arisen from a common ancestral plexus, with *N. incana* being an early offshoot from this stock. *Nerisyrenia camporum* and *N. gypsophila* are thought to be later, perhaps contemporaneous,derivatives from this stock, after a dysploid reduction from $x = 10$ to $x = 9$ had occurred. Or, *N. gypsophila* may have arisen directly from a peripheral, somewhat aberrant, population of *N. camporum,* through the process of quantum speciation or disruptive selection. Although these species are closely related, they are easily separated and are contrasted below:

N. camporum	**N. gypsophila**	**N. incana**
Herbaceous perennials.	Suffruticose.	Suffruticose.
Variously pubescent but never incanous.	Canescent but never incanous.	Incanous.

Leaves not succulent.	Succulent-subsucculent.	Succulent-subsucculent.
Silique apex entire.	Entire.	Notched.
Siliques 1.5–4.0 mm	1.9–3.0 mm broad.	4.0–9.0 mm broad.
Replum 1.0–1.4 mm broad.	0.5–1.1 mm broad.	1.5–3.6 mm broad.

Apparently drawing from the label on the holotype, Rollins (1939) listed the type locality for *Nerisyrenia camporum* as "W. Texas-El Paso, Oct, 1849". However, Gray (1850, p. 9) in his original description of this species referred to the type locality as "High prairies and calcareous hills, at the head of the San Felipe; July (in flower and fruit)." Presumably, Gray was drawing upon Wright's original collection data in the citation quoted above.

Gray often united two or more of Wright's collections, if they represented the same species, and assigned a different number to the united collections (Johnston, 1940). Therefore, it is difficult or impossible to ascertain the original number on which Gray based his description. However, in studying Wright's original collection data for 1849 (transcribed by Johnston, 1940), and assuming that Gray drew on Wright's locality citations, two collections appear as likely sources upon which Gray based his description of *Nerisyrenia camporum.* One collection, *610,* is listed by Wright as having been collected from "calcareous hills of the San Felipe"; the second, number *636,* is listed as "hills, head of S. Felipe"; both collections were made in July. The "San Felipe" referred to in the above quotations is San Felipe Creek or San Felipe Springs, the source for the creek, both of which are located near present day Del Rio in Val Verde County, Texas (Johnston, 1940). The locality data for the two collections cited above is very similar to that given by Gray, suggesting that one (or both) of the above collections represents the type of the species to which Gray assigned the number *11.* Although Wright collected in far western Texas during September, October and November of 1849, none of his collections from that region or during that time span bear any reference to a "San Felipe".

6. **Nerisyrenia gypsophila** Bacon sp. nov. Type: **México.** Chihuahua: Jurassic gypsum ca. 15 miles SE of Estación Morreon on Rio Conchos lake road, Sierra de las Monillas. 26 May 1971. *A. M. Powell et al. 2108.* (Holotype, TEX!; Isotypes, to be distributed).

Suffrutices 2.5–3.5 dm alta. Radix palaris crassa. Caules plures vel multi erecti vel adscendentes, ramis praecipue ad partem superiorem restrictis, dense pubescentes saepe canescentes trichomatibus nonnihil adpressis dendriticis brevistipitatis longistipitatisve, vetustiores ad 7 mm crassi cortice exarata aliquantum exfolianti saepe glabrata. Folia 16–40 mm longa (2–)5–8(–11) mm lata, plus minusve succulenta, oblanceolata vel anguste elliptica base attenuato-subpetiolata apice acuta vel subacuta margine integra vel repando-dentata saepe leviter revoluta, dense pubescentia saepe pannosa trichomatibus dendriticis brevistipitatis longistipitatisve. Sepala 6.5–8.5 mm longa 1.1–1.2 mm lata lanceolata vel oblanceolata apice acuta per anthesin effusa demum reflexa dense pubescentia trichomatibus dendriticis sessilibus brevistipitatisve. Petala 9.5–11.5 mm longa 4.5–8.5 mm lata anguste obovata vel elliptica base conspicue dilatata denticulataque. Stamina 5.5–8.5 mm longa, filamenta 4–6 mm longa, antherae 2.4–3.4 mm longae. Infructescentia admodum rigida 4–30 cm longa parte superiore in folia non inclusa parte inferiore saepe inclusa; pedicelli 8–12 mm longi, satis recte adscendentes raro effusi haud divaricati, dense pubescentes trichomatibus dendriticis longistipitatis brevistipitatisve, inferiores pauxillum dispersi superiores leniter congesti. Siliquae ad maturitatem imbricatae dense vel leniter congestae, 17–30 mm longae 1.9–3.0 mm late lineari-oblongae valde obcompressae, rectae haud arcuatae; valvae apice rotundatae truncataeve, dense pubescentes trichomatibus saepe flocculosis. Stylus 2.7–4.0 mm longus glaber, vel raro trichomatibus dendriticis paucis. Stigma 0.6–1.0 mm longum sagittatum vel rotundatum raro aliquantum decurrens. Replum 0.5–1.1 mm latum. Semina 0.6–1.0 mm longa 0.5–0.7 mm lata, ovata vel anguste oblonga, turgida vel leviter compressa, ochracea. Chromosomatum numerus: $2n = 18$.

Distribution: Presently known only from the type locality and immediate vicinity (Figure 3), occupying crusty gypsum exposures and gypseous soil of alluvial fans. Flowering from March to September.

REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: 1.2 mi SE of Hwy 16 on road to Rio Conchos Lake, *Powell et al. 2102 & 2103* (TEX); 11.8 mi S of Aldama-Ojinaga Hwy, 27.4 mi N Aldama, *Bacon & Hartman 1348* (TEX); 8.8 mi E of RR, Hwy 16, *Powell, Turner & McGill 2069* (TEX); 11 mi E of Hwy 16 on road to new lake on Rio Conchos, *Powell, Turner & McGill 2026* (TEX); 1.7 mi S of Placer de Guadalupe, *Powell, Turner & McGill 2054* (TEX).

This species is most closely related to *Nerisyrenia camporum.* It is, however, easily distinguished from that taxon by several morphological features (see discussion under *N. camporum*).

The taxon is thought to have arisen through some quantum event or disruptive selection, as its ancestors encountered gypseous localities; its impoverished flavonoid chemistry, as compared to *Nerisyrenia camporum,* might reflect, in part, physiological variation associated with individuals in the ancestral population which were genetically predisposed towards occupation of this unusual soil type.

7. **Nerisyrenia linearifolia** (S. Watson) Greene, Pittonia **4:** 225. 1900. For synonymy and typification, see varietal designations.

Herbaceous to somewhat woody, rhizomatous perennial, 0.5–4.0 dm tall, moderately to densely pubescent throughout with sessile to long-stalked, dendritically branched hairs; stems few to several from a woody caudex, erect to somewhat spreading, older stems to 5 mm thick. Leaves 16–70 mm long, 1.2–8.0 mm broad, more or less succulent, terete to flattened, over-lapping on the stem; linear to narrowly oblanceolate-spathulate, attenuate at base, obtuse to acute at apex; margins entire, weakly sinuate to rarely dentate. Sepals 4.8–7.5 mm long, 1.0–2.0 mm broad, broadly lanceolate, ovate to elliptic in outline. Petals 8.5–13.0 mm long, 5.0–8.5 mm wide, obovate to spathulate in outline; blade margins entire; dilate and denticulate at base. Stamens 6.0–8.5 mm long; filaments 4–6 mm long; anthers 2.5–3.5 mm long. Infructescence 5–35 mm long, lax; pedicels 6–16 mm long, ascending, divergent to divaricate, not congested toward the apex. Siliques 9–30 mm long, 1.0–3.6 mm broad, oblong to weakly obclavate-subulate in outline, terete to usually somewhat obcompressed, straight to incurved; valves somewhat angled to the margin, rounded-truncate at apex, rarely tapered to the style. Style glabrous, 0.9–4.0 mm long. Stigma deltoid-sagittate, 0.4–1.5 mm long, somewhat decurrent on the style. Replum 0.7–1.3 mm broad. Seeds 30–80 per silique, ovate-elliptic to oblong, plump to slightly flattened; yellow.

KEY TO THE VARIETIES

Plants low and clump forming, branching throughout, siliques widest at base, weakly obclavate-subulate in outline. . . . . 7a. var. *mexicana.*

Plants more erect, branching restricted to upper 2/3 of stems, siliques not widest at base, oblong in outline. . . . . 7b. var. *linearifolia.*

7a. **Nerisyrenia linearifolia** var. **mexicana** Bacon var. nov. TYPE: **México.** COAHUILA: Agua Nuevo, 18 Apr 1905, *E. Palmer 560.* (Holotype, GH!; Isotype, US!).

Herbae perennes humiles 1–2 dm altae. Caules decumbentes vel adscendentes omnino ramosi. Folia 19–70 mm longa 1.5–8.0 mm lata complanata anguste oblanceolato-spathulata, basi attenuata apice obtusa vel acuta. Infructescentia 6–19 cm longa. Pedicelli 8–16 mm longi divaricate adscendentes vel effusi vel aliquando recurvati. Siliquae 15–27 mm longae (1.5–)2.3–3.6 mm latae, plerumque basi latissimae, paululum obclavato-subulatae. Replum ad 1 mm latum. Chromosomatum numerus: $2n = 36$.

DISTRIBUTION: A gypsum endemic, found in loamy to hard-packed clays in the southeastern quarter of Coahuila, southern half of Nuevo León and adjacent areas of Tamaulipas and San Luis Potosí (Figure 6). Flowering from April to December.

REPRESENTATIVE SPECIMENS: **México.** COAHUILA: Agua Nuevo, *Palmer 560* (GH); 15 mi S of Saltillo, *Rollins & Tryon 58130* (GH, TEX); 31 mi SW of Monterrey, *Warnock & Barkley 14740m* (TEX); Hipólito, *Viereck 516* (US); S of Paila (Valle Seco), *Hinton 16552* (US); Parras, *Palmer 1047* (GH, US). NUEVO LEÓN: 4.5 mi N of Matehuala, *Beaman 1860* (GH, US); 4.5 mi E of San Roberto Jct on Hwy 60, *Bacon & Hartman 1337* (TEX); 5.3 mi E of San Roberto, *Bacon 1008* (TEX); 11.5 mi E of San Roberto Jct on road to Linares, *Turner & Crutchfield 6315* (TEX); 29 mi W of Galeana, *Rollins & Tryon 58175* (GH); on a flat W of Galeana, *Rinehart 328* (GH); near Pablillo, *Shreve & Tinkham 9748* (GH); 21 mi E of Saltillo, *Rollins & Tryon 58105* (GH, TEX). SAN LUIS POTOSÍ: 18 km S of San Luis Potosí, *Rollins & Tryon 58211* (GH, TEX); 15 mi E of La Presa, *Barkley, Rowell & Paxson 844* (TEX); along road between Dr. Arroyo and Matehuala, *Nelson 4526* (GH, US). TAMAULIPAS: Reservoir of Miquihuana, *Stanford, Lauber & Taylor 2372* (US); Miquihuana, *Viereck 541* (US).

Nerisyrenia linearifolia var. *mexicana,* on further study, may prove to be worthy of specific status. I have had little field experience with the variety, and consequently, my knowledge of the taxon is derived primarily from herbarium specimens. In overall morphological expressions, it appears quite distinctive. However, it is difficult to find specific characteristics, singly or in combination, which readily distinguish the two varieties. Until I have a better acquaintance with this taxon, I have opted for a conservative view and treat the entity as only varietally distinct.

7b. **Nerisyrenia linearifolia** (S. Watson) Greene var. **linearifolia.**

Greggia linearifolia S. Watson, Proc. Am. Acad. **18:** 191. 1883. TYPE here designated: **Texas.** CULBERSON CO.: bluffs of Delaware Creek, 1882, *V. Havard s. n.*, right-hand members on sheet. (Hololectotype, GH!).

Greggia camporum Gray var. *angustifolia* Coulter, Contr. U. S. Nat. Herb. **1:** 31. 1890. TYPE: **Texas.** IRION CO.: Camp Charolette, *Nealley 702.* (Holotype, US!).

Greggia camporum Gray var. *linearifolia* (S. Watson) M. E. Jones, Proc. Calif. Acad. **5:** 625. 1895.

Parrasia linearifolia (S. Watson) Greene, Erythea **3:** 75. 1895.

Herbaceous to somewhat woody, rhizomatous perennial, 1.5–4.0 dm tall; stems ascending-erect, rarely spreading; branching confined to upper 2/3 of stem. Leaves 16–65 mm long, 1.2–4.5 mm broad, terete to flattened; linear to narrowly oblanceolate-spathulate, attenuate at base, acute to obtuse at apex. Infructescence 5–35 cm long; pedicels 6–14 mm long, ascending to divergent. Siliques 9–30 mm long, 1.0–2.2 mm broad, oblong in outline. Replum 0.7–1.3 mm broad. Chromosome number: $2n$ = 18, 19, 20, 34, 36.

DISTRIBUTION: Southeastern New Mexico and west Texas; a single outlying population known in the Sierra de la Paila, Coahuila (Figure 6); an edaphic endemic restricted to gypsum outcrops or heavily gypseous sandy or loamy-clay soils. Flowering sporadically throughout the year, primarily February to September.

REPRESENTATIVE SPECIMENS: **México.** COAHUILA: Mina la Abundancia in upper reaches of Cañón Corazón del Toro, SW quadrant of Sierra de la Paila, *Chiang, Wendt & Johnston 10118* (TEX); Sierra de la Paila, SW quadrant, *Wendt, Chiang & Johnston 10111A* (TEX); Sierra de la Paila at one of the lower mine levels in the Mina la Abundancia area, *Johnston, Wendt & Chiang 10510* (TEX).

United States. NEW MEXICO: Chaves Co.: ½ mi SW of Fraier, *Waterfall 6132* (GH, SMU); 20 mi NE of Roswell, *Goodman & Hitchcock 1133* (GH); Ft. Sumner-Roswell, *Nelson 11311* (GH); E embankment of Pecos River by Roswell, Hwy 380, *Solbrig 3177* (GH). Doña Ana Co.: White Sands, *Wooton 158* (US). Eddy Co.: 16.5 mi SE of Carlsbad on Hwy 128, *Bacon & Hartman 1397* (TEX); Lakewood, 6 Aug 1909, *Wooton s. n.* (US). Lincoln Co.: 35 mi S of Torrance, 10 Aug 1909, *Wooton s.n.* (US). Otero Co.: 32.1 mi NE of Las Cruces, *Bacon 1046* (TEX); 18 mi SW of entrance to White Sands Nat'l Monument, *Turner & Turner 8017* (TEX); White Sands, *Berkman, Lee & Tharp 46060* (SMU, TEX). Socorro Co.: 21 mi W of

Carrizozo on Hwy 380, *Bacon & Hartman 1389* (TEX). TEXAS: Crane Co.: off US 67, 6 mi W of McCamey, *Lundell & Lundell 10220* (SMU, TEX, US); 6.5 mi W of McCamey on Hwy 67, *Bacon 1468* (TEX); 5 8 mi N of Imperial, *Warnock 15438* (TEX); ca. 10 mi E of Grandfalls, *Hinckley & Hinckley 208* (SMU, US). Culberson Co.: 31 mi NW of Kent, *Muller 8492* (SMU); 33 mi W of Orla on Hwy 652, *Bacon & Hartman 1406* (TEX); 6 mi E of Delaware Springs, *Correll & Johnston 18538* (GH, TEX); ca. 15 mi E of Pasotex pipeline headquarters on Delaware Creek, Pasotex pipeline road, *Rollins & Correll 61147* (GH, TEX); 22 mi SE of State Line Cafe, Texas RR 652, *Rollins & Correll 6642*, in part, (GH); 1 mi S of Texas-New Mexico line on Hwy 62, *Waterfall 3749* (GH); 30 mi N of Van Horn, *Waterfall 4129* (GH); 44 mi N of Van Horn, on Hwy 84, *Correll & Johnston 18468* (GH, TEX); 1.5 mi E of Daugherty, *Waterfall 5183* (GH); 5 mi N of Daugherty, *Waterfall 4471* (GH); 22 mi SE of State Line Cafe, Texas RR 652, *Rollins & Correll 6643* (GH, TEX); 1.7 mi S of NM State line, Texas RR 1108, *Rollins & Correll 6640* (TEX); 2 mi SE of US routes 62 & 180 at New Mexico line, *McVaugh 8162* (GH, SMU, TEX). Hudspeth Co.: W side of Salt Lake on Hwy 62, *Whitehouse 17001* (SMU); SE base of Malone Mts, *Correll & Johnston 19295* (TEX). Pecos Co.: along Pecos River Girvin, *Warnock 208* (US). Reeves Co.: 5 mi E of Pecos, Toyah Lake, *Warnock 5252* (SMU, TEX); 6 mi E of jct FM 1450 & 285, on 1450, *Bacon & Hartman 1360* (TEX); 12 mi NW of Toyah, *Tharp & Gimbrede 51-997* (TEX); 7 mi SE of Pecos, *Turner 931* (SMU); 4 mi N of Pecos, *Waterfall 4226* (GH); 56 mi N of Pecos, *Waterfall 4255* (GH); 12 mi W of Mentone on Hwy 285, *Bacon & Hartman 1405* (TEX). Ward Co.: 12 mi S of Monahans, *Turner & Warnock 59* (GH); 5 mi E of Barstow, *Cory 45096* (TEX); 6.4 mi S of Pyote, near FM 1927, *Powell 2146* (TEX); 2 mi W of Pyote, *Warnock 7872* (SMU, TEX). Winkler Co.: 10 mi S of Kermit on State Hwy 18, 1 mi W on county road, *Collins 1304* (SMU); 12 mi SSE of Kermit, *Rowell 11540* (SMU).

This variety often occurs in marginal sympatry with *Nerisyrenia camporum*. The two species are ecologically isolated, however, since *N. camporum* is, for the most part, calciphilic instead of gypsophilic. Morphologically, these two species are easily separable since the one species is rhizomatous with relatively narrow leaves, while *N. camporum* is taprooted with much broader leaves.

This taxon is restricted, for the most part, to western Texas and southeastern New Mexico. Nevertheless, I refer here, albeit with hesitation, three collections from the Sierra de Paila in southern Coahuila. These collections exhibit the upright, more robust habit, with narrow linear leaves typical of *Nerisyrenia linearifolia* var. *linearifolia*. The fruits of these plants (available only on one collection, *Johnston, Wendt & Chiang 10510*) are much reduced in length and more strongly obcompressed than is typically found in this variety. These collections may represent another as yet undescribed species of *Nerisyrenia;* however, until more field observations and further study of plants from the above area can be made, I accept them as relatively atypical members of this taxon.

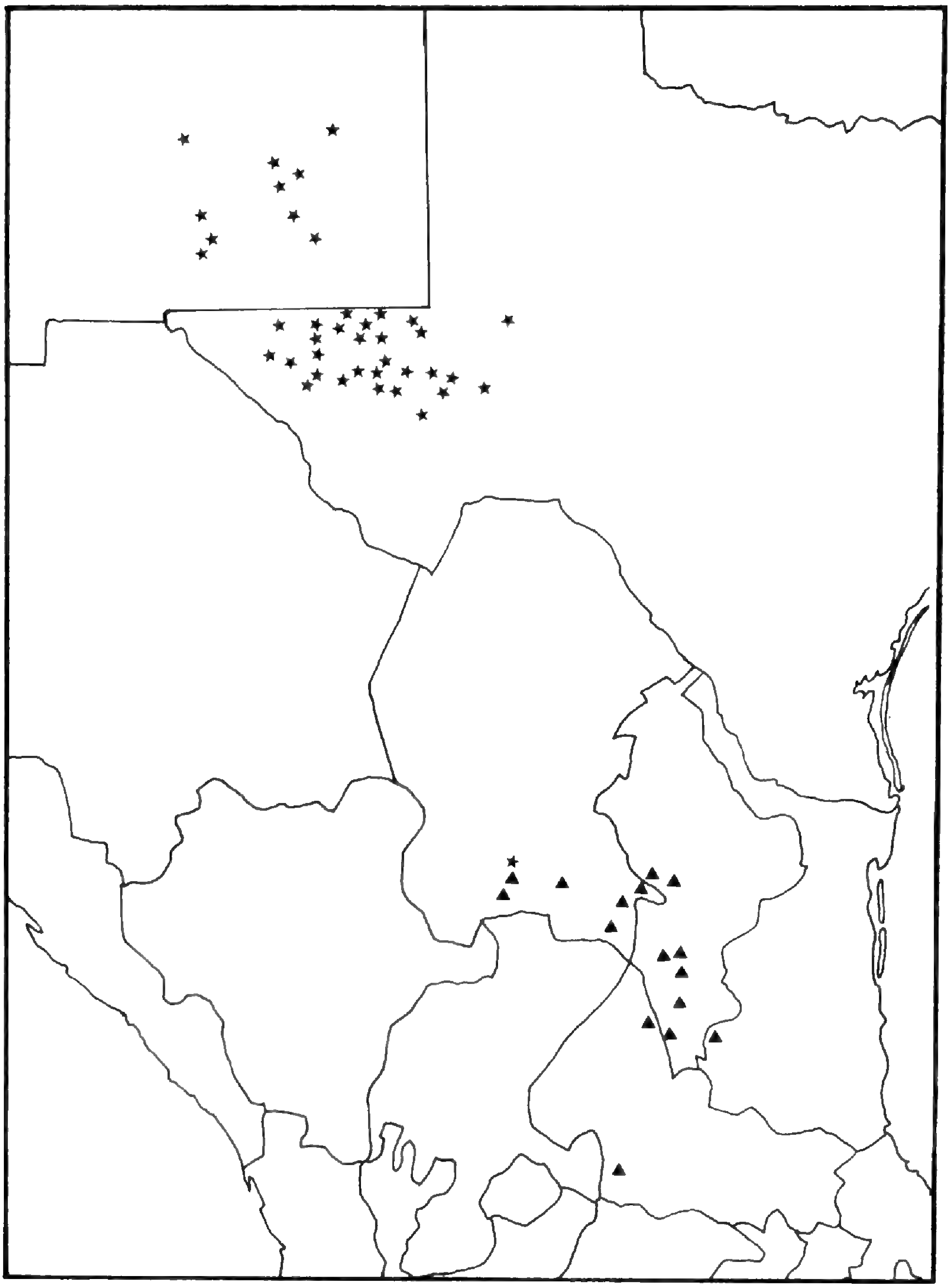

Figure 6. Distribution of *Nerisyrenia linearifolia:* var. *linearifolia,* closed stars; var. *mexicana,* closed triangles.

8. **Nerisyrenia gracilis** I. M. Johnston, Jour. Arnold Arb. **22:** 157. 1941. TYPE: **México.** SAN LUIS POTOSÍ: gypsum plains near sinkholes; stems decumbent; corolla white; 2 miles south of Cedral, 11–12 Sep 1938, *I. M. Johnston 7583.* (Holotype, GH!).

Herbaceous to somewhat woody, rhizomatous perennials, 0.5–1.5 (rarely to 4) dm tall, scattered to densely pubescent throughout with sessile or short-stalked dendritically branched trichomes; stems several from a slender, woody caudex, usually decumbent, occasionally ascending; older stems to 3 mm thick, often with furrowed bark, glabrate. Leaves succulent, 20–70 mm long, 0.7–2.5(–6) mm broad linear-oblanceolate to spathulate, terete to flattened, attenuate at base, obtuse to acute at apex; margins entire, rarely with 1 or 2 dentations. Sepals 3.5–6.5 mm long, 0.7–1.5 mm broad, lanceolate, subulate, rarely oblong in outline, acute-obtuse at apex. Petals 7–10 mm long, 3.5–6.0 mm broad, obovate-spathulate in outline, obtuse at apex, margins entire to somewhat undulate; dilated and denticulate at base. Stamens 5–8 mm long; filaments 4–6 mm long; anthers 2.0–3.5 mm long. Infructescence rather lax, (2.0–)4–17(–20) cm long, often the apical fruits barely exceeding the leaves, basal fruits included within the leaves; pedicels 5–9 mm long, ascending to spreading, rather evenly spaced throughout. Siliques slender, 6–30(–35) mm long, 0.7–1.3(–2.0) mm broad, terete, rarely compressed, straight to curved inward to tortuous; valves commonly somewhat thin and outlining the seeds, tapering to the style. Style 1.8–3.8 mm long, glabrous. Stigma 0.5–1.1 mm long, deltoid-sagittate, decurrent on the style. Replum 0.9–1.2(–1.6) mm broad. Seeds 30–90 per silique, 0.5–0.7 mm long, 0.5–0.6 mm broad, broadly ovate to oblong, plump; yellow. Chromosome number: $2n = 18, 34, 36, 38$.

DISTRIBUTION: Southwestern Nuevo León, southeastern corner of Coahuila, eastern Zacatecas and northeastern San Luis Potosí, Mexico, occupying crusty to hard-packed or exposed gypsum plains and flats (Figure 3). Flowering from March to September.

REPRESENTATIVE SPECIMENS: **México.** COAHUILA: Hipólito, *Viereck 516* (US); 6 mi N of La Ventura, *Johnston 7638* (GH). NUEVO LEÓN: Minas "Manto Blanco" y "Sabana Blanco", just N of the Cañón de Portrerillas, *Johnston, Wendt & Chiang 10251a* (TEX); 16 mi N of Rancho de Estacas, on the road to Rancho Lechuguillal, *Johnston, Wendt & Chiang 10214* (TEX); Km 100 on Hwy between Monterrey and Monclova, *Bacon, Leverich & Turner 1077* & *1079* (TEX); 105 km on Monterrey-

Monclova Hwy, *Bacon, Leverich & Turner 1081 & 1082* (TEX); 29.5 mi SE of jct Mex 53–57, near Mex 53, *Powell & Turner 2297* (TEX); 100 km NW of Monterrey, *Turner 6365* (TEX); ca. 10 mi S of San Jose de Raices on Mex 57, *McVaugh 18230* (GH); ca. 28 mi N of San Roberto on Hwy 57, *Bacon, Leverich & Turner 1104* (TEX); 7.3 mi N of San Roberto Hwy 57, *Bacon 1013* (TEX); Km 154 on Hwy 57, *Bacon, Leverich & Turner 1108 & 1109* (TEX); 8 mi S of Galeana, *Correll & Johnston 19870* (TEX); 4 mi S of Galeana, *McGregor et al. 71* (GH); 2.5 mi S of Pueblo Galeana, *Irving 152* (TEX), *Stuessy 268* (TEX); 15 mi S of San Roberto, *Turner 6215* (TEX); 15 mi S of San Roberto Jct on Mex 57, *Sanderson 293* (TEX); 17 mi S of San Roberto on Hwy 57, *Bacon, Leverich & Turner 1119* (TEX); 66 km S of San Roberto jct on road to San Luis Potosí, *Chiang, Wendt & Johnston 8258B* (TEX); 40 mi N of Matehuala, *Waterfall 15756* (SMU). SAN LUIS POTOSÍ: 6 mi N of San Vicente, *Johnston 7616* (GH); 13 mi N of Matehuala, *Shreve 8709* (US); 3.5 mi N of Matehuala, *Bacon & Hartman 1335* (TEX); 3.5 mi N of Matehuala, towards Cedral, *Henrickson 6551* (TEX); just W of Hwy 57 on road to Cedral, *Bacon Leverich & Turner 1127* (TEX); 4.3 mi W of Hwy 57, on hwy to Cedral, *Bacon 1001* (TEX); 7.5 mi W of Hwy 57, on road to Cedral, *Bacon 1002* (TEX); 1.7 mi S of Cedral, *Bacon 1004* (TEX); 5 mi S of Cedral, *Johnston 7525* (GH); 38 mi S of Matehuala, *Johnston 7509* (GH); gravelly plain E of Catorce, *Pennell 17554* (TEX). ZACATECAS: Vanegas-Saltillo road, *Lundell 5725* (TEX, US); 35 mi NNW of Concepción del Oro, 10 mi W of Cedros, *Henrickson 6349* (TEX); Cedros, *Lloyd 111* (US); Sierra Hermosa, *Johnston 7402* (GH, US).

Johnston (1941) suggested that this species was most closely related to *Nerisyrenia linearifolia* (var. *linearifolia* of this treatment). However, due to the distinctive differences in flavonoid chemistry and, also, to morphological differences between this species and *N. linearifolia,* I consider *N. gracilis* to be most closely related to *N. powellii.*

9. **Nerisyrenia powellii** Bacon sp. nov. TYPE: **México.** COAHUILA: gypsum outcrops between El Rey and Laguna del Rey on road from El Rey to La Chemica, 19 Oct. 1971, *J. D. Bacon & W. R. Leverich 1257.* (Holotype, TEX!; Isotypes, to be distributed).

Suffrutex rhizomatosus 2–4 dm altus; caules plures erecti vel aliquantum effusi copiose ramosi, vetustiores ad 0.7 cm crassi glabrescentes cortice exarata. Folia succulenta 15–40 mm longa 2–5 mm lata lineari-spathulata basi attenuata apice obtusa vel acuta margine integra vel raro 1–2 dentibus. Sepala 5–7 mm longa 1–1.5 mm lata, subulata vel oblanceolata, apice acuta, patentia demum reflexa, dense pubescentia trichomatibus dendriticis brevistipitatis vel longistipitatis. Petala 6–9 mm longa 3–5 mm lata, spathulata vel anguste obovata basi dilatata. Stamina 5–8 mm longa, filamenta 4–6 longa, antherae 3–4 mm longae. Infructescentia laxa

15–23 cm alta plerumque multo elevata super folia; pedicelli 5–10 mm longi adscendentes raro recurvati, dense pubescentes trichomatibus dendriticis brevistipitatis longistipitatisque. Siliquae 9–25 mm longae 1–1.5 mm latae teretes vel saepius parum compressae, rectae vel parum introrsum arcuatae; valvae versus stylum angustatae, apice acutae vel subacutae saepe ad maturitatem tenuiores et leniter constrictae inter semina. Stylus 2.3–2.8 mm longus. Stigma 0.6–0.9 mm altum, plus minusve decurrens in stylo. Replum 1–2 mm latum elliptico-oblongum apice saepe acutum. Semina 30–80 ovato-oblonga turgida flava. Chromosomatum numerus: $2n = 38$.

DISTRIBUTION: Plants endemic to northern Coahuila, occupying chalky gypsum outcrops, crusty gypsum knolls and gypseous clay flats of valley floors (Figure 3). Flowering from March to October.

REPRESENTATIVE SPECIMENS: **México.** COAHUILA between la Víbora and Matrimonio Viejo, about lat. 27°6′N, *I. M. Johnston 9336* (GH); 4½ km E of Matrimonio Viejo, *M. C. Johnston, Wendt & Chiang 10898* (TEX); 76.3 mi W of Cuatro Ciénegas, *Bacon & Leverich 1159* (TEX); 3 mi from San Vicente, *Stewart & Johnston 1953* (GH, TEX); along road from San Vicente to southern end of Laguna de Jaco, *Johnston & Muller 1078* (GH, TEX); *Johnston & Muller 1099* (GH, TEX); 16 mi S of Laguna del Rey, *I. M. Johnston 7814* (GH); E side of Picacho San José, S of Santa Elena, *I. M. Johnston 9406* (GH).

Nerisyrenia powellii is most closely allied to *N. gracilis*. The two species are allopatric, however, and cannot be confused since *N. powellii* is an erect, suffruticose perennial while *N. gracilis* is a decumbent, herbaceous perennial. (See discussion under *N. castillonii*).

This species is known from only a few collections and may yet be found over a larger region. However, in at least some areas it forms large, rather uniform populations such as those which I have seen occupying extensive gypsum exposures on the northwest side of Laguna del Rey.

The species is named for Dr. A. M. Powell, whose teachings and personal attitudes greatly influenced my appreciation of botany.

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THE VASCULAR FLORA OF ST. BARBE SOUTH DISTRICT, NEWFOUNDLAND: AN INTERPRETATION BASED ON BIOPHYSIOGRAPHIC AREAS

André Bouchard, Stuart Hay and Ernest Rouleau

The Gulf of St. Lawrence region harbours a rich and diverse vascular flora which lacks study despite several previously published regional floras such as those of Scoggan (1950), Erskine (1960), Marie-Victorin and Rolland-Germain (1969), and Roland and Smith (1969). The flora of Newfoundland is known for the most part from the journals of Fernald (1911, 1926–27, & 1933) and the only complete checklist is that of Rouleau (1949, 1956). St. Barbe South occupies a large sector of the west coast of this province. The comprehensive study of its flora is an outgrowth of research on the vegetation and flora of the recently created Gros Morne National Park in the southern part of the District. This earlier research, carried out in conjunction with the park's natural resources analysis, began to reveal a complex and rich nordic flora (numbering some 780 vascular plant species), which warranted further study.

The objective of the work is to provide an analysis of the flora in essentially two parts. One section compiles, in the form of an annotated catalogue (Hay, 1976, Appendix II. 228 pp.), an exhaustive record of vascular plant collections with accompanying information describing their diverse habitats. The other section draws on the information contained in the catalogue to describe the region's flora in terms of biophysiographic units discernable within the study area. This latter approach is well suited to St. Barbe South because abrupt variation, particularly in bedrock geology and altitude, results in locally steep environmental gradients along which different elements of the flora are sorted out. The basic changes in landform, with resultant changes in microclimate, soils, drainage, etc., can be translated in terms of a scheme of physiographic units coupled with corresponding changes in the vegetation and flora. These integrated categories are described as biophysiographic areas. Limited by both a lack of floristic information and the complexity of factors controlling the manner in which elements of the flora are associated, an exhaustive analysis of each biophysiographic area was not attempted. Nevertheless, the general description for each unit attempts to highlight the significant associations in the flora of the study area.

METHODS

The inventory of herbarium collections from the study area dates from 1820 to 1974 (Hay, 1976, Appendix II). The annotations of earlier contributions to the flora are in large part unpublished information compiled by Professor E. Rouleau of the Université de Montréal. They are the fruit of his research on Newfoundland's flora in various North American and European herbaria as well as of his own field studies. The more recent collections, mainly made in the course of this study and related work on the vegetation and flora of Gros Morne National Park (Bouchard, 1974; Airphoto Analysis Associates, 1975; Bouchard & Hay, 1976a), substantiate most of the records of earlier botanists. Many of these later collections, made during the summers of 1972, 1973, and 1974, represent additions or extensions to the flora.

The sequence adopted for the taxonomic arrangement of families in the inventory (Hay, 1976) is taken from Rouleau (1970). Lower taxonomic units follow alphabetically. The latin nomenclature, with few exceptions, follows that of *Gray's Manual of Botany* (Fernald, 1950).

Generally, the level of precision sought in the taxonomic treatment has been limited to the rank of species. Occasionally, for reasons of interpretation in the text, subspecific taxa have been included. In difficult genera needing revision such as *Antennaria, Euphrasia,* etc., no attempt has been made to revise earlier collections (in many cases the only collections) even though their taxonomic status is dubious.

Each citation in the catalogue (Hay, 1976) includes the geographic provenance of the specimen followed by a habitat description, date, collector, collecting number and the abbreviation (in accordance with Holmgren & Keuken, 1974) of the herbarium where the specimen has been deposited. For example:

Lycopodium alpinum L.

> Gros Morne: north slope of Gros Morne Mountain near summit with *Salix herbacea, Cassiope hypnoides, Phyllodoce caerulea.* 6/7/73. *Bouchard & Hay 73201* (CAN, MT). Long

> Range Mts., Western Brook Pond: *Scirpus cespitosus, Carex oligosperma, Sphagnum* bog with numerous flashets and exposed boulders; on felsenmeer. 25/7/73. *Bouchard & Hay 73305* (CAN, MT).

For the most part, the collections are housed in the following herbaria: British Museum (Natural History), London (BM); National Herbarium of Canada, National Museums of Canada, Ottawa (CAN); Biosystematics Research Institute, Dept. of Agriculture, Ottawa (DAO); Gray Herbarium of Harvard University, Cambridge, Massachusetts (GH); Botanical Museum, University of Helsinki, Helsinki (H); Herbier Marie-Victorin, Institut Botanique, Université de Montréal, Montréal (MT); and the Agnes Marion Ayre Herbarium, Memorial University of Newfoundland, St. John's (NFLD). Although containing relatively fewer pertinent specimens, the following herbaria preserve additional historical contributions to the flora: Herbarium of the Royal Botanic Gardens, Kew (K); Botanical Museum, Oslo (O); and the Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris (P). A large number of additional herbaria which have received exchange specimens are also listed.

To present an overview of the vascular flora of the region, the study area was divided into a scheme of major biophysiographic areas. Although the choice of these categories was somewhat arbitrary, the units were selected to best reflect the manner in which different elements of the flora are associated. Much of the information used in the interpretation of the physiography and geology of St. Barbe South is taken from earlier research on the natural resources of Gros Morne National Park. Expeditions made in 1974, to northern areas in the District lying outside the national park, provided additional information concerning the major physiographic sites and related vegetation required to adequately describe the flora.

DESCRIPTION OF STUDY AREA

St. Barbe South District is situated on the west coast of Newfoundland where the Gulf of St. Lawrence narrows into the Strait of Belle Isle (Figure 1). The District, which covers an area of roughly 7,000 km.^{2}, lies between 49°30′ and 50°50′ north latitude, and between 56°40′ and 58°20′ west longitude (Figure 2). It is subdivided on the basis of altitude into two topographic land regions; a low-lying coastal plain, and an alpine plateau region.

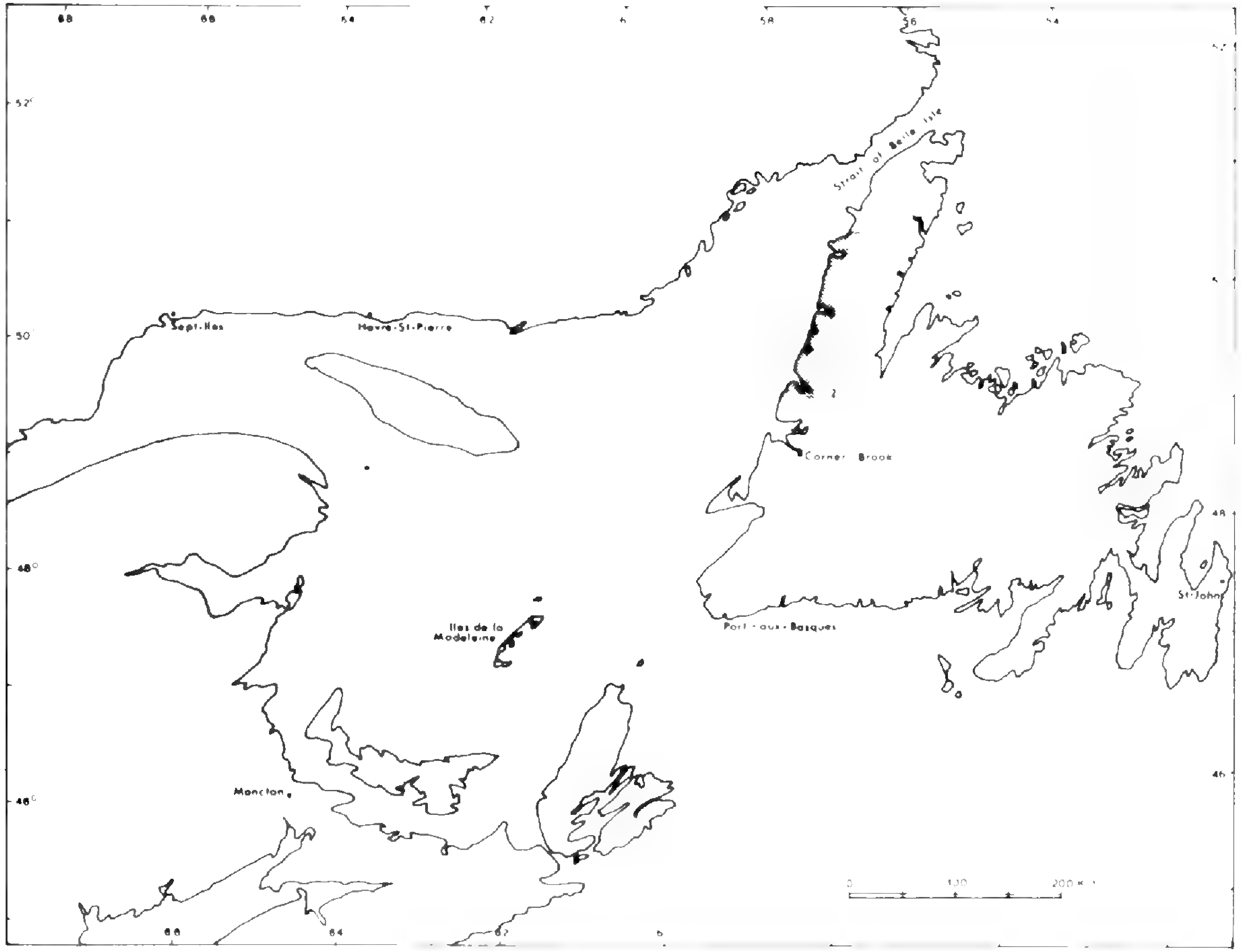

Figure 1. St. Barbe South District, Newfoundland, in the Gulf of St. Lawrence.

PHYSIOGRAPHY AND GEOGRAPHY

Coastal Plain. This gently rolling sedimentary plain, of up to 150 m. elevation, is bordered by the Gulf of St. Lawrence on its western side. The abrupt western scarp of the Long Range Mountains marks its interior eastern margin (Figure 2).

The coastal plain extends from Bonne Bay in the south, to the extreme north of the study area, a straight line distance of 175 km. Although it is reduced to a narrow coastal bench at both its northern and southern extremes, the width of the coastal lowland may stretch inland for up to 25 km. to the base of the Long Range Mountains. Numerous fjords, carved into the mountains, emerge onto the coastal plain creating large landlocked, freshwater forebays which drain into the Gulf. The basins of Bonne Bay and St. Pauls Inlet open directly into the sea and are partly saline. Abundant rivers, streams, lakes, ponds and bog pools constitute much of the surface area of the poorly drained, relatively flat coastal lowland.

Alpine Plateau. The high altitude land region, of 450 to 800 m. elevation, is an almost continuous plateau extending from Trout River Pond (Table Mountain) at the southern boundary of the study area, to the South Summit of the Highlands of St. John at the extreme north. Its eastern boundary is the plunging western escarpment of the Long Range Mountains, the axis of which roughly parallels the coastline. The eastern boundary of St. Barbe South marks the western limit of the alpine region in the study area.

The alpine plateau is a relatively flat, rugged peneplain surface (Oxley, 1953). It is a part of the Long Range Mountain complex which forms the backbone of the Northern Peninsula. The precipitous western escarpment is breached by numerous spectacular glacier-carved canyons and previously mentioned fjords.

The rolling surface of the plateau, which for the most part is gradually inclined to the east, retains abundant freshwater lakes and ponds. The watershed, draining to the west, discharges onto the coastal lowland, whereas east-flowing drainage is discharged by such numerous rivers as the Humber, Main and Soufflets Rivers.

GEOLOGY

Coastal Plain. The southern sector of the coastal lowland, between Bakers Brook and Daniels Harbour, is composed mainly of three groups of interbedded sedimentary formations, the Humber Arm Group, the Green Point-St. Pauls Group and the St. George Group which alternate in bands parallel to the coast (Geologic map; Baird, 1958). Except for some breccia of Middle Cambrian, and some Pennsylvanian and/or Mississippian sedimentaries, these groups are Ordovician.

The Humber Arm Group is found throughout this southern area. It is composed mainly of sandstones, conglomerates, and grey shales (Baird, 1958). It alternates with the Green Point-St. Pauls Group, composed of thin bedded limestone, abundant Cow Head type breccia, shale and siltstones. The St. George Group, composed of massive limestones, dolomites and interbedded shales, constitutes an important part of the bedrock which forms the low rolling piedmont area along the front flank of the Long Range. Some exceptional exposures of this group form the high stratified cliffs along the southern shore of the East Arm of Bonne Bay (Airphoto Analysis Associates, 1975) south of the coastal plain. The limestone breccia is most abundant at Broom Point and Cow Head.

With the exception of the St. George Group, these Ordovician sedimentary rocks do not represent the original, in situ deposits of the coastal plain. They are part of a complex alternating sequence of tilted thrust sheets which have overridden the original lowland deposits. This sequence is the result of a deformation of the interbedded formations during transport (allochtonous klippen) from their original site of deposition to the east of the Northern Peninsula (Airphoto Analysis Associates, 1975; Cumming, 1973; Fleming, 1973).

The northern sector of the coastal lowland, from Daniels Harbour to Eddies Cove West, is composed of the original, undeformed, sedimentary deposits which were laid in place (autochtonous) while the Northern Peninsula was part of the submerged continental shelf of eastern North America (Fleming, 1973). These marine deposits consist of Lower Cambrian to Middle Ordovician carbonates; mainly St. George dolomite and Table Head limestone, with some shale and interbedded limestone, dolomite and slate of Labrador Group sediments. They are best exposed at Bellburns (Table Point and Bateau Barrens), the Pointe Riche Peninsula, and the vertical cliffs forming the western face of Doctor Hill (the South Summit of the Highlands of St. John).

Except for a few protruding rock ridges, exposed coastal headlands, and occasional uplifted cliffs along the Long Range escarpment, the sedimentary rocks of the coastal lowland are generally buried beneath organic, marine, glacial, waterlaid and eolian deposits. This complex array of surficial deposits is easier to understand when interpreted in terms of a piedmont glacier phase characterized by expanded-foot valley glaciers which formerly terminated in a sea that stood about 100 m. higher than present-day sea level, and which transgressed inland to that elevation as the glaciers receded up the troughs of the Long Range Mountains (Grant, 1969b, 1972a, 1973a).

Alpine Plateau. The predominant geological formation of this alpine area is the Precambrian Long Range plateau, an uplifted block of Grenville basement rock. These rocks, which are so extensively exposed at the margin of the Canadian Shield, consist principally of metamorphic and igneous granite or granite gneiss (Cumming, 1973).

Also in this land region are several geologically distinct alpine summits situated as outliers against the western escarpment of the Precambrian massif. They are uplifted monadnocks of Lower Cambrian Labrador Group sediments (Cumming, 1973) which were formerly part of the coastal lowland. These exposures of interbedded limestone, dolomite slate and quartzite were thrust upward along the major tectonic fault which separated the coastal lowland and the alpine Long Range. Gros Morne, Killdevil, Blue Mountain and Doctor Hill form these alpine summits and are protected by caps of more resistant quartzite.

In the southwestern sector of the study area, the broad summits of Table Mountain, Lookout Mountain, and the northern portion of the Gregory Plateau also form a major outlying highland area of the alpine land region. These mountains are a confluence of various geological formations that have been laterally transported (klippen), due to tectonic movement, from their site of origin. They represent the northern portion of the Bay of Islands Igneous Complex, comprised mainly of ultramafic serpentine, altered gabbroic rocks and quartz diorite (Smith, 1958). In particular, the denuded serpentine tableland of Table Mountain forms an impressive uplifted, deeply dissected peneplain bounded by steep cliffs.

The extensive summit area of much of the alpine region is characterized by scoured bedrock surfaces with surficial deposits of glacial drift, erratic boulders and colluvial material as a result of Pleistocene glaciation. Local accumulations of felsenmeer on some of the higher summits are interpreted by Grant (1969b, 1973a) as being partly relict from a nunatak phase of valley deglaciation and partly due to permafrost effects of present climate.

CLIMATE

Newfoundland's climate is known primarily from the work of Hare (1952). In the west coast sector, the maritime and northern geographic situation, and the great variation in altitude between the coastal lowland and the alpine plateau, result in important regional climatic differences. The following factors have an important influence on the vegetation and flora of the study area: a cool climate with a short growing season, a moderating influence of the ocean, a continual moisture excess, and the strong prevailing winds.

The cool climate and short growing season are responsible for the predominantly boreal aspect of the vegetation. The mean air temperature (mean of daily maximum and minimum) in July ranges from 15.6°C in the south to 10°C in the north (Hare, 1952). In January, this range is from –6.7°C to –12.2°C. A striking feature of the winter temperatures is that, due to the warming maritime influence on the coast, the 9.4°C isotherm for mean air temperature lies along the boundary between the coastal plain and the Long Range Mountains. The coastal plain has a cooler summer than the interior of the Island of Newfoundland due to the moderating effect of the Labrador Current. Sea surface temperatures vary between 10°C and 12.8°C in July.

The vegetative growing season ranges from 120 to 150 days (Hare, 1952), the lag being particularly pronounced in the northern sector of the Long Range. The start of the vegetative season, when mean air temperature passes 6.1°C, is between May 20 and May 25 in the southern part of the study area. In the northern Long Range sector, a possible late starting date of June 5 is more than 50 days

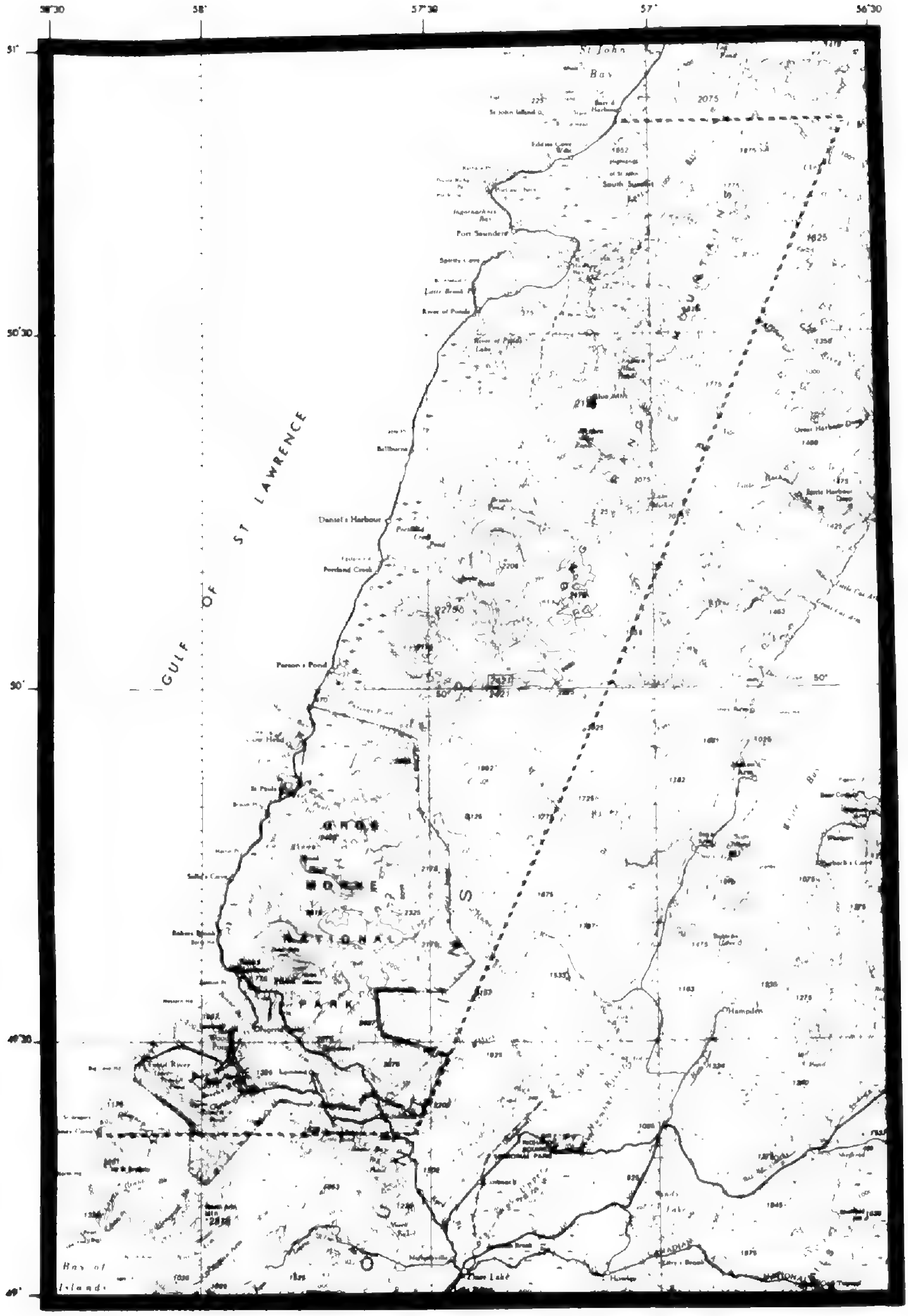

Figure 2. St. Barbe South District. Dotted line represents the boundary of the District. One and three-eighths inches equals 20 km.

behind the corresponding period for Montreal and Ottawa. The extreme contrast results from the constant presence on both sides of the northern half of the Northern Peninsula of Labrador Current water which is often ice-laden well into July. The higher summit areas in the more southern sector of the alpine plateau region probably have a similarly tardy vegetative season.

Relatively high precipitation, low potential evapotranspiration, and poor water drainage due to the general flatness of both the coastal lowland and the alpine plateau region have resulted in the formation of extensive peatland. The mean annual precipitation is between 89 and 114 cm. (Hare, 1952). The potential evapotranspiration, or the "landscape water need", varies from 31 cm. in the north to 48 cm. in the south, leaving an annual moisture surplus greater than 40 cm. The mean annual snowfall ranges from 250 to 380 cm.

The predominant southwest onshore winds are an important environmental factor responsible for the structure of several plant communities, especially the coastal krummholz and upland tuckamoor.

VASCULAR FLORA OF THE REGION

HISTORY OF FLORISTIC STUDIES

The history of botanical exploration of this part of the west coast of Newfoundland dates from the early part of the nineteenth century. However, the inaccessibility of the Island, and even more so of the Northern Peninsula, has greatly hindered studies of the little known flora of this region.

The earliest records concerning the flora appeared in the journal of the French naturalist, Bachelot de la Pylaie, who briefly explored the region of Port au Choix and Ingornachoix Bay in 1820 (Leroy, 1957). Most of his observations concerned cryptogamic species and only the algae section of his *Flore de Terre-Neuve et des Iles Saint-Pierre et Miquelon* was published (Fernald, 1911). Nevertheless, specimens of his vascular plant collection have been preserved at the Muséum National d'Histoire Naturelle de Paris.

The nineteenth century epoch of botanical explorations also includes meagre collections of several amateur botanists. James Richardson explored this west coast area for the Geological Survey of Canada in 1861, and concomitantly made vascular plant collections for the National Museum of Canada. In 1873, an extensive list of flowering plants and ferns was compiled by H. Reeks, a naturalist who convalesced for some time at Cow Head (Robinson & von Schrenk, 1896). The herbarium collections of the "Arethusa Expedition" to the Pointe Riche Peninsula, led by Bartlett and Budingham in 1885, are preserved at Harvard University. Finally, late in the century, the Rev. A. C. Waghorne published a partial flora of Newfoundland (Waghorne, 1893, 1895, 1898), compiled with the assistance of the Dominion botanist, J. Macoun. Waghorne's catalogue was never completed. The little collecting he did in St. Barbe South was restricted to Chimney Cove.

This rather meagre record of botanical studies prompted Professor M. L. Fernald of Harvard University to write that, "in spite of notes already published, the flora of Newfoundland as a whole has been among the least known of any flora in civilized America" (Fernald, 1911). He consequently led a series of expeditions to Newfoundland to fill a void in the botanical knowledge of the territory about the Gulf of St. Lawrence.

On the first expedition of 1910, two members, Professor K. M. Wiegand and J. Kittredge, spent only a few days collecting specimens from three localities in St. Barbe South. Some of their more interesting discoveries on the limestones of Cow Head and Ingornachoix Bay included *Arabis alpina, Botrychium lunaria, Cochlearia cyclocarpa* (type), *Dryas integrifolia, Gentiana nesophila, Hedysarum alpinum, Lesquerella purshii, Salix reticulata, Saxifraga cespitosa* and *Tanacetum huronense*. At Bonne Bay, the serpentine tableland (Table Mountain) and Lookout Mountain yielded interesting mentions for the flora in *Adiantum pedatum* var. *aleuticum, Arenaria humifusa, Armeria maritima, Lychnis alpina, Potamogeton oakesianus* and *Schizaea pusilla.*

Wiegand and Kittredge's collections of 1910 from Pointe Riche and "l'avant-goût" of a brief stopover at Port Saunders in 1924 prompted a return voyage in 1925. The expedition mainly botanized Bard Harbour Hill (the North Summit of the Highlands of St. John) and St. John Island which lie adjacent to, but outside the northern limit of, St. Barbe South. Fernald profited by an afternoon trip to the calcareous talus of the western escarpment of Doctor Hill (the South Summit of the Highlands of St. John) to collect such rareties as *Gentiana propinqua, Polystichum lonchitis, Senecio pauciflorus* and the endemic *Epilobium scalare* (type).

Fernald's 1929 expedition included botanists B. Long and J. M. Fogg. They spent two weeks exploring the limestone barrens of the Pointe Riche Peninsula collecting such "discriminatingly selected specialties" (Fernald, 1933) as the taxonomically complex *Antennaria, Arnica, Salix* and *Taraxacum,* which abound there. An excursion to the southern slopes of Doctor Hill led to the discovery of such rare species for the study area as *Athyrium alpestre, Phyllodoce caerulea, Salix herbacea, Streptopus* × *oreopolus, Vaccinium* × *nubigenum* and *Viola palustris* even though Fernald (1933) qualified the botanical status of the siliceous tableland as "a poor place when contrasted with Bard Harbour Hill and the calcareous western slope of Doctor Hill at John Kanes Ladder." The final leg of this voyage was spent at Bonne Bay, where for three weeks the group continued to display their uncanny knack for ferreting out many rare and interesting species enumerated in Fernald's journal (1933). Their itinerary included such outstanding physiographic features as the limestone cliffs and coves of East Arm, the serpentine Table Mountain, Lookout Mountain, Killdevil Mountain and the barachois of the Lomond River.

Fernald's voyages culminated in the most completely documented study of the vascular flora of Newfoundland (Fernald, 1911, 1918a, 1918b, 1924, 1925, 1926–27, 1930, 1933). His ensuing theories concerning the phytogeographic distribution of different elements of the flora as well as his highly readable journals did much to stimulate further study. The calcareous exposures of Bonne Bay and the adjacent serpentine of Table Mountain subsequently attracted such botanists as Kimball, 1919; Bishop, 1928; Simpson, 1928; Jansson, 1930; Rishbeth, 1937; and Penson, 1941. The limestone barrens at Pointe Riche were explored by Abbe and Pease, 1931; Ayre, 1936; and Penson, 1941. These expeditions added little or no published information on the flora of the region.

In 1948, Professor E. Rouleau of the Université de Montréal began serious botanizing of the entire province over a period of time that would span twenty years. His painstaking compilation of previous collection records and of distribution maps, as well as his considerable contribution of collected material represents the second major phase in the development of a comprehensive view of the flora of St. Barbe South. Part of this information was published as a checklist of the vascular plants of Newfoundland (Rouleau, 1949, 1956).

The inventory of the flora continued to grow with additions by Professor R. Tuomikoski, 1949, from the University of Helsinki, Finland, and by Elkington, 1958, of the British Museum. Expeditions from the Canada Department of Agriculture, Ottawa, to the west coast of Newfoundland resulted in collections by Basset, 1949; Savile, 1951; and Donly, 1955, from numerous localities in the study area.

In more recent years, ecological studies in the region have served to increase our knowledge of the flora. The description by Rowe (1959) of boreal forest sections which dissect the study area, and a subsequent more detailed vegetation analysis by Damman (1967) were the first steps toward an understanding of possible environmental factors responsible for the presence of certain elements of the flora and the manner in which they are associated.

The recent creation of Gros Morne National Park in the southern part of St. Barbe South gave rise to the third major phase in the study of the flora. In 1972, a vegetation study of the coastal plain area of the park (Bouchard, 1974) was the first comprehensive analysis of all the vascular flora within a circumscribed sector of the study area. The floristic part of a later report (Bouchard & Hay, 1976a) presents integrated data concerning frequency of occurrence, manner of association and habitats for all the coastal plain vascular plants. Rouleau *et al.* (1975) published an exhaustive checklist of the vascular flora of the entire park. This was followed by a complete biophysical resource inventory by Airphoto Analysis Associates (1975). The latter report incorporates useful information concerning the floristic composition and the environmental controls of many vegetation associations.

GEOGRAPHIC AFFINITIES

Newfoundland lies entirely within the Boreal Forest Region of Canada (Rowe, 1959) and includes large areas of forest-tundra, a subsection of this region grading into the arctic tundra. Overall, the flora of St. Barbe South is characterized by the core of species which typify, or are associated with, the essentially transcontinental boreal forest vegetation. While the dominant tree species vary, *Abies balsamea, Betula papyrifera, Picea glauca* and *P. mariana* are all characteristically present. Due to regional differences in the physiognomy of the vegetation, and in the flora, this sector of the west coast embraces three boreal forest subsections (Rowe, 1959). Thus, the Corner Brook Section, encompassing the area south of Bonne Bay, is distinguished because of more demanding southern species such as *Betula alleghaniensis* and *Fraxinus nigra.* The Northern Peninsula Section includes the flanks and piedmont area of the Long Range Mountains as well as the coastal plain. The Newfoundland-Labrador Section, which includes the Precambrian alpine plateau, is part of Rowe's broader forest-tundra section.

The flora of the west coast sector of Newfoundland has long attracted the attention of phytogeographers because of the high proportion of vascular plants which are not typical of the boreal forest flora. Some of these species show varying degrees of disjunction with their main centres of geographic distribution, while others are endemic to the Gulf of St. Lawrence region. Rowe (1966), following the individualistic concept of plant association of Gleason (1939), summarized the difficulty in defining sharp boundaries for floristic and vegetation zones stating "every species while sharing area with others, has its unique pattern of prominence and distribution." As an alternative, Rousseau (1974) identified eleven major phytogeographic groups in the flora of Quebec-Labrador. Similarly, the flora of St. Barbe South, although confined to a much smaller area, contains elements representative of nearly all of these chorologic groups.

Cosmopolitan Element. Species of wide ecological amplitude (often colonizing open habitats) such as *Cystopteris fragilis, Deschampsia flexuosa* and *Equisetum arvense* are examples of this group with a world wide distribution.

Circumpolar Element — Northern Hemisphere. This element of the flora consists primarily of two groups: (1) circumpolar boreal forest species such as *Circaea alpina, Moneses uniflora* and *Pyrola minor;* and (2) arctic-alpine species of arctic circumpolar distribution with southern extensions of range in suitable, usually alpine, habitats. Within the latter group, the tundra barrens of the Long Range Mountains yield numerous examples such as *Arctostaphylos alpina, Loiseleuria procumbens* and *Lycopodium alpinum* (Bouchard & Hay, 1974). Several examples such as *Dryopteris limbosperma* (syn. *Thelypteris limbosperma,* Bouchard & Hay, 1976b; syn. *Oreopteris limbosperma,* Bouchard, et al., 1977) show

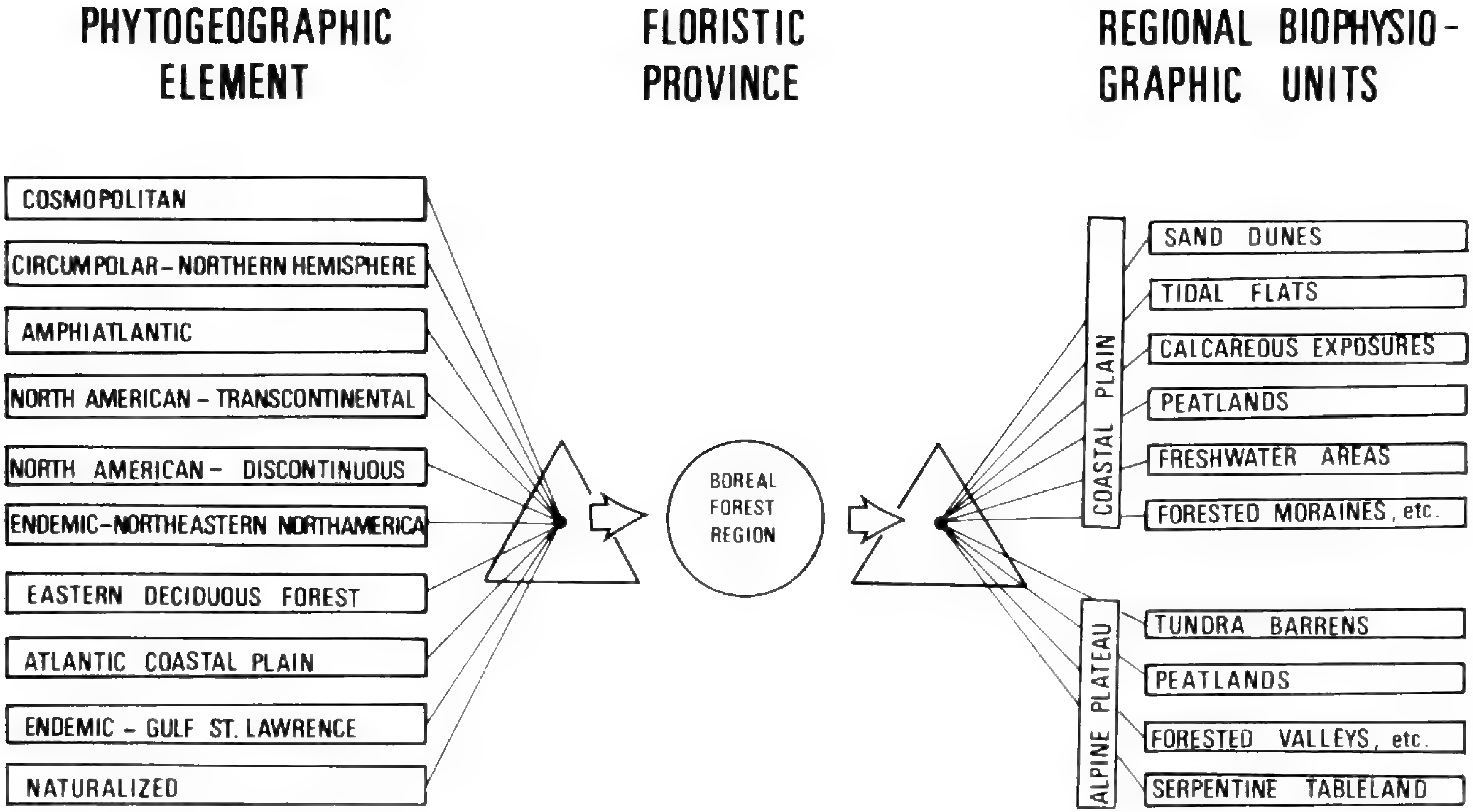

Figure 3. "Refraction" of the flora of St. Barbe South due to a prism-like influence of environmental, historic and biotic controls.

a highly disjunct distribution in the North American part of their range. Other species such as *Androsace septentrionalis, Potentilla nivea* and *Woodsia alpina* have extended their range into the Gulf of St. Lawrence region on barren alkaline soils such as occur on the calcareous coastal plain exposures. Additional representative species including *Lycopodium selago* and *Silene acaulis* are found on limestone, granite and serpentine barrens throughout the study area.

Amphiatlantic Element. This flora, with a macrodistribution pattern ranging mainly along both sides of the Atlantic, includes *Armeria maritima, Diapensia lapponica, Salicornia europaea, Saxifraga paniculata* and *Viola palustris*. These plants are found mainly in restricted habitats of the study area such as the tidal flats, tundra barrens and calcareous barrens.

North American Element-Transcontinental at Canadian Latitudes. Two major groups comprise this element: (1) boreal forest species such as *Abies balsamea, Cornus canadensis, Gaultheria hispidula, Kalmia poliifolia* and *Picea glauca* which characterize the forested landforms of the study area; and (2) several arctic-alpine species including *Dryas integrifolia, Rubus acaulis* and *Vaccinium cespitosum* colonizing coastal limestone barrens or alpine tundra. Rousseau also distinguished a "quasi-transcontinental" group with similar North American distribution including *Aster puniceus, Cypripedium acaule* and *Potentilla tridentata*.

North American Element-Discontinuous in Continental Interior. Plants of this group, which includes *Orobanche uniflora* (including *O. terrae-novae*), *Parnassia parviflora* and *Viola pallens* from the study area, show discontinuity, often in the midwest of their continental distribution.

Endemic Element in Northeastern North America. Several species typical of peatland flora such as *Andromeda glaucophylla, Carex exilis, Sarracenia purpurea* and *Vaccinium angustifolium* show this more restricted regional distribution pattern. *Lycopodium sabinifolium* and *Salix uva-ursi* are arctic-alpine examples of this group.

Eastern Deciduous Forest Element. Although several species representative of this element extend their range further north in the study area (e.g. *Vaccinium macrocarpon*), tree species such as *Acer rubrum, Betula alleghaniensis* and *Fraxinus nigra* appear to be at or near their northern limit at Bonne Bay and are rare and restricted to forested slopes at this locality.

Atlantic Coastal Plain Element. This distribution pattern is represented mainly by distinctive plants which have been only rarely recorded from the alpine peatlands of the plateau region south of Bonne Bay. They include *Bartonia paniculata, Habenaria blephariglottis, Potamogeton oakesianus* and *Schizaea pusilla.*

Endemic Element. Species of this group have been mainly described by Fernald (1911, 1926-27, 1933, 1950) and many are of questionable taxonomic status. Several are endemic essentially to the Gulf of St. Lawrence centred-region and include *Arnica chionopappa, Lesquerella purshii, Oxytropis johannensis, Streptopus* × *oreopolus, Taraxacum ambigens, Triglochin* × *gaspense* and *Vaccinium* × *nubigenum.* Other such species are more narrowly endemic to the study area and include *Antennaria bayardii, A. columnaris, Epilobium scalare* and *Salix wiegandii.* The majority of these species are found on the calcareous exposures of the coastal plain. Many await revision and are probably only edaphic ecotypes of closely related species.

Naturalized Element. These species, introduced mainly from Eurasia, include *Aconitum bicolor, Agropyron repens, Plantago major, Ranunculus acris, Rumex crispus, Trifolium repens* and *Tussilago farfara.* They are relatively few and favour habitats of the coastal plain which have been disturbed due to road construction, settlement, logging and livestock grazing.

In conclusion, there has been much discussion in response to the phytogeographic questions raised by the existence, particularly in the Gulf of St. Lawrence region, of the many vascular plants which are apparently endemic or which have geographic affinity with floristic elements other than the core of species that characterize the general boreal forest region. The merging together of distinct floristic elements around the Gulf has been described in Nova Scotia (Roland & Smith, 1969), in Newfoundland (Fernald, 1911, 1925, 1933; Damman, 1965), and in Quebec (Marie-Victorin, 1938). Theories proposed to account for these diverse elements in the flora range from survival in the wake of Pleistocene glaciation in alpine or coastal refugia (Fernald, 1925; Drury, 1969; Wynne-Edwards, 1937, 1939), to the importance of opportunities for migration (long distance dispersal), competition and disturbances such as fire (Rowe, 1966). Rousseau (1974) brought these many hypotheses into perspective, discussing in detail their importance in relation to his phytogeographic groups for the flora of Quebec-Labrador. He summarized, "en plus des facteurs climatiques qui influencent manifestement la répartition des plantes, il en existe d'autres tels la composition du sol, les éléments biotiques (constitution génétique et concurrence avec d'autres plantes) ainsi que les éléments historiques (glaciation et submersion postglaciaire), lesquels modifient grandement certaines modalités de distribution qui autrement devraient être plutôt réguliéres."

The interplay of environmental (especially climate), historical and biotic factors responsible for the presence of different phytogeographic elements in the flora, and the manner in which they are associated, can be visualized in terms of a model (Figure 3). These factors have permitted the segregation of some plants from their affiliated geographic groups and integrated them into an essentially boreal forest flora. These same factors, particularly with the locally steep environmental gradients, have had a "prismatic" effect on the different elements of the flora causing their "refraction" into different plant communities colonizing diverse physiographic units of the study area.

BIOPHYSIOGRAPHIC AREAS

Coastal Plain, Sand Dunes.

PHYSIOGRAPHY. The coastal sand dunes of St. Barbe South (Figure 5A) are a conspicuous landform of the coastal plain due to their elevation above the surrounding lowland. They are beach dunes, as defined by Way (1973), of a smaller scale than examples occurring elsewhere in the Gulf of St. Lawrence such as les Iles-de-la-Madeleine (Grandtner, 1967).

Sufficient sand required for dune formation occurs infrequently on the sedimentary coastal terrain. However, large surficial deposits have accumulated at the mouth of several rivers which drain the Long Range Mountains and the coastal plain. The source of sand appears to be the Precambrian granite of the Long Range. In each case, the river-transported sand is discharged into a bay which opens directly on the sea and which is bounded immediately to the north by a retaining rocky peninsula. The rock promontory arrests the littoral drift of the sand and the ensuing dune formation occurs behind the bay-shore according to the processes outlined by McHarg (1969) and Way (1973).

The dunes form behind the brackish sandy seashore (vegetation described in the following section on Tidal Flats). They form two distinct zones which have characteristic vegetation: (1) the hummocky foredunes or primary dunes of recent deposition which are exposed to salt spray and sand movement, and which are continually being broken and reformed by onshore winds; and (2) the higher fixed dunes which are normally stable and colonized by scrub vegetation.

VEGETATION AND FLORA.

Foredunes. The unstable foredune area is colonized almost exclusively by *Ammophila breviligulata* and to a lesser extent by *Elymus arenarius.* The plant cover for this zone is well below 50% (Bouchard, 1974). Frequent blow-outs occur where the stabilizing marram-grass or beach-grass cover has been disturbed. Once the foredunes have been secured, other psammophytes or halophytic species such as *Carex maritima, Gentiana amarella, Juncus balticus, Lathyrus japonicus, Plantago juncoides, Rumex pallidus, Senecio pseudo-arnica* and *Smilacina stellata* may become established. *Ammophila breviligulata* is the only species which grows uniquely on this landform. The others (*Carex maritima, Gentiana amarella,* etc.) are found occasionally in other physiographic sites such as the tidal flats and the sea cliffs.

Numerous opportunistic, turf-forming grasses such as *Agrostis alba, Festuca rubra, Poa palustris* and *Poa pratense* may consolidate local areas in the foredune zone. Other species which are also found in this protective turf include *Equisetum arvense, Potentilla anserina, Trifolium repens* and *Sagina nodosa.* Weedy species such as *Anaphalis margaritacea, Senecio vulgaris, Ranunculus repens* and *Rhinanthus crista-galli* also become established as scattered individuals in this herbaceous community.

Fixed Dunes. The higher fixed dunes are usually stabilized by a scrub formation of *Abies balsamea* and *Picea glauca.* This vegetation is often destroyed by sand movement or sand blasting where the front-lying dunes have been disturbed. Other species commonly found in this scrub thicket, especially on the exposed front face of the dune, are *Alnus crispa, Cornus alba, Juniperus communis, Ribes lacustre* and *Shepherdia canadensis.*

This vegetation unit grades into the balsam fir scrub or forest communities (Bouchard, 1974) which dominate the well drained areas of the coastal plain. This front-lying scrub is consequently composed mostly of species coming from this latter vegetation type.

GEOGRAPHIC DISTRIBUTION. The essential physiographic conditions leading to the formation of major sand dunes have occurred at three localities along the coast. At the mouth of Western Brook, the sand dune system has been built up in the bay bounded on the north by Broom Point. The dunes which surround Shallow Bay at the mouth of the Stanford River have accumulated between the peninsula of Lower Head and the village of Cow Head. They are the largest example of this landform in the region. The Portland Creek sand dunes have been retained in Portland Cove which abuts on Eastern Head peninsula. Other surficial deposits of sand in the interior of the coastal plain are very local and have been covered by fir scrub or forest vegetation.

Coastal Plain, Tidal Flats and Brackish Shores.

PHYSIOGRAPHY. In comparison with the salt marshes which rim the shores of the Atlantic provinces such as Nova Scotia (Harvey, 1973), the tidal flat marshes (Figure 5B) of St. Barbe South District are neither extensive nor well developed. They nevertheless conform to the general concept in that they originate as coastal sand or mud flats which are subject to periodic inundation by the tide. These flats are colonized by a characteristic halophytic vegetation which may lead to the development of a closed marsh community. The brackish soil water and/or tidal submergence are clearly the chief factors controlling the formation.

Shallow bays and river estuaries which are protected from the heavy wave erosion of the open coast permit gradual siltation leading to the formation of tidal flats and brackish shores.

VEGETATION AND FLORA. In this biophysiographic unit, three general vegetation units can be described; (1) the open tidal mud flats which are partially colonized by turfy herbaceous communities, (2) the upper salt marsh rimming the lower tidal flats, and (3) the vegetation of the brackish sand or gravel shores which do not necessarily form a part of the tidal flats.

Tidal Mud Flats. The zonation of the vegetation on the lower tidal flats depends on the depth and duration of inundation by the

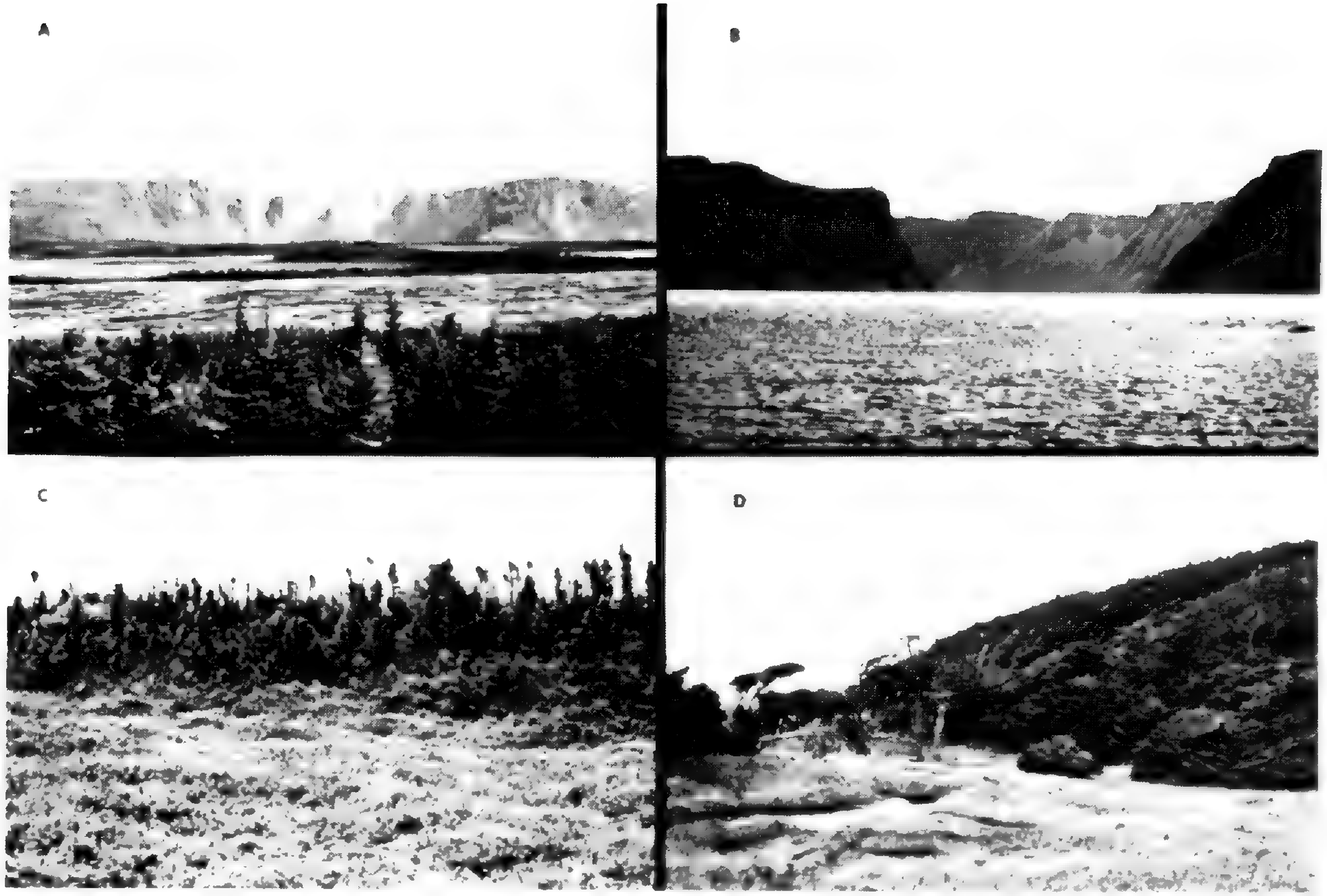

Figure 4. A. Western Brook Pond "fjord" and the coastal plain. B. A view of Western Brook Pond from the coastal plain. C. Dwarf black spruce scrub in the foreground; black spruce scrub in the background. D. Coastal krummholz of wind-shaped balsam fir and white spruce scrub.

tides and is well developed only where the change in elevation is very gradual. In the seaward sector, which is normally submerged by salt water, a single vascular plant *Zostera marina* is found growing with abundant marine algae. The more elevated open mud flats, which are flooded to shallow depths with each tidal cycle, are virtually bare of vegetation except for *Salicornia europaea* which may form extensive monospecific populations in which the plant cover is probably less than 10% (Bouchard, 1974). However, towards their upper extreme, these mud flats are covered by a turfy herbaceous community dominated by *Eleocharis halophila, Festuca rubra, Plantago oliganthos, Ranunculus cymbalaria, Salicornia europaea, Scirpus rufus* and *Triglochin palustre.* Some other characteristic species include *Eleocharis parvula, Lomatogonium rotatum, Puccinellia paupercula, Spergularia canadensis, Stellaria humifusa, Triglochin* × *gaspense* and *T. maritimum.* The wet depressions and frequent tide pools, which form on the flats, contain colonies of aquatic species such as *Potamogeton filiformis, Ruppia maritima, Zannichellia palustris* and *Zostera marina.*

Most of the preceding species are halophytes which, by virtue of their tolerance to the severe conditions of the lower tidal mud flats, have been able to colonize this open habitat. The distribution of this unique assemblage of species is nearly exclusively restricted to this zone.

Upper Salt Marsh. The physiognomy of the upper salt marsh shoreline, which occurs at the upper limit of the tides, is quite different from that of the lower tidal flats because of its closed herbaceous structure. This community is rarely flooded by salt water but the soil is nevertheless saline and supports a diverse halophytic flora. The dominant species *Eleocharis halophila, Carex mackenziei, C. paleacea* and *C. salina* are accompanied by many other characteristic species such as *Arenaria peploides, Atriplex glabriuscula, A. patula, Carex maritima, Catabrosa aquatica, Glaux maritima, Iris hookeri, Juncus balticus, J. bufonius, J. gerardii, Lomatogonium rotatum, Plantago juncoides, Potentilla anserina, P. egedei, Sagina nodosa, Scirpus americanus, Stellaria humifusa* and *Triglochin maritimum.* This last zone abuts on normal coastal plain vegetation and consequently many species of general distribution are capable of invading it despite the limitations imposed by the brackish environment. Such opportunistic species as *Agros-*

tis alba, Aster foliaceus and *Festuca rubra* are frequent examples of species which encroach on this community from the mosaic of herbaceous communities along the coast.

Brackish Shores. The brackish sand or gravel shores are sparsely colonized by several halophytic species including *Arenaria peploides, Atriplex glabriuscula, A. patula, Cakile edentula, Elymus arenarius, E. virginicus, Glaux maritima, Hierochloe odorata, Hordeum jubatum, Ligusticum scothicum, Lathyrus japonicus, Mertensia maritima, Poa eminens, Polygonum fowleri, P. raii, Salsola kali, Sagina nodosa, S. procumbens, Senecio pseudo-arnica, Solidago sempervirens* and *Spartina pectinata.* These species are infrequent and are usually restricted to this open brackish habitat although a few, such as *Ligusticum scothicum* and *Lathyrus japonicus* are occasionally found growing on wet sea cliffs. Because these shores are often adjacent to the salt marsh, some of the same species occur in both habitats. This vegetation unit also grades into the mosaic of coastal herbaceous communities described by Bouchard (1974).

GEOGRAPHIC DISTRIBUTION. The forebay of St. Pauls Inlet and the entrance to Parsons Pond contain the only large saline mud flats with rich salt marsh vegetation. The St. Pauls flats (Figure 5B) are a particularly outstanding feature of the coastal plain.

Tidal mud flats are also located in Bonne Bay at Glenburnie and Lomond in the estuaries of Mackenzies Brook and the Lomond River respectively. Less extensive brackish shores are also found at the mouth of Deer Brook and in the Southeast Arm.

In the northern part of the District, the only locality where there is some minor development of this vegetation is in Hawkes Bay at the mouth of the East River.

Numerous brackish gravel shores occur in protected coves of Bonne Bay, St. Pauls Inlet, Parsons Pond, Port Saunders and Hawkes Bay. The only examples of brackish sandy shores lie in front of the sand dunes at Western Brook, Stanford River and Portland Creek.

Coastal Plain, Calcareous Exposures.

The calcareous exposures of the coastal plain are described in two subsections, calcareous maritime exposures (Figure 5C) and calcareous inland exposures (Figure 5D). Although these two habitats are characterized by calcareous bedrock, the maritime influence is such an important ecological variable that this division is necessary to adequately describe the flora.

Calcareous Maritime Exposures

PHYSIOGRAPHY. The geomorphology of the calcareous maritime exposures in the northern part of the coastal plain is very different from that in the southern sector. In the latter part of the region the exposures are promontories with low cliffs which jut out from the coastline. These headlands are the exposed, terminal sections of ridges of interbedded sedimentary rock which underlie the coastal plain. These ridges, which parallel each other in this part of the coastal lowland, are the result of thrust faulting and massive lateral displacement (klippen) of the interleaved sedimentary beds of several distinct geological formations. The geomorphology of this section of the coastal plain has been discussed in detail by Cumming (1973) and is summarized in the geology section of this text (see previous Geology section). In contrast the calcareous maritime exposures of the northern sector are extensive flat barrens which intermittently form long sections of the coastline. These barrens are composed of horizontal beds of the autochthonous sedimentary deposits of sandstone and carbonate rock which form the bedrock of the coastal plain in this northern sector (Fleming, 1973). They lie exposed and are maintained as barrens by the constant erosion processes of the seashore. The surface of this landform is a mosaic of bedrock outcrops and gravel barrens where frost weathering of the bedrock has led to the accumulation of unconsolidated gravel. The seaward section of these barrens may slope gradually to sea level or terminate as low sea cliffs.

Much of the floristic composition of the vegetation of these exposures is determined by the alkaline calcareous bedrock. Additional parameters which also have an important influence are the salt spray, due to the proximity of the sea, and the exposure to high winds which maintain the open, unstable nature of the habitat.

VEGETATION AND FLORA. Despite the differing geomorphology of the coastal calcareous exposures in the northern and southern halves of the region, their flora is very similar. The lower cliff face and boulder beaches of both the headlands and barrens are normally completely open. Only in protected coves of Pointe Riche Peninsula is there some development of brackish shore vegetation (see previous Tidal Flats section). The vegetation which becomes established behind the open seaward sector can be described in two principal zones: (1) the unstable upper cliff face and exposed rock barrens facing directly on the sea, and (2) the turfy heath scrub which stabilizes areas on the crest or top of the barrens and cliffs which are less disturbed. This heath community grades into the coastal formation of fir scrub situated inland of the exposed seaward zones.

Sea Cliffs and Rock Barrens. The steep sea cliffs are sparsely colonized on their upper face by a few hardy species such as *Plantago juncoides* and *Sedum rosea.* The latter is unique to this landform in the study area. On more protected high ledges there is some formation of turf composed of such ubiquitous coastal species as *Agrostis alba, Campanula rotundifolia, Festuca rubra, Ligusticum scothicum* and *Potentilla anserina.*

The weathered gravels and outcrops on the northern barrens support a more diverse flora than the previous habitat. They are colonized mainly by a very patchy vegetation cover of severely wind-pruned shrubs. The dominant species forming this low-lying mat include such rampant woody species as *Betula pumila, Juniperus communis, J. horizontalis, Potentilla fruticosa,* and the characteristic calciphile *Dryas integrifolia.* The latter species is a commonly occurring example of the calciphilous element of the flora, the distribution of which is restricted to this calcareous physiographic unit. The apparent rarity of these species, or at least their restriction to a unique habitat at various isolated localities around the Gulf of St. Lawrence, has attracted the attention of botanists such as Fernald (1925), Marie-Victorin (1938), Scoggan (1950), Damman (1965), Roland and Smith (1969), Rousseau (1974) and Grandtner and Rousseau (1975). Whether the edaphic specificity of this element of the flora is indicative of a particular physiological dependency on the calcareous substrate (calciphilous) or whether they are ecologically specialized plants which find sanctuary in this unstable, low-competition habitat, is a question which has long engendered debate (Wynne-Edwards, 1937, 1939; Griggs, 1940). More recently authors such as Drury (1969) and Morisset (1971, 1974) have discussed this group of vascular plants and the biogeographic implications of their endemism or disjunct distribution.

Most of the species occurring in the study area, which have been described as calciphiles in the Gulf of St. Lawrence region (Fernald, 1950; Scoggan, 1950; Rousseau, 1974), are found growing sparsely either on the open weathered gravels or shallow soils of the turf carpet overlying the barrens. The main examples are species which are characteristic of the biophysiographic unit as a whole in that they are found on these coastal sites and also on the inland calcareous sites. They include *Allium schoenoprasum, Arnica chionopappa, A. terrae-novae, A. tomentosa, Asplenium viride, Cypripedium calceolus, Cryptogramma stelleri, Cystopteris fragilis, Draba arabisans, D. glabella, D. norvegica, Erigeron hyssopifolius, Hedysarum alpinum, Lesquerella purshii, Malaxis brachypoda, Polystichum lonchitis, Salix vestita* and *Tofieldia pusilla.*

Other species such as *Carex microglochin, Cochlearia cyclocarpa, C. tridactylites, Gentiana nesophila, Habenaria hookeri, Parnassia parviflora* and *Salix reticulata,* though generally described as calciphilous, are restricted in their distribution to the maritime barrens and apparently are not found on the inland calcareous sites.

Another group of species which colonize this biophysiographic unit is also found growing sparsely on the serpentine tableland (see following Serpentine Tableland section). These species include *Arctostaphylos uva-ursi, Anemone parviflora, Arenaria humifusa, A. rubella, Armeria maritima, Artemisia canadensis, Cerastium arvense, Oryzopsis asperifolia, Oxytropis terrae-novae, Salix arctica, S. glauca, Saxifraga aizoides, S. oppositifolia, Senecio pauperculus, Solidago hispida* and *S. multiradiata* and show a close affinity with the strictly calciphilous species in that they colonize an open unstable habitat on a highly alkaline rock substrate.

The flora of this biophysiographic unit is very diverse and contains numerous species of wide arctic distribution which, though not defined as calciphiles, are restricted to this landform in the study area. The calcareous sites provide a favourable habitat at the limit of the range of *Arabis alpina, Artemisia borealis, Braya purpurescens, Carex rupestris, Festuca saximontana, Potentilla nivea, P. pectinata, Primula egaliksensis, Saxifraga cespitosa, S. paniculata, Sedum rosea, Woodsia alpina,* and *W. glabella* and permit their southern extension of distribution into the Gulf of St. Lawrence.

In addition to species which are characteristic or unique, these naturally disturbed open barrens are also successfully colonized by weedy species such as *Achillea millefolium, Deschampsia flexuosa* and *Trisetum spicatum* which are frequent in man-disturbed or open habitats everywhere on the coastal plain. Because some localized turfy areas are sufficiently influenced by salt spray from the sea, some species more typical of the salt marsh or gravel beaches (see previous Tidal Flats section) such as *Iris hookeri, Juncus balticus, Ligusticum scothicum, Mertensia maritima* and *Scirpus rufus* may be found.

Turfy Heath Scrub. The turfy heath scrub, which lies behind the seaward-facing gravel barrens and cliffs, is a structurally closed vegetation unit on a hummocky peat layer on the calcareous maritime exposures. The vegetation of this zone is permanently maintained as a poorly developed low-lying scrub and peaty turf due to exposure to high winds and frost kill. The peaty carpet is sufficiently removed vertically from the underlying limestone so that in comparison with the open gravel barrens, the flora in this zone is much more diverse. Fernald (1933) attributes the reduced alkalinity of these superficial soils to leaching and accumulation of acid peats. As a result the turfy heath barren is dominated by a wind-pruned scrub composed of species of general distribution such as *Abies balsamea, Betula pumila, Empetrum nigrum, Juniperus communis, J. horizontalis, Larix laricina, Myrica gale, Picea mariana,* and *Potentilla fruticosa.* Uncommon but characteristic shrubs include *Cornus alba, Rhamnus alnifolius, Shepherdia canadensis* and *Viburnum edule.* Ericaceous species such as *Andromeda glaucophylla, Vaccinium angustifolium, Kalmia angustifolia* and *Ledum groenlandicum* which characterize the raised bogs of the coastal plain (see following section on Peatlands) are relatively common in this heath scrub formation. Several uncommon herbaceous species including *Castilleja septentrionalis, Comandra richardsiana, Geocaulon lividum* and *Selaginella selaginoides* are not considered as calciphiles but often favour calcareous boggy soil. They have a general distribution in the study area but are more frequently found in the protective heath scrub of these calcareous barrens.

GEOGRAPHIC DISTRIBUTION. The calcareous coastal headlands in the southern half of the coastal plain are situated at isolated localities between Bonne Bay and Parsons Pond. These scarped promontories jut into the Gulf at Lobster Cove Head, Green Point,

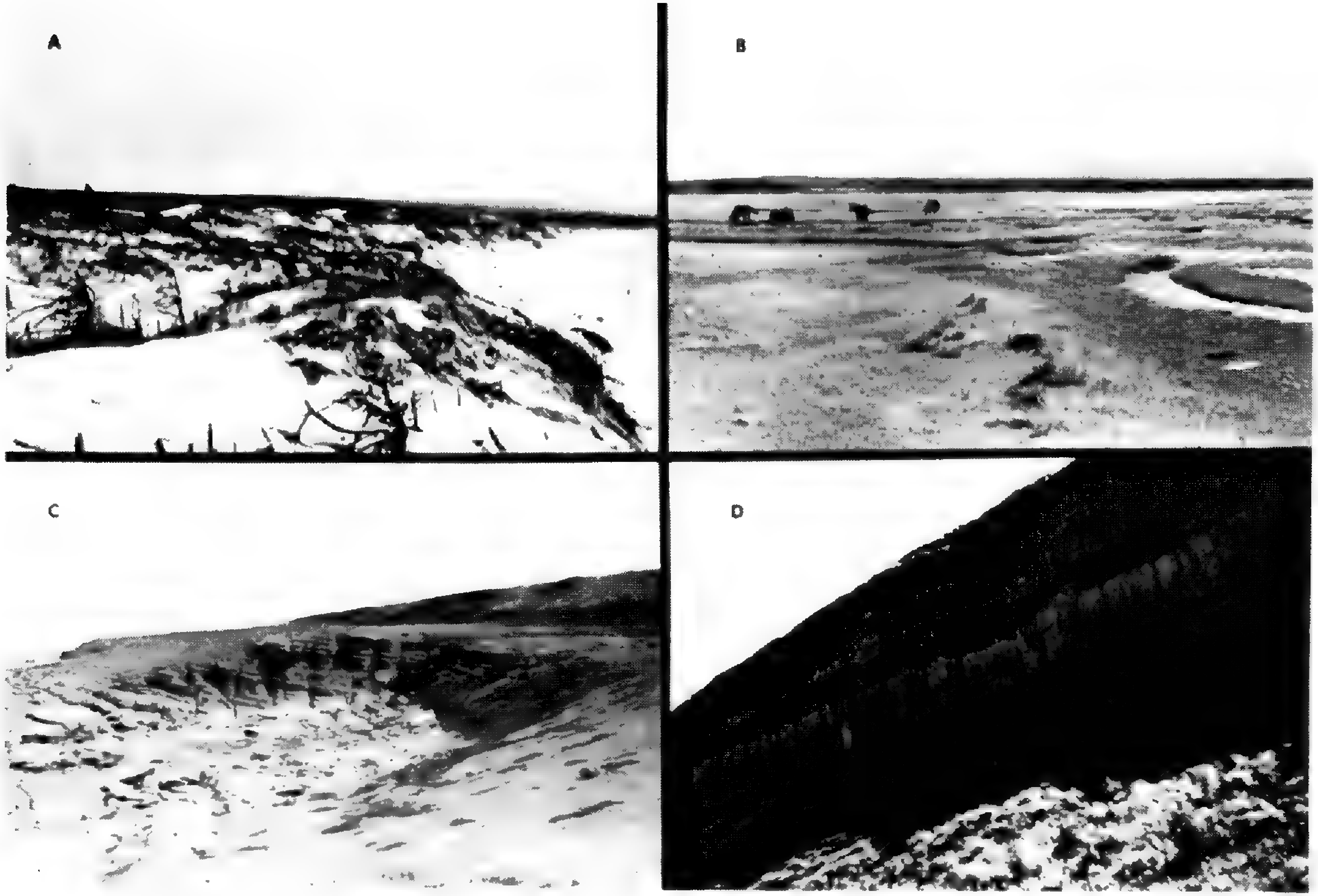

Figure 5. A, Sand dunes at Shallow Bay. B, St. Pauls tidal flats at low tide. C, Limestone barrens at Pointe Riche. D, Limestone escarpment along the South Summit of the Highlands of St. John.

Martin Point, Broom Point, Cow Head and Lower Head. Stearing Island and White Rock Islets at Cow Head are part of the same formation.

The coastal limestone barrens of the northern sector are much more extensive tablelands and constitute long sections of the seashore. The Eastern Head formation extends from Portland Creek to Daniels Harbour. Bateau Barrens dominates the coastline between Bellburns and Bateau Cove at LaFontaine Point. The Pointe Riche Peninsula (Figure 5C) at Port au Choix, including the barrens on the mainland between Gargamelle and Eddie's Cove West, is the largest exposure of this landform.

Calcareous Inland Exposures

PHYSIOGRAPHY. The inland calcareous exposures of the study area are major outcrops of sedimentary rock which lie at scattered locations along the western escarpment of the Long Range Mountains. They are not a continuous geological formation but rather occur as local exposures along the thrust fault which divides, from north to south, the low-lying sedimentary coastal plain and the Precambrian Long Range plateau. With the uplift of the Long Range, sections of the coastal lowland, lying along the fault, were displaced. Less major displacements along the fault have been reduced by erosion to hogback foothills (Cumming, 1973) along the base of the escarpment and are covered with fir scrub or fir forest vegetation. The major displacements are still represented by vertical cliffs of interbedded shale, limestone and sandstone with steep talus slopes at their base. Despite the almost montane elevation of a few of these cliffs, this landform is treated as part of the coastal plain complex because these displaced sedimentary formations are closely allied geologically with the calcareous exposures of the actual coastal lowland.

The sedimentary cliffs and their talus slopes constitute an extremely unstable habitat because of the continual disturbance by exposure, ice and falling rock. Consequently the vegetation cover is minimal and it is maintained in a pioneer stage of succession. The drainage of this habitat is rapid.

The vegetation shows no maritime influence because these outcrops are situated along the interior of the coastal plain and well inland from the sea. The outcrops exposed around the East Arm of Bonne Bay are somewhat exceptional because this basin opens directly onto the sea and the bay is partly saline. Nevertheless, the flora of these latter scarps is similar to the more strictly interior examples of this landform.

VEGETATION AND FLORA. The boulder screes at the base of these calcareous cliffs are usually covered on their lower slopes by fir forest or fir scrub vegetation, which towards its upper extreme grades into patchy dwarf scrub composed usually of *Abies balsamea, Betula papyrifera, Juniperus communis, Picea glauca* and *P. mariana.* Above this stabilized area, the talus slope and vertical cliff face are completely open and the vegetation cover is less than 5%. The lack of dominant species and a high diversity of uncommon or rare species, including a rich calciphilous element, characterize this vegetation. Those calciphiles which have ubiquitous distribution on calcareous sites within the region, whether they be coastal headlands or inland exposures, have been described for the coastal calcareous exposures (see previous Calcareous Maritime Exposures section). Conversely, examples of those species which are conceived to be true calciphiles by several authors (Fernald, 1950; Rousseau, 1974; Scoggan, 1950) and whose distribution is restricted to the rocky ledges and crevices of this physiographic site include *Alchemilla minor, Androsace septentrionalis, Anemone multifida, Arabis drummondii* and *Cystopteris bulbifera.* Within the study area, these species apparently cannot tolerate the ecological influence of salt spray and increased exposure which are important factors in the corresponding coastal habitats.

The crest and flat summit of these outcrops often provide a more stable, undisturbed site for colonization by fir scrub or fir forest communities similar to those found at the base of the talus slopes and elsewhere on the coastal plain. The barren summit of Sandy Barren at St. Pauls Inlet is exceptional and its sparse vegetation cover is strikingly similar to that of the exposed maritime rock barrens.

GEOGRAPHIC DISTRIBUTION. The East Arm basin of Bonne Bay provides some of the most striking examples of this landform with high stratified cliffs and steep talus slopes at Lomond, Tuckers Head, and Shag Cliff along the south shore; and at Killdevil along the north shore.

Further north, major exposures occur at Sandy Barren at the interior end of St. Paul's Inlet and at the eastern end of Parsons Pond where these basins meet the escarpment of the Long Range plateau.

The cliffs of the sedimentary outcrop at Portland Head are curiously isolated in the coastal plain but are probably indirectly associated with the major fault dividing the coastal lowland and the Long Range.

The most northern and most extensive exposure in the study area is the western escarpment of Doctor Hill, the South Summit of the Highlands of St. John (Figure 5D).

Coastal Plain, Peatlands.

The following description of this biophysiographic unit is a simplified version of that which appeared in previous reports on the vegetation and flora of the coastal plain of Gros Morne National Park (Bouchard, 1974, 1975; Bouchard and Hay, 1976a). It has been expanded to fit the description of the entire coastal lowland of the study area.

PHYSIOGRAPHY. Fen and bog peatland overlie much of the coastal plain (Figure 4A) forming a patchwork of flat, wet herbaceous terrain between adjacent forest and scrub communities.

Except for a few exposed rock ridges and coastal headlands, the bedrock foundation of the coastal plain lies buried beneath deep marine and glacial deposits. Its geomorphology is an important factor controlling the drainage and hence the formation of these peatlands (Bouchard, 1975). The complex geology of the sedimentary bedrock formations and of the mantle of surficial deposits has been summarized in the geology section (see previous Geology section) of this text and has been discussed in detail by Cumming (1973) and Grant (1972a, 1973a).

The most extensive peatland formations occur in the southern and central part of the coastal plain where in some areas these organic deposits cover as much as 43% of the terrain (Bouchard, 1975). The peat deposits usually lie between adjacent outcrops of parent bedrock or glacial deposits which are more elevated and better drained landforms. Many of the bogs in this sector are of a linear pattern due to their formation between ridges created by the faulted bedrock. In the northern sector the deep surficial moraines of glacial till, which mantle most of this coastal plain area (Grant, 1972a), have greatly limited the development of peatlands.

The coastal plain bogs may have been formed following the same successional steps described by Sjörs (1963) for the Attawapiskat River in northern Ontario (Bouchard, 1974). Forest or scrub would have invaded the newly exposed land after its postglacial emergence from the sea. Much of this early forest was probably swampy. The peaty but well decomposed types of humus made the soil more impermeable and more water retaining. The general development was then in the direction of greater wetness or paludification. Mosses spread (as the conditions that allowed their establishment continued), gradually occupying more and more of the forest floor until the sodden conditions killed off the forest and a bog was formed (Drury, 1956). Most of the peatland can be classified as "raised bogs." These bogs have grown above their site of origin, and have centers which are higher than the margins and surfaces which are convex (Drury, 1956). Growth is by peatmoss proliferation and deposition of peat. Deposit depth varies tremendously and can exceed 3.5 meters. The high rate of peat decomposition on the edge of the raised bog is probably the cause of the convexity of the dome. Numerous flashets or ponds are found at right angles to the slope in the direction of the contours. According to Sjörs (1961), the flashets are primarily dependent on the water flow across the peatland. The poor drainage in these ombrogenous bogs is by seepage from the center to the edge.

Sjörs (1963) wrote that "if the present non-glacial period continues long enough, growing peat deposits will ultimately reach a state of instability inducing either drought or bog-burst, depending on the type of topography and climate. In many cases the peats will be destroyed earlier by erosion, corrosive oxidation, or fire thus never reaching a final state of maturity." Because of the short growing season and low nutrient conditions, successional changes are expected to be extremely slow. The present structure and composition will be maintained for a long period of time.

The vegetation on the flat, wet terrain of the peatlands can be zonally subdivided according to the trophic level of the site. Pollett *et al.* (1970) have made a detailed analysis of peatland vegetation based on this principle. In this study a somewhat simpler segregation is adopted: (a) the large raised bogs and adjacent surrounding dwarf black spruce scrub which are the predominant community types on wet, oligotrophic sites; and (b) sedge meadows (or fens) and larch scrub which favour the richer eutrophic sites.

VEGETATION AND FLORA.

Raised Bogs. The physiognomy of the raised bog landform is distinct as an expansive, hummocky blanket of *Sphagnum* peat and reindeer moss (*Cladina*) with very dwarf vegetation of tundra type structure. The dominant herbaceous vascular species composing the vegetation cover is *Scirpus cespitosus.* Several dwarf ericaceous shrubs such as *Andromeda glaucophylla, Chamaedaphne calyculata, Empetrum nigrum, Kalmia angustifolia, K. polifolia, Ledum groenlandicum, Vaccinium angustifolium, V. oxycoccos* and *V. uliginosum* are also dominant or very frequent species. These woody plants are maintained in an extremely dwarf or stunted stage of development due to the low nutrient level and exposure to high wind and frost kill in the bogs. Rarely will these species exceed 5 cm. in height (Bouchard, 1974). Less common or infrequent dwarf shrubs including *Abies balsamea, Aronia melanocarpa, Betula pumila, Gaylussacia dumosa, Juniperus communis, Larix laricina, Lonicera villosa, Myrica gale, Nemopanthus mucronatus, Picea mariana* and *Vaccinium vitis-idaea* are characteristic of the vegetation of the raised bogs. The wetness of the habitat favours the colonization by several important Cyperaceae such as *Carex aquatilis, C. exilis, C. limosa, C. rariflora, Eriophorum angustifolium, E. spissum, E. virginicum* and *Rhynchospora alba.* Other frequent and characteristic vascular plants of the flora include *Arethusa bulbosa, Aster nemoralis, Coptis groenlandica, Drosera rotundifolia, Equisetum fluviatile, Rubus chamaemorus, Sarracenia purpurea* and *Smilacina trifolia.*

The raised bogs are usually surrounded by a belt of dwarf black spruce scrub (Figure 4C) in which ericaceous shrubs are co-dominants. This community, which is maintained as a dwarf formation less than 50 cm. in height (Bouchard, 1974) due to the pruning action of the wind, grades into taller more pure formations of black spruce scrub. The dominant species in the dwarf scrub formation are *Kalmia angustifolia* and *Picea mariana.* Ericaceous shrubs such as *Chamaedaphne calyculata, Empetrum nigrum, Ledum groenlandicum, Vaccinium angustifolium* and *V. vitis-idaea* are common accompanying species. The flora of this association is not rich and is very similar to that of the raised bog proper.

Several uncommon but characteristic shrubs not encountered in the raised bog include *Alnus rugosa, Amelanchier bartramiana, Juniperus horizontalis, Rhododendron canadense* and *Viburnum cassinoides,* Additional infrequent herbaceous species such as *Geocaulon lividum, Linnaea borealis* and *Sanguisorba canadensis* are also found in this more protected habitat.

Sedge Meadows. The sedge meadows (or fens) are not common on the coastal plain, nor do they cover large areas in contrast with the raised bogs. They are found primarily in well mineralized, eutrophic zones having active water seepage (Pollett *et al.*, 1970) such as depressed "lagg" areas adjacent to the raised bogs or floating vegetation mats around ponds or lakes.

The vegetation on this flat, wet habitat is primarily herbaceous and dominated by one or several cyperaceous species such as *Carex exilis, C. lasiocarpa, C. livida* or *Scirpus cespitosus.* The community has a tendency to develop towards a shrub-carr by the invasion of woody plants (Curtis, 1959). As a result such shrubby species as *Andromeda glaucophylla, Aronia melanocarpa, Betula michauxii, B. pumila, Chamaedaphne calyculata, Empetrum nigrum, Kalmia polifolia, Larix laricina, Ledum groenlandicum, Lonicera villosa, Myrica gale* and *Picea mariana* are common accompanying species. The flora of these communities is one of the richest of vegetation types found on the coastal plain. In addition to *Aster nemoralis, A. radula, Drosera anglica, D. rotundifolia, Menyanthes trifoliata, Sanguisorba canadensis, Scirpus hudsonianus* and *Vaccinium oxycoccos,* many other vascular plants listed by Bouchard (1974) are found which are characteristic of this hydric flora.

The sedge meadow communities often grade into an adjacent larch scrub formation. These two vegetation types have much the same floristic composition but their structure is quite different, the latter being an open scrub formation dominated in the shrub stratum by *Larix laricina.* Other common shrub species are *Betula pumila, Ledum groenlandicum, Myrica gale, Potentilla fruticosa* and *Rhamnus alnifolius. Drosera rotundifolia, Equisetum fluviatile, Galium labradoricum, Gaultheria hispidula, Iris versicolor, Mitella nuda, Sanguisorba canadensis, Scirpus cespitosus, Smilacina trifolia, Solidago uliginosa, Thalictrum alpinum, T. pubescens, Triglochin maritimum* and *Vaccinium oxycoccos* dominate the rich ground flora. Many sedges such as *Carex disperma, C. interior,* *C. lasiocarpa, C. leptalea, C. limosa, C. livida* and *C. tenuiflora* are a common element of this habitat. The added protection afforded by this shrub phase of the sedge meadow and its nutrient enriched seepage, which is often calcareous, may partially explain the colonization by many species which are mostly restricted to this zone in the peatlands. *Angelica atropurpurea, Caltha palustris, Epilobium palustre, Pinguicula vulgaris, Salix candida, Selaginella selaginoides* and orchid species such as *Cypripedium reginae, Habenaria dilatata* and *Listera convallarioides* are examples of this latter group.

GEOGRAPHIC DISTRIBUTION. The peatlands overlie the entire coastal lowland but are most extensive in the southern and central regions of the study area. The major formations extend from Rocky Harbour in the south to Daniels Harbour in the central sector of the District. Back from the coastline, this landform stretches inland from one to fifteen kilometers toward the base of the Long Range escarpment. To the north of Daniels Harbour, this biophysiographic unit becomes less important although there is some development south of River of Ponds and to the interior of Hawkes Bay.

Coastal Plain, Freshwater Areas.

PHYSIOGRAPHY. The watershed of the coastal plain is an interconnected network of freshwater rivers, streams and ponds which constitutes much of the surface area. The complex drainage patterns are determined by the underlying sedimentary bedrock formations and the surficial marine and glacial deposits.

Running Water. The major drainage basins of the coastal lowland are associated with the rivers draining the land-locked, freshwater fjords (Figure 4A). Water from the rivers is supplied mainly by these fjords which are reservoirs of the nutrient-poor meltwater from the high altitude, granitic Long Range plateau. The rivers are also fed by the network of meandering streams and creeks which dissect the wet peatlands of each drainage basin.

Standing Water. The abundant lakes, ponds and bog pools (or flashets) in the lowland area are filled by accumulated spring meltwater and summer precipitation. The larger ponds and lakes are generally shallow depressions in surficial glacial till and the bottoms are covered with a mineral substrate. The high water retaining capacity of the surrounding peatlands assures a slow run-off and maintains a high water table and a constant water supply to these ponds throughout the summer. Occasional marl ponds have formed in areas where there has been an accumulation of calcium rich, alkaline seepage water from underlying calcareous bedrock. The forebays, which lie at the mouths of several of the landlocked fjords, form the deepest and largest bodies of freshwater in the coastal plain. The numerous flashets, which characterize the physiognomy of the raised bogs, are depressions of varying depth which are formed in the peat deposits due to the eccentric growth and drainage of the bogs (see previous Peatlands section). Some of these pools may be completely drained during the summer, exposing the partially decomposed peat deposits of the bottom.

VEGETATION AND FLORA.

Running Water. The rivers and larger streams of the coastal plain support little or no aquatic vegetation due to limiting physical conditions such as swift current or rapids, sterile sandy or rocky substrate, and the low nutrient level. Where large ponds (locally called "steadies") form in the river bed and physical factors become less restrictive, aquatic vegetation similar to that which colonizes the edge of lakes may become established.

Despite the virtual absence of any hydrophytic vegetation in the rivers, the narrow fringe of alluvial soils along these drainage courses may be extensively colonized by *Alnus rugosa* thickets. Other woody species characteristic of this riparian zone include *Cornus alba, Rhamnus alnifolius, Salix cordata* and *S. pellita.* Pteridophytes such as *Onoclea sensibilis* and *Matteuccia struthiopteris* occasionally form an important ground cover. Some species which are mainly restricted to this habitat in the study area are *Cirsium muticum, Corylus cornuta, Dryopteris thelypteris, Eupatorium maculatum, Lycopus americanus, Mentha arvensis, Scutellaria epilobiifolia, S. lateriflora* and *Trillium cernuum.* Though not strictly situated in the coastal plain, the river estuaries of Bonne Bay are colonized by similar alder swales. *Fraxinus nigra* and *Sambucus pubens* are found in this [illegible]t and appear to reach the northern limit of their distribution in Newfoundland at Bonne Bay.

The oligotrophic, meandering creeks, which drain the wet peatlands, are not significant for aquatic flora although a few true hydrophytes such as *Potamogeton alpinus, P. natans* and *Hippuris vulgaris* may become established in the slow flowing water. On the banks of these entrenched channels a characteristic community develops. This vegetation unit, as described by Bouchard (1974), is a scrub formation dominated by *Alnus rugosa, Calamagrostis canadensis, Myrica gale, Sanguisorba canadensis, Spiraea latifolia* and *Thalictrum pubescens.*

Standing Water. The freshwater lakes and ponds of the study area can be described as oligotrophic, eutrophic and dystrophic as defined by Dansereau (1957). The deep fjord basins are oligotrophic bodies of water. They contain no vascular plants although occasional species such as *Isoëtes muricata* may rarely colonize shallow water areas along the edge of their forebays.

Most of the larger lakes and ponds of the coastal plain are more eutrophic. They contain some shoreline vegetation but it is variable and shows no uniformity from one pond to another. Some of the more common emergent hydrophytes are *Carex aquatilis, Eleocharis palustris* and *Equisetum fluviatile.* Uncommon to rare species such as *Callitriche verna, Eriocaulon aquaticum, Glyceria borealis, Littorella americana, Lobelia dortmanna, Myriophyllum alterniflorum, M. exalbescens, M. tenellum, Potamogeton amplifolius, P. epihydrus, P. gramineus, Ranunculus trichophyllus, Sagittaria graminea, Scirpus acutus, Sparganium minimum* and *Utricularia vulgaris* are found locally in the shallow water of these ponds. Occasional lakes are bordered by areas of emersed muck deposits. In this littoral zone, uncommon but characteristic species such as *Caltha palustris, Cardamine pensylvanica, Carex michauxiana, Glyceria canadensis, Hypericum boreale, Juncus pelocarpus* and *Ranunculus reptans* are found in a sparse herbaceous community where sedges such as *Carex aquatilis, C. flava* and *C. lasiocarpa* predominate.

The dystrophic pools and flashets in the raised bogs harbour a very limited flora due to their acidity and nutrient deficiency. Those which are shallow often contain emergent hydrophytes such as *Carex limosa, C. rostrata, Equisetum fluviatile* and *E. palustre.* Occasional species which are found either anchored in the organic peat bottom or floating in the shallow water of these pools include *Drosera rotundifolia, Menyanthes trifoliata, Nuphar variegata, Sparganium angustifolium, S. hyperboreum, Triglochin palustre, Utricularia cornuta, U. intermedia* and *U. minor.*

GEOGRAPHIC DISTRIBUTION. The rivers which drain the major landlocked fjord basins as well as the surrounding coastal plain are Deer Brook, Bakers Brook, Western Brook and Portland Creek. Stag River, Stanford River, River of Ponds and Torrent River drain only the coastal plain and are not connected to the fjords.

The largest freshwater lakes or ponds are the forebays at the mouths of the major fjords. They are found at Deer Pond, Bakers Brook Pond, Western Brook Pond, Portland Creek Pond, Western and Eastern Blue Pond. Lakes which occur along the drainage course of a river, such as River of Ponds Lake and the Torrent River Lakes, are common in the coastal plain.

Coastal Plain, Forested Moraines, Ridges and Foothills.

PHYSIOGRAPHY AND GEOGRAPHIC DISTRIBUTION. Within the coastal plain, much of the surface area is occupied by several elevated landforms including glacial moraines, bedrock ridges and foothills of the Long Range escarpment. Because of several shared features, these distinct landforms have been grouped together as a single biophysiographic unit despite the unique geomorphology of each. Their mineral soils, improved drainage and their elevated sloping topography (compared with adjacent low-lying peatlands) constitute a habitat which has been pervasively colonized by several similar vegetation types, usually dominated by *Abies balsamea* and *Picea mariana.*

Low, rolling ground moraines covered by forest and scrub vegetation are typical of this biophysiographic unit. These sites are more common in the central and northern sector of the coastal plain (Grant, 1972a). Other major landforms with similar physiography are elevated marine beaches, weathered ridges of faulted sedimentary bedrock and frontal slopes and foothills of the Long Range escarpment including the heads of the fjord valleys. The forested slopes and valleys surrounding much of Bonne Bay, although situated outside the coastal plain area, are included in this general biophysiographic unit.

These landforms are found throughout the altitudinal range of the coastal plain. They have been described as separate, detailed land systems in the southern part of the study area located within Gros Morne National Park (Airphoto Analysis Associates, 1975).

VEGETATION AND FLORA. Although this general biophysiographic unit represents a somewhat arbitrary grouping of heterogeneous landforms, the floristic composition of the colonizing forest and scrub vegetation is very constant. Nevertheless, the structure of the forest or scrub vegetation found on the different landforms is variable depending mainly on the level of disturbance which has occurred. Three major formations can be distinguished: (1) second growth, closed-crown forests of *Abies balsamea* which colonize most of the inland examples of this biophysiographic unit where wind is not an important controlling factor; (2) wind-shaped krummholz (Figure 4 D) colonizing the coastal fringe of elevated beaches and moraines which are highly exposed to onshore winds; and (3) early successional scrub colonizing these sites which have been disturbed by man as a result of fire or logging.

Closed-crown Balsam Fir Forests. The most representative examples of this forest association are found on the frontal slopes of the Long Range escarpment where secondary succession has replaced the disturbance of past logging. Continued logging of the more accessible forested parts of the coastal lowland has maintained the vegetation in early successional scrub communities.

The closed-crown forests are typically dominated by *Abies balsamea* and *Betula papyrifera, Picea glauca* and *Picea mariana* are scattered throughout. Quantitative data concerning this vegetation type has been tabulated by Bouchard (1974), who concluded that mature forests of this type represent the terminal successional stage for this biophysiographic unit.

The ground flora of these forests is not rich, but a typical boreal forest element is well represented. *Dryopteris spinulosa* is very common and may dominate the herb layer. Other herbs of these latter forests are *Clintonia borealis, Coptis groenlandica, Cornus canadensis, Linnaea borealis, Maianthemum canadense, Trientalis borealis;* infrequent boreal orchids (*Goodyera repens, G. tesselata, Habenaria obtusata, Listera cordata*) and several ericaceous species (*Gaultheria hispidula, Moneses uniflora,* and *Monotropa uniflora*) comprise the majority of sparse ground cover. Several uncommon to rare species such as *Aralia nudicaulis, Corallorhiza maculata, Dryopteris phegopteris, Habenaria orbiculata, Lycopodium lucidulum, L. obscurum, Mitella nuda, Pyrola minor, P. secunda, Solidago macrophylla, Streptopus amplexifolius, S. roseus* and *Viola renifolia* are typically associated with these forests.

Understory shrub coverage is very sparse and is composed largely of regeneration from the canopy trees. Other occasional shrubs which are typically associated with this forest formation are *Acer spicatum, Alnus crispa, Nemopanthus mucronatus, Pyrus decora, Ribes glandulosum, R. lacustre* and *Taxus canadensis.*

Within the study area, these forests include several species which appear to be at or near the extreme northern limit of their Newfoundland distribution. *Acer rubrum, Betula alleghaniensis, Epigaea repens, Pinus strobus* and *Populus tremuloides* have been recorded from only rare stations at Bonne Bay.

A transition black spruce scrub community (Figure 4 C) lies in a buffer zone between the balsam fir forest of the richer, better drained sites and the dwarf black spruce scrub of the oligotrophic peatland soils (see previous Peatlands section). Its physiognomy differs sufficiently from the adjacent formations in that it has been described as a discrete vegetation type by authors such as Damman (1967) and Bouchard (1974, 1975). Although it is a continuum between the two adjacent vegetation types, the flora of this transition scrub more closely resembles the dwarf black spruce scrub than the fir forest community. *Abies balsamea* is an important element but *Picea mariana* becomes the dominant species in this transition zone. There is also a predominance of ericaceous shrubs such as *Kalmia angustifolia* and *Ledum groenlandicum* which is indicative of its close relationship to the adjacent dwarf black spruce scrub community.

Wind-shaped Coastal Krummholz. The wind-shaped component of the balsam fir forests and scrub includes the coastal krummholz and the upland tuckamoor. Both communities are physiognomically and botanically similar but only the former occurs in the coastal plain.

The coastal krummholz is found mainly on elevated beaches and reworked moraines along the seashore. Similar stands are found where these landforms occur around large bodies of water in the coastal plain. Settlement and logging have decimated many of the former stands of this vegetation type. The exposure to the pruning action of high winds and frost kill is responsible for the notable flattened crown of this scrub formation.

The dominant tree species is *Abies balsamea. Picea glauca* is frequent and may dominate some small isolated stands. It is noteworthy that *Picea mariana* does not occur in this scrub formation. Botanically, these isolated wind-disturbed communities are not as rich as the homologous, protected forest stands. Nevertheless, species which are common in the latter forest communities, such as *Dryopteris spinulosa, Maianthemum canadense, Moneses uniflora,* etc. also comprise the sparse ground flora of the krummholz.

Early Successional Scrub. The closed-crown balsam fir forests of this biophysiographic unit were formerly more widespread on the coastal plain. Due to continued logging of these accessible areas, many of the original stands are now maintained as early successional scrub communities dominated by *Abies balsamea.* These were described by Bouchard (1974) as homogeneous second growth scrub of balsam fir and heterogeneous second growth scrub of balsam fir and deciduous shrubs. Because balsam fir can reoccupy almost all sites occupied before logging (Damman, 1967), this scrub vegetation is a successional step toward the closed-crown balsam fir forest. Consequently the flora of this community is composed of essentially the same species which comprise the fir forests. The open structure of the heterogeneous second growth scrub permits an increase in frequency of invading deciduous shrubs such as *Acer spicatum, Alnus crispa, A. rugosa* and *Betula papyrifera.*

Fire-disturbed areas are infrequent. Their occasional occurrence on formerly forested moraines, such as in the area south of Western Brook Pond, has led to recolonization either by a heterogeneous *Betula papyrifera-Alnus crispa* dominated scrub or by *Kalmia angustifolia-Vaccinium angustifolium* dwarf scrub communities (Bouchard, 1974). These burned site communities are likely early successional stages toward balsam fir forest and black spruce dwarf scrub, respectively, as their evolving flora is much the same as the previously described flora of these latter natural communities.

Additional studies concerning the structure, composition and reconnaissance of these vegetation types within Gros Morne National Park have been done by Bouchard (1974, 1975) and Airphoto Analysis Associates (1975).

Alpine Plateau, Tundra Barrens.

PHYSIOGRAPHY AND GEOGRAPHIC DISTRIBUTION. The barrens of the Long Range Mountain plateau are the most characteristic feature of the highland landscape (Figure 6 A). The principal landforms of this biophysiographic unit are glacially scoured bedrock ridges and knobs often covered with thin deposits of surficial glacial drift and extensive flat boulder fields (or felsenmeer) of frost-shattered bedrock.

Within the study area, this biophysiographic unit is mainly concentrated in two widely separated areas of the Long Range plateau. In the northern sector, the barrens are found on the Highlands of St. John and the extensive plateau area to the interior. The second major area is found on that section of the plateau which lies between Bonne Bay and Portland Creek Pond. Some of the higher plateau surfaces in both regions are possible nunataks (periglacial ice-free zones) of the Wisconsin phase of Pleistocene glaciation (Airphoto Analysis Associates, 1975; Grant, 1969 a, b, 1973 a).

The shattered quartzite (felsenmeer) crests of Killdevil, Gros Morne and the South Summit of the Highlands of St. John (or Doctor Hill) as well as the barren highland peaks south of Bonne Bay at Lookout Hills and at Pic à Teneriffe are of different geological formations than the Precambrian Long Range plateau. Nevertheless, these outlying alpine peaks and the barrens of the main Long Range massif have been grouped into the same unit because of their botanical and physiographic similitude. The complex geomorphology of these highland areas has been summarized previously in section Geology.

Much of the surface of the barrens is exposed, lichen-covered bedrock. The major factors maintaining the colonization of these sites by tundra vegetation are the open exposure of the habitat and the inadequate, patchy veneer of gleyed, mineral soil. Due to the impervious granitic bedrock, the shallow siliceous soils are poorly drained. Savile (1972) and Bliss (1962) describe other pertinent physical factors such as wind abrasion and desiccation, low summer and winter temperatures and short growing period which are typical of this arctic-like environment. Barrens occur almost exclusively in the highland area but several isolated stations of limited size are found in the coastal plain area (Bouchard, 1974). These rare localities are on elevated, exposed knolls of the piedmont moraines situated in the foothills of the Long Range escarpment.

Zones of snow accumulation (or zabois) often occur on sheltered slopes or ravines adjacent to the barrens on the highland plateau. These protected sites are distinguished from the barrens per se by

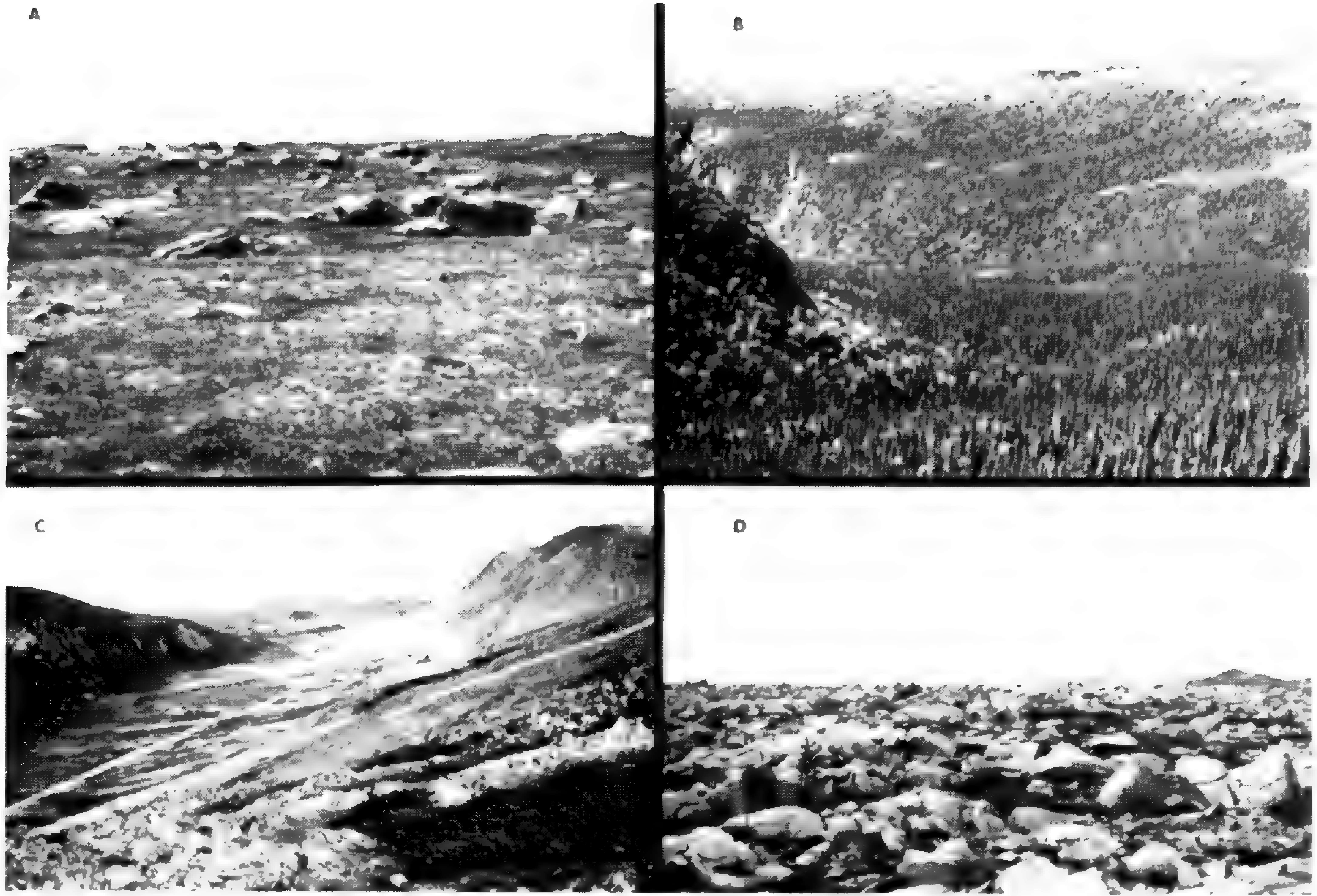

Figure 6. A, Alpine tundra barrens, Long Range Mountains. B, Forested valley within the Long Range Mountain plateau. C, Serpentine talus slopes between Trout River and Bonne Bay. D, Serpentine barren on the summit of Table Mountain

snowbanks which may persist well into the summer, pockets of accumulated soil, and frequent wet seepage areas. Local differences in temperature and effective growing season in this unique habitat within the barrens have been discussed by Bliss (1969) for alpine peaks in the Appalachians.

VEGETATION AND FLORA. The tundra community which colonizes the highland barrens presents a generally discontinuous 60-80% vegetation coverage with intervening bare rock surfaces. The patchy heath carpet is consistently dominated by lichens (*Cladina alpestris, C. rangiferina,* etc.), mosses (*Rhacomitrium lanuginosum,* etc.), and dwarf ericaceous shrubs (*Empetrum nigrum* and *Vaccinium uliginosum*). Although the latter dwarf shrub species are quite ubiquitous throughout the study area, they typically dominate the severely wind-pruned vegetation of this biophysiographic unit.

The attenuated flora of this alpine community is remarkable for its characteristic arctic-alpine element. The xerophytic adaptations of many of these plants to the arid conditions of this habitat have been described by Bliss (1962), Porsild (1964, 1969), and Savile (1972). Such species as *Arctostaphylos alpina, Carex bigelowii, Diapensia lapponica, Empetrum eamesii, Juncus trifidus, Loiseleuria procumbens* and *Potentilla tridentata* are common. Less frequent examples include *Agrostis borealis, Hierochloe alpina, Lycopodium annotinum* var. *pungens* and *L. selago.* With the exception of *Potentilla tridentata,* these species are largely on the limit of a wide-ranging, arctic circumpolar distribution (Hultén, 1962, 1971; Porsild, 1964). Their range extends southward in isolated, suitable alpine habitats such as occur around the Gulf of St. Lawrence. Other uncommon species in this community (*Lycopodium sabinifolium* and *Salix uva-ursi*) are of eastern American arctic-alpine distribution (Rousseau, 1974).

Despite the severity of the habitat, several non-alpine or boreal herbaceous species sporadically colonize the barrens. These include *Cornus canadensis, Deschampsia flexuosa, Eriophorum spissum, Maianthemum canadense, Rubus chamaemorus, Scirpus cespitosus* and *Trientalis borealis.* Infrequent dwarf shrubs of the patchy vegetation mat are represented by *Abies balsamea, Betula papyrifera, B. pumila, Juniperus communis, Kalmia angustifolia, Ledum groenlandicum, Picea mariana, Vaccinium angustifolium* and *V. vitis-idaea.* These species encroach on the barrens community from adjacent sheltered ravines and slopes which are colonized by upland tuckamoor thickets.

In the zabois or snowbank zones, the tundra vegetation of the adjacent barrens grades into a richer, predominantly herbaceous community. This habitat falls within the tolerance limits of subalpine as well as alpine species (Bliss, 1969) and consequently the vegetation is usually dominated by species such as *Dryopteris spinulosa* and *Sanguisorba canadensis. Calamagrostis canadensis, Clintonia borealis, Coptis groenlandica, Polygonum viviparum, Solidago macrophylla, Streptopus amplexifolius* and *S. roseus* are some of the common non alpine herbs making up the diverse flora of this community. Dwarf ericaceous shrubs such as *Kalmia polifolia* and *Vaccinium angustifolium,* and patchy areas of turf dominated by *Scirpus cespitosus* are also found in this heterogeneous vegetation. *Alnus crispa* thickets sometimes colonize the lower slopes or meltwater drainage channels in these zabois areas. The tundra barren species grade into this community. In addition, these protected sites harbour several rare alpine species which have been recorded mainly from only a few localities on the Long Range plateau. *Carex stylosa, Cassiope hypnoides, Cornus suecica, Deschampsia atropurpurea, Epilobium hornemannii, Gnaphalium norvegicum, G. supinum, Lycopodium alpinum, Phleum alpinum, Phyllodoce caerulea, Salix herbacea, Sibbaldia procumbens, Stellaria calycantha, Streptopus* × *oreopolus, Vaccinium cespitosum, V.* × *nubigenum* and *Viola palustris* are examples of this highly restricted flora.

Alpine Plateau, Peatlands.

PHYSIOGRAPHY AND GEOGRAPHIC DISTRIBUTION. In contrast to the raised bog peatlands of the coastal plain (see previous Peatlands section), the alpine peatland biophysiographic unit consists of comparatively local shallow peat deposits and does not have the characteristic hummocky surface and numerous eccentrically oriented flashets of the lowland bogs.

The peat of this consolidated organic mat seldom exceeds 40 cm. in depth (Airphoto Analysis Associates, 1975). It has generally accumulated on areas of flat or gently sloping alpine terrain where the underlying impermeable bedrock impedes drainage. Such sites occur on gently sloping deposits of shallow glacial drift adjacent to exposed barren bedrock knobs and on flat areas of felsenmeer formation. Exposed erratic boulders frequently protrude through the peat mat. Seepage from adjacent, more elevated barren exposures or from the underlying granitic bedrock is nutrient deficient. In contrast to the highly exposed, often snow-free barrens, the protection afforded by snow cover on these sites may further explain the development of these peat deposits.

This biophysiographic unit generally occurs in conjunction with the tundra barrens and is concentrated in the same northern and southern sectors of the Long Range plateau. In addition, similar peat deposits occur on the alpine plateaus which lie immediately south of Bonne Bay. Thus the flat summit of the Serpentine Tableland, the central plateau area of the Lomond Peninsula, and the highland terraces of Lookout Hills are included in this biophysiographic unit. Although these latter areas differ geologically (see previous Geology section) from the Precambrian Long Range plateau, the peat mantle creates similar physiographic conditions on these sites and the same vegetation type is maintained.

The very poor drainage and the high water table of this biophysiographic unit may lead to the formation of flashets where the peat accumulations are sufficiently deep. These bog pools form in shallow depressions of the peat mat when it is on flat terrain such as in felsenmeer areas. On gradually sloping terrain, a series of descending terraces may be formed in the peat mat with a reticulate pattern of flashets oriented at right angles to the slope. There are several possible explanations for the formation of this flashet pattern. It may be the result of gravitational downslope movement (peat flow) of water saturated organic material (Hanson, 1950). Alternatively, the origin of the flashets may be explained by a differential freeze-thaw cycle of hummocks and hollows in the peat (similar to solifluction movement). Research by Sjörs (1959, 1961, 1963) indicated that such a pattern might be due merely to the formation of fissures as a result of the intrinsic expansion of the peat biomass on an inclined plane. He also emphasized the importance of downslope water flow to maintain this reticulate pattern.

VEGETATION AND FLORA. The vegetation cover of this essentially closed herbaceous community averages 80-100% with intervening exposed boulders and bog pools. It is composed predominantly of *Scirpus cespitosus* and numerous *Carex* species. Unlike the deep, spongy, hummocky *Sphagnum-Cladina* raised bogs of the coastal plain, these sedge peats are relatively shallow and flat. Moss species (*Rhacomitrium lanuginosum* and *Sphagnum* spp.) are an important but not dominant element in the organic mat. Lichen species are virtually absent in contrast to their abundance in the vegetation of both the tundra barrens and the raised bogs.

This alpine sedge vegetation type has been defined as sedge bog or patterned fen (Airphoto Analysis Associates, 1975). Both its species composition and physiognomy tend to be a mixture of the raised bog and the sedge meadow vegetation of the coastal plain. The dominant vascular species of this dwarf herbaceous community are *Scirpus cespitosus* and several common sedges *Carex exilis, C. limosa, C. oligosperma* and *C. pauciflora.* Uncommon but characteristic graminoid species include *Carex bigelowii, C. miliaris, C. stylosa, Calamagrostis pickeringii, Eriophorum spissum, Juncus filiformis* and *Rhynchospora alba.* Although this dwarf vegetation has a tundra-like structure, the flora has virtually none of the arctic-alpine element which characterizes the tundra barrens. Only *Carex bigelowii, C. miliaris* and *C. stylosa* have an arctic-alpine distribution. Non-alpine dwarf heath shrubs and herbs such as *Chamaedaphne calyculata, Drosera rotundifolia, Kalmia polifolia* and *Sanguisorba canadensis* are sparsely scattered throughout this community. Flashets harbour an aquatic flora which is similar to, but less diverse than, the flora of the coastal plain bog pools. Species such as *Carex limosa, C. rostrata, Isoëtes muricata, Nuphar variegata, Sparganium angustifolium* and *S. hyperboreum* are rare to uncommon in these sterile alpine pools.

Immediately south of Bonne Bay, on the plateau areas of Lookout Hills and Lomond Peninsula, the flora of this alpine peatland contains several rare vascular plants. Species such as *Bartonia paniculata, Habenaria blephariglottis, Potamogeton oakesianus* and *Schizaea pusilla* have been recorded from this one boggy alpine habitat within the study area and these plants are at or near the extreme northern range of their eastern American distribution. Other rare species which appear to be restricted mainly to these sedge bogs at Bonne Bay include *Lycopodium inundatum, Potamogeton confervoides* and *Scheuchzeria palustris.*

Toward the central region of the highland Precambrian plateau, where fir forest and scrub vegetation become more predominant, this peatland formation is frequently invaded by isolated clumps of *Abies balsamea* and/or *Picea mariana*. In addition to these tree species, several shrubs such as *Andromeda glaucophylla, Chamaedaphne calyculata, Kalmia polifolia, Ledum groenlandicum, Myrica gale, Nemopanthus mucronatus* and *Rhododendron canadense* frequently dominate these dense, isolated thickets. This "savanna" type of vegetation could be interpreted as a transition stage between the open dwarf herbaceous vegetation which is typical of this biophysiographic unit and the more protected forested sites (see next section).

Alpine Plateau, Forested Valleys, Ravines, and Talus.

PHYSIOGRAPHY AND GEOGRAPHIC DISTRIBUTION. Sites on the highland plateau, which are suitable for the development of forest or scrub vegetation, are typical of this general biophysiographic unit (Figure 6 B). In comparison with the tundra barrens and open peatlands, local environmental factors which distinguish these forested sites are adequate protection from wind and frost exposure, sufficient soil accumulation and improved drainage. Several landforms meet these physiographic requirements. The glacier-carved valleys and adjacent talus slopes, which constitute much of the rolling topography of the alpine plateau region, are usually densely forested. Here there is less impedance to drainage by underlying bedrock due to the deep colluvial deposits. Smaller ravines or depressions in the barrens create a sheltered habitat with adequate soil deposits for frequent colonization of scrub vegetation (or tuckamoor). Similar upland tuckamoor is frequent on alpine talus where the unstable colluvial slopes and exposure to the pruning action of high winds maintain the vegetation in a scrub stage.

Although these landforms are found scattered throughout the highland plateau, forested slopes become progressively more common toward the central interior region which is bounded on the south by the headwaters of the Upper Humber River system, to the north by the headwaters of Soufflets River, and to the interior by the eastern boundary of St. Barbe South District. Outside this extensive area of concentration, sloping terrain with forest or tuckamoor vegetation occurs at high altitude along the western escarpment of the Long Range. This biophysiographic unit also includes the U-shaped fjord valleys which emerge at high altitude onto the alpine plateau. Similarly, the forested slopes which are found at alpine elevations to the south of Bonne Bay (on the Lomond Peninsula, on Lookout Hills and on the Gregory Plateau), correspond with the botanical and physiographic interpretation of this unit.

VEGETATION AND FLORA. Due to the inaccessibility of the alpine sites occupied by this vegetation type, the following brief description is based on relatively few field observations. It is inferred from the few sites visited that floristically, these forest and scrub communities do not vary appreciably. In fact, the vegetation of this biophysiographic unit is essentially a repetition of the corresponding forest communities of the coastal lowland.

As is the case of the coastal plain, the composition of the forest and scrub communities in the alpine region is very constant despite the variability in colonized landform. Structurally, the major vegetation formations can be described as a function of natural disturbance levels: (a) closed-crown mature forests of *Abies balsamea* which occur mainly on the stable slopes of alpine valleys either at the heads of the fjords or in the central interior region of the Precambrian plateau; (b) wind-shaped upland tuckamoor or scrub which colonizes the unstable and highly exposed talus slopes such as occur along the western escarpment of the Long Range and occasional exposed, well drained moraines and smaller depressions or ravines on the highland plateau; and (c) deciduous shrub thickets generally colonizing the disturbed talus at the base of alpine cliffs and bluffs. This scrub is maintained by falling rock and ice, as well as colluvial ground and snow movement.

Closed-crown Balsam Fir Forests. Most of these alpine forests occur in inaccessible areas of the interior and are consequently mature, undisturbed stands. Like the previously described second growth forests of the coastal plain (see previous Forested Moraines section), the alpine stands are dominated by *Abies balsamea. Betula papyrifera, Picea glauca* and *P. mariana* are often scattered as associated tree species.

With few exceptions, the shrub and herb strata are of the same composition as their coastal plain counterparts. They are dominated in the same manner by strong regeneration from the canopy trees and similar understory species such as *Acer spicatum, Alnus* *crispa, Clintonia borealis, Dryopteris spinulosa,* etc. The ericaceous shrubs, *Rhododendron canadense* and *Vaccinium ovalifolium* are much more common at these higher elevations and may be locally dominant.

Where these forest communities are adjacent to the open slopes of the alpine peatland biophysiographic unit, invasion of the peat slopes by isolated thickets of forest species creates a "savanna" type of vegetation.

Upland Tuckamoor. This wind-shaped alpine scrub resembles very closely the wind-shaped component of the lowland balsam fir forests (i.e. coastal krummholz, see previous Forested Moraines section). These dense stunted thickets are similarly dominated by *Abies balsamea. Picea glauca* which occurs frequently in the krummholz is generally replaced by *Picea mariana* on these alpine slopes. The latter species is absent from the coastal formation, but may locally dominate the tuckamoor. One atypical stand was observed where *Picea glauca* was dominant. *Betula papyrifera* occurs frequently.

The tuckamoor includes additional shrub species of *Amelanchier bartramiana, Empetrum nigrum, Gaultheria hispidula, Kalmia angustifolia, Ledum groenlandicum, Nemopanthus mucronatus, Rhododendron canadense, Taxus canadensis, Vaccinium angustifolium, V. uliginosum* and *V. vitis-idaea* which are virtually absent from the lowland krummholz. The sparse ground flora is made up of the recurring forest herbs *Clintonia borealis, Cornus canadensis, Dryopteris spinulosa, Maianthemum canadense,* etc.

The tuckamoor may grade into a very dense, homogeneous, dwarf black spruce mat which colonizes severely wind-eroded talus slopes. Stunted, prostrate *Picea mariana* invariably dominates this depressed dwarf community. The underlying herb layer is drastically reduced, but the overall floristic composition remains the same as in the *Abies balsamea* dominated tuckamoor.

Deciduous Shrub Thicket (on disturbed talus). This disturbed heterogenous scrub is generally dominated by deciduous shrubs (or small trees) such as *Alnus crispa* and *Betula papyrifera.* Nevertheless, *Abies balsamea* is abundant and locally dominant especially in more stabilized zones. Continual disturbance on the boulder talus maintains an open-structured community and tree stems are usually bent or prostrate due to colluvial ground movement and downslope snow-creep.

The flora is closely related to that of the forest and tuckamoor communities and includes frequent shrubs such as *Acer spicatum, Amelanchier bartramiana, Pyrus decora, Ribes glandulosum, Vaccinium uliginosum* and *Viburnum trilobum.* Small colonies of *Vaccinium cespitosum* form on these disturbed alpine screes and appear to be mainly restricted to this habitat in the study area. Herb coverage among the often exposed boulders on these talus consists largely of pteridophytes such as *Dryopteris spinulosa, D. phegopteris, Osmunda cinnamomea, O. claytoniana* and common recurring species of the *Abies balsamea*-dominated forest and scrub communities.

Alpine Plateau, Serpentine Tableland.

PHYSIOGRAPHY AND GEOGRAPHIC DISTRIBUTION. Table Mountain (Figures 6 C & 6 D) is one of the outstanding physiographic features of the alpine land region of St. Barbe South District. This serpentine massif occupies an area roughly circumscribed by the South Arm of Bonne Bay, the road to Trout River village, and Trout River Pond.

Geologically, this plateau is very distinct from the granitic Precambrian Long Range which predominates the alpine region of the study area. The peculiar geology of this serpentine formation is largely responsible for its unique physiographic and botanical nature. The geomorphology (laterally displaced klippen) of this unit is summarized previously in section Geology.

The principal landforms comprising this biophysiographic unit include the frost-shattered felsenmeer accumulation on the broad summit, till-mantled slopes, actively eroding escarpments, talus slopes, and alluvial scree fans receding from the base of the cliffs.

The serpentine plateau has the appearance of a rock wasteland, colonized by only scanty vegetation cover. Similar barren serpentine outcrops occur in widely scattered areas of Quebec (Scoggan, 1950; Raymond, 1950; Legault et Blais, 1968, map for eastern North America; Hamel, 1970), and elsewhere in Newfoundland (Fernald, 1911, 1933). The remarkable vegetation of these serpentine barrens owes its poverty and uniqueness to the influence of several environmental factors. Rune (1953) and Whittaker *et al.* (1954) concluded that the infertility of serpentine soils for most plants can mainly be attributed to the unfavorable balance of several important elements. Low levels of calcium appear to be most influential.

High concentrations of chromium, nickel and magnesium may possibly attain levels which are toxic to most plants, but which stimulate or at least are tolerated by serpentinicolous plants. Low nutrient levels (particularly of calcium) and the high alkalinity of these ultrabasic rocks are also restrictive factors. There are also exacting physical limitations to prospective colonizing plants. The talus slopes, escarpments, and much of the plateau surface are barren, unstable rock exposures. These alpine landforms are exposed to wind erosion and snow abrasion which create arid, arctic-like conditions. Soil accumulation is minimal due to the lack of biological breakdown processes. The proximity to the surface of the underlying parent bedrock and the absence of insulating vegetation cover, result in mechanical frost-churning or congeliturbation of the surface material.

VEGETATION AND FLORA. Distinctive characteristics generally common to serpentine floras (attenuation, presence of unique edaphic ecotypes, endemism and relic species, disjunctive distributions, etc.) throughout the world have been discussed in detail by Rune (1953) and Whittaker *et al.* (1954).

The physiognomic response of the vegetation to this physiographic unit permits three distinct units to be described: (1) the barrens, comprised of various landforms practically destitute of vegetation such as scree slopes, vertical escarpments, and felsenmeer on the plateau summit; (2) the peat bog covering much of the interior of the flat summit; (3) scrub vegetation at the base of some talus slopes. These categories are most easily interpreted as an opening, lowering, and reduction of the community with less favourable environment (Whittaker *et al.*, 1954).

Serpentine Barrens. Vegetation on the precipitous, rotting cliff faces is virtually absent. The surface of other barren landforms is usually greater than 80% exposed bedrock, interspersed with solitary, wind-pruned shrubs and tufts of grass or other herbs. What scanty vegetation is able to colonize the rock barrens, is restricted to small patches of mineral soil between boulders or along streams.

The sparse vegetation cover consists largely of tolerant shrubby species of wide ecological amplitude. *Juniperus communis* and *Larix laricina* are the most common examples. Other stunted or creeping shrub species which are sporadic on the barren landscape include *Alnus crispa, Betula pumila, Juniperus horizontalis, My-*

rica gale, and *Potentilla fruticosa*. *Rhododendron lapponicum* is found exclusively on the serpentine barrens within the study area. Species such as *Arctostaphylos uva-ursi, Salix arctica* and *S. glauca* are also equally characteristic of open calcareous barrens.

The moss, *Rhacomitrium lanuginosum*, and a wide diversity of herbaceous vascular plants sparsely colonize the open barrens. They are mostly restricted to moist patches of weathered gravels which commonly occur along drainage channels or in seepage areas. A characteristic group of plants with an affinity for these open, unstable, serpentine soils — hence, serpentinicolous plants (Rune, 1953) — is known exclusively from this biophysiographic unit within the study area. They include *Adiantum pedatum* var. *aleuticum, Arenaria marescens, Lychnis alpina* and the previously mentioned shrub *Rhododendron lapponicum*. In addition, a closely related group of plants is found growing preferentially on the serpentine gravels, and may occasionally colonize the similarly open, alkaline barrens of the calcareous coastal plain exposures. This list includes *Anemone parviflora, Arenaria humifusa, A. rubella, Armeria maritima, Artemisia borealis, A. canadensis, Cerastium arvense, Danthonia intermedia, D. spicata, Deschampsia cespitosa, Festuca scabrella, Oryzopsis asperifolia, O. canadensis, Oxytropis terrae-novae, Saxifraga aizoides, S. oppositifolia, Senecio pauperculus, Solidago hispida,* and *S. multiradiata.* Local areas of calcareous seepage may account for the presence of some of these species which might otherwise be excluded from the serpentine biophysiographic unit. Minor surface deposits of precipitated calcium carbonate or travertine (Airphoto Analysis Associates, 1975) occur at several sites in the serpentine barrens. Restricted colonies of truly calciphilous species such as *Cypripedium calceolus* and *Dryas integrifolia* owe their presence to these calcareous inclusions.

Several species of the coastal plain peatlands recur inconspicuously on wet, sterile gravels of the serpentine barrens. These include *Carex exilis, Drosera rotundifolia, Sanguisorba canadensis, Sarracenia purpurea, Selaginella selaginoides, Thalictrum pubescens* and *Triglochin maritimum.*

Arctic-alpine plants, found both on coastal plain limestone barrens and on granitic alpine barrens throughout the study area, are also sparsely distributed in this biophysiographic unit. *Carex scirpoidea, Juncus trifidus, Lycopodium selago,* and *Silene acaulis* are examples.

The flora includes a few species of wider ecological amplitude such as *Campanula rotundifolia, Conioselinum chinense, Potentilla tridentata, Primula mistassinica,* and *Thalictrum alpinum.* Opportunistic species such as *Anaphalis margaritacea* and *Festuca rubra* sporadically invade this open, sterile habitat.

Peat Bog. The interior area of the flat summit of the tableland is partially covered with peat deposits. The somewhat paradoxical peat bog on an otherwise barren plateau which is toxic to most vegetation, is probably due to the particular physiography of the site. The flat, stable terrain, poor drainage, and decreased exposure of the interior plateau area have permitted a gradual accumulation of residual organic debris. This peatland is both botanically and physiographically similar to the peatlands occurring elsewhere in the alpine region of the study area (see Alpine Plateau, Peatlands section). The vegetation on these organic deposits is apparently not influenced by the underlying serpentine bedrock.

Scrub. The barrens grade into a transition zone of more dense scrub vegetation on some of the lower, more stabilized, and less exposed slopes; especially where these talus abut on adjacent geological formations. These scrub communities are dominated by *Larix laricina.* Co-dominant species include *Abies balsamea, Betula papyrifera,* and *Picea mariana.*

The dense undergrowth consists of the same shrub species which colonize the open barrens (*Juniperus communis, J. horizontalis, Myrica gale, Potentilla fruticosa,* etc.), common additional deciduous shrubs (*Acer rubrum, Alnus crispa, A. rugosa, Nemopanthus mucronatus, Viburnum cassinoides, Pyrus decora,* etc.), and common heath shrubs (*Andromeda glaucophylla, Empetrum nigrum, Epigaea repens, Gaultheria hispidula, Kalmia angustifolia, Kalmia polifolia, Ledum groenlandicum, Rhododendron canadense, Vaccinium angustifolium, V. oxycoccos, V. uliginosum, V. vitis-idaea,* etc.). Very stunted *Pinus strobus* (forma *prostrata* of Fernald, 1933) is occasional. Despite the underlying serpentine bedrock, the flora of this scrub community is similar to the upland tuckamoor found on talus slopes elsewhere in the alpine land region (see previous Forested Valleys section). There are, nevertheless, important differences such as the dominance of *Larix laricina,* and the presence of several species which are at or near the northern limit of their distribution such as *Acer rubrum*, *Epigaea repens*, and *Pinus strobus*. In addition to the anticipated, sparse ground flora of the tuckamoor communities (*Cornus canadensis*, *Clintonia borealis*, *Maianthemum canadense*, etc.), exceptional herbaceous species of the open serpentine such as *Oryzopsis asperifolia*, *Senecio pauperculus* and *Solidago hispida* are found within this dense scrub.

CONCLUSIONS

The complex interplay of environmental, historic and biotic factors has caused a remarkable diversity in the flora of St. Barbe South District in a region where boreal forest is the predominant vegetation type. This flora integrates about 780 vascular plant species from ten distinct phytogeographic groups in the North American flora: Cosmopolitan Element, Circumpolar Element-Northern Hemisphere, Amphiatlantic Element, North American Element-Transcontinental at Canadian Latitudes, North American Element-Discontinuous in Continental Interior, Endemic Element in Northeastern North America, Eastern Deciduous Forest Element, Atlantic Coastal Plain Element, Endemic Element-Gulf of St. Lawrence, and Naturalized Element. This highly diverse flora sorts itself out in the study area in terms of ten major biophysiographic units. Within the lowlying coastal plain occur: Sand Dunes, Tidal Flats and Brackish Shores, Calcareous Exposures, Peatlands, Freshwater Areas, and Forested Moraines, Ridges and Foothills. The alpine region includes: Tundra Barrens, Peatlands, Forested Valleys, Ravines and Talus Slopes, and Serpentine Tableland.

This approach is based on the interaction of factors controlling, on the one hand, the continental "macrodistribution" of species, and on the other, their local "microdistribution" associated with the diverse units making up the biophysiography of the study area. Although the latter categories are particular to the study area, the use of this concept as a tool for describing patterns in vegetation and flora could be successfully applied elsewhere.

The interpretation of the overall geographic distribution or range limits of vascular plants necessitates comprehensive regional floristic studies such as that of the flora of St. Barbe South. The perception of the distribution pattern of a species, or of factors controlling this distribution, is dependent on the continual input of additional information from such intensive local research.

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CANADA

APPENDIX I

ALPHABETICAL LIST OF THE VASCULAR FLORA

Abies balsamea (Linnaeus) Miller
Acer rubrum Linnaeus
Acer spicatum Lamarck
Achillea borealis Bongard
Achillea millefolium Linnaeus
Achillea ptarmica Linnaeus
Aconitum bicolor Schultes
Actaea rubra (Aiton) Willdenow
Adiantum pedatum Linnaeus
Agrimonia striata Michaux
Agropyron repens (Linnaeus) Beauvois
Agropyron trachycaulum (Link) Malte
Agrostis alba Linnaeus
Agrostis borealis Hartman
Agrostis geminata Trinius
Agrostis scabra Willdenow
Agrostis tenuis Sibthorp
Alchemilla filicaulis Buser
Alchemilla minor Hudson
Allium schoenoprasum Linnaeus
Alnus crispa (Aiton) Pursh
Alnus rugosa (DuRoi) Sprengel
Alopecurus aequalis Sobolowski
Alopecurus pratensis Linnaeus
Amelanchier bartramiana (Tausch) Roemer
Amelanchier fernaldii Wiegand
Amelanchier laevis Wiegand
Amelanchier spicata (Lamarck) K. Koch
Ammophila breviligulata Fernald
Anaphalis margaritacea (Linnaeus) Bentham & Hooker
Andromeda glaucophylla Link
Androsace septentrionalis Linnaeus
Anemone canadensis Linnaeus
Anemone multifida Poiret
Anemone parviflora Michaux
Angelica atropurpurea Linnaeus

Angelica laurentiana Fernald
Antennaria albicans Fernald
Antennaria bayardii Fernald
Antennaria brunnescens Fernald
Antennaria cana (Fernald & Wiegand) Fernald
Antennaria columnaris Fernald
Antennaria confusa Fernald
Antennaria eucosma Fernald & Wiegand
Antennaria foggii Fernald
Antennaria gaspensis Fernald
Antennaria neodioica Greene
Antennaria rupicola Fernald
Antennaria spathulata Fernald
Antennaria straminea Fernald
Antennaria vexillifera Fernald
Antennaria wiegandii Fernald
Anthoxanthum odoratum Linnaeus
Arabis alpina Linnaeus
Arabis drummondii A. Gray
Aralia nudicaulis Linnaeus
Arceuthobium pusillum Peck
Arctostaphylos alpina (Linnaeus) Sprengel
Arctostaphylos uva-ursi (Linnaeus) Sprengel
Arenaria dawsonensis Britton
Arenaria humifusa Wahlenberg
Arenaria lateriflora Linnaeus
Arenaria marcescens Fernald
Arenaria peploides Linnaeus
Arenaria rubella (Wahlenberg) J. Smith
Arethusa bulbosa Linnaeus
Armeria maritima (Miller) Willdenow
Arnica chionopappa Fernald
Arnica louiseana Farr
Arnica terrae-novae Fernald
Arnica tomentosa J. M. Macoun
Aronia melanocarpa (Michaux) Elliott
Artemisia borealis Pallas
Artemisia canadensis Michaux
Asplenium viride Hudson
Aster adscendens Lindley

Aster foliaceus Lindley
Aster nemoralis Aiton
Aster novi-belgii Linnaeus
Aster puniceus Linnaeus
Aster radula Aiton
Aster umbellatus Miller
Astragalus alpinus Linnaeus
Astragalus eucosmus Robinson
Athyrium alpestre (Hoppe) Rylands
Athyrium filix-femina (Linnaeus) Roth
Atriplex glabriuscula Edmondston
Atriplex patula Linnaeus
Avena fatua Linnaeus
Avena sativa Linnaeus

Barbarea vulgaris R. Brown
Bartonia paniculata Michaux
Bellis perennis Linnaeus
Betula alleghaniensis Britton
Betula borealis Spach
Betula glandulosa Michaux
Betula michauxii Spach
Betula minor (Tuckerman) Fernald
Betula papyrifera Marshall
Betula pumila Linnaeus
Botrychium lunaria (Linnaeus) Swartz
Botrychium matricariifolium A. Braun
Botrychium multifidum (Gmelin) Ruprecht
Botrychium virginianum (Linnaeus) Swartz
Brachyelytrum erectum (Schreber) Beauvois
Braya purpurescens (R. Brown) Bunge
Bromus ciliatus Linnaeus

Cakile edentula (Bigelow) Hooker
Calamagrostis canadensis (Michaux) Nuttall
Calamagrostis inexpansa A. Gray
Calamagrostis neglecta (Ehrhart) Gaertner, Meyer & Scherbius
Calamagrostis pickeringii A. Gray
Callitriche anceps Fernald
Callitriche hermaphroditica Linnaeus

Callitriche verna Linnaeus
Calopogon tuberosus (Linnaeus) Britton, Sterns & Poggenburg
Caltha palustris Linnaeus
Calypso bulbosa (Linnaeus) Oakes
Campanula rotundifolia Linnaeus
Capsella bursa-pastoris (Linnaeus) Medikus
Cardamine pensylvanica Muhlenberg
Carex angustior Mackenzie
Carex aquatilis Wahlenberg
Carex arctata Boott
Carex atratiformis Britton
Carex aurea Nuttall
Carex bebbii Olney
Carex bicolor Bellardi
Carex bigelowii Torrey
Carex bipartita Bellardi
Carex brunnescens (Persoon) Poiret
Carex buxbaumii Wahlenberg
Carex canescens Linnaeus
Carex capillaris Linnaeus
Carex castanea Wahlenberg
Carex cephalantha (Bailey) Bicknell
Carex chordorrhiza Ehrhart
Carex concinna R. Brown
Carex crawei Dewey
Carex crawfordii Fernald
Carex debilis Michaux
Carex deflexa Hornemann
Carex demissa Hornemann
Carex deweyana Schweinitz
Carex diandra Schrank
Carex disperma Dewey
Carex eburnea Boott
Carex exilis Dewey
Carex flava Linnaeus
Carex glacialis Mackenzie
Carex gracillima Schweinitz
Carex gynocrates Wormskjold
Carex hormathodes Fernald
Carex hostiana DeCandolle

Carex interior Bailey
Carex intumescens Rudge
Carex langeana Fernald
Carex lasiocarpa Ehrhart
Carex lenticularis Michaux
Carex lepidocarpa Tausch
Carex leporina Linnaeus
Carex leptalea Wahlenberg
Carex leptonervia (Fernald) Fernald
Carex limosa Linnaeus
Carex limosa × *C. rariflora*
Carex livida (Wahlenberg) Willdenow
Carex mackenziei Kreczetowicz
Carex maritima Gunnerus
Carex × *mendica* Lepage
Carex michauxiana Boeckeler
Carex microglochin Wahlenberg
Carex miliaris Michaux
Carex misandroides Fernald
Carex muricata Linnaeus
Carex nigra (Linnaeus) Reichard
Carex oligosperma Michaux
Carex paleacea Wahlenberg
Carex pallescens Linnaeus
Carex pauciflora Lightfoot
Carex paupercula Michaux
Carex pedunculata Muhlenberg
Carex × *pieperiana* P. Junge
Carex projecta Mackenzie
Carex rariflora (Wahlenberg) J. E. Smith
Carex rostrata Stokes
Carex rupestris Bellardi
Carex salina Wahlenberg
Carex scirpoidea Michaux
Carex scoparia Schkuhr
Carex serotina Mérat
Carex sterilis Willdenow
Carex stipata Muhlenberg
Carex stylosa C. A. Meyer
Carex × *subviridula* (Kukenthal) Fernald

Carex tenuiflora Wahlenberg
Carex trisperma Dewey
Carex vaginata Tausch
Carex vesicaria Linnaeus
Carex viridula Michaux
Carex viridula × *C. lepidocarpa*
Carex wiegandii Schkuhr
Carex × *Xanthina* Fernald
Carum carvi Linnaeus
Cassiope hypnoides (Linnaeus) D. Don
Castilleja septentrionalis Lindley
Catabrosa aquatica (Linnaeus) Beauvois
Centaurea nigra Linnaeus
Cerastium arvense Linnaeus
Cerastium beeringianum Chamisso & Schlechtendahl
Cerastium terrae-novae Fernald & Wiegand
Cerastium vulgatum Linnaeus
Chamaedaphne calyculata (Linnaeus) Moench
Chelone glabra Linnaeus
Chenopodium album Linnaeus
Chrysanthemum leucanthemum Linnaeus
Cichorium intybus Linnaeus
Cinna latifolia (Treviranus) Grisebach
Circaea alpina Linnaeus
Cirsium arvense (Linnaeus) Scopoli
Cirsium muticum Michaux
Cirsium vulgare (Savi) Tenore
Clintonia borealis (Aiton) Rafinesque
Cochlearia cyclocarpa Blake
Cochlearia tridactylites Banks
Comandra richardsiana Fernald
Conioselinum chinense (Linnaeus) Britton, Sterns & Poggenburg
Conioselinum pumilum Rose
Convolvulus sepium Linnaeus
Coptis groenlandica (Oeder) Fernald
Corallorhiza maculata Rafinesque
Corallorhiza trifida Chatelain
Cornus alba Linnaeus
Cornus canadensis Linnaeus
Cornus suecica Linnaeus

Cornus × *unalaschkensis* Ledebour
Corylus cornuta Marshall
Cryptogramma stelleri (S. G. Gmelin) Prantl
Cypripedium acaule Aiton
Cypripedium calceolus Linnaeus
Cyripedium reginae Walter
Cystopteris bulbifera (Linnaeus) Bernhardi
Cystopteris fragilis (Linnaeus) Bernhardi

Dactylis glomerata Linnaeus
Danthonia intermedia Vasey
Danthonia spicata (Linnaeus) Beauvois
Deschampsia atropurpurea (Wahlenberg) Scheele
Deschampsia cespitosa (Linnaeus) Beauvois
Deschampsia flexuosa (Linnaeus) Trinius
Diapensia lapponica Linnaeus
Digitalis purpurea Linnaeus
Draba arabisans Michaux
Draba glabella Pursh
Draba incana Linnaeus
Draba lactea Adams
Draba norvegica Gunnerus
Drosera anglica Hudson
Drosera intermedia Hayne
Drosera linearis Goldie
Drosera × *obovata* Mertens & Koch
Drosera rotundifolia Linnaeus
Dryas integrifolia Vahl
Dryopteris × *boottii* (Tuckerman) Underwood
Dryopteris cristata (Linnaeus) A. Gray
Dryopteris disjuncta (Ledebour) Morton
Dryopteris filix-mas (Linnaeus) Schott
Dryopteris limbosperma (Allioni) Becherer
Dryopteris noveboracensis (Linnaeus) A. Gray
Dryopteris phegopteris (Linnaeus) Christensen
Dryopteris robertiana (Hoffmann) Christensen
Dryopteris spinulosa (O. F. Mueller) Watt
Dryopteris thelypteris (Linnaeus) A. Gray

Eleocharis acicularis (Linnaeus) Roemer & Schultes

Eleocharis elliptica Kunth
Eleocharis halophila (Fernald & Brackett) Fernald & Brackett
Eleocharis nitida Fernald
Eleocharis palustris (Linnaeus) Roemer & Schultes
Eleocharis parvula (Roemer & Schultes) Link
Eleocharis pauciflora (Lightfoot) Link
Eleocharis smallii Britton
Elymus arenarius Linnaeus
Elymus virginicus Linnaeus
Empetrum eamesii Fernald & Wiegand
Empetrum nigrum Linnaeus
Epigaea repens Linnaeus
Epilobium alpinum Linnaeus
Epilobium anagallidifolium Lamarck
Epilobium angustifolium Linnaeus
Epilobium ciliatum Rafinesque
Epilobium davuricum Fischer
Epilobium glandulosum Lehmann
Epilobium hornemanii Reichenbach
Epilobium latifolium Linnaeus
Epilobium nesophilum (Fernald) Fernald
Epilobium palustre Linnaeus
Epilobium scalare Fernald
Equisetum arvense Linnaeus
Equisetum fluviatile Linnaeus
Equisetum palustre Linnaeus
Equisetum pratense Ehrhart
Equisetum scirpoides Michaux
Equisetum sylvaticum Linnaeus
Equisetum variegatum Schleicher
Erigeron hyssopifolius Michaux
Erigeron philadelphicus Linnaeus
Erigeron strigosus Muhlenberg
Eriocaulon aquaticum (Hill) Druce
Eriophorum angustifolium Honckeny
Eriophorum brachyantherum Trautvetter & Meyer
Eriophorum chamissonis C. A. Meyer
Eriophorum gracile W. D. J. Koch
Eriophorum × *Pylaieanum* Raymond
Eriophorum spissum Fernald

Eriophorum tenellum Nuttall
Eriophorum virginicum Linnaeus
Eriophorum viridi-carinatum (Engelmann) Fernald
Erysimum cheiranthoides Linnaeus
Erysimum coarctatum Fernald
Eupatorium maculatum Linnaeus
Euphrasia americana Wettstein
Euphrasia arctica Lange
Euphrasia disjuncta Fernald & Wiegand
Euphrasia randii Robinson
Euphrasia rigidula Jordan
Euphrasia williamsii Robinson

Festuca brachyphylla Schultes
Festuca elatior Linnaeus
Festuca ovina Linnaeus
Festuca prolifera (Piper) Fernald
Festuca rubra Linnaeus
Festuca saximontana Rydberg
Festuca scabrella Torrey
Festuca vivipara (Linnaeus) J. E. Smith
Fragaria virginiana Duchesne
Fraxinus nigra Marshall

Galeopsis tetrahit Linnaeus
Galium asprellum Michaux
Galium kamtschaticum Steller
Galium labradoricum (Wiegand) Wiegand
Galium palustre Linnaeus
Galium trifidum Linnaeus
Galium triflorum Michaux
Gaultheria hispidula (Linnaeus) Bigelow
Gaylussacia baccata (Wangenheim) K. Koch
Gaylussacia dumosa (Andrews) Torrey & A. Gray
Gentiana amarella Linnaeus
Gentiana nesophila Holm
Gentiana propinqua Richardson
Geocaulon lividum (Richardson) Fernald
Geranium pratense Linnaeus
Geranium robertianum Linnaeus

Geum macrophyllum Willdenow
Geum rivale Linnaeus
Glaux maritima Linnaeus
Glechoma hederacea Linnaeus
Glyceria borealis (Nash) Batchelder
Glyceria canadensis (Michaux) Trinius
Glyceria fluitans (Linnaeus) R. Brown
Glyceria grandis S. Watson
Glyceria striata (Lamarck) Hitchcock
Gnaphalium norvegicum Gunnerus
Gnaphalium supinum Linnaeus
Gnaphalium sylvaticum Linnaeus
Gnaphalium uliginosum Linnaeus
Goodyera repens (Linnaeus) R. Brown
Goodyera tesselata Loddiges

Habenaria blephariglottis (Willdenow) Hooker
Habenaria clavellata (Michaux) Sprengel
Habenaria dilatata (Pursh) Hooker
Habenaria hookeri Torrey
Habenaria hyperborea (Linnaeus) R. Brown
Habenaria obtusata (Banks) Richardson
Habenaria orbiculata (Pursh) Torrey
Habenaria psycodes (Linnaeus) Sprengel
Habenaria straminea Fernald
Habenaria viridis (Linnaeus) R. Brown
Halenia deflexa (J. E. Smith) Grisebach
Hedysarum alpinum Linnaeus
Heracleum maximum Bartram
Hieracium aurantiacum Linnaeus
Hieracium florentinum Allioni
Hieracium floribundum Wimmer & Grabowski
Hieracium groenlandicum Arvet-Touvet
Hieracium kalmii Linnaeus
Hierochloe alpina (Swartz) Roemer & Schultes
Hierochloe odorata (Linnaeus) Beauvois
Hippuris vulgaris Linnaeus
Hordeum jubatum Linnaeus
Hordeum vulgare Linnaeus
Hypericum boreale (Britton) Bicknell

Impatiens capensis Meerburgh
Iris hookeri Penny
Iris versicolor Linnaeus
Isoetes muricata Durieu

Juncus albescens (Lange) Fernald
Juncus × *alpiniformis* Fernald
Juncus alpinus Villars
Juncus articulatus Linnaeus
Juncus balticus Willdenow
Juncus brevicaudatus (Engelmann) Fernald
Juncus bufonius Linnaeus
Juncus canadensis J. Gay
Juncus dudleyi Wiegand
Juncus effusus Linnaeus
Juncus filiformis Linnaeus
Juncus gerardii Loiseleur
Juncus × *nodosiformis* Fernald
Juncus nodosus Linnaeus
Juncus pelocarpus E. Meyer
Juncus stygius Linnaeus
Juncus tenuis Willdenow
Juncus trifidus Linnaeus
Juniperus communis Linnaeus
Juniperus horizontalis Moench

Kalmia angustifolia Linnaeus
Kalmia polifolia Wangenheim
Kobresia simpliciuscula (Wahlenberg) Mackenzie

Lactuca biennis (Moench) Fernald
Lamium purpureum Linnaeus
Lappula myosotis Moench
Larix laricina (DuRoi) K. Koch
Lathyrus japonicus Willdenow
Lathyrus palustris Linnaeus
Ledum groenlandicum Oeder
Leontodon autumnalis Linnaeus
Lesquerella purshii (S. Watson) Fernald
Ligusticum scothicum Linnaeus

Linnaea borealis Linnaeus
Linum catharticum Linnaeus
Listera auriculata Wiegand
Listera borealis Morong
Listera convallarioides (Swartz) Torrey
Listera cordata (Linnaeus) R. Brown
Littorella americana Fernald
Lobelia dortmanna Linnaeus
Lobelia kalmii Linnaeus
Loiseleuria procumbens (Linnaeus) Desvaux
Lomatogonium rotatum (Linnaeus) Fries
Lonicera villosa (Michaux) Roemer & Schultes
Luzula multiflora (Retzius) Lejeune
Luzula parviflora (Ehrhart) Desvaux
Luzula spicata (Linnaeus) DeCandolle
Luzula sudetica (Willdenow) DeCandolle
Lychnis alpina Linnaeus
Lycopodium alpinum Linnaeus
Lycopodium annotinum Linnaeus
Lycopodium clavatum Linnaeus
Lycopodium complanatum Linnaeus
Lycopodium inundatum Linnaeus
Lycopodium lucidulum Michaux
Lycopodium obscurum Linnaeus
Lycopodium sabinifolium Willdenow
Lycopodium selago Linnaeus
Lycopus americanus Muhlenberg
Lycopus uniflorus Michaux
Lysimachia terrestris (Linnaeus) Britton, Sterns & Poggenburg
Lythrum salicaria Linnaeus

Maianthemum canadense Desfontaines
Malaxis brachypoda (A. Gray) Fernald
Malaxis unifolia Michaux
Matricaria maritima Linnaeus
Matricaria matricarioides (Lessing) Porter
Matteuccia struthiopteris (Linnaeus) Todaro
Mentha arvensis Linnaeus
Menyanthes trifoliata Linnaeus
Mertensia maritima (Linnaeus) S. F. Gray

Milium effusum Linnaeus
Mimulus moschatus Douglas
Mitella nuda Linnaeus
Moneses uniflora (Linnaeus) A. Gray
Monotropa hypopithys Linnaeus
Monotropa uniflora Linnaeus
Montia lamprosperma Chamisso
Montia rivularis Gmelin
Muhlenbergia glomerata (Willdenow) Trinius
Myosotis laxa Lehmann
Myosotis scorpioides Linnaeus
Myrica gale Linnaeus
Myriophyllum alterniflorum DeCandolle
Myriophyllum exalbescens Fernald
Myriophyllum tenellum Bigelow

Nemopanthus mucronatus (Linnaeus) Baillon
Nuphar variegata Engelmann

Odontites rubra (Baumgarten) Opiz
Oenothera biennis Linnaeus
Oenothera parviflora Linnaeus
Oenothera perennis Linnaeus
Onoclea sensibilis Linnaeus
Orobanche terrae-novae Fernald
Oryzopsis asperifolia Michaux
Oryzopsis canadensis (Poiret) Torrey
Osmorhiza chilensis Hooker & Arnott
Osmorhiza obtusa (Coulter & Rose) Fernald
Osmunda cinnamomea Linnaeus
Osmunda claytoniana Linnaeus
Osmunda regalis Linnaeus
Oxyria digyna (Linnaeus) Hill
Oxytropis johannensis (Fernald) Fernald
Oxytropis terrae-novae Fernald

Parnassia glauca Rafinesque
Parnassia parviflora DeCandolle
Pastinaca sativa Linnaeus
Pedicularis palustris Linnaeus

Phalaris arundinacea Linnaeus
Phleum alpinum Linnaeus
Phleum pratense Linnaeus
Phyllodoce caerulea (Linnaeus) Babington
Picea glauca (Moench) Voss
Picea mariana (Miller) Britton, Sterns & Poggenburg
Pinguicula vulgaris Linnaeus
Pinus strobus Linnaeus
Plantago juncoides Lamarck
Plantago lanceolata Linnaeus
Plantago major Linnaeus
Plantago oliganthos Roemer & Schultes
Poa alpigena (Fries) Lindman fil.
Poa alpina Linnaeus
Poa annua Linnaeus
Poa compressa Linnaeus
Poa eminens Presl
Poa fernaldiana Nannfeldt
Poa glauca Vahl
Poa nemoralis Linnaeus
Poa palustris Linnaeus
Poa pratensis Linnaeus
Poa saltuensis Fernald & Wiegand
Poa subcaerulea J. E. Smith
Poa trivialis Linnaeus
Pogonia ophioglossoides (Linnaeus) Ker-Gawler
Polygonum amphibium Linnaeus
Polygonum aviculare Linnaeus
Polygonum convolvulus Linnaeus
Polygonum cuspidatum Siebold & Zuccarini
Polygonum fowleri Robinson
Polygonum hydropiper Linnaeus
Polygonum persicaria Linnaeus
Polygonum raii Babington
Polygonum viviparum Linnaeus
Polypodium virginianum Linnaeus
Polystichum braunii (Spenner) Fée
Polystichum lonchitis (Linnaeus) Roth
Populus balsamifera Linnaeus
Populus × *gileadensis* Rouleau

Populus tremuloides Linnaeus
Potamogeton alpinus Balbis
Potamogeton amplifolius Tuckerman
Potamogeton confervoides Reichenbach
Potamogeton epihydrus Rafinesque
Potamogeton filiformis Persoon
Potamogeton gramineus Linnaeus
Potamogeton natans Linnaeus
Potamogeton oakesianus Robbins
Potamogeton perfoliatus Linnaeus
Potentilla anserina Linnaeus
Potentilla crantzii (Crantz) G. Beck
Potentilla egedei Wormskjold
Potentilla fruticosa Linnaeus
Potentilla nivea Linnaeus
Potentilla norvegica Linnaeus
Potentilla palustris (Linnaeus) Scopoli
Potentilla pectinata Rafinesque
Potentilla tridentata Aiton
Prenanthes trifoliolata (Cassini) Fernald
Primula egaliksensis Wormskjold
Primula laurentiana Fernald
Primula mistassinica Michaux
Prunella vulgaris Linnaeus
Prunus pensylvanica Linnaeus fil.
Prunus virginiana Linnaeus
Pteridium aquilinum (Linnaeus) Kuhn
Puccinellia coarctata Fernald & Weatherby
Puccinellia paupercula (Holm) Fernald & Weatherby
Pyrola asarifolia Michaux
Pyrola chlorantha Swartz
Pyrola minor Linnaeus
Pyrola rotundifolia Linnaeus
Pyrola secunda Linnaeus
Pyrus americana (Marshall) DeCandolle
Pyrus decora (Sargent) Hyland

Ranunculus abortivus Linnaeus
Ranunculus acris Linnaeus
Ranunculus cymbalaria Pursh

Ranunculus hyperboreus Rottboell
Ranunculus macounii Britton
Ranunculus pensylvanicus Linnaeus fil.
Ranunculus repens Linnaeus
Ranunculus reptans Linnaeus
Ranunculus trichophyllus Chaix
Rhamnus alnifolius L'Héritier
Rhinanthus borealis (Sterneck) Chabert
Rhinanthus crista-galli Linnaeus
Rhododendron canadense (Linnaeus) Torrey
Rhododendron lapponicum (Linnaeus) Wahlenberg
Rhynchospora alba (Linnaeus) Vahl
Rhynchospora capillacea Torrey
Rhynchospora fusca (Linnaeus) Aiton fil.
Ribes glandulosum Grauer
Ribes hirtellum Michaux
Ribes lacustre (Persoon) Poiret
Ribes triste Pallas
Rorippa islandica (Oeder) Borbas
Rosa nitida Willdenow
Rosa virginiana Miller
Rubus acaulis Michaux
Rubus arcticus Linnaeus
Rubus chamaemorus Linnaeus
Rubus idaeus Linnaeus
Rubus pubescens Rafinesque
Rumex acetosa Linnaeus
Rumex acetosella Linnaeus
Rumex crispus Linnaeus
Rumex fenestratus Greene
Rumex longifolius DeCandolle
Rumex mexicanus Meissner
Rumex obtusifolius Linnaeus
Rumex orbiculatus A. Gray
Rumex pallidus Bigelow
Ruppia maritima Linnaeus

Sagina nodosa (Linnaeus) Fenzl
Sagina procumbens Linnaeus
Sagittaria graminea Michaux

Salicornia europaea Linnaeus
Salix arctica Pallas
Salix arctophila Cockerell
Salix bebbiana Sargent
Salix candida Fluegge
Salix cordata Michaux
Salix discolor Muhlenberg
Salix glauca Linnaeus
Salix glaucophylloides Fernald
Salix herbacea Linnaeus
Salix lanata Linnaeus
Salix lucida Muhlenberg
Salix myrtillifolia Andersson
Salix pedunculata Fernald
Salix pellita Andersson
Salix planifolia Pursh
Salix reticulata Linnaeus
Salix rigida Muhlenberg
Salix serissima (L. H. Bailey) Fernald
Salix uva-ursi Pursh
Salix vestita Pursh
Salix wiegandii Fernald
Salsola kali Linnaeus
Sambucus pubens Michaux
Sanguisorba canadensis Linnaeus
Sanicula marilandica Linnaeus
Sarracenia purpurea Linnaeus
Satureja vulgaris (Linnaeus) Fritsch
Saxifraga aizoides Linnaeus
Saxifraga cespitosa Linnaeus
Saxifraga oppositifolia Linnaeus
Saxifraga paniculata Miller
Scheuchzeria palustris Linnaeus
Schizachne purpurascens (Torrey) Swallen
Schizaea pusilla Pursh
Scirpus acutus Muhlenberg
Scirpus americanus Persoon
Scirpus atrocinctus Fernald
Scirpus cespitosus Linnaeus
Scirpus cyperinus (Linnaeus) Kunth

Scirpus hudsonianus (Michaux) Fernald
Scirpus rubrotinctus Fernald
Scirpus rufus (Hudson) Schrader
Scirpus subterminalis Torrey
Scrophularia nodosa Linnaeus
Scutellaria epilobiifolia A. Hamilton
Scutellaria lateriflorus Linnaeus
Secale cereale Linnaeus
Sedum rosea (Linnaeus) Scopoli
Selaginella selaginoides (Linnaeus) Link
Senecio aureus Linnaeus
Senecio gaspensis Greenman
Senecio pauciflorus Pursh
Senecio pauperculus Michaux
Senecio pseudo-arnica Lessing
Senecio vulgaris Linnaeus
Shepherdia canadensis (Linnaeus) Nuttall
Sibbaldia procumbens Linnaeus
Silene acaulis (Linnaeus) Jacquin
Sisyrinchium montanum Greene
Smilacina stellata (Linnaeus) Desfontaines
Smilacina trifolia (Linnaeus) Desfontaines
Solidago × *calcicola* Fernald
Solidago canadensis Linnaeus
Solidago hispida Muhlenberg
Solidago lepida DeCandolle
Solidago macrophylla Pursh
Solidago multiradiata Aiton
Solidago purshii Porter
Solidago rugosa Miller
Solidago sempervirens Linnaeus
Solidago uliginosa Nuttall
Sonchus arvensis Linnaeus
Sonchus oleraceus Linnaeus
Sparganium angustifolium Michaux
Sparganium chlorocarpum Rydberg
Sparganium eurycarpum Engelmann
Sparganium hyperboreum Laestadius
Sparganium minimum (Hartman) Fries
Spartina pectinata Link

Spergularia canadensis (Persoon) Don
Spergularia rubra (Linnaeus) Presl & Presl
Sphenopholis intermedia Rydberg
Spiraea latifolia (Aiton) Borkhausen
Spiranthes romanzoffiana Chamisso
Stachys palustris Linnaeus
Stellaria calycantha (Ledebour) Bongard
Stellaria crassifolia Erhart
Stellaria graminea Linnaeus
Stellaria humifusa Rottboell
Stellaria longipes Goldie
Stellaria media (Linnaeus) Cyrillo
Streptopus amplexifolius (Linnaeus) DeCandolle
Streptopus × *oreopolus* Fernald
Streptopus roseus Michaux

Tanacetum huronense Nuttall
Tanacetum vulgare Linnaeus
Taraxacum ambigens Fernald
Taraxacum ceratophorum (Ledebour) DeCandolle
Taraxacum lapponicum Kihlman
Taraxacum latilobum DeCandolle
Taraxacum officinale Weber
Taxus canadensis Marshall
Thalictrum alpinum Linnaeus
Thalictrum pubescens Pursh
Tofieldia glutinosa (Michaux) Persoon
Tofieldia pusilla (Michaux) Persoon
Trientalis borealis Rafinesque
Trifolium agrarium Linnaeus
Trifolium hybridum Linnaeus
Trifolium pratense Linnaeus
Trifolium repens Linnaeus
Triglochin × *gaspense* Lieth & D. Löve
Triglochin maritimum Linnaeus
Triglochin palustre Linnaeus
Trillium cernuum Linnaeus
Trisetum melicoides (Michaux) Vasey
Trisetum spicatum (Linnaeus) Richter
Triticum aestivum Linnaeus

Tussilago farfara Linnaeus
Typha latifolia Linnaeus

Urtica dioica Linnaeus
Utricularia cornuta Michaux
Utricularia intermedia Hayne
Utricularia minor Linnaeus
Utricularia vulgaris Linnaeus

Vaccinium angustifolium Aiton
Vaccinium cespitosum Michaux
Vaccinium macrocarpon Aiton
Vaccinium × *nubigenum* Fernald
Vaccinium ovalifolium J. E. Smith
Vaccinium oxycoccos Linnaeus
Vaccinium uliginosum Linnaeus
Vaccinium vitis-idaea Linnaeus
Verbascum thapsus Linnaeus
Veronica americana (Rafinesque) Schweinitz
Veronica arvensis Linnaeus
Veronica officinalis Linnaeus
Veronica scutellata Linnaeus
Veronica serpyllifolia Linnaeus
Veronica tenella Allioni
Viburnum cassinoides Linnaeus
Viburnum edule (Michaux) Rafinesque
Viburnum trilobum Marshall
Vicia cracca Linnaeus
Viola adunca J. E. Smith
Viola cucullata Aiton
Viola incognita Brainerd
Viola labradorica Schrank
Viola nephrophylla Greene
Viola pallens (Banks) Brainerd
Viola palustris Linnaeus
Viola renifolia A. Gray
Viola renifolia × *pallens*
Viola selkirkii Pursh
Viola septentrionalis Greene

Woodsia alpina (Bolton) S. F. Gray
Woodsia glabella R. Brown
Woodsia ilvensis (Linnaeus) R. Brown

Zannichellia palustris Linnaeus
Zostera marina Linnaeus

CONTRIBUTIONS TO THE VASCULAR FLORA OF OXFORD COUNTY, MAINE

C. S. CAMPBELL AND L. M. EASTMAN

Oxford County includes about 5570 sq. km. (2150 sq. mi.) of mostly hilly and mountainous land in the northwest corner of Maine. It is bordered to the north by Frontenac County of the Province of Quebec, Canada; to the east and south by Franklin, Androscoggin, Cumberland and York Counties of Maine; and to the west by Carroll and Coos Counties of New Hampshire. Oxford County, which has a population of 45,000, resembles the state of Delaware in size and shape.

In 1824 Thomas Nuttall collected *Subularia aquatica* L. in the town of Waterford. This was the first known collection of a vascular plant in Oxford County as well as the first of this species in North America. Since that time many keen-eyed botanists have collected extensively here. The most notable contributors to the knowledge of the local flora were John C. Parlin, Kate Furbish, Leston A. Wheeler, Arthur S. Pease and Ralph C. Bean. Over the past few years our botanizing has added many new species sites to the county and the state. The most fruitful localities are the northern and southern ends of the county where relatively little collecting of herbarium specimens of vascular plants had been done.

Our distribution records are based on the collections in the herbaria of the New England Botanical Club, the University of Maine, and the University of New Hampshire. In the following account, the species followed by an asterisk (*) are first collections for Oxford County while those followed by a double asterisk (**) are new for the state. Voucher specimens have been donated to the University of Maine Herbarium. Except where indicated, nomenclature follows Fernald (1950).

On the basis of topography and climate, Oxford County may be divided into a northern and a southern half (Toppan, 1935). Mountain ranges interspersed with some lowlands fill the northern half. On the other hand, the southern half, or the southern interior to distinguish it from the coastal region of Maine, has a lower relief with a warmer, wetter climate and a longer growing season.

A boreal forest of *Picea* spp. and *Abies balsamea* (L.) Mill. covers higher elevations and cold valleys on the northern uplands. On midslopes northern hardwoods (*Acer saccharum* Marsh., *Betula alleghaniensis* Britton [Brayshaw, 1966; *B. lutea* Michx. f. of Fernald, 1950], and *Fagus grandifolia* Ehrh.) predominate over a flora considerably more diverse than that of the boreal forest. In favorable conditions, such as east-facing midslopes of the Boundary Mountain Range at the very northern end of Oxford County, several species of pteridophytes are prominent. *Adiantum pedatum* L., *Diplazium acrostichoides* (Sw.) Butters (Butters, 1917; *Athyrium thelypteroides* (Michx.) Desv. of Fernald, 1950), and *Polystichum braunii* (Spenner) Fee form large populations. The northern *Botrychium virginianum* (L.) Sw. var. *europaeum* Anstr.* and *Dryopteris goldiana* (Hook.) Gray* are less prominent. The only other station for the latter species is a very similar stand of pure hardwoods in Haystack Notch (549 m., 1800 ft.) near the southern end of the northern uplands. The same three common ferns also dominate the slopes of Haystack Notch.

Galium kamtschaticum Steller* and *Milium effusum* L.* are infrequent and frequent respectively in these northern hardwoods. *Impatiens pallida* Nutt.* grows in the hardwoods of the Boundary Mountains and, again, Haystack Notch, but it is most characteristic of the borders of woods and roadside thickets in the northernmost township of Bowmantown.

One of the Boundary Mountains, Twin Peaks (917m, 3010 ft.) in Bowmantown has a remarkable flora. Above the rich hardwoods on the eastern midslope, at about 793 m., 2600 ft., a band of wet cliffs traverses the mountain and supports a northern, calciphytic flora. *Woodsia glabella* R. Br.* is frequent here, and we found one small colony of what we are calling *W. alpina* (Bolton) S. F. Gray*. It may also be a hybrid of *W. glabella* and *W. ilvensis* (L.)R.Br. which occurs nearby on drier rocks. Three northern sedges *Carex capillaris* L. var. *Major* Blytt.*, *C. atratiformis* Britt.*, and *C. media* Br.** grow on moist ledges or in the boulders at the base of the cliff. The first two sedges are infrequent or rare in Maine and the third, which enters the United States from Canada only in the northern midwest, is a new record for New England. Just under the summit of the mountain there is a large dry cliff, presumably formed by glacial plucking and now surrounded by boreal forest. Growing on shelves and in crevices amongst the three dominant species of the cliff — *Thuja occidentalis* L., *Potentilla fruticosa* L., and *P. tridentata* Ait. — is a mixture of northern and subalpine calcyphiles: *Lycopodium selago* L.*, *Dryopteris fragrans* (L.) Schott, *Poa glauca* Vahl.*, *Trisetum spicatum* (L.) Richter var. *pilosiglume* Fern.*, *Carex aurea* Nutt., *C. capillaris***, and *Juncus trifidus* L. Of particular note in this assemblage are three considerable range extensions. First, *Carex eburnea* Boott** was previously known in New England only from calcareous rocks of western New England. *Saxifraga aizoon* Jacq. var. *neogaea* Butters* is found in several localities in Vermont and has recently been added to the flora of the White Mountains (Churchill, 1967). In Maine it grows elsewhere only on the ledges of the South Basin of Mt. Katahdin. Finally, the only other localities in New England for *Antennaria rupicola* Fern.* are the rocky shores of the St. John River and Mattawamkeag River (the type locality) in Aroostook County, Maine.

Eight other species of the northern uplands had not previously been reported from Oxford County. *Geum macrophyllum* Willd.* is frequent in moist, open woods. *Veronica tenella* All.* we found on a rocky brookbank. *Aster junciformis* Rydb.* and *Senecio aureus* L. var. *intercursus* Fern.* were both found in alluvial woods of the Magalloway River. Three native ruderals occur in disturbed soil bordering dirt roads in the northern uplands, *Euphrasia canadensis* Townsend*, *Rhinanthus crista-galli* L.*, and *Gnaphalium sylvaticum* L.* *Carex bigelowii* Torr.* from the summit of Baldpate Mt. (1244 m., 4080 ft.) joins 14 other species of the flora defined as alpine (Pease, 1964).

In contrast to the flora of predominantly northern affinities of the northern uplands, there is a strong southern element in the flora of the southern interior. This is especially the case in the drainage of the Saco River where *Juniperus virginiana* L. var. *crebra* Fern. & Grisc., *Betula lenta* L., *Quercus alba* L., *Q. velutina* Lam., *Q. ilicifolia* Wang., *Ceanothus americanus* L., and *Kalmia latifolia* L. all reach the northern limits of their ranges. Of the 28 additions to the county and state that we report from this region, the majority are also at the northern limits of their ranges.

The two most prominent physiographic features of the region are the extensive Wisconsin glacial deposits and the numerous low, rounded hills. Sand and gravel carried by the melt waters of the receding glacier were deposited on the bottom of a large lake covering the valley of the present Saco River in the towns of Fryeburg, Stow, Lovell, Sweden, Denmark, Brownfield, and Hiram. At present, what remains of this glacial lake are many lakes and ponds and extensive sand plains cut by the meandering Saco.

On the sandy shores of Kimball Pond in Fryeburg grow *Eleocharis engelmanii* Steud. f. *detonsa* (Gray) Svenson* and *E. tuberculosa* (Michx.) R. & S.* Other notable plants found around this pond are *Carex michauxiana* Boeckl. (swale), *Utricularia gibba* L. (muddy shore), and *U. resupinata* B. D. Greene (shallow water, apparently only blooming during years when the water is sufficiently shallow).

In the same town centuries of flooding by the Saco have created the largest farming acreage of contiguous alluvial soils in Maine (Rourke & Hardesty, 1966). Where the woods along the river have been allowed to grow up to *Acer saccharinum* L. and *Tilia americana* L., as at Snow Falls, a diverse flora persists including *Leersia virginica* Willd. var. *ovata* (Poir.) Fern.*, another southern species.

The sand plains of the region are an outpost for a small maritime element in the flora: *Myrica pennsylvanica* Loisel*, *Hudsonia tomentosa* L. and var. *intermedia* Peck, and *Lechea maritima* Leggett. Also in the sandy outwash of the area and previously not collected are two rather common species, *Lysimachia quadrifolia* L.* and *Aster vimineus* Lam.*

Many northerly range extensions come from the low rounded hills of the Saco River valley. The most important of these are Frost Mt. (373 m., 1225 ft.) in Brownfield, Peaked Mt. (329 m., 1080 ft.) and Bill Merrill Mt. (488 m., 1600 ft.) in Hiram, and Rattlesnake Mt. (359 m., 1179 ft.) in Porter (Eastman, 1977). In the dry, mixed woods on the lower slopes of these hills, we found *Phytolacca americana* L.*, *Chimaphila maculata* (L.) Pursh*, *Corallorhiza odontorhiza* (Willd.) Nutt.* and *Triphora trianthophora* (Sw.) Rydb. The spotted wintergreen has recently been collected in Maine from four widely scattered and very small populations. Unlike *Chimaphila*, the two orchids are rare in New England. Our station for the *Corallorhiza* collection is the second in the state, the first being from a similar habitat about 64 km. (40 mi.) due south, in South Berwick, where John Parlin found it in 1898. *Triphora trianthophora* was first discovered in Maine and Oxford County in 1899 on Frost Mt. (Harvey, 1900). This station was apparently destroyed by fire in 1947, but the plant also occurs in nearly pure stands of beech at the base of Bill Merrill Mt. and in several localities and sometimes in large populations in the Evans Notch region of the County (Eastman, 1969, 1972; Campbell, 1975).

In the rocky woods above the dry woods at the bases of these low hills, we added *Bromus pubescens* Willd.** (Wagnon, 1950; *B. purgans* L. of Fernald, 1950), *Muhlenbergia sobolifera* (Muhl.) Trin.**, *Carex cephalophora* Muhl.*, and *C. virescens* Muhl.* Where the rocky woods turn to open or shaded ledges there are plants such as *Woodsia obtusa* (Spreng.) Torr.*, *Panicum latifolium* L., *Chenopodium boscianum* Moq.*, *Ranunculus fascicularis* Muhl.**, *Arabis missouriensis* Greene, *Geranium carolinianum* L.*, *Ceanothus americanus* L., *Vitis aestivalis* Michx. var. *argentifolia* (Munson) Fern.**, *Cerastium arvense* L.*, *Epilobium ciliatum* Raf.*, *Antennaria petaloidea* Fern.*, and *A. plantaginifolia* (L.) Hook.* Of particular note in this group of plants are the *Bromus, Muhlenbergia,* and *Ranunculus* collections. The nearest localities for all three are one or two stations in southern New Hampshire.

Five other species from the Saco River drainage are also new county records: *Carex incomperta* Bickn.* (swale in Porter), *C. artiteca* Mackenz.* (dry bank in Porter), *Isotria verticillata* (Willd.) Raf.* (under *Pinus strobus* in Waterford), *Nyssa sylvatica* Marsh* (mixed woods in Denmark), and *Vaccinium atrococcum* (Gray) Heller* (heath bog in Stow).

Carex sparganioides Muhl.* (reported from Franklin County, Maine, but otherwise not known north of southern New Hampshire) and *Rhododendron viscosum* (L.) Torr.* (rare in southern York County, Maine) were collected within two and one half miles of one another in northwestern Woodstock. These stations appear to be isolated populations far removed from the main part of their ranges.

Carex is the largest genus in the flora with 107 species, 23 varieties, and four forms. In addition to the ten new records reported so far, five others have been added, all growing in full sun in moist to dry soil: *C. annectans* Bickn.*, *C. alopecoidea* Tuckerm.*, *C. echinata* Murr.*, *C. wiegandii* Mackenz.* and *C. granularis* Muhl. var. *haleana* (Olney) Porter*. The latter two species were both found growing near *C. aurea,* a good indicator of neutral or alkaline soil. Another calcyphile found associated with *C. aurea* is *Equisetum variegatum* Schleich.* from a moist bank in Hebron.

Caltha palustris L.*, *Amelanchier intermedia* Spach* (vel aff.), and *Aster novae-angliae* L.* are all more or less frequently occurring species which had not previously been collected in Oxford County. On several rocky, wooded slopes, we saw non-reproductive plants of what we suspected to be *Clematis verticillaris* DC.* We saw only one plant in flower in a recently cleared roadside thicket in Albany. *Typha angustifolia* L.* in a roadside ditch in West Paris has perhaps recently come this far inland in response to the presence of roadside salts.

The genus *Crataegus* is not prominent in the Oxford flora. There are seven infrequent to rare species of roadsides, hedgerows, old fields, and ledges. Two of these are new: *C. anomala* Sarg.* and *C. compta* Sarg.*

Two of the nine additions to the aquatic flora are common species, *Lemna minor* L.* and *Spirodela polyrhiza* (L.) Schleid.* The others are rare or infrequent: *Potamogeton confervoides* Reichenb.*, *P. obtusifolius* Mert. & Koch*, *P. praelongus* Wulfen.*, *Elodea canadensis* Michx., *Ceratophyllum demersum* L.*, *Myriophyllum humile* (Raf.) Morong*, and *M. exalbescens* Fern.*

Anemone riparia Fern.* from coniferous woods in Hebron is the last of 74 indegenes reported here as new for Oxford County.

Additions to the adventive flora number 88 species. They are for the most part weedy and closely associated with man's alteration of the environment. Some species are characteristically found in railroad ballast: *Eragrostis poaeoides* R. & S.*, *E. pectinacea* (Michx.) Nees*, *Hordeum jubatum* L.*, *Triticum aestivum* L.*, *Avena sativa* L.*, *Sporobolus vaginiflorus* (Torr.) Wood var. *inaequalis* Fern.*, *Kochia scoparia* (L.) Roth*, *Silene cserei* Baumg.*, *Diplotaxis tenuifolia* (L.) DC.**, *Plantago indica* L.*, and *Lactuca scariola* L. f. *integrifolia* (Bogenh.) G. Beck.*

Alopecurus pratensis L.*, *Lupinus polyphyllus* Lindl.*, *Veronica chamaedrys* L.*, *Galium erectum* Huds.*, and *Achillea ptarmica* L.* have become more or less prominent in old fields.

Abutilon theophrasti Medic.* has established itself sparingly on the sand plains of Brownfield. *Epipactis helleborine* (L.) Crantz* has invaded vacant lots but is more characteristically found in rich hardwoods in populations of one or two individuals where its capacity for self-fertilization will allow it to spread itself from one parent plant.

Eighteen new adventive species are garden escapes, persisting and spreading only near their cultivation: *Allium schoenoprasum* L.*, *Iris germanica* L.*, *Lychnis chalcedonica* L.*, *Dianthus plumarius* L.*, *Aquilegia vulgaris* L.*, *Delphinium exaltatum* L.*, *Sedum acre* L.*, *S. sarmentosum* Bunge**, *S. spurium* Bieb*, *Filipendula rubra* (Hill) Robins.*, *Rosa multiflora* Thunb.*, *R. spinosissima* L.*, *R. rugosa* Thunb.*, *Thermopsis mollis* (Michx.) M. A. Curtis*, *Geranium sanguineum* L.*, *Ajuga reptans* L.*, *Digitalis purpurea* L.*, *Echinops sphaerocephalus* L.*, and *Valeriana officinalis* L.*

The majority of the additions to the adventive flora are from waste places, roadsides, dumps, and vacant lots: *Eragrostis neomexicanus* Vasey*, *Lolium multiflorum* Lam.*, *Secale cereale* L.*, *Panicum miliaceum* L.*, *P. dicotomiflorum* Michx.*, *Lilium tigrinum* L.*, *Convallaria majalis* L.*, *Iris pseudoacorus* L.* (also on muddy shores), *I. sibirica* L.*, *Populus nigra* L. var. *italica* Muenchh.*, *Cannabis sativa* L.*, *Rumex domesticus* Hartm.*, *Stellaria media* (L.) Cyrillo*, *Lychnis dioica* L.*, *L. alba* Mill.* (the last two frequent to common), *L. coronaria* (L.) Desr.*, *Dianthus armeria* L.*, *Berberis thunbergii* DC.*, *Chelidonium majus* L.* (a common weed), *Lepidium sativum* L.*, *Conringia orientalis* (L.) Dumort*, *Armoracia lapathifolia* Gilib.*, *Physocarpus opulifolius* (L.) Maxim.*, *Rosa cinnamomea* L.*, *Robinia viscosa* Went.*, *R. hispida* L.*, *Lathyrus tuberosus* L.*, *Geranium molle* L.*, *G. maculatum* L.*, *Celastrus orbiculatus* Thunb.*, *Acer platanoides* L.*, *Oenothera pilosella* Raf.*, *Aegopodium podagraria* L.*, *Vinca minor* L.*, *Convolvulus arvensis* L.*, *Phlox paniculata* L.*, *Borago officinalis* L.*, *Lamium purpureum* L.*, *Mentha alopecuroides* Hull**, *Physalis alkekengi* L.*, *Datura stramonium* L.*, *Petunia violacea* Lindl.*, *Campanula rapunculoides* L.*, *C. linifolia* Jacq.**, *C. latifolia* L.*, *Helianthus annuus* L.*, *H. laetiflorus* Pers.*, *Artemisia ludoviciana* Nutt. var. *brittonii* (Rydb.) Fern.*, *Centauria maculosa* Lam.*, *Tragopogon pratensis* L.*, and *Sonchus arvensis* L.*

In summary, the vascular flora of Oxford County includes 1345 native and adventive species (Campbell & Eastman, manuscript in preparation). One hundred and sixty-two of these are reported here as new records.

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NEW STATIONS FOR CHIMAPHILA MACULATA (L.) PURSH IN MAINE

The discovery of spotted wintergreen, *Chimaphila maculata* (L.) Pursh at the base of Mount Agamenticus in York, York County, in 1971, was the first for this species to be recorded in Maine (see Rhodora **75:** 162 165). Since then, four new stations have been discovered.

On June 3, 1976, Harry Tyler of Westport Island and Christopher S. Campbell, graduate student at Harvard University discovered *Chimaphila maculata* on a dry wooded slope at Norridgewock, Somerset County, at latitude 44° 45′N. This is believed to be the most northern station for the species in North America. An interesting feature of this area is the occurrence of large colonies of *Cypripedium arientinum* R.Br., *Habenaria Hookeri* Torr., and *Orchis spectabilis* L.

During the summer of 1975, Philip Keenan of Dover, New Hampshire, and I discovered twelve plants of *Chimaphila maculata* in low, rich, rocky woods, off route 114, North Sebago, Cumberland County. On a subsequent visit to the area on June 6, 1976, only two plants were found. Dry leafless stalks were visible, indicating that some animal or bird had eaten the plants.

On July 4, 1975, I discovered eleven plants of spotted wintergreen on a poorly wooded slope in thin, rocky soil on Peaked Mountain, Hiram, Oxford County. Rock piles throughout the area indicate the land had been cleared during an earlier time.

In early July, 1976, Richard O'Connell of Portland discovered a single plant on a gravelly slope among *Ostrya virginiana* (Mill.) K. Koch on the southeast side of Pleasant Mountain, Denmark, Oxford County. The plants had but four leaves and showed no signs of budding.

In lieu of specimens, color photographs, taken at all the stations mentioned, have been deposited at the University of Maine Herbarium.

L. M. EASTMAN
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A NATIONAL LIST OF SCIENTIFIC PLANT NAMES

The Department of Botany, Smithsonian Institution, was recently asked by the Soil Conservation Service of the United States Department of Agriculture to produce an updated, revised, and corrected edition of the *National List of Scientific Plant Names,* which was originally issued by the Service in 1971. The Department of Botany has agreed to undertake the revision of this checklist and looks forward to bringing the list to the attention of a much wider circle of botanists and conservationists. It will include the correct scientific names of all vascular plant taxa (including subspecies and varieties) in North America, Hawaii, Puerto Rico and the Virgin Islands.

In the process of revising the list, we will be soliciting the highly valued cooperation of numerous botanical colleagues early in 1978. In the published revision, full acknowledgment will be given to the people making individual contributions of data.

Please address your correspondence regarding the checklist to: The Chairman, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560.

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THE TAXONOMY OF ASTER SECTION MULTIFLORI (ASTERACEAE)
I. NOMENCLATURAL REVIEW AND FORMAL PRESENTATION OF TAXA

ALMUT G. JONES

Aster sect. *Multiflori* A. Gray (1884) is one of the more stable and well delimited groups in this highly variable and polymorphic genus. Nevertheless, the entities included within this group have posed problems for virtually every floristic botanist who has had to deal with them. Asters are notorious for their high degree of interspecific compatibility and, in the view of several authors, hybridization is one of the major causes of confusion of taxa in the field (Burgess, 1906; Cronquist, 1952a; Shinners, 1941; Wiegand, 1928). The genus is characterized by nearly complete self-sterility and obligatory outcrossing. The resulting heterozygosity and a ready phenotypic response to environmental fluctuations find expression in a wide range of structural variability, as well as extensive geographic ranges for most species.

A difficulty confronting the monographer who relies principally on herbarium material is the inadequacy of many specimens, particularly of older collections, including many types. They often lack underground parts or consist of single branches that fail to display some very diagnostic characteristics of the plants, e.g., habit of stems and rhizomes. Habitat data are frequently lacking on specimen labels, although these data can provide critical information for the identification and characterization of *Aster* species (Jones, 1978).

The views presented in previous taxonomic treatments of *Aster* sect. *Multiflori* vary considerably. At one extreme, seven species are recognized (Rydberg, 1917), and at the other only one (Boivin, 1962). However, none of the previous investigators has studied the group over its entire geographic range. The taxa under consideration are widely distributed, ranging from New England to Washington, north to Alaska, and south to Mexico. The plants are absent in the southeastern United States, California, and Nevada.

This treatment recognizes two species, *Aster ericoides* Linnaeus and *A. falcatus* Lindley, on the basis of morphology, cytology, and the presence of a strong reproductive barrier. In each species, the major morphological variants are treated at the subspecific level, while several less well defined entities are given varietal rank. The conclusions are based, in part, on the examination of over 7,000 herbarium specimens from about 40 herbaria. Experimental, cytological, phytogeographical, and statistical data in support of this interpretation will be presented in the sequel to this paper.

ACKNOWLEDGMENTS

I am greatly indebted to W. W. Payne, now at the Cary Arboretum, Millbrook, New York, who directed my dissertation study, and to D. P. Rogers, who helped me with the nomenclature. Acknowledgment is due the curators of the following herbaria (identified by their acronyms) for loans of specimens and provision of study facilities: ALTA, ASC, AUA, BM, BRY, CAN, COLO, DAO, GA, GH, ILL, ILLS, IND, ISC, ISM, K, KSC, KY, MAINE, MICH, MISS, MO, MSC, NCU, NDA, ND-G, NEBC, NY, OKL, OS, OSU, PH, RM, TEX, UARK, UBC, UC, US, WIS, WS, and WVA. Several people kindly provided photographs and living material: L. C. Anderson, G. K. Arp, W. T. Barker, B. Boivin, K. L. Chambers, M. G. Dumais, R. A. Evers, G. J. Goodman, R. W. Pohl, C. S. Sheviak, and P. Shildneck. Financial support was received through a dissertation research grant from the National Science Foundation (GB-32016). This study is based, in large part, on my doctoral dissertation, deposited at the University of Illinois in Urbana-Champaign.

NOMENCLATURAL REVIEW

Nomenclatural problems connected with *Aster* sect. *Multiflori* are quite formidable. A list of 48 names and combinations has been compiled, and several names must be excluded altogether. The oldest names date back to Linnaeus (1753), Aiton (1789), Muhlenberg ex Willdenow (1804), Persoon (1807), Lindley (in Hooker, 1834, and in DeCandolle, 1836), and to Torrey and Gray (1841).

Aster ericoides Linnaeus is the oldest name for a species in sect. *Multiflori.* Linnaeus (1753) based the description of this species not on a specimen but on three references, the first from Gronovius (1739), the second from Royen (1740), and the third from Dillenius (1732). The specimen underlying the Gronovius citation is *John Clayton 194* (BM!); it has been marked "type," but I do not know by whom. Royen merely referred to Dillenius' diagnosis and illustration. The Dillenius reference provides the name-bringing citation and a drawing based on a plant cultivated by James Sherard.

Great confusion was caused when, sometime after 1755, a specimen from the Uppsala Botanic Garden was included in the Linnaean herbarium. It was labeled *Aster ericoides* but was, in reality, a plant of the taxon we now call *A. pilosus* Willdenow. Solander (in Aiton's *Hortus Kewensis,* 1789) used this specimen for the diagnosis of *A. ericoides.* The Dillenius (1732) reference under *A. ericoides* L. in *Species Plantarum* and a specimen from a cultivated plant, designated as type and annotated: "Sol. in Hort. Kew. iii: 203" (BM!), were used to define *A. multiflorus* Aiton. Later authors followed the interpretation given in *Hortus Kewensis,* but in the citation of range, the confusion was quite apparent. Hooker (1834), for example, cited Drummond's collection from "Saskatchawan and toward the Rocky Mountains" and Douglas' "Red River" [Canada] collection for *A. ericoides* sensu Aiton, which cannot possibly apply as *A. pilosus* does not extend that far west. Nees (1833) cited Pursh's collection *"a Canada ad Carolinam usque"* for *A. multiflorus* Aiton, which can apply only in part because this species, except for one doubtful record, does not occur in the Carolinas. Persoon (1807) placed *A. multiflorus* as a variety under *A. ericoides* sensu Aiton, which possibly accounts for the conflicting geographic information. The locality for *Clayton 194,* i.e., the type for *A. ericoides* in the proper Linnaean sense, is "Virginia." Only one authentic herbarium collection from Virginia was found among those examined (*Allard 12196,* US), but geographic information for very early collections from North America is often not very precise. Lamarck (1783) used the epithet *ericoides* in the correct Linnaean sense, and Michaux (1803) and Schkuhr (1808) applied the name to plants that were only varietally separable from the Linnaean species.

The error in application of the epithet *ericoides* persisted in the

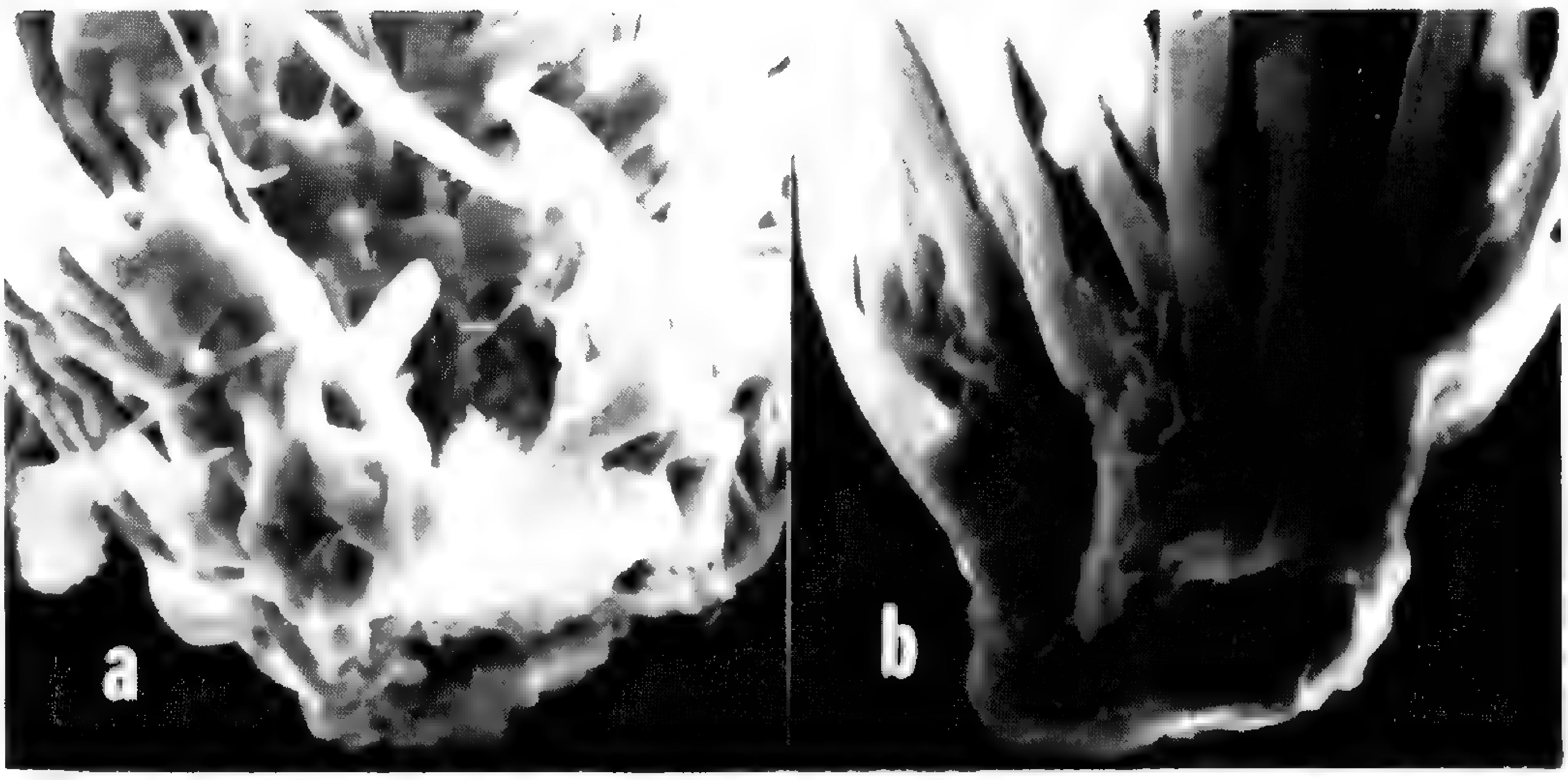

Figure 1. Scanning electron micrographs of achene bases. a, *Aster ericoides* ssp. *ericoides;* voucher *905* (ILL); b, *Aster falcatus* ssp. *commutatus; Raup 963* (DAO).

literature until Mackenzie (1926) clarified the nomenclatural situation. He pointed out that Gray (1882) recognized the misapplication but did not correct it. The story was summarized by Blake (1930) who stated that the correct name for *Aster ericoides* sensu Aiton is *A. pilosus* Willdenow. Ten varietal names of *A. ericoides* sensu authors belong in synonymy under *A. pilosus* and related taxa. As many of the older manuals are still extensively used, and many collectors are unaware of the nomenclatural confusion surrounding these taxa, herbaria abound with specimens for which the name *A. ericoides* was misapplied.

The name *Ericoidei* Nees (1833) cannot be used for the section of *Aster* that includes *A. ericoides* Linnaeus. Nees and all subsequent authors based this infra-generic epithet on *A. ericoides* sensu Aiton (1789) and on the misidentified specimen in the Linnaean herbarium, i.e., on a different "type." Torrey and Gray (1841) included *A. multiflorus* Aiton and *A. falcatus* Lindley in *Ericoidei,* but A. Gray (1884) segregated these species from that section and placed them, for the first time, in their proper conspectus under sect. *Multiflori.*

In *Flora of North America,* Torrey and Gray (1841) recognized under *Aster multiflorus* the varieties *β stricticaulis* and *γ commutatus.* The type for *β stricticaulis* is a Drummond collection from "Saskatchawan and toward the Rocky Mountains" (K!). There is a second Drummond collection on the type sheet of *A. ramulosus* Lindley (K!), which was marked by Asa Gray as var. "*β*" and probably is a syntype of var. *stricticaulis* but, erroneously, was cited by Torrey and Gray under var. γ *commutatus*. The type citation for the epithet *commutatus* [= *A. falcatus* ssp. *commutatus* in this interpretation] is "Upper Missouri [River] *Dr. James* (NY!). One of the Richardson collections (Ft. Franklin) mounted on the type sheet for *A. ramulosus* was marked "γ" by Asa Gray and cited for var. *commutatus* in *Flora of North America*.

In *Synoptical Flora of North America*, A. Gray (1884) elevated var. *commutatus* to the rank of species. Under *Aster multiflorus*, he cited as synonyms *A. scoparius* [sensu] DeCandolle (1836) [not *A. scoparius* Nees (1818)], and *A. hebecladus* DeCandolle. These two taxa were recognized as good species by Torrey and Gray and based on Berlandier collections from Texas. Examination of isotypes and microfiche photographs of the types from the DeCandolle herbarium proved Gray's interpretation correct; the plants are *A. ericoides* Linnaeus. Type material of *A. scoparius* appears to have somewhat larger heads than typical *A. ericoides*. This was noted by Rydberg (1906a) when he reinstated the species under the name *A. polycephalus*.

There has been little doubt about the name *Aster falcatus* Lindley. The type citation, as given in Hooker's (1834) *Flora Boreali-americana*, is "Arctic America, *Dr. Richardson*." The type specimen (K!) and two of the five different plants on the type sheet of *A. ramulosus* Lindley, also collected by Dr. Richardson, are identical. Date and place of original publication are the same for both names. *Aster ramulosus* was placed in synonymy under *A. falcatus* by Torrey and Gray (1841).

The name *Aster ciliatus* Muhlenberg ex Willdenow (1804) also created nomenclatural confusion. As it is a later homonym of *A. ciliatus* Walter (1788), the epithet is unavailable. The Muhlenberg collection is a plant of *A. ericoides* with spreading stem pubescence. Fernald (1899) placed the name *ciliatus* in synonymy under his *A. multiflorus* var. *exiguus*, which represents a slender-stemmed plant with few heads, and was subsequently reduced to forma status by the author himself (1949). It was on the basis of the Muhlenberg specimen, however, that Rydberg (1901) chose the name *exiguus* to recognize, at the rank of species, plants allied to *A. multiflorus* but with hirsute stem pubescence. Rydberg's choice created a nomen ambiguum, but the name was introduced, with his interpretation, into several floristic works, some of which are still widely used.

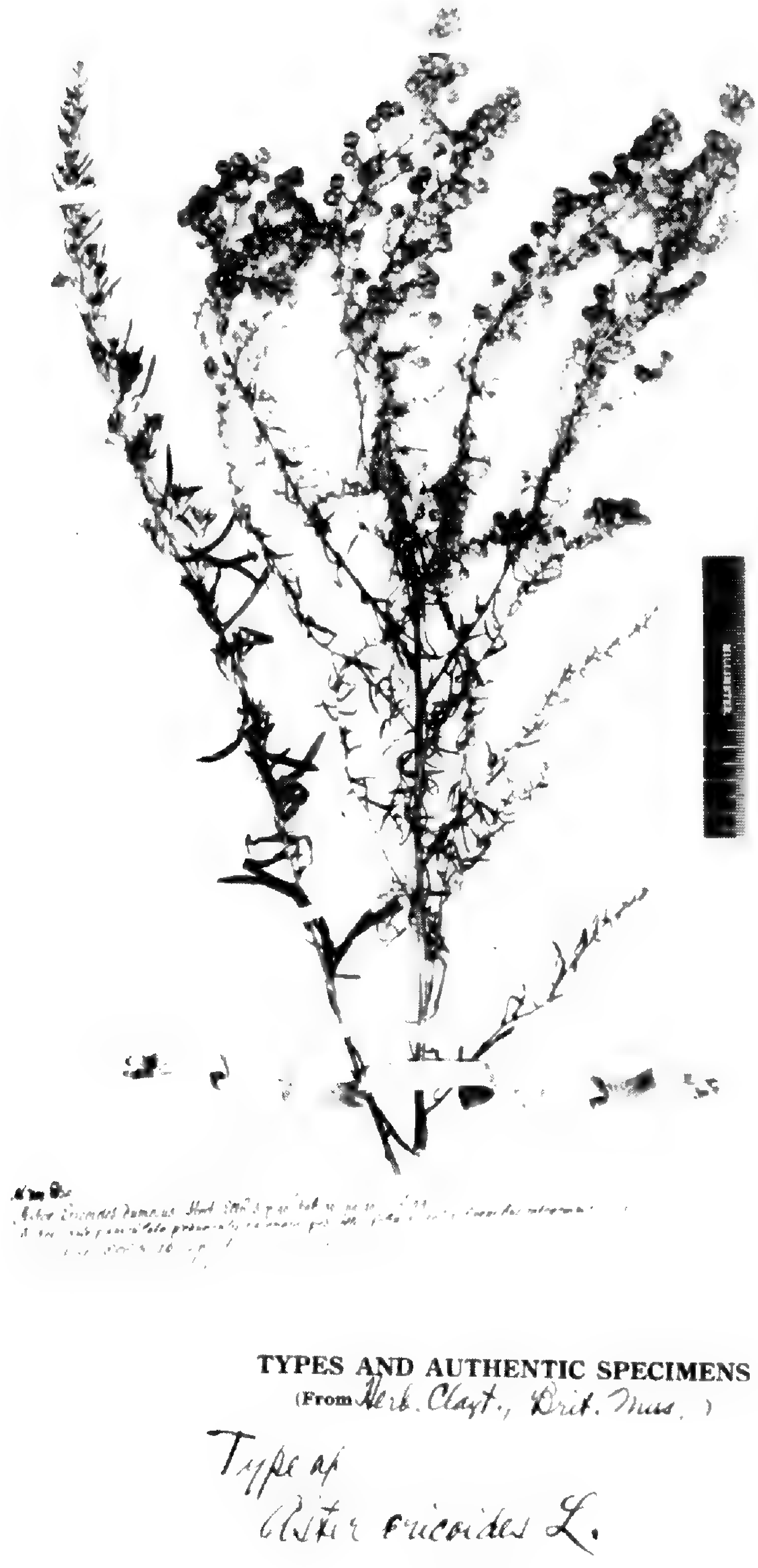

Figure 2. Type of *Aster ericoides* L.; *Clayton 194* (BM). (Photograph courtesy of B. Boivin).

Since the species cannot be upheld taxonomically, the nomenclatural problem will resolve itself. The earliest name available for the variety of *A. ericoides* ssp. *ericoides* with spreading stem pubescence is *A. multiflorus β prostratus* Kuntze (1891).

The epithet *pansus* was coined by Blake (1928) to replace the untenable epithet *exiguus* sensu Rydberg. At the time, Blake felt that Kuntze's varietal epithet *prostratus* also did not apply to plants with spreading stem pubescence, since Kuntze did not interpret his variety in that particular sense. As the type for *Aster multiflorus* var. *pansus,* Blake designated a collection from Washington: *Whited 853* (US!). When the article by Mackenzie (1926) on the status of *A. ericoides* had come to his attention, Blake placed var. *pansus* in synonymy under *A. ericoides* var. *prostratus.* Cronquist (1950) noted the distinctness in habit of the small-headed western populations of sect. *Multiflori,* and he elevated var. *pansus* to specific rank. In this interpretation, these populations are recognized as *A. ericoides* ssp. *pansus.*

Rydberg elevated all the morphological entities he could recognize to the rank of species, and in his *Flora of the Rocky Mountains* (1917), he placed seven species in sect. *Multiflori.* Six of these are based on previously named taxa; the seventh is *Aster crassulus* Rydberg, described in 1901 as a plant with stoloniferous rootstock, erect or ascending stems, and densely hirsute indument. In this interpretation, this taxon is reduced to varietal rank under *A. falcatus* ssp. *commutatus.*

Basionyms in sect. *Multiflori* not discussed so far include: *Aster cordineri* A. Nelson (1905), a plant with exceptionally large heads, to be placed in synonymy under *A. falcatus* ssp. *commutatus; A. elegantulus* Porsild (1950), the type (CAN!) of which is a perfect match to that of typical *A. falcatus;* and *Aster incanopilosus* (Lindley in Hooker) Sheldon (1893), which is a nomen nudum based on *A. ramulosus β incanopilosus.* According to Rydberg (1901), the term *"incanopilosus"* was used by Lindley in a descriptive sense, not as a varietal epithet. The name belongs, at least in the sense of Sheldon's authentic collections [Battle Lake, Otter Tail County, Minnesota, Aug. 1892 (WS, UC, RM)] in synonymy under *A. falcatus* ssp. *commutatus.*

Aster Section **Multiflori** A. Gray, Synopt. Fl. N. Am. **1**(2): 185. 1884.

Aster [subseries] *Densiflori* Nees von Esenbeck, Gen. et Sp. Ast., 110. 1833. – In part. — DeCandolle (1836) 242, as section, in part.
Aster sect. *Leucanthi* sensu DeCandolle, Prodromus **5:** 239. 1936. — In part, not Nees von Esenbeck (1833).
Aster sect. *Ericoidei* Torrey & Gray, Fl. N. Am. **2:** 123. 1841. — In part, not Nees von Esenbeck (1833), nor A. Gray (1884).
Aster sect. *Multiflori* A. Gray, Synopt. Fl. N. Am. **1**(2): 185. 1884. — Rydberg (1917) 880, in part, (1932) 804; R. A. Nelson (1933) **35:** 323–327.
Aster sect. *Squarrosa* Sheldon, Bull. Torrey Bot. Club **20:** 286. 1893.
Aster subsect. *Dumosi* House, Annot. List Pl. N. Y. 706. 1924. — In part.

Diagnostic Characteristics of the Section. Rhizomatous perennial herbs of variable habit. Stem pubescence uniformly distributed, not in lines, often scabrous, or glabrescent toward the base. Rosette leaves linear to somewhat spatulate, 2–6(–8) cm long, usually not more than 1 cm wide, with an entire, ciliolate margin, a mucronate apex, and a somewhat sheathing base. Cauline leaves in 3–4 size classes, linear to linear-lanceolate, sessile, entire, except for the ciliolate and often scabrous margin, the apex acute or obtuse, always armed with a slender bristle, the base often clasping or dilated; midrib prominent but lateral veins obscure or lacking; rameal leaves much reduced in size. Leaf pubescence uniform on both surfaces, usually more copious on cauline than on basal leaves. Inflorescence variable, depending on the species, but usually paniculate, never corymbiform. Heads radiate. Phyllaries in 3–4 series which may be subequal in height, or more commonly are imbricated; outer phyllaries linear or somewhat spatulate, with a ciliolate or fimbriolate margin and an obtuse or acute, mucronate apex, at least somewhat squarrose, pubescent on the outside and often also on the inside; inner phyllaries linear to linear-lanceolate, acute to attenuate, with an erose upper margin, somewhat pubescent or glabrous. Head size variable, depending on the species, ranging from 1–2 cm in diameter and from 20–60 florets per head. Ligules white, or occasionally slightly lavender. Disk florets yellow when young, turning purple after anthesis; corolla-tubes widening gradually, not distinctly differentiated into tube and limb portions. Pappus of white or somewhat discolored but never tawny capillary bristles, about as long as the disk corolla. Mature achenes purple or chocolate brown, 1.2–2.5 mm long, plump, strigillose, with 7 ribs.

Pollen grains with a spinulose exine. TYPE SPECIES: *Aster ericoides* Linnaeus. Sp. Pl. **2:** 875. 1753.

ANALYTICAL KEY

1. Heads small, the involucre 2.5–4.5 mm high; phyllaries strongly imbricated and graduated, the outer 2–3(–3.5) mm long; ligules 10–18(–20), typically less than 6.5 mm long; inflorescence compound-racemiform, the numerous crowded heads usually secund on arching branches. . . . . 2.
    2. Habit colonial, the plants with erect stems; rhizome system stoloniferous, typically lacking cormoid portions; rosette shoots formed mostly some distance removed from old stems; involucre in fresh material cylindrical-campanulate. . . . . 1a. *Aster ericoides* ssp. *ericoides.*
        i. Stem pubescence sparse, strigose or ascending. . . . . var. *ericoides.*
        ii. Stem pubescence copious, divaricate-hirsute. . . . . var. *prostratus.*
    2. Habit cespitose, the plants forming clusters of erect or ascending stems; rhizomes cormoid, not strongly stoloniferous; rosette shoots mostly ascending from or near the base of old stems; involucre in fresh material broadly campanulate. . . . . 1b. *Aster ericoides* ssp. *pansus.*
        i. Plants forming many-stemmed clumps, the stems erect, sturdy, typically with copious spreading indument. . . . . var. *pansus.*
        ii. Plants forming few-stemmed clusters, the stems decumbent or ascending, slender; indument typically sparse and appressed-strigose. . . . . var. *stricticaulis.*
1. Heads larger, the involucres 5–8 mm high; outer phyllaries (3–)4–7 mm long; ligules 22–35, 7 mm long or longer; inflorescence variable, but heads typically not secund. . . . . 3.
    3. Habit cespitose, the plants forming few-stemmed clusters; rhizomes cormoid; rosette shoots and buds arising nearly vertically at or near the base of old stems; inflorescence with heads terminally disposed on long, slender, few-bracted peduncles; phyllaries not strongly squarrose, subequal in length, or the outer ones longest, largely herbaceous; plants sparsely pubescent, mostly appressed-strigose. . . . . 2a. *Aster falcatus* ssp. *falcatus.*
    3. Habit scattered colonial, or plants forming sod-like patches; rhizomes tangled, strongly stoloniferous; rosette shoots formed some distance removed from the old stems; peduncles stout, often relatively short and with many bracts; phyllaries strongly squarrose, at least somewhat imbricated, with a conspicuous indurate basal portion; plants usually copiously pubescent. . . . . 2b. *Aster falcatus* ssp. *commutatus.*
        i. Stems decumbent or ascending, usually branched from near the base; inflorescence diffuse-paniculate, or sometimes a simple raceme; heads rarely secund, usually with 40–50(–60) florets. . . . . var. *commutatus.*
        ii. Stems erect, usually divaricately branched near the middle; inflorescence compound-racemiform; heads often somewhat secund, with 35–40(–45) florets. . . . . var. *crassulus.*

SYNONYMY AND DESCRIPTION OF TAXA

1. **Aster ericoides** Linnaeus, Sp. Pl. **2:** 875. 1753. TYPE: "Virginia," *John Clayton 194* (BM!). Figure 2.

Lamarck (1783) **1:** 304; Michaux (1803) **2:** 113; Schkuhr (1808) 105, *pl. 245;* Poiret (1823) 492; Hooker (1834) **2:** 12 [exclusive of description and synonyms; applicable only to the collections cited]; Mackenzie (1926) 65; Blake (1930) 138; Rydberg (1932) 809; R. A. Nelson (1933) 325; Small (1933) 1389; Raup (1934) 204; Palmer & Steyermark (1935) 663; Raup (1935) 166, (1936) 320; Benke (1936) 121; Cory & Parks (1937) 101; Dole (1937) 257; Reeves & Bain (1947) 255; St. John (1937) 426; Deam (1940) 943; Gates (1940) 241, (1941) 238; Kittell (1941) 406; Tidestrom & Kittell (1941) 406; G. N. Jones (1945) 254; Norton & Brown (1945) 41; Tatnall (1946) 262; Breitung (1947) 97; Cronquist (1947) 144; Hanes & Hanes (1947) 250; Ogden, et al. (1948) 63; W. C. Stevens (1948) 403; Hodgdon & Friedlander (1949) 112; Rosendahl & Cronquist (1949) 511; Turner (1949) 25; Fernald (1950) 1432; G. N. Jones (1950) 276; O. A. Stevens (1950) 278; Cronquist in Gleason (1952) **3:** 464; Weber (1953) 181; Harrington (1954) 576; Evers (1955) 439; Jones & Fuller (1955) 468; St. John (1956) 426; Guldner (1960) 187; Massey (1961) 197; Weber (1961) 181; Boivin (1962) 66; Waterfall (1962) 214; Gleason & Cronquist (1963) 730; G. N. Jones (1963) 251; St. John (1963) 463; Steyermark (1963) 1518; Lakela (1965) 364; Rickett (1966) **1**(2): 578, *pl. 157;* Boivin (1967) 1032; Cormack (1967) 355; Barkley (1968) 341; Porsild & Cody (1968) 96; Seymour (1969) 353; Correll & Johnston (1970) 1597; Klein (1970) *f. 720;* Van Faasen (1971) 100; Waterfall (1972) 214; Weber (1972) 121; Jones & Bell (1974) 22; Swink (1974) 47; Mohlenbrock (1975) 429. — not sensu Aiton (1789).

Characters of the Species. Plants up to one meter tall, the stems usually branched above the middle. Rosette leaves mostly 2–5 cm long; stem leaves reduced in size, the larger and medium ones withered and deciduous at flowering time; ultimate rameal leaves typically phyllary-like, squarrose, stiff, intergrading with the involucre. Inflorescence racemiform, many-flowered, with heads on densely bracteate short peduncles, or subsessile and crowded, mostly secund on arching or ascending branches. Heads 1 cm or less in diameter; receptacle conspicuously alveolate; involucre 2.5–4.5(–5) mm high, strongly imbricated, the outer phyllaries squarrose, firm, 1.2–2.5(–3) mm long, with a spatulate herbaceous portion covering about 60% of the area, the basal portion chartaceous and indurate; inner phyllaries longer and narrower, and more flexible. Ligules 10–18(–20), about 4–6.5 mm long, including the corolla-tube; disk florets 6–12(–20), the corolla about 2.5–4 mm long. Pappus of 30–40 bristles. Achenes purple, or brown when weathered, 1.2–1.8 (–2.0) mm long, and about 0.4–0.5 mm in diameter, lacking a conspicuous callus base (Figure 1a).

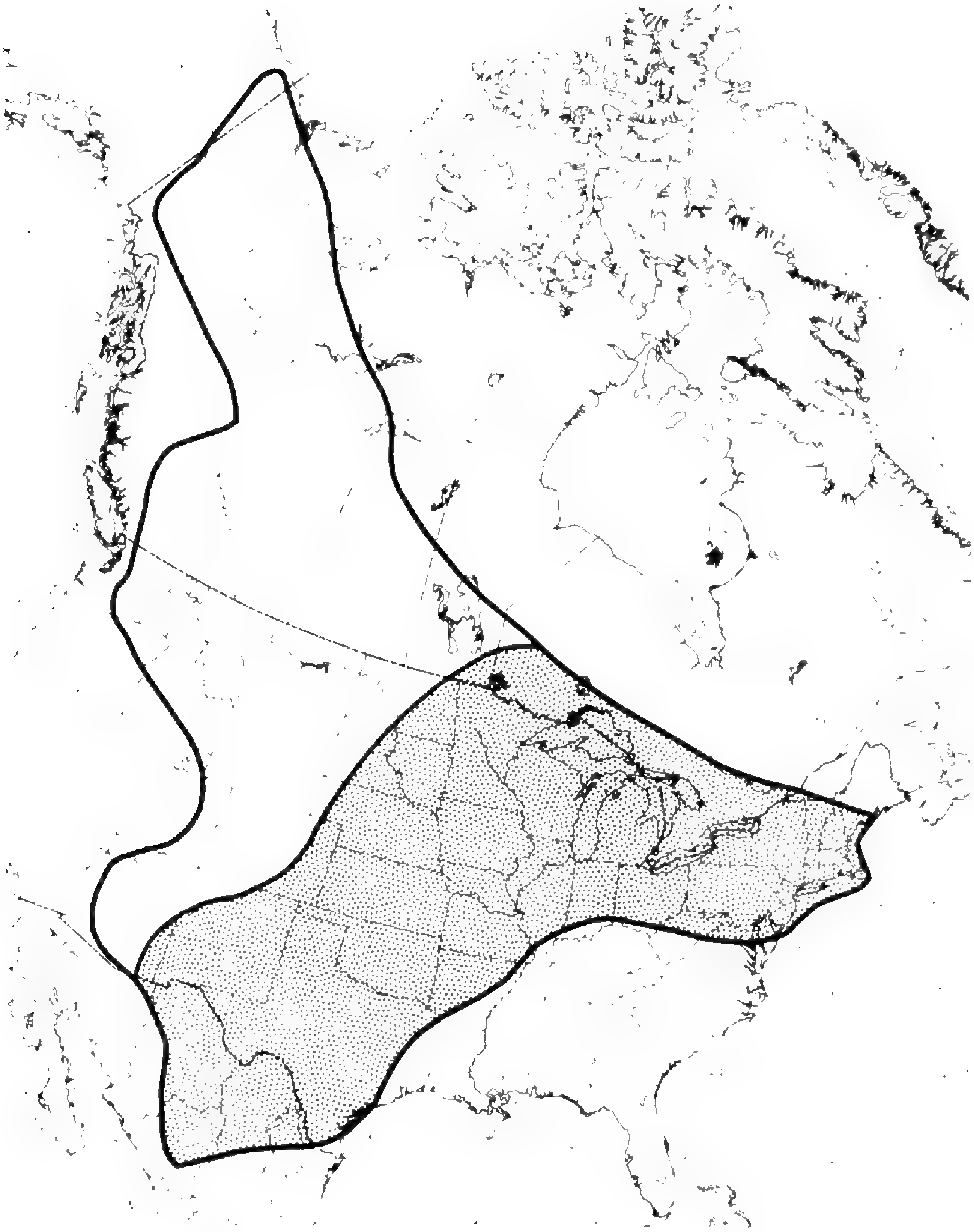

Figure 3. Range of *Aster ericoides* ssp. *ericoides*.

1a. **Aster ericoides** Linnaeus ssp. **ericoides**

Aster multiflorus Aiton, Hort. Kew., Ed. 1, **3:** 203. 1789. - [Based on Dillenius (1732) cited by Linnaeus (1753) as one of the references for *A. ericoides*]. - Willdenow (1804) 2027; Muhlenberg (1813) 74; Pursh (1814) **2:** 546; Hornemann (1815) **2:** 813; Nuttall (1818) **2:** 155; Barton (1818) 117; Nees von Esenbeck (1818) 31; Link (1822) **2:** 331; Sprengel (1826) 531; Link (1829) **1:** 740; Nees von Esenbeck (1833) 116; Hooker (1834) **2:** 13; DeCandolle (1836) **5:** 243; Torrey & Gray (1841) 124; Torrey (1843) 341; Gray (1848) 201, (1850) 90; Chapman (1860) 202; Darby (1860) 3641; Lesquereux (1861) 367; Porter & Coulter (1874) 56; Gray (1882) 165; Watson (1883) 103; Gray (1884) **1**(2): 185; Macoun (1884) 223; J. M. Coulter (1885) 161, in part; Brendel (1887) 50; Britton (1889) 138; Gray (1889) 260; Watson & Coulter (1890) 260; Kuntze (1891) **1:** 313; J. M. Coulter (1892) 195; MacMillan (1892) 520; Porter (1894) 325; Rydberg (1895) 163; Britton & Brown (1898) **3:** 381; Porter (1898) 493; S. Coulter (1899) 976; Britton (1901) 964; Mohr (1901) 783; Porter & Small (1903) 326; Rydberg (1906b) 355, in part; Robinson & Fernald (1908) 811; G. T. Stevens (1910) 666; Petersen (1912) 176; Small (1913) 1224; Monroe (1913) 99; Brainerd (1915) 251; Hegi (1915) **6**(1): 420; Wooton & Standley (1915) 685; Rydberg (1917) 885; Lowe (1921) 278; Rydberg (1922) 885; Britton & Brown (1923) **3:** 427; House (1924) 707; Pepoon (1927) 501; Schaffner (1928) 535; Pammel & King (1930) 3851; Peattie (1930a) 376, (1930b) 141; Harned (1931) 554; Benner (1932) 293; Over (1932) 139; Zenkert (1934) 256; Stemen & Myers (1937) 563; Madison (1938) 150, *f. 734;* Harper (1944) 225; Taylor (1955) 520; Voss & Eifert (1967) 235. - *Aster ericoides* L. * *multiflorus* (Ait.) Persoon, Synops. Sp. Pl. **2:** 443. 1807. TYPE: cult. "Sol. Hort. Kew. iii: 203" (BM!); photograph of type, ILL.

Aster ciliatus sensu Muhlenberg ex Willdenow, Sp. Pl. **3:** 2027. 1804. - Persoon (1807) **2:** 443; Pursh (1814) **2:** 546; Nees von Esenbeck (1818) 30; Poiret (1823) **1:** 492. — *Aster multiflorus* Ait. [var.] *ciliatus* (Muhl. ex. Willd.) Barton, Compend. Fl. Philad. **2:** 117. 1818. -Nees von Esenbeck (1833) 117. — Not *A. ciliatus* Walter (1788). TYPE CITATION: "*Muhlenberg in litt. Habitat in America boreali.*"

[A specimen, presumably from Muhlenberg's type, sent to Asa Gray by Nees von Esenbeck (GH!) was annotated by Fernald: "*A. multiflorus* Ait., var. *exiguus* Fernald, n. var.", and the name *A. ciliatus* was placed in synonymy under Fernald's (1899) var. *exiguus*. Rydberg's (1901) choice of the name *exiguus* for plants with divaricate pubescence was based on this specimen, not on Fernald's type].

Aster hebecladus DeCandolle, Prodromus **5:** 242. 1836. — Torrey & Gray (1841) 146; Coulter & Nelson (1909) 515, in part; Wooton & Standley (1915) 685; Cory & Parks (1937) 101. TYPE: "In Mexicanae prov. Texas". *Berlandier 2085* (Holotype, G; Isotype, GH!) — Jones (1973) *pl. 3a.*

Aster scoparius sensu DeCandolle, Prodromus **5:** 242. 1836. — Torrey & Gray (1841) 146. — Not Nees von Esenbeck (1818, 1833). TYPES: "Comancheros orientalis, Texas". *Berlandier 1868, 1871, 1894* (Lectotype designated herein = *Berlandier 1871,* G; Isolectotypes, GH!, MO!, WIS!) — Jones (1973) *pl. 3c.*

Figure 4. Holotype of *Aster multiflorus* Ait. var. *pansus* Blake (= *A. ericoides* ssp. *pansus*); *Whited 853* (US).

Aster multiflorus Aiton *α normalis* Kuntze, Rev. Gen. Pl. **1:** 313. 1891.

Aster multiflorus Aiton *β prostratus* Kuntze, Rev. Gen. Pl. **1:** 313. 1891. [This is the basionym of *A. ericoides* L. ssp. *ericoides* var. *prostratus* (Kuntze) Blake.] — *Aster ericoides* L. var. *prostratus* (Kuntze) Blake, Rhodora **32:** 138. 1930. Palmer & Steyermark (1935) 663; Gates (1940) 241; Hanes & Hanes (1947) 250; Fernald (1950) 1432; Cronquist in Gleason (1952) **3:** 464; Gleason & Cronquist (1963) 730; Mohlenbrock (1975) 429. — *Aster ericoides* L. f. *prostratus* (Kuntze) Fernald, Rhodora **51:** 96. 1949. — Steyermark (1963) 1518. TYPE: Nebraska, *O. Kuntze*, Sept. 1874 (Holotype, NY!) — Jones (1973) *pl. 4b.*

Aster multiflorus Aiton var. *exiguus* Fernald, Rhodora **1:** 187. 1899. Robinson & Fernald (1908) 811; House (1924) 707. — *Aster ericoides* L. f. *exiguus* (Fernald) Fernald, Rhodora **51:** 96. 1949. — Fernald (1950) 1433. — Not *A. exiguus* Rydberg (1901). TYPE: Dedham, Massachusetts, *C. E. Faxon* (Holotype, GH!) — Jones (1973) *pl. 5e.* [The name was applied to specimens of delicate and slender habit].

Aster exiguus Rydberg, Bull. Torrey Bot. Club **28:** 505. 1901. — In part. — [Based on *A. multiflorus* Ait. var. *exiguus* Fernald only as to name-bringing synonym, not as to type]. — Britton (1901) 964; Mackenzie & Bush (1902) 196; Rydberg (1906b) 355, in part; Daniels (1911) 233; Petersen (1912) 177; Small (1913) 1224; Rydberg (1917) 884, in part, (1922) 884, in part, (1932) 808; Deam (1940) 943; G. N. Jones (1945) 254; Reeves & Bain (1947) 255; G. N. Jones (1950) 275; Jones & Fuller (1955) 468; Mohlenbrock & Voigt (1959) 346; Guldner (1960) 187; G. N. Jones (1963) 251. [This epithet belongs in synonymy under *A. ericoides* L. ssp. *ericoides* var. *prostratus* (Kuntze) Blake].

Aster polycephalus Rydberg, Bull. Torrey Bot. Club **33:** 153. 1906. [This name is based on the type of *A. scoparius* sensu DeCandolle (1836), which is a later homonym of *A. scoparius* Nees (1818). As to the interpretation of authors, including Rydberg, the name belongs in synonymy under *A. falcatus* ssp. *commutatus*].

Aster multiflorus Aiton var. *caeruleus* Benke, Rhodora **30:** 78. 1928. — *Aster ericoides* L. f. *caeruleus* (Benke) Blake, Rhodora **32:** 139. 1930. — Fernald (1950) 1433; Steyermark (1963) 1518. TYPE: Illinois [near Bushnell], *H. C. Benke 4373* (Holotype, FM).

[This is a form with blue or purplish rays, possibly the result of introgressive hybridization].

Aster Batesii Rydberg, Brittonia **1:** 102. 1931. — *Aster ericoides* L [var.] *Batesii* (Rydb.) Gates, Trans. Kansas Acad. Sci. **42:** 138. 1939. — Gates (1940) 241. at least in part. TYPE: Nebraska, St. Paul, *J. M. Bates 5440* (Holotype, NY!).

[This is a slightly glandular form with lavender rays, possibly the result of introgressive hybridization].

Aster ericoides Linnaeus f. *gramsii* Benke, Am. Midl. Nat. **13:** 326. 1932 — Fernald (1950) 1433; Guldner (1960) 187. TYPE: Illinois. Cook County, Schiller Park, *H. C. Benke 4948* (Holotype, FM).

[A form with rose-red ligules, possibly the result of introgressive hybridization].

Illustrations in Literature: Dillenius (1732) *t. 36, f. 40;* Schkuhr (1808) *pl. 245;* Bois (1896) *t. 136* [as *multiflorus*]; Robinson & Fernald (1908) *f. 952* [as *multiflorus*]; G. T. Stevens (1910) 666, *pl. 183* [as *multiflorus*]; Hegi (1915) **VI**(1):420 [as *multiflorus*]; Britton & Brown (1923) 3: *f. 4337* [as *multiflorus*]; Pammel & King (1930) *f. 384, 385* [as *multiflorus*]; Madison (1938) *f. 734* [as *multiflorus*]; Gates (1941) *f. 346;* W. C. Stevens (1948) *f. 702* [not *f. 701,* which may be *A. simplex*]; Fernald (1950) *f. 1660;* O. A. Stevens (1950) *f. 305;* Gleason (1952) **3:** 465; Steyermark (1963) *pl. 360, f. 5;* Rickett (1966) **1**(2): *pl. 157;* Klein (1970) *f. 720.*

Distinctive Characteristics of the Subspecies. Plants colonial, the stems erect, 50–100 cm tall, typically only one emerging at any point, rhizome system horizontal, lacking distinct cormoid portions, strongly stoloniferous; winter rosettes produced at tips of elongate stolons some distance removed from the old stems; only the ultimate rameal leaves persisting at flowering time, these linear, not dilated at the base, and not strongly clasping. Involucre mostly short-cylindric (turbinate in dry specimens); disk florets usually less than 12, up to 14 in populations of the southern or western part of the range.

Two varieties are recognized, mainly on the basis of pubescence characteristics, var. *ericoides* with indument relatively sparse, appressed to ascending, var. *prostratus* (Kuntze) Blake (1930) with copious spreading, often scabrous pubescence. Heads and number of florets average somewhat smaller in var. *prostratus* than in var. *ericoides* (Jones, 1974).

FLOWERING PERIOD. Late August to October (to November in the South).

HABITAT. Dry ground, roadsides, railroad sidings, prairies, open ranges, grassy hillsides, glades, and dunes.

RANGE. Southern Maine, northern Virginia, Ohio, Illinois, Arkansas, Oklahoma, Texas, northern Mexico, Arizona, eastern Colorado, Nebraska, eastern Dakotas, southeastern Manitoba, southern Ontario, and perhaps southwestern Quebec (Figure 3).

REPRESENTATIVE SPECIMENS. **Arizona:** GILA CO., Payson, *R. E. Collom 183* (GH, MICH, MO, NY). **Arkansas:** WASHINGTON CO., Fayetteville, *F. L. Harvey 37* (ILL, MICH, MO, NY). **Colorado:** BACA CO., Pritchett, *C. M. Rogers 6422* (COLO, MICH, TEX, US). **Connecticut:** LITCHFIELD CO., South Canaan, *J. M. Greenman 41* (MO). **Illinois:**

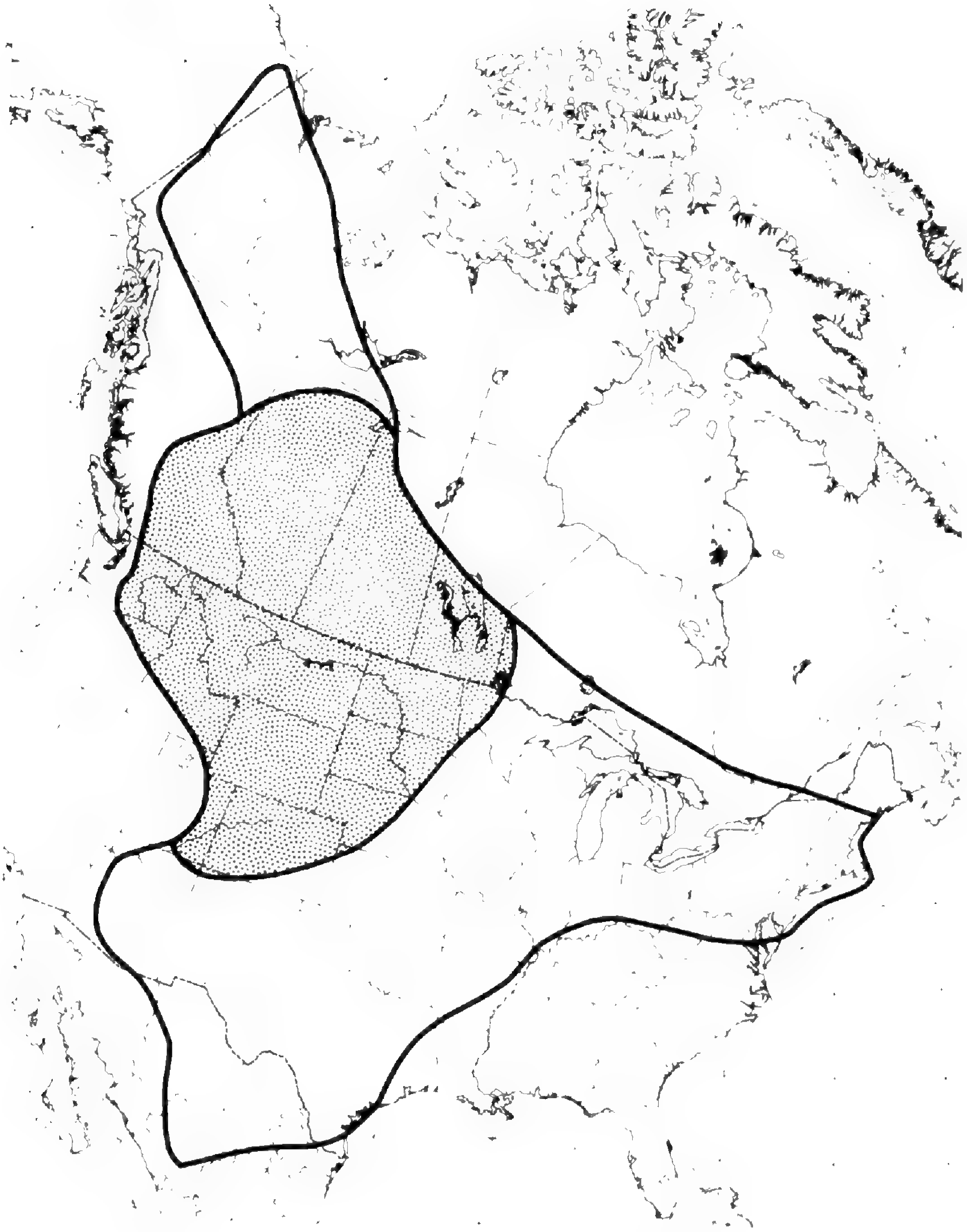

Figure 5. Range of *Aster ericoides* ssp. *pansus*.

CHAMPAIGN CO., Urbana, *G. N. Jones 16312* (ILL). **Indiana:** BENTON CO., Fowler, *C. C. Deam 32718* (IND). **Iowa:** ADAMS CO., Washington Twp., *M. J. Fay 5700* (TEX). **Kansas:** SALINE CO., Bavaria, *K. L. Johnson 1729* (NCU, NDA). **Maine:** LINCOLN CO., Monhegan, *N. C. Fassett 21558* (MO, WIS). **Massachusetts:** MIDDLESEX CO., Woburn, *A. R. Hodgdon & M. Hopkins, s.n.* (COLO, DAO, GA, GH, ILL, ISC, KY, MAINE, MO, MSC, NY, OSU, PH, RM, TEX, UBC, UC, US, WIS, WS). **Michigan:** WASHTENAW CO., Dixboro, *F. J. Herman 7348* (GH, MICH, MO, MSC, NY, PH). **Minnesota:** CLEARWATER CO., Squaw Lake, Itasca Park, *M. L. Grant 6776* (ISC, WIS). **Missouri:** PUTNAM CO., Livonia, *B. F. Bush 7747* (GH, ILL, MO, NDA, NY). **Nebraska:** RICHARDSON CO., Humboldt, *H. C. Reynolds 2607* (WIS). **New Hampshire:** STRAFFORD CO., Durham, *C. H. Knowlton, s.n.* (NCU, PH). **New Jersey:** CAPE MAY CO., Wildwood, *H. M. Moldenke 4030* (NY). **New Mexico:** GRANT CO., Silver City, *O. B. Metcalfe 781* (GH, ILL, MO, NY, RM). **New York:** ALBANY CO., Loudonville, *H. D. House 27073* (ILL, OKL). **North Dakota:** GRAND FORKS CO., Larimore, *P. Bates 676* (NDA, WIS). **Ohio:** ASHTABULA CO., West Jefferson, *E. C Leonard 2035* (US). **Oklahoma:** MAYES CO., Locust Grove, *J. G. Brown 13* (OKL, TEX). **Pennsylvania:** NORTHAMPTON CO., Easton, *T. C. Porter 16808* (MO). **Rhode Island:** PROVIDENCE CO., Diamond Hill, *E. J. Palmer 46580* (NEBC). **South Dakota:** SPINK CO., Redfield, *A. E. Ricksecker 140* (ILL). **Texas:** BEXAR CO., San Antonio, *F. Lindheimer 876* (MO, NY, OKL, TEX, UC, US). **Virginia:** FAUQUIER CO., *H. A. Allard 12196* (TEX, US, WIS). **Wisconsin:** IOWA CO., Ridgeway, *H. H. Iltis 19395* (WIS). **Manitoba:** Winnipeg, *G. N. Jones 23566* (ILL). **Ontario:** YORK CO., Toronto, *H. H. Brown 1432* (DAO), *5035* (UBC). **Mexico:** Coahuila, Parras, *E. Palmer 439* (MO, UC, US).

1b. **Aster ericoides** Linnaeus ssp. **pansus** (Blake) A. G. Jones, stat. nov.

Aster multiflorus sensu authors. – J. M. Coulter (1885) 161; A. Nelson (1896) 127; Rydberg (1900) 393; Piper & Beattie (1901) 186; Piper (1906) 572; Rydberg (1906b) 355, in part; Coulter & Nelson (1909) 515; Piper & Beattie (1914) 270; Henry (1915) 293; Clements & Clements (1945) 259. — Not Aiton (1789).

Aster multiflorus β stricticaulis Torrey and Gray, Fl. N. Am. 2: 125. 1841. - [This is the basionym for *A. ericoides* L. ssp. *pansus* (Blake) A. G. Jones var. *stricticaulis* (Torr. & Gray) Gates]. - Macoun (1884) 223; Rydberg (1895) 163. - *Aster stricticaulis* (Torr. & Gray) Rydberg, Fl. Rocky Mountains, p. 885. 1917. – Rydberg (1922) 885, (1932) 809. — *Aster ericoides* L. [var.] *stricticaulis* (Torr. & Gray) Gates, Trans. Kansas Acad. Sci. **42:** 138. 1939. Gates (1940) 241. TYPE: "Saskatchawan, and towards the Rocky Mountains". *Drummond* (Lectotype, designated herein, K!).

[The type material is mounted on two sheets, each consisting of several different collections: Jones (1973) *pl. 2c* = lectotype, *pl. 1c* = *Drummond 584* (syntype or isolectotype) on the type sheet of *A. ramulosus* (K!). The individual specimens have been annotated by Asa Gray].

Aster exiguus Rydberg, Bull. Torrey Bot. Club **28:** 505. 1901. – In part. – Rydberg (1906b) 355, (1917) 884, in part; Standley (1921) 424. – Not *A. multiflorus* Ait. var. *exiguus* Fernald (1899).

Figure 6. Holotype of *Aster falcatus* Lindl. in Hook.; *Dr. Richardson* (K). (Photograph courtesy of B. Boivin).

Aster multiflorus Aiton var. *pansus* Blake, Rhodora **30:** 227. 1928. – [This is the basionym of *A. ericoides* L. ssp. *pansus* (Blake) A. G. Jones]. – *Aster pansus* (Blake) Cronquist, Leaflets West. Bot. **6:** 45. 1950. – Cronquist in Davis, et al. (1952) 705; Breitung (1954) 89, 92; Cronquist in Hitchcock, et al. (1955) **5:** 91; Scoggan (1957) 526; Moss (1959) 457; Abrams & Ferris (1960) **4:** 322, *f. 5546;* Peck (1961) 781; Thieret (1961) 120; Hitchcock & Cronquist (1973) 492. – *Aster ericoides* L. var. *pansus* (Blake) Boivin, Nat. Canad. **89:** 70. 1962. TYPE: Washington, Kittitas County, Ellensburg, *K. Whited 853* [Holotype (Figure 4), US!; Isotypes OSU!, WS!].

Aster ericoides Linnaeus var. *commutatus* sensu Boivin, Nat. Canad. **89:** 67. 1962. – In part. – Boivin (1967) 1032, (1972) 32, in part. – Not *A. multiflorus* γ *commutatus* Torrey and Gray (1841).

Illustrations in Literature: Hitchcock, et. al. (1955) **5:** 96; Abrams & Ferris (1960) **4:** 323, *f. 5546.*

Distinctive Characteristics of the Subspecies. Plants forming distinct cespitose clusters or many-stemmed clumps, with several stems arising from a cormoid rhizome portion. Several clumps often interconnected by horizontal strands, but these produced only at times of little moisture stress in early spring. Winter rosettes formed at or near the base of old stems, not at the tips of elongate stolons; leaves of larger size often persistent at flowering time in addition to the numerous rameal leaves; smaller leaves usually somewhat dilated or clasping at the base. Involucre campanulate or turbinate; disk florets 10–20; achenes similar to those of the typical subspecies, but often somewhat paler purple.

Two varieties are recognized which appear to be well separated geographically. Variety *pansus* (Blake) Boivin (1962) is distinct by forming sturdy, many-stemmed clumps, the stems erect, up to 100 cm tall at maturity, mostly densely spreading pubescent; heads strongly secund. Variety *stricticaulis* (Torrey & Gray) Gates (1939) is more delicate and slender in every respect. Stems decumbent or ascending, the cormoid rhizome portions more widely spaced; stem pubescence mostly appressed-strigose; heads not strongly secund.

FLOWERING PERIOD. Mid-July to end of September, rarely into October.

HABITAT. Dry or well-drained sandy or gravelly soil, lake shores, salt flats, open ranges, hillsides, river banks and sandbars.

RANGE. Variety *pansus:* British Columbia, Washington, Oregon, and Idaho, with slight representation in adjacent regions east of the

Continental Divide; variety *stricticaulis:* Alberta, Saskatchewan, southern Manitoba, Dakotas, Nebraska, Kansas, Colorado, Utah, Wyoming, and Montana, with slight representation in adjacent regions (Figure 5).

REPRESENTATIVE SPECIMENS. **Colorado:** JEFFERSON CO., Arvada, *I. W. Clokey 3908* (GH, ILL, ISC, MICH, MO, RM, UC, US, WS). **Idaho:** LATAH CO., Moscow, *L. T. Henderson 2804* (GH, US). **Minnesota:** GRANT CO., Sanford Twp., *J. W. & M. F. Moore 10126* (ILL, ISC). **Montana:** JEFFERSON CO., Helena, *M. A. Carleton 224* (ILL, KSC). **Nebraska:** CUSTER CO., Arnold, *K. L. Johnson 2879* (NDA). **North Dakota:** STARK CO., Dickinson, *O. A. Stevens 1506* (NDA). **Oregon:** MORROW CO., Rhea Creek, *J. B. Leiberg 896* (MO, US). **South Dakota:** HARDING CO., Table Mountain, *S. S. Visher 342* (RM). **Utah:** SAN JUAN CO., Lost Canyon, *S. L. Welsh, G. Moore, & M. Olsen 3770* (BRY). **Washington:** ASOTIN CO., Asotin, *A. Cronquist & S. Preece 6816* (DAO, OSU, US, WS). **Wyoming:** FREMONT CO., Jeffrey City, *G. N. Jones 35187* (ILL). **Alberta:** ACADIA D., Craigmyle, *A. H. Brinkman 293* (DAO), *788* (ALTA, US). **British Columbia:** EAST KOOTENAY D., Windermere, *J. A. Calder & D. B. O. Savile 11180* (*DAO*). **Manitoba:** PORTAGE LA PRAIRIE D., Langruth, *A. & D. Löve 5662* (DAO). **Ontario:** RAINY RIVER D., 10 miles below Rainy River, *C. E. Garton 9424* (DAO, UC). **Saskatchewan:** LAKE CENTRE D., Watrous, *H. A. Senn 2947* (DAO).

2. **Aster falcatus** Lindley in Hooker, Fl. Bor.-Am. **2:** 12. 1834. TYPE: "Arctic America," *Dr. Richardson* (Holotype, K!, Isotype, GH!). Figure 6.

DeCandolle (1836) **5:** 241; Torrey & Gray (1841) 125; Porter & Coulter (1874) 56; Gray (1884) 185; Macoun (1884) 223; Rydberg (1896) 506, (1906b) 355; Henry (1915) 293; Rydberg (1917) 885, (1922) 885; R. A. Nelson (1933) 326; Raup (1936) 303; Cronquist (1947) 144; Rosendahl & Cronquist (1949) 511; Hultén (1950) 1492; Cronquist in Gleason (1952) **3:** 464; Cronquist in Davis, et al. (1952) 702; Weber (1953) 181; Harrington (1954) 576; Cronquist in Hitchcock, et al. (1955) **5:** 82; Scoggan (1957) 527; Moss (1959) 456; Cody (1960) 97; Weber (1961) 181; Gleason & Cronquist (1963) 730; Barkley (1968) 341; Porsild & Cody (1968) 96; Weber (1972) 121; Hitchcock & Cronquist (1973) 492.

Specific Characteristics. Habit of plants variable, the stems mostly branched below the middle. Rosette leaves 3–8 cm long; stem leaves in 3–4 size classes, mostly with somewhat clasping base, usually only the midrib strongly expressed, but sometimes lateral veins present in larger leaves. Inflorescence diffuse-paniculate or compound-racemiform, or sometimes a simple raceme. Heads not crowded, usually single or few at tips of branches, not secund, 1–1.5(–2) cm in diameter, the receptacle not as strongly alveolate as in *Aster ericoides.* Involucre 5–8 mm long; outer phyllaries 3–8 mm long, usually at least somewhat squarrose; inner phyllaries 4–7 mm long, more slender. Ligules 20–35, 7–10 mm long, including the corolla-tube; disk florets (16–)18–30, the corolla (3.5–)4–5.5 mm long. Pappus of 40–55 bristles. Achenes chocolate brown, or sometimes pale purple, 2–2.5 mm long, with a short callus base (Figure 1b).

2a. **Aster falcatus** Lindley in Hooker ssp. **falcatus**

Aster ramulosus Lindley in Hooker, Fl. Bor.-Am. **2:** 13. 1834. — DeCandolle (1836) **5:** 243; Nuttall (1841) 293; Macoun (1884) 223. Type: "Fort Franklin, and Cumberland House Fort", *Dr. Richardson* (K!); Jones (1973) *pl. 1c.*

[The type sheet consists of five different plants from three localities. Asa Gray annotated the specimens and determined that the Richardson collections are identical with *A. falcatus*].

Aster elegantulus Porsild, Canad. Field-Nat. **64:** 43. 1950. Type: Yukon Territory, Whitehorse, *A. E. Porsild & A. J. Breitung 10703* (Holotype, CAN!) — Jones (1973) *pl. 2a.*

Aster ericoides Linnaeus var. *commutatus* sensu Boivin, Nat. Canad. **89:** 67. 1962. — In part. — Boivin (1967) 1032, (1972) 32, in part. — Not *A. multiflorus* γ *commutatus* Torrey and Gray (1841).

Illustration in Literature: Gleason (1952) **3:** 465.

Distinctive Characteristics of the Subspecies. Plants in distinct cespitose clusters, with several stems arising from a cormoid rhizome portion; connecting horizontal strands formed mostly in spring. Winter rosettes arising at a steep angle from or near the base of old stems, often not emerging until spring. Stems usually ascending, not erect, typically with sparse appressed pubescence, or sometimes thinly hirsute. Cauline leaves of all sizes usually persistent at flowering time, the smaller leaves dilated and often clasping at the base; rameal leaves flexible, not phyllary-like. Inflorescence typically diffuse-paniculate, with heads single or few at ends of branchlets, usually on long, slender peduncles with few, distant, flexible bracts. Terminal heads conspicuously larger than lateral heads. Involucre hemispherical, or broadly turbinate when pressed, not strongly imbricated, and not strongly squarrose, the phyllaries subequal in length, or often the outer ones longer than the inner ones. Outer phyllaries thinly appressed pubescent to nearly glabrous, sparingly ciliolate, spatulate, largely herbaceous, the indurate base covering less than 30% of the area; disk florets typically more than 20, the total number of florets 40 or more per head.

Flowering Period. End of July to mid-September.

Habitat. In well-drained soil; river banks and slopes; edges of alkali lakes and flats; prairies and plains; in the southern part of the range in the montane zone up to 8,000 feet elevation, mostly in somewhat more mesic situations, as compared to the subspecies *commutatus*.

Range. Alaska, Yukon D., southwestern Mackenzie D., British Columbia, Utah, Arizona, New Mexico, Colorado, western Dakotas, western Manitoba, and Alberta. The plants are more commonly found in the northern than in the southern part of range (Figure 7).

Representative specimens. **Alaska:** Ft. Yukon, *O. S. Bates, 1888* (US). **Arizona:** COCONINO CO., Flagstaff, *G. A. Pearson 307* (US). **Colorado:** GUNNISON CO., Gunnison, *I. W. Clokey 2973, 2975* (ILL, RM, UC, US, WIS). **Montana:** GLACIER CO., Babb, *D. Lynch 6696* (WS). **New Mexico:** SIERRA CO., Kingston, *O. B. Metcalfe 1406* (MO, UC, US). **North Dakota:** BILLINGS CO., Medora, *N. Zaczkowski 1492, 4293, 6177* (NDA). **South Dakota:** PENNINGTON CO., Black Hills Nat. For., *A. S. & B. Tomb 576* (TEX). **Utah:** DAGGETT CO., Sheep Creek, south of Manila, *L. L. Welsh & G. Moore 6736* (BRY). **Wyoming:** ALBANY CO., Centennial, *A. Nelson 8792* (NY). **Alberta:** VEGREVILLE D., Fort Saskatchewan, *G. H. Turner 2747, 6492, 7395, 7421, 8623, & 8628* (ALTA), *2809* (DAO, ALTA, WIS). **British Columbia:** CARIBOO D., Chilcotin, *W. A. Newcombe 101* (UBC). **Manitoba:** CHURCHILL D., The Pas, *W. Krivda 2104* (COLO, DAO, WIS). **Northwest Territories:** MACKENZIE D., Fort Liard, *W. J. Cody & K. W. Spicer 11749* (UBC); YUKON D., Haines Junction, *J. A. Calder & I. Kukkonen 28250* (ALTA, COLO, UC, WS). **Saskatchewan:** MAPLE CREEK D., Cypress Hills, *A. J. Breitung 5673* (DAO, MO).

2b. **Aster falcatus** Lindley ssp. **commutatus** (Torrey & Gray) A. G. Jones, stat. & comb. nov.

Aster ramulosus β incanopilosus Lindley in Hooker, Fl. Bor.-Am. 2: 13. 1834. Nomen nudum. — DeCandolle (1836) **5:** 243. – *Aster incanopilosus* (Lindl.) Sheldon, Bull. Torrey Bot. Club **20:** 286. 1893. Porter (1894) 323; Britton & Brown (1893) **3:** 381, *f. 3803;* Rydberg (1900) 393. [Authentic specimens: Battle Lake, Otter Tail County, Minnesota, Aug. 1892, *E. P. Sheldon* (RM!, UC!, WS!)]. *Aster multiflorus* Ait. [var.] *incanopilosus* (Lindl.) Rydberg, Fl. Sand Hills, Nebraska. Contr. U.S. Nat. Herb. **3:** 163. 1895. – Nomen. – Rydberg (1896) 506.

Aster multiflorus Aiton γ *commutatus* Torrey and Gray, Fl. N. Am. 2: 125. 1841. [This is the basionym for *A. falcatus* Lindl. in Hook. ssp. *commutatus* (Torr. & Gray) A. G. Jones]. – Macoun (1884) 223. – *Aster commutatus* (Torr. & Gray) A. Gray, Synopt. Fl. N. Am. **1**(2): 185. 1884. – J. M. Coulter (1885) 161; Williams (1892) 192; A. Nelson (1896) 126; Howell (1897) 308; Britton (1901) 965; Henshaw (1906) 68, *pl. 21;* Rydberg (1906b) 355; Robinson & Fernald (1908) 811; Coulter & Nelson (1909) 515; Daniels (1911) 234; Pétersen (1912) 177; Henry

(1915) 293; Wooton & Standley (1915) 685; Rydberg (1917) 885, (1922) 885; Britton & Brown (1923) **3:** 427; Tidestrom (1925) 559; Rydberg (1932) 809; Ashton (1933) 122; R. A. Nelson (1933) 326; Palmer & Steyermark (1935) 664; Cory & Parks (1937) 101; Gates (1940) 241; Kittell (1941) 406; Shinners (1941) 416; Tidestrom & Kittell (1941) 406; Kearney & Peebles (1942) 918; Cronquist (1947) 144; Turner (1949) 25; Fernald (1950) 1433; O. A. Stevens (1950) 278; Kearney & Peebles (1951) 871; Harrington (1954) 576; Steyermark (1963) 1519, *pl. 360;* Barrell (1969) 94. — *Aster ericoides* L. var. *commutatus* (Torr. & Gray) Boivin, Nat. Canad. **89:** 67. 1962. — In part. — Boivin (1967) 1032, (1972) 32, in part. TYPE: "Upper Missouri". Long's Expedition, *Dr. James* (Holotype, NY!) — Jones (1973) *pl. 5c.*

Aster adsurgens sensu authors. — R. A. Nelson (1933) 325; Peck (1941) 724. — Not E. L. Greene (1900).

[The status of this species is the subject of a separate publication (Jones, 1975)].

Aster crassulus Rydberg, Bull. Torrey Bot. Club **28:** 504. 1901. — [This is the basionym for *A. falcatus* Lindl. in Hook. ssp. *commutatus* (Torr. & Gray) A. G. Jones var. *crassulus* (Rydb.) Cronquist]. — Rydberg (1906b) 355; Daniels (1911) 234; Wooton & Standley (1915) 685; Rydberg (1917) 884; Standley (1921) 424; Rydberg (1922) 884, (1932) 809. — *Aster commutatus* (Torr. & Gray) A. Gray, var. *crassulus* (Rydb.) Blake, in Tidestrom, Fl. Utah and Nevada. Contr. U. S. Nat. Herb. **25:** 560. 1925. — Blake (1940) 470; Kittell (1941) 406; Tidestrom & Kittell (1941) 407; Kearney & Peebles (1942) 918, (1951) 871; Shields (1951) 63; Harrington (1954) 576. — *Aster falcatus* Lindl. in Hook. var. *crassulus* (Rydb.) Cronquist, Bull. Torrey Bot. Club **74:** 144. 1947. — Cronquist in Gleason (1952) **3:** 464; Breitung (1954) 88, 92; Cronquist in Hitchcock, et al. (1955) **5:** 82; Moss (1959) 456; Abrams & Ferris (1960) **4:** 322, *f. 5545.* TYPE: Colorado, La Veta, *F. K. Vreeland 690a* [Holotype, NY! (Figure 8); Possible Isotype, RM!, misnumbered as *Vreeland 190a*].

Aster cordineri A. Nelson, Bot. Gaz. **40:** 64. 1905. — Coulter & Nelson (1909) 515. TYPE: Colorado, Estes Park, *W. S. Cooper 151* (Holotype, RM!) — Jones (1973) *pl. 5d.*

[This specimen has very large heads and traits, generally, somewhat intermediate between typical *A. falcatus* and ssp. *commutatus*].

Aster polycephalus Rydberg, Bull. Torrey Bot. Club **33:** 153. 1906. - In part, not including the type, which is that of *A. scoparius* DC. - Rydberg (1906b) 355; Daniels (1911) 234; Petersen (1912) 177; Rydberg (1917) 885; Standley (1921) 424; Rydberg (1922) 885, (1932) 809. - *Aster commutatus* (Torr. & Gray) A. Gray var. *polycephalus* (Rydb.) Blake, in Tidestrom, Fl. Utah and Nevada. Contr. U. S. Nat. Herb. **25:** 560. 1925. — Blake (1940) 470; Kittell (1941) 406; Tidestrom & Kittell (1941) 407; Kearney & Peebles (1942) 918, (1951) 871; Harrington (1954) 576. — *Aster ericoides* L. [var.] *polycephalus* (Rydb.) Gates, Trans. Kansas Acad. Sci. **42:** 138. 1939. — Gates (1940) 241.

Aster hebecladus sensu Coulter & Nelson, Man. C. Rocky Mts., p. 515. 1909. — In part. — Not DeCandolle (1836).

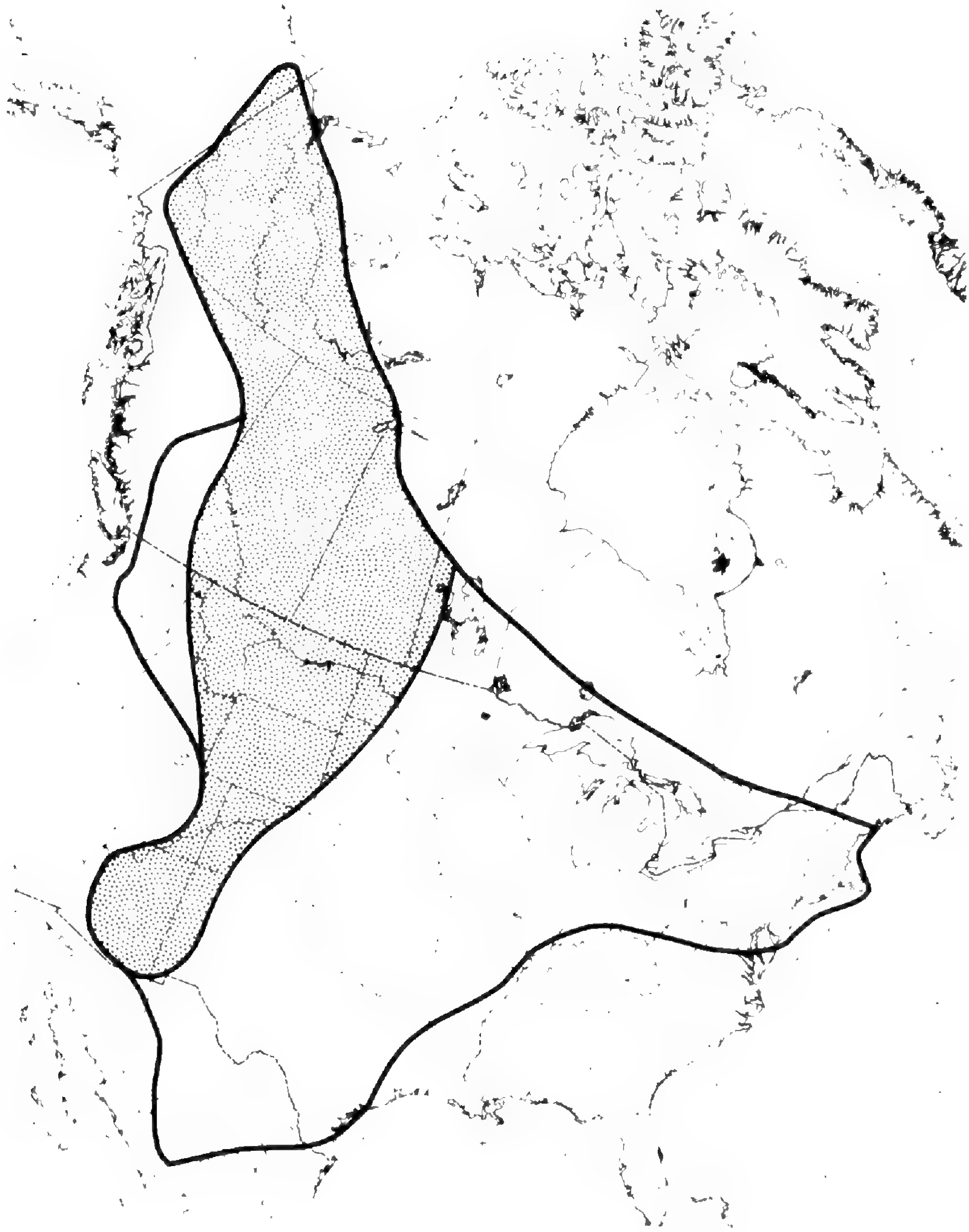

Figure 7. Range of *Aster falcatus* ssp. *falcatus*.

Illustrations in Literature: Britton & Brown (1898) **3:** *f. 3803* [as *incanopilosus*]; Henshaw (1906) 65. *pl. 21;* Britton & Brown (1923) **3:** *f.4338;* Hitchcock, et al. (1955) **5:** 85 [as *falcatus*]; Abrams & Ferris (1960) **4:** *f. 5545* [as var. *crassulus*]; Steyermark (1963) *pl. 360, f. 2.*

Distinctive Characteristics of the Subspecies. Plants forming sod-like patches or colonies, the stems typically single or few from each point of emergence, erect, or more commonly ascending; height of stems variable, depending on the variety, as well as the habitat; rhizomes creeping or densely tangled, horizontal, lacking distinct cormoid portions. Winter rosettes produced at the tips of elongate stolons, some distance removed from the old stems. Pubescence generally copious, appressed or spreading; leaves of all sizes often persistent at flowering time; rameal leaves usually not conspicuously dilated or clasping. Inflorescence diffuse-paniculate or compound-racemiform or, in pastured habitats, a simple raceme. Heads uniform in size; peduncles often densely bracteate and the bracts stiff, intergrading with the phyllaries; involucre hemispherical, typically strongly imbricated, the outer phyllaries shorter than the inner ones, copiously pubescent on the back, squarrose, obtuse or acute, the chartaceous indurate basal portion covering 35% or more of the area.

Two varieties are distinguished, mainly on characteristics of habit. Variety *commutatus* forms bushy or sprawling plants, about 20–60 cm high, with stems usually decumbent or ascending, branched near the base; inflorescence typically diffuse-paniculate, the heads mostly terminal, not secund, large, with more than 20 disk florets, the total number of florets 40–50(–60). Variety *crassulus* (Rydberg) Cronquist (1947) has stems erect, 60–100 cm tall, usually branched near the middle; inflorescence compound-racemiform, usually with strongly divaricate branches; heads often somewhat secund, with (14–)18–20 disk florets, the total number of florets 35–40(–45).

FLOWERING PERIOD. August-October (or November in the southern part of range).

HABITAT. Dry soil; plains, hills, river banks, prairies, roadsides, and railroad sidings.

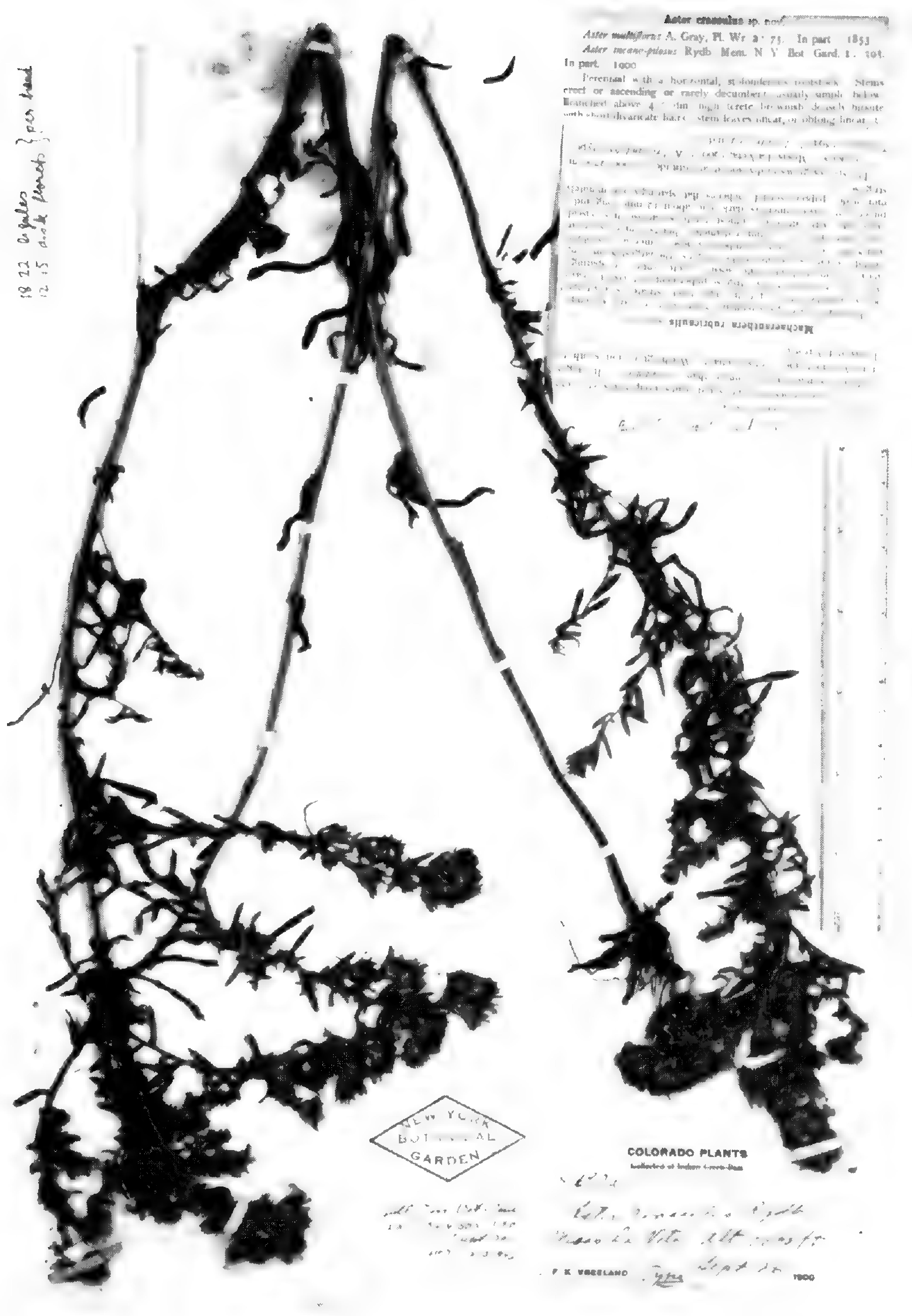

Figure 8. Holotype of *Aster crassulus* Rydberg (= *A. falcatus* ssp. *commutatus* var. *crassulus*); *Vreeland 690a* (NY).

RANGE. Southern Alberta, Montana, Wyoming, Colorado, Arizona, Mexico, Texas, Oklahoma, Kansas, Nebraska, Dakotas, Manitoba, and Saskatchewan (Figure 9).

REPRESENTATIVE SPECIMENS. **Arizona:** COCONINO CO., south of Flagstaff, *O. M. Clark 12152* (GH, OKL). **Colorado:** PUEBLO CO., Rye, *I. W. Clokey 4344* (MICH, MO, NY, RM, UC, US, WS). **Kansas:** BARTON CO., Claflin, *H. C. Benke 6211* (KSC, TEX). **Minnesota:** OTTER TAIL CO., Battle Lake, *E. P. Sheldon, s. n.* (RM, UC, WS). **Montana:** MADISON CO., Montana Valley, *A. & E. Nelson 6839* (ILL, ISC, NY, RM, US). **Nebraska:** SHERIDAN CO., Hay Springs, *E. S. Nixon 241, 242* (RM). **New Mexico:** RIO ARRIBA CO., Tank Canyon, Santa Fé Nat. For., *H. W. Springfield 418* (TEX). **North Dakota:** CASS CO., Fargo, *O. A. Stevens 299* (DAO, GA, NDA, OKL, UC, US, WIS). **Oklahoma:** WOODS CO., Alva, *G. W. Stevens 2857* (ILL, MO, OKL). **South Dakota:** CUSTER CO., Custer, *S. Stevens 45432* (NY). **Texas:** YOUNG CO., Graham, *J. Reverchon 3316* (MO). **Wyoming:** SHERIDAN CO., Sheridan, *S. S. Sharp 233* (RM). **Alberta:** CALGARY D., Calgary, *W. C. McCalla 9028, 10207* (ALTA, UBC). **Manitoba:** BRANDON D., Brandon, *G. A. Stevenson 497, 1046, 1059, 1626, & 1972* (DAO). **Saskatchewan:** MAPLE CREEK D., *A. J. Breitung 5680* (DAO, US). QU'APPELLE D., north of Regina, *A. J. Breitung 3893* (DAO, MO, RM). **Mexico:** Chihuahua, Villa Ahumada, *H. Le Sueur 365* (MO, TEX).

REPORTED HYBRIDS

Aster × amethystinus Nuttall, (*pro sp.*), Trans. Am. Phil. Soc. **2**(7): 294. 1841. (*Aster ericoides* Linnaeus × *novae-angliae* Linnaeus). TYPE: "Hab. In Massachusetts, near Cambridge and Salem; rare" *Nuttall* (BM!).

[Nuttall's paper was read before the American Philosophical Society on April 4, 1837]. — Torrey & Gray (1841) **2:** 144; Gray (1884) **1**(2): 185, (1889) 260; Porter (1894) 322; Porter & Small (1903) 323; Robinson & Fernald (1908) 810; Monroe (1913) 99; Britton & Brown (1923) 418; House (1924) 703; Knowlton (1930) 185; Peattie (1930a) 375; Benner (1932) 293; Rydberg (1932) 809; Palmer & Steyermark (1935) 664; Shinners (1941) 417; G. N. Jones (1945) 225, (1950) 275; Fernald (1950) 1432; G. N. Jones (1963) 251; Boivin (1967) 1032; Seymour (1969) 353; Van Faasen (1971) 100.

Aster bostoniensis Hort. ex Baker, *in* Gard. Chron. **2:** 744. 1884. [Type unknown; the name was applied to a plant cultivated in Europe].

Aster multiflorus Aiton × *novae-angliae* Linnaeus, H. C. Benke, Rhodora 32: 1–3, *pl. 192.* 1930. TYPE: Wisconsin, Kaukauna, *H. C. Benke 767* (Holotype, MIL).

Aster amethystinus Nuttall f. *leucerythros* Bemis, Rhodora **32:** 3. 1930. TYPE: Massachusetts, Worcester, *E. W. Bemis*, Oct. 5, 1924 (Holotype, GH!). [A rose-rayed form].

Aster amethystinus Nuttall f. *leucos* Bemis, Rhodora **33:** 63. 1931. TYPE: Massachusetts, Worcester, *E. W. Bemis*, Sept. 24, 1930 (Holotype, GH!). [A white-rayed form].

Benke (1930) was the first to present circumstantial evidence for the hybrid nature of these plants, noting that they were rare, and were always found in conjunction with the putative parent species. Hybrid status was experimentally verified by Wetmore and Delisle (1939) and confirmed by my own work (Jones, 1973).

Diagnostic Characteristics. Perennials with stoloniferous rhizomes; stems erect, 30 cm high or more, with ascending branches and densely hirsute pubescence. Cauline leaves linear, entire with ciliolate margins, sessile and somewhat auriculate-clasping, hirsutulous on both sides, the apex acute or nearly obtuse, armed with a bristle. Inflorescence racemiform or somewhat corymbiform, the heads on leafy branches. Involucre campanulate, about 4–5 mm high, the outer phyllaries linear to oblanceolate, squarrose, mucronate, hispidulous and somewhat glandular on the back. Receptacle alveolate; florets about 60, the ligules 20–30, 6–8 mm long, typically purple; pappus tawny; achenes brown, strigillose and somewhat glandular-puncticulate.

FLOWERING PERIOD. Late August to early October.

HABITAT. The same as the parent species: dry soil; in prairie vegetation along roads and railroads.

REPRESENTATIVE SPECIMENS. **Connecticut:** HARTFORD CO., Stony Brook, *H. A. Ahles 65409* (NCU). **Illinois:** COOK CO., Palatine, *H. C. Benke 5943* (UC). **Iowa:** CLAY CO., Ruthven, *A. Hayden 11137, 11134* (ISC). **Massachusetts:** BERKSHIRE CO., Williamstown, *C. H. Knowlton, s.n.* (KY). **Michigan:** WAYNE CO., River Rouge, *O. A. Farwell 8800, 8784, & 8804* (MICH). **Rhode Island:** PROVIDENCE CO., Providence, *J. F. Collins, s.n.* (GH). **Wisconsin:** RACINE CO., Racine, *S. C. Wadmond, s.n.* (KSC). **Ontario:** WENTWORTH CO., Hopkins Creek area, *J. S. Pringle 639* (WIS).

Aster × Batesii Rydberg, (*pro sp.*), Brittonia **1:** 102. 1931. (*Aster ericoides* Linnaeus × *?oblongifolius* Nuttall). TYPE: Nebraska, St. Paul, *J. M. Bates 5440* (Holotype, NY!).

Aster ericoides L. [var.] *Batesii* (Rydb.) Gates, Trans. Kansas Acad. Sci. **42:** 138. 1939. — Gates (1940) 241. — Perhaps, in part.

This hybrid has not been experimentally verified. In the original publication, Rydberg suggests: "mistaken for *A. amethystinus* Nutt. Perhaps a hybrid, *A. ericoides* × *Kumleini.*" *Aster kumleini* is a synonym for *A. oblongifolius.* The type and other specimens labeled *A. batesii* resemble plants of *A. ericoides,* but leaf margins are slightly glandular scabrous and ligules lavender. Introgression may be involved, but the proposed parentage of *A. oblongifolius* is questionable. My own experimental work does not lend support to Rydberg's suggestion, and I have listed *A. batesii* in synonymy under *A. ericoides* ssp. *ericoides.*

Aster × **columbianus** Piper, (*pro sp.*), Contr. U.S. Nat. Herb. **16** (5): 210. 1913. (*Aster ericoides* Linnaeus × *campestris* Nuttall). TYPE: Washington, Waitsburg, *Horner 559* [Holotype, US, apparently lost (Blake, 1928); Isotype, WS! (Jones, 1973, *pl. 4d*)].

Piper & Beattie (1914) 270; Cronquist in Hitchcock et al. (1955) **5**: 91; St. John (1956) 424; Abrams & Ferris (1960) 322; St. John (1963) 461. — *Aster multiflorus* Ait. var. *columbianus* (Piper) Blake, Rhodora **30**: 227–228. 1928.

Aster amethystinus sensu authors. - Piper & Beattie (1901) 186; Piper (1906) 572. - Not Nuttall (1841).

This hybrid has not been experimentally verified. The isotype and two other collections from Washington that I have seen [Whitman Co., *H. St. John 9265* (WS); Okanogan River, *S. Watson 191* (GH)] do have characteristics intermediate between the putative parent species. The plants resemble those of *Aster ericoides* ssp. *pansus,* but ligules are purple; phyllaries, leaf margins, and peduncles somewhat glandular; pappus sordid; achenes canescent.

Aster exiguus Rydberg × **pilosus** Willdenow, Ahles ex Jones & Fuller, Vasc. Pl. Illinois. 468. 1955. — Nomen nudum. (*Aster ericoides* Linnaeus × *pilosus* Willdenow) TYPE: Illinois, Cook Co., Palatine, *V. H. Chase 9105* (Holotype, ILL!; Isotype, ILLS).

This hybrid has not been experimentally verified. Specimens from Illinois cited in addition to the type are: Champaign Co., Rantoul, *H. A. Gleason, s.n.* (ILL); Normal Park, *E. J. Hill, s.n.;* Du Page Co., Wheaton, *W. S. Moffatt 462.* I have seen only the type and the Gleason collection, and they are somewhat atypical

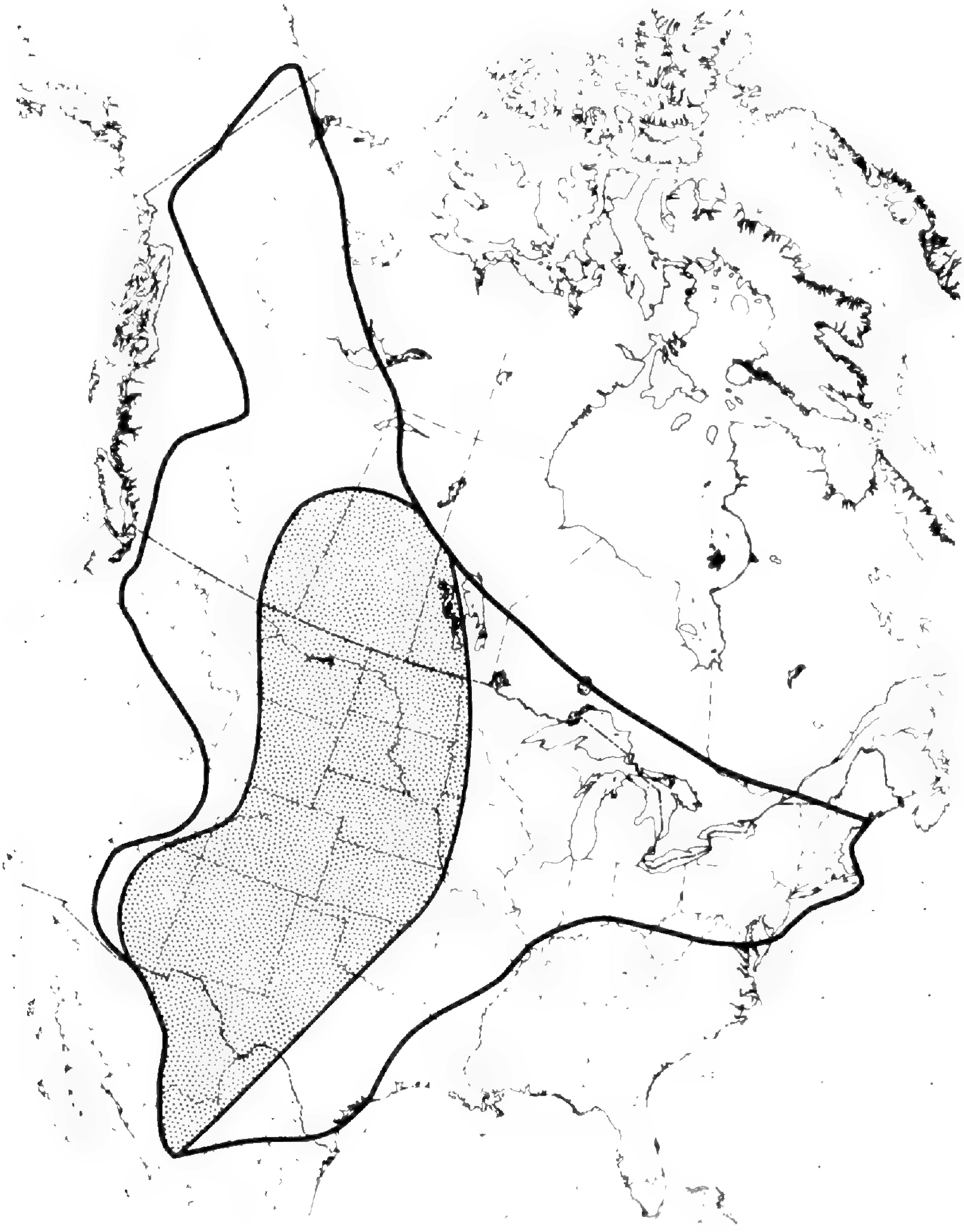

Figure 9. Range of *Aster falcatus* ssp. *commutatus*.

late-season specimens of *Aster ericoides* ssp. *ericoides* var. *prostratus*. Plants of this kind, characterized by stems with relatively soft spreading pubescence, a leafy inflorescence with heads not conspicuously secund, and leaves with long soft bristles, can often be found on mowed roadsides. They are usually still in flower when adjacent undisturbed stands have finished. The only specimen that looks somewhat like an intermediate between the two putative parent species is a collection from dry sandy soil, Mason County, Illinois, *R. T. Rexroat 1255* (ISM).

EXCLUDED NAMES

The following is a list of names that have been applied to *Aster ericoides* but properly belong in synonymy under taxa unrelated to sect. *Multiflori.*

Synonyms of **Aster pilosus** Willdenow, or varieties of that species:

Aster ericoides var. *pilosus* (Willdenow) Porter, Mem. Torrey Bot. Club **5:** 323. 1894.

Aster ericoides γ *platyphyllus* Torrey & Gray, Fl. N. Am.**2:** 125. 1841.

Aster ericoides var. *Pringlei* A. Gray, Synopt. Fl. N. Am. **1**(2): 184. 1884.

Aster ericoides var. *Randii* Britton in Britton & Brown, Ill. Fl. **3:** 379. 1898.

Aster ericoides var. *Reevesii* A. Gray, Synopt. Fl. N. Am. **1**(2): 184. 1884.

Aster ericoides var. *strictus* Porter, in Porter & Coulter, Synops. Fl. Colorado, 56. 1874.

Aster ericoides β *villosus* (Michaux) Torrey & Gray, Fl. N. Am. **2:** 124, 503. 1841.

Synonyms of **Aster parviceps** Mackenzie & Bush:

Aster ericoides var. *parviceps* Burgess, in Britton & Brown, Ill. Fl. **3:** 379. 1898.

Aster ericoides var. *pusillus* A. Gray, Synopt. Fl. N. Am. **1**(2): 184. 1884.

Synonym of **Aster depauperatus** (Porter) Fernald:

Aster ericoides var. *depauperatus* Porter. Mem. Torrey Bot. Club **5:** 323. 1894.

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SYSTEMATICS, DISTRIBUTION, AND NOMENCLATURE OF THE POLYMORPHIC VACCINIUM ANGUSTIFOLIUM

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Since 1950 and 1952, when Fernald and Gleason respectively published their floras of northeastern United States and adjacent Canada, the taxonomic treatment of the lowbush blueberry has been the centre of considerable controversy. While Fernald recognized but one polymorphic species, Gleason followed Camp's (1945) treatment and recognized three distinct entities *viz. Vaccinium angustifolium* Aiton, *V. brittonii* Porter ex Bicknell, and *V. lamarckii* Camp. In 1942, Camp had stated that *V. angustifolium* is the basic diploid ($2n = 24$) of this trilogy, having a distribution centered in the eastern subarctic of North America and existing only as relic populations in the southern parts of its range. He considered *V. lamarckii* to be a tetraploid ($2n = 48$) derived from *V. angustifolium* (Camp, 1945: 234), and *V. brittonii* another tetraploid of unknown affinity but possibly a mutant derived from *V. lamarckii* (Camp, 1945: 237).

However, Camp's evidence for these generalizations is meagre: he assumed that *Vaccinium angustifolium* was a diploid species on the basis of a single count reported by Darrow *et al.* (1944). Furthermore, no supporting voucher specimen could be located. The material for this count might have come from the White Mountains in which case *V. boreale* Hall & Aalders cannot be ruled out. Camp argued that *V. boreale* was merely a stunted form of *V. angustifolium* although it had previously been recognized at the varietal level by both Wood (1861) and Gray (1848). Recently, the taxonomic status of this taxon has been clarified (Vander Kloet, 1977).

Subsequent cytological studies by Hall and Aalders (1961) and Whitton (1964) of the lowbush blueberry in eastern Canada and Maine respectively showed that *Vaccinium angustifolium, V. brittonii* and *V. lamarckii* were consistently tetraploid ($2n = 48$).

I have also tried to find a diploid *Vaccinium angustifolium* in Ontario where I took clonal material as well as open pollinated seeds from plants which fell within Camp's (1945) morphological description of *V. angustifolium,* i.e. colonies 10–15 cm high, twigs of the current season green, abaxial surface of leaves glabrous or with a line of pubescence along the midvein, less than 10 mm wide and 30 mm long, margin sharply serrate, corolla cylindraceous, 3–5 mm long and fruit bright blue, glaucous, 5–7 mm in diameter. However, these plants (parents and progeny) were all tetraploid (Bent & Vander Kloet, 1976; Hersey & Vander Kloet, 1976).

Additional experimental analysis by Aalders and Hall (1963) demonstrated that the diagnostic features of *Vaccinium brittonii* (i.e. glaucous leaves and twigs, which serve to distinguish itfrom *V. angustifolium*) are controlled in part by a semidominant gene and in part by exposure to sunlight.

Finally, numerical studies of *Vaccinium* sect. *Cyanococcus* in northeastern Ontario by Smith (1969) and in eastern Ontario and adjacent New York by Vander Kloet (1972) failed to detect any substantive morphological discontinuity among *V. angustifolium, V. lamarckii* and *V. brittonii.*

While the data, cited above, have not corroborated Camp's hypothesis that the lowbush blueberry complex is composed of three biological entities ("morphs" in the following discussion), neither have they weakened it substantially; therefore, the purpose of this paper is to bring evidence against the hypothesis by showing (1) that the three morphs cross-pollinate freely in the field; (2) that the three morphs do not breed true in the field; (3) that the three morphs frequently intermingle at each site; (4) that the three morphs flower at the same time at each site; and (5) that greenhouse grown plants from the three morphs interbreed freely with one another. From this evidence and the studies cited above the conclusion is reached that reduction of these three morphs to a single species, *Vaccinium angustifolium* Aiton, is appropriate.

METHODS AND MATERIALS

Sampling space was arbitrarily restricted to 40 blueberry habitats located within 23 regions scattered throughout eastern North America (for details of geographical location see APPENDIX I.) At each of the 40 sites a minimum of one hectare was systematically searched and a few mature twigs from each different phenotype of *Vaccinium* sect. *Cyanococcus* were collected and dried[1]. In addition to taking soil samples and making ecological and habitat notes for each

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[1] Voucher specimens in ACAD. Acronyms follow *Index Herbariorum,* Holmgren & Keuken (1974).

collection, a few, usually five, ripe berries were harvested so that small, random populations could be reared under glass for later analysis of potential gene exchange within and between the different morphological groups.

In order to assess the frequency of each species at a given site, transects were run through nine lowbush blueberry habitats (marked with an asterisk in APPENDIX I). At each of the nine sites, 50-metre tapes were laid down 20 metres apart and at each 10 metre mark the *Vaccinium* species, if any, touching the mark or falling within a 10 cm diameter circle centered on the mark was recorded.

To follow flowering, pollination, and fruiting a minimum of 5 colonies was permanently marked in 1970 at Kaladar, Ontario; at Chaffey's Locks, Ontario; at Rock Dunder, Morton, Ontario; at Mt. Fitzsimmons, Ivy Lea, Ontario; Well's Island, Jefferson County, New York; and Biorachan Road, West Branch of River John, Nova Scotia. Observations have been made from 1970 to 1975 not only on these permanent colonies but also on adjacent colonies.

Next, the dried specimens were scored for the following four features: plant height (from field data); mean leaf width; type of leaf margin (entire or serrate); and type of abaxial leaf indumentum (glaucous, glabrous, or pubescent). These are the features most frequently used to separate taxa of *Vaccinium* sect. *Cyanococcus* in the field.

For the gene exchange trial, small populations (three to 59 plants) were grown from seed of a single colony. In all, 24 such populations from ten sites were begun for the polymorphic *Vaccinium angustifolium*, and were kept for two years in a cold frame. The provenance of the 24 populations was as follows: Kaladar, Ontario — three populations *"lamarckii," "brittonii,"* and *"angustifolium"* 59 plants; Rock Dunder, Morton, Ontario — two populations *"lamarckii"* and *"brittonii"* 18 plants; Blue Mountain, Lansdowne, Ontario — two populations *"angustifolium"* and *"brittonii"* 14 plants; Mt. Fitzsimmons, Ivy Lea, Ontario — three populations *"angustifolium," "brittonii,"* and *"lamarckii"* 17 plants; Port Maitland, Nova Scotia — two populations *"lamarckii"* and *"angustifolium"* 12 plants; Port Franks, Ontario — one population *"lamarckii"* three plants; Wolfville, Nova Scotia — three populations *"lamarckii," "brittonii,"* and *"angustifolium"* 27 plants; West Branch, Pictou County, Nova Scotia — three populations *"la-*

marckii," *"brittonii,"* and *"angustifolium"* 27 plants; Flat River, Prince Edward Island — one population *"angustifolium"* 24 plants; and Bonavista, Newfoundland — one population *"lamarckii"* 24 plants.

All these plants were moved from the cold frame into the greenhouse on 17 April 1974, where they began to flower after 20 days. And for the next 30 days, every morning open corollas were removed from several plants, the pollen removed and applied only once to mature stigmata on different plants from the same locality (population cross) or from another locality (local cross) or from a locality more than 100 km distant (regional cross).

RESULTS

Following the foraging behaviour of individual bumblebee queens of *Bombus ternarius, B. terricola* and *B. bimaculatus* during May of 1971 and 1972 in eastern Ontario, I noted a polylectic feeding strategy. Table 1 shows a typical set of results which can best be explained by chance foraging behaviour on the part of individual bees.

This foraging behaviour has been verified by Vander Kloet (1976a) when he investigated the composition corbicular pollen loads of both solitary and colonial bees on *Vaccinium angustifolium, V. corymbosum, V. myrsinites* and *V. darrowii.* Microscopic examination of stigmata also showed that they are encrusted by a variety of pollen grains including those from neighbouring *Vaccinium* taxa.

Furthermore, pollination biology studies of the *Vaccinium angustifolium* complex have shown that the flower is functionally and physiologically self sterile (Camp, 1942; Aalders & Hall, 1961; Wood, 1968; Vander Kloet, 1972, & 1976a). Therefore, which of these "alien" pollen grains contribute to seed set can be determined by growing the seedlings from open pollinated berries.

Table 2 gives the results from one such germination trial. Open pollinated berries, collected from *"angustifolium," "brittonii,"* and *"lamarckii"* give a progeny of the other two morphs that indicates that these three morphs do not breed true under field conditions. The observed difference in frequency of progeny has been correlated with the frequency of the parental populations (Vander Kloet, 1976b).

The frequency of occurrence of the species and morphs at the nine different sites is given in Table 3. Not only does the frequency of *"brittonii"* vary sharply from site to site, but, also, it always occurs with *"angustifolium"* and *"lamarckii."* Additional observations made in 1974 and 1975 also support this conclusion: *"brittonii"* does not occur in the absence of *"angustifolium"* or *"lamarckii";* the last two, however, always occur together. The other *Vaccinium* species which occasionally occur with the *V. angustifolium* complex have a distinct geographical range as well as habitat differences (Vander Kloet, 1977).

Moreover, that these three morphs intermingle on a given site has been observed, among others, by Scoggan (1957) in Manitoba, by Lakela (1965) in northeastern Minnesota, by Roland and Smith (1969) in Nova Scotia, by Duis (1941) in West Virginia, and Deam (1940) in Indiana. Collection data gleaned from herbarium specimens examined at DAO, CAN, TRT, ACAD, QK, GH, NYS, US, NY, MTMG, SFS, and QFA indicate not only that the three morphs share the same habitat, but also that the geographical ranges of *"brittonii"* and *"lamarckii"* are entirely contained within the range of *"angustifolium"* mapped collectively in Figure 1.

Field observations revealed no pattern or sequence of flowering that would permit me to partition the three morphs in the field. Indeed, location, exposure, and age of colony seemed to govern timing of anthesis. In Leeds County, Ontario, shrubs on steep, exposed, south-facing slopes of Precambrian outcrops began to flower in 1970 on May 5th regardless of morph disposition. Moreover, adjacent to these precocious colonies were several serotinous shrubs which did not begin to flower until May 19th. The same absence of a flowering pattern was observed in Pictou County, Nova Scotia, during 1973 and 1974 in spite of the fact that flowering does not begin until the first week in June.

According to McMillan and Pagel (1958), at least two variables affect the phenology of plants: (1) the site variable involving both differences from point to point, i.e. the microhabitat, and from year to year, the annual fluctuation, and (2) the genetic variable, i.e. differences in response to the same habitat due to different genetic potentials of the individuals involved.

To minimize these variables, I decided to follow the phenology of the even aged population prepared for the gene exchange trial and kept in the greenhouse since 17 April 1974 at 18° C at night and

22°C during the day and a light regime of 16 hours. The first shrub began to flower after 20 days, the last after 31 days. But no significant difference in flowering sequence was discovered among these three morphs.

That these greenhouse grown plants from the three morphs interbreed freely with one another is demonstrated in Table 4. The relatively low set success (41%), which does not significantly vary among the morphs, I attribute to low pollen production. Boulanger *et al.* (1967) also reported low pollen production in *Vaccinium angustifolium* sensu lato. But under field conditions, each corolla is visited a minimum of three times by pollinators whose bodies are covered with pollen, and these visitations result in high set success. However, Wood (1971) discovered that the addition of hives of honey-bees to blueberry fields did not increase the number of seeds per berry.

Finally, the morphological data accumulated in this study again failed to give me a criterion to separate these three morphs efficiently.

Although each of these lines of evidence is insufficient in itself, when they are combined and added to the cytological and genetic data cited in the introduction, the degradation of these three "species" to a lower rank is fully warranted. In effect, all of these moderately strong individual probabilities are combined to produce an overall certainty — namely that these morphs comprise one polymorphic species, *Vaccinium angustifolium* Aiton.

TAXONOMY

Vaccinium angustifolium Aiton, Hort. Kew, ed. 1. **2:** 11. 1789.

V. pensylvanicum Lamarck, Encycl. **1:** 74. 1783, non *V. pensylvanicum* Miller, Gard. Dict. ed. 8. 1768 = *Royena glabra,* nec *V. pensylvanicum* var. *angustifolium* (Aiton) Gray, Man. ed. **1:** 261. 1848, misapplied to *V. boreale* Hall & Aalders.

V. pensylvanicum var. *nigrum* Wood, Classbook ed. 1861. p. 252.

V. nigrum (Wood) Britton, Mem. Torr. Bot. Club **5:** 252. 1894.

V. pensylvanicum f. *leucocarpum* Deane, Rhodora **3:** 264. 1901.

V. brittonii Porter ex Bicknell, Bull. Torr. Bot. Club **41:** 420. 1914.

V. angustifolium var. *laevifolium* House, Bull. N.Y. State Mus. **243, 244:** 61. 1923.

V. angustifolium var. *nigrum* (Wood) Dole, Fl. Vermont ed. 3. 210. 1937.

V. lamarckii Camp, Bull. Torr. Bot. Club **71:** 180. 1943.

V. angustifolium var. *hypolasium* Fernald, Rhodora **51:** 104. 1949.

V. angustifolium f. *nigrum* (Wood) Boivin, Nat. Can. **93:** 437. 1966.

Cyanococcus angustifolius (Aiton) Rydberg, Brittonia **1:** 94. 1931.

Shrub (10–)20(–60) cm high, in dense, extensive colonies. Twigs of the current season green or glaucous, angular, verrucose, glabrous to pubescent. Leaves elliptic to narrowly elliptic; (5–)11(–20) mm wide, (15–)26(–41) mm long; green or blue green; glabrous, glaucous or pubescent beneath; margin sharply serrate, rarely entire. Calyx and pedicel glaucous or glabrous, rarely pubescent. Corolla cylindrical to urceolate; (4–)5(–6) mm long; white, occasionally with pink striping. Filaments ciliate along the margins, occasionally pubescent. Style glabrous. Pollen tetrads (36–)39(–41) μm in diameter. Berry blue and glaucous, dull black, or shining black, rarely white, (3–)6(–10) mm in diameter; each containing 36–(56)–86 seeds. Chromosome number: $2n = 48$.

Whether or not segments of this polymorphic species should be recognized at an infraspecific level remains a moot point. Apparently, character sets are not constant from generation to generation and novel recombinations occur from time to time. Moreover, Mosquin (1971) argues that, while such descriptions are useful in drawing attention to such segments, the names more often than not turn out to be useless and, even worse, a misleading burden to biological literature.

Range: Labrador and Newfoundland, west to southern Manitoba and Minnesota, south to northern Illinois, Pennsylvania, and Delaware and in the mountains to Virginia and West Virginia (Figure 1).

Type locality: "Native of Newfoundland and Labrador". Pouch Cove, Newfoundland, *fide* W. G. Dore (pers. com.). Introduced at Kew about 1776 by Benjamin Bewick. Type at BM, seen in 1975.

Since both *Vaccinium angustifolium* and *V. boreale* occur in Newfoundland and Labrador, some confusion has prevailed as to whether the type, taken from material cultivated at Kew, applies to *V. angustifolium* or *V. boreale.* Using stomata peels, Aalders and Hall (1962) showed that the type fitted better in the tetraploid *V. angustifolium.* Regarding leaf size and shape, the Morse (1971) polyclave system for plant identification also suggests that the type fits better into *V. angustifolium* than *V. boreale.*

Habitat: headlands, high moors, dry sandy areas, peaty barrens, exposed rocky outcroppings of the Canadian Shield, jack-pine barrens, pitch-pine barrens, oak parklands, poplar regeneration forests

Table 1.

Foraging behaviour of Bombus ternarius, B. terricola, and B. bimaculatus on a granite outcropping 3 km west of Chaffey's Locks, Ontario.[1]

To FROM	"angustifolium"	"brittonii"	Arctostaphylos uva-ursi
"angustifolium"	36	67	49
"brittonii"	31	60	49
A. uva-ursi	58	87	80
	$X^2 = 1.54$	P (.05 = 9.488)	

[1] Observation times: May 14, 1971 to May 18, 1971 and May 20, 1972 to May 28, 1972.

Table 2.

Distribution of progeny from 12 berries collected at random in 1970, 1971, & 1974 from colonies of "angustifolium," "brittonii" & "lamarckii" at Kaladar, Ontario.

PROGENY PARENTS	"brittonii"	"angustifolium"	"lamarckii"
KE 127* "brittonii" (4 berries)	22	20	6
KE 130 "angustifolium" (4 berries)	12	35	9
KE 134 "lamarckii" (4 berries)	1	17	4

*Voucher specimens in ACAD.

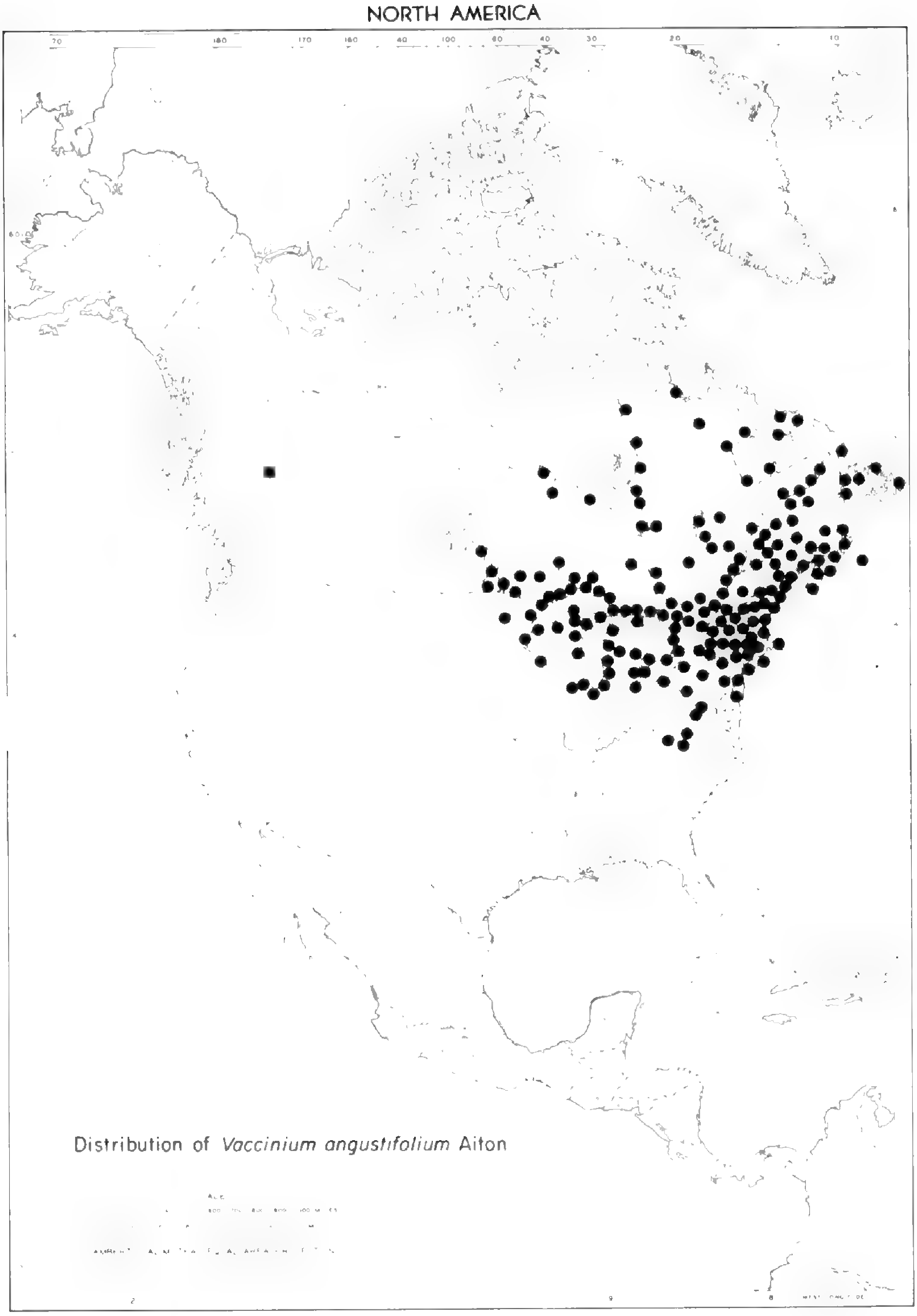

Figure 1. Distribution of *Vaccinium angustifolium* Aiton.

and in the Maritimes and New England especially abandoned pastures and bogs.

The natural habitats of *Vaccinium angustifolium* sensu lato were briefly described by Camp (1945) and Vander Kloet (1977). It is tolerant of a wide range of temperature, including frequent burning, but is intolerant of dense shade and grows most luxuriantly on fired barrens. Occurrence is restricted to acid soils. The average pH for 60 soils in which it was growing was 4.4 with a range between 2.8 and 6.6 (Vander Kloet, 1972, & unpublished).

Floral Biology: flower buds are formed in late summer and open the following April (in New Jersey), May (in Ontario) or June (in Nova Scotia). Occasional plants may bloom in September and October and a few precocious buds may open in March in very favoured situations. Reproduction is amphimictic, the flowers perfect, entomophilous; the most frequent pollinators are *Andrena vicina, A. carlini, Bombus bimaculatus, B. terricola, B. ternarius* and *B. perplexus* (Boulanger *et al.*, 1967; Vander Kloet, 1972 & 1976a).

Dispersal of the fruit and seed is primarily effected by birds and mammals. In the Maritimes and New England, robins and bears are particularly effective dispersal agents. Seedling establishment varies sharply throughout the species' range — from frequent in the Maritimes to none during the last forty years in eastern Ontario (Vander Kloet, 1976c).

Finally, I have postulated a recent hybrid origin followed by autoploidy for *Vaccinium angustifolium* sensu stricto (Vander Kloet, 1977). Subsequent introgression with *V. corymbosum* has resulted in the addition of glaucescence and pubescence to this taxon to give *V. angustifolium* its present polymorphic status.

ACKNOWLEDGMENTS

I wish to thank Dr. Larry Morse for his several critical readings of the manuscript, his valuable suggestions, and his notes on typification. Secondly, my thanks go to all those curators of herbaria cited above who gave me free access to their *Vaccinium* collections.

Table 3.

Frequency of occurrence of "angustifolium," "brittonii," "lamarckii" on several sites in eastern North America.

Sites	"brittonii"	"lamarckii"	"angustifolium"	V. myrtilloides	V. boreale	V. pallidum
Kaladar, Ont.	24	7	42	0	0	0
Delta, Ont.	42	43	12	0	0	0
Degelis, P.Q.	0	4	5	8	0	0
Gagetown, N.B.	0	1	8	4	0	0
Liberty, Me.	9	3	12	3	0	0
Lee, N.H.	0	18	34	0	0	1
West Branch, N.S.	23	16	40	6	0	0
Flat River, P.E.I.	1	6	21	0	0	0
Bonavista, Nfld.	0	18	34	0	2	0

Table 4.

Single link reciprocal crosses among "angustifolium," "lamarckii" and "brittonii"

Taxa	Population cross (plants from a single hm.)			Local cross (plants from a 50 km radius)			Regional cross (plants more than 100 km apart)		
	crosses	berries	seedlings	crosses	berries	seedlings	crosses	berries	seedlings
angustifolium × angustifolium	19	10	33	26	15	81	94	37	84
angustifolium × lamarckii	32	12	6	58	27	61	100	31	193
angustifolium × brittonii	36	21	36	62	24	44	141	53	176
lamarckii × brittonii	13	5	—	41	22	68	33	15	28
lamarckii × lamarckii	12	2	8	13	6	7	19	9	52
brittonii × brittonii	10	6	20	21	7	36	14	3	—

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APPENDIX I. LOCATION OF SAMPLING SITES*

1. West St. Modeste, Labrador, 51°36′N/56°45′W.
2. St. Anthony Hill, St. Anthony, Newfoundland.
3. Blomidon Mountain, Humber West, Newfoundland.
4. Mt. Sykes, Birch Bay, Humber East, Newfoundland.
5. Massive headlands, 2 km SW of Bonavista, Newfoundland.*
6. Ballyhack Point, Avondale, Harbour Maine, Newfoundland.
7. Pouch Cove, St. John's North, Newfoundland.
8. French Mountain, Cape Breton Highlands, Inverness County, Nova Scotia.

9. Kennington Cove, Cape Breton County, Nova Scotia.
10. Margaree Municipal Airport, Frizzleton, Inverness County, Nova Scotia.
11. Biorachan Road, Earltown, Colchester County, Nova Scotia.
12. A 2 ha poverty grass meadow 3.2 km west of West Branch, Pictou County, Nova Scotia.*
13. Red Head, Port Maitland, Yarmouth County, Nova Scotia.
14. Lake George, Yarmouth County, Nova Scotia.
15. An open white spruce regeneration forest along the Trans Canada Highway 1 km south of Flat River, Queen's County, Prince Edward Island.*
16. North River, Queen's County, Prince Edward Island.
17. Point Deroche, Queen's County, Prince Edward Island.
18. A popular regeneration forest in CFB Gagetown along hwy 7, 7.8 km south of Geary, Sunbury County, New Brunswick.*
19. A disturbed margin of a raised bog, along hwy 2, 500 m NW of the New Brunswick border, Temiscouata County, Quebec.*
20. Beaven Lake, near Arundel, Argenteuil County, Quebec.
21. A 1.7 ha granite-gneiss outcrop, 0.5 km north of Kaladar, Lennox and Addington County, Ontario.*
22. Rock Dunder, 3 km SW of Morton, Leeds County, Ontario.
23. Lake Opinicon, Chaffey's Locks, Leeds County, Ontario.
24. Blue Mountain, Charleston Lake, near Lansdowne, Leeds County, Ontario.
25. Red Horse Lake, near Lansdowne, Leeds County, Ontario.
26. Mt. Fitzsimmons, near Ivy Lea, Leeds County, Ontario.
27. A 2.4 ha quartzite outcrop 4 km south of Delta, Leeds County, Ontario.*
28. Hebert Bog, Upper Rock Lake, Frontenac County, Ontario.
29. Washburn, Frontenac County, Ontario.
30. Turkey Point, Norfolk County, Ontario.
31. Pinery, Port Franks, Lambton County, Ontario.
32. Wells Island, Jefferson County, New York.
33. Butterfield Lake, Jefferson County, New York.
34. Sag Harbor, Long Island, Suffolk County, New York.
35. An old field, 8 km west of Liberty along hwy 3, Waldo County, Maine.*
36. Mt. Washington, White Mountains, Coos County, New Hampshire.
37. An oak-hickory forest surrounding Wheelwright Pond at Lee, Strafford County, New Hampshire.*
38. Mast Way, Lee, Strafford County, New Hampshire.
39. Reservoir System, Framingham, Middlesex County, Massachusetts.
40. Jeremy Run, Skyline Drive, Shenandoah National Park, Rappahannock County, Virginia.

*Frequency sampling site.

APPENDIX II. CITATION OF SELECTED SPECIMENS

Newfoundland. HUMBER DISTRICT: Hannah's Head (Mt. Patricia), *Rouleau 335* (DAO); Cornerbrook, *Rouleau 42* (DAO). FOGO DISTRICT: Gander River, First Pond, *Rouleau 5406* (DAO); Joe Batt's Arm, *Brett* in 1945 (ACAD); Fredericton, *Ludlow 156* (ACAD). GANDER DISTRICT: south side of Gander, *Bassett 1036* (DAO). FERRY-

LAND DISTRICT: Witless Bay line, *Rouleau 5401* (DAO). CARBONEAR — BAY DE VERDE DISTRICT: Old Pelican, Cooks Pond, *Rouleau 5708* (DAO). GREEN BAY DISTRICT: Springdale Turn-off, *Rouleau 7318* (ACAD). LABRADOR: Brule, Happy Valley, *Gardner & Desroches 846* (QFA); Bassin de la R. Saint John, 51°07′N/63°47′W, *Dutilly & Lepage 41392* (QFA); Area 25, *Judd GB47* (DAO). Hodgewater, *Cameron 12222* (ACAD). Holyrood, Butter Pot Ponds, *Erskine 3014* (ACAD). Port de Grave, *Lear 11988* (ACAD). **Nova Scotia.** VICTORIA COUNTY: Ingonish, *Roland 41647* (DAO); Slaty Point, Clyburne Brook, *Smith et al. 4368* (DAO); Black Brook Cove, *Smith et al. 4356* (ACAD); Lockhart Brook, Salmon River, *Smith et al. 6366* (ACAD). LUNENBURG COUNTY: Deep Cove, Aspotogan Mt., *Hart 1152* (DAO); Indian Lake, *Smith et al. 8980* (ACAD). KINGS COUNTY: Auburn Barrens, *McLellan DA024* (DAO); Cambridge Station, *Webster 7* (ACAD). HALIFAX COUNTY: Sable Island, *Erskine 53-1091* (DAO); Melville Cove near Halifax, *Gorham 451368* (DAO); Peggy's Cove, *Smith et al. 17518* (ACAD). DIGBY COUNTY: Brier Island, *Roland et al. 299* (ACAD). PICTOU COUNTY: Pictou Landing, *Smith et al. 16683* (ACAD); 5 miles NW of Pictou, *Smith et al. 11572* (ACAD). HANTS COUNTY: Sackville River S of Mt. Uniacke, *Smith et al. 17610* (ACAD); Lantz, *Smith et al. 6028* (ACAD); Kennetcook Corners, *Smith et al. 9212* (ACAD). CUMBERLAND COUNTY: Crossroads, *Schofield & Bentley 4709* (ACAD); Jeffers Brook, *Smith et al. 19079* (ACAD). ANTIGONISH COUNTY: Linwood, *Smith et al. 10763* (ACAD); Pomquet Point, *Smith et al. 13681* (ACAD). SHELBURNE COUNTY: Clarke's Harbour, Cape Sable Island, *Smith et al. 7191* (ACAD). GUYSBOROUGH COUNTY: Lincolnville, *Smith et al. 7441* (ACAD). QUEEN'S COUNTY: Caledonia, *Smith et al. 11532* (ACAD). ANNAPOLIS COUNTY: 4 miles W of West Dalhousie, *Smith et al. 14540* (ACAD). INVERNESS COUNTY: head of MacGregor Brook, *Smith et al. 3807* (ACAD). CAPE BRETON COUNTY: Eastern Harbour, Scatari Island, *Smith et al. 8398* (ACAD). **Prince Edward Island.** PRINCE COUNTY: Alberton, *Fernald & St. John 7919* (NASP). KINGS COUNTY: Bristol, Lot 40 Station, *Erskine & Smith 2299* (DAO); Basin Head, *Griffin & Griffin* in 1972 (ACAD); 5 miles SE of Mt. Stewart, *Erskine 1603* (ACAD); Peake's Station, *Erskine 1603* (DAO); Bothwell, 10 miles E of Souris, *Erskine & Smith 2010* (ACAD). QUEEN'S COUNTY: Brackley Point, *Erskine 1780* (DAO); Charlottetown, *Erskine & Smith 1755* (DAO). **New Brunswick.** QUEEN'S COUNTY: W of New Canaan, *Roberts & Bateman 641742* (DAO); Starkey Bridge, *Smith et al. 15950* (ACAD). ALBERT COUNTY: Top of Gowland Mountain, *Roberts & Bateman 641542* (DAO); Nixon, *Smith et al. 18646* (ACAD); Weldon, *Smith et al. 18636* (ACAD). CHARLOTTE COUNTY: Tower Hill, near Moore's Mills, *Dore & Hall 13718* (DAO); Grand Harbour, Grand Manan, *Perry 13653* (ACAD); St. Stephen, *Haley 12755* (ACAD). WESTMORELAND COUNTY: Upper Rockport-Wood Point, *Roberts & Bateman 642463* (DAO); Moncton, *Perry* in 1920 (ACAD). KENT COUNTY: Cocagne, *Smith et al. 16635* (DAO); Nr. Cocagne River on road to Shediac Bridge, *Roberts & Bateman 64-2853* (ACAD). NORTHUMBERLAND COUNTY: Mount Carleton, *Smith & Clattenburg 20076* (ACAD); Doaktown, *Smith et al.* 18714 (ACAD); Portage Brook near Popple Depot, *Roberts & Bateman 64-4254* (ACAD); Newcastle, *Scoggan 12101* (ACAD). GLOUCESTER COUNTY: Bass River, *Smith et al. 16575* (ACAD). KINGS COUNTY: Berwick, *Smith et al. 18878* (ACAD). ST. JOHN COUNTY: Lily Lake, St. John, *Hay 271* (ACAD). **Quebec.** KAMOURASKA COUNTY: Ste. Anne, *Hamel & Payette 730* (DAO). RIMOUSKI COUNTY: Bic, *Breitung 490* (DAO). SAGUENAY COUNTY: Port-Cartier, *Sherk & Cinq-Mars 516* (DAO); Ile Ouapitagone, Archipel Ouapitagone, *St. John 90663* (GH); Harrington Harbour, 50°30′N/59°29′W, *Swales 745* (MTMG). CHARLEVOIX COUNTY: Baie St-Paul, *Raymond & Champagne 56-879* (DAO); Baie St-Paul, *Marie-Victorin et al. 56879* (ACAD). TEMISCOUATA COUNTY: Rivière-du-Loup, *Cody et al. 695* (DAO); Rivière-du-Loup, *Soper & Fraser 3663* (TRT). PORTNEUF COUNTY: Saint-Gilbert, *Marie-Victorin et al. 2487* (ACAD). ROBERVAL COUNTY: Péribonka, *Lavoie 9* (ACAD). LÉVIS COUNTY: St-Romuald, *Gravel & Tessier 69-23* (ACAD). JACQUES-CARTIER COUNTY: Ile-Perrôt, *Cinq-Mars 64-441* (ACAD). CHAMBLY COUNTY: Chemin du Lac, Longueuil, *Rolland-Germain 485* (ACAD). WOLFE COUNTY: Garthby Twp., Chalet Hill, *Blais & Hamel 11250* (ACAD). ARTHABASKA COUNTY: Sainte-Clothilde, *Marie-Victorin et al. 2068* (ACAD). CHICOUTIMI COUNTY: Saint-Fulgence, *Cayouette 7005* (ACAD). ABITIBI-EAST COUNTY: Maizeret Twp., Harricanaw River, 49°12′N/78°03′W, *Bentley 58142* (MTMG). East Coast of Hudson Bay, Old Factory, 52°33′N/78°15′W: *Dutilly & Lepage 12291* (GH). East Coast of Hudson Bay, Head of Richmond Gulf, *Spreadborough 14404* (CAN). Richmond Gulf, East Coast of Hudson Bay, Wiachewan River, *Abbe & Abbe 3380* (GH). Lac Mistassini, Baie Rousseau, 51°04′N/73°20′W: *Rousseau & Rouleau 747* (GH). Côte-Nord, Pointe-aux-Esquimaux, *Marie-Victorin & Rolland-Germain 18358* (GH). New Quebec, entre Fort George et la Baie aux Oies, 53°54′N/79°07′W: *Lepage 12635* (DAO). New Quebec, Lac Ayde, 52°20′N/73°25′W: *Haber & Bergeron 2262* (CAN). James Bay, Harricanaw River, 48°20′N: *Dutilly & Lepage 15168* (QFA). James Bay, Lac Desaulniers, 53°35′N/77°35′W: *MacCulloch* in 1973 (MTMG). Ungava Oriental, River George, 55°55′N: *Rousseau 413* (DAO); Central Ungava, Knob Lake Area, Lake Gillard, 30-35 miles NW of Burnt Creek, *Mustich 621* (CAN). Rupert House, 51°29′N/78°46′W: *Spafford 17* (DAO). Lac Pomerleau, Mt. Otish, 52°20′N/70°35′W: *Rousseau & Pomerleau 166* (DAO). Péribonka Region, around Lake Alex and Patrick West River: *Hustich 621* (CAN). Opinac Lake Quad, 52°03′N/77°08′W: *Argus 9529* (CAN). Longue Pointe de Mingan, 50°18′N/64°01′W: *Gillett 4986* (ACAD). **Ontario.** ELGIN COUNTY: near St. Thomas, Malahide Twp., *James* DAO114 (DAO). CARLETON COUNTY: "The Sand Hills" Torbolton Twp. (LI9C5), *Breitung* in 1946 (DAO); Constance Bay, *Senn 708* (NY). RENFREW COUNTY: Petawawa, *Breitung 6905* (DAO). THUNDER BAY DISTRICT: Paradise Island (off SW corner of St. Ignace Island), *Garton 6616* (DAO). GRENVILLE COUNTY: 3 mi. SW of Prescott, *Dore 18036* (DAO). GLENGARRY COUNTY: Raisin River, W of the 401 Lancaster Bridge, *Gogo 507* (DAO). ALGOMA DISTRICT: vicinity of Michipicoten Harbour 48°00′N/85°00′W, *Hosie et al. 1283 & 1312* (ACAD); 48°00′N/84°49′W, 47°56′N/84°52′W, 48°06′N/84°30′W, Wawa, *Garton et al. 14669, 14041, 14430* (ACAD); John Island, *Grassl 2438* (NY). HASTINGS COUNTY: Marmora Twp. 5 miles ENE of Marmora, *Gillett & Calder 6280* (NY). MUSKOKA DISTRICT: Gravenhurst, *Biltmore Herbarium 5617* (NY). LEEDS COUNTY: La Rue Island, 1000 Islands, *Bicknell* in 1905 (NY). **Manitoba.** Maskwa Rapids, *Löve & Löve 5515* (DAO). Sandilands Forest Reserve, 60 miles SE of Winnipeg, *Breitung 7907* (DAO). Victoria Beach, East shore of Lake Winnipeg, *Breitung 7832* (DAO). Whiteshell Provincial Park, 100 miles E of Winnipeg, *Wishart 19* (MTMG).

Michigan. CHARLEVOIX COUNTY: Beaver Island, *Voss 3886* (MICH). OSCEOLA COUNTY: 6.5 miles SE of Marion, *Voss 9464* (MICH). KALKASKA COUNTY: 5 miles E of Kalkaska, *Voss 3807* (MICH); Coldsprings Twp., *LaRue 35* (MICH). WEXFORD

COUNTY: 5 miles WSW of Hoxeyville, *Voss 4489* (MICH). NEWAGO COUNTY: 1.5 miles S of Bridgetown, *Hermann 8632* (MICH). **Minnesota.** ST. LOUIS COUNTY: 4 miles S of Gilbert, *Lakela 3472* (NY); Grand Lake, 18 miles N of Duluth, *Lakela 2875* (NY). WINONA COUNTY: Trempealeau Ridge, *Holzinger* in 1901 (NY). HUBBARD COUNTY: Park Rapids, *Palmer 36829* (NY). CHISAGO COUNTY: Taylors Falls, *Rydberg 9619* (NY). CLEARWATER COUNTY: Itasca Park, headwaters of the Mississippi River, *Moyle 37* (NY). Benedict, *Bergman 3146* (NY). **Ohio.** TRUMBULL COUNTY: *Shanks 2264* (NY). LUCAS COUNTY: *Bartley & Pontius 761* (NY). **Illinois.** KANKAKEE COUNTY: near St. Anne, *Jones 11400* (NY). **Wisconsin.** WASHBURN COUNTY: Township 40 N, Range 13 W Casey, *Galletta 8101* (NCSC). BURNETT COUNTY: Section 12, Twp. 41N, Range 14W (13 mi E of Minnesota line), *Galletta 812* (NCSC). VILAS COUNTY: Plum Creek Avenue, St. Germain, 2.2 mi from Hwy 70, *Galletta 8163 & 8162* (NCSC). SAUK COUNTY: West Bluff, Devils Lake, *Fassett 3313* (NY). MARINETTE COUNTY: Marinette, *Phuette* in 1891 (NY). Wisconsin Point, Lake Superior, *Gillman* in 1876 (NY). West De Pere, Wolf River Dells, *Keefe* in 1938 (NY). **Maine.** PENOBSCOT COUNTY: Stillwater River, 3 miles NW of Old Town, *Rossbach 4840 & 4841* (ACAD); Upper Stillwater, *Fernald 362* (NY). KNOX COUNTY: Dodge Mt. near Rockland Line, Rockport, *Rossbach 1821* (ACAD); between Athearn's and North Hope Corners, *Rossbach 4017* (ACAD); Union, *Cole 905* (NY); Jones Mt., Hope, *Cole 937* (NY). FRANKLIN COUNTY: near summit of Sugarloaf Mt., *Rossbach 5266* (ACAD); summit ridge of Saddleback Mt., *Rossbach 5991* (ACAD). WALDO COUNTY: Grindel Point, Islesboro, *Rossbach, 3587* (ACAD); Little River, SW of Belfast, *Rossbach 4780* (ACAD); Spear's Mountain, at 1000 ft. elevation, Montville, *Rossbach 4700* (ACAD); Swanville, *Chamberlain 1905* (NY). PISCATAQUIS COUNTY: Mount Katahdin, *Walker 1883* (NY). LINCOLN COUNTY: Dodge's Point, Damariscotta River, *Wilson 221* (NY). WASHINGTON COUNTY: between Jonesboro and Meddybemps, *Eggleston et al. 22236* (NY); Cherryfield, *Coville US1489770* (US). AROOSTOOK COUNTY: township X1, Range 16, *St. John & Nichols 2439* (NY). YORK COUNTY: Ocean Park, *Moldenke 1581* (NY); York, *Bicknell 6911* (NY). **New Hampshire.** GRAFTON COUNTY: Black Mountain near East Haverhill, *Muenscher & Clausen* in 1934 (NY). COOS COUNTY: Lancaster, *Blanchard* in 1911 (NY). CHESHIRE COUNTY: Hinsdale, *Batchelder* in 1919 (NY); Marlboro, *Rusby* in 1919 (NY). Greenfield, *Coville US494774* (US). **Vermont.** RUTLAND COUNTY: Proctor, *Banker 201* (NY); Twin Mountains, West Rutland, *Eggleston 1451* (NY). WINDHAM COUNTY: Westminster, *Blanchard 140* (NY); Jamaica, *Moldenke 9560* (NY). CHITTENDEN COUNTY: Camels Hump, *Blanchard* in 1918 (NY); The Chin, Mt. Mansfield, *Edmondson 5216* (NY); Mt. Mansfield, *Blanchard* in 1912 (NY). **Massachusetts.** NANTUCKET COUNTY: Nantucket Island, *Mackeever 562* (NY). MIDDLESEX COUNTY: Melrose, *Morong* in 1877 (NY); Winchester, *Smith 1171* (NY). DUKES COUNTY: Martha's Vineyard, West Tisbury, *Mackeever 134* (NY). BARNSTABLE COUNTY: Dennis, *Fernald & Long 17276* (NY). WORCESTER COUNTY: Worcester, *Edmondson 334* (NY). BERKSHIRE COUNTY: Tyringham, *Vail* in 1897 (NY). HAMPDEN COUNTY: Granville, *Seymour 142* (NY). **Connecticut.** MORRIS COUNTY: Bantum Lake, *Rosalie 41* (NY). FAIRFIELD COUNTY: Bridgeport, *Eames* in 1895 (NY). LITCHFIELD COUNTY: Salisbury, *Druslar* in 1937 (NY). HARTFORD COUNTY: Burlington, *Enequist 21 & 27* (NY); Southington, *Bissell 148* (NY). MIDDLESEX COUNTY: East-Hampton, *Chamberlain* in 1924 (NY). WINDHAM COUNTY: Thompson, *Weatherby 4681* (NY). **Rhode Island.** WASHINGTON COUNTY: Westerly, *Moldenke 1620* (NY).

KENT COUNTY: Warwick, *Congdon* in 1878 (NY). **New York.** TOMPKINS COUNTY: Ithaca, *Coville US295392* (US); South Hill, Ithaca, *Allen* in 1934 (NY). SUFFOLK COUNTY: Long Island, Riverhead, *Latham 20504* (NYS); Long Island, Sag Harbor, *Latham 33287* (NYS); Long Island, Deer Park, *Latham 22380* (NYS). CORTLAND COUNTY: Valley of Fall Creek, *Allen* in 1934 (NY). ULSTER COUNTY: Lake Awosting, *Woodward* in 1938 (NY); High Falls, *Taylor 1821* (NY). HERKIMER COUNTY: Adirondack Mountains, Fourth Lake, Fulton Chain, *Killip 31802* (NY). GREENE COUNTY: Tannersville, *Vail* in 1891 (NY); New Baltimore, *Taylor 230* (NY). Catskill Mts., *Camp 3029* (NY). DELAWARE COUNTY: Stamford, *Taylor 592* (NY). ROCKLAND COUNTY: Palisades Interstate Park, *Lehr 720* (NY). ORANGE COUNTY: Black Rock Forest, *Raup 7220* (NY). SCHUYLER COUNTY: Hector, *Allen* in 1934 (NY). Shawangunk Mountains, *Woodward* in 1936 (NY). RENSSELAER COUNTY: Berlin, *House 24961* (NY). ST. LAWRENCE COUNTY: Morristown, *Phelps 763* (NY). **Pennsylvania.** BRADFORD COUNTY: Barclay Twp., State Game Lands #12, *Westerfield 1133* (NY). LYCOMING COUNTY: 3.5 miles S of So. Williamsport, *Fogg 17702* (NY). LENNOX COUNTY: Pocono Summit, *Porter* in 1891 (NY). SOMERSET COUNTY: Jenner Plateau, 2.5 km SSW of Tire Hill, Johnstonn, *Clausen & Shetler 236* (NY). SNYDER COUNTY: Selingsgrove, *Moldenke 3140* (NY). SCHUYLKILL COUNTY: *Parker* in 1864 (NY). ELK COUNTY: 1 mile E of Caledonia, *Wahl 623* (NY). PIKE COUNTY: Saw Hill Falls, *Nash* in 1909 (NY). LUZERNE COUNTY: Bear Run, *Taylor 2130* (NY). MONROE COUNTY: Pocono Plateau, Long Pond, *Britton* in 1893 (NY). CENTRE COUNTY: Thickhead Mt., *Mathias 1108* (NY). SULLIVAN COUNTY: Lake Ganoqua, *Smith* in 1902 (NY). **New Jersey.** MONMOUTH COUNTY: 1.5 miles ESE of Clarksburg, *Fogg 14112* (NY); Shark River, *Taylor 2292* (NY); 1 mile N of Holmeson, *Long 52029* (NY). ATLANTIC COUNTY: Mays Landing, *Pennell 12015* (NY); Atsian Road, Hammonton, *Bassett 89* (NY). MORRIS COUNTY: Succa-summa, *Mackenzie 3962* (NY). PASSAIC COUNTY: Greenwood Lake, *Mackenzie 2558* (NY). SUSSEX COUNTY: High Point, *Mackenzie 4182* (NY). **Virginia.** GILES COUNTY: vicinity of Mt. Lake, *Camp 3002* (NY). PAGE COUNTY: Luray, *Steele 124* (NY). PULASKI COUNTY: Peak Mt., along Peak Creek, *Small* in 1892 (NY). Shenandoah National Park, Hogback Mountain, *Camp 1289* (NY). **West Virginia.** GRANT COUNTY: Alleghany Plains, 20 miles W of Petersburg, *Batchelor* in 1940 (NY); Stony River Dam, *Core* in 1931 (NY). AUGUSTA COUNTY: Mt. Rogers, *Heller 823* (NY). PENDLETON COUNTY: Panther Mt., *Rydberg 9157* (NY). **Delaware.** East of Mt. Culea, Pyles Mill, *Commons* in 1875 (NY).

TAXONOMIC NOTES ON SPIRANTHES CASEI CATLING & CRUISE AND SPIRANTHES × INTERMEDIA AMES

PAUL M. CATLING

Only recently described, *Spiranthes casei* Catling & Cruise (1974) was previously confused with other sympatric species of *Spiranthes,* and when recognized as being distinct, it had been referred to *S. vernalis* Engelm. & Gray (Mousley, 1941, 1942; Correll, 1950; Whiting & Catling, 1971). Shortly after *S. casei* had been formally described, Luer (1975, p. 108) referred it to the previously described *S.* × *intermedia* Ames (1903) assigning to it a true specific status. It was briefly explained in the description of *S. casei* (Catling & Cruise, *loc. cit.*) that the name *S. intermedia* could not apply to the newly discovered species. Since Luer's interpretation occurs in a major and very recent reference work on North American orchids that actually postdates the description of *S. casei,* it is not surprising that I have received a considerable number of requests for an explanation concerning the correct choice of name. The purpose of this paper is to demonstrate that the specific epithet *"intermedia"* applies to a northeastern coastal plain complex probably involving both *S. vernalis* and *S. lacera* (Raf.) Raf. var. *gracilis* (Bigelow) Luer, and that it does not apply to the more northern taxon recently described as *S. casei.* It should be emphasized that *Spiranthes* is a taxonomically problematic genus in North America, and in the absence of a critical review of the literature, thorough morphological, ecological and distributional study, and especially, reference to the type specimens, one is unlikely to treat the genus without error.

METHODS

In the following paragraphs I have included a review of the relevant literature, and presented data collected from type material personally examined, and from specimens borrowed from various herbaria throughout the northeast (ACAD, AMES, CAN, CM, DAO, MICH, MTMG, NEBC, NFLD, PENN, PH, QUC, TRT, US, WIS). The type material of the taxa in question display an abundance of flowers, and a few could be removed without seriously affecting the specimens. Dried flowers were reconstituted with dilute ammonium hydroxide and warm soap solution, and camera lucida drawings were prepared. The dissected flowers were later mounted on slides with glycerin and placed in the collections of the Ames Orchid Herbarium at Harvard University. Scatter diagrams are based on about 100 randomly selected herbarium sheets of each taxon from throughout its area of distribution in the northeast, with no more than two plots per locality.

TAXONOMY

Spiranthes × *intermedia* Ames (1903) was originally described as a putative hybrid involving *S. praecox* (Walter) S. Watson and *S. gracilis* (Bigelow) Beck (=*S. lacera* var. *gracilis*). A year later the erroneously identified *S. praecox* of New England was described as a new species, *S. neglecta* Ames (Ames, 1904). Therefore *S.* × *intermedia* became the hybrid of *S. neglecta* (=*S. vernalis*) and *S. gracilis* (Ames, 1904, p. 28). St. John (1918) discussed the hybrid complex in southeastern Massachusetts, referring to the hybrids of *S. vernalis* and *S. cernua* (L.) Rich. as *S.* × *intermedia*. *Spiranthes cernua* × *S. gracilis* Ames was described in 1921, and at that time Ames considered *S. neglecta* to be synonymous with *S. vernalis* (Ames 1921, p. 81). He postulated *S.* × *intermedia* to be, "one of the variants of a cross between *S. cernua* and *S. gracilis* in which the characters of *S. gracilis* are clearly predominant" (Ames, *loc. cit.*). In 1924 Ames included *S.* × *intermedia, S. neglecta* and *S. cernua* × *S. gracilis* in synonymy with his × *S. vernalis.*

Drawings accompanied the descriptions of *Spiranthes* × *intermedia* (Ames, 1903, *pl.* 47), *S. neglecta* (Ames, 1904, p. 29, *fig.* 1), and *S. cernua* × *S. gracilis* (Ames, 1921, *pl.* 128). The drawings accompanying the description of *S. cernua* × *S. gracilis* were later used in Correll's "Native Orchids of North America" (1950), to illustrate *S. vernalis.* Although Correll placed both *S.* × *intermedia* and *S. neglecta* in synonymy with *S. vernalis* it was not indicated that *S. cernua* × *S. gracilis* was also a synonym despite his use of the plate.

Although the early literature treated *Spiranthes* × *intermedia* as a hybrid involving either *S. vernalis* and *S. lacera* var. *gracilis,* or *S. vernalis* and *S. cernua,* or *S. cernua* and *S. lacera* var. *gracilis,* it was never considered a true species. It is clear that New England taxonomists had difficulty with a complex of plants likely involving *S.*

vernalis and *S. lacera* var. *gracilis,* and perhaps also *S. cernua;* but the important point is that both Ames and Correll finally admitted the confusing plants (*S.* × *intermedia* etc.) within the variation of *S. vernalis,* and Ames at least had studied the group in great detail.

Another clue relating to the inappropriateness of applying the name *"intermedia"* to a taxon clearly distinct from the *Spiranthes vernalis* complex can be obtained from the earlier literature. In his original description of *S.* × *intermedia,* Ames (1903) stated, "The coloring of lip was distinctive; yellow-green at the apical, greenish near the proximal end; the callosities or nipples were green at their base with a whitish apex." Ames (1903, p. 262) further writes, "As far as observed the color of the callosities was decisive in the determination of the hybrids." Later St. John (1918, p. 112) described the lip of *S.* × *intermedia* from Dover, Massachusetts, "It has a suffusion of yellowish-green color down its centre and in the callosities, suggestive of the deep green color of the body of the lip of *S. gracilis.*" Although I have critically observed flower color of *S. casei* in Ontario, Quebec, New England, and the Canadian Maritimes, I have never found a specimen with yellowish-green coloration in the lip.

It was noted in the type description (Catling and Cruise, 1974) that *Spiranthes vernalis,* and also *S.* × *intermedia, S. neglecta* and *S. cernua* × *S. gracilis* differed from *S. casei* "in exhibiting a light-colored and frequently more dense, non-glandular pubescence on the rachis, and a denser, less robust spike with a larger number of narrower and slightly longer flowers." With the exception of the pubescence these characteristics are clear from the plate of *S.* × *intermedia* provided by Ames (Ames, 1903, *pl.* 47). In addition, it was pointed out that *S. casei* and *S. vernalis* each have discrete distributions.

Luer (1975) recognized the northern taxon as quite distinct from the southern *Spiranthes vernalis* and assumed that the description and illustration of *S.* × *intermedia* were applicable to it, and that its distribution ranged into southeastern Massachusetts (the type locality of *S.* × *intermedia*). The basis of these assumptions remains a mystery to me. Although the range of *S. casei* has been extended in the east and west since it was described, there are no new distribution records for areas substantially to the south of the range previously indicated (Catling and Cruise, 1974, p. 534). *Spiranthes* *casei* (*S. intermedia* Ames *sensu* Luer) remains unknown from southeastern Massachusetts.

As previously mentioned, when *Spiranthes casei* was first recognized as distinct from other sympatric species of the genus, it was referred to *S. vernalis*. The late recognition of *S. casei* must certainly have resulted from northern botanists' lack of familiarity with the southern *S. vernalis* and a lack of familiarity on the part of the botanists further south with the distinct northern taxon (now *S. casei*). In addition there may have been a fear of complicating the group further with the publication of new names which may only represent local extremes of variation, obscure hybrids, or freaks. Thus when Henry Mousley sent his Quebec specimens to Correll, Correll referred them to *S. vernalis;* both Mousley (1941, 1942) and Correll (1950) published the Quebec occurrence under the name "*S. vernalis*". It is surprising to find that the distribution map of *S. vernalis* prepared by Luer (1975, p. 103) shows this species occurring in the eastern townships of Quebec, when he himself recognized the northern plants, previously referred to *S. vernalis,* as a different species. It is now clear that *S. vernalis* does not occur in the eastern townships of Quebec or anywhere else in Canada (based on field work and on material from northeastern herbaria). The fact that Mousley's specimens represent *S. casei* is not only obvious from his published photographs (1942, *pl.* I and II) but also from the actual examination of his specimens (AMES, DAO, MTMG). *Spiranthes casei* and *S. vernalis* appear to be allopatric.

TAXONOMIC CHARACTERS

Having summarized the literature that has plagued botanists for the past fifty years regarding the true identity of certain northeastern *Spiranthes* species, it is now appropriate to present some detailed information about *S. casei* resulting from recent morphological re-evaluation. Since there is some precedent for grouping the types of *S.* × *intermedia, S. neglecta,* and *S. cernua* × *S. gracilis* with *S. vernalis* (Ames, 1921; Correll, 1950), and as it facilitates comparison, these may subsequently be referred to as the "*S. vernalis* complex" (of southern New England).

The specimens of *Spiranthes vernalis, S.* × *intermedia, S. neglecta,* including the types, and also the specimens of the putative *S. cernua* × *S. gracilis* are similar to each other in appearance but differ from *S. casei* in having a light-colored, and frequently more dense, non-glandular pubescence on the rachis. This pubescence varies from 0.1 to 0.4 mm. in length and with 20–80 hairs per square mm., the hairs frequently being about 0.1 mm. apart. In *S. casei,* the pubescence is 0.1–0.4 mm. long and much less dense with 10–30 hairs per square mm. The pubescence of *S. casei* is also more slender and always gland-tipped. Usually the capitate glandular tips, as well as from two to seven septa, are dark reddish or amber in color. The trichomes of the *S. vernalis* complex are frequently thicker and the septa are more difficult to discern. Clubbed trichomes occasionally occur but the pubescence is essentially pointed at the tip and cannot be described as glandular. In both *S. casei* and the *S. vernalis* complex, pubescence similar to that of the rachis extends onto the ovary and the outer surfaces of the basal perianth parts, but is usually less than 0.1 mm. long. Only in *S.* × *intermedia* and one other specimen from southeastern Massachusetts (Ames 2247) was some intermediacy in pubescence noticeable.

Similarly the lips of the type specimens of *Spiranthes* × *intermedia, S. neglecta, S. cernua* × *S. gracilis* and *S. vernalis* differ from those of the type specimen of *S. casei,* as well as *S. casei* from areas far removed from the type locality (Figure 1). In the *S. vernalis* complex the lips are narrower, have a cuneate base and somewhat smaller basal calli. The cordate bases of the relatively wider lips of *S. casei* are clearly shown in Figure 1, g-k. Moreover, the lip of *S. casei* tends to be more apically truncated and occasionally notched and the dilation tends to be more proximal. Although no attempt has been made to illustrate pubescence of the lips here (thus bases and calli size be amply illustrated), it was noticed that *S. casei* usually has the edges of the cordate base and region of the calli distinctly and often densely ciliolate, while in the types of *S.* × *intermedia, S. neglecta, S. cernua* × *S. gracilis* and *S. vernalis* this area varies from sparsely or locally ciliolate to puberulent. Although only a few flowers from the type specimens were examined in detail, over 20 flowers of each of *S. vernalis, S. casei* and *S. lacera* var. *gracilis* (from throughout their range) have been examined, and the floral parts represented here are characteristic.

Spiranthes casei also differs from the *S. vernalis* complex of southeastern Massachusetts in having relatively broader lateral petals (Figure 2) reflecting the characteristically more robust nature of the flowers. Specifically, *S. casei* differs from *S.* × *intermedia* in possessing three major veins in the lateral petals whereas *S.* ×

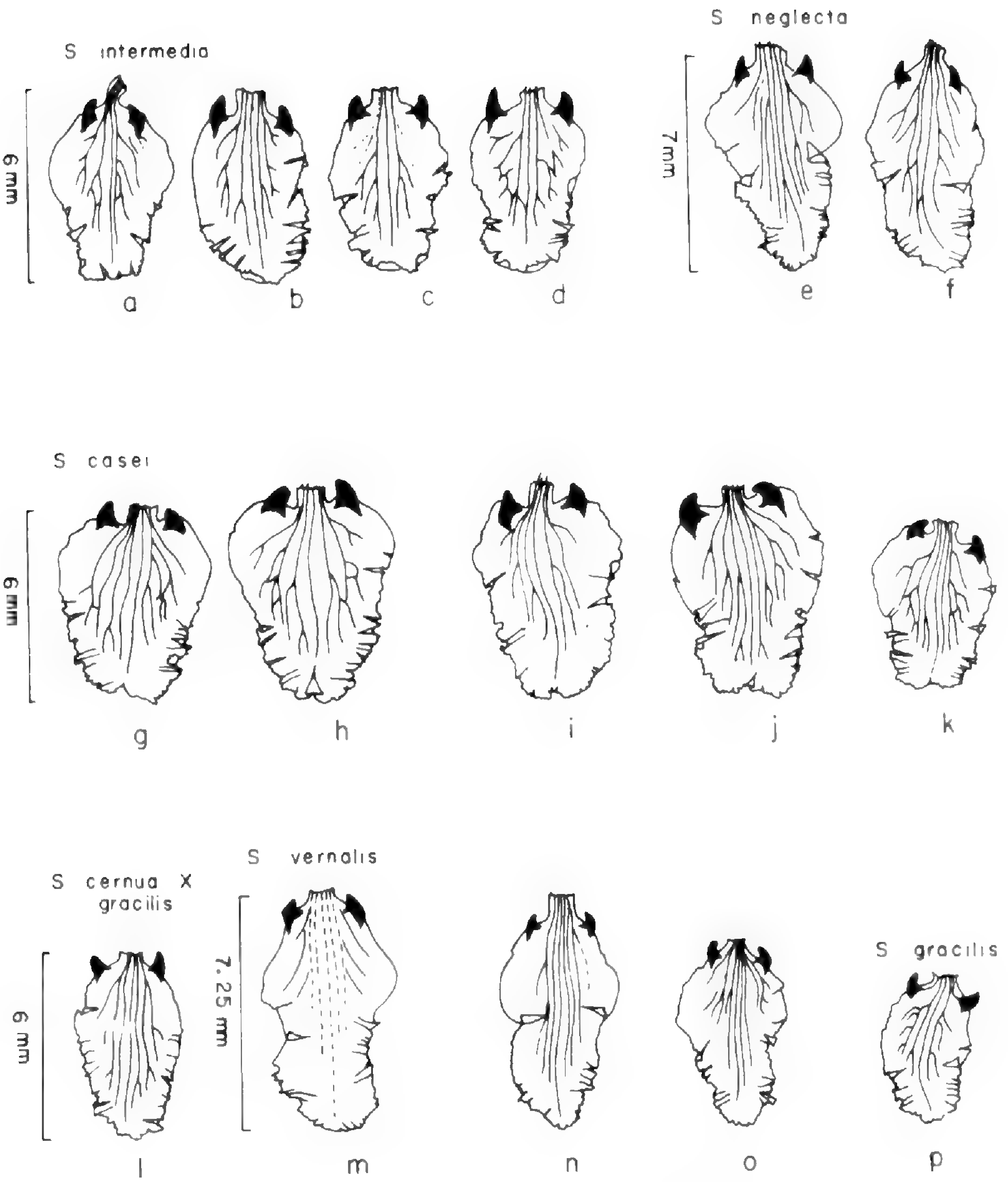

Figure 1. **Camera-lucida drawings of the lips of Spiranthes spp.** a, b, c, d, *S. intermedia* Ames, Type (AMES 2246); e, f, *S. neglecta* Ames, Type (AMES 2518); g-k, *S. casei* Catling & Cruise; g, h, Type (TRT 169205); i, New Hampshire (AMES 67224); j, Quebec (AMES 63778); k, Michigan, *Bob & Fassett 9484* (WIS); l, *S. cernua* × *gracilis* Ames, Type (AMES 17391); m-o, *S. vernalis* Engelm & Gray; m, Type, redrawn from a drawing by Ames accompanying the type (AMES 82967); n, Missouri, *Palmer*, 14 June 1958 (WIS); o, Connecticut, *Eames*, 8 Aug. 1897 (WIS); p, *S. gracilis* (Bigel.) Beck., Massachusetts, *Wiegand* (WIS).

intermedia has only two or a secondary third. Interestingly, *S. lacera* var. *gracilis* usually has only two.

The robust nature of the flowers of *Spiranthes casei* is also manifest in the value of the length versus width ratio of the lateral sepals. When sepal width is plotted against sepal length (Figure 3), with the pubescence characters represented symbolically, it becomes clear that the types of *S.* × *intermedia, S. neglecta* and *S. cernua* × *S. gracilis* belong with *S. vernalis* and not with *S. casei;* furthermore, the types of *S. casei* fall well within the boundaries of that species, differing markedly from *S. vernalis.*

Certain other floral characters distinguish *Spiranthes casei* from *S.* × *intermedia,* and from the *S. vernalis* complex in general. A flower from the type of *S.* × *intermedia,* reconstituted with ammonium hydroxide (Figure 4) certainly resembles the relatively narrow and delicate flowers of *S. vernalis* and *S. lacera* var. *gracilis.* The dorsal perianth parts extend conspicuously beyond the lip in the flowers of *S.* × *intermedia* (Figure 4c) and are usually upcurved at the tip, but in *S. casei* the dorsal perianth parts barely extend beyond the lip and they are usually not upcurved (Figure 4d). Due to their narrowness, their somewhat greater divergence, and their plane of attachment, the lateral sepals in the *S. vernalis* complex frequently leave a space below the lip in lateral view, but in the robust flowers of *S. casei* no such space is apparent and less of the lip is visible (Figure 4c&d).

There is also a notable difference in the nature of the column (Figure 4a&b). In the types of *Spiranthes* × *intermedia, S. neglecta* and the specimens of the putative *S. cernua* × *S. gracilis,* as well as in several flowers of *S. vernalis* from widely separated localities, the column was found to be distinctly stipitate (Figure 4a) while in numerous flowers of *S. casei* examined, including the type, the column is not stipitate, but rather only slightly and gradually constricted toward the base. Although some other differences in the column structure appear to exist, it would be difficult to discuss them with certainty on the basis of reconstituted dried flowers alone.

The characteristic floral density of the spike in *Spiranthes* spp. may be expressed in quantitative terms by calculating the value for a ratio of spike length (mm.) to flower number. Since *S. casei* has a relatively more open spike, this ratio will have a relatively greater value. In Figure 5 the floral density ratio is plotted against the ratio

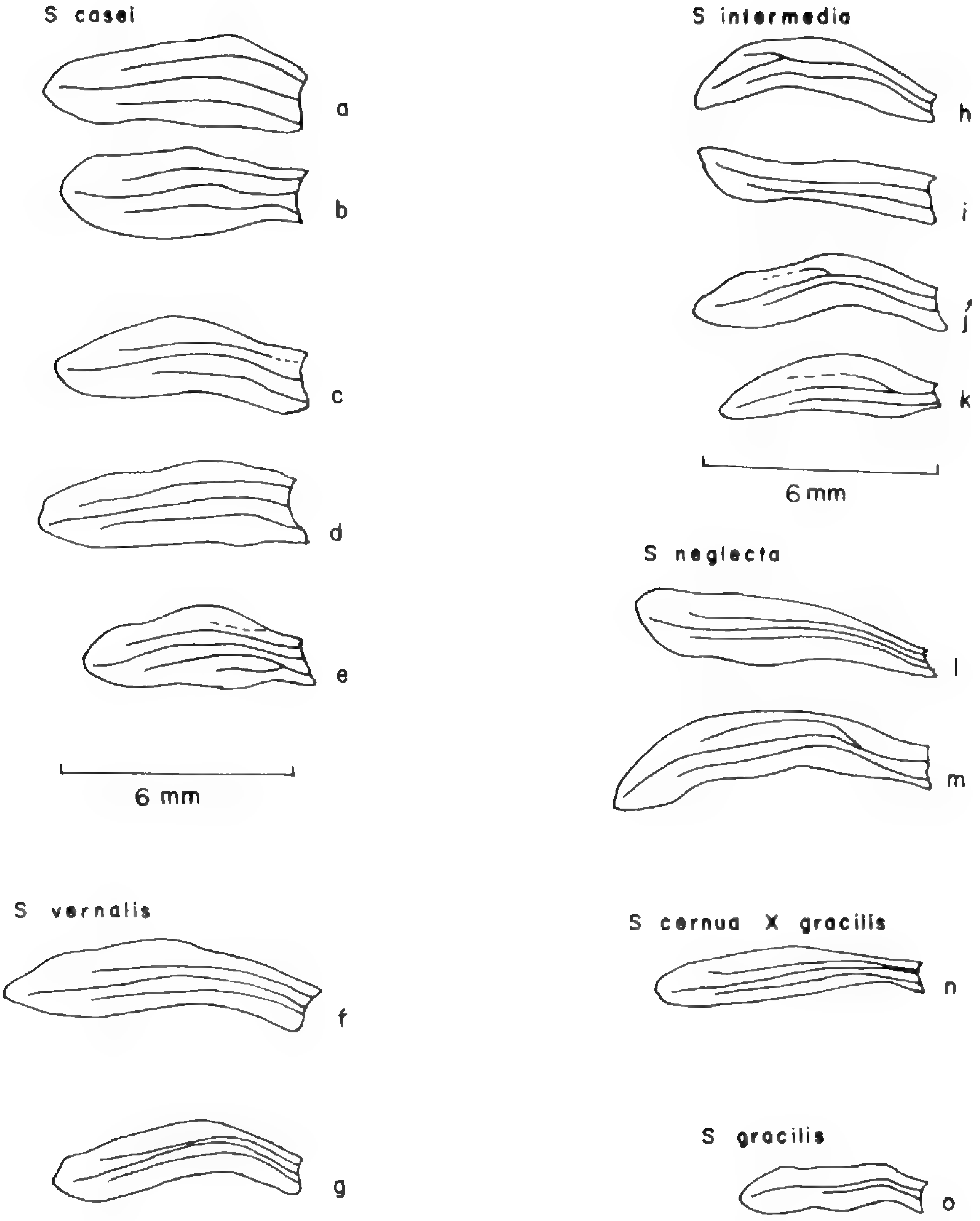

Figure 2. **Camera-lucida drawings of lateral petals of Spiranthes spp.** a-e, *S. casei* Catling & Cruise; a, b, TYPE (TRT 169205); c, New Hampshire (AMES 67224); d, Quebec (AMES 63778); e, Michigan, *Bob & Fassett 9484* (WIS); f, g, *S. vernalis* Engelm. & Gray; f, Missouri, *Palmer,* 14 June 1958 (WIS); g, Connecticut, *Eames,* 8 Aug. 1897 (WIS); h-k, *S. intermedia* Ames, TYPE (AMES 2246); l, m, *S. neglecta* Ames, TYPE (AMES 2518); n, *S. cernua* × *gracilis* Ames, TYPE (AMES 17391); o, *S. gracilis* (Bigel.) Beck., Massachusetts, *Wiegand* (WIS).

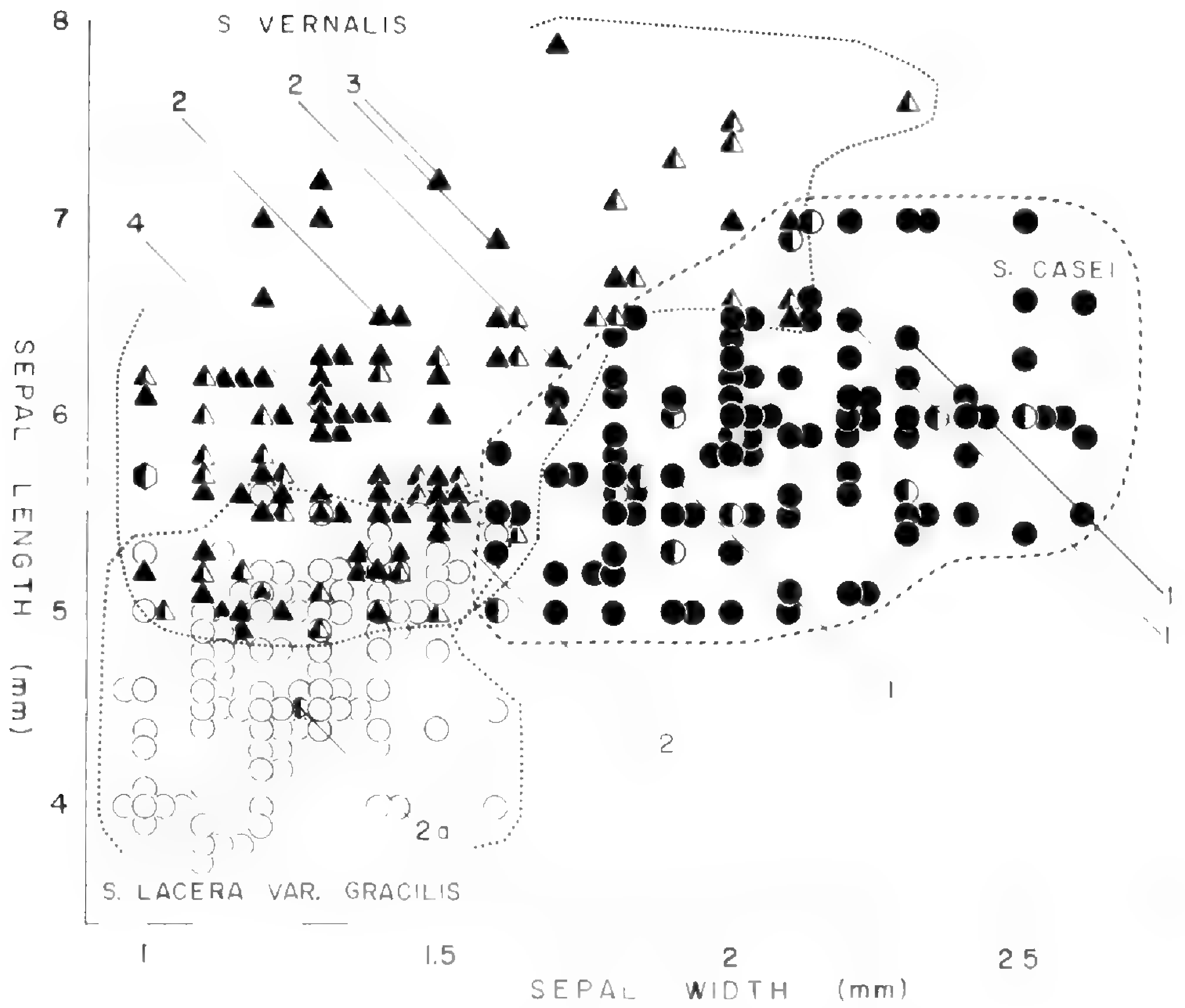

Figure 3. Sepal width plotted against sepal length for *S. lacera* var. *gracilis*, *S. vernalis*, and *S. casei*, with various symbols representing different pubescence types, and shading representing different pubescence lengths. 1, *S. casei* Catling & Cruise TYPE (TRT 169205); 2, *S. intermedia* Ames TYPE (AMES 2246); 2a, *S. intermedia* Ames COTYPE (AMES 2246); 3, *S. neglecta* Ames TYPE (AMES 2518); 4, *S. cernua* × *gracilis* Ames TYPE (AMES 17391). The triangles represent pointed non-glandular pubescence, whereas the circles indicate glandular-capitate pubescence. Intermediate pubescence is shown with a hexagonal symbol. Relative lengths of pubescence are indicated with three degrees of shading. No shading indicates pubescence 0–0.12 mm. in length, partial shading indicates 0.13–0.25 mm., and full shading indicates pubescence 0.26–0.43 mm. long.

of lateral sepal length versus lateral sepal width, again with pubescence characters represented symbolically to reduce species identification prejudice. The types of *S.* × *intermedia*, *S. neglecta* and *S. cernua* × *S. gracilis* again fall with *S. vernalis*, while *S. casei* and its types are altogether discrete.

This morphological re-evaluation, including type material, demonstrates that *Spiranthes casei* is quite distinct from the *S. vernalis* complex (including *S.* × *intermedia*) in the type of pubescence; in

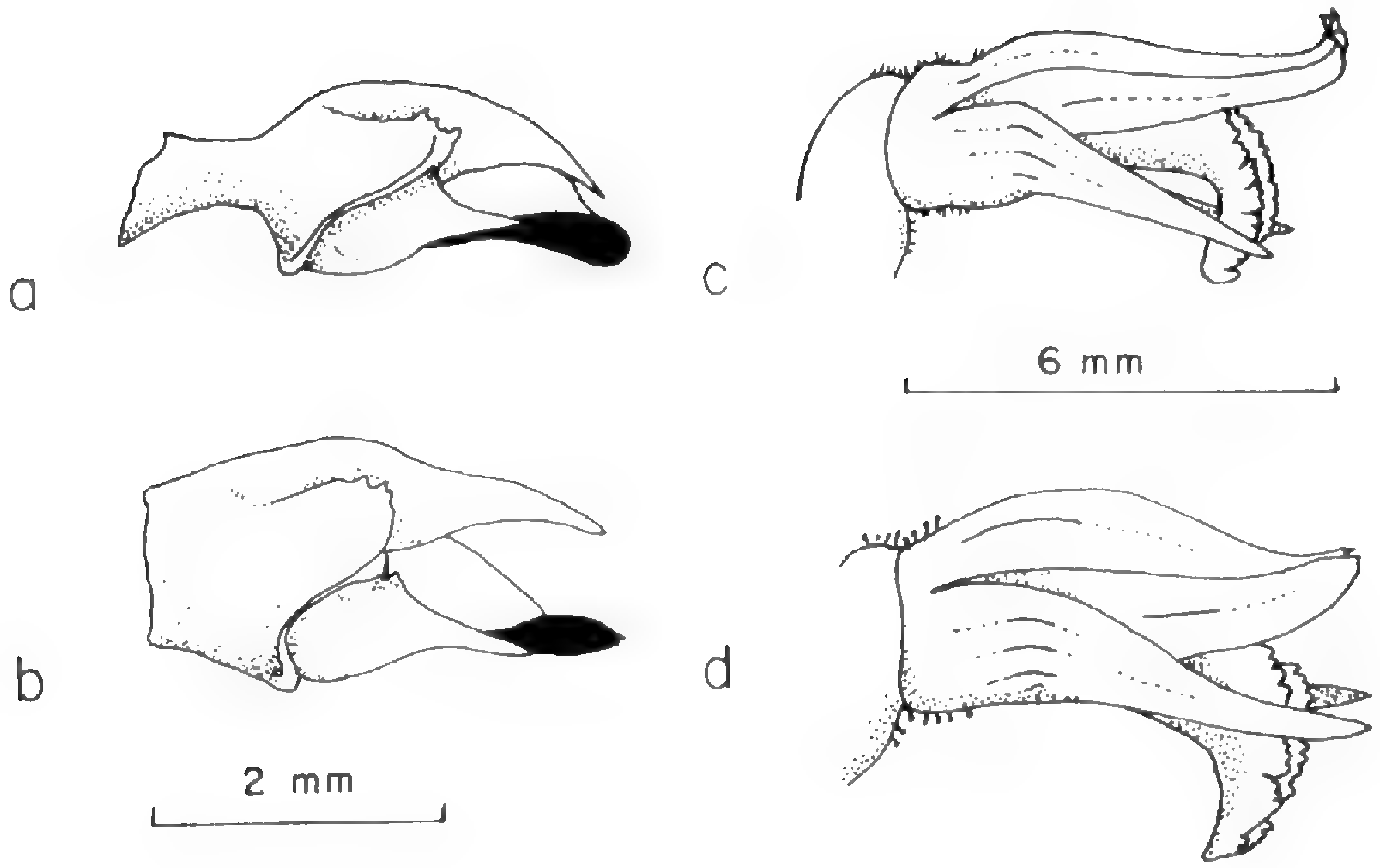

Figure 4. a,b, lateral view of column of a, *S. intermedia* Ames (AMES 2246 holotype), b, *S. casei* Catling & Cruise (AMES 63778); c,d, lateral view of flowers of c, *S. intermedia* Ames (AMES 2246 holotype), d, *S. casei* Catling & Cruise (AMES 63778).

the shape, size and venation of lateral petals; in the shape of the lateral sepals; in the morphology of the lip; in the structure of the column; in certain details of floral structure and in the floral density of the spike.

Although the types of *Spiranthes neglecta* and the specimen of the putative *S. cernua* × *S. gracilis* appear to closely resemble *S. vernalis*, *S.* × *intermedia sensu* Ames does seem to demonstrate some intermediacy between *S. vernalis* and *S. lacera* var. *gracilis* with respect to lip size, shape and major venation (Figure 1). An intermediate condition is apparent in the lateral petals, where, although some variability in shape occurs, the venation frequently involves a third secondary vein as opposed to the two veins of *S. lacera* var. *gracilis* and the characteristic three veins of *S. vernalis* (Figure 2). Intermediacy of *S.* × *intermedia* is also apparent in its variability in pubescence (Figure 3), the general appearance of the flowers, the floral density of the spike (Figure 5), and notably in flower color (see above). The type specimens of *S.* × *intermedia* are remarkably diverse, with one falling in the blend area of *S. vernalis* and *S. lacera*

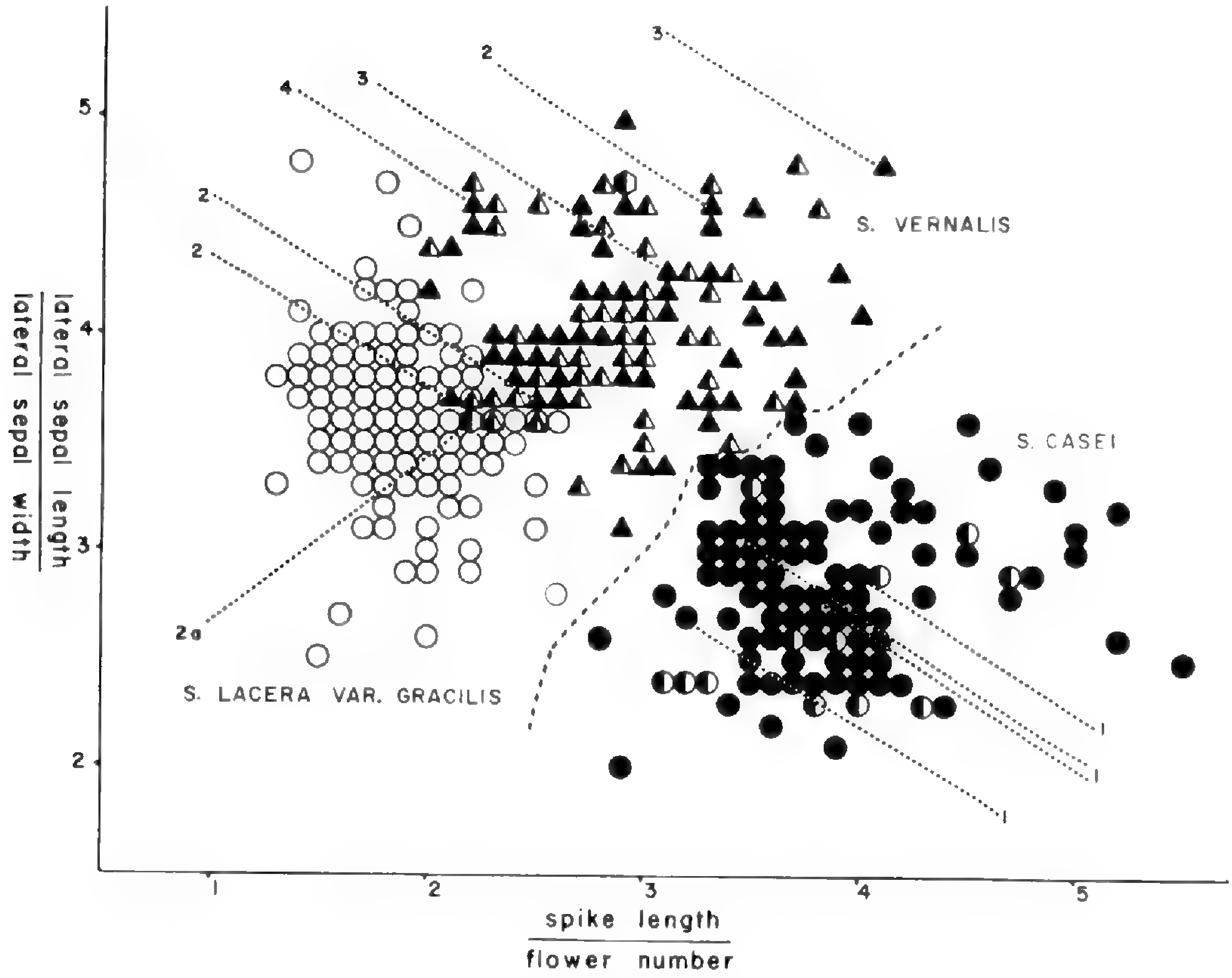

Figure 5. The ratio of lateral sepal length/lateral sepal width plotted against the ratio of spike length/flower number. Symbols and types as in Figure 3.

var. *gracilis* in both Figures 3 and 5. An isotype specimen of *S.* × *intermedia* with pubescence characters unlike *S. vernalis*, appears in the middle of *S. lacera* var. *gracilis* in Figure 3 and along the peripheral blend zone in Figure 5, further suggesting its possible hybrid origin.

Spiranthes × *intermedia* is reported to grow in close association with its putative parents, *S. vernalis* and *S. lacera* var. *gracilis*, and it also flowers at the same time (Ames, 1903; St. John, 1918). This habit is in keeping with a hybrid interpretation. Although *S. lacera* var. *gracilis* and *S. vernalis* flower simultaneously in southern New England, further to the south *S. vernalis* flowers much earlier. In New Jersey, when *S. lacera* var. *gracilis* is in anthesis in late August, *S. vernalis* has already passed flowering. The simultaneous flowering in southern New England may have led to the hybridization that created the taxonomic difficulties that prompted Ames to study this hybrid complex and resulted in his broad concept of *S. vernalis* (Ames, 1924).

Of course, it would be desirable to study this hybrid complex in the field, but unfortunately the open meadow habitats at the type localities around Easton, Mass., appear to have been largely destroyed by urban development, and also by natural succession to scrub and woodland. Perhaps 70 years ago with the forest cleared by cutting and burning, and a farming community based on pasturelands, *Spiranthes* spp. were much more frequent in the area.

Field and cytological study is certainly desirable to demonstrate further the probable hybrid nature of *S.* × *intermedia.* The possibility of *S. cernua* contributing to the hybrid complex is also worthy of investigation.

CONCLUSIONS

Based on a critical review of existing literature and on actual re-examination of type specimens, the plants described and illustrated as *Spiranthes intermedia* Ames (*pro* hybr.) by Luer (1975) fall into synonymy with *S. casei* Catling & Cruise (1974). Reports of *S. vernalis* in the eastern townships of Quebec actually refer to *S. casei,* which has a more northern distribution and is absent from southern New England. The name *S.* × *intermedia* should be retained for hybrids which may still occur in southern New England where *S. vernalis* and *S. lacera* var. *gracilis* occur together and flower simultaneously. *Spiranthes cernua* × *S. gracilis* Ames and *S. neglecta* Ames, although perhaps a part of a hybrid complex, appear to be sufficiently similar to *S. vernalis* to be placed in synonymy.

ACKNOWLEDGEMENTS

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NOTES ON THE GENUS ERAGROSTIS (GRAMINEAE) IN THE SOUTHEASTERN UNITED STATES

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In the 20 years since the last major treatment of *Eragrostis* for the United States (Hitchcock, 1950), our knowledge of the genus has grown, largely as a result of the numerous recent floras of many parts of the world. As a consequence, there are a number of taxonomic and nomenclatural changes involving members of the genus which are found in the southeastern United States and which have been overlooked in the more recent floras of the region (Radford, et al., 1968; Long & Lakela, 1971). These are discussed together with results of my own investigations.

In the following only names which are relevant to the discussion or are basionyms for such names are included. More nearly complete synonymy is available in Harvey (1948) and Hitchcock (1950).

Eragrostis N.M. von Wolf, Gen. Pl. Vocab. Char. Def. 23. 1776. TYPE SPECIES: *E. eragrostis* (Linnaeus) von Wolf (= *E. minor* Host).

Eragrostis Host, Icon. Gram. Austr. **4:** 14. 1809. Nom. nud.

Eragrostis P. de Beauvois, Ess. Agrost. 70. 1812. TYPE SPECIES: *E. eragrostis* (Linnaeus) Beauvois (= *E. minor* Host).

Neeragrostis Bush, Trans. Acad. St. Louis **13:** 178. 1903. *Emend.* Nicora, Rev. Argent. Agron. **29:** 3. 1962. TYPE SPECIES: *Neeragrostis weigeltiana* (Reichenbach) Bush [≑ *E. reptans* (Michaux) Nees].

Diandrochloa de Winter, Bothalia **7:** 387. 1960. TYPE SPECIES: *Diandrochloa namaquensis* (Nees) de Winter (= *E. namaquensis* Nees).

As pointed out by Ross (1966), von Wolf's valid and effective publication of *Eragrostis* antedates that by Palisot de Beauvois. This fact has unfortunate consequences for the name of a common weed, *E. poaeoides* Beauv. ex Roem. et Schult. (see below).

Two segregate genera of *Eragrostis* have been proposed. Bush regarded the creeping habit and unisexual nature of the spikelets of *E. hypnoides* (Lam.) B.S.P. and *E. reptans* (Michx.) Nees sufficient grounds to erect a new genus, *Neeragrostis* Bush. Hitchcock (1926) later pointed out that *E. hypnoides* has uniformly hermaphroditic florets, but that *E. reptans* is truly dioecious. He also returned the two species to *Eragrostis*, a placement with which

Harvey (1948) agreed. Nicora (1962) thoroughly re-examined the matter and concluded that *Neeragrostis* is a valid segregate, but that the hermaphroditic *E. hypnoides* should be excluded, thus reducing the genus to a single species, *N. reptans* (Michx.) Nicora. She based her conclusions on five characters: 1. *Neeragrostis* is dioecious, *Eragrostis* hermaphroditic. 2. The creeping habit of *Neeragrostis* is unusual in *Eragrostis.* 3. The styles in *Neeragrostis* are attached to the ovary at a single point, and are unusually elongate, while they are shorter and attached at two separate points on top of the ovary in *Eragrostis.* 4. The bicellular microhairs in *Neeragrostis* are extremely long, due to the elongation of the basal cell to 70–230μm. 5. The silica bodies in *Neeragrostis* are dumbbell-shaped.

Further examination of these characters in *Eragrostis,* especially in *E. hypnoides,* shows that the differences are really not as clear as they seem at first. Dumbbell-shaped silica bodies are the predominant type in *E. tenella* (L.) Beauv. ex Roem. et Schult., and are one of several types present in *E. capillaris* (L.) Nees and *E. hypnoides.* While the basal cells of the bicellular microhairs in *Neeragrostis* are considerably longer than the 20–30 μm typical of *Eragrostis,* those of *E. hypnoides* are also longer than usual (40–65 μm). Furthermore, the unusual length of these hairs in *Neeragrostis* may well be related to their function as glands, since the hairs in all species of *Eragrostis* with which I am familiar are eglandular. The long, thin styles in *Neeragrostis* allow the stigmas to be exserted near the distal end of the floret, as Nicora points out. This is probably an adaptation to compensate for the extremely condensed pistillate inflorescence in this species, but it is also seen in *E. hypnoides.* The placement of the styles on the ovary in *Neeragrostis* is different from all species of *Eragrostis* that I have examined. However, this condition is approached in *E. hypnoides,* in which the style bases are separated during anthesis but come to lie in contact at maturity because the part of the ovary between the bases does not enlarge with the rest of the ovary, and the bases themselves swell. The growth habitat of *Neeragrostis* and *E. hypnoides* is essentially the same, and, furthermore, a creeping, stoloniferous habit is also found in the apparently unrelated, African *E. barbinodis* Hack. and *E. bergiana* (Kunth) Trin. Thus, the only character in which *Neeragrostis* is clearly distinct from *Eragrostis* is in its sexuality. It is approached in all other characters by *E. hypnoides,* which appears to be the evolutionary link between *Neeragrostis reptans* and the rest of the genus *Eragrostis,* to which it properly belongs.

As pointed out by its author, the recent discovery (Pohl, 1977) of *Eragrostis contrerasii* R. W. Pohl further supports this conclusion. This Central American species with a creeping habit occupies an intermediate position between *E. reptans* and *E. hypnoides* in that it is dioecious like the former, but both its pistillate and staminate inflorescences are open like those of *E. hypnoides* and staminate plants of *E. reptans.*

De Winter's segregate *Diandrochloa* (1960), is based on two African species, *Eragrostis namaquensis* Nees and *E. pusilla* Hack. He also recommends the transfer of several other species, among which is *E. glomerata* (Walt.) Dewey, a species of the southeastern United States. This segregate genus is based on the species having membranaceous ligules (vs. ligules of hairs), two (vs. three) stamens per floret, and spikelets which are small and delicate, morphologically very similar to those of *E. ciliaris* (L.) R. Br., except that the paleas lack long cilia on their keels. In addition, they are hydrophilous and have somewhat smaller chromosomes than is usual in *Eragrostis.* Of these, the only character which is truly unique and distinctive is the membranaceous ligule. Only two stamens are found in the florets of many American species, e.g., *E. bahiensis* Schrad., *E. secundiflora* Presl, and *E. elliottii* S. Wats. The similarity in spikelet structure between *Diandrochloa* and *E. ciliaris* et aff. is in their small size and disarticulating rachillas. The latter is a widespread character in *Eragrostis,* and spikelet size is quite variable in the genus. The spikelets of *E. spicata* Vasey and *E. frankii* C. A. Meyer, both of which have ligules composed of hairs, are nearly as small as those of *Diandrochloa.* With respect to other spikelet characters, especially the shape and texture of the lemma and the prominence of its lateral nerves, there is at least as strong a similarity between *E. ciliaris* et aff. and the American *E. spectabilis* (Pursh) Steud. or the African *E. aspera* (Jacq.) Nees as between *E. ciliaris* et aff. and the species included in *Diandrochloa.* Hydrophilly is found in several unrelated species, e.g., *E. refracta* (Muhl.) Scribn., *E. lutescens* Scribn., and *E. frankii,* and the differences in chromosome size need further examination since chromosome size is quite difficult to measure accurately. I feel that as there is only one unique character which separates the species included in *Diandrochloa* from the rest of *Eragrostis,* recognition at the sectional level is more appropriate.

Eragrostis atrovirens (Desfontaines) Trinius ex Steudel, Nom. Bot., ed. 2. **1:** 562. 1840.

Poa atrovirens Desfontaines, Fl. Atlant. **1:** 73, *tab. 14.* 1789.

Eragrostis chariis (Schultes) A. S. Hitchcock, Lingan Sci. Jour. **7:** 193. 1929 [1931]. Sensu Hitchcock, *ibid.;* Manual. 166. 1935; Manual, ed. 2. 167. 1950 [1951], not Schultes.

Eragrostis nutans (Retzius) Nees ex Steudel, Nom. Bot., ed. 2, **1:** 563. 1840. Sensu Long & Lakela, Flora Trop. Florida. 148. 1971, not Retzius.

In making the new combination, *Eragrostis chariis* (Schult.) Hitchc., Hitchcock misapplied Schultes' *Poa chariis* to this widespread African and Asian species, which has been introduced into the southeastern United States. Bor (1960) corrected the error finding that *Poa chariis* Schult., and therefore *E. chariis,* is a synonym of *E. nutans* (Retz.) Nees ex Steud. Long and Lakela (1971) then applied the name *E. nutans* to our representatives of this species. This application is incorrect, for *E. nutans* clearly differs from our plants in several respects, among which are the smaller spikelets (lemmas 1.25 mm long vs. ca. 2 mm long), paleas which persist after the lemma and caryopsis have fallen (vs. paleas falling with the lemmas and caryopsis), and the contracted (vs. open) panicles of *E. nutans.* The determination of our plants as *E. atrovirens* has been confirmed by N. L. Bor (pers. comm.).

Eragrostis bahiensis Schrader ex Schultes, Mantissa **2:** 318. 1824.

Eragrostis expansa Link, Hort. Berol. **1:** 190. 1827.

Eragrostis bahiensis Schrad. ex Schult. has been introduced into the United States from South America, where it is found from Bolivia and southern Brazil south to central Argentina (Burkart, 1969; Cabrera 1970; Hitchcock, 1927). In South America it has been a source of confusion because of its variable panicle morphology and spikelet color. On the basis of this variation, Hitchcock (1927) recognized two taxa, *E. bahiensis* sensu stricto, and *E. expansa* Link. Both of these are found in the United States, although

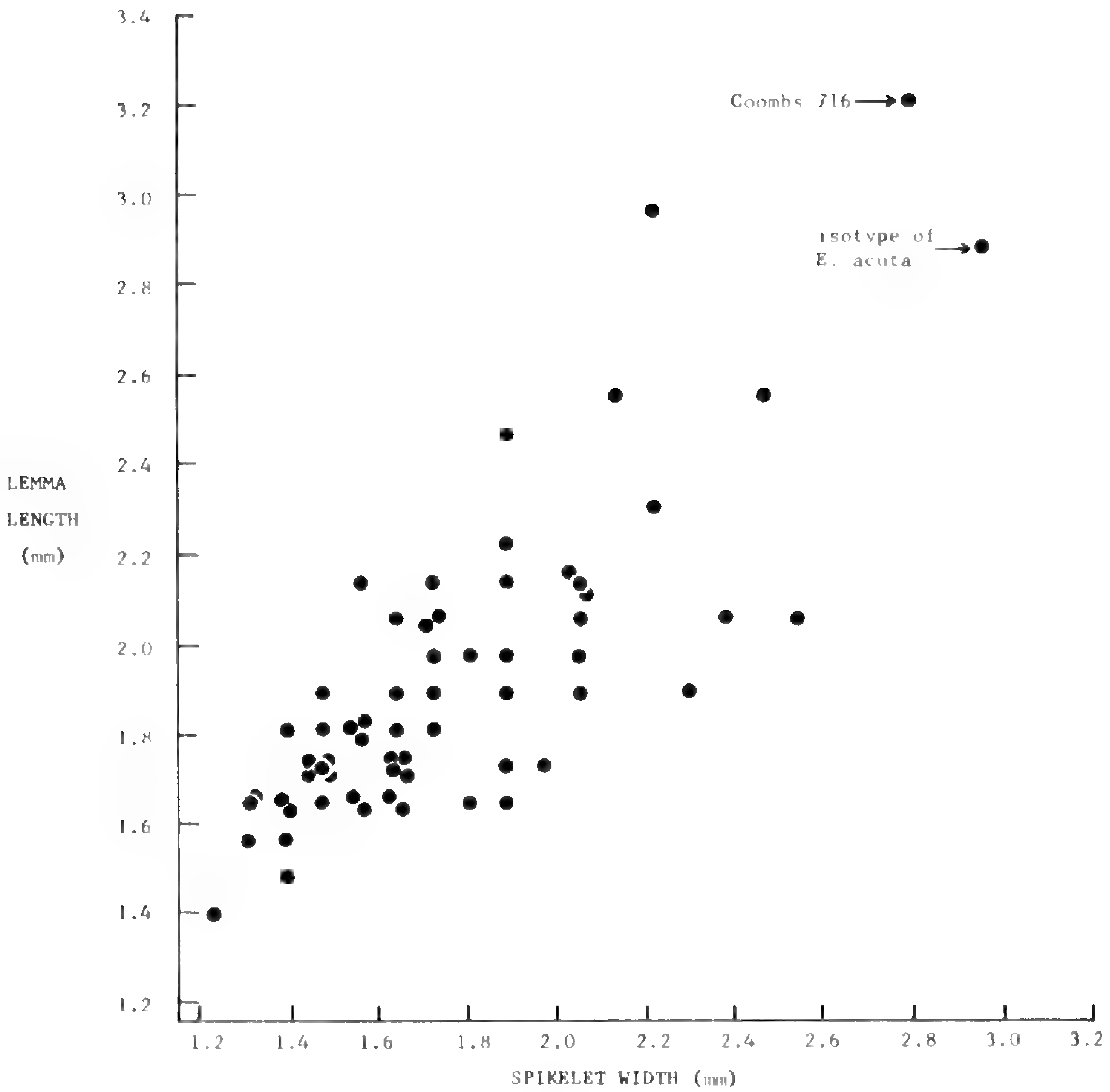

Figure 1. *Eragrostis elliottii.* Scatter diagram showing variation in characters used to separate *E. elliottii* and *E. acuta.* $n = 63$. *Coombs 716* was cited in the original description of *E. acuta.*

the occurrence here of *E. expansa* has not previously been reported.

Burkart (1969) united these under *Eragrostis bahiensis* sensu lato, with the approval of E. Nicora, who has been interested in *Eragrostis* in South America for years, and who assisted in his treatment of the genus. As Hitchcock had done, Rosengurtt et al. (1970) recognized both species, distinguishing them on the basis of the degree of panicle contraction. Examination of the South American material at the U.S. National Herbarium convinced me that this is a highly variable character in *E. bahiensis,* as it is in many other *Eragrostis* species. Consequently, I agree with Burkart that *E. expansa* and *E. bahiensis* sensu stricto, are the same.

Eragrostis cumingii Steudel, Syn. Pl. Glum. **1:** 206. 1854.

Eragrostis simplex Lamson-Scribner, U. S. Dept. Agric. Div. Agrost. Bull. 7 (ed. 3): 250. *fig. 244.* 1900. LECTOTYPE, **Florida:** Istachatta, dooryard, 26 Aug. 1897, *A. H. Curtiss 6073,* (U. S. Nat. Herb. no. 314,483), US! Isotype, US!.

On the basis of Jansen's (1953) study of the closely related *Eragrostis elongata* (Willd.) Jacq., *E. zeylanica* Nees et Meyer, and *E. cumingii* Steud., and the Old World material of these three species at the U. S. National Herbarium, it is clear that our *E. simplex* Scribn., of Florida, southern Georgia, and Alabama, is the same as *E. cumingii,* a species native to Burma, Malaysia, the Philippines, and Australia (Bor, 1960). Although the Old World material is somewhat more variable than ours with respect to plant size and degree of pilosity of the blades and sheaths, both share such important characters as open panicles with rather distant primary branches which spread at right angles to the panicle axis; short-pedicelled spikelets which are usually crowded onto very short secondary panicle branches; more or less flattened spikelets which are 1.5–2 mm wide; lemmas 1.5–2 mm long and identically shaped; paleas with short-ciliate keels which persist after the lemma and caryopsis have fallen; a tendency for the spikelets to break up both from above and below by the lemmas and caryopses falling from below and the rachilla disarticulating from above at maturity, three stamens per floret; identical, dark to pale brown, ovoid caryopses; and an annual life cycle.

The phytogeographical problem presented by the wide disjunction between the Old and New World distributions of this species is probably best explained by assuming that it was introduced into the New World by European man. This hypothesis is supported by (1) the earliest collection I have seen was made rather recently, in 1894; (2) it is a "rather common species, locally very abundant" (Jansen, 1953, p. 271) in Malaysia; (3) its closest relatives occur in the Old World part of its distribution; (4) according to herbarium labels it occurs in typically weedy habitats in the United States; (5) it is an annual and appears to be cleistogamous as suggested by the dehisced anthers that are common inside the florets and the lack of exserted anthers or stigmas on any of the specimens I examined; and (6) there is a precedent among grasses for such wide disjunctions between the United States and distant countries, e.g., the occurrence of the Australian *Eragrostis elongata* (Willd.) Jacq.

in Florida (see Casual Introductions), Gould and Lonard's (1970) report of the African *Eragrostis plana* Nees from Jamestown, South Carolina, and R. Kologiski's discovery of *Dinebra retroflexa* (Vahl) Panzer, an African species, growing in Charlotte, North Carolina (pers. comm.).

Eragrostis elliottii S. Watson, Proc. Am. Acad. Arts & Sci. **25:** 140. 1890. Based on *Poa nitida* Elliott.

Poa nitida Elliott, Botany of S.C. and Ga. **1:** 162. 1816. Not Lamarck, 1791, nor *Eragrostis nitida* Link, 1827. HOLOTYPE. **South Carolina:** Charleston, Paris Island, *Elliott s. n.*, CHARL.

Eragrostis acuta A. S. Hitchcock, Proc. Biol. Soc. Wash. **41:** 159. 1928. HOLOTYPE, **Florida:** Punta Rassa, Jul. 1900, *Hitchcock 263,* (U.S. Nat. Herb. no. 7,311,236), US!. Isotype, (U.S. Nat. Herb. no. 1,503,824), US!.

As noted in the original description of *Eragrostis acuta* Hitchc., this rare species from western Florida strongly resembles the more widely distributed *E. elliottii* S. Wats., the only differences being that *E. acuta* has longer lemmas and wider spikelets. Harvey (1948) reduced *E. acuta* to synonymy under *E. elliottii,* but it was treated as a distinct species in both editions of Hitchcock's *Manual* (1935 & 1950).

Examination of type material failed to turn up any additional differences except that both the isotype and *Coombs 716* (US), cited in the original publication, were nearly sterile, and, on many spikelets, one to several of the lower lemmas was unusually elongate. Measurements of spikelet width and lemma length on the 63 specimens of *E. acuta* and *E. elliottii* (including 7 from western Florida) at DUKE and NCU demonstrated that the isotype and *Coombs 716* are merely extremes in a pattern of variation which is typical for a single species (Figure 1).

The geographic distribution of plants referable to *Eragrostis acuta* also conforms to the pattern expected for extreme individuals within a normal pattern of variation. There are only about a dozen, widely scattered collections of *E. acuta,* and they are all found within the distribution of *E. elliottii.* Nor are these extreme individuals restricted to western Florida. I have seen collections referable to *E. acuta* from Dade, Leon, Madison, Monroe, and Palm Beach counties in Florida, as well as locations in Alabama.

The high degree of sterility and atypical elongation of some of the lemmas suggest that possibly the spikelets were infected with a fungus, some of which are known to induce enlargement of the infected parts. There were, however, no externally visible signs of such an infection. In any case, it seems clear to me that *Eragrostis acuta* should be reduced to synonymy under *E. elliottii.*

Eragrostis minor Host, Icon. Descr. Gram. Aust. **4:** 15. 1809. Based on *Poa eragrostis* Linnaeus.

Poa eragrostis Linnaeus, Sp. Pl. **1:** 68. 1753. HOLOTYPE, *Habitat in Italia supra muros. D. Baecker s. n.,* LINN. Microfiche!

Eragrostis eragrostis Beauvois, Ess. Agrost. 71, 174; *pl. 14, fig. 11.* 1812. Based on *Poa eragrostis* Linnaeus.

Eragrostis poaeoides Beauvois ex Roemer et Schultes, Syst. Veg. **2:** 574. 1817. Based on *Poa eragrostis* Linnaeus.

Unfortunately, as a result of the change of date of valid publication of the genus, the name of this worldwide weed must be changed from *Eragrostis poaeoides* Beauv. ex. Roem. et Schult. to *E. minor* Host. Although Host validly and effectively published *E. minor* in 1809, his name has been rejected until now because, prior to Ross' paper in 1966, *Eragrostis* was not considered to be validly published until 1812.

Eragrostis secundiflora Presl ssp. **oxylepis** (Torrey) S. D. Koch, comb. nov. Based on *Poa oxylepis* Torrey.

Poa interrupta Nuttall, Trans. Amer. Phil. Soc., n. s., **5:** 296. 1837. Not Lamarck, 1791. HOLOTYPE, **Arkansas:** In bushy prairies near the sandy banks of the Arkansas River, *Nuttall s. n.,* PH!

Poa oxylepis Torrey in Marcy, Expl. Red. River. 301, *pl. 19.* 1853. Based on *Poa interrupta* Nuttall.

Eragrostis oxylepis (Torrey) Torrey, U.S. Expl. Miss. Pacif. Rept. **4:** 156. 1857.

Eragrostis beyrichii J. G. Smith, Rept. Mo. Bot. Gard. **6:** 117. *pl. 56.* 1895. Type specimen apparently lost; see Harvey (1948).

Eragrostis secundiflora Presl, Reliq. Haenk. **1:** 276. 1830. HOLOTYPE, **Mexico,** *Haenke s. n.,* PR. Photograph and fragment at US! Sensu Small, Manual. 124. 1938; Hitchcock, Manual. 144. 1935, not Presl.

Eragrostis oxylepis var, *beyrichii* (J. G. Smith) Shinners, Field & Lab. **20:** 34. 1952.

The work of Koch and Currie (1973) has shown that although extreme specimens of *Eragrostis oxylepis* (Torr.) Torr. and *E. beyrichii* J. G. Smith can be distinguished, there is continuous variation between the two in all characters. Therefore, all taxonomic distinctions between the two are abandoned, as was done by Correll and Johnston (1970) and Harvey (1975).

There is little doubt that *Eragrostis oxylepis,* from the southeastern United States, and the Mexican *E. secundiflora* Presl are part of the same species, as was indicated by Harvey (1975). Furthermore, the Brazilian *E. compacta* Steud. is also part of *E. secundiflora,* as suggested by Pilger (1939) and Harvey (1948), who actually reduced *E. compacta* to synonymy under *E. secundiflora.* All three elements in this species share the important characters of a perennial life cycle; a robust habit; spikelets which are generally densely clustered on elongate to very short, usually somewhat distant panicle branches, and which are strongly laterally flattened; reddish, leathery, strongly keeled and prominently nerved lemmas; disarticulating rachillas; and two stamens with very small anthers in each floret.

Within this species, however, there are two distinct elements separated by rather minor morphological differences and a major geographical disjunction. One of these, subspecies *oxylepis* (Torr.) S. D. Koch, is relatively common, being found primarily in Texas, but with significant extensions along the Gulf Coast east to Florida, and south to the city of Veracruz, Mexico. Subspecies *secundiflora* (= *E. compacta*), also appears to be relatively common, but it occurs in eastern Brazil, east of the states of Maranhão, Goias, and São Paulo. In northern South America, Central America, and the West Indies, both subspecies are absent. Surprisingly, subspecies *secundiflora* is known from two localities in southern Mexico, Acapulco, Guerrero (*Haenke, s. n.,* US), and Pochutla, Oaxaca (*Liebmann 12864,* US).

The subspecies differ morphologically in two respects: 1. In subspecies *oxylepis,* the plants have glabrous sheaths and blades, except for a tuft of hairs flanking the base of the blade at the top of the sheath; in some specimens the adaxial side of the base of the blade is densely hirsute, the hairs occasionally arising from papillae. In subspecies *secundiflora,* the sheaths and both sides of the blades are typically densely invested with long, pustulate-based hairs; in a few specimens these hairs are restricted to the upper third of the sheath and lower third of the blade. 2. In subspecies *oxylepis,* the caryopses are elongate-ovoid, 0.7–1.2 mm long and

0.4–0.6 mm wide, the length : width ratio being about 2. In subspecies *secundiflora,* the caryopses are ovoid, 0.6–0.7 mm long and 0.4 mm wide, the length : width ratio being about 1.5. The southern Mexican specimens have caryopses like those of subspecies *secundiflora,* but are intermediate with respect to hairs — the adaxial sides of the blades are pilose, the abaxial sides glabrous, and the sheaths have fringe of long hairs along the upper third of their margins.

Because of this classical pattern of correlated morphological and geographical discontinuity, I feel that the two components of *Eragrostis secundiflora* should be recognized as separate subspecies. It seems likely that there was once a connection between the two, and that the very rare southern Mexican collections are representatives of relict populations.

The type collection, which consists of two sheets, is from one of these relict populations in Mexico. According to L. H. Harvey (pers. comm.), who has seen the holotype, the hairs of the sheaths and blades vary from the intermediate condition typical of plants from this area to the nearly glabrous condition seen in subspecies *oxylepis.* However, as the caryopses of the holotype and the panicle fragment at the U.S. National Herbarium are typical of subspecies *secundiflora,* I am assigning the holotype to the Brazilian subspecies.

Eragrostis tenella (Linnaeus) Beauvois ex Roemer et Schultes, Syst. Veg. **2:** 576. 1817.

Poa tenella Linnaeus, Sp. Pl. **1:** 69. 1753. HOLOTYPE, **India.** Annotated "14 tenella" by Linnaeus. LINN. Microfiche!

Poa amabilis Linnaeus, Sp. Pl. **1:** 68. 1753. LECTOTYPE, *Plukenet,* Alm. bot., *tab. 300, fig. 2!* 1696.

Eragrostis amabilis (Linnaeus) Wight et Arnott ex Nees in Hooker et Arnott, Bot. Beechey Voyage. 251. 1838.

Basing his conclusions on the unpublished research of Otto Stapf, Bor (1960 and pers. comm.) pointed out that *Eragrostis amabilis* (L.) Wight et Arn. ex Nees is the same species as *E. tenella* (L.) Beauv. ex Roem. et Schult. Since Hooker (1896, p. 315) was the first to unite the two, and he used the latter name, *E. tenella* is the correct name for this species (Art. 57, Internatl. Code Bot. Nom., 1972).

Eragrostis tracyi Hitchcock, Amer. Jour. Bot. **21:** 130, *fig. 1.* 1934. HOLOTYPE, **Florida:** Lee Co., Sanibel Island, 19 May, 1901, *S. M. Tracy 1768.* (U.S. National Herbarium no. 441,983). US!

Koch (1972) showed that this "apparently perennial" (Hitchcock, 1950) Florida endemic is really an annual. Although closely related to *Eragrostis tephrosanthos* Schult., a widespread, annual species of the southwestern United States, Mexico, Central America, the West Indies, and the Gulf Coast of the United States, it is easily distinguished from the latter by its anthers.

CASUAL INTRODUCTIONS

The small caryopses, tendency toward weediness, and self-fertility or even cleistogamy of many species of *Eragrostis* make casual introductions of members of the genus outside their natural distributions very likely. It comes as no surprise, then, that there are a number of species native to distant areas which have been collected once, twice, or even thrice in the Southeast.

While admitting the highly subjective nature of such decisions, I have indicated with an asterisk those species which I feel are likely to be introduced repeatedly and should be considered part of the flora.

Eragrostis barrelieri Daveau. This is a Mediterranean species which has become naturalized in Mexico, the West Indies, and the southwestern United States, east to Texas and Kansas (Hitchcock, 1950). In the southeast, it has been collected once on manganese ore piles in Baltimore, Maryland (*C. F. Reed 43644,* US).

***Eragrostis domingensis** (Pers.) Steud. This West Indian and Central American species has been reported from Plantation Key, Monroe Co., Florida by Lakela (1969). It was also collected on 20 June 1935 "near border of Georgia" (*W. A. Silveus 2279,* US).

Eragrostis elongata (Willd.) Jacq. A single specimen of this species, previously unreported from the United States, was found in the U.S. National Herbarium (Florida: Collected in 1897, *Simpson s. n.,* [Herb. Chas. H. Mohr], US). It was misidentified as *E. simplex* Scribn. (= *E. cumingii* Steud.), but is clearly distinct from the latter in that it has two (vs. three) anthers per floret; spikelets which break up only from above, the lemmas and paleas persisting and the rachillas disarticulating at maturity (vs. spikelets which break up from both above and below, the lemmas falling away below and the rachillas disarticulating above at maturity); paleas with scabrous (vs. short-ciliate) keels; very short panicle branches with dense, sessile clusters of spikelets (vs. more elongate branches with more distant spikelets); and a perennial (vs. annual) life cycle. Simpson's specimen fits Jansen's (1953) description of *E. elongata,* a common Australian species, and also matches perfectly the Australian material of this species in the U.S. National Herbarium.

Eragrostis gangetica (Roxb.) Steud. has been collected near Biloxi, Mississippi (Harvey, 1948; Hitchcock, 1950), and near Lake Trafford, Collier Co., Florida (*Koch 7127,* NSC). This annual Indian species has been known as *E. stenophylla* Hochst. ex Miq., but, as Bor (1960) pointed out, *E. gangetica* has priority.

Eragrostis mexicana (Hornem.) Link is a weedy species native to Mexico and the southwestern United States. It was reported from Delaware by Fernald (1950), but not by Hitchcock (1950) or Harvey (1948).

***Eragrostis neomexicana** Vasey may be only a more robust form of *E. mexicana,* as is the opinion of Gleason and Cronquist (1963). It too is native to the southwestern United States and Mexico, but has been found in Delaware and Maryland (Fernald, 1950; Harvey, 1948; Hitchcock, 1950).

Eragrostis plana Nees. Gould and Lonard (1971) reported that this tropical African species has been collected twice at the Santee Wool Combing Mill at Jamestown, South Carolina.

Eragrostis scaligera Salz. ex Steud., a species native to northeastern Brazil was found growing in a vacant lot at Naples, Collier Co., Florida (Koch, 1975).

Eragrostis virescens Presl. This Chilean species, which is morphologically nearly identical to *E. orcuttiana* Vasey of California, has been collected in Maryland (Harvey, 1948; Hitchcock, 1950) and Appalachicola, Florida (*Chapman s. n.,* US).

SUMMARY

A review of the taxonomy and nomenclature of a number of *Eragrostis* species which occur in the southeastern United States establishes the following: 1. The author of the genus is N. M. von Wolf, not P. de Beauvois. 2. Neither *Neeragrostis* nor *Diandrochloa* should be recognized as valid segregates. 3. The name *E. atrovirens* must replace *E. chariis* and *E. nutans,* as applied in the United States. 4. *Eragrostis expansa,* a segregate of *E. bahiensis* which occurs in the United States, should not be recognized as valid. 5. *Eragrostis cumingii,* an Asiatic species, is conspecific with and has priority over *E. simplex.* 6. *Eragrostis acuta* should be considered a synonym of *E. elliottii.* 7. The name *E. minor* must replace *E. poaeoides.* 8. *Eragrostis oxylepis* should be reduced to subspecific status under *E. secundiflora.* 9. The name *E. tenella* must replace *E. amabilis.* 10. It is pointed out that *E. tracyi* is an annual, closely related to, but distinct from *E. tephrosanthos.* A list of introduced species which have had only limited success is included, with a brief discussion of each.

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STUDIES ON NEW ENGLAND AGARICS II

Howard E. Bigelow

In the continuing survey of the mycoflora of New England and adjacent areas, several uncommon species belonging to the genera *Stropharia* and *Psilocybe* have been collected. These species are seldom reported and described completely, and there are little data available about their distribution in North America. *Stropharia coronilla, S. hardii, Psilocybe thrausta, P. coprophila, P. merdaria, P. bullacea,* and *P. rhombispora* are described below.

The colors given in quotation marks in the descriptions are those of Ridgway (1912).

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Stropharia coronilla (Fries) Quélet, Champ. Jura et Vosges, p. 255. 1872. Figures 1–3.

Pileus 1.3–5 cm broad, convex or hemispheric at first with an incurved and narrowly inrolled margin, remaining so for some time but becoming unrolled and vertical, not striate, expanding finally to broadly convex, surface moist and dull when fresh, sometimes rather shining when partially dried, glabrous and smooth, light orange yellow (about "ochraceous buff") young and fresh, paler in age (near "cream buff"); context white, moderately thick on disc, pliable. Odor rather fragrant. Taste not distinctive.

Lamellae adnate or rounded at times to sinuate or emarginate, close, broad (3–7 mm), whitish soon pinkish vinaceous, then vinaceous gray and finally chocolate brown, edges crenate, whitish marginate.

Stipe 2.5–4 cm long, apex 3.5–9 mm thick, tapering downward to narrowed base, 2–7 mm, surface glabrous, solid stuffed, often curved, white.

Annulus superior, white with dark striations on upper side, thick, persistent.

Spores 7–8(–8.5) × 5–5.5 μm, elliptic to ovate, one side flattened in side view, smooth, brown in KOH, wall thickened, apiculus hyaline and small, apical pore present, truncate at times, deposit blackish brown. Basidia 17.5–28 × 7–8 μm, 4-spored. Cheilocystidia 22–28 × 7.5–12.5 μm, subsaccate to cylindric, clavate and pedicellate or clavate and bulbous, smooth, walls thin (empty appearing and not with granular content like basidioles). Pleurocystidia of two types: (1) rostrate to mucronate, 27–30 × 8.5–10 μm, with crystalline refractive bodies (chrysocystidia), hyaline to bright yellow, (2) irregular basidioid, 23–26.5 × 6.5–7.5 μm, contents homogeneous, walls smooth and thin. Pileus: cutis hyphae mostly cylindric, 3–8.5(–16) μm diam, golden yellow in KOH, pigment distinctly encrusted, often appearing scalariform, some hyphae smooth, occasional end cells protruding beyond surface; context hyaline, hyphae cylindric to inflated, 11–25 μm diam, cells often short. Hymenophoral trama of subparallel to parallel hyphae, mostly cylindric, 5–9(–15) μm diam, narrow near subhymenium, broad in mediostratum. Oleiferous hyphae present, 5–9 μm diam. Clamp connections present.

Gregarious to subcespitose on lawn. Fall.

MATERIAL EXAMINED. **Massachusetts:** *Bigelow 11558* (collected by H. Hinds) (MASS).

Smith (1949) notes that the pileus may be viscid if very wet conditions prevail at the time of fruiting. Under such circumstances, it would be possible to confuse *Stropharia coronilla* with the viscid *S. semiglobata.* However, the latter grows attached to manure, and the stipe lacks a persistent annulus. The spores are considerably larger (15–19 × 7–9 μm) than those of *S. coronilla.*

Smith (1949) and Hesler (1960) have illustrated the appearance of fresh specimens of *Stropharia coronilla.*

Stropharia hardii Atkinson, Jour. Mycol. **12:** 194. 1906. Figures 4–6.

Pileus (2–)4.5–7 cm broad, hemispheric to convex at first with an incurved margin attached to the partial veil, becoming convex to broadly convex, finally plane, margin even and slightly appendiculate with white veil remains, surface smooth, appressed fibrillose on the disc under a hand lens, matted fibrillose to fibrillose scaly near margin, opaque, subviscid at first soon only moist, finally dry, disc orangish ("warm buff," "ochraceous buff"), becoming paler and more yellowish toward the margin ("maize yellow"); context moderately thick except at edge, white, firm. Odor slightly of green corn or raw potato. Taste mild, pleasant and rather nutty.

Lamellae adnexed or adnate, seceding and rounded in age, close to crowded, narrow to medium broad (3–7 mm), not forked nor intervenose, whitish at first (near "tilleul buff"), darkening to "avellaneous" then "drab," finally to dark purplish brown, edges crenate or fimbriate under a lens, slightly undulate.

Stipe 3.5–8 cm long, apex 8–15 mm thick, base slightly enlarged (up to 2 cm) and tapering gradually upward, blunt in soil, base with a few rhizoids, solid and white within but becoming cavernous from insects, surface whitish, silky to scabrous below annulus, dull and smooth above.

Annulus superior, whitish, membranous, narrow (± 4 mm), ridged on top, cottony underneath, edge rather ragged.

Spores 5.5–7 × 4–5 μm, ovate, smooth, ochraceous brown in KOH, wall thickened, small hyaline apiculus, apical pore minute, deposit "cinnamon drab," "benzo brown," "olive brown," "bister." Basidia 15–26 × 5–7.5 μm, 4-spored. Cheilocystidia 32–40 μm long, 8–16 μm broad, saccate to broadly cylindric or subclavate, pedicellate, mucronate at times, smooth, thin walled, with interior crystal at times (chrysocystidia). Pleurocystidia 28–33 μm long, 8–11 μm broad, mucronate to papillate or mammillate, broadly cylindric to subclavate, usually with interior refractive crystal or two, smooth, thin walled. Pileus: cutis bright ochraceous to golden yellow in KOH, pigment distinctly encrusted, hyphae cylindric to inflated, 2–14 μm diam, cells often short; context yellowish, hyphae mostly inflated, 7.5–26 μm diam, cells often short, walls sinuous at times. Hymenophoral trama of parallel hyphae, yellowish in KOH, hyphae mostly somewhat inflated, 3–21 μm diam, cells short. Oleiferous hyphae present. Clamp connections present.

Gregarious. On humus under hemlock and hardwoods. August and September.

MATERIAL EXAMINED. **Maine:** *Bigelow 16652* (MASS); **Massachusetts:** *Bigelow 9798, 12382, 15808, & 17492* (MASS); **New Hampshire:** *Bigelow 17501* (MASS); **Ohio:** *Hard 8,* 17 Oct 1906, Chillicothe (TYPE) (CUP *20118*).

In the field *Stropharia hardii* could be mistaken for *Pholiota schraderi,* or vice versa, and it is necessary to check all specimens microscopically. *Pholiota schraderi* has longer spores, 6.5–8(–10) × 4–4.5(–5.5) μm, and its cystidia are larger, 40–60(–78) × 9–20 μm, according to Smith and Hesler (1968).

Photographs of *Stropharia hardii* may be found in Smith and Hesler (1940) and Hesler (1960).

Psilocybe thrausta (Schulz.) Bon, Docums mycol. **4:** 17. 1974. Figures 10 & 11.

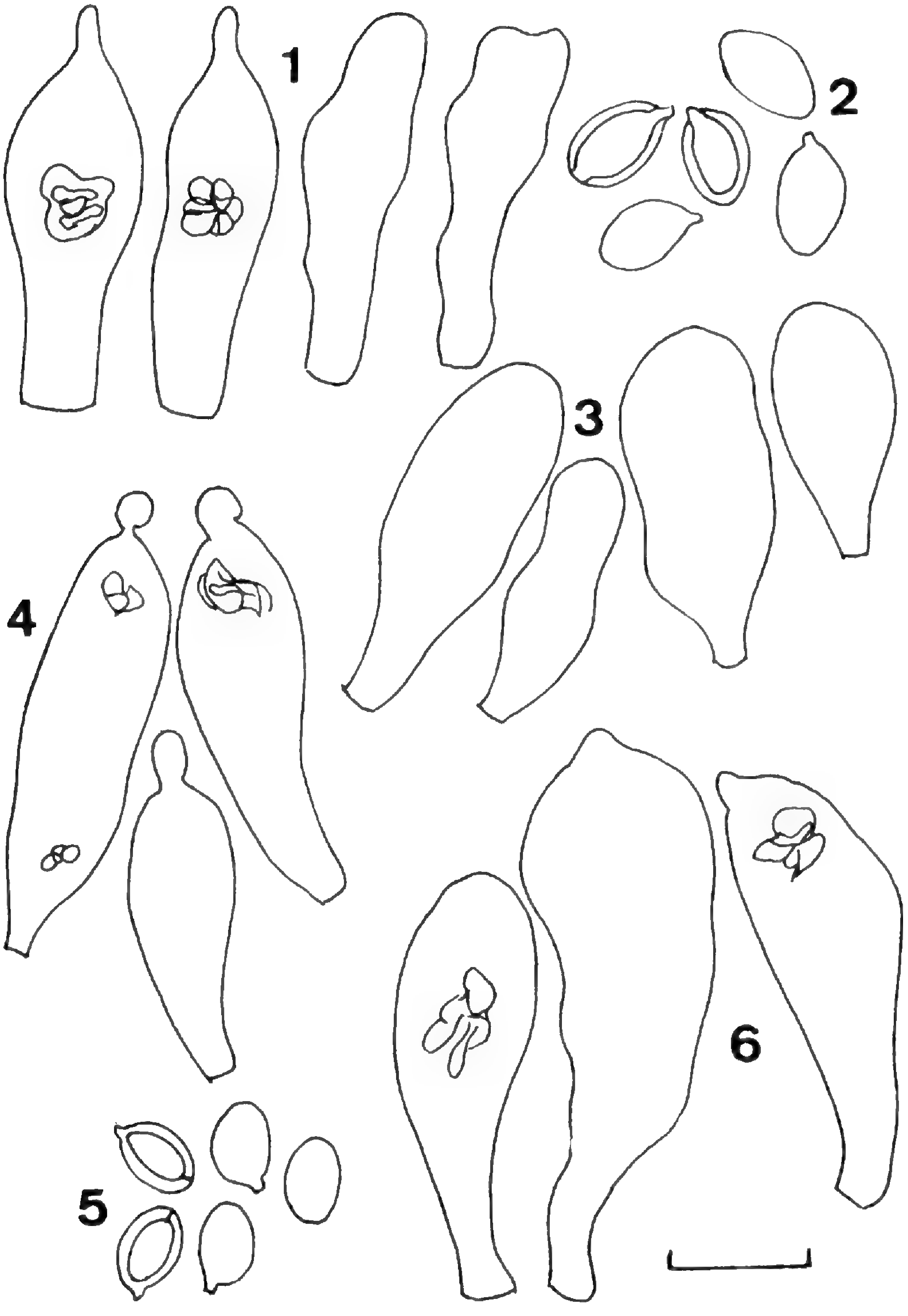
Pileus 2.5–6 cm broad, convex to broadly convex with the margin incurved at first and attached to a partial veil, finally nearly plane, margin not striate but dentate appendiculate from ruptured veil, surface squarrose with scales in 1–3 concentric rings, whitish to cream or buff to pale yellowish, appressed in age, slightly viscid, ground color dull orange ("zinc orange" to "ochraceous orange"); context thin, soft or brittle, watery concolorous with cap or a pale salmon buff or whitish. Odor slightly fragrant or odor and taste absent.

Lamellae broadly adnate with a decurrent tooth, or decurrent, broad (5–10 mm), narrowed at margin, arched when young, close to subdistant, purplish gray to dark purple brown, edges white fimbriate.

Stipe 10–16 cm long, apex 3–8 mm thick, equal or base enlarged and tapering upward, often curved and flexuous, squarrose from base to annulus, scales yellowish to buff, ground color pale ochraceous orange to ochraceous brown, becoming rather shining as scales appressed, white pruinose to furfuraceous above annulus, silky white beneath, solid stuffed (watery buff core, becoming hollow at times, cortex whitish), base slightly enlarged at times and strigose.

Annulus superior, thin, small, whitish with yellowish fibrillose particles on under side, striate on upper side, membranous, projecting to 6 mm.

Spores 11–14 × 6–7 μm, elliptic, apex truncate and with distinct broad apical pore, smooth, brownish yellow in KOH, small hyaline apiculus. Basidia 20–32 × 9–11 μm, 4-spored. Cheilocystidia 55–80 μm long, 3.5–5 μm broad, cylindric to narrowly fusoid, wavy and flexuous near base, walls thin. Pleurocystidia absent. Pileus: cutis an ixotrichodermium, hyphae 1.5–4 μm diam, wavy and erect or



Figures 1–6. *Stropharia coronilla:* 1. pleurocystidia; 2. spores; 3. cheilocystidia. *Stropharia hardii:* 4. pleurocystidia; 5. spores; 6. cheilocystidia. Standard line = 10 μm.

loosely interwoven, cylindric and branched, yellow with dilute pigment in cell contents; context hyphae cylindric to inflated, 3–16 μm diam, hyaline or yellow. Hymenophoral trama of subparallel hyphae, cylindric, 3.5–7.5 μm diam, hyaline. Oleiferous hyphae present (up to 20 μm diam). Clamp connections present.

Solitary, scattered, or gregarious. On stump or other wood debris. In mixed woods. September.

MATERIAL EXAMINED. **Massachusetts:** *Bigelow 7771 & 15544* (MASS).

This species is placed in *Stropharia* by several workers and indeed its stature and presence of an annulus do recall such species as *S. hardii* and *S. hornemanii.* The diagnostic characters and taxonomic level of *Stropharia* have been in debate for some time, but if the presence of chrysocystidia is considered an essential diagnostic character of *Stropharia, P. thrausta* is properly placed in *Psilocybe.*

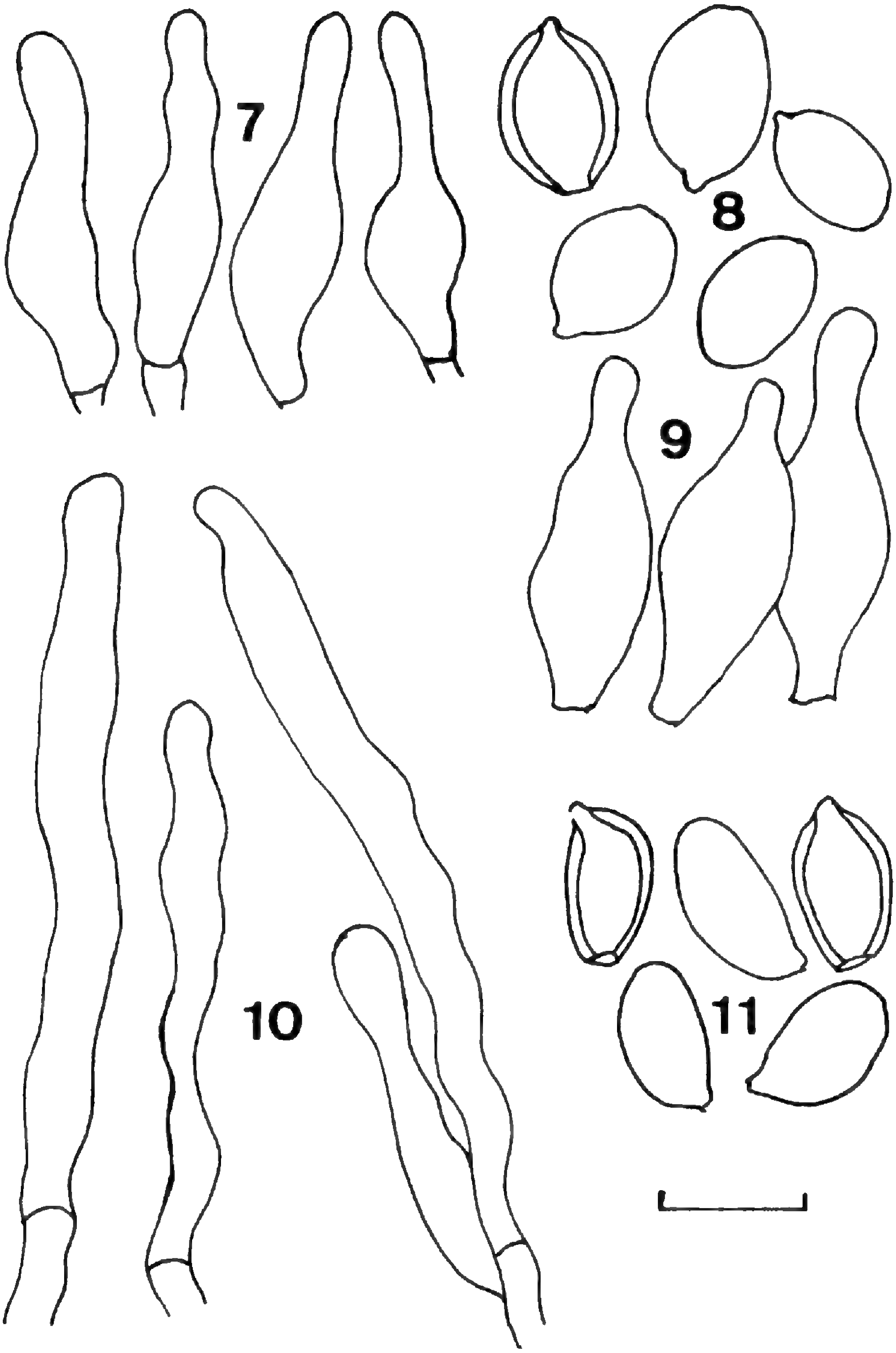
Psilocybe coprophila (Fries) Kummer, Der Führer in die Pilzkunde, p. 71. 1871. Figures 7–9.

Pileus up to 12 mm broad, obtuse at first and margin attached to stipe by whitish veil, expanding soon to hemispheric then convex, usually with low broad umbo when mature, surface viscid and hygrophanous, brown (near "ochraceous tawny") with darker brown striations, fading to buff (near "cream buff") and then opaque, disc tinged ochraceous for some time, margin whitish crenate from veil remnants; context thin, concolorous and fading with pileus surface. Odor and taste not distinctive.

Lamellae broadly adnate to short decurrent, subdistant, broad, purple brown, edges white marginate.

Stipe up to 25 mm long and 2 mm thick, equal, surface with whitish fibrillose patches, ground color light brown, base with white tomentum and often a small bulb.

Spores 11.5–13.5(–14.5) × 7–8(–9) μm, lentiform and slightly angular, smooth, wall thick (up to 1 μm), apex truncate and with distinct pore, light violaceous with yellowish cast in KOH. Basidia 19–34 × 8–11 μm, 4-spored. Cheilocystidia abundant, 26–34 μm long, apex 2.5–4 μm thick, base 6–8 μm thick, ventricose rostrate, hyaline, smooth, thin walled, contents granular. Pleurocystidia scattered, similar in shape to cheilocystidia but more robust, apex up to 5 μm thick, base up to 10 μm thick. Pileus: gelatinous pellicle pres-



Figures 7–11. *Psilocybe coprophila:* 7. cheilocystidia; 8. spores; 9. pleurocystidia. *Psilocybe thrausta:* 10. cheilocystidia; 11. spores. Standard line = 10 μm.

ent, hyaline in KOH, subpellicular layer light yellowish brown in KOH, pigment finely encrusted, hyphae cylindric, 2–4 μm diam; context hyphae cylindric to inflated, 3–15 μm diam, smooth, cells often short. Hymenophoral trama of parallel hyphae, cylindric or occasionally inflated, (2.5–)5–13 μm diam. Clamp connections present.

Gregarious. On horse manure. October.

MATERIAL EXAMINED. **Massachusetts:** *Bigelow 16284* (MASS).

Psilocybe coprophila resembles several other species which grow on dung, e.g., *P. subcoprophila* (Britz.) Sacc., *P. subviscida* (Peck) Kauffman, *P. angustispora* Smith, but as far as is known *P. coprophila* is the only one of the group which has pleurocystidia.

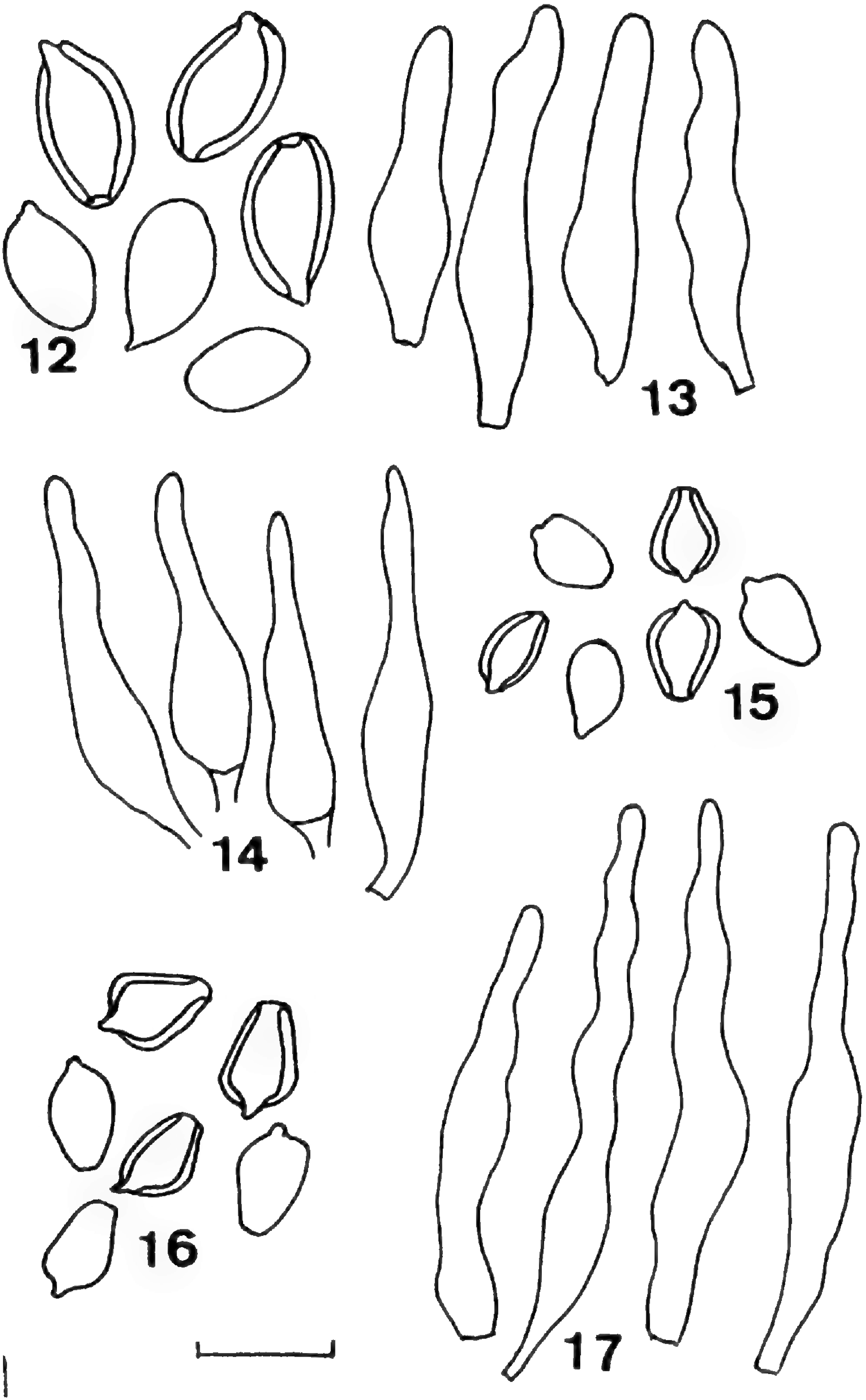
Psilocybe merdaria (Fries) Ricken, Die Blatterpilze, p. 251. 1915. Figures 12, 13, & 18.

Pileus 5–35 mm broad, obtuse at first with margin connected to stipe by white fibrillose partial veil, expanding to broadly conic then broadly convex, at times subumbonate in largest caps, margin becoming white crenate with rupture of veil, then appressed, not striate, completely glabrous and viscid when expanded, ochraceous at first then paler and yellower ("cream buff," "Naples yellow," "maize yellow"), disc sometimes tinged ochraceous, olivaceous tinged when water soaked; context thin, creamy white to yellowish, firm but brittle. Odor fragrant fungoid.

Lamellae broadly adnate to subdecurrent, close, broad (up to 7 mm), subacute at pileus margin, broad at stipe, soft, easily separable from stipe, whitish at first then violaceous gray, finally dark purplish brown to blackish brown, edges crenate to white fimbriate.

Stipe (1–)2–4(–8) cm long, 1–4 mm thick, at times radicate, equal or base slightly enlarged, hollow, fibrous texture, surface heavy silky fibrillose at first and attached near apex to pileus margin by white partial veil, veil rupturing with expansion to give fibrillose zone but no persistent annulus, fibrils appressed and diffracted below with stipe expansion, thinly scabrous in age, white then pale dingy yellowish.

Spores 10–13(–14.5) × 6.5–8(–9) μm, elliptic to ovate, slightly angular at times, smooth, dark brown in KOH, wall thick, smooth, apex with pore, ± truncate, deposit dark purple brown ("dusky brown"). Basidia 20–28 × 8–10 μm, 4-spored, protruding when mature, sterigmata delicate, short, basidioles short. Cheilocystidia



Figures 12–17. *Psilocybe merdaria:* 12. spores; 13. cheilocystidia. *Psilocybe bullacea:* 14. cheilocystidia; 15. spores. *Psilocybe rhombispora:* 16. spores; 17. cheilocystidia. Standard line = 10 μm.

abundant, clustered, cylindric or somewhat ventricose below, 25–40 μm long, 5–8 μm diam in ventricose portion, smooth, hyaline. Pleurocystidia absent. Pileus: cutis an ixotrichodermium, hyphae slender, 0.5–2 μm diam, contorted, subsurface layer with encrusted hyphae, cylindric or slightly inflated, 2–6 μm diam; context hyphae cylindric or inflated, 3–21 μm diam, smooth. Hymenophoral trama of interwoven hyphae, appearing rather cellular, hyphae cylindric to broad cylindric, 3–9(–11) μm diam, cells short. Clamp connections present.

Gregarious, on cow or horse dung, or straw and dung. In field or near stable. June-August.

MATERIAL EXAMINED. **Massachusetts:** *Bigelow 8109, 9537, & 17070* (MASS); **Quebec:** *Bigelow 6118 & 6143* (MASS).

With fresh specimens, the viscid, light yellow pileus of *Psilocybe merdaria* and its substrate might lead to misidentification as *Stropharia semiglobata* or perhaps even as *Agrocybe pediades*. A microscopic examination is necessary — *S. semiglobata* is conveniently identified by its chrysocystidia and the *A. pediades* group by the cellular pileus cutis.

Psilocybe bullacea (Fries) Kummer, Der Führer in die Pilzkunde, p. 71. 1871. Figures 14 & 15.

Pileus 4–12 mm broad, convex or subcampanulate, margin incurved at first, appendiculate with white veil remains for some time, faintly pellucid striate, surface glabrous except at edge, viscid, brown ("mikado brown" at first, then "verona brown" or "snuff brown"); context thin, pliant, concolorous with pileus surface. Odor and taste not distinctive.

Lamellae broadly adnate, broad (up to 5 mm), narrowed at pileus edge, close, violaceous brown ("benzo brown"), edges white fimbriate.

Stipe 1–4 cm long, 1–1.5 mm thick, equal, hollow, tough, apex pruinose, fibrillose (heavy) below, fibrils grayish, ground color cinnamon color.

Spores 6.5–7.5 × 5–6 × 4–4.5(–5) μm, elliptic to ovate, often angular, wall smooth and thick, apical pore truncate at times, yellowish with purplish cast in KOH. Basidia 17–23 × 5–6.5 μm, 4-spored. Cheilocystidia abundant, 23–35 μm long, 6–7 μm at widest portion, 2 μm at apex, fusoid ventricose to ventricose rostrate,

Figure 18. *Psilocybe merdaria. Bigelow 17070* (MASS). ×1.

smooth, hyaline. Pleurocystidia absent. Pileus: cutis an ixotrichodermium, ± 25 μm thick, hyphae within ± 1.5 μm thick, subsurface layer dull yellowish in KOH, hyphae cylindric or slightly inflated, 2.5–7.5 μm, distinctly encrusted; context hyaline, hyphae cylindric to inflated, 6.5–11 μm diam, smooth, cells often short. Hymenophoral trama of ± parallel hyphae, cylindric to inflated, 4–20 μm diam, hyaline, smooth, cells short. Clamp connections present. Stipe cortex composed of cylindric hyphae, 2–6 μm diam, spirally encrusted, walls and septa thickened.

Gregarious. On deer pellets in cedar bog. July.

MATERIAL EXAMINED. **Maine:** *Bigelow 10423* (MASS).

Psilocybe subviscida (Peck) Kauffman differs from this species by the "brownish ferruginous" lamellae. Smith (1948) found pleurocystidia to be present in his study of the type of *P. subviscida*, although he did not think their occurrence to be significant. He also found that the spores were not angled distinctly, and that the pileus did not have distinctive coloration in section.

Another coprophilous species with relatively small spores is *Psilocybe caespitosa* Murrill. It has a larger pileus (1–2.5 cm), grows in a cespitose fashion, but otherwise should closely resemble *P. bullacea* in the field. According to Smith's type study, the species should be distinguishable on microscopic characters for the cheilocystidia are short (22–28 μm), the spores not angular in face view, and encrusted hyphae are absent in the pileus.

Psilocybe rhombispora (Britz.) Saccardo, Syll. Fung. **11:** 72. 1895. Figures 16 & 17.

Pileus 4–15 mm broad, hemispherical at first with an incurved margin, whitish fibrillose veil present, soon expanding to convex, margin appendiculate with veil remains at first then appressed, not striate, surface glabrous, moist and hygrophanous, a dark vinaceous brown moist (near "auburn," "chestnut brown"), fading to a dingy buff (near dingy "pinkish buff"); context thin, firm, watery appearing and concolorous with moist pileus at first, fading to pale ochraceous buff. Odor absent. Taste slightly bitter.

Lamellae adnate, close, broad (up to 3.5 mm), arched, narrowed at pileus edge, brown (near "snuff brown"), edges straight, white fimbriate.

Stipe 1–2 cm long, apex 1–3 mm thick, enlarged and tapered downward, surface with heavy coating of grayish fibrils, ground color blackish, solid (whitish in center, cortex blackish like surface), central, often curved, base with white mycelium.

Spores 6–7.5(–8.5) × 5–5.5(–6) × 3.5(–4) μm, ovate and angular to lentiform, smooth, wall thick, distinct apical pore, truncate, drab yellow to yellow brown in KOH. Basidia 26–29 × 6–8 μm, 4-spored. Cheilocystidia subcylindric to subventricose and rostrate, 35–50 μm long, apex 2–3 μm diam, ventricose portion 5–6 μm diam, walls thin, hyaline. Pleurocystidia absent. Pileus: cutis an ixotrichodermium, hyphal fragments 1.5–3 μm diam, hyaline, subsurface hyphae cylindric to slightly inflated, 3–10 μm diam, smooth or finely encrusted, cells often short; context hyphae often inflated, 5–15(–33) μm diam, walls often slightly thickened or very finely encrusted, cells short, tissue yellow brown in KOH. Hymenophoral trama of parallel hyphae, cylindric or somewhat inflated, 4–12 μm diam, walls slightly thickened or finely encrusted, yellowish brown in KOH, cells short. Clamp connections present.

Cespitose, on sawdust and wood chips. July.

MATERIAL EXAMINED. **Massachusetts:** *Bigelow 6934* (MASS).

Deconica rhomboidospora Atkinson (Ann. Mycol. **7:** 368. 1909.) appears to be closely related, although not identical, to *Psilocybe rhombispora.* The specimens of the type of *D. rhomboidospora* (CUP *18245*) have spores (6–)6.5–7 × 4.5–5.5 μm, which are broadly ovate and only slightly angular, and cheilocystidia 30–53 μm long, 2.5–4 μm broad at apex, 5–7.5 μm near the base. The pileus cutis is subgelatinous in sections mounted in KOH, but there is no pellicle as in *P. rhombispora. Deconica rhomboidospora* also has encrusted pigments on the pileus hyphae, but these are confined to the cutis. In the field, the species should be distinguishable from *P. rhombispora* by the dry, ochraceous to clay color pileus. Both species grow on wood debris.

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DEVELOPMENT OF DIATOM COMMUNITIES ON POTAMOGETON ROBBINSII OAKES

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One of the most important groups of organisms in the aquatic system is the periphyton, the organisms that grow attached to macrophytes, logs, rocks, mud or other submersed objects. Periphyton species which are primarily composed of Bacillariophyceae (diatoms) are often found in large numbers producing slimy mats (Young, 1945). The periphyton are important in overall lake productivity (Wetzel, 1964), and recently have been used as tools in studying critical environmental problems (Rashke & Weber, 1970; Baker, 1974). Despite the importance of periphyton in aquatic systems and their usefulness as environmental tools, there has been much neglected research. The objective of this study was to broaden the information regarding periphyton ecology.

The attached diatom communities on *Potamogeton robbinsii* Oakes, a submerged pondweed, were observed throughout 1975 in Wheelwright Pond in Lee, New Hampshire. The communities were qualitatively and quantitatively described from leaves along various intervals of the shoot. Seasonal fluctuations in concentrations of the diatom species were observed. Temporal changes in community composition were also observed on *P. robbinsii* leaves. Whitford (1959) developed a method to study pioneer versus climax communities of diatoms by comparing the attached communities on young and old parts of vertically-oriented aquatic plants. In this study the influence of depth was eliminated because *P. robbinsii* grows parallel to the bottom sediments. Hence, young and old portions of the plant are at a similar depth, which eliminates differences in light, temperature and nutrients along the axis. To my knowledge no one has conducted studies on the periphyton of New Hampshire.

METHODS

Biweekly or monthly trips during 1975 were made to Wheelwright Pond to collect stems of *Potamogeton robbinsii* plants. The stems were carefully harvested with a garden hoe and placed gently in buckets with lake water to minimize loss of periphyton.

Two sets of leaves, with approximately equal areas, were selected

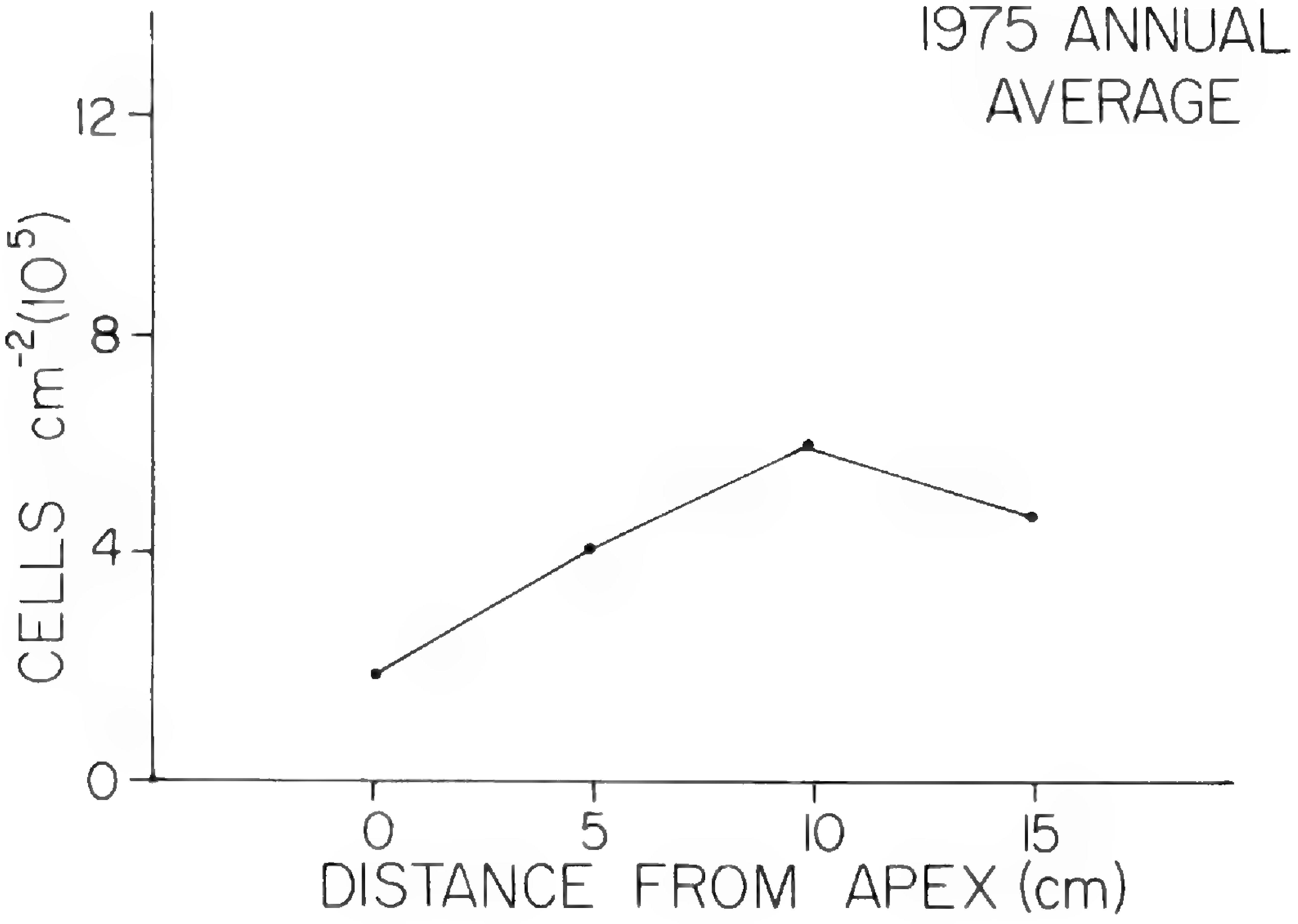

Figure 1. Average concentration of diatoms on *Potamogeton robbinsii* leaves (1975).

from at least five different randomly-chosen plants; one set was used to obtain the total surface area and the other set for quantification of diatom concentrations. From each plant two leaves were clipped at 0, 5, 10, and 15 cm. intervals from the apex and placed into separate 100 ml. beakers.

The first group of leaves was photographed and the total leaf area was determined gravimetrically. The second group of leaves was put directly through a cleaning process which oxidized all of the organics (both the leaf substrate and the diatom cell contents) leaving behind the silica frustules. Approximately 10 ml. of 50% H_2SO_4, 10 ml. of distilled water and a few crystals of potassium dichromate were placed in each beaker with the leaves and boiled for twenty minutes. After fifteen minutes a few more potassium dichromate crystals were added to insure complete oxidation of organics. After boiling, the sample was centrifuged for seven minutes at 2,500 R.P.M. Observation of the supernatant indicated no loss of diatoms. The supernatant was then removed with a specially designed vacuum decanter. The diatoms were resuspended and washed several times with distilled water, with repeated centrifugation. After the last washing, the pellet was suspended in 8 ml. distilled water and preserved with a few crystals of thymol to prevent the growth of fungus (Patrick & Reimer, 1966).

A volume from 0.12–0.500 ml. of the oxidized sample was pipetted with a micropipette onto a number one cover slip and gently heated on a hot plate until dry, leaving the clean frustules from the known volume of the sample on the cover slip. The cover slip was inverted and mounted onto a glass slide with a drop of Kleermount mounting medium (Carolina Biological Supply). A minimum of four permanent slides was made from each sample and each was scanned under low power. The slide with the most even distribution of frustules was chosen for quantitative microscope analysis. The slide was then scanned once, twice, or until at least 1000 individual cells were identified and counted at ×1000 with a Wild M20 microscope.

Taxa were identified with the help of Hustedt (1930), Patrick and Reimer (1966, 1975), Hansmann (1973), and the Fritsch microfiche collection.

RESULTS

Along the shoot of *Potamogeton robbinsii* an increase in diatom concentration was observed from the apex to approximately 10 cm. From 10 to 15 cm. the concentration of diatoms decreased or remained approximately the same (Figure 1). At the apex the annual average was 1.9×10^5 diatoms/cm^2 while at 5 and 10 cm. from the apex the average was two and three times higher. At 15 cm. the average cell concentration was 4.7×10^5 cells/cm^2.

Monthly variations in the concentrations of epiphytes were observed (Figures 2a-d). The range in concentrations was from 0.2×10^5 at the apex on 4 June to 13.2×10^5 cells/cm^2 at 10 cm. from the apex on 5 April. Spring and fall maxima occurred from April through June and October through November, respectively. A marked decline in diatom concentrations occurred during May. A mid-summer minimum occurred between June and September. The decline in diatom concentration in the shoot section from 10 to 15 cm. did not occur during July and August. During the summer very low concentrations occurred at the apex. The concentration profile along the axis became uniform during the late winter.

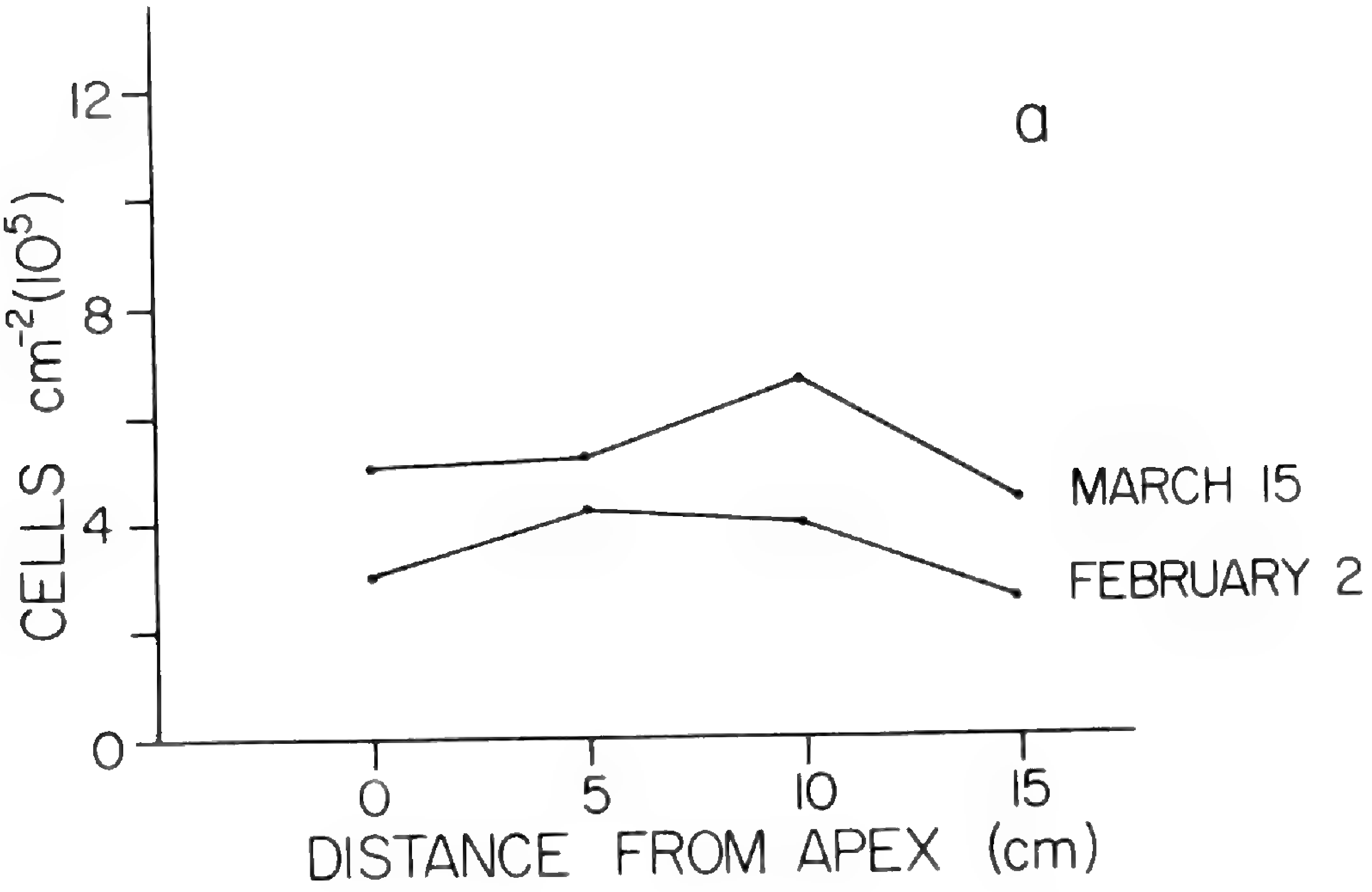

Figure 2a. Concentration of diatoms on *Potamogeton robbinsii* leaves, February 2 and March 15, 1975.

A total of 133 taxa of epiphytic diatoms were encountered (Species List). The three most abundant species were *Achnanthes minutissima, Cocconeis placentula* var. *euglypta,* and *Eunotia incisa. Anomoeoneis vitrea* was occasionally abundant. Of lesser importance were *Tabellaria fenestrata, Fragilaria capuncina* var. *mesolepta, Navicula radiosa,* and *Navicula radiosa* var. *tenella.*

Maxima and minima of the dominant epiphytic taxa occurred at various times during the year. *Achnanthes minutissima* had a maximum in the late spring (April through June) followed by a summer minimum that extended into the early fall (Figure 3a). Late in the year a smaller maximum occurred. An abrupt decrease in concentration occurred in May. The decrease was from 7.4 × 10^5 cells/cm^2, the largest concentration of an individual species found throughout the year, to 1.4 × 10^5 cells/cm^2.

Cocconeis placentula var. *euglypta* had maxima in June and November of 2.5 × 10^5 and 2.9 × 10^5 cells/cm^2 and a minimum in late September of 0.45 × 10^5 cells/cm^2 (Figure 3b). In these respects the seasonal pattern is similar to that of *Achnanthes minutissima.* The seasonal profiles differ in that the decrease in numbers of *C. placentula* var. *euglypta* in May was slight and its maximum values

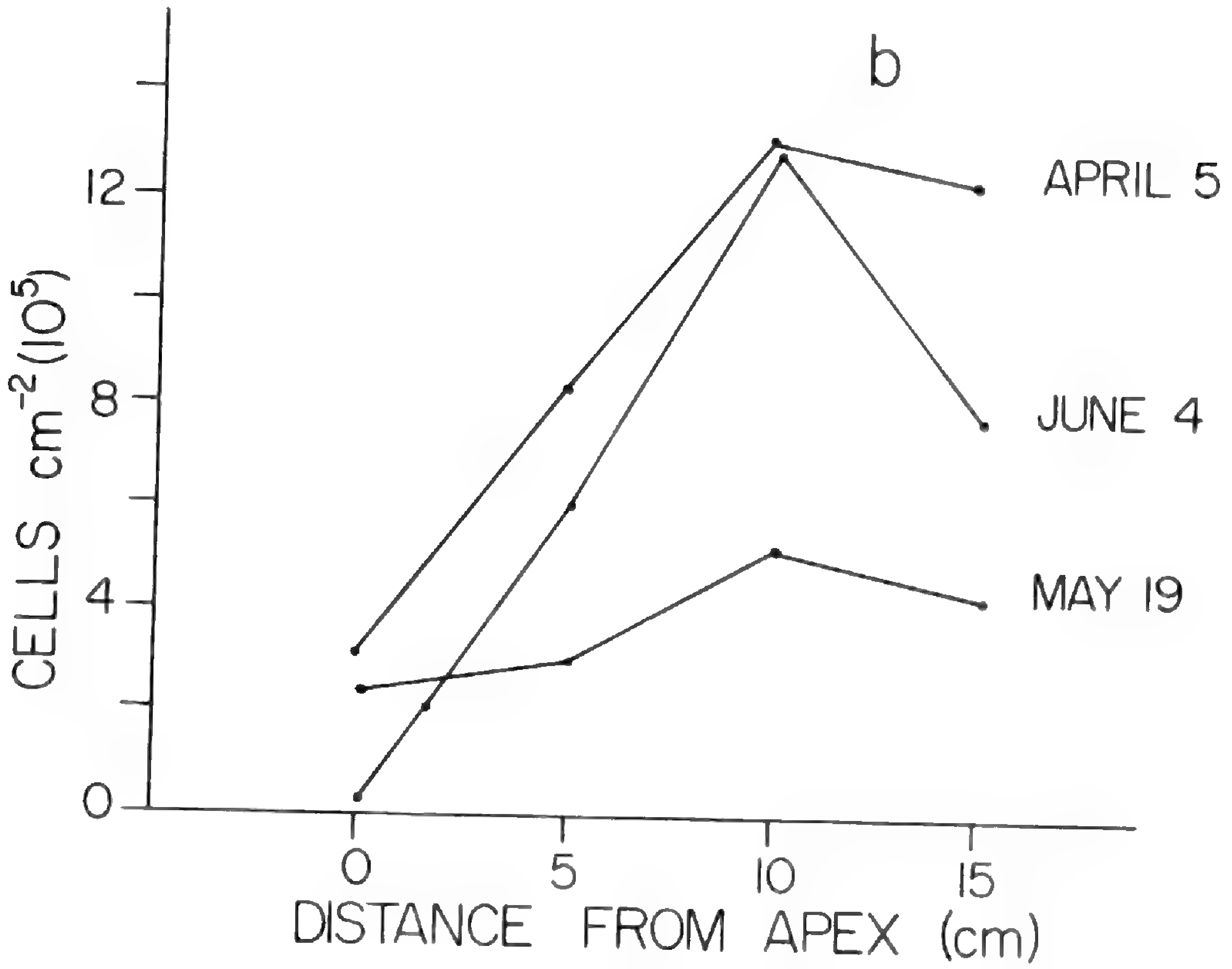

Figure 2b. Concentration of diatoms on *Potamogeton robbinsii* leaves, April 5, May 19, and June 4, 1975.

did not approach those of *A. minutissima.*

Eunotia incisa had a seasonal profile markedly similar to that of *Cocconeis placentula* var. *euglypta* (Figure 3c). Both had spring and fall maxima, a summer minimum and only a slight decline in concentration during May.

The community structure along the shoot of *Potamogeton robbinsii* varied throughout the year. During late winter (February and March) the community structure was similar from 0 to 15 cm. along the shoot (represented by March, Figure 4a). During these months no apical growth of *P. robbinsii* was observed.

During spring through late fall (April through November) distinct changes in community structure occurred along the shoot (represented by April 5, July 7 and November 22, Figures 4b, c, & d). The dominant taxa increased in concentration from 0 to 10 cm. and decreased slightly from 10 to 15 cm. Changes in dominance or relative abundance of these taxa shifted as the leaves aged. One group of two species, *Eunotia incisa* and *Cocconeis placentula* var. *euglypta,* had a parallel pattern of decreasing relative abundance

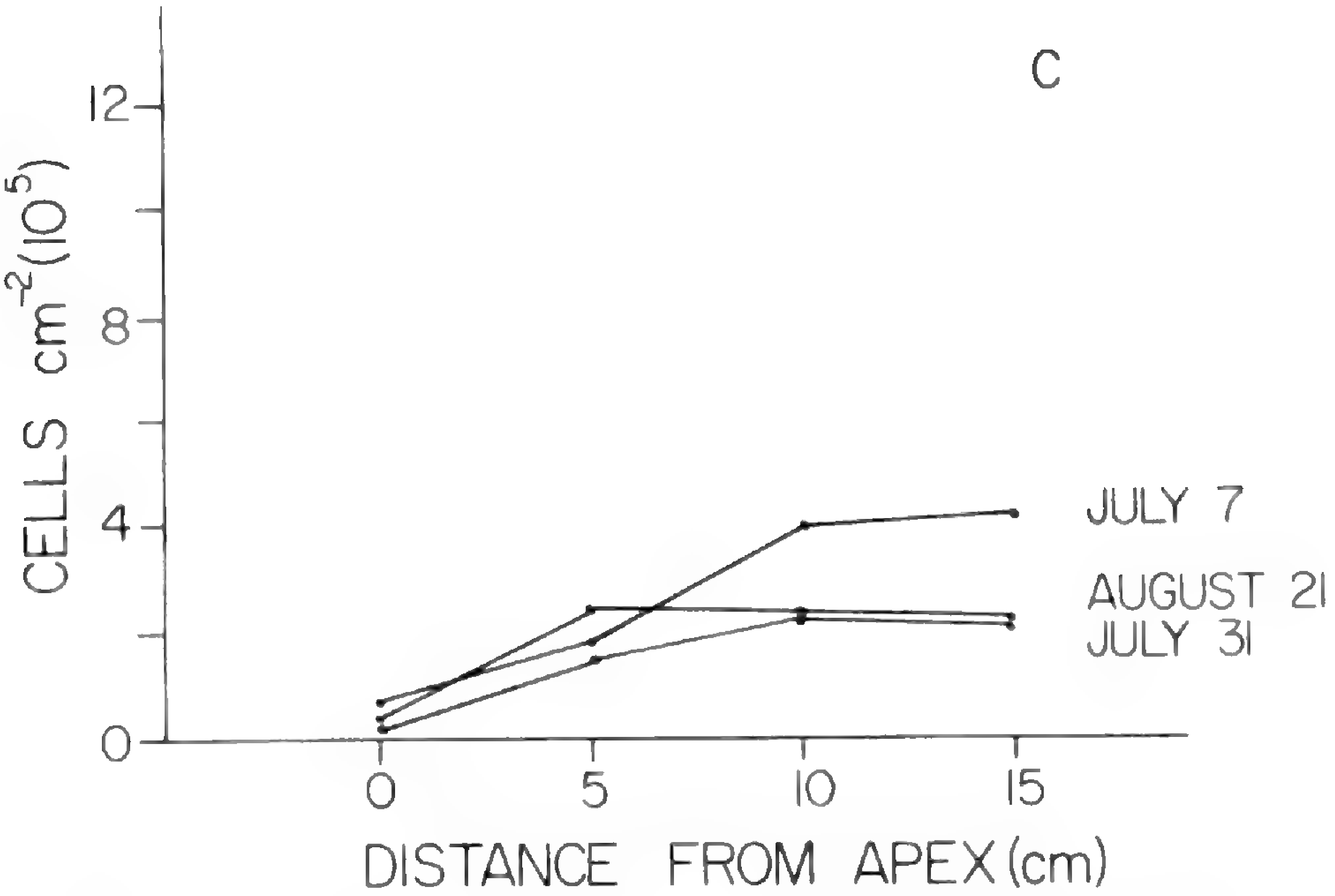

Figure 2c. Concentration of diatoms on *Potamogeton robbinsii* leaves, July 7, July 31, and August 21, 1975.

along the shoot. A second group, *Achnanthes minutissima* and *Anomoeoneis vitrea* had a parallel pattern of increasing relative abundance along the shoot. Between 10 and 15 cm., when the total number of diatoms/cm^2 decreased, a reversal of this trend occurred, i.e. the importance of *C. placentula* var. *euglypta* and *E. incisa* again increased, while that of *A. minutissima* and *A. vitrea* decreased.

Although the trends of relative abundance of *Anomoeoneis vitrea* were similar to those of *Achnanthes minutissima* the concentration was much lower. The average concentrations of *Eunotia incisa* and *Cocconeis placentula* var. *euglypta* were similar to each other.

DISCUSSION

The horizontal growth habit of *Potamogeton robbinsii* eliminates light, temperature, and depth as factors resulting in the observed changes in the epiphytic community along the shoot. Therefore, the only apparent causal factor is leaf age. As a newly formed leaf becomes exposed to the aquatic environment, algae and bacteria coat it with mucilage (Young, 1945; Patrick & Reimer, 1966). The mucilage then captures silt and particulate matter and enables other microorganisms to attach. The cumulative increase of mucilage as the leaves mature may be the primary cause of the increase of epiphytes from 0 to 10 cm.

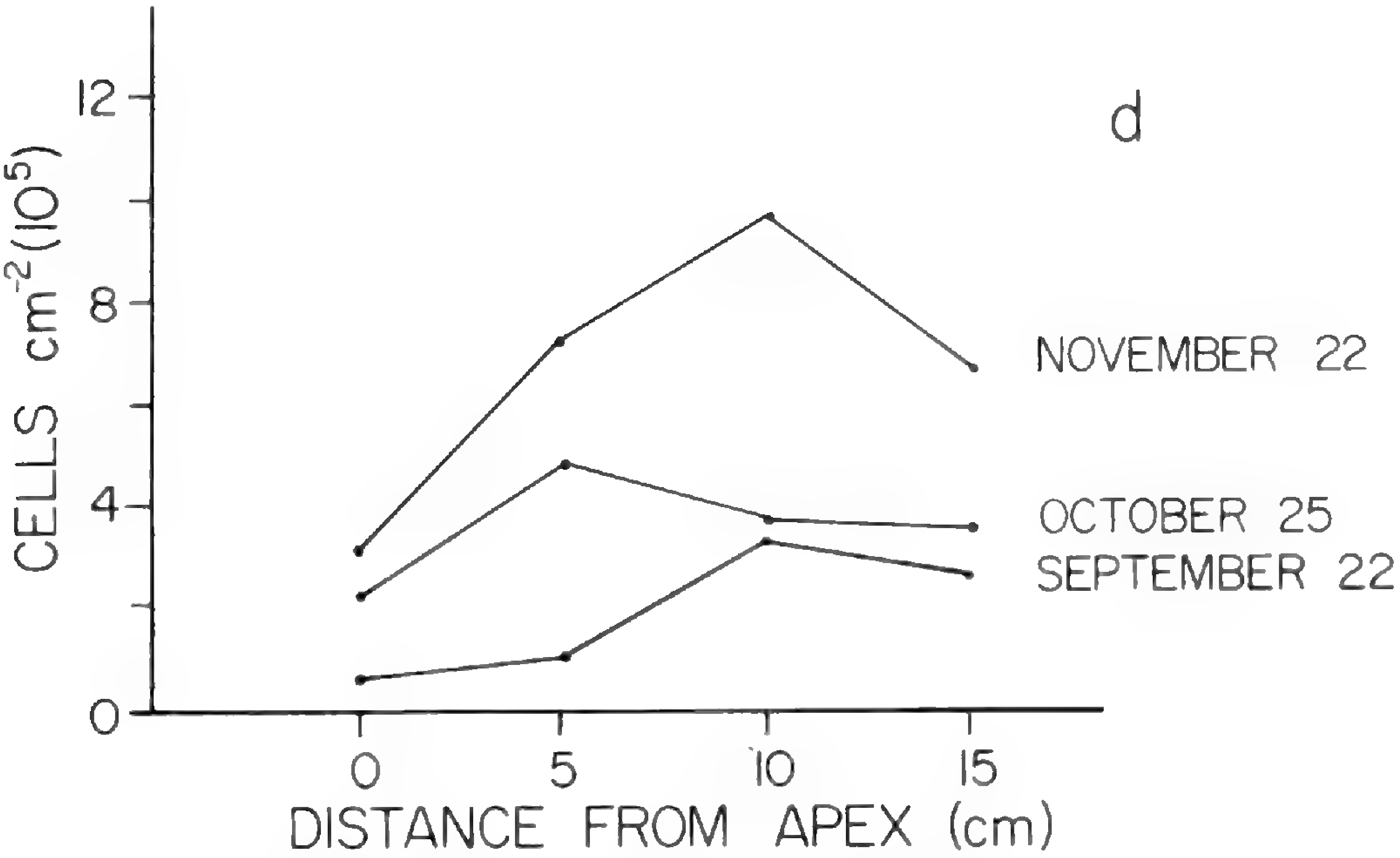

Figure 2d. Concentration of diatoms on *Potamogeton robbinsii* leaves, September 22, October 25, and November 22, 1975.

Associated with the increase in diatoms from 0 to 10 cm. was an increase in the blue-green algae on the older leaves. These algae apparently behave as successional species, requiring a mucilage layer before they become part of the periphyton. The increase in blue-green algae may also account for some of the increase in total numbers of diatoms by increasing the surface area available for attachment. Most of the blue-green algae present had thick mucilage sheaths which enabled further colonization by diatoms.

The decrease in diatom numbers between the 10 and 15 cm. level is also accountable due to the interplay of physical factors. It is apparent that for a given substrate the periphytic mat may only attain a finite size, above which a "sloughing off" occurs, enhanced by the breakdown of the macrophyte substrate. Also, fewer blue-green algae were present at the 15 cm. level, so that their loss also accounted for part of the decrease in diatoms.

Differences between the monthly distribution patterns of diatoms along the axis of the *Potamogeton robbinsii* plants (Figures 2a-d) are explained on the basis of differential growth of the macrophyte itself. For example, in February and March the distribution was relatively uniform and the macrophytes were not actively growing. As a result the diatom communities on all sections of the axis were similar in concentration. Winter environmental conditions such as

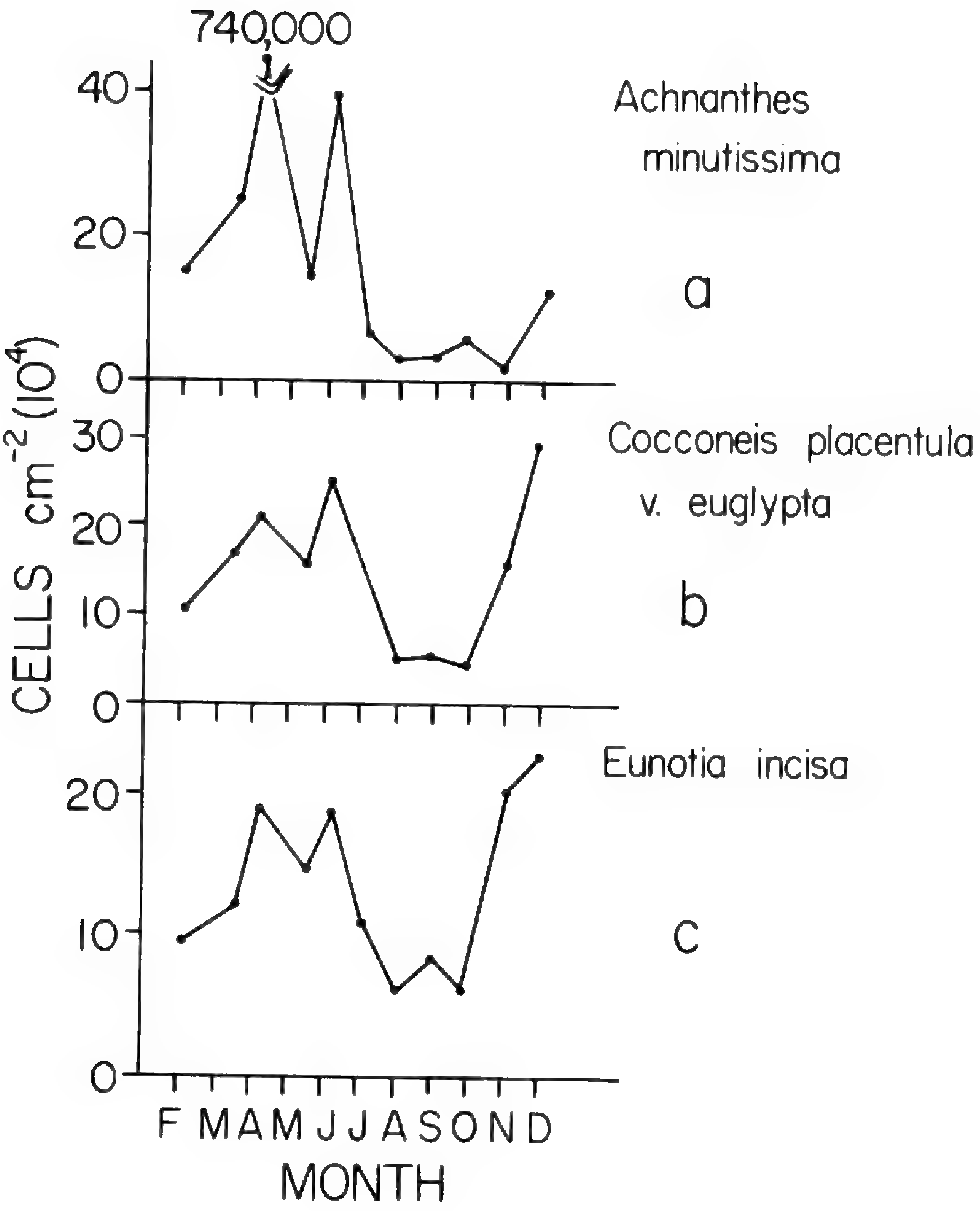

Figure 3. Seasonal concentration of dominant diatoms on *Potamogeton robbinsii.* a. *Achnanthes minutissima;* b. *Cocconeis placentula* var. *euglypta;* c. *Eunotia incisa.*

very low levels of light and temperature limited diatom concentrations to approximately one-third of the yearly maximum.

Another distribution pattern was the low concentration of epiphytes on the apical leaves relative to the concentration on older leaves during April through September. This distribution is explained on the basis of the macrophyte growth cycle. During these months, new leaves were constantly produced by the apical meristem providing new substrate for colonization. The epiphyte community on the young leaves was always at a "pioneer" stage with low cell concentration. As the leaves aged, "successional" stages appeared. During July and August the decline in cell concentration from 10 to 15 cm. was not present; this distribution is attributable to both the high growth rate of *Potamogeton robbinsii* and to reduced degradation of leaves in that segment. In future studies the growth rate and age of the individual leaves of the macrophyte should be quantified in order to determine the specific rate of colonization by diatoms.

The seasonal fluctuations of diatoms on *Potamogeton robbinsii,* which include a large spring maximum, a summer minimum, and a small fall maximum, are in agreement with previous seasonal studies of diatoms. Most diatoms favor low light levels and temperature, and many investigators suggest that these factors are the triggering mechanisms for the spring and fall blooms (Smith, 1950; Patrick & Reimer, 1966). Such seasonal fluctuations of diatoms are similar in a variety of habitats: attached diatoms in streams (Patrick, 1948; Douglas, 1958); epilithic communities in oligotrophic lakes (Stockner & Armstrong, 1971; Fox et al., 1969); epiphytic communities in lake systems (Foerster & Schlichting, 1969; Godward, 1937); and studies of colonization of artificial substrates in river systems (Flemer, 1970; Baker, 1974).

The marked May decrease in the spring maximum in Wheelwright Pond was probably caused by increased wave action due to overturn which scoured away many of the loosely attached forms. With overturn completed by June and the growth rate of the diatoms high, large concentrations of epiphytes developed.

The similar seasonal growth curves of *Cocconeis placentula* var. *euglypta* and *Eunotia incisa* suggest that these taxa have similar environmental requirements, growth rates, and abilities to retain substrates. The decline in *Achnanthes minutissima* and *Anomoeoneis vitrea* during May was much larger than that of *C. placentula* var. *euglypta* or *E. incisa* and suggests a weaker attachment mechanism.

The ability of a diatom to attach onto a substrate helps determine whether it is a "pioneer" or "climax" species. This study shows that there are definite changes in species composition over time; there is a group of species which can cling to the freshly formed leaves while

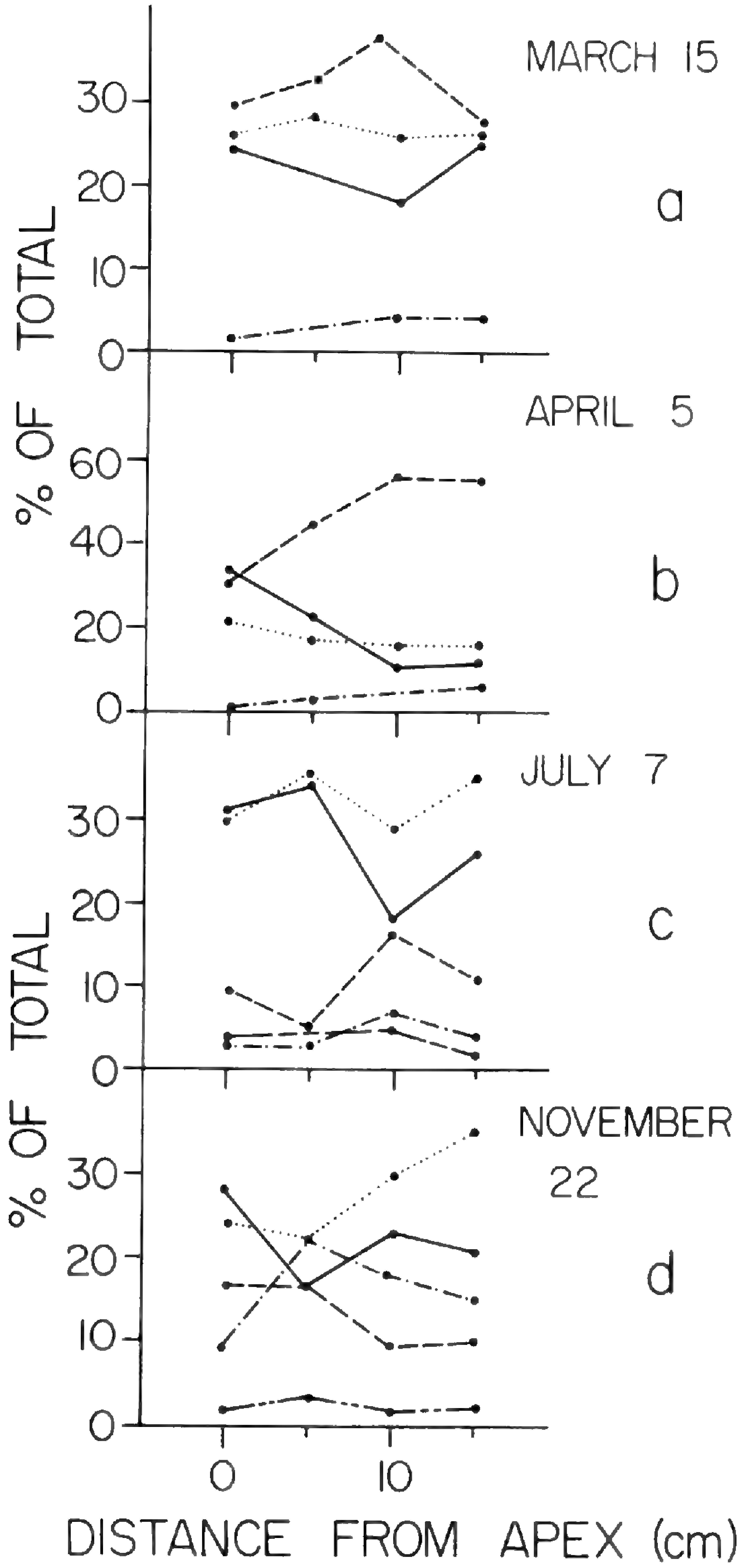

Figure 4. Relative abundance of dominant diatoms on *Potamogeton robbinsii* leaves (1975). a. March 15; b. April 5; c. July 7; d. November 22.— — — — = *Achnanthes minutissima;* .... = *Cocconeis placentula* var. *euglypta;* __________ = *Eunotia incisa;* . __ . __ . __ = *Anomoeoneis vitrea;* ___ _ _ ____ = *Tabellaria fenestra.*

other diatoms do not adhere until a mucilage layer is formed. The former group represents the "pioneers" and the latter the "climax" species.

In observing "pioneer" communities on the *Potamogeton robbinsii* leaves one should consider only those dates where growth of the substrate occurred. These were the only times that new leaves were added at the shoot apex. I found that communities at 0 cm. were primarily dominated by two species, *Eunotia incisa* and *Cocconeis placentula* var. *euglypta* (Figure 4). At the 5 and 10 cm. levels *Achnanthes minutissima* and *Anomoeoneis vitrea* became more important. A few additional species had their highest frequency at 0 cm. (the "pioneer" stage) although most of the minor species had their highest frequencies in the older communities.

Additional evidence supports the successional pattern as outlined above. First, *Eunotia incisa* and *Cocconeis placentula* var. *euglypta* were the only two species attached to newly formed leaves and represent very early "pioneer" stages. Second, it was observed that *E. incisa* and *C. placentula* var. *euglypta* had superior attachment mechanisms as they were eroded to a lesser extent than were *Achnanthes minutissima* and *Anomoeoneis vitrea* in May.

Superior attachment mechanisms for *Cocconeis placentula* var. *euglypta* and *Eunotia incisa* are evident. *Cocconeis* has a broad, flat, slightly curved morphology and secretes a layer of mucilage. Such characteristics enable it to cling firmly to substrate (Smith, 1950; Sieburth & Thomas, 1973; Stockner & Evans, 1972). *Eunotia* secretes large quantities of mucilage, has a curved symmetry, and can form filaments, all of which enable it to adhere to and entangle with fresh substrates.

Achnanthes minutissima and *Anomoeoneis vitrea* are both smaller than the other major contributors and, hence, probably have a larger specific growth rate (Fogg, 1965). This is one possible means by which *A. minutissima* and *A. vitrea* may have a higher concentration than the "pioneer" forms once they become attached in successional stages of community development.

Other workers have recorded similar successional patterns. Dillard (1969) found *Eunotia pectinalis* var. *minor* to be the "pioneer" organism of epilithic diatom communities, although the species was not dominant in the mature communities where *Achnanthes minutissima* and *Gomphonema parvulum* were codominant. Stockner and Evans (1972) observed a well defined successional pattern where

A. minutissima was most dominant in later stages of community development. Sieburth and Thomas (1973) found a *Cocconeis* species attached to eelgrass in large numbers, completely covering the plant, causing it to break down. It was not until later stages in the development of the community that other diatoms colonized the substrate.

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Species list of diatoms found on Potamogeton robbinsii leaves during 1975.

Cyclotella bodanica Eul., *C. kutzingiana* Thwaites, *C. meninginiana* Kutz., *C. stelligera* (Cleve) Grun., *C.* sp. (unknown), *Melosira distans* (Ehrb.) Kutz., *M. granulata* (Ehrb.) Ralfs., *M.* sp., *Stephanodiscus astraea* var. *minutula* (Kutz.) Grun., *Thalassiosira tumida* Hustedt, *Achnanthes affinis* Grun., *A. clevei* Grun., *A. clevei* var. *rostrata* Hustedt, *A. detha* Horn & Hellerman, *A. gibberula* Grun., *A. lanceolata* Breb., *A. lanceolata* var. *elliptica* Cleve, *A. lanceolata* var. *rostrata* Hustedt, *A. linearis* W. Sm., *A. microcephala* Kutz., *A. minutissima* Kutz., *Amphipleura pellucida* Kutz., *Amphora ovalis* Kutz., *Anomoeoneis vitrea* (Grun.) Ross, *Asterionella formosa* Hassall, *Bacillaria paradoxa* var. *tumidula* Grun., *Caloneis bacillum* (Grun.) Mereschkowsky, *Caloneis silicula* (Ehrb.) Cleve, *C. schumanniana* (Grun.) Cleve, *Cocconeis placentula* (Ehrb.) var. *euglypta* (Ehrb.) Cleve., *Cymbella aspera* (Ehrb.) Cleve, *C. cistula* (Hemprich) Grun., *C. cistula* var. *maculata* (Kutz.) Van Heurck, *C. gracilis* (Rabh.) Cleve, *C. naviculiformis* Aversw. ex Heib. Auerswald, *C. sinuata* Greg., *C. turgida* (Greg.) Cleve, *C. ventricosa* Kutz., *Diploneis marginestriata* Hustedt, *Epithemia turgida* (Ehrb.) Kutz., *Eunotia curvata* Lagerst., *E. flexuosa* Kutz., *E. flexuosa* var. *eurycephala* Grun., *E. incisa* W. Sm. ex Greg., *E. incisa* (large) W. Sm. ex. Greg., *E. major* (W. Sm.) Rabh., *E. pectinalis* (Kutz.) Rabh., *E. pectinalis* (Kutz.) Rabh. var. *minor* (Kutz.) Rabh., *E. impressa* (Ehrb.) Rabh., *E. pectinalis* var. *ventricosa* Grun., *E. serra* var. *diadema* (Ehrb.) Patr., *E. valida* Hustedt, *E. vanheurckii* Patr., *Fragilaria capucina* Desmazieres, *F. capucina* Desmazieres var. *mesolepta* (Rabh.) Grun., *F. construens* (Ehrb.) Grun., *F. crotonensia* Kitton, *F. harrissonii* W. Sm., *F. intermedia* Grun., *F. pinnata* Ehrb., *F.* sp., *F. virescens* var. *mesolepta* Rabh., *Frustulia rhomboides* (Ehr.) de Toni, *Gomphocymbella* sp., *Gomphonema acuminatum* Ehrb., *G. acuminatum* Ehrb. var. *brebissonii* (Kutz.) Clev., *G. acuminatum* Ehrb. var. *coronata* (Ehrb.) W. Sm., *G. angustatum* (Kutz.) Rabh., *G. augur* Ehrb., *G. constrictum* Ehrb., *G. constrictum*

Ehrb. var. *capitata* (Ehrb.) Cleve., *G.* sp. (girdle), *G. gracile* Ehrb., *G. gracile* Ehrb. var. *lanceolata* (Kutz.) Cleve., *G. intricatum* Kutz., *G. olivaceum* (Lyngbye) Kutz., *G. parvulum* (Kutz.) Grun., *Gyrosigma obscurum* (W. Sm.) Griff. & Henfr., *G. spencerii* (Quek.) Griff. & Henfr., *Hantzschia amphioxys* (Ehrb.) Grun. var. *virox* (Hantzsch) Grun., *Meridion circulare* Agardh, *M. circulare* Agardh var. *constricta* (Ralfs.) van Heurck., *Navicula bacillum* Ehrb., *N. cryptocephala* Kutz., *N. cuspidata* var. *ambigua* (Ehrb.) Cleve, *N. falaisiensis* Grun., *N. hungarica* var. *capitata* (Ehrb.) Cleve, *N. minima* Grun., *N. protracta* Grun., *N. pseudoscutiformis* Hustedt, *N. pupula* Kutz., *N. pupula* Kutz. var. *elliptica* Hustedt, *N. pupula* var. *rectangularis* (Greg.) Grun., *N. radiosa* Kutz., *N. radiosa* (Kutz.) var. *tenella* (Breb.) Grun., *N. rhyncocephala* Kutz., *N. tridentula* Krasske, *N. verecunda* Hustedt, *Neidium affine* (Ehrb.) Cleve, *Neidium iridis* var. *ampliata* (Ehrb.) Cleve, *Nitzschia acicularis* W. Sm., *N. acuta* Hantzsch, *N. amphibia* Grun., *N. obtusa* var. *scalpelliformis* Grun., *N. paleacea* Grun., *N. recta* Hantzsch, *N.* sp., *N. subtilis* (Kutz.) Grun., *Rhopalodia gibba* (Ehrb.) O. Mull., *Pinnularia abaujensis* (Pont.) Ross, *P. gibba* Ehrb., *P. intermedia* (Lagerst.) Cleve, *P. nodosa* (Ehrb.) W. Sm., *P.* sp.,*P. sudetica* Hilse, *Stauroneis anceps* Ehrb., *S. anceps* var. *hyalina* Brun & Peragallo, *S. anceps* Ehrb. f. *linearia* (Ehrb.) Cleve, *S. ignorata* Hustedt, *S. kriegeri* Patr., *S. livingstonii* Reim., *S. perminuta* Hustedt, *S. phoenicenteron* Ehrb., *Surirella delicatissima* Lewis, *Synedra arcus* Kutz., *S. parasitica* W. Sm., *S. pulchella* Kutz., *S. rumpens* Kutz., *S. tenera* W. Sm., *S. ulna* (Nitzsch) Ehrb., *S. vaucheriae* Kutz., *Tabellaria fenestrata* (Lyngbye) Kutz., *T. flocculosa* (Roth) Kutz., and one unidentifiable specimen.

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CHROMOSOME NUMBERS OF MISCELLANEOUS UNITED STATES DICOTYLEDONS

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During my academic year at the Department of Botany, Smithsonian Institution, Washington, D.C., in 1970 1971, I had the opportunity to make collections of material for cytological study. A previous report on this study, listing chromosome numbers of some Asteraceae, has been published (Kovanda, 1972). In the present paper, chromosome counts for 38 collections are reported. These include 36 taxa of specific rank, representing 31 genera and 15 families. The majority of these counts reinforce earlier observations and support current studies in cytogeography. In some taxa, the present counts confirm the presence in the United States of two or more chromosome races. New ploidy levels are established for *Solidago flexicaulis* and *Krigia virginica*. Chromosome counts are reported for the first time for *Ranunculus micranthus, Stellaria gonomischa, Cubelium concolor* and *Senecio eremophilus*. Notes on previous cytological work, variation and geographical distribution have been added wherever appropriate but no attempt has been made to produce generalizations of a taxonomic or evolutionary nature.

MATERIALS AND METHODS

The material upon which the present counts are based was collected from different localities in Washington, D.C., Maryland, Virginia, Tennessee, Colorado, New Mexico, Arizona, Nevada and California. To count the somatic numbers, tips were taken from primary roots of young seedlings grown in Petri dishes. The techniques were identical to those described in my 1972 paper. Determinations of gametic chromosome numbers were made by the use of squashes of pollen mother cells. For these studies, young flower buds of the various species were collected in the field and fixed in Carnoy solution. After a period of 24 to 48 hours, the fixative was replaced by 70 per cent ethyl alcohol in which the material was held without refrigeration until it could be examined. The anthers were stained in lacto-propionic orceine, but for *Aquilegia canadensis* and *Saxifraga virginiensis* aceto-carmine was used as a stain. Meiotic behavior was quite regular in all the species investigated. Voucher specimens for all of the plants examined are on deposit at the Herbarium of the National Museum in Prague (PR). Those collection numbers preceded by K. are by Kovanda; by K.&S., Kovanda and Shetler.

OBSERVATIONS

CARYOPHYLLACEAE

Silene acaulis (L.) Jacq. ssp. *acaulescens* (T. N. Williams) Hitch. & Maguire

Colorado, Grand County: Berthoud Pass, 12400 ft., *K.&S. 3313.* $2n = 24$.

This circumboreal species, embracing a host of infraspecific taxa, has been counted many times on both New and Old World material (for references, see Fedorov, 1969) but no variation in the chromosome number was observed.

Stellaria gonomischa Boivin

Colorado, Grand County: Berthoud Pass, 12400 ft., *K.&S. 3328.* $2n = 26$.

This is possibly the first report for one of the segregates of *Stellaria umbellata* Turcz. The latter sensus stricto seems to be the only member of sect. *Umbellatae* which has been counted previously, with $2n = 26$ (Zhukova, 1967). Hartman's (1971) report of $2n = 26$ for a Wyoming collection of *S. umbellata* Turcz. may be referable either to *S. gonomischa* Boivin or to *S. weberi* Boivin.

RANUNCULACEAE

Aquilegia canadensis L.

Maryland, Montgomery County: Bear Island, *K. 4031.* $n = 7$.

Ranunculus abortivus L.

Virginia, Fairfax County: Turkey Run, *K. 4059.* $n = 8$.

Ranunculus micranthus Nutt.

Virginia, Fairfax County: Turkey Run. *K. 4081.* $n = 8$.

While several reports are available for *Ranunculus abortivus, R. micranthus,* which is closely related, has as yet been chromosomally unknown (Keener, 1976).

BRASSICACEAE

Arabis laevigata (Muhl.) Poir.
Maryland, Montgomery County: Bear Island, *K. 4043.* $n = 7$.

SAXIFRAGACEAE

Saxifraga virginiensis Michx.
Maryland, Montgomery County: Bear Island, on rocky ledges, *K. 4025.* $n = 14$.
Virginia, Fairfax County: Difficult Run, dry open wood, *K. 4047.* $2n = 28$.

The chromosome numbers reported here represent the first counts for United States plants of this species and correspond with one based on a collection from near Tulibi Lake, Manitoba (Löve & Ritchie, 1966).

FABACEAE

Desmodium dillenii Darl.
Maryland, Montgomery County: Dry wood on road from Cabin John to Cabin John Bridge, *K. 3526.* $2n = 22$.

The report of $2n = 22$ concurs with three counts presented for meiotic material from North Carolina and Connecticut (Young, 1940). The genus seems to be entirely diploid, based on $x = 11$.

Oxytropis deflexa (Pall.) DC.
Colorado, Park County: 2 mi. N. of Fairplay on Route 9, 9900 ft., *K.&S. 3374.* $2n = 16$.

VIOLACEAE

Cubelium concolor (Forst.) Raf.
Maryland, Montgomery County: Plummers Island, *K. 4166.* $n = 24$.

The huge genus *Cubelium,* mainly tropical in its geographical distribution, is poorly known cytologically. The limited data available (Gadella et al., 1969; Davidse 1971) would indicate that at least two polyploid series are present, one based on $x = 6$, the other on $x = 8$. *Cubelium concolor,* which does not appear to have been previously counted, obviously fits within this pattern.

ONAGRACEAE

Ludwigia alternifolia L.

Virginia, Fairfax County: Great Falls of the Potomac, *K. s.n.* $2n = 16$

The only chromosome counts made hitherto in this species are $n = 8$ and $2n = 16$ for var. *pubescens* Palmer & Steyerm. from Florida (Gregory & Klein, 1960).

PLUMBAGINACEAE

Armeria maritima (Mill.) Willd. var. *californica* (Boiss.) G.H.M. Lawr.

California, Marin County: Ocean View, on coastal bluffs, *K. 6156.* $2n = 18$.

POLEMONIACEAE

Phlox divaricata L.

Maryland, Montgomery County: Bear Island, *K. 4024.* $n = 7$.

Phlox subulata L.

Maryland, Montgomery County: Bear Island, *K. 4022.* $n = 7$.

HYDROPHYLLACEAE

Phacelia dubia (L.) Trel.

Maryland, Montgomery County: Plummers Island, *K. 4175.* $n = 5$.

BORAGINACEAE

Mertensia virginica (L.) Pers.

Washington, D.C.: Moist alluvial wood along the Potomac River, between Three Sisters and Chain Bridge, *K. 4016.* $n = 12$.

To date, all of the members of this genus have had the base chromosome number of $x = 6$ (e.g., Britton, 1951; Sokolovskaya, 1968).

RUBIACEAE

Houstonia caerulea L.

Maryland, Montgomery County: Bear Island, *K. 4031.* $n = 16$.

This wide-ranging species has been shown to consist of three chromosomal races, diploid ($n = 8$), tetraploid ($n = 16$) and hexaploid ($n = 24$) of which the first is more southern in its distribution. Only tetraploids have been reported from Maryland (Lewis & Terrell, 1962).

CAMPANULACEAE

Campanula divaricata Michx.

Virginia, Warren County: Along Skyline Drive, near Stony Man, *K. 3573*. $2n = 34$.

This is a curious member of subsect. *Heterophylla* of the genus *Campanula*, aberrant in any of the proposed serial subdivisions (Kovanda, 1977). The count of $2n = 34$ is in agreement with the only previously published record based on a West Virginia collection (Gadella, 1964). A reported count of $2n = 40$ (Darlington & Janaki-Ammal, 1945) is doubtfully correct.

ASTERACEAE

Tribe Astereae

Acamptopappus shockleyi A. Gray

Nevada, Nye County: Beatty, on road to Daylight Pass, *K. 5728*. $2n = 18$.

This species has been reported as having $n = 9$ by Raven et al. (1960) from Esmeralda County, Nevada.

Erigeron pulchellus Michx.

Virginia, Fairfax County: Difficult Run, *K. 4234*. $2n = 18$.

Erigeron simplex Greene

Colorado, Grand County: Berthoud Pass, 12400 ft., *K.&S. 3329*. $2n = 18$.

This species is now known to be composed of at least two chromosome races, one diploid, with $2n = 18$, one tetraploid, with $2n = 36$ (Wiens & Halleck, 1962; Taylor & Brockman, 1966). Montgomery and Yang (1960) have reported a triploid number, $2n = 27$, for cultivated material from the Royal Botanic Garden, Edinburgh. The species would clearly be worth a thorough cytogeographical study.

Solidago flexicaulis L.

Maryland, Montgomery County: Bear Island, *K. 3631*. $2n = 27, 36$.

Previous counts have revealed that *Senecio flexicaulis* comprises diploid ($2n$ = 18) and tetraploid ($2n$ = 36) cytotypes (Beaudry & Chabot, 1959; Solbrig et al., 1964; Kapoor & Beaudry, 1966; Beaudry, 1969; Kapoor, 1970). Their geographical distribution does not appear to form a definite pattern but the simultaneous presence of triploids and tetraploids in one locality would indicate that they are at least partly sympatric. No diploids were found in the present collection but they are known to occur in Maryland (Kovanda, 1972).

Solidago speciosa Nutt. var. *pallida* Porter
Colorado, Larimer County: Rist Canyon, about 8 mi. W. of Bellevue, 6800 ft., *K.S. 3164*. $2n$ = 36.

The tetraploid chromosome number reported here is in accord with Beaudry's (1963) results for this species. Morton (1970) has, however, counted n = 9 for var. *rigidiusculus* T. & G. from Missouri, indicating the presence of at least two ploidy levels within this variable species. A detailed study is needed to ascertain whether this variation in chromosome number is correlated with the taxonomic treatment. The collection upon which the present count is based may be referred to var. *pallida* Porter, but differs in having densely hairy achenes.

Tribe Heliantheae

Bebbia juncea (Benth.) Greene
Arizona, Pima County: Robles Ranch, on road to Ryan Field Coffee Shop, *K. 5255*. $2n$ = 18.

Bidens tenuisecta A. Gray
New Mexico, Santa Fe County: Sangre de Christo Mountains, along the Chamisa Trail, *K. 3446*. $2n$ = 24.

The count of $2n$ = 24 is the second report for this species and the first for a United States collection (Turner & Johnston, 1961).

Chrysogonum virginianum L.
Maryland, Montgomery County: Cabin John, *K. 4216*. n = 16.

This number was reported previously by Jones (1968) for material from Georgia.

Helianthus annuus L.
California, Fresno County: Squaw Valley, *K. 5891*. $2n$ = 34.

Madia elegans D. Don ssp. *vernalis* Keck
California, Tulare County: Three Rivers, *K. 5819*. $2n$ = 16.

Tribe Senecioneae

Arnica mollis Hook.

Colorado, Grand County: Berthoud Pass, 12400 ft., *K.&S. 3321.* $2n = 38$.

This is another species containing two cytotypes, one diploid, with $2n = 38$, one tetraploid, with $2n = 76$, the latter being apparently more common (Ornduff et al., 1967). The only diploid record was from Jackson County, Colorado. Additional determinations are required to correlate the cytological information with morphological variation.

Senecio aureus L.

Maryland, Montgomery County: Bear Island, *K. 4032.* $n = 22$.

Washington, D.C.: Theodore Roosevelt Island, *K. 4292.* $n = 22$.

Senecio douglasii DC.

California, Fresno County: Squaw Valley, *K. 5890.* $2n = 40$.

Senecio eremophilus Richards

Colorado, Summit County: Alluvial ground at Breckenridge, *K.&S. 3369.* $2n = 40$.

This seems to be the first count for the species, placing it at the same level as *Senecio ambrosioides* Rydb., the only member of sect. *Eremophili* which has been counted previously (Ornduff et al., 1967). Assuming that the basic chromosome number of the majority of the Senecioneae is $x = 10$ (Ornduff et al., 1963), *S. eremophilus* is to be regarded as a tetraploid.

Tribe Cichorieae

Hieracium gronovii L.

Tennessee, Henry County: Puryear Clay Pit, *K. 3072.* $2n = 18$.

Hieracium venosum L.

Maryland, Montgomery County: Great Falls of the Potomac, *K. 4181.* $2n = 18$.

This count, made from young corolla tissue, confirms previous reports by Gustafsson (1933), Smith (1966) and Jones (1968).

Hypochoeris glabra L.

California, Fresno County: Squaw Valley, *K. 5893.* $2n = 10$.

Krigia virginica (L.) Willd.

Virginia, Fairfax County: Great Falls of the Potomac, *K. 4231.* $2n = 20$.

The only previous report for *Krigia virginica* was diploid, $2n = 10$

(Stebbins, Jenkins, & Walters, 1953). Surprisingly enough, the Great Falls gathering proved to be tetraploid, with a chromosome couplement of $2n = 20$. Obviously, two ploidy levels exist within this species, and further study is needed, to determine possible differences in their morphology, habitat requirements and geographical distribution.

Youngia japonica (L.) DC.

Maryland, Montgomery County: Chesapeake and Ohio Canal, picnic area near Lock 14, *K. 4223*. $n = 8$.

ACKNOWLEDGMENTS

I am indebted to Drs. S. G. Shetler, Department of Botany, Smithsonian Institution, Washington, D.C., and W. A. Weber, University of Colorado, Boulder, for valued advice on the identity of some species. The Rocky Mountain field trip was supported by the Smithsonian Research Foundation (Sg-0653061/C2).

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INSTITUTE OF BOTANY
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BASICLADIA CHELONUM (COLLINS) HOFFMANN & TILDEN AND BASICLADIA CRASSA HOFFMANN & TILDEN (CLADOPHORALES) IN SOUTHERN ILLINOIS

Louis L. Lipsey, Jr.

Since the works of Tiffany and Britton (1952), the algal flora of southern Illinois has been studied extensively. However, reports of *Basicladia* are absent in the literature (Dillard & Mohlenbrock, 1962; Dillard, Weik, & Mohlenbrock, 1963; Weik & Mohlenbrock, 1963; Wunderlin & Wunderlin, 1968; Wunderlin, 1971; Dillard & Tindall, 1973; Williams & Tindall, 1975).

On March 25, 1977, while collecting for phytoplankton in Little Grassy Lake, Williamson County, Illinois, *Basicladia chelonum* (Collins) Hoffman & Tilden was found epizoic upon the musk turtle, *Sternotherus odoratus* Latreille. Although *B. chelonum* had a general distribution upon the turtle's shell, on the plastron it was found sporadically in small bunches, only a few millimeters in diameter, and on the carapace it was present in massive tufts. The alga on the anterior portion of the carapace was very grass-green in appearance, whereas that on the posterior half was darkened greatly by the presence of epiphytic diatoms, whose taxa included: *Gomphonema acuminatum* Ehrb., *G. gracile* Ehrb. emend V.H., *G. parvulum* Kutz., and *Achnanthes minutissima* Kutz.

A few days later, on March 31, 1977, two other turtles were collected at Prairie Creek Pond in Franklin County, Illinois. One of the turtles examined was a musk turtle. Algae were absent from its plastron, but its carapace was covered by a luxurious green growth of *Basicladia chelonum* (Figure 1). The filaments of *B. chelonum* were generally free of epiphytic algae although cells of *Eunotia curvata* (Kutz.) Lagerst. were encountered occasionally. The second turtle collected at this locality was a painted turtle, *Chrysemys picta* Schneider. *Basicladia crassa* Hoffman & Tilden was found on the carapace of this specimen. Its plastron was free of algal growth. Filaments of *B. chelonum* were encountered but to a lesser extent than *B. crassa.* The filaments of *B. crassa* were yellow-green in appearance, darkened somewhat by the extreme abundance of epiphytes. *Oedogonium* sp., *Eunotia curvata* (Kutz.) Lagerst., *Gom-*

Figure 1. A musk turtle with the epizoic alga, *Basicladia chelonum*.

phonema gracile Ehrb. emend. V.H., and *G. parvulum* Kutz. were the most abundant epiphytes observed. However, cells of *Surirella angustata* Kutz. and *Synedra* sp. were also frequent upon the filaments. In addition to the epiphytes, numerous filaments of *Draparnaldia plumosa* (Vauch.) C. A. Agardh. and *Tribonema minus* (Wille) Hazen. were intermingled among the erect thalli of *Basicladia*.

Edgren et al. (1953) conducted a major study of the genus *Basicladia* in relation to its epizoic existence upon turtles. They found that the musk turtle (*Sternotherus odoratus*) and the painted turtle (*Chrysemys picta*) were colonized to a greater extent than were other species of turtles. Their findings further showed that *Basicladia chelonum* was usually more abundant than was *B. crassa* upon *S. odoratus*. When the carapaces of *C. picta* were analyzed, Edgren et al. found *B. crassa* to be more frequent than *B. chelonum*. My observations support these findings.

Interestingly enough, two of the three turtles in this study had their epizoic *Basicladia* heavily populated by a large variety of epiphytes. Edgren et al. (1953) found only one epiphyte in their study of over 700 turtles. It is quite possible that these investigators overlooked the diatoms upon examination of their specimens. This matter of epiphytic algae upon the epizoic *Basicladia* warrants further investigation.

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A NEW SPECIES OF XYRIS (SECT. XYRIS) FROM TENNESSEE AND NORTHWESTERN GEORGIA

Robert Kral

An examination of the rather small collection of Tennessee Xyrids at the Vanderbilt University Herbarium has revealed a specimen labeled "*X. caroliniana* Walt." (this name now applied to a much different taxon) but which, in regard to a combination of characteristics, is distinct from any other *Xyris.* It is hereby described as follows:

Xyris tennesseensis Kral, sp. nov.
Herba solitaria vel dense caespitosa; basis plerumque bulbosa, foliis extimis squamiformibus fuscis inclusa. Folia lineari-gladiata, 15–45 cm. longa; basis equitans, quam lamina 3–8-plo brevior, rosea vel purpurea, margine pallida scariosa; lamina viridis 0.5–1.0 cm. lata, plana vel leviter torta, ad apicem obtusa, incrassata, margine leviter incrassata, paginis glabris vel subtiliter papillosis. Vagina foliis brevior, basin versus rufa vel fusca; lamina brevis. Scapus linearis 30–70 cm. longus, apicem versus complanatus 2–5-costatus necnon saltem duabus costis alis similibus et tuberculo-scabridis. Spica ovoidea 1.0–1.5 cm. longa, obtusa; bracteae multae arcte et spiraliter imbricatae. Bracteae fertiles suborbiculatae, rotundatae, integrae vel leviter erosae, corylinae, area dorsali ovato-triangulari viridi. Sepala laterali inclusa curvata, carina tenui, basin versus angusta, integra, apicem versus latiora lacerata, ferruginea. Semina non translucida.

Perennial, solitary or densely caespitose, the plant base soft, somewhat fleshy, often bulbous, usually enclosed in dark, scale-like outer leaves (as in *Xyris torta, X. platylepis*). Leaves linear, 15–45 cm. long, the blades linear-gladiate, 0.5–1.0 cm. broad, flat or slightly twisted, bright green, the apex incurved, bluntly acute, somewhat thickened, the margins slightly thickened, entire; equitant base 1/3–1/8 the length of the blade, pink, red or purple, the margin, pale, broad, scarious, the surfaces smooth or finely papillate. Sheaths shorter than the foliage leaves, reddish or brownish proximally and with short blades. Scapes linear, straight, 30–70 cm. long, usually flattened and 2–5-costate distally and with at least two ridges quite wide and tuberculate-scabrid, subterete and 2–several ribbed proximally. Mature spikes broadly ovoid, 1.0–1.5 cm. long, blunt, of several tightly and spirally imbricated bracts. Fertile bracts suborbicular, rounded entire or slightly erose, tan save for greenish, ovate-triangular dorsal areas. Lateral sepals included, curvate, the keels thin, narrow, the distal half lacerate, broader, reddish brown. Petal blades obovate, ca. 4.5 mm. long, 3.0 mm. broad, yellow, apically rounded, lacerate. Staminodes bi-brachiate, the long hairs moniliform. Fertile anthers ca. 2 mm. long, lance-linear, the sacs near parallel, their tips projecting apically 0.4 mm. beyond the flat connective apex. Seeds ellipsoidal, ca. 0.5–0.6 mm. long, slightly to very farinose, with 18–20 fine, longitudinal lines, these sometimes irregular or joining. Flowering in late summer, early fall. Flowers opening in morning. Chromosome number: $n = 9$.

Seepage over calcareous sandstone or fine, wet, sandy, peaty soil of meadow-swales, Valley and Ridge of northwestern Georgia and southwestern Highland Rim of Tennessee (Lewis County).

TYPE: **United States.** TENNESSEE. Lewis Co.: 3.5 mi. SW of Hampshire just over Maury Co. line by Tenn. 99; locally abundant in *Parnassia* bog, 26 Aug. 1969, *R. Kral 36370*. Holotype at US (this and isotypes soon to be distributed!). Additional material: GEORGIA. Bartow Co.: muddy open area at edge of runway from large spring just S of Aubrey Lake 5.6 mi. N 12 deg E of Cartersville, *Duncan & Harris 12958* (GA). GORDON CO.: 14 mi. S of Chatsworth by UA 411; sunny seep ca. 8 mi. N Fairmount, *Kral 51519* (VDB, dupls. to be distributed). TENNESSEE. Lewis Co.: Meriwether Lewis Nat. Monument. Spring Branch, *C. B. King 318* (VDB); type locality, *Kral 36370;* shaley banks of Little Swan Creek above Natchez Trace Parkway, ca. 1.5 mi. NE of Park Headquarters, *Kral 44471*D (VDB, dupls. to be distributed).

Because of its somewhat bulbous, fleshy base, and twisted leaf blades, this species superficially resembles either *Xyris torta* or *X. platylepis*. However, *X. torta* has ciliate, strongly-curvate, apically hair-tufted lateral sepals, together with strongly raised-nerved leaves; and *X. platylepis* has more strongly bulbous, gelatinous coated, bases and larger spikes. Neither of these have farinose seed, a character which, when combined with lateral sepal features, seems

Xyris tennesseensis Kral. a. Habit sketch. b. Spike. c. Lateral sepal. d. Petal blade and stamen. e. Seed.

to relate this new taxon with the *Xyris difformis* complex. In that complex of forms, *X. tennesseensis* is closest to *X. difformis* Chapm. var. *floridana* Kral, the only one with farinose seeds; however that variety lacks bulbous bases, has a lower stature, more spreading leaves which are liberally tuberculate-scabrid over their surfaces, and smaller, sharper-pointed, darker colored spikes.

Xyris tennesseensis has been found in five localities and always in populations unmixed with those of other *Xyris* species. Thus far it appears to be spatially isolated from other Xyrids, and the nearest geographical relatives are *X. difformis* var. *difformis* and *X. torta.* It is curious that to date this plant is known to be local in two different and separate physiological provinces. However, this situation may merely indicate a lack of botanical collection in the intervening area. It is perhaps of some interest that in all presently known localities, a common associate is *Juncus brachycephalus* (Engelm.) Buch., an essentially northern rush, only recently reported (1973, 1975) from further south than Indiana and Illinois.

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CENTAURIUM PULCHELLUM IN NEW ENGLAND

On July 29th, 1977, a few plants collected by the roadside on Route 30 near the north end of Lake Bomoseen in the Town of Castleton, Vt. were brought to Jesup Herbarium for identification. By a process of elimination it was determined that these specimens did not belong to our local flora. By reference to the keys, descriptions, and illustrations in Gustav Hegi's *Flora von Mittel Europa* the plants have been identified as *Centaurium pulchellum* (Sw.) Druce (Gentianaceae). Hegi describes the species as annual or biennial and native to southern Europe. It is listed in the eighth edition of Gray's *Manual of Botany* as occurring occasionally from New York to Illinois and south to east Virginia. Reference to other Floras and to a number of herbaria in New England indicates that this is the first report of the species in New England. An item of interest is that the collection station is described as an area of several square feet covered by several hundred plants, giving the appearance of a well established colony. The collection was made by C. L. Wilson, Professor of Botany Emeritus, Dartmouth College, T. M. Frost, graduate student in Biology, Dartmouth, and Paul Martin Brown, a Vermont botanist. On October 4th at the same station, Paul Martin Brown collected mostly fruiting specimens of the species. Voucher specimens have been deposited in the Pringle Herbarium (VT) at the University of Vermont, Burlington, Vt., the Hodgdon Herbarium (HNA) at the University of New Hampshire, Durham, N.H., the University of Massachusetts Herbarium at Amherst (MASS) at the University of Massachusetts, Amherst, Mass., the Jesup Herbarium (HNH), Dartmouth College, Hanover, N.H., and the New England Botanical Club Herbarium (NEBC), Harvard University, Cambridge, Mass.

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EUPHORBIA DENTATA IN NEW ENGLAND

NANCY A. MCNELLY

On August 19, 1976, I collected specimens of *Euphorbia dentata* Michx. from a stand found in Cambridge, Middlesex County, Massachusetts. The plants were growing in cracks in the pavement of a vacant lot.

In the eighth, corrected edition of *Gray's Manual of Botany* (1) and the revised edition of *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada* (2), the easternmost range of *Euphorbia dentata* Michx. is listed as New York state. No mention of this species is made in *The Flora of New England* (3). Because it appears that there are no previous records of the presence of this species in New England, I felt it important to report this collection. A specimen of this spurge has been submitted to the herbarium of the New England Botanical Club.

I would like to thank Henry G. Wendler of the Massachusetts Horticultural Society for his confirmation of my identification of this plant, and James W. Hinds for his encouragement.

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THREE ADDITIONS TO THE VERMONT FLORA

ERIC SUNDELL

The following species are not unexpected in Vermont, and this note confirms their presence in the flora.

Aristida basiramea Engelm. WINDSOR COUNTY: sandy soil of railroad yard, White River Junction, *Sundell 1308,* 31 July 1975. Reported from both New Hampshire and New York by Hitchcock and Chase (*Manual of the grasses of the United States,* 1950). Specimen verified with a Fernald and Griscom collection from Bedford, New Hampshire, distributed as number 513 of the *Plantae Exsiccatae Grayanae.*

Sedum spurium Bieb. WINDSOR COUNTY: a few thriving colonies on rock ledges along U.S. Route 5, within the village of White River Junction, *Sundell 1512,* 12 July 1976. Clausen (*Sedum of North America north of the Mexican Plateau,* 1975) cites 14 collections from "Nfld. to Pa." but has informed me in a personal communication that he knows of no previous Vermont collections.

Bellis perennis L. WINDSOR COUNTY: abundant lawn weed in South Woodstock village, *Sundell 1384,* 28 May 1976. This is the little daisy that inspired William Wordsworth to at least four poems. A Vermont specimen is, in fact, cited in the Check-list of Vermont Plants (Vermont Botanical and Bird Club, 1973) as on deposit at Windham College herbarium, but in answer to an inquiry there it is no longer retrievable.

Specimens of all three species are filed in the Jesup Herbarium, Dartmouth College, in Hanover, New Hampshire. I wish to thank Dr. James Poole for his cheerful help, especially for forwarding voucher sheets of *Bellis* and *Sedum* to the Pringle Herbarium, University of Vermont, and a sheet of the *Sedum* collection to Dr. Clausen at Cornell University.

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CAREX WIEGANDII MACKENZIE (CYPERACEAE): NEW FOR PENNSYLVANIA

PAUL E. ROTHROCK

While completing a taxonomic study of the genus *Carex* in Pennsylvania, I critically examined several collections which seemed to be related to *C. atlantica* Bailey var. *incomperta* (Bailey) Hermann, a plant of common occurrence in Pennsylvania. The collections differed from this species, however, in having obviously broader leaves (up to 5 mm wide), inflorescences of strongly aggregated spikelets, ventrally nerveless perigynia, and strongly thickened, brownish sheath orifices.

The above diagnostic features best describe *Carex wiegandii* Mack. (sect. *Stellulatae*), a species formerly known from Newfoundland to Ontario and south to Massachusetts and northern New York. My determination was kindly confirmed by Dr. F. J. Hermann through examination of a duplicate specimen. The collections from northern Pennsylvania (now deposited at PAC) therefore represent an appreciable range extension.

REPRESENTATIVE SPECIMENS. **Elk Co.**: Open boggy ground 0.75 mile ENE of Rasselas (N 41°37′W 78°37′), *Rothrock 473;* **McKean Co.**: Open *Sphagnum* bog (Catherine Swamp) ca. 5 miles SE of Mt. Jewett (N41°41′W 78°34′), *Rothrock & Keener 488.*

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NOTICE OF PUBLICATION

The New England Botanical Club has received a copy of James L. Hodgins' *A Guide to the Literature on the Herbaceous Vascular Flora of Ontario.* The booklet contains entries on references to checklists and surveys (by area and author), monographs, periodicals and journals, maps, and public herbaria. This 25 page publication may be purchased at $2.00 a copy by writing the author at: 90 Wolfrey Avenue, Toronto, Ontario, Canada M 4 K 1 K 8.

Vol. 80, No. 822, including pages 159–318, was issued April 21st, 1978.

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THE TAXONOMY OF ASTER SECTION MULTIFLORI (ASTERACEAE) — II. BIOSYSTEMATIC INVESTIGATIONS

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This paper is a continuation of the study presented in Rhodora Vol. 80, No. 823, pages 319–357, and it constitutes a summary of the biosystematic and phytogeographic data compiled in support of the taxonomic treatment of *Aster* sect. *Multiflori.* The core of the findings is based on my doctoral dissertation, deposited with the Graduate College of the University of Illinois at Urbana-Champaign in 1973, but research has been continued. Acknowledgments and bibliographic entries given in Part I will not be repeated. Two species are recognized: *Aster ericoides* Linnaeus [with the typical ssp. *ericoides* and ssp. *pansus* (Blake) A. G. Jones], and *A. falcatus* Lindley in Hooker [with the typical ssp. *falcatus* and ssp. *commutatus* (Torrey & Gray) A. G. Jones].

MATERIALS AND METHODS

For hybridization and uniform culture experiments, populations were transplanted to a research field in Urbana, Illinois, and to a greenhouse. Copious field notes were taken at the collection sites. The following states and provinces were visited: Alberta, Arizona, British Columbia, Colorado, Illinois, Indiana, Iowa, Kansas, Massachusetts, Minnesota, Montana, Nebraska, North and South Dakota, Oklahoma, Oregon, Washington, Wisconsin, and Wyoming. Vouchers (identified by numbers only) are deposited in the herbarium of the University of Illinois (ILL).

Morphological characteristics were examined in over 7,000 herbarium specimens covering the entire geographic range for *Aster* sect. *Multiflori.* In addition to specimens held at ILL, loans were obtained from 40 other herbaria. The institutions for cited specimens are identified by their respective acronyms, as listed in *Index Herbariorum,* Ed. 6 (Holmgren & Keuken, 1974).

The technique for preparation and staining of chromosome squashes has been published (Jones, 1977). Countable figures were photographed at a camera magnification of 500 × using Kodak High Contrast copy film. Brovira No. 6 paper was used for printing.

MORPHOLOGICAL CONSIDERATIONS

In order to delimit the taxa in *Aster* sect. *Multiflori,* about 2,000 specimens were subjected to a quantitative and qualitative evaluation. The following diagnostic character groups presented themselves:

1. Number of florets per head (only number of disk flowers was scored).
2. Relative height of head, determined by adding height of the involucre to length of ligule (in mm).
3. Length and texture (firm vs. flexible) of the bract-like leaves of the peduncle.
4. Length of the peduncle.
5. Imbrication of the involucre, calculated as a ratio: length of outer to inner phyllaries.
6. Degree of herbaceousness of outer phyllaries, i.e., the fraction of the area that is green, in contrast to the chartaceous, indurate, basal portion.
7. Degree of squarrose spreading of outer phyllaries (this character is generally correlated with the previous: plants with stiff indurate outer phyllaries have a more strongly squarrose involucre than those with flexible green phyllaries).
8. Habit of rhizomes: stoloniferous vs. cormoid.
9. Habit of above-ground stems: cespitose vs. single-stemmed colonial.
10. Habit of the inflorescence: compound-racemiform, with heads secund, vs. diffuse-paniculate, with heads at apex of branchlets, not secund.
11. Type of stem pubescence, scored (on the major branches of the inflorescence) for three categories: divaricately hirsute, appressed strigose, and ascending (= intermediate).

Originally, seven of the contrasting character combinations were mapped for presence; data for some characters were subjected to an analysis of statistical significance, and those of others were employed for the construction of scatter diagrams (Jones, 1973, 1974).

Among the herbarium collections examined, many specimens exhibited intermediacy between the extremes of certain characteristics. In my own field work, I have also found many examples. The highest degree of intermediacy was observed among populations from Alberta, Saskatchewan, Montana, and western North Dakota, where three of the four subspecies are sympatric. Collections made by A. J. Breitung, A. H. Brinkman, B. Boivin, W. C. McCalla, E. H. Moss, H. M. Raup, and G. H. Turner in Alberta and Saskatchewan bear numerous annotations attesting to the problem of delimiting taxa within *Aster* sect. *Multiflori.* Only rarely can a collection from this area be identified with certainty on the basis of only one or two characters. However, specimens can usually be assigned to the subspecies by a combination of at least six or seven of the characteristics listed above, and most flowering or fruiting specimens can readily be distinguished at the specific level.

A comparison of mean, range, and standard deviation for quantifiable diagnostic characteristics in taxa of *Aster* sect. *Multiflori* is presented in Table 1. Four of the six categories in the table pertain to characters of the capitulum, one concerns the ultimate rameal leaves, and one constitutes the sum of four measurements.

Capitulum. Head size is the most evident and constant morphological character by which the two species of *Aster* sect. *Multiflori* can be distinguished. *Aster ericoides* is a relatively small-headed species, while *A. falcatus* is relatively large-headed (Figure 1). Several traits contribute to head size: height of head, number of ligules, and number of disk florets. For statistical tests, relative height of head was computed by adding height of involucre in mm to the length of the ligule. In a 2 × 7 contingency table, a test of significance was performed on 956 samples, comparing relative height of head with number of disk florets (Table 2). Both the observed and the expected numbers are listed in each size class. The chi square value obtained corresponds to a probability of much less than 0.0005 for equal or more extreme deviations from a random distribution on the basis of chance alone. The correlation between these two characters is, therefore, statistically highly significant.

Table 1. **Comparison of morphological measurements for the taxa recognized in Aster sect. Multiflori.**

Characteristics		*A. ericoides ssp. ericoides*	*A. ericoides ssp. pansus*	*A. falcatus ssp. falcatus*	*A. falcatus ssp. commutatus*
1. Number of disk	mean	9.0	14.7	20.5	18.6
florets per head	range	5–18	6–25	14–34	13–32
[Standard deviation]	S (±)	2.85	4.33	4.70	4.16
2. Length of ligule	mean	5.14	5.33	7.18	7.52
(including corolla-tube),	range	3.0–8.0	3.0–8.0	6.0–10.0	6.0–11.0
in mm	S(±)	0.98	0.85	1.06	1.07
3. Height of involucre,	mean	4.06	4.36	5.41	5.81
in mm	range	2.5–5.5	3.0–5.0	5.0–8.5	4.5–9.0
	S (±)	0.66	0.57	0.74	0.89
4. Length of peduncular	mean	2.23	3.07	5.13	4.54
bract-like leaves,	range	1.5–4.5	1.5–5.5	3.5–9.0	2.0–10.0
in mm	S (±)	0.75	1.05	1.46	1.49
5. Sum of the above	mean	20.11	26.33	37.48	35.49
(1–4) measurements	range	14–31	15–34	29–52	27–55
	S (±)	3.85	4.77	5.03	6.87
6. Imbrication of involucre	mean	0.60	0.70	0.93	0.71
= ratio: length of outer	range	0.4–0.8	0.4–0.95	0.7–1.3	0.3–1.1
to inner phyllaries	S (±)	0.11	0.15	0.14	0.17

Number of disk florets was chosen for numerical evaluation, because ligules are often removed or broken off and cannot readily be scored with accuracy. Ligule number in *Aster ericoides* varies from (8–)10–18(–20), and in *A. falcatus* from (18–)22–32(–36). Consequently, the total number of florets separates the two species, with an approximate range of 18–33 in *A. ericoides* and 35–60 in *A. falcatus.* In reality, the correlation between height of head and number of florets is even stronger than is indicated in the statistical analysis. In typical *A. falcatus,* secondary heads on minor branchlets of the inflorescence are often considerably shorter than those terminating major branchlets. Number of florets, however, usually is not significantly affected by variability in height. There is hardly any overlap between the two species, as far as overall head size is concerned.

Table 2. **Comparison of relative height and number of disk florets per head.**

Number of Florets per Head		Relative Height of Head 11.5 mm or less	12.0 mm or more	Totals
6 or less	observed	128	2	130
	expected	94.10	35.90	
7–10	observed	290	11	301
	expected	217.88	83.12	
11–14	observed	144	63	207
	expected	149.84	57.16	
15–18	observed	79	64	143
	expected	103.51	39.49	
19–22	observed	40	72	112
	expected	81.07	30.93	
23–26	observed	10	30	40
	expected	28.95	11.05	
27 or more	observed	1	22	23
	expected	16.65	6.35	
Totals		692	264	956

Chi Square: 330.24 (6 degrees of freedom)
Probability: $<<0.0005$

Degree of imbrication of the involucre, on the other hand, is subject to much variability. The character is significant, at best, at the subspecific level and must be evaluated in combination with other characteristics. When compared with height of head and rhizome habit in a scatter diagram, the results present a continuum (Jones, 1973, *f. 10*).

Inflorescence. Certain very diagnostic characters cannot readily be scored. Features of the inflorescence, for example, are very useful for separation of taxa in sect. *Multiflori.* In most populations of *Aster ericoides,* the inflorescence is a dense many-headed panicle with arching branches, the heads racemiform, on short peduncles, and typically secund. Within ssp. *pansus,* the secund exposure of heads is not as pronounced in plants of var. *stricticaulis* as in those of typical var. *pansus.* In var. *stricticaulis* the heads are nearly sessile, crowded, and inserted more or less uniformly around the flowering stalk.

Populations of both subspecies of *Aster falcatus* typically exhibit open panicles. The heads are long-pedunculate, not crowded, and not secund. Simple, short-stemmed, racemose inflorescences, observed in matted populations of *A. falcatus* ssp. *commutatus,* result from a phenotypic response to certain environmental conditions.

In a 2 × 2 contingency table, a sample of 956 specimens was tested statistically for correlation between height of head and type of inflorescence (Table 3). The extremely high chi square value indicates that the probability for a chance distribution of deviations from randomness is infinitesimal. The two species can, therefore, usually be distinguished on the basis of these two characteristics alone.

Many populations of the transition zone between the ranges of *Aster falcatus* ssp. *commutatus* and *A. ericoides* ssp. *ericoides* (i.e., from Manitoba, the Dakotas, western Minnesota, and Nebraska) tend toward intermediacy; the branches of the inflorescence are often arching and heads disposed more or less racemiform. Number of florets and height of head, however, are relatively high. If characters of pubescence are disregarded, many specimens of this kind identify with the description and the type of Rydberg's (1901) *A. crassulus* (=*A. falcatus* ssp. *commutatus* var. *crassulus*).

Collections from the southern portion of the range of *Aster* sect. *Multiflori* (Oklahoma, New Mexico, Texas, Mexico) often exhibit a particular inflorescence trait. The ultimate rameal leaves are very small and closely appressed to the peduncle or stem. They are stiff, often squarrose and phyllary-like and, in fact, usually intergrade with the phyllaries (Figure 2). This trait is predominantly correlated with appressed stem pubescence. Although mostly recorded for specimens of *Aster ericoides* ssp. *ericoides,* it has also been found in southern populations of *A. falcatus* ssp. *commutatus.* One trans-

Table 3. **Comparison of relative height of head with type of inflorescence.**

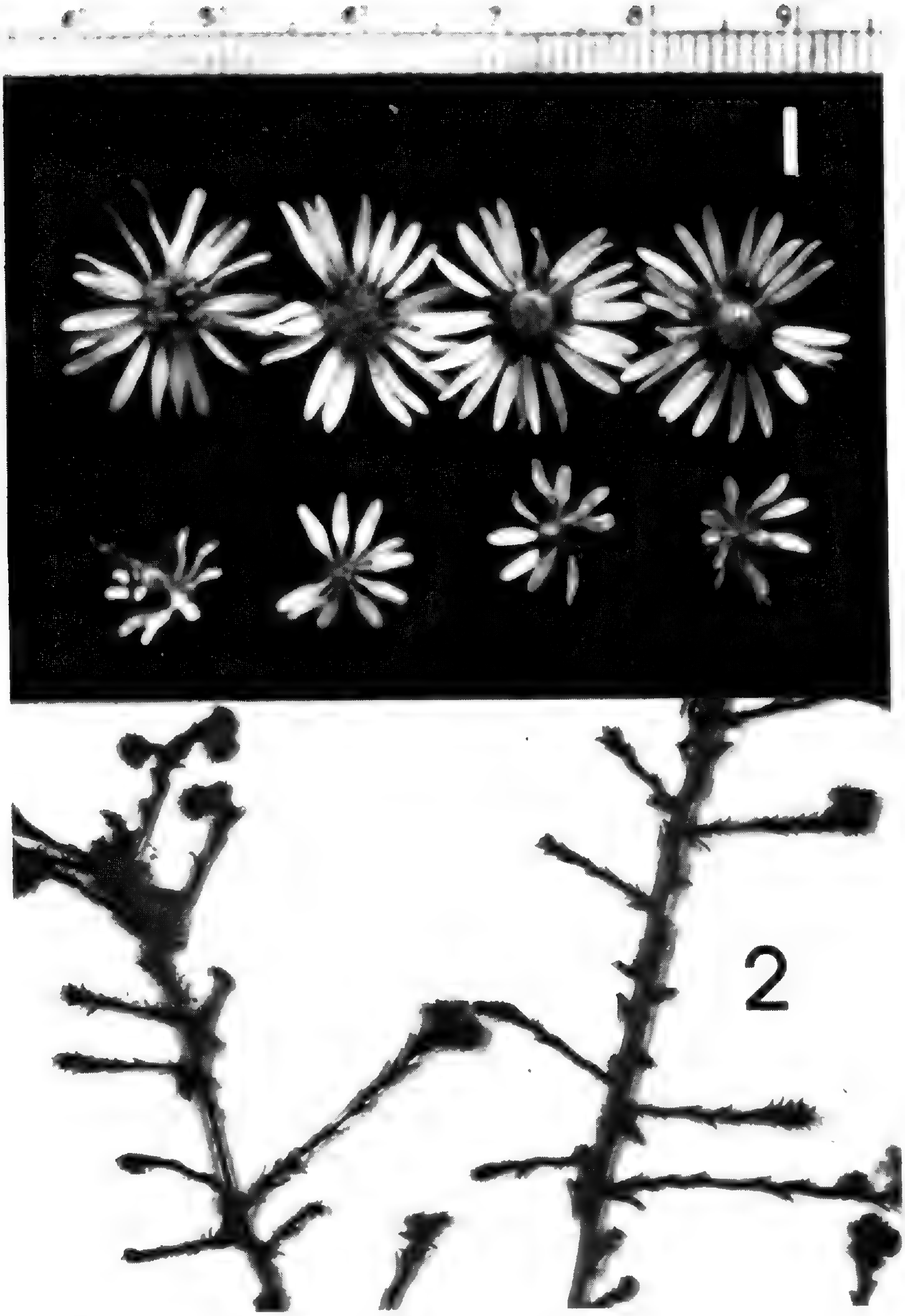
		Inflorescence		
Relative Height of Head		racemiform, with heads short-peduncled or subsessile, secund, crowded on arching branches.	diffuse-paniculate, with heads long-peduncled, on divaricate or ascending branches, not secund.	Totals
11.5 mm or less	observed	567	125	692
	expected	457.47	234.53	
12.0 mm or more	observed	65	199	264
	expected	174.53	89.47	
Totals		632	324	956

Chi Square: 277.65 (1 degree of freedom)
Probability: $<<0.0005$

plant population of this form from southern Oklahoma (*893*) was successfully crossed with a population of typical *A. ericoides* from Indiana (*471*). Populations exhibiting the trait probably cannot be recognized above forma rank. In older floristic works, the plants may key out as *A. hebecladus* DC. Examples are: **Texas:** *W. F. Mahler 1396* (TEX); *H. Wurzlow 1891* (ILL); *E. Whitehouse 9491* (MICH, NY); *V. L. Cory 50291* (GH, ILL, MICH) and *50182* (MICH, NY); **New Mexico:** *F. R. Fosberg S3405* (COLO, GH) and *S3476* (UC); *O. E. Wooten, s.n.* (ILL, RM, KSC, UC); **Oklahoma:** *R. M. House 164* (OKL); *R. Bebb 5926* (OKL); *F. A. Waugh 229* (MO); *F. B. McMurry 1082* (OKL).

Habit. This character is subject to extreme variability in response to environmental fluctuations. There is evidence of clinal variation along ecological gradients (Jones, 1978a), but there is also evidence of good morphological separation of genetically fixed features, at least at the subspecific level.

Ruth A. Nelson (1933) was the first to recognize the significance of underground parts as a diagnostic character in sect. *Multiflori.* She noted that plants with small heads (*Aster ericoides*) have a



Figures 1 and 2. **1.** Comparison of head size. Large heads: *Aster falcatus* ssp. *commutatus* var. *crassulus* (*424*, Nebraska); small heads: *A. ericoides* ssp. *ericoides* var. *prostratus* (*428*, South Dakota); **2.** *Aster ericoides* ssp. *ericoides*: form with appressed rameal leaves [portion of *W. F. Mahler 1396* (TEX)].

cespitose habit and short rhizomes, while plants with large heads (*"A. commutatus"*) form extensive masses and have a creeping rhizome system. As she studied only Rocky Mountain collections from south of the Canadian border, her story was incomplete, and her interpretation led to confusion. Cronquist (1947) pointed out that all collections of *A. ericoides* from east of the Mississippi River have a creeping rhizome system, and that occasional large-headed specimens from the Cordilleran region have the cespitose habit. Later (1950) he gave specific status to the western small-headed taxon [*A. pansus* (Blake) Cronquist = *A. ericoides* ssp. *pansus* (Blake) A. G. Jones]. The holotype, Ellensburg, Washington, *K. Whited 853* (US! — Jones, 1978b, p. 337), lacks underground parts, but there is no doubt about the prevalence of this habit form in small-headed populations from the western states and provinces (Figure 3).

In populations with large heads, a similar dichotomy of underground habit can be observed. Plants of typical *Aster falcatus* have a short cormoid rhizome correlated with cespitose ascending stems (Figure 4). The type, "Arctic America," *Dr. Richardson* (K! — Jones, 1978b, p. 339), again lacks underground parts, but a nearly identical Richardson collection from Fort Franklin that is part of the type collection of *A. ramulosus* (K!) does exhibit a cormoid rhizome. In 68 specimens from Alberta, identified as typical *A. falcatus,* 60 had a short cormoid rhizome, and eight had a stoloniferous rhizome system. Over much of the range of *A. falcatus,* the typical subspecies is sympatric with ssp. *commutatus.* Plants of the latter taxon characteristically form extensive colonies or mats and exhibit a tangled, often woody and knobby, but clearly stoloniferous rhizome system (Figure 5). A certain degree of morphological intermediacy can be observed between the two subspecies, but they occupy somewhat different habitats and, in most places, plants of one taxon are much more abundant than those of the other.

Boivin (1962, 1972) considered the rhizome habit of mere ecological rather than taxonomic importance and, under *Aster ericoides* var. *commutatus,* he combined all elements of the large-headed *A. falcatus* plus the small-headed Great Plains variant of *A. ericoides* (= ssp. *pansus* var. *stricticaulis*). This judgment was based on the observation that, during the rainy spring season or in disturbed habitats, occasional horizontal rhizome strands may be produced by cormoid-cespitose plants. Herbarium specimens selected for me by

ANNOTATION LABEL

PLANTS OF SASKATCHEWAN
University of Saskatchewan, Regina

No 3973 Date August 18, 1964

Aster pansus (Blake) Cronquist

dry open sandy plains, 3 miles E of Dry Lake, Strawberry Lakes area, 12 m. S of Indian Head

J. F. Ledingham, G. J. Jones et al.

Figure 3. *Aster ericoides* ssp. *pansus* var. *stricticaulis* — specimen with characteristic cormoid rhizome [*Ledingham, et al. 3973* (DAO)].

Boivin in support of his viewpoint included *McCalla 12101 & 12338; Boivin & Alex 10199; Boivin & Dore 8202* (DAO). For the far-western var. *pansus,* on the other hand, Boivin did accept the cormoid-tufted condition as a taxonomic character, and he also cited the stoloniferous condition as a diagnostic feature for the eastern var. *ericoides.* According to my observations, however, rhizome habit is a genetically fixed character in all the taxa because transplants of northwestern populations of *A. falcatus* (both subspecies) and *A. ericoides* ssp. *pansus* to the experimental field in Urbana always retained their original underground habit, season after season (Jones, 1978a).

Rhizome habit is correlated with above-ground habit. Populations of *Aster ericoides* ssp. *ericoides* form colonies; the stems are erect, inserted singly, and typically branched above the middle in what is referred to as an excurrent growth habit (R. A. Nelson, 1933). Two variants have been observed in populations of *A. ericoides* ssp. *pansus.* The habit is cespitose in both, but in var. *pansus,* stems are erect and sturdy, with an excurrent branch system similar to ssp. *ericoides.* In var. *stricticaulis,* the stems are somewhat decumbent or ascending, typically more slender and not quite as tall as in var. *pansus.* In transplants to the experimental field in Illinois, populations of var. *pansus* from Oregon and British Columbia (*1130, 1152, 1153, & 1159*) retained the erect habit, while plants of var. *stricticaulis* from Alberta and western Minnesota (*450, 451, & 1203b*) exhibited a phenotypic response toward enhancement of the decumbent habit.

The habit of *Aster falcatus* ssp. *falcatus* resembles that of *A. ericoides* ssp. *pansus* var. *stricticaulis,* except that the stems are usually taller and sturdier, often nearly erect, and more diffusely branched. The colonial stands of *A. falcatus* ssp. *commutatus* are variable. In semi-arid regions of the Great Plains, they form matted growth with relatively short stems. In somewhat more mesic sites, the plants tend to be bushy, with stems decumbent or ascending, branched divaricately from near the base, often strongly sprawling. Transplants of both subspecies of *A. falcatus* from a more northern latitude (**Alberta:** *911, 1178, 1194, & 1195;* **Montana:** *1212;* **North Dakota:** *912, 914, & 1208;* **Wyoming:** *1082*) to the experimental field in Illinois experienced a phenotypic change toward more decumbent stems than were observed in their native habitats. A concurrent change in phenology was noted (Jones, 1978a). By contrast, trans-

PLANTS OF MACKENZIE DISTRICT
NORTHWEST TERRITORIES CANADA

Aster ericoides L., s. l.

Norman Wells.

Moist disturbed ground by buildings,

No. 7813 Coll: W. J. Cody Aug. 5, 195[illegible]
R. J. Gutteridge

Figure 4. *Aster falcatus* ssp. *falcatus* — specimen with characteristic cormoid rhizome [*Cody & Gutteridge 7813* (NCU)].

plants from western states of the same latitude as Illinois (**Colorado:** *996, 1001, & 1053;* **Nebraska:** *424*) showed little or no change, either in habit or phenology.

As in the inflorescence characteristics, many populations especially in the eastern portion of the range for *Aster falcatus* ssp. *commutatus* approach the habit of *A. ericoides* and match the type of *A. crassulus* Rydberg (1901). Stems are erect and sturdy, with somewhat excurrent branches (western **Iowa:** *553;* eastern **Nebraska:** *541;* eastern **South Dakota:** *553–556;* eastern **Colorado:** *1050*).

Another series of intermediates combines the sprawling divaricate branching habit of ssp. *commutatus* with floral characteristics of *Aster ericoides* (both subspecies). These plants were observed in the short-grass prairies and plains of Colorado, Kansas, Nebraska, Oklahoma, and Texas (*892, 893, 1045, 2199, 2204, & 3036*). Since the sprawling habit is found in both species, as well as in both plants with cormoid and stoloniferous rhizome systems, the populations are not taxonomically recognized. Examples are: *U. T. Waterfall 1821* (OKL) *& 10394* (MICH); *A. & R. Nelson & G. J. Goodman 5292* (OKL, RM) *& 5329* (OKL, RM, TEX); *G. Engelmann, s.n.* (MO); *J. W. Blankinship, s.n.* (MICH, RM, US); *W. C. Muenscher 11457* (GA); *F. D. Kelsey, s.n.* (ILL); *V. L. Cory 50291* (GH, ILL, MICH).

Pubescence. In many older studies involving *Aster* sect. *Multiflori,* stem pubescence has been considered a character of primary taxonomic importance (Rydberg, 1906, 1917, & 1932). Most recent authors, however, recognize the significance of this character only at an inferior level. According to my observations, the dichotomy of spreading vs. appressed stem pubescence can be employed for each subspecies. In *A. ericoides,* colonies of either pubescence type often occur side by side in the same population, while the plants are nearly indistinguishable in other respects. Occasionally, stem pubescence may vary within one plant, especially in young vegetative growth (*413, 448, & 452*). Herbarium specimens of *A. ericoides* which exhibit this phenomenon are appressed strigose in the lower stem portion and divaricately hirsute in the upper branches, e.g., *E. Pammel, s.n.* (ISC) and *B. Shimek, s.n.* (ISC). Nearly all specimens of *A. falcatus* ssp. *commutatus* have spreading hairs in the lowermost few centimeters of the stem, regardless of whether the main stem portion has appressed or divaricate indument. If these plants were keyed out with the aid of one of Rydberg's manuals, a collector might conceivably come up with a different name, depending on the portion of the stem he examined.

Many herbarium specimens of *Aster* sect. *Multiflori* have both appressed and spreading pubescence forms in different plant pieces on the same sheet, for example *G. H. Turner 2747* (ALTA); *A. H. Brinkman 788* (ALTA); *W. Krivda 2104* (COLO); *R. I. Cratty, s.n.* (ISC); *E. J. Hill, s.n.* (ILL), and *J. R. Churchill, s.n.* (MO). In other collections, one form may be represented on a sheet in one herbarium, while the other is represented on a duplicate sheet in another institution. Often the names originally applied to these specimens vary accordingly. For the most part, there is no doubt that the plants were collected in the same place and, with few exceptions, they are of the same species and subspecies.

Nevertheless, the results of experimental work indicate that the kind of indument is genetically determined. Both forms occur in all taxa, but ascending stem pubescence is a truly intermediate state between the appressed and the divaricate form. Within each subspecies, plants of the two forms can usually be successfully crossed. Stem pubescence cannot, therefore, be utilized as a key character in the separation of the species or subspecies.

Frequency of occurrence in any habitat or area usually favors one form over the other. At least to some extent, the differential distribution appears to be controlled by ecological forces. Tolerances and adaptations are not identical for the two pubescence forms (Jones, 1974). In my experimental work, I have found that plants of *Aster ericoides* with relatively sparse appressed pubescence were more adversely affected by excessive spraying with insecticides and fungicides than plants with copious hirsute pubescence. A 2:1 frequency ratio found in Illinois in favor of plants with spreading indument suggests that plants of the sparsely strigose form may be less well adapted to disturbance of habitat.

Stem pubescence was quantitatively compared with other characteristics for all four subspecies. The results for *Aster ericoides* ssp. *ericoides* have been published (Jones, 1974) and, on the basis of differential abundance and a combination of correlated morphological characteristics, varietal rank was assigned to the two pubescence types in that subspecies.

In *Aster ericoides* ssp. *pansus,* the two varieties can readily be distinguished on the basis of several characters other than pubes-

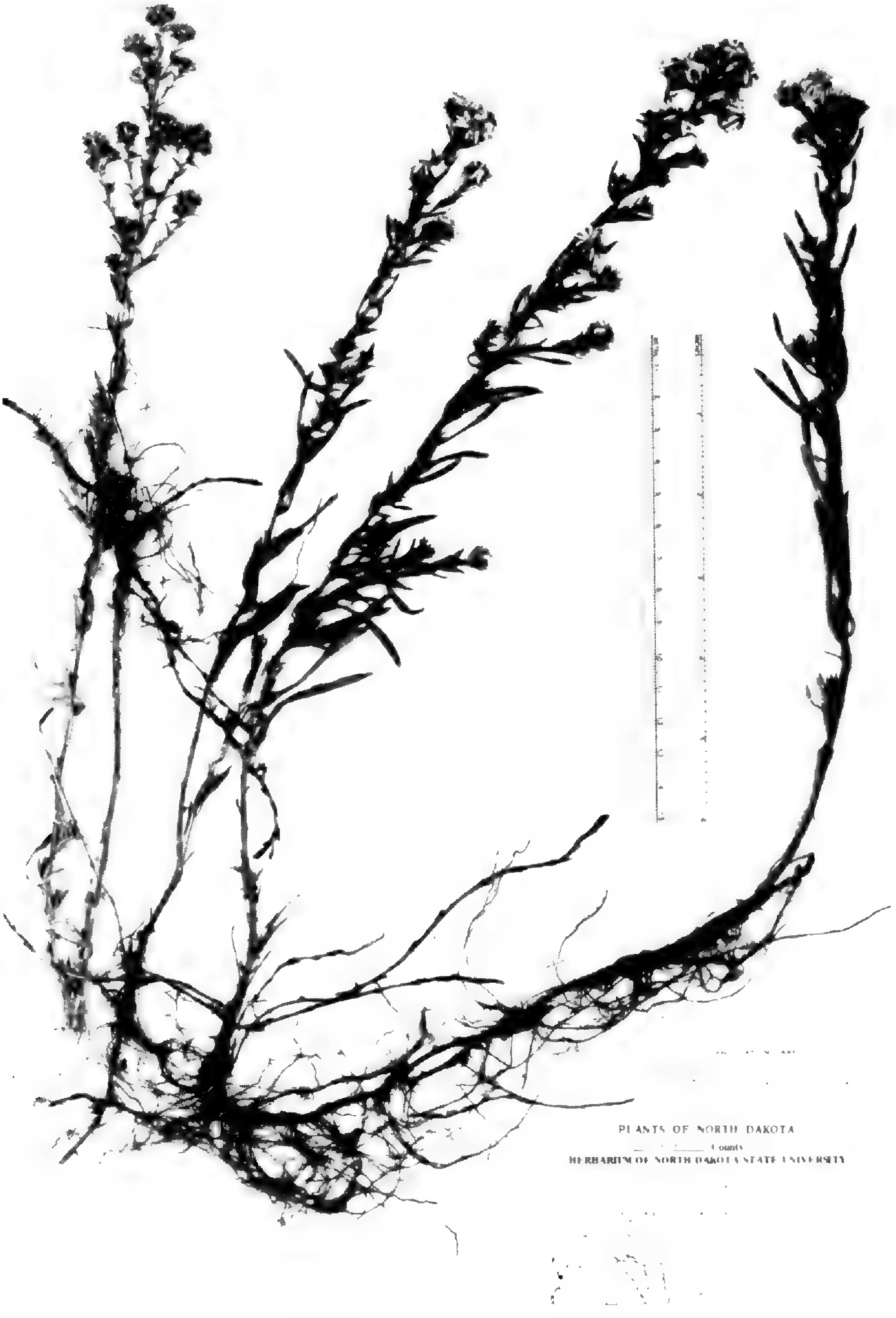


Figure 5. *Aster falcatus* ssp. *commutatus* — specimen with characteristic stoloniferous rhizome system [*Zaczkowski 1225* (NDA)].

cence. Plants of var. *pansus* have erect and sturdy stems, the inflorescences ample, with heads strongly secund. In plants of var. *stricticaulis* stems are slender, ascending or decumbent; inflorescences few-stemmed, with heads crowded, not strongly secund. A sample of 338 specimens was tested with a 2 × 2 contingency table for correlation of these character combinations with stem pubescence (Table 4). Intermediates, found to be only few in number, were omitted from the analysis. Expected frequencies were calculated under the null hypothesis that stem pubescence is of no significance. The high chi square value indicates, however, that the null hypothesis must be rejected. Probability for a chance association of the tested characters is less than 0.0005 and stem pubescence is a significant taxonomic character at the varietal level in ssp. *pansus*. Most plants in var. *pansus* have divaricate or reflexed trichomes, while plants of var. *stricticaulis* typically have appressed-strigose indument.

Specimens of *Aster falcatus* ssp. *falcatus* appear to be uniform. Quantity of indument is characteristically sparse in these plants. In a sample of 267 northwestern collections assigned to this subspecies, 24.7% were of the spreading pubescence form and 75.3% were of the strigose or closely ascending form. The strigose form clearly prevails in typical *A. falcatus;* the spreading form may have been introduced into the subspecies population by way of hybridization and introgression.

For *Aster falcatus* ssp. *commutatus,* the situation with regard to stem pubescence is complex. This subspecies is highly variable in several characteristics. It also has a wide geographic range, and is in contact and partly sympatric with all other subspecies of sect. *Multiflori.* The type, Upper Missouri, *Dr. James* (NY!), consists of a small branchlet with a few heads and appressed stem pubescence. Rydberg (1901) described *A. crassulus* to accommodate large-headed plants of the Great Plains and Rocky Mountains with spreading pubescence. The holotype, La Veta, Colorado, *Vreeland 690a* (NY! — Jones, 1978b, p. 341), as well as a possibly misnumbered duplicate (isotype), *Vreeland 190a* (RM!), are clearly of that pubescence form. Several paratypes, however, are strigose, except for the lowermost portion of the stem, e.g., Custer, South Dakota, *Rydberg 773* (NY); Rio Dolores, New Mexico, *Newberry* (NY); Madison County, Montana, *A. & E. Nelson 6839,* in part (GH, ILL, NY, US).

Table 4. **Significance of stem pubescence in Aster ericoides ssp. pansus.**

Stem Pubescence		Habit Characteristics var. *pansus*	var. *stricticaulis*	Totals
divaricate or reflexed	observed	82	38	120
	expected	37.633	82.367	
appressed	observed	24	194	218
	expected	68.367	149.633	
Totals		106	232	338

Chi Square: 115.504 (1 degree of freedom)
Probability: <<0.0005

Re-examination of the type material of *Aster multiflorus* γ *commutatus* and *A. crassulus,* evaluation of about 500 herbarium specimens, and observations made in the field revealed the presence in *A. falcatus* ssp. *commutatus* of two natural habit variants which are correlated with several other characteristics. The holotype of *A. crassulus* is a tall erect plant with spreading branches and a more or less racemiform inflorescence, the heads medium-large with about 16 disk florets and 20–22 ligules. Habit of the type for *A. multiflorus* γ *commutatus* can only be inferred by comparison with other collections from the same region, and with specimens annotated by A. Gray, as being that of a large-headed bushy plant with ascending stems and a diffuse-paniculate inflorescence.

A statistical analysis was made to determine the degree of correlation between stem pubescence and habit characteristics of specimens assigned to *Aster falcatus* ssp. *commutatus.* The sample consisted of 419 herbarium collections (duplicates not counted) from the entire range. The statistic used was a 2 × 2 contingency table solved for chi square (Table 5), and expected frequencies were calculated under the null hypothesis that stem pubescence is not correlated with habit characters. The small chi square value indicates that equal or more extreme deviations from random distribution would occur 70 times in 100 by chance alone, so that the null hypothesis is highly acceptable. In a comparison of habit with inflorescence characteristics, stem pubescence is of no taxonomic significance within this subspecies. On a populational and geographic basis, one form is usually predominant, but in my own field work, intensive search revealed both pubescence forms in most collection sites.

GENETIC CONSIDERATIONS

Chromosome numbers. Literature reports of chromosome counts for *Aster* sect. *Multiflori* are as follows: $2n = 10$ for *A. amethystinus* [= *A. ericoides* × *novae-angliae*] (Van Faasen, 1963; Wetmore & Delisle, 1939). $2n = 10$ for *A. ericoides* (Delisle, 1937; Semple, 1976; Van Faasen, 1963; Wetmore & Delisle, 1939). $2n = 10$ for *A. pansus* [= *A. ericoides* ssp. *pansus*] (Löve & Löve, in Löve & Solbrig, 1964). $2n = 18$ (as $n = 9$) for *A. falcatus* (Anderson, et al., 1974). The voucher, *Raven 20610* (NY), from New Mexico, is *A. ericoides* with, perhaps, some intermediacy toward *A. falcatus* ssp. *commutatus*. The plant has relatively small heads, a divaricate branch system, spreading stem pubescence, and a stoloniferous rhizome.

My own cytological work consisted mostly of meiotic counts and revealed the presence of three ploidy levels in *Aster* sect. *Multiflori* (Figures 6–16). Plants of the small-headed *Aster ericoides* are usually diploid with a gametic chromosome number of $n = 5$, but tetraploid populations with $n = 10$ are not uncommon, especially in the southern part of the range. No hexaploid plants have been found in *A. ericoides*. The large-headed *A. falcatus*, by contrast, is typically a hexaploid with a gametic number of $n = 15$. Toward the eastern and southern part of the range, populations with $n = 10$ are common, but the meiotic number of $n = 5$ has not been encountered in large-headed plants. In most cases, chromosome number is correlated to head size, but not consistently.

Populations of *Aster ericoides* from east of the Mississippi River are morphologically very uniform, and most plants examined were diploid (*204, 239, 346, 347, 364, 365, 370, & 884* from Illinois, *474 & 905* from Indiana, and *586 & 1226* from Wisconsin). However, three populations from Indiana (*470, 471, & 904*) and one from Illinois (*457*), while morphologically indistinguishable from adjacent populations, were tetraploid with $n = 10$ chromosomes. Several populations from Kansas (*895*), eastern Colorado (*1045*), and Oklahoma

Table 5. **Significance of stem pubescence in Aster falcatus ssp. commutatus.**

Stem Pubescence		Habit Characteristics var. *commutatus*	 var. *crassulus*	Totals
divaricate or reflexed	observed	119	87	206
	expected	116.52	89.48	
appressed	observed	118	95	213
	expected	120.48	92.52	
Totals		237	182	419

Chi Square: 0.153 (1 degree of freedom)
Probability: 0.70 = 70%

(*892* & *894*) also were tetraploid. Although head size was small, some of these plants had the divaricate branching habit characteristic for *A. falcatus* ssp. *commutatus.* Again, there is no consistency, as one population from southern Oklahoma had the meiotic number of $n = 5$ (*891*). In populations from Nebraska, Iowa, South Dakota, and Minnesota, the correlation between ploidy level and head size was quite evident. Most diploid plants resembled populations from east of the Mississippi River, while tetraploid plants were characterized by slightly longer ligules and phyllaries, a somewhat higher number of florets, and a much stouter, often sprawling habit, approaching *A. falcatus* ssp. *commutatus* in appearance. Representative vouchers of diploid plants from these states are: *412, 413, 415, & 528* (Iowa), *428* (South Dakota), and *443, 445, & 1215* (Minnesota). Vouchers of tetraploid plants are: *424* (eastern Nebraska), *427* (western Iowa), *432* (South Dakota), and *450 & 451* (western Minnesota). Most populations from British Columbia and many from Alberta had a gametic chromosome number of $n = 5$ (*1151, 1159, 1202, & 1204,* occasionally $n = 10$ (*1152*). They all belong in *A. ericoides* ssp. *pansus.*

Hexaploid populations with $n = 15$ chromosomes were found in both subspecies of *Aster falcatus.* Collections of this kind were made in southern Alberta (*1178, 1194, & 1203a*), Wyoming (*1082*), Montana (*1206*), and North Dakota (*1208*). All tetraploid popula-

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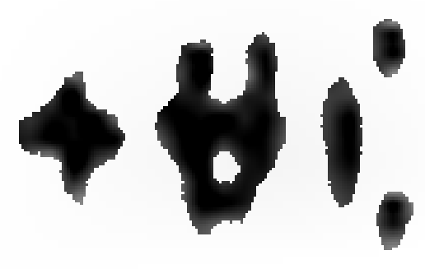

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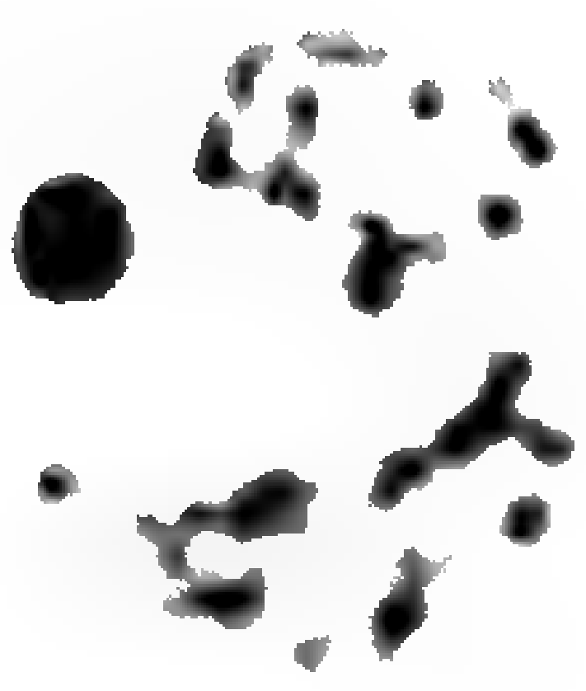

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tions found in this species belonged morphologically in *A. falcatus* ssp. *commutatus*. Collections were made in North Dakota (*912, 914, & 915*) and Colorado (*996, 1001, & 1050*).

Meiosis was regular in most preparations, although laggards and bridges during anaphase I were not uncommon (Figure 17). Occasionally pairing was incomplete, and univalents were observed during prophase and metaphase.

Hybridization. Of the many putative hybrids proposed in *Aster,* relatively few have been produced experimentally, for example, *A.* × *amethystinus* [= *A. ericoides* × *novae-angliae*] by Wetmore and Delisle (1939), *A.* × *herveyi* [= *A. macrophyllus* × *spectabilis*] by Uttall (1962), and *A.* × *blakei* [= *A. acuminatus* × *nemoralis*] by Pike (1970). A few experimentally produced interspecific hybrids that survived for several seasons can be added to the list from my work (Jones, 1973, and unpublished).

The procedure used for hybridization experiments and their evaluation has been published (Jones, 1974). Individual experimental results and tabulation of data obtained during the season of 1972, presented in my doctoral dissertation (Jones, 1973), are not repeated here. The results for sect. *Multiflori* can be summarized as follows.

Figures 6–20. **6.** Diakinesis: *Aster ericoides* ssp. *ericoides* (*891s,* Oklahoma); $2n = 5_{II}$; **7.** Metaphase I: *Aster ericoides* ssp. *ericoides* var. *prostratus* (*239,* Illinois); $2n = 5_{II}$; **8.** Metaphase I: *Aster ericoides* ssp. *pansus* (*1159,* British Columbia); $2n = 4_{II} + 2_{I}$; **9.** Anaphase II: *Aster ericoides* ssp. *ericoides* (*346,* Illinois); $n = 5$; **10.** Diakinesis: *Aster falcatus* ssp. *commutatus* (*1050,* Colorado); $2n = 10_{II}$; **11.** Late Diakinesis: *Aster ericoides* ssp. *ericoides* (*471,* Indiana); $2n = 10_{II}$; **12.** Metaphase I: *Aster falcatus* ssp. *commutatus* var. *crassulus* (*424,* Nebraska); $2n = 9_{II} + 2_{I}$; **13.** Early Anaphase I: *Aster ericoides* ssp. *ericoides* (*457* × *470* = cross: Illinois × Indiana); $2n = 20$; **14.** Early Diakinesis: *Aster falcatus* ssp. *falcatus* (*1203b,* Alberta); $2n = 15_{II}$; **15.** Diakinesis: *Aster falcatus* ssp. *commutatus* (*1082,* Wyoming); $2n = 15_{II}$; **16.** Late Metaphase — Incipient Anaphase I: *Aster falcatus* ssp. *commutatus* (*1206,* Montana); $2n = 15_{II}$; **17.** Anaphase I: *Aster falcatus* ssp. *falcatus* (*1203b,* Alberta); note laggards and bridge resulting from translocation; **18.** Early Diakinesis: *Aster hesperius* × *falcatus* ssp. *commutatus* (*1111* × *1001,* Utah × Colorado); $2n = 2_{I} + 5_{II} + 1_{III} + 2_{IV}$ (= 23); **19.** Diakinesis: *Aster ericoides* × *falcatus* (*451* × *1178,* Minnesota × Alberta) $2n = 3_{I} + 8_{II} + 2_{III}$ (= 25); **20.** Early Anaphase I: *Aster ericoides* × *falcatus* (*451* × *1178*); $2n = 25$.

Many attempts were made to cross members of *Aster* sect. *Multiflori* with 15 species of other sections, but hybridization succeeded only if the species were cytologically related, with one exception. This exception was a cross between a population of *A.* cf. *hesperius* from Utah (*1110 & 1111*), with a gametic number of n = 13 chromosomes, and a population of *A. falcatus* ssp. *commutatus* from Colorado (*1001*), with n = 10 chromosomes. The hybrid exhibited $2n$ = 23 chromosomes (Figure 18) in varying combinations of univalents, bivalents, and multivalents. The plants are vigorous and have survived for several seasons (*2595, 2780, 2965, 3072, 3155, 3206, 3278, 3684, 3687,* and others).

The work of Wetmore and Delisle (1939) was reproduced, with the difference that *Aster ericoides* (*314*) was the seed parent and *A. novae-angliae* (*348*) the pollen parent. The hybrids are vigorous and have survived for four seasons (*1565, 1644, 1826, 1845, 1990, 2519, 2782, 2847, 3115, 3223, 3657,* and others).

Hybrids between *Aster ericoides* (*365*) and *A. sericeus* (*608*) survived as weak plants in the greenhouse (*2715, 3178, & 3371*), but they did flower and set seed. The seedlings were the progeny from the only successful cross. Nine other crossing attempts failed to produce seed. Both parents and the hybrid had $n = 5$ chromosomes.

A cross between *Aster falcatus* ssp. *commutatus* (*996*) and *A. ascendens* (*1201c*) produced a few full achenes, but the seedlings died soon after emergence of the cotyledons and first rosette leaves.

In contrast to published reports (Ahles, in Jones & Fuller, 1955) and labeled herbarium specimens, I have not yet succeeded in crossing *Aster ericoides* and *A. pilosus.* Fourteen attempts were made involving about 5,000 potential achenes. One cross yielded a few achenes, but the seedlings died soon after emergence of the cotyledons.

Five attempts were made to cross *Aster ericoides* ssp. *pansus* from British Columbia with *A. campestris* from Alberta. These species are the putative parents of *A.* × *columbianus* Piper (pro sp., 1913). One cross (*1130* × *1184*) yielded a few full achenes, but the hybrid seedlings never grew beyond the rosette stage and died after one year.

Spontaneous hybrids between *Aster ericoides* and *A. falcatus* possibly would be difficult to recognize with certainty. A considerable number of intermediates was found among herbarium specimens. In the field, however, most populations could readily be placed into the respective species. Intermediacy and gene flow in areas of contact and overlap of taxa are evident but probably not found to the extent inferred from the prevalence of variants in collections of certain botanists who were cognizant of the existing taxonomic problems.

Average seed set of a total of over 130 crossing attempts between populations of *Aster ericoides* and *A. falcatus* was about 1%. This indicates the existence of a strong reproductive barrier between the two taxa. Even if only the 49 random crosses between typical *A. ericoides* and *A. falcatus* ssp. *commutatus* var. *crassulus* are evaluated, average seed set amounts to a mere 2%. A somewhat higher success is to be expected in these crosses, as the majority of populations of var. *crassulus* were found to be tetraploid with $n = 10$ chromosomes, and a considerable number of populations of *A. ericoides* also were tetraploid.

Crosses between *Aster* populations that were only varietally distinct generally yielded high, often nearly full (12% or more) seed set. In no case was a sterility barrier detected between the two different pubescence forms in populations of the same region that were morphologically similar in other respects. The reproductive barrier between var. *pansus* and var. *stricticaulis* appears to be somewhat stronger (7% average seed set in 4 attempts) than the barrier between var. *ericoides* and var. *prostratus* (17% average seed set in 12 attempts). Average seed set in 20 crosses between plants of typical *A. ericoides* and ssp. *pansus,* involving about 4,200 potential achenes, amounted to 9%.

Data for crosses within typical *Aster falcatus* are somewhat biased because a population from Edmonton, Alberta (*911*) could not be crossed with any other population in the whole section. Cytological examination suggests meiotic irregularity. Several other populations have been successfully crossed with an average seed set of about 10% in 4 attempts. Within *A. falcatus* ssp. *commutatus,* seed set in crosses between the two pubescence forms averaged about 13% in 5 attempts. When the two habit variants (var. *crassulus* and var. *commutatus* of this interpretation) were crossed, average seed amounted to 12% in 7 crossing attempts. Crosses between typical *A. falcatus* and ssp. *commutatus* yielded an average seed set of about 5% in 20 attempts, involving about 7,000 potential

Figure 21. Geographic distribution of rhizome habit. Circles: stoloniferous; full dots: cormoid.

achenes. This relatively low yield indicates that genetic compatibility between the two subspecies of *A. falcatus* is somewhat impaired, but a considerable degree of intermediacy must be expected in regions of sympatry.

Cytological data offer an explanation for the fact that certain populations could not successfully be crossed with other morphologically indistinguishable populations from the same region. As far as tested, tetraploid plants could only rarely be hybridized with diploid plants. The few full achenes resulting from such crosses usually yielded plants that had the meiotic number of the seed parent, which may be the result of occasional selfing or contamination.

If artificial crosses between *Aster ericoides* and *A. falcatus* produced more than occasional full achenes, both parent plants were usually tetraploids, e.g., in a cross between *A. ericoides* from Oklahoma (*894*) and *A. falcatus* from Colorado (*996*), and another between *A. ericoides* from Minnesota (*451*) and *A. falcatus* from Colorado (*1001*). Exceptional hybrids between plants of different ploidy levels were obtained, however, e.g., *1194* (n = 15 from Alberta) × *457* (n = 10 from Illinois) and *451* (n = 10 from Minnesota) × *1178* (n = 15 from Alberta). Full seed set was obtained in these two crosses, and the progeny had $2n$ = 25 chromosomes which exhibited irregular pairing during meiosis (Figures 19 & 20).

ECOLOGICAL CONSIDERATIONS

As a result of their extremely wide geographic range, species of *Aster* sect. *Multiflori* are found in a variety of ecological situations. However, the plants always grow in open places, never in woodlands; their natural habitat is grassland. In the forest-prairie ecotone, they have been recorded on glades and wind-exposed slopes that do not support tree growth, but these asters are absent from true forest areas. In the mountains, they are found on meadows, in the vicinity of streams and lakes, on well-drained ground in river valleys, occasionally on gravel bars, but not in wet seepage areas or low, moist, alluvial bottomlands. I have not found them in the extremely dry overgrazed plains which are dominated by *Artemisia tridentata,* but they are common in the bunch-grass prairies of the Great Plains. They are also found in dune habitats. In the tall-grass prairies, populations of sect. *Multiflori* generally grow in relatively dry situations, while wet ground and ditch margins are favored by other *Aster* species, e.g., *A. simplex, A. praealtus,* and *A. puniceus.*

Tolerance of *Aster ericoides* toward disturbance of the natural vegetation appears to be very low. Occasional populations may be found at the margins of plowed fields but, at least in the region east of the Mississippi River, this species is mostly confined to remnants of prairie vegetation along railroads, to bluff prairies, and to dune areas (Jones, 1974).

By contrast, *Aster falcatus* may show a favorable response to disturbance or, at least, a considerable tolerance. This was noted by Boivin (1972), and it is evident from the exceptional vigor exhibited by several collections made in the vicinity of cities in Alberta [*McCalla 10218 & 12393; G. H. Turner 2812* (ALTA)]. Label data indicate that the plants grew in disturbed ground. The matted low-stemmed habit form with simple racemose inflorescences often found in plains populations of *A. falcatus* ssp. *commutatus* is commonly associated with pastured areas, and is probably a response to grazing. The plants form an integral part of the plant community in these man-made habitats. Observations made in my experimental fields, which during the spring season are much visited by rabbits and other wildlife, suggest that these asters may be of some importance as forage plants in the ranges of the Great Plains. A collection of this habit form (*G. H. Turner 7421*) was transferred by Dr. Turner to his garden and, in cultivation, grew into broadly branching sturdy plants about 60 cm tall, with paniculate inflorescences, the heads borne on long peduncles at the tips of branchlets [*G. H. Turner 7621, 7626, & 7627* (ALTA, DAO)].

My collecting experience with *Aster falcatus* ssp. *falcatus* is limited. This taxon appears to tolerate a wide climatic range, as it occurs from Alaska southward to Arizona and New Mexico. According to label data, northern populations were collected in dry prairie, on bluffs, and on river banks. In the southern portion of the range, the plants are found in grassland openings of the juniper-pine zone, at altitudes between 1,500 and 2,500 meters, i.e., in climatically moderate situations, rather than the hot deserts.

Asters of sect. *Multiflori* seem to display a notably high tolerance for salinity and alkalinity. Habitat information on herbarium sheets indicates that these plants were frequently collected in alkali flats and at edges of salt marshes. The presence of *A. ericoides* on the islands of the Atlantic seaboard, in places exposed to salt spray, is also indicative of this tolerance. This adaptation appears to be correlated with a prevalence of the spreading pubescence form. Quantity of indument is usually exceptionally copious, often resulting in a cinereous appearance. Collections characteristic for this phenomenon are: **Montana:** *J. F. Brenkle & L. H. Shinners 41* (WIS); **New York:** *R. L. Crockett, s.n.* (GA); **Washington:** *W. J. Eyerdam 6382* (ILL); *H. St. John, W. D. Courtney & C. S. Parker 5499* (MO, UC, WS); **Manitoba:** *J. S. Rowe 197* (DAO); *H. J. Scoggan 4417 & 10404* (ALTA); **Mackenzie District:** *C. C. Loan 314* (DAO).

When the distribution of populations of sect. *Multiflori* is mapped, not with regard to taxa but to contrasting pairs of characteristics, one branch of the dichotomy always transcends the entire range, while the other finds expression only in the western half (Jones, 1973, and Figure 21). The eastern limit for the western element roughly coincides with the 100th meridian. Several writers in the fields of ecology and plant geography have recognized this meridian as a climatic and vegetational boundary (Jenny, 1930; Livingston & Shreve, 1921; McDougall, 1925; Merriam, 1892; Oosting, 1956; and Transeau, 1935); it separates the true prairies from the more sparsely vegetated Great Plains. The controlling climatic parameter is precipitation.

Ranges of the four subspecies recognized in sect. *Multiflori* are determined largely by their response to climatic factors. *Aster ericoides* ssp. *ericoides* grows predominantly in the true prairie under moderate moisture stress. In the northern portion of its range, this taxon does not extend west of the 100th meridian. In the southern portion, for example Texas, the plants occur in the blackland prairies, in open areas associated with the *Dalea-Prosopis-Populus* community, and in the post-oak belt, again under fairly mesic conditions.

Aster ericoides ssp. *pansus* is limited to the area west of the 95th meridian. Variety *pansus* grows mostly west of the continental divide, in the narrow grassland strips of river valleys and in the Palouse Prairie. The tall erect habit exhibited by these plants may be indicative of their association with the relatively dense, tall vegetation prevailing in this region of moderate climatic conditions. The somewhat decumbent or sprawling var. *stricticaulis,* on the other hand, is more common in the dry plains east of the continental divide. These plants are found in thinly vegetated habitats dominated by bunch-grasses. Other forbs in association with these asters are *Lesquerella ludoviciana, Tephrosia virginiana, Astragalus* spp., *Sphaeralcea coccinea, Artemisia frigida, Heterotheca villosa, Penstemon* spp., *Geum triflorum,* and *Solidago* spp. All these plants are characterized by a similar cespitose habit. In the early-season stage, several stems arise from a caudex-like rhizome in all directions at an angle of less than 90° with the horizontal, thereby providing maximum ground cover (Jones, 1973, *pl. 11 a, c, & f*). The general prevalence of this habit form in many unrelated plains species strongly suggests an adaptive response toward protection against wind and excessive soil moisture loss.

Aster falcatus ssp. *commutatus* is found in habitats of variable climatic conditions, which is to be expected from the morphological heterogeneity found in this taxon. Variety *commutatus* tolerates the xeric conditions that prevail in the high plains and is often sympatric with plants of *A. ericoides* ssp. *pansus* var. *stricticaulis.* Populations of the var. *crassulus* prevail in the transition zone between the true prairies and the dry plains, i.e., in more mesic situations. Populations of typical *A. falcatus* also seem to favor somewhat more moderate situations than those of var. *commutatus.* My own collections of ssp. *falcatus* (e.g. *1160, 1178, 1194, & 1208*) were made mostly in the vicinity of rivers or on gravelly slopes.

GEOGRAPHIC DISTRIBUTION

An understanding of the geographic distribution of sect. *Multiflori* proved to be critical for a solution of the taxonomic problems. After extensive field and experimental work, all herbarium collections available were again scrutinized. Using the morphological criteria established and summarized in Table 1, it was possible to estimate relative frequency of occurrence of the four subspecies in any given area. Representation in the herbarium is, of course, often biased and, at best, a crude approximation of the conditions that actually prevail. Bias can be minimized, however, by having a large sample from a variety of sources. Not counting duplicates, the total sample for this particular presentation consisted of 3,209 collections. After sorting them geographically, the specimens under each subspecies were counted, and the frequencies calculated in percent of total sample from each state or province. On the basis of the

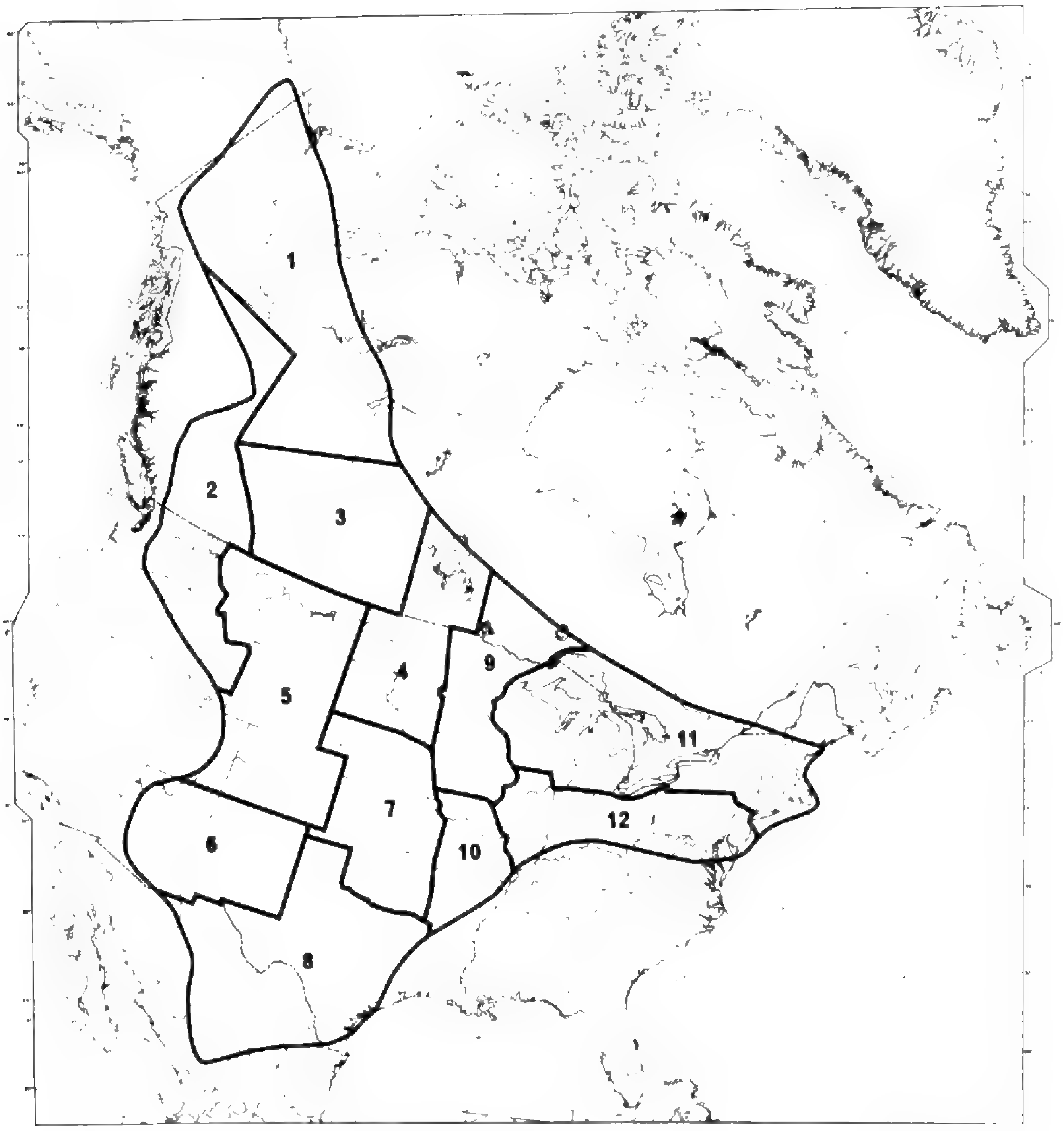

Figure 22. Range of *Aster* sect. *Multiflori,* subdivided into 12 more or less natural zones.

percentages obtained, the total range for sect. *Multiflori* was subdivided into 12 zones (Figure 22). Although they follow political boundaries (except in Canada), these zones represent more or less natural assemblages. The tabulated results (Jones, 1973, p. 217) are not repeated here, but the summaries are presented diagrammatically (Figures 23–25). Shaded sections in the large pies for each zone represent the subspecies occurring in that zone, and the blank sections represent morphological intermediates. Smaller pies below each of the zones give a breakdown of the varietal frequencies.

Discussion of Results. Zone 1 represents the northern extreme of range, northern Alberta, the Northwest Territories, and Alaska, a large area, in which relatively few collections were made. While both species occur in the area, typical *Aster falcatus* is predominant. In *A. ericoides* ssp. *pansus,* variety *stricticaulis* prevails. A high percentage of intermediates is, at least in part, a reflection of small sample size.

Zone 2, the northwestern limit of range, hosts the same two subspecies as Zone 1, but the frequencies differ significantly. This zone is separated from all the others by the continental divide. Populations of the small-headed *Aster ericoides* ssp. *pansus* var. *pansus* predominate in British Columbia and in the Palouse Prairie.

Zone 3 reveals the presence, in nearly equal proportions, of three subspecies, the two subspecies of *Aster falcatus* plus *A. ericoides* ssp. *pansus.* This zone constitutes the "trouble" area of southern Alberta and Saskatchewan referred to before. The number of morphological intermediates is relatively small, however, in comparison to the number of collections that can readily be placed. Similar to Zone 1, in *A. ericoides* ssp. *pansus,* variety *stricticaulis* is more common than typical var. *pansus.* In *A. falcatus* ssp. *commutatus,* variety *commutatus* is predominant. If pubescence forms are considered in this subspecies, the proportions of the two variants are approximately equal.

Zone 4 is characterized by the occurrence of all four subspecies. Manitoba and the Dakotas form the northern half of a corridor bounded by the 95th and 105th meridians, i.e., the transition zone between the true prairies and the plains. *Aster falcatus* ssp. *commutatus* and *A. ericoides* ssp. *pansus* are more common than typical *A. falcatus* and *A. ericoides.* In *A. ericoides* ssp. *pansus,* only var. *stricticaulis* is represented, while frequency ratios are about equal between the varieties of ssp. *ericoides* and *A. falcatus* ssp. *commutatus.* This equal division also applies to the pubescence forms.

Zone 5 comprises the states of the high plains. *Aster falcatus* ssp. *commutatus* predominates, providing nearly half of the sample of 334 collections. Typical *A. falcatus* also has fairly high representation, and the degree of morphological intermediacy is considerable. Plants with hirsute pubescence are about twice as abundant as plants with strigose indument. *Aster ericoides* is mostly represented by ssp. *pansus* var. *stricticaulis,* while ssp. *ericoides* barely enters the eastern portion of this zone.

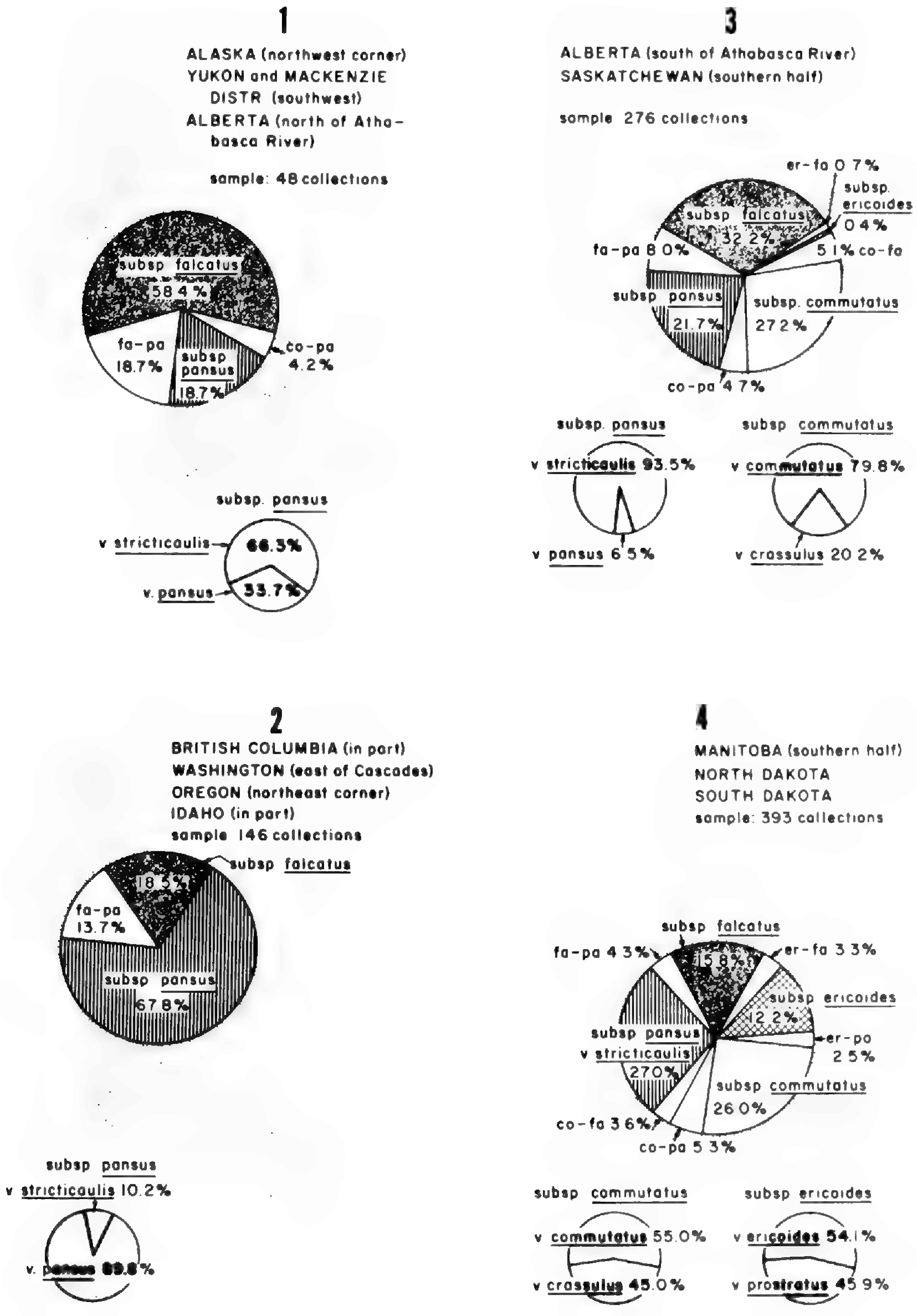

Figure 23. Frequency of occurrence for taxa represented in zones 1–4.

Zone 6 reveals that the southern limit of *Aster ericoides* ssp. *pansus* has been reached; this taxon is essentially absent in Arizona and New Mexico. Instead, ssp. *ericoides* occurs with increased frequency. *Aster falcatus* is mostly represented by ssp. *commutatus,* but ssp. *falcatus* has been collected at higher altitudes. Within ssp. *commutatus,* variety *crassulus* prevails with 63%. Approximately 56% of the collections have hirsute stems.

Zone 7, comparable to Zone 4 in the north, forms the southern half of a corridor bounded by the 95th and 105th meridians. Distribution of taxa is different, however; *Aster ericoides* ssp. *ericoides* is the predominant taxon in Nebraska, Kansas, and Oklahoma, and the strigose var. *ericoides* is more abundant than the hirsute var. *prostratus. Aster falcatus* ssp. *commutatus* is represented mostly by var. *crassulus* and, again, the form with strigose pubescence prevails, with ratios similar to those found for *A. ericoides.*

Zone 8 forms the southern limit of range for sect. *Multiflori.* The plants are mostly *Aster ericoides* ssp. *ericoides,* although southern populations often differ morphologically somewhat from populations east of the Mississippi River. *Aster falcatus* ssp. *commutatus* occurs mostly in the form of var. *crassulus,* with plants of the strigose pubescence form prevalent. Representation of typical *A. falcatus* is minor in Texas and Mexico.

Zones 9–12 can be considered as a unit. This is the area east of the 95th meridian, where populations of sect. *Multiflori* are characterized by considerable uniformity. Only along the northwestern boundary do plants of *Aster falcatus* enter the area to any extent, mostly in the form of ssp. *commutatus* var. *crassulus. Aster ericoides* ssp. *pansus* usually exhibits some intermediate traits. Without underground parts, herbarium specimens are indistinguishable from the typical subspecies. All populations in Zones 11 and 12 are typical *A. ericoides.* This area (east of the Mississippi River) was the subject of an earlier publication (Jones, 1974).

Brief mention must be made of regions adjoining the range of sect. *Multiflori.* I have seen no specimens from either California or Nevada which can be placed in this section. Most specimens from these states labeled as such were misidentified plants with affinities to *Aster ascendens* (e.g., *E. Palmer 143,* from San Diego Co., California — NY). There are two sheets from Fremont's expedition

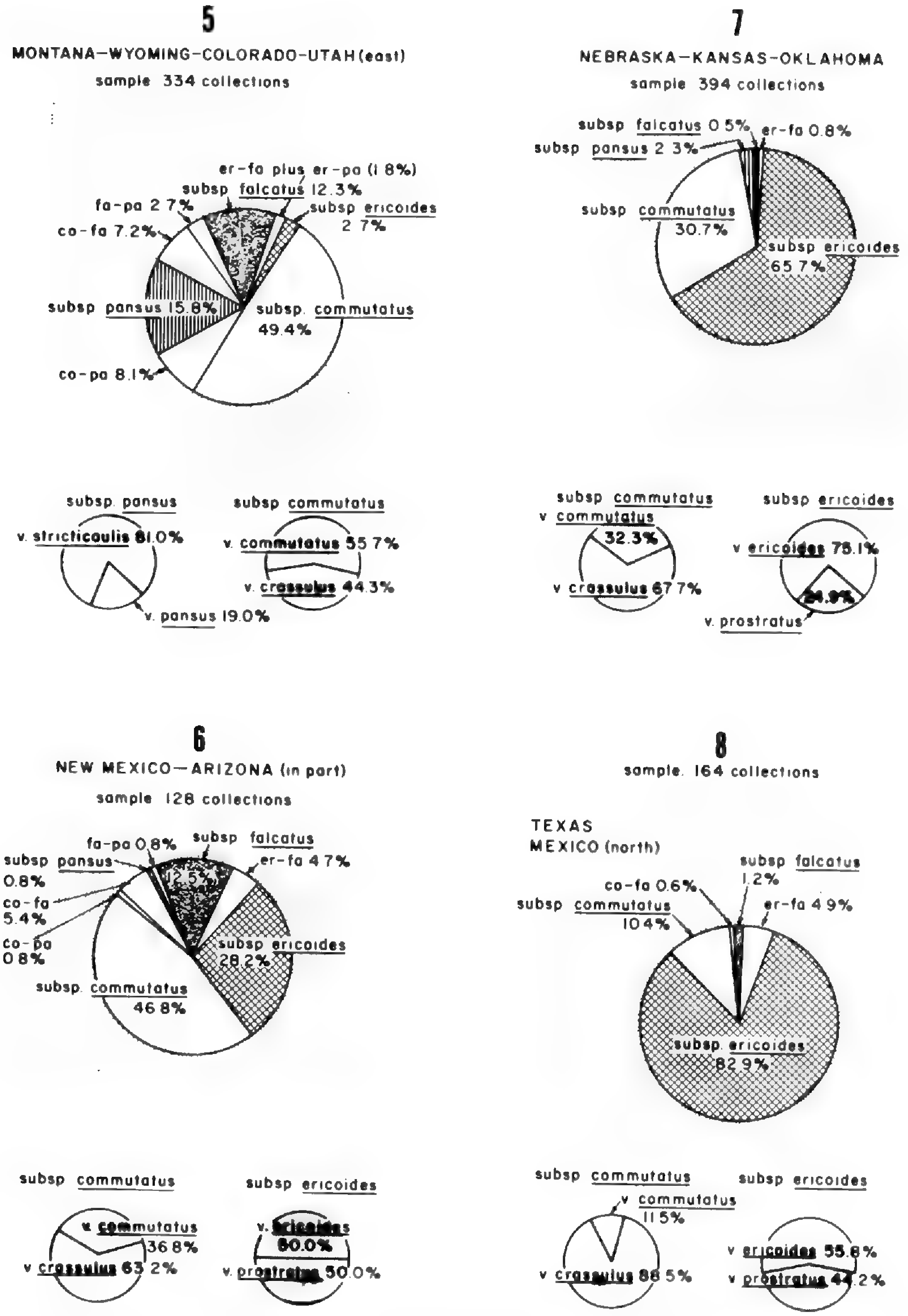

Figure 24. Frequency of occurrence for taxa represented in zones 5–8.

to California, 1845–47, one of which is *A. ericoides* (labeled *A. multiflorus*) from "Turkey Creek"; the other consists of two dissimilar pieces, one of which is *A. falcatus* ssp. *commutatus*. That sheet bears Nuttall's number *64* (NY); it was labeled *A. Nuttallii* by Asa Gray and annotated by him: "or new — Nuttall's specimen is poor." One does not know where these plants were collected. In *Botany of California*, Asa Gray (1876) does not list sect. *Multiflori* among the asters from that state.

In the northeastern part of the range, the sect. *Multiflori* does not extend beyond southeastern Ontario and the extreme southwest corner of Quebec. Although I have seen no specimens from Quebec, I have seen a photograph of a stand of *Aster ericoides* labeled Hull County, Templeton, *W. Scott 13342* (DAO). The locality is in the vicinity of Ottawa.

In the southeastern United States, there is only one authentic record from Virginia [Fauquier County, 8 miles from Aldie, etc., *H. A. Allard 12196* (TEX, US, WIS)], but I have found many misidentified sheets from that state, which probably account for some of the counties listed for the occurrence of *Aster ericoides* in Virginia (Massey, 1961). Peattie (1930) cited his own collection *2521* from Polk County, North Carolina. I have not located that collection, but all other collections from the Carolinas were misidentified, except one piece on a sheet marked Anderson, South Carolina, John Davis. The other piece on that sheet is *A. parviceps*, and a collection exists with the same date, also by John Davis, from Hannibal, Missouri (MICH). Another questionable North Carolina record is a collection by P. O. Schallert, marked Winston-Salem (GH). Schallert was a prolific collector in the Southwest, and Winston-Salem was his place of residence.

Two authentic disjunct collections are: **Alabama:** Hale County, Rosemary, *R. M. Harper, s.n.* (NY); **Mississippi:** Oktibbeha County, Starkville, *J. D. Ray 7669* (NCU).

In this age of long-distance motor travel, it would be surprising if one would not occasionally find plants growing outside their natural range. The fact that so few specimens do exist outside the range of sect. *Multiflori* indicates that these plants have no weedy tendencies. In my own recent travels, I have been unable to find *Aster ericoides* in southern Indiana, Kentucky, Tennessee, the Carolinas, and Georgia.

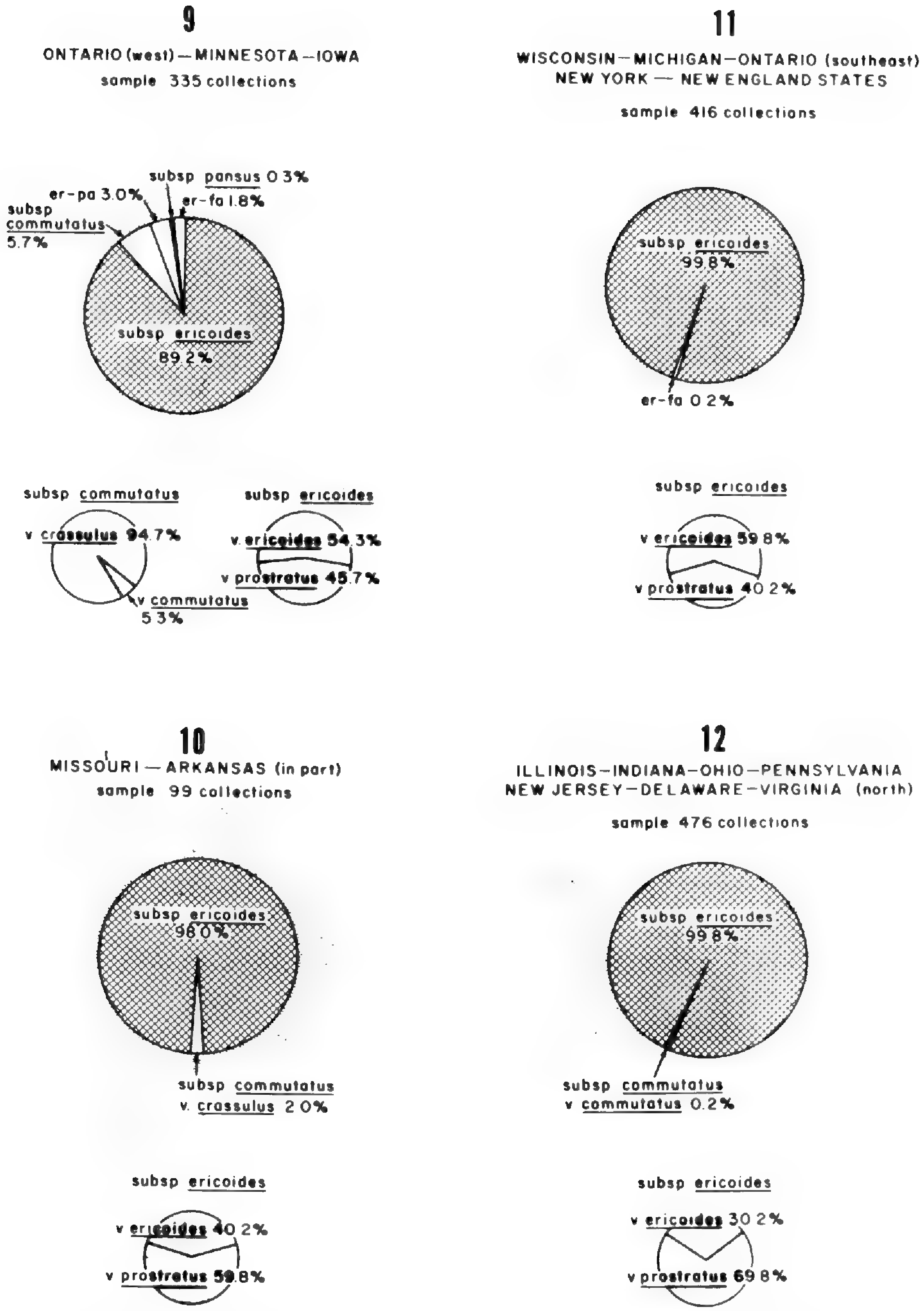

Figure 25. Frequency of occurrence for taxa represented in zones 9–12.

PHYLOGENETIC CONSIDERATIONS

The ease with which many *Aster* species can be hybridized suggests that the genus is actively evolving. Three series of chromosome numbers occur in *Aster*, with the basic numbers $x = 5$, 8, and 9. Considerations of chromosome evolution in the genus revolve around the question of which base number is the ancestral one, the high $x = 9$ or the low $x = 5$. Literature on the subject has been discussed in a previous paper (Jones, 1977). The available evidence suggests that the progenitor of *Aster* had a basic chromosome number of $x = 4$, and that all taxa of the three extant chromosome number series are derived by way of aneuploidy and polyploidy.

Species of *Aster* sect. *Multiflori* belong in the $x = 5$ series. According to accepted criteria, *A. ericoides* is phylogenetically older than *A. falcatus*. Populations of *A. ericoides* are predominantly diploid and, with the exception of the far northern reaches, this taxon has been recorded throughout the range for the whole group. The typical ssp. *ericoides* is characterized by a high degree of morphological uniformity and by relatively limited ecological requirements and tolerances. The taxon is predominant in the southwestern portion of range and the sole representative of the section in the eastern one-third of the area. There is hardly any sympatry with ssp. *pansus*, which is confined to the northwestern part of range. The two subspecies are morphologically and ecologically well differentiated, but a genetical barrier is lacking or very weak. Data on abundance of populations, and information on postglacial migration of floras (Benninghoff, 1964; Hanson, 1947; Hultén, 1937) suggest that the probable center of distribution for *A. ericoides* is the prairie area between the Missouri and Mississippi Rivers. Several factors suggest that ssp. *pansus* is a derivative of the typical subspecies, for example, a higher degree of heterogeneity and a relatively narrow range, as compared to typical *A. ericoides*. Gene flow from sympatric populations of *A. falcatus* may be partly responsible for the lack of uniformity in *A. ericoides* ssp. *pansus*.

Aster falcatus is typically hexaploid, but a considerable number of populations were found to be tetraploid. On the basis of the polyploidy, one can assume that this species is a derivative of *A. ericoides*, and the wide northern extent of range, into Alaska, suggests that differentiation of the two species took place before the Wisconsinan glaciation. Typical *A. falcatus* is, perhaps, a species of the flora element that survived maximum glaciation in nunataks or unglaciated pockets in the mountains (Fernald, 1925; Hultén, 1937). Highest frequency of occurrence for this subspecies is recorded from the northwestern portion of range. In the extreme north, it is the only representative of sect. *Multiflori.*

The hexaploid chromosome number has been found in both subspecies of *Aster falcatus,* although no populations from north of Edmonton, Alberta, have been examined. The two subspecies are well differentiated morphologically but rather weakly in their ecological requirements. *Aster falcatus* ssp. *commutatus* is sympatric with all other recognized taxa of sect. *Multiflori* over at least part of their ranges, but it is absent from the extreme northern region. These plants appear to be more tolerant toward disturbance of habitat, and reproductively more aggressive than plants of typical *A. falcatus,* a fact which suggests that the ssp. *commutatus* may be phylogenetically younger than the typical subspecies. However, hexaploidy can have arisen more than once. A certain degree of genetic isolation between the two subspecies is indicated by a relatively low average seed set (5% of the potential) in the successful crosses. Perhaps the two subspecies originated separately, and the species boundaries were obliterated relatively recently, after the Pleistocene.

Tetraploid populations are found mostly in the central range of sect. *Multiflori,* and they are characterized by a high degree of heterogeneity. At least theoretically, this ploidy level may have originated in two ways: by duplication of the chromosomes in diploid parents, or by hybridization between hexaploid and diploid plants. Subsequent crossing and recombinations between populations, followed by fixation of genotypes, may account for the heterogeneity observed.

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CHROMOSOMES OF MEXICAN SEDUM II. SECTION PACHYSEDUM

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This is the second of several papers reporting altogether the chromosomes of about 90 species of Mexican *Sedum*. A general introduction, materials and methods, and acknowledgements are included in the first paper (Uhl, 1976b).

Berger (1930) proposed sect. *Pachysedum* to include those shrubby and subshrubby Mexican species of *Sedum* that have thickened, terete or subterete leaves. He also proposed sects. *Dendrosedum, Fruticisedum,* and *Leptosedum* to include certain other, mostly large, Mexican species, some of which resemble sect. *Pachysedum.* Clausen (1943) considered that Berger's four sections plus his own new sect. *Craigia* warranted status as subg. *Pachysedum* (Berger) Clausen. In the most recent general treatment, Jacobsen (1974) followed Berger closely, adding some more recently described species and sect. *Centripetalia* Alexander.

However, Walther (1931) was more impressed with the lateral inflorescences of many of these species, and he proposed sect. *Bergerosedum* to include those species of Berger's sects. *Pachysedum* and *Dendrosedum* having this character. (In doing so he excluded *Sedum cremnophila* and *S. corynephyllum,* which have lateral inflorescences and which Berger had included in his sect. *Pachysedum,* and he inadvertently included two species whose floral stems are not truly lateral.) The evidence from cytology presented here and also the evidence obtained from many artificially produced hybrids (Uhl, 1976a, and unpublished) indicates that the mostly large and thick-leaved species with lateral inflorescences, or at least most of them, form a natural group, referred to here as sect. *Pachysedum.* All of these species have $n = 30$ to $n = 36$ or a multiple (except for $n = 26$ in *S. hultenii*). Most of them can be intercrossed readily in cultivation, and the resulting hybrids exhibit mostly bivalent chromosome pairing at meiosis, which indicates that their genomes are organized in very similar ways (Uhl, 1976a, and unpublished). The same kind of evidence also indicates that species of sect. *Pachysedum* are less closely related to other species of *Sedum* having terminal inflorescences.

Of the species listed under sect. *Pachysedum* by Jacobsen (1974), *Sedum eichlamii* is a horticultural name without taxonomic standing, and *S. guatemalense* Hemsley and *S. morganianum* Walther are excluded from the present treatment because of their terminal inflorescences. On the other hand, *S. confusum* Hemsley, including its synonym *S. aoikon* Ulrich (Clausen, 1975), and *S. dendroideum* DC of Jacobsen's sect. *Dendrosedum* and *S. cuspidatum* Alexander and *S. hultenii* Fröderström of his sect. *Frutisedum* are included with sect. *Pachysedum* here because of their lateral inflorescences and for other reasons. The recently named *S. batallae* Barocio (1973), *S. clavatum* Clausen (1975), *S. decumbens* Clausen (1975), *S. macdougallii* Moran (1977), possibly *S. suaveolens* Kimnach (1978), and one species as yet unnamed also are considered to belong to sect. *Pachysedum* and are reported here.

This paper reports numbers of 82 collections, representing all 19 species here considered to constitute sect. *Pachysedum,* modified as indicated from Jacobsen (1974), and including sect. *Craigia* Clausen. Three additional named species are reported here because they are considered to be natural or garden hybrids each probably having a species of sect. *Pachysedum* as one parent.

Four of the 19 species treated here, *Sedum corynephyllum, S. craigii,* the new *S. suaveolens,* and the unnamed *UC58.858,* have corollas that are anomalous for *Sedum:* erect in the lower half or more, instead of spreading from the base as in the other 15 species of sect. *Pachysedum* and in typical species of *Sedum.* In this character they resemble members of subfam. Echeverioideae, but they do not fit well into any genera of that subfamily. Jacobsen (1974) assigned *S. corynephyllum* and *S. craigii* to his sect. *Pachysedum,* and their subshrubby habit, very thick leaves, lateral inflorescences, and basic chromosome numbers ($x = 30$–34) are all compatible with this treatment. The same situation applies also to the undescribed *UC58.858.* Furthermore, in certain hybrids the chromosomes of *S. corynephyllum* and *UC58.858,* at least, have a very high degree of homology with those of certain other species of sect. *Pachysedum,* as shown by very extensive chromosome pairing (Uhl, unpublished). (*Sedum craigii* flowers at a different season from all the other species, and this has limited opportunities for hybridizing.) Details of the hybrids involving species of sect. *Pachysedum* will be published separately, but a few hybrids of special interest are mentioned below in the accounts of their parental species.

Although vegetatively of very different aspect from other species of sect. *Pachysedum,* the recently discovered and named *Sedum suaveolens* is included in this treatment because of similarity of its flowers to those of *S. craigii* (Kimnach, 1978).

SPECIES

Sedum adolphii, Sedum nussbaumerianum.

Sedum adolphi Hamet and *S. nussbaumerianum* Bitter are very similar and possibly conspecific (Clausen, 1959). All plants studied cytologically came from cultivation, where both species are widespread. No field locality has been reported for *S. adolphii,* and Clausen (1959) was unable to find *S. nussbaumerianum* in the large barranca which is its type (and only) locality. Plants discovered this year by Felipe Otero and by myself in two locations at low elevations in the state of Veracruz have not been studied cytologically as yet. In terms of the basic chromosome numbers of the section ($x = 30$–36), both species are tetraploid ($n = 64$), and most plates at metaphase I include some apparent multivalents, which makes exact counts very difficult (Figures 1 & 21). In hybrids most or all of the chromosomes of polyploid parents belonging to other genera of the Mexican Crassulaceae pair among themselves, indicating that they are autopolyploids (Uhl, 1970, and unpublished; Uhl & Moran, 1973). It is likely that the same is true also for these and other polyploids of sect. *Pachysedum,* but direct evidence from chromosome pairing in their hybrids is not yet available.

Sedum × amecamecanum.

Sedum × *amecamecanum* Praeger, according to Clausen (1959), is probably a natural hybrid between *Villadia batesii* and *Sedum dendroideum* ssp. *monticola* (later renamed *S. praealtum* ssp. *monticola,* Clausen, 1975). It is morphologically intermediate between the two parents, and Clausen found it only where they occur together. I have noted both terminal and axillary inflorescences, as might be expected in such a hybrid. Clausen also reported that in nature most anthers of *S. amecamecanum* are undeveloped, that in cultivation many pollen grains are small and undeveloped, and that ovules do not develop into seed. No chromosome count is available for *S. praealtum* ssp. *monticola,* but the other two subspecies of *S. praealtum* have $n = 34$–36 (see below); *Villadia batesii* has $n = 25$, and its hybrid with subspecies *monticola* might be expected to have about 60 somatic chromosomes.

The cytological evidence reported here strongly supports the conclusion that *Sedum amecamecanum* is a hybrid, probably of the parentage suggested. Meiosis was highly irregular in both collections studied, with univalents on and off the plate at metaphase I (Figure 2), with many laggards and occasionally a bridge at anaphase I (Figure 3) and sometimes restitution nuclei after meiosis I, and with most quartets including extra spores and/or spores of different sizes after meiosis II (Figure 5).

The two collections studied are not identical. *U483* has pale yellowish flowers and fewer chromosomes, with about 57 univalents counted in one cell. An average of about 15 bivalents and multivalents is estimated for most of its cells at metaphase I, plus a large number of univalents (usually 20 or more), and with 25–32 elements counted on metaphase II plates. This may well be an F_1 hybrid. *M7800,* said to have originated at 3000 meters on Popocatepetl, has white flowers and more chromosomes, usually with 55–57 elements of all kinds at metaphase I and 40–46 elements on each plate at metaphase II (Figure 4). This may be a triploid hybrid, with two sets of chromosomes from *Villadia batesii:* either an F_1 hybrid which received an unreduced gamete from *V. batesii,* or the result of a backcross of an unreduced gamete of the F_1 hybrid to *V. batesii.* Although Clausen (1959) studied different plants from those reported here, he also noted two variants of *Sedum amecamecanum* and concluded on morphological grounds that one may be an F_1 hybrid and the other "the result of a single backcross to *V. batesii*". He also reported subspecies *monticola* only from Iztaccihuatl and subspecies *parvifolium* from Popocatepetl. Therefore, *S. amecamecanum* from Popocatepetl—if the locality data for *M7800* are correct—might result from *V. batesii* crossed there with *S. praealtum* ssp. *parvifolium.*

Sedum batallae.

Sedum batallae Barocio ($n = 34$, Figure 6) is known only from a few square meters on a sheer cliff in southern Hidalgo. In describing this species, Barocio (1973) considered that it shows some similarity to *S. compactum* ($n = 58$) of Fröderström's (1935) group *Minimum.* However, its lateral inflorescence, its thickened leaves, and its chromosome number suggest that it is a diminutive member of sect. *Pachysedum.* Furthermore, like larger sect. *Pachysedum* species, it is easily hybridized with species of subfam. Echeverioideae, and extensive chromosome pairing occurs in these hybrids (7 analyzed, Uhl, 1976a, and unpublished).

Sedum clavatum.

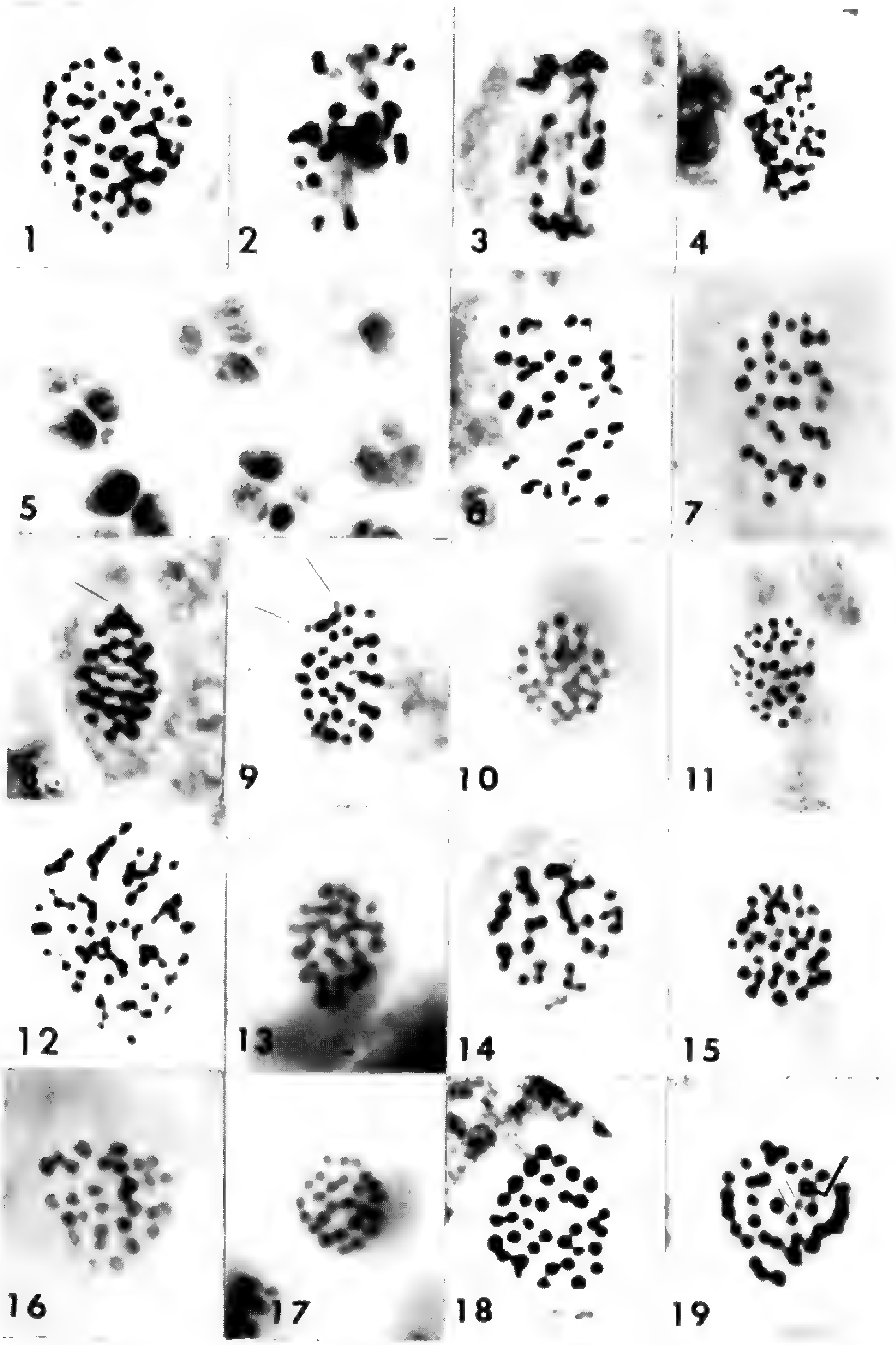
Sedum clavatum Clausen (1975) ($n = 33$) is only recently named, although it was earlier described in detail as the "*Sedum* of the Tiscalatengo Gorge" (Clausen, 1959). It is known only from one locality, a canyon southeast of the Nevado de Toluca in the southern part of the state of Mexico, and probably all three collections came from the same population. The type clone (*TMV-T-Tis 1*) has a small extra (B-) chromosome, and some of its cells at anaphase I show a chromosome bridge, but another plant of the type collection (*TMV-T-Tis 3,* Figure 7) has no B-chromosomes or bridges. One B-chromosome also was noted in one of the other collections (*M19058,* Figure 8), and two in the third (*U1566,* Figure 9). Clausen (1975) considered the species to be closest to *S. lucidum* but did not assign it to a section.

Sedum confusum, Sedum decumbens.

Sedum confusum Hemsley ($n = 34$, Figure 10) was earlier described in detail by Clausen (1959) as *S. aoikon,* which he now considers to be a synonym (Clausen, 1975). It resembles the common *S. praealtum* ($n = 34, 35, 36$) but is smaller. Long known only in cultivation, it has recently been reported from northern Puebla (Clausen, 1975). The newly described *S. decumbens* Clausen ($n = 34$) also is similar, but smaller still and of unknown origin in the wild.

Sedum corynephyllum.

Sedum corynephyllum Fröderström ($n = 34, 68$) was first described as a monotypic genus, *Corynephyllum viride* Rose. This treatment has generally not been accepted (e.g., Berger, 1930; Fröderström, 1935), and Jacobsen (1974) lists the species in his sect. *Pachysedum* as *S. viride* (Rose) Berger (a name preëmpted by the earlier *S. viride* Makino). The collections studied all came from the Atlantic slope of the Sierra Madre Oriental, from southern San Luis Potosi southeast for nearly 200 km into eastern Hidalgo. The three tetraploid collections ($n = 68$, Figure 12) all came from the Barranca de Metztitlan, Hidalgo, in the southeastern part of the range and possibly all from the same population. All collections from farther north and west were diploid ($n = 34$, Figure 11).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Sedum craigii.

Sedum craigii Clausen ($n = 30$, Figure 13) until recently was the only *Pachysedum* known to be native to western Mexico, and it is the only species that usually flowers in the fall. Apparently only one plant, thought at first to be *Graptopetalum amethystinum*, has ever been collected (Lindsay, 1943), and both collections reported here probably had the same origin (rim of Barranca del Cobre, in western Chihuahua). In describing this species, Clausen (1943) commented on its unusual combination of characters, especially its erect but separate petals, recurved at the tips. However, he felt that it "seemed as near to *Sedum*" as to any other genus, and he assigned it to a new section, *Craigia*, of his subg. *Pachysedum*. Jacobsen (1974) did not accept Clausen's section and listed *S. craigii* with sect. *Pachysedum*.

Sedum craigii differs in its chromosome number ($n = 30$) from all other species of sect. *Pachysedum* except *S. dendroideum*, which does not seem particularly close to it morphologically. A surprisingly close relative is *Echeveria affinis*, also $n = 30$, also native to western Mexico, and which also flowers during the fall, when few other Mexican Crassulaceae are in bloom. A hybrid between these two species shows completely bivalent chromosome pairing in nearly every cell, produces 17.7% stainable pollen, and appears to be slightly fertile (Uhl, unpublished). Also similar to *S. craigii* in floral structure (but not in vegetative aspect) is the anomalous new *S. suaveolens* (Kimnach, 1978).

Sedum cremnophila.

Sedum cremnophila Clausen (*Cremnophila nutans* Rose) ($n = 33$, Figure 14) is known only from cliffs within a few kilometers north and south of Tepoztlan, Morelos. It has all of the morphological

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Figures 1–19. Chromosomes of *Sedum* sect. *Pachysedum* at metaphase I in pollen mother cells, ×2000 (except as indicated). Thin lines point to univalents or B-chromosomes, thicker lines to multivalents. 1, *S. adolphii*, *C45-97*, $n = 64$; 2–5, *S.* × *amecamecanum: 2, U483*, spindle view, with univalents off the metaphase I plate; 3, *U483*, lagging univalents at anaphase I; 4, *M7800*, 42 elements at metaphase II; 5, *U483*, abnormal quartets with undersized microspores, ×800; 6, *S. batallae*, *M13411*, $n = 34$; 7–9, *S. clavatum:* 7, *TMV-T-Tis 3*, $n = 33$; 8, *M19058*, $n = 33 + 1$B; 9, *U1566*, $n = 33 + 2$B; 10, *S. confusum*, *C44–14*, $n = 34$; 11–12, *S. corynephyllum;* 11, *U258*, $n = 34$; 12, *M7796*, $n = 68$; 13, *S. craigii*, *C43-2*, $n = 30$; 14, *S. cremnophila*, *M10174*, $n = 33$; 15, *S. cuspidatum*, *U1263*, $n = 34$; 16, *S. dendroideum*, *M7779*, $n = 30$; 17, *S. hultenii*, *C7472*, $n = 26$; 18, *S. lucidum*, *C44–12*, $n = 34$; 19, *S.* × *luteoviride*, *M7801*, 31 bivalents, 1 trivalent, and 2 univalents.

and cytological characteristics of sect. *Pachysedum*, and hybrids with three other species of sect. *Pachysedum* (*S. batallae, S. cuspidatum, S. lucidum*, and *S. praealtum*, all having $n = 34$) show almost completely bivalent chromosome pairing, indicating close homology (Uhl, 1976a). *Sedum cremnophila* is also very similar vegetatively to *Echeveria linguifolia*, which also has $n = 33$, and these two species have been crossed reciprocally in cultivation to give fertile hybrids with normal meiosis (Uhl, 1976a). The F_1 hybrids have been back-crossed in various combinations to both parents to give second-generation progeny which also have apparently normal meiosis. Clearly *Sedum cremnophila* and *Echeveria linguifolia* are very closely related, and their traditional classification into the type genera of different subfamilies does not correspond to their natural relationship. Hybrids of *Echeveria linguifolia* with three other species of sect. *Pachysedum* (*S. batallae, S. cuspidatum*, and the undescribed *UC58.858*, all with $n = 34$) also show mostly bivalent chromosome pairing (Uhl, 1976a), adding strong additional evidence for close relationship of *Echeveria linguifolia* with sect. *Pachysedum*.

Considering the similarity in their morphology and in their chromosomes, Moran (1978) has proposed to revive the genus *Cremnophila* Rose for *Sedum cremnophila* and *Echeveria linguifolia*. However, the chromosomes of both of these species are so closely homologous also with the chromosomes of various other species of sect. *Pachysedum* (Uhl, 1976a) that it seems desirable to keep them all together taxonomically, either as sect. *Pachysedum* of *Sedum* or possibly as a separate genus, *Cremnophila*.

Sedum cuspidatum.

Sedum cuspidatum Alexander ($n = 34$, Figure 15) originated from two localities about 125 km. apart in eastern Oaxaca and western Chiapas. A greenhouse hybrid with *S. cremnophila* is partly fertile and served as seed parent of a second-generation hybrid having as pollen parent the F_1 hybrid *S. cremnophila* × *E. linguifolia* (Uhl, 1976a). The second-generation hybrid shows nearly normal meiosis, produces 59% stainable pollen, and may itself be fertile. Hybrids of *S. cuspidatum* with *S. lucidum* ($n = 34$) and with *S. treleasei* ($n = 34$) also show essentially normal meiosis, with 34 bivalents in nearly all cells, but neither of these hybrids is fertile.

Sedum dendroideum.

Sedum dendroideum DC (sensu strictu) differs in its chromosome number ($n = 30$, Figure 16) from the similar *S. praealtum* ($n = 34$, 35, 36, Figures 23, 24, 25), formerly included under it (Clausen, 1959), and from the smaller *S. confusum* and *S. decumbens* (both $n = 34$). Clausen (1959) considered the species to be native only to the Sierra Madre del Sur and to Guatemala, but apparently some populations occur considerably farther north. The five plants reported here came from Hidalgo to eastern Oaxaca, a distance of more than 600 kilometers, and I have a collection (that has not flowered) from the state of Mexico. Both *S. dendroideum* and *S. praealtum* are reputed to have medicinal value (Clausen, 1959), and possibly their original distributions have been extended by man.

Sedum hultenii.

Sedum hultenii Fröderström consistently has $n = 26$ (9 collections, Figure 17). The plants studied came from an area of the Sierra Madre Oriental extending from northern Hidalgo more than 200 km. southeastward into northern Puebla. One collection (*U485*) received in 1957 from Uppsala, Sweden, may have originated from Fröderström's type collection of 1932, which he reported (1935) as being in cultivation in Sweden.

Sedum hultenii has lateral inflorescences and in vegetative appearance it seems to lie at the end of a morphological series: *S. dendroideum* — *S. praealtum* — *S. confusum* — *S. decumbens* — *S. hultenii.* It is included here with sect. *Pachysedum,* but its chromosome number ($n = 26$) is anomalous, and it may not be closely related to the other species of the section. Most other species of sect. *Pachysedum* hybridize readily with each other and with most Echeverioideae, but only one of 22 attempts at crossing *S. hultenii* with 10 of these species has resulted in progeny (with *S. cremnophila, U1881* × *M10174*).

Sedum lucidum.

Sedum lucidum Clausen ($n = 34$, Figure 18) is known only from a small area in the Rio Blanco valley, south of the peak of Orizaba, state of Veracruz. Clausen (1959) considered it closest to *S. dendroideum* ($n = 30$) and *S. clavatum* ($n = 33$). It must also be closely related to *S. cuspidatum* ($n = 34$) and to *S. treleasei* ($n = 34$), for hybrids with those species (*U1263* × *U1462* and *O-RB6* × *U1205*, respectively) show essentially normal meiosis and produce 10.3% and 19.5% stainable pollen.

Sedum × luteoviride.

Sedum × luteoviride Clausen appears to be a natural hybrid. Clausen (1948) originally assigned this species to subg. *Pachysedum*, and Jacobsen (1974) included it with his sect. *Pachysedum*. However, Clausen later (1975) transferred it to subg. *Sedum*. Meiosis was irregular in all five collections studied, and many abnormal microspores are produced. The species was described from cultivated material, with no locality then known for it in the wild (Clausen, 1959). In 1959, near San Vicente, Hidalgo, Dr. Reid Moran and Myron Kimnach found a single plant of *S.* × *luteoviride* (*M7808*) with *S. praealtum* ssp. *parvifolium* (*M7806*, $n = 35$) and *S. greggii* (*M7807*, $n = 33$), and these may be its parents.

Although the total chromosome number appears to be about the same in all collections studied, the amount of pairing at metaphase I differs. The greatest amount of chromosome pairing was noted in *M7801*, where 28–33 bivalents and multivalents (average 30.8) plus 1–10 univalents (average 4.3) were noted in 26 cells analyzed at metaphase I (32 + 2 in Figure 19). Anaphase I has several laggards and occasionally a bridge or two, and one or more chromosomes are sometimes left out of the principal nuclei at telophase I. Most quartets include small extra microspores. By contrast, slides made in two different years of *M7808* (which was collected in the wild) show only 10–26 paired chromosomal elements at metaphase I (average 16.8) plus 15–46 univalents (average 31.6) in 14 cells for which approximate analyses could be made. About 5% of the pollen grains of this plant stained in aniline blue-lactophenol, including many that were abnormal in size.

The morphology of *Sedum luteoviride* and the number and irregular behavior of its chromosomes at meiosis are compatible with its origin as a hybrid between *S. praealtum* of sect. *Pachysedum* and the diminutive *S. greggii*, which has a terminal flowering stem. A vigorous specimen of *M7808* produced both terminal and lateral inflorescences in cultivation. Plants of *M7801* are smaller and produce smaller leaves than *M7808*. Populations of both *S. praealtum* and *S. greggii* differ somewhat in morphology and in chromosome number, and it is likely that *M7801* and *M7808* resulted from crosses involving different subspecies and/or chromosome races of the two species. A recent attempt to hybridize the two species (*U1187* × *M7807*) has resulted in seven seeds, just planted.

Sedum macdougallii.

Sedum macdougallii Moran ($n = 34$, Figure 20), only recently named, appears most similar to *S. treleasei* (Moran, 1977). It is known only from its type locality, northeast of Tehuantepec in eastern Oaxaca.

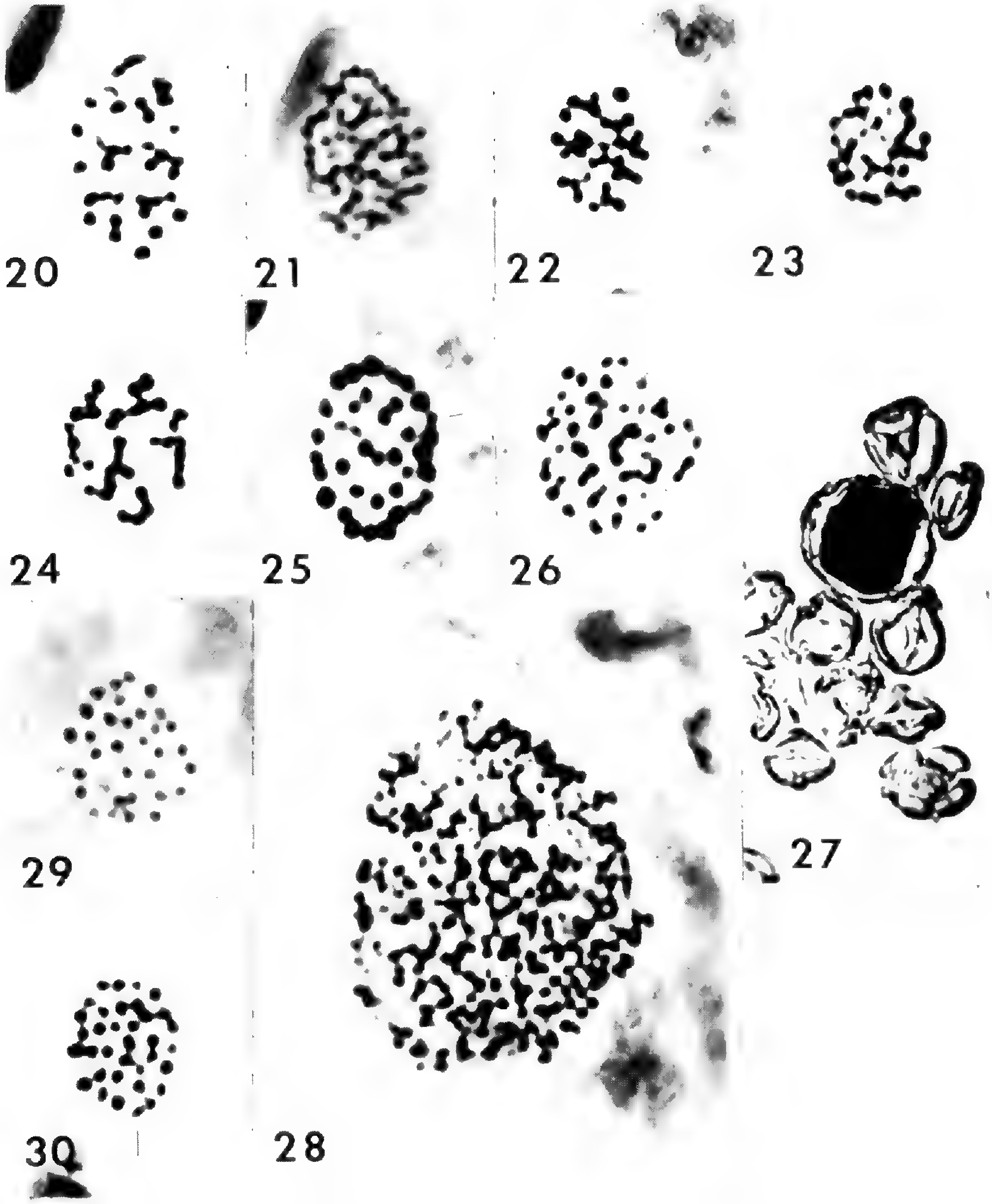
Sedum pachyphyllum.

Sedum pachyphyllum Rose ($n = 34$, Figure 22) has been studied only from cultivated material of unknown origin in the wild. The species is native to the Sierra Mixteca of northwestern Oaxaca.

Sedum praealtum.

Sedum praealtum DC was previously treated as one of four subspecies under *S. dendroideum* (Clausen, 1959). However, Clausen (1975) has recently restricted *S. dendroideum* to include only the one of its former subspecies that has marginal leaf glands and he has reinstated *S. praealtum* to include the other three subspecies. This treatment accords better with the cytological evidence, which shows *S. dendroideum* (sensu strictu) with consistently $n = 30$ (5 collections, Figure 16), whereas *S. praealtum* ssp. *praealtum* has $n = 34$ (2 collections, Figure 23) and ssp. *parvifolium* has $n = 34$ (9 collections), $n = 35$ (4 collections, Figure 24) and $n = 36$ (1 collection, Figure 25).

Sedum praealtum and the similar *S. dendroideum* are widely cultivated, perhaps because of their reputed medicinal value (Clausen, 1959), and this makes their native distribution difficult to establish. The collections studied here exhibit much more overlap in their distributions than previously indicated (Clausen, 1959). Furthermore, the subspecies of *S. praealtum* apparently intergrade, and some collections are not easily assigned to them. Subspecies *praealtum* ($n = 34$) is probably native in the Rio Blanco valley of Veracruz (Clausen, 1959) and possibly elsewhere. Subspecies *parvifolium* is more widely distributed, occurring from northern Hidalgo to Oaxaca and possibly to Guatemala. No geographic pattern is evident in the distribution of the dysploid chromosome races ($n = 34, 35, 36$).



Figures 20–30. Chromosomes of *Sedum* sect. *Pachysedum* at metaphase I in pollen mother cells, ×2000 (except as indicated). Thin lines point to univalents or B-chromosomes, thicker lines to multivalents. 20, *S. macdougalli, SSM-SL1, n* = 34; 21, *S. nussbaumerianum, C44-93, n* = 64; 22, *S. pachyphyllum, U1751, n* = 34; 23, *S. praealtum* ssp. *praealtum, O-RB3, n* = 34; 24–25, *S. praealtum* ssp. *parvifolium:* 24, *M7806, n* = 35; 25, *M10074, n* = 36 + 1B; 26–27, *S.* × *rubrotinctum:* 26, *UC32.3009,* about 10 bivalents (with greater depth of focus) plus about 43 univalents, equivalent to 2*n* = 63; 27, *UC55.098,* pollen, mostly unstained and abortive, ×500; 28, *S. suaveolens, U2323, n* = ca. 320; 29, *S. treleasei, U1205, n* = 34; 30, *S.* sp., *UC58.858, n* = 34 + 1.

Sedum × rubrotinctum.

Sedum × rubrotinctum Clausen is known only in cultivation (Clausen, 1975), and it appears to be a garden hybrid. Meiosis is extremely irregular, and probably most chromosomes are unpaired at metaphase I. About 50–55 elements, including about 10 bivalents and multivalents, were noted in the best cells seen (Figure 26), equivalent to a somatic chromosome number of about 63. Laggards and occasional chromosome bridges are present at anaphase I and more laggards also at anaphase II. Virtually all quartets include extra and/or markedly undersized microspores, and most spores seem to degenerate soon after meiosis. At anthesis only 14 of 1286 pollen grains (1.1%) appeared reasonably normal when stained in aniline blue-lactophenol (Figure 27).

Walther (1931), who incorrectly identified *Sedum rubrotinctum* as *S. guatemalense* Hemsley (Clausen, 1948), noted the "subapical mucros" at the tips of its petals and compared them with similar appendages in *S. stahlii,* which has terminal floral stems. He also commented on other similarities between the two, notably the subshrubby habits and the subterete leaves strongly flushed with bright red. An artificial hybrid, *S. cremnophila* (of sect. *Pachysedum*) × *S. stahlii* (Uhl, 1976a) is a good match for *S. rubrotinctum* in most characters, including size, coloring and petal tips, but it has broader, thicker leaves. It seems reasonably certain that *S. stahlii* ($n = 29$) was one parent of *S. rubrotinctum.* The other parent must have been a subshrubby, yellow-flowered *Sedum* with terete leaves, most likely *S. pachyphyllum* ($n = 34$, Figure 22). A single seedling resulted from the cross *S. pachyphyllum* (*U1751*) × *S. stahlii* (*M7774*) but died before it could be studied. The chromosome number in *S. rubrotinctum* is compatible with this parentage ($2n =$ ca. 63), and the degree of irregularity in behavior of its chromosomes at meiosis is similar to that seen in artificially produced hybrids between *S. stahlii* and two other species of sect. *Pachysedum* (*S. cremnophila* and *S. cuspidatum,* Uhl, 1976a, and unpublished).

Sedum suaveolens.

The recently discovered and described *Sedum suaveolens* Kimnach (1978) has the dubious distinction of having the highest chromosome number yet found in seed plants, $n = 320$, or very close to that (Figure 28). In terms of the basic chromosome number in sect. *Pachysedum* ($n = 30$–34), this is apparently 20-ploid. Vegetatively this species differs sharply from all other species of sect. *Pachysedum,* and its sessile rosettes closely resemble those of some species of *Echeveria* (e.g., *E. elegans*) and *Graptopetalum* (e.g., *G. macdougallii*). However, its flowers do not conform to those of *Echeveria* or *Graptopetalum* but seem most similar to those of *S. craigii,* and Kimnach (1978) tentatively assigned it to Clausen's sect. *Craigia,* along with *S. craigii.* Further study may suggest a different classification for this very anomalous species. It is known only from its type locality, near Topia, in northwestern Durango about 230 km. southeast of the locality of *S. craigii.*

Sedum treleasei.

Sedum treleasei Rose ($n = 34$, Figure 29) is native to southeastern Puebla. All collections studied are of unknown origin in the wild, although one (*U1205*) is traceable back to Rose himself. The collections differ somewhat, with *U1205* having thicker, broader leaves than the others.

Sedum sp.

One collection (*UC58.858*) is clearly an undescribed species ($n = 34$). It has very blue-glaucous, obovate, reddish-tipped leaves up to about 25 mm. long and 8 mm. thick, and vegetatively it somewhat resembles *Sedum pachyphyllum.* However, its petals are pale yellowish and erect in the lower half, then chocolate brown and strongly recurved above. Its only known locality is in the Sierra Madre del Sur of south central Oaxaca, where it was collected by Thomas MacDougall (*B-188*) in 1957. The only plant studied happens to be a trisomic ($2n + 1$), and about half of the metaphase I figures show 34 bivalents and a univalent (Figure 30), and the other half show only 34 elements, presumably including a trivalent.

The floral characters of this species (*UC58.858*) make it difficult to assign it to an existing genus. However, its vegetative characters, its lateral inflorescence, its chromosome number, and especially the pairing behavior of its chromosomes in several hybrids (Uhl, 1976a, and unpublished) clearly favor its assignment to sect. *Pachysedum.* In particular, a hybrid with *Sedum lucidum* (*U1462* × *UC58.858*) shows nearly normal meiosis, and only bivalent chromosome pairing was noted in about half its cells at metaphase I, with the other cells showing 1–4 univalents and sometimes probably a multivalent or two. A single chromosome bridge was noted in two cells at anaphase I, but many other cells at this stage appeared normal, and 7.0% stainable pollen is produced. These observations indicate that, in spite of the differences in their flowers, the parental genomes are very similarly organized and probably bear no more than a few small differences in chromosome structure and gene arrangements. Clearly the genes that regulate the morphology and pigmentation of the corolla in the parental species have evolved along different lines, but the overall arrangement and organization of the genes in the parental chromosomes are very much alike. Similar observations also were made for a hybrid with *Echeveria linguifolia* (*UC61.583* × *UC58.858*) (Uhl, 1976a).

DISCUSSION

The apparent basic chromosome number in sect. *Pachysedum* ($n =$ 30–36) is so high as to suggest that it is polyploid. However, no other evidence supports this conclusion. No similar species with substantially lower chromosome numbers are known that might represent diploid close relatives or ancestors of sect. *Pachysedum*. Species with $n = 30$ to $n = 36$ exhibit no tendency to form multivalents at meiosis, as known polyploids in this family generally do (Uhl, 1976a, and unpublished). Strongest evidence for diploidy of these species with $n = 30$–36 comes from study of many hybrids. Details of this have been published for *Sedum cremnophila* and *Echeveria linguifolia* (Uhl, 1976a). Study of many hybrids involving other species of sect. *Pachysedum* leads to the same conclusion for them also, and for the same reasons: (1) the chromosomes contributed to a hybrid by these species with $n = 30$–36 are no more potent in determining the phenotype of the hybrid than are other genomes contributing as few as 12 chromosomes, the lowest chromosome number in the comparium; and (2) in the hybrids the chromosomes are unable to pair with other chromosomes from the same parent (autosyndesis), although most of them usually pair successfully with at least some part(s) of one or more chromosomes from the other parent (allosyndesis) (Uhl, unpublished). Both of these properties contrast sharply with the properties of chromosomes from known tetraploids in these groups. If the high basic chromosome numbers here are the result of ancient polyploidy, the original diploid ancestors, if they exist, are no longer apparent, and the genomes here have now become so thoroughly diploidized that none of the cytological or genetical traits of polyploids, except the high numbers, remain. Similar conclusions have been reached on similar grounds for *Graptopetalum* and *Thompsonella* ($x = 30$–34 and $x = 26$, respectively) (Uhl, 1970) and for *Pachyphytum* ($x = 31$–33, Uhl & Moran, 1973).

Although hybrids are easily produced between most species of sect. *Pachysedum* and subfam. Echeverioideae, attempted crosses between species of sect. *Pachysedum* and other species of *Sedum* are less likely to result in any progeny. And although very extensive chromosome pairing occurs in most hybrids between sect. *Pachysedum* and subfam. Echeverioideae, most hybrids between sect. *Pachysedum* and other species of *Sedum*, when obtained, usually exhibit considerably less chromosome association at meiosis (i.e., they usually have more univalents) (Uhl, 1976a, and unpublished). This observation applies to hybrids of sect. *Pachysedum* with the relatively large species of *Sedum* with terminal inflorescences (*S. allantoides, S. obcordatum, S. palmeri, S. platyphyllum,* & *S. stahlii*), as well as to hybrids with smaller, more "typical" species of *Sedum*.

Thus, as judged by the extent of their association at meiosis, the chromosomes of sect. *Pachysedum* of *Sedum* are more closely homologous with the chromosomes of most species of subfam. Echeverioideae than they are with most or all other species of *Sedum*. Since the ability of chromosomes to synapse at meiosis is a strong indicator of their homology and genetic similarity, sect. *Pachysedum* seems to be significantly closer genetically to subfam. Echeverioideae than it is to the rest of *Sedum*.

The genera of subfam. Echeverioideae appear to have ancestral chromosome numbers in the range of 30–35 (Uhl, 1970, 1976a, and unpublished; Uhl & Moran, 1973), the same as in sect. *Pachysedum*. The latter appear to be an intermediate group between typical *Sedum* and subfam. Echeverioideae, and they may resemble the ancestral stocks from which the latter were derived. Walther (1931) stressed the close resemblance between *Sedum cremnophila* and *Echeveria linguifolia* and suggested that "possibly the transition between *Echeveria* and the more primitive genus *Sedum* may be sought in this vicinity". The evidence from the chromosome numbers, presented here, and the evidence from study of many hybrids, to be presented elsewhere, support this idea.

Traditionally classification of the Mexican Crassulaceae into subfamilies and genera has been based chiefly upon characters of the corolla, especially its attitude and connation. However, the cytological evidence indicates that corolla characters are of limited taxonomic value here, since parallel conditions appear to have evolved independently several times in related lines. Some taxonomic revision seems appropriate to bring the classification of sect. *Pachysedum* into closer harmony with its natural relationships. One possible improvement might be to expand the recently revived *Cremnophila* (Moran, 1978) to include most or all species of *Pachysedum* (and probably also several species of *Echeveria*) and to assign the genus to subfam. Echeverioideae.

Table 1. Chromosome Numbers in Sedum Section Pachysedum

Sedum adolphii Hamet $n = 64$

U1938, UC62.241, C45-97 (Figure 1), *C46-32* All cultivated.

Sedum × amecamecanum Praeger Meiosis irregular.

U483 (Figures 2, 3, 5) Cultivated.

M7800 (Figure 4) Cultivated in Mexico. Said to have come from 3000 m. on Popocatepetl.

Sedum batallae Barocio $n = 34$

M13411 (Figure 6) Topotype. Hidalgo: sheer cliffs of Cerro Alto, 2½ km. S. of Epazoyucan, 2600 m. (R. Moran, C. H. Uhl, & H. Sanchez-Mejorada).

Sedum clavatum Clausen $n = 33$

TMV-T-Tis. 1 & Tis. 3 (Figure 7) State of Mexico: Tiscalatengo Gorge, 4 km. WSW of Tenancingo (R. T. Clausen) Type Collection.

M19058 (Figure 8) Same locality (H. Fittkau) $n = 33 + 1$B.

U1566 (Figure 9) Same locality (J. Meyran 1306) $n = 33 + 2$B.

Sedum confusum Hemsley $n = 34$

C44-14 (Figure 10), *C46-14, UC45.323* All cultivated.

Sedum corynephyllum Fröderström $n = 34$

M13386 San Luis Potosi: Sierra La Aquitaria, 34 km. SW of Rioverde (R. Moran & C. H. Uhl).

U2339 Hidalgo: Palo Hueco, 28 km. NE of Jacala, 1700 m.
U2127 Queretaro: 24 km. NE of Vizarron.
M10042, M10047 Hidalgo: Barranca de Toliman (R. Moran).
C48-55 Hidalgo: near Zimapan (R. T. Clausen).
M7802, U258 (Figure 11), *C47-71* All cultivated.

Sedum corynephyllum Fröderström $n = 68$
U1286 Hidalgo: 7 km. N. of Metzquititlan (M. Kimnach).
M7796 (Figure 12) Same or nearby locality (R. Moran).
UC57.577 Hidalgo: Barranca de Venados (P. C. Hutchison).

Sedum craigii Clausen $n = 30$
C43-2 (Figure 13) Isotype. Chihuahua: Canyon wall of Barranca del Cobre 2135 m. (R. T. Craig & G. Lindsay).
U1206. Cultivated. Probably same collection.

Sedum cremnophila Clausen $n = 33$
M10174 (Figure 14) Tep 2, Tep 3, Tep 6 ($n = 33 + 1$B), Tep 7 Morelos: above Aztec temple, N. of Tepoztlan (R. Moran, R. T. Clausen).
U1291, U1435, M7687 Morelos: Sierra de Chalchi, S. of Tepoztlan, on cliffs (M. Kimnach, C. H. Uhl, & R. Moran).

Sedum cuspidatum E. J. Alexander $n = 34$
U1263 (Figure 15) Oaxaca: Sierra Madre above Zanatepec (T. MacDougall, *B-236*).
C46-62 Clonotype. Chiapas: near Ocozocoautla (T. MacDougall).
C49-25 Chiapas: WSW of Tuxtla Gutierrez.
UC52.1881 Cultivated (Coll. by T. MacDougall).

Sedum decumbens Clausen $n = 34$
C44-119 Cultivated. Type collection.

Sedum dendroideum Moc. & Sesse $n = 30$
M7785 Hidalgo: Pachuca (R. Moran).
M7779 (Figure 16) Puebla: San Hipolito (R. Moran).
SJC Oaxaca: San Jose Chiltepec (T. MacDougall).
M7736 Oaxaca: Cañada de Tutla (R. Moran).
UC56.799 Oaxaca: Cerro Atravesado, Juchitan (T. MacDougall, *B-176*).

Sedum hultenii Fröderström $n = 26$

U1864 Hidalgo: 8 km. S. of Santa Ana, 1600 m.

U1865 Hidalgo: 10 km. S. of Santa Ana, 1600 m.

U1937 Hidalgo: Cantil de Tambor, 11 km. S. of Santa Ana, 1650 m.

U1868 Hidalgo: 23 km. N. of Jacala.

C7472 (Figure 17) Puebla: Near Huauchinango (Topotype?) (R. T. Clausen).

U2349 Puebla: 2 km. W. of dam at Nuevo Necaxa, 1600 m.

U1881 Puebla: 8 km. N. of Zacapoaxtla, 1375 m.

U485 Cultivated: Uppsala, Sweden. Likely from the type collection.

M14783 Cultivated. Said to be from Hidalgo (H. Fittkau).

Sedum lucidum R. T. Clausen $n = 34$

C44-12 (Figure 18) Type collection. Veracruz: Orizaba (E. Walther).

RB6 5 km. SW of Orizaba city (R. T. Clausen).

U1462 Veracruz: E. of town of Rio Blanco.

M3179, C48-24, C49-13 All cultivated.

Sedum × luteoviride R. T. Clausen Meiosis irregular.

M7808 Hidalgo: Near San Vicente, ca. 35 km. S. of Jacala, 2300 m. (R. Moran).

C47-76, M7616, M7801 (Figure 19) All cultivated.

Sedum macdougallii Moran $n = 34$

SSM = SL1 (Figure 20) Topotype. Oaxaca: Santiago Lachiguiri. (T. MacDougall).

Sedum nussbaumerianum Bitter $n = 64$

C44-93 (Figure 21), *C46-27* Both cultivated (R. T. Clausen).

Sedum pachyphyllum Rose $n = 34$

U191, U1751 (Figure 22), *FL1420* All cultivated.

Sedum praealtum DC ssp. **praealtum** $n = 34$

U1887 Veracruz: S. side of valley opposite city of Rio Blanco.

RB3 (Figure 23) Same or nearby locality (R. T. Clausen).

Sedum praealtum DC ssp. **parvifolium** Clausen $n = 34$

U1468 Hidalgo: 3.6 km. N. of Pueblo Nuevo.

C7437 Hidalgo: Rocks by waterfall near Pueblo Nuevo, 3050 m. (R. T. Clausen).

C7430 Hidalgo: Rocks beside road, Real del Monte, 2745 m. (R. T. Clausen).
C7533 Hidalgo: Barranca de los Marmoles, 37 km. N. of Zimapan, 2300 m. (R. T. Clausen).
M-M Tlaxcala: NE side of Malinche (5 plants) (R. T. Clausen).
M7770 Oaxaca: Las Flores, Sierra Juarez (R. Moran).
M10130 Oaxaca: Cerro San Felipe (R. Moran).
SSM-SL1 Oaxaca: San Luis (R. T. Clausen).
U842 Guatemala: Dept. El Quiche. Chichicastenango, possibly cultivated (H. E. Moore, Jr.).

Sedum praealtum DC ssp. **parvifolium** Clausen $n = 35$
M7806 (Figure 24) Hidalgo: San Vicente, ca. 35 km. S. of Jacala, 2300 m. (R. Moran).
U1882 Puebla: E. of Teziutlan.
U1461 Veracruz: 1 km. NE of Cumbres de Acultzingo.
UC58.842 Oaxaca: below Neveria, Santo Domingo Ozolotepec, 2600 m. (T. MacDougall, *B-189*).

Sedum praealtum DC ssp. **parvifolium** Clausen $n = 36 + 1B$
M10074 (Figure 25) Hidalgo: El Carmen (R. Moran).

Sedum × rubrotinctum Clausen Meiosis irregular
M3090, UC32.3009 (Figure 26), *UC55.098* (Figure 27) All cultivated.

Sedum suaveolens Kimnach $n = 320\pm$
U2323 (Figure 28) Type collection. Durango: vertical cliff face in river canyon 3 km S. of Topia. *M. Kimnach & H. Sanchez-Mejorada 1784.*

Sedum treleasei Rose $n = 34$
U1205 (Figure 29) Cultivated, Univ. of Mich. Bot. Garden *9375,* from J. N. Rose in 1921.
U475, U2444 Cultivated.

Sedum sp. $n = 34 + 1$
UC58.858 (Figure 30) Oaxaca: Below Neveria, Santo Domingo Ozolotepec, 2600 m. (T. MacDougall, *B-188*).

SUMMARY

Section *Pachysedum* is defined as consisting of 19 Mexican species having lateral floral stems and mostly shrubby or subshrubby habit and *Sedum*-like flowers. Chromosome numbers are reported for 82 collections representing all 19 species: one species has $n = 26$, two each have $n = 30$ and $n = 33$, 11 have $n = 34$, two have $n = 64$, and one has $n = 320\pm$, probably 20-ploid and the highest known in seed plants. One species includes diploid and tetraploid populations ($n = 34, 68$); another has populations with 3 different dysploid numbers ($n = 34, 35, 36$); one trisomic was noted; and B-chromosomes were found in 3 species. Chromosome numbers are also reported here for three other named species which have very irregular meiosis and appear to be sterile; they are believed to be natural or garden hybrids each having a species of sect. *Pachysedum* as one parent. In many artificial hybrids the very extensive homology and pairing between chromosomes of different species of sect. *Pachysedum* supports the conclusion that most or all of them represent a natural group. In spite of their relatively high numbers, the 30–34 gametic chromosomes contributed by most species of sect. *Pachysedum* do not pair among themselves in hybrids, and such species are considered effectively diploid. Substantial chromosome pairing occurs in hybrids between species of sect. *Pachysedum* and subfam. Echeverioideae, whereas considerably less chromosome pairing occurs in most hybrids between species of sect. *Pachysedum* and other Mexican species of *Sedum* that have terminal floral stems. This indicates that sect. *Pachysedum* is more closely related genetically to subfam. Echeverioideae than it is to most or all other species of Mexican *Sedum*. Some taxonomic realignment seems desirable here to bring the classification into closer agreement with the genetic relationships.

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PUTATIVE HYBRIDIZATION IN THE GENUS EUPATORIUM (COMPOSITAE)[1]

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Fryar (1964) and Maurushat (1969) gave evidence for the hybrid origin of several anomalous biotypes in the genus *Eupatorium*. Hybridization in the genus has also been reported by others (Radford, et. al., 1968; Gleason & Cronquist, 1963; Gleason, 1952). This paper concerns the putative hybrid origin of *E. fernaldii* Godfrey from *E. sessilifolium* L. and *E. album* L., the hybridization of *E. sessilifolium* with *E. perfoliatum* Brit., the hybridization of *E. semiserratum* DC. and *E. lecheaefolium* Greene, and a possible hybrid origin for *E. saltuense* Fern.

MATERIALS AND METHODS

Flowering plants were collected throughout the summer and early fall. Rootstocks to be used as source materials for determining chromosome numbers and investigating breeding systems were taken from the field and replanted in a greenhouse or garden at Florida State University. Herbarium specimens were made of the flowering stems from the field collected plants.

Chromosome analysis was made from the root tips of mature plants, seedlings, or from the pollen mother cells (PMC's) at meiosis. All material was fixed in acetic alcohol, stained with aceto-orcein, and prepared by the squash technique for observation. Root tips were hydrolyzed in 10% 1N HCl for three to five minutes before staining and squashing. Mitotic material was treated with 0.9% colchicine for an hour prior to fixation. Voucher specimens for chromosome counts (Appendix) were deposited in the FSU Herbarium.

RESULTS AND DISCUSSION

Eupatorium fernaldii Godfrey (putative *E. album* × *E. sessilifolium*).

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Plants of *Eupatorium fernaldii* were studied from twenty-four locations in Georgia and North Carolina. The habitats were gravelly clay and rocky cliff faces adjacent to roads, and open hilly pastures adjacent to pinewoods and mixed hardwood forests in the Montane and Piedmont provinces. Large populations of the biotype occur.

Chromosome counts were made of plants of seven of the populations. Six populations were tetraploid and one was triploid (Appendix). Those plants for which chromosome counts were made and those of the remaining seventeen populations studied failed to produce pollen. A few plants produced grossly malformed pollen without proper wall formation. In order to determine achene setting ability, plants from the seven populations were isolated from pollen sources in a greenhouse; they produced full heads of viable achenes indicating reproduction by agamospermy. Among many of the plants, achene development was observed to occur before anthesis. These are characteristics of polyploid plants of other *Eupatorium* species (Sullivan, 1976).

Plants of *Eupatorium fernaldii* resemble *E. album* L. in having petaloid phyllaries, leaves of similar shape, and a similar habit. However, unlike *E. album,* the leaves are nearly glabrous. Because of the similarity between *E. album* and *E. fernaldii,* Fernald (1937), who originally described this biotype, named it *E. album* var. *monardifolium* Fern. Later, Godfrey (1950) elevated it to the species level. Godfrey (pers. comm.) recently examined an isotype of *E. vaseyi* Porter and found it to be phenotypically like the type of *E. fernaldii.* Previously, Fernald (1945) had reassigned *E. vaseyi* Porter to *E. sessilifolium* var. *vaseyi* (Porter) Fern. and Grisc.

Since diploids of this taxon were not found and due to its similarity to *Eupatorium album,* and its occurrence as male-sterile, polyploid agamics, the hypothesis of a hybrid origin seemed reasonable. Based on the morphological similarity previously mentioned, one obvious hypothetical parent is *E. album.* The other hypothetical parent should occur within the prescribed area of distribution of *E. fernaldii,* as does *E. album,* as a sexual diploid, and have nearly glabrous leaves as does *E. fernaldii.* The only *Eupatorium* with these characteristics is *E. sessilifolium* L. (Sullivan, 1976).

Measurements were made of the three entities, putative parents and hybrid (Table 1). In addition to similarities between *Eupatorium fernaldii* and the putative parents mentioned above, shape and

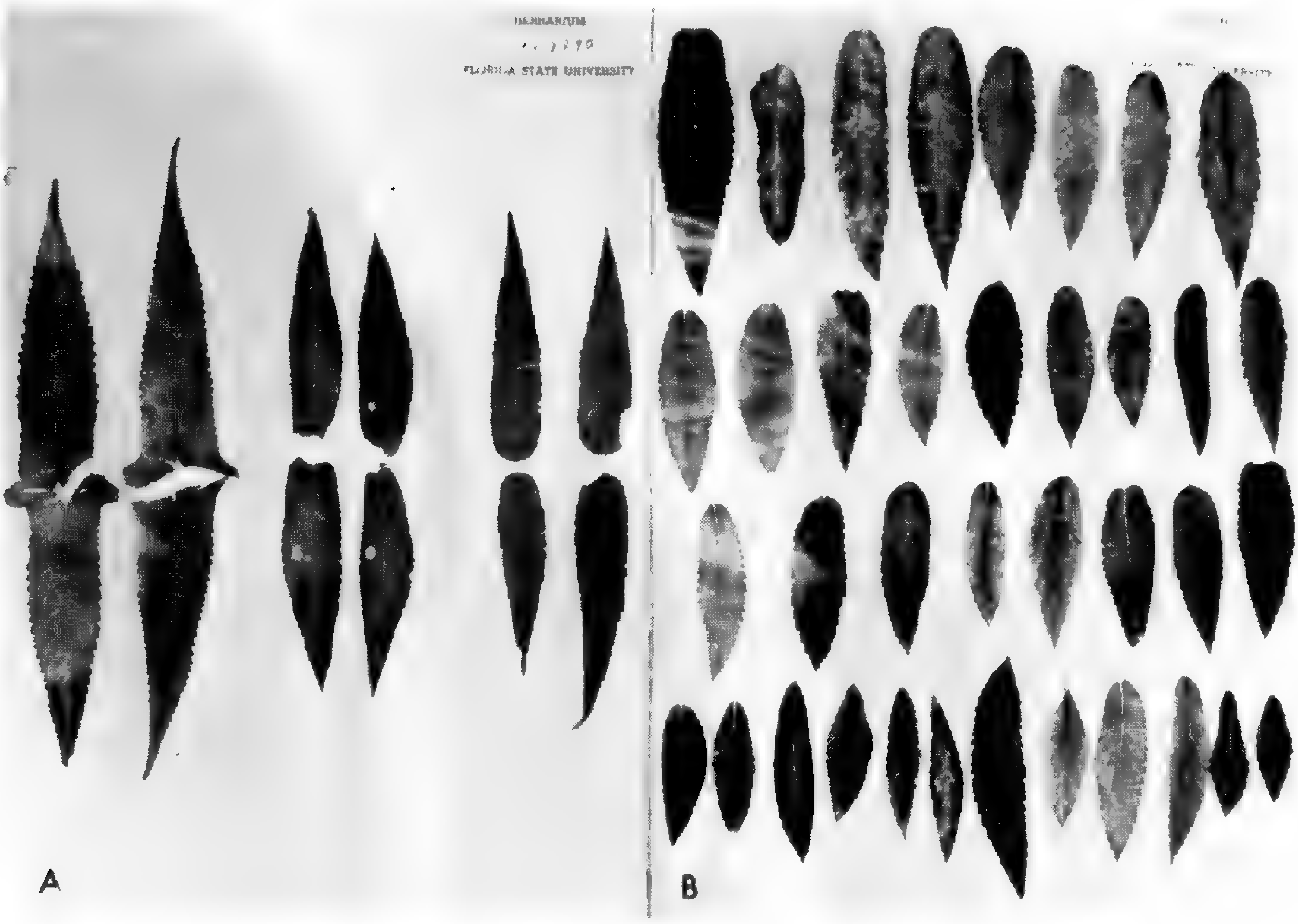

Figure 1A and B. A. (left to right): Two pairs of leaves each of *Eupatorium perfoliatum*, hybrid, and *E. sessilifolium*. B. Leaves from backcross hybrid plants, *Eupatorium sessilifolium* × hybrid.

serration of leaves of *E. fernaldii* plants were intermediate between *E. album* and *E. sessilifolium;* leaf length tended to be like *E. album,* while leaf width exceeded that of both the parental plants. The lengths of capitulary characters of hybrid plants tended to equal or to exceed those of *E. album* plants.

Although further evidence is needed, the morphological evidence provided suggests a hybrid origin for *Eupatorium fernaldii*. Evidence from phytochemical and karyotypic work might provide further information not readily apparent from the morphology.

Eupatorium sessilifolium × perfoliatum.

The distributions of *Eupatorium sessilifolium* (discussed above) and *E. perfoliatum* overlap throughout the range of the former. *Eupatorium perfoliatum* has a broad distribution throughout eastern North America and parts of the midwest. While collecting in the southern Appalachians in Graham County, North Carolina, I found one plant intermediate in morphology between *E. sessilifolium* and

Table 1. **Morphological comparison of Eupatorium album, E. sessilifolium and E. fernaldii.**

	E. album var. *album*	*E. fernaldii*	*E. sessilifolium*
Leaves:	4.8–11 cm long, 1–3.4 cm wide, elliptic with acute tips and attenuate bases, 10–30 teeth; crenate and double crenate, irregularly spaced, nearly cleft in some upper leaves, short petiolate, densely pilose on upper and lower surfaces	4.8–11 cm long, 2–3.8 cm wide, elliptic to lanceolate, acute to acuminate tips, bases sessile, 5–23 teeth doubly serrate, scattered pilose along veins of upper and lower surfaces	6–10 cm long, 1.6–3.2 cm wide, lanceolate with acuminate tips, clasping to rounded bases, sessile, 8–20 teeth, serrate; pilose on upper veins, lower surfaces glabrous except mid veins
Head:	7–10 mm	7–9 mm	6–7 mm
Corolla:	4–5 mm	4–5.5 mm	2.5–3 mm
Pappus:	4–5.5 mm	4–6 mm	3.5–4 mm
Phyllaries:	10–15, white petaloid, little green, 7–10 mm, acuminate	10–14 white petaloid margins and tip, 7–9 mm mucronate-caudate	9–12 green with hyaline margin, 3.5–5 mm, acute

E. perfoliatum; the intermediate plant was growing within a large population of diploid *E. sessilifolium* plants along a disturbed and eroded bank. *Eupatorium perfoliatum* was nearby in a poorly drained area on a road bank.

The diploid intermediate was transplanted to a greenhouse where reciprocal backcross hand-pollinations were made to diploid *Eupatorium sessilifolium.* The achenes were sown, and the resulting progeny were like those of *E. sessilifolium;* however, a few had clasping to perfoliate bases, like the *E. perfoliatum* and intermediate plant (Figures 1A and B), indicating hybridity.

Meiosis in most PMC's of the hybrid was normal; however, in 7.3% of the cells observed two univalents were formed (Table 2). In 2.5% of the cells at Telophase II two micronuclei were found; those probably resulted from failure of laggards to be included in the large nuclei.

Despite the paucity of hybrid collections of this combination, hybridization could occur more frequently than observed since the species are sympatric in a part of their range. However, ecological barriers might prevent establishment. The high degree of interfertility, as indicated by chromosomal compatibility, and the capacity to form backcross progeny with at least the one parent tested indicate that genetic isolating barriers are poorly defined. Further examination of the two species could reveal that introgression is occurring, if sufficiently strong ecological barriers to hybrid establishment do not exist.

Eupatorium semiserratum × lecheaefolium.

Eupatorium semiserratum plants occur as sexual diploids throughout their distributional range; the distribution is Coastal Plain and adjacent areas from Florida to eastern Texas, north to Virginia, Tennessee, and southeastern Missouri (Sullivan, 1976). The habitats include moist to boggy, peaty, sandy soils in pine flatwoods, margins of seasonal ponds, gum swamps, and bayheads. In addition the plants are abundant in disturbed habitats such as firelanes, margins of roadside ditches, and clear-cut pine flatwoods. Plants of *E. lecheaefolium* Greene occur as diploids ($n = 10$) and triploids (Sullivan, 1976). The triploids were male-sterile and agamospermous; the diploids are sexual, male-fertile and self-incompatible (Sullivan, 1976). Diploid plants of *E. lecheaefolium* are narrowly

Table 2. **Meiosis in the field hybrid Eupatorium perfoliatum × sessilifolium.**

No. MI cells	% MI with 2 univalents	No. AI cells	%AI with laggards:		No. TII cells	%TII with micronuclei	
			1	2		1	2
27	7.3	20	0	5	39	0	2.5

distributed in southern Georgia and midnorthern Florida. Grant (1953) made chromosome counts of a diploid from Alexander County, North Carolina; however, field work in that area during this study failed to reveal diploid plants of *E. lecheaefolium.* Herum specimens which were identified as polyploids by their male-sterility were collected in the Coastal Plain and Piedmont from North Carolina to southern New Jersey, and from Georgia to southern Louisiana and to eastern Tennessee (Sullivan, 1976). Plants of this species occur in dry, upland pinewoods and edges of rich woods. Disturbed areas such as firelanes, highway rights-of-way, and old fields also provide favorable habitats.

Diploids of the two species are found intermixed occasionally in disturbed sites where their habitats are contiguous. From one such location (Leon County, Florida) where intermediate plants were present, seeds were collected from putative parental and hybrid plants and progeny tests were made in a greenhouse.

With few exceptions, progeny from the parental plants were like the respective species, indicating that backcrosses are infrequent or unsuccessful. However, progeny from hybrid plants were morphologically diverse, recombining characteristics of the parental species (Figure 2). Figure 3 is a scatter diagram made by using leaf width and number of teeth per one leaf margin of the progeny. The figure illustrates the intermediacy and recombinance of parental characters in the hybrids.

A year later over half the greenhouse progeny had died. The remaining plants were remeasured and a second scatter diagram constructed (Figure 4) again using leaf width and number of teeth per margin. The surviving progeny, as illustrated in the scatter diagram, were the plants resembling the parents; the intermediate plants had died. These results suggest that the intermediate condition is intrinsically unstable. No competition occurred in the greenhouse pots and no other apparent extrinsic selection occurred.

F_1 hybrid plants were synthesized by reciprocal hand pollination between diploids of *Eupatorium semiserratum* and *E. lecheaefolium.* A total of six hybrids was obtained from the *E. semiserratum* parent and none from the *E. lecheaefolium* parent. Self-pollinations, intersibling crosses, and reciprocal backcrosses to *E. semiserratum* were made using the F_1 hybrids. Self-pollinations and intersibling crosses failed to produce viable seeds; however backcrosses

Figure 2. Leaves from sixth node of plants from progeny test. Left, leaves from progeny of *Eupatorium lecheaefolium;* center, leaves from progeny of intermediate plants; right, leaves from progeny of *E. semiserratum.*

yielded thirteen progeny from the *E. semiserratum* seed parent and seven progeny from the F_1 seed parent.

Analyses of meiosis were made of three F_1 hybrids (Table 3). Meiosis was irregular with a high frequency of two and four univalents, one or two nondisjunct bivalents, and lagging univalents at Anaphase I. In one hybrid, one to three chromatids were excluded from the Metaphase II plate.

The differences in habitats of the parental species, intrinsic selection against intermediate hybrids, apparent infrequency of backcrossing in the field and meiotic irregularities are factors which isolate the species.

Some of the hybrid progeny resembled plants referred to as *Eupatorium hyssopifolium* L. var. *laciniatum* Gray and var. *hyssopifolium.* Numerous collections from populations of these varieties were made for greenhouse culture and study. From those plants, chromosome numbers were determined to be triploid and tetraploid (Appendix). The plants were male-sterile; however, when isolated in a greenhouse from pollen sources, they produced full heads of viable achenes. Progeny grown from these achenes had the same chromosome numbers as the respective parent plants. Those results reveal the plants to be agamic, as has been discovered in other *Eupatorium* polyploids (Sullivan, 1976). Grant (1953) gave triploid chromosome counts for *E. hyssopifolium* also.

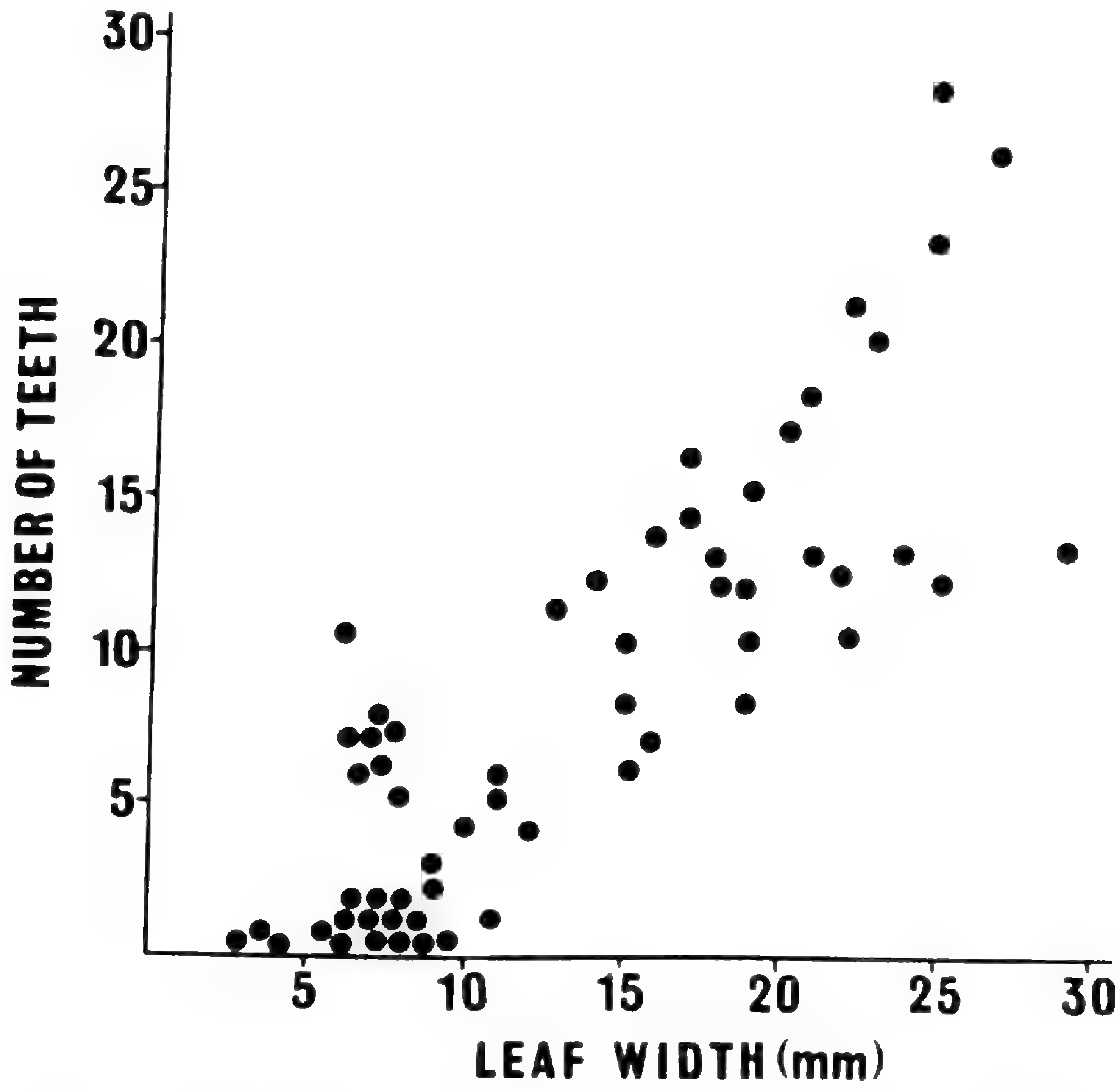

Figure 3. Scatter diagram of progeny from test of naturally occurring hybrids of *Eupatorium semiserratum* × *lecheaefolium* and parental plants.

Plants of those varieties are variable. Fernald (1950) suggested that the two mentioned above and *Eupatorium hyssopifolium* L. var. *calcaratum* Fern. and Schub., which is synonymous with *E. lecheaefolium*, are confluent. The relationship of plants of those varieties to hybrids of *E. lecheaefolium* × *semiserratum* are being investigated through karyotyping and phytochemical studies.

Eupatorium saltuense (putative *E. album* × *E. lecheaefolium*).

Eupatorium saltuense was described by Fernald (1942) from southeastern Virginia. Radford et al. (1968) reported the species from Caswell, Granville, and Warren counties in the North Carolina Piedmont.

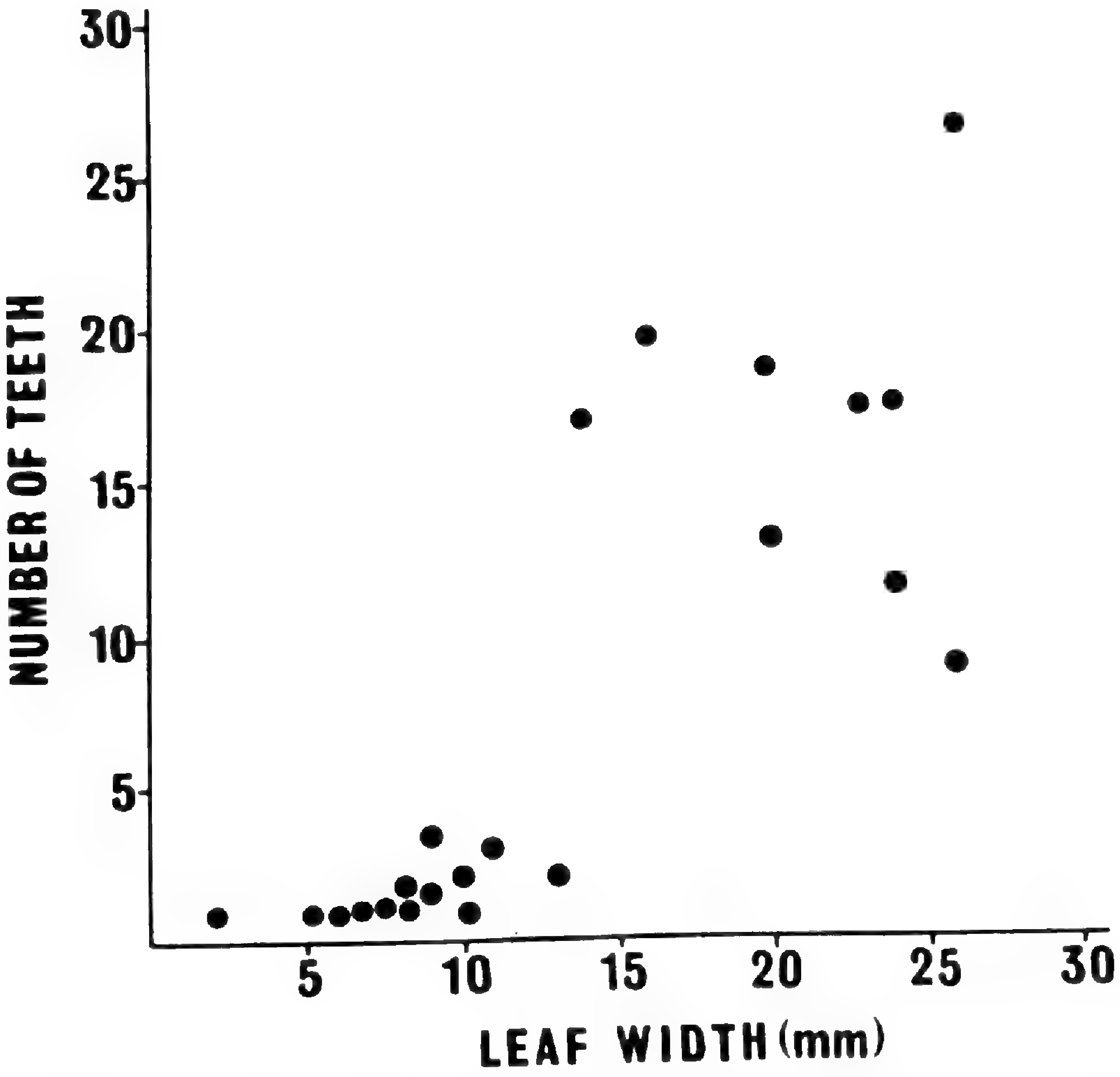

Figure 4. Scatter diagram of same progeny as measured in Figure 2 a year later (after most had died).

Population samples of *Eupatorium saltuense* were obtained from various sites in southeastern Virginia. These were grown in a greenhouse. Chromosome numbers of *E. saltuense* were found to be $2n = 30$, a triploid count based on $x = 10$ (Sullivan, 1976; Grant, 1953). The plants were male-sterile and when isolated from pollen sources in a greenhouse, they set full heads of viable achenes revealing their agamic reproductive ability. The male-sterile agamic nature of polyploid eupatoria has been repeatedly found by the author (1976).

The plants were found in disturbed habitats intermixed with polyploid *Eupatorium altissimum* L., triploid *E. lecheaefolium* Greene and two other anomalous polyploids. Diploid plants of *E. album* L. were in the near vicinity.

Table 3. **Meiosis in diploid F_1 hybrids of Eupatorium lecheaefolium × semiserratum.**

		% MI with			% AI with laggards:							% MII with					% TII with micronuclei		
					I		II					I II	Excluded I						
Plant	No. MI cells	9II, 2I	8II, 4I	No. AI cells	1	2	1	2	3	4	No. MII cells		1	2	3	No. TII cells	1	2	3
A	28	39	35	[1]												61	16	13	0
B				33	3	3	9	6	0	0									
C	8	62	0	82	9	1.2	11	12	1.2	1.2	36	5.4	11	3	3	121	2.4	12	0.8

[1] None examined.

Table 4. **Morphological descriptions of Eupatorium album (2*n*), E. lecheaefolium (2*n*), and E. saltuense.**

	E. album	*E. lecheaefolium*	*E. saltuense*
Leaves:	4.8–11 cm long, 1–3.4 cm wide, elliptic with acute tips and attenuate bases, 10–30 teeth; crenate and double crenate, irregularly spaced, nearly cleft in some upper leaves, short petiolate, densely pilose on upper and lower surfaces	2–4 cm long, 0.2 cm wide, linear with acute tip and cuneate base, lower surfaces hispid, upper nearly glabrous, margins entire	4–11.2 cm long, 0.6–3.6 cm wide, elliptic to elliptic-lanceolate, attenuate-acuminate tip, and acute base, glabrous above, pubescent beneath, 2–25 coarse teeth per margin
Phyllaries:	10–15, white petaloid, little green, 7–10 mm, acuminate	mucronate, 3.2–4 mm long	mucronate, 4–6 mm long
Head:	7–10 mm	4.3–5.5 mm long	5–8 mm long
Corolla:	4–5 mm	2.5–3.5 mm long	3–5 mm long
Pappus:	4–5.5 mm	3.2–4 mm long	4–5 mm long

Plants of *Eupatorium saltuense* resemble *E. lecheaefolium* in several respects: suppressed axillary shoots, similar inflorescences, and three prominent veins from the leaf base (Table 4). On the other hand, the leaf is elliptic-lanceolate and its margins are coarsely dentate, unlike the narrow linear one of *E. lecheaefolium* but similar to that of *E. album.*

For the reason stated above, measurements were made of population samples of diploid *Eupatorium lecheaefolium, E. album,* and *E. saltuense.* Type and isotype specimens from the Gray Herbarium were also measured and these data are included in the scatter diagram (Figure 5) using involucral bract length and teeth/margin. In the diagram, the type and isotype measurements fall directly

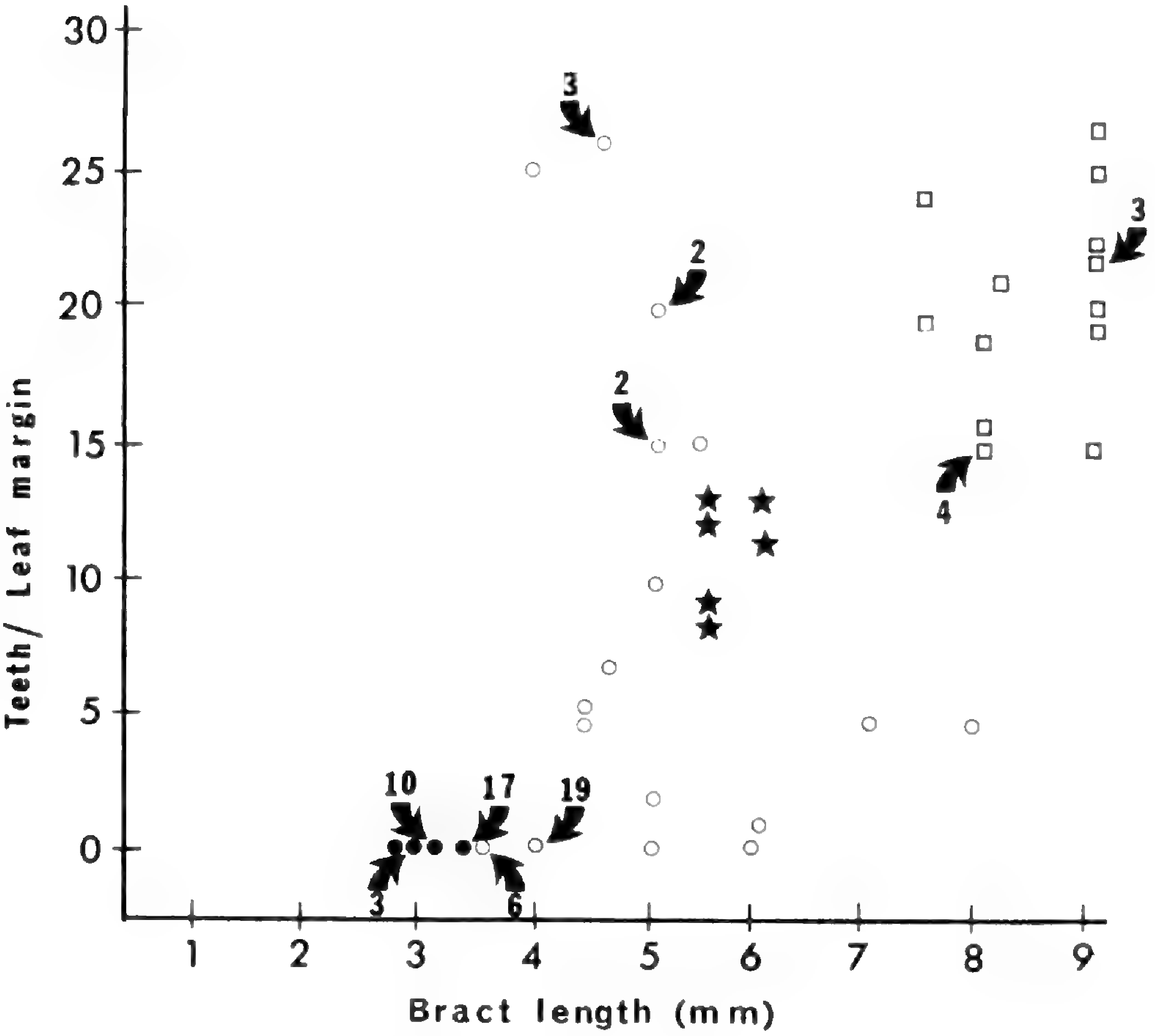

Figure 5. Scatter diagram using measurements of diploid *Eupatorium lecheaefolium* (●) and diploid *E. album* (□), Fernald's types and isotypes of *E. saltuense* (★), and other collections of *E. saltuense* (o). The numbers refer to the specimens with similar measurements represented by the symbol indicated by arrows.

intermediate between the putative parents. Most of the plants collected during this study also fell intermediate; however, some plants exceeded *E. album* in number of teeth per margin.

The origin of *Eupatorium saltuense* from *E. album* × *lecheaefolium* is uncertain because of the distribution of diploids of the putative parents. Field work during this study revealed that diploids of *E. lecheaefolium* are narrowly distributed in northern Florida and southern Georgia (Sullivan, 1976); Grant (1953) determined diploidy of a specimen from Rocky Face Mountain in the Piedmont Province in Alexander County, North Carolina. A vain search was made for diploids in that vicinity during this study. (By examining pollen, it is a relatively simple matter to determine diploidy of *Eupatorium* specimens.) Because of the apparent dearth of diploid *E. lecheaefolium* in that area it is probable that the origin of *E. saltuense* through hybridization could have occurred in the ancient past when diploids of *E. lecheaefolium* were more prevalent.

Further evidence regarding the origin of *E. saltuense* is being sought from phytochemical and karyotypic studies.

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APPENDIX

Eupatorium sessilifolium × album: 4*n, 3786 R. L. Lazor & V. I. Sullivan,* Rabun Co., Ga.; 4*n, 3809 RLL & VIS,* Jackson Co., N. C.; 4*n, 3807 RLL & VIS,* Jackson Co., N. C.; 4*n, 3810 RLL & VIS,* Jackson Co., N. C.; 4*n, 3816 RLL & VIS,* Jackson Co., N. C.; 4*n, 67873 R. K. Godfrey,* Jackson Co., N. C.; 3*n, 68270 RKG,* Buncombe Co., N. C.

Eupatorium sessilifolium × perfoliatum: 2*n, 3795A RLL & VIS,* Graham Co., N. C.

Eupatorium hyssopifolium var. **hyssopifolium** & var. **laciniatum:** 4*n, 69777 RKG,* Coffee Co., Tenn.; *4n, 69659 RKG,* Monroe Co., Ala.; 4*n, 68098 RKG,* Lamar Co., Miss.; 4*n, 69706 RKG,* Tuscaloosa Co., Ala.; 3*n, 69854 RKG,* Montgomery Co., Ala.

Eupatorium lecheaefolium × semiserratum: 2*n, 68430 RKG,* Leon Co., Fla.; 2*n, 69860 RKG,* Houston Co., Ala.

ON THE PLANKTONIC AND EPIPHYTIC DESMIDS (DESMIDIALES, CHLOROPHYTA) OF SOUTHERN WISCONSIN HARD WATERS

STEPHEN B. GOUGH[1]

Our knowledge of the desmid flora of southern Wisconsin hard waters (here defined as waters with > 30 mg per l Ca^{+2}, following the scheme of Sawyer & McCarthy, 1967) is limited. Smith (1924) examined the desmid plankton of selected lakes throughout the state but gave no indication of the chemical conditions at his study sites, nor did he examine the aufwuchs component. Sloey and Blum (1972) investigated the algal flora of hard water Lake Winnebago and reported the presence of two species of desmids in the aufwuchs and one in the plankton, but accounts of other investigations (e.g., Marsh, 1903) are restricted to generic determinations.

Desmid generic diversity is decidedly lower in hard waters than in soft waters (Hutchinson, 1967; Gough & Woelkerling, 1976) and the same appears to be true for desmid species (Smith, 1924; West & West, 1896). Smith (1920, p. 8), for example, states that fewer than one or two species were found in the plankton of the hard water lakes of southern Wisconsin whereas soft water bogs may harbor hundreds of species.

The factors responsible for the low diversity in hard water environments are not clear but may involve pH levels, calcium concentrations, conductivity levels or an interaction of these parameters (see Woelkerling & Gough, 1976, for a review of the literature on this subject). With few exceptions, the desmids occurring in hard waters are species of *Closterium, Cosmarium* or *Staurastrum* (Gough & Woelkerling, 1976; Smith, 1924; and others) and of these taxa, most are considered to be unusually tolerant forms which grow in soft waters as well; only a few have been suspected of preferring a hard water environment (Hutchinson, 1967). However, little attempt has been made to determine the chemical tolerance of individual taxa. Moreover, the chaotic state of desmid systematics

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makes it difficult to make comparisons between studies, especially when few authors cite the taxonomic sources used in the identification of their taxa.

Two major hard water lentic environments exist in Wisconsin: lakes (particularly those in the southern part of the state) and calcareous spring ponds. The latter type consists of impoundments fed by artesian sources from aquifers within or running through limestone bedrock or glacial till; these are especially prevalent in southeastern Wisconsin. The lakes and spring ponds differ in the ranges and mean levels of certain chemical parameters (Table 2), particularly conductivity, pH, CO_2, some nitrogen compounds, calcium and alkalinity.

To further our understanding of desmids in hard water environments, this report presents a floristic account of the species found in 20 hard water lakes and six calcareous spring ponds in southern Wisconsin. Comments on diversity, the frequency of occurrence of taxa in the plankton and aufwuchs, morphological variation within populations and distribution in relation to water chemistry are also included.

Table 1. **Conspectus of Desmid Species in Southern Wisconsin Hard Water Lakes and Spring Ponds.**

1\. Plants without a median constriction.................................. 2.
  2\. Distance between apices less than 100μ.............. *Closterium venus.*
  2\. Distance between apices greater than 200μ..... *Closterium moniliferum.*
1\. Plants with a median constriction. .... 3.
  3\. Semicells with an apical incision................. *Euastrum pinnatum.*
  3\. Semicells without an apical incision.............................. 4.
    4\. Semicells with divergent processes............................ 5.
      5\. Semicell base inflated. .... *Staurastrum longiradiatum.*
      5\. Semicell base tapered to the isthmus.... *Staurastrum manfeldtii.*
    4\. Semicells without processes.................................. 6.
      6\. Plants greater than 6 times longer than broad. .... *Pleurotaenium maximum.*
      6\. Plants less than 2 times longer than broad. .... 7.
        7\. Semicells with lateral incisions....... *Micrasterias truncata.*
        7\. Semicells without lateral incisions...................... 8.
          8\. Semicells granulate. .... 9.
            9\. Semicell apex flattened. ...... *Cosmarium botrytis.*
            9\. Semicell apex rounded. .. *Cosmarium punctulatum.*
          8\. Semicells pitted................. *Cosmarium granatum.*

Geographic and biological host data for the study sites are listed in Table 2 and a summary of the water chemistry is found in Table 3. Scanning electron micrographs referenced in the checklist are found in Figures 1–15.

MATERIALS AND METHODS

Ten to 25 l of water were strained through a No. 25 silk mesh plankton net and the plankton concentrate was preserved with FAA (10 : 7 : 2 : 1 :: 95% EtOH : distilled H_2O : formalin : acetic acid). Portions of macrophytes were collected and subjected to agitation and hydrolysis for removal and examination of the aufwuchs (see Gough & Woelkerling, 1976, for procedural details). Several glass slides were made of each plankton and aufwuchs concentrate using a glycerin jelly-fast green mounting medium and Hoyer's solution. The former provided stained cytoplasm which allowed recognition of characters such as pyrenoid arrangement and chloroplast structure whereas the latter provided cleared cells for examination of cell wall sculpturing. Voucher material has been deposited in my personal herbarium.

Living samples were taken twice at most sites during the period of June 1-August 30, 1973. Collections were transported on ice to the lab where clonal isolates were established in modified Waris medium (Waris, 1953; 90% medium + 10% soil water extract) using the capillary tube isolation technique (Hoshaw, et al., 1973). Established cultures which were representative of field populations were then used for scanning electron microscopy (SEM) and SEM micrographs (Figures 1–15) were produced for those taxa in which wall ornamentation is of primary taxonomic value. The advantages of SEM and the procedures used and the difficulties encountered in the preparation of desmid samples for SEM are outlined elsewhere (Gough, Garvin, & Woelkerling, 1976).

Tests for CO_2 and pH were done in the field with a HACH Chemical Company Water Analysis Field Kit, Model DR-EL, and calcium was determined in the lab by the EDTA titrimetric method (APHA, 1971). Other parameters were analyzed by the Wisconsin Department of Natural Resources, Delafield Laboratory (see Woelkerling, 1976, for details of the methods used).

Table 2. **Study sites: Geographic and Biological Host Data.**

COUNTY	SITE	LOCATION T	R	S	AREA (ha)	AUFWUCHS HOSTS*
Dane	Bruner's Pond	6N	7E	11	1	C,M,PP
	Fish L.	9N	7E	3	102.06	C,M,N,U
	L. Waubesa	6N	10E		855.76	M
	L. Wingra	7N	9E	27	139.72	C,M
Green Lake	Green L.	15N	12E		2966.62	M,N
Iowa	Cox Hollow L.	6N	4E	10,11	38.88	A,C
	Twin Valley L.	6N	3E	1	59.54	C,PC
Jefferson	Ripley L.	6N	13E	7	175.37	M,N,PC,U
	Rock L.	7N	13E		555.26	C,M
Racine	Tichigan L.	4N	19E		360.86	C
Walworth	L. Beulah	4N	18E		338.99	A,M,PP,U
	L. Geneva	1,2N	16,17E		2131.11	C,M
	Whitewater L.	3,4N	15E		259.20	PP
Waukesha	Fowler L.	8N	17E	33	31.59	A,Ch,M,PP
	Golden L.	7N	17E	30,31	101.25	M,Na,PP
	L. Nagawicka	7N	18E	8,17	371.38	A,M
	Okauchee L.	8N	17E	18	480.74	M,PP
	Pewaukee L.	7N	18,19E		1009.66	Ca,M
	School Section L.	6N	17E	16,17	50.62	M,PC
	Silver L.	7N	17E	9,16	89.91	Ch,S
	Spring Pond "A"	5N	17E	3	0.01	A,H
	Spring Pond "B"	6N	18E	21	0.01	A,Ch
	Spring Pond "C"	6N	18E	21	0.01	Ch,RL
	Spring Pond "D"	6N	18E	21	0.005	Ch,RL
	Spring Pond "E"	6N	18E	21	0.002	Ch
	Spring Pond "F"	6N	18E	21	0.002	Ch

*A = *Anacharis*, C = *Ceratophyllum*, Ca = *Carex*, Ch = *Chara*, H = *Hippuris*, M = *Myriophyllum*, N = *Nuphar* (petioles), Na = *Najas*, PC = *Potamogeton crispus*, PP = *Potamogeton pectinatus*, RL = *Ranunculus longirostris*, S = *Scirpus*, and U= *Utricularia*.

RESULTS AND DISCUSSION

TAXA PRESENT

The following is a checklist of the ten species of desmids found at the study sites. Populations of each taxon conformed to all descriptions and illustrations cited, and a conspectus of the taxa is found in Table 1. Percentage figures are based on presence/absence data from all sites (lakes and spring ponds).

Closterium Nitzsch ex Ralfs

Closterium moniliferum (Bory) Ehrenberg ex Ralfs **1848:** 166. *pl. 28, fig 3.* Irénée-Marie **1939:** 66. *pl. 5, figs. 1, 2.* Krieger **1937:** 289. *pl. 18, figs. 6, 7.* Sloey and Blum **1972:** 139. Smith **1924:** 9. *pl. 52, fig. 10.*

Plants of this species were common in the aufwuchs of the hard water lakes, occurring at 19% of all study sites, but none were found in the plankton.

A few cells (ca. 2%) in about half of the populations displayed a slightly scattered pyrenoid arrangement rather than the typical single row positioning.

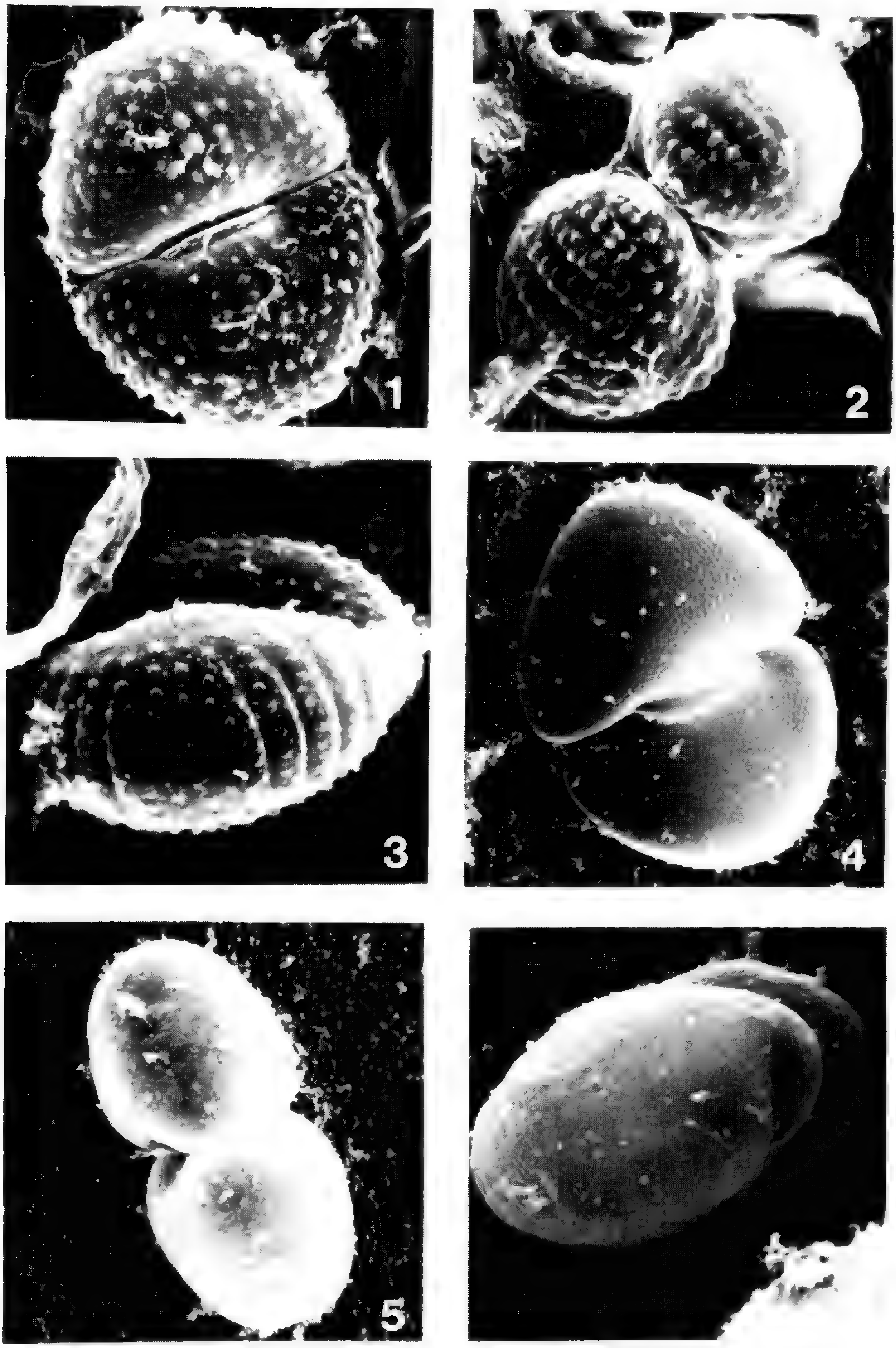
Closterium venus Kützing ex Ralfs **1848:** 220. *pl. 35, fig. 12.* Irénée-Marie **1939:** 70. *pl. 4, figs. 14–16. Krieger* **1937:** 272. *pl. 16, figs. 1–5.* Smith **1924:** 9. *pl. 52, fig. 9.*

Like *Closterium moniliferum,* no cells were found in the spring ponds or in the plankton of the lakes. However, the taxon was commonly encountered in the lake aufwuchs (found at 27% of all sites) where it often occurred on *Myriophyllum* and *Ceratophyllum.*

Cosmarium Corda ex Ralfs 1848

Cosmarium botrytis (Bory) Meneghini ex Ralfs **1848:** 99. *pl. 16, fig. 1.* Hirano **1957:** 182. *pl. 27, fig. 13.* Irénée-Marie **1939:** 210. *pl. 26, fig. 4.* Smith **1924:** 33. *pl. 57, fig. 22.* Text figures 1–3.

Although these plants were seldom confused with other taxa, the prominence of the basal cluster of granules varied within most populations and a few cells with larger granules resembled *Cosmarium sportella* Brébisson ex Ralfs 1848, as described by Irénée-Marie, 1939, p. 200, *pl. 24, fig. 9.*



Figures 1–6, **Cosmarium.** 1, *C. botrytis* (Bory) Meneghini ex Ralfs (1200×); 2, *C. botrytis* (Bory) Meneghini ex Ralfs (1600×); 3, *C. botrytis* (Bory) Meneghini ex Ralfs (2000×); 4, *C. granatum* Brébisson ex Ralfs (1900×); 5, *C. granatum* Brébisson ex Ralfs (2100×); 6, *C. granatum* Brébisson ex Ralfs (3000×).

Cells of this species were found in the aufwuchs of 54% of the sites (in lakes only) and in one lake plankton sample, making it the most commonly found *Cosmarium* taxon.

Cosmarium granatum Brébisson ex Ralfs **1848:** 96. *pl. 32, fig. 6.* Hirano **1957:** 129. *pl. 20, fig. 25.* Irénée-Marie **1939:** 167. *pl. 23, fig. 13.* Smith **1924:** 31. *pl. 57, fig. 18.* Text figures 4–6.

The distinction between this taxon and *Cosmarium subtumidum* Nordstedt as described by Irénée-Marie, 1939, p. 167. *pl. 27, fig. 17,* is tenuous since it is based on a minor variation in cell shape which is not readily evident in the illustrations.

This species never occurred in the spring ponds or in the lake plankton but was found in the aufwuchs at 23% of the sites where it often displayed high population densities.

Cosmarium punctulatum Brébisson **1856:** 129. *pl. 1, fig. 16.* Hirano **1957:** 183. *pl. 27, fig. 15.* Irénée-Marie **1939:** 204. *pl. 31, fig. 1.* Text figures 7–9.

The semicircular semicells and prominence and arrangement of granules in this taxon were stable characters in the populations examined.

No cells occurred in the spring ponds but one lake harbored the species in its plankton and 42% of all sites contained it in their aufwuchs.

Euastrum Ehrenberg ex Ralfs 1848

Euastrum pinnatum Ralfs **1848:** 81. *pl. 13, fig. 1.* Hirano **1959:** 255. *pl. 32, fig. 15.* Irénée-Marie **1939:** 120. *pl. 13, fig. 3.* Krieger **1937:** 522. *pl. 68, figs. 5–7.* Smith **1924:** 24. *pl. 56, fig. 5.* Text figure 10.

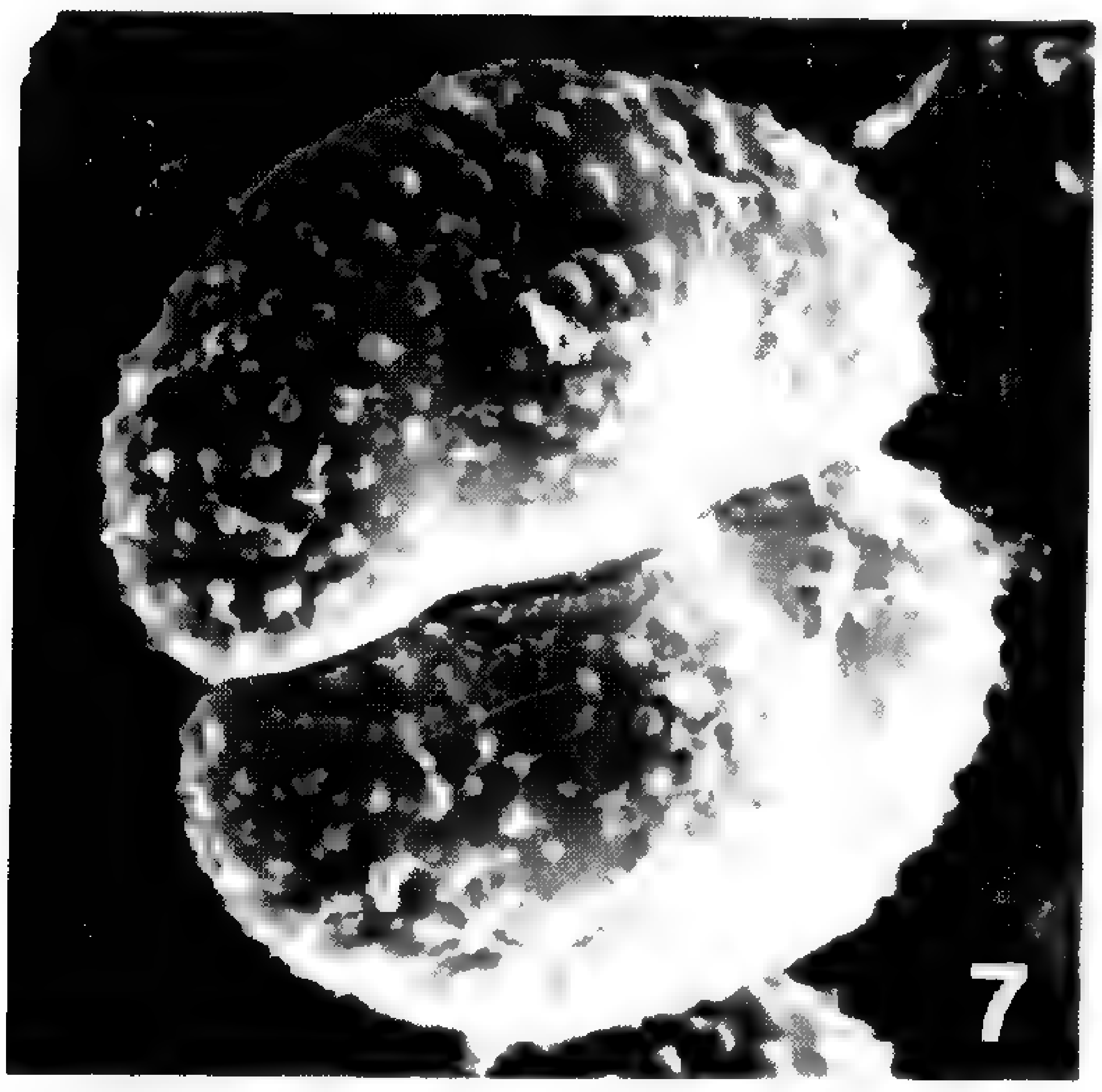
This taxon was found in the aufwuchs of only one lake.

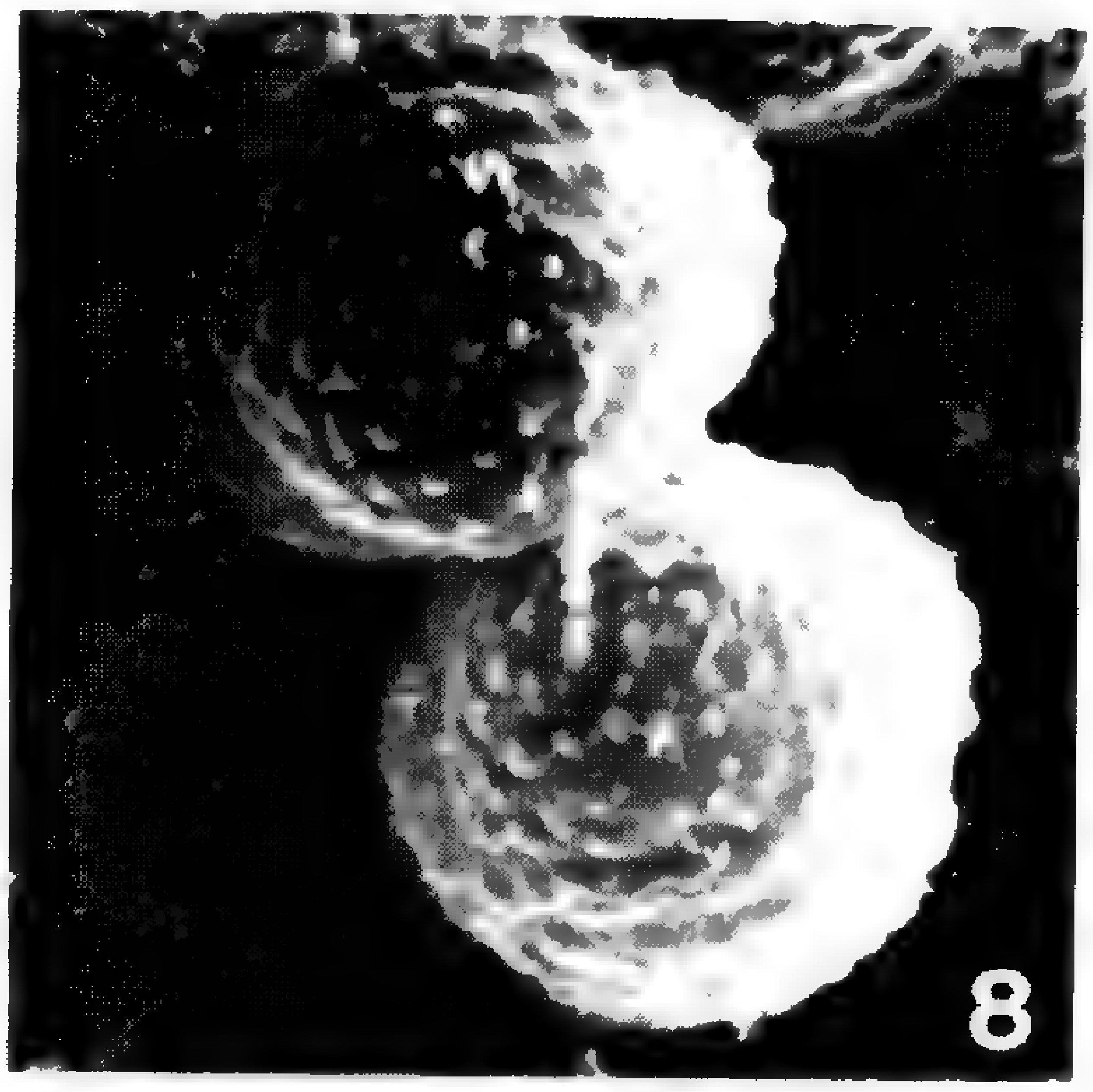
Micrasterias Agardh ex Ralfs 1848

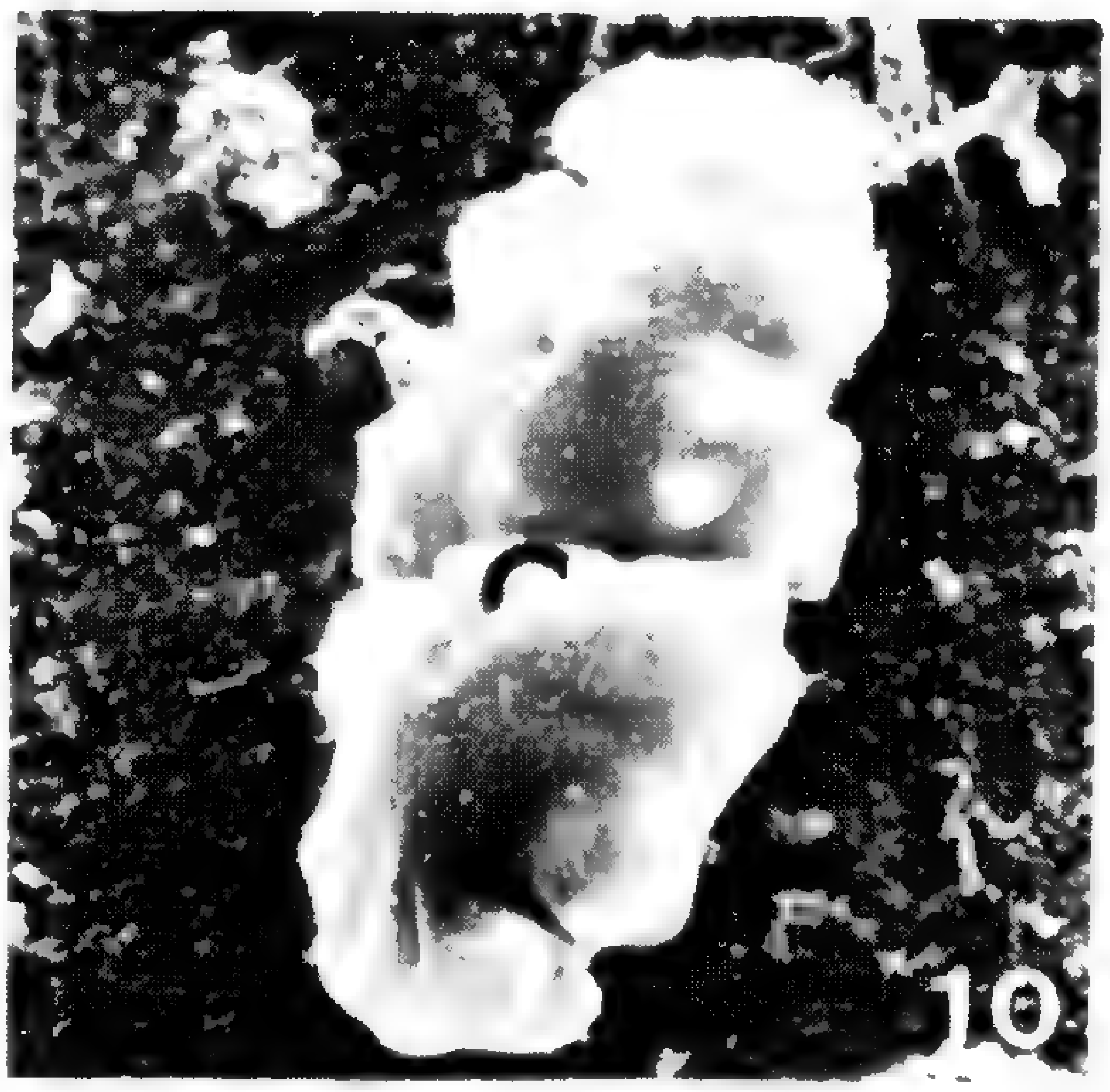
Micrasterias truncata (Corda) Brébisson ex Ralfs **1848:** 75. *pl. 8, fig. 4; pl. 10, fig. 5.* Hirano **1959:** 272. *pl. 36, figs. 4, 5, 17.* Irénée-Marie **1939:** 221. *pl. 33, figs. 2–7; pl. 34, fig. 2.* Krieger **1937:** 25. *pl. 102, figs. 1–4.* Smith **1924:** 43. *pl. 60, figs. 1, 2.* Text figure 11.

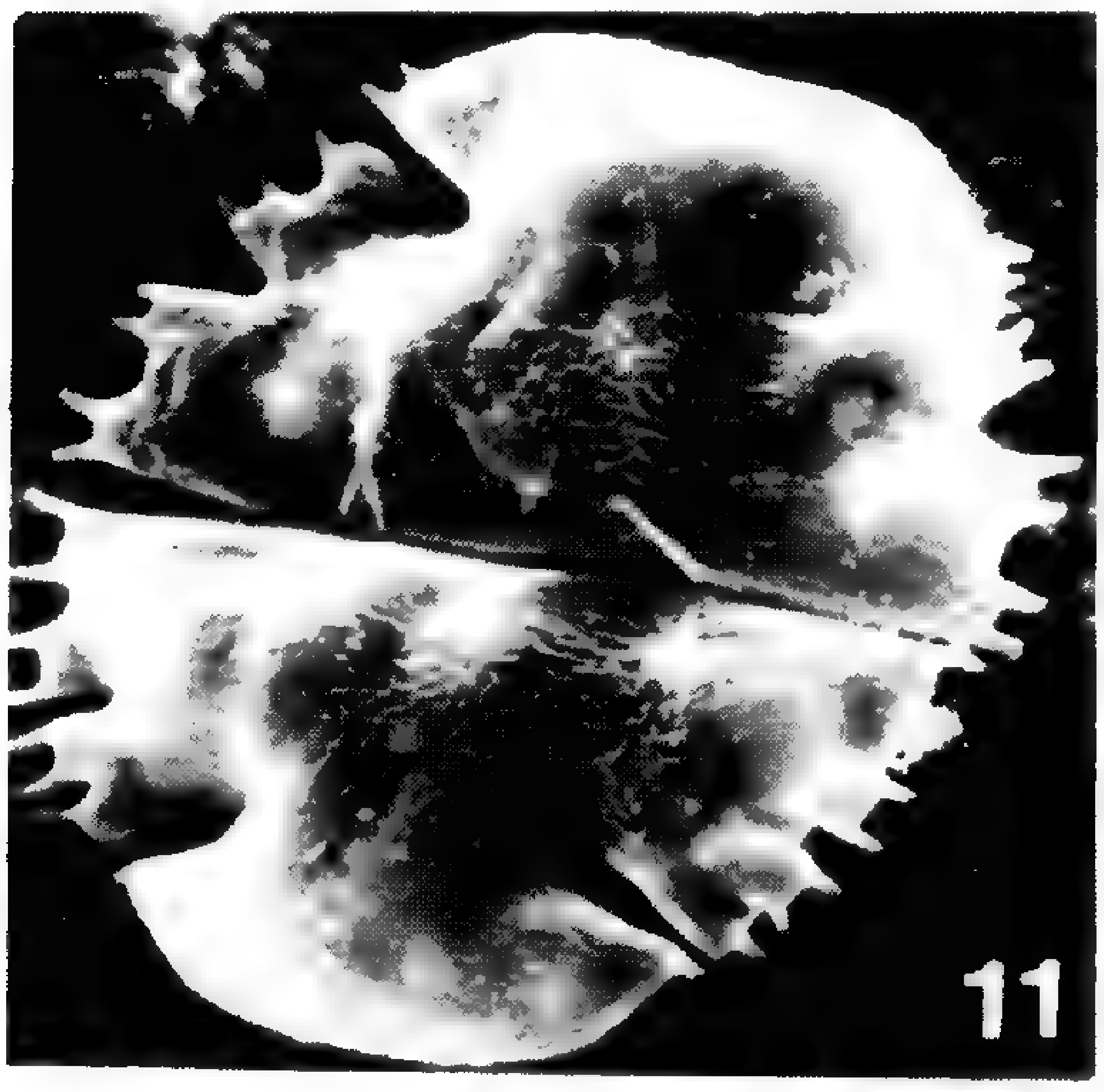
This taxon was found in the aufwuchs of only one lake.

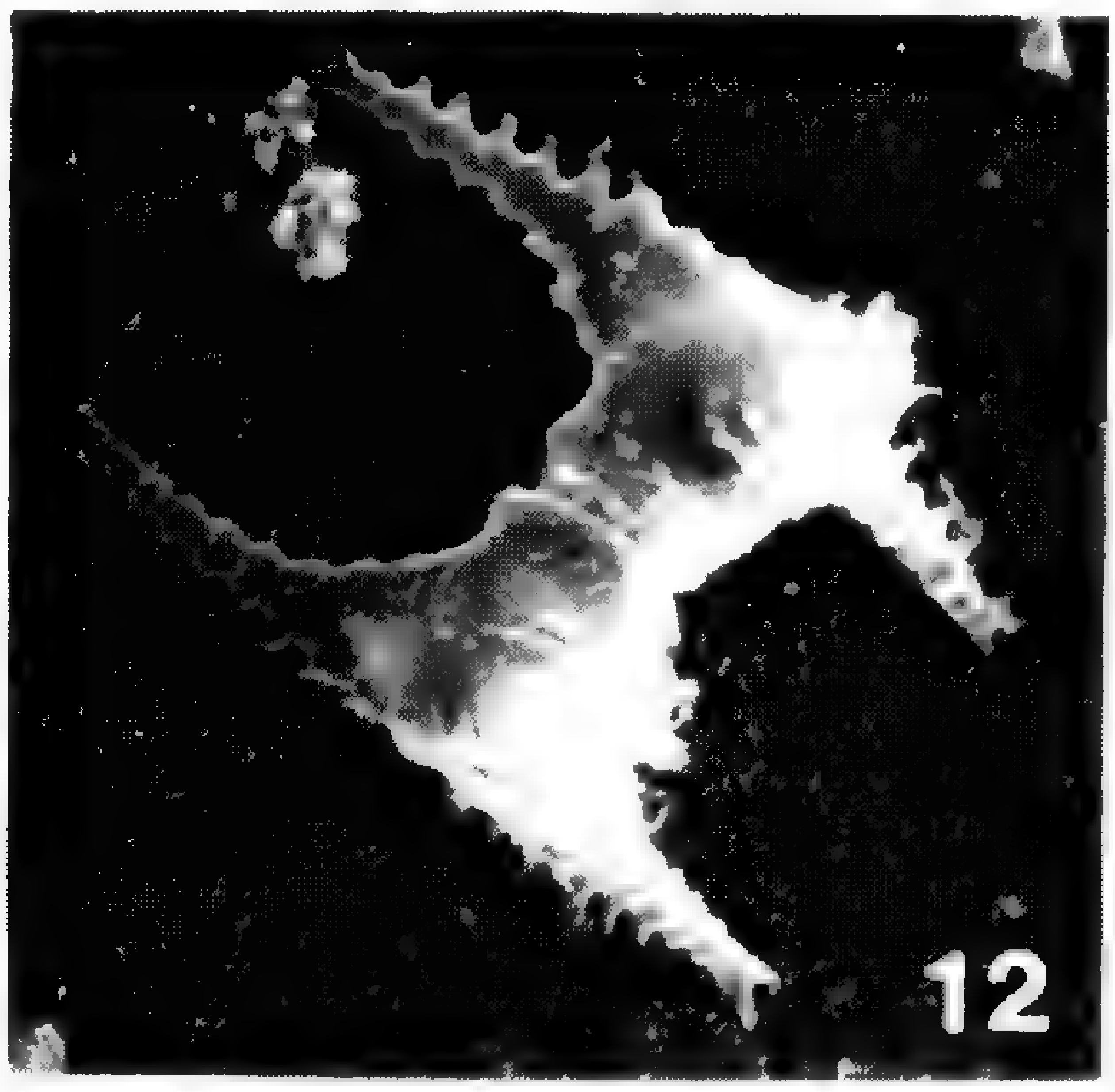
Pleurotaenium Nägeli 1849











Figures 7–12, **Cosmarium, Euastrum, Micrasterias, and Staurastrum.** 7, *C. punctulatum* Brébisson (2600×); 8, *C. punctulatum* Brébisson (2200×); 9, *C. punctulatum* Brébisson (2700×); 10, *E. pinnatum* Ralfs (600×); 11, *M. truncata* (Corda) Brébisson (1000×); 12, *S. longiradiatum* W. & G. S. West (1000×).

Pleurotaenium maximum (Reinsch) Lundell **1871:** 89. *pl. 4, fig. 2.* Irénée-Marie **1939:** 94. *pl. 10, figs. 3, 4.*

Although only found in the aufwuchs of one lake, *Pleurotaenium maximum* occurred there in abundance.

Staurastrum Meyer ex Ralfs 1848

Staurastrum longiradiatum W. & G. S. West **1896:** 267. *pl. 17, fig. 23.* Hirano **1959:** 363. *pl. 46, figs. 1, 2.* Smith **1924:** 90. *pl. 74, figs. 5–11.* Text figures 12, 13.

The prominence of the basal inflation on each semicell was variable but consistently distinctive.

Found commonly in the lake plankton (encountered at 27% of all sites), the species only occurred in the aufwuchs of one lake, possibly adventitiously.

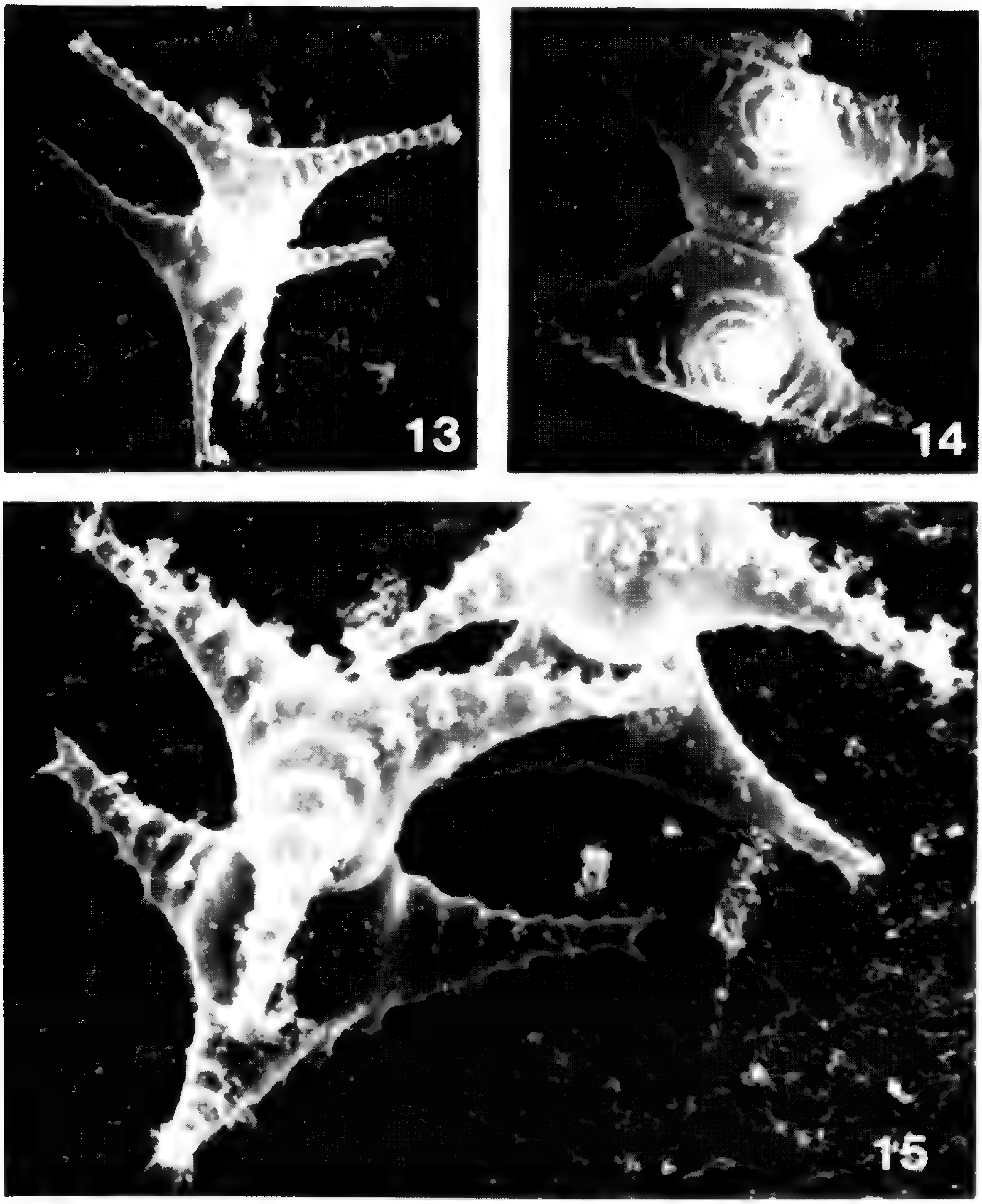
Staurastrum manfeldtii Delponte **1873:** 64. *pl. 13, figs. 6–19.* Hirano **1959:** 368. *pl. 48, fig. 1.* Irénée-Marie **1939:** 309. *pl. 48, fig. 4.* Text figures 14, 15.

Like *Staurastrum longiradiatum,* this species was only found in the aufwuchs of one lake. However, it occurred in 15% of the plankton samples, including one spring pond (where it represented the only desmid taxon recovered from such environments).

ECOLOGICAL OBSERVATIONS.

No *Closterium, Euastrum, Micrasterias* or *Pleurotaenium* species were found in the plankton, and the latter three were only found at single localities. Likewise, *Cosmarium* was rarely found in plankton but was common in the aufwuchs, whereas the opposite was true of *Staurastrum.* The only taxon occurring in the spring ponds (one locality) was *Staurastrum manfeldtii.*

Zero to three desmid species occurred in the plankton of the lakes (consistent with Smith's (1920) observations of low diversity in hard waters) with a mean of 0.7 per site; 0–1 planktonic taxa occurred at the calcareous spring ponds where the mean was only 0.2 per site. The aufwuchs of the lakes harbored greater species numbers (range 0–8, mean 3.1 per site) whereas no desmid species were encountered in the spring pond aufwuchs samples. These data parallel results found at the generic level (Woelkerling & Gough, 1976) where



Figures 13–15, **Staurastrum**. 13, *S. longiradiatum* W. & G. S. West (1100×); 14, *S. manfeldtii* Delponte (1300×); 15, *S. manfeldtii* Delponte (1500×).

diversity was generally greatest in softer water and in the aufwuchs of any given site. Moreover, *Utricularia* was found to harbor more desmid species than any other macrophyte at each site, a result also consistent with findings at the generic level (Woelkerling & Gough, 1976). However, no obvious specificity of a taxon for a particular macrophyte was noted.

Table 4 lists the ranges of chemical parameters under which the 10 desmid species were found. Such a listing does not indicate the tolerance of the taxa to the chemical parameters as only a select group of environments (which do not cover the full potential water chemistry range) were analyzed. However, the table does indicate that most taxa, particularly the *Cosmarium* species, are capable of occurring under widely different chemical regimes. *Cosmarium botrytis*, for example, which occurred in the aufwuchs of 54% of the sites, was found at the extremes of virtually all the chemical parameters. The three taxa occurring at only one locality (*Euastrum pinnatum, Micrasterias truncata* and *Pleurotaenium maximum*) were found at rather high levels of conductivity, pH and calcium. Since most species within these genera seem confined to soft waters, it is curious that these taxa, if they represent eurytopic species within the genera, were not found at more localities.

Apart from the observation that the number of desmid species was lower in the spring ponds than in the lakes sampled, no obvious correlations were found between water chemistry and species diversity. Factors potentially responsible for the lower diversity in spring ponds are discussed in Woelkerling and Gough (1976) and may involve the frequent occurrence of higher levels of calcium, conductivity and alkalinity in the ponds or a possible competitive advantage of other algae at the lower temperatures. The low diversity is in apparent disagreement with Moss's (1973a) findings that high levels of free CO_2 are conducive to desmid development.

Determination of the occurrence of desmid taxa in relation to the full range of water chemistry requires a look at several additional habitats, including, in particular, acid bogs and soft water lakes. Unfortunately such studies are hampered by the chaotic state of the systematics. If several distinct taxa can be recognized, however, their distribution in nature and behavior in culture under different chemical regimes might lead to a better understanding of desmid ecology. Although Gough (1977), Moss (1972, 1973, a,b,c), Tassigny (1971) and others have reported on such studies, many taxa under several different culture conditions will need to be evaluated before generalizations can be attempted.

Tyler (1973) has remarked that the state of confusion in desmid systematics has virtually necessitated the determination of species by comparative iconography. Problems with the use of existing

Table 3. **Summary of water chemistry conditions. All values expressed in mg/l except for conductivity (μmho/cm) and pH (units).**

	SPRING PONDS		HARD WATER LAKES	
PARAMETER	RANGE	MEAN	RANGE	MEAN
Conductivity	520-619	584	228-495	396
pH	7.3-7.5	7.4	8.3-9.8	8.7
CO_2	24-32	29	0-15	1
O_2	4.0-9.0	7.7	—	
PO_4-P	.014-.030	.020	.009-.112	.039
Total P	.03-.06	.042	.01-.17	.08
NO_2-N	.002-.021	.010	.000-.032	.009
NO_3-N	2.35-2.94	2.62	.04-1.13	.19
NH_3-N	.05-.23	.15	.03-.51	.10
Org. N	.34-.66	.57	.62-2.10	1.13
Total N	3.07-3.63	3.34	.76-2.73	1.40
Total Alkalinity	247-290	271	110-324	192
Ca++	50-74	66	30-74	45
Mg++	25-43	36	—	—
Cl^-	21-32	26	8-61	23
$SO_4^=$	27-32	30	3-36	22

taxonomic works, particularly keys to the species of *Cosmarium* and *Staurastrum,* to which hundreds of taxa are assigned, are several: (1) the use of cryptic morphological distinctions such as elliptical vs. semielliptical (e.g., Hirano, 1959), (2) the apparent tendency to recognize every polymorphic variant as a taxon, and (3) the frequent lack of correlation between the representations of the same taxa by different authors (e.g., cf. *Staurastrum gracile* Ralfs 1858 in Smith (1924, p. 88. *pl. 73, figs. 16–18*) and Irénée-Marie (1939, p. 313. *pl. 48, fig. 13*)). Thus, until extensive monographic work, which incorporates an evaluation of polymorphism in field and culture populations, reduces the confusion attending desmid systematics, it seems imperative that citations to specific taxonomic works accompany every taxon reported in the literature. Moreover, the prevalent use of desmids in various indicator schemes (e.g., Fjerdingstad, 1965; Nygaard, 1949; Palmer, 1969; Thunmark, 1945) which require species determinations suggests the need for careful taxonomic work in their application and possible revision of the schemes as the taxonomy is revised.

Table 4. **Range of chemical conditions under which desmid species occurred.***

TAXON	CONDUCTIVITY	pH	CO_2	PO_4-P	TOTAL P	NO_2-N	NO_3-N
Closterium moniliferum	377–495	8.3–9.1	0–6	.017–.112	.05–.17	.003–.026	<.04–.59
C. venus	361–474	8.3–9.3	0–3	.015–.100	.02–.12	.000–.020	<.04–1.13
Cosmarium botrytis	228–490	8.3–9.8	0–15	.009–.112	.01–.17	.000–.032	<.04–1.13
C. granatum	228–490	8.3–8.7	0–15	.015–.051	.02–.07	.000–.032	.06–.39
C. punctulatum	228–490	8.3–8.8	0–15	.014–.061	.01–.12	.000–.032	<.04–.39
C. subtumidum	228–490	8.3–9.8	0–15	.015–.064	.03–.07	.000–.032	.06–1.13
*Euastrum pinnatum**	441	8.5	0	.037	.03	.000	.08
*Micrasterias truncata**	461	8.3	0	.017	.05	.020	.11
*Pleurotaenium maximum**	375	8.8	0	.023	.08	.003	<.04
Staurastrum longiradiatum	228–474	8.5–9.3	0–3	.009–.112	.02–.17	.000–.023	<.04–.12
S. manfeldtii	323–520	7.4–8.8	0–28	.014–.064	.05–.08	.002–.020	<.04–2.72

Table 4 continued

TAXON	NH_3-N	ORG. N	TOTAL N	TOTAL ALKALINITY	Ca^{++}	Cl^-	SO_4^-
Closterium moniliferum	.04–.51	1.08 1.88	1.28–2.73	150 254	41–74	14 61	23–32
C. venus	<.03–.12	.64–1.48	.76–2.11	150 240	34–58	13 61	3–28
Cosmarium botrytis	<.03–.38	.62 2.10	.76 2.16	110–324	30 63	10 61	3 36
C. granatum	<.03–.12	.64–.99	.76 1.53	110–324	34 63	13–27	3 36
C. punctulatum	<.03 .51	.64–1.88	.76 2.73	110–324	34 74	13–61	3 36
C. subtumidum	<.03 .12	.84 2.10	.98 2.16	110–324	33–63	10–27	3–14
*Euastrum pinnatum**	<.03	.72	.80	190	54	16	36
*Micrasterias truncata**	.07	1.08	1.28	150	41	61	23
*Pleurotaenium maximum**	.04	1.48	1.52	188	45	18	27
Staurastrum longiradiatum	<.03–.16	.62 1.67	.85–1.91	110 204	30–58	13–49	3 28
S. manfeldtii	.03 .38	.34–1.48	1.00–3.29	171 247	35 50	8–25	8 32

*Denotes taxon occurred at a single locality.

SUMMARY

The poorly known desmid flora of southern Wisconsin hard waters was investigated in 20 lakes and 6 calcareous spring ponds. Ten species (2 *Closterium*, 3 *Cosmarium*, 1 *Euastrum*, 1 *Micrasterias*, 1 *Pleurotaenium* and 2 *Staurastrum* taxa) were found. A few species displayed some polymorphism but most were clearly distinguishable entities. *Closterium*, *Euastrum*, *Micrasterias* and *Pleurotaenium* were confined to the aufwuchs, and *Cosmarium* was seldom found elsewhere, whereas *Staurastrum* usually only occurred in the plankton. *Cosmarium botrytis* was the most common taxon encountered, whereas species of *Euastrum*, *Pleurotaenium* and *Micrasterias* were only recorded at single localities. Species diversity was greatest in the aufwuchs at all sites and was lower in the spring ponds than in the lakes. Many of the taxa (especially *Cosmarium* species) occurred over a wide range of chemical conditions but no correlations were found between water chemistry and species diversity.

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PLANT ECOLOGY OF CEDAR GLADES IN THE BIG BARREN REGION OF KENTUCKY

JERRY M. BASKIN AND CAROL C. BASKIN

The state of Kentucky is located entirely within the Eastern Deciduous Forest Formation, and thus deciduous forests are considered to be the climatic climax vegetation (Braun, 1950). Braun (1950) recognizes two plant associations within the state: the Mixed Mesophytic Forest of the Cumberland Mountains and Plateau and the Western Mesophytic Forest of other physiographic regions of the state.

Prairies or barrens once covered extensive areas of the Mississippian Plateau and the Mississippi Embayment Sections (Loughridge, 1888; Garman, 1925; Dicken, 1935; McInteer, 1942, 1946), and Transeau (1935) included the Kentucky barrens on his map of the Prairie Peninsula. However, these grasslands have, when left undisturbed, reverted to deciduous forests, and it is believed that frequent fires played a major role in maintaining them (Shull, 1921; Sauer, 1927; Dicken, 1935; McInteer, 1946). Dicken (1935) believed that, "The Barrens in Kentucky certainly represented a transition phase of the grassland, not merely from prairie to forest, however, but probably from forest through a temporary grassland back to forest. There can be no reasonable doubt that the Barrens were originally forested." In the Big Barren Region of the Mississippian Plateau there are small areas where the soil is so shallow that, even when left undisturbed, it does not support forest vegetation but instead maintains an herbaceous flora. These openings are surrounded by thickets in which *Juniperus virginiana* L. is an important component and are here referred to as cedar glades. No accounts have been written of the plant ecology of cedar glades within the barren region, and the only cedar glades described in Kentucky are located in Bullitt County, outside the barren region (Baskin & Baskin, 1975).

Within Warren, Simpson, Hart and Logan counties, we have found several small cedar glades (Figure 1) and have prepared a list of the plants occurring on them. The locations for the glades are as follows: (1) Hart County along Rider's Mill Road, 1.6 miles north of state road 728 (north of Priceville), (2) Warren County east of US

31W, 0.2 miles north of the Warren-Simpson County line, (3) Simpson County west of US 31W, 0.4 miles south of the Warren-Simpson County line, (4) Logan County, 0.3 miles south of Dennis and (5) Logan County south of Kentucky state road 100, 2.4 miles east of its intersection with US 68. The Warren and Simpson County glades are developed on Ste. Genevieve limestone, the Logan County glades on Girkin limestone, and the Hart County glades on Reelville limestone. The topography of the glades is mostly flat, and soil depth ranges from 0 to about 25 cm.

A checklist of the herbaceous vascular plants collected on these five cedar glades is given below. Following the name of each species are letters indicating the collection sites: H = Hart Co., W = Warren Co., S = Simpson Co., L-1 = Logan Co. south of Dennis, and L-2 = Logan Co. along Kentucky state road 100. Species which are non-native elements of the flora are indicated by an asterisk. Voucher specimens are on deposit at the University of Kentucky.

CATALOG OF SPECIES

ISOETACEAE

Isoëtes butleri Engelm. W

OPHIOGLOSSACEAE

Ophioglossum engelmannii Prantl S, L-1, W

GRAMINEAE

Andropogon gerardii Vit. S, H
A. scoparius Michx. S, H, L-1, L-2
A. virginicus L. L-1
Aristida longespica Poir. L-1
A. oligantha Michx. S, H, L-1, L-2
A. purpurascens Poir. L-1
Danthonia spicata (L.) Beauv. S
Eragrostis cilianensis (All.) Link.* S
E. spectabilis (Pursh) Steud. S, L-1
Festuca elatior L.* L-2
Hordeum pusillum Nutt. L-1
Panicum capillare L. S, L-1, L-2
P. flexile Scribn. H, L-2

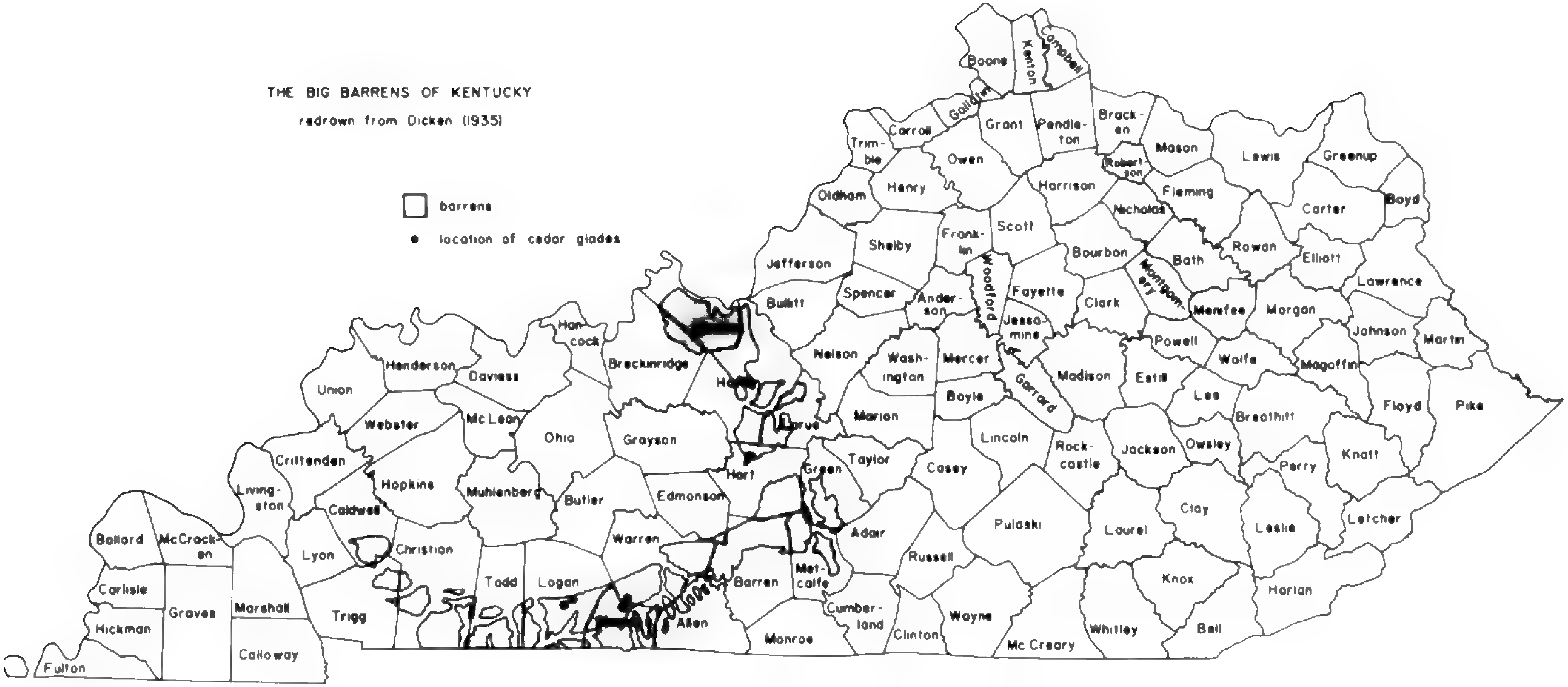

Figure 1. A county map of Kentucky showing the location of cedar glades in the Big Barren Region.

P. lanuginosum Ell. L-1
P. polyanthes Schult. L-1
P. sphaerocarpon Ell. L-1
Paspalum ciliatifolium Michx. L-1
Poa compressa L.* S
Setaria glauca (L.) Beauv.* L-1
Sorghastrum nutans (L.) Nash S, H, L-2
Sporobolus vaginiflorus (Torr.) Wood S, L-1, L-2, W, H
Triodia flava (L.) Smyth S, L-1

CYPERACEAE

Carex complanata Torr. & Hook. S
C. laxiflora Lam. L-1
Cyperus inflexus Muhl. S, L-1, L-2

LILIACEAE

Allium vineale L.* S, L-1, L-2, H
A. cernuum Roth L-2
Nothoscordum bivalve (L.) Britt. S, L-1, W

AMARYLLIDACEAE

Agave virginica L. S, H, L-1, L-2
Hypoxis hirsuta (L.) Coville L-1

IRIDACEAE

Belamcanda chinensis (L.) DC.* L-1
Sisyrinchium albidum Raf. S, H

PORTULACACEAE

Portulaca oleracea L.* S, L-1

CARYOPHYLLACEAE

Arenaria patula Michx. var. *patula* S, H; var. *robusta* (Stey.) Maguire W
Cerastium brachypodum (Engelm.) Robins. S, L-1, L-2
Dianthus armeria L.* L-1
Holosteum umbellatum L.* S, L-1, L-2, W

RANUNCULACEAE

Delphinium virescens Nutt. L-1

CRUCIFERAE

Arabidopsis thaliana (L.) Heynh.* S
Cardamine hirsuta L.* S
Draba verna L.* S, L-1, L-2, W
Leavenworthia torulosa Gray W
L. uniflora (Michx.) Britt. S, L-1, L-2
Lepidium campestre (L.) R. Br.* L-1
L. virginicum L.* L-1

CRASSULACEAE

Sedum pulchellum Michx. S, L-1, L-2, W

ROSACEAE

Potentilla simplex Michx. S, H, L-1
Rosa carolina L. S, H, L-2

LEGUMINOSAE

Baptisia australis (L.) R. Br. L-2
Cassia fasciculata Michx. L-1, L-2
Galactia volubilis (L.) Britt. S, L-1
Lespedeza capitata Michx. H
L. cuneata (Dumont) G. Don* H
L. stipulacea Maxim.* S, L-1, L-2
Melilotus officinalis (L.) Lam.* S, L-1
Petalostemon candidum (Willd.) Michx. L-1, L-2
P. purpureum (Vent.) Rydb. L-2
Strophostyles umbellata (Muhl.) Britt. H
Stylosanthes biflora (L.) BSP. H, L-1

LINACEAE

Linum sulcatum Riddell H, L-2

POLYGALACEAE

Polygala alba Nutt. L-2

OXALIDACEAE

Oxalis violacea L. S, L-1

GERANIACEAE

Geranium carolinianum L. S

EUPHORBIACEAE

Croton capitatus Michx. S, L-1, L-2
C. monanthogynus Michx. S, H, L-1, L-2
Crotonopsis elliptica Willd. L-1
Euphorbia corollata L. H
E. dentata Michx. S, L-1, L-2
E. maculata L. S, L-2
E. supina Raf. S, L-1

MALVACEAE

Sphaeralcea angusta (Gray) Fern. S, L-1

GUTTIFERAE

Hypericum dolabriforme Vent. S, L-1, L-2, H
H. gentianoides (L.) BSP. L-1
H. perforatum L.* L-1

CISTACEAE

Lechea tenuifolia Michx. L-1

VIOLACEAE

Viola rafinesquii Greene S

PASSIFLORACEAE

Passiflora incarnata L. S.

CACTACEAE

Opuntia compressa (Salisb.) Macbr. S, L-1, L-2

ONAGRACEAE

Gaura filipes Spach L-1, H, L-2

UMBELLIFERAE

Aethusa cynapium L.* H
Chaerophyllum tainturieri Hook. S, L-1
Daucus carota L.* S, L-1, H, L-2
Eryngium yuccifolium Michx. H
Zizia aptera (Gray) Fern. H

GENTIANACEAE

Sabatia angularis (L.) Pursh S, H, L-1, L-2

APOCYNACEAE

Apocynum cannabinum L. H.

ASCLEPIADACEAE

Asclepias verticillata L. S, H, L-2
A. viridiflora Raf. S, H

CONVOLVULACEAE

Ipomoea pandurata (L.) G. F. W. Mey. S

BORAGINACEAE

Heliotropium tenellum (Nutt.) Torr. S, H, L-2
Lithospermum canescens (Michx.) Lehm. S

VERBENACEAE

Verbena simplex Lehm. S, L-1, L-2, H

LABIATAE

Hedeoma hispida Pursh L-1
Isanthus brachiatus (L.) BSP. S, H, L-2
Monarda fistulosa L. H

Physostegia virginiana (L.) Benth. H, L-2
Prunella vulgaris L.* L-1, L-2
Pycnanthemum flexuosum (Walt.) BSP. H, L-2
Salvia lyrata L. S, H, L-1, L-2
Scutellaria leonardii Epling H
S. parvula Michx. S, L-1

SOLANACEAE

Physalis heterophylla Nees S
Solanum nigrum L.* S

SCROPHULARIACEAE

Gerardia tenuifolia Vahl L-1, L-2
Leucospora multifida (Michx.) Nutt. S
Penstemon tenuiflorus Pennell S, H, L-1
Veronica peregrina L. L-1

ACANTHACEAE

Ruellia humilis Nutt. S, L-1, L-2, H

PLANTAGINACEAE

Plantago aristida Michx. L-1, L-2
P. lanceolata L.* H, L-1, L-2
P. pusilla Nutt. L-1
P. virginica L. S, L-1, L-2

RUBIACEAE

Diodia teres Walt. S, L-1, H, L-2
Galium pilosum Ait. S
Houstonia lanceolata (Poir.) Britt. S, L-1, L-2
H. patens Ell. L-1

VALERIANACEAE

Valerianella radiata Dufr. S

CAMPANULACEAE

Lobelia spicata Lam. H, L-2
Specularia perfoliata (L.) A. DC. L-1

COMPOSITAE

Achillea millefolium L.* S, L-1
Ambrosia artemisiifolia L. S, H, L-1, L-2
Aster oblongifolius Nutt. H
A. pilosus Willd. S, H, L-1, L-2
Chrysanthemum leucanthemum L.* S, H, L-1, L-2
Cirsium discolor (Muhl.) Spreng. S
Coreopsis tripteris L. H
Echinacea angustifolia DC. H, L-2
Erigeron strigosus Muhl. S, H, L-1
Eupatorium altissimum L. S, H, L-2
E. incarnatum Walt. S
Helenium amarum (Raf.) H. Rock L-2
Helianthus hirsutus Raf. H, S, L-1
H. mollis Lam. L-2
Krigia virginica (L.) Willd. L-2
Kuhnia eupatorioides L. S
Liatris squarrosa (L.) Michx. H, L-1, L-2
L. spicata (L.) Willd. L-2
Parthenium integrifolium L. H
Ratibida pinnata (Vent.) Barnh. H, L-2
Rudbeckia fulgida Ait. H
Silphium terebinthinaceum Jacq. var. *pinnatifidum* (Ell.) Gray L-2
S. trifoliatum L. H, L-2
Solidago nemoralis Ait. H, L-1, L-2
Tragopogon pratensis L.* S
Verbesina virginica L. S

DISCUSSION

A total of 148 taxa, representing 41 families, was collected and all except *Ophioglossum engelmannii* and *Isoëtes butleri* are angiosperms. The two families with the largest number of representatives are the Compositae (26 species) and the Gramineae (22 species).

Characteristic plants of the barrens listed by Garman (1925) that also occurred on the cedar glades are little bluestem (*Andropogon scoparius*), tall bluestem (*A. gerardii*), Indian grass (*Sorghastrum nutans*), white prairie-clover (*Petalostemon candidum*), purple prairie-clover (*P. purpureum*), butterfly-weed (*Asclepias viridiflora*), puccoon (*Lithospermum canescens*), Venus's looking-glass (*Specularia perfoliata*), blazing-star (*Liatris squarrosa*), partridge pea (*Cassia fasciculata*) and button snakeroot (*Eryngium yuccifolium*).

The prairie element in the cedar glade flora is represented by a number of species including *Andropogon gerardii, A. scoparius, Aristida purpurascens, Sorghastrum nutans, Allium cernuum, Delphinium virescens, Baptisia australis, Lespedeza capitata, Petalostemon candidum, P. purpureum, Euphorbia corollata, Gaura filipes, Eryngium yuccifolium, Asclepias verticillata, Lithospermum canescens, Monarda fistulosa, Pycnanthemum flexuosum, Lobelia spicata, Echinacea angustifolia, Kuhnia eupatorioides, Liatris spicata, Ratibida pinnata* and *Silphium terebinthinaceum* var. *pinnatifidum.*

Leavenworthia torulosa was the only cedar glade endemic found in the glades of the barren region. A small population of this species occurs in the Warren County glade. The only other known location for this species in Kentucky is on a small limestone outcrop in Logan County (Baskin & Baskin, 1977).

Of the fifteen characteristic cedar glade species listed by Baskin and Baskin (1975) as occurring in Bullitt County, Kentucky, eleven were collected from cedar glades in the barren region (*Ruellia humilis, Agave virginica, Isanthus brachiatus, Ophioglossum engelmannii, Sporobolus vaginiflorus, Heliotropium tenellum, Scutellaria parvula, Nothoscordum bivalve, Sisyrinchium albidum, Asclepias verticillata* and *Croton monanthogynus*). Other non-weedy species found on the glades in the barren region that frequently are found on cedar glades in the southeastern United States (Baskin, Quarterman & Caudle, 1968; Baskin & Baskin, 1975) are *Isoëtes butleri, Andropogon scoparius, Aristida longespica, Cyperus inflexus, Delphinium virescens, Leavenworthia torulosa, L. uniflora, Sedum pulchellum, Baptisia australis, Oxalis violacea, Arenaria patula, Croton capitatus, Opuntia compressa, Hypericum dolabriforme, Leucospora multifida, Penstemon tenuiflorus,* and *Houstonia lanceolata.* Several of these species also occur on cedar glades in Missouri (Steyermark, 1934).

None of these glades have been left undisturbed which apparently accounts for the large number of weedy species growing on them. All of the glades discussed in this paper, except possible portions of the Hart County glade, have been pastured.

The distribution of plants on a cedar glade is largely determined by soil depth, and zones of vegetation may be distinguished. In the Simpson County glade, which is the largest glade we studied, several relatively distinct zones of vegetation can be recognized. In soils that are from 2–5 cm in depth *Portulaca oleracea, Cyperus inflexus, Euphorbia supina, Sedum pulchellum* and *Leavenworthia uniflora* are the most important species. During summer when the three summer annuals (*E. supina, P. oleracea* and *C. inflexus*) are in the active part of their life cycles, these shallow soils are extremely dry. During late autumn, winter and early spring when the two winter annuals (*S. pulchellum* and *L. uniflora*) are active the soil is moist. In soils 5–10 cm deep *Sporobolus vaginiflorus* is the dominant species. Other plants of some importance in the deeper soils are *Croton monanthogynus, Euphorbia dentata, E. maculata, Panicum capillare* and *Isanthus brachiatus.* These plants are summer annuals and complete their life cycles between spring and autumn. In deep soil (10–20 cm) *Sporobolus vaginiflorus* shares dominance with *Ruellia humilis, Agave virginica, Hypericum dolabriforme, Croton monanthogynus, Heliotropium tenellum* and *Isanthus brachiatus.* Four of these (*S. vaginiflorus, C. monanthogynus, H. tenellum* and *I. brachiatus*) are summer annuals, while *Ruellia humilis, A. virginica* and *H. dolabriforme* are summer-active perennials. In certain areas *Andropogon scoparius* (a summer-active perennial) is the obvious dominant (Figure 2). *Andropogon gerardii* and *Sorghastrum nutans* also occur with *A. scoparius.* Little bluestem does not form a continuous cover but instead occurs in clumps or bunches. *Sporobolus vaginiflorus, Heliotropium tenellum, Agave virginica* and *Ruellia humilis* are the most frequently occurring species in the spaces between the bunches of little bluestem. Soil depths taken in and near clumps of *A. scoparius* ranged from 15 to 25 cm, and in the interclump areas soil depths ranged from 10 to 15 cm. In one small area of the glade, on a gentle slope where the substrate is extremely rocky and soil depths range from 4–8 cm, *Ruellia humilis* is the dominant species. Other species occurring on this rocky slope include *Andropogon scoparius, Sporobolus vagini-*

Figure 2. A portion of the cedar glade in Simpson County, Kentucky dominated by *Andropogon scoparius*. Picture was taken 4 May, 1971.

florus, Heliotropium tenellum and *Aster pilosus*. A few woody plants have become established in small areas where the soil apparently is deeper and/or where there are cracks in the limestone. These species include *Celtis laevigata* Willd., *Forestiera ligustrina* (Michx.) Poir., *Fraxinus americana* L., *Symphoricarpos orbiculatus* Moench, *Rhamnus caroliniana* Walt., *Ulmus alata* Michx., *Juniperus virginiana* L., and *Cercis canadensis* L.

Since many prairie species occur in the cedar glades, we suggest that (1) prairie species may have been present in the glades prior to establishment of the barrens and that the cedar glades served as centers of dispersal of prairie species after the Indians destroyed the forest by burning, or (2) prairie species were not part of the original cedar glade flora and they migrated into the area after the burning of the forests. The cedar glades, along with the few remaining small prairie patches, may be serving as refugia for a once wide-spread prairie flora that existed in the Big Barren Region prior to settlement of the area by European immigrants or their descendants.

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NEW ENGLAND FERNS (FILICALES)

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This list of species of the New England ferns and their hybrids documented in the New England Botanical Club Herbarium has been compiled to provide names to be used for computer documented distribution maps. Comments included under some genera pertain to changes in application of names, particularly in regard to usage in *Gray's Manual of Botany.* References are also included to special studies supplying data on cytology or geography of the species that is pertinent to their systematics. There is a greater correspondence to the treatment of C. V. Morton in *Britton and Brown's Illustrated Flora of the Northeastern United States and Adjacent Canada* (1952) than to the treatment by M. L. Fernald in *Gray's Manual.* Many forms and varieties were recognized in Fernald's work, as was often done during his period when lesser variants were considered of greater importance than at present. None of the forms and only two of the varieties he used are included here, although as more systematic work is done some may merit recognition. There are few modern monographic works on New England species that encompass their entire geographic range. Many New England ferns have broad circumboreal affinities involving the same species or species groups occurring in eastern Asia and (or) Europe. The general geographic patterns of New England ferns are discussed in relation to studies on *Thelypteris* (Tryon & Tryon, 1974).

Preparation of distribution maps

Maps for all of the pteridophytes of Europe have been issued in the *Atlas Flora Europaeae* (1972) and for the British species in *Atlas of Ferns of the British Isles* (1978). Preparation of distribution maps for New England ferns has been stimulated by these recent publications, and work is in progress by the Plant Distribution Committee of the New England Botanical Club. Club records of the committee's work show that it has been active since its formation at the instigation of M. L. Fernald in April, 1917. This originally was named the Committee on the Topographical Survey of the Flora of New England and consisted of C. E. Knowlton, Chairman, C. A. Weatherby and W. S. Ripley, Jr. The purpose of the committee as directed to the Club membership, in the minutes of the meeting, was for "determining the limits of the different floral areas and the great advantage which would accrue from all plants observed in any given region being turned in. This committee would compile the results and in time be able to establish the limits of each species. It is quite as important moreover in this sort of work to know what does not grow in a region as what does." The title of the committee was shortened to the Plant Distribution Committee in 1920, and in 1927 the membership changed to C. A. Weatherby, Chairman, C. E. Knowlton and R. C. Bean. As a result of work of the committee over the years a series of manuscript distribution maps was prepared for species in the New England flora through the Rosaceae. These are maintained in the Club herbarium. An early series was completed for the ferns about 1920. The present series of maps are designed to document each locality with a particular collection. The state, county, town and date have been recorded for each specimen. The New England Botanical Club herbarium is regarded as the core collection for the region. The work of recording the data was done by members of the Plant Distribution Committee consisting of: Judith Vickers Burlingame, Clifford David, Martha Fisher, Walter Judd, Aminta Kitfield, Michael Lamson, Larry Morse, Mary Perry, Alice Tryon, and Russell Walton, Chairman. Larry Morse, Walter Judd and Michael Lamson have worked out methods of recording the data. Larry Morse wrote the initial program for the computer and has followed the entire project through the final phase of editing the tape. Preparation of printed material and conversion of data from cards to tape was done by Michael Lamson. The distribution records are currently being transferred to maps by Russell Walton.

Accepted names are listed in bold face type at the left, the common names at the right, and abbreviations used in computer processing are in the center column. Synonyms under the accepted names are mainly from the eighth edition of *Gray's Manual of Botany* (1950) and indicated by an asterisk; others from state or regional floras are indicated by a number in parentheses corresponding to the numbered references.

OSMUNDACEAE

OSMUNDA

A number of aberrant forms have been recognized in *Gray's Manual* in each of the species of *Osmunda* but they are not of systematic consequence. American plants of *O. regalis* are not as robust as those of Europe and have been distinguished as var. *spectabilis* but the difference in stature and some other characters may not be taxonomically significant.

Osmunda cinnamomea L.	Osmun cinn	Cinnamon Fern
O. Claytoniana L.	Osmun Clay	Interrupted Fern
O. regalis L.	Osmun reg	Royal Fern

SCHIZAEACEAE

LYGODIUM

Lygodium palmatum (Bernh.) Sw.	Lygo palm	Climbing Fern

POLYPODIACEAE

ADIANTUM

Adiantum pedatum L.	Adian ped	Maidenhair

ASPLENIUM

Two of the five New England species of *Asplenium*, *A. montanum* and *A. platyneuron,* and also the closely related *Camptosorus rhizophyllus,* are considered as basic diploids and hybrids are well known between them (Wagner, 1954). The most notable of the hybrids in New England, *Asplenium platyneuron* × *Camptosorus rhizophyllus,* is commonly called Scott's Spleenwort. Hybrids between species and related genera have been intensively studied in Europe. Cytological work on American plants is largely based on plants of the southern United States and the Appalachian region. The American plants of *A. Ruta-muraria* are differentiated from those of Europe as *A. cryptolepis* in *Gray's Manual.* The American material was distinguished largely on quantitative characters that appear to fall within the range of those of Europe. The species is tetraploid with $n = 72$ in North America and most of Europe except for diploid plants in northern Italy (Lovis & Reichstein, 1964).

Asplenium montanum Willd.	Asple mont	Mountain Spleenwort
A. platyneuron (L.) Oakes	Asple platy	Ebony Spleenwort

A. platyneuron × Camptosorus rhizophyllus		Scott's Spleenwort
A. Ruta-muraria L.	Asple Rut-m	Wall-rue Spleenwort
A. cryptolepis Fern.*		
A. Ruta-muraria × A. Trichomanes	Asple Rut-m × Trich	
A. Trichomanes L.	Asple Trich	Maiden-hair Spleenwort
A. viride Huds.	Asple viri	Green Spleenwort

ATHYRIUM

Athyrium Filix-femina is considered a highly variable, widely distributed species in North America and Eurasia. The treatment of four varieties and six forms in *Gray's Manual,* adapted from the work of Butters, notes the extreme variability of the plants. The species has been studied in Europe by J. J. Schneller (pers. comm., 1975) and it has been shown that the red color of the petioles and rachis, which characterizes forma *rubellum,* is a simple genetic trait without taxonomic significance.

Athyrium Filix-femina (L.) Roth	Athyr Fi-fe	Lady Fern
Asplenium Filix-femina (L.) Bernh. (6)		
Athyrium angustum (Willd.) Presl (14, 6)		

CAMPTOSORUS

Camptosorus rhizophyllus (L.) Link	Campt rhiz	Walking Fern

CHEILANTHES

This genus centers in the southwestern United States and Mexico and is represented in New England by a single species known from an early collection from the face of cliffs at West Rock, New Haven, Connecticut, where it has long been extinct.

Cheilanthes lanosa (Michx.) D. C. Eaton	Cheil lano	Hairy Lip Fern
C. vestita (Spreng.) Sw.*		

CRYPTOGRAMMA

Cryptogramma Stelleri (Gmel.) Prantl	Crypt Stell	Slender Cliff-brake

CYSTOPTERIS

American plants of *Cystopteris fragilis* appear to be largely tetraploid and distinct from the diploid *C. protrusa* which occurs west and south of New England. *Cystopteris fragilis* var. *Mackayii* has been distinguished by the shape of the indusium and segments. It is not recognized here since the characters do not appear to be sufficiently constant.

Cystopteris bulbifera (L.) Bernh.	Cyst bulb	Bulblet Fern
C. fragilis (L.) Bernh.	Cyst frag	Fragile Fern

DENNSTAEDTIA

Dennstaedtia punctilobula (Michx.) Moore	Denns punct	Hay-scented Fern

DIPLAZIUM

These species are clearly distinct from *Athyrium* where they have been treated in many of the works on New England ferns. *Diplazium acrostichoides* has been placed in *Lunathyrium* Koidz. and *D. pycnocarpon* in the monotypic genus *Homalosorus* Small ex Pic. Ser. Studies on Asiatic species by Sledge (1962) and Kato (1977) distinguish *Diplazium* and its segregates from *Athyrium*. However, a broader survey of this large complex is required to confirm the appropriate generic groups.

Diplazium acrostichoides (Sw.) Butters	Dipla acros	Silvery Spleenwort
Asplenium acrostichoides Sw. (6)		
Athyrium thelypterioides (Michx.) Desv.*		
D. pycnocarpon (Spreng.) Broun	Dipla pycno	Narrow-leaved Spleenwort
Asplenium angustifolium Michx. (6)		
Athyrium pycnocarpon (Spreng.) Tidestr.*		

DRYOPTERIS

Dryopteris is the largest and most complex genus of ferns in New England where there are nine species with cytological levels from diploid with $n = 41$ to hexaploid with $n = 123$. Complexity is due to hybridization between most of the species. Other species occur to the north and west of New England but the largest concentration of species and hybrids is in the Appalachian area. The New England species *D. cristata, D. Filix-mas,* and *D. spinulosa* also occur in Europe and hybridize there with other species. Problems of relationships of the species are compounded by their designation by different names. The well known name, *D. spinulosa,* used in *Gray's Manual* and many other floras, is retained here in the traditional sense although it is not correct according to the present rules of nomenclature. *Dryopteris austriaca* (Jacq.) Woynar was substituted by Morton and *D. carthusiana* (Vill.) H. P. Fuchs has been used in the *Atlas Florae Europaeae* (1972). However, *D. austriaca* is probably a synonym of another fern, perhaps *Pteridium,* and the application of *D. carthusiana* is uncertain until the type can be verified. The genus has been intensively studied in Europe and to a lesser extent in America. The work of Wagner (1971) and Hickok and Klekowski (1975) in this country and Gibby (1977) and Gibby and Walker (1977) in England brings out new cytological and genetic evidence but different concepts on the relationships of the species. These recent studies emphasize the need for additional field work and experimental studies especially in the New England region.

Dryopteris campyloptera (Kze.) Clarkson	Dryop camp	Mountain Wood Fern
D. spinulosa var. *americana* (Fisch.) Fern*		
D. Clintoniana (D.C. Eaton) Dowell	Dryop Clint	Clinton's Wood Fern
D. cristata var. *Clintoniana* (D.C. Eaton) Underw.*		
Aspidium cristatum var. *Clintonianum* D. C. Eaton (6)		
D. Clintoniana × Goldiana	Dryop Clint × Gold	
D. Clintoniana × D. intermedia	Dryop Clint × inter	

D. Clintoniana × D. marginalis	Dryop Clint × margi	
D. Clintoniana × D. spinulosa	Dryop × spin	
D. cristata (L.) A. Gray	Dryop crist	Crested Wood Fern
D. cristata × D. Goldiana	Dryop crist × Gold	
D. cristata × D. intermedia	Dryop crist × inter	Boott's Wood Fern
D. cristata× D. marginalis	Dryop crist × margi	
D. cristata × D. spinulosa	Dryop crist × spin	
D. Filix-mas (L.) Schott	Dryop Fixma	Male Fern
D. Filix-mas × D. marginalis	Dryop Fixma × margi	
D. fragrans (L.) Schott	Dryop frag	Fragrant Fern
D. Goldiana (Hook.) A. Gray	Dryop Gold	Goldie's Fern
Aspidium Goldianum Hook. (6)		
D. Goldiana × D. intermedia	Dryop Gold × inter	
D. Goldiana × D. marginalis	Dryop Gold × margi	
D. Goldiana × D. spinulosa	Dryop Gold × spin	
D. intermedia (Willd.) A. Gray	Dryop inter	Glandular Wood Fern
D. spinulosa var. *intermedia* (Willd.) Underw.*		
D. austriaca var. *intermedia* (Muhl.) Morton (12)		
D. intermedia × D. marginalis	Dryop inter × marg	
D. intermedia × D. spinulosa	Dryop inter × spin	
D. marginalis (L.) A. Gray	Dryop margi	Marginal Shield Fern
Aspidium marginale (L.) Sw. (6)		
D. marginalis × D. spinulosa	Dryop margi × spin	

D. spinulosa (Muell.) Watt Dryop spin Spinulose Wood Fern
D. spinulosa var. *spinulosa**
D. austriaca var. *spinulosa* (Muell.) Fiori (12)
Aspidium spinulosum (Muell.) Sw. (6)

GYMNOCARPIUM

This species was treated in *Dryopteris* in *Gray's Manual* but it and the related *Gymnocarpium Robertianum* (Hoffm.) Nieuwl. are morphologically distinct and the chromosome number $n = 80$ also differs from the series based on 41 in *Dryopteris.*

Gymnocarpium Dryopteris (L.) Newm. Gymno Dryop Oak Fern
Dryopteris disjuncta (Ledeb.) Morton*
Phegopteris Dryopteris (L.) Fée (6)

MATTEUCCIA

Matteuccia Struthiopteris (L.) Todaro Matte Strut Ostrich Fern
M. pensylvanica (Willd.) Raym. (15, 23)
Onoclea Struthiopteris (L.) Hoffm. (6)
Pteretis pensylvanica (Willd.) Fern.*

ONOCLEA

Onoclea sensibilis L. Onoc sensi Sensitive Fern

PELLAEA

Pellaea is one of the exceptional genera of New England ferns in that its geographic range extends northward from a concentration of species in the southwestern United States and Mexico. Both species of New England are apogamous, *P. atropurpurea* is triploid with n, $2n = 87$, and the tetraploid *P. glabella* var. *glabella* with n, $2n = 116$ is the only one of the three varieties of the species in this region.

Pellaea atropurpurea (L.) Link Pella atro Purple Cliff-brake

P. atropurpurea var. *atropurpurea* (12)		
P. glabella Mett.	Pella glab	Smooth Cliff-brake
P. atropurpurea var. *Bushii* Mack. (12)		

POLYPODIUM

Plants of eastern America allied to the *Polypodium vulgare* complex have been studied cytologically along with those of Europe by Shivas (1961). The investigation of American material was based largely on plants from the southeastern United States but a collection from Smuggler's Notch, Lamoile County, Vermont was reported as a diploid with $n = 37$. Diploids and tetraploids are known from eastern Canada, and in the southern United States both of these levels as well as a triploid are reported. The diploid is morphologically distinct with broader, somewhat deltoid lamina with acuminate segment lobes in contrast to the tetraploid with a relatively linear lamina and rounded segment lobes. Cytotypes may have been recognized in the designation of several forms as *acuminatum, deltoideum* or *elongatum* in the treatment of the species in *Gray's Manual.* Cytological work on the species complex in New England similar to studies on *P. vulgare* in Europe will clarify relationships.

Polypodium virginianum	Poly virg	Polypody
Polypodium vulgare (L.) (12)		

POLYSTICHUM

The American complex of *Polystichum Braunii* is comprised of two disjunct elements, the eastern var. *Purshii* which occurs in New England and the western var. *alaskense* (Maxon) Hult. Both of these varieties and the European element of the species are consistently tetraploid with $n = 82$. In western America and Europe there are complexes involving hybridization. A hybrid has been proposed between our two species on morphological characters (Thompson & Coffin, 1940) but neither this nor the parents have been cytologically studied in New England.

Polystichum acrostichoides (Michx.) Schott	Polys acros	Christmas Fern
P. Braunii (Spenn.) Fée	Polys Braun	Braun's Holly Fern

PTERIDIUM

Pteridium is exceptional among New England ferns in the occurrence of two geographic varieties within the region. The coastal plain variety *pseudocaudatum* extends north to Cape Cod. The more common New England plants are var. *latiusculum,* a wide-ranging variety in eastern North America with disjunct stations in the west, and also northern Europe and eastern Asia.

Pteridium aquilinum var. **latiusculum** (Desv.) Underw.	Pteri aqui v lat	Bracken
P. aquilinum var. **pseudocaudatum** (Clute) Heller	Pteri aqui v pseud	Bracken

THELYPTERIS

Five species treated under *Dryopteris* in *Gray's Manual* represent discrete elements in *Thelypteris* based on morphological aspects and especially different chromosome numbers. *Thelypteris Phegopteris* is an apogamous triploid with n, $2n = 90$, and *T. hexagonoptera* is diploid with $n = 30$. Three other species formerly regarded as an allied group are readily distinguished on differences in spores and chromosome numbers: *T. noveboracensis* $n = 27$, *T. palustris* $n = 35$, and *T. simulata* $n = 64$. A study of populations in New England (Tryon & Tryon, 1973) indicated the species are more closely related to species in western North America or eastern Asia than to each other.

Thelypteris hexagonoptera (Michx.) Weatherby	Thely hexa	Broad Beech Fern
Dryopteris hexagonoptera (Michx.) C. Chr.*		
Phegopteris hexagonoptera (Michx.) Fée (6)		
T. noveboracensis (L.) Nieuwl.	Thely nove	New York Fern
Dryopteris noveboracensis (L.) A. Gray*		
Aspidium noveboracensis (L.) Sw. (6)		
T. palustris Schott	Thely palus	Marsh Fern
Dryopteris Thelypteris (L.) A. Gray*		
Aspidium Thelypteris (L.) Sw. (6)		

T. Phegopteris (L.) Slosson	Thely phego	Long Beech Fern
Dryopteris Phegopteris (L.) C. Chr.*		
Phegopteris connectilis (Michx.) Watt (23)		
P. polypodioides Fée (6)		
T. simulata (Davenp.) Nieuwl.	Thely simu	Massachusetts Fern
Dryopteris simulata (Davenp.) Underw.*		
Aspidium simulatum Davenp. (6)		

WOODSIA

Woodsia alpina (Bolton) S. F. Gray	Woods alpin	Northern Woodsia
W. alpina × **W. ilvensis**	Woods alpin × ilven	
W. glabella R. Br.	Woods glab	Smooth Woodsia
W. ilvensis (L.) R. Br.	Woods ilven	Rusty Woodsia
W. obtusa (Spreng.) Torr.	Woods obtus	Blunt-lobed Woodsia

WOODWARDIA

Woodwardia areolata (L.) Moore	Woodw areo	Netted Chain Fern
Lorenseria areolata (L.) Presl (23)		
W. virginica (L.) J. Sm.	Woodw virg	Virginia Chain Fern

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A NEW MEXICAN SPECIES OF PHYLLANTHUS (EUPHORBIACEAE) WITH SOUTHERN HEMISPHERE AFFINITIES

GRADY L. WEBSTER

In June, 1976, I received from Dr. Neil Harriman at Wisconsin State University (Oshkosh) an unidentified *Phyllanthus* which he had collected in the highlands of southwestern Tamaulipas, Mexico. The specimen was entirely pistillate and obviously represented a species unlike any other known from that area. Fortunately, I was planning a field trip to Mexico in the summer of 1976 and it was not difficult to locate the plant along the road (route 101) from Victoria to Tula, growing in scrub on limestone near the turn-off to the village of Bustamante. Here there were many staminate plants, and it was immediately apparent that the species is unusual in several respects: 1) dioecious inflorescence distribution; 2) unusually high elevation (between 5000 and 6000 ft) for *Phyllanthus* species in Mexico other than temperate ones such as *P. polygonoides;* and 3) deviant vegetative structure, with deciduous branchlets as in many species of *Phyllanthus* (Webster, 1956) but with the leaves on the permanent branches not reduced to cataphylls. This systematically isolated species is herewith described and named in honor of its discoverer, Dr. Neil Harriman.

Phyllanthus harrimanii Webster, sp. nov., ab omnibus speciebus Mexicanis differt foliis ramorum non reductis sed ramulis deciduis, plantis dioicis, staminibus 3 liberis, pollinis granis globosis 3-colporatis grosse reticulatis.

Glabrous bushy shrub 0.5–1.5 m high; branches brownish, terete, slender; branchlets ± deciduous, the branching subphyllanthoid, leaves on persistent axes not reduced to cataphylls (but tending to be smaller than those on branchlets); branchlet axes (1.5–) 3–6 (–8) cm long, terete, straight or zig-zag, smooth, stramineous, with (3–) 6–15 leaves, occasionally with an iterative side-branch. Leaves with stipules lanceolate, acuminate, 1.5–3 mm long, ± stramineous becoming brownish and indurate (especially on persistent axes); petioles 1–3 mm long; blades elliptic or ovate, thinly but firmly subcoriaceous, acute or obtuse and minutely apiculate at the tip, obtuse to rounded and somewhat oblique at base, about 1–3.5 cm long, 0.5–2 cm broad, greenish above, below glaucous (minutely stomatiferous-pustulate under a lens), veins about 4–6 on a side, rather obscure, veinlets not visible; margins entire, recurved or subrevolute. Dioecious; flowers axillary on branchlets; staminate flowers 1 or 2 per axil, pistillate flowers solitary. Staminate flower: pedicel capillary, 5–12 mm long; calyx lobes 5, ovate to obovate, entire, yellowish, midrib with ± prominent branching lateral veins, 1.5–2.3 mm long, 1.2–2.0 mm broad; disk segments 5, reniform, flat, smooth, about 0.3–0.4 mm long and 0.6–0.7 mm broad; stamens 3, free; filaments terete, 0.6–1.0 mm long; anthers broadly elliptic, compressed, with connective enlarged, muticous, slightly emarginate, longitudinally dehiscent, about 0.5 mm long, 0.6–0.7 mm broad; pollen grains globose, about 20–25 μm in diameter, tricolporate, colpi elongated and rather narrow, not bordered, reticulum rather coarse. Pistillate flower: pedicel slender, terete, 9–14 mm long; calyx lobes 5, oblong to broadly ovate or obovate, blunt, greenish, rather obscurely pinnately veined, 2.0–2.5 mm long, 2.4–3.0 mm broad; disk angular, 2.0–2.5 mm across, smooth, flat, slightly fleshy, ± dissected into 5 closely contiguous segments 0.9–1.2 mm broad; ovary oblate, smooth, about 1.5 mm across; styles free from the base, spreading, 1.3–1.7 mm long, bifid, the subulate branch-tips 0.7–1.0 mm long. Capsules oblate, about 6 mm broad; columella rather slender, about 2 mm long; seeds obtusely angular, irregularly mottled-banded with elongated brownish cells on a yellowish background, 2.6–3.2 mm long, 2.0–2.4 mm broad. (Figure 1)

TYPE: Mexico, Tamaulipas, dense scrub on limestone slopes 6 mi W of Palmillas, alt. 5300 ft, associated with *Astrocasia neurocarpa,* 1 August 1976, *G. L. Webster & W. S. Armbruster 20496* (Holotype, DAV; isotypes to be distributed).

ADDITIONAL COLLECTION EXAMINED: Mexico, Tamaulipas, Bustamante, alt. 5900 ft, 12 August 1975, *Neil A. Harriman 11615* (DAV).

The two localities are very close to one another in a floristically rich area of limestone ridges in the Sierra Madre Oriental. However, although there are many interesting species of Euphorbiaceae in this region west of the Jaumave Desert, *Phyllanthus* is extremely rare. The new species is therefore isolated geographically and ecologically as well as systematically.

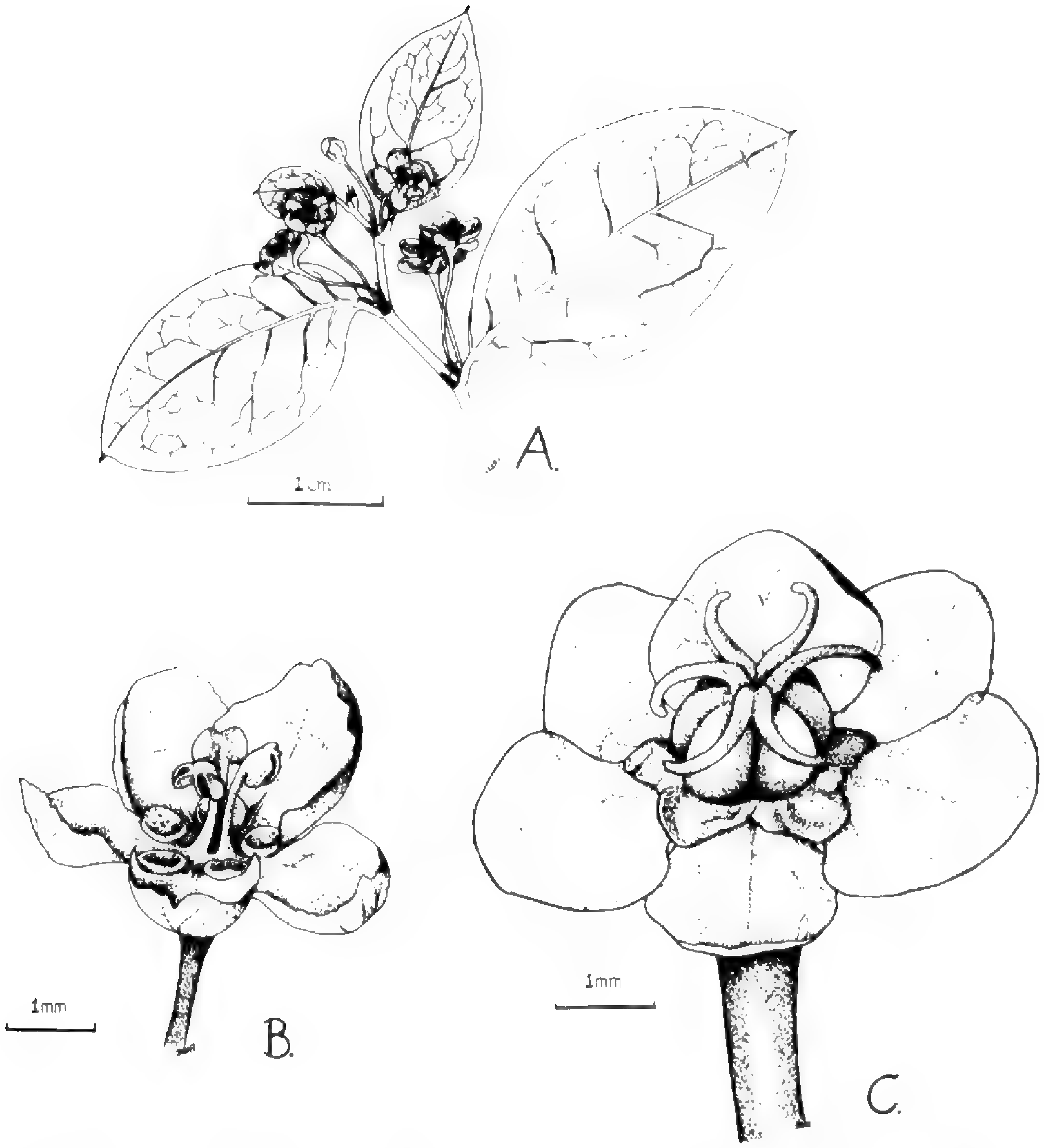

Figure 1. *Phyllanthus harrimanii.* A, Tip of branch of staminate plant; B, Staminate flower; C, Pistillate flower.

The affinities of *Phyllanthus harrimanii* are not at all clear. It does not appear to be close to any other species of Mexico or Central America. The aspect of the foliage is reminiscent of certain Cuban species, but those have true phyllanthoid branching and areolate pollen grains. Perhaps the most striking resemblance is with the South American *P. sellowianus,* which resembles *P. harrimanii* in its subphyllanthoid branching, elliptic leaves, dioecious flower production, and staminate flowers with three free stamens whose anthers dehisce longitudinally. However, the areolate pollen grains of *P. sellowianus* are very different, and, in fact, necessitate placing that species in subg. *Xylophylla.*

The pollen grains of *Phyllanthus harrimanii* are not closely similar to any of those illustrated by Köhler (1967), Punt (1967), or Punt & Rentrop (1973). However, they do somewhat resemble those of certain Brazilian species which were placed in "subsect. 2" of sect. *Phyllanthus* by Mueller (1873), although none of these are particularly close in overall morphological characters. *Phyllanthus subemarginatus* Muell. Arg. agrees in its dioecious flowers and subphyllanthoid branching, but has very different leaves and much more discrete anther locules. *Phyllanthus lacteus* Muell. Arg., although monoecious, has glaucous leaves suggestive of the Mexican plant. Several species, such as *P. glaziovii,* show some resemblance but have truly phyllanthoid branching. More surprisingly, there is a resemblance with the Australian species *P. subcrenulatus* F. Muell., which has subphyllanthoid branching.

Pending a revision of the entire genus, it seems preferable not to place such species as *Phyllanthus harrimanii* in sect. *Phyllanthus,* where they would appear discordant with the many herbaceous species that are much more specialized morphologically. Ferdinand Mueller created a special group, subg. *Lysiandra,* for *P. subcrenulatus;* and it is here proposed to recognize that as a section within subg. *Phyllanthus,* to accommodate some of the woodier presumably primitive species of the subgenus.

Phyllanthus sect. **Lysiandra** (F. Mueller) Webster, stat. nov.

Phyllanthus subg. *Lysiandra* F. Mueller, Fragm. Phyt. Austral. **1:** 108. 1859.

Glabrous shrubs with subphyllanthoid branching, the leaves on the main stem and branches tardily or not at all reduced to cataphylls; leaves orbicular to elliptic; monoecious or dioecious; calyx lobes 5 or 6; stamens 3, free or rarely basally united, anthers with ± enlarged connective, anther-sacs discrete, dehiscing longitudinally; pollen grains subglobose or globose, tricolporate, reticulum mostly coarse; seeds finely striate-banded.

TYPE SPECIES: *Phyllanthus subcrenulatus* F. Mueller.

ADDITIONAL SPECIES: *Phyllanthus dallachyanus* Benth., *P. gunnii* Hook. f. (Australia); *P. amoenus* Muell. Arg., *P. subemarginatus* Muell. Arg. (South America); *P. harrimanii* Webster (Mexico).

In the narrow circumscription of sect. *Lysiandra* adopted here, species such as *Phyllanthus claussenii* Muell. Arg. are excluded because of their phyllanthoid branching, even though they are similar in having anthers with enlarged connectives and tricolporate globose pollen grains. When the South American taxa of *Phyllanthus* are revised, it may be necessary to broaden the circumscription of sect. *Lysiandra* to permit the inclusion of some species with phyllanthoid branching.

The referral of *Phyllanthus harrimanii* to an otherwise antipodal section raises some provocative phytogeographic questions. This new species from Tamaulipas does appear to be a relict of a relatively primitive neotropical element which now survives in Brazil and which is absent from the West Indies. It shares with *Phyllanthus tuerckheimii* of Guatemala (Webster, 1967) the distinction of showing the greatest taxonomic isolation of any species in North America. At present both taxa point to austral connections in an enigmatic manner, which remains to be clarified by further revisional and palynological studies.

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SUBMERSED AQUATIC VASCULAR PLANTS IN ICE-COVERED PONDS OF CENTRAL OHIO

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Few observations of submersed aquatic vascular plants persisting in vegetative condition during the winter season in northern temperate regions have been recorded in the standard references on aquatic plants written in the English language (Arber, 1920; Fassett, 1940; Muenscher, 1944; Sculthorpe, 1967; Hutchinson, 1975). Recently, Boylen and Sheldon (1976) called attention to certain growth phenomena of leafy aquatic plants in water under ice cover. Our observations were made on plants in small, shallow, man-made ponds during the severe winter of 1976–1977, when ambient air temperatures remained below freezing continuously from 28 December to 2 February and below 10° C (50° F) until 22 February. Our observations confirm the perennial growth habits of six species which overwintered as submersed, whole, intact leafy plants. The species studied were *Najas guadalupensis, Potamogeton crispus, Ceratophyllum demersum, Elodea canadensis, Myriophyllum spicatum,* and *Ranunculus longirostris.*

Field observations were made on these species in three ponds (1, 1B and 16) in the Delaware Reservoir Wildlife Area, Delaware County, about 67 kilometers (42 miles) north of Columbus, between U.S. Routes 23 and 42. In the area, approximately 50 ponds were constructed by damming small streams or waterways in the period 1953–1955 (Ross, 1974). Since then various species of submersed aquatic vascular plants have become established. The ponds studied have varying depths with a maximum of 1 to 2 meters, mud bottoms, and are surrounded by shore vegetation of willows, elms, maples, cottonwoods, and cat-tails. Locations of populations of aquatic plants in the ponds were marked with metal stakes in the fall of 1976 to locate the populations during the winter season. Ice cover developed to 30 centimeters with a maximum snow cover of 12.5 centimeters over the ice at the time of measurement. Water temperatures under the ice ranged from 1° C to 4° C (34° F to 39° F). Incident radiation penetrating the snow and ice cover was measured with a Protomatic Underwater Photometer as described by Rich and Wetzel (1969). As measured 25 February 1977, on a hazy sunny day, light intensity directly beneath the ice was 120 foot candles and at the bottom of the pond at 1.5 meters, light was at 1 foot candle. Above the pond, light intensity was 1300 foot candles. On a cloudy day, light intensity was reduced to 29 foot candles directly below the ice and less than 1 foot candle at the bottom of the pond. Depth of occurrence of the aquatic plants was approximately 0.5 to 1.5 meters. The populations were sampled on 22 January, 12 February, and 25 February, and were followed with frequent observations during the spring season. To ascertain during the winter season whether the plants were indeed alive and physiologically active, all of the above-cited species were transplanted into ten-gallon aquaria maintained at room temperature, approximately 18° C (65° F). All of the species showed continued elongation of stems and the formation of new leaves, with the exception of *Ranunculus longirostris.* To reveal the vegetative condition of the plants as they existed under natural conditions during the winter season and the new growth in the spring season, voucher specimens were prepared and deposited in the herbaria at The Ohio State University (OS) and University of Michigan (MICH).

In most of the standard references on aquatic plants and in the more general manuals of the temperate flora, the winter growth habit of aquatic vascular plants is either not noted or authors are in disagreement as to the overwintering conditions. Our observations of these six species under the ice during the winter season confirm that they persisted as whole plants in a vegetative state. The plants had stems with cauline leaves and, with the exception of *Ceratophyllum demersum,* these leaves or leaf segments were smaller in width than usually occurs in the summer foliage.

COMMENTARY ON SPECIES STUDIED

Najas guadalupensis (Spreng.) Magnus

Fernald (1950) and Lawrence (1951) state that the genus *Najas* consists of herbaceous annuals. However, Rosendahl (1939) noted that *N. olivacea* overwintered as a perennial vegetative plant. In agreement with Rosendahl, Sculthorpe (1967, p. 347) considered all members of the genus to be annuals, with the exception of *N. olivacea.* In a comprehensive study of life forms of Indiana vascular plants, McDonald (1937) listed *N. guadalupensis* as an annual.

A large colony of this species has been observed by the first author in Pond 1B every summer and fall since 1968. It had been speculated that the plants in this colony were perennial. During the 1976–1977 winter season we repeatedly observed whole intact vegetative plants. In the spring, new shoots emerged from the persisting stem apices confirming the perennial habit of this species in central Ohio. The growth phenomena observed on these plants are very similar to that reported for *Najas olivacea* by Rosendahl (1939) who noted that the plant "renews freely from the persistent lower portions of stems of the previous season."

Potamogeton crispus L.

Butcher (1933) and Gessner (1959, p. 300) state that the vegetative plant body "dies down" with the onset of winter. In discussing the overwintering of this species, Sculthorpe (1967, pp. 348–349), Harmon (1974), and Hutchinson (1975, p. 236) do not allow for the possibility that the species may overwinter as a vegetative plant body. Our observations confirm those of Moore (1915, p. 264), Glück (1924, pp. 120–123), and Waisel (1971), who described the winter vegetative form of *Potamogeton crispus*. The leaves of the winter form are flat, blue-green, and narrow in contrast to the undulate, reddish-brown, wider leaves of the summer form.

Ceratophyllum demersum L.

This species is usually considered to overwinter by means of densely crowded dormant stem apices as discussed by Pearl (1907), Arber (1920, p. 216), Evermann and Clark (1920, pp. 165, 302), Glück (1924, pp. 133–134), Muenscher (1944, p. 228), and Sculthorpe (1967, p. 346). With the exception of Sculthorpe, these authors also mention that *Ceratophyllum demersum* may overwinter as an intact vegetative plant body. Muenscher (1944, p. 228) states that "In deep water vegetative plants may be found throughout the winter even under ice." Although the plants in Pond 1 occurred in shallow water, our observations confirm the report of Muenscher, as well as those cited above.

Elodea canadensis Michx.

Sculthorpe (1967, p. 346) describes this species as perennating by densely crowded apices. Our observations were that *Elodea canadensis* remained as a leafy green plant throughout the winter confirming similar statements by Evermann and Clark (1920, pp. 122, 174).

Myriophyllum spicatum L.

Most of the general reference works on aquatic plants report that species of *Myriophyllum* overwinter by the formation of turions or winter buds. With considerable confusion existing among the morphological characters used to separate the non-indigenous *M. spicatum* from the native *M. exalbescens,* it is difficult to ascertain which descriptions of overwintering structures are applicable to *M. spicatum.* Our observations confirm those of Evermann and Clark (1920, pp. 196, 374–375), Glück (1924, p. 102), and Stanley *et al.* (1976) who indicate that entire plants overwinter.

Ranunculus longirostris Godr.

Our observations coincide with those of Goebel (1892, pp. 354–355), Evermann and Clark (1920, pp. 187, 313), and Glück (1924, p. 230), who report that this species overwinters in the form of leafy green plants. However, in the spring the leafy portions of these plants disappeared from the population we studied during the winter. This species has been observed regularly by the first author in Pond 1 during September for the past several years, and its absence at this time may be temporary suggesting that additional study is necessary on its life history. The plants from this population did not initiate new growth when transplanted into aquaria in the laboratory during the winter season.

SUMMARY AND CONCLUSIONS

The presently accepted life histories of many submersed aquatic vascular plants, which assume perennation exclusively by various types of specially formed dormant structures, deserve reevaluation. It may mean that an additional slow-growing or dormant phase in the vegetative condition could appropriately be integrated into our present concepts of the life histories of many of these species. In addition, the success of several of the above-cited species as "weedy" invaders or as aggressive competitors may be correlated with their ability to remain in a vegetative condition throughout the winter season. With the onset of melting ice, such plants are already active photosynthetically and occupy considerable area in the habitat long before the germination of the seeds of annuals or the development of foliage of species perennating from rhizomes.

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FUNGI FROM NANTUCKET SALT MARSHES AND BEACHES

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Marine fungi on intertidal and submerged wood, salt marsh plants, and algae have been collected from coastal areas of Massachusetts by Barghoorn and Linder (1944), Meyers (1957), and Webber (1966, 1970). Kohlmeyer (1971) added to the number of species reported and compiled an annotated list of the New England marine fungi. The above authors have not, however, reported on the fungi from the islands off the coast. During June 1977, we had the opportunity to spend a few days on Nantucket Island and were able to collect fungi from a number of different substrates from some salt marsh and beach habitats. The collecting sites and substrates sampled were as follows:

J. B. Jetties Beach, a sandy beach on the north side of the island; salinity 30 o/oo; water temperature 21° C; 25 June 1977; washed up and submerged dead *Zostera marina* L., RVG *109*[1]; wood on beach, RVG *110*.

P. R. Salt marsh behind Nantucket Public Works Dept. garage, north side of island off Polpis Rd.; salinity of adjacent tidal creek 20 o/oo; water temperature 21° C; 25 June 1977; dead standing *Spartina alterniflora* Loisel., RVG *111a; S. alterniflora* debris at the high tide mark, RVG *111b;* dead standing *Salicornia* sp., RVG *111c;* dead *Zostera marina* at the high tide mark, RVG *111d*.

S. Surfside, a sandy beach on the south side of the island; 25 June 1977; wood on the beach, RVG *112a;* dead *Zostera marina* on the beach, RVG *112b*.

Specimens (RVG *109–112*) are deposited as slides and/or dried material at the mycological collection of the University of North Carolina, Institute of Marine Sciences (IMS). Cultures of *Pleospora gaudefroyi* Patouillard and *Camarosporium roumeguerii* Saccardo have been deposited at the American Type Culture Collection, Rockville, Maryland.

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[1] Collection numbers preceded by RVG are housed in the author's personal herbarium.

ASCOMYCOTINA

Buergenerula spartinae Kohlm. et Gessner; dead standing *Spartina alterniflora;* P. R.; RVG *111a.* This is the first report of *B. spartinae* from Massachusetts. It is ubiquitous along the east coast of the United States on *S. alterniflora* (Gessner & Kohlmeyer, 1976).

Corollospora maritima Werdermann; *Zostera marina* and wood with attached sand grains; J. B.; RVG *109 & 110. Corollospora maritima* has been reported previously on wood and in foam from Massachusetts (Kohlmeyer, 1971).

Halosphaeria sp.; dead standing *Spartina alterniflora;* P. R.; RVG *111a.* This fungus is similar to *H. hamata* but the appendages are atypical.

Leptosphaeria albopunctata (Westend.) Sacc.; dead standing *Spartina alterniflora;* P. R.; RVG *111a. Leptosphaeria albopunctata* has not been reported previously from Massachusetts.

Leptosphaeria halima Johnson; leaves of dead standing *Spartina alterniflora;* P. R.; RVG *111a.* This is the first report of *L. halima* from New England. It has been reported previously from North Carolina and Florida (Johnson, 1956; Johnson & Sparrow, 1961).

Leptosphaeria obiones (Crouan et Crouan) Sacc.; *Spartina alterniflora:* debris at the high tide mark and dead standing plants; P. R.; RVG *111a.*

Phaeosphaeria typharum (Desmaz.) Holm; *Spartina alterniflora:* debris at the high tide mark and dead standing plants; dead standing *Salicornia* sp. P. R.; RVG *111a,b,&c.*

Pleospora gaudefroyi Patouillard; dead standing *Salicornia* sp.; P. R.; RVG *111c.* This collection represents the first report of *P. gaudefroyi* from North America. It has been reported previously from Europe and South America (Kohlmeyer, 1962; Kohlmeyer, unpublished; Kohlmeyer & Kohlmeyer, 1964–1969). Cultures derived from transferring a few ascospores to GYPSR/2 agar (glucose, lg; yeast extract, 0.lg; agar, 18g; penicillin G, 0.lg; streptomycin SO_4, 0.lg; 500 ml Rila Marine mix and 500 ml distilled water) produced ascocarps with mature ascospores in about four weeks.

Pleospora pelagica Johnson; dead standing *Spartina alterniflora;* P. R.; RVG *111a.* This represents the first account of *P. pelagica* from Massachusetts. It has been reported previously from Rhode Island (Gessner & Kohlmeyer, 1976).

Pleospora vagans var. **vagans** Niessl; dead standing *Spartina alterniflora;* P. R.; RVG *111a. Pleospora vagans* var. *vagans* has been reported previously on *S. alterniflora* from Rhode Island and New Jersey (Gessner & Kohlmeyer, 1976).

Pleospora cfr. **valesiaca** (Niessl) E. Müller; dead standing *Salicornia* sp.; P. R.; RVG *111c.* The fungus reported here has sheathed ascospores similar to *P. valesiaca* which has been found on *Salicornia* spp. in Argentina, New Jersey, and North Carolina (Kohlmeyer, unpublished).

BASIDIOMYCOTINA

Uromyces cfr. **acuminatus** Arth.; dead standing *Spartina alterniflora;* P. R.; RVG *111a.* Teliospores agreeing in shape and size with those of *U. acuminatus* were found on the leaves of *S. alterniflora.* Cummins (1971) has previously reported this fungus on salt marsh cordgrass from Massachusetts.

DEUTEROMYCOTINA

Alternaria sp.; dead standing *Salicornia* sp. and dead *Zostera marina* on beach. P. R.; S.; RVG *111c & 112b.*

Asteromyces cruciatus F. et Mme. Moreau ex Hennebert; dead *Zostera marina* on beach. S.; RVG *112b.* This sand-inhabiting fungus from temperate waters has been reported from foam in Massachusetts (Kohlmeyer, 1971).

Camarosporium roumeguerii Saccardo; dead standing *Salicornia* sp.; P. R.; RVG *111c.* Saccardo (1880) and Kohlmeyer (unpublished) have found this fungus on *Salicornia* spp. This is the first report of *C. roumeguerii* from the United States. It readily produced pycnidia in culture when isolated on GYPSR/2 agar.

Dendryphiella salina (Suth.) Pugh et Nicot; driftwood and dead *Zostera marina* on beach. S.; RVG *112a&b.* A collection of this fungus from a crustaceous alga on an intertidal branch was made previously in Massachusetts by Kohlmeyer (1971).

Phoma sp. and spermogonia; *Spartina alterniflora:* debris at the high tide mark and dead standing plants; dead standing *Salicornia* sp. P. R.; RVG *111a,b,&c.*

Septoria sp.; *Spartina alterniflora:* debris at the high tide mark and dead standing plants; P. R.; RVG *111a&b.*

Stagonospora sp. II; *Spartina alterniflora:* debris at the high tide mark and dead standing plants; P.R.; RVG *111a&b.* A common fungus on *S. alterniflora, Stagonospora* sp. II has been reported from numerous locations along the east coast of North and South America (Gessner & Kohlmeyer, 1976).

DISCUSSION

The fungi of Nantucket salt marshes and beaches, reported in this limited study, appear to be similar to those of mainland New England (Kohlmeyer, 1971; Gessner & Goos, 1973; Gessner, 1977). Studies by other workers on off shore islands (Cavaliere, 1968; Kohlmeyer, 1967, 1969; Kohlmeyer & Kohlmeyer, 1977; Schaumann, 1969) have reported species commonly found on the mainland. The geographical distribution of the marine fungi reported here, as for other islands in Atlantic temperate waters, appears to be influenced by water temperatures and the host plants. Host specific fungi such as *Buergenerula spartinae* and *Pleospora pelagica* have been reported from *Spartina alterniflora* along the east coast of the United States. *Camarosporium roumeguerii* has only been collected on members of the Chenopodiaceae. *Phaeosphaeria typharum* and *Pleospora vagans* var. *vagans* occur on a number of graminicolous hosts (Holm, 1957; Gessner & Kohlmeyer, 1976; Wehmeyer, 1961). Other fungi such as *Leptosphaeria albopunctata, L. halima, L. obiones,* and *Pleospora gaudefroyi* are commonly found on the remains of salt marsh plants but are occasionally reported from wood. The discovery of *P. gaudefroyi* and *C. roumeguerii* for the first time in North America and the United States, respectively, probably relates to the few studies of fungi on hosts in the Chenopodiaceae. *Asteromyces cruciatus* is a common fungus in temperate waters on plant material, on sandy shores, and in foam. Fungi such as *Corollospora maritima* and *Dendryphiella salina* appear to be ubiquitous on plant material from sandy beaches and the intertidal zone. This study further supports the host-influenced distribution of many salt marsh fungi and the ubiquitous distribution of some plant debris-sand inhabiting species on beaches.

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ISOTRIA MEDEOLOIDES, THE SMALLER WHORLED POGONIA, NEW TO CANADA

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The orchid genus *Isotria* is very rare in Canada and is known from only a few records. Previous records have been for *Isotria verticillata* (Willd.) Raf. which is known from one old record from Middlesex County and currently from a site in Norfolk County, Ontario.

On April 26, 1977, while on a fern foray near Calton Swamp in Elgin County, Ontario, attention was attracted to two overwintering stems of what appeared to be an orchid of the genus *Isotria*.

Its vernal appearance was first recorded on May 19 when two monocotyledonous stalks had appeared about 8 cm. above the leafy humus. By May 22 each had expanded into the characteristic whorl of leaves and terminal flower bud and were 15 cm. tall.

Initially its identity was assumed to be *Isotria verticillata* (Willd.) Raf. commonly known as the Whorled Pogonia which had been recorded previously from Ontario and is certainly the more common of the two species of *Isotria* in North America.

By May 26 the plants had reached anthesis and were 22 cm. tall (Figure 1). On May 31 the plants had been in flower for five days and I became curious about some discrepancies between literature descriptions and the plants at the site.

Although I had had no previous field experience with the genus *Isotria* it became clear to me that these plants were not the Whorled Pogonia but the Smaller Whorled Pogonia, *Isotria medeoloides* (Pursh.) Raf. The plants were smaller than the descriptions of the Whorled Pogonia and the sepals were much shorter and less spider-like in appearance. In addition, they had shown no tendency to produce any purple coloration, either on the lip and sepals of the flower or on the stem of the plant itself.

The descriptions for *Isotria medeoloides* fit these plants exactly and all the details of habitat and flowering were suitable. However, one problem still remained. *Isotria medeoloides* had not been previously reported from Canada.

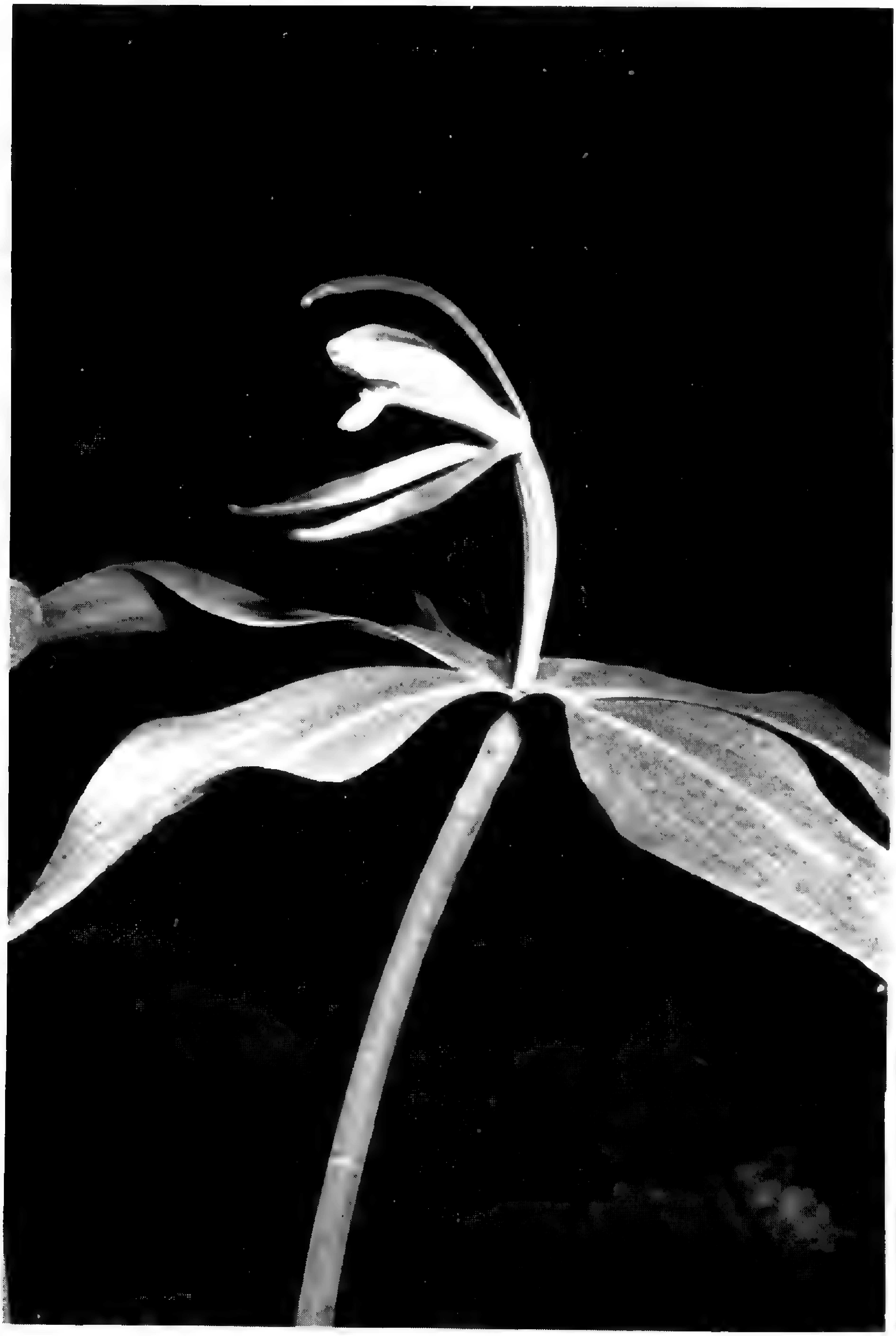

Figure 1. *Isotria medeoloides* (Willd.) Raf. in Elgin County, Ontario.

Its range in North America is given as New England, New York, Pennsylvania, New Jersey, Virginia, North Carolina and Missouri (Correll, 1950). It has been described as very rare and local, growing in rich sub-acid leaf mold under hemlocks and this was precisely the type of habitat where the Elgin County, Ontario, plants were found.

The site is located in partial shade of an open edge of deciduous second growth, adjacent to a stand of mature hemlocks (*Tsuga*). Other tree species in the area include *Betula lutea* Michx. f., *Acer rubrum* L. and *Fraxinus* sp. Herbaceous plant associates include an abundance of *Maianthemum canadense* Desf., *Medeola virginica* L., *Lonicera canadensis* Bartr., *Trientalis borealis* Raf. and *Polygonatum* sp. A fine colony of *Dryopteris disjuncta* (Ledeb.) C. V. Mort. occurs within sight distance and *Osmunda cinnamomea* L., *Onoclea sensibilis* L., *Botrychium virginianum* (L.) Sw. and *Botrychium matricariaefolium* A. Br. occupy the dried-up melt water pools and lower areas surrounding the site.

Orchid species in the near vicinity include *Goodyera pubescens* (Willd.) R. Br., *Cypripedium calceolus* var. *pubescens* (Willd.) Correll, *Habenaria lacera* (Michx.) Lodd., *Malaxis brachypoda* (Gray) Fern., *Liparis Loeselii* (L.) Richard, and *Aplectrum hyemale* (Muhl.) Torr.

In an account of the discovery of *Isotria medeoloides* in Michigan (Case with Schwab, 1971),Mr. Schwab reported that plants dropped their flowers after just a day or two. In contrast, the Elgin County, Ontario, plants remained at anthesis from May 26 through June 4, an interval of at least ten days. This longevity may be attributed in part to a dip in temperature during the latter part of anthesis from an average daytime high of 24° C and early morning low of 10° C to a daytime high of 12° C and early morning low of 1.5° C. These temperatures were recorded at the Burwell Road Weather Station near St. Thomas and reflect some degree of modification due to the proximity of the city. This is evidenced by the fact that in some localized areas near the site of *Isotria,* planted corn crops received damage from frost. Temperatures then returned to near those at the start.

On June 11 two additional plants were discovered approximately 200 meters from the original site. One of these was in flower and one had only the characteristic whorl of leaves. This flower was never pollinated and the flower dropped from its attachment near the whorl of leaves. In contrast to this, the flowers at the original site were pollinated and the flowers parted from the top of the long ovary, which by this time had begun to swell noticeably, standing well above the whorl of leaves.

The plants at this site have been well documented by photographs taken by many naturalists and orchid enthusiasts of Ontario and a specimen was collected, dated May 31, 1977, (*Stewart 2500*) and deposited in the herbarium of the Department of Plant Sciences, University of Western Ontario, in London, Canada.

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POTAMOGETON GRAMINEUS WITH ADNATE STIPULES

C. B. HELLQUIST

While conducting field work during the summer of 1972 I collected a peculiar pondweed. The plant (Figure 1) initially appeared to be a multi-branched, shallow water form of *Potamogeton oakesianus* Robbins. It was found in an unnamed pond on the north side of Browns Ridge Road at the junction of New Hampshire Route 16, Ossipee, Carroll County, New Hampshire. This pond is a small (about 15 × 25 m), shallow (45 cm), muddy-bottomed body of water with a pH of 6.2 and an alkalinity of 6.0 mg/1 $CaCO_3$. Aquatic plants present were *Sparganium chlorocarpum* Rydb., *Potamogeton epihydrus* Raf., and *Nuphar variegatum* Engelm.

Collected specimens (*4486*) were shown to Eugene C. Ogden who located a few adnate stipules on the plants. This discovery led to a taxonomic problem since *Potamogeton oakesianus* is not known to produce adnate stipules. Leaf-stipule adnation is a character found in *Potamogeton filiformis* Pers., *P. vaginatus* Turcz., *P. pectinatus* L., *P. robbinsii* Oakes, *P. spirillus* Tuckerm., *P. bicupulatus* Fern., *P. diversifolius* Raf. and *P. tennesseensis* Fern.

This plant has been observed during several seasons. In September, 1974, Dr. Ogden and I visited the pond and collected a number of specimens (*Hellquist, 9939 & Ogden*). The stem anatomy was studied by Dr. Ogden. The anatomical pattern agrees well with that of *Potamogeton gramineus,* but could include that of some specimens of *P. oakesianus.* Neither is known to have adnate stipules. Although fruits were not found, a young pistil indicated that the coil of the embryo agrees with that for *P. gramineus* and *P. oakesianus.* Its general appearance is that of *P. tennesseensis* but the embryo coil and the shape of the endodermis cells are not of that species.

The population is sterile, suggesting a possible hybrid exists. The possibilities of *Potamogeton oakesianus* or *P. gramineus* crossed with *P. filiformis* or *P. pectinatus* are not likely probabilities since the latter two species are found in alkaline waters and not within 50 miles of the pond. The possibility of a cross with either *P. bicupulatus* (*P. capillaceus* Poir.) or *P. spirillus* seems more reasonable since these acid water taxa are common in the area.

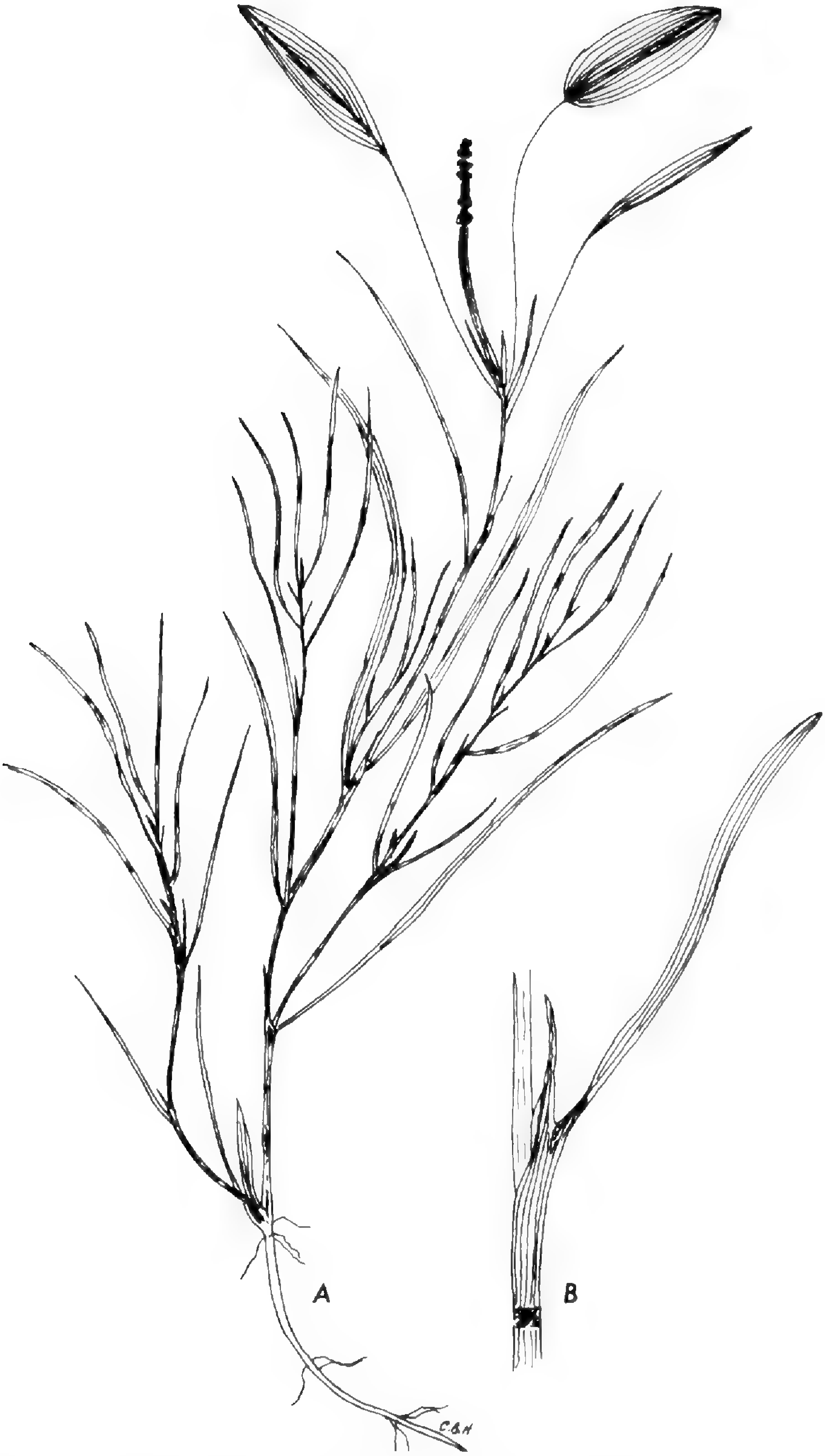

Figure 1. A, Habit of Browns Ridge Road Pond population of *Potamogeton gramineus*, × ½; B, Adnate stipule × 5.

Paper chromatography was conducted on this population along with other populations of *Potamogeton filiformis, P. pectinatus, P. spirillus, P. bicupulatus, P. epihydrus, P. gramineus* and *P. oakesianus.* The chromatographic technique utilized a 4:1:5 n-butanol, acetic acid, water mixture in the first dimension and a 5% acetic acid solution in the second dimension. Upon observing spot patterns of the populations from the above taxa it appeared that the Browns Ridge Road material best matched *P. gramineus.*

In addition to the adnate stipules on some of the leaves, this particular population differs from other collections of *Potamogeton gramineus* in other characters. The submersed leaves are narrower and many have only one vein. This is similar to that of *P. gramineus* L. forma *minimus* Morong (Morong, 1893). These plants are even more delicate than those of *P. gramineus* L. var. *myriophyllus* Robbins. Specimens have been deposited in the herbaria of Boston State College and various other institutions.

ACKNOWLEDGMENT

I wish to thank Dr. Eugene C. Ogden for his assistance and review of the manuscript.

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NOTES ON THE CHROMOSOME NUMBER OF GAULTHERIA PROCUMBENS L. (ERICACEAE)

GUY L. NESOM

Gaultheria procumbens L., has at least two chromosome numbers different from the single one previously reported by Newcomer (1941) of $n = 12$ from plants collected at an unspecified locality in either North Carolina or Tennessee. The present report is of three North Carolina populations, one from the Piedmont Province in Durham County (tetraploid with $n = 22$), one from the Blue Ridge Province in Macon County ($n = 22$), and one from the Blue Ridge Province in Burke County (octoploid with $n = 44$). Clear meiotic counts were obtained from pollen mother cells at late anaphase II of the Piedmont population; the tetraploid count from Macon County was made at metaphase I; and counts of $n = 44$ from the Burke County population were made at late prophase I as well as counts of $n =$ ca. 44 at late anaphase I and II.

Specific collection data for the North Carolina populations are as follows: **Burke Co.**: with *Galax* in heath at the summit of Tablerock Mountain, ca. 16 mi NW of Morganton, Blue Ridge Province; *G. Nesom & D. Wickland s.n.*, $n = 44$. **Durham Co.**: North-facing slope on tributary of Little River, just NE of Co. Rd. 1628, ca. 9 mi N of Durham, Piedmont Province; *J. Moore & P. Olwell s.n.*, $n = 22$. **Macon Co.**: edge of rock in chestnut oak-heath community, near Sunset Rock, Highlands, Blue Ridge Province; *A. E. Radford s.n.*, $n = 22$. Vouchers from all three populations have been deposited in NCU.

Three base numbers ($x = 11, 12, 13$) are known in this large genus, though only twelve species have as yet been cytologically investigated; ten of these have $x = 11$. Most are diploid, but besides *Gaultheria procumbens,* two other species from widely separate geographic areas are known to have tetraploid populations with respect to $x = 11$ (Callan, 1941). A single species, *G. Itoana* Hay of Formosa, is known to have a base number of 13 ($2n = 26$, Callan, 1941). The three species reported to have a base number of 12 are all from North America. *Gaultheria hispidula* (L.) Muhl. var. *hispidula* is diploid with $2n = 24$ (Löve & Löve, 1966); the other two, *G. Shallon* Pursh from along the Pacific coast and *G. procumbens,* are both apparently dibasic with $x = 11$ and 12. *Gaultheria Shallon* is reported as an octoploid with respect to both base numbers ($2n = 88$, Callan, 1941; $2n = 96$, Hagerup, 1928).

It is interesting to note that although these three North American species have a variant base chromosome number in common, Airy-Shaw (1940) placed *Gaultheria Shallon* in sect. *Brossaeopsis* Airy-Shaw and the other two in different subsections of sect. *Gaultheria* (sect. *Eugaultheria* Airy-Shaw). In his treatment *G. procumbens* was discussed as "morphologically one of the most isolated species known." This species seems to be morphologically rather uniform throughout its range, though several striking but local variants have been noted in the northeastern United States (e.g., MacKeever, 1961; Fernald & Hodgdon, 1934). The strong probability that both aneuploidy and autopolyploidy exist within the species and within the area of the southern Appalachians offers an intriguing study.

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NOTES ON THE FLORA OF RHODE ISLAND

As part of an undergraduate thesis on the vegetation of the area, I have done extensive field work, since 1974, with the native plants of southern Rhode Island. I have found several species of flowering plants not previously documented from Rhode Island. I have also found stations for two other noteworthy species. Irene Stuckey and Elmer Palmatier, of the University of Rhode Island, have been most helpful in confirming the status of these species. Lisa Standley, formerly of the Bailey Hortorium, and A. W. H. Damman, of the University of Connecticut, verified identifications of the *Carex* species mentioned.

Of the seven taxa discussed below, five are new records for the state and are marked (*). The significance of the other two species is indicated.

**Sagittaria teres* S. Wats. Plentiful in shallow water, sandy bottom. School House Pond, Charlestown. 3 August 1976.

**Carex artitecta* Mack. Numerous plants in crevices in quartzite rock. Hemlock Ledges, Gloucester. 24 July 1977.

Carex collinsii Mack. Growing with *Gaultheria hispidula* on sphagnum tussocks, in a swamp of Atlantic white cedar. Genessee Swamp, South Kingstown. 7 July 1975. This is possibly the same station at which this species was collected by J. F. Collins in 1932. The northernmost occurrence for this coastal plain species.

**Carex tonsa* (Fern.) Bickn. Plentiful under pitch pines in a sand plains area. South Kingstown. 7 July 1977.

**Drosera filiformis* Raf. Six vigorous plants were found in a gravel bank, in moist, fine silt with *Lycopodium inundatum, Rhexia virginica,* and *Vaccinium macrocarpon.* These plants flowered in early July, 1977. A careful search located about fifty seedlings surrounding the mature individuals, so the plants are reproducing. Near Wordens Pond, South Kingstown.

Helianthemum dumosum (Bickn.) Fern. The only previously known station in Rhode Island was on Block Island. Two healthy plants, with fully developed cleistogamous flowers, were found growing with the *Carex tonsa* mentioned above. Irene Stuckey confirmed my identification. South Kingstown. 1 July 1977.

**Hudsonia tomentosa* Nutt. var. *intermedia* Peck. Growing with the typical variety, in a sand plains area on the north edge of the Charlestown Moraine, South Kingstown. 15 July 1977.

Voucher specimens of the species discussed above have been deposited in the Wiegand Herbarium of Cornell University. A specimen of the *Drosera filiformis* has been deposited in the Herbarium of the New England Botanical Club.

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EUPHORBIA DENTATA IN CONNECTICUT

On September 12, 1977, I found a large patch of *Euphorbia dentata* (Michx.) growing along the Amtrak railroad right-of-way in Branford, Connecticut. *Gray's Manual of Botany,* 8th edition, reports the range of this species as "N.Y. to Minn., S.D. and Wyo. s. to Va., La., Tex. and Mex.". According to Joseph Dowhan of the Connecticut State Natural History and Geological Survey, the species has been reported from Connecticut in 1822 and 1884, but no voucher specimens exist. A specimen was collected in New Hampshire in 1866 (Blake *s.n.*), but the species does not seem to have been found again in New England until 1967. Since then, it has been collected, always along railroad tracks, by L. E. Charette and H. E. Ahles in various localities in Vermont, Massachusetts and Rhode Island.

Specimens of the Connecticut plants have been deposited in the herbaria of Yale University (YU), University of Connecticut (CONN) and the Connecticut Botanical Society (CBS).

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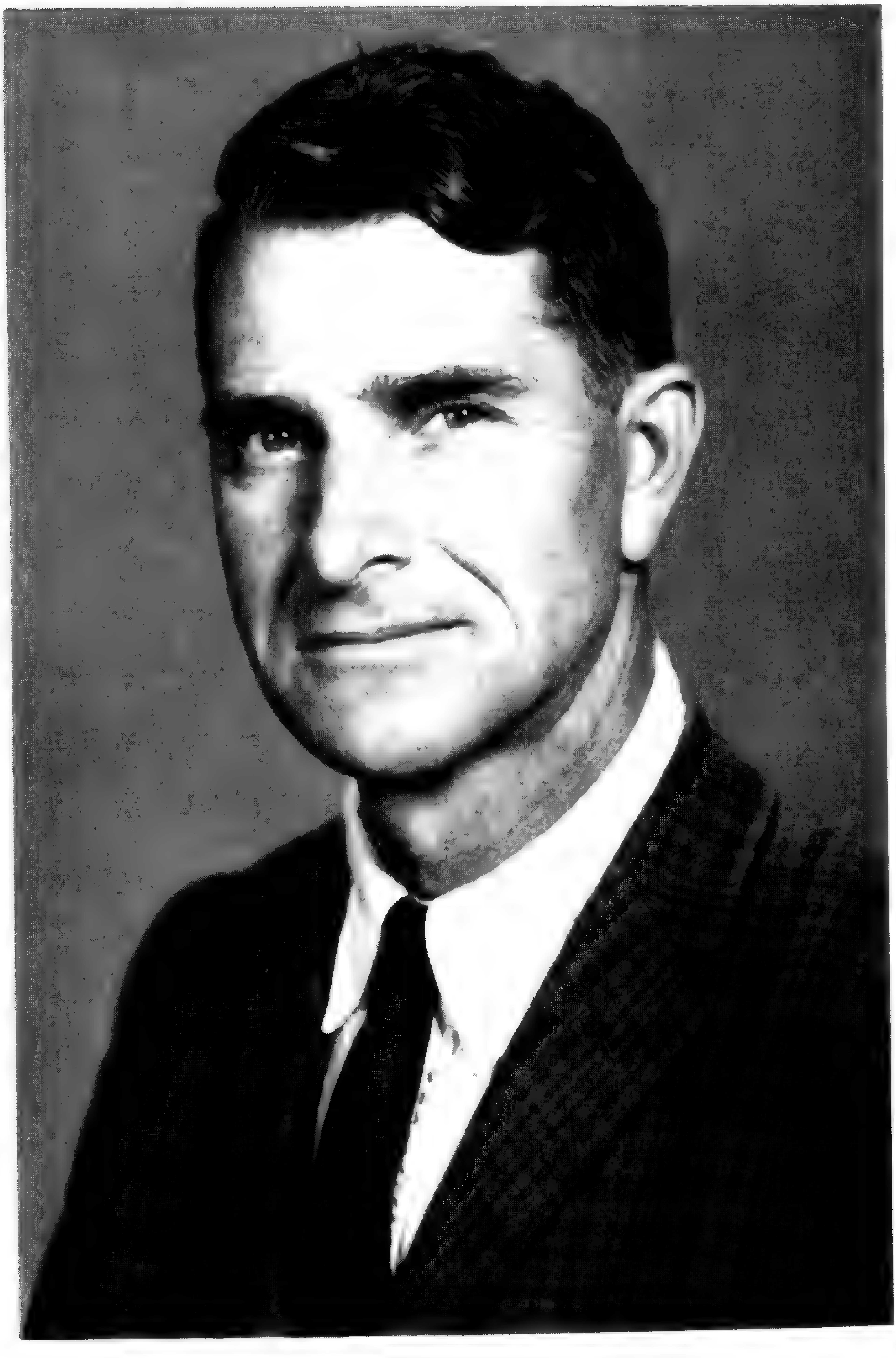
ALBION R. HODGDON

1909-1976

Albion Reed Hodgdon was born November 1, 1909, on Sawyer's Island, in Boothbay, Maine. He spent much of his boyhood on a farm in southeastern New Hampshire, attending grades one through seven in a one-room schoolhouse in Dover, where his family moved in 1914. In his early teens he developed a strong interest in native plants and vegetation, perhaps as the result of periodic "expeditions" into the surrounding countryside with his older brother Melville and another friend to study the local plants, birds and animals. Initially, at least, Melville was to keep track of the plants and Albion the birds, and an interest in birds remained with Albion throughout his life. A growing interest in plants led him to enroll in the Botany curriculum at the University of New Hampshire. He received a B.S. in Botany in 1930, then stayed on in the position of Assistant in Botany from 1930–1932, while working toward a Master's Degree. He received his M.S. in 1932 on completion of his thesis, entitled "The Flora of Strafford County, New Hampshire." He then enrolled in the graduate program at Harvard University where he worked as an Instructor in Botany while studying for his Ph.D. in plant taxonomy with Dr. Merritt Lyndon Fernald. His dissertation took the form of a monographic study of the genus *Lechea* (Cistaceae).

Upon conferral of the doctorate in 1936 Dr. Hodgdon returned to the University of New Hampshire as Instructor in Botany, a position he held until 1941, when he was promoted to Associate Professor. From 1942 to 1947, while the Botany faculty was united with Zoology and Microbiology in a Biology Department, Dr. Hodgdon served as Head of the Botany section and of the Agricultural Research Station. In 1947 he became Head of an independent Botany Department, and served in that capacity for twenty years, resigning as Head in 1967 to devote more time to teaching, research and professional activities.

In 1940 he married Audrey McKown. She was his distant cousin, whom he had first met as a boy of about seven during childhood visits to the family seat in Boothbay. They were both from seafaring stock; Audrey, as the daughter of a sea captain, had spent a goodly part of her childhood with her family aboard ship, sailing to all



ALBION R. HODGDON

parts of the world. Courtship followed graduate study, and they were eventually married in Malden, Massachusetts. He is survived by his wife, a daughter, Ariel, two sons, Alan and Anthony, and four grandchildren.

Throughout his career Dr. Hodgdon's research activities centered largely on the flora of New Hampshire and adjacent areas. He maintained a special interest in the taxonomy of the genus *Rubus*. He was an acknowledged authority on the flora of New England and published many papers on New England plants in RHODORA, either as sole author, or jointly with his principal collaborators, Radcliffe B. Pike and Frederic L. Steele. Other associates in research and publication include John A. Churchill, David S. Conant, William D. Countryman, Lesley M. Eastman, Merritt L. Fernald, Joanne Flint, Herbert Friedlander, Dominic P. Gange, P. Giguere, A. D. Hastings, Edward J. Hehre, Stanley B. Krochmal, Henry R. Tyler, Jr., and Leonard P. Wolfe, Jr.

In the 1960's, in collaboration with Radcliffe Pike, he devoted considerable attention to the floristics and phytogeography of the coastal islands of Maine and New Brunswick, Canada, especially Grand Manan and the Wolf Islands in the Bay of Fundy.

Dr. Hodgdon's broad taxonomic and ecological interests led him to travel widely, to Tennessee, Michigan and New Brunswick, Canada, while working on *Lechea;* to Cuba in 1936; to Mexico and California, accompanied by brother Melville, in 1938; to the Arctic Slope of Alaska in 1952; to Great Britain in 1964; to Scotland and Ireland in 1966; to Europe in 1968; to the islands of the Caribbean for several summer vacations; and to the Galapagos Islands in 1973.

Over the years Dr. Hodgdon held memberships in a number of national professional organizations, including the American Association for the Advancement of Science, Botanical Society of America, American Society of Plant Taxonomists, Ecological Society of America, Nature Conservancy, Society of the Sigma Xi, and the Society for the Study of Evolution. However, he concentrated most of his activity and energy in dedicated service to such New England organizations as the New Hampshire Academy of Sciences (now disbanded), the Society for the Protection of New Hampshire Forests, the Audubon Society, and especially the New England Botanical Club. He was a regular participant in Audubon bird counts and was frequently called on to lead bird watching trips as he knew the birds by their calls as well as by sight, and had only to stand in the stillness of the forest and listen to know what birds might be present. He was elected to membership in the New England Botanical Club on December 2, 1932, and was an active member until incapacitated in 1974. He served the Club from 1962 until 1974 as Editor-in-Chief of its journal, RHODORA, an effort in which he enjoyed the close collaboration of Radcliffe Pike. He was elected President of the Club in 1974.

A champion of sensible environmental causes, Dr. Hodgdon was instrumental in the preservation for public use and enjoyment of such New Hampshire natural areas as Odiorne State Park in Rye, the University of New Hampshire Natural Area in Durham, the U.N.H. Squam Lake Refuge, the Spruce Hole Bog in Lee, and *Rhododendron* colonies in Harrisville, Hopkinton, and Fitzwilliam. Some of these activities became the subjects of papers in RHODORA. At U.N.H. he played a significant part in the establishment of the first doctoral program, and in 1957 the first two doctoral awards made by the University went to botany graduate students.

Dr. Hodgdon considered as one of his major achievements the development of the herbarium at U.N.H., now designated as the Albion R. Hodgdon Herbarium. Starting with a small nucleus of perhaps 1500 specimens, which were present in the early 1930's, he developed a collection which today numbers about 82,000 specimens of vascular plants and approximately 36,000 specimens of marine algae. Included in the herbarium are several historically important personal or institutional collections of New England plants which have been donated or placed on permanent or long-term loan. The associated Sumner Pike Library contains about 1500 volumes of floristic and taxonomic literature.

As a teacher Dr. Hodgdon excelled. His field-oriented courses on the flora of New Hampshire, aquatic plants, taxonomy, and phytogeography attracted innumerable students, few of whom could match his stamina or stride on a White Mountains trail. To many of these he became simply and affectionately known as "Doc". In him they found a genuine and sincere friend and mentor, a gentle philosopher who was always helpful, kind and generous with his time. He had an enthusiasm for art, science, and life that was a source of inspiration to many. In this respect his unique personality is perhaps best summed up in the words of the following poem by Helen Field Watson (1949):

HODGDON OF DURHAM

Hodgdon of Durham is a timeless man
Mature in judgement, in emotions prime
One might imagine that a century's span
Had left Thoreau of Concord past his time
And Hodgdon — like the man who planted beans,
Translated Plato and the woodchuck's talk —
Now prowls for mosses where a moist rock leans
And travels miles to show where lichens walk.
He treats as kin of his a Pine or Man
And looks at each with something near surprise.
His life is clean-cut, built on Nature's plan;
He seems appraising self with other's eyes,
And yet is heedless of unruly hair,
Frayed coat, worn shoes, assuming friends will know
Tree bark and clothes but give protective care
To finer inside portions as they grow.
All that he owns he uses for one end —
To bring together Nature and a Man
on equal terms — an honor to each friend —
Though Nature long was here when Man began.
He walks at ease in any company
With quiet born of years of listening,
With eagerness on leash, alert to see
The other's silent need of anything.
Well-meaning folks, consumed with misplaced zeals,
Remind him of his duty to implore
New grace, not knowing this man often kneels
In fervid worship on God's forest floor.

Through his generous and unstinting contributions of time, effort, and knowledge over a period of more than forty years "Doc" Hodgdon touched the lives of many, earning the love and respect of his many students, colleagues and friends in New England, as well as the respect of the botanical community. On December 31, 1976, he passed away after a long convalescence resulting from an automobile accident in August, 1974. In his honor the Albion R. Hodgdon Memorial Fund has been established with gifts from friends, family, former students and associates. The fund will be used to support the work of the Hodgdon Herbarium. Friends who wish to may send contributions designated for this fund to: Chairman, Department of Botany and Plant Pathology, University of New Hampshire, Durham, N.H. 03824.

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