Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 81 January, 1979 No. 825

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

RHODORA. — A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes, and single copies are available. For information and prices write RHODORA at address given below.

Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes, relating to the plants of North America, and floristically related areas, will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. All manuscripts should be submitted in duplicate, and must be double- (at least ⅜ of an inch) or triple-spaced throughout. Please conform to the style of recent issues of the journal. Extracted reprints, if ordered in advance, will be furnished at cost.

Address manuscripts and proofs to:
Russell R. Walton
Managing Editor, RHODORA
Harvard University Herbaria Building
22 Divinity Avenue
Cambridge, Mass. 02138

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Scirpus Longii Fernald

In New England, this rare species grows in a few marshes and wet meadows in central Connecticut and eastern Massachusetts.

Original artwork by Frances S. Chew

Rhodora

(ISSN 0035-4902)

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 81 January, 1979 No. 825

THE SYSTEMATICS OF THE AMERICAN SPECIES OF ALNUS (BETULACEAE)[1]

JOHN J. FURLOW

INTRODUCTION

All of the American species of *Alnus* are morphologically variable, and in several cases they are polymorphic. Many species and infraspecific taxa, in addition, are neither morphologically nor genetically well-differentiated. Taxa which are isolated geographically or ecologically pose few problems, but when their ranges intersect or overlap, they often become more difficult. Nevertheless, the taxa are all distinguishable, though the simultaneous use of several different characters may sometimes be required for accurate determinations.

The literature dealing with the genus in North America reveals considerable confusion in the circumscriptions, ranks, and classification of taxa at all infrageneric levels. Single-character variants have repeatedly been treated as distinct species, subspecies, or varieties, and there have been no unified concepts of these taxa. In order to confront these problems, I have assembled data from a number of sources not previously used in revisions of *Alnus*, including numerical taxonomic and chemosystematic studies. The detailed results of this experimental work will be discussed separately in a later paper.

The purpose and scope of this work is primarily monographic; the experimental aspects were conducted solely for the data they could provide and not as ends in themselves. In the work as a whole, traditional taxonomic methods predominated; that is, data were

---

[1] Editor's note: this is part one of two. Part II, including the remainder of the Taxonomic Treatment and all references, will be published in Vol. 81, No. 826 (April, 1979).

collected from a wide variety of sources, herbarium and field studies were undertaken in order to gain an intimate familiarity with the group, and, finally, the most phylogenetically accurate as well as practical system possible was synthesized.

The genus *Alnus* is not particularly large, but in order to perform a comprehensive investigation, I limited the present study to those taxa occurring in the New World. Thus I was able to see all of the species in the field and to obtain an ample supply of herbarium and experimental material. In instances where species occur in both the New and Old Worlds, as much material from the Old World as could be obtained was used.

Considerable work remains to be done, especially with regard to the Latin American taxa (for which herbarium material is not abundant). I feel that I have made significant improvements in the classification of these taxa, but the system proposed here must be regarded as somewhat tentative, pending additional exploration of the areas in which they occur and the accumulation of a great deal more material. In all of the species and infraspecific taxa, more detailed study of individual populations will have to be made before a true understanding of this group can be achieved. Especially important will be genetic and cytogenetic investigations, which are practically nonexistent. The present work should provide a basis, in terms of both classification and nomenclature, for such future investigation.

ACKNOWLEDGMENTS

I am most grateful to Dr. John H. Beaman for his interest, encouragement, and guidance throughout this study and for providing the principal facilities and materials with which it was conducted. I am expecially indebted to him for a research assistantship funded through a grant from the National Science Foundation (No. GJ-573) under which he was Principal Investigator. This grant supported computer use and a portion of the field work. Dr. Beaman also supplied funds from a Ford Foundation Grant (No. 71-3511), administered through the Michigan State University Studies Center, to support travel in Mexico, and he accompanied me during a part of this field work.

Much of the field work was financed by a Doctoral Dissertation Grant from the National Science Foundation (No. GB-28662), and this award is gratefully acknowledged. Support was also provided by the Department of Botany and Plant Pathology of Michigan State University in the form of both teaching assistantships and a graduate fellowship.

Sincere appreciation is also extended to Dr. James W. Hanover for his assistance and for the use of his laboratory and equipment, to Dr. William Tai for the use of his microscopes and photographic equipment and for his helpful advice, to Dr. Melinda E. Denton for her guidance during a portion of the study, and to Dr. Stephen Stephenson for his interest and assistance. Drs. Beaman, Hanover, Stephenson, and Tai read the entire manuscript; parts were also reviewed by Drs. Denton, Ralph E. Taggert, and Lynn E. Murray. The valuable suggestions made by all of these individuals are greatly appreciated.

Specimens for study were collected by Drs. Beaman, Denton, James H. Anderson, Loran C. Anderson, C. Eugene Jones, and Warren Douglas Stevens.

I wish to thank the curators of the herbaria I visited and from which I borrowed specimens for their helpfulness. These institutions are listed preceding the taxonomic treatment. Thanks are also extended to the director and staff of the Electron Microscope Laboratory of Michigan State University, where scanning electron microscopy was carried out.

Sincere thanks are extended to my parents, Mr. and Mrs. Wilbur S. Furlow, and to my parents-in-law, Mr. and Mrs. Donald H. Lotz, for both moral and financial support during this effort.

Finally, without the devoted and unselfish support and assistance of my wife, Gretchen, this work would not have been possible.

HISTORICAL ACCOUNT

Although *Alnus* was regarded as a distinct genus by Tournefort (1700) and most others before him, Linnaeus included it as a single species of *Betula* in the first edition of *Species Plantarum* (1753). This treatment was not widely accepted, however, and the separate genera continued to be used by such authors as Miller, Hill, and Ehrhart. Miller, in the 7th edition of *The Gardener's Dictionary* (1759) wrote: "Dr. *Linnaeus* has joined this Genus to the *Betula,* and places it in the fourth Division of his twenty-first Class of Plants, intitled, *Monaecia tetrandria,* from the Plants having male and female flowers, and the male having four Stamina. But as the Fruit of the Alder is of a conical Form, and that of the Birch cylindrical, so we shall keep them separate, whereby the Work will be rendered more intelligible to the Generality of Readers." The compound name *Betula-Alnus* was used for the alders in 1770 by Weston and in 1785 by Marshall (the genus *Betula* being retained in both cases for the birches). Above the level of genus, *Alnus* was included with such gymnospermous cone-bearing trees as *Abies, Pinus,* and *Larix* by Ray (1682) and Tournefort (1700). The development of supra-generic concepts applying to the alders is reviewed by Stearn (1973).

The genus was first divided into segregate genera in the revision by Spach (1841) who separated *Alnaster* and *Clethropsis* from *Alnus,* those segments being equivalent to the subgenera recognized in the present treatment. *Alnaster* included only *A. viridis; Clethropsis, C. nitida* and *C. nepalensis,* two Asiatic species; and *Alnus* the remaining species. Spach separated the South American species of *Alnus* into sect. *Phyllothyrsus* and the remaining species into sect. *Gymnothyrsus,* disregarding the great similarity between *A. acuminata* and the Mexican and Central American taxa.

The next revision of the genus was the monograph of Regel (1861), who viewed the genus as a single unit, but divided it into sections corresponding to Spach's genera and sections. In this work *Alnus jorullensis* was first treated as a variety of *A. acuminata. Alnus serrulata* was treated as a variety of the European *A. glutinosa,* and *A. rubra* was considered a variety of *A. incana.* Elements of *A. incana* ssp. *rugosa* were included in both *A. incana* and *A. glutinosa.* In 1865 Regel completed a second revision of the genus in which he used subgenera instead of sections as his major infrageneric divisions and changed many names and circumscriptions as well. Here he recognized *A. jorullensis, A. rubra,* and *A. serrulata* as separate species; the treatment of *A. incana* ssp. *rugosa* remained confused as before. *Alnus maritima* appeared in the second of Regel's works, but was placed in his subg. *Gymnothyrsus* rather than in subg. *Clethropsis.* A third treatment by Regel appeared in de Candolle's *Prodromus* (1868) and closely followed his 1865 system except for a return to the use of sections rather than subgenera.

Winkler revised the genus in *Das Pflanzenreich* in 1904. In this treatment only two sections are recognized, sect. *Alnobetula* (equivalent to Spach's genus *Alnaster*) and sect. *Gymnothyrsus* (including Spach's genus *Clenthropsis*). Major changes introduced in this work include the use of the names *Alnus alnobetula* (for *A. viridis*), *A. rugosa,* and *A. tenuifolia. Alnus serrulata* was treated as a variety of *A. rugosa,* and all of the Latin American taxa were considered varieties of *A. jorullensis.*

Although not monographic, several important revisionary works by Callier appeared about this time (1892, 1904, 1911, & 1918). In these publications a large number of new names and combinations are found.

The most recent revisions of the genus are those of Czerepanov (1955) and Murai (1964). Czerepanov erected an intricate structure of genera, sections, subsections, series, and species, but he did not make many real changes in the previous systems. Several of his groupings are quite artificial, such as the placing of *Alnus serrulata* in the same section as *A. rhombifolia* while putting *A. incana* ssp. *rugosa* in another section, and show a lack of understanding of the taxa, as in the recognition of both *A. tenuifolia* and *A. densiflora* as species. In a few cases, however, his choices seem to be wise, including the close placement of *A. jorullensis* and *A. firmifolia* in the same series. Murai's treatment (1964) is the most recent for the genus, but unfortunately it is practically unobtainable in American libraries. In an earlier version, Murai (1963) recognized two genera, *Alnaster* and *Alnus,* but in 1964 he combined these into one genus with two subgenera and six sections. That treatment follows popular current usage fairly closely, but it differs in several important respects. First, Murai treats *Alnus crispa* and *A. sinuata* as subspecies of a single species, *A. crispa* (the treatment used by Hultén, 1944). Second, he attempts to show a very close phylogenetic relationship between the Latin American and eastern Asian species by placing them all in sect. *Japonicae* of subg. *Gymnothyrsus* (probably not a correct interpretation). Third, he recognizes the close relationship of *Alnus maritima* with the Asian species of his sect. *Clethropsis.*

The most neglected aspect of the taxonomy of *Alnus* in the New World involves the complex of species and infraspecific taxa of Latin America. Besides the original descriptions of these taxa and more or less superficial treatments in the monographs and revisions listed above, the only study of this group has been the work of Fernald (1904b), Bartlett (1909), and Standley (1920), all based solely on a very limited supply of herbarium material.

TAXONOMIC CONCEPTS

The alders form a well-defined group easily circumscribed on the basis of morphological similarities and discontinuities. Although they have sometimes been segregated into a number of separate genera, as discussed above, the species share many features distinctive to the group as a whole and should properly be treated as a single genus. This view is widely accepted today. *Alnus* is separated from its closest ally, *Betula,* by several major discontinuities, including its woody infructescences with persistent scales, the structure of its buds, and the number of stamens in the flowers. Within the genus there are three distinct evolutionary lines, these being treated here as subgenera and distinguishable on the basis of leaf venation, exposure of the pistillate catkins during the winter, structure of the buds, season of blooming, and flower structure. One can find still smaller natural groups of species within the subgenera, but these are not as distinct morphologically, and it does not seem useful to subdivide the subgenera into sections.

Species in *Alnus* consist of apparently allogamous populations, these often showing incomplete intrinsic reproductive barriers among themselves (at least within subgenera), but usually isolated by their habitats. In spite of a relatively high level of morphological variability, especially in vegetative features, the species are nevertheless rather easily distinguished on the basis of morphology.

Previous workers have described numerous species and infraspecific taxa on the basis of variation in the shape, margin, pubescence, and gland characteristics of the leaves of already-known species in the genus. When a large number of specimens from throughout the ranges of such taxa are examined, however, these features are nearly always found to vary continuously from one extreme to the other without clear breaks. Taxa that were based mainly on extremes in pubescence (*Alnus crispa* var. *mollis, A. ferruginea, A. pringlei, A. rhombifolia* var. *bernardina, A. rugosa* f. *emersoniana, A. serrulata* f. *noveboracensis*), leaf shape (*A. arguta* var. *subsericea, A. crispa* var. *harricanensis, A. ovalifolia, A. serrulata* var. *subelliptica*), and infructescence form (*A. crispa* var. *elongata*) are consequently no longer recognized.

It has been suggested by Raven (1962) that the degree of reproductive isolation between taxa where they come into contact is of fundamental taxonomic importance, providing information dealing with the relationship between groups of plants as they actually occur in nature. Groups which intergrade in such areas are considered to be subspecies of the same species, while populations which may hybridize but do not intergrade are treated as separate species (*loc. cit.*). This concept is a useful one in *Alnus*, and it has been applied in the present treatment.

In several instances wide-ranging species have been treated previously as separate species where they occur in different geographical regions. From the degree of morphological similarity between the populations in these regions and the amount of intergradation seen where their ranges overlap, it is evident that these taxa are conspecific. *Alnus tenuifolia* in western North America, *A. rugosa* in eastern North America, and *A. incana* in Eurasia are seen as representing parts of a single species, as are *A. crispa* in eastern and northern North America, *A. sinuata* in western North America, and *A. viridis* in Eurasia. In Latin America, the same pattern is shown by *A. arguta* in Mexico and Central America and *A. acuminata* in South America. In these taxa, however, in spite of the clear relationships at the species level, one can see a degree of differentiation in each case. The geographically separated populations are therefore considered to be subspecies of *A. incana, A. viridis,* and *A. acuminata,* respectively.

Subspecies, as employed in the present treatment, are segments of species having relatively large geographical ranges and which are distinct in morphology and (to at least some degree) habitat (cf. Du Rietz, 1930; Camp & Gilly, 1943; Mayr, 1947; Steenis, 1957). The category is used not only for those taxa showing distinct geographical distributions, but also for ecotypes, as seen in *Alnus acuminata* spp. *arguta* and *glabrata* and *A. jorullensis* spp. *jorullensis* and *lutea.* The biological nature of geographical and ecological races in *Alnus* appears to be essentially the same, warranting the use of the same formal category.

Putative hybridization frequently occurs where closely related species of *Alnus* grow sympatrically (e.g., *A. incana* ssp. *rugosa* and *A. serrulata*). In such cases, the taxa are otherwise morphologically distinct and do not appear to intergrade except for the occurrence of intermediate individuals in the putative hybrid populations. Many species of *Alnus* are extrinsically isolated, as shown by successful artificial hybridization between such distinct and isolated taxa as *A. glutinosa* of western Europe and *A. rubra* of western North America (Ljunger, 1959).

EVOLUTION AND PHYTOGEOGRAPHY

Alnus is distributed throughout the Northern Hemisphere, extending below the Equator along the Andes in South America. It is absent from the Antilles in both modern and fossil floras, though floristically related genera (*Fagus, Salix, Myrica, Liquidambar,* and *Nyssa*) existed there in the Tertiary (Graham, 1972b). Distributional centers can be recognized in the following regions: 1) circumpolar Europe, Asia, and North America, 2) mountainous southern Europe, Asia Minor, and Iran, 3) the Himalayas and adjacent mountainous central China, 4) coastal eastern Asia from northern Manchuria to the Tropic of Cancer, 5) mountainous parts of Mexico, Central America, and northern South America, 6) coastal eastern North America from Nova Scotia to the Gulf of Mexico, and 7) western North America from southern Alaska to northern Mexico. In addition, alleged fossils of *Alnus* have been reported from Australia and Tasmania, where the genus does not occur today, but these are of questionable identity (Berry, 1923).

Alnus is represented in the early fossil record of the angiosperms, appearing in the upper Cretaceous, where it was associated with other early woody genera, including *Betula, Acer, Corylus, Cercis, Ginkgo,* and *Sequoia.* The earliest "definite *Alnus* pollen" in North America appears in the Maestrichtian of the Rocky Mountains, and the first mega-fossils are of the same age in British Columbia (Wolfe, 1973). During the Tertiary the genus became prominent and is represented by wood, leaves, fruits, cones, and pollen in numerous fossil floras. Over 40 Cenozoic species are recognized by LaMotte (1952) for North America alone. Pollen of *Alnus* is common in bog deposits of Pleistocene age and is an indicator of changes in climate and vegetation during that period. Many Cenozoic fossil alders bear a striking resemblance to present-day species, and it may be possible to trace the migrations and evolution of these taxa using such evidence, although the record is somewhat sketchy.

Origin of the Genus and Subgenera.

According to Takhtajan (1969), *Alnus* may have evolved in southwestern Asia. He shows that subg. *Clethropsis* (which he considers to be the most primitive segment of the genus) is presently more or less restricted to the Himalayas, Assam, and southwestern China, a region he believes to have been important in early angiosperm evolution. However, recent evidence, summarized by Raven and Axelrod (1972, 1974), points away from this region as the site of early angiosperm evolution. These authors (1974) conclude that the angiosperms most likely originated in western Gondwanaland before the separation of Africa and South America, spreading northward from this region into Laurasia, where the Hamamelidiflorae (including the Fagales) then differentiated. Furthermore, as discussed below, much evidence suggests that subg. *Clethropsis* may not actually be the most primitive aspect of the genus after all.

Murai (1964) states that *Alnus* originated in eastern Asia, specifically in an area including or near present-day Japan, basing this conclusion on the large total number of species and the large number of supposedly relict distributions occurring there today. He regards members of his sect. *Bifurcatus* (of subg. *Alnobetula*), today completely restricted to Japan, as the most primitive taxa of the genus. There is evidence, however, that while this area, like the Himalayan region, has been an important center of preservation, it was not a major center of angiosperm evolution (Raven & Axelrod, 1974).

It is difficult to deduce the true site of origin of *Alnus* on the basis of present information. A number of methods have been proposed for locating possible points of origin or centers of dispersal of plant groups, including the use of measures of diversity, degree of differentiation, size of area, presence of disjunct distributions, and fossil evidence. Various reviews of these techniques (e.g., Cain, 1944; Cracraft, 1975) have shown that none is completely satisfactory for all taxa. But one or more of them may be useful in a particular group. All of the above criteria, and especially the principle that the greatest diversity in a group of plants occurs in the area of its origin (Vavilov, 1951), suggest that the genus did, in fact, originate on the Asian land mass. Present distributional patterns and the fossil record indicate that subg. *Clethropsis* evolved in southern Asia, while subg. *Alnobetula* differentiated in northern and northeastern Asia. Subgenus *Alnus*, considered here to be the most primitive part of the genus, most likely originated at southern and mid-latitudes in Asia, later further specializing in cooler, more northern areas. Following this original divergence, each of the subgenera spread throughout the Northern Hemisphere.

On the basis of wood anatomy, it appears that the Betulaceae arose from an ancient Hamamelidaceous stock derived from Magnoliaceous ancestors (Tippo, 1938). Wolfe (1973), in discussing the origin of patterns of leaf venation in the Amentiferae, supports this view, stating: "in their consistent craspedrodromy and intercostal venation, the various members of the Betulaceae are highly similar to the *Corylopsis* type and could well be the end products of this hamamelid line". Continuing, he shows that the leaf venation of the Betulaceae (*Corylus* pattern) is entirely absent from the Magnoliidae, Dilleniidae, and Asteridae, and is rare in the Rosidae. In the Hamamelidae, however, it is common in the Fagaceae and Ulmaceae as well as the Betulaceae. Early in the history of the family, *Betula* and *Alnus* apparently formed one line while *Corylus, Ostrya, Ostryopsis,* and *Carpinus* diverged and formed another. *Betula* and *Alnus,* on the basis of anatomical features, have been shown to be the most primitive members of the family (Tippo, 1938; Hall, 1952). As seen from their similar morphology and anatomy, these two genera show relatively little divergence.

An early hypothesis as to the events which may have followed the evolution of *Alnus* is outlined by Kryshtofovich (1929). According to this theory, the early Tertiary flora of Europe became divided into three principal "floristic provinces". The northwestern division forest (Greenland Province) was made up of *Populus* species and other temperate deciduous trees showing no Asiatic relationship. *Alnus* and *Betula* were rare in this region during the early Tertiary. The second region (Turgai Province) occupied the middle zone of Siberia, America, and Alaska, and it was covered by deciduous forest in which *Betula* and *Alnus* occupied an important place. To the south was the third region (Poltava Province) which included the Ukraine and southern Russia, and which was characterized by remnants of the older evergreen tropical vegetation. As the climate cooled, the Turgaian vegetation enlarged, spreading into the Greenlandian and Poltavan regions. Thus, the fossil record was interpreted by Kryshtofovich as showing that *Alnus* originated in the southern Asian highlands, spreading east across Siberia and western North America, but not moving west until later in the Tertiary to complete the circumpolar distribution seen today. In fact, the present distribution and fossil record of *Alnus* in North America do suggest such an early introduction from the west followed by a much more recent migration from the east.

The species comprising subg. *Alnus* are divided into two sections by Murai (1964), one of these (sect. *Japonicae*) including several eastern Asian taxa as well as all of the Latin American taxa, and the other (sect. *Glutinosae*) including *A. incana* and its various allies. Murai concludes that both of the sections originated in the vicinity of Japan, sect. *Japonicae* directly from his sect. *Clethropsis,* and sect. *Glutinosae* from ancestors common to itself and sect. *Clethropsis.* All of the evidence, however, suggests that subgenera *Alnus* (sects. *Glutinosae* and *Japonicae* of Murai) and *Clethropsis* are monophyletic, which would make the derivation of Murai's sections in this manner impossible. Murai's sect. *Glutinosae* appears, rather, to be derived from his sect. *Japonicae* and adapted to a cooler climate. Close relationships between taxa of eastern Asia and northern Latin America were first noted by Hara (1948) and later discussed briefly by Matuda (1953) and Sharp (1953a, 1972). Pollen said to resemble that of *Alnus japonica* has been reported from the early Oligocene of Colorado by Van Alstine (1969), though it seems doubtful that such an identification could be made with much precision. Comparative morphology does not substantiate the relationship suggested by Murai between the alders of Mexico and eastern Asia. Additional study will be needed to establish the true relationship.

Dispersal in the New World

Axelrod and Raven (1972), in discussing plate tectonic theory and evolutionary biogeography, hypothesize that the Amentiferae had its primary radiation on the Laurasian land mass before Europe and America were separated by the North Atlantic Ocean. They conclude that "migration across Laurasia was direct and essentially uninterrupted during much of the Cretaceous . . ." This connection between Europe and America may have lasted well into the Eocene (cf. Raven, 1972; Ryan & Axelrod, 1974). However the evidence seems to point away from an early introduction of *Alnus* from the east, as discussed below.

Alnus has generally been regarded as a remnant of widespread mesophytic Arcto-Cretaceous and Arcto-Tertiary geofloras (Axelrod, 1952). However Wolfe (1972) has questioned the validity of the concept of a uniform mesophytic flora in the early Tertiary on the basis of paleobotanical data, noting that "no known Cretaceous or Paleocene flora contains 20 or more mixed mesophytic genera." Pollen data suggest the existence of two major floristic provinces during the late Cretaceous and early Tertiary, the first including eastern North America and Europe, and the second occupying western North America and eastern Asia (Wolfe, 1975). *Alnus* may first have been represented in the tropical vegetation, and not become a component of the temperate forest until the Oligocene (Wolfe, 1972). During warmer periods in the Oligocene the alders, along with the maples and other such presently temperate genera, are seen as again occupying lowland regions. Cooler climates following this period removed the tropical vegetation, though a true mixed mesophytic vegetation did not appear until the Miocene (Wolfe, 1972).

In discussing the vegetational history of the Rocky Mountains, Leopold and MacGinitie (1972) show affinities between the early Eocene floras of this region and modern plants of southeastern Asia. However, Raven and Axelrod (1974) point out that this Rocky Mountain fossil flora could just as easily represent a remnant of an older widespread subtropical Laurasian vegetation as a flora with such southeastern Asian connections. Chaney (1947) shows that during Eocene time the neotropical flora extended north to about 49 degrees on the western edge of the continent. The flora of the Rocky Mountains had taken on a tropical American aspect by mid-Eocene, while in far northwestern America the termination of Asiatic affinities was more gradual, lasting until mid-Miocene, by which time the modern coniferous forest had already developed in the Rocky Mountains (Leopold & MacGinitie, 1972).

According to Graham (1972a), the lower Tertiary vegetation of the southern United States probably consisted of neotropical warm-temperature to tropical elements with some broad-leaved deciduous species (including *Alnus*), while a broad-leaved deciduous community with paleotropical components existed in the Pacific Northwest. After the Palaeogene, the Rocky Mountain and western floras lost their Asiatic element, which was gradually replaced by an expanding mixed mesophytic forest in mid-Tertiary. Later, mountain building resulted in changing climates, eliminating the mixed mesophytic element in much of the western United States, Canada, and western Europe.

The ancestors of both *Alnus maritima* and the present Latin American species were doubtless components of the early Tertiary vegetation of America, having arrived from Asia via the Bering land bridge, although Murai (1964) shows *A. maritima* entering by a route through southeastern Asia and South America before the division of Gondwanaland, an idea not in accord with the fossil evidence (see below). Although fossils of *Alnus* from Latin America are few, enough exist to show that the genus reached this region from the north at a relatively early time. Using a fossil pollen flora from Veracruz, Graham (1972b, 1973) shows that *Alnus* (along with *Abies, Juglans, Fagus, Liquidambar, Ulmus, Celtis, Picea, Myrica,* and *Populus*) reached southern Mexico by the mid-Miocene but is not present in older sediments there. Three genera from this flora (*Alnus, Juglans,* and *Myrica*) are found in late Miocene pollen deposits in Panama, being absent from earlier floras there. The earliest abundant *Alnus* pollen in northern South America is mid-Pleistocene in age, although infrequent, isolated grains are also found in lower Pleistocene sediments (Hammen, 1972; Graham, 1972b, 1973). A Pliocene species based on leaf material from Bolivia (*Alnus preacuminata*) was published in 1922 by Berry and is often cited in connection with the southward migration of northern temperate genera, but this fossil is not generally accepted today as representing *Alnus*. Pollen of *Myrica* appears in South America before *Alnus* (in the lower Pliocene), but *Juglans* is not found until the lower Quaternary (Graham, 1972b). By the middle to late Jurassic, orogenies had produced islands between North and South America, but presumably *Alnus* did not migrate south, at least in numbers, until the last fold of the isthmus (Talamanca Ridge) became fully emerged in the Miocene (Bartlett & Barghoorn, 1973).

Alnus viridis and *A. incana* may not have been introduced to North America until after the Miocene, when the northern climate became cooler. *Alnus viridis* ssp. *crispa* and *A. incana* ssp. *rugosa* may be the most primitive segments of these species, both existing as apparent relicts in northeastern North America today. The origin of

A. serrulata is obscure, but it undoubtedly occurred at a very early time. It, like *A. maritima,* may be a remnant of the early Tertiary flora, but its affinity to *A. incana* suggests a later origin, perhaps in the Miocene or Pliocene. *Alnus rubra* appears to be a remnant of the western mesophytic Miocene forest, as are *A. rhombifolia, A. oblongifolia,* and the species of the Latin American complex. The stock which formed this group moved south into Mexico and Central America, where it diverged to form the taxa seen in those regions today.

Historical Factors Affecting Distributions.

Of the present alders occurring in eastern North America, other than *Alnus maritima, A. serrulata* appears to be the most ancient, judging from its high degree of morphological specialization. The species today has a predominantly coastal distribution, although it occurs in the Appalachian and Ozark highlands as well, where it may have evolved. Braun (1955) points out that there are many disjunctions of vegetation from upland areas (the Appalachian and Interior Highlands) on the younger Atlantic Coastal Plain and explains that these occurred during the Tertiary, followed by dissection of the intermediate peneplane, which resulted in the loss of suitable habitats there. During the Pleistocene glacial periods, the range of *A. serrulata* may have been decreased in the north, especially in the mountains. Braun (1951) feels that glaciation did not strongly disrupt the deciduous forest zone in the southeastern United States as far north as the Appalachian Plateau in southern Ohio and Kentucky. Evidence from numerical analysis (Furlow, in preparation) suggests that *A. serrulata* survived the Pleistocene in two widely-separated localities, the southeastern Atlantic Coastal Plain and the Ozark Highlands, where the populations have diverged significantly.

Alnus viridis ssp. *crispa* must have been separated from *A. viridis* of Europe more recently, as shown by the relatively very small divergence of these taxa. Hultén (1963) argues that the North Atlantic floras are very ancient, and that "the phytogeographical conditions around the North Atlantic . . . give poor support for a land bridge that could have existed in Quaternary or late Tertiary times." He allows, however, that "circumpolar plants of the far North" probably migrated by wind over the frozen polar sea or on floating ice. It would not be difficult to imagine *Alnus* being dispersed in this manner. This taxon probably survived glacial advances in several refugia, including the southern Appalachians, where it occurs as a relict today. A. Löve (1959, 1967) and Löve and Löve (1967) provide evidence that refugia existed in parts of Scandinavia, Iceland, and the Canadian arctic archipelago west of Baffin Island, and Ives (1963) concludes that large parts of northern Labrador, where ssp. *crispa* occurs today, remained ice-free during the maximum extent of Wisconsin glaciation. That the species could have withstood the severe conditions of the Pleistocene in such northern refugia is shown by Thorarinsson (1963), who cites fossil alder leaves in Pleistocene volcanic sediments in Iceland.

Harshberger, as early as 1903, rejected the idea of massive migrations of plants before advancing Pleistocene glaciers and accepted the Appalachians as a glacial refugium in the eastern United States. The Scandinavian element, according to him, invaded the New World in the late Pleistocene, remaining after the final glacial retreat. *Alnus incana* ssp. *rugosa,* which is scarcely differentiated from *A. incana* of southwestern Europe, could have arrived in this way, but if so, the populations of *A. incana* present in Scandinavia today must have displaced the Pleistocene forms by migrating from the east at a later time since these are quite different from either spp. *rugosa* or *incana* of southwestern Europe, as shown below. It is possible that ssp. *rugosa* entered the New World at an earlier period, that ssp. *incana* then became extinct in northern Europe, and that the present northern European ssp. *incana* stock invaded Scandinavia from the east, all before the Pleistocene. Subspecies *rugosa* probably survived in refugia at low elevations, either east or west of the Appalachian highlands and immediately south of the ice (D. Löve, 1959).

It has been shown by Hultén (1928) from the distributions of a number of species that a flow of plants has occurred in both directions between Siberia and North America. *Alnus incana* ssp. *tenuifolia* and *A. viridis* ssp. *sinuata* apparently entered this region following the extinction of the mixed mesophytic forest in the middle Miocene, because their first fossils are in the Miocene of Alaska (Wolfe, 1969). Fossil species corresponding to these present taxa, *A. harneyana* and *A. fossilis* (*A. carpinoides*), respectively, were present in the western United States and Canada during the Miocene in habitats similar to the ones they have today (Chaney, 1959; Chaney & Axelrod, 1959). During the Pleistocene *A. incana* ssp. *rugosa* was separated from ssp. *tenuifolia* and *A. viridis* ssp. *crispa* from ssp. *sinuata* by a "wide gap in the continuity of the northern coniferous forest" (Raup, 1947). Subspecies *sinuata* may have survived the glacial advances in refugia in unglaciated Alaska (Hultén, 1937b; Livingstone, 1955) and points southward to Washington (Heusser, 1960) as well as in its present habitats in the mountains of the northwestern United States, though probably at lower elevations. Its Pleistocene presence in these localities is supported by geological, paleobotanical, and botanical evidence (Heusser, 1960). *Alnus incana* ssp. *tenuifolia* probably survived in its present habitats in the Sierra Nevada and Rocky Mountains as far south as New Mexico and Arizona. After the Pleistocene, *A. incana* ssp. *rugosa* again extended across northern Canada and met ssp. *tenuifolia* in northern Alberta or Saskatchewan. At the same time, the range of *A. viridis* ssp. *crispa* became continuous with that of ssp. *sinuata* in Alaska.

Alnus incana spp. *rugosa* and *tenuifolia* fit the pattern shown by Iltis (1966) in which western species range north and south across the glacial boundary while their eastern vicariants are restricted to glaciated land. Iltis interprets this pattern as evidence for the ultimate western origin of these eastern taxa, but in this case at least, it seems more likely that the restriction of ssp. *rugosa* to glaciated soil in the eastern United States and Canada is an artifact caused by climate. In the mountainous West, ssp. *tenuifolia* occurs south of the glacial boundary only at high elevations in the mountains or in the far North. The cool climatic conditions required by *A. incana* do not exist south of the glacial boundary in the East. In fact, a considerable amount of glaciated land exists south of the southern limits of the range of *A. incana* ssp. *rugosa* in eastern North America.

It is probable that *Alnus maritima* was formerly much more widespread in North America than it is today. Its closest allies are found only in Asia, following a pattern shared by many other woody genera of eastern North America and that region (Li, 1971, 1972). Other members of subg. *Clethropsis* are known in the fossil record of the western United States and Canada. These taxa have the same distinctive leaf features (margin and venation) of modern representatives of this group. One such species, *Alnus relatus,* occurred in Idaho and Oregon during the Miocene in habitats similar to those of

A. maritima in the eastern United States today (Chaney, 1959). Another fossil species, *A. cremastogynoides,* described from the Eocene or Oligocene of British Columbia, differs in certain respects, but also shows the characteristic leaf features of this group (cf. Berry, 1926; Brown, 1937).

The presence of *Alnus maritima* on the Delaware Peninsula might best be regarded as of relatively recent achievement since this species is not hardy further north and probably could not have survived the Pleistocene there. It most likely migrated to its present location on the coastal plain during the climatic moderation following the Pleistocene glaciation from some location further to the south. The cause of the wide disjunction of this species in Delaware and Oklahoma is not known, but the two populations are shown in the numerical taxonomic and chemosystematic studies (below) to have diverged somewhat, pointing away from a recent achievement of the disjunction (cf. Fryxell, 1967). This evidence, together with the indications of great antiquity discussed above, indicates an origin of the disjunct distribution by isolation of the populations following range restriction.

The Latin American taxa, along with *Alnus rubra, A. rhombifolia,* and *A. oblongifolia,* apparently have been in their present locations for a very long time, as suggested by McVaugh (1952). *Alnus rubra,* today restricted to the Pacific coastal fog belt, appears to be a relict from the moist mixed forest of the Northwest in the Miocene. *Alnus rhombifolia* may have also been a part of this forest, having adapted to summer-dry conditions since the Pleistocene (Wolfe, 1969). Miocene fossils of *Alnus hollandiana* (*A. corrollina*), a species morphologically similar to modern *A. rhombifolia,* are described from western lowland and slope forests by Chaney (1959), in association with such mesophytic genera as *Acer, Fraxinus, Fagus, Ulmus, Liquidambar, Ostrya, Juglans,* and *Nyssa.* Benson (1962) lists *A. rhombifolia* and *A. oblongifolia* as vicariants in the California and Southwestern Oak Woodlands and Chaparral, respectively. He feels that the Southwestern Oak Woodlands and Chaparral have been "relatively little modified from the Oligocene prototype, which also had summer rain," these two regions apparently being separated by intervening arid lands by the Pliocene.

The antiquity of the temperate flora of Mexico and Central America has been a subject of dispute among various workers. An excellent review of this problem was made by Rzedowski in 1965.

One view holds that "the present temperate flora of Mexico must have come from the north during the late Pleistocene" because prior to the Pliocene "there was little continuous area with sufficient elevation to support a temperate vegetation . . ." (Sharp, 1953b). Dressler (1954), however, after reviewing the paleobotanical and physiographic evidence, concludes that the temperate types were introduced from the western part of North America as early as the Miocene and reached Guatemala by the Pliocene, the eastern North American plants probably not migrating into Mexico until the early Pleistocene. Chaney (1936), in discussing the movement of temperate forests southward during the cooling period of the Cenozoic states that "a modified type of Miocene forest had migrated as far south as southern Guatemala . . ." by this time, including such genera as *Alnus, Arbutus, Crataegus, Ostrya, Pinus, Quercus,* and *Salix.* Axelrod (1939) lists the genera *Quercus, Cornus, Ulmus,* and *Juglans* in Mexico as possibly having differentiated in that area and thus having "no floristic relationship to the northern species of the same genera." McVaugh (1952) states that "such genera as *Alnus, Arbutus, Carpinus,* and others have persisted in Mexico and adjacent Central America since early Tertiary or even since Cretaceous time . . .". *Alnus rubra, A. rhombifolia,* and *A. oblongifolia* all show strong affinities to the species of Latin America and may be remnants of stocks which either did not migrate further south originally, or which originated from a northward-moving Madro-Tertiary flora during or before the Pliocene.

Little is known of the history of the Latin American species of *Alnus* due to the scanty fossil record. All of the taxa are very closely related, and they are not strongly differentiated, indicating relatively recent speciation. Numerical analysis (Furlow, in preparation) indicates the most primitive present segment of the complex to be the population of *A. acuminata* ssp. *arguta* in southwestern Mexico. *Alnus jorullensis,* as well as the other subspecies of *A. acuminata* appear to have diverged primarily in response to differing climates at various altitudes.

ECOLOGY

Most of the alders are associated with wet habitats. The plants may occur in standing water, on stream banks, on wet floodplains, in bogs and muskegs, or on moist mountain slopes. A few are adapted to somewhat drier conditions. *Alnus viridis* ssp. *crispa,* for example, is found sometimes in apparently dry woods, and *A. jorullensis* often occurs on mountain slopes away from standing or running water. In both of these species, however, the plants are nevertheless usually associated with some source of moisture, even though it may not be as obvious as in the other species. Most alders grow only in full sunlight, an exception again being *A. viridis* ssp. *crispa,* which may occur as an understory component in conifer woods. Where this is the case, the forest is usually very open, and the alder stratum may actually represent a declining successional stage. Nearly all of the taxa are isolated by habitat where their geographical distributions overlap, although some have fairly wide tolerances and may actually occur sympatrically.

All species of *Alnus* are mycotrophic, with root nodules (Figure 1) containing nitrogen-fixing microorganisms (cf. Bond, 1956, 1963; Bond *et al.,* 1954; Hawker & Fraymouth, 1951). That nitrogen-fixation actually occurs has been established by chemical means for *Alnus viridis* ssp. *crispa* (Dalton & Naylor, 1975), and, in a recent paper, Fleschner *et al.* (1976) have measured the rate of nitrogen-fixation in *Alnus incana* ssp. *tenuifolia.* The exact identity of the endophytes has been a matter of dispute since early in the nineteenth century (cf. Kelley, 1950). Whatever their identity, there is evidence (Bond, 1963; Rodriquez-Barrueco & Bond, 1968) that the nitrogen-fixing endophytes of *Alnus* are specific for the species upon which they are growing.

Symbionts forming mycorrhizae on *Alnus* have also been reported (Masui, 1926; Klečka & Vukalov, 1935; Trappe, 1964; Neal *et al.,* 1968). These organisms apparently have a role in nutrient absorption and the minimization of root diseases, but their biology is not yet well understood.

The role of *Alnus* in plant succession has been studied by a number of investigators, especially in areas recently deglaciated in southern Alaska. In studies at Glacier Bay, Cooper (1923a, 1923b, 1931, & 1939) showed that *Alnus* plays an important part in the succession of recently deglaciated land. He demonstrated that from a pioneer stage of mosses, horsetails, *Epilobum,* and *Dryas,* the community moves through a thicket stage of willows and alders before reaching the forest climax of spruce. This work has been continued by Crocker and Major (1955), Crocker and Dickson (1957), Lawrence (1958), Heilman (1966), Mitchell (1968), Ugolini

(1968), Hurd (1971), Reiners *et al.* (1971), and others. Reiners *et al.* (1971) estimate the length of stages in the successional sere at Glacier Bay as follows: horsetails, sedges, *Epilobium, Salix,* and *Populus,* 0 to 5 years; *Dryas,* 5 to 20 years; *Alnus viridis* ssp. *sinuata,* 20 to 40 years; *Populus* and *Picea sitchensis,* 50 to 70 years; *Picea sitchensis* forest, 75 to 100 years; and *Tsuga* forest, over 100 years. One of the roles of *Alnus* may be the addition of nitrogen to the soil. Lawrence (1958) found that nitrogen entering the soil originates mainly from the dropped leaves rather than from the nodules themselves. He showed that the autumn foliage of *Alnus viridis* ssp. *sinuata* contains up to 3% (dry weight) combined nitrogen and estimated that an alder thicket five years old and five feet tall adds 140 pounds of nitrogen to the soil per acre per year from the fallen leaves. Crocker and Dickson (1957) found that the soil in alder thickets had accumulated over one ton of nitrogen per acre by the end of 70 years. Another study, by Dalton and Naylor (1975), showed insignificant nitrogen accumulation in soil containing plants of *Alnus viridis* ssp. *crispa,* though these workers apparently failed to consider fallen leaves as a possible source of the nitrogen.

Crocker and Major (1955) found that the soil in alder thickets can change in pH from values over 8.0 to less than 5.0 within 35 to 50 years. In this period, organic matter (with a pH of 4.2 to 4.6) six to seven centimeters deep had accumulated below the plants. The 18-inch deep mineral soil profile and forest floor combined had accumulated almost 4.0 kilograms of organic carbon per square meter.

Other species of *Alnus* cited by authors as pioneers in succession include *Alnus rubra* in the Pacific Northwest (Worthington *et al.,* 1962; Newton *et al.,* 1968) and *A. acuminata* ssp. *arguta* in southern Mexico and in Guatemala (Standley & Steyermark, 1952). From information on the labels of herbarium specimens used in this study, it appears that virtually every species plays this role, occurring regularly on cut or burned-over land and in abandoned fields. Many species (*A. incana* ssp. *rugosa, A. serrulata, A. viridis* ssp. *crispa*) are regarded as weeds, growing in ditches, along embankments, on pond shores, in wet pastures, and other places where they are not desired.

In some cases where *Alnus* might be expected as an important pioneer in succession, it is absent. Tisdale *et al.* (1966) point out that

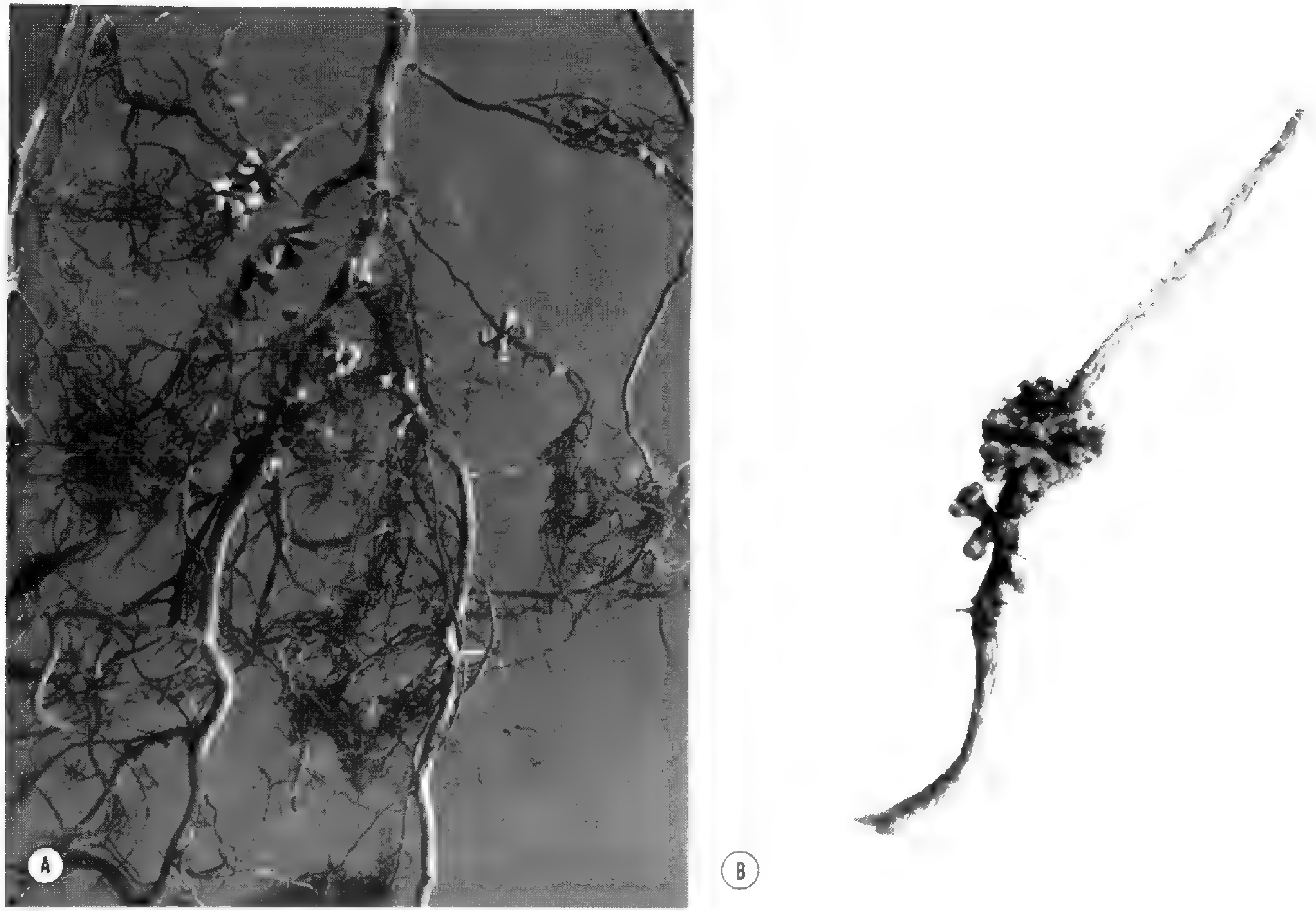


Figure 1. Nodules of nitrogen-fixing endophytes on roots of *Alnus serrulata*. A, ×0.7. B, ×1.5.

alders are not present in the successional vegetation occurring on recently glaciated land on Mt. Robson in the Canadian Rocky Mountains even though the environmental conditions seem to be favorable for its development there. Additional study will be necessary for a more complete understanding of this problem as well as the general role of these plants in succession.

McVean, in a series of papers on the ecology of *Alnus glutinosa* in England (1953a, 1953b, 1955, 1956a, & 1956b) makes a number of observations that also appear to be true for the American species. Among these is the fact that the root system has both surface and deep branches, enabling the plant to survive in either waterlogged soil or where the water table is deeper. Only the surface roots bear nodules, however. He also shows that seed germination is independent of light, normal temperature variation, and pH within the range of 3.5 to 8.0, but is sensitive to low oxygen and moisture levels. He (1953a) lists a large number of animal feeders, parasites, insect pests, and destructive fungi and discusses the effects of each on plants in various stages of their life histories.

MORPHOLOGY AND ANATOMY

Habit. Members of the genus *Alnus* are woody plants ranging in size from small shrubs to large trees. In general, the species of warm climates are arborescent while those of cool-temperate, boreal, and montane regions are fruticose in form. Two American shrubby species (*Alnus maritima* and *A. incana*) approach tree stature. Even those species which normally attain the size of trees usually possess several main trunks, pointing, perhaps, to a shrubby ancestral habit. The fruticose form in modern taxa, however, is regarded as an adaptation to cool climates which has arisen from the tree habit independently in a number of lines. Photographs showing the habits of representative taxa are provided in Figures 2 and 3.

Stems. Mature stems in *Alnus* range in diameter from about one centimeter to more than two meters. In most species the bark is smooth, though in larger trees it is sometimes broken into flat plates or can be furrowed and corky (Figure 4). All of the Latin American taxa develop transverse constrictions, as shown in Figure 4. It is unknown whether this feature is caused by external environmental factors. On smooth bark, the lenticels are visible and range from very

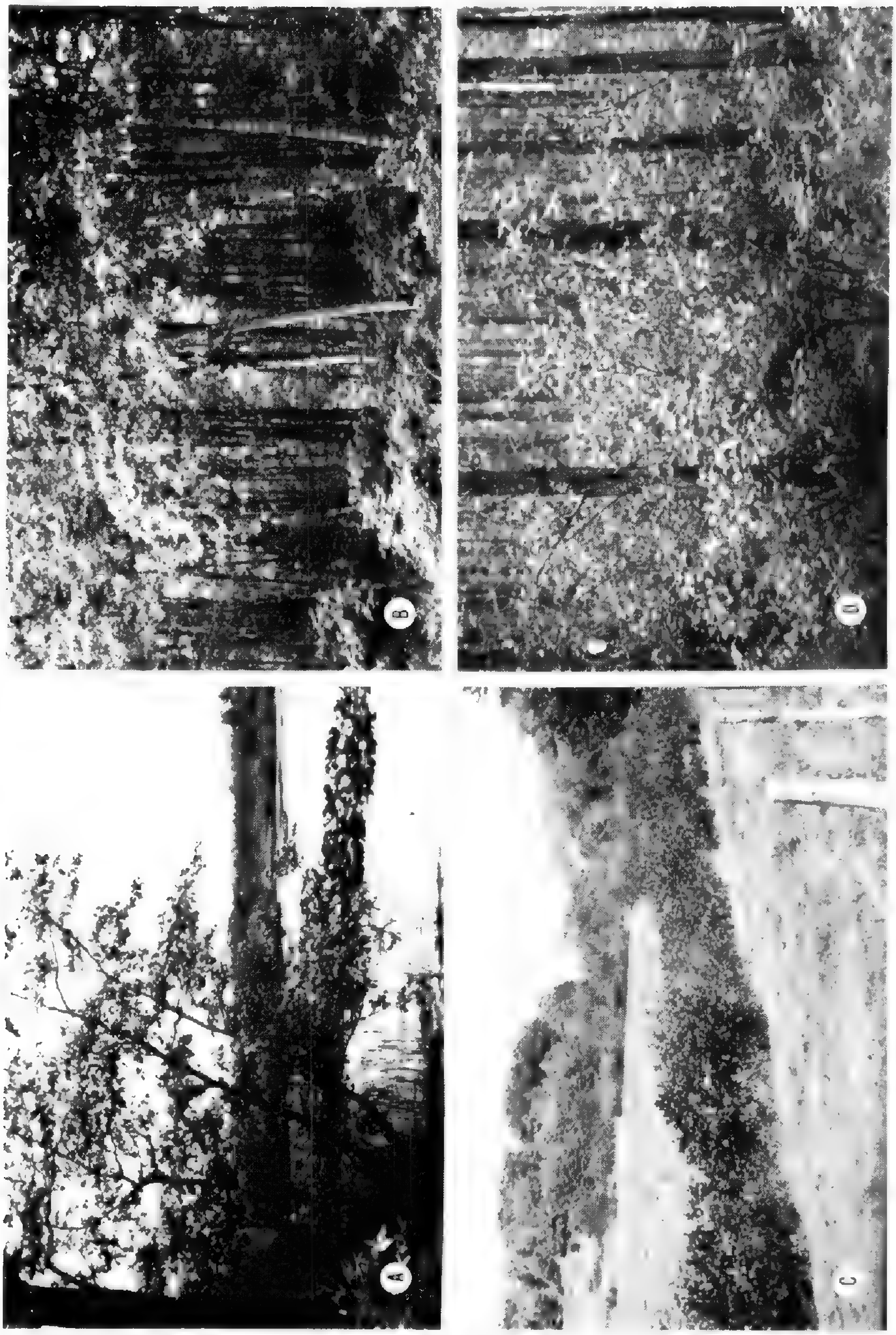


Figure 2. Habits and habitats of representative species of *Alnus*. A, *Alnus incana* ssp. *rugosa*, large shrub on the bank of the Pigeon River in northern Indiana. B, *A. rubra*, medium-sized trees forming a dense stand on a river floodplain in west-central Washington. C, *A. serrulata*, medium-sized shrubs growing on the banks of a small stream in the Blue Ridge Mountains of southern Virginia. D, *A. viridis* ssp. *crispa*, medium-sized shrubs forming an understory in pine woods in central Alberta.


A
B
C
D

small and inconspicuous round spots (e.g., *A. serrulata* and *A. maritima*) to large, prominent, transverse markings (e.g., *A. incana* ssp. *rugosa*). The presence of smooth bark in the shrubby species, as well as the shrub habit itself, may be a result of neoteny, these species never reaching "maturity" in an anatomical sense (Hall, 1952).

The twigs are terete, but in cross-section have a triangular-shaped region of pith in the center which varies in form from that of a symmetrical (equilateral) triangle in *Alnus maritima* and *A. rhombifolia* to nearly linear in *A. viridis* ssp. *crispa*. In *A. incana* and *A. serrulata*, the pith is equilaterally-triangular, but with strongly concave sides. The color ranges from a light buff in *A. viridis* and *A. rhombifolia* to a dark brown in *A. incana, A. serrulata,* and *A. acuminata*. Sometimes pronounced longitudinal ridges are evident on the surface of the twigs, expecially in *Alnus acuminata* and *A. maritima*. In transection these ridges are seen to contain air chambers.

The epidermis of young shoots is usually somewhat pubescent, glandular, and resin-coated. The pubescence and glands vary in density, color, and size, but are otherwise similar from species to species. The glands are invariably denser and larger at the nodes than along the internodes of the stems. On the youngest twigs, the lenticels are always oriented longitudinally, but these rapidly become laterally elongate with secondary growth of the stem. The leaf scars are triangular and about as high as broad. They bear five bundle scars, the upper two much larger than the lower three, which may be fused together. In *Alnus rhombifolia, A. acuminata, A. rubra,* and *A. jorullensis* the lower two lateral bundle scars are more elongate than those of the other species, although this feature varies from specimen to specimen.

In *Alnus viridis* one can usually see a differentiation in the length of the twigs. The leaves are borne on short spur shoots growing laterally on longer branches. In other species the leaves are borne directly on the long shoots. After one to several seasons, the short shoots may elongate and become long branches.

Figure 3. Habits and habitats of representative species of *Alnus*. A, *Alnus oblongifolia*, trees ca. 17 m tall in a stream on Mt. Graham in southern Arizona. B, *A. jorullensis* ssp. *jorullensis*, tree ca. 10 m tall on Volcan Popocatepetl, Mexico. C, *A. rhombifolia*, trees ca. 4 m tall on the banks of the Trinity River in northern California. D, *A. viridis* ssp. *sinuata*, shrubs ca. 2.5 m tall covering a subalpine mountainside in Glacier National Park, Montana.

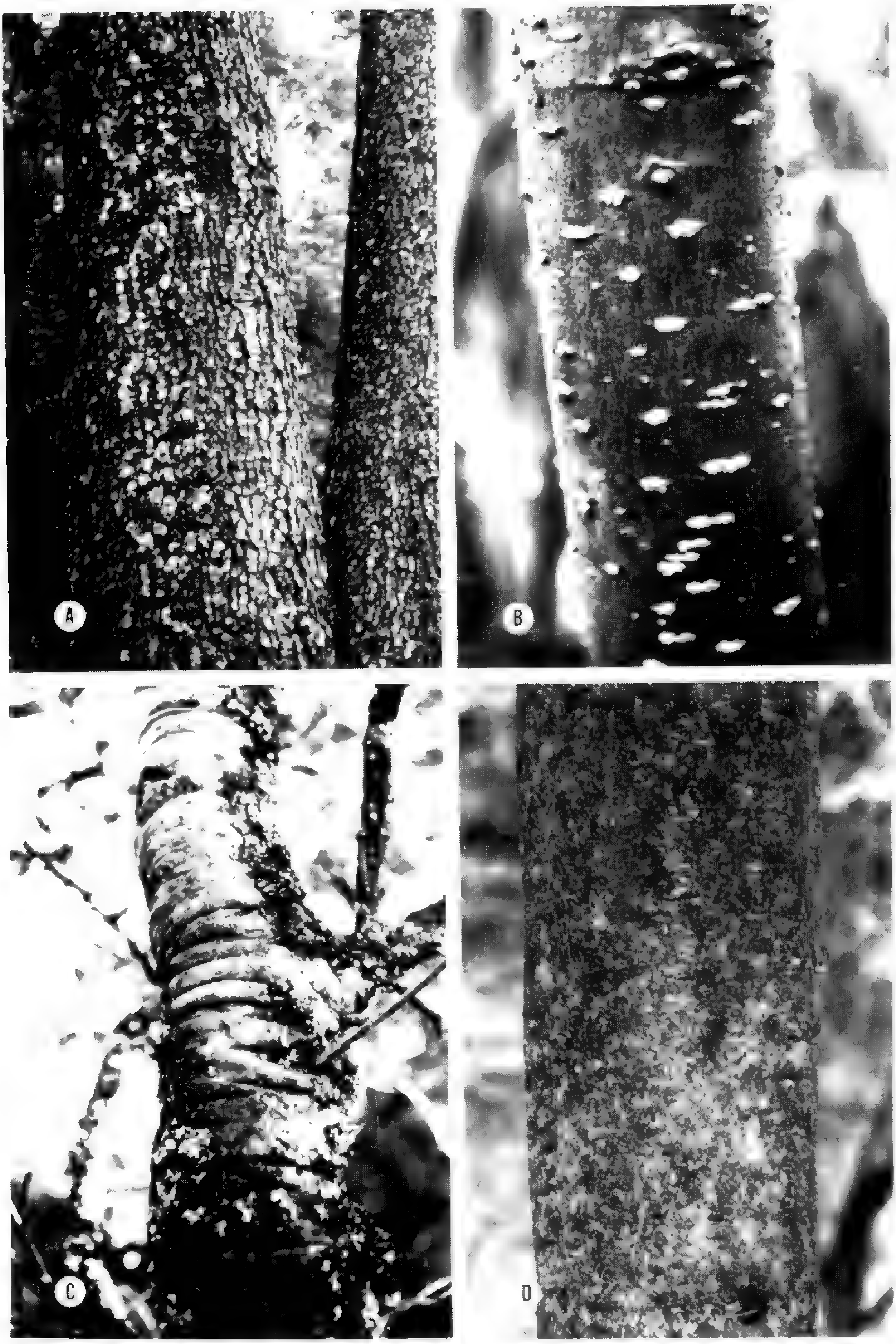


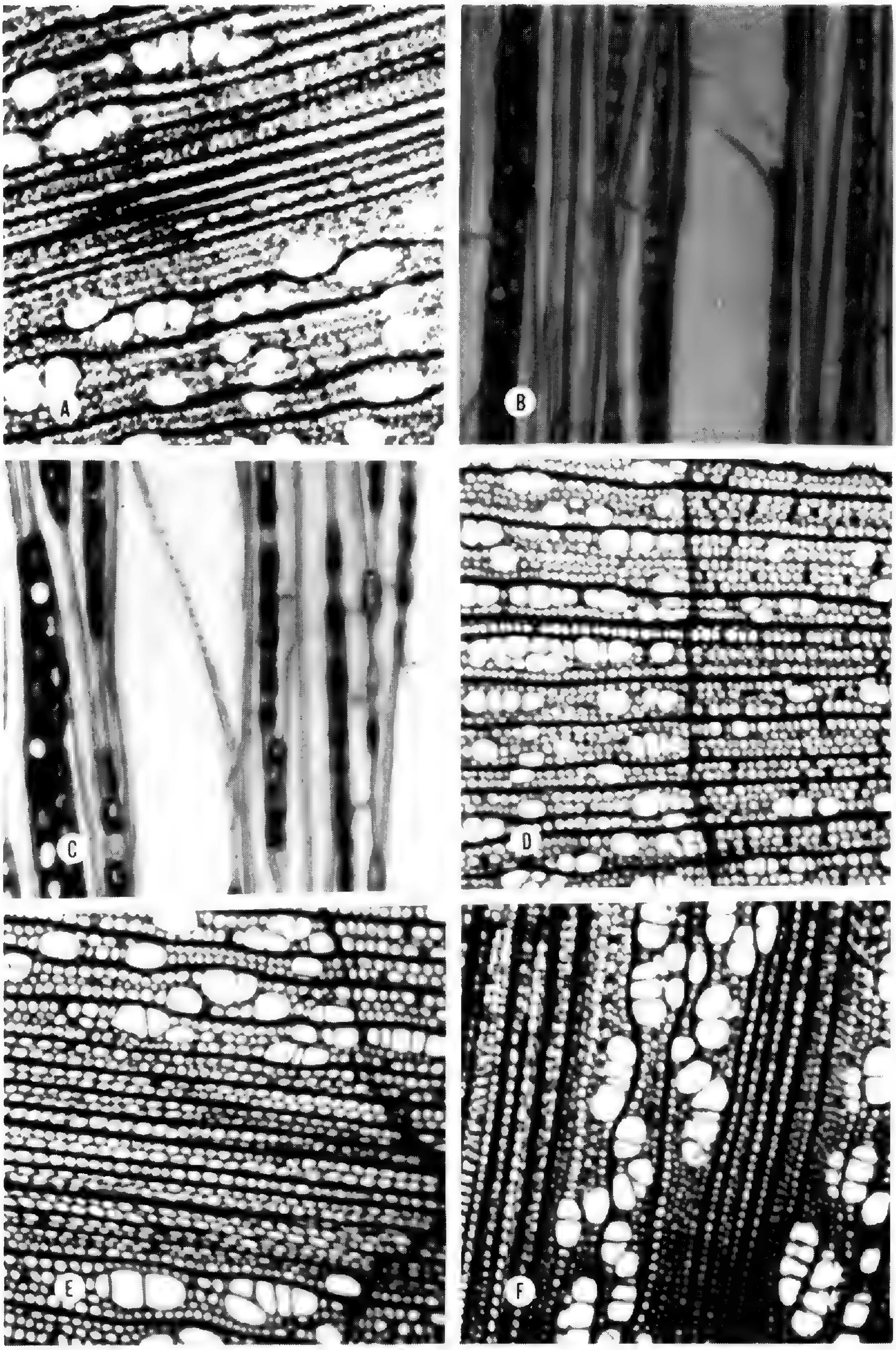
Figure 4. Bark of a representative species of *Alnus*. A, Alnus oblongifolia, ×0.03. B, *A. incana* ssp. *rugosa*, ×0.2. C. *A. jorullensis* ssp. *jorullensis*, ×0.17. D, *A. serrulata*, ×0.33.

The wood of *Alnus* has long interested plant anatomists. Bailey (1911) first showed a phylogenetic series involving the building up of large multiseriate rays from uniseriate ones. He noted that there is no inclination of any aggregation in *A. incana, A. rubra,* and *A. maritima. Alnus rhombifolia* was shown to have completely fused aggregate or compound rays. In a second paper (Bailey, 1912) he discusses in detail the evolution of the compound ray and shows a reversal in the trend (from multiseriate to uniseriate) in several species, including *A. viridis* ssp. *crispa* and "*A. acuminata*". This phenomenon has also been discussed by Hoar (1916), Forsaith (1920), Anderson and Abbe (1934), and Hall (1952). The latter states that aggregate rays are absent in *A. oblongifolia, A. jorullensis, A. ferruginea,* and *A. mirbelii.*

All of the above authors describe the wood of "*Alnus acuminata*" as having uniseriate rays, and several of them note that growth rings are absent in this species. It is not certain, however, that *A. acuminata* of South America is what these workers actually had in mind. In each case, anatomical material apparently was obtained from cultivated plants, although the authors are not clear on this point. Examination of wood of all the species showed that multiseriate rays are present in all of them except *A. viridis,* which does, in fact, have uniseriate or partly biseriate rays. Some species, such as *A. incana* ssp. *rugosa, A. serrulata,* and *A. maritima,* possess rather poorly-developed multiseriate rays, however (Figures 5 & 6). All species have uniseriate rays between the multiseriate ones.

The wood is made up primarily of vessels and fiber tracheids, although some true tracheids may be present in certain species. The outer part of the primary cortex is always collenchymatous (Metcalf & Chalk, 1950). The pericycle contains a composite and continuous ring of sclerenchyma, and the secondary phloem contains stone cells. The cork cells are almost tabular in shape.

Hall (1952), in characterizing the family Betulaceae, its tribes, and its genera on the basis of wood anatomical features, provides the most complete description of *Alnus* wood available. Species differences are shown to occur with respect to vessel length, diameter, frequency, shape in cross-section, and the number of bars in the scalariform perforation plates. Both tracheids and fiber tracheids are present in some species, while only fiber tracheids occur in others. Intervascular pitting may be opposite, alternate, or transitional, depending on the species.

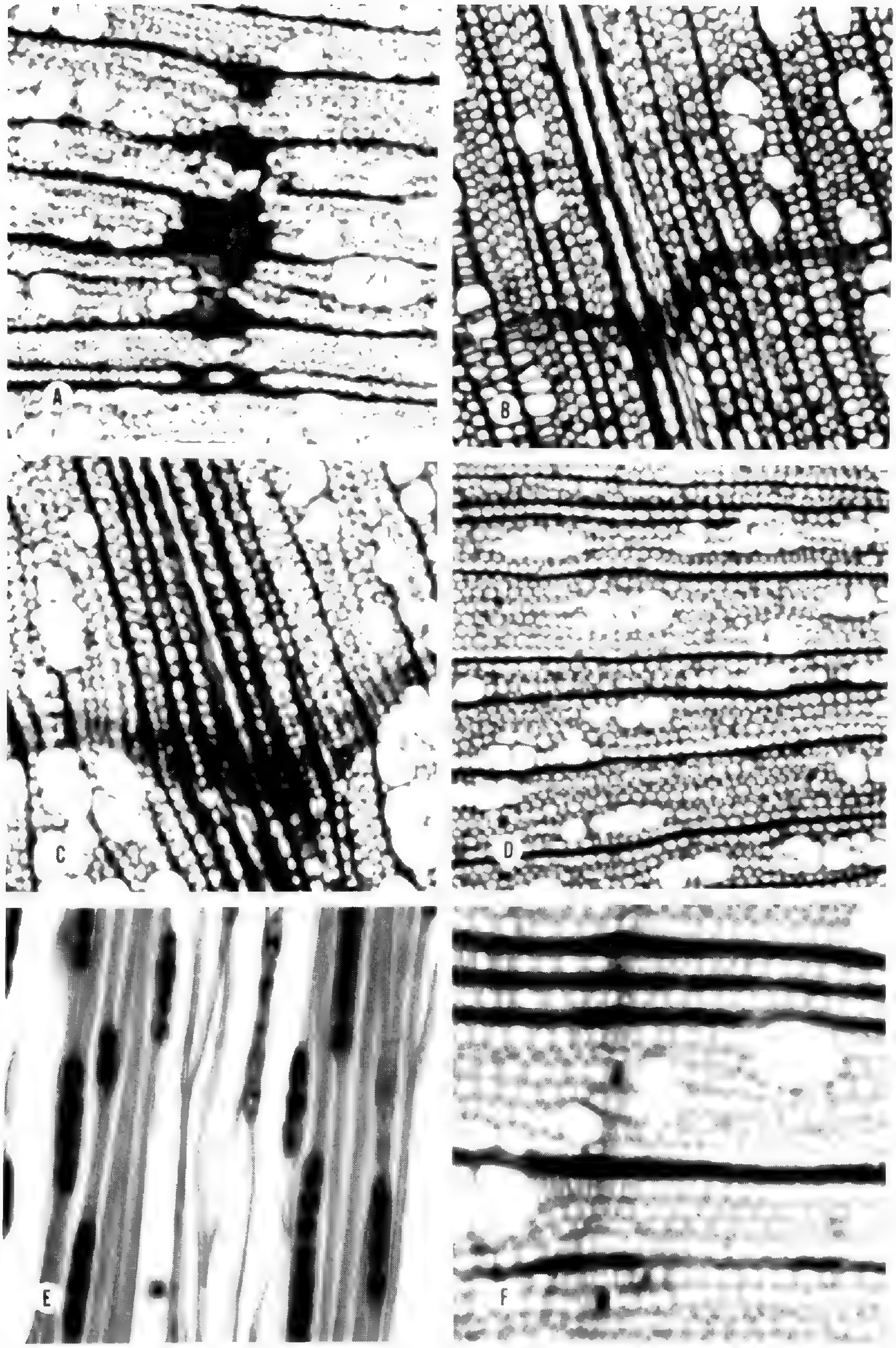

A
B
C
D
E
F

Specialized features, according to Hall (1952), include alternate intervascular pitting, as opposed to opposite; a large or small number of bars in the perforation plates rather than an intermediate number; the absence of true tracheids; and uniseriate rays by reduction from aggregate rays. Other features in an advanced state include a reduced frequency of vessels, angular vessel shape in cross section, and a large number of vessels per cluster. Unfortunately, Hall did not examine fossil alder wood in the collection of his data. Such a study might have proved useful in the determination of primitive and advanced conditions in wood traits.

Many of the species names used by Hall are of uncertain application, and he does not include documentation of the specimens studied. In addition, in many cases he does not name the species showing the particular features discussed, so his work is of limited value at the species level. From the information available, however, and from my own observations, it is possible to make the following general statements.

The wood of *Alnus viridis* is specialized in that it possesses uniseriate rays apparently derived from multiseriate ones by reduction and a relatively large number of vessels per unit area. It is primitive, however, in that the vessels are small and intervascular pitting is opposite. The wood of *A. incana* and *A. serrulata* is somewhat advanced in that it possesses moderate-sized vessels of intermediate frequency and with alternate intervascular pitting, but it is primitive in that it has only moderately well-developed multiseriate rays. Wood of *A. maritima* is advanced in that its vessels are small and infrequent, but it is primitive in possessing aggregate rays. *Alnus jorullensis* is distinct from the other species in having very angular vessels of medium size. The wood of this species is primitive with respect to its high frequency of vessels and its multiseriate rays.

Figure 5. Photomicrographs of *Alnus* wood. A, *Alnus acuminata* ssp. *arguta, transverse section showing aggregate rays and large diameter vessels,* ×107. B, *A. acuminata* ssp. *arguta,* tangential section showing rays and details of the vessel wall, ×263. C, *A. acuminata* ssp. *glabrata,* tangential section showing uniseriate and biseriate rays and details of the perforation plate of a vessel, ×263. D, *A. incana ssp. rugosa,* transverse section showing little tendency for aggregation of the rays, ×107. E, *A. incana* ssp. *tenuifolia,* transverse section showing aggregation of rays and moderate diameter vessels, ×107. F, *A. jorullensis* ssp. *lutea,* transverse section showing multiseriate rays, ×107.


A
B
C
D
E
F

Wood of *A. rhombifolia, A. oblongifolia,* and *A. acuminata* is generally primitive in having aggregate rays, but advanced in showing numerous, large, circular vessels. Thus, each species can be seen as specialized in some wood features and not in others, probably in response to the particular environmental conditions present in its habitat.

Stipules. The stipules vary greatly in size, ranging from about 4 to 15 mm in length and from about 0.5 to 6 mm in width, as shown in Figure 7. *Alnus viridis, A. serrulata,* and *A. acuminata* possess relatively large stipules, while *A. maritima* and *A. oblongifolia* have much smaller ones, being particularly reduced in width. Mostly, they are ovate in shape with acute tips. Like the leaves, they are pubescent and glandular on the abaxial surface. The margins are lined with longer and coarser hairs than those borne on the surface.

Winter Buds. The buds of *Alnus* are stalked (though nearly sessile in *A. viridis*).The bud stalks are very short modified branches, often with one or more nodes which bear reduced leaves as the buds are forming. In all of the species except *A. viridis* the buds are protected by two slightly modified stipules and sometimes one or more of the stipules of the next level of the bud (Figures 8 & 9). These may cover the entire bud or be reduced in size or entirely absent (*A. maritima* and *A. oblongifolia*). The stipular scales are equal in size, and when large enough, valvate. Buds of *Alnus viridis* are covered by several unequal bud scales apparently derived from stipules. In all species the stalks and scales are pubescent, glandular, and covered with resinous secretions. Within the buds the leaves are conduplicate and usually more or less plicate within their stipules. However, the degree of development of the young leaves varies considerably in different species.

Figure 6. Photomicrographs of *Alnus* wood. A, *Alnus jorullensis* ssp. *lutea,* transverse section showing "wax chambers", ×107. B, *A. maritima,* transverse section showing small-diameter vessels and a small multiseriate ray, ×107. C, *A. rhombifolia,* transverse section showing a well-developed multiseriate ray, ×107. D, *A. viridis* ssp. *crispa,* transverse section showing small-diameter vessels and uniseriate rays, ×107 E, *A. viridis* ssp. *crispa,* tangential section showing the vertical nature of the rays, ×263. F, *A. viridis* ssp. *sinuata,* transverse section showing slight aggregation of the rays, ×263.

Figure 7. Stipules and expanding leaves of representative species of *Alnus*, all ×1.0. A, *Alnus incana* ssp. *rugosa*. B, *A. maritima*. C, *A. rhombifolia*. D, *A. viridis* ssp. *crispa*.

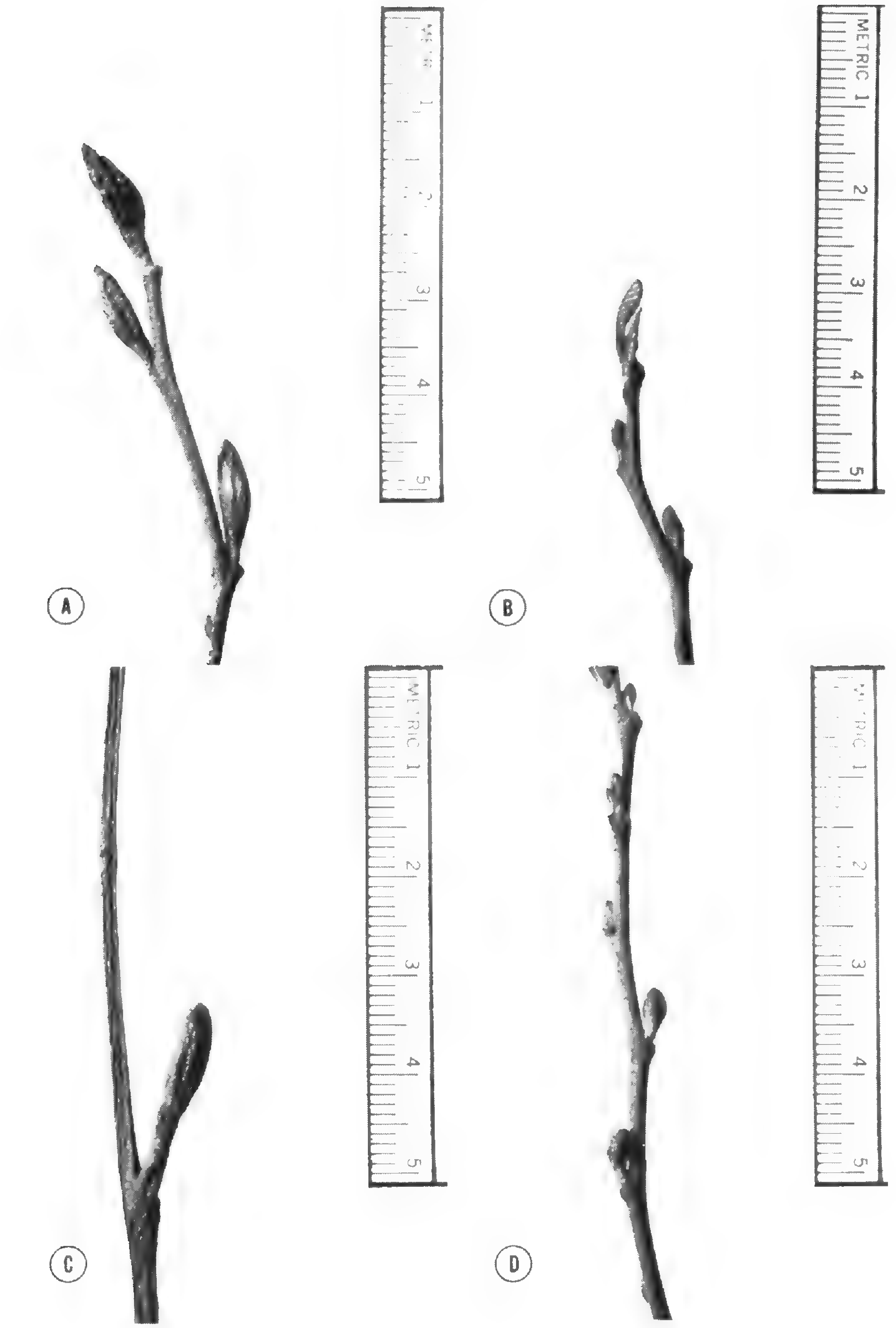


Figure 8. Twigs with winter buds of representative species of *Alnus*. A, *Alnus oblongifolia*. B, *A. maritima*. C, *A. rubra*. D. *A. serrulata*.

Leaves. The leaves of *Alnus* are borne alternately along the twigs. The petioles are terete and are usually rather deeply grooved above The leaves are typically ovate and double-serrate. However, *Alnus maritima* and other members of subg. *Clethropsis* have much narrower leaves with low, distant, upturned, single teeth (though the leaves of seedlings of *A. maritima* may sometimes be ovate and double-serrate). Many species in the genus have laciniate forms (cf. Hylander, 1957). In North America, local populations of *A. incana* ssp. *rugosa, A. viridis* ssp. *sinuata,* and *A. rubra* demonstrate this condition. Several species, including *A. maritima, A. serrulata,* and *A. jorullensis,* have obovate leaves, apparently derived from the ovate form by suppression of linear development accompanied by increased lateral growth in the apical region. The range of variation in shape and margin for each American taxon is shown in the series of leaf outlines pictured in Figures 10, 11, and 12.

The leaves are pinnately veined, the lateral veins sometimes branching one or two additional times to form subsecondaries near the margins, especially toward the base. Venation in *Alnus maritima* is semicraspedodromous to eucamptodromous, while in all the other species it is simply-craspedodromous (cf. Hickey, 1973). The size of the leaf is not correlated with the number of lateral veins but with their distance from each other. The lateral veins of all species form about the same angle with the midrib (30 to 40 degrees). Between the lateral secondary veins are tertiary cross-veins. These are well-developed, forming ladder-like reticulations in some species, but they may be incomplete in others. Within these reticulations are areoles containing simple to branching veinlets.

Leaf margins are somewhat thicker than other parts of the blade, especially at the apices of major teeth, giving them a glandular-tipped appearance. In some species (best illustrated by *Alnus rubra*) the margin is revolute (Figure 13). The base is usually rounded, truncate, or cordate, but it may be extended or even attenuate. The apex is usually acute, but its shape ranges from long-acuminate to truncate to deeply notched in some species (Figures 10, 11, & 12).

The foliage of all the alders is pubescent, especially along the major veins on the abaxial surface, although a few taxa such as *Alnus viridis* ssp. *sinuata* and *A. acuminata* ssp. *glabrata* are essentially glabrous. The hairs are simple, straight, and borne mainly on the veins and veinlets, even in densely-pubescent forms. They vary in length, color, and density, but not in general shape or appearance.

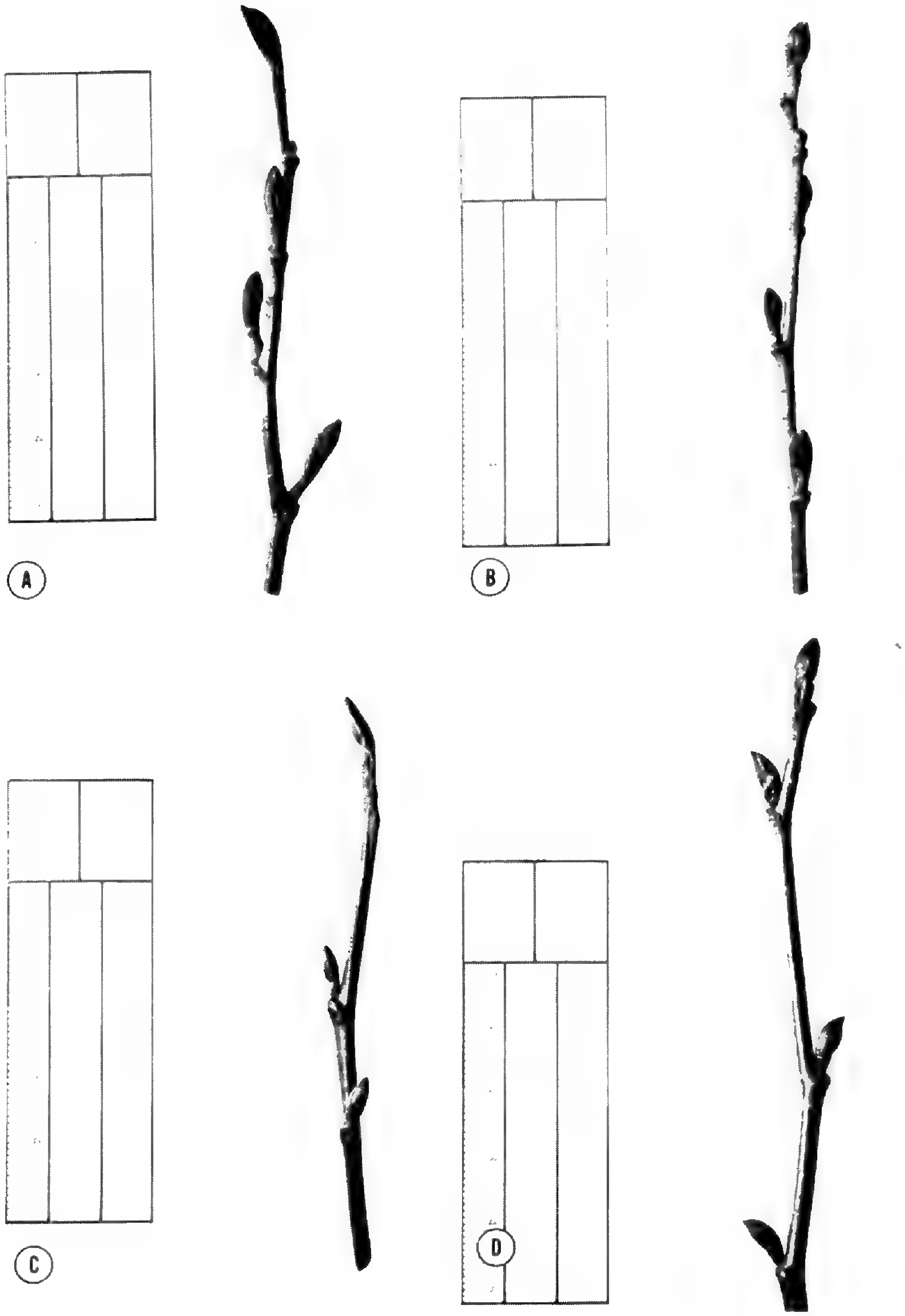


Figure 9. Twigs with winter buds of representative species of *Alnus*. A, *Alnus incana* ssp. *rugosa*. B, *A. incana* ssp. *tenuifolia*. C, *A.rhombifolia*. D, *A. viridis* ssp. *crispa*.

The leaves of all species of *Alnus* are glandular as well as pubescent (Figure 14). The glands, which are more frequent on the lower surface and petiole than above, are described by Metcalf and Chalk (1950) as "consisting of a short but broad stalk composed of low, suberized cells and a shield-like head made up of cells appearing to be polygonal in surface view, but resembling a palisade in sections of the gland." The development of the glands is described by Dorman (1924), who found that they secrete a high molecular weight polyterpene. The glands may be large, yellow, and crowded, as in *Alnus jorullensis* ssp. *lutea,* or they may appear small, dark, and sparse, as in *A. incana* ssp. *rugosa.* They often darken with age, especially on the adaxial surface. The leaves, like the twigs and buds, are often covered with a thick deposit of resinous material, the amount varying from species to species. Of the American species, *A. viridis* is by far the most glutinous.

The anatomy of leaves of the Betulaceae was comprehensively treated by Boubier (1896), who shows that *Alnus* varies considerably in its leaf structure and describes the blade, veins, and petiole histologically (cf. also Solereder, 1908). The stomata are ranunculaceous (surrounded by several irregularly-arranged epidermal cells) and present only on the abaxial surface (Figure 15). A hypodermis is present just below the epidermis in some species, being better developed in some than in others (Boubier, 1896). The hypodermis is found in species of all subgenera.

Inflorescences. *Alnus* is monoecious with the flowers borne in catkins, the staminate pendent and the pistillate erect (Figure 23). The pistillate catkin was shown by Abbe (1935) to be composed of numerous cymules arranged spirally on a primary axis. Each cymule bears three levels of bracts, only the two tertiary florets being present except in rare cases. The staminate catkins are likewise made up of tiny cymules, but all three florets are usually present. *Alnus viridis* and *A. maritima* lack one of the two tertiary bracts of the staminate cymule, while both are usually present in all of the other species.

Alnus maritima and its allies of southern Asia bear the staminate catkins singly in the axils of leaves at the tips of branches and the pistillate catkins singly in leaf axils on the same branch just below the staminate. All of the other species bear the pistillate catkins in racemose clusters just below the solitary and axillary staminate

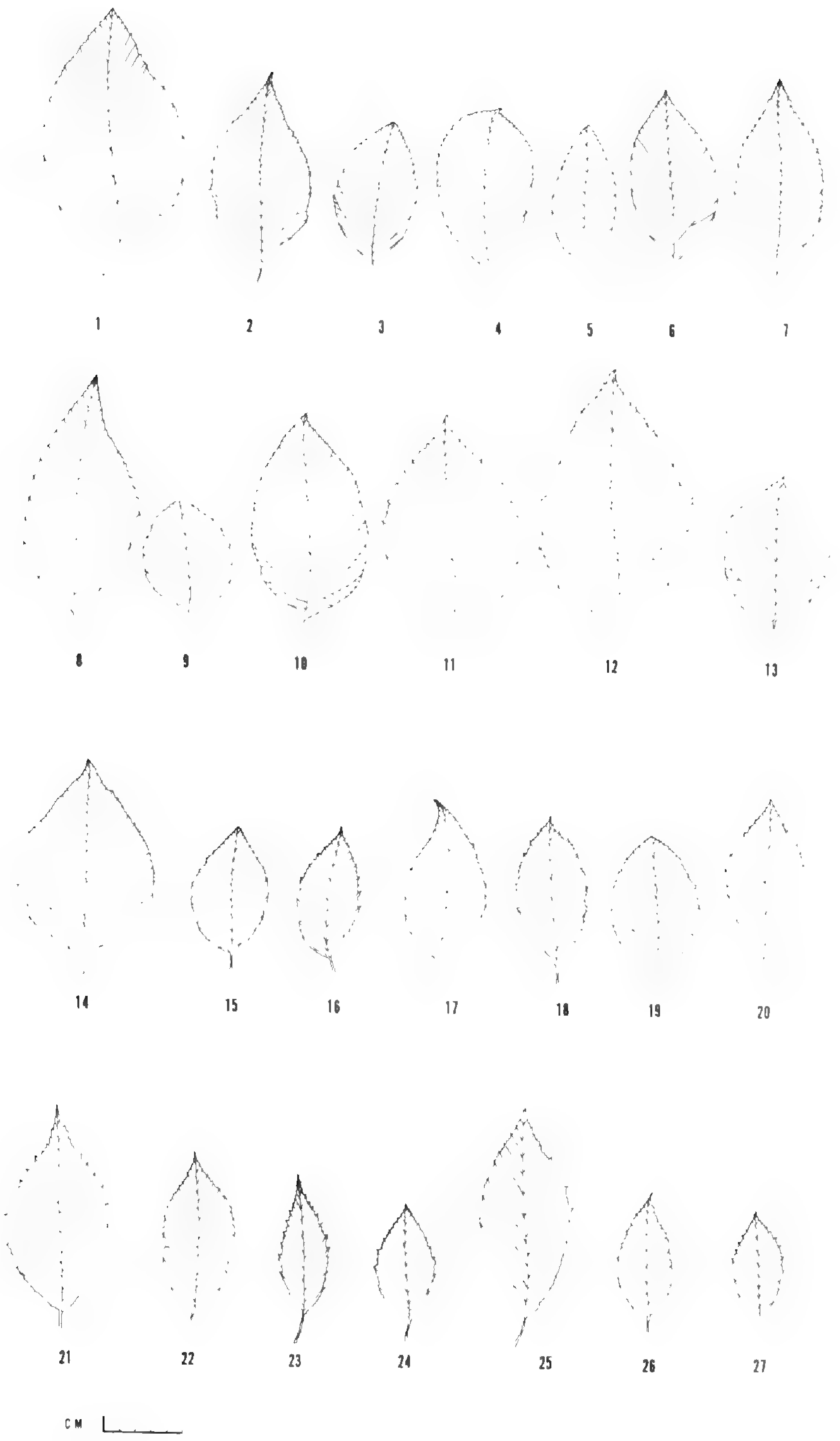


Figure 10. Outlines of leaves of *Alnus* showing extremes in the patterns of shape and margin variation: 1–10, *Alnus acuminata* ssp. *acuminata;* 11–20, *A. acuminata* ssp. *arguta;* 21–27, *A. acuminata* ssp. *glabrata.*

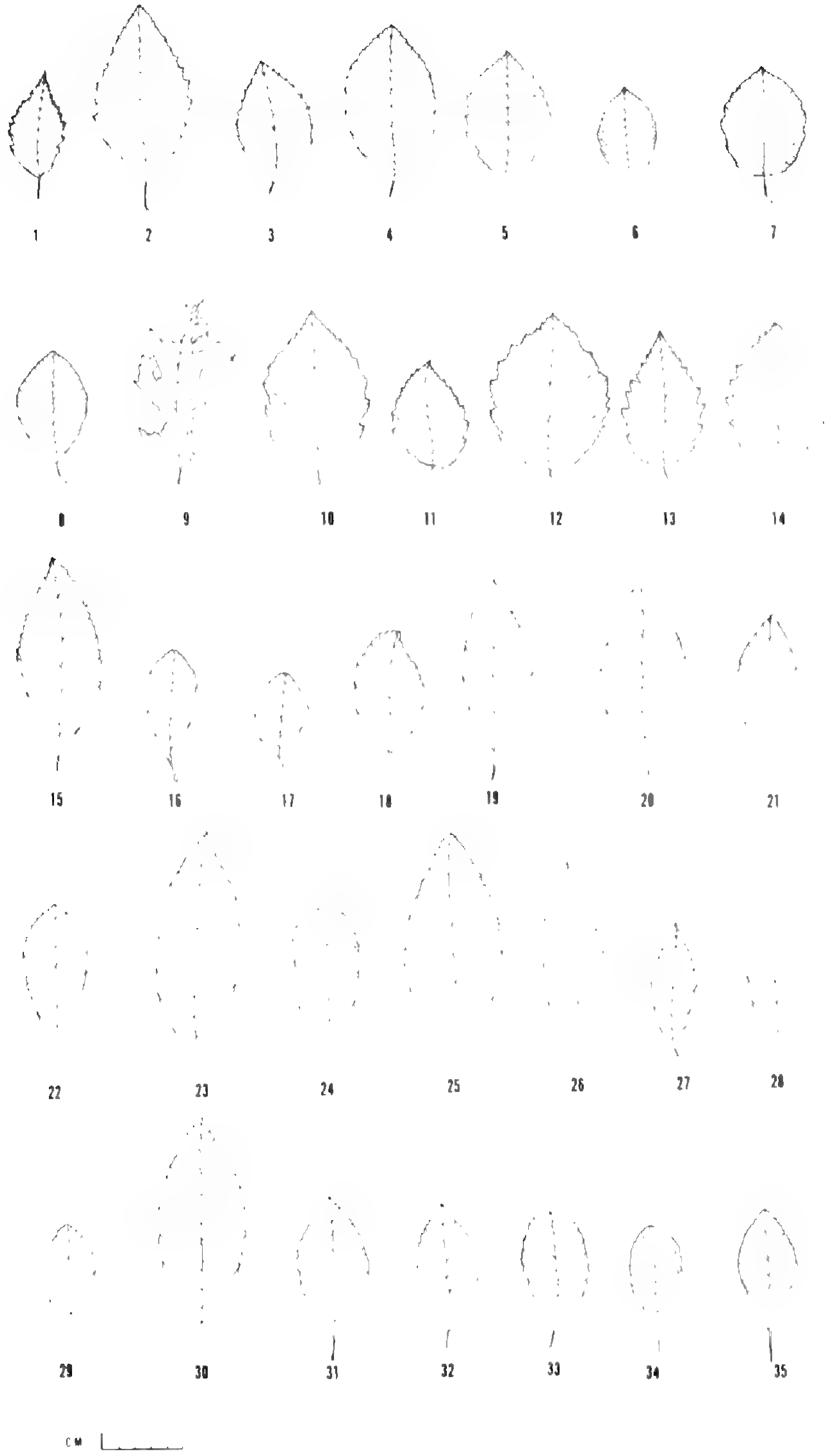


Figure 11. Outlines of leaves of *Alnus* showing extremes in the patterns of shape and margin variation: 1–4, *Alnus oblongifolia;* 5–9, *A. incana* ssp. *rugosa;* 10–14, *A. incana* ssp. *tenuifolia;* 15–21, *A. jorullensis* ssp. *jorullensis;* 22–30, *A. jorullensis* ssp. *lutea;* 31–35, *A. maritima.*

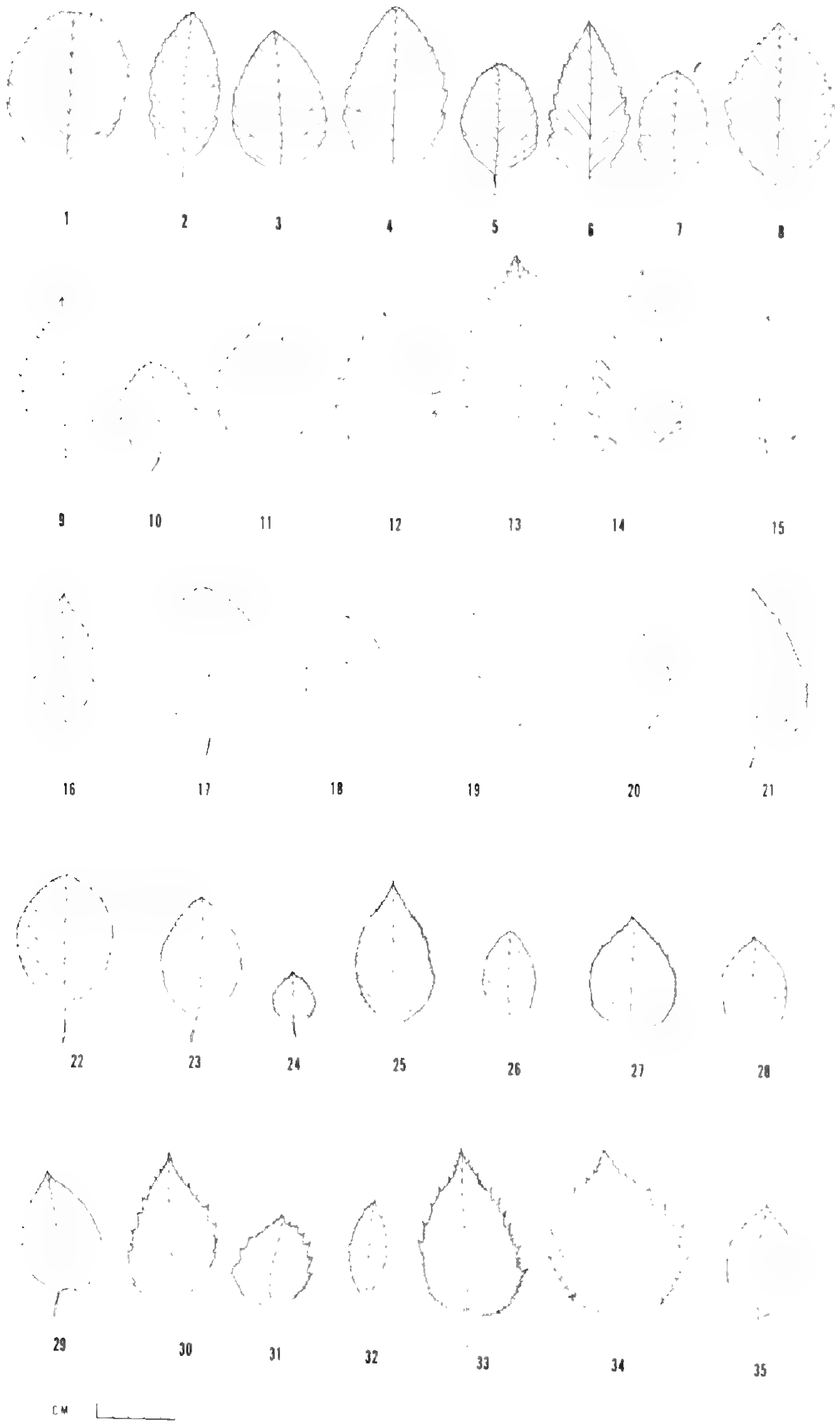


Figure 12. Outlines of leaves of *Alnus* showing extremes in the patterns of shape and margin variation: 1–7, *Alnus rhombifolia;* 8–15, *A. rubra;* 16–20, *A. serrulata;* 21–28, *A. viridis* ssp. *crispa;* 29–35, *A. viridis* ssp. *sinuata.*

catkins, which occasionally also appear in branched clusters on vigorous plants. In *A. viridis* and other members of subg. *Alnobetula,* the staminate and lower pistillate catkins retain the subtending leaves, which may be somewhat reduced in size, while in the other species, all or most of the leaves are lost and the internodes appreciably shortened. Sometimes pistillate catkins are seen on the staminate branches just below the staminate catkins, or staminate catkins may appear at the tips of the pistillate branches above the pistillate catkins. Occasionally, both pistillate and staminate flowers may appear in the same catkin and, in this case, the staminate are apical.

The pistillate catkins of *Alnus viridis* are pendent on long, thin peduncles. *Alnus maritima* has somewhat stouter and shorter peduncles, and the remainder of the species have still shorter ones, becoming nearly sessile in *A. incana* and *A. serrulata.* Where the pistillate catkins occur in racemose clusters, the catkins near the base of the cluster always have longer peduncles than those at the tip.

Murai (1964) regards the single, axillary pistillate catkins of *Alnus maritima* as advanced over the clustered type and shows a phylogenetic series of reduction leading to this state in the Asian members of subg. *Clethropsis.* In *Alnus maritima* nodes are evident on the "peduncle" of each solitary pistillate catkin, suggesting this reduction. That the short axillary pistillate branches in the subgenera *Alnus* and *Alnobetula* are already reduced from a primitive condition in which both pistillate and staminate catkins were present is suggested by the occasional presence of both kinds of inflorescences on the same branch. Similarly, that simple axillary staminate catkins are derived from branched systems is indicated by the occasional appearance of such systems in vigorous specimens.

At maturity, the pistillate catkins of all the alders become woody and cone-like, the five bracts of each cymule fusing into a single persistent scale bearing two fruits. These woody mature cones are often useful in identification, varying considerably in shape and size (Figures 16, 17, & 18). The cone scales also vary in shape and size, but this is mostly correlated with the dimensions of the cone itself. Other variation in the cone scales involves the shape, degree of thickening, and amount of reflexing of the terminal lobe. These woody infructescences are one of the most distinctive features of *Alnus* and the most useful in distinguishing it from the genus *Betula.*

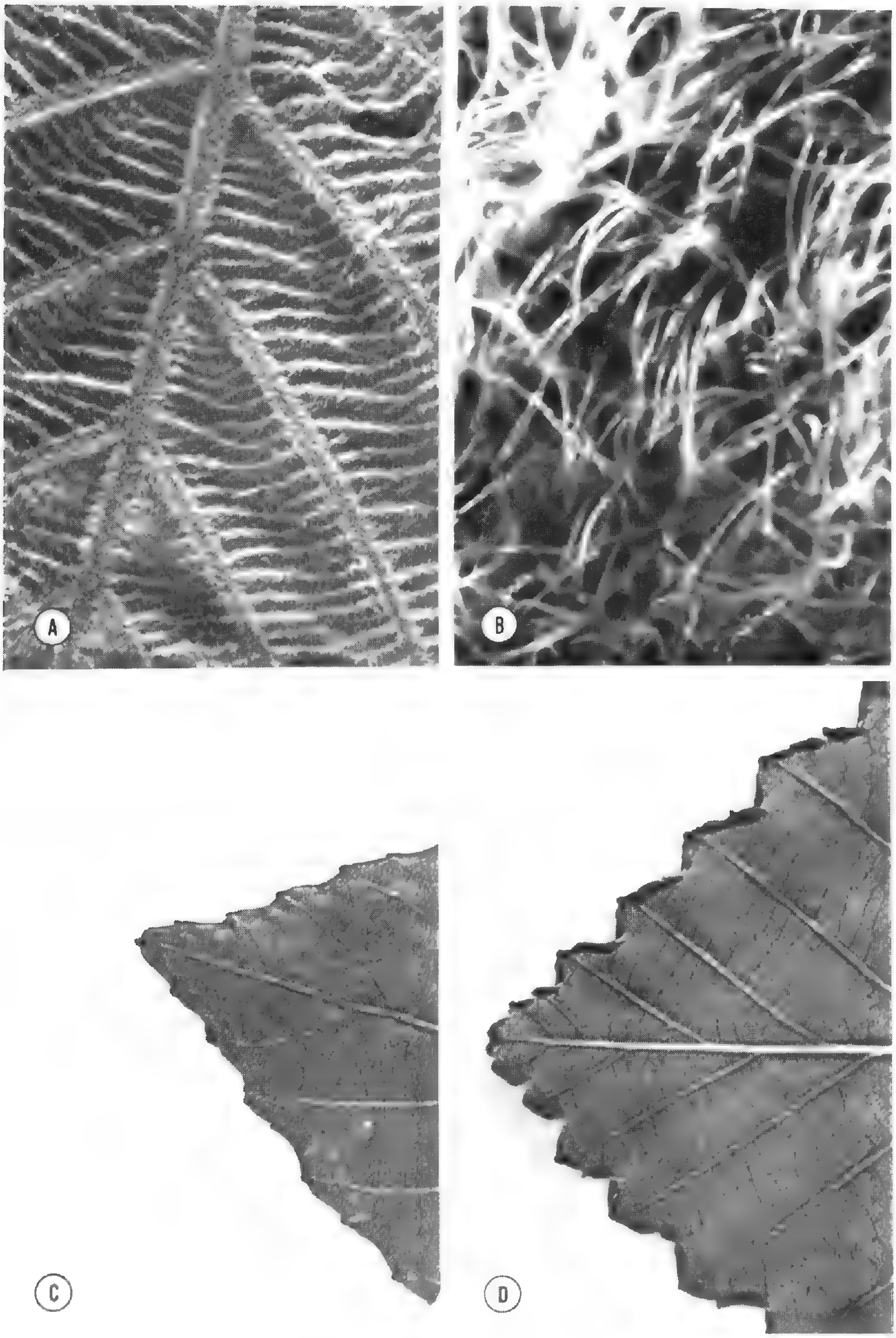


Figure 13. Macroscopic features of *Alnus* leaves. A, *Alnus viridis* ssp. *crispa*, pubescent extreme (*A. crispa* var. *mollis* Fern.), ×2. B, same as A, ×30. C, *A. maritima*, glandular teeth, ×2. D, *A. rubra*, revolute margin, ×2.

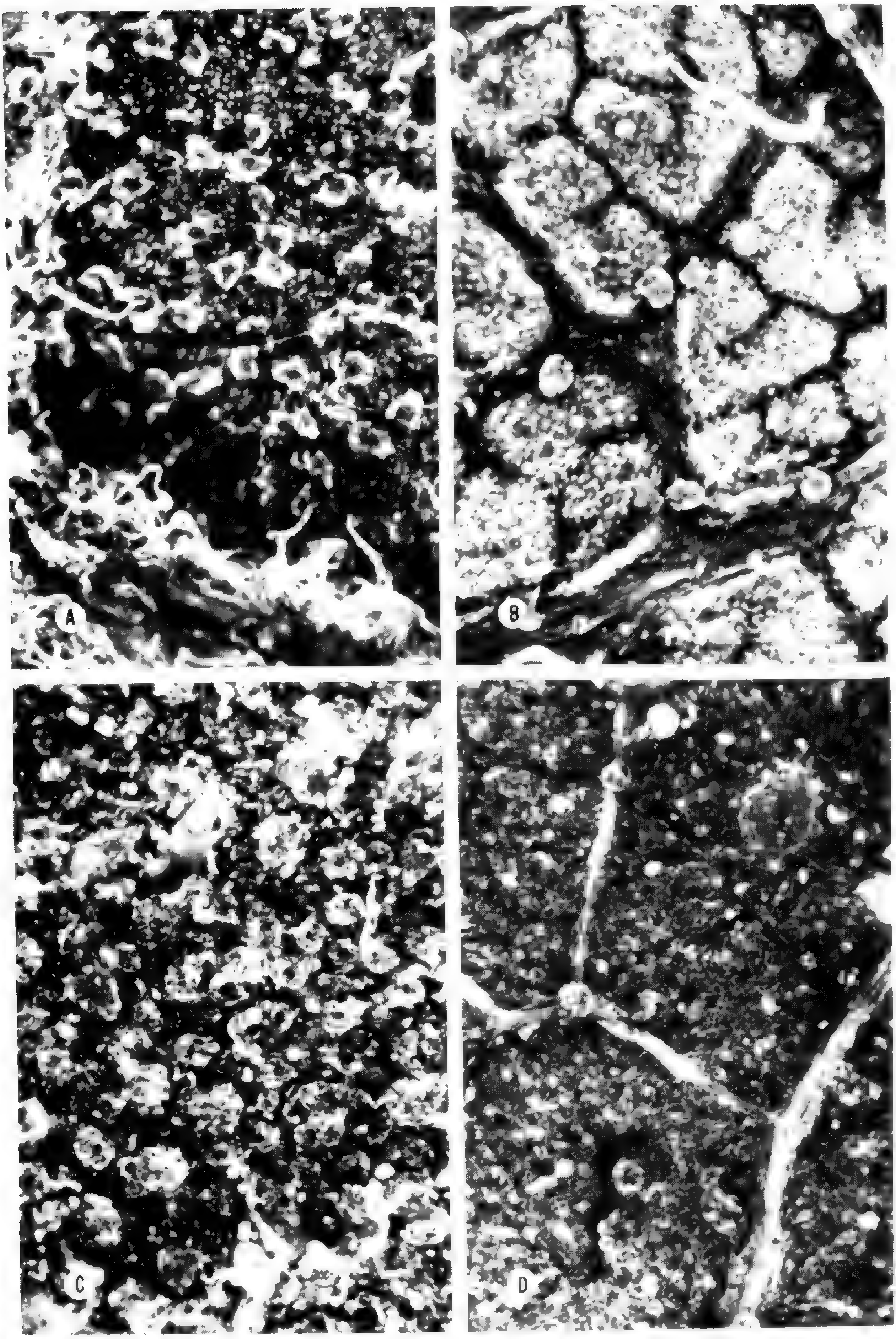


Figure 14. Epi-illuminated microscopic views of abaxial leaf surfaces of *Alnus* showing veins, resinous deposits, and glands, all ×30. A, *Alnus acuminata* ssp. *arguta*. B, *A. jorullensis* ssp. *jorullensis*. C, *A. jorullensis* ssp. *lutea*. D, *A. viridis* ssp. *sinuata*.

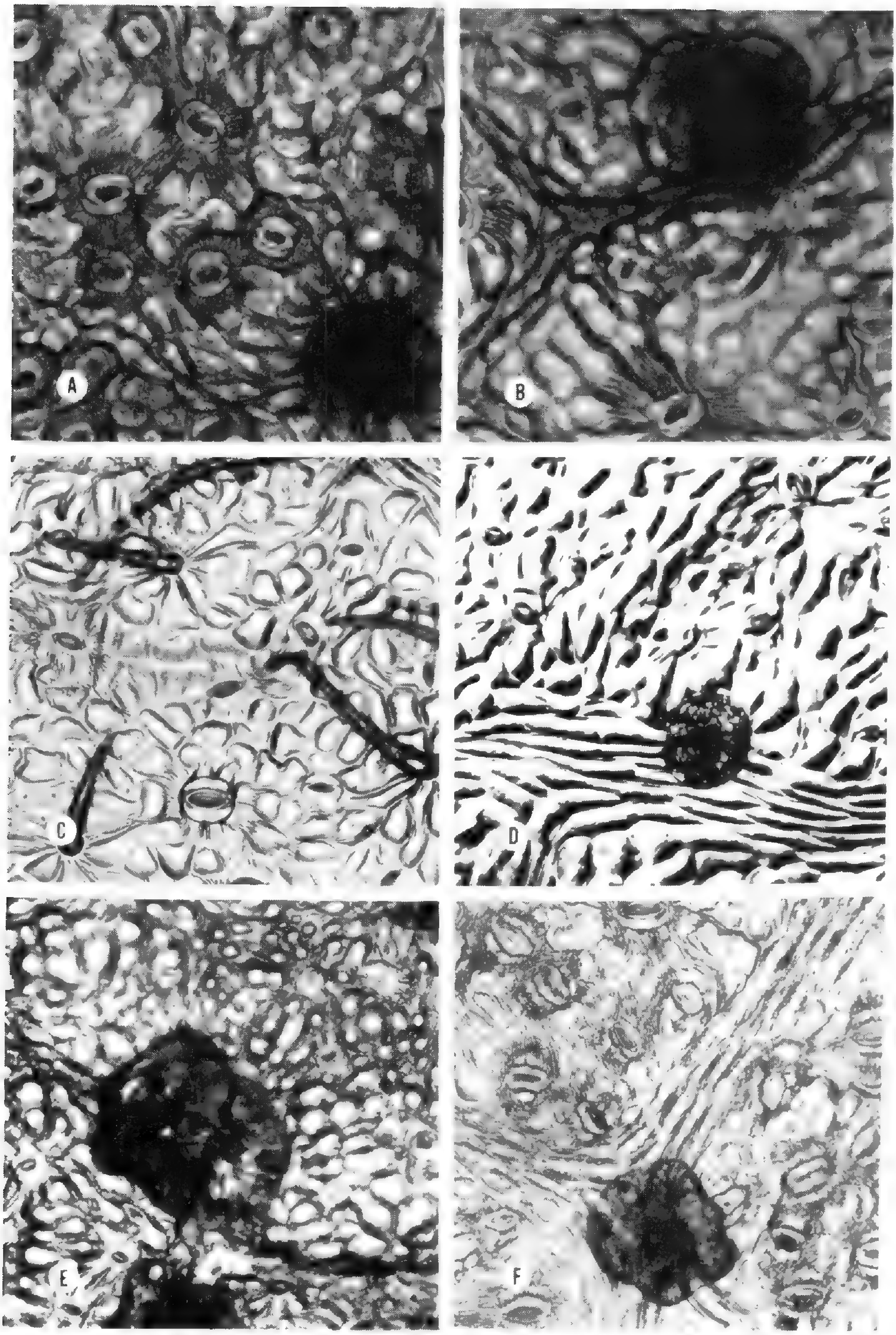


Figure 15. Photomicrographs of abaxial leaf cuticle imprints of *Alnus* made on thin acetate sheets showing stomata, epidermal cells, hairs, and glands, all ×105. A, *Alnus acuminata* ssp. *arguta*. B, *A. acuminata* ssp. *glabrata*. C, *A. oblongifolia*. D, *A. incana* ssp. *tenuifolia*. E, *A. jorullensis* ssp. *lutea*. F, *A. maritima*.

Flowers. The flowers of *Alnus* are unisexual and minute, as in most other wind-pollinated plants. The staminate flowers have a tiny but well-formed perianth with from two to six parts, usually appearing to be a single whorl. Most species of *Alnus* and *Clethropsis* have four perianth parts and an equal number of stamens opposite them. *Alnus rhombifolia* commonly has only two perianth segments and two stamens, and *A. oblongifolia* usually has four, sometimes with two tepals and two stamens smaller than the other two. In *Alnus viridis,* four or five tepals and stamens are the rule, but occasionally up to six perianth parts and six stamens may be present, each in two whorls (Abbe, 1935).

The stamens vary in length and degree of fusion to the perianth parts. They are tetrasporangiate and never exserted very far from the catkin. In *Alnus incana,* the filaments are subsessile, never exceeding the length of the tepals. They are long in *A. viridis, A. maritima, A. oblongifolia, A. rhombifolia, A. rubra,* and *A. serrulata,* and intermediate in the remaining species. In *Alnus incana* of Europe, the filament length is variable.

The pistillate flowers are normally without a perianth, consisting mainly of a single bicarpellate ovary derived from a tricarpellate one, together with a simple two-branched style (Abbe, 1935; Hjelmqvist, 1948). Abbe (1938) noted that single tricarpellate pistils are often found in the axils of foliage leaves below the catkins. The ovary has two poorly-defined locules, becoming one above the single ovule in each section. The placentation is basically axile according to Abbe (1935); the ovules are anatropous, unitegmic, and crassinucellar (Davis, 1966).

The ovary in *Alnus* was shown to be inferior by Abbe (1935, 1938), who found that three or four small elongate glands of the type occurring on the edges of the perianth parts of the staminate flowers sometimes appear at the summit. In several specimens of *Alnus rubra* he found true tepals in this position, with the glands now at their apices. Four such glands were seen on the perianth parts of flowers from the Asian *A. subcordata,* while two appeared in specimens of *A. maritima, A. incana,* and *A. rubra* from North America. Vestigal vascular traces were seen running to the glands in the specimen of *A. incana.*

On the basis of staminate floral morphology, *Alnus viridis* is the most primitive species, having lost the fewest parts, and *A. oblongifolia* is the most advanced, having lost the most. Likewise, with

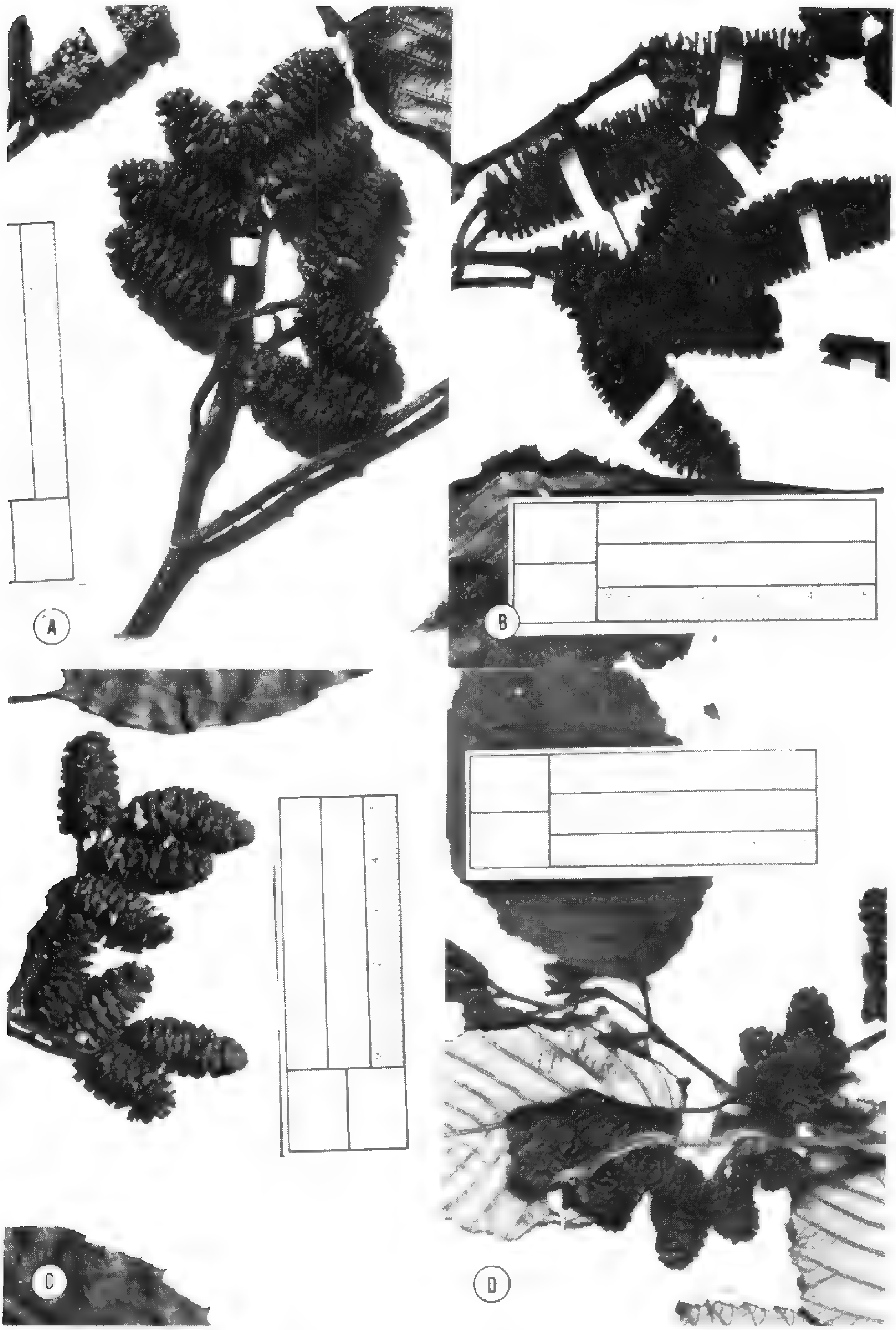


Figure 16. Mature infructescences of representative species of *Alnus*. A, *Alnus acuminata* ssp. *acuminata*. B, *A. acuminata* ssp. *arguta*. C, *A. acuminata* ssp. *glabrata*. D, *A. incana* ssp. *rugosa*.

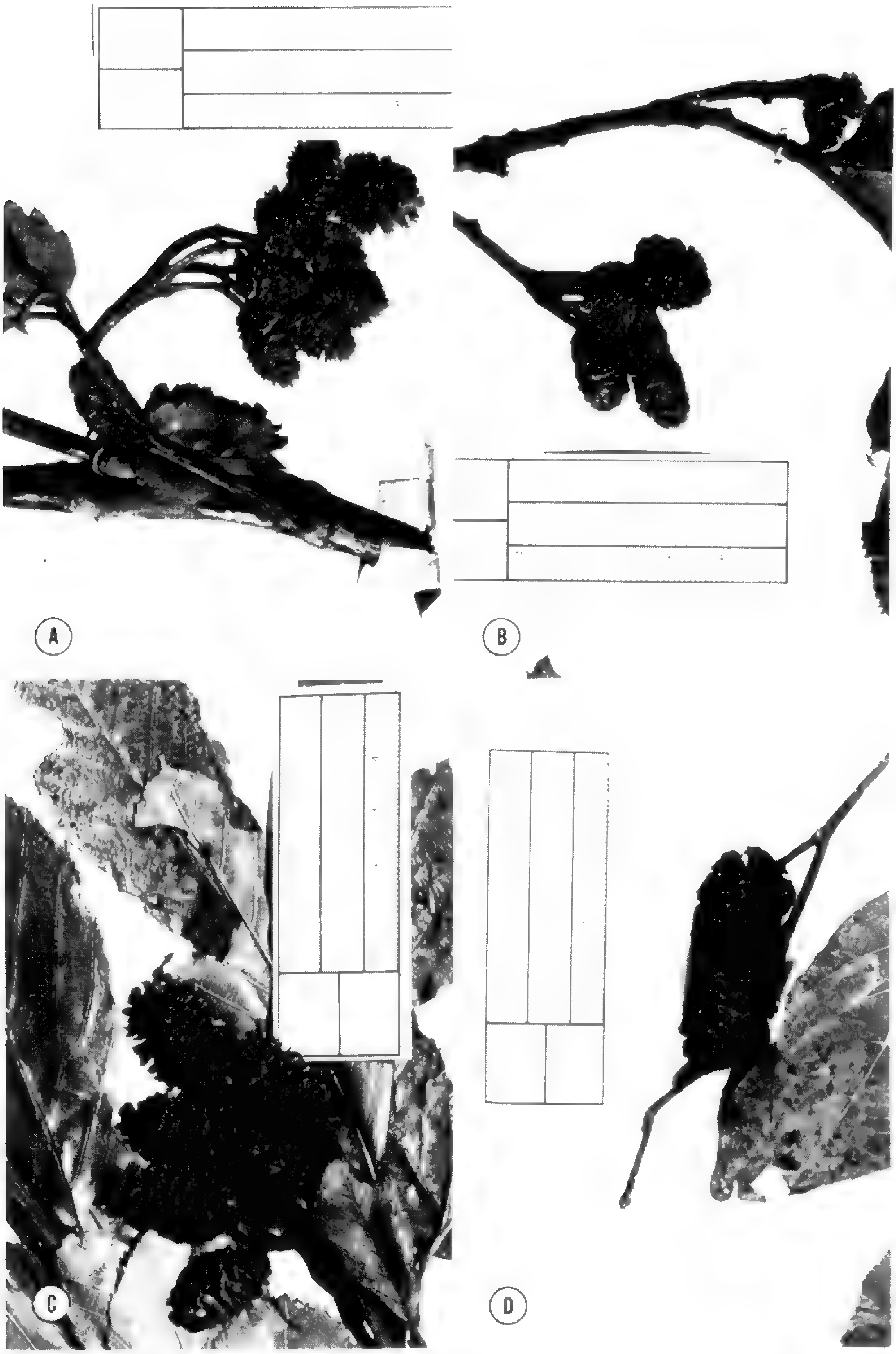


Figure 17. Mature infructescences of representative species of *Alnus*. A, *Alnus incana* ssp. *tenuifolia*. B, *A. jorullensis* ssp. *jorullensis*. C, *A. jorullensis* ssp. *lutea*. D, *A. maritima*.

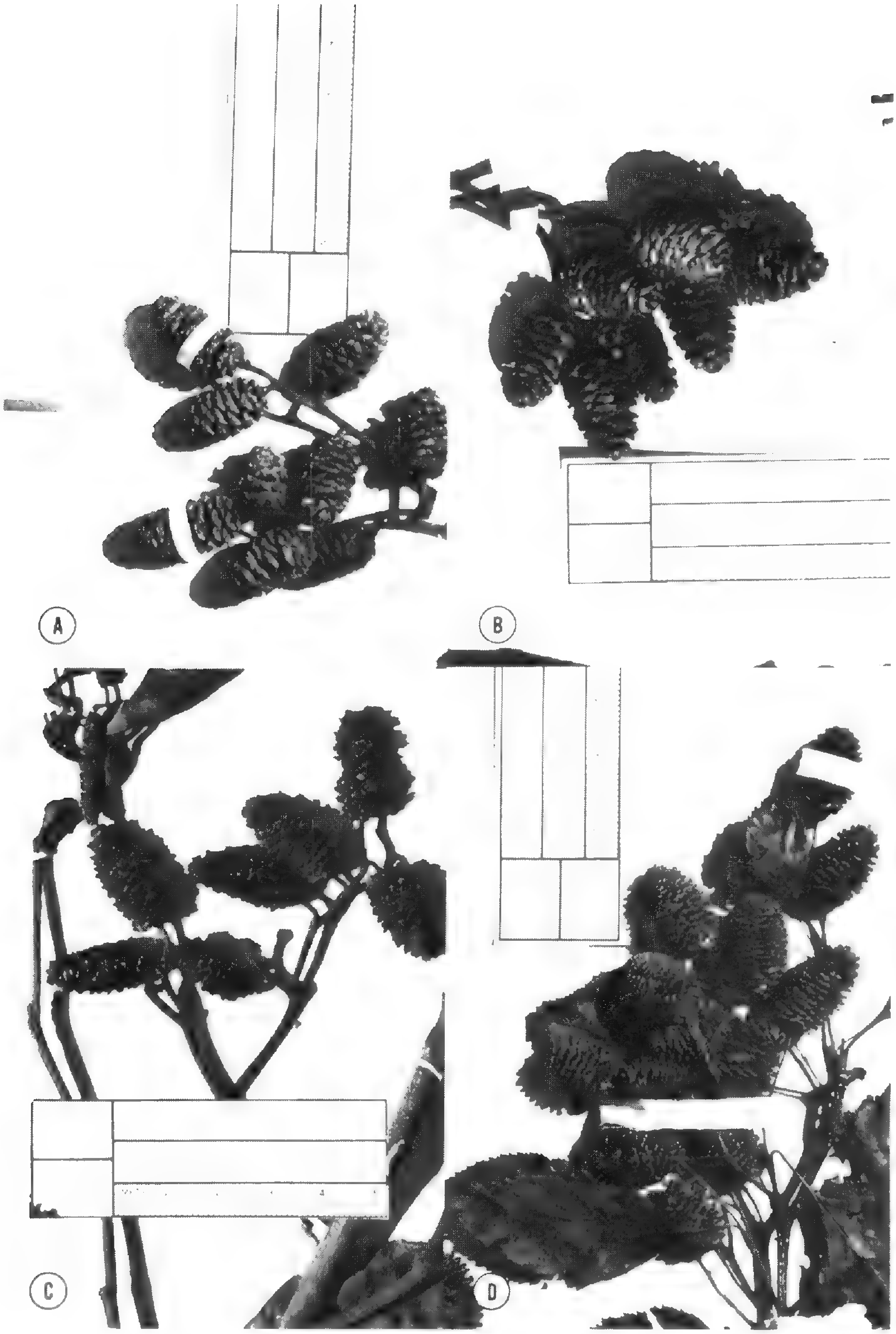


Figure 18. Mature infructescences of representative species of *Alnus*. A, *Alnus rhombifolia*. B, *A. rubra*. C, *A. serrulata*. D, *A. viridis* ssp. *sinuata*.

regard to inflorescences, *A. viridis* is the most primitive, but for this character *A. maritima* is the most advanced.

Pollen. Pollen grains of *Alnus* are small, light in weight, and produced in abundance. Erdtman (1969) estimates that a single catkin of *Alnus glutinosa* produces as many as 4,500,000 grains, compared with 1,250,000 in *Quercus robur* and 175,000 in *Fagus sylvatica.* The weight of a single grain is about 6.5×10^{-9} gm, compared with 3.8×10^{-9} gm in *Juniperus* and 37.0×10^{-9} gm in *Fagus* (Erdtman, 1969). Wodehouse (1935) states that alder pollen is "caught in great abundance on pollen slides exposed several miles from any trees." Where *Alnus* is abundant, the windborn pollen is sometimes responsible for causing hayfever in susceptible individuals (Chamberlain, 1927).

The grains are isopolar, radiosymmetric, stephanoporate monads ranging from 17 to 35 microns in diameter. They are somewhat flattened, and they typically have from three to six apertures, though occasionally more than six pores may be present. The apertures are aspidate and often somewhat elliptical, ranging from 2.5 to 4.5 microns long. Each aperture has an annulus. The surface is smooth or slightly granular in appearance under the compound microscope (Figure 19) but can be seen to be covered with very minute verrucae, gemmae, or spinules (nanoverrucae, nanogemmae, or nanospinules) positioned on low ridges when viewed with the scanning electron microscope (Figure 20). The sexine is pertectate and thicker than the nexine (Erdtman, 1969). Thickened bands (arcus) in the exine (tectum and nexine) run in pairs from aperture to aperture, giving a very characteristic appearance to shrunken or collapsed grains (Figure 20), although these bands are not always evident in fully expanded and unstained material. Below the pores, the intine is thickened considerably to form large onci.

To find morphological differences in the pollen of *Alnus* species, grains were examined using both light and scanning electron microscopy, as discussed by Ridgway and Skvarla (1969). Pollen from three to seven herbarium specimens of each species was collected and mounted in glycerine jelly prepared by the formula of Johannsen (1940) and stained light red with safranin-O. Within one week after preparation these grains were studied, measured, and photographed under oil immersion at a magnification of 630 × with a Zeiss Photomicroscope II. Seven grains on each slide (21 to 49

Table 1. **Herbarium specimens from which pollen was obtained for study.**

Alnus acuminata ssp. *acuminata:*
- *Balls 6924,* Peru (F)
- *Killip & Smith 17928,* Dept. Santander, Colombia (NY)
- *Tovar 2770,* Prov. Huancayo, Peru (UC)
- *Venturi 1047,* Prov. Tucumán, Argentina (F)
- *Venturi 3865,* Prov. Tucumán, Argentina (MO)

Alnus acuminata ssp. *arguta:*
- *Breedlove 7851,* Chenalho, Chiapas, México (F)
- *Breedlove 8572,* San Juan Ixcoy, Guatemala (F)
- *Breedlove 9063,* Tenejapa, Chiapas, México (MICH)
- *Carlson 2412,* Las Casas, Chiapas, México (MICH)
- *Espinosa 641,* Cañada de Contreras, D. F., México (ENCB)
- *Hinton 15415,* Distr. Mina, Guerrero, México (MICH)
- *Lems 5031,* Prov. Cartago, Costa Rica (NY)
- *Palacios s.n.,* Jan. 19, 1968, Zacapoaxtla, Puebla (ENCB)
- *Standley 80553,* Volcán de Pacaya, Guatemala (F)
- *Steyermark 34605,* Volcán Zunil, Guatemala (F)

Alnus acuminata ssp. *glabrata:*
- *Mexia 8979,* Petlacala, Guerrero, México (NY)
- *Pringle 8022,* Tizapán, D. F., México (MEXU)
- *Rzedowski 19301,* Los Remedios, México, México (MSC)
- *Rzedowski 26680,* Distr. Coixtlahuaca, Oaxaca, México (ENCB)
- *Torres 345,* D. F., México (MEXU)

Alnus incana ssp. *incana:*
- *Jaques s.n.,* Switzerland (RM)
- *Markland s.n.,* Finland (DAO)
- *Rozsembersky s.n.,* Hungary (UC)
- *Tullberg s.n.,* Sweden (NY)

Alnus incana ssp. *rugosa:*
- *Blanchard s.n.,* Caledonia Co., Vermont (GH)
- *Dodge s.n.,* St. Clair Co., Michigan (RM)
- *Fernald & Bartlett 10,* Essex Co., Massachusetts (GH)
- *Gilbert s.n.,* Berkshire Co., Massachusetts (UC)
- *Lakela 1341,* Louis Co., Minnesota (NY)
- *Lucy 3238,* Chenago Co., New York (F)
- *Minshall 2707,* Carleton Co., Ontario (DAO)
- *Pepoon 630,* Cass Co., Michigan (MSC)
- *Ricard & Boivin 600,* Quebec (UC)

Alnus incana ssp. *tenuifolia:*
- *Breitung s.n.,* Alberta (DAO)
- *Frost s.n.,* Colorado (UC)
- *Keck 5526,* Douglas Co., Nevada (UC)

Table 1 (continued)

Robbins 1699, El Dorado Co., California (UC)
Russell 4862, Sutherland, Saskatchewan (DAO)
Turner 4784, Alberta (DAO)

Alnus jorullensis ssp. *jorullensis:*
Rzedowski 2239, San Angel, D. F., México (ENCB)
Rzedowski 22045, Cerro Ajusco, D. F., México (ENCB)
Rzedowski 27147, El Guajolote, Hidalgo, México (ENCB)

Alnus jorullensis ssp. *lutea:*
Breedlove 16518, Sierra Surutato, Sinaloa, México (MICH)
Rzedowski 19395, Nevado de Colima, Jalisco, México (ENCB)
Salazar 5, San Angel, D. F., México (MEXU)

Alnus maritima
Commons s.n., Wicomico Co., Maryland (NY)
Furlow 205, Sussex Co., Delaware (MSC)
Robbins 2795, Pontotoc Co., Oklahoma (DAO)
Smith s.n., Sussex Co., Delaware (RM)
Waterfall 9258, Johnston Co., Oklahoma (OKLA)

Alnus oblongifolia:
Foster & Arnold 108, Gila Co., Arizona (US)
Furlow s.n., Graham Co., Arizona (MSC)
Greene s.n., Grant Co., New Mexico (MO)
Hartman 322, Huchuerachi, Sonora, México (F)
Toumey s.n., Pima Co., Arizona (RM)

Alnus rhombifolia:
Applegate 960, Jackson Co., Oregon (UC)
Heller 11167, Butte Co., California (NY)
Parks & Parks 24084, Del Norte Co., California (RM)
Plaskett 14, Monterey Co., California (RM)
Suksdorf s.n., Klickitat Co., Washington (F)
Tracy 5306, Humboldt Co., California (UC)
Wapole 150, Jackson Co., Oregon (US)

Alnus rubra:
Henderson 312, Hood River Co., Oregon (NY)
Lawfer 131, Marin Co., California (WTU)
Macoun s.n., Victoria, British Columbia (CAN)
Sheldon S.11680, Clarke Co., Washington (UC)
Tracy 6151, Humboldt Co., California (UC)

Alnus serrulata:
Demaree 16650, Hot Springs Co., Arkansas (NY)
Furlow 344, Brown Co., Indiana (MSC)

Table 1 (continued)

Godfrey 55316, Jefferson Co., Florida (NY)
Johnson 2619, Easton Co., Connecticut (F)

Alnus viridis ssp. *crispa:*
Baldwin et al. 559, Baie James Co., Quebec (CAN)
Churchill s.n., July 10, 1937, Coos Co., New Hampshire (MSC)
Cody & Webster 5362, Alaska (DAO)
Dumais & Rankin 1002, Alberta (CAN)
Forbes s.n., May 11, 1912, Franklin Co., Massachusetts (UC)
Furlow 251, Mitchell Co., North Carolina (MSC)
Young s.n., May 21, 1940, Kenora Distr., Ontario (DAO)

Alnus viridis ssp. *sinuata:*
Anderson 6479, Alaska (RM)
Bacigalupi et al. 3469, Josephine Co., Oregon (UC)
Furlow 279, Lemhi Co., Idaho (MSC)
Sanson 1630, Alberta (DAO)
Schmantz 367, Missoula Co., Montana (DAO)

Alnus viridis ssp. *viridis:*
Bornmüller s.n., Oct., 1919, Germany (A)
Kampstein s.n., without date, Austria (US)
Prerowsky s.n., Apr., 1893, Bohemia (DAO)
Vautier et al. s.n., May 28, 1963, France (WTU)

grains per species) were measured to determine diameters, and 100 grains per slide (300 to 900 grains per species) were examined to establish the average number of pores per grain. For scanning electron microscopy, pollen collected from herbarium specimens was attached to metal stubs by means of double-adhesive cellophane tape, coated with gold, and examined with an Advanced Metals Research Model 900 scanning electron microscope at Michigan State University. Herbarium specimens used for the collection of pollen grains are listed in Table 1.

Few tangible differences, other than pore number and grain diameter, were noted in the material studied, although slight variations in the color of the grains, the sculpturing of the surface, and the size of the aspides and onci were detectable. The size ranges of the grains of all species overlap (Table 2, Figure 21), but the mean values of some, such as *Alnus maritima,* which has very small grains, are useful in distinguishing them from the other taxa. The least significant difference among the mean values (L.S.D. Test) was found to be 0.836 microns at the 5% probability level and 1.099 microns at the 1% level. Based on pollen diameter, three major groups can be recognized readily, these corresponding roughly to the three subgenera. *Alnus maritima* (subg. *Clethropsis*) has the smallest grains, showing an average diameter of only 19.7 microns. Subgenus *Alnobetula*, represented by *A. viridis*, has larger grains, with mean diameters ranging from 21.1 to 22.1 microns, and the remaining species, members of subg. *Alnus*, have still larger mean diameters, ranging from 21.1 to 25.0 microns.

Aperture number is often a better criterion for distinguishing species than is grain diameter, as shown in Table 2. *Alnus maritima* and *A. serrulata* typically have grains with four pores, while five taxa (*A. viridis* ssp. *crispa*, *A. viridis* ssp. *sinuata*, *A. viridis* ssp. *viridis*, *A. jorullensis*, and *A. rubra*) usually demonstrate a five-pored configuration. Two taxa (*A. incana* spp. *rugosa* and *incana*) have either four- or five-pored grains, these occurring in about a one to one ratio, and six taxa (*A. oblongifolia*, *A. rhombifolia*, *A. incana* ssp. *tenuifolia*, *A. acuminata* ssp. *acuminata*, *A. acuminata* ssp. *arguta*, and *A. acuminata* ssp. *glabrata*) have both four- and five-pored grains in ratios of two or three to one. In most cases, variability in pore number is high, with up to 35% of the grains of a particular specimen lying outside the "typical" number.

Alnus incana ssp. *tenuifolia* demonstrates a tendency toward the four-pored condition shown by *A. serrulata*. The four-pored condition might be considered advanced in *Alnus*, even though a small number of apertures is probably the ultimate primitive condition, as suggested by Doyle (1969). That four pores is an advanced condition in *Alnus* is indicated by the fact that it occurs mainly in species that are otherwise quite specialized (*A. serrulata* and *A. maritima*) while those taxa having five or six pores (*A. viridis* subspecies) are otherwise more generalized. In addition, the fact that "in fossil alder pollen from the Tertiary of west Scotland, increased aperture number is linked with a tendency towards a panotreme condition" (Erdtman, 1969) could be interpreted to support this idea.

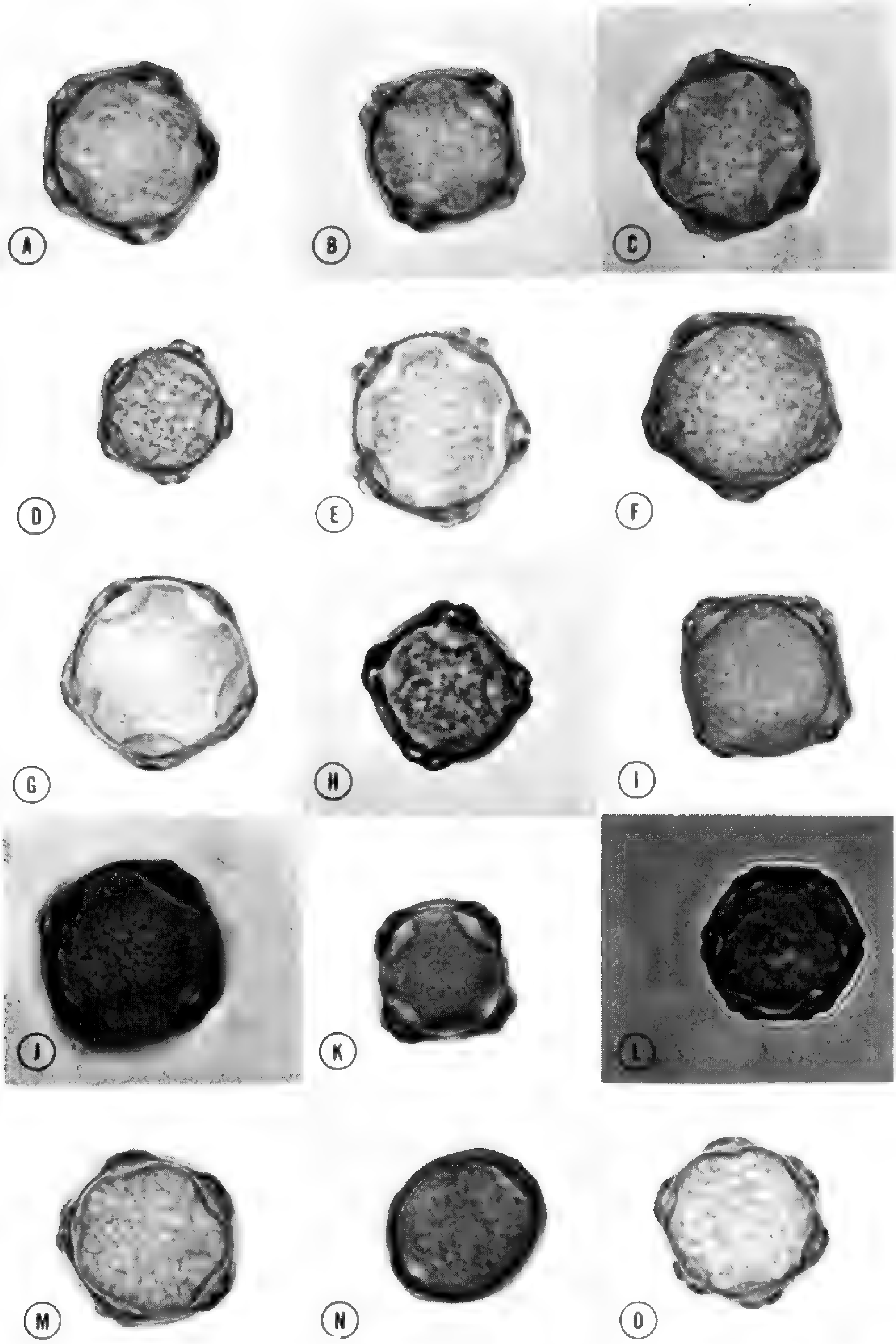
Four groups of species can be distinguished on the basis of surface sculpturing, as seen in scanning electron micrographs (Figure 20). The first of these, represented by *Alnus viridis* spp. *crispa* and *sinuata*, shows grain surfaces densely covered with prominent gemmae positioned along short low ridges, the elements being larger in ssp. *sinuata*. A second group, represented by *A.*

Table 2. **Size of *Alnus* pollen grains (microns)**

Taxon	Mean Diameter	Range	Standard Deviation
A. acuminata ssp. *acuminata*	24.22	20.9-28.7	1.80
A. acuminata ssp. *arguta*	20.80	18.6-27.1	1.61
A. acuminata ssp. *glabrata*	23.78	20.2-26.4	1.52
A. incana ssp. *incana*	24.49	18.6-29.5	3.10
A. incana ssp. *rugosa*	22.80	19.4-25.6	1.62
A. incana ssp. *tenuifolia*	23.60	18.6-27.9	2.00
A. jorullensis ssp. *jorullensis*	23.14	20.2-26.4	2.11
A. jorullensis ssp. *lutea*	24.34	21.7-27.9	1.60
A. maritima	19.67	17.1-23.3	1.72
A. oblongifolia	24.34	20.2-27.9	1.94
A. rhombifolia	24.51	21.7-28.7	1.52
A. rubra	25.02	20.0-27.9	1.99
A. serrulata	21.06	18.6-24.8	1.90
A. viridis ssp. *crispa*	21.06	18.6-23.3	1.46
A. viridis ssp. *sinuata*	21.83	17.1-26.4	2.01
A. viridis ssp. *viridis*	22.08	18.6-26.4	1.84

Table 3. **Percent of *Alnus* pollen grains having various numbers of pores.**

Species	Number of Pores			
	3	4	5	6
A. acuminata ssp. *acuminata*	0.0	23.8	73.0	3.2
A. acuminata ssp. *arguta*	0.0	34.6	65.4	0.0
A. acuminata ssp. *glabrata*	0.0	31.6	67.8	0.6
A. incana ssp. *incana*	0.0	38.0	58.6	3.4
A. incana ssp. *rugosa*	0.0	46.8	51.4	1.8
A. incana ssp. *tenuifolia*	0.0	70.3	29.8	0.0
A. jorullensis ssp. *jorullensis*	0.0	14.3	82.0	3.7
A. jorullensis ssp. *lutea*	0.0	14.4	82.0	3.4
A. maritima	6.0	86.0	8.0	0.0
A. oblongifolia	0.0	33.2	64.6	2.2
A. rhombifolia	0.0	23.4	76.0	0.6
A. rubra	0.0	7.8	76.0	16.2
A. serrulata	11.0	80.6	8.4	0.0
A. viridis ssp. *crispa*	0.4	10.2	82.0	7.4
A. viridis ssp. *sinuata*	0.0	9.6	82.4	0.0
A. viridis ssp. *viridis*	0.0	7.4	77.2	15.4


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O

serrulata, A. incana ssp. *rugosa,* and *A. incana* ssp. *tenuifolia,* has fairly dense verrucae, these positioned along longer and more prominent ridges. The verrucae are very dense in *A. incana* ssp. *tenuifolia* and *A. serrulata* and somewhat less so in *A. incana* ssp. *rugosa.* A third group, containing *A. acuminata* ssp. *acuminata, A. acuminata* ssp. *glabrata, A. jorullensis, A. rubra,* and *A. rhombifolia,* has low, moderately long ridges with only moderately dense verrucae. Finally, *A. maritima* shows pronounced long ridges with very small and infrequent elements.

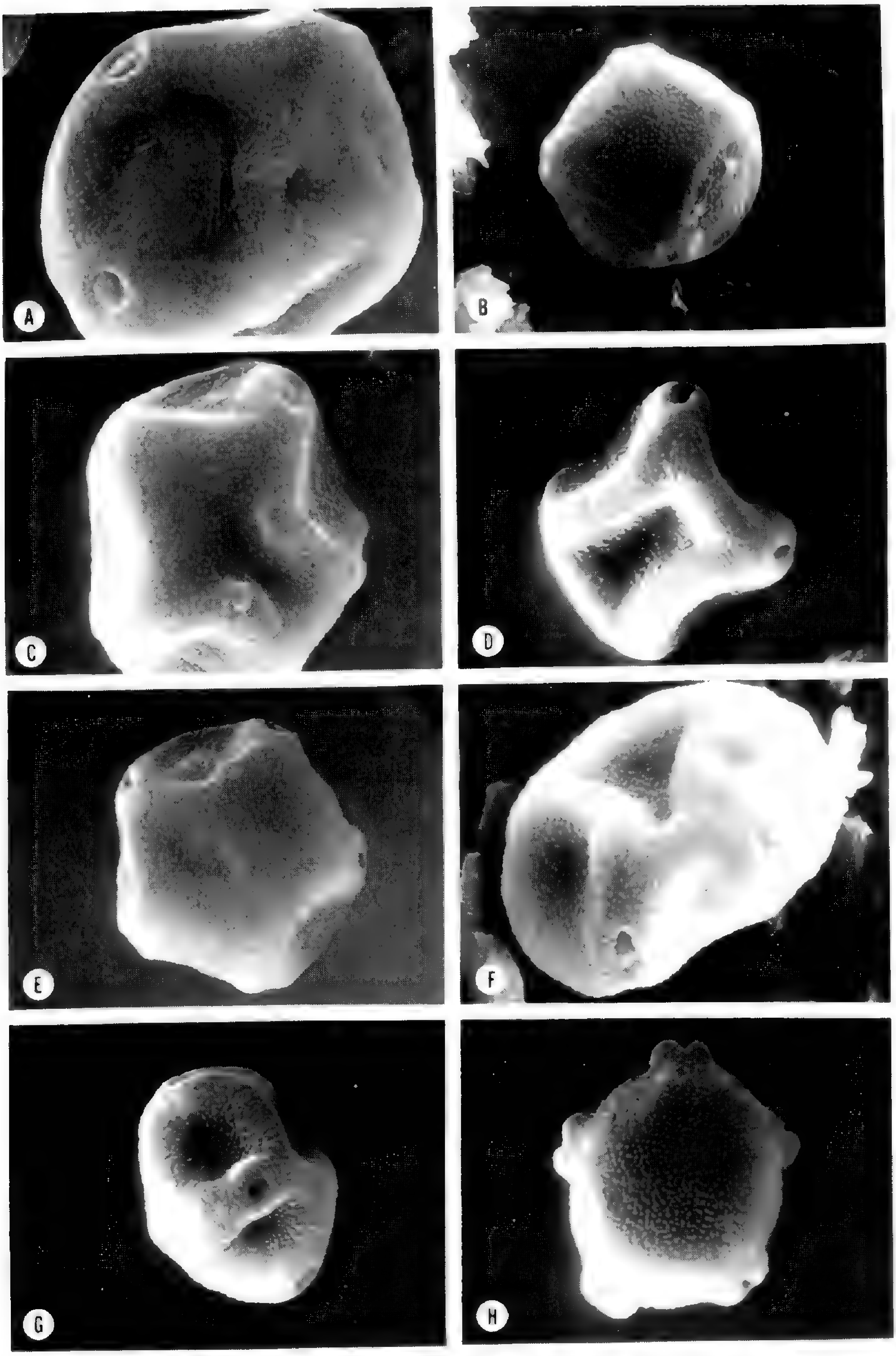
With the light microscope, pollen from subg. *Alnobetula* may be distinguished from that of species in the other subgenera in that it is generally lighter in color (not as deeply stained by safranin) and has smaller onci and aspides, which give the grains a rounder or less angular appearance. *Alnus acuminata* has rather light-appearing grains, but not as light as those of subg. *Alnobetula,* and they bear medium to large aspides and onci. *Alnus incana* spp. *rugosa* and *tenuifolia,* as well as *A. serrulata, A. oblongifolia,* and *A. rhombifolia* all have medium to large aspides and onci and dark walls, while *A. maritima* and *A. rubra* have grains of similar shape but of intermediate shade. Finally, *A. jorullensis* bears relatively small aspides, medium-sized onci, and is of intermediate darkness.

Major groups of species based on pollen characteristics correlate well with clusters formed using gross plant structure. The subspecies of *Alnus viridis* form one group, *A. incana* and *A. serrulata* another, and *A. acuminata* a third. *Alnus jorullensis,* while clearly related to the *A. acuminata* complex, retains an identity of its own. *Alnus rubra, A. rhombifolia,* and *A. oblongifolia* appear to be most closely allied to the *A. acuminata* group.

Fruits. The fruits of *Alnus* are small, smooth-surfaced, light, dry, indehiscent, and laterally-winged (Figure 22). In the literature they have been termed both nutlets and samaras. In *Alnus viridis,* each wing is as wide as or wider than the body of the fruit itself, while

---

Figure 19. Pollen grains of representative species of *Alnus,* all ×865. A, *Alnus acuminata* ssp. *arguta.* B, *A. oblongifolia.* C, *A. acuminata* ssp. *glabrata.* D, *A. incana* ssp. *incana.* E, *A. incana* ssp. *tenuifolia.* F, *A. jorullensis* ssp. *jorullensis.* G, *A. jorullensis* ssp. *lutea.* H, *A. maritima.* I, *A. rhombifolia.* J, *A. rubra.* K, *A. serrulata.* L, *A. viridis* ssp. *crispa.* M & N, *A. viridis* ssp. *sinuata.* O, *A. viridis* ssp. *viridis.*


A
B
C
D
E
F
G
H

other species have narrower wings. A few taxa (e.g., *A. maritima*) are characterized by essentially wingless fruits, there being only low ridges where the wings would otherwise occur. In these species dispersal is apparently by water, although even without wings the fruits may be carried some distance by moderately strong winds. The summit of the fruit is crowned by two persistent styles. The fruit body is usually elliptical in shape, and the wings, when present, are normally wider at the summit than below and extend further, both at the apex and base, than the body.

REPRODUCTIVE BIOLOGY

The alders are anemophilous, although insects are sometimes attracted to the staminate catkins (Figure 23). Species of subgenera *Alnus* and *Alnobetula* flower early in the spring in the temperate zone, from November to February in southern Mexico and Central America, and as late as July in northern Canada, while those of subg. *Clethropsis* bloom in the early autumn (September or October in *Alnus maritima*). In subg. *Alnus*, both staminate and pistillate catkins are produced during the growing season prior to blooming and are exposed during the winter. In subg. *Alnobetula*, only the staminate catkins are produced during the prior growing season and exposed during the winter, the pistillate catkins appearing along with the new foliage. Members of subg. *Clethropsis* produce both staminate and pistillate catkins during the same season as flowering. Anthesis takes place before the leaves appear in subg. *Alnus*, while the leaves are still small or just emerging from the bud in subg. *Alnobetula*, and when the plants are fully leafed out in subg. *Clethropsis*.

Staminate meiosis was found by Wetzel (1929) to occur in late summer (September) in members of subg. *Alnus* (*A. rubra*, *A. glutinosa*, and *A. cordata*) and somewhat earlier (July and August) in subg. *Alnobetula* (*A. viridis*). Meiosis occurs in August and September (immediately before anthesis) in subg. *Clethropsis* (*A. maritima*).

Figure 20. Scanning electron micrographs of pollen grains of representative species of *Alnus*. A, *Alnus incana* ssp. *rugosa*, ×1667. B, *A. incana* ssp. *tenuifolia*, × 1000. C, *A. jorullensis* ssp. *lutea*, ×1500. D, *A. maritima*, ×1500. E, *A. rubra*, ×1500. F, *A. viridis* ssp. *crispa*, ×1500. G, *A. viridis* ssp. *sinuata*, ×1500. H, *A. viridis* ssp. *sinuata*, ×1500.

McVean (1953a) reports that *Alnus glutinosa* is nearly always protogynous, although up to 12 percent protandry has been observed. Casual observation of the American species indicates that this general pattern may be true for them as well, although no definite data are available.

The age of first flowering of most species of *Alnus* is not known, but it probably occurs early in the life of at least the shrubby species. Lawrence (1958) reports that *A. viridis* ssp. *sinuata* in Alaska reaches flowering age in less than seven years. A specimen of *A. maritima* grown in an experimental garden in East Lansing, Michigan reached reproductive maturity at the age of three years, as determined from annual rings. Individuals of *A. viridis* ssp. *crispa, A. incana* ssp. *rugosa,* and *A. serrulata* grown in the same garden all reproduced first at the age of five years. The tree-sized species (*A. rubra, A. rhombifolia, A. acuminata, A. jorullensis,* etc.) were in general not seen reproducing in the field until they were relatively large.

To plants living in an environment with a relatively short growing season and a severe winter (such as that of far northern and subalpine climates) the parallel development of the shrub habit and an earlier reproductive maturity would be advantageous. Structural reduction under such environmental conditions seems to be associated with anatomical immaturity in otherwise adult plants (i.e., neoteny), as noted by Forsaith (1920) and Hall (1952).

Alnus frequently occurs in thickets, but it is not known whether such groups of plants always (or ever) represent clones. In the field, small plants of *A. serrulata, A. incana* spp. *rugosa* and *tenuifolia, A. viridis* ssp. *sinuata,* and *A. oblongifolia* were occasionally found to be interconnected by their roots when dug for transplanting. Sprouting from exposed roots in streams was noted in *Alnus incana* ssp. *tenuifolia, A. viridis* ssp. *sinuata,* and *A. oblongifolia.* Both layering and cuttings are effective methods of propagating alders, and submerged branches in nature are sometimes observed with adventitious roots. On the other hand, *Alnus* produces abundant seed (fruits), and one would expect thickets of individual plants to develop in suitable habitats from natural seeding alone. Steele (1961), judging from the amount of variation observed in clumps of *A. incana* ssp. *rugosa* and *A. serrulata,* concluded that these were not clones.

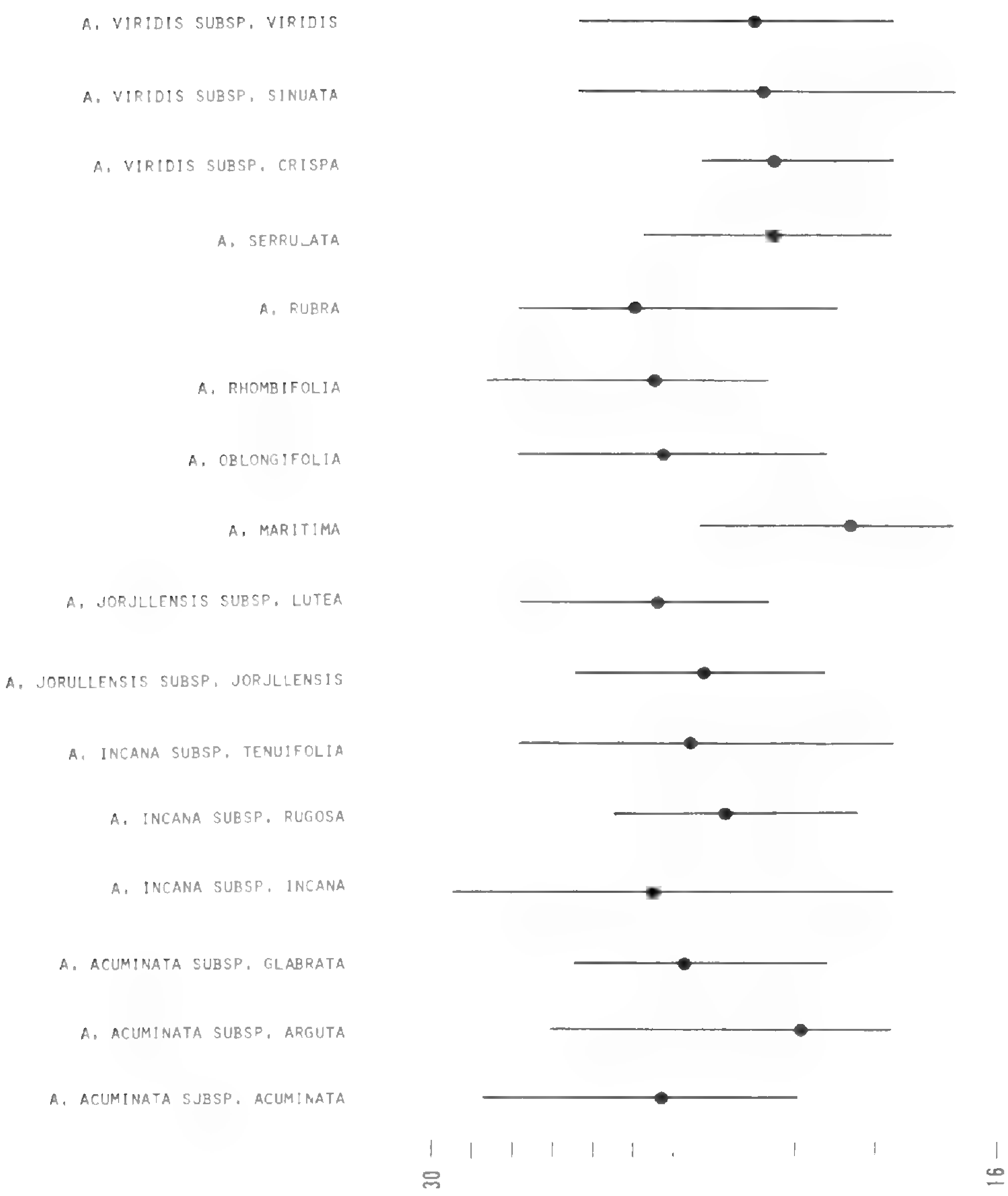


Figure 21. Range of variation in diameter of *Alnus* pollen grains (microns).

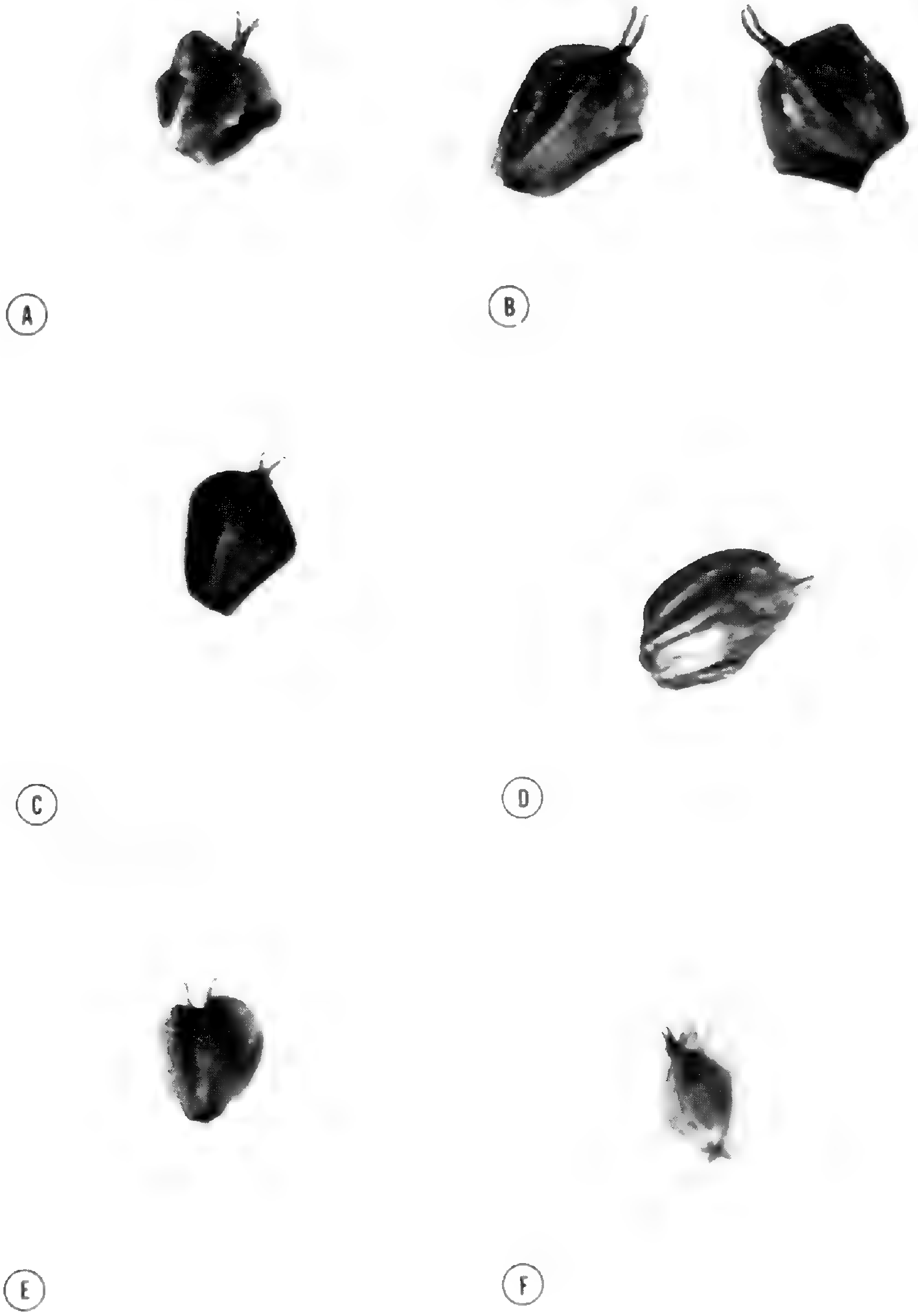


Figure 22. Fruits of representative species of *Alnus*, all ×8. A, *Alnus acuminata* ssp. *acuminata*. B, *A. oblongifolia*. C, *A. incana* ssp. *rugosa*. D, *A. maritima*. E, *A. serrulata*. F, *A. viridis* ssp. *sinuata*.

The fruits of *Alnus* are small and usually winged. Their dispersal in most cases is probably by wind. In some species, however, the wings are much reduced and somewhat corky, apparently serving as floatation mechanisms for water dispersal. McVean (1955) found that the fruits of *A. glutinosa* would float in still water for a period of over 12 months without decomposing. Although no similar study has been made of any of the American species, it seems clear that such essentially wingless-fruited species as *A. maritima* are likewise dispersed mainly by water.

Schalin (1968), using X-ray techniques to determine the developmental stage of the embryo and endosperm in seeds of *Alnus incana* and *A. glutinosa*, found that approximately half of the viable seed contained incompletely-developed embryos. Germination was increased to nearly 100% of viable seed by stratification and cold treatment. This system presumably insures that part of a plant's seed crop will germinate immediately while a portion is delayed until later. Germination in *Alnus* is epigeal and appears to be relatively independent of normal variation in light, temperature, and pH, but it is sensitive to low oxygen and moisture levels (McVean, 1953a).

Many species of *Alnus* hybridize, and numerous putative natural hybrids have been named (Winkler, 1904; Murai, 1964, 1968). Of the New World species, three pairs of taxa have long been suspected of hybridizing naturally. The ranges of *A. incana* spp. *rugosa* and *tenuifolia* overlap in north-central Canada, and the two intergrade morphologically in this region. An extremely variable putative hybrid swarm exists where *A. viridis* spp. *crispa* and *sinuata* occur sympatrically in central and northern Alaska (Hulten, 1944), as does one in the region where *A. incana* ssp. *rugosa* and *A. serrulata* come in contact. In the latter case, Steele (1961) found that hybrids "normally occur in places that may be regarded as somewhat intermediate, and that have almost invariably been disturbed by man" and concludes that *A. serrulata* is introgressing into *A. incana* in this area. No conclusive evidence for hybridization among the various Latin American taxa exists, but the range of variation in some of the species strongly suggests that it does occur. Intermediate forms between *A. acuminata* spp. *arguta* and *glabrata*, between *A. acuminata* ssp. *arguta* and *A. jorullensis*, and between *A. jorullensis* spp. *jorullensis* and *lutea* are rather frequently observed, and these occur in places where hybridization could be expected.

Because putative hybridization is so frequent in the genus, one

Figure 23. A, pistillate and staminate inflorescences of *Alnus serrulata*. B, syrphid flies visiting staminate catkins of *Alnus viridis* ssp. *crispa* in Terra Nova National Park, Newfoundland (photograph courtesy of Garrett E. Crow). C, pistillate inflorescences of *Alnus serrulata* showing the typical erect axis. D, pistillate inflorescences of *Alnus incana* ssp. *rugosa* showing the typical geniculate axis.

may conclude that reproductive isolation in *Alnus* species is mainly extrinsic in nature. Successful crossing among the three subgenera has not been reported, however. *Alnus maritima* is effectively isolated from all the other species by its flowering season. Several species of the subgenera *Alnus* and *Alnobetula* grow sympatrically, but they do not produce hybrid offspring. Within each subgenus, the species or infraspecific taxa are all separated either geographically or altitudinally and climatically.

Apomixis was described in *Alnus serrulata* from New England by Woodworth (1929, 1930). Meiosis in the plants studied (called *A. rugosa* by the author) was found to be extremely abnormal. Pistillate catkins were found to have no embryo sac development at the time of pollen release, and the pollen was judged to be less than 5% morphologically normal, yet the plants produced an abundance of viable seed. Embryo sac development began about three months after the pollen was shed without a reduction of chromosome number. From one to four embryo sacs developed in each ovule, one to five embryos maturing in each embryo sac. The embryos were seen developing from the diploid egg and by nucellar budding. In a later paper, Woodworth (1931) showed that *A. serrulata* from Virginia produced almost perfect pollen and concluded that the cytological irregularities seen in the New England populations were the result of hybridization with *A. incana* ssp. *rugosa.*

Pollen of specimens selected from throughout the range of each taxon was examined (as described above), but such morphological abnormalities were not found in any other species or in any other part of the range of *Alnus serrulata.* From these results it appears that apomixis is rare or absent in most of the American species of the genus. Further work, especially on a population basis, is needed for a better understanding of this problem.

CHROMOSOME NUMBERS

All of the American species of *Alnus* for which chromosome information is available have numbers of $2n = 28$ (Table 4). Unfortunately, there are no data for *Alnus rhombifolia, A. oblongifolia,* nor for any of the Latin American taxa.

In 1934, Wanscher predicted that the basic chromosome number in the Betulaceae is $x = 7$, based on numbers of $x = 8$ in *Carpinus* and *Ostrya* and $x = 14$ or higher in the other genera. In 1962, Chiba found a diploid number of 14 in root tip cells of Japanese *Alnus hirsuta* var. *microphylla* (*A. inokumae* Murai & Kusaka), a taxon which may be conspecific with *A. incana*. In the typical variety of *A. hirsuta*, the number was found to be $2n = 28$. The basic chromosome number in *Alnus* is therefore taken to be $x = 7$.

Four levels of polyploidy occur in *Alnus*, although $2n = 28$ is by far the most common condition. In addition to the number reported by Chiba ($2n = 14$) and the many species having $2n = 28$, several European and Asian species have numbers of $2n = 42$ and $2n = 56$. *Alnus glutinosa* has been reported with somatic chromosome numbers of both $2n = 28$ and $2n = 56$ (Woodworth, 1929, 1931), while *A. subcordata* and *A. japonica* may have either $2n = 28$, $2n = 42$, or $2n = 56$ (Gram *et al.*, 1941; Jaretzky, 1930; Woodworth, 1929, 1931). *Alnus cordata* has been found with either $2n = 28$ or $2n = 42$ (Jaretzky, 1930). *Alnus orientalis* has been found with $2n = 42$ (Gram *et al.*, 1941). In addition, Kodama (1967) reported a chromosome number of $2n = 112$ from root nodule tissue of *Alnus firma* in Japan, but it is not known whether other parts of the plant had this number.

Jaretzky (1930) and Gram *et al.* (1941) report that meiosis is irregular and the pollen quality poor in the species having 42 chromosomes (*Alnus cordata, A. subcordata,* and *A. orientalis*). In plants having $2n = 56$ chromosomes, meiosis is nearly regular and almost all the pollen is well-formed (Gram *et al.*, 1941). All reports for species in which $2n = 28$ (except those involving putative hybrids between *A. incana* ssp. *rugosa* and *A. serrulata* by Woodworth, 1929, 1930, 1931) likewise indicate a normal meiosis.

It seems clear that the alders with chromosome numbers of $2n = 28$ and $2n = 56$ represent a simple polyploid series. Those with 42 chromosomes may have resulted from hybridization between $2n = 28$ and $2n = 56$ types.

PHYLOGENETIC TRENDS

Divergence and Convergence. From anatomical evidence (Tippo, 1938; Hall, 1952) the Betulaceae are not primitive but are regarded as low in the Amentiferae. Tippo considers *Betula* and *Alnus* to be the most primitive genera, *Corylus* and *Ostryopsis* less so, and *Carpinus* and *Ostrya* least primitive. Within *Alnus* itself, considerable morphological and biochemical variation suggests extensive specialization and divergence among various species and groups of species.

Table 4. **Chromosome numbers reported for American species of Alnus and their Eurasian vicariants.**

Species	Number (2*n*)	Reference
A. incana ssp. *incana*	28	Gram, et. al., 1942
	28	Löve, 1954
	28	Wetzel, 1928
A. incana ssp. *rugosa*	28	Löve, 1954
	28	Woodworth, 1929
	28	Woodworth, 1931
A. incana ssp. *tenuifolia*	28	Gram, et al., 1942
A. maritima	28	Wetzel, 1929
	28	Woodworth, 1929
	28	Woodworth, 1931
A. rubra	28	Taylor & Mulligan, 1968
	28	Gram, et al., 1942
	28	Jaretzky, 1930
	28	Wetzel, 1927
	28	Wetze, 1928
A. serrulata	28	Woodworth, 1929
	28	Woodworth, 1930
	28	Woodworth, 1931
A. viridis ssp. *crispa*	28	Löve, 1954
	28	Löve & Löve, 1965
	28	Löve & Löve, 1966
	28	Pouques, 1949
	28	Woodworth, 1929
	28	Woodworth, 1931
A. viridis ssp. *sinuata*	28	Taylor & Mulligan, 1968
	28	Löve. 1954
A. viridis ssp. *viridis*	28	Contandriopoulos, 1964
	28	Jaretzky, 1930
	28	Pouques, 1949
	28	Wetzel, 1928
	28	Wetzel, 1929

At the infrageneric level, the alders have diverged into three distinct groups, treated here as the subgenera *Alnus*, *Alnobetula*, and *Clethropsis*. Subgenus *Alnobetula* is adapted to a cold environment, as shown by its present distribution in the boreal latitudes and at high elevations, and by morphological features including the shrub habit and reduction in the size of many structures. At the same time, several other characters, such as the presence of long peduncles, appear to remain primitive in the subgenus.

The basic morphological pattern seen in the "primitive" members of subgenus *Alnus* (illustrated best in America by *A. rubra*, *A. oblongifolia*, and *A. acuminata*) suggests adaptation to a mesic, temperate existence. The Latin American members of this subgenus have diverged from this pattern to a greater or lesser extent, being adapted to a somewhat warmer climate with rainy and dry seasons. None becomes dormant for an extended period as do their northern relatives. One species of this group (*A. jorullensis*) has gained the ability to exist in drier and colder habitats. Individuals of this taxon often have thicker, smaller leaves, thicker bark, and other characters suggesting adaptation to more xeric conditions. *Alnus serrulata* and *A. rhombifolia* of the southern United States have also diverged in this direction and possess many of the same specializations. *Alnus incana*, like *A. viridis*, has become adapted to a cool environment, but not to the same extent. Here may be seen convergence in such characters as the shrub habit and smaller leaves, while the subgeneric characteristics (e.g., the pistillate catkins exposed during the winter before anthesis) are retained.

Although some phylogenetic taxonomists have concluded that subg. *Clethropsis* represents the most primitive segment of the genus (Takhtajan, 1960; Murai, 1964), *Alnus maritima* is seen to possess a host of apparently derived characters, including reduced fruit wings, a semi-shrub habit, autumn flowering, reduced inflorescences, and relatively small obovate leaves. Its peculiar geographical distribution in America suggests great antiquity, but it is not primitive morphologically, at least in readily-observable characters, when compared with such species as *A. oblongifolia*, *A. rubra*, and *A. acuminata*.

Three American species of *Alnus* are represented regionally as subspecies. In each of these, the subspecies have diverged, but they intergrade where their ranges overlap. The strongest divergence occurs in *A. viridis* spp. *crispa* and *sinuata*, ssp. *crispa* being better adapted to low elevations and ssp. *sinuata* to montane conditions;

both are more or less flexible in this respect (ssp. *sinuata* also sometimes occurring in moderate lowland regions along the Pacific coast and ssp. *crispa* sometimes occurring in rather severe montane conditions in the East). There is less morphological differentiation between the subspecies of *A. incana,* although ssp. *rugosa* is shrubbier in habit than ssp. *tenuifolia* (apparently a derived state since the other subspecies of *A. incana* are all more treelike). *Alnus acuminata* has diverged to a lesser extent than *A. viridis* and *A. incana* in North and South America, and it has not adopted a radically different habitat in either area, probably because the two populations have been separated only since the Pleistocene.

Alnus is an old genus, and convergence has apparently occurred repeatedly in many characters. This is especially true for some of the easily-seen features by which the species are recognized in the field (habit, leaf shape, pubescence, and cone size), and in most cases, the specializations have developed under similar environmental conditions where they have appeared in two or more otherwise distinct species. Similar phenomena have been described in many other temperate woody genera, most recently by Tucker (1974) in the genus *Quercus.*

Phylogeny. The relatively large amount of convergence in *Alnus,* together with its wide distribution and apparent repeated migrations over a long period of time make the construction of a phylogeny difficult. However, certain patterns are repeated in the results of the various studies reported here. A phylogenetic tree, synthesized from all of this data, is provided in Figure 24. The base of this figure represents the supposed origin of the genus, and the tips of the branches the present American species and subspecies, together with the Eurasian vicariants of American taxa. Taxa toward the center of the tree are regarded as relatively unspecialized, while those away from the center are seen as more advanced, though in a few cases it was not possible to accurately represent the taxa in this way and still show their true cladistic relationship (e.g., in the case of *A. rhombifolia, A. oblongifolia,* and *A. acuminata*). While they represent progressive development in a qualitative sense, neither the horizontal nor the vertical axis is intended to indicate relationship or time quantitatively. Because extinction has certainly occurred many times in the genus, there are bound to be gaps and missing branches, and because the tree is necessarily drawn in only two

Figure 24. Phylogenetic tree of the New World taxa of *Alnus* and their Eurasian vicariants.

dimensions, some additional distortion has to be present. Nevertheless, this scheme provides an approximate picture of the relationships among the present taxa of North and South America based on the present study.

ECONOMIC IMPORTANCE

Alnus has long been used by man, especially for lumber, in tanning and dyeing, for the production of charcoal, and as an astringent medication. It was important to the ancient Greeks and Romans for shipbuilding, and medieval builders, seeing that alders grew near water, concluded that the wood of this tree must be resistant to moisture and constructed much of Venice and Amsterdam on piles made from its trunks.

Among the more obscure uses for alders is one reported by Nicholas Culpeper in 1653, who writes that "leaves gathered while the morning dew is on them, and brought into a chamber troubled with fleas, will gather them thereonto, which being suddenly cast out, will rid the chamber of those troublesome bedfellows." Coon (1963) states that "the twigs, bark, and catkins are a source of a black dye that has been known and used for centuries. Used alone, it dyes wool a reddish color and used with copperas, produces a good black. Young shoots produce colors from yellow to cinnamon, while the leaves will produce a dye for leather." Other uses of *Alnus* in Europe, including the manufacture of wooden shoes and clog soles, are reviewed by Eldin (1964).

Although seldom a major timber source in America, *Alnus* is nevertheless important for a variety of wood products. In the Pacific Northwest the wood of *Alnus rubra* is used in cabinetry as well as for the manufacture of toys, trays, brush handles, spools, shoe soles, boxes, and other small items (cf. Worthington *et al.*, 1962). It is also an important source of pulp for paper in this region, and research into its productivity, management, etc. has been increasing in recent years (cf. Smith, 1968; Williamson, 1968). *Alnus acuminata* finds similar uses throughout its range from Mexico to Argentina. Acosta-Solis (1939) states that in Ecuador alder wood "is used in carpentry, furniture making, and cabinet work, and before Eucalypt lumber became available, was employed in general construction in the same way as Calupf, Sauce, Algarrobo, and Arrayan. In the province of Tungurahua it is used for making the boxes and packing cases in which fruit is exported."

Commenting on the shrubby stature of the alders of eastern North America, Michaux (1859) states that "common alder[1] is too small to be applicable to any use in the arts: from its inferiority of size, it will probably one day give place to the European Alder" and "the dwarfish stature of all the species of Alder that have hitherto been discovered in North America excludes them from that class of vegetation to the description of which I have restricted my labors; but I could not forbear mentioning the two most remarkable species, of which one[2] merits attention on account of its abundant diffusion, and the other[3] on account of a striking peculiarity in the color of its leaves." In spite of their small size, even the shrubby alders of the New World have important uses. Among these is their use as a source of firewood for the natives of regions where other fuels are scarce, including parts of Alaska (Porsild, 1939) and the high Andes of South America (Record & Hess, 1943).

The ability of alders to fix atmospheric nitrogen may someday benefit the forestry industry. According to Tarrant (1968), "evidence from many studies indicates that alder (*Alnus* spp.) has a potential relation to forestry similar to that of legumes to Agriculture." Presently, however, members of the genus have not found extensive use in this way in North America.

The bark and foliage of *Alnus* are very astringent and are used in primitive American societies for medicinal purposes. Smith (1923, 1928, 1932, & 1933) reports a number of such uses among American Indians, including the making of poultices to reduce swellings and infusions or teas to treat sores, the passing of blood in stools, cases of piles, and the flux. He (1923) states that "the white man has held valuable its astringent properties in the treatment of diarrhea and haematuria. The liquid has been used as a mouth wash or gargle in the treatment of stomatitis and pharyngitis. When injected into the vagina, it is said to cure leucorrhaea." Standley (1920) mentions that in Mexico an infusion of bark is used as a lotion for cutaneous diseases and that a decoction of the bark is sometimes taken internally for scrofula and venereal diseases. Martinez (1959) reports that the bark of *A. firmifolia* (=*A. jorullensis*) is sold in Mexican markets for such purposes. In Peru, the leaves of alders are crushed

---

[1] *Alnus serrulata.*

[2] *Alnus serrulata.*

[3] *Alnus incana* ssp. *rugosa.*

with butter to cicatrize wounds and also used without fat to protect against inflammation. Applied to recent wounds, the leaves are used to stop bleeding (Macbride, 1936). In the United States, according to Vines (1960), the bark of *A. serrulata* was formerly used in the treatment of "intermittent fever". Smith (1932) states that "the eclectic practitioner in the United States and Canada employed it [the bark] in a powdered condition for dusting upon chafed body surfaces."

Other native American uses of the alders include the tanning and dyeing of leather and textiles with preparations of the bark (Macbride, 1936; Smith, 1923, 1932, & 1933; Standley, 1920; Standley & Steyermark, 1952). In some regions alders are of limited value for livestock forage. All of the species are important in the reduction of soil erosion since *Alnus* is among the first of the colonizers to follow fires, lumbering, volcanic eruptions, and other disturbances of the natural vegetation. In Great Britain, the Netherlands, and Germany, alders have been used for some time in the rehabilitation of mine spoils (Tarrant, 1968).

SPECIMENS EXAMINED

Approximately 9,000 specimens were examined during this study. In the treatment of each taxon on the following pages, only representative specimens are cited, but the collection sites of all the material seen have been plotted on the maps. The specimens cited were chosen for use in the numerical taxonomic part of the work and represent the complete range of phenotypic and geographical variation observed. A list of all the specimens used has been prepared and placed on file in the Beal-Darlington Herbarium of Michigan State University. This is also available to interested individuals from the author.

In the citation of specimens, herbaria have been given the abbreviations used in the sixth edition of Index Herbariorum (Holmgren & Keuken, 1974). Collections from the following institutions were examined: The Arnold Arboretum, Harvard University (A); The University of Alberta (ALTA); The University of Arizona (ARIZ); The National Museum of Canada (CAN); Biosystematics Research Institute, Canada Department of Agriculture (DAO); The Dudley Herbarium, Stanford University (DS); Herbario de la Escuela Nacional de Ciencias Biologicas, Instituto Polytécnico

Nacional, México (ENCB); The Searle Herbarium, Field Museum of Natural History (F); The Gray Herbarium, Harvard University (GH); Indiana University (IND); The Jepson Herbarium, The University of California (JEPS); Herbario Nacional del Instituto de Biología de la Universidad Nacional Antónoma de México (MEXU); The University of Michigan (MICH); The Missouri Botanical Garden (MO); The Beal-Darlington Herbarium, Michigan State University (MSC); The University of Notre Dame (ND); The Greene Herbarium, The University of Notre Dame (NDG); The New England Botanical Club Herbarium (NEBC); The New York Botanical Garden (NY); The Bebb Herbarium, The University of Oklahoma (OKL); The Ohio State University (OS); The University of Pennsylvania (PENN); The Academy of Natural Sciences of Philadelphia (PH); The Rocky Mountain Herbarium, The University of Wyoming (RM); The University of California at Berkeley (UC); United States National Herbarium, Smithsonian Institution (US); The University of Wisconsin (WIS); The University of Washington (WTU).

TAXONOMIC TREATMENT

Alnus P. Miller, Gard. Dict., Abbr. ed. 4. 1754.

Alnus Tournefort, Inst. Rei Herb. 1: 587. 1700; Ehrhart, Oekon. Pfl. Hist. 2: 211. 1753; Miller, Gard. Dict., Abbr. ed. 4. 1754.
Betula Linnaeus, Sp. Pl. 2: 983. 1753, in part as to species 5.
Betula-alnus Weston, Bot. Univers. Hortul. 1: 1770, not validly published.
Betula-alnus Marshall, Arb. Amer. p. 20. 1785, *nom. illeg.*

Deciduous monoecious trees and shrubs with narrowly to broadly ovate to obovate leaves, watery sap, smooth to (in age) scaly astringent bark, and terete branchlets with triangular pith and (usually) conspicuous circular to elliptic lenticels, the twigs, buds, and foliage sparsely to densely covered with simple straight hairs and minute peltate glands; sapwood white, soft, close, straight-grained, and brittle, becoming red when exposed to the air before dry; heartwood reddish-brown, usually forming only a small core; roots often stoloniferous, the rootlets fibrous, bearing nodules containing nitrogen-fixing endophytes. Leaf buds with 2 or 3 equal mostly valvate stipular scales or 5 or more imbricate scales, raised on well-defined minute stems (stipitate), elongate, often slightly three-angled, ovoid to oblong and acuminate, acute, or rounded at the apex, resin-coated; apical bud pseudoterminal. Leaves alternate, simple, pinnately-veined, singly- or doubly-serrate to nearly entire, petiolate, deciduous, shed while still green; in the bud enclosed in their stipules, becoming conduplicate in expansion, plicately-folded along the lateral veins. Leaf scars often elevated, obtuse to rounded below and somewhat notched above, with three large approximately equidistant circular to crescent-shaped bundle scars, the lowest often obviously composed of three smaller scars. Stipules ovate, elliptic, or obovate, acute to rounded at the apex, glandular, glabrous to densely pubescent, ciliate-margined, deciduous or moderately persistent. Flowers unisexual, sessile, in modified cymules reduced and arranged into pedunculate bracteate aments, the peduncles from the axils of leaves or minute leafy bracts, opening in the early spring before or with the unfolding of the leaves, or in later summer or autumn, often partially developed during the previous growing season and either exposed or enclosed in the bud during dormancy. Pistillate inflorescences ovoid to oblong or cylindric, erect, pedunculate, formed in the axils of the leaves of a branchlet developing in the axil of one of the upper leaves on the main axis below the staminate inflorescences, appearing as a racemose cluster or solitary on the main stem; bracts subtended by and adnate with 4 bracteoles, imbricate, and somewhat fleshy. Pistillate flowers 2 per bract, without perianth. Pistil 1, compressed, 2- (or rarely 3-) carpellate; ovary inferior, 2- (rarely 3-) locular below and 1-locular above; ovules 2, one per locule, axially attached near the summit of the locule, pendulous, anatropous; styles 2, linear, free, each stigmatic near the apex. Pistillate inflorescences enlarging, the bracts becoming thick and woody after anthesis; mature scales obovate, 3- to 5-lobed or truncate at the apex, forming a persistent subglobose, ovoid, or cylindric strobilus-like infructescence. Staminate catkins elongate, pendulous, in one or more racemose clusters or solitary in the axils of leaves or leafy bracts; bracts short-stalked, peltate, adnate at the base to 3 or 5 bracteoles, subtending 3 (to rarely 6) minute flowers. Perianth of one series, 4- (or infrequently 1- to 6-) parted, the segments ovate, elliptic, or obovate and connate at the base, glandular-margined; stamens 2 or 4 (occasionally 5 or 6), short (never much exserted from the catkin), inserted at the base of the perianth parts and often basally adnate to them; filaments short to long, undivided; anthers erect, dorsifixed, introrse, 4-sporangiate and 2-locular, the thecae parallel, partially separate, contiguous, dehiscing longitudinally. Fruit a small, flattened, ovate, elliptic, orbicular, or obovate nutlet or samara, pointed and crowned at the apex by the remnants of the styles, wingless (with a narrow wing-like chartaceous border) or broadly membranaceous winged on 2 margins; pericarp of 2 coats, the outer thin and membranaceous, the inner thick and crustaceous. Seed solitary by abortion, filling the cavity of the fruit, the hilum apical, testa membranaceous, without endosperm. Embryo large, straight, the radicle superior and shorter than the flat, fleshy cotyledons.

LECTOTYPE SPECIES: *Alnus glutinosa* (Linnaeus) Gaertner (*Betula alnus α glutinosa* Linnaeus).

Alnus is the classical Latin name for the alder tree and for objects made from its wood, including ships and boats. In this connection it was used by Virgil, Pliny, and others. It is presumably derived from the Latin verb *alo* (to nourish), referring to its usual close association with water.[1] The English name *alder* is derived from the Old English *alor, aler* (Murray *et al.,* 1933).

The genus was generally considered distinct from *Betula* until the two were combined as *Betula* by Linnaeus in *Species Plantarum* (1753). Phillip Miller was the first to resurrect *Alnus* in the *Gardner's Dictionary, Abridged,* ed. 4 (1754), but since he did not use binomial nomenclature one of his species cannot be designated the type. In the 8th edition of the *Gardner's Dictionary* (1768), where he first used binomials, Miller omitted the genus altogether, apparently partly by mistake, referring the reader first under "Alder-Tree" to *Alnus,* and then under *"Alnus"* to *Betula,* but not including any alder species there. The first treatment employing binomial nomenclature to list *Alnus* species, excluding Hill's *The British Herbal* of 1757 because of its inconsistency in the use of binomials (cf. Stafleu *et al.,* 1972), is Gaertner's *De Fructibus et Seminibus Plantarum* (1790). The only species of *Alnus* cited in this work is *A. glutinosa* (Linnaeus) Gaertner, based on Linnaeus' *Betula alnus α glutinosa* (Sp. Pl. **2:** 983. 1753). This species has therefore been chosen as the lectotype of the genus.

---

[1] Wood (1880) states that the Latin name is derived from the Celtic *al* (near) and *lan* (riverbank), also referring to its usual habitat.

ARTIFICIAL KEY TO THE SUBGENERA, SPECIES, AND INFRASPECIFIC TAXA

1. Winter buds stalked, covered (sometimes incompletely) by 2 or 3 equal stipular scales; leaf-bearing stems usually not forming both long and short shoots; staminate and pistillate inflorescences produced mid to late in the growing season, not with new growth in the spring. .... 2.
    2. Lateral veins of the leaves terminating in teeth at the margin; pistillate inflorescences (and later infructescences) borne on short branchlets in racemose clusters; flowering occurring at the beginning of the growing season (spring). Subg. *Alnus*. .... 3.
        3. Leaves mostly ovate (rarely elliptic), finely serrate or serrulate to rather coarsely double-serrate. .... 4.
            4. Leaf margins finely and evenly serrate or serrulate, sometimes slightly lobed; trees of the western United States. ... 3. *A. rhombifolia.*
            4. Leaf margins serrate or double-serrate to irregularly-toothed.. 5.
                5. Margin of leaf blade strongly revolute; large trees of northwestern coastal North America. .... 1. *A. rubra.*
                5. Margin of leaf blade flat or only slightly to moderately revolute; trees and shrubs. .... 6.
                    6. Leaves lanceolate to narrowly ovate or ovate........ 7.
                        7. Major teeth of the leaves sharp and acuminate, usually standing out well above the secondary teeth. .... 8.
                            8. Internodes, petioles, and lower leaf surfaces and veins glabrous; staminate flowers with 4 stamens and perianth parts; trees of central and southern Mexico.........4c. *A. acuminata* ssp. *glabrata.*
                            8. Internodes, petioles, and lower leaf surfaces and veins at least sparsely pubescent, often villous to velutinous; staminate flowers with either 2 or 4 stamens and perianth parts................. 9.
                                9. Stamens and perianth parts 4, equal in size; trees of South America. ....4a. *A. acuminata* ssp. *acuminata.*
                                9. Stamens and perianth parts 2 or 4, if 4, then 2 large and 2 smaller; trees of the southwestern United States and adjacent northern Mexico. .... 2. *A. oblongifolia.*
                        7. Major teeth of the leaves acute to obtuse, short to long. .... 2. *A. oblongifolia.*
                    6. Leaves moderately to broadly ovate, the major teeth obtuse to rounded.................................... 10.
                        10. Leaves usually large, the blade 5–19 cm long, relatively finely double-serrate or serrate, the apex usually acuminate, densely glandular below; infructescences 11–45 mm long; bark usually with transverse constrictions or ridges; trees of Mexico, Central America, and South America. .... 11.

11. Leaves usually finely serrate or serrulate; trees of South America.4a. *A. acuminata* ssp. *acuminata.*
11. Leaves usually double serrate; trees of Mexico and Central America. 4b. *A. acuminata* ssp. *arguta.*

10. Leaves usually smaller, the blade 4–10 cm long, more coarsely double-serrate, the apex usually acute to obtuse, sparsely to only moderately glandular below; infructescences 10–17 mm long; bark without transverse constrictions; large shrubs and small trees of Canada and the northern and western United States. .... 12.

12. Leaf blade moderately thick, the major teeth acute; large shrubs of eastern Canada and the northeastern United States. .... 6a. *A. incana* ssp. *rugosa.*
12. Leaf blade thin and papery, the major teeth usually rounded; large shrubs or small trees of the western United States and Canada. ....6b. *A. incana* ssp. *tenuifolia.*

3. Leaves mostly elliptic, oblong-elliptic, or obovate, occasionally tending toward ovate. .... 13.

13. Leaves more or less orbicular, the apices usually retuse (occasionally rounded); moderately large trees naturalized in the northeastern United States and adjacent Canada. ....8. *A. glutinosa.*
13. Leaves ovate, elliptical, oblong, or obovate, the apices acute to obtuse or sometimes slightly rounded; trees and shrubs of the United States, Canada, Mexico, and Central America. .... 14.

14. Leaf margins finely and evenly serrulate; leaf texture papery to moderately coriaceous. .... 15.

15. Leaf blades broadly elliptic to obovate, the apices often more or less rounded; staminate flowers with 4 stamens; large shrubs of eastern North America. . 7. *A. serrulata.*
15. Leaf blades narrowly elliptic or rhombic, the apices usually not rounded; stamens 2 (or 4 with 2 reduced in size); large trees of the western United States. .. 3. *A. rhombifolia.*

14. Leaf margins rather coarsely and unevenly toothed or wavy, especially near the apex; leaf texture very firm and leathery; large trees of southern Mexico and Guatemala. .... 16.

16. Lower leaf surface with relatively few small widely-spaced whitish, yellowish, or brownish glands. .... 5a. *A. jorullensis* ssp. *jorullensis.*
16. Lower leaf surface densely covered with large whitish to bright yellow glands. ..... 5b. *A. jorullensis* ssp. *lutea.*

2. Lateral veins of the leaves usually terminating by anastomosing with other veins near the margin (infrequently ending in the teeth); pistillate inflorescences (and later infructescences) solitary in leaf axils along the main stems; flowering occurring near the end of the growing season (late summer or autumn). Subg. *Clethropsis.* .... 10. *A. maritima.*

1. Winter buds sub-sessile (stalks not over 1 mm long), covered by 5 or more unequal imbricate scales; leaf-bearing stems usually with both long shoots and short spurs, the latter bearing the leaves; staminate inflorescences produced late in the previous growing season, pistillate inflorescences produced along with the first new growth of the season. Subg. *Alnobetula*. .... 17.
   17. Leaves finely serrate or serrulate (rarely double-serrate), leathery, dark green, and sometimes sparsely to densely pubescent below; shrubs of the eastern United States and adjacent Canada, northern Canada to Alaska, and the Pacific coast south to northern California. .... 9a. *A. viridis* ssp. *crispa*.
   17. Leaves moderately to coarsely double-serrate (rarely singly or finely serrate), thin to membranaceous, light or yellowish green, glabrous; shrubs of the mountainous and coastal western United States and Canada. .... 9b. *A. viridis* ssp. *sinuata*.

Alnus Miller subg. **Alnus**

Alnus Miller, Gard. Dict., Abbr. ed. 4 1754; *Alnus* c. *Alnus* Endlicher, Gen. Pl. suppl. 2, p. 28. 1842; *Alnus* sect. *Alnus* Sargent, Silva North Amer. **9**: 68. 1896; *Alnus* subg. II. *Alnus* Schneider in Sargent, Pl. Wilson. **2**(3): 490. 1916.

Alnus sect. II. *Clethra* W. D. J. Koch, Syn. Fl. Germ. Helvet., p. 663. 1837. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.

Alnus sect. II. *Gymnothyrsus* Spach, Ann. Sci. Nat. ser. 2, **15**: 204. 1841; *Alnus* IV. subgen. *Gymnothyrsus* (Spach) Regel, Bull. Soc. Nat. Mosc. **38**(3): 425. 1865. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.

Alnus sect. I. *Phyllothyrsus* Spach, Ann. Sci. Nat. ser. 2, **15**: 204. 1841; *Alnus* sect. *Gymnothyrsus* subsect. *Phyllothyrsus* (Spach) Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 98. 1955. LECTOTYPE: *A. acuminata* Humboldt, Bonpland, & Kunth.

Alnus subgen. *Euclethrus* Petermann, Deutschl. Fl. p. 516. 1849. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.

Alnus sect. II. *Betulaster* Regel, Mem. Soc. Nat. Mosc. **13**(2): 144. 1861. TYPE: *A. lindeni* Regel (= *A. acuminata* Humboldt, Bonpland, & Kunth).

Alnus sect. IV. *Eualnus* Regel, Mem. Soc. Nat. Mosc. **13**(2): 152. 1861. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.

Alnus sect. III. *Pseudalnus* Regel, Mem. Soc. Nat. Mosc. **13**(2): 145. 1861. LECTOTYPE: *A. acuminata* Humboldt, Bonpland, & Kunth.

Alnus sect. *Pycnantha* Muller, Madroño **5**: 152. 1940. TYPE: *A. densiflora* Muller (= *A. incana* (Linnaeus) Moench).

Alnus sect. *Gymnothyrsus* subsect. *Hedroiostachys* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 101. 1955. TYPE: *A. glabrata* Fernald (= *A. acuminata* Humboldt, Bonpland, & Kunth).

Alnus sect. *Gymnothyrsus* subsect. *Phyllothyrsus* ser. *Acutissimae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 99. 1955. TYPE: *A. acutissima* (Winkler) Callier (= *A. acuminata* Humboldt, Bonpland, & Kunth).

Alnus sect. *Gymnothyrsus* subsect. *Phyllothyrsus* ser. *Ferrugineae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 99. 1955. TYPE: *A. ferruginea* Humboldt, Bonpland, & Kunth (= *A. acuminata* Humboldt, Bonpland, & Kunth).

Alnus sect. *Gymnothyrsus* subsect. *Podostachys* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 99. 1955. TYPE: *A. serrulatoides* Callier.

Alnus sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Glutinosae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 100. 1955. TYPE: *A. glutinosa* (Linnaeus) Gaertner.

Alnus sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Jorullenses* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 101. 1955. TYPE: *A. jorullensis* Humboldt, Bonpland, & Kunth.

Alnus sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Rhombifoliae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 100. 1955. TYPE: *A. rhombifolia* Nuttall.

Alnus sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Rubrae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 100. 1955. TYPE: *A. rubra* Bongard.

Alnus sect. *Proskeimostemon* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 102. 1955. TYPE: *A. hirsuta* Turczaninov (= *A. incana* (Linnaeus) Moench).

Alnus sect. *Proskeimostemon* ser. *Incanae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 104. 1955. TYPE: *A. incana* (Linnaeus) Moench.

Alnus sect. *Proskeimostemon* ser. *Hirsutae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 103. 1955. TYPE: *A. hirsuta* Turczaninov (= *A. incana* (Linnaeus) Moench).

Alnus sect. *Glutinosae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154:** 63. 1963, *nom. nud.; Alnus* subgen. *Gymnothyrsus* sect. *Glutinosae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154:** 67. 1963, *pro. syn.; Alnus* subgen. *Gymnothyrsus* sect. *Glutinosae* Murai, Bull. Gov. For. Expt. Sta. Jap. **171:** 50. 1964, not validly published.

Alnus sect. *Maritimae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154:** 66. 1963, not validly published; *Alnus* subgen. *Gymnothyrsus* sect. *Maritimae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154:** 66. 1963, *pro syn.*

Large shrubs and small to large trees; twigs and young branches not differentiated into long and short shoots; bud stalks well developed; buds covered by 2 (or sometimes 3) equal stipular valvate scales. Leaves coarsely to very finely double-serrate or serrulate; lateral veins ending in major teeth at the margin. Pistillate inflorescences borne on short, stout peduncles, usually without subtending leaves, in racemose clusters on short branchlets along a major branch, the latter bearing the staminate catkins at the upper nodes, usually without subtending leaves, in one or more racemose clusters. Pistillate and staminate inflorescences both formed during the previous growing season and exposed during the dormant period (where present); anthesis occurring in the spring before new growth commences; fruits maturing at the end of the current growing season; staminate flowers with 4 (occasionally 2) stamens; perianth parts 4, 2 sometimes reduced in size. Fruits lacking wings or merely narrowly wing-margined on two sides.

1. **Alnus rubra** Bongard

Alnus rubra Bongard, Mem. Acad. Sci. St. Petersb. ser. 6, **2:** 162. 1833; *Alnus incana η rubra* (Bongard) Regel, Mem. Soc. Nat. Mosc. **13**(2): 157. 1861. TYPE: *Mertens*, "a l'ile de Sitcha" (LE?, not seen).

Alnus castaneaefolia Douglas ex Hooker, Fl. Bor. Amer. **1:** 158. 1838, *non* Mirbel, Mem. Mus. Hist. Nat. **14:** 463. 1827, *pro syn.*

Alnus oregona Nuttall, North Amer. Sylva **1:** 44. 1842. TYPE: *Nuttall s.n.*, "on the borders of the rivers Boisée and Brulée, which pass into the Shoshonée not far from Walla-Walla, and at intervals it continues more or less common to Point Chinhook, near the shores of the Pacific" (Holotype, BM?, not seen; Isotype, PH!).

Alnus maritima hort. ex Wetzel, Bot. Archiv **25:** 264. 1929, *non* Spach, Ann. Sci. Nat. ser. 2, **15:** 206. 1841, *pro syn.*

Alnus washingtonia hort. ex Wetzel, Bot. Archiv **25:** 264. 1929, *pro syn.*

Alnus rubra var. *pinnatisecta* Starker, Jour. For. **37:** 415. 1939; *Alnus rubra* f. *pinnatisecta* (Starker) Rehder, Bibl. Cult. Trees and Shrubs, p. 104. 1949. TYPE LOCALITY: "T. Norman Nelson farm, 16 miles northwest of Portland, Ore." (original material not seen).

Narrow, somewhat pyramidal-crowned trees, up to 28 m in height; trunks usually several, erect, up to 1.5 m in diameter; bark thin, gray, whitish, or irregularly mottled, smooth to slightly rough with small bumps and irregularities, with inconspicuous lenticels when young, broken into shallow plates on older individuals; young stems medium to dark red-brown, dull to moderately lustrous, not glaucous to slightly glaucous, usually without a heavy resinous coating, not differentiated into noticeable long and short shoots, often with prominent longitudinal ridges originating at the nodes; internodes usually glabrous, moderately glandular, the glands small to medium in size, brown or dark brown; nodes and stems bearing inflorescences densely glandular; lenticels oval to elongate, 0.5–1.2 mm long, 0.3–1.1 mm wide, whitish to yellowish, moderately prominent; leaf scars 1.5–2 mm high, 2–4 mm wide, the bundle scars moderately prominent. Buds ellipsoid, acute to slightly rounded at the apex, heavily resin-coated; stalk 2–8 mm long, 1.2–2.5 mm in diameter, glabrous, densely glandular; body 6–10 mm long, 3–5 mm in diameter; scales 2 (–3), stipular, equal, more or less valvate, glabrous to moderately pubescent, glandular; pubescence and glands usually obscured by the heavy coat of resin. Leaves ovate to elliptic; apex acute to obtuse; base broadly cuneate to rounded; blade (3.5–) 6–11 (–15) cm long, (2.5–) 3.5–7 (–9.5) cm wide, medium to dark green and dull to moderately lustrous above, light to medium green or green-brown and dull below, coriaceous; margin strongly revolute, double-serrate or crenate; major teeth (3–) 5–15 (–25) mm apart, 2–6 mm deep (up to 35 mm deep in forma *pinnatisecta* (Starker) Rehder), regular; secondary teeth 3–6 per cm, 0.2–1 mm deep, regular; adaxial surface glabrous to sparsely pubescent, sparsely to moderately glandular; abaxial surface and veinlets glabrous to sparsely pubescent, densely to very densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base usually moderately pubescent to tomentose or wooly-pubescent (rarely only sparsely pubescent); pubescence whitish to yellowish; glands small to medium in size, whitish to yellowish (rarely brownish). Lateral veins 9–14, 4–11 mm apart at mid-leaf, straight or slightly ascending, usually not branching again, terminating in major teeth at the margin; cross veins between lateral veins poorly to well developed. Petioles (7–) 8–18 (–22) mm long, 0.7–2 mm in diameter, sparsely pubescent to moderately villous, moderately to densely glandular. Stipules ovate, elliptic, or obovate, the apex acuminate, acute, or obtuse, 6–8 mm long, 1.7–2.5 mm wide, green to light brown, glabrous to sparsely pubescent, moderately glandular; hairs, when present, yellowish; glands yellowish. Pistillate inflorescences borne in racemose groups of (3–) 4–5 (–8) on short branches diverging moderately to strongly from the main axis, produced during the previous growing season, erect, ovate to elliptic, at anthesis (3.5–) 5–7 mm long, 1.7–2.1 mm in diameter, on peduncles 1–2 mm long, 0.5–1.5 mm in diameter; staminate catkins borne in one or more racemose clusters of (2–) 3–6 at the end of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 3.5–14 cm long, 6–10 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic to obovate, obtuse to rounded at the apex, 1.6–2.1 mm long, 1.2–1.6 mm wide, lined with minute glands at the margin; stamens 4, opposite and separate from or only slightly basally adnate to the perianth parts, usually appearing much longer than the perianth, filaments 0.8–1.6 mm long, anthers 1.3–1.8

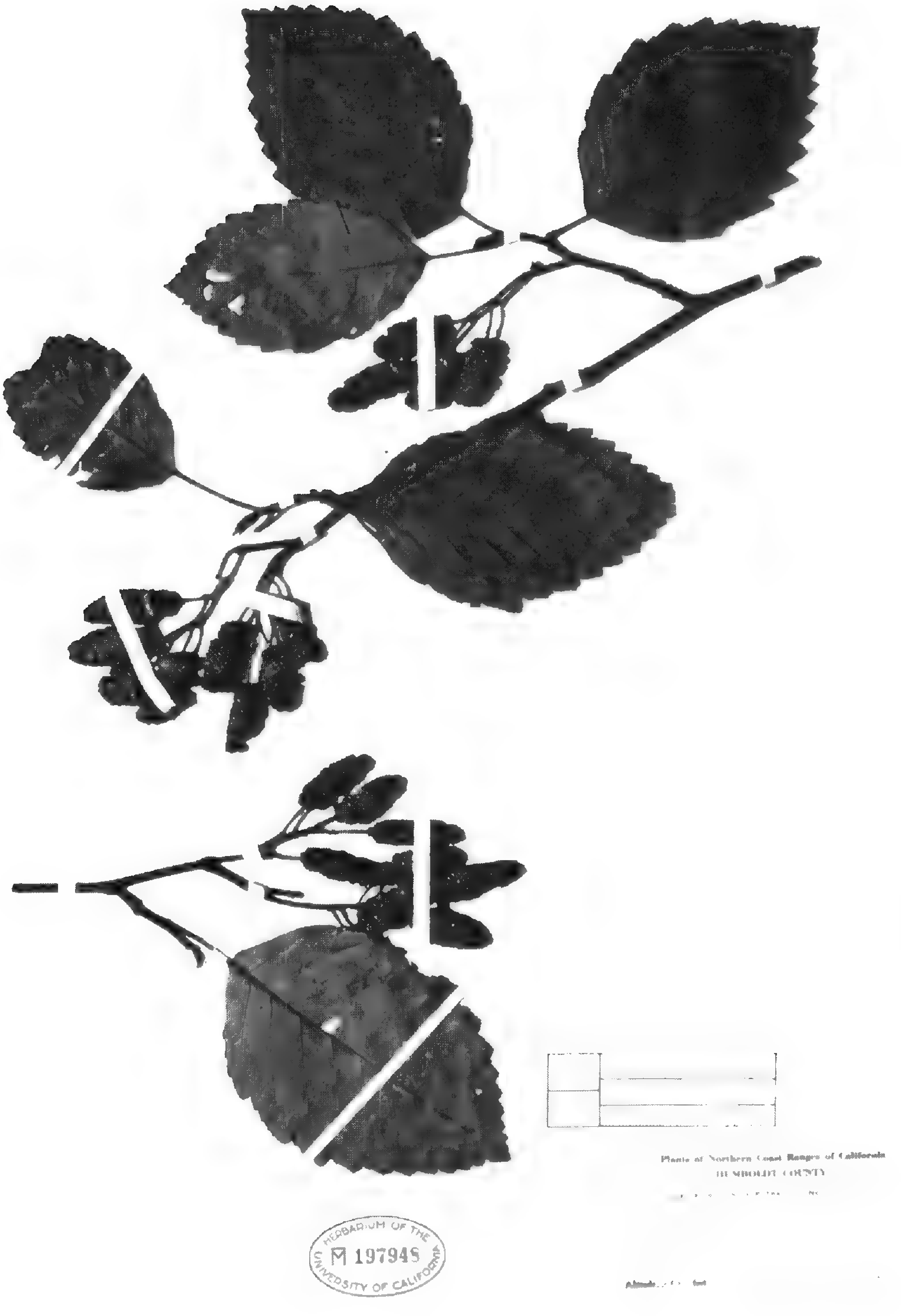


Figure 25. Representative specimen of *Alnus rubra* Bongard.

mm long and 1.3–1.8 mm in diameter, thecae separate for 30–60% of their length. Mature infructescences ovoid (sometimes ellipsoid) or subglobose, (10–) 14–25 (–34) mm long, (6–) 8–14 (–16) mm in diameter, on peduncles 0.5–7 (–10) mm long, 1–1.8 mm in diameter; scales 4–7 mm long, 4.5–6 mm wide at the apex, 1.7–2 mm wide at the base; apex moderately thick to very thick, flat, the terminal lobe truncate, not extended. Fruits narrowly wing-margined, brown; body ovate or elliptic, 2–2.5 mm long, 1–1.5 mm in diameter; wings 2.5–4 mm long, 0.5–1 mm wide, chartaceous; persistent styles 0.5–0.7 mm long. Figures 2B, 8C, 13D, 18B, and 25.

DISTRIBUTION AND HABITAT: Along the Pacific coast from the southwestern corner of Alaska to central California; east along the Columbia River and its tributaries to eastern Washington and western Idaho. On rocky, gravelly, sandy, or humus stream banks and moist floodplains, lake shores, coasts, and open slopes, at elevations mostly below 300 meters (but occasionally occurring as high as 1,000 meters). Often with *Acer, Sequoia, Pseudotsuga, Thuja,* or *Larix.* Figure 26.

COMMON NAMES: Red alder, Oregon alder, alder.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA. North Arm of Cowichan Lake, *Allen s.n.,* Aug. 5, 1938 (cut-leafed) (UC); Bull Harbour, Hope Island off N end of Vancouver Island, *Calder & MacKay 31311* (DAO, UC); 21 mi by road W of Terrace along road to Prince Rupert, *Calder et al. 14928* (DAO, NY, UC); about 2.5 mi E of Masset, Graham Island, *Calder et al. 21299* (DAO); just S of Lawnhill on road from Tiell to Skidegate, Graham Island, *Calder et al. 21737* (DAO); Bowen Island, ca. 5 mi W of Horseshoe Bay, *Huber 1025* (UC); Elk Lake near Victoria, *Macoun s.n.,* Mar. 9, 1914 (CAN); Cowichan Station near Duncan, Vancouver Island, *Wessel 59* (DAO); Prospect Lake near Victoria, *Young 17* (DAO). **United States.** ALASKA. Juneau, *Anderson 6230* (CAN, DAO, F, NY, RM); 13 mi NW of Juneau on Glacier Highway, *Argus & Chunys 6101* (CAN); Washington Bay, Kuiu Island, *Eyerdam 5345* (WTU); on the banks of Indian River in Sitka National Monument, just E. of Sitka, *Heller 14932* (UC, WTU). CALIFORNIA. Alameda Co.: Berkeley, *Bioletti s.n.,* Apr., 1894 (UC); Berkeley, *Blasdale s.n.,* Mar. 12, 1896 (RM). Del Norte Co.: Crescent City, *Applegate 5294* (F, UC). Humboldt Co.: 3 mi NW of Neafus Peak, *Nelson 154* (UC); Trinidad, *Reed s.n.,* July 26, 1941 (DAO); near Carlotta, on Van Duzen River, *Tracy 6149* (UC). Marin Co.: W side of Mount Tamalpais, *Lawfer 131* (WTU). San Mateo Co.: Tunitas, *Rose 36743* (US); Tunitas, *Rose 55189* (RM). IDAHO. Bonner Co.: Whiskey Rock Bay, Pend Oreille Lake, *Johnson 4781* (RM, UC). OREGON. Clatso Co.: Seaside, *Demaree 13441* (NY). Hood River Co.: without location, *Henderson 312* (MO). Lane Co.: 8 mi SW of Cottage Grove, *Furlow 299* (MSC). Washington Co.: Portland, *Lunnell s.n.,* June 20, 1903 (RM); T. Norman Nelson farm, Dixie Mountain, *Matthews s.n.,* Oct. 3,

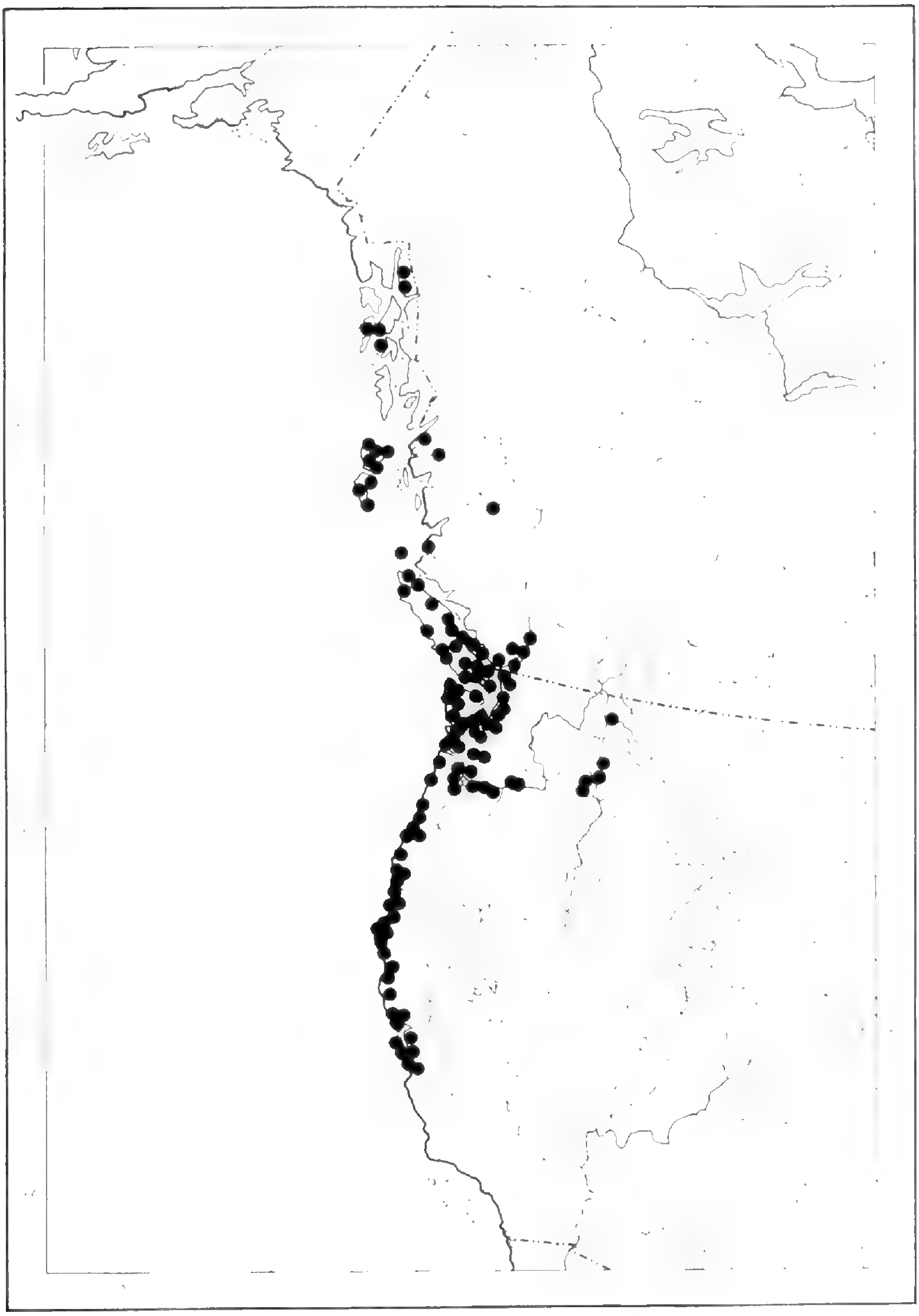


Figure 26. Distribution of *Alnus rubra* Bongard.

1940 (cut-leafed) (UC). WASHINGTON. Clark Co.: Vancouver Lake, *Sheldon 11680* (UC). Grays Harbor Co.: 5 mi SE of Humptulips, *Furlow 293* (MSC). King Co.: Seattle, *Eyerdam 1329* (F, MO); North Seattle, *Eyerdam s.n.*, Aug. 29, 1936 (F, UC); near Seattle, *Thompson 5128* (WTU). Pierce Co.: along the White River 6 mi NW of Cayuse Pass, Mount Rainier National Park, *Furlow 290* (MSC); 7 mi SE of Enumclaw, *Furlow 292* (MSC). Skeminana Co.: E bank of Clearwater Creek, Columbia National Forest, *Matthews s.n.*, Sept. 9, 1940 (cut-leafed) (UC).

Morphologically, *Alnus rubra* appears to be the most generalized species of the genus in America. It is little specialized in terms of habit, leaf shape, leaf size, cone size, and many other features, although it appears to be more or less advanced in a few other characters (including the reduced wings of the fruits).

Nuttall (1842), and later Kuntze (1891), recognized strong affinities between *Alnus rubra* and the alders of Latin America, though this relationship has not frequently been discussed by other authors. Numerical results from the present study, based on both morphological and chemical data, support such a link. *Alnus rubra*, together with *A. acuminata*, *A. jorullensis*, and *A. oblongifolia*, apparently represents a remnant of an ancient complex of species in the New World. Their relationship to the Eurasian species is thus far not well understood, however.

In the western United States and Canada this species was formerly widely known as *Alnus oregona* Nuttall, and this name continues to find limited use today. The name *Alnus rubra* Tuckerman, based on *Betula-alnus rubra* Marshall, is a later homonym applying to *A. serrulata* (Aiton) Willdenow.

Alnus rubra is readily recognized by its large size, gray mottled bark, and ovate, coarsely-toothed, revolute-margined leaves. The largest reported individual occurs in Polk Co., Washington, and has a trunk circumference of 4.1 m, a height of 27.6 m, and a spread of 16.2 m (Pomeroy & Dixon, 1966). In two or three widely-separated locations a form with deeply-cut leaves (*Alnus rubra* f. *pinnatisecta* (Starker) Rehder) occurs sporadically, growing along with individuals of the ordinary kind. The depth of the leaf lobes in such plants is not the same in specimens from various trees or locations.

Alnus rubra is found in varying habitats, ranging from exposed coastal bluffs to river floodplains and pond shores, sometimes forming great expanses of forest in low-lying areas of Washington and Oregon. Mainly restricted to the mesic coastal fog belt, it follows the Columbia River system eastward away from the Pacific

Ocean, reaching western Idaho in several disjunct populations (Johnson, 1968a & b). The limiting factors responsible for the restricted distribution of this species are not well understood. Although it occurs in a rather moderate climate naturally, plants transferred to an experimental garden in central Michigan, where the winters are relatively severe, were found to be perfectly hardy.

2. **Alnus oblongifolia** Torrey

Alnus oblongifolius Torrey *in* Emory, Rept. U.S. Mex. Bound. Surv. **2:** 204. 1859; *Alnus serrulata* γ *oblongifolia* (Torrey) Regel, Bull. Soc. Nat. Mosc. **38**(3): 432. 1865. Type: *Wright 1864,* "banks of the Mimbres and near Santa Barbara, New Mexico" (Holotype, NY!; Isotype, US!). Figure 27.

Open, round-crowned trees up to 15 (–30) m in height; trunks usually several, erect, up to 1.5 m in diameter; bark light gray to brown and smooth when young, dark brown and broken into plates on old individuals, the lenticels usually inconspicuous on smooth trunks and branches; young stems medium red-brown, slightly to moderately lustrous, slightly to moderately resin-coated, not differentiated into long and short shoots, sometimes with slightly to moderately conspicuous longitudinal ridges originating at the nodes; internodes sparsely pubescent to velutinous, sparsely to moderately glandular; nodes and stems bearing inflorescences very densely glandular; hairs yellowish to brownish; glands small to medium in size, yellowish to brownish; lenticels of twigs circular to elliptic, 0.2–0.7 mm long, 0.1–0.5 mm wide, whitish, inconspicuous. Buds ovoid, slightly rounded at the apex, moderately to heavily resin-coated; stalk 1.5–4 mm long, 1–1.5 mm in diameter, glabrous to sparsely pubescent, densely glandular; body 4–8 mm long, 1.5–4 mm in diameter; scales 2, stipular, equal, valvate or often incompletely covering the underlying unexpanded leaves, glabrous to moderately villous, glandular; pubescence and glands usually obscured by the resinous coat. Leaves narrowly ovate or lanceolate to elliptic (or occasionally rhombic); apex long to short acuminate or acute (rarely obtuse or rounded); base narrowly to broadly cuneate or rounded; blade (3–) 5–9 (–11) cm long, (2–) 3–6 (–7) cm wide, medium to dark green and dull (sometimes lustrous when young) above, medium green and dull to moderately lustrous below, chartaceous to moderately coriaceous; margin flat, slightly thickened, sharply to coarsely double-serrate to serrulate; major teeth

Figure 27. Right: holotype of *Alnus oblongifolia* Torrey. Left: specimen of *A. acuminata* Humboldt, Bonpland, & Kunth.

usually acuminate, standing well above the secondary teeth, 5–13 (–16) mm apart at mid-leaf, up to 5 mm deep, regular to irregular; secondary teeth 3–8 per cm, 0.5–2 mm deep, slightly uneven to irregular; adaxial surface sparsely pubescent to (rarely) moderately villous (sometimes glabrous), moderately to densely glandular; abaxial surface and veinlets sparsely to moderately villous, moderately to densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base densely tomentose to wooly-pubescent; pubescence whitish to yellowish; glands small to medium in size, whitish to yellowish (rarely brownish). Lateral veins 9–13 (–15), 3–8 mm apart at mid-leaf, straight or slightly ascending, often branching once again, especially near the base, terminating in major teeth at the margin; cross veins between lateral veins poorly developed and usually not meeting. Petioles (3–) 7–18 (–22) mm long, (0.7–) 1–1.5 mm in diameter, moderately villous to velutinous, moderately to densely glandular. Stipules ovate to elliptic or obovate, acute to obtuse at the apex, 5–7 mm long, 1–1.5 mm wide, green to light brown, glabrous to velutinous, the hairs yellowish, moderately glandular, the glands yellow or pale brown. Pistillate inflorescences borne in racemose groups of (2–) 4–5 (–7) on short branchlets not diverging strongly from the main axis, these sometimes subtended by leaves, several such groups also often clustered together, produced during the previous growing season, erect, ovate to elliptic, at anthesis 4–5 mm long, 2–2.8 mm in diameter, on peduncles 1.5–5 mm long, 1–5 mm in diameter; staminate catkins borne in one or more racemose clusters of 3–6 at the summit of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 3.2–8.5 (–10) mm long, 5–8 mm in diameter, on peduncles 3–13 mm long, 1–1.5 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–4) mm wide. Staminate flowers usually 3 per bract; perianth of 4 parts, these elliptical to obovate, rounded at the apex, 1.3–1.8 mm long, 0.8–1.2 mm wide, 2 frequently reduced in size, the margins lined with minute glands or glands absent; stamens 2 or 4, if 4 then 2 frequently reduced in size, opposite and basally adnate to the perianth parts, usually appearing much longer than the perianth, the filaments 1–1.3 mm long, the anthers 0.9–1.6 mm long, 1–1.4 mm in diameter, the thecae separate for 50–70% of their length. Infructescences ovoid, ellipsoid, or cylindric, (9) 15–24 mm long, 0.5–1.5 mm in diameter; scales 3–4 mm long, 2.5–4 mm wide at the apex, 0.5–1.3 mm wide at the base, the apex thin to moderately thickened, flat, the terminal lobe-tip acute, somewhat to very extended. Fruits narrowly winged, brown; body broadly elliptic to obovate, 1.8–3 mm long, 1.2–2.3 mm in diameter; wings 2.2–3.5 mm long, 0.5–1 mm wide, chartaceous; persistent styles 0.6–1 mm long. Figures 3A, 4A, 8A, 15C, 22B, and 27.

DISTRIBUTION AND HABITAT: Central Arizona and west-central New Mexico south to south-central Chihuahua and northeastern Sonora. Occurring on sandy or rocky streambanks and adjacent moist slopes, often in mountain canyons, from elevations of about 1,500 to 2,300 meters (occasionally as low as 1,000 meters). Often associated with *Pinus, Quercus, Juniperus,* or *Pseudotsuga,* sometimes fairly dense groves. Figure 28.

COMMON NAMES: Arizona alder, New Mexican alder, Mexican alder, aliso.

REPRESENTATIVE SPECIMENS: **Mexico:** CHIHUAHUA. Cuiteco, S of Creel near Río Cuiteco, *Knobloch 948* (MSC); Batopilitas River, *LeSueur 1304* (ARIZ, F). Sonora. Huchuerachi, *Hartman 322* (F, NY, UC, US); 6 mi N of Huachinera, *Hastings & Turner 65–53* (ARIZ); Cañon Palpito, Mun. de Agua Prieta, *Muller 3728* (MICH); Cañon de Bavispe, *White 3116* (MEXU, MICH); Cañon Internacional, *White 3481* (F, MICH). **United States.** ARIZONA. Apache Co.: Bog Creek, 10 mi E of McNary, *Goddard 687* (UC). Gila Co.: bank of East Verde River, at bridge N of Payson, *Foster & Arnold 108* (US); Sierra Ancha, *Jackson 13* (US); without definite location, *Johnson 8581* (NY, UC, US). Graham Co.: Mt. Graham, near Wet Canyon Recreation Area, *Furlow 351* (MSC); Graham Mountains, *Thornber & Shreve 7849* (ARIZ); Graham Mountains, *Thornber & Shreve 8011* (ARIZ). Greenlee Co.: Clifton. A.T., *Rusby 383* (F, NY, UC). Pima Co.: Mt. Lemmon, *Loomis et al. 2180* (ARIZ). Beaver Creek, *Fernow s.n.,* Aug., 1896 (US). Oak Creek, *Pearson 338* (US). NEW MEXICO. Grant Co.: Pinos Altos Mts., *Greene s.n.,* Oct. 11 (F). Luna Co.: banks of the Mimbres and near Santa Barbara, *Bigelow s.n.,* without date (NY); without location, *Wright 1864* (NY, US). Socorro Co.: in the Mogollon Mountains in or near the W fork of the Gila River, *Metcalfe 365* (ARIZ, MO, NY, RM, UC); near Halt's Ranch, in the Mogollon Mountains, *Wooton s.n.,* July 20, 1900 (ARIZ, RM). Pecos Cañon, *Eastwood 15503* (NY).

Alnus oblongifolia possesses a quite restricted distribution relative to the other North American species of the genus. In Sonora this species intergrades with *A. acuminata* ssp. *arguta,* and a case might be made to combine it with that taxon. Sargent, in *The Silva of North America* (1896), tentatively included it in *Alnus acuminata* pending the accumulation of additional specimens, noting that it appeared to be identical with certain of the Mexican material. In

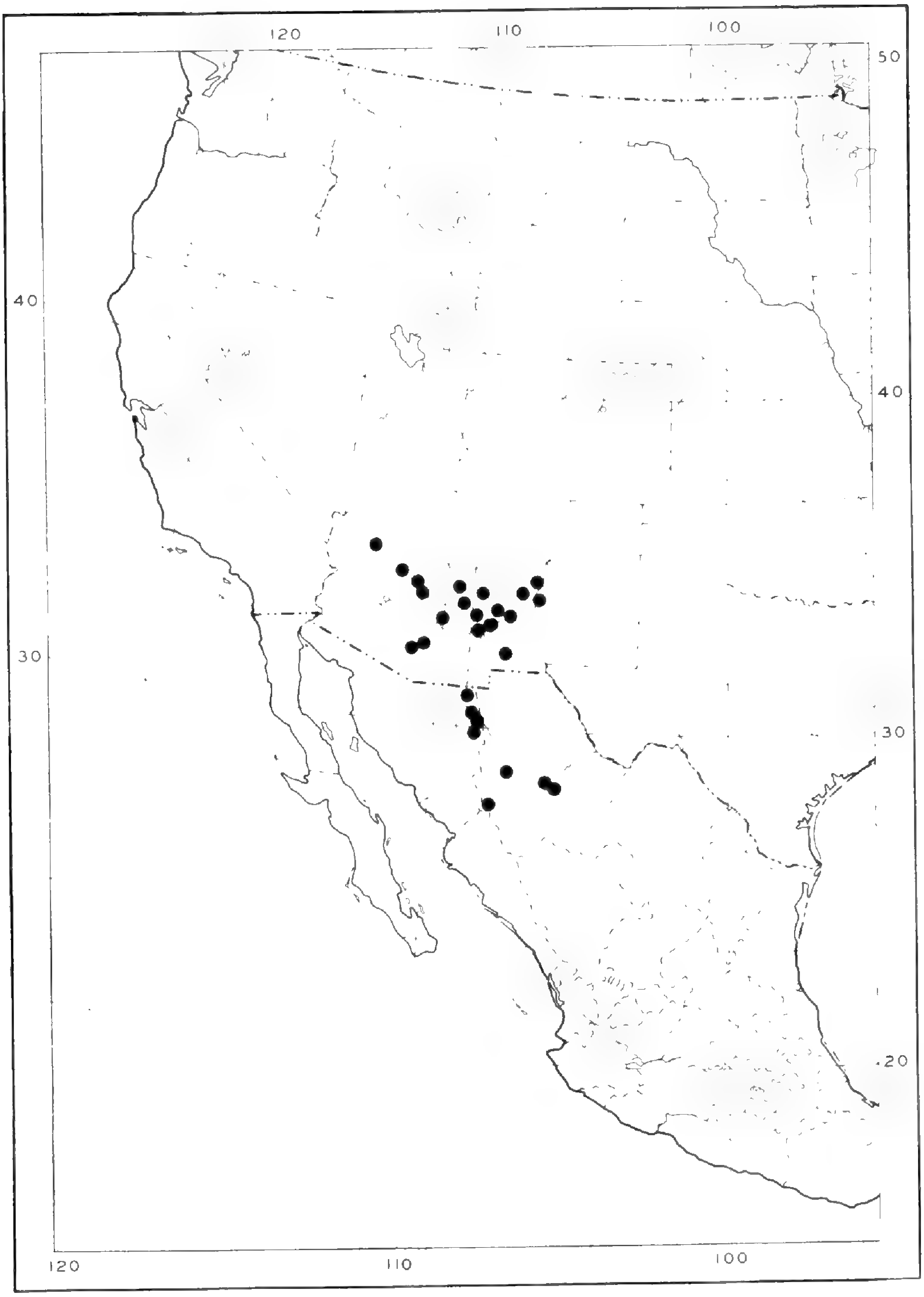


Figure 28. Distribution of *Alnus oblongifolia* Torrey.

many ways, however, *A. oblongifolia* shows affinities to *A. rhombifolia,* with which it is sometimes confused. Characters in *A. oblongifolia* suggesting this relationship include the presence of only two stamens, a tendency to take on a serrulate and rhombic leaf form, and the smooth bark (lacking the transverse constrictions of *A. acuminata*). Its leaf shape varies, often on the same branch, from a distinctive sharp-toothed, lanceolate, acuminate-tipped form to one which is more or less elliptical or rhombic with very small teeth, reminiscent of *Alnus rhombifolia,* to a double-serrate ovate type similar to that of *A. incana* ssp. *tenuifolia* (which occurs in the same geographical region, though at a higher elevation). Identification is usually difficult, however, only with herbarium specimens having few leaves.

Alnus oblongifolia is found at relatively high elevations in the mountains of the southwestern United States and adjacent northern Mexico. The habitat of this species in Arizona is described in detail by Whittaker and Niering (1965) in their study of the vegetation of the Santa Catalina Mountains.

Alnus oblongifolia, like *A. rubra,* is unspecialized in morphology and similarly occupies a mesophytic habitat. Both taxa are probably remnants of wider-ranging species which existed during cooler periods.

3. **Alnus rhombifolia** Nuttall

Alnus rhombifolia Nuttall, North Amer. Sylva **1:** 49. 1842; *Alnus rhombifolia* var. *typica* Callier, Fedde Rep. Sp. Nov. **10:** 229. 1911. TYPE: *Nuttall s.n.,* "in the vicinity of Monterey in Upper California" (BM?, not seen).

Alnus glutinosa δ serrulata (Aiton) Regel, Mem. Soc. Nat. Mosc. **13**(2): 166. 1861, in part.

Alnus glutinosa δ serrulata lusus d. *californica* Regel, Mem. Soc. Nat. Mosc. **13**(2): 166. 1861. TYPE LOCALITY: "aus Californien" (original material not seen).

Alnus rhombifolia var. *ovalis* Winkler, Pflanzenreich **19**(4.61): 115. 1904. TYPE LOCALITY: "Californien" (original material not seen).

Alnus californica hort. ex Winkler, Pflanzenreich **19**(4.61): 115. 1904, *pro syn.*

Alnus rhombifolia var. *bernardina* Munz & Johnston, Bull. Torr. Bot. Cl. **52:** 222. 1925. TYPE: *Munz & Johnston 8468,* junction of South Fork and Santa Ana River, San Bdno. Mts., San Bernardino Co., California (Holotype, POM; Isotypes, F!, NY!). Figure 29.

Somewhat pyramidal open-crowned trees up to 25 (–28) m in height; trunks usually several, erect, up to 1 m in diameter; bark light gray, whitish, or irregularly mottled, smooth to slightly rough, with inconspicuous lenticels when young, brown and broken into scales on old individuals; young stems light green to red-brown, slightly to moderately lustrous, slightly to moderately glaucous, lightly to moderately resin-coated, not differentiated into long and short shoots, usually without longitudinal ridges; internodes glabrous to moderately villous, sparsely to moderately glandular; nodes and stems bearing inflorescences very densely glandular; hairs whitish to yellowish; glands small, yellowish to brownish; lenticels of twigs circular to elliptic, 0.1–0.7 mm long, 0.1–0.3 mm wide, whitish, inconspicuous; leaf scars 1.7–2 mm high, 1.5–2.5 mm wide, the bundle scars moderately prominent. Buds ellipsoid to obovoid, slightly rounded at the apex, moderately to heavily resin-coated; stalk 3–5 mm long, 1.2–1.5 mm in diameter, glabrous to sparsely pubescent, moderately to densely glandular; body 3–9 mm long, 2–3 mm in diameter; scales 2, stipular, equal, mostly valvate, often incompletely covering the underlying organs or even apparently absent from the buds nearest the apex of the stem, glabrous to moderately villous, glandular; pubescence and glands often obscured by the heavy resin coat. Leaves ovate, elliptic, or rhombic; apex acute, obtuse, or rounded (rarely acuminate); base broadly cuneate to rounded; blade (3–) 4.5–8.5 (–13) cm long, (1.5–) 2.5–4.5 (–7.5) cm wide, medium to dark green and dull (sometimes lustrous when young) above, light to medium green and dull to moderately lustrous below, chartaceous to coriaceous; margin flat, not thickened, finely serrate, serrulate, or (rarely) double-serrate (mainly on very vigorous shoots), sometimes slightly lobed; major teeth 5–8 (–10) mm apart at mid-leaf, up to 3 mm deep, regular to irregular; secondary teeth 4–9 per cm at mid-leaf, 0.7–1.5 mm deep, slightly uneven to irregular; adaxial surface glabrous, sparsely pubescent, or moderately villous, moderately to densely glandular; abaxial surface and veinlets sparsely pubescent to velutinous, moderately to densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base densely tomentose to wooly-pubescent; pubescence whitish to yellowish; glands small to medium in size, yellowish to brownish. Lateral veins 9–12 (–15), (2–) 4–7 (–10) mm apart at mid-leaf, straight, often branching once again, especially near the base, terminating in major teeth at the margin; cross veins between

Figure 29. Specimen of *Alnus rhombifolia* Nuttall. Isotype of *Alnus rhombifolia* var. *barnardina* Munz & Johnston.

lateral veins usually poorly developed. Petioles (3–) 7–15 (–23) mm long, 0.7–1.2 (–1.8) mm in diameter, moderately villous to velutinous, moderately to densely glandular. Stipules mostly elliptic, the apex acute, 6–11 mm long, 2–2.5 mm wide, green to light brown, glabrous to moderately villous, the hairs yellowish, moderately glandular, the glands yellowish. Pistillate inflorescences borne in racemose groups of 3–6 on short non-strongly-divergent branchlets, produced during the previous growing season, erect, ovate to elliptic, at anthesis 3–6 mm long, 1.5–2 mm in diameter, on peduncles 0.5–1.5 mm long, 0.6–1 mm in diameter; staminate catkins borne in one or more racemose clusters of 3–7 at the end of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 3–10 cm long, 4–7 mm in diameter, on peduncles 2–12 mm long, 1–1.5 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic or obovate, the apex obtuse to rounded, 0.9–1.7 mm long, 0.4–1.1 mm wide, 2 frequently reduced, the margin lined with minute glands or glands absent; stamens usually 2 (occasionally 4, but if so 2 reduced), opposite and basally adnate to the perianth parts, usually appearing much longer than the perianth; filaments 0.8–1.7 mm long, anthers 1.1–1.9 mm long and 1.2–1.7 mm in diameter, the thecae separate for 35–45% of their length. Infructescences ovoid, ellipsoid, or cylindrical, 10–17 (–22) mm long, (6–) 7–9 (–10) mm in diameter, on peduncles 0.2–7 (–10) mm long, 0.7–1.2 mm in diameter; scales 3–3.5 mm long, 3.5–4.2 mm wide at the apex, 1–1.2 mm wide at the base, the apex moderately thickened, flat, the terminal lobe-tip acute to rounded and somewhat extended. Fruits narrowly wing-margined, brown; body broadly elliptic, 2–2.5 mm long, 1.5–2 mm in diameter; wing margins 2.5–3 mm long, 0.1–0.3 mm wide; persistent styles 1–1.5 mm long. Figures 3C, 7C, 9C, 18A, 29, and 30.

DISTRIBUTION AND HABITAT: Southern Washington and adjacent western Idaho southwest to northern California and south to the Mexican border. On rocky streambanks and adjacent slopes from near sea level at the coast to elevations of over 2,300 meters inland. Often associated with *Pinus, Quercus,* or *Abies.* Figure 31.

Figure 30. Representative specimen of *Alnus rhombifolia* Nuttall.

COMMON NAMES: Alder, white alder, California alder, mountain alder, western alder.

REPRESENTATIVE SPECIMENS: **United States.** CALIFORNIA. Alameda Co.: along Redwood Creek, NE of Redwood Peak, *Constance 380* (UC). Contra Costa Co.: Alamo Canyon, Mount Diablo, *Bowerman 1058* (UC). Del Norte Co.: Kelley's Flat, Darlingtonia, Smith River, *Parks & Parks 24084* (RM). Humboldt Co.: along the Trinity River 7 mi SE of Willow Creek, *Furlow 304* (MSC). Los Angeles Co.: San Antonio Cañon near Clarmont, *Baker 3667* (F, MO, NY, RM, US); Little Dalton Canyon, San Gabriel Mts., *Campbell 82* (DAO). Mariposa Co.: along the Merced River, 5 mi W of Yosemite Village, Yosemite National Park, *Furlow 307* (MSC). Mendocino Co.: by streams, Ukiah, *Pringle s.n.*, Aug. 14, 1902 (F); 12 mi N of Leggett along US 101, along S fork of Eel River, *Stevens 1072* (MSC). Nevada Co.: W of Greenhorn Creek, T16N, R9E, S24, *Raven 8014* (F). Riverside Co.: along stream, Snow Creek, N base of San Jacinto Mts., *Roos 2403* (WTU); Whitewater, *Rose 38003* (NY, WTU). San Bernardino Co.: junction of South Fork and Santa Ana Rivers, San Bdno. Mts., *Munz & Johnston 8468* (F, WTU); mouth of Mill Creek, *Munz & Johnston 8679* (NY); San Bernardino Valley, *Parish & Parish 542* (F, JEPS, UC). San Diego Co.: on bank of San Felipe Creek above ranch house of San Felipe Ranch, *Wiggins 2031* (WTU). Siskiyou Co.: Shasta River, *Butler 10* (UC). Tehama Co.: Cold Fork of the Cottonwood Creek, near foot of Tom's Head, Yollo Bolly Mtns., *Jepson s.n.*, Apr. 28, 1899 (JEPS). Trinity Co.: along the Trinity River 5 mi NW of Del Loma, *Furlow 305* (MSC). Ventura Co.: 1¼ mi NW of Casitas, *Sowder 145* (UC); Horn Cañon, Ojai, *Thacher s.n.*, Apr. 24, 1918 (JEPS). IDAHO. Canyon Co.: Big Willow, *Macbride 128* (RM). Clearwater Co.: Orofino, *Christ 7511* (NY). Latah Co.: near Kendrick, *Christ 10151* (NY). Nez Perces Co.: about Lewiston, *Heller & Heller 3117* (DAO, MO, NY, UC). OREGON. Hood River Co.: E line of county, *Henderson 813* (MO). Jackson Co.: Neil Creek, 6 mi S of Artland, *Applegate 960* (UC); Gold Hill, *Walpone 150* (US). Malheur Co.: upper end of Sucker Creek Canyon, 25 mi S of Adrian, *Clarkson 264* (DAO). Wasco Co.: along the Deschutes River, *Jones 8582* (WTU). WASHINGTON. Klickitat Co.: along creeks near Bingen, *Suksdorf s.n.*, Feb. 13, Mar. 18, 1893 (UC); streams, W Klickitat Co., *Suksdorf s.n.* Mar. 2, May, 1881 (F, UC). Whitman Co.: along stream on N side of Snake River, 14 mi W of Lewiston, *Hitchcock & Muhlick 22029* (RM, UC, WTU).

In certain populations *Alnus rhombifolia* has very pubescent leaves. Such a variant was designated var. *bernardina* by Munz and Johnston (1925). However, study of the species in all parts of its range in western North America showed that this form merely represents one extreme in the overall pattern or variation and does not warrant formal recognition.

Occasionally, especially on vigorous sprouts and young plants, the leaves assume a more lanceolate form with the tip becoming acuminate and the margin double-serrate, suggesting somewhat the shape of *Alnus oblongifolia,* to which it is closely allied. The largest

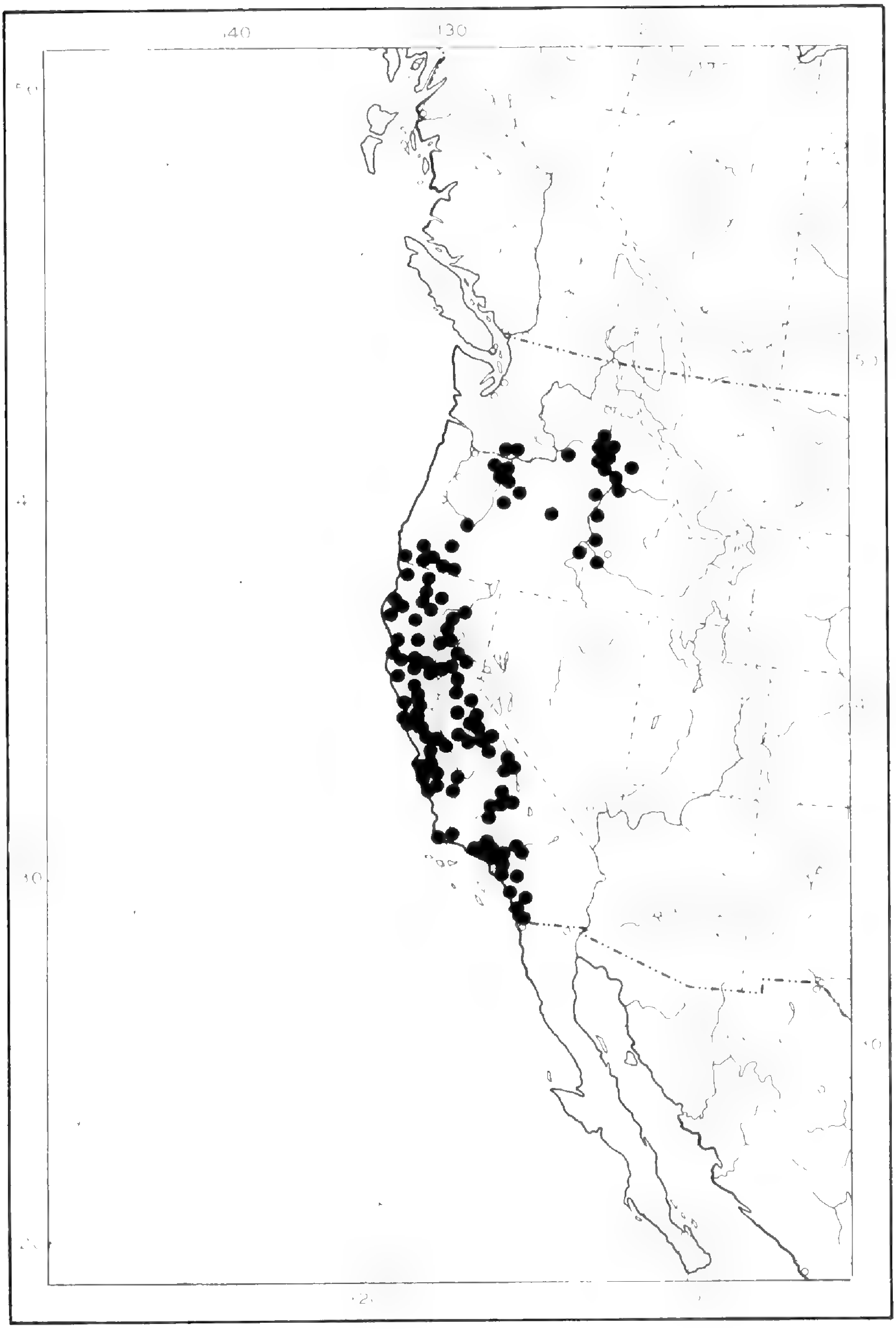


Figure 31. Distribution of *Alnus rhombifolia* Nuttall.

known individual, as reported by Dixon (1961), occurs in the Angeles National Forest in California, measuring 28.4 meters in height, 13.7 meters in spread, and 3.4 meters in trunk circumference.

This alder often occurs in habitats with moderately warm winters; in the southern part of its range it retains its leaves most of the year, though in the North it is deciduous during the winter. It survives, as well, in some more rigorous situations (e.g., in the Sierra Nevada Mountains). Young plants from Shasta Co., California (collected at an elevation of about 20 meters above sea level), when transplanted to an experimental field at Lansing, Michigan, were killed back to ground level during each of four consecutive winters, but they always resumed vigorous growth the following spring.

Specimens from northern Mexico were not seen, but since *Alnus rhombifolia* is known to occur as far south as San Diego, California, populations might be expected to exist in adjacent Baja California as well.

4. **Alnus acuminata** Humboldt, Bonpland, & Kunth

Alnus acuminata Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. **2**: 20. 1817.

Narrow-crowned trees up to 30 m in height; trunks one or several, erect to spreading, up to 1 m in diameter; bark gray to gray-brown, smooth to slightly rough, scaly on old individuals, often broken by transverse ridges or constrictions encircling the stem; young stems medium green-brown, brown, or dark red-brown, dull to moderately lustrous, sometimes slightly to heavily glaucous, without conspicuous longitudinal ridges originating at the nodes; internodes glabrous to moderately villous or velutinous, moderately to densely glandular; nodes and stems bearing inflorescences densely glandular; hairs yellowish to brown (occasionally dark brown); glands small to medium in size, yellowish, brownish, or dark brown; lenticels of twigs circular to elliptic or elongate, 0.3–1.5 mm long, 0.2–1 mm wide, whitish or yellowish, inconspicuous to moderately prominent; leaf scars 1–3 mm high, 1.5–4 mm wide, with inconspicuous bundle scars. Buds ovoid, ellipsoid, or obovoid, acuminate or acute (to slightly rounded) at the apex, lightly to heavily resin-coated; stalk 1–7 mm long, 1–2 mm in diameter, glabrous to moderately villous or velutinous, densely glandular; body 3–10 mm long, 2–4.5 mm in diameter; scales 2, more or less equal, stipular, valvate, often incompletely covering the underlying organs, glabrous to sparsely pubescent (to rarely densely villous), glandular; pubescence and glands usually obscured by the resinous coating. Leaves lanceolate, narrowly to broadly ovate, oblong-ovate, elliptic, or (infrequently) obovate; apex long-acuminate, acuminate, acute, obtuse, or rounded; base acute, cuneate, obtuse, or rounded, sometimes oblique; blade (3.5–) 5.5–14 (–19) cm long, (2–) 3–9 (–10.5) cm wide, medium to very dark green and dull, moderately lustrous, or very lustrous above, light to medium green or brown and dull below, chartaceous to coriaceous; margin slightly to moderately revolute or sometimes nearly flat, unthickened or slightly thicker than the blade itself, coarsely, moderately, or finely double-serrate to serrulate; major teeth 8–14 (–20) mm apart, up to 5 mm deep, regular, slightly uneven, or irregular; secondary teeth (2–) 4–8 (–10) per cm, (0.1–) 0.3–1.5 mm deep, regular, slightly uneven, or irregular; adaxial surface glabrous to sparsely pubescent (rarely moderately villous), sparsely to densely glandular; abaxial surface and veinlets glabrous to moderately villous (sometimes tomentose), densely glandular, moderately resin-coated; major veins and vein axils near the base tomentose to wooly-pubescent; pubescence whitish, yellowish, or brown; glands small to medium in size, whitish, yellowish, or brownish (rarely dark brown). Lateral veins (7–) 10–15 (–18), (3–) 5–8 (–15) mm apart at mid-leaf, straight to slightly ascending, usually branching once again, especially near the base, terminating in major teeth at the margin; cross veins between lateral veins poorly to well-developed. Petioles (4–) 7–23 (–35) mm long, (0.8–) 1–2 (–2.5) mm in diameter, glabrous to velutinous, moderately to densely glandular. Stipules ovate to elliptic, the apex acuminate to acute, 4–8 mm long, 1–1.5 mm wide, green to light brown, sparsely pubescent to velutinous, the hairs yellowish to brownish, moderately glandular, the glands yellowish. Pistillate inflorescences borne in racemose groups of (2–) 3–6 on short non-strongly-divergent to strongly-divergent branchlets, these generally subtended by leaves, produced during the previous growing season, erect, ovate to elliptic, at anthesis 3–6 (–8) mm long, 1.5–2.2 (–3) mm in diameter, on peduncles (1–) 2–5 (–6) mm long, 1–1.5 (–2) mm in diameter; staminate catkins borne in one or more racemose clusters of 2–6 at the end of the main branch above the pistillate inflorescences, the lowermost often subtended by small leaves, produced during the previous season, pendent during and before anthesis, at anthesis (3–) 5–11 (–15) cm long, 5–10 (–11) mm in diameter, on peduncles 2–10 (–22) mm long, 1–1.8 (–2) mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5 mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic or obovate, the apex rounded to obtuse, 1.2–1.8 mm long, 0.6–1.2 mm wide, the margins lined with small to large glands; stamens 4, opposite and basally adnate to the perianth parts, appearing shorter than to longer than the perianth, the filaments 1.1–1.8 mm long, the anthers 1.2–2 mm long and 0.9–1.9 mm in diameter, the thecae separate for 35–55% of their length. Infructescences ovoid, ellipsoid, or cylindric, 11–28 (–45) mm long, 8–12 (–15) mm in diameter, on peduncles 0.2–10 mm long, 1–2 mm in diameter; scales 3–5 mm long, 2.5–5 mm wide at the apex, 1–1.8 mm wide at the base, the apex moderately thickened and flat, the terminal lobe-tip acute to rounded and not much extended to very extended. Fruits narrowly wing-margined, dark brown; body elliptic, to obovate, 1.5–3 (–5) mm long, 1.5–1.8 (–2) mm in diameter; wings 2–3 (–5.5) mm long, 0.2–1 mm wide, chartaceous to coriaceous; persistent styles 0.5–1 mm long.

The taxonomic status of *Alnus acuminata* and the other species of this genus described by Humboldt, Bonpland, and Kunth, *A. jorullensis* and *A. ferruginea*, has long been confused. Virtually all of the Latin American alders have gone under each of these names in one treatment or another. In his monograph of the Betulaceae, Regel (1861) used the name *A. acuminata* for the South American alders, including *A. jorullensis* of Mexico as a variety. The remaining Mexican forms were separated as *A. arguta* (Schlechtendal) Spach, and the extremely narrow-leafed *A. castaneifolia* Mirbel of South America was left as a separate species. Winkler (1904), in his monograph of the family, transferred all of the forms, including *A. castaneifolia,* to *A. jorullensis,* where they were retained in the most recent treatment of the genus by Murai (1964). These taxa are very closely related, but there are consistent differences, at least between *A. acuminata* and *A. jorullensis.*

Photographs of the types at Paris show that the leaves of *Alnus acuminata* are broadly ovate and acuminate-tipped, while those of *A. jorullensis* are more elliptical or obovate with acute or rounded apices. On the basis of the material examined in this study, *A. jorullensis* does not occur farther south than Guatemala, while *A. acuminata* extends deep into South America.

Alnus ferruginea has frequently been used as the name of an extremely pubescent alder, whether in South America, where it was originally collected, or in Mexico and Central America. This pubescent-leaved form is much more frequent in extreme southern Mexico (Chiapas and Oaxaca), Central America, and northern South America than in other parts of the range of the complex, but it represents no more than an extreme in the continuous variation pattern of the pubescence character in this species.

Alnus acuminata is considerably variable throughout its range, but probably not much more so than such other wide-ranging species of the genus as *A. viridis, A. incana,* and *A. glutinosa.* Especially variable characters in *Alnus acuminata* include leaf pubescence (which ranges from almost totally absent in some plants to very dense in others), the density and size of the glands covering the lower leaf surface, leaf shape (varying from narrowly lanceolate to nearly orbicular), and the shapes of the leaf apices and bases. The fact that the foliage is so variable sometimes makes this species confusing and difficult to determine, but taken as a whole, it forms a discrete and natural unit.

The area of best development of *Alnus acuminata,* and also of its greatest variability, is southern Mexico and northern Central America, pointing to this region as a possible site of origin. This species is relatively unspecialized, as discussed above, and it may have been derived from a widespread prototype similar to present day *Alnus rubra,* having a mesophytic habitat and a large stature. *Alnus acuminata* and *A. rubra* are similar in many ways, indicating such a close relationship, but these taxa also possess numerous differences, suggesting a long period of isolation.

4a. **Alnus acuminata** Humboldt, Bonpland, & Kunth ssp. **acuminata**

Alnus acuminata Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. **2:** 20. 1817; *Alnus acuminata α genuina* Regel, Mem. Soc. Nat. Mosc. **13**(2): 147. 1861; *Alnus jorullensis* var. *acuminata* (Humboldt, Bonpland, & Kunth) Kuntze Rev. Gen. Pl. **2:** 638. 1891. TYPE: *Humboldt & Bonpland s.n.,* "crescit in Andibus Peruviae inter Caxamarca et Micuicampa, regione Escalloniae et Valleae stipularis alt. 1700–1800 hex." (Holotype, P; microfiche photograph of type, MSC!).

Alnus ferruginea Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. **2:** 21. 1817; *Alnus acuminata γ ferruginea* (Humboldt, Bonpland, & Kunth) Regel, Mem. Soc. Nat. Mosc. **13**(2): 148. 1861; *Alnus jorullensis* var. *ferruginea* (Humboldt, Bonpland, & Kunth) Kuntze, Rev. Gen. Pl. **2:** 638. 1891; *Alnus ferruginea* var. a.

Figure 32. Representative specimen of *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*.

typica Callier, Mitt. Deutsch. Dendr. Ges. **27:** 161. 1918, in part. TYPE: Humboldt & Bonpland s.n., "crescit locis excelsis frigidis Andium Novogranatensium prope Santa Fé de Bogota, alt. 1400–1600 hex." (Holotype, P; microfiche photograph of type, MSC!).

Alnus castaneaefolia Mirbel, Mem. Mus. Hist. Nat. **14:** 463. 1827; *Alnus jorullensis β castanifolia* (Mirbel) Regel, Bull. Soc. Nat. Mosc. **38**(3): 425. 1865. TYPE: *Dombey,* "á Tarma au Perou" (P?, not seen).

Alnus mirbelii Spach, Ann. Sci. Nat. ser. 2, **15:** 204. 1841; *Alnus acuminata β mirbelii* (Spach) Regel, Mem. Soc. Nat. Mosc. **13**(2): 148. 1861; *Alnus jorullensis* var. *ε mirbelii* (Spach) Winkler, Pflanzenreich**19** (4.61): 126. TYPE LOCALITY: "Peruvia" (original material not seen).

Alnus arguta δ punctata Regel, Mem. Soc. Nat. Mosc. **13**(2): 152. 1861. TYPE: *Ruiz,* " in Peru und Chili" (not seen).

Alnus lindeni Regel, Mem. Soc. Nat. Mosc. **13**(2): 144. 1861. TYPE: *Linden,* "auf der Sierra Nevada von Neugranada . . . in einer Höhe von 15000 fuss über dem Meere" (original material not seen).

Alnus acuminata γ spachii Regel, Bull. Soc. Nat. Mosc. **38**(3): 424. 1865; *Alnus spachii* (Regel) Callier in Schneider, Ill. Handb. Laubh. **1:** 132. 1904, *pro syn.; Alnus spachii* (Regel) Callier, Mitt. Deutsch. Dendr. Ges. **27:** 163. 1918. Original material not seen.

Alnus lanceolata Philippi, Anal. Univ. Chile **91:** 514. 1895. TYPE: *Paulus Ortega s.n.,* "Januario 1881, prope Lurin haud procul a Lima in regione litorali Peruviae" (not seen).

Alnus rufescens Liebman ex Hemsley, Biol. Centr. Amer. Bot. **55:** 165. 1882, in part, *pro syn.*

Alnus jorullensis var. *ζ acutissima* Winkler, Pflanzenreich **19**(4.61): 127. 1904; *Alnus acutissima* (Winkler) Callier, Mitt. Deutsch. Dendr. Ges. **27:** 163. 1918; *Alnus mirbelii* var. *acutissima* (Winkler) Callier, Mitt. Deutsch. Dendr. Ges. **27:** 163. 1918, *pro syn.* (erroneously attributed to Winkler). TYPE: *Peoppig,* "Peru: an Bächen des Huanuca-Thals" (Syntype, B?, not seen); *Weberbauer 182,* "Thal von Huillapolschi, südwörts von Matucana" (Syntype, B?, not seen).

Alnus ferruginea var. *aliso* Lorenz & Hieronymus ex Winkler, Pflanzenreich **19**(4.61): 126. 1904, *pro syn.*

Alnus ferruginea var. *obtusifolia* Callier, Mitt. Deutsch. Dendr. Ges. **27:** 162. 1918. TYPE: *Hartwig 1319,* "Colombia: Bogotá, in Andibus" (BRM?, not seen).

Rather narrow-crowned trees up to 25 m in height, sometimes shrubby, sprawling, or prostrate on exposed sites; trunks one to several, up to 1 m in diameter; young stems dull to moderately lustrous, occasionally slightly to moderately glaucous, the internodes sparsely pubescent to velutinous, the glands small to medium in size, yellowish to brownish. Lenticels of twigs 0.3–1 mm long, 0.2–0.7 mm wide, yellowish, moderately prominent. Buds ovoid to ellipsoid, acuminate to acute at the apex, lightly to moderately resin-coated; stalk 1–5 mm long, moderately villous to velutinous; scales sparsely pubescent to densely villous. Leaf apex long-acuminate to acute, obtuse, or rounded; base cuneate to rounded, sometimes oblique; blade 3.6–9.5 (–19) cm long, (2–) 3.5–9 (–11) cm wide; margin slightly to moderately revolute, the major teeth 8–17 mm apart, slightly uneven to irregular; secondary teeth (2–) 3–7 per cm, 0.1–1.5 mm deep, slightly uneven to irregular; abaxial surface and veinlets sparsely to moderately villous or velutinous. Lateral veins (7–) 10–16 (–18), (3–) 4–8 (–15) mm apart at mid-leaf, slightly to moderately ascending; cross veins between lateral veins well-developed. Petioles (4–) 7–16 (–28) mm long, 1–1.8 (–2.5) mm in diameter, glabrous to moderately villous or velutinous. Stipules 7–15 mm long, 2.5–4 mm wide, moderately villous to velutinous. Pistillate inflorescences at anthesis 3–8 mm long, 1.5–3.2 mm in diameter, on peduncles 1.5–6 mm long, 1–1.8 (–2) mm in diameter. Staminate catkins at anthesis 3.5–15 cm long, 5–11 mm in diameter, on peduncles 4–22 mm long, 1–2 mm in diameter. Staminate flowers with 4 perianth parts, these obtuse to rounded at the apex, 1.2–2.2 mm long, 0.6–2 mm wide, the margins lined with small to medium-sized glands; stamens appearing shorter than, equal to, or longer than the perianth, the filaments 0.8–1.8 mm long, the anthers 1.2–2 mm long and 1.1–1.9 mm in diameter, the thecae separate for 20–50% of their length. Infructescences (11–) 15–30 mm long, 8–12 (–15) mm in diameter, on peduncles 1–8 (–10) mm long, 1.2–2 mm in diameter; scales 3–5 mm long, 2.5–4.5 mm wide at the apex, 1–1.7 mm wide at the base. Fruits narrowly wing-margined; body 2.7–3 (–4) mm long, 1.2–1.8 mm in diameter; wings 2–3 mm long, 0.2–1 mm wide, chartaceous to coriaceous; persistent styles 0.5–1 mm long. Figures 16A, 32, and 33.

DISTRIBUTION AND HABITAT: Eastern Venezuela and northern Colombia south along the Andes to northern Argentina. On streambanks and moist slopes at elevations from 2,000 to 2,800 meters (occasionally extending as low as 1,500 meters). Figure 34.

COMMON NAMES: Aliso, jaul.

REPRESENTATIVE SPECIMENS: **Argentina.** Villa Nougues, Prov. Tucumán, *Krapovickas & Cristobal 14529* (MO, UC); Saladillo, Prov. Tucumán, *Mayer 13.956* (MO); de Yala a Lagunas de Yala, Prov. Jujuy, *O'Donell 2854* (NY); Cerro la Cuera Sta. Cruz, Prov. Salta, Dept. Orau, *Pierotti 323* (NY, UC); Sierra del Cajón, Prov. Salta, *Rodrequez 1291* (NY); Hogava, *Venturi 1047* (UC); Siacubon, *Venturi 3865* (MO); la lagunita, Prov. Tecumán, Dept. Tafí, *Xescole s.n.,* Jan., 1944 (NY, UC). **Bolivia.** La Paz, *Buchtien 680* (MO, NY); location illegible, *Buchtien 3146* (NY, US); Tunari, *Kuntze*

Figure 33. Specimen of *Alnus castaneifolia* Mirbel (=*A. acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*).

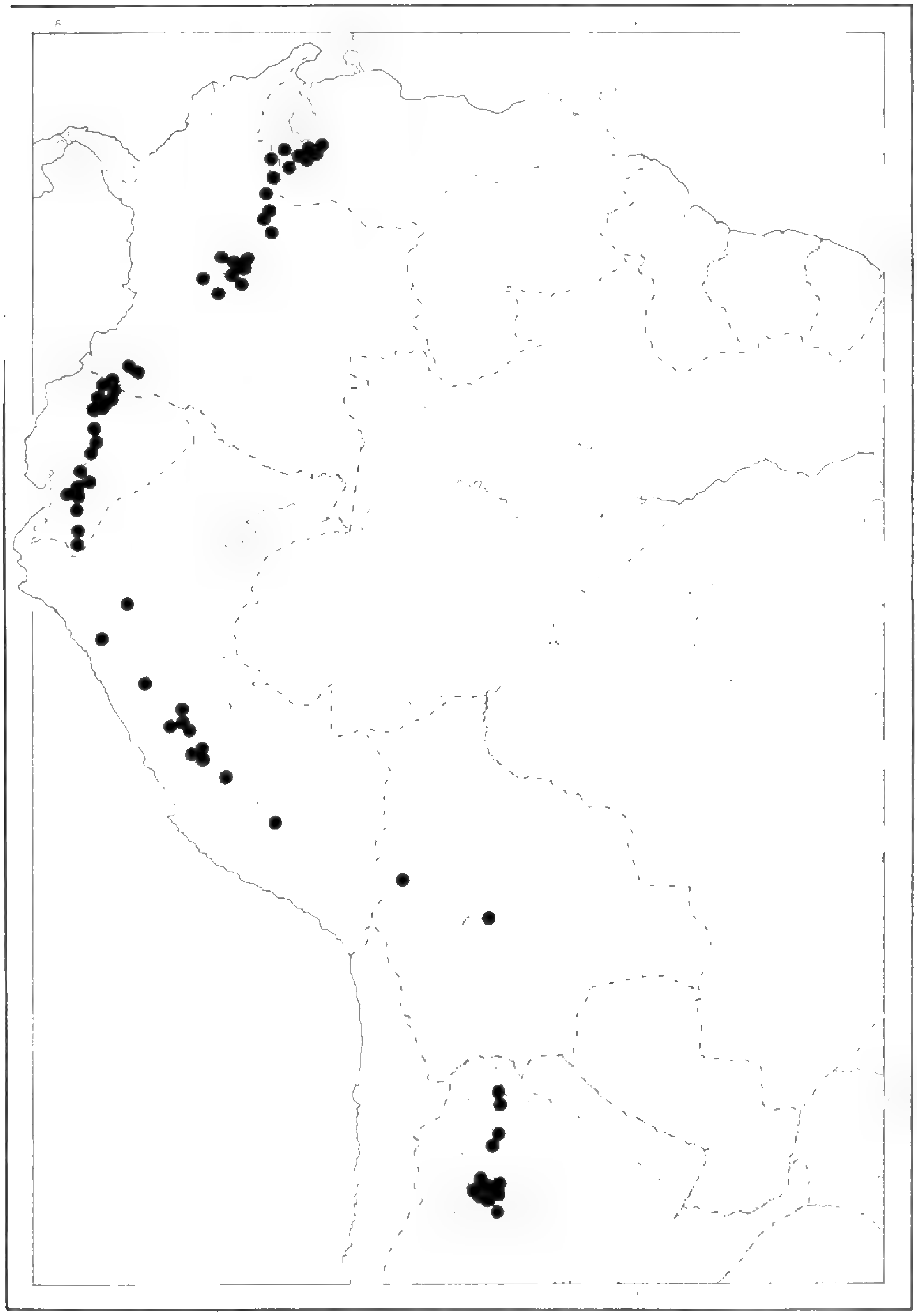


Figure 34. Distribution of *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata* in South America.

s.n., Apr. 5, 1892 (NY, US); Pulcheri *White 234* (MICH, NY). **Colombia.** Boqueron de Bogotá, *Andre 720* (NY); Páramo de Guasca, Cundinamarca, *Balls B5768* (UC); Caldas E of Neira, near Cemento de Caldas, *Breteler 4472* (NY); Dept. Norte de Santander, E slope of Páramo de Santurbán, toward Mutiscus, *Killip & Smith 19615* (NY); canoncito in sabrano, Dept. of Cundinamarca SW of Las Cruces, Bogotá, *Pennell 2131* (NY); Páramo de San Antonio, entre la Laguna de La Cocha y el Valle de Sibundoy, Prov. Putumayo, *Schultes 3221A* (F). **Ecuador.** Chillo Valley, Río Pita, *Anthony & Tate 229* (US); Prov. Loja, Cerro Villanaco, ca. 7 km W of the city of Loja, *Camp E-676* (NY); Prov. Azuay, along the Río Cumbe, 25–30 km S of Cuenca, *Camp E-2070* (F, NY); valley of the Río Matadero, a few km W of Cuenca, *Giler 37* (US); Provs. Imbabura and Pichincha, Otavato to Maichiugui, *Hitchcock 20820* (NY); Río Tasquasa near Angel, *Mexia 7536* (UC); vicinity of Cuenca, *Rose 22855* (NY); in Andibus Equadorensibus, *Spruce 5755* (NY); N side of valley of el Río Leon, 85 km S of Cuenca, *Wiggins 10846* (MO, NY, UC). **Peru.** Valle del Urubamba, Calca, *Herrera 2092* (F); Canyon of Río Huasahuasi below Huasahuasi, *Hutchinson 1057* (NY, UC); Tarma, *Macbride & Featherstone 1021* (F); Cerro Puma Urco, SE of Chachapoyas, *Pennell 15526* (US); Río Acopalca, *Rauh s.n.*, July 3, 1957 (F); in Peruviae memonibus, *Ruiz 11652* (F, photograph); without location, *Ruiz & Pavon s.n.*, in 1788 (F); km 40, Dept. Huanuco, Huanuco to Carpish, *Seibert 2222* (MO, US); alrededores de Huancayo, *Tovar 2770* (UC); Cuzco, *Vargas C. 8109* (MO); Dept. Apurimac, *Vargas C. 8766* (MO); vicinity of Panao, *Woytkowski 112* (F). **Venezuela.** Chama valley, Apartaderos, *Breteler 4475* (NY); Chama valley, between Nueuchies and San Rafael, *Breteler 4480* (NY); Valle Río Chama, 9 km from Mérida along road to Tabay, *Breteler 4481* (NY); Quebrada de Saisay, *Gehriger 24* (NY); Mérida, *Jahn 788* (NY); Moconoque, Mer., everywhere, *Pittier 13239* (MO, NY).

Alnus acuminata ssp. *acuminata* is the only alder occurring in South America. Several minor variants, including *A. mirbelii* Spach, *A. spachii* Callier, and *A. acutissima* Callier, differ only in leaf margin and indumentum, and in these characters not consistently; therefore these taxa are not recognized as distinct. Regionally, *Alnus acuminata* ssp. *acuminata* has generally smaller leaves and infructescences toward the southern part of its range (Argentina) than it does in the center (Bolivia and Peru). Farther north, in populations in Venezuela, Colombia, and Ecuador, the leaves are broader and more rounded at the apex, although acuminate-tipped foliage is not entirely absent, while the infructescences are somewhat smaller than those from populations in the central part of the range.

The foliage of South American *Alnus acuminata* is variable, the apices ranging from long-acuminate to very rounded, the bases varying from rounded to long-cuneate, the general shape varying from narrowly lanceolate to broadly ovate, and the pubescence ranging from nearly absent to quite dense.

Alnus castaneifolia Mirbel is a form with extremely narrow leaves having sharp teeth (Figure 33). I have seen only one specimen (and one photograph of a specimen) of this taxon, both collected by Ruiz in Peru. Although this alder may, in fact, represent another subspecies, it seems more likely that it is only a sporadic or local variant of *A. acuminata* ssp. *acuminata.* Without seeing additional material, however, it is impossible to determine this with certainty, and the form is tentatively included in ssp. *acuminata.*

4b. *Alnus acuminata* ssp. *arguta* (Schlectendal) Furlow

Alnus acuminata ssp. *arguta* (Schlechtendal) Furlow, Ann. Mo. Bot. Gard. **63:** 380. 1977; *Betula arguta* Schlechtendal, Linnaea **7:** 139. 1832; *Alnus arguta* (Schlechtendal) Spach, Ann. Sci. Nat. ser. 2, **15:** 205. 1841; *Alnus arguta α genuina* Regel, Mem. Soc. Nat. Mosc. **13**(2): 151. 1861. TYPE: *Schiede 21,* "prope San Miguel del Soldado, Naulingo, Acatlan, et Chiconquiaco" (HAL?, not seen; ISOTYPE or ISOSYNTYPE, MO!). Figure 36.

Alnus rufescens Liebman ex Hemsley, Biol. Centr. Amer. Bot. **55:** 165. 1882, in part, *pro syn.*

Alnus jorullensis var. *η acuminata* f. *media* Winkler, Pflanzenreich **19**(4.61): 127. 1904, in part.

Alnus pringlei Fernald, Proc. Amer. Acad. **43:** 62. 1907. TYPE: *Pringle 10125,* Michoacan, by streams near Uruapan, alt. about 1525 m., 13 November, 1905 (HOLOTYPE, GH!; ISOTYPES, DAO!, F!, MEXU!, MICH!, MSC!, NY!, PH!, UC!, US!).

Alnus arguta var. *cuprea* Bartlett, Proc. Amer. Acad. **44:** 610. 1909. TYPE: *Pringle 10251,* "Oaxaca: wet canon near base of the summit ridge of the Sierra de San Felipe above the city of Oaxaca" (LECTOTYPE, GH!; ISOLECTOTYPES, DAO!, ENCB!, F!, MICH!, MSC!, UC!, US!).[1]

Alnus arguta var. *subsericea* Bartlett, Proc. Amer. Acad. **44:** 610. 1909. TYPE: *Pringle 10252,* "Oaxaca: wet canon near the base of the summit ridge of the Sierra de San Felipe, above the city of Oaxaca"(HOLOTYPE, GH!; ISOTYPES, DAO!, ENCB!, F!, MICH!, MSC!, UC!, US!).[2]

Alnus ovalifolia Bartlett, Proc. Amer. Acad. **44:** 611. 1909. TYPE: *Smith 2199,* Guatemala, San Lucas, Dept. Zacatepequez, alt. 5500 ft. (HOLOTYPE, GH!; ISOTYPE, US!).

---

[1] Bartlett does not indicate a type specimen. Of the material cited, *Pringle 10251* best fits the description of the variety and was apparently its primary basis. This collection is therefore chosen as the lectotype.

[2] Although a type is not designated, this is the only specimen cited in connection with the description of the variety. A paragraph later Bartlett refers *Ghiesbreght 160* from Chiapas to this taxon, but it is clear from the context that he regards *Pringle 10252* as the type.

Alnus ferruginea var. a. *typica* Callier, Mitt. Deutsch. Dendr. Ges. **27:** 161. 1918, in part.

Alnus guatemalensis Gandoger, Bull. Soc. Bot. Fr. **66:** 289. 1919. TYPE: *Von Türckheim,* "Guatemala, ad Alta Verapaz."[3]

Narrow-crowned trees up to 30 m in height; trunks usually several, erect, up to 1 m in diameter; young stems dull to moderately lustrous, sometimes slightly to heavily glaucous, the internodes glabrous to moderately villous, the glands small to medium in size and brownish to dark brown. Lenticels of twigs 0.3–1.5 mm long, 0.2–1 mm wide, whitish or yellowish, inconspicuous to moderately prominent. Buds ellipsoid to obovoid, acuminate, acute, or slightly rounded at the apex, moderately to heavily resin-coated; stalk 2–7 mm long, glabrous to moderately villous; scales glabrous to sparsely pubescent. Leaf apex acuminate, acute, or obtuse (rarely rounded); base acute, cuneate, obtuse, or rounded, sometimes oblique; blade (3.5–) 5.5–15 (–16) cm long, 3–8.5 (–11) cm wide; margin slightly to moderately revolute; major teeth 8–14 (–20) mm apart, slightly uneven; secondary teeth (2–) 4–8 (–10) per cm, (0.1–) 0.3–1.5 mm deep, slightly uneven; abaxial surface and veinlets glabrous to moderately villous or (rarely) tomentose. Lateral veins (7–) 10–15 (–18), (3–) 5–8 (–12) mm apart at mid-leaf, straight to slightly ascending. Cross-veins between lateral veins well developed. Petioles (5–) 11–23 (–35) mm long, (0.8–) 1–2 (–2.5) mm in diameter, glabrous to sparsely pubescent. Stipules 4–8 mm long, 1–1.5 mm wide, sparsely pubescent to velutinous. Pistillate inflorescences at anthesis 3–8 mm long, 1.5–3 mm in diameter, on peduncles (1–) 2–5 (–6) mm long, 1–1.5 (–2) mm in diameter; staminate catkins at anthesis (3–) 5–11 (–15) cm long, 5–10 (–11) mm in diameter, on peduncles 2–10 (–17) mm long, 1–1.8 (–2) mm in diameter. Staminate flowers with 4 perianth parts, these obtuse to rounded at the apex, 1.2–1.9 mm long, 0.6–1.2 mm wide, the margin lined with small to minute glands; stamens appearing equal to or longer than the perianth; filaments 1.1–1.8 mm long; anthers 1.2–2 mm long, 0.9–1.7 mm in diameter, the thecae separate for 35–55% of their

---

[3] Gandoger provides no collection number or date for the type collection cited. Von Türckheim collected at least twice at this locality; I have examined his no. 351, collected there in 1886 (MICH!, US!), and his no. II-1013, collected in 1906 or 1907 (F!, MO!, NY!).

Figure 35. Type specimen of *Betula arguta* Schlechtendal (=*Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow).

Figure 36. Specimen of *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow Isotype of *Alnus pringlei* Fernald.

length. Infructescences 11–28 (–45) mm long, 8–12 (–15) mm in diameter, on peduncles 0.2–10 mm long, 1–2 mm in diameter; scales 3–4.5 mm long, 3–4.5 mm wide at the apex, 1–1.7 mm wide at the base. Fruits narrowly wing-margined; body 1.5–3 mm long, 1.5–1.8 mm in diameter; wings 2–2.3 mm long, 0.2–1 mm wide, chartaceous to coriaceous; persistent styles 0.5–0.8 mm long. Figures 14A, 15A, 22A, 35, and 36.

DISTRIBUTION AND HABITAT: Mexico from central Sonora southeast along the Sierra Madre Occidental and the Sierra Madre del Sur to Oaxaca; east and north from Michoacan to southern San Luis Potosi and northern Veracruz, and in central Chiapas; southern Guatemala; central Costa Rica and southwestern Panama. Along streams and adjacent moist slopes at elevations from about 2,000 to 3,200 meters (though sometimes found as low as 1,500 or as high as 3,700 meters). Usually with *Pinus, Quercus,* or *Abies.* Figure 37.

COMMON NAMES: Aile, jaul, aliso.

REPRESENTATIVE SPECIMENS: **Costa Rica.** Roads above San Isidro de Coronado, *Allen 548* (F); Las Nubes, Coronado, *Echeverria 123* (F, UC); Prov. Cartago, Cordillera de Talamanca, *Lems 5031* (NY); near Sanatorio de Tierra Blanca, Cartago, slopes of Volcán Irazu, *Rodriquez C. 145* (MICH, UC); bords des rivieres su Copez, *Tonduz 11680* (MEXU, MICH, NY). **El Salvador.** Northern slopes of Santa Ana Volcano, Dept. of Santa Ana, area known locally as "El Comun", *Allen & Van Severen 6880* (F); cloud forest Mountain Cerro Verde, Dept. Santa Ana, *Molina R. & Montalvo 21520* (NY). **Guatemala.** 5 mi N or San Juan Ixcoy on road to Soloma, *Breedlove 8572* (F); bank of Río Panajuchel near Lake Atitlan, *Hatch & Wilson 288* (F); Antigua, Dept. Sacatepéquez, *Kellerman 4966* (US); about 11 mi W of Quezaltenango, *King 3193* (NY, UC, US); road to Iximche Ruins, Tecpán, Dept. Chimaltenango, *Molina R. et al. 16127* (F); S. Rafael, *Rittier 55* (US); Dept. of Huehuetenango, *Skutch 1110* (F, NY); San Lucas, Dept. Zacatepéquez, *Smith s.n.,* M. Apr., 1800 (US); Dept. Guatemala, slopes of Volcá de Pacaya, between San Francisco Sales and the base of the active cone, *Standley 80553* (F); Dept. Huehuetenango, Aguacatán road, 10 km E of Huehuetenango, *Standley 82135* (F); Dept. Huehuetenango, about Leguna de Ocubilá, E of Huehuetenango, *Standley 82695* (F); Dept. San Marcos, mountains along the road between San Marcos and Serchil, *Standley 85337* (F); Dept. Quezaltenango, Cerro Quemado, *Standley 86026* (F); Dept. Quezaltenango, above Los Vahos, Cerro Quemado, *Standley 86107* (F); Dept. Quezaltenango, Volcán Zunil, *Steyermark 34605* (F); Dept. El Progreso, between Calera and summit of Volcán Siglo, *Steyermark 43037* (F, NY); Dept. Alta Verapaz, Coban, 4200 ft., *von Türckheim 351* (MICH, US); Dept. Alta Verapaz, Coban, 1350 m, *von Türckheim II-1013* (F, MO, NY); pine forest region in Sierra Madre Mountains where Depts. of

Huehuetenango, Totonicapán, and Quezaltenango join, *Williams et al. 22718* (F). **Panama.** Llano del Volcán, *Allen 3468* (F, MICH, MO, NY, UC); Volcán de Chiriquí, *Davidson 997* (F); 8 mi NE of El Volcán, *Tyson & Dwyer 828* (MO); Finca Lérida to Peña Blanca, *Woodson & Schery 317* (MO). **Mexico.** CHIAPAS. Along road to Zontehuitz, *Breedlove 6649* (ENCB, F, MICH); along the road to Chenalho near the school house of Yal Ichin, *Breedlove 7851* (ENCB, F); along creek near road 1 km N of Aguacatenango, *Breedlove 7909* (ENCB, MICH); on road from San Cristóbal Las Casas to Tenejapa, *Breedlove 9063* (F, MICH); 1 mi W of Nabenchauk, *Breedlove 9522* (MICH); creek bank at NE boundary of Aguacatenango, *Breedlove 9649* (MEXU, MSC, US); SE city limits of Teotisca, *Breedlove 11300* (MEXU); near the center of Amatenango, *Breedlove 12150* (MSC); in the barrio of Tuk, paraje of Matsab, *Breedlove 12457* (MSC); between Las Casas and Tenejapa, *Carlson 2412* (MEXU, MICH); on the NW side of Muk'ta vits (Cerro Huitepec), *Laughlin 1870* (MSC); near Zinacantán Center, *Laughlin 2347* (MEXU); de S. Cristóbal a Buenavista (Chepetic), *Miranda 4987* (MEXU); Cerro del Boqueron, *Purpus 6981* (NY, UC); paraje de Mohosik', *Ton 1134* (MSC); in the paraje of Yash'anal, *Ton 2130* (MEXU, NY). CHIHUAHUA. Basigochi, SE of Creel, *Knobloch 498* (ENCB, MSC, WIS); near Concheño, *LeSueur 594* (F); 44 mi S of Creel, steep barranca wall, *Straw & Foreman 1901* (ENCB, MEXU, MICH). DISTRITO FEDERAL. On hwy. 16, 1.9 mi W of San Bartolo, *Denton 1922* (MSC, WTU); Cañada de Contreras, cerca de 2° dinamo, *Espinosa 641* (ENCB). DURANGO. North slopes of Cerro Huehueto, S of Huachicheles, about 75 mi W of Cd. Durango, *Maysilles 7257* (MEXU, MICH); San Ramón, *Palmer 207* (NY, UC, US). GUANAJUATO. Mountains ESE of San José Iturbide and about 5 mi W of Cerro Zamorano, wooded canyons in oak forests near summits called Mesa del Gato, *McVaugh 10381* (MEXU, MICH); San Luís de la Paz, *Salazar 5* (MEXU). GUERRERO. Pilas, Distr. Mina, *Hinton 10705* (NY, UC); approximately 6 mi W of Mazatlán, *Rowell 3913* (MICH); 2 km al E de Omiltemi, *Rzedowski 16044* (ENCB); 5 km al W de Camotla, Mun. de Chichihualco de Leonardo Bravo, *Rzedowski 16405* (ENCB, MEXU, MSC); 11 km al E del Aserradero Agua Fria, *Rzedowski & McVaugh 260* (ENCB, MSC). HILDAGO. Alrededores de Zacualtipán, *González Quintero 318* (ENCB, MEXU, MSC); Santiago Tepepa, Mun. de Acoxochitlan, *González Quintero 493* (ENCB); Rancho Viejo, Mun. de La Mision, *González Quintero 1005* (ENCB); 30 km al NE de Jacala, *González Quintero 1337* (ENCB); Xochicoatlan, Mun. de Molango, *González Quintero 1560* (ENCB); Santuario, 22 km al NNE de Ixmiquilpan, *González Quintero 2272* (ENCB); cerca de Chapulhauacan, *Rzedowski 12265* (ENCB, MSC); Lindavista, sobre el camino a Tenango de Doria, *Vela & Rzedowski 349* (ENCB). JALISCO. Etat de Jalisco, *Liquet s.n.*, without date (NY); mountain in oak-pine forest, near summit of pass 7–8 road mi NW of Los Volcanes along road between Ayulta and Mascota, *McVaugh 12208* (MICH, US); about 6–10 mi SW of Talpa de Allende, in the valley of Río Charco Verde and near its headwaters, *McVaugh 14330* (MICH); 10 12 mi W of Talpa de Allende, in the headwaters of an E branch of Río de Talpa, 3 mi above Los Sauces, *McVaugh 21440* (MICH); headwaters of Río Mascota, about 20 km, airline, SE of Talpa de Allende, *McVaugh 21474* (MICH); 16 km S of El Chante (ca. 25 km SE of Autlán), *McVaugh 23055* (ENCB, MICH); Sierra del Halo, near a lumber road leaving the Colima highway 7 mi SSW of Tecalitlan and extending SE toward San Isidro, *McVaugh & Koelz 1123* (MICH). MÉXICO. Rancho Tobias near Villa Guerrero, *Alexander & Hernandez X. 1978* (NY); Rancho Santo Tobias near Villa Guerrero, *Gilly 104* (MSC); along small stream just N of Amecameca, *Gilly & Dodds 1* (MSC, NY);

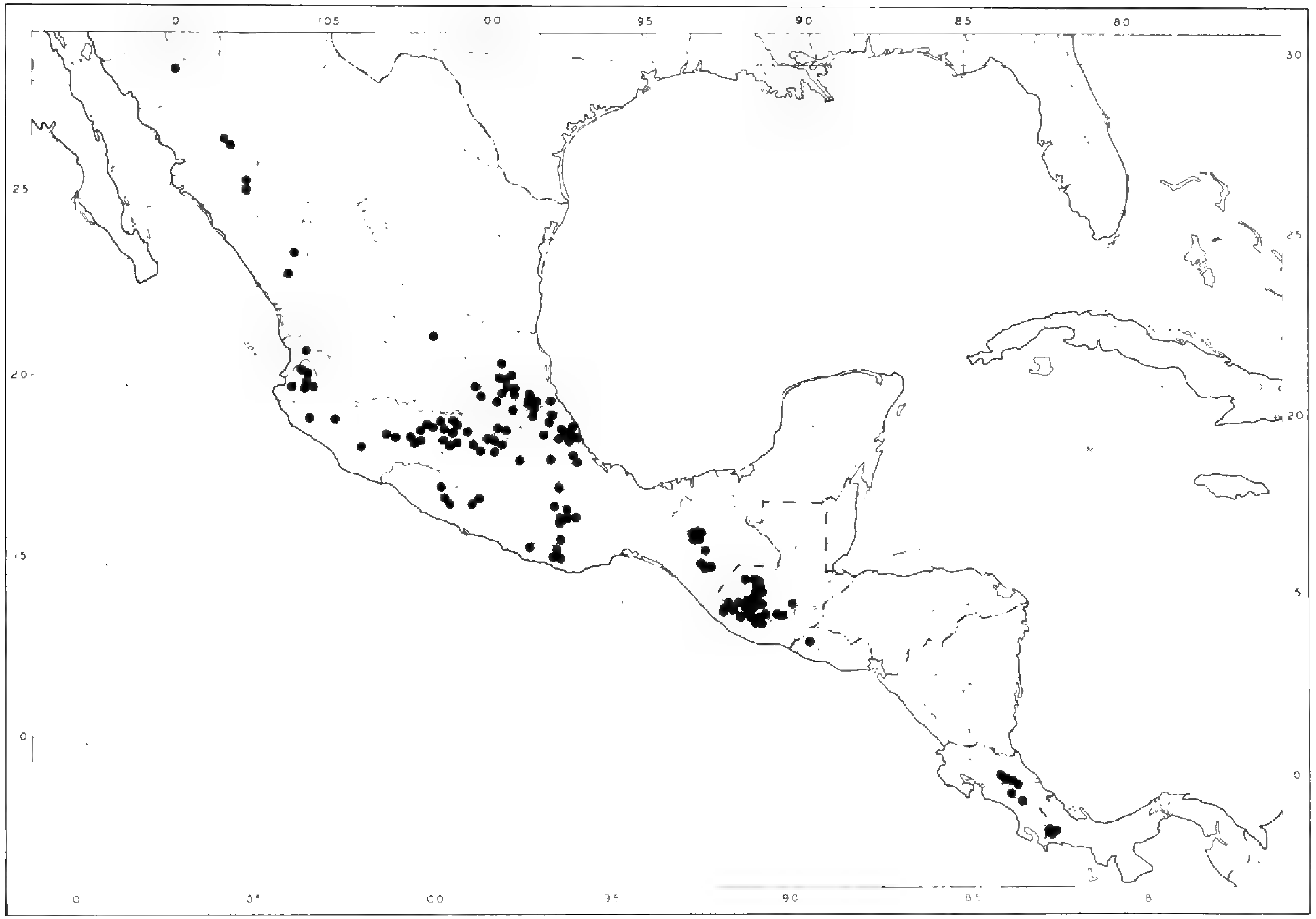


Figure 37. Distribution of *Alnus acuminata* Humboldt, Bonpland, and Kunth ssp. *arguta* (Schlechtendal) Furlow in Mexico and Central America.

Rancho Santo Tobias near the town of Villa Guerrero, *Gilly et al. 103* (MSC); 5 km SW de Cahuacan, *González Quintero 870* (ENCB, MSC); La Labor, Distr. of Temascaltepec, *Hinton 2780* (US); Rincón, Distr. Temascaltepec, *Hinton 8785* (NY). MICHOACÁN. South of Morelia at km 263, *Barr 63-586 & Niles 313* (UC); 1.5 km S of Opopeo, *Furlow 337* (MSC); Zitácuaro-Carpinteros, *Hinton 11875* (DS, NY, UC); west-facing slopes of Cerro de Carboneras above the Río Cupa, *King & Soderstrom 4893* (MICH, NY, UC); 8–10 mi NW and WNW of Ciudad Hidalgo, along mountains W of Cerro San Andrés and 6–7 mi N of village of San Pedro Aguaro, *McVaugh 9992* (MEXU, MICH, MO); San José Purua, *Paray 2203* (ENCB); by streams near Uruapan, 5000 ft, *Pringle 10125* (DAO, F, MEXU, MICH, MO, MSC, PH, UC, US); 14 km al E de Zitácuaro, sobre la carretera a Toluca, *Rzedowski & de la Sota 18324* (ENCB, MEXU). MORELOS. Al N de Coajomulco, *Palacios s.n.*, Jan. 9, 1965 (ENCB). NAYARIT. 5 mi N of Compostela, near the bridge over Río Miravalles, *McVaugh & Koelz 627* (MICH). OAXACA. San Miguel Suchistepec, *Alexander 596* (MEXU); between Ayulta and Santa Maria, *Camp 2751* (MICH, NY, UC); Cerro San Felipe, *Conzatti 2215* (F); Hacienda Guadulupe, *Conzatti e hijos 4768* (MICH); vicinity of Cerro Zempoaltepetl, *Hallberg 943* (ENCB, MICH); Cerro de San Felipe, *Mexia 9121* (F, MO, NY, UC, WTU); by brooks, Sierra de San Felipe, *Pringle 10251* (DAO, ENCB, MICH, MSC, UC, US, WIS); by brooks, Sierra de San Felipe, *Pringle 10252* (DAO, ENCB, F, MICH, MSC, UC, US, WIS); Puertecillo de Lanchao, *Rzedowski 19624* (ENCB, MEXU, MSC). PUEBLA. Huauchinango, *Aguirre & Reko 150* (NY); entre Teziutlán y Atempan, *Ern 434* (ENCB); 5 km al SW de Huauchinango, *Espinosa 601* (ENCB, MEXU); Los Molinos, near Atlixco, *Gilly 128* (MSC); Tezuitlán, *Orcutt s.n.*, Sept. 6, 1910 (F, MO); Sierra de Zacapoaxtla, *Palacios s.n.*, Jan. 19, 1968 (ENCB); El Paraiso, V. Juarez, *Sarukhan et al. s.n.*, Apr. 12, 1962 (MEXU). QUERETARO. 51 mi NE of Zimapan, *Waterfall 14209* (US). SAN LUÍS POTOSÍ. El Guajolote, 10 km al W de Rosa de Castilla, *Rzedowski 8529* (ENCB). SINALOA. Along the Arroyo El Surutato, 2 mi N of Surutato, Sierra Surutato, *Breedlove 16484* (MICH); 3 mi N of Los Ornos along road to Ocurahui, *Breedlove & Thorne 18415* (MICH). SONORA. Horconcitos, Río Huachinera, *White 2965* (ARIZ, MEXU, MICH). VERACRUZ. Orizaba Mexique, *Bilimek 404* (NY); 32 km SW of the city of Orizaba, *Furlow 341* (MSC); San Miguel del Soldado E de Jalapa, *Gomez-Pompa 1472* (MEXU); orillas del Río Jamapa, cerca de Ixhualtlan del Cafe, *Lot 882* (GH, MEXU); Acatlan, *Rosas R. 600* (GH); Malpais, entre la Joya, Ver. y Rancho Dos Hermanos, Ver., *Vela Galves 108* (ENCB); Champilico, *Ventura A. 58* (ENCB, MSC); La Florida, Mun. de Atzalan, *Ventura A. 243* (ENCB, MSC); valley NW of La Perla (vicinity of Orizaba), *Weaver et al. 1700* (MICH).

Several variants of *Alnus acuminata* ssp. *arguta* have been treated as separate species or varieties of *Alnus arguta*. One such taxon is *Alnus pringlei* Fernald, which differs from ssp. *arguta* mainly in that the petioles and veins of the leaves are more densely pubescent. *Alnus arguta* var. *subsericea* Bartlett, *A. arguta* var. *cuprea* Bartlett, and *A. ovalifolia* Bartlett, similarly, represent minor variations in leaf shape and indumentum characters. Throughout the range of this subspecies, infructescences vary considerably, both in length and diameter. The leaves are almost always ovate, though they sometimes become elliptic or (infrequently) even obovate, and the apices range from acuminate to rounded. Pubescence on the abaxial leaf surface varies from absent to very dense. Leaf surface glands may appear either large and densely-arranged or smaller and sparser. The glands are never entirely absent, however, contrary to the statements of Fernald (1904b), Standley (1920), and Standley and Steyermark (1952).

Alnus acuminata ssp. *arguta* is most easily distinguished from ssp. *acuminata* by its coarser more deeply toothed leaves. The leaves of ssp. *acuminata* are often toothless or nearly so, while this is only infrequently the case in ssp. *arguta*. The foliage of ssp. *acuminata* is also somewhat broader and more elliptical than that of ssp. *arguta*.

This subspecies occurs throughout much of the mountainous parts of Mexico and northern Central America. Small disjunct populations are also found in Costa Rica and Panama (Furlow, 1977), and specimens from these areas are to a certain degree distinct from those of both Mexico and South America. Sometimes the leaves approach *Alnus jorullensis* in shape and indumentum, though they retain the overall aspect of *A. acuminata*. It is difficult to place these populations in a particular subspecies. However, numerical analysis (unpublished, to be presented in a later paper) indicates that they possess somewhat stronger affinities with ssp. *arguta* than with ssp. *acuminata*. They are thus treated here as belonging to ssp. *arguta*.

Alnus acuminata ssp. *arguta* is usually found growing along mountain streams or on moist slopes in pine-oak forests at relatively high elevations in Mexico and northern Central America. Toward the south of its range it show a preference for moderate moisture conditions, being largely absent on the Pacific Slope, where rainfall is more abundant (Standley & Steyermark, 1952).

4c. **Alnus acuminata** ssp. **glabrata** (Fernald) Furlow

Alnus acuminata ssp. *glabrata* (Fernald) Furlow, Ann. Mo. Bot. Gard. **63:** 381. 1977; *Alnus glabrata* Fernald, Proc. Amer. Acad. **40:** 26. 1904. Type: *A. Dugés s.n.*, April, 1882, "Monte San Nicolas, Guanajuato" (Lectotype of Standley, (GH!, 1920). Figure 38.

Alnus jorullensis var. *η acuminata* f. *media* Winkler, Pflanzenreich **19**(4.61): 127. 1904, in part.

Alnus glabrata var. *durangensis* Bartlett, Proc. Amer. Acad. **44:** 611. 1909. Type: *Palmer 965*, in the vicinity of the City of Durango, State of Durango, April to November 1896 (Holotype, GH!; Isotypes, F!, NY!, UC!, US!).

Narrow-crowned trees up to 30 m in height; young stems dull to slightly lustrous, not glaucous to moderately glaucous; internodes glabrous, moderately glandular; lenticels 0.3–1 mm long, 0.2–0.7 mm wide, whitish or yellowish, moderately prominent; leaf scars 1–1.5 mm high, 1.5–2.5 mm wide. Buds ovoid to ellipsoid, slightly rounded to rounded at the apex, moderately to heavily resin-coated; stalk 2–6 mm long, 1–2 mm in diameter, glabrous, densely glandular; body 5–9 mm long, 3–4 mm in diameter. Leaves narrowly ovate to lanceolate (or rarely elliptic), the apex long-acuminate (or sometimes acute), the base acute to obtuse or rounded; blade (3–) 6–13 (–15) cm long, (2–) 3–6.5 (–8) cm wide, medium to dark green above, light to medium green (or brown) below, chartaceous; margin flat, unthickened, usually sharply double-serrate; major teeth 8–16 (–18) mm apart at mid-leaf, 2–5 mm deep, regular, usually more or less acuminate; adaxial surface glabrous; abaxial surface and veinlets glabrous (rarely very sparsely pubescent), moderately to densely glandular; major veins and vein axils near the base glabrous to sparsely pubescent; pubescence, when present, whitish to pale yellowish. Lateral veins 8–13, 4–8 (–11) mm apart at mid-leaf, straight or slightly ascending; cross veins between lateral veins poorly developed. Petioles (8–) 12–21 (–27) mm long, 0.8–1.5 mm in diameter, glabrous. Stipules 7–9 mm long, 1–2 mm wide, green to light brown, sparsely to moderately pubescent, the hairs yellowish, moderately glandular, the glands yellowish. Pistillate inflorescences at anthesis 4–6 mm long, 2–3 mm in diameter, on peduncles 1–4 mm long, 1–1.7 mm in diameter; staminate catkins at anthesis 6.5–9.5 cm long, 6–8 mm in diameter, on peduncles 2–14 mm long, 1–2 mm in diameter. Staminate flowers with 4 perianth parts, these elliptic to obovate, the apex obtuse to rounded, 1.5–2.1 mm long, 0.8–1.1 mm wide, the margin lined with minute to small glands; stamens usually appearing equal to or longer than the perianth, the filaments 1–1.7 mm long, the anthers 1.6–1.8 mm long and 1.5–1.8 mm in diameter, the thecae separate for 35–45% of their length. Infructescences (10–) 15–25 (–30) mm long, 6–12 (–15) mm in diameter, on peduncles 0.2–3 mm long, 1.2–1.8 mm in diameter; scales 4.5–5 mm long, 3.7–5 mm wide at the apex, 1.2–1.5 mm wide at the base, the apex moderately thickened, the terminal lobe-tip acute to rounded, often somewhat extended. Fruits narrowly wing-margined; body 2.2–4 mm long, 1.2–2 mm in diameter; wings 2.5–3 mm long, 0.3–0.8 mm wide, firm to coriaceous; persistent styles 0.6–1 mm long. Figures 15B, 16C, 38, and 39.

Figure 38. Lectotype of *Alnus glabrata* Fernald (=*Alnus acuminata* ssp. *glabrata* (Fernald) Furlow).

Figure 39. Representative specimen of *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow.

DISTRIBUTION AND HABITAT: Central Durango southeast to Guanajuato, México, Tlaxcala, and north-central Oaxaca. Usually found along streams and on moist slopes, often with *Pinus* and *Quercus*, at elevations from 1,500 to 2,500 (or rarely to 3,000) meters. Figure 40.

COMMON NAMES: Aile, aliso.

REPRESENTATIVE SPECIMENS: **Mexico.** DISTRITO FEDERAL. By streams, Valley of Mexico, *Pringle 4361* (F, MO, MSC, NY, UC); by streams near Tizapán, 7500 ft, *Pringle 8022* (F, MEXU, MO, MSC, NY, UC); San Angel, *Torres 354* (MEXU). DURANGO. At the city of Durango and vicinity, *Palmer 965* (F, NY, UC, US). GUANAJUATO. Monte de San Nicolas, *Dugés s.n.* in 1882 (GH); 14.5 mi from Guanajuato on the road to Dolores Hidalgo, *Johnston 2641* (MEXU, MICH, MSC); ca 15 mi from Guanajuato on road to Dolores Hidalgo, *Solbrig & Ornduff 4509* (UC). GUERRERO. Petlascala, *Mexia 8979* (F, MO, NY, UC). HIDALGO. Barrancas W of El Salto Station, Distr. Tula de Allende, *Moore 1457* (MEXU, MICH, UC); Tula, *Rose 8330* (NY). MÉXICO. Atlacomulco, *Detling 8920* (ENCB); just N of Amecameca, *Gilly & Dodds 2* (MSC, NY); Parque Nacional "Los Remedios", *Rzedowski 19301* (ENCB, MSC); 2 km al SE de San Pablo Ixayoc, *Rzedowski 24161* (ENCB, MSC). OAXACA. 5 km adelante de Tlaxiaca, *Pennington & Sarukhan K. 9216* (NY); Rancho del Cura cerca de Concepción, Buenavista, Distr. de Coixlahuaca, *Rzedowski 25713* (ENCB); 1 km al E de Ihuitlan Plumas, *Rzedowski 26680* (ENCB, MSC). PUEBLA. Vicinity of Puebla, *Arsene 135* (US); alrededores de Atzala, *Ern 328* (ENCB); Los Molinos near Atlixco, *Sharp 45406* (MEXU). TLAXCALA. Rancho Nuevo, Tlaxco, *Aguilar 8-A-42* (ENCB); 4 km al W de Apizaco, *Ruiz Bedolla s.n.*, July 9, 1967 (ENCB); orillas del Rio Zahuapan, cerca de Tlaxcala, *Weber 169* (ENCB).

In describing *Alnus glabrata,* Fernald (1904b) did not designate one of his cited specimens as the type. In 1920, Standley, in *Trees and Shrubs of Mexico,* listed the type of this species as from "Monte San Nicolas, Guanajuato," thus establishing one of Fernald's elements (*A. Dugés s.n.,* April, 1882) as the lectotype. This specimen is the first listed by Fernald in the protologue, and its selection by Standley may represent an arbitrary choice of the first listed element, as explicitly prohibited in the Rules of Nomenclature (Stafleu *et al.,* 1972). Without stronger evidence of this, however, the specimen of Dugés should be allowed to stand as the lectotype.

This subspecies occurs at generally lower elevations than ssp. *arguta,* but the habitats of the two overlap altitudinally, and they are sometimes found growing in close proximity. It may eventually prove to be only a minor variant of ssp. *arguta,* but from the material seen, it appears distinct enough to be given subspecific

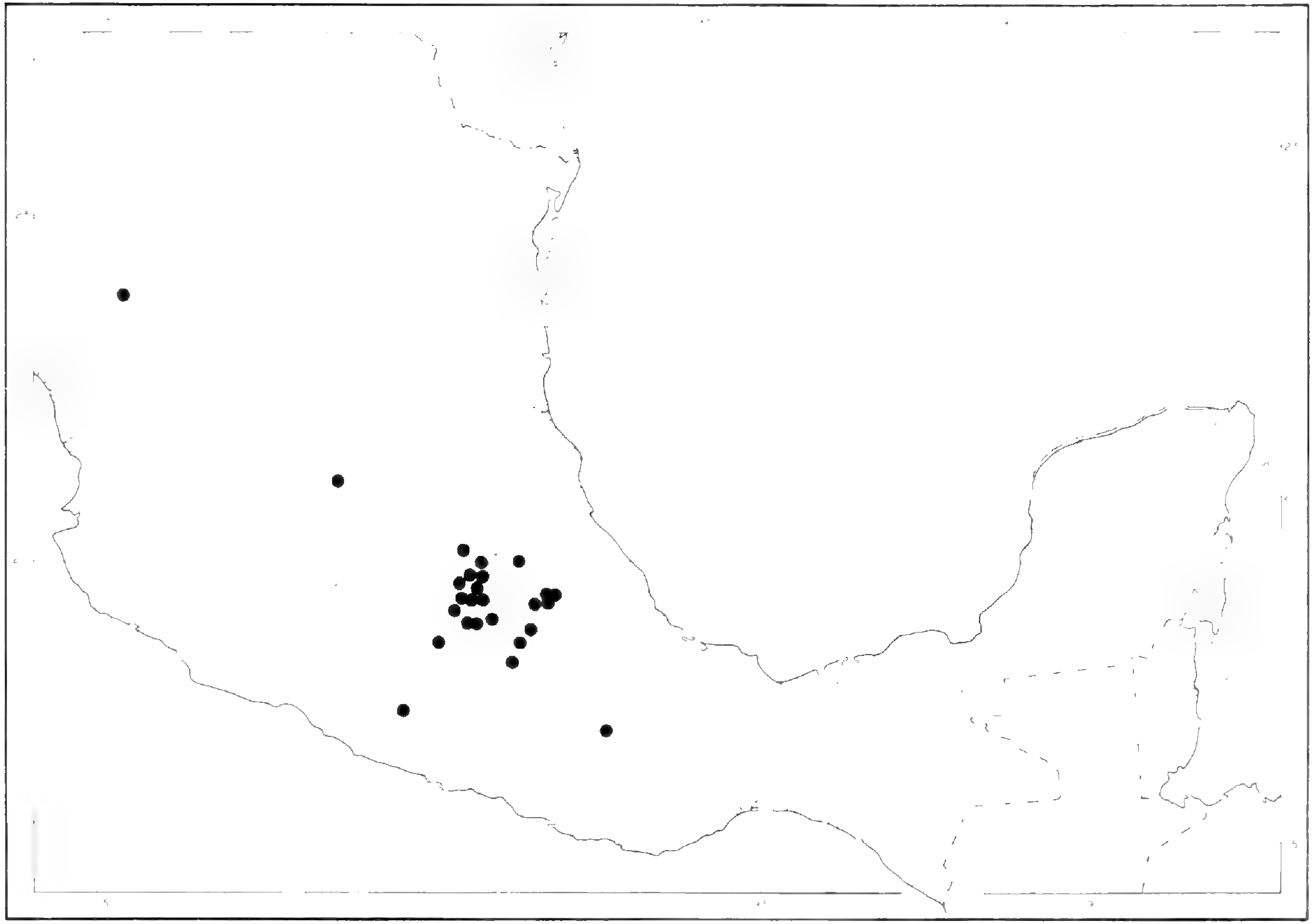


Figure 40. Distribution of *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow.

status. The most useful distinguishing characters are the completely (or nearly) glabrous lower leaf surface and the lanceolate or narrowly ovate, acuminate, sharp-toothed leaf form.

There is abundant evidence of natural hybridization between spp. *glabrata* and *arguta* throughout the range, as shown by numerous specimens having intermediate leaf shapes and indumentum. Where such putative hybridization occurs, it is often difficult to determine these taxa. In the specimens cited here, such intermediates have been assigned to one variety or to the other, depending on their closest affinity. They have not been taken into consideration in constructing the key.

To be concluded in Vol. 81, No. 825 (April, 1978)

THE TYPIFICATION AND TAXONOMIC STATUS OF SPARTINA CAESPITOSA A. A. EATON

MARK J. MCDONNELL AND GARRETT E. CROW[1]

In 1898 Alvah Augustus Eaton described a new species of *Spartina* growing in the salt marshes of New Hampshire and Massachusetts (Eaton, 1898). It was similar to *Spartina patens* (Ait.) Muhl. but somewhat larger and with a distinctive caespitose growth habit, thus its name *Spartina caespitosa* A. A. Eaton. He had discovered it two years earlier as stated in his original text:

> "On August 26, 1896 while collecting the peculiar large form of *Spartina patens* growing on the border of the salt marsh at Seabrook, N.H. I noticed a taller, more slender plant growing in a clump of bushes." (Eaton, 1898, pg. 338)

A recent assessment of the taxonomy of this species for the Flora of New Hampshire Project revealed a problem with the typification of *Spartina caespitosa.* While examining the supposed type specimen at the Gray Herbarium the senior author noted that it was collected from Seabrook, N.H. on September 29, 1896, rather than August 26, as described by Eaton. This supposed type has "TYPE" stamped on it, but there is no evidence from the label data that Eaton regarded it as the type specimen (Fig. 1A). The specimen was stamped "TYPE" by a member of the Gray Herbarium staff at some later date during a period in which all the type specimens in the herbarium were being located. The discrepancy between the published date and the date on the supposed type has apparently gone unnoticed until now.

In an effort to resolve the confusion an attempt was made to locate all of Eaton's specimens of *Spartina caespitosa* in hopes that the true type specimen would be found.[2] A total of 17 specimens of

---

[1] Published with the approval of the Director of the University of New Hampshire Agricultural Experiment Station as Scientific Contribution No. 931.

[2] Specimens were sought from NEBC, NHA, HNH, MASS, and CONN and from those listed in *Index Herbariorum:* Part II., Collectors (Lanjouw & Stafleu, 1957) as having specimens of A. A. Eaton: BUF, COCO, GH, NY, and US. Index Herbariorum also lists MANCH as having A. A. Eaton specimens but upon inquiry it was found they do not. There appears to have been some confusion between MANCH (Manchester Museum, Manchester, England) and the Institute of Arts and Science, Manchester, N.H., U.S.A. which did have A. A. Eaton specimens. These specimens are now in the Hodgdon Herbarium of the University of New Hampshire (NHA).

S. caespitosa collected by Eaton were located. No specimen could be found which agreed completely with the collection site or date published in the original description.

The only specimen (*Eaton 501,* NEBC) collected on August 26, 1896, agrees well with Eaton's original description and has "TYPE SPECIMEN" printed on the label (Fig. 1B). But hand written on the label is: "First collection, one root in Hampton Falls, N.H." The original description however, states that it was first collected in Seabrook, N.H., on this date.

The earliest collection from Seabrook, N.H. (*Eaton 505,* US), was on August 27, 1896, one day after the date cited by Eaton as the original collection of *Spartina caespitosa* (Fig. 1C). Eaton (1898) does state that he made an extended search of this area on August 27, the day after the original discovery. This specimen has two culms, one of which is the typical *S. caespitosa* Eaton described, but the other does not fit his original description. The date of this specimen was misinterpreted by Merrill (1902) as 1891. Eaton apparently did not collect specimens from Seabrook, N.H., again until September of 1896.

The fact that the Hampton Falls specimen (*Eaton 501,* NEBC) collected on Aug. 26, 1896, has "TYPE SPECIMEN" printed on the label would seem to suggest that Eaton regarded this as a type specimen regardless of the location and date published with the original description. However, the matter is further complicated as Eaton also had "TYPE SPECIMEN" printed on the label of a specimen (*Eaton 898,* NY) of *Spartina caespitosa* collected from Salisbury, Mass. in October, 1896 (Fig. 1D). It is clear that Eaton held a broad type concept. It is also possible that "TYPE SPECIMEN" may have meant "typical" (R. Tryon, personal communication, 1978).

A critical analysis of all of Eaton's specimens reveals that his original description does not refer to any one specimen but is based on all the specimens he had collected up to that time. In light of this and the subsequent confusion over the actual type specimen a lectotype must be designated.

Research into the early land records and field studies of the Hampton Falls-Seabrook salt marshes provided valuable insight into the discrepancy between the published account of the original collection of *Spartina caespitosa* and the label data on Eaton's specimens. It appears that Eaton first collected *S. caespitosa* in the upper edges of the salt marsh surrounding Brown's Creek. This creek forms the boundary between Hampton Falls and Seabrook, N.H. Field studies revealed that *S. caespitosa* occurs on both sides of the creek. In view of this there is apparently little difference between the Seabrook and Hampton Falls sites. Thus the one specimen Eaton collected on August 26, 1896 (*Eaton 501,* NEBC), which agrees well with the original description and has "TYPE SPECIMEN" printed on the label, is here designated the lectotype for *Spartina caespitosa* A. A. Eaton (Fig. 1B).

Since Eaton's original description of *Spartina caespitosa* its taxonomic status has been the center of much controversy. Merrill (1902), in the first monograph on North American Spartinas, felt it looked sufficiently like *Spartina juncea* (Michx.) Willd. (=*S. patens* (Ait.) Muhl. var. *monogyna* (M. A. Curtis) Fern.) to place it in that taxon. Hitchcock (1906; 1935, pg. 493) relegated it to varietal status under *S. patens* (*S. patens* var. *caespitosa* (A. A. Eaton) Hitchc.) while stating: "An ambiguous form resembling *S. patens* but growing in large tufts without rhizomes." Robinson and Fernald (1908) and Blomquist (1948, pg. 109) used Hitchcock's treatment, the latter stating it ". . . should perhaps be considered an ecological form rather than a distinct entity". Swallen (1939) and Chase (*in* Hitchcock, 1950) on the other hand treat it as a distinct species.

Church (1940), on the basis of cytological studies, was the first to suggest that *Spartina caespitosa* was of hybrid origin. He felt it arose from a cross between the hexaploid segment of the *S. patens* complex and the hexaploid *S. pectinata* Link. Recent studies by Reeder and Singh (1971), Marchant (1968, 1970) and Gould (1968) have shown that *S. patens* is not a polyploid and that this species, *S. pectinata,* and *S. caespitosa* all have a chromosome count of $2n = 40$.

Fernald (1950), apparently noticing the similarities between *Spartina caespitosa* and its putative parents, *S. patens* and *S. pectinata,* was the first to give it hybrid status (× *S. caespitosa* (A. A. Eaton) Fern.).

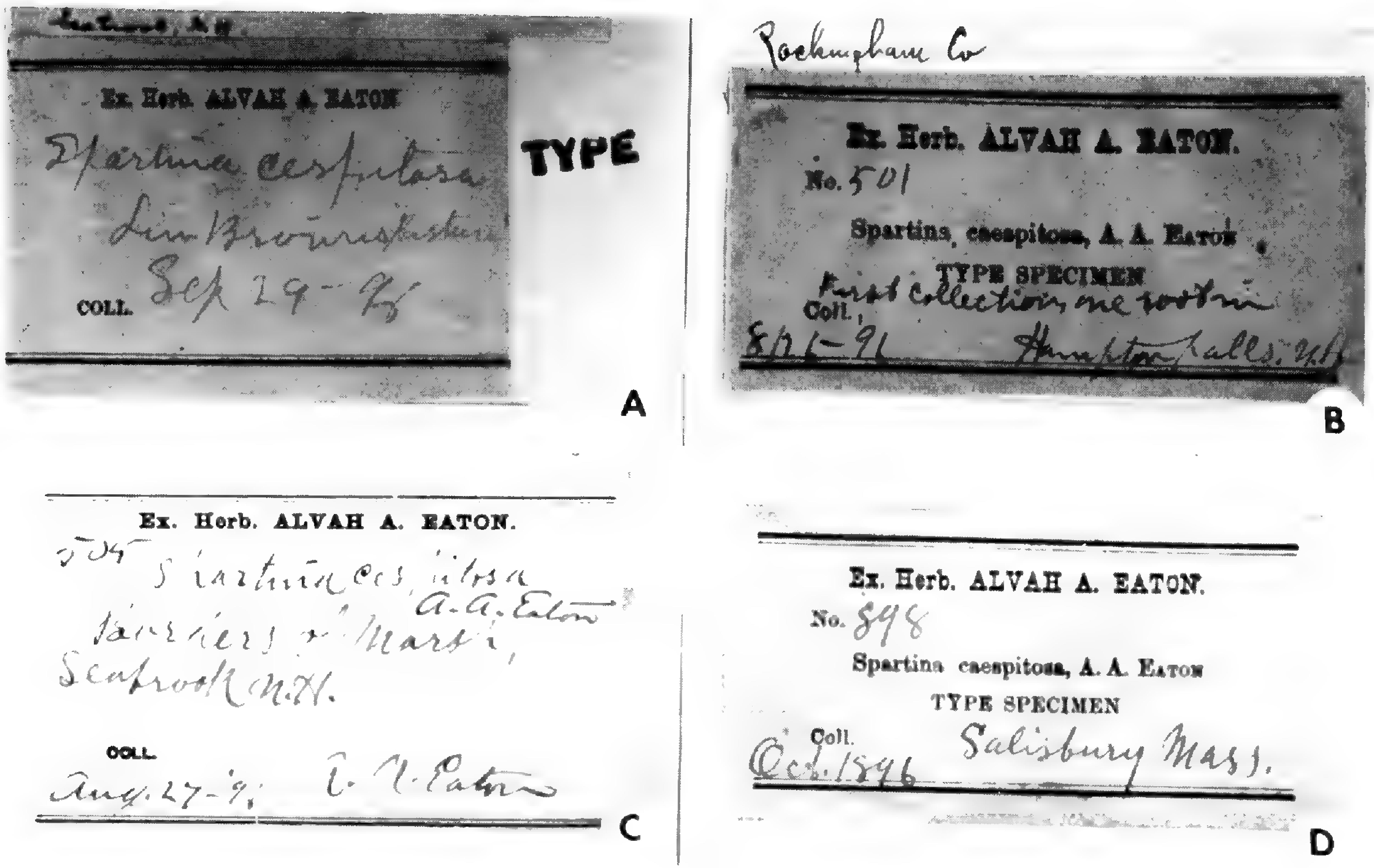
Marchant (1970), studying the cytology and breeding behavior of *Spartina caespitosa* and its putative parents, found that all three exhibited regular meiotic pairing and high pollen stainability. He went on to state that regular meiotic pairing is by no means unique in interspecific hybrids. In crossing experiments between *S. patens* and *S. pectinata* he was able to produce plants similar to *S.*

caespitosa. However, during these experiments he found that self-pollination can take place in this protandrous grass genus, causing him some uncertainty about the results. Marchant (1970, pg. 188) concludes:

> ". . . it is clear that *S.* × *caespitosa* is by no means unique in its almost regular cytological behavior and fertility but at the same time the data give only small support for a hybrid origin. Indeed the taxon behaves as a descrete species in many characteristics."

Among the most convincing evidence for the hybrid origin of *Spartina caespitosa* is Mobberly's (1956) hybrid index, based on twenty different morphological characteristics discernible from herbarium specimens. The distribution of the hybrid index scores generated showed *S. caespitosa* to be distinctly intermediate between *S. patens* and *S. pectinata.* In contrast, we found from a preliminary analysis of the readily distinguishable characteristics of *S. caespitosa* and its putative parents that *S. caespitosa* does not exhibit morphological characteristics distinctly intermediate between *S. patens* and *S. pectinata.* Instead there is a gradation in morphological characteristics from the smaller *S. patens* to the slightly larger *S. caespitosa* and finally to the large *S. pectinata.* The differences between *S. caespitosa* and *S. patens* are, at times, very difficult to perceive.

The most distinct characteristics of *Spartina caespitosa* are its caespitose habit and the fact that it does not produce elongate rhizomes. However, an examination of over 50 specimens of *S. caespitosa* from throughout its range revealed that some plants do in fact produce elongate rhizomes. As Hitchcock (1935) noted, those in the southern portion of the range (Chesapeake Beach, Md., and Virginia Beach, Va.) commonly produce elongated rhizomes, but these rhizomes are thick and more closely resemble those of *S. pectinata* than *S. patens.* In addition the floral morphology of the *S. caespitosa* plants at the southern end of the range differs somewhat from the northern plants in having more spikelets per spike, smaller first glumes, and more acuninate second glumes. One possible explanation for this difference between the northern and southern forms is that the plants exhibit different morphological characteristics depending on which putative parent was the female. Dore and Marchant (1968) observed this type of variability in *S. caespitosa* populations growing in Charlottetown, P.E.I., Canada.



[illegible], N.H.

Ex. Herb. ALVAH A. EATON

Spartina cespitosa

[illegible]

COLL. Sep 29-96

TYPE

Rockingham Co

Ex. Herb. ALVAH A. EATON.

No. 501

Spartina caespitosa, A. A. Eaton

TYPE SPECIMEN

First collection, one root in

Coll. 8/26-96 Hampton Falls, N.H.

Ex. Herb. ALVAH A. EATON.

504 Spartina caespitosa A. A. Eaton

borders of Marsh, Seabrook N.H.

COLL. Aug. 27-96 A. A. Eaton

Ex. Herb. ALVAH A. EATON.

No. 548

Spartina caespitosa, A. A. Eaton

TYPE SPECIMEN

Coll. Oct. 1896 Salisbury Mass.

Figure 1. Labels from original collections of *Spartina caespitosa* by A. A. Eaton. A. Specimen in Gray Herbarium which was previously considered the "TYPE" specimen (GH). B. Earliest collection of this species, dated August 26, 1896 (NEBC). C. Earliest collection from Seabrook, N.H., dated August 27, 1896 (US). D. A specimen from Salisbury, Mass., which also has "TYPE SPECIMEN" on the label (NY).

The caespitose habit, therefore, appears to be the one characteristic which holds *Spartina caespitosa* apart from both *S. patens* and *S. pectinata*. But herbarium specimens and field studies revealed a number of plants with the morphological characteristics of *S. patens* which exhibited a tall caespitose habit. Indeed, some of the herbarium specimens had been incorrectly determined as *S. caespitosa*. It is interesting to note that many of the *S. patens* specimens from the southern states, especially Florida, Mississippi, and Louisiana, have short, clustered, developing shoot tips and a caespitose habit characteristic of *S. caespitosa*. Also occurring in the southern United States is *Spartina bakeri* Merr., which is separated from *S. patens* solely by the fact that it has a taller caespitose habit and grows in both fresh and brackish marshes. As Mobberly (1956) stated, it is extremely difficult to separate herbarium specimens of this species from *S. patens* unless the particular habit has been noted on the label. This species, like all the other Spartinas in this complex, has a chromosome count of $2n = 40$ (Marchant, 1968). A subsequent examination of the morphology of *S. bakeri* revealed that except for the caespitose habit it was more closely aligned with *S. patens* than *S. caespitosa*.

SUMMARY

While providing few answers this study has produced a number of new insights into the taxonomy of *Spartina caespitosa*. An analysis of herbarium specimens of *S. caespitosa* and its putative parents, *S. patens* and *S. pectinata*, from throughout their ranges revealed that the morphological criteria used to distinguish *S. caespitosa* are not as clear cut as previously described. The current taxonomic treatment of *S. caespitosa* appears unsatisfactory. A more complete analysis of the chemistry, morphology, cytology, ecology, and taxonomy of *S. caespitosa*, its putative parents and such related species as *S. bakeri*, needs to be done in order to obtain a better understanding of this entire complex.

ACKNOWLEDGMENTS

We would like to thank the curators of the herbaria from which specimens were borrowed for this study (BUF, GH, NEBC, NY, ISC, and US). Irene Storks examined HNH, MASS, and CONN for A. A. Eaton specimens. We are grateful to Dr. A. Linn Bogle for reviewing the manuscript.

LITERATURE CITED

Blomquist, H. L. 1948. The Grasses Of North Carolina. Duke Univ. Press. Durham, N.C. 276 pp.

Church, G. L. 1940. Cytotaxonomic studies in the Gramineae *Spartina, Andropogon,* and *Panicum.* Am. Jour. Bot. **27:** 163-271.

Dore, W. G., & C. J. Marchant. 1968. Observations on the hybrid cord-grass *Spartina* × *caespitosa* in the Maritime Provinces. Canad. Field-Naturalist **82:** 181-184.

Eaton, A. A. 1898. Two new species. Bull. Torrey Bot. Club **25:** 338-342.

Fernald, M. L. 1950. Gray's Manual of Botany. Ed. 8, Corrected Edition, 1970. Van Nostrand Reinhold Company. New York. 1632 pp.

Gould, F. W. 1968. Chromosome numbers of Texas grasses. Can. Jour. Bot. **46:** 1315-1319

Hitchcock, A. S. 1906. Notes on grasses. Rhodora **8:** 202-212.

Hitchcock, A. S. 1935. Manual Of The Grasses Of The United States. U.S.D.A. Misc. Publ. **200** U.S. Government Printing Office. Washington, D.C. 1040 pp.

Hitchcock, A. S. 1950. Manual Of The Grasses Of The United States. (Revised by Agnes Chase). U.S.D.A. Misc. Publ. **200.** U.S. Government Printing Office. Washington, D.C. 1051 pp.

Lanjouw, J., & F. A. Stafleu. 1957. Regnum Veg. Vol. **9.** Index Herbariorum, II. Collectors E-H. Utrecht-Netherlands. 295 pp.

Marchant, C. J. 1968. Evolution in *Spartina* (Gramineae) III. Species chromosome numbers and their taxonomic significance. Linn. Soc., Bot. **60:** 411-417.

Narchant, C. J. 1970. Chromosome pairing and fertility in *Spartina* × *caespitosa.* Can. Jour. Bot. **48:** 183-188.

Merrill, E. D. 1902. The North American species of *Spartina.* U.S.D.A. Bur. Pl. Indust. Bull. No. 9.

Mobberly, D. G. 1956. Taxonomy and distribution of the genus *Spartina.* Iowa State Coll. J. Sci. **30:** 471-574.

Reeder, J. R. & D. N. Singh. 1967. *In:* IOPB chromosome number reports XI. Taxon **16:** 215-222.

Robinson, B. L., & M. L. Fernald. 1908. Gray's New Manual Of Botany. American Book Co. New York. 926 pp.

Swallen, J. R. 1939. Tribe Chloridae. *In:* North American Flora Vol. **17:** 579-638.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE 03824

RANGE EXTENSIONS OF CAREX IN MINNESOTA

GERALD A. WHEELER

During the winter of 1974 an examination of the distribution of the genus *Carex* in Minnesota was begun. The Minnesota *Carex* distribution maps on file at the University Herbarium were examined; these distributions were then compared with published accounts of *Carex* distribution in the surrounding states and Canadian provinces. It quickly became apparent that it was highly probable that several species of *Carex* remained to be discovered in Minnesota. This article deals with three *Carex* taxa that frequent the floodplains of southeastern and east-central Minnesota which previously had not been reported from the state, as well as a species of *Carex* which frequents the same floodplains but which had not been collected in Minnesota since 1885. Under "Representative Collections" cited at the end of this report, the letter W refers to those specimens collected by the writer; O & W indicates specimens collected jointly with Prof. Gerald B. Ownbey; S indicates specimens placed at the disposal of the writer by Mr. Steven Swanson, a student at the University of Wisconsin, LaCrosse. All specimens cited are deposited in the University of Minnesota Herbarium (MIN).

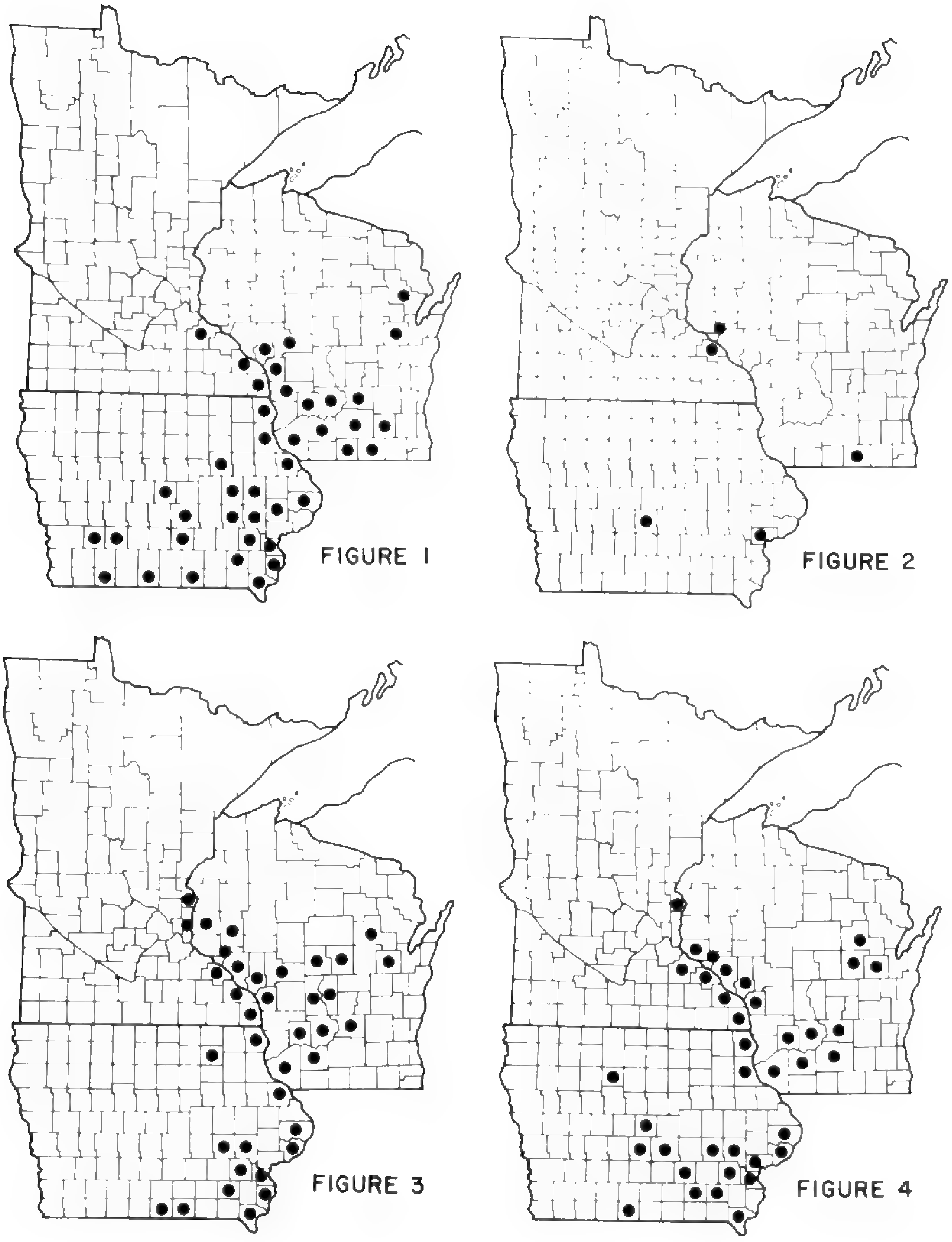
Although the species was reported by Mackenzie (1935) for Wisconsin and Iowa, the finding of *Carex grayi* Carey in Minnesota represents an extension of the known range. During the 1975–1977 field seasons, this species was collected in floodplain woods bordering the Mississippi River at scattered locations in Houston, Winona, and Goodhue counties. Based on the presently known distribution of this species, the station in northern Goodhue County represents the northwesternmost site for it in the United States (Fernald, 1942) and Canada (Reznicek, 1974).

Fernald (1942) reported *Carex grayi* Carey var. *hispidula* Gray as occurring both in Wisconsin and Iowa, but not in Minnesota. In September, 1976, the writer collected this plant in a floodplain woods bordering the Mississippi River near Read's Landing in eastern Wabasha County. Of the thirty or more plants observed at this location, all had very hispidulous perigynia; no glabrous plants of *C. grayi* were found at this station.

Although *Carex typhina* Michx. was reported for both Wisconsin and Iowa, Mackenzie (1935) did not include Minnesota within the species range. A specimen of this species was collected by J. M. Holzinger in October, 1900, but misidentified by him as *C. retrorsa* Schwein. It was correctly identified as *C. typhina* by Dr. J. H. Zimmerman, University of Wisconsin, in 1963. The specimen label states only that the plant was collected on the Mississippi River bottoms in Winona County. Prior to 1976, this was the only Minnesota specimen of this species in the University Herbarium. In August, 1976, Prof. Ownbey and the writer collected *C. typhina* in a floodplain woods bordering the Mississippi River about 2.5 miles south of Reno in Houston County and also from a floodplain woods near LaCrescent, Houston County. Subsequently, the writer found this species about 3.5 miles south of Franconia in southeastern Chisago County. As far as can be determined, the latter location represents the northwesternmost site for this species in the United States and Canada (Fernald, 1970).

Prior to 1976, *Carex muskingumensis* Schwein. was represented by a single specimen from Minnesota in the University Herbarium. The specimen was collected by J. H. Sandberg in June, 1885, in a meadow near Center City, Chisago County, and identified by him as *C. arida* Schwein. and Torr. At a later date the specimen was examined by K. K. Mackenzie and annotated to *C. muskingumensis.* Minnesota was included within the geographical range of the species by Mackenzie (1935) apparently on the basis of this record. In 1976 this species was found at several localities along the wooded floodplains of the Mississippi River from Houston to Goodhue counties. Evidently it has been overlooked for several years because of lack of intensive collecting in its special habitat. It is interesting to note that efforts made during the past two years to recollect *C. muskingumensis* at Sandberg's original site in Chisago County have failed.

Distribution maps show the distribution, by county, of each of the four above discussed *Carex* taxa in Minnesota, Wisconsin, and Iowa. Specimens deposited at the University of Wisconsin, University of Iowa and Iowa State University, as well as those at the University of Minnesota, were utilized in the preparation of the maps.



Carex distributions, by county, in Minnesota, Wisconsin, and Iowa.
Figures 1–4. **1,** *Carex grayi;* **2,** *Carex grayi* var. *hispidula;* **3,** *Carex typhina;* **4,** *Carex muskingumensis.*

ACKNOWLEDGEMENTS

The writer wishes to thank the following individuals for their help: Prof. Gerald B. Ownbey for many enjoyable collecting trips and for much valuable help with the manuscript; Dr. James H. Zimmerman, who suppiied information on recent collections of these four taxa in Wisconsin; and the curators of those herbaria whose specimens were used in the preparation of the maps.

REPRESENTATIVE COLLECTIONS

CAREX GRAYI Carey. **Goodhue Co.:** 4.5 mi. WNW of Red Wing, T113N, R15W, Sec. 19, *W1145*. **Houston Co.:** Navigation Pool No. 8 on the Mississippi River, Site 31, *S 835;* Rte. 26, 1.3 mi. N. of Iowa Border, *O & W 5327;* just north of U.S. 14, 16, and 61 at LaCrescent, *O & W 5384*. **Winona Co.:** 5 mi. S. of John A. Latsch State Park on U.S. 61, T108N, R8W, Sec. 34, *W 846*.

CAREX GRAYI Carey var. HISPIDULA Gray. **Wabasha Co.:** 0.25 mi. E. of Read's Landing, T111N, R11W, Sec. 24, *W976*.

CAREX TYPHINA Michx. **Chisago Co.:** just N. of Rte. 243, 0.5 mi. E. of the jct. of Rte. 95 and Rte. 243, T33N, R19W, Sec. 28, *W 934*. **Houston Co.:** Rte. 26, 2.6 mi. S. of its jct. with Rte. 249 (to Caledonia), *O & W 5356;* just N. of U.S. 14, 16, and 61 at LaCrescent, *O & W 5374*. **Wabasha Co.:** 0.25 mi. E. of Read's Landing, T111N, R11W, Sec. 24, *W 978*. **Washington Co.:** 3 mi. S. of Marine on the St. Croix, *W 960*. **Winona Co.:** Mississippi River bottoms, *Holzinger, s.n.,* October, 1900.

CAREX MUSKINGUMENSIS Schwein. **Chisago Co.:** Center City, meadows, *Sandberg, s.n.,* June, 1885. **Goodhue Co.:** 0.25 mi. N. of the Red Wing City Park, *W 893*. **Houston Co.:** 3.5 mi. S. of LaCrescent, *W 834;* Rte. 26, 1.3 mi. N. of Iowa border, *O & W 5342;* Rte. 26, 2.6 mi. S. of its jct. with Rte. 249 (to Caledonia), *O & W 5359;* just N. of U.S. 14, 16, and 61 at LaCrescent, *O & W 5381*. **Wabasha Co.:** 0.25 mi. E. of Read's Landing, T111N, R11W, Sec. 24, *W 977*. **Winona Co.:** 5 mi. S. of John A. Latsch State Park on U.S. 61, T108N, R8W, Sec. 34, *W845;* U.S. 61, 1.1 mi. N. of its jct. with Rte. 248 at Minnesota City, *O & W 5392*.

LITERATURE CITED

Fernald, M. L. 1942. Critical notes on *Carex*. Rhodora **44:** 281–331.

Fernald, M. L. 1970. Gray's Manual of Botany. 8th ed., corrected printing. D. Van Nostrand Co., New York.

Mackenzie, K. K. 1935. Cyperaceae, Cariceae. North American Flora, Vol. **18.** New York Botanical Garden, New York.

Reznicek, A. A. 1974. The taxonomy of *Carex* series *Lupulinae* in Canada. Canadian Journal of Botany **52:** 2387–2399.

DEPARTMENT OF BOTANY
UNIVERSITY OF MINNESOTA
ST. PAUL, MINNESOTA
55108

A NAME CHANGE FOR LYCOPODIUM FLABELLIFORME

R. JAMES HICKEY AND JOSEPH M. BEITEL

The epithet *flabelliforme* is firmly established in the literature concerning North American lycopods. It has, with one exception (Nessel, 1939), gone unchallenged since it was first described as a variety of *Lycopodium complanatum* by Fernald in 1901. With these facts in mind we decided to examine the nomenclatural change proposed by Holub (1975a). Our investigation showed that the epithet *flabelliforme* is not only incorrect at the specific level but at the varietal level as well. The present article reviews some of the nomenclatural history of the taxon and gives what we believe to be its complete synonymy.

In 1741, Dillenius published a plate (Figure 1) and an excellent description of a lycopod obtained from John Bartram of Pennsylvania. This plant, *Lycopodium digitatum foliis arboris vitae, spicis bigemellis teretibus,* now commonly goes by the name *L. flabelliforme* (Fern.) Blanchard (Wilce, 1965). As pointed out by Holub (1975b), however, the correct name for this species is *L. digitatum* A. Braun. Unfortunately, Braun's binomial was inconspicuously published in a footnote to a paper by Kunze (1848). Later authors (Marie-Victorin, 1925; Holub, 1975 a, b) have further obscured this combination through incorrect literature citations.

Marie-Victorin (1925) was the first author to consider *Lycopodium digitatum* as an alternative name for *L. flabelliforme.* He rejected it, arguing that the condensation of a prelinnaean adjectival phrase and the lack of both an explicit literature citation and a description made Braun's combination unacceptable. Some fifty years later, Holub (1975a) took up Braun's name as the basionym for the combination *Diphasiastrum digitatum* (A. Braun) Holub. Holub (1975b) reasoned that according to Article 32 of the International Code of Botanical Nomenclature (Stafleu, 1972) the reference "Dillen." in the authority citation of Braun's binomial constituted an indirect reference to a previous and effectively published description.

In 1857, Döll compared the plant pictured in Dillenius' plate LIX with the European varieties of *Lycopodium complanatum* and stated that "Diese varietas *Dilleniana* ist bis jetzt nur in America beobachtet worden. . . ." This mention of a variety *Dillenianum* constitutes valid publication for precisely the same reasons advanced by Holub (1975b) for *L. digitatum*. Fernald's name, *L. complanatum* var. *flabelliforme*, and the subsequent elevation of it to species level by Blanchard (1913) are both predated by earlier names and are therefore both incorrect.

When treated as a species, the correct name is *Lycopodium digitatum* and when treated as a variety of *L. complanatum* it must be called *L. complanatum* var. *Dillenianum*. The complete synonymy of this taxon (grouped by basionym) is as follows:

Lycopodium digitatum A. Braun

Lycopodium digitatum A. Braun, Am. J. Sci. & Arts, ser. II, **6:** 81. 1848; *L. complanatum* var. *digitatum* (A. Braun) Nessel, Die Bärlappgewächse, p. 335. 1939; *L. chamaecyparissus* var. *digitatum* Nessel, Die Bärlappgewächse, p. 335. 1939, *pro syn; Diphasiastrum digitatum* (A. Braun) Holub, Preslia, Praha **47:** 108. 1975. LECTOTYPE: plate LIX in Dillenius, Historia Muscorum, 1741 (see below).

Lycopodium complanatum var. *Dillenianum* Döll, Fl. Gross. Bad. p. 80. 1857, as *"Dilleniana"; L. Dilleniana* Nessel, Die Bärlappgewächse, p. 333. 1939, *pro syn.* LECTOTYPE: plate LIX in Dillenius, Historia Muscorum, 1741 (see below).

Lycopodium complanatum var. *flabelliforme* Fern., Rhodora **3:** 280. 1901; L. flabelliforme (Fern.) Blanchard, Rhodora **13:** 168. 1911; *L. complanatum* ssp. *flabelliforme* (Fern.) Clausen, Am. Fern J. **35:** 17. 1945; *Diphasium anceps* ssp. *flabelliforme* (Fern.) Löve & Löve, Nucleus **1:** 7. 1958. *Diphasium flabelliforme* (Fern.) Rothm., Fedde, Rep. Spec. Nov. **66:** 235. 1962; *Diphasium complanatum* ssp. *flabelliforme* (Fern.) Löve & Löve, Univ. Colorado Stud., Biol. Ser. **17:** 4. 1965. LECTOTYPE: Vermont, Manchester, *Day 219* (GH!), selected by Wilce, 1965.

From the comments made by both Döll (1857) and Braun (in Kunze, 1848) it is obvious that both these authors were aware of and relied heavily on Dillenius' plate LIX and the accompanying description for their understanding of this taxon. Since Dillenius' plate (Figure 1) is so diagnostic (note the superficial rhizome, the regularly fan-shaped lateral branches, the wide, ultimate branchlets without annual constrictions, and the four strobili per peduncle, often with sterile tips) that there can be no doubt as to the plant he was describing, and since there are no other references in either work or cited specimens from which to select a lectotype, we choose plate LIX as lectotype for both *Lycopodium digitatum* and *L. complanatum* var. *Dillenianum*.

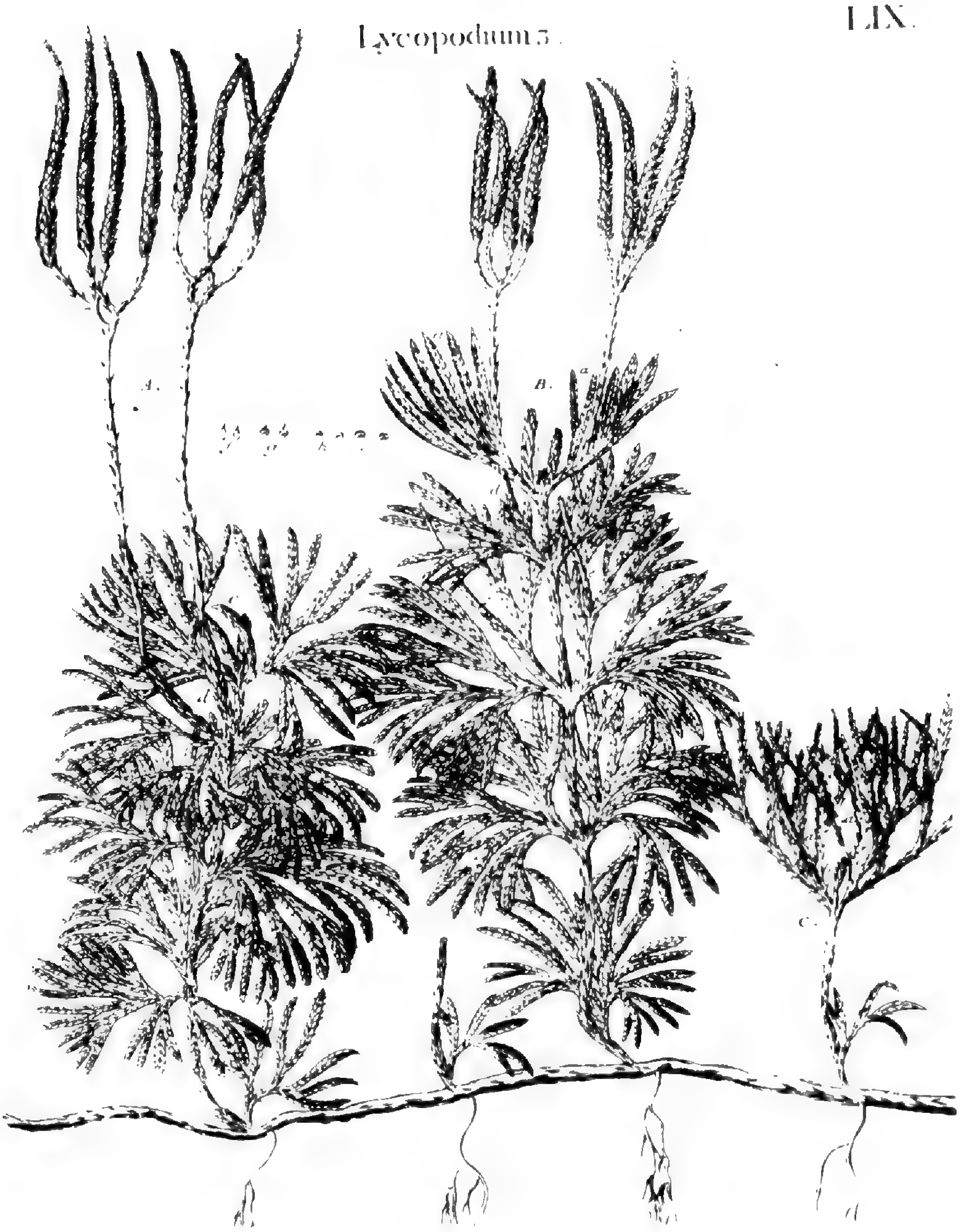


Figure 1. Dillenius' plate LIX, *Lycopodium digitatum foliis arboris vitae, spicis bigemellis teretibus,* from Historia Muscorum 1741. The lectotpe of *Lycopodium digitatum* A. Braun and of *L. complanatum* var. *Dillenianum* Döll.

ACKNOWLEDGEMENTS

The authors would like to thank Drs. Alice and Rolla Tryon, Dr. Christopher Haufler, and Dr. David Conant for their advice and suggestions during this study.

LITERATURE CITED

BLANCHARD, W. H. 1911. *Lycopodium flabelliforme*. Rhodora **13:** 168 171.

DILLENIUS, J. J. 1741. Historia muscorum, ed. I., Oxonii.

DÖLL, J. CH. 1857. Flora des Grossherzogthums Baden, Carlsruhe.

FERNALD, M. L. 1901. The True *Lycopodium complanatum* and its common American representative. Rhodora **3:** 278 281.

HOLUB, J. 1975a. *Diphasiastrum*, a new genus in Lycopodiaceae. Preslia, Praha **47:** 97 110.

______. 1975b. Notes on some species of *Diphasiastrum*. Preslia, Praha **47:** 232 240.

KUNZE, G. 1848. Notes on some ferns of the United States. Am. J. Sci. & Arts, ser II, **6:** 80 89.

MARIE-VICTORIN, FR. 1925. Les Lycopodinées du Quebec et leurs formes minueres. Contrib. Lab. Bot. Univ. Montréal **3.** Montréal.

NESSEL, H. 1939. Die Bärlappgewächse. G. Fischer, Jena.

STAFLEU, F. A. (Chairman). 1972. International Code of Botanical Nomenclature, 426 pp. Utrecht, Netherlands.

WILCE, J. H. 1965. Section Complanata of the genus *Lycopodium*. Beih. Nova Hedwigia **19:** i-ix, 1-233.

R.J.H.
HARVARD UNIVERSITY HERBARIA
22 DIVINITY AVENUE
CAMBRIDGE, MA 02138

J.M.B.
DEPARTMENT OF BOTANY
DIVISION OF BIOLOGICAL SCIENCES
THE UNIVERSITY OF MICHIGAN
ANN ARBOR, MI 48109

GEOCAULON LIVIDUM IN THE MAHOOSUC RANGE, NEW HAMPSHIRE AND MAINE

ROGER STERN

Geocaulon lividum (Richards) Fern. is among the more obscure components of the northern New England flora. Its distribution is the low arctic and boreal regions of Canada and Alaska, reaching its southern limit in our area in northern New England. It is the northernmost Santalaceae in North America. In the literature it is sometimes referred to as semi-parastic; capable of both autotrophic and phagotrophic nutrition. Semi-parasitism is common in the Santalaceae and is achieved by haustorial suckers (Moss, 1926).

Prior to 1965, *Geocaulon lividum* had been collected or sighted in New England but twelve times, these stations mainly from the mountains of northern New Hampshire and Maine while one coastal station was reported from Washington County in Maine. In 1965, S. K. Harris reported six stations, five of them from the Mahoosuc Range. He comments on the difficulty in distinguishing the plant from *Vaccinium* ssp., and concludes, "A thorough search for the plant in favorable habitats may reveal that *Geocaulon lividum* is a much more common plant in northern New England than present collections indicate."

A. R. Hodgdon (1974) found the species in South Bay Bog, Pittsburg, N.H., at an elevation of about 1700 ft. He suggests that botanists have overlooked *Geocaulon lividum* at intermediate elevations in northern New England such as the Pittsburg station.

In 1976 C. S. Richards (pers. comm.) reported another coastal station from Washington County, Maine.

OBSERVATIONS IN THE MAHOOSUCS

In 1975 I encountered the species in a study site on Mahoosuc Arm (elev. — 3777 ft.), Oxford County, Maine. After learning to distinguish it from *Vaccinium angustifolium* varieties and *V. uliginosum* var. *alpinium,* I found the plant on peaks and forests throughout the Mahoosuc Range at elevations between 2500 ft. and 3800 ft. I found 40 stations between Mt. Success, Coos County, New Hampshire, and Old Speck, Oxford County, Maine, excluding Goose Eye, which was the subject of Harris' observations. I ceased enumerating the stations at 40, satisfied that *Geocaulon lividum* had a general distribution within the Mahoosuc Range. Like Harris (1965), I found the plant both on the "boggy summits," which Pease (1964) states as the local habitat and on moist forest sites. New boggy summit stations include Mahoosuc Arm summit area (13), Old Speck west arm (1), Mt. Carlo (2), and Mt. Success (9). Moist forest stations along the Mahoosuc Trail occur on Old Speck's southwest ridge (4), near May Cut-Off on Mahoosuc Arm (4), along the north slope of Mt. Success (5), and just south of Success summit (1).

On the summits of the Mahoosuc Range *Geocaulon lividum* occurs in all the plant associations delineated by Fahey (1976) and Marchand (1977), although it went undetected in these studies. In forests it occurs most commonly along trailsides with *Cornus canadensis, Maianthemum canadense, Clintonia borealis,* and *Coptis groenlandica* or with a slightly more ericaceous association of *Vaccinium angustifolium, V. myrtilloides,* and *Gaultheria hispidula* upon an extensive moss carpet often including the less common *Thuidium* spp. The forest canopy is most often fir but white birch, red spruce, and mountain ash are sometimes found.

Moss (1926) describes dwarfed individuals of *Geocaulon lividum* from Banff, Alberta. A particular underground stem bore normal shoots or abnormal only. This appears to be the case with Mahoosuc individuals as well.

CONCLUSIONS

Geocaulon lividum is not a rare plant in the Mahoosuc Range and it seems likely that this is true of northern New England as a region. Stations enumerated from the Range more than triple the recorded stations from New England. The distribution and physiological ecology of this semi-parasite are worthy of further study.

Voucher specimens are on deposit at the Hodgdon Herbarium, University of New Hampshire.

LITERATURE CITED

FAHEY, T. J. 1976. The vegetation of a heath bald in Maine. Bulletin of the Torrey Botany Club. **103:** 23 29.

GLEASON, H. A. 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Canada. 3 vols. Hafner Publ. Co., New York.

HARRIS, S. K. 1965. *Geocaulon lividum* in New England. Rhodora **67:** 407 409.

Hodgdon, A. R. 1974. *Carex exillis, Geocaulon lividum* and other plants of interest in Pittsburg, New Hampshire. Rhodora **76:** 307–309.

Marchand, P. J. 1977. Subalpine bogs of the Mahoosuc Range, Maine: Physical Characteristics and Vegetation Development. Center for Northern Studies **#11,** Wolcott, Vt.

Moss, E. H. 1926. Parasitism in the genus *Commandra.* New Phytologist **25:** 264–276.

Pease, A. S. 1964. A Flora of Northern New Hampshire. New England Botanical Club, Cambridge, Ma.

RESEARCH DEPARTMENT
APPALACHIAN MOUNTAIN CLUB
GORHAM, N.H. 03581

DROSERA LINEARIS GOLDIE REDISCOVERED IN CRYSTAL BOG, CRYSTAL, MAINE

S. C. ROONEY, C. S. MCKELLAR, AND F. GAFFNEY

Crystal Bog (alt. 480 feet) in Crystal, Aroostook County, Maine, has long been recognized as the site of many unique and rare plants. Fortunately, most of the area now belongs to the Maine chapter of The Nature Conservancy.

There are seven herbarium specimens of *Drosera linearis* from Maine — all from Crystal Bog — as recorded by Eastman (1978). The most recent of these is a specimen collected in 1935 by C. D. Chamberlain and R. E. Delano.

On June 30, 1978, two groups of *Drosera linearis* were found growing in the wettest depressions in the bog, in association with *D. rotundifolia* and *D. intermedia*. Each group consisted of a little more than 100 plants. One plant was collected for verification and 35 mm slides were taken of the one specimen seen in flower. The collected specimen will be deposited in the herbarium of the University of Maine.

The Crystal Bog Stewardship Committee gratefully acknowledges the assistance of Mr. Les Eastman with our ongoing inventory of the plants of the bog.

LITERATURE CITED

EASTMAN, L. M. 1978. "Rare vascular Maine plants, a compilation of herbarium and literature citations", Maine Critical Areas Program Report.

SCR
HOULTON, MAINE

CSMcK
SHERMAN MILLS, MAINE

FG
SYRACUSE, NEW YORK

Preliminary Announcement

THIRTEENTH INTERNATIONAL BOTANICAL CONGRESS

Sydney, Australia 21–28th August, 1981

The Programme will consist of 12 sections — molecular, metabolic, cellular and structural, developmental, environmental, community, genetic, systematic and evolutionary, fungal, aquatic, historical, and applied botany. There will be plenary sessions, symposia, and sessions for submitted contributions (papers and posters). Chairman of the Programme Committee: Dr. L. T. Evans.

Field Trips will include visits to arid and semi-arid regions, eucalypt forest, rain forest, heath, coastal vegetation (e.g. Great Barrier Reef, mangroves) etc., and specialist trips. Chairman of the Field Trips Committee: Prof. L. D. Pryor.

First Circular, containing details, will be mailed in August, 1979. Send your name and full address, preferably on a postcard, to ensure your inclusion on the mailing list.

Enquiries should be sent to the Executive Secretary, Dr. W. J. Cram.

Congress Address: 13th I.B.C., University of Sydney, N.S.W. 2006, Australia.

Sponsored by the Australian Academy of Science

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Manuscripts should be submitted in **duplicate** and **must** be **double-spaced** or preferably triple-spaced (at least ⅜ of an inch) **throughout,** including foot-notes, figure legends, and references. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly, as they are often not necessary. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens, except that the names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distributions. Systematic revisions and similar papers should be prepared in the format of "The Systematics and Ecology of Poison-Ivy and the Poison-Oaks", W. T. Gillis, Rhodora 73: 161–237, 370–443. 1971, particularly with reference to indentation of keys and synonyms. Papers of a floristic nature should follow, as far as possible, the format of "Contribution to the Fungus Flora of Northeastern North America. V., H. E. Bigelow & M. E. Barr, Rhodora 71: 177–203. 1969. For bibliographic citations, please refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides a complete set of standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the CBE Style Manual, 3rd ed. (original title: Style Manual for Biological Journals). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches and be sure that your illustrations are proportioned to reduce correctly. (Some "turn-page" figures with brief legends will be 3½ × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size.

Vol. 80, No. 824, including pages 453–612, was issued Oct. 27, 1978

RHODORA INDICES

Volumes 1-50 (1899-1948)

$10.00 per copy

This index consists of 415 double column pages arranged in two parts. Part I is an Index to Plant Names in the 50 volumes. Part II is an Index to Authors and Titles. Bound in paper wrapper.

Volumes 51-75 (1949-1973)

$20.00 per copy

This index consists of 287 double column pages arranged in two parts. Part I is an Index to Taxa Cited in the 25 volumes. Part II is an Index to Authors and Titles. Bound in paper wrapper.

Remittance should be made payable, in United States funds, to RHODORA. Please direct all orders to:

RHODORA
Botanical Museum
Oxford Street
Cambridge
Massachusetts 02138

RHODORA **January, 1979** **Vol. 81, No. 825**

CONTENTS

ANNOUNCING A SYMPOSIUM

"RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND"

4, 5 May 1979
at Harvard University

Biology of Endangered Species

Plant Conservation Concerns in New England

Conserving Rare Plants and Their Habitats

Further information, contact:
Dr. Garrett E. Crow
Dept. of Botany and Plant Pathology
University of New Hampshire
Durham, New Hampshire 03824
Organized by the
New England Botanical Club

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 81 April, 1979 No. 826

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Conducted and published for the Club, by
ROLLA M. TRYON, Editor-in-Chief

RHODORA. — A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes, and single copies are available. For information and prices write RHODORA at address given below.

Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes, relating to the plants of North America, and floristically related areas, will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. All manuscripts should be submitted in duplicate, and must be double- (at least ⅜ of an inch) or triple-spaced throughout. Please conform to the style of recent issues of the journal. Extracted reprints, if ordered in advance, will be furnished at cost.

Address manuscripts and proofs to:
Russell R. Walton
Managing Editor, RHODORA
Harvard University Herbaria Building
22 Divinity Avenue
Cambridge, Mass. 02138

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Scirpus Longii Fernald

In New England, this rare species grows in a few marshes and wet meadows in central Connecticut and eastern Massachusetts.

Original artwork by Frances S. Chew

Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 81 April, 1979 No. 826

THE SYSTEMATICS OF THE AMERICAN SPECIES OF ALNUS (BETULACEAE)[1]

JOHN J. FURLOW

TAXONOMIC TREATMENT — CONTINUED

5. **Alnus jorullensis** Humboldt, Bonpland, & Kunth

Alnus jorullensis Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. 2: 20. 1817.

Spreading trees up to 20 m in height; trunk usually single, up to 1.8 m in diameter, the branches sometimes massive; bark gray to dark brown, smooth to corky, often broken by deep transverse constrictions which encircle the stem, the lenticels inconspicuous on smooth branches; young stems light to medium brown or dark red-brown, dull to slightly lustrous, not glaucous to heavily glaucous, without conspicuous resin-coating, not differentiated into long and short shoots, usually without conspicuous longitudinal ridges originating at the nodes; internodes glabrous, sparsely pubescent, or velutinous, moderately to densely glandular; nodes and branchlets bearing inflorescences very densely glandular; hairs yellowish to brown; glands medium to large, yellow to brown. Lenticels of twigs circular to elliptic, 0.5–1.5 mm long, 0.3–0.7 mm wide, whitish to yellowish or brownish, moderately prominent; leaf scars 1–2 mm high, 1.5–2.7 mm wide, with inconspicuous bundle scars. Buds ellipsoid, slightly rounded to rounded at the apex, moderately to heavily resin-coated; stalk 1–3 mm long, 1–2 mm in diameter, sparsely pubescent to moderately villous, densely glandular; body 2–7 mm long, 1.5–3 mm in diameter; scales 2, stipular, equal, valvate, glabrous to moderately pubescent, glandular; pubescence

---

[1] This continues and completes the article started in the January issue, Volume 81 (825), pp. 1–121.

and glands obscured by the resin coating. Leaves narrowly elliptic, elliptic, elliptic-oblong, oblong, or obovate (rarely ovate); apex acute, obtuse, or rounded; base attenuate, acute, or narrowly cuneate; blade (4–) 5–16 (–20) cm long, (2–) 3–7 (–9) cm wide, dark to very dark green and dull to very lustrous above, light to medium green, brown, or yellow-brown and dull below; coriaceous; margin flat to moderately revolute, unthickened, double-serrate or sinuate to shallow-lobed and serrate or serrulate, up to 50% entire from the base; major teeth or lobes (7–) 9–17 (–22) mm apart at mid-leaf, up to 3 mm deep, irregular; secondary teeth (1–) 3–5 (–8) per cm, 0.1–1.2 mm deep, irregular; adaxial surface glabrous to sparsely pubescent, moderately to densely glandular; abaxial surface and veinlets glabrous to sparsely pubescent or moderately villous, moderately to very densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base glabrous to tomentose; pubescence yellowish to brownish; glands small to large, bright or pale yellow to brown. Lateral veins 7–17, (4–) 5–8 (–14) mm apart at mid-leaf, slightly to strongly ascending, sometimes branching once again, especially near the base, terminating in major teeth at the margin; cross veins between lateral veins poorly to well developed. Petioles (2–) 6–12 (–23) mm long, 1–1.5 (–3) mm in diameter, glabrous to sparsely pubescent, moderately to densely glandular. Stipules ovate to elliptic, the apex acute, ca. 5 mm long, ca. 1.5 mm wide, green to light brown, moderately villous to velutinous, the hairs yellowish, moderately glandular, the glands yellowish. Pistillate inflorescences borne in racemose groups of 3–5 on short non-divergent to strongly diverging branchlets, these generally subtended by leaves, produced during the previous growing season, erect, ovate to elliptic, at anthesis 2–3 (–4) mm long, ca. 2 mm in diameter, on peduncles 0.2–4 mm long, 1–1.5 mm in diameter; staminate catkins borne in one or more racemose clusters of (2–) 3–5 at the end of the main branch above the pistillate inflorescences, the lowermost usually subtended by small leaves, produced during the previous growing season, pendent before and during anthesis, at anthesis (3–) 3.5–11 cm long, 3–9 mm in diameter, on peduncles 1–7 mm long, 0.8–1.5 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these ovate, elliptic, or obovate, the apex acute to rounded, 1.3–1.5 mm long, 0.4–1.1 mm wide, the margin lined with minute to moderately large glands;

stamens 4, opposite and free of or basally adnate to the perianth parts, appearing equal to or longer than the perianth, the filaments 1.2–1.4 mm long, the anthers 1.1–1.6 mm long and 1.1–2 mm in diameter, the thecae separate for 35–65% of their length. Infructescences ovoid to ellipsoid, (11–) 13–25 (–29) mm long, (8–) 9–15 mm in diameter, on peduncles 0.2–5 mm long, 1.5–2 mm in diameter; scales 3.5–5 mm long, 3.5–5.5 mm wide at the apex, 1–1.8 mm wide at the base, the apex moderately to greatly thickened and flat, the terminal lobe-tip truncate and not extended to somewhat extended. Fruits narrowly winged or merely wing-margined, dark brown; bodies elliptic to obovate, 1.7–3.5 mm long, 1.2–3 mm in diameter; wings 1.5–3.5 mm long, 0.2–1 mm wide, firm; persistent styles 0.7–1.2 mm long.

Alnus jorullensis is more morphologically specialized than is *A. acuminata* and occurs in somewhat less mesic habitats. The leaves are often laterally expanded at the apex and narrowed near the base, the veins rising more abruptly near the tip than in most other species. The teeth at the apex are usually larger than those at mid-leaf, and the lower margin may appear entire for a considerable distance above the base. The tree is scrubby in appearance, although it becomes quite large and bears massive spreading limbs.

This species is closely related to *Alnus acuminata,* from which it was most likely derived. It shares with it such unique characteristics as the deep transverse constrictions in its bark and well-developed abaxial leaf glands. It is more specialized, however, in leaf shape, density of the glands, and habitat, and it is quite distinct as a species.

The name "*Alnus jorullensis*" is frequently misapplied to various Latin American alders. In recent years the concept of this species has become somewhat less confused, but it is still difficult to distinguish *A. jorullensis* from the other taxa using current keys. Standley (1920), in his key to the species of Mexico, separates *A. jorullensis* from all the other species in the first couplet, stating that its leaves are "densely covered beneath with yellow wax glands" while the other species have "leaves without glands beneath or the glands remote and inconspicuous." As explained above, this second lead really fits none of the Latin American taxa, even though the former may be applied to ssp. *lutea* of *A. jorullensis.*

In comparison with the usually ovate form of *A. acuminata,* the type of *Alnus jorullensis* (Figure 41) demonstrates the distinctively

Figure 41. Holotype of *Alnus jorullensis* Humboldt, Bonpland, & Kunth (photograph courtesy of John H. Beaman).

elliptic to obovate leaves of the species. Other characters of diagnostic value include the ascending lateral veins of the leaves, the scrubby habit of the trees, and (in ssp. *lutea*) the heavy accumulation of large, bright-yellow glands on the abaxial leaf surfaces.

In the current literature, *Alnus jorullensis* is usually seen as the densely glandular-leafed alder discussed above. Humboldt and Bonpland's specimen does not represent this glandular form, however, instead corresponding closely to Fernald's *A. firmifolia,* which is described by its author as "resembling large-leaved *A. jorullensis* HBK., but quite lacking the close covering of waxy or granular atoms which characterize the lower leaf-surface of that species." The types of both *A. jorullensis* and *A. firmifolia* have glands on the lower leaf surface, but these are relatively small, dark, and widely spaced.

Two forms of *Alnus jorullensis* do, in fact, exist. One of these has leaves bearing densely-arranged yellow glands on the lower surface, while the other has foliage as that described above. Individuals of the sparsely glandular form bear more irregularly and obovately shaped leaves which are usually more coarsely toothed, especially near the apex. The glandular form (ssp. *lutea*) occurs in relatively warmer habitats than any of the other Mexican taxa of *Alnus,* in the pine-oak zone, at elevations generally below 2,500 meters (described by Goldman, 1951, as the "arid lower tropical subzone"). The sparsely glandular form (ssp. *jorullensis*) is found at higher elevations in similar (though necessarily somewhat cooler and moister) habitats. Where the two occur together (usually at intermediate elevations), they interbreed freely, producing a wide variety of intermediate individuals. Both types occur throughout central and southern Mexico, but only ssp. *jorullensis* reaches south as far as Guatemala.

5.a **Alnus jorullensis** Humboldt, Bonpland, & Kunth ssp. **jorullensis**

Alnus jorullensis Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. **2:** 20. 1817; *Alnus acuminata δ jorullensis* (Humboldt, Bonpland, & Kunth) Regel, Mem. Soc. Nat. Mosc. **13**(2): 149. 1861; *Alnus jorullensis α typica* Regel, Bull. Soc. Nat. Mosc. **38**(3): 425. 1865. Type: *Humboldt & Bonpland s.n.,* "crescit in aridis, arenosis montis ignivomi Mexicani, Volcan de Jorullo, altit. 630 hex." (Holotype, P; photograph of type, MSC!). Figure 41.

Alnus firmifolia Fernald, Proc. Amer. Acad. **43:** 61. 1907. Type: *Pringle 10040,* "Federal District, mountains about Cima Station, alt. 9800 ft., 30, August, 1905" (Holotype, GH!; Isotypes, DAO!, F!, MICH!, MSC!, NY!, PH!, UC!, US!, WIS!). Figure 42.

Figure 42. Holotype of *Alnus firmifolia* Fernald (= *Alnus jorullensis* Humboldt, Bonpland, & Kunth ssp. *jorullensis*).

Spreading trees up to 20 m in height; trunk up to 1.8 m in diameter; bark brown, smooth to corky; young stems light to dark red-brown, rarely glaucous; internodes mostly glabrous (occasionally sparsely pubescent), moderately glandular; nodes and stems bearing inflorescences densely glandular; glands small, brown to dark brown. Lenticels of twigs circular to elongate, 0.5–1 mm long, yellowish to brownish, somewhat prominent; leaf scars 1–1.8 mm high, 1.7–3.5 mm wide. Buds ellipsoid; stalk 1–2 mm long, 0.7–2 mm in diameter, more or less glabrous; body 3–4 mm long, 1.5–3 mm in diameter; scales glabrous. Leaves elliptic, elliptic-oblong, or obovate (rarely ovate), the apex usually obtuse or rounded (but occasionally acute), the base acute to broadly cuneate; blade (3.5–) 4.5–11 (–13) cm long, (2.5–) 3.5–5.5 (–7) cm wide, medium to dark green or brown below; margin flat, double-serrate, serrate, or serrulate, up to 25% entire from the base; major teeth (7–) 10–17 mm apart, up to 3 mm deep, very irregular; secondary teeth (3–) 5–8 per cm, 0.2–1.1 mm deep, slightly uneven to irregular; adaxial surface and veinlets moderately to rather densely glandular; leaf pubescence yellowish to brownish; leaf glands small to medium in size, yellowish, brownish, or dark brown. Lateral veins 7–10 (–15), (4–) 6–10 (–11) mm apart at mid-leaf, slightly to moderately ascending, sometimes branching once again near the base; cross veins between lateral veins usually well-developed. Petioles (4–) 10–15 (–18) mm long, 1–1.5 (–2) mm in diameter, glabrous or sparsely pubescent, moderately to densely glandular. Pistillate inflorescences borne on branchlets diverging strongly from the main axis, at anthesis ca. 4 mm long, ca. 2.5 mm in diameter, on peduncles 0.2–1.5 mm long, ca. 1 mm in diameter; staminate catkins borne in clusters of 2–4, at anthesis (3–) 5–6.5 cm long, 7–8 mm in diameter, on peduncles 3–5 mm long, 1–1.5 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers with 4 perianth parts, these elliptic to obovate, acute at the apex, 1.2–1.5 mm long, 0.4–0.8 mm wide, the margin lined with small to moderately large glands; stamens basally adnate to the perianth parts, appearing equal to or longer than the perianth, the filaments 0.6–0.9 mm long, the anthers 1.2–1.6 mm long, 1.3–1.7 mm in diameter, the thecae separate for 40–65% of their length. Infructescences 11–28 mm long, 8–13 mm in diameter, on peduncles 0.2–5 mm long, 1.5–2 mm in diameter; scales 3.5–5 mm long, 3.5–5 mm wide at the apex, 1–1.7 mm wide at the base, the apex moderately thickened and flat, the terminal lobe-tip truncate to rounded and not extended to somewhat extended. Fruits narrowly wing-margined, dark brown; body 1.7 2.2 mm long, 1.2–1.7 mm in diameter; wings 1.5-2.5 mm long, 0.2–0.7 mm wide, firm; persistent styles 0.7–1 mm long. Figures 3B, 4C, 14B, 17B, 19F, and 42.

DISTRIBUTION AND HABITAT: Central Durango south and east to Jalisco, northern Michoacán, Mexico, and central Veracruz; central Oaxaca; southeastern Guatemala. Along rocky streams, intermittent streams, and slopes near streams or arroyos from elevations of 2,800 to 3,800 meters (occasionally as low as 2,200 meters). Usually associated with *Pinus, Quercus,* or *Abies* in open woodland associations. Figure 43.

COMMON NAMES: Aile, aliso.

REPRESENTATIVE SPECIMENS: **Guatemala.** Sierra de los Cuchumatanes, about 28 mi from Huehuetenango, *Hawkes et al. 1746* (F); cumbre de la Sierra de los Cuchumatanes, *Standley 81150* (F); vicinity of Tojquia, *Steyermark 50128* (F); summit of Sierra de los Cuchumatanes, *Steyermark 50148* (F). **Mexico.** CHIAPAS. Paraje of Matsab, Mun. of Tenejapa, *Ton 1961* (NY). DISTRITO FEDERAL. Mountains about Cima Station, *Pringle 10040* (DAO, F, MICH, MSC, NY, UC, US, WIS); parte occidental del Pedregal de San Angel cerca del Río Eslava, *Rzedowski 2239* (ENCB). DURANGO. North slopes of Cerro Huehueto (Huehuento) S of Huachicheles, about 75 mi W of Cd. Durango, *Maysilles 7994* (MICH, NY). GUERRERO. Teotepec, Distr. Mina, *Hinton 14794* (MICH, NY). HIDALGO. Cerca de Tezuantla, *Espinosa 402* (ENCB); 2 km al E de El Guajolote, *Rzedowski 27417* (ENCB). JALISCO. Northeastern slopes of the Nevado de Colima, *McVaugh 12845* (MICH); La Joya, en la ladera E del Nevado de Colima, *Rzedowski 19361* (ENCB, MEXU). MÉXICO. Paraje Provincial, Mount Popocatépetl, *Balls B4168* (UC); 19 km E of Amecameca along the road to Popocatépetl, *Furlow 320* (MSC); Cerro Papayo, Río Frío, *Matuda 28227* (MEXU); on Nevado de Toluca, *Rose & Painter 7884* (US); Netzcualango, vertiente NW del Ixtaccíhuatl, *Rzedowski 21616* (ENCB, MSC). MICHOACÁN. Cerro Burro, 11.2 km S. of Opopeo, *Furlow 326* (MSC); ca. 18 mi S of Pátzcuaro, *King & Soderstrom 5218* (MEXU, MICH, NY, UC). MORELOS. Yautepec, *Gomez Murga 87* (ENCB); between Huitzilac and Tres Cumbres, *Hatheway 1184* (MO); Tres Marias Mts., *Pringle 15039* (F, DAO, MO, MSC, UC); Lagunas de Zempoala, *Straw & Gregory 1060* (MEXU, MICH). OAXACA. Mountains N of Ixlán de Juárez, lumber road along ridges of sierra, departing highway 13.5 mi N of Ixtlán, *Anderson & Anderson 5413* (ENCB, MICH); vicinity of Cerro Zempoaltepetl, *Hallberg 894* (MICH); vicinity of Cerro Zempoaltepetl, *Hallberg 909* (MICH); Sierra de San Felipe, *Pringle 10248* (DAO, ENCB, MICH, MSC, UC). PUEBLA. La Cumbre, Zacapoaxtla, *Vela G. 1087* (ENCB). VERACRUZ. P. Orizaba, *Miranda 319* (MEXU); 9 mi E of Perote, *Spetzman 1412* (MEXU).

The original specimen of *Alnus jorullensis* was reported by Humboldt, Bonpland, and Kunth (1817) to have been collected on Volcán de Jorullo, Michoacán. This locality does not seem a likely

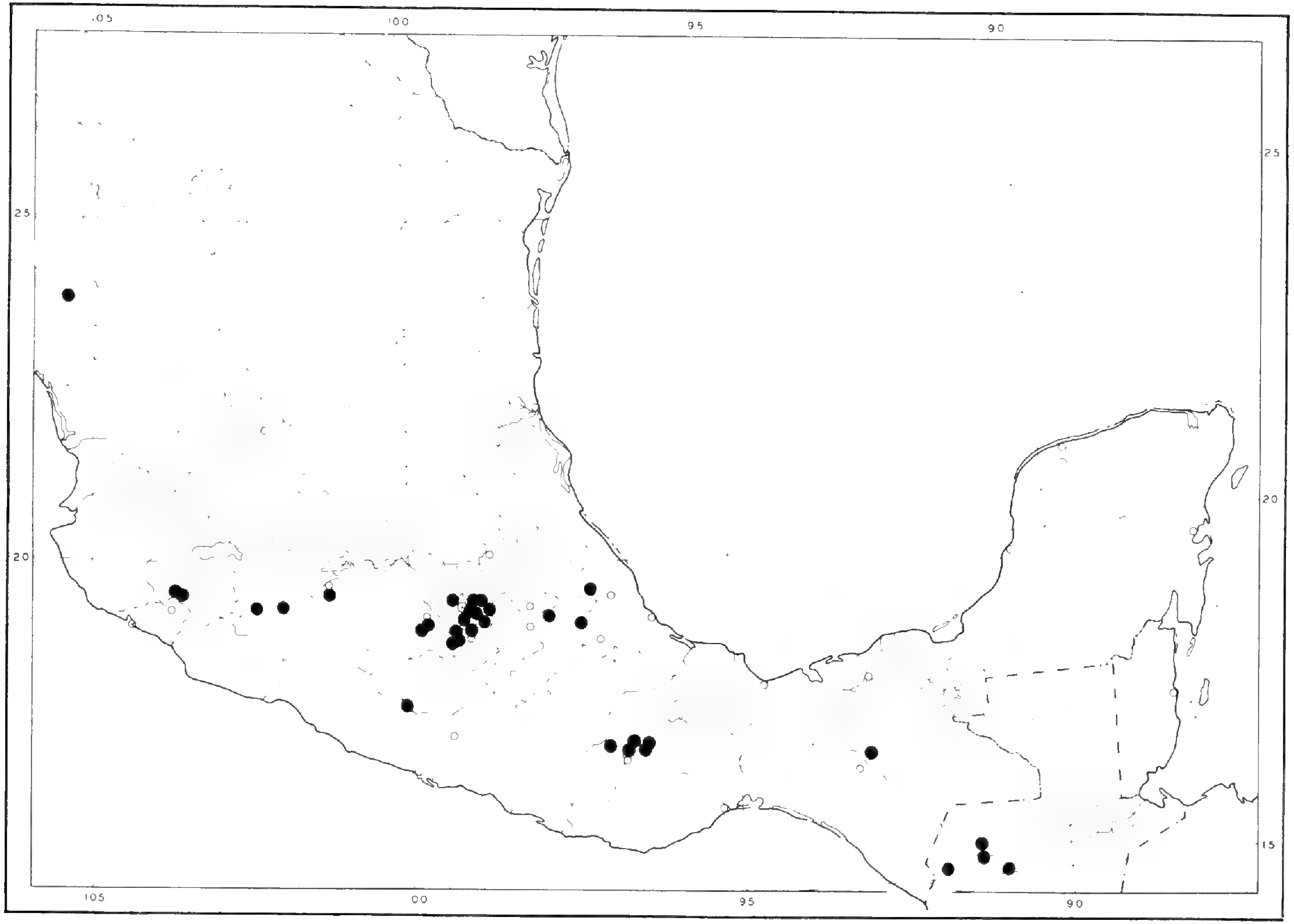


Figure 43. Distribution of *Alnus jorullensis* Humboldt, Bonpland, & Kunth ssp. *jorullensis*.

habitat for *Alnus,* however, having a maximum elevation of only 630 meters, a semi-arid climate, and vegetation including such plants as acacias and palms. On a trip to the site in 1971, I was unable to locate any alders, though I collected *A. jorullensis* (ssp. *lutea*) at nearby Pátzcuaro, in a forest of *Pinus* at an elevation of about 2,000 meters. Subspecies *jorullensis* is a frequent tree at several of the other sites visited by Humboldt and Bonpland in central Mexico (e.g., Nevado de Toluca), and it seems likely that the type actually came from one of those places.

Alnus jorullensis ssp. *jorullensis* is easily distinguished from the other Latin American taxa of *Alnus* by its large mature size and scrubby habit, and by its leathery obovate to elliptical leaves bearing small pale-yellowish to brown (often inconspicuous) glands on the lower surface. The leaves, when dry, are usually very dark green above and rather dark brown or dark greenish brown below. This taxon occurs as far south as Guatemala, though material was seen from only a single region of that country. It is the common alder of high elevations in its range, occurring at altitudes greater than those of any of the other taxa.

5b. **Alnus jorullensis** ssp. **lutea** Furlow

Alnus jorullensis ssp. *lutea* Furlow, Ann. Mo. Bot. Gard. **63:** 381. 1977. TYPE: *Furlow 330,* Michoacán: 8 kilometers north of Uruapan along the roadside; elevation 2,000 meters. Tree, 5 meters high; trunk 15 cm in diameter; bark smooth with transverse constrictions. Occasional. November 28, 1971 (HOLOTYPE, MSC!). Figure 44.

Alnus jorullensis var. *exigua* Fernald, Proc. Amer. Acad. **40:** 27. 1904. TYPE: *A. Dugés s.n.,* Guanajuato and vicinity, without date (reported in the protologue as from "mtns. of Santa Rosa, April 1901") (HOLOTYPE, GH!).

Spreading trees up to 15 (–20) m in height; trunk up to ca. 0.6 m in diameter; bark gray-brown to dark brown, usually corky; young stems medium brown to dark red-brown, not glaucous to heavily glaucous; internodes glabrous, sparsely pubescent, or velutinous, moderately to densely glandular; nodes and stems bearing inflorescences very densely glandular; hairs yellowish to brownish; glands medium to large in size, yellowish to brownish. Lenticels of twigs circular to elliptic, 0.5–1.5 mm long, whitish to yellowish, moderately prominent; leaf scars 1–2 mm high, 1.5–2.7 mm wide. Buds with stalks 1–3 mm long, 1–2 mm in diameter, sparsely pubescent to moderately villous; bodies 2–7 mm long, 1.5–3 mm in diameter; scales sparsely to moderately pubescent, densely glandular. Leaves narrowly elliptic, oblong, or obovate (rarely ovate); apex acute, obtuse, or rounded; base attenuate, acute, or cuneate; blade (4–) 5–15 (–20) cm long, (2–) 3–7 (8.5) cm wide, light to medium brown or yellow-brown below; margin flat to moderately revolute, double-serrate or sinuate to shallow-lobed and serrate or serrulate, up to 50% entire from the base; major teeth or lobes 9–17 (–22) mm apart, up to 1.5 mm deep, irregular; secondary teeth (1–) 3–5 per cm, 0.1–0.5 mm deep, irregular; adaxial surface glabrous to sparsely pubescent; abaxial surface and veinlets glabrous to sparsely pubescent, densely to very densely glandular; pubescence yellowish to brownish; glands medium to large in size, crowded, bright yellow (occasionally brownish or pale yellow). Lateral veins 8–10, (4–) 5–8 (–14) mm apart at mid-leaf, moderately to strongly ascending, sometimes branching once again near the base; cross veins between lateral veins usually poorly developed. Petioles (2–) 6–12 (–23) mm long, 1–1.5 (–3) mm in diameter, glabrous to sparsely pubescent, moderately to densely glandular. Pistillate inflorescences borne on non-diverging branches, at anthesis 2–3 mm long, ca. 2 mm in diameter, on peduncles 0.2–4 mm long, 1.2–1.5 mm in diameter; staminate catkins borne in clusters of 3–5, at anthesis 3.5–11 cm long, 3–9 mm in diameter, on peduncles 1–7 mm long, 0.8–1.5 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers with 4 perianth parts, these usually obovate, rounded at the apex, 1.2–1.4 mm long, 0.6–0.9 mm wide, the margin lined with very minute glands; stamens free or basally adnate to the perianth parts, usually appearing longer than the perianth, the filaments 1.2–1.5 mm long, the anthers 1.1–1.6 mm long and 1.1–2 mm in diameter, the thecae separate for 35–45% of their length. Infructescences (11–) 13–25 mm long, 9–15 mm in diameter, on peduncles 0.2–2 mm long, 1.5–1.8 mm in diameter; scales 4.5–5 mm long, 4.5–5.5 mm wide at the apex, 1.5–1.7 mm wide at the base, the apex moderately to greatly thickened, the terminal lobe-tip truncate and not extended. Fruits narrowly winged or merely wing-margined; bodies 2.5–3.5 mm long, 1.7–2 mm in diameter; wings 3–3.5 mm long, 0.5–1 mm wide, firm; persistent styles 1–1.3 mm long. Figures 5F, 6A, 14C, 15E, 17C, 19G, 20C, and 44.

Figure 44. Holotype of *Alnus jorullensis* ssp. *lutea* Furlow.

DISTRIBUTION AND HABITAT: Central Sinaloa and Durango south and east to southern Jalisco, Michoacán, México, and central Veracruz; central Oaxaca. Rocky streambanks, intermittent streams, and moist to moderately dry slopes from elevations of about 1,000 to 2,500 (rarely to 3,000) meters. Usually associated with *Pinus, Quercus,* or *Abies.* Figure 45.

COMMON NAMES: Aile, aliso.

REPRESENTATIVE SPECIMENS: **Mexico.** DISTRITO FEDERAL. Bosque de Santa Rosa, *Matuda 20970* (MEXU); Pedregal de San Angel, *Rzedowski 514* (ENCB). DURANGO. Perfil de la Sierra Madre Occidental a lo largo de la carretera Durango-Mazatlán, *Martin et al. 315* (ENCB); from El Salto S along lumber road toward Pueblo Nuevo (about 60 air mi SW of Cd. Durango, *Maysilles 7807* (MICH); Laguna del Progreso, 34 road mi N of railroad at Coyotes, *Maysilles 8333* (NY). GUANAJUATO. Guanajuato and vicinity, *A. Dugés s.n.,* without date; 30 km al E de San Luís de Paz, *Rzedowski 9082* (ENCB). GUERRERO. Cerro Azul, Distr. Mina, *Hinton 14943* (NY, WTU); Petlacala, Distr. Mina, *Hinton 15406* (MICH, NY, UC, WTU). HIDALGO. San Vincinte, *Fisher s.n.,* Aug. 16, 1937 (F, NY, RM); Jacala, *Kenoyer 641* (MO); Omitlan-Huasca, *Miranda 4472* (MEXU); hills, Cuyamaloya, 8000 ft, *Pringle 10288* (F, MEXU, MSC, MO, NY, UC); ca. 3 mi S of Tepiji del Río, *Straw & Gregory 1166* (MEXU, MICH, UC). JALISCO. Nevado de Colima above the sawmill called Piedra Ancha and just E of the first great cañon W of the sawmill site, *McVaugh 11673* (MEXU, MICH); Real Alto, trail to Poso Hedionda, *Mexia 1717* (F, MICH, MO, NY, UC); camino de Atenquique al Nevado de Colima, *Rzedowski 19395* (ENCB, MEXU, MSC). MÉXICO. Pantoja, Distr. Temascaltepec, *Hinton 3545* (NY); Ixtaccíhuatl, *Purpus 1792* (F, NY, UC). MICHOACÁN. 13 km W of Pátzcuaro on a dry hillside with pines and oaks, *Furlow 328* (MSC); 8 km N of Uruapan along the roadside, *Furlow 330* (MSC); steep mountainside NW of Aquililla, ca. 5–7 km S of Aserradero Dos Aguas, *McVaugh 22683* (ENCB, MICH). MORELOS. 2½ mi S of Tres Cumbres on old hwy 95 to Cuernavaca, *Gibson 1035* (MEXU); 1 km al N de Cuajumulco, *Palacios Ch. s.n.,* Feb. 15, 1965 (ENCB, MSC). OAXACA. Cerro San Felipe, *Conzatti 4074* (MEXU); Loma del encino, El Carrizal, Yolox, *May Nah 788* (ENCB, MEXU); summit ridge, Sierra de San Felipe, 7000 ft, *Pringle 10249* (DAO, ENCB, MICH, MSC, UC). PUEBLA. 38 km W of the city of Orizaba on a steep hillside with pines, *Furlow 339* (MSC); Mt. Orizaba, *Purpus 3003* (NY, UC); ca. 4.5 km E Río Frío, Mun. Tlahuapan, *Weber 802* (ENCB). SINALOA. 7 mi W of Santa Rita along a side road E of the Los Hornos to Surutato road, *Breedlove 16518* (MICH); along road to Surutato, 3 mi SE of Los Ornos, *Breedlove & Thorne 18614* (MICH); El Batel, 70 km NE of Mazatlán, *Pitekla 293* (UC). ZACATECAS. Sheltered east-facing valley, steep mountainsides near summits ca. 20 km westward toward Tlaltenango from the road junction S of Jalpa, *McVaugh 25638* (MICH).

Alnus jorullensis ssp. *lutea* is readily distinguishable from all the other American taxa of the genus by the profusion of moderately to very bright yellow glands covering the lower leaf surfaces. These glands produce in the leaves a peculiar yellowish brown or yellowish

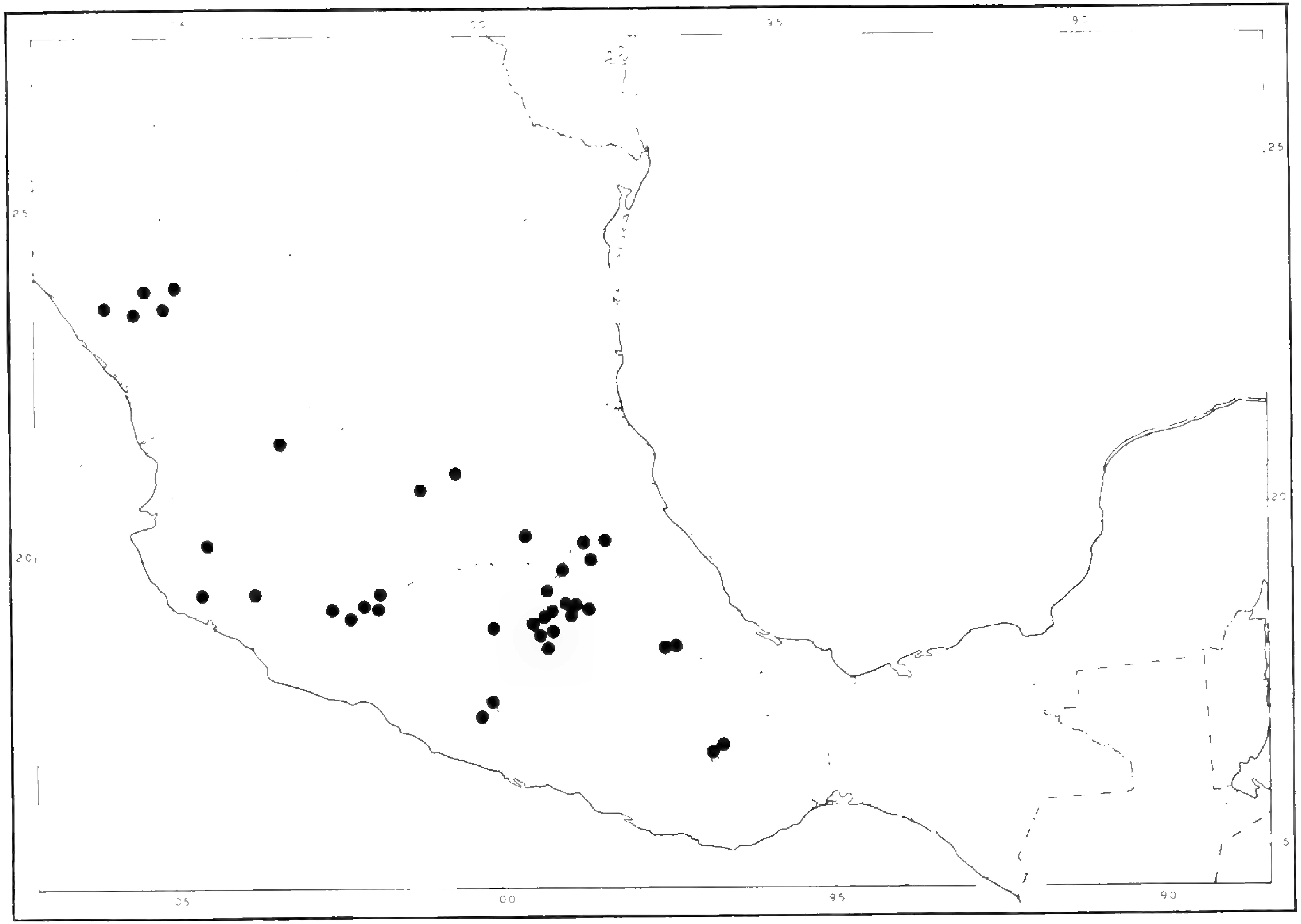


Figure 45. Distribution of *Alnus jorullensis* ssp. *lutea* Furlow.

green-brown color when viewed without magnification. The subspecies has therefore been given the epithet *"lutea"* in reference to this characteristic. Other diagnostic features, as already mentioned, include leaves which are narrower and more ovate in shape, bear more sharply-pointed apices, and have less coarsely-toothed margins than those of ssp. *jorullensis.*

This and the previous subspecies represent ecotypes, *Alnus jorullensis* ssp. *jorullensis* occurring at generally higher and ssp. *lutea* occurring at generally lower elevations throughout much of mountainous southern Mexico. Subspecies *lutea* does not reach Central America as does ssp. *jorullensis.*

6. **Alnus incana** (Linnaeus) Moench

Alnus incana (Linnaeus) Moench, Meth. Pl. p. 424. 1794; *Betula alnus* Linnaeus, Sp. Pl. **2:** 983. 1754, in part; *Betula alnus β incana* Linnaeus, Sp. Pl. **2:** 983. 1754; *Betula incana* (Linnaeus) Linnaeus f., Suppl. Pl. p. 417. 1781.

Trees or shrubs up to 25 m in height; trunks up to 3.5 dm in diameter, erect or ascending, bark light to dark gray, reddish, or purplish-brown, smooth or broken into plates (on old individuals); young stems light to dark red-brown, dull to slightly lustrous, slightly to heavily glaucous, usually without conspicuous resinous coating, not differentiated into long and short shoots, without longitudinal ridges originating at the nodes; internodes sparsely pubescent to velutinous or tomentose, moderately to densely glandular; nodes and stems bearing inflorescences very densely glandular; hairs yellowish to brownish to dark brown; glands small to medium in size, pale yellowish to brown; lenticels of twigs circular to elliptic, 0.2–1.2 mm long, 0.2–0.7 mm wide, whitish to yellowish, moderately prominent; leaf scars 1–2 mm high, 1.5–2.5 mm wide, the bundle scars inconspicuous to somewhat prominent. Buds ellipsoid, acute to slightly rounded at the apex, moderately to heavily resin-coated; stalk 2–4 mm long, 1–2 mm in diameter, sparsely pubescent to velutinous, densely glandular; body 3–7 mm long, 1.5–3 mm in diameter; scales 2 (–3), stipular, equal, valvate, moderately villous to velutinous, glandular; pubescence and glands usually obscured by the resin coating. Leaves ovate to oblong-ovate, elliptic, or nearly orbicular (rarely somewhat obovate), the apex acute to obtuse or rounded; base attenuate, broadly cuneate to acute, obtuse, or rounded, sometimes oblique; blade (2.5–) 4–9 (–11) cm long, (1–)

3–9 cm wide, medium to dark green and dull to moderately lustrous above, light to medium green and dull (sometimes slightly to heavily glaucous) below, membranaceous, chartaceous, or somewhat coriaceous; margin flat to slightly revolute, slightly to moderately thickened, double-serrate to nearly serrulate; major teeth (4–) 8–13 (–16) mm apart at mid-leaf, up to 7 mm deep, regular; secondary teeth 3–11 (–13) per cm, 0.3–1.2 mm deep, regular; adaxial surface glabrous, sparsely pubescent, or somewhat pilose, sparsely to moderately glandular; abaxial surface and veinlets glabrous to velutinous or tomentose, sparsely to moderately glandular, slightly to moderately resin-coated; major veins and vein axils near the base tomentose to wooly-pubescent; pubescence whitish to yellowish or brownish; glands small to medium, whitish, yellowish, or brownish. Lateral veins 7–14, (3–) 4–9 (–10) mm apart at mid-leaf, straight to slightly ascending, sometimes branching once again, especially near the base, terminating in major teeth at the margin; cross veins between lateral veins poorly to well developed. Petioles (4–) 8–17 (–25) mm long, (0.5–) 0.8–1.5 mm in diameter, moderately villous to tomentose, sparsely to moderately glandular. Stipules ovate, elliptic, or obovate, the apex acute to obtuse, 5–10 mm long, 2–3.5 mm wide, green, glabrous to velutinous, the hairs yellowish, moderately glandular, the glands yellowish. Pistillate inflorescences borne in racemose groups of (2–) 3–6 (–8) on short branchlets non-divergent to strongly divergent from the main axis, produced during the previous growing season, erect, ovate to elliptic, at anthesis 2–5 mm long, 1.2–3 mm in diameter, on peduncles 0.2–2 mm long, 0.8–2 mm in diameter; staminate catkins borne in one or more racemose clusters of 2–4 at the end of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during both dormancy and anthesis, at anthesis 3–7 (–10) cm long, 5–9 mm in diameter, on peduncles 1–18 mm long, 0.8–2.2 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic to obovate, the apex rounded, 1.2–1.9 mm long, 0.4–1.3 mm wide, the margin lined with small to medium or large glands; stamens 4, opposite and basally to nearly completely adnate to the perianth parts, usually appearing somewhat shorter than to equal in length to the perianth; filaments 0.4–1.2 mm long; anthers 0.8–1.4 mm long and 0.7–1.2 mm in diameter, the thecae separate for 30–55% of their length. Infructescences ovoid to ellipsoid, (6–)

10–17 (–22) mm long, (6–) 8–11 (–14) mm in diameter, on peduncles 0.2–6 (–8) mm long, (0.8–) 1–1.5 (2) mm in diameter; scales 3–5.5 mm long, 3–5.5 mm wide at the apex, 0.8–1.5 mm wide at the base, the apex thin to moderately thickened and flat, the terminal lobe-tip acute and depressed to somewhat or very extended. Fruits narrowly winged or wing-margined, brown; body ovate, elliptic, or obovate, 2.5–3.5 mm long, 1.2–2.5 mm in diameter; wings 2.5–3.5 mm long, 0.4–0.8 (–1.2) mm wide, firm to coriaceous; persistent styles 0.5–1.2 mm long.

Alnus incana was one of two alders included by Linnaeus in *Species Plantarum* as varieties of his *Betula alnus.* It occurs in a circumpolar distribution, occupying habitats ranging from lowlands to nearly subalpine conditions. Among several morphologically and geographically well-marked segments of the species are subspecies *rugosa* of north-eastern North America and subspecies *tenuifolia* of western North.America. Although the typical subspecies of Europe becomes a tree, *Alnus incana* in the New World seldom attains a stature greater than that of a large shrub. Fernald (1945b) emphasized this in arguing for separate specific status for the North American forms. There are too many affinities between New and Old World plants, however, to continue to separate them as different species.

Alnus incana, especially in Europe and Asia, is extremely variable (cf. Hultén, 1971), and this has led to the application of a profusion of species, variety, and form names to it. Leaf shape is usually ovate, but it ranges from this form to obovate or orbicular. Pubescence and glaucousness of the leaves are likewise quite variable, as are habit and bark characters. In spite of this diversity, however, there is usually little confusion in determining the species.

Best development, as with greatest variability, is in Europe, pointing to an origin there, although this species has been greatly affected by Pleistocene glaciation, complicating the tracing of its history.

6a. **Alnus incana** ssp. **rugosa** (DuRoi) Clausen

Alnus incana ssp. *rugosa* (DuRoi) Clausen, Mem. Cornell Univ. Agr. Expt. Sta. **291:** 8. 1949; *Betula alnus* (*rugosa*) DuRoi, Diss. Inaug. Obs. Bot. p. 32. 1771; *Betula rugosa* (DuRoi) Ehrhart, Beitr. Naturk. **3:** 21. 1788; *Alnus rugosa* (DuRoi) Sprengel, Syst. Veg. ed. 16, **3:** 848. 1826; *Alnus glutinosa δ serrulata* lusus c. *rugosa* (DuRoi) Regel, Mem. Soc. Nat. Mosc. **13**(2): 165. 1861; *Alnus*

Figure 46. Representative specimen of *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

serrulata β rugosa (DuRoi) Regel, Bull. Soc. Nat. Mosc. **38**(3): 432. 1865; *Alnus rugosa* var. *α typica* Winkler, Pflanzenreich **19**(4.61): 119. 1904. Type location: "habitat in America septentrianali" (original material not seen).

Alnus glauca Michaux, Hist. Arb. For. Sept. **3**: 322. 1813; *Alnus incana* var. 3 *glauca* (Michaux) Laudon, Arboret. Fruticet. Brit. **3**: 1688. 1838; *Alnus incana α glauca* (Michaux) Regel, Mem. Soc. Nat. Mosc. **13**(2): 154. 1861. Original material not seen (P?).

Alnus glutinosa α serrulata (Aiton) Regel, Mem. Soc. Nat. Mosc. **13**(2): 165. 1861, in part.

Alnus incana β americana Regel, Mem. Soc. Nat. Mosc. **13**(2): 155. 1861; *Alnus incana* var. ι . *americana* (Regel) Winkler, Pflanzenreich **19**(4.61): 123. 1904; *Alnus rugosa* var. *americana* (Regel) Fernald, Rhodora **47**: 350. 1945; *Alnus americana* (Regel) Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 103. 1955, *non* Petzold & Kirchner, Arb. Musc. p. 597. 1864. Type: *Sartwell,* "Penn Yan in Nordamerika" (LE?, not seen).

Alnus argentea hort. ex Petzold & Kirchner, Arb. Musc., p. 600. 1864, *pro syn.*

Alnus canadensis hort. ex Winkler, Pflanzenreich **19**(4.61): 119. 1904, *pro syn.*

Alnus oblongata hort. ex Winkler, Pflanzenreich **19**(4.61): 119. 1904, *non* Willdenow, Sp. Pl. ed. 4, **4**: 335. 1805, *pro syn.*

Alnus incana var. *glauca* f. *tomophylla* Fernald, Rhodora **16**: 56. 1914; *Alnus incana* var. *tomophylla* (Fernald) Rehder, Man. Cult. Tr. Shrbs., p. 147. 1927, erroneously attributed to Fernald; *Alnus rugosa* var. *americana* f. *tomophylla* (Fernald) Fernald, Rhodora **47**: 353. 1945. Type: *Fernald & Wiegand 5303,* Newfoundland: border of a wet thicket, Norris Arm, Aug. 21, 1911 (Holotype, GH!). Figure 47.

Alnus rugosa var. *typica* f. *emersoniana* Fernald, Rhodora **47**: 347. 1945. Type: *Fernald & Bartlett 14,* Massachusetts: Round Pond, Tewksbury, Middlesex Co., Apr. 14 & Oct. 14, 1906 (Holotype, GH!).[1]

Alnus rugosa var. *americana* f. *hypomalaca* Fernald, Rhodora **47**: 353. 1945. Type: *Weatherby & Weatherby 7015,* New Brunswick: Seal Cove Brook, Grand Manan, Charlotte Co., July 24, 1941 (Holotype, GH!).

Spreading shrubs up to 10 (–17) m in height; trunks up to ca. 17 (–25) cm in diameter, the bark dark gray, reddish, or purplish-brown, with large, conspicuous whitish or grayish elliptic or elongate lenticels; young stems light to dark red-brown, dull; internodes sparsely pubescent to velutinous; lenticels of twigs 0.2 1.2 mm long, 0.2–0.7 mm wide, moderately prominent, whitish to yellowish; leaf scars 1–2 mm high, 1.5–2.5 mm wide, the bundle scars somewhat prominent. Buds acute (or sometimes slightly rounded) at the apex; stalk 2–4 mm long, 1–2 mm in diameter, sparsely pubescent to

---

[1] Another collection from the same locality (*Fernald & Bartlett 18*) was erroneously annotated "type number" by Fernald on sheets now at the following (and possibly other) herbaria: CAN, F, GH, NY, US (2 sheets), and WIS.

velutinous; body 3–7 mm long, 1.5–3 mm in diameter. Leaves ovate to elliptic (rarely obovate), the apex acute to obtuse; blade (2.5–) 4–9 (–11) cm long, (1.3–) 3–7.5 cm wide, medium to dark green and dull above, usually medium green and dull below, often slightly to heavily glaucous below, chartaceous; margin flat to slightly revolute, slightly to moderately thickened, double-serrate to nearly serrulate; major teeth (4–) 8–13 (–15) mm apart at mid-leaf, up to 4 mm deep, regular; secondary teeth 6–11 (–13) per cm, 0.3–1 mm deep, regular; adaxial surface glabrous to sparsely pubescent, sparsely to moderately glandular; abaxial surface and veinlets glabrous to velutinous, sparsely to moderately glandular; pubescence yellowish to brownish; glands small to medium in size, yellowish to brownish. Lateral veins 11–14, (3–) 4–9 (–10) mm apart at mid-leaf; cross veins between lateral veins well developed. Petioles (4–) 8–17 (–20) mm long, 0.5–1.5 mm in diameter, moderately villous to tomentose, sparsely to moderately glandular. Stipules 6–10 mm long, 2–3.5 mm wide. Pistillate inflorescences borne in groups of (2–) 3–6 on short branchlets non-divergent to strongly divergent from the main axis, at anthesis 2–5 mm long, 1.2–2 (–2.5) mm in diameter, on peduncles 0.2–2 mm long, 0.8–1 mm in diameter; staminate catkins borne in one or more clusters of 2–4, at anthesis 2–7 cm long, 5–8 mm in diameter, on peduncles 1–9 (–11) mm long, 0.8–2 (–2.2) mm in diameter. Staminate flowers with 4 perianth parts, these elliptic or obovate, the apex rounded, 1.4–1.9 mm long, 1.1–1.3 mm wide, the margin lined with medium to large glands; stamens basally adnate to the perianth parts, usually somewhat shorter than to equal in length to the perianth; filaments 0.4–0.9 mm long, anthers 0.9–1.2 mm long and 0.8–1.2 mm in diameter, the thecae separate for 30–45% of their length. Infructescences (6–) 10–17 mm long, (6–) 8–11 mm in diameter, on peduncles 0.2–6 (–8) mm long, 1–1.5 (–2) mm in diameter; scales 3.5–4.5 mm long, 3–4 mm wide at the apex, 0.8–1.5 mm wide at the base. Fruits narrowly winged or wing-margined; body elliptic to obovate, 2.5–3.5 mm long, 1.3–2.5 mm in diameter; wings 2.5–3.5 mm long, 0.4–0.8 (–1) mm wide, firm to coriaceous; persistent styles 0.5–1 (–1.3) mm long. Figures 2A, 4B, 7A, 9A, 16D, 22C, 46, and 47.

DISTRIBUTION AND HABITAT: North-central Manitoba east to southern Labrador, south to southeastern North Dakota, northeastern Iowa, northern Indiana, central Ohio, and southern Pennsylvania. Streambanks, lakeshores, borders of bogs, edges of

Figure 47. Specimen of *Alnus incana* ssp. *rugosa* (DuRoi) Clausen. Holotype of *Alnus incana* var. *glauca* f. *tomophylla* Fernald.

swamps, wet fields and swales, often forming fairly dense thickets. Found at elevations of nearly sea level along the north Atlantic coast to about 825 meters in the Appalachian highlands. Figure 48.

COMMON NAMES: Speckled alder, tag alder, swamp alder, hazel alder, hoary alder, aulne blanchatre (Quebec).

REPRESENTATIVE SPECIMENS: **Canada.** LABRADOR. Paradise River, Sandwich Bay, *Bishop 275* (A); platiere pres de la route de la riv. Hamilton, rive N du lac Gabbro, *Dutilly & Lepage 41117* (DAO); Goose Bay, *Schofield 781* (DAO). MANITOBA. Lac Du Bonnet, *Breitung 7473* (DAO); E end Singoosh Lake, Duck Mts., *Halliday 66-1933* (CAN); Lake Winnipeg, *Moyer s.n.*, Aug. 28, 1889 (NY). NEW BRUNSWICK. Charlotte Co.: Grand Manan, *Weatherby & Weatherby 7015* (CAN, GH, US). Restigouche Co.: Campbellton, low grounds, *Chalmers s.n.*, Aug. 8, 1877 (CAN). Sunbury Co.: Mill Settlement, Blissville Parish, *Christie 637* (DAO); Bass River, *Fowler s.n.*, May 1, 1835 and Sept. 23, 1875. NEWFOUNDLAND. SE of Tompkins, 1 mi N of St. Andrews, Codroy Village, *Basset 846* (DAO); valley of the Exploits River, Norris Arm, *Fernald & Weigand 5305* (CAN, GH, NY, US); Humber Arm, Bay of Islands, McIver's Cove, *Fernald et al. 1646* (GH, NY). NORTHWEST TERRITORIES. Keewatin District: Robinson Portage, *Peeble & Peeble 18* (US). NOVA SCOTIA. Antigonish Co.: Merland, *Smith et al. 13598* (CAN). Halifax Co.: Musquodobolt Harbour, *Rouseau 35623* (CAN). Lunenburg Co.: wet thickets and swales back of brackish shore of Lahave River, Bridgewater, *Fernald & Long 23779* (A, CAN, GH, MO). Yarmouth Co.: Sloan Lake, Pleasant Valley, *Fernald et al. 21015* (GH). ONTARIO. Algoma District: N shore of Lake Superior, 10 mi SE of White River, *Crow 1268* (MSC). Carleton Co.: Dow's Swamp, Ottawa, *Minshall 2707* (DAO). Kenora District: Moose Factory, *Dutilly & Lepage 13795* (A). Rainy River District: along C.N.R. ¾ mi W of Rainy R. Town, *Garton 8524* (DAO). Thunderbay District: 24 mi S of Nipigon along Rt. 17, *Furlow 312* (MSC). PRINCE EDWARD ISLAND. Prince Co.: woods just E of Wellington, *Smith 161* (DAO). Queens Co.: Mount Albion, *Erskine & Smith 1733* (DAO). QUEBEC. Abitibi Co.: Harricanaw River, *Bentley 58204* (CAN). Gaspe-Est Co.: York, *Collins et al. s.n.*, Aug. 25, 1904 (GH). Mantane Co.: Riviere Blanche, wet ground, *Forbes 69585* (CAN, DS). Nouveau Quebec Region: Fort George, *Baldwin et al. 565* (CAN). Portneuf Co.: Station Agionomique, *Cinq-Mars 64498* (DAO). Stanstead Co.: North Hatley, *Jack s.n.*, Sept. 26, 1914 (A). **United States.** CONNECTICUT. Litchfield Co.: Berkshire Mountains, *Barkley et al. 38162* (MEXU). Woodbury Co.: Woodbury, *Clark s.n.*, Aug. 25, 1908 (DAO). ILLINOIS. Winnebago Co.: shallow bog near Sugar River, Sec. 20, Shirland Twp., *Fell & Fell 49 382* (DAO). INDIANA. Legrange Co.: Pigeon River State Fish and Game Area, on the N shore of the marsh along the Pigeon River, *Furlow 243* (MSC); along streams, 3 mi SE of Mongo, *Palmer 40375* (NY). Lake Co.: valley of Deep River, below schoolhouse, N of Liverpool, about 2½ mi NW of Hobart, *Steyermark 63551* (F). Porter Co.: just E of Tremount, in the ditch beside the road, *Furlow 245* (MSC). IOWA. Allamakee Co.: margin of Yellow River near Old Stone House, 7 mi NE of Postville, *Thorne 12449* (F, NY). Fayette Co.: about 8 mi SW of Oelwein, *Pammel 475* (MO). MAINE. Hancock Co.: 3 mi E Franklin, *Friesner 6308* (RM, UC). Lincoln Co.: Ocean Point, *Fassett 15802* (F). Penobscot Co.: swamps,

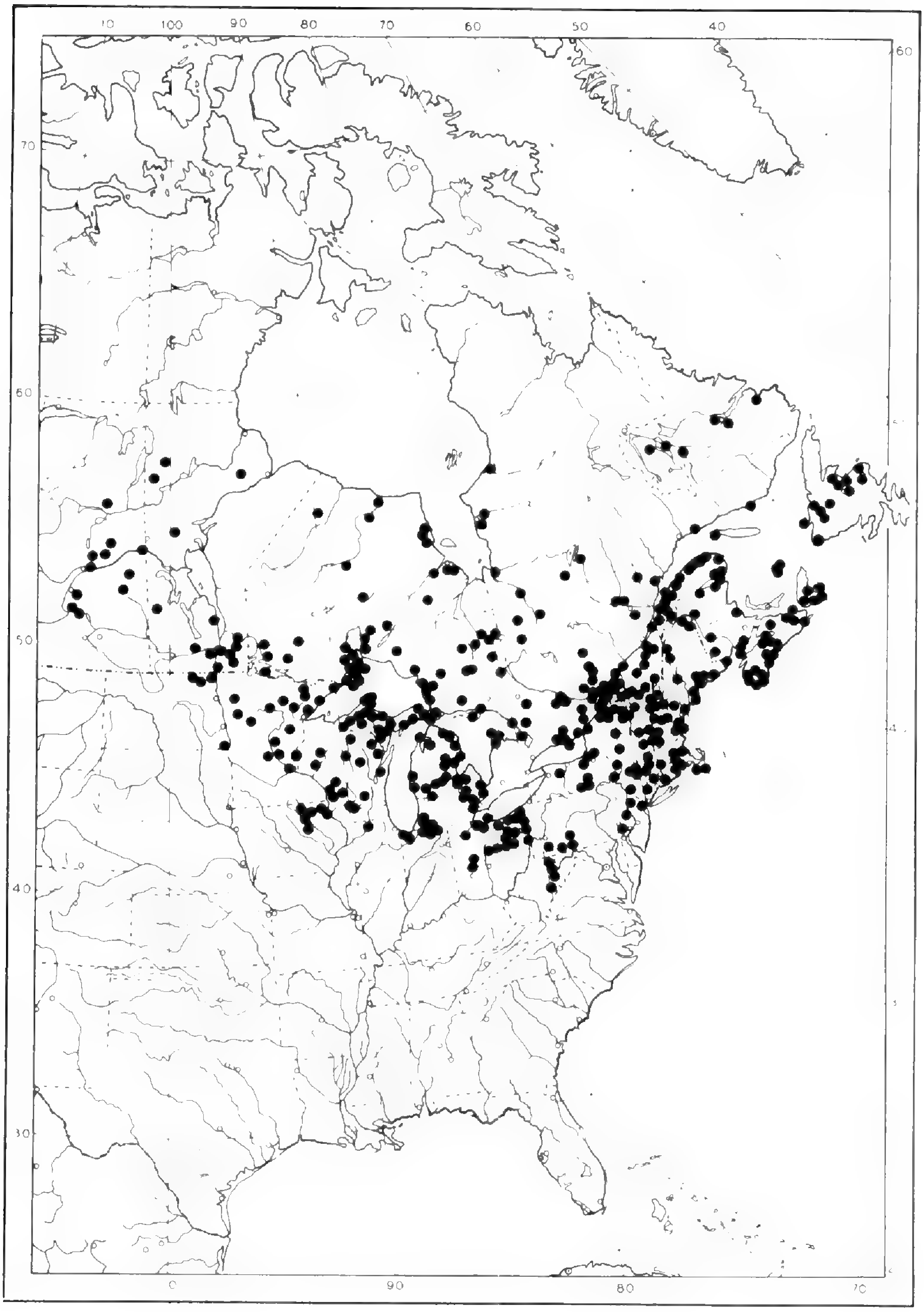


Figure 48. Distribution of *Alnus incana* ssp. *rugosa* (DuRoi) Clausen.

Bangor, *Knight s.n.,* Apr. 22, Oct. 8, 1905 (RM). York Co.: York and vicinity, York Harbor, *Bicknell 3445* (NY); Cape Heddick, *Jack 3388* (A, UC, US). MARYLAND. Mountain Lake Park, *Carter s.n.* Sept. 2, 190? (NY). MASSACHUSETTS. Berkshire Co.: Hoosac R., *Churchill s.n.,* July 26, 1915 (MO); E Mt. Williamstown, *Gilbert s.n.,* in 1883 (UC). Dukes Co.: Martha's Vineyard, head of cove, Great Pond, *Bicknell 3443* (NY). Middlesex Co.: swampy woods, Winchester, *Fernald & Bartlett 7* (GH, NY); clay-bottomed swamp, Winchester, *Fernald & Bartlett 10* (GH, NY); Round Pond, Tewksbury, *Fernald & Bartlett 14* (GH) & *Fernald & Bartlett 18* (CAN, F, GH, NEBC, NY, US). MICHIGAN. Alpena Co.: on the E shore of Long Lake, *Furlow 234* (MSC). Cass Co.: without location, *Pepoon 630* (MSC). Chippewa Co.: Whitefish Point, crest of foredune, *Gillis 2435* (MSC). Livingston Co.: low border of Douglas Lake near mouth of Maple River, *Deam 28814* (NY). Luce Co.: Dear Park, shore of Muskallonge Lake, *Gillis 5534* (MSC). Ontonagon Co.: 1.5 mi E of Silver City, edge of dunes on Lake Superior shore, *Beaman 1849* (MSC). St. Clair Co.: near Port Huron, *Dodge s.n.,* July 21, 1896 (RM). MINNESOTA. Anoka Co.: ¾ mi due N from Little Cook Lake, edge of Carlos Avery Game Refuge, S of Linwood, *Thieret 8462* (F). Clearwater Co.: Lake Itasca State Park, *Furlow 261* (MSC). Hubbard Co.: Benedict, *Bergman 3035* (NY). Louis Co.: border of bog, bay side, Duluth, *Lakela 1341* (NY). Marrison Co.: 12 mi W of Brainerd along US rt. 210, *Furlow 260* (MSC). NEW HAMPSHIRE. Coos Co.: shore of Lake Umbagog, Cambridge, *Pease 18150* (GH). Grafton Co.: along Batchelders Brook ½ mi from Baker River, *Churchill s.n.,* Aug. 6, 1936 (MSC). Sullivan Co.: along rocky streams near Acworth, *Palmer 42735* (A). NEW JERSEY. Sussex Co.: Cranberry Lake, *Mackenzie s.n.,* Aug. 19, 1906 (RM). NEW YORK. Cayuga Co.: on the W shore of Sterling Pond, Fair Haven Beach State Park, *Furlow 191* (MSC). Chemung Co.: without location, *Lucy 9673* (RM). Chenago Co.: without location, *Lucy 3235* (F, RM). St. Lawrence Co.: 3 mi NW of Canton on the floodplain of the Grasse River, *Furlow 194* (MSC). NORTH DAKOTA. Cavalier Co.: Walhalli, *Bergman 2025* (MO). Richland Co.: Leonard, *Stevens 1340* (UC). OHIO. Ashtabula Co.: springs along lower Ashtabula R., *Hicks s.n.,* June 18, 1932 (OS). Henry Co.: along the Maumee River about 3 mi NE of Napoleon, *Weishaupt s.n.,* July 1, 1956 (OS). Richland Co.: Mansfield, *Wilkinson 9673* (NY, OS). PENNSYLVANIA. Bedford Co.: 3/16 mi S of Woodvale, *Berkheimer 10591* (UC). Lehigh Co.: meadows S of trolley tracks just SW of Trexlertown, *Pretz 5917* (UC). Monroe Co.: ½ mi E of Tannersville, *Earle 1186* (DAO). RHODE ISLAND. Providence Co.: bank E of gate, Hauterive, East Providence, *Collins s.n.,* Oct. 17, 1906 (NY); North Providence, *Olney s.n.,* without date (NY). VERMONT. Bennington Co.: Manchester, *Day 163* (GH). Caledonia Co.: Peacham, very common near stream, *Blanchard s.n.,* May 1, 1884 (UC). Chittenden Co.: shore of Lake Champlain, near Buckington, *Rehder s.n.,* Aug. 4, 1902 (A). Rutland Co.: Twin Mountains, W. Rutland, *Eggleston 3210* (NY). Windsor Co.: 1 mi W of Bridgewater Corners along the Ottauguechee River, *Furlow 201* (MSC). WEST VIRGINIA. Preston Co.: Cranesville, *Davis & Davis 107* (NY). Tucker Co.: George Thompson Farm, Canaan Valley, *Core & Strausbaugh s.n.,* July 25, 1947 (DAO). WISCONSIN. Florence Co.: Tifler, *Haynie 28752* (F). Jackson Co.: 1 mi E of Black River Falls, *Furlow 256* (MSC). Marinette Co.: marsh near Green Bay at City of Marinette, *Grassl 3327* (NY). Sauk Co.: swampy ground near Kilburn, *Palmer 27679* (MO, UC).

This taxon was generally considered conspecific with *Alnus incana* of Europe until Fernald (1945b) argued in favor of its being given specific status and treated it so in the 8th edition of *Gray's Manual of Botany* (1950). In the former work, the author lists differences between the taxa of America and Eurasia, especially emphasizing the fact that the Old World taxon is usually a tree while that of the New World is a shrub. He concludes by stating: "surely no argument beyond the mere facts and the plates is needed to show that we have been far astray in calling our northern Swamp Alder the same as the Eurasian *A. incana.*" The differences cited by Fernald, however, all seem minor when compared with the striking similarities of the two taxa.

The original material of *Betula alnus rugosa* DuRoi was a cultivated shrub in the botanic garden of Harbke near Brunswick. The existence of the type is not known. Fernald (1945b) provides a photograph taken by Rehder at B (and presumed since destroyed) of a specimen of *"Betula rugosa"* distributed by Ehrhart and coming from the Harbke Garden[1].

Alnus incana ssp. *rugosa* is often indistinguishable from the typical subspecies on the basis of herbarium material. In northeastern North America the foliage is often moderately to heavily glaucous below (*A. rugosa* var. *americana* Fern., *A. incana* var. *glauca* Ait. f.), this trait gradually disappearing to the west and the south. As noted by Steele (1961), this character is consistent throughout the geographical range of the variety, but it is difficult to use since it doesn't appear until after the leaves are fully matured late in the summer.

A cut-leafed form of this subspecies, *Alnus rugosa* f. *tomophylla,* was described by Fernald (1914) from Newfoundland (Plate 34). Unlike the cut-leafed form of *A. rubra,* this taxon is represented by only a single collection. Cut-leafed variants of *Alnus incana* in Europe are numerous and have a very involved nomenclature (cf. Hylander, 1957).

Alnus incana ssp. *rugosa* is easily distinguished from the other species with which it occurs by its smooth, dark, conspicuously-lenticeled bark and by its acute-tipped, double-serrate leaves. It is

---

[1] Termed a "topotype" by Fernald.

predominantly a lowland shrub, more common in swamps and bogs than along running streams like most of the other species of *Alnus*. The largest recorded specimen of *A. incana* ssp. *rugosa*, occurring at Holland, Michigan, has a height of 17 meters, a trunk circumference of 80 centimeters, and a spread of 8 meters (Pomeroy & Dixon, 1966).

The exact western limit of the geographical range is difficult to establish since this subspecies intergrades gradually into subspecies *tenuifolia* in northern Saskatchewan and Manitoba. To the south and east its range overlaps that of *Alnus serrulata*, and in this region occurs a putative hybrid swarm of intermediate forms. Such specimens seem to be especially common in material from Massachusetts. In both areas of overlap with other taxa, *Alnus incana* ssp. *rugosa* may be difficult to determine. No attempt has been made to resolve this problem in the present key.

6b. **Alnus incana** ssp. **tenuifolia** (Nuttall) Breitung

Alnus incana ssp. *tenuifolia* (Nuttall) Breitung, Amer. Midl. Natr. **58:** 25. 1957; *Alnus tenuifolia* Nuttall, North Amer. Sylva **1:** 48. 1842. Type: *Nuttall s.n.*, "on the borders of small streams within the range of the Rocky Mountains, and afterward in the valleys of the Blue Mountains of Oregon (Holotype, BM?; isotype, GH!). Figure 49.

Alnus incana var. *virescens* Watson, Bot. Calif. **2:** 81. 1880, *non* Wahlenberg, Fl. Lapponica, p. 250. 1812; *Alnus glutinosa* var. *virescens* (Watson) Kuntze, Rev. Gen. Pl. **2:** 638. 1891; *Alnus tenuifolia* var. a. *virescens* (Watson) Callier *in* Schneider, Ill. Handb. Laubh. **1:** 133. 1904. Type: *Watson 1090*, Parley's Park, Utah, June, 1869, alt. 7000 ft. (Lectotype, GH!).[1]

Alnus communis Desfont. ex Kuntze, Rev. Gen. Pl. **2:** 638. 1891, *pro syn.*

Alnus occidentalis Dippel, Handb. Laubh. **2:** 158. 1892; *Alnus tenuifolia* var. b. *occidentalis* (Dippel) Callier *in* Schneider, Ill. Handb. Laubh. **1:** 133. 1904; *Alnus incana* ssp. *rugosa* var. *occidentalis* (Dippel) Hitchcock *in* Hitchcock et al., Vasc. Plts. Pac. Northwest **2:** 73. 1964. Type: *Dieck*s, *Purpus*, "in Nordwest-Amerika heimische" (not seen).

Alnus densiflora Muller, Madroño **5:** 152. 1940. Type: *Allen 514*, Nevada, Storey Co.: southwest of Virginia City on the Jumbo Canyon Road, September 3, 1937 (Holotype, US!).

Spreading shrubs or trees up to 9 (–15) m in height; trunks usually several, ascending, up to 30 cm in diameter; bark light gray to dark brown, smooth, speckled with moderately-prominent to inconspicuous round to elliptic lenticels; young stems often moderately to

---

[1] Another Watson specimen from the King Expedition, also labeled "No. 1090," but from Carson City, Nevada, is at US.

heavily glaucous; lenticels of twigs 0.2–0.7 mm long, usually inconspicuous; leaf scars 1–2 mm high, 1.8–2.5 mm wide, with moderately-prominent bundle scars. Buds ellipsoid to obovoid, usually somewhat rounded at the apex, lightly to moderately resin-coated; stalk 1–3 mm long, 1–2 mm in diameter, glabrous to velutinous; body 4–7 mm long, 1.5–3 mm in diameter. Leaves ovate to elliptic; apex acuminate, acute, or obtuse; base usually broadly cuneate to rounded; blade (3–) 4–8.5 (–9.5) cm long, 2.5–8 cm wide, usually medium to dark green and dull to moderately lustrous above, light to medium green or brownish and dull below, membranaceous to chartaceous; margin flat, not thickened, double-serrate; the major teeth often more or less rounded, (5–) 7–10 (–16) mm apart at mid-leaf, (2–) 4–7 mm deep, regular; secondary teeth (3–) 4–9 per cm, 0.5–1.2 mm deep, regular; adaxial surface glabrous to sparsely pubescent, abaxial surface and veinlets glabrous to sparsely pubescent, slightly or not at all resin-coated. Lateral veins 8–13, (3–) 5–7 (–9) mm apart at mid leaf, usually branching once again, especially near the base; cross veins between lateral veins poorly to well developed. Petioles (4–) 7–18 (–25) mm long, 0.8–1.5 mm in diameter, glabrous to moderately villous or velutinous, moderately to densely glandular. Stipules elliptic to obovate, the apex rounded, 5–7 mm long, 2–3 mm wide, green to light brown, glabrous to moderately villous. Pistillate inflorescences borne in groups of (2–) 3–5, at anthesis 2.5–4 mm long, 1.5–2.8 mm in diameter, on peduncles 0.2–1 mm long, 0.8–2 mm in diameter; staminate catkins borne in groups of 3–5 at the end of the main branch above the pistillate inflorescences, this branch moderately to strongly divergent from the main axis, at anthesis 4–10 cm long, 7–9 mm in diameter, on peduncles 2–18 mm long, 1–1.5 mm in diameter. Staminate flowers with 4 perianth parts, these obovate, 1.6–2 mm long, 1.2–1.6 mm wide, the margin lined with very minute glands; stamens almost completely adnate to the perianth parts, usually appearing shorter than the perianth, the filaments 0.4–1.1 mm long, the anthers 0.8–1.1 mm long and 0.8–1.1 mm in diameter, the thecae separate for 45–55% of their length. Infructescences 9–18 (–20) mm long, (5–) 8–13 mm in diameter, on peduncles 0.2–3 (–6) mm long, 0.8–1.5 mm in diameter; scales 4–5.2 mm long, 3.7–5 mm wide at the apex, (0.8–) 1.2–1.5 mm wide at the base, the apex moderately thickened, the terminal lobe-tip acute to rounded and somewhat extended. Fruits narrowly winged or merely wing-margined, brown;

Figure 49. Lower left: isotype of *Alnus tenuifolia* Nuttall (= *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung). Upper right: specimen of *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung.

body mostly elliptic or obovate, 2.5–3.5 mm long, 1.2–2.5 mm in diameter; wings 3–3.5 mm long, 0.5–1.2 mm wide, firm to coriaceous; persistent styles 0.5–1.2 mm wide, firm to coriaceous; persistent styles 0.5–1.2 mm long. Figures 9B, 17A, and 49.

DISTRIBUTION AND HABITAT: Southern Alaska east to Mackenzie District (as far north as the Mackenzie Delta), south to south-central California, southern Arizona, and central New Mexico. Streambanks, lake shores, wet fields and meadows, bog and muskeg margins, and moist slopes at elevations from about 100 meters in Alaska to over 3,000 meters in Colorado and Arizona. Occurring singly or forming fairly dense thickets. Often associated with *Populus, Salix, Abies, Pinus,* or *Pseudotsuga.* Figure 50.

COMMON NAMES: Thinleaf (or thin-leafed) alder, mountain alder, alder, river alder.

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA. Cold Lake, French Bay E of peninsula along the Alberta-Saskatchewan border, *Dumais & Rankin 1233* (CAN); about 20 mi SE of Smith, *Furlow 262* (MSC); Jasper National Park, about 7 mi SW of the N park entrance, *Furlow 270* (MSC); river valley adjacent to Fort Saskatchewan, *Turner 4784* (DAO). BRITISH COLUMBIA. Dawson Creek, *Breitung 1823* (DAO); 4 mi NNE of Nelson, *Calder & Saville 9395* (DAO, UC); Merritt, bank above Nocola River, *McCabe 4438* (UC); 25 mi S of Ft. St. James, *McCabe 7589* (UC, WTU); Queen Charlotte Isl., *Newcombe s.n.,* Apr. 25, 1901 (F); N slopes of Peace R. valley, vicinity of Hudson Hope, *Raup & Abbe 3699* (CAN, NY). NORTHWEST TERRITORIES. Mackenzie District: near Basworth Creek, Norman Wells, *Cody & Gutteridge 7385* (DAO, F); Mackenzie River 4 mi E of Trout River, *Cody & Spicer 11371* (DAO, UC); Liard River, 2 mi above Blue Bill Creek, 42 mi N of Fort Liard, *Cody & Spicer 11910* (DAO, UC); flat alluvial island in delta at junction of Mackenzie E Channel with Kugwallet Bay of Arctic Ocean, *Lindsey 706* (CAN). SASKATCHEWAN. South shore of Lake Athabaska, E of William River, vicinity of Little Gull Lake, shore of small lake to the E, *Argus 319-62* (DAO); Meadow Lake Forest Reserve, 20 mi S of Meadow Lake, *Breitung 8203* (DAO); Lazy Edward Bay, Cree Lake, *Maini 150* (DAO, RM). YUKON TERRITORY. Whitehorse, *Anderson 9610* (CAN); Bear Creek area about 8 mi E of Dawson, *Calder & Billard 3220* (DAO, RM, UC); Dawson, *Eastwood 17 & Eastwood 20* (CAN); Rampart House on the Alaska-Yukon border, *Loan 359* (DAO). **United States.** ALASKA. Fairbanks, *Anderson 1579* (NY); floodplain of the Chena River at mi 3.2 on Chena Pump Road, *Anderson s.n.,* Sept. 6, 1971 (MSC); Kenai River near mouth of Cooper Creek, Kenai Peninsula, *Calder 5122* (DAO); foot of Chugash Mts., Anchorage, *Dutilly et al. 21669* (DAO, US); bank of Naknek River, King Salmon, *Schofield 2295* (DAO, WTU). ARIZONA. Apache Co.: Greer, *Fulton 8216* (ARIZ); 3 mi N of Alpine, *Furlow 350* (MSC); bottom of Canyon de Chelly, ¼ mi above Monument Canyon, *Goodman & Payson 3253* (WTU). Graham Co.: Riggs Flat, Graham Mts., *Shreve 5251* (ARIZ). Pima Co.: Rincon Mts., Manning Trail, *Blumer 3420* (ARIZ, UC). CALIFORNIA. El Dorado Co.: ca. 2 mi S of Meyers, Upper Truckee River Basin, *Crampton 6690* (UC); about 1 mi E of Pyramid Ranger Station, *Robbins 1699* (UC). Glen Co.: Plaskett Meadows, *Baker 9896* (UC). Humboldt Co.: Croghan Hole on Trinity Summit, *Tracy 19286* (UC, WTU). Placer Co.: 4 mi S of Truckee on Truckee-Tahoe Road, *Mason 5463* (UC). Siskiyou Co.: shore of Castle Lake, *Bacigalupi 6800* (JEPS). COLORADO. Boulder Co.: Boulder, *Moseley s.n.*, in 1896 (RM); Lower Boulder Cañon, *Osterhout 2404* (NY, RM); Allan's Park, *Ramaley 902* (RM); along streams at mouth of Gregory Canyon W of Boulder, *Robbins 346* (UC). Eagle Co.: near Walcott, *Palmer 38127* (NY). Gunnison Co.: Crested Butte, 8 mi NE of Gothic, *Booth 49c334* (WTU). Larimer Co.: 2 mi below Bear Lake, Rocky Mountain National Park, *Furlow 308* (MSC). Ouray Co.: Red Mountain road S of Ouray, *Underwood & Selby 280* (NY). IDAHO. Bonneville Co.: 17 mi SW of Victor, Targhee National Forest, *Furlow 277* (MSC). Elmore Co.: Sawtooth Primitive Area, along stream 7 mi S of Spangle Lakes, *Hitchcock & Muhlick 10171* (NY, WTU). Idaho Co.: 6 mi SW of Lolo Pass, Clearwater National Forest, *Furlow 285* (MSC). Lewis Co.: Cottonwood Canyon, *Mulford s.n.*, June 14, 1892 (NY). MONTANA. Flathead Co.: along Logan Creek 10 mi NE of Lake McDonald, Glacier National Park, *Furlow 274* (MSC); Columbia Falls, *Williams 405* (MSC, NY). Missoula Co.: Missoula, *Elrod 2* (NY). Park Co.: Livingston, along Yellowstone River, *Mason 3506* (UC). NEVADA. Douglas Co.: Edgewood, Lake Tahoe, at California line, *Keck 5526* (UC). Lyon Co.: Carson Creek Cañon, *Brandegee s.n.*, without date (UC); Carson City, *Watson 1090* (US). Storey Co.: 2 3½ mi SW of Virginia City, *Allen 514* (A, NY). Washoe Co.: 8 mi W of Reno Hot Springs, *Archer 5474* (DAO); Hunter Creek Canyon, *Kennedy s.n.*, Apr. 5, 1901 (UC). NEW MEXICO. Catron Co.: upper Willow Creek drainage, Mogollon Range, 60 mi NW of Silver City, 18 mi E of Mogollon, *Band 256* (WTU). San Juan Co.: 7 mi NW of Washington Pass near E base of Chuska Mts., *Watson s.n.*, Aug. 27, 1958 (ARIZ). San Miguel Co.: low woods along Pecos River, Pecos, *Drouet & Richards 3312* (F). Crook Co.: Strawberry Range, Blue Mountains, between Mitchell and Prineville, *Mason 3550* (UC). Harney Co.: opposite Tumtum Lake, 7.6 mi S of Fields, *Ferris 12851* (UC). R. & Blue Mts., *Nuttall s.n.*, without date (GH). UTAH. Salt Lake Co.: Murray, *Jones s.n.*, Apr. 11, 1917 (UC). Sevier Co.: head of Salina Canyon, *Jones 3429* (MSC, NY, UC). Wasatch Co.: along bank of small stream W of Strawberry Res., *Foster 268* (NY). WASHINGTON. Chelan Co.: lower end of Lake Chelan, *Sudworth s.n.*, Oct. 2, 1904 (US). Spokane Co.: base of Mt. Carleton (Mt. Spokane), *Kreager 226* (NY, UC, WTU). Stevens Co.: 28 mi E of Colville on hillside above Little Pend Oreille Lake, *Beattie 11682* (NY). Yakima Co.: Surveyor's Creek, Toppenish, *Heidenreich 26* (WTU). WYOMING. Albany Co.: Medicine Bow National Forest, W of Eagle Rock, *Holliday 34* (RM). Park Co.: Yellowstone National Park, Soda Butte Creek, *Nelson & Nelson 5868* (NY, RM, WTU). Teton Co.: Two Ocean Lake, *Churchill s.n.*, July 20, 1958 (MSC).

This taxon differs from ssp. *rugosa* mainly in the coarser teeth of its leaves, its larger, more tree-like habit, its lighter bark with less-conspicuous lenticels, and its montane riparian habitat. Although variable, it is not as much so as ssp. *rugosa*. In the North it occurs nearly at sea level, but it is found primarily in the mountains throughout most of its range.

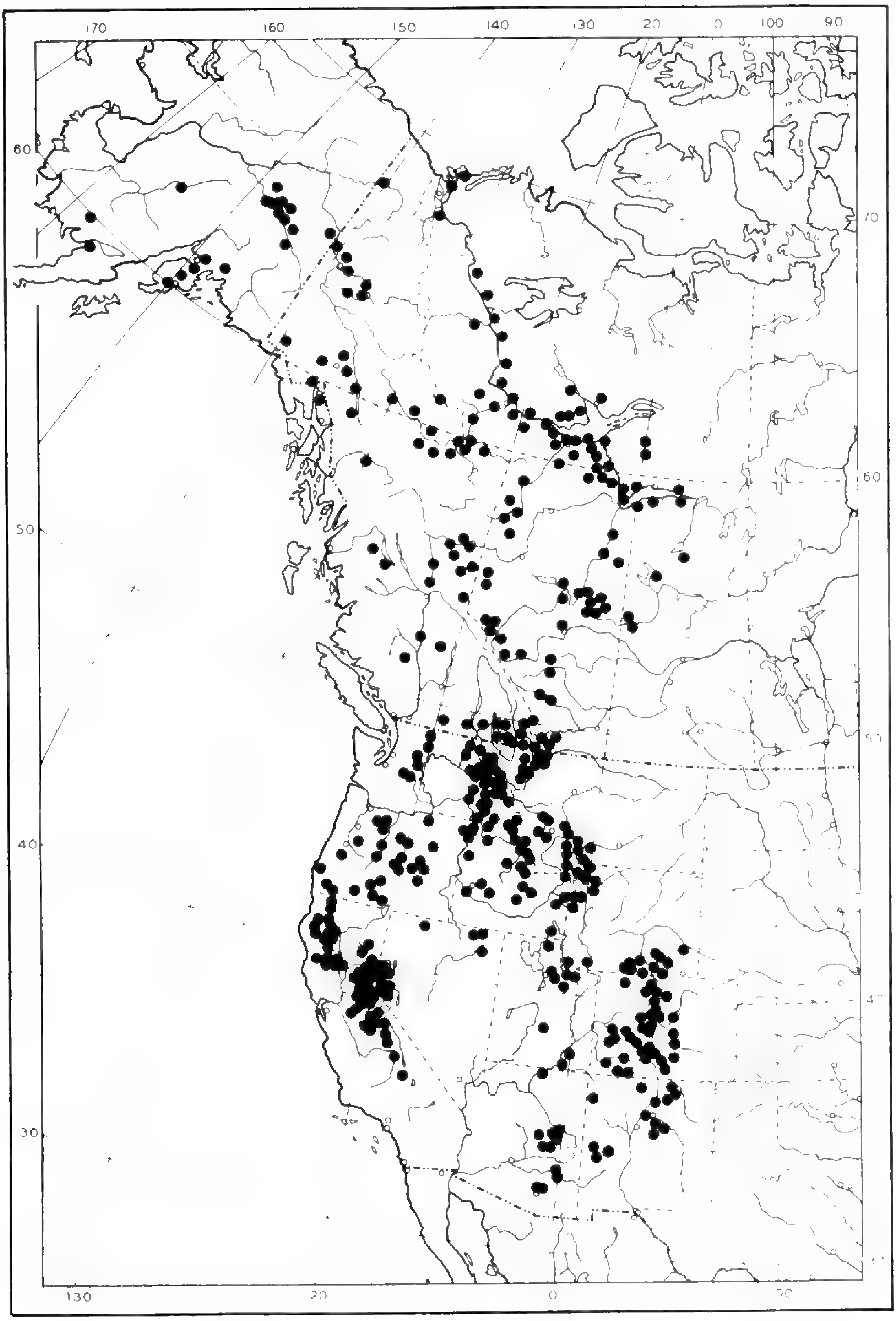


Figure 50. Distribution of *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung in North America.

In 1940, Muller described what he thought to be a new species of *Alnus, A. densiflora,* based on a specimen collected in the Sierra Nevada Mountains of Nevada, noting that the staminate flowers were borne in very "compact" inflorescences. The type of this species (*Allen 514*) is a specimen of typical *A. incana* ssp. *tenuifolia,* the crowded staminate inflorescences being merely the unexpanded catkins of the following season, although it is clear from Muller's description that he thought them to be in anthesis (in September).

Hitchcock, in his recent treatment of this taxon (Hitchcock *et al.*, 1964), views all of *Alnus incana* in North America as belonging to one subspecies and the European material to another, the eastern and western North American segments being treated as varieties. From the degree of divergence among these taxa, however, especially between the eastern and western New World forms, it seems better to consider them all of the same rank (cf. Hultén, 1967, 1971).

The only other taxa with which *Alnus incana* ssp. *tenuifolia* could be confused in its normal range are *Alnus rhombifolia* and *A. oblongifolia,* with which it sometimes occurs sympatrically. In leafless material, these species can usually be distinguished from *A. incana* by the buds, which are more rounded at the apex and more completely covered by the bud scales in *A. incana.* Flowering material can be determined by the number of stamens and by the fact that the stamens are shorter than the perianth only in *A. incana* ssp. *tenuifolia.*

Several floras (including Gleason, 1963, and Gleason & Cronquist, 1963) state that the range of *Alnus incana* ssp. *tenuifolia* extends east to Minnesota and North Dakota. No material was seen from that area, however, that could be referred to this subspecies (all being *A. incana* ssp. *rugosa*). Although no material of *A. incana* ssp. *tenuifolia* was seen from Mexico, it might be expected to occur there in the area adjacent to its range in Arizona and New Mexico. Gleason (1963) and Gleason and Cronquist (1963) state that this taxon exists in Baja California.

7. **Alnus serrulata** (Aiton) Willdenow

Alnus serrulata (Aiton) Willdenow, Sp. Pl. ed. 4, **4**(1): 336. 1805; *Betula serrulata* Aiton, Hort. Kew, **3**: 338. 1789; *Betula alnus serrulata* (Aiton) Michaux, Fl. Bor. Amer. **2**: 181. 1803; *Alnus serrulata—α: vulgaris* Spach, Ann. Sci. Nat. ser. 2, **15**: 206. 1841; *Alnus glutinosa δ serrulata* (Aiton) Regel, Mem. Soc. Nat. Mosc.

13(2): 164. 1861, in part; *Alnus glutinosa δ serrulata* lusus a. *genuina* Regel, Mem. Soc. Nat. Mosc. **13**(2): 164. 1861; *Alnus serrulata α genuina* Regel, Bull. Soc. Nat. Mosc. **38**(3): 432. 1865; *Alnus rugosa* var. *β. serrulata* (Aiton) Winkler, Pflanzenreich **19**(4.61): 120. 1904: *Alnus serrulata* var. *vulgaris* Fernald, Rhodora **47**: 358. 1945; *Alnus incana* var. *serrulata* (Aiton) Boivin, Le Nat. Canad. **94**: 651. 1967. TYPE: "nat. of Pennsylvania. Cult. 1769 by Peter Collinson, Esq." (BM?, not seen).

Alnus carpinifolia Desfontaines ex Spach, Ann. Sci. Nat. ser. 2, **15**: 206. 1841, *pro syn.*

Alnus maritima hort. ex Spach, Ann. Sci. Nat. ser. 2, **15**: 206. 1841, *pro syn.*

Alnus rubra Desfontaines ex Spach, Ann. Sci. Nat. ser. 2, **15**: 206. 1841, *non* Bongard, Mem. Akad. Sci. St. Petersb. ser. 6, **2**: 162. 1833, *pro syn.*

Alnus serrulata—β : macrophylla Spach, Ann. Sci. Nat. ser. 2, **15**: 206. 1841; *Alnus macrophylla* Desfontaines ex Spach, Ann. Sci. Nat. ser. 2, **15**: 206. 1841, *pro syn.*

Alnus rubra Tuckerman, Amer. Jour. Sci. ser. 2, **45**: 32. 1843, *non* Bongard, Mem. Akad. Sci. St. Petersb. ser. 6, **2**: 162. 1833.

Alnus latifolia Desfontaines ex Hartig, Vollst. Naturgesh. Forstl. Kulturpfl., p. 336. 1851, *pro syn.*

Alnus glutinosa δ serrulata lusus b. *obtusifolia* Regel, Mem. Soc. Nat. Mosc. **13**(2): 165. 1861; *Alnus serrulata δ obtusifolia* (Regel) Regel, Bull. Soc. Nat. Mosc. **38**(3): 433. 1865; *Alnus rugosa* var. *obtusifolia* (Regel) Winkler, Pflanzenreich **19**(4.61): 120. 1904. TYPE: "gesehen vom Ohio und in kultivirten Exemplaren" (not seen).

Alnus americana hort. ex Petzold & Kirchner, Arb. Musc., p. 597. 1864, *non* Hartig, Vollst. Naturgesh. Forstl. Kulturpfl., p. 337. 1851.

Alnus obtusifolia Mertens ex Regel, Mem. Soc. Nat. Mosc. **13**(2): 165. 1861, *pro syn.*

Alnus noveboracensis Britton, Torreya **4**: 124. 1904; *Alnus serrulata* var. *vulgaris* f. *noveboracensis* (Britton) Fernald, Rhodora **47**: 358. 1945. TYPE: *Britton s.n.*, New York, Grant City, Staten Island (HOLOTYPE, NY!).

Alnus undulata hort. ex Winkler, Pflanzenreich **19**(4.61): 119. 1904, *pro syn.*

Alnus serrulata var. *subelliptica* Fernald, Rhodora **47**: 358. 1945. TYPE: *Fernald & Bartlett 16*, "Massachusetts: sandy swamp, Tewksbury, April 14 and Oct. 14, 1906" (HOLOTYPE, GH!; ISOTYPES, CAN!, F!, NY!, US!, WIS!). Figure 51.

Alnus serrulata var. *subelliptica* f. *emarginata* Fernald, Rhodora **47**: 359. 1945. TYPE: *Bissell & Weatherby* (*Weatherby 2031*), "Connecticut: open, rather sphagnous swamp, Rainbow, Windsor, Hartford Co., Sept. 16, 1906 and April 6, 1907" (HOLOTYPE, GH!).

Alnus serrulata var. *subelliptica* f. *mollescens* Fernald, Rhodora **47**: 359. 1945. TYPE: *St. John 2681*, "New York: wet hollow. Riverbed, Southampton. Suffolk Co., July 25-Aug. 3, 1920" (HOLOTYPE, GH!).

Alnus serrulata var. *subelliptica* f. *nanella* Fernald, Rhodora **47**: 360. 1945. TYPE: *Fernald & Lewis 14596*, "Virginia: Ram Hole Swamp, Seward Forest, near Triplett, Brunswick Co., June 22 and Sept. 13, 1944" (HOLOTYPE, GH!; ISOTYPES, PH!, US!).

Compact shrubs up to 10 (–14) m in height; trunks up to 16 cm in diameter, ascending; bark light gray, smooth to slightly rough, the lenticels inconspicuous; young stems light brown to dark red-brown, dull, often slightly to moderately glaucous, without noticeable resinous coating, not differentiated into long and short shoots, without longitudinal ridges; internodes glabrous to velutinous, moderately to densely glandular; nodes and branchlets bearing inflorescences very densely glandular; hairs whitish to yellowish or brownish; glands small to medium in size, yellowish to dark brown; lenticels of twigs circular to elliptic, 0.3–0.6 mm long, 0.2–0.4 mm wide, yellowish, inconspicuous; leaf scars 0.7–3 mm high, 1.5–2.5 mm wide, the bundle scars moderately prominent. Buds ellipsoid to obovoid, slightly rounded to rounded at the apex, moderately to heavily resin-coated; stalk 1.5–3 mm long, 1–1.5 mm in diameter, sparsely to moderately pubescent, densely glandular; body 3–6 mm long, 2–3 mm in diameter; bud scales 2, stipular, equal, valvate, moderately pubescent, glandular; pubescence and glands usually obscured by the resin coat. Leaves usually elliptic or obovate (rarely ovate); apex obtuse to rounded (rarely acute); base broadly cuneate (sometimes rounded); blade (4–) 5–9 (–14.5) cm long, (2–) 3.5–6.5 (–7.5) cm wide, medium to dark green and dull to moderately lustrous above, light to medium green or green-brown and dull below, chartaceous to somewhat coriaceous; margin flat to slightly revolute, slightly to moderately thickened, serrulate to somewhat double-serrate; major teeth (when present) (5–) 7–18 (–22) mm apart at mid-leaf, less than 2 mm deep, irregular; secondary teeth (5–) 7–11 (–15) per cm, 0.1–0.8 (–1) mm deep, regular to slightly uneven; adaxial surface glabrous to sparsely pubescent, moderately to densely glandular; abaxial surface and veinlets glabrous to moderately villous, moderately to densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base tomentose to wooly-pubescent; pubescence whitish to yellowish; glands small to medium in size, whitish to yellowish or brownish. Lateral veins 8–11, (3–) 4–8 (–10) mm apart at mid-leaf, straight or slightly ascending, sometimes branching once again, especially near the base, terminating in teeth at the margin; cross veins between lateral veins poorly (to rarely well) developed. Petioles (2–) 6–15 (–22) mm long, 0.5–1.5 (–2) mm in diameter, glabrous, moderately villous, or tomentose, sparsely to moderately glandular. Stipules elliptic to

Figure 51. Specimen of *Alnus serrulata* (Aiton) Willdenow. Holotype of *Alnus serrulata* var. *subelliptica* Fernald.

Figure 52. Representative specimen of *Alnus serrulata* (Aiton) Willdenow.

obovate, the apex obtuse to rounded, 2.5–5.5 mm long, 1.6–3 mm wide, green to light brown, glabrous to moderately villous, the hairs yellowish, moderately glandular, the glands pale yellow. Pistillate inflorescences borne in racemose clusters of (2–) 3–5 on short non-strongly-divergent branchlets, produced during the previous growing season, erect, ovate to elliptic, at anthesis 3–6 mm long, 1.5–2.5 mm in diameter, on peduncles 0.5–2 (–3) mm long, 0.8–1 mm in diameter; staminate catkins borne in one or more racemose clusters of 3–5 at the end of the main branch above the pistillate inflorescences, this branch usually strongly divergent, bending sharply away from the main axis, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 3–8.5 cm long, 4–10 mm in diameter, on peduncles 1.5–8 mm long, 0.5–1.2 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic to obovate, the apex obtuse to rounded, 0.7–1.1 mm long, 0.3–1.1 mm wide, the margin lined with minute glands; stamens 4, opposite and basally adnate to the perianth parts, usually appearing much longer than the perianth, the filaments 0.6–0.9 mm long, the anthers 0.8–1.1 mm long and 0.8–1 mm in diameter, the thecae separate for 15 40% of their length. Infructescences ovoid to ellipsoid, 10–17 (–22) mm long, (6–) 8–11 mm in diameter; on peduncles 0.2–5 (–8) mm long, 0.8–1.2 mm in diameter; scales 3–4.5 mm long, 3–4 mm wide at the apex, 0.8–1 mm wide at the base, the apex moderately thickened, flat, the terminal lobe-tip acute and somewhat to very extended. Fruits narrowly winged or wing-margined, brown; body obovate, 2.2–3.3 mm long, 1.2–2 mm in diameter; wings 2–2.5 mm long, 0.2–0.5 mm wide, firm to coriaceous; persistent styles 0.7–1.4 mm long. Figures 2C, 4D, 8D, 18C, 22 E, 23A, 51, and 52.

DISTRIBUTION AND HABITAT: South-central Quebec east to southern Nova Scotia, southwest to northern Ohio and Indiana, central Missouri and eastern Oklahoma, south to the Gulf of Mexico and northern Florida. Streambanks, edges of sloughs, swampy fields, margins of bogs, and lake shores from near sea level to elevations of about 750 meters in the Appalachian and Ozark highlands. Figure 53.

COMMON NAMES: Smooth alder, common alder, hazel alder (erroneously), tag alder, red alder.

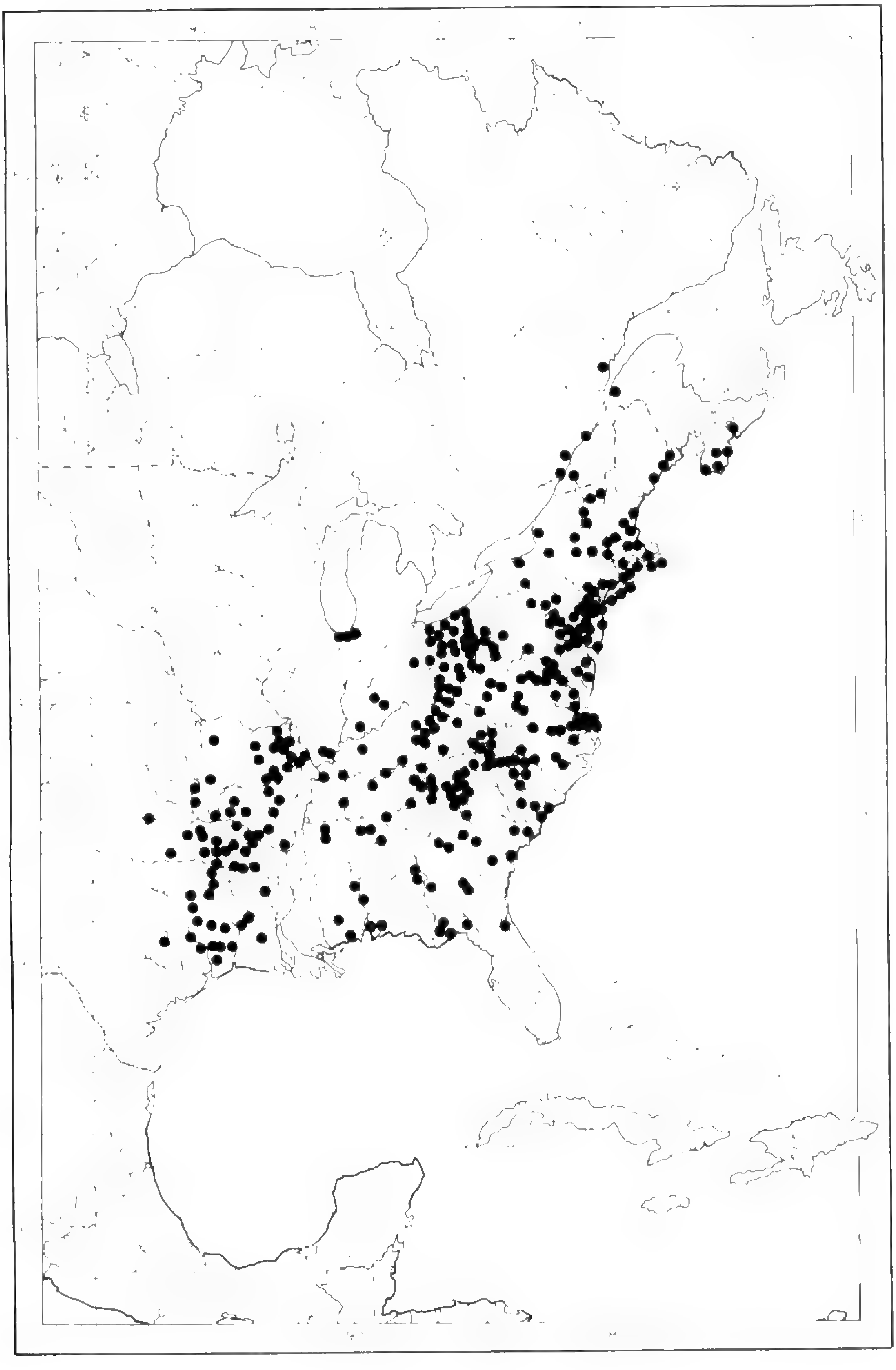


Figure 53. Distribution of *Alnus serrulata* (Aiton) Willdenow.

REPRESENTATIVE SPECIMENS: **Canada.** NOVA SCOTIA. Lunenburg Co.: outlet of Wallace Lake near Italy Cross, *Donly 876* (DAO). Queens Co.: Ponhook Lake, *Smith et al. 10323* (DAO). Yarmouth Co.: Butler's Lake, Gavelton, *Fernald et al. 21021* (GH). QUEBEC. Chambly Co.: Chambly, *Cleonique 5001* (DAO). Lotbiniere Co.: Lotbiniere, rivages du Saint-Laurrent, *Marie-Victorin et al. 56117* (CAN). Temiscouata Co.: Lac Naud, *Blouin et al. 7006* (DAO). **United States.** ALABAMA. Baldwin Co.: E shore of Mobile Bay at Battles Warf, *Brinker 338* (MO). Franklin Co.: vicinity of Russellville, *James 46* (MO). Russell Co.: 11 mi W of Phoenix City, *Furlow 346* (MSC). ARKANSAS. Hot Springs Co.: Magnet Cove, *Demaree 16650* (NY). Pike Co.: banks of Little Mo. River, New Hope, *Demaree 9749* (NY). Pulaski Co.: Little Rock, *Hasse s.n.*, Apr. 20, 1860, Aug., 1860 (NY); along Broadie Creek, near Little Rock, *Merrill 1465* (MO). Yell Co.: Ola, creek bottoms, *Demaree 18227* (MO). CONNECTICUT. New Haven Co.: Waterbury, Cooke St., *Lucian W. 4* (NY). New London Co.: Norwich, *Setchell s.n.*, Mar. 19, 1883, Aug. 22, 1883 (UC). DELAWARE. New Castle Co.: region about Newark, *Tidestrom 3104* (MICH). Sussex Co.: moist thicket near Georgetown, *Britton 13* (NY); 4 mi S of Milford, near the W shore of Hudson's Pond, *Furlow 247* (MSC). DISTRICT OF COLUMBIA. At edge of natural woods in U.S. Nat. Arboretum, *Mazzeo 1170* (WTU); common at Terra Cotta, *Tidestrom 4337* (NY). FLORIDA. Gadsden Co.: along a very small stream 19 mi W of Tallahassee, *Godfrey 52793* (GH, NY). Jefferson Co.: 1 mi E of Lloyd, *Godfrey 55316* (NY). Wakulla Co.: near the Sopchoppy River, about 5 mi N of Sopchoppy, *Godfrey 55213* (GH, WTU). GEORGIA. Clark Co.: just S of Athens, *Duncan 3877* (RM, UC). Randolph Co.: banks of small creek S of Cuthbert, *Harper 1782* (A, F, GH, MO, NY). Wilcox Co.: 11.5 mi S of Abbeville on US rt. 129, *Furlow 345* (MSC). ILLINOIS. Johnson Co.: Tunnel Hill, *Palmer 15176* (MO). Pope Co.: creekbank, Belle Smith Spring, SE of McCormick, *Evers 51637* (WIS). INDIANA. Brown Co.: on the N bank of Salt Creek just E of Belmont, *Furlow 315* (MSC). DuBois Co.: 1 mi N of Bretzville along Ind. rt. 64, *Furlow 316* (MSC). Jackson Co.: in the wet woods about ¼ mi S of Chestnut at the intersection of US rt. 202 and Interstate rt. 89, *Furlow 202* (MSC). NEW JERSEY. Cape May Co.: NE branch of Pond Creek near Ray Road, *Stone s.n.*, Aug. 9, 1918 (MO). Ocean Co.: Barnegat, *Long 22066* (UC). Salem Co.: along Delaware River, N of Penns Grove, *Adams & Adams 1889* (UC). NEW YORK. Oneida Co.: E end of Oneida Lake, *House 27158* (NY, UC, WTU). Richmond Co.: Grant City, Staten Id., *Britton s.n.*, Aug. 3, 1894 (NY). Warren Co.: island in Lake George, *Engelmann s.n.*, Aug. 24, 1856 (MO). NORTH CAROLINA. Buncombe Co.: bordering the Swannanoa River, *Biltmore 1240* (F, NY, RM). Mitchell Co.: Roan Mountain and vicinity, *Meehan et al. s.n.*, July, 1880 (NY). Rowan Co.: China Grove, *Eggleston 4607* (NY); on Dunn's Mountain, *Small s.n.*, Aug. 10-27, 1884 (NY). Wilkes Co.: Blue Ridge Parkway, just S of the intersection with NC rt. 18, *Furlow 210* (MSC). OHIO. Athens Co.: between rt. 124 and the River, 1¾ mi SW of the Washington Co. line, *Herrick s.n.*, July 3, 1956 (OS). Columbiana Co.: rt. 164, 4 mi N of rt. 39, *Herick s.n.*, July 2, 1954 (OS). Hocking Co.: Neotoma, *Wolfe et al. s.n.*, May 26, 1940 (OS). Wooster Co.: in low ground, Wooster, *Duvel 488* (OS). OKLAHOMA. Delaware Co.: open creek bank on Flint Creek, Flint, *Wallis 1945* (OKL). Johnston Co.: along Pennington Creek, NW of Tishomingo, *Goodman 5445* (UC). McCurtain Co.: Broken Bow, along Yanubbee Creek, *Furlow 348* (MSC). PENNSYLVANIA. Dauphin Co.: Harrisburg, *Small s.n.*, Apr. 16, 1888 (F). Lancaster Co.: in the vicinity of Conewago, *Small s.n.*, Sept., 1892 (NY). Lehigh Co.: meadows along Trout Creek E of 12th Ward, Allentown, *Pretz 6107* (UC). Philadelphia Co.: along head of

Cresheim Creek, Mermaid, *Adams & Thebes 1191* (UC). RHODE ISLAND. Newport Co.: N outlet of Middle Quarry Pond, *Collins s.n.*, Oct. 19, 1906 (NY). Providence Co.: Limerock, Lincoln, *Collins 15006* (F). SOUTH CAROLINA. Dorchester Co.: Charleston, *Sargent s.n.*, Feb. 12, 1880 (A). Georgetown Co.: river swamp 14 mi NW of Georgetown, *Godfrey & Tryon 788* (NY, UC). Jasper Co.: 1 mi NW of Gillesonville, *Bell 1672* (UC). TENNESSEE. Campbell Co.: in shallow water, Cove Lake, *Isely 3351* (MSC). Knox Co.: Knoxville, *Kearney s.n.*, Feb. 25, 1893 (F, NY). Lumnen Co.: along brooks W Mitchelville, *Eggert s.n.*, Aug. 17, 1897 (MO). Roane Co.: Harriman, *McMorine s.n.*, Apr. 17, 1893 (DAO). TEXAS. Cherokee Co.: Larissa, *Palmer 8628* (MO). Newton Co.: near Newton, *Nogle s.n.*, Oct., 1961 (F). Polk Co.: Livingston, *Palmer 6766* (MO). VERMONT. Addison Co.: shore of Lake Dunmore, *Dutton s.n.*, Aug. 23, 1908 (MO). Caledonia Co.: Lyndon, *Bartlett 30* (NY). VIRGINIA. Amherst Co.: along Otter Creek, Blue Ridge Parkway, *Freer 2475* (US). Brunswick Co.: Seward Forest, near Triplett, *Fernald & Lewis 14596* (GH, PH, US). Isle of Wight Co.: dry sandy woods S of Zuni, *Fernald et al. 6582* (GH, MO). Prince William Co.: half way between Beverly Mill and Hopewell Gap, E slope of Bull Run Mountains, *Allard 3911* (F, GH, NY). Princess Anne Co.: on the banks of the Dismal Swamp Canal about 7 mi N of the North Carolina state line, *Furlow 207* (MSC). Southampton Co.: Franklin, *Eggleston 4916* (NY). WEST VIRGINIA. Fayette Co.: Gauley Bridge, *Eggleston 5522* (MO, NY). Mingo Co.: near mouth of Little Huff Creek, *Berkley 1042* (MO). Upshur Co.: without location, *Pollock s.n.*, Apr. 13, 1896 (MICH).

The name *Alnus rugosa* has been widely and erroneously used for this species since about the beginning of the nineteenth century, most recently by Ball (1964) in *Flora Europaea.* Since Fernald's (1945b) review of this problem, however, most of the confusion between these two species has been resolved.

The leaves of *Alnus serrulata* are easily recognized by their serrulate margins and elliptic to obovate shape. In other respects, however, herbarium specimens may be difficult to distinguish from *A. incana* ssp. *rugosa,* with which it is sympatric in the northern part of its range. The problem of identification is most difficult when the leaves are absent. A useful feature (employed by Fernald, 1945b, 1950) to distinguish these species is the form of the branchlet bearing the staminate inflorescences. In *A. serrulata* this stem bends abruptly away from the main axis at the point of attachment, while this is not the case in *A. incana* ssp. *rugosa* (Figure 23). However the character is not absolutely reliable and should be used in combination with other distinctive features, including the more globose or rounder-tipped winter buds and lighter-colored bark with less-prominent lenticels. The largest known individual, as noted by Pomeroy and Dixon (1966), occurs near Shreve, Ohio and has a trunk circumference of 50 cm, a height of 14 m, and a spread of 7 m.

When *Alnus serrulata* and *A. incana* ssp. *rugosa* overlap in distribution, they apparently hybridize (cf. Steele, 1961), although an artificial hybrid between these species has not been reported. *Alnus serrulata* var. *subelliptica* Fern. occurs in the region of overlap and may represent part of the putative hybrid swarm found there. Fernald's forms of this variety vary in leaf shape, size, and pubescence.

Alnus serrulata is primarily coastal in distribution, although it also occurs over a considerable portion of non-coastal southeastern North America and at moderate elevations in the Appalachian and Ozark Mountains. Like a number of other species of the Atlantic Coastal Plain, *A. serrulata* occurs disjunctly in the sand dunes of the southern end of Lake Michigan. A gap in its distribution occurs in the Mississippi River delta region (Figure 53). Comparable gaps occur in the distributions of several other southeastern American taxa, including *Toxicodendron toxicarium* (cf. Gillis, 1971) and *Lyonia ligustrina* var. *foliosiflora* (cf. Judd, 1978).

The closest relative of *Alnus serrulata* in North America is *A. incana*, though these species are quite distinct morphologically. *Alnus serrulata* is regarded here as more highly specialized than *A. incana* in its shrubbier habit, obovate leaf form, and serrulate leaf margin. Both species occur in rather similar lowland habitats in eastern North America, though *A. serrulata* is more often found along flowing streams than is *A. incana* and generally occurs in a warmer climate.

8. **Alnus glutinosa** (Linnaeus) Gaertner

Alnus glutinosa (Linnaeus) Gaertner, Fruct. Sem. **2:** 54. 1790; *Betula alnus α glutinosa* Linnaeus, Sp. Pl. **2:** 983. 1753; *Betula glutinosa* (Linnaeus) Linnaeus, Syst. Nat. ed. 10, **2:** 1265. 1759; *Alnus glutinosa* (*vulgaris*) Persoon, Syn. Pl. **2:** 550. 1807; *Alnus glutinosa — α: vulgaris* Spach, Ann. Sci. Nat. ser. 2, **15:** 207. 1841.

Betula alnus Linnaeus, Sp. Pl. **2:** 983. 1753, in part.

Alnus vulgaris Hill, Brit. Herb., p. 510. 1757, *nom. illeg.*

Broadly pyramidal trees up to 20 (–35) m in height; trunks usually one to several, up to about 0.5 or 0.7 m in diameter; bark dark brown, smooth when young, fissured or broken into shallow plates when older, lenticels moderately conspicuous on smooth stems; young stems green to light reddish-brown, moderately lustrous, usually not glaucous, with a moderately heavy to very heavy resinous coating, not differentiated into long and short shoots, sometimes with slightly noticeable longitudinal ridges originating at the nodes; internodes glabrous to sparsely pubescent, moderately to densely glandular; nodes and branchlets bearing inflorescences glabrous to sparsely pubescent, very densely glandular; hairs whitish to light brownish; glands usually medium in size, yellowish; lenticels of twigs elliptic to circular, 0.7–1.2 mm long, 0.2–0.5 mm wide, yellowish or whitish, more or less inconspicuous; leaf scars ca. 1.5 mm high, ca. 2.5 mm wide, the bundle scars not prominent. Buds ellipsoid to obovoid, obtuse to rounded at the apex, usually heavily resin-coated; stalk 2–5 mm long, 1.5–2.5 mm in diameter, glabrous to sparsely pubescent, densely glandular; body 6–10 mm long, 2.5–5 mm in diameter; bud scales 2 (–3), stipular, equal, valvate, more or less glabrous, moderately to densely glandular; pubescence and glands usually obscured by the resin coat. Leaves obovate to suborbicular; apex retuse to obcordate (sometimes merely rounded); base obtuse to broadly cuneate (rarely rounded); blade (3–) 4–7.5 (–9) cm long, (2.5–) 3–7 (–8) cm wide, dark green and moderately to very lustrous above, medium green and dull below, chartaceous to coriaceous; margin flat, usually not thickened, double-serrate to denticulate (sometimes deeply lobed in cut-leafed forms); major teeth (5–) 9–15 (–20) mm apart at mid-leaf, 1.5–7 mm deep, regular to irregular; secondary teeth 3–8 per cm, 0.5–1 mm deep, regular to irregular; adaxial surface glabrous to sparsely pubescent, sparsely glandular; abaxial surface and veinlets glabrous to sparsely pubescent, moderately glandular, moderately to heavily resin-coated; major veins and vein axils near the base pilose to densely tomentose; pubescence whitish to brownish; glands small, medium, or large in size, whitish to brownish. Lateral veins (5–) 7–9 (–10), 4–12 mm apart at mid-leaf, usually slightly ascending, sometimes branching once again, especially near the apex, terminating in teeth at the margin; cross veins between lateral veins poorly to well developed. Petioles 7–27 mm long, 1–1.5 mm in diameter, usually sparsely pubescent, moderately to densely glandular. Stipules elliptic to obovate, rounded to obtuse at the apex, 6–9.5 mm long, 3–5 mm wide, medium green, glabrous to sparsely pubescent, the hairs whitish, sparsely to moderately glandular, the glands yellowish to brownish. Pistillate inflorescences borne in racemose groups of 2–4 (–5) on short non-strongly-divergent branchlets, produced during

Figure 54. Representative specimen of *Alnus glutinosa* (Linnaeus) Gaertner.

the previous growing season, erect, ovoid to ellipsoid, at anthesis (3–) 4–5 (–6) mm long, 2–3 mm in diameter, on peduncles 1–6 mm long, 1–1.5 mm in diameter; staminate catkins borne in one or more racemose clusters of 2–5 at the end of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 4–12.5 cm long, 4.5–12 mm in diameter, on peduncles 2–11 mm long, 0.7–1.5 mm in diameter; floral bracts 1.5–2.5 mm high, 2–3 mm wide. Staminate flowers 3 per bract, perianth of 4 parts, these generally obovate, the apex rounded, ca. 1.5 mm long, ca. 1.3 mm wide, the margin lined with glands of moderate size; stamens 4, opposite and basally adnate to the perianth parts, usually appearing shorter than to equal in length to the perianth, the filaments 0.5–0.8 mm long, the anthers 1.2–1.6 mm long, 0.8–1.3 mm in diameter, the thecae separate for 30–50% of their length. Infructescences ovoid to ellipsoid, (12–) 16–22 mm long, 10–13 mm in diameter; peduncles 1–22 mm long, 0.5–1.5 mm in diameter; scales 4–5.5 mm long, 4–6 mm wide at the apex, 1.5–2.5 mm wide at the base, the apex moderately thickened, flat to slightly reflexed, the terminal lobe-tip acute to rounded, not usually extended. Fruits narrowly bordered, brown; body obovate, 2.5–3.5 mm long, 2–2.7 mm wide; wing-borders 2.5–3.5 mm long, 0.2–0.5 mm wide; persistent styles 0.5–1.2 mm long. Figure 54.

DISTRIBUTION AND HABITAT: In Europe from central Scandinavia south to southern Spain, Italy, and Asia Minor; in America escaped from cultivation and naturalized from Massachusetts and southern New York, southern Ontario, southern Michigan, and northern Illinois south to southern New Jersey, southern Ohio, and central Illinois. Riverbanks, lake shores, and wet areas. Figure 55.

COMMON NAMES: Black alder, common alder, European alder.

SPECIMENS EXAMINED: **Canada.** ONTARIO. Elgin Co.: Port Burwell, sandy beach, *James 1670* (DAO); shore of Lk. Erie near St. Williams, *James 2148* (DAO). Oxford Co.: along edge of stream, about 3 mi N of Conning, *Soper & Shields 4770* (CAN). **United States.** CONNECTICUT. Hartford Co.: open, rather sphagnous swamp, Windsor, *Weatherby 2031* (US). ILLINOIS. Cook Co.: low ground near Stony Island, Chicago, *Johnson 1474* (US). Piatt Co.: Monticello, *Jones 34385* (UC). INDIANA. Marion Co.: bank of Williams Creek S of the Indiana School for the Blind, Indianapolis, *Furlow 480* (MSC). MASSACHUSETTS. Barnstable Co.: Cape Cod, just E of Brewster, *Furlow 204* (MSC). Norfolk Co.: wet ground, Brookline, *Forbes 17130*

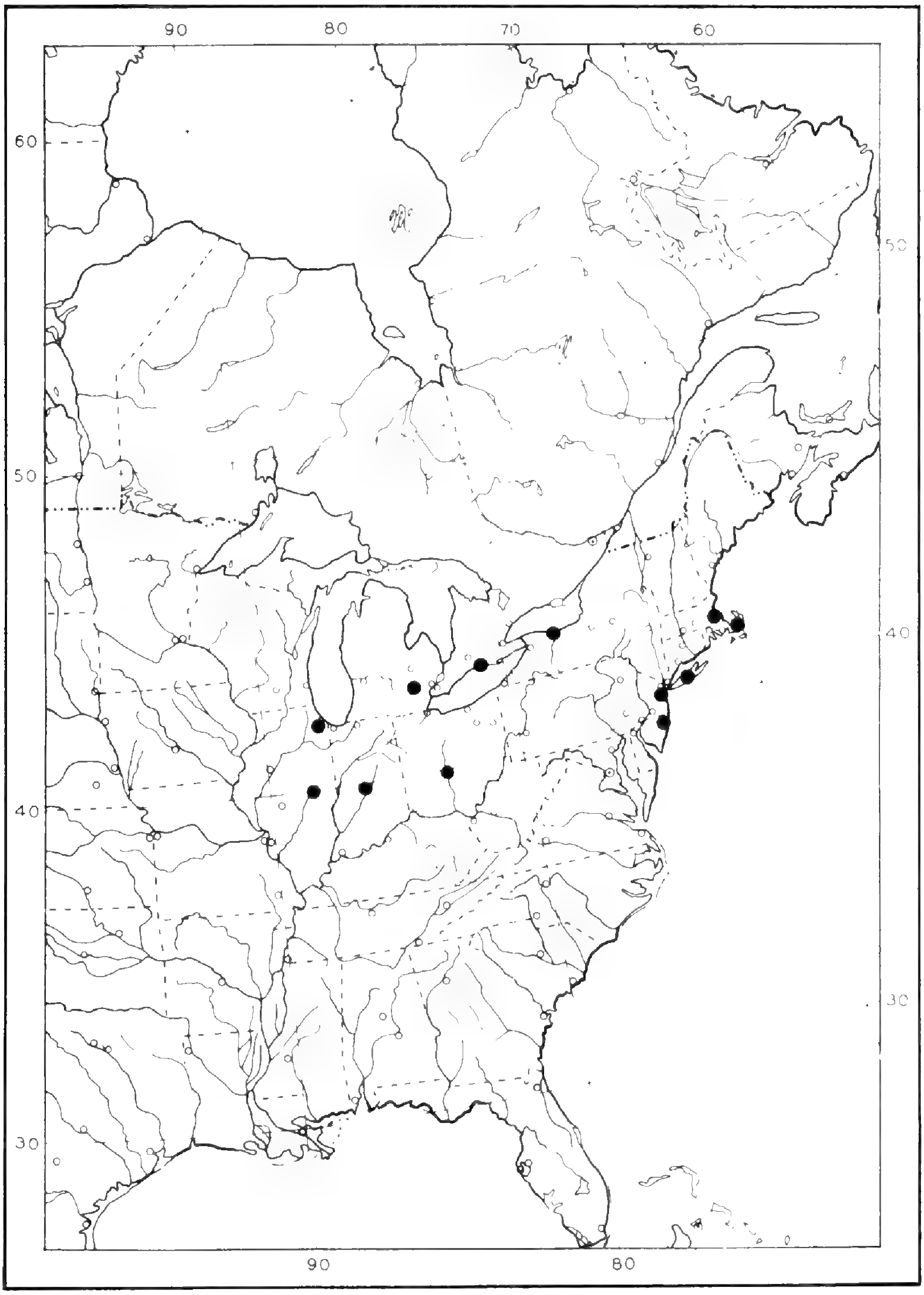


Figure 55. Distribution of *Alnus glutinosa* (Linnaeus) Gaertner in North America.

(WIS); brackish marsh, Brookline, *Forbes s.n.,* Mar. 25, 1904 (MSC); swamp, Beacon St., Brookline, *Forbes s.n.,* Mar. 29 & Sept. 7, 1903 (RM, UC). MICHIGAN. Washtenaw Co.: Dexter-Huron Drive, shoreline of Huron River, *Denton 980* (MSC). NEW JERSEY. Ocean Co.: S tip on the W side of Island Beach, growing in a *Phragmites* swamp, *Bio-Ecology Class* (*Rutgers University*) *s.n.,* Oct. 2, 1955 (DAO). NEW YORK. Monroe Co.: banks of Genesee River, Plymouth Ave., Rochester, *Matthews 4436* (NY); low places along Lake Ontario on Edgemere Dr., *Matthews 4749* (DAO, MSC, RM, UC, WIS). Queens Co.: W side of track to Flushing, L.I., *Schrenk s.n.,* Apr. 5, 1878 (NY). Richmond Co.: Todt Hill, Staten Island, *Britton s.n.,* Sept. 20, 1891 (NY); near Egbertville, Staten Island, *Britton s.n.,* July 18, 1894 (NY). OHIO. Franklin Co.: along Alum Creek near the Main Street Bridge, Columbus, *Furlow 355* (MSC). PENNSYLVANIA. Philadelphia Co.: West Philadelphia, in swamps on Indian Run, *MacElwee 2141* (NY).

Alnus glutinosa is the common alder throughout much of western Europe. In the eastern United States and Canada it is the most frequently cultivated species, and it often escapes and becomes naturalized in that region. The most useful characters for distinguishing this species from the native American taxa include the arborescent habit and the obovate to orbicular leaves with notched tips. *Alnus glutinosa* is the lectotype species of the genus *Alnus.*

Alnus subg. **Alnobetula** (Ehrhart) Petermann

Alnus subg. *Alnobetula* (Ehrhart) Petermann, Deutschl. Fl., p. 516. 1849 (based on *Betula alnobetula* Ehrhart, Bietr. Naturk. **2:** 72. 1788); *Alnus* sect. I. *Alnobetula* (Ehrhart) W.D.J. Koch, Syn. Fl. Germ. Helvet., p. 663. 1837; *Alnobetula* (Ehrhart) Schur, Vehr. Sieb. Ver. Naturw. **4:** 68. 1853; *Alnus* subg. a. *Alnobetula* (Ehrhart) Callier *in* Schneider, Ill. Handb. Laubh. **1:** 120. 1904; *Alnaster* sect. *Alnobetula* (Ehrhart) Murai, Bull. Gov. For. Expt. Sta. Jap. **154:** 62. 1963, not validly published; *Alnus* subg. *Alnaster* sect. *Alnobetula* (Ehrhart) Murai, Bull. Gov. For. Expt. Sta. Jap. **154:** 62. 1963, *pro syn.; Alnus* subg. *Alnaster* sect. *Alnobetula* (Ehrhart) Murai, Bull. Gov. For. Expt. Sta. Jap. **171:** 32. 1964, not validly published. TYPE: *Alnus viridis* (Villars) Lamarck & De Candolle.

Duschekia Opiz, Oekon. Neuigk. Verhandl. **1839:** 524. 1839. TYPE: *Betula ovata* Schrank (= *Alnus viridis* (Villars) Lamarck & De Candolle).

Alnaster Spach, Ann. Sci. Nat. ser. 2, **15:** 183. 1841; *Alnus* a. *Alnaster* (Spach) Endlicher, Gen. Pl. suppl. **2,** p. 28. 1842; *Alnus* sect. I. *Alnaster* (Spach) Regel, Mem. Soc. Nat. Mosc. **13**(2): 134. 1861; *Alnus* subg. *Alnaster* (Spach) Regel, Bull. Soc. Nat. Mosc. **38**(3): 421. 1865. TYPE: *Alnaster viridis* (Villars) Spach (= *Alnus viridis* (Villars) Lamarck & De Candolle).

Semidopsis Zumaglini, Fl. Pedemont. **1:** 249. 1849. TYPE: *Semidopsis viridis* (Villars) Zumaglini (= *Alnus viridis* (Villars) Lamarck & De Candolle).

Alnus subg. *Alnaster* ser. a. *Virides* Schneider *in* Sargent, Pl. Wilson. **2**(3): 491. 1916; *Alnaster* sect. *Virides* (Schneider) Czerepanov, Notul. Syst. Herb. Inst.

Bot. Kom. Acad. Sci. U.R.S.S. **17:** 94. 1955. TYPE: *Alnus viridis* (Villars) Lamarck & De Candolle.

Alnaster sect. *Virides* ser. *Fruticosi* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 96. 1955. TYPE: *Alnaster fruticosa* (Ruprecht) Ledebour (= *Alnus viridis* ssp. *crispa* (Aiton) Turrill).

Alnaster sect. *Virides* ser. *Sinuati* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 96. 1955. TYPE: *Alnaster sinuata* (Regel) Czerepanov (= *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve).

Small to large spreading shrubs with ascending branches; twigs and young branches differentiated into long stems and short spur shoots; buds sub-sessile, covered with ca. 5 or 6 unequal, imbricate scales. Leaves double-serrate; venation craspedodromous. Pistillate inflorescences borne on long, slender peduncles, each subtended by a leaf (often reduced), in racemose clusters on short shoots along a major branch, the latter bearing the staminate catkins in a racemose arrangement at the apex, the lowermost sometimes subtended by leaves; pistillate inflorescences produced along with new growth at the beginning of the season; staminate inflorescences produced during the previous season and exposed during the dormant season, more or less erect during dormancy, anthesis occurring in spring (at the beginning of new growth), fruit maturation occurring at the end of the current growing season; staminate flowers with 4, or occasionally 5 or 6 stamens. Fruits with 2 large lateral membranaceous wings.

The citation "*Alnus* subgen. *Alnaster* (Spach) Endlicher" is sometimes used for this taxon (cf. Murai, 1964). Endlicher, however, did not specify a rank when he published this name, and the first author to subsequently assign a rank was Regel (1861), who used "*sectio,*" thus establishing Endlicher's name as a section, not a subgenus (cf. Article 35, *International Code of Botanical Nomenclature,* Stafleu et al., 1972). The name *Alnus* subg. *Alnaster* was first published in 1865 by Regel, while *Alnus* subg. *Alnobetula* (with the same type and circumscription) was published earlier, in 1849, by Petermann, making the latter the correct subgeneric name.

9. **Alnus viridis** (Villars) Lamarck & De Candolle

Alnus viridis (Villars) Lamarck & De Candolle, Fl. Fr. ed. 2, **3:** 304. 1805; *Betula viridis* Villars, Hist. Pl. Dauph. **3**(1): 789. 1789; *Alnaster viridis* (Villars) Spach, Ann. Sci. Nat. ser. 2, **15:** 201. 1841; *Semidopsis viridis* (Villars) Zumaglini, Fl. Pedemont. **1:** 250. 1849; *Duschekia viridis* (Villars) Opiz, Seznam Rostl. Kvet.

Ceske, p. 38. 1852; *Alnobetula viridis* (Villars) Schur, Vehr. Sieb. Ver. Naturw. **4:** 68. 1853. Type locality: "en Valgaudemar, en l'Oysans, le Champsaur, &c." (original material not seen).

Alnus alpina Villars, Hist. Pl. Dauph. **1:** 295. 1786, *nom nud.; Betula alpina* (Villars) Borkhausen, Theor.-prakt. Handb. Forstbot. **1:** 477. 1800. Type: "la maotagne de Sept-Laux" (original material not seen).

Betula alnobetula Ehrhart, Beitr. Naturk. **2:** 72. 1788; *Alnus alnobetula* (Ehrhart) Hartig, Vollst. Naturgesh. Forstl. Kulturpfl., p. 372, 1851, *pro syn; Alnus alnobetula* (Ehrhart) K. Koch, Dendrol. ed. 2, **2**(1): 265. 1873; *Alnaster alnobetula* (Ehrhart) Schweinfurth ex Ascherson, Fl. Prov. Brandenb. **1:** 622. 1864. Type: *Herrenhaufen,* June 1782 (GOET?, not seen).

Betula ovata Schrank, Baiersche Fl. **1:** 419. 1793; *Alnus ovata* (Schrank) Loddiges, Bot. Cab. **12:** no. 1141. 1826; *Duschekia ovata* (Schrank) Winkler Pflanzenreich **19**(4.61): 105. 1904, *pro syn.,* erroneously attributed to Opiz. Type locality: Bavaria (original material not seen).

Spreading shrubs up to ca. 12 m in height; trunks up to 20 cm in diameter, ascending to prostrate, bark light gray to reddish-brown, smooth, covered with prominent whitish or grayish lenticels; young stems medium to dark red-brown, slightly to moderately (or sometimes very) lustrous, not glaucous to highly glaucous, moderately to heavily resin-coated, differentiated into long and short shoots, sometimes with longitudinal ridges originating at the nodes; internodes glabrous to velutinous, sparsely to densely glandular; nodes and stems bearing inflorescences very densely glandular; pubescence whitish to yellowish; glands yellowish to light brown; lenticels of twigs circular to elliptic, 0.2–1.2 mm long, 0.2–1 mm wide, whitish to yellowish, usually very prominent; leaf scars 1–2 mm high, 1.5–3.5 mm wide, the bundle scars inconspicuous to moderately prominent. Buds short-stalked and often appearing sessile, ovoid, acuminate or acute at the apex, moderately to heavily resin-coated; stalk 0.2–2 mm long, 1.5–2 mm in diameter, glabrous to velutinous, densely glandular; body 5–11 mm long, 2–6 mm in diameter; scales ca. 5, unequal in size, glabrous to velutinous, glandular; pubescence and glands usually obscured by the resin coat. Leaves narrowly to broadly ovate or elliptic; apex acuminate, acute, obtuse, or (sometimes) rounded; base acute, obtuse, rounded, or cordate; blade 2–16 cm long, 1.3–13 cm wide, light yellowish green to dark green and dull to lustrous (usually very lustrous when young) above, light to medium green and dull to lustrous below, membranaceous to coriaceous, usually very glutinous; margin nonrevolute, often somewhat puckered, slightly to much thickened, serrulate to coarsely double-serrate; major teeth 3–25 mm apart at mid-leaf, up to 6 mm deep, slightly uneven to regular or irregular; secondary teeth 5–18 per cm, 0.3–3 mm deep, slightly uneven to irregular; adaxial surface glabrous to sparsely pubescent, sparsely to moderately (or rarely densely) glandular; abaxial surface and veinlets glabrous to velutinous, moderately to densely glandular, lightly to moderately resin-coated; major veins and vein axils near the base tomentose to wooly-pubescent; pubescence whitish to yellowish or brownish. Lateral veins 5–12, 2–13 mm apart at mid-leaf, straight or slightly ascending, often branching once or twice again, especially near the base, terminating in major teeth at the margin; cross veins between lateral veins absent or poorly developed. Petioles 3–26 mm long, 0.7–2.5 mm in diameter, glabrous to moderately villous or velutinous, sparsely to densely glandular. Stipules ovate, ovate-oblong, or elliptic; apex acute, obtuse, or rounded; 3–9 mm long, 2–5 mm wide, green or light brown, glabrous to sparsely pubescent, moderately glandular; pubescence whitish to yellowish; glands yellowish. Pistillate inflorescences borne in racemose clusters of 2–10 at the apices of short shoots, the lowermost often appearing somewhat separate from the group and subtended by reduced leaves, produced with new growth in the spring, more or less erect, ovate to cylindric, at anthesis 5–8 mm long, 1.5–2.5 mm in diameter, on peduncles 2–18 mm long, 0.2–0.8 mm in diameter; staminate catkins borne in a single racemose cluster of 2–4 at the end of the main branch above the pistillate inflorescences, produced during the previous growing season, erect during dormancy, pendent at anthesis, at anthesis 2.5–14 cm long, 5–12 mm in diameter, on peduncles 0.2–2 mm long, 0.5–2 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers (2–) 3 per bract; perianth of 4 (–5) parts, these elliptic to obovate, rounded at the apex, 1.1–1.4 mm long, 0.7–1.2 mm wide, with conspicuous medium to large glands along the margin; stamens 4 (or rarely 5), opposite, separate from, and usually appearing much longer than the perianth parts; filaments 0.7–1.7 mm long; anthers 1–1.7 mm long and 0.7–1.3 mm in diameter, the thecae separate for 40–80% of their length. Infructescences ovoid to ellipsoid or cylindric, 8–23 mm long, 4–16 mm in diameter, on peduncles 3–20 mm long, 0.5–1.2 mm in diameter; scales 3–6 mm long, 2.7–4.5 (–6) mm wide at the apex, 0.7–1.7 mm wide at the base, the apex thin to moderately thickened, flat, the terminal lobe-tip acute and somewhat extended. Fruits winged, light yellowish brown; body elliptic to obovate, 1.7–3.2 mm long, 1.2–2 mm in diameter; wings obovate, extending beyond the apex of the body, 2.5–4 mm long, 0.7–2 mm wide at the widest point, membranaceous; persistent styles 0.3–0.8 mm long.

Alnus viridis has a circumpolar distribution with a gap in northern Europe. Subspecies *crispa* and *sinuata* in northern and northwestern North America, respectively, occur as well in adjacent northeastern Asia, being replaced there to the south by subspecies *maximowiczii* (Callier) Löve & Löve, and to the west by subspecies *viridis*.

This species is perhaps the easiest of our taxa to identify because of its distinctive sub-sessile, multi-scaled buds and long, thin infructescence peduncles. Although most present keys and descriptions state that the winter buds of *Alnus viridis* are sessile, they are, in fact, always at least somewhat short-stipitate. The inflorescences are generally subtended by leaves or leafty bracts, these being narrower, more rounded at the tip, more obovate, and more cuneate at the base than the normal vegetative leaves. This is by far the most glutinous and fragrant-leafed of the American species of the genus.

9a. **Alnus viridis** ssp. **crispa** (Aiton) Turrill

Alnus viridis ssp. *crispa* (Aiton) Turrill, Curtis' Bot. Mag. **173:** tab. 382. 1962; *Betula crispa* Aiton, Hort. Kew. **3:** 339. 1789; *Betula alnus crispa* (Aiton) Michaux, Fl. Bor. Amer. **2:** 181. 1803; *Alnus crispa* (Aiton) Pursh, Fl. Amer. Sept., p. 623. 1814; *Alnus alnobetula* var. ζ. *crispa* (Aiton) Winkler, Pflanzenreich **19**(4.61): 107. 1904; *Alnus viridis* var. *crispa* (Aiton) House, Bull. N.Y. St. Mus. **254:** 271. 1924; *Alnaster crispus* (Aiton) Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Akad. Sci. U.R.S.S. **17:** 96. 1955. *Duschekia crispa* Pouzar, Preslia **36:** 339. 1964. Type: "nat. of Newfoundland and Hudson's Bay" (Holotype, BM).

Alnus undulata Willdenow, Sp. Pl. ed. 4, **4**(1): 336. 1805. Type: "habitat in Canada" (B?, not seen).

Alnus viridis α Hooker, Fl. Bor.-Amer. **1:** 157. 1838, *nom. illeg.*

Alnus repens Wormskjold ex Hornemann, Fors. Dansk. Oecon. Pl. ed. 3, **1:** 957. 1821; *Alnus ovata* var. *repens* (Hornemann) Wormskjold ex Lange, Fl. Dan. **16**(46): 12, tab. 2738. 1871; *Alnus ovata* f. *repens* (Hornemann) Kjellman *in* Nördenskjold, Vege. Exp. Vet. Aktt. **2:** 52. 1883; *Alnus alnobetula* var. ϵ. *repens* (Hornemann) Winkler, Pflanzenreich **19**(4.61): 107. 1904; *Alnus alnobetula* var. a. *typica* f. *repens* (Hornemann) Callier *in* Schneider, Ill. Handb. Laubh. **1:** 121. 1904; *Alnus viridis* var. *repens* (Hornemann) Callier, Fedde Rep. Sp. Nov. **10:** 225. 1911; *Alnus viridis* var. *repens* f. *typica* Callier, Fedde Rep. Sp. Nov. **10:**

225. 1911; *Alnus viridis* I. *typica* d. *repens* (Hornemann) Ascherson & Graebner, Syn. Mitteleur. Fl., p. 415. 1911. Type: "Leutenant Wormskiold har fundet den i det sudlige og Prof. Gieseke i det nordlige Gronland" (not seen).

Alnus orbiculata Lopylaie ex Spach, Ann. Sci. Nat. ser. 2, **15:** 201. 1841, *pro syn.*

Alnus mitchelliana Curtis ex A. Gray, Amer. Jour. Sci. **42:** 42. 1842. Type: *Gray & Carey s.n.*, in monte Roan dicto, Carolina Septentrionalis, July, 1841 (Lectotype, GH!; isolectotypes, MO!, NY!).

Alnus(*Alnobetula*) *fruticosa* Ruprecht, Beitr. Pfl. Russ. Reich. **2:** 53. 1845; *Alnaster fruticosus* (Ruprecht) Ledebour, Fl. Ross. **3**(2): 655. 1850; *Alnus viridis* * *A. fruticosa* (Ruprecht) Nyman, Conspect. Fl. Europ., p. 672. 1881; *Alnus alnobetula* var. *β* . *fruticosa* (Ruprecht) Winkler, Pflanzenreich **19**(4.61): 106. 1904; *Alnus fruticosa* var. a. *typica* Callier *in* Schneider, Ill. Handb. Laubh. **1:** 121. 1904; *Alnus fruticosa* var. *typica* f. *normalis* Callier, Fedde Rep. Sp. Nov. **10:** 227. 1911; *Alnus fruticosa* var. *typica* forma *vulgaris* Callier, Fedde Rep. Sp. Nov. **10:** 226. 1911; *Duschekia fruticosa* (Ruprecht) Pouzar, Preslia **36:** 339. 1964. Type: "in sylvis ad fl. Mesen fere ubique, hic terminus maxime occidentalis videtur fruticis per Siberiam facile totam (v.g. Ircutzk! Baical!) ad Kamtschatkam ins Karaginsk! Unalaschkam! et Sitcham! usque diffusi" (LE?, not seen).

Alnus viridis β sibirica Regel, Mem. Soc. Nat. Mosc. **13**(2): 137. 1861, in part; *Alnus viridis* var. *sibirica* (Regel) Callier, Mitt. Deutsch. Dendr. Ges. **27:** 49. 1918, erroneously attributed to Regel, in part.

Alnus viridis β sibirica lusus a. *communis* Regel, Mem. Soc. Nat. Mosc. **13**(2): 138. 1861, in part.

Alnus viridis β sibirica lusus c. *subglabra* Regel, Mem. Soc. Nat. Mosc. **13**(2): 138. 1861. Type locality: "aus Dahurien, vom Kotzebouesund, aus Kamtschatka, Sitka, Grönland und Labrador" (original material not seen).

Alnus tristis Wormskjold ex Regel, Mem. Soc. Nat. Mosc. **13**(2): 138. 1861, *pro syn.*

Alnus viridis β, parvifolia Regel *in* De Candolle, Prodromus **16**(2): 183. 1868, in part; *Alnus alnobetula* a. *parvifolia* (Regel) Dippel, Handb. Laubh. **2:** 146. 1892, in part; *Alnus alnobetula* var. *θ. parvifolia* (Regel) Winkler, Pflanzenreich **19**(4.61): 107. 1904, excl. American element; *Alnus viridis* var. *parvifolia* Sauter ex Winkler, Pflanzenreich **19**(4.61): 107. 1904, *pro syn.* Type locality: "in alpibus altioribus Helvetiae australis, in alpibus tyrolensibus et in Labrador" (original material not seen).

Alnus ovata var. *repens* f. *macrophylla* Lange, Med. om Gronl. **3:** 280. 1887. Type: *Majuola*, Greenland (Holotype, S).

Alnus fruticosa var. *typica* f. *macrophylla* Callier, Fedde Rep. Sp. Nov. **10:** 226. 1911. Original material not seen.

Alnus mollis Fernald, Rhodora **6:** 162. 1904; *Alnus crispa* var. *mollis* (Fernald) Fernald, Rhodora **15:** 44. 1913; *Alnaster crispa* f. *mollis* (Fernald) Murai, Bull. Gov. For. Expt. Sta. Jap. **171:** 36. 1964, *pro syn; Alnus crispa* f. *mollis* (Fernald) Murai, Bull. Gov. For. Expt. Sta. Jap. **171:** 36. 1964, *pro syn.* Type: *Fernald, s.n.*, Maine, rocky river bank, Orono, May & Aug. 1890 (Lectotype, GH!). Figure 56.

Alnus fruticosa var. *typica* f. *grandifolia* Callier, Fedde Rep. Sp. Nov. **10:** 227. 1911. Original material not seen.

Alnus viridis var. d) *repens* f. 1. *groenlandica* Callier, Mitt. Deutsch. Dendr. Ges. **27:** 48. 1918. Type locality: Grönland, Labrador (original material not seen).

Alnus viridis var. *sibirica* lus. c. *glabra* Callier, Mitt. Deutsch. Dendr. Ges. **27:** 49. 1918, erroneously attributed to Regel (probably intended to refer to *Alnus viridis β sibirica* lusus *subglabra* Regel), *nom. illeg.*

Alnus viridis var. *fernaldii* House, Bull. New York St. Mus. **254:** 271. 1924. Original material not seen.

Alnus crispa var. *elongata* Raup, Jour. Arn. Arb. **17:** 243. 1936. Type: *Raup & Abbe 4665,* Alberta, sandy beach on the north shore of Lake Athabasca a few miles west of Sand Point, Sept. 9, 1932 (Holotype, GH!; isotypes, CAN!, F!, MO!, US!).

Alnus crispa f. *stragula* Fernald, Rhodora **47:** 144. 1945. Type: *Pease & Smith 25707,* Quebec, Matane Co., Mt. Logan, July 13, 1923 (Holotype, GH!).

Alnus crispa var. *harricanensis* Lepage, Le Natr. Canad. **77:** 44. 1950. Type: *Dutilly & Lepage 15164,* Quebec, riviere Harricana, sur une ile granitique a environ trois milles en bos de l'embouchure de la riviere Samson, 2 juillet 1946 (Holotype, CAN!; isotype, GH!).

Spreading shrubs up to 6 (–9) m in height; trunks ascending to decumbent where the climate is severe, up to ca. 10 cm in diameter; bark light gray, smooth; young stems usually strongly differentiated into long and short shoots, often with prominent longitudinal ridges originating at the nodes; internodes glabrous to velutinous, densely glandular; lenticels of twigs 0.5–1 mm long, 0.3–0.7 mm wide, whitish, often quite conspicuous; leaf scars 1–2 mm high, 1.7–3.5 mm wide, the bundle scars inconspicuous. Leaves broadly to narrowly ovate or elliptic; apex usually obtuse (sometimes acute or rounded); base acute, obtuse, or rounded, sometimes cordate; blade (2–) 3.5–8.5 (–15.5) cm long, (1.3–) 3–6 (–12.8) cm wide, medium to dark green and dull (lustrous when young) above, light to medium green and dull to moderately lustrous below, coriaceous; margin slightly to much thickened, finely double-serrate or serrulate; major teeth (3–) 5–11 (–25) mm apart at mid-leaf, up to 4 mm deep, irregular; secondary teeth (5–) 8–15 (–18) per cm, 0.5–2.5 mm deep, irregular; adaxial surface glabrous to sparsely pubescent, sparsely to moderately glandular; abaxial surface and veinlets glabrous to velutinous, moderately to densely glandular, moderately to heavily resin-coated; pubescence whitish to yellowish or brownish; glands small to medium in size, yellowish to brownish. Lateral veins 7–12, 3–9 (–11) mm apart at mid-leaf. Petioles (3–) 5–15 (–24) mm long, 0.7–1.5 (–2.5) mm in diameter, glabrous to moderately villous or velutinous, sparsely to densely glandular. Stipules ovate, ovate-oblong, or elliptic, the apex obtuse to rounded, 7–9 mm long, 2–5

Figure 56. Specimen of *Alnus viridis* ssp. *crispa* (Aiton) Turrill. Lectotype of *Alnus mollis* Fernald.

Figure 57. Specimen of *Alnus viridis* ssp. *crispa* (Aiton) Turrill.

mm wide. Pistillate inflorescences at anthesis 5–8 mm long, 1.5–2.5 mm in diameter, on peduncles 2–7 mm long, 0.4–0.8 mm in diameter; staminate catkins at anthesis 2.5–9 (–12) cm long, 5–10 mm in diameter, on peduncles 0.2–1 mm long, 0.5–1 (–2) mm in diameter. Filaments of stamens 0.7–1 mm long; anthers 1–1.5 mm long, 0.7–1.3 mm in diameter, the thecae separate for 50–80% of their length. Infructescences 11–15 (–20) mm long, 0.5–1.2 mm in diameter; scales 4–6 mm long, 2.7–4.5 (–6) mm wide at the apex, 0.7–1.2 mm wide at the base, the apex moderately thickened. Fruits winged, light brown; body elliptic to obovate, (2–) 2.5–3.2 mm long, (1.2–) 1.5–2 mm in diameter; wings 2.5–5 mm long, (0.7–) 1–2 mm wide at the widest point; persistent styles (0.3–) 0.6–1 mm long. Figures 2D, 7D, 9D, 13A, 56, and 57.

DISTRIBUTION AND HABITAT: Alaska and adjacent Siberia east to northern Labradór and the southwestern coast of Greenland, south to northern California, south-central Alberta and Manitoba, northern Minnesota, Wisconsin, and Michigan, southern Ontario, central New York, and northern Massachusetts; disjunct populations in south-central Pennsylvania and west-central North Carolina (on the border with Tennessee). Occurring singly or forming dense thickets along streams, lakeshores, coasts, and bog or muskeg margins, or on sandy or gravelly slopes or flats from near sea level in the North to about 2,000 meters in New Hampshire (1,900 meters in North Carolina). Often growing with *Picea, Pinus, Populus, Salix,* or *Betula,* usually in sandy, gravelly, or rocky soil. Figure 58.

COMMON NAMES: Green alder, mountain alder, alder, aulne vert (Quebec).

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA. 6 mi SSE of Ellscott, *Dumais & Rankin 1002* (CAN); about 1 mi SW of Smith, *Furlow 267* (MSC); Saskatchewan Mountains, SE of Jasper, *Malte 10* (CAN); Saskatoon Mountains near Beaverlodge, Peace River District, *Raup 1941* (DAO); on N shore of L Athabasca just W of Sand Point, *Raup & Abbe 4665* (CAN, F, GH, MO, US); 1 mi N of Kootenay Crossing, *Taylor & Ferguson 2555* (DAO). BRITISH COLUMBIA. Quarantine Lake, about 20 mi W of Victoria, Vancouver Island, *McCabe 5551* (UC); Muncho Lake, Alaska Highway, *Szczawinski s.n.,* July 27, 1962 (DAO). LABRADOR. Flint Island, near Port Manvers, *Bryant 103* (GH); Goose Bay, *Gillett & Findlay 5541* (NY, RM, UC, US, WTU). MANITOBA. 7 mi SW of Lac Du Bonnet, *Breitung 7777* (DAO); Clear Lake, *Heimburger s.n.,* July 27, 1939 (CAN); Whiteshell Forest Reserve, E of Winnipeg, *Scoggan 10606* (CAN). NEW BRUNSWICK. Gloucester Co.: bank along Tete-a-Gouche River, Bathurst, *Blake 5474*

(GH, NY, US). King's Co.: Springfield, *Roberts & Bateman 64-401* (DAO). York Co.: McAdam, *Dore 9839* (DAO). NEWFOUNDLAND. SE of Tompkins, 1 mi N of St. Andrews, Codroy Valley, *Bassett 840* (DAO); Burchy Cove (Curling), *Fernald & Wiegand 3275* (A, CAN, GH, NY); St. John's, *Robinson & Schrenk 24* (CAN, GH, MO, NY). NORTHWEST TERRITORIES. Keewatin District: NW extremity of Nuettin Lake, Little River, 1 mi above mouth, *Harper 2225* (CAN); McConnell R., 7 mi inland from mouth, *MacInnis 42* (DAO); Beralzon Lake, *Scoggan & Baldwin 8366* (CAN). Mackenzie District: Great Bear Lake, Gunbarrel Inlet, *Cody 2852* (DAO); Aklavik, Mackenzie River Delta, *Cody & Ferguson 9680* (DAO); valley of Caribou Hills behind Reindeer Station, *Cody & Ferguson 10442* (DAO); S shore of Mackenzie River 2 mi E of Trout River, *Cody & Matte 8631* (DAO); Yellowknife, N end of Kam Lake, *Cody & McCanse 2166* (DAO); Louise Falls on Hay River, *Lewis 387* (DAO); Moraine Point, Great Slave Lake, *Lewis 469* (DAO); NW shore of Thelon River, ca. 20 mi SW of Hornby Pt., *Rossbach 6435* (CAN). NOVA SCOTIA. Annapolis Co.: Roadside, Lily Lake, North Mountain, *Smith et al. 10521* (CAN). Digby Co.: Centreville, common alder at edge of Midway Lake, *Smith et al. 15450* (DAO). Kings Co.: Newtonville, *Cunningham s.n.*, July 30, 1957 (DAO). Pictou Co.: without location, *Robinson 577* (NY); roadside thickets near Pictou, *Smith et al. 13572* (DAO). Yarmouth Co.: dry fields and clearings near St. John (Wilson's) Lake, *Fernald et al. 23776* (GH). ONTARIO. Algoma District: 12 mi S of Wawa, Lake Superior Prov. Park, *Furlow 309* (MSC). Kenora District: Kenora, *Dudley s.n.*, July 8, 1939 (DAO); Kenora, *Young s.n.*, May 21, 1940 (DAO). Thunder Bay District: Terrace Bay, *Crow 1293* (MSC); 1 mi S of Fort William, *Garton 2492* (DAO). PRINCE EDWARD ISLAND. Prince Co.: O'Leary, borders of second growth woods, *Erskine 1950* (DAO). Queens Co.: Wood Islands, cleared edge of swampy ground, *Erskine 1313* (DAO, NY). QUEBEC. Baie James Co.: Beaver River, islands in, *Baldwin et al. 559* (CAN); Harricanaw Riv., James Bay, *Dutilly & Lepage 15164* (CAN, DAO). Gaspe Co.: Riviere a Claude, *Chrysler s.n.*, Aug. 4, 1935 (US); SW side of Mt. St. Pierre, *Clausen & Trapido 2905* (UC); sea-cliffs, Cap Blanc, Pruce, *Collins et al. s.n.*, Aug. 17, 1904 (GH); rocky baut, Gaspe Bay, *Collins et al. s.n.*, Aug. 25, 1904 (GH); on bank of St. Lawrence River near Ruisseau, Castor, *Cooley & Pease 6727* (GH); on terraces and bluffs, Ste. Anne des Monts, *Fernald & Collins 534* (A, CAN, GH); Allen's Ravine, N slope of Mt. Albert, *Fernald & Collins 585* (GH). Isles de la Madeleine Co.: Amherst, *Johansen s.n.*, July, 1917 (CAN). Kamouraska Co.: Lac Disparu, Ste-Anne-de-la-Pocatiere, *Hamel 573* (DAO). Matane Co.: Razorback Ridge, Mt. Logan, *Pease & Smith 25707* (GH). Mistassini Co.: Riviere Takwa, dans un bois tourbeus le long du premier portage, *Rosseau & Rouleau 940* (GH). Nouveau-Quebec: Baie d'Hudson, *Brisson & Forest 20784* (UC). Riviere-du-Loup Co.: Riviere-du-Loup, 3 mi N de la ville, *Hamel & Payette 837* (DAO); Saint-Epiphane, *Lemieux 7411* (DAO). SASKATCHEWAN. S shore of Lake Athabasca, E of William River, *Argus 446-62* (DAO); Cree Lake, *Maini 201* (DAO, RM); Archibald R., vicinity of Wolverine Pt., L. Athabasca, *Raup 6740* (CAN, NY); 2 mi S of Reserve, *Rowe 234* (DAO). YUKON TERRITORY. Dawson, *Anderson 1578* (NY); Rampart House, *Loan 669* (DAO, UC); Mackenzie River Delta, Aklavik, *Porsild & Porsild 1864* (CAN). **Greenland.** Sydvestgrönland, *Dahl s.n.*, Sept. 17, 1937 (CAN); Groenl. Occid., ca. Neria 61° 33′ N lat. bor., *Eugenius s.n.*, June 30, 1928 (CAN); Groenl. Occid., ca. Neria 61° 33′ N lat. bor., *Eugenius s.n.*, June 26, 1930 (F, MO, US); Björnedalen v. Ivigtut., *Grontved 736* (CAN, DAO); Torssukatak, *Hansen et al. 1890*

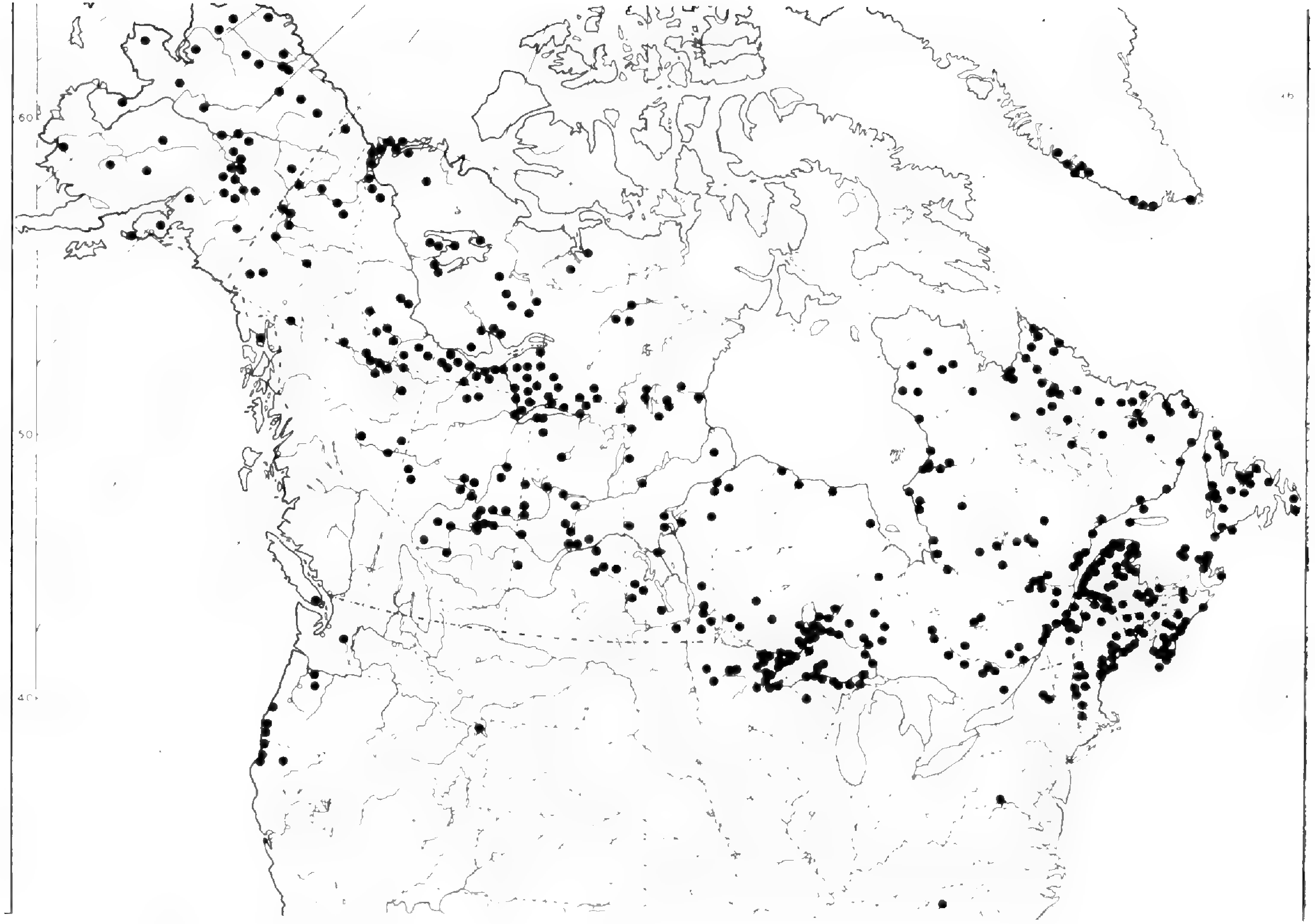


Figure 58. Distribution of *Alnus viridis* ssp. *crispa* (Aiton) Turrill in North America.

(CAN); 64° 12′N Lat., *Lyngl. sn.*, Sept. 6, 1927 (CAN, MO, RM); FREDERIKSHAAB DISTR., *Porsild 7975* (CAN); SYD.-GRONL., Bjornedal. Arsuk-Fjord, *Porsild & Porsild s.n.*, July 13, 1925 (CAN, GH, NY). **United States.** ALASKA. Talkeetna, *Anderson 7620* (CAN); College, University of Alaska Campus, *Anderson s.n.*, Sept. 6, 1971 (MSC); Killik R. valley, *Cantlon 4799* (MSC); Big Delta Camp area, Richardson Highway, *Cody 6254* (DAO); 6 mi E of Delta Junction, *Cody & Webster 4890* (DAO); between Circle and Central Road House, *Cody & Webster 5362* (DAO); Rampart, *Hollich s.n.*, July 10, 1903 (NY); Anchorage area, *York 361* (F). CALIFORNIA. Del Norte Co.: near coast meadows, Crescent City, *Dudley s.n.*, July 1, 1899 (DS); Coopers Flat, Smith River, *Parks & Parks 24152* (DS, NY, RM, UC, WTU); adjacent to S end of Elk Valley, *Tracy 19180* (UC); 1 mi S of Crescent City, *Wolf 9097* (DS, NY). Siskiyou Co.: Spirit Lake, Marble Mts., *Howell 14956* (DS). MAINE. Androscoggin Co.: Norway, *Smith s.n.*, May 1, 1865 (NY). Aroostook Co.: gravelly shores, St. Francis, *Fernald 98* (MSC, NY, RM, UC). Penobscot Co.: rocky river bank, Orono, *Fernald s.n.*, May and Aug., 1890 (GH). MASSACHUSETTS. Franklin Co.: Charlemont, *Churchill & Woodward s.n.*, May 15, 1915 (UC); Shelburne, banks of Deerfield River, *Forbes s.n.*, May 11, 1912 (UC). MICHIGAN. Alger Co.: Pictured Rocks, Lake Superior, *Wheeler s.n.*, Aug. 28, 1900 (MSC). Baraga Co.: tip of Point Abbaye, on maple woods border near lake shore, *Beaman 1829* (MSC). Houghton Co.: edge of pond in Jacobsville Quarry, *Richards 3622* (DAO). Keewenaw Co.: rocky shore of Lake Superior, 3 mi NW of Copper Harbor, *Bennett 33* (F). Schoolcraft Co.: thickets on E bank of Manistique River, 5 mi NW of Blaney Park, *Voss 9935* (MSC). MINNESOTA. Clearwater Co.: Itasca Park, Douglas Lodge, *Grant 3125* (F, MO, NY, UC). Cook Co.: on the Lake Superior shore 1½ mi N of Cascade River, *Furlow 314* (MSC). St. Louis Co.: 18th St. on Minnesota Ave., Duluth, *Lakela 1681* (F, NY, US). NEW HAMPSHIRE. Coos Co.: Mt. Washington at 5500 ft. altitude among rocks at the base of the summit cone and Bigelow's lawn, *Churchill s.n.*, July 10, 1937 (MSC); Tuckerman's Ravine Trail, Mt. Washington, *Eggleston & Eggleston 22353* (NY); upper wall of Tuckerman's Ravine, *Kennedy s.n.*, July 10, 1891 (RM). Grafton Co.: White Mountains, *Chickering s.n.*, July 15, 1877 (F). NEW YORK. Essex Co.: Whiteface Mountain, Adirondacks, *Dore 14274* (DAO); shore of Elk Lake, North Hudson, *House 25957* (UC). NORTH CAROLINA. Mitchell Co.: Roan Mtn., *Alexander s.n.*, June 23, 1939 (NY); Roan Mountain, near the lower edge of the spruce forest zone, *Furlow 251* (MSC); in monte Roan dicto Carolina Septentrionalis, *Gray & Cary s.n.*, July, 1841 (GH, MO, NY); summit Roan, *Gray et al. s.n.*, in 1879 (A); Roan Mountain, *Rydberg 8269* (NY). OREGON. Clackamas Co.: Government Camp Meadow, vicinity of Mt. Hood, *Abrams 11373* (DS). Coos Co.: cliffs at Bandon Beach, *Abrams & Benson 10620* (DS, RM). Curry Co.: in coastal scrub, about 600 ft. back from the ocean, about 7 mi S of Ophir, *Bacigalupi 8976* (JEPS); Cape Blanco, *Ferris & Lorrains 10629* (DS, UC); Brookings, *Kildale 8498* (DS). PENNSYLVANIA. Bedford Co.: ⅜ mi ENE of Martin Hill Fire Tower, *Berkheimer 9883* (UC). TENNESSEE. Carter Co.: Roan Mountain, *Hernandez et al. 11739* (DAO, DS, MSC, NY). VERMONT. Chittenden Co.: Mt. Mansfield, *Pringle s.n.*, June 5 and 6, Aug. 10, 1877 (F, US). Washington Co.: Plainfield, *Eggleston s.n.*, May 20, 1894 (NY). WASHINGTON. Snohomish Co.: Stevens Pass Region, Cascade Mountains, *Grant s.n.*, May, Aug. 1929 (UC). WISCONSIN. Bayfield Co.: along Lake Superior Shore at tip of Bayfield Peninsula, *Voss 10030* (MICH). Douglas Co.: Sauntry Lake, *Wilson 1755* (RM). Vitas Co.: highest ground E of Diamond L., *Fassett 13778* (MO). WYOMING.

Park Co.: S shore of Yellowstone Lake, *Adams s.n.*, Aug. 9, 1871 (US); timber reserve, Crandall Creek, *Rose 287* (US).

This subspecies is often difficult to distinguish from ssp. *viridis* of mountainous central Europe on the basis of herbarium material. However, as noted by Turrill (1962), it possesses a significant number of differences, including taller growth, larger leaves, finer and more regular leaf serrations, longer and more slender petioles, and larger cones. Populations in northeastern Asia (frequently called *Alnus fruticosa*) are continuous with the American members, both in distribution and morphology (cf. Porsild, 1939), and are considered here as belonging to ssp. *crispa.*

In both Europe and America, the names *Alnus alnobetula* and *A. viridis* have been extensively used for this species, but in recent years segregating the New World form as a separate species, *A. crispa,* has been the most common treatment. The unity of *A. viridis* in Europe, America, and Asia seems to be gaining renewed recognition in the literature, however, and the results of the present studies support this view.

The leaves of *Alnus viridis* ssp. *crispa* occurring in Quebec, Ontario, Michigan, and adjacent areas are usually more or less pubescent below (*A. crispa* var. *mollis* Fernald). To the west and south this form passes gradually into the generally glabrous typical form. Other character differences do not correlate with the pubescent extreme, and the variety is therefore not recognized here. To the west, through northern Canada, the leaves become gradually narrower and the habit somewhat taller.

In northwestern North America the ranges of *Alnus viridis* ssp. *crispa* and ssp. *sinuata* overlap, and in this region is found an extremely variable apparent hybrid swarm (cf. Hultén, 1944). Where allopatric, the subspecies are easily distinguished by leaf texture and serration, although vigorous shoots of ssp. *crispa* often have very coarsely-toothed leaves, appearing much like those of ssp. *sinuata.*

Subspecies *crispa* has not heretofore been recognized as occurring in western North America south of northern British Columbia and central Alberta. Actually, it reaches the northern counties of California along the Pacific coast and, farther inland, northwestern Wyoming. Although no specimens from Montana or Idaho could be assigned to this subspecies, many appeared to be intermediate between it and ssp. *sinuata,* as frequently did specimens from Oregon, Washington, and southern British Columbia, suggesting that the putative hybrid swarm extends much further to the south than previously realized.

Throughout its normal range, *Alnus viridis* ssp. *crispa* occurs either along streams and in other damp places or in somewhat drier habitats. It is often found in rocky or sandy and acid soil, and occurs from low to subalpine elevations, depending on latitude and other ecological conditions. The subspecies occurs disjunctly on the summit of Roan Mountain on the North Carolina-Tennessee border in a population that has long interested American botanists (cf. Gray, 1842; Clarkson, 1960). Recently a second and intermediate disjunct population, lying in southern Pennsylvania, has been noted (Wherry, 1960). The habitat on the summit of Roan Mountain is described in detail by Brown (1941), who gives an account of the climate, soil, vegetational history, etc., together with an analysis of each of the various communities found there. *Alnus viridis* ssp. *crispa* occurs on Roan Mountain on "balds" in the spruce-fir forest occupied also by *Rhododendron* and grasses. The summit is often shrouded by clouds, and it is therefore very humid, a factor which may be important in the maintenance of this relict population so far south of the normal southern limit of its range.

9b. **Alnus viridis** ssp. **sinuata** (Regel) Löve & Löve

Alnus viridis ssp. *sinuata* (Regel) Löve & Löve, Univ. Colo. Stds. ser. Biol. **17:** 20. 1965; *Alnus viridis δ sinuata* Regel, Bull. Soc. Nat. Mosc. **38**(3): 422. 1865; *Alnus sinuata* (Regel) Rydberg, Bull. Torr. Bot. Club **24:** 190. 1897; *Alnus sinuata* var. a. *typica* Callier *in* Schneider, Ill. Handb. Laubh. **2:** 888. 1912; *Alnus fruticosa* var. *sinuata* (Regel) Hultén, Fl. Aleut. Isls., p. 153. 1937; *Alnus crispa* ssp. *sinuata* (Regel) Hultén, Fl. Alaska Yukon, p. 587. 1944; *Alnaster sinuatus* (Regel) Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17:** 97. 1955; *Alnus crispa* var. *sinuata* (Regel) Breitung, Canad. Fld.-Natrl. **71:** 51. 1957; *Duschekin sinuata* (Regel) Pouzar, Preslia **36:** 339. 1964; *Alnaster crispa* ssp. *sinuata* (Regel) Murai, Bull. Gov. For. Expt. Sta. Jap. **171:** 35. 1964, *pro syn.* TYPE: "in Kamtschatka und dem nordwestlichem Amerika" (LE?, not seen).

Alnus viridis β Hooker, Fl. Bor.-Amer. **1:** 157. 1838, *nom. illeg.*

Alnus viridis β sibirica Regel, Mem. Soc. Nat. Mosc. **13**(2): 137. 1861, in part.

Alnus viridis β sibirica lusus b. *sitchensis* Regel, Mem. Soc. Nat. Mosc. **13**(2): 138. 1861; *Alnus sitchensis* (Regel) Sargent, Silva of N. Amer. **14:** 61. 1902; *Alnus sitchensis* var. a. *typica* Callier *in* Schneider, Ill. Handb. Laubh. **1:** 123. 1904. TYPE: *Mertens* ?, "nur aus Sitka" (LE?, not seen).

Alnus viridis β sibirica lusus d. *kamtschatica* Regel, Mem. Soc. Nat. Mosc. **13**(2): 139. 1861; *Alnus kamtschatica* (Regel) Kudo ex Masamune, Jour. Jap. Bot. **10**: 498. 1934. Type: "nur aus Kamtschatka gesehen" (LE?, not seen).

Alnus glandulosa Sargent, Silva of N. Amer. **14**: 62. 1902, *pro syn,* erroneously attributed to J. Richardson *in* J. Franklin, Narr. Journ. Pol. Sea. 1823 (probably mistakenly referring to *A. glutinosa* in that account).

Alnus sitchensis var. b. *kamtschatica* Callier *in* Schneider, Ill. Handb. Laubh. **1**: 123. 1904; *Alnus sinuata* var. *kamtschatica* (Callier) Callier *in* Schneider, Ill. Handb. Laubh. **2**: 888. 1912; *Alnus fruticosa* var. *kamtschatica* (Callier) Komorov, Fl. Peinis. Kamtsch. **1**: 47. 1927; *Alnus kamtschatica* Komorov, Fl. S.S.S.R. **5**: 310. 1936, *non* Kudo ex Masamune, Jour. Jap. Bot. **10**: 498. 1934; *Alnaster kamtschaticus* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 96. 1955. Type locality: "nur Kamtschatka" (original material not seen).

Alnus alnobetula var. *η stenophylla* Winkler, Pflanzenreich **19**(4.61): 107. 1904; *Alnus sinuata* var. *stenophylla* Callier, Fedde Rep. Sp. Nov. **10**: 227. 1911. Type: *Elmer 365,* Clarkia, Kootenai Co., Idaho (Syntype, B?; isosyntype, NY!); *Elmer 887,* Cedar Mts., Latah Co., Idaho (Syntype, B?; isosyntype, NY!); *Rydberg & Bessey 3933,* Emigrant Gulch, Mont. (Syntype, B?; isosyntypes, NY!, RM!); *Sandberg, MacDougal, & Heller 427,* Cedar Mountain, Latah Co., Idaho (Syntype, B?; isosyntypes, DS!, NY!, US!).

Alnus crispa ssp. *sinuata* var. *laciniata* Hultén, Fl. Alaska Yukon, p. 598. 1944. Type: *Hutchison 595,* Kodiak, Pillar Mtn., July 2, 1936 (Holotype, H).

Spreading shrubs up to 10 m in height; trunks up to 13 cm in diameter, bark light gray to reddish-brown, smooth; young stems usually strongly differentiated into long and short shoots, the spur shoots usually much shorter than those of ssp. *crispa,* without pronounced longitudinal ridges; lenticels of twigs 0.3–1.2 mm long, 0.2–1 mm wide, yellowish; leaf scars 1–2 mm wide, with moderately prominent bundle scars; internodes glabrous (rarely sparsely pubescent), sparsely to moderately glandular. Leaves narrowly to broadly ovate (or sometimes almost elliptic); apex acuminate, acute or obtuse; base rounded to cordate, often oblique; blade (3–) 4–9 (–14) cm long, (2–) 3–7 (–10) cm wide, light (usually yellowish) to medium green and dull to moderately lustrous above, light to medium yellowish green and moderately to very lustrous below, membranaceous to chartaceous; margin slightly thickened, double-serrate; major teeth (6–) 8–13 (–22) mm apart at mid-leaf, up to 6 mm deep, slightly uneven to regular; secondary teeth 6–14 per cm, 0.3–3 mm deep, slightly uneven to irregular; adaxial surface glabrous to sparsely pubescent, sparsely to moderately glandular; abaxial surface and veinlets glabrous to sparsely pubescent, lightly resin-coated; pubescence whitish to yellowish; glands small to medium, yellowish to brownish. Lateral veins 7–11, (3–) 5–7 (–13) mm apart at mid-leaf. Petioles (4–) 8–16 (–26) mm long, 0.8–1.8 mm in diameter, glabrous to sparsely pubescent, moderately to densely glandular. Stipules ovate, the apex acute, 3–3.5 mm long, 2.3–3 mm wide. Pistillate inflorescences at anthesis 6–8 mm long, 2–2.5 mm in diameter, on peduncles 2–18 mm long, 0.4–0.8 mm in diameter; staminate catkins at anthesis 2.5–13.5 cm long, 5–12 mm in diameter, on peduncles 0.2–2 mm long, 1.2–2 mm in diameter. Stamens with filaments 1.2–1.7 mm long; anthers 1–1.6 mm long, 0.8–1.2 mm in diameter, the thecae separate for 40–50% of their length. Infructescences (10–) 14–20 (–23) mm long, (6–) 8–13 mm in diameter, on peduncles 4–19 mm long, 0.7–1.2 mm in diameter; scales 3–5 mm long, 3.5–4.5 mm wide at the apex, 1–1.8 mm wide at the base, the apex thin to moderately thickened. Fruits light yellowish brown; body elliptic to obovate, 1.7–2.5 mm long, 1.2–2 mm in diameter; wings 2.7–4 mm long, 0.9–1.5 mm wide at the widest point; persistent styles 0.5–0.7 mm long. Figures 3D, 14D, 18D, 22F, and 59.

Distribution and Habitat: Alaska and adjacent Siberia east to western Yukon Territory, south to northern California, southern Idaho, and northwestern Wyoming. Occurring singly or in open to dense thickets along gravelly or rocky streambanks, lakeshores, and coasts; on moist rocky slopes, outcrops, and avalanche trails; and in open coniferous woodlands from near sea level along the Pacific coast from Alaska to northern California, to the subalpine zone at elevations over 2,500 meters in Montana and Idaho. Often associated with *Picea, Pinus, Salix,* or *Populus.* Figure 60.

Common Names: Sitka alder, mountain alder, alder.

Representative specimens: **Canada.** ALBERTA. The Whistlers, Jasper, *Comte 1658* (MO); Cavell Creek, *Macoun s.n.,* Aug. 17, 1917 (F, NY); Lake Louise, *McCabe 5236* (UC); Banff National Park, 2 mi SW of Eisenhower Junction, *Mosquin & Seaborn 7161* (DAO); Banff, Stony Squaw Mt., *Sanson 1630* (DAO). BRITISH COLUMBIA. A few mi N of Lower Post Alaska Highway, *Calder & Gillett 24470* (DAO, US, WTU); upper Victoria Lake, near S end of Moresby Island, *Calder & Taylor 35789* (DAO); 10 mi NW of Houston on road between Smithers and Burns Lake, *Calder et al. 12863* (UC, WTU); trail to summit of Mt. Arrowsmith, Vancouver Island, *Calder et al. 16421* (DAO); rocky point N of Fraser River, Mission, *Ledingham 49–508* (DAO); Cowichan Lake, *Spreadborough s.n.,* May 24, 1911 (CAN). NORTHWEST TERRITORIES.

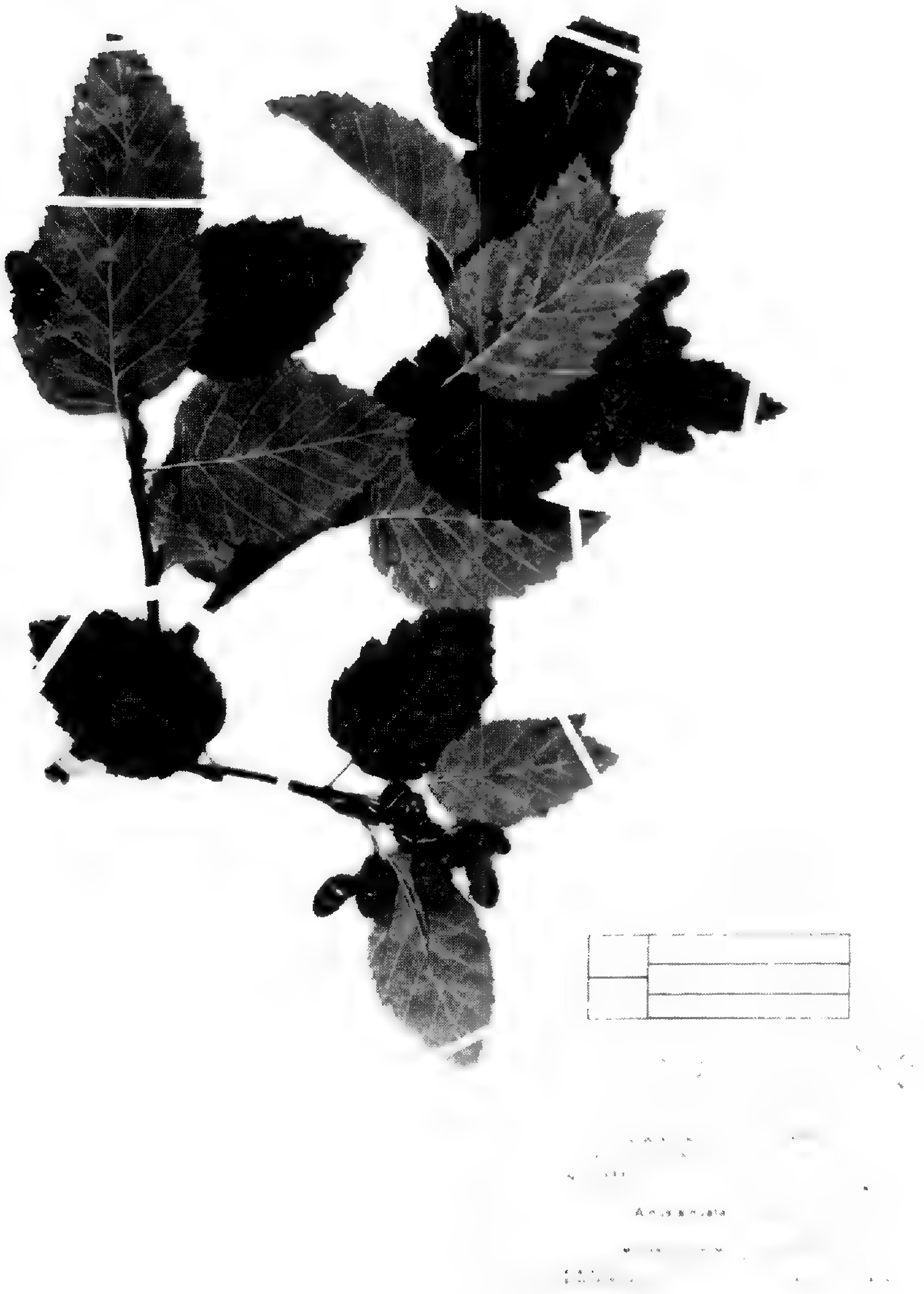


Figure 59. Representative specimen of *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve.

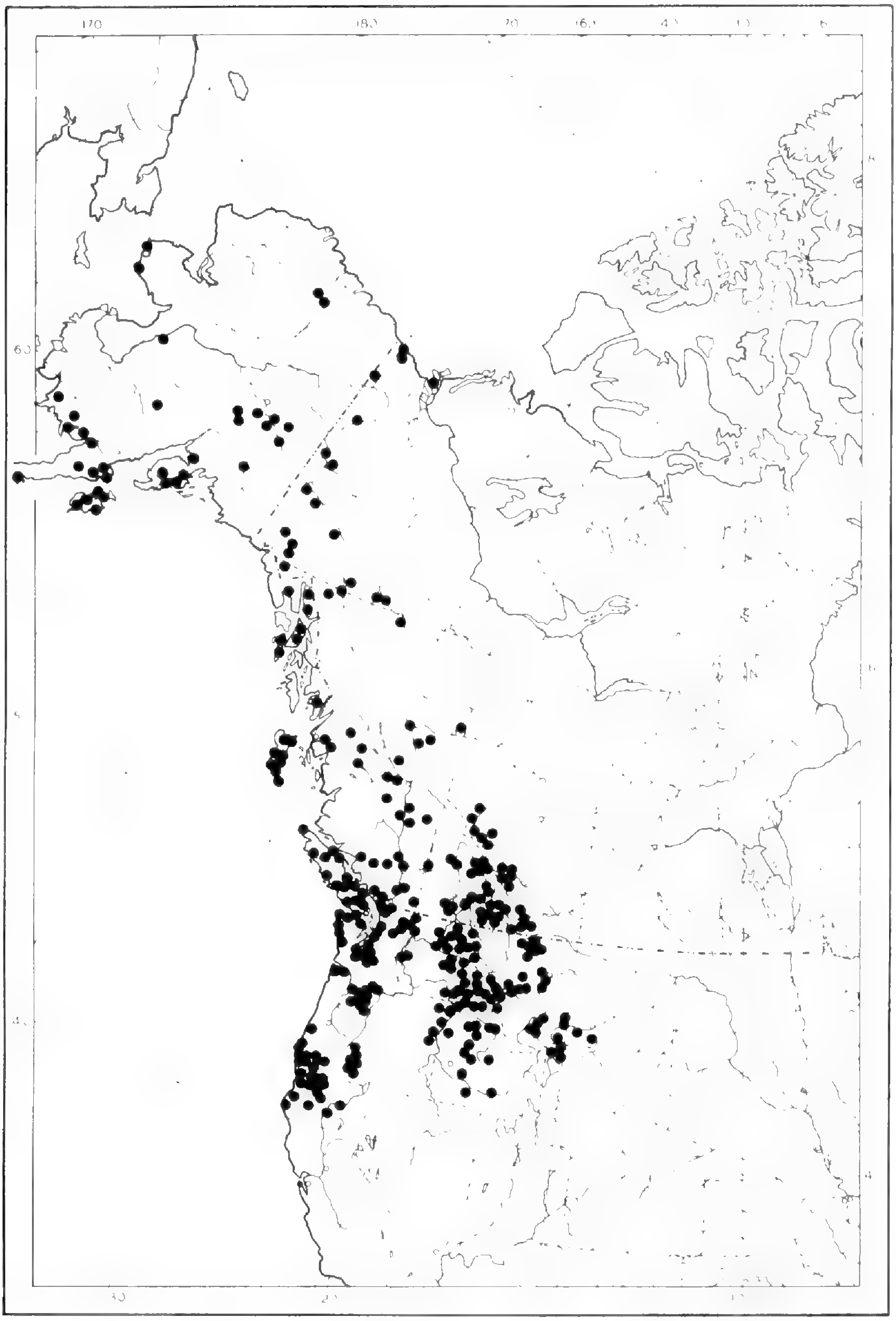


Figure 60. Distribution of *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve in North America.

Mackenzie District: Mackenzie Delta, *Sowan 35* (DAO). YUKON TERRITORY. Moosehide Mtn., Dawson, *Calder & Billard 2879* (DAO); vicinity of Carcross, *Porsild 18460* (CAN). **United States.** ALASKA. Moose Pass, *Anderson 6479* (RM); Fairbanks Quadrangle, end of Ballaine Road at crest of hill, *Argus 435* (DAO, RM); junction of Ukak and Savanoski Rivers, *Cahalane 164* (US); about 1 mi on road to Kenai from Soldatna, Kenai Peninsula, *Calder 4995* (DAO); road from Palmer to Willow, bank of Little Susitna River, *Dutilly et al. 21868* (DAO, US); Washington Bay, Kuiu Island, along seashore, *Eyerdam 8167* (DAO, F); Kodiak Island, Kodiak, *Kincaid s.n.,* July 30, 1899 (CAN); Palmer Creek Road, S of Hope, Kenai Penninsula, *Langenheim 4255* (UC, WTU); between Fire Lake and Eklutna, *Lepage 23048* (DAO); Hyder, river flats, *McCabe 8459* (UC, WTU); Ketchikan Lakes, Revillagigedo Island, *McCabe 8612* (NY, UC); about Anchorage, *Nelson & Nelson 3506* (RM); Petersburg, *Palmer 681* (DAO). CALIFORNIA. Del Norte Co.: 2 mi N of Crescent City, *Abrams & Benson 10727* (US); coastal plain, Crescent City, *Parks 4290* (DS, F, NY, RM, UC); low flats E of Crescent City, *Tracy 13519* (UC, WTU). Humboldt Co.: Trinity Summit, near Box Camp, *Tracy 17913* (DS, UC). Salmon Mountain Range, along Sugar Creek, *Parker s.n.,* May 26, 1949 (UC). IDAHO. Bonner Co.: roadside, Priest River Exptl. Forest, *Daubenmire 44487* (WTU); Rock Creek, Upper Priest River, *Epling 7646* (F). Idaho Co.: 6 mi SW of Lolo Pass, Clearwater National Forest, *Furlow 284* (MSC). Latah Co.: Cedar Mountains, *Sandberg et al. 427* (DS, NY, US); W slope of Moscow Mountains, *Sharesmith 3561* (RM, UC, WTU). MONTANA. Flathead Co.: mountainside near Swan River E of Big Fork, *Butler 233* (NY). Glacier Co.: 3 mi E of Logan Pass, Glacier National Park, *Furlow 272* (MSC). Mineral Co.: near Taft, 5 mi SE of state boundary, *Bartlett & Grayson 1038* (NY). Missoula Co.: Silver Butte-Fisher Road, *Schmautz 367* (DAO). Park Co.: Emigrant Gulch, *Rydberg & Bessey 3933* (NY, RM); Kersey Lake, about 5 mi E of Cooke City, *Witt 1699* (MO, UC, WTU). Powell Co.: Garnet, *Scheuber s.n.,* June 1, 1901 (NY, UC). Ravalli Co.: 3 mi N of Lost Trail Pass, Bitterroot National Forest, *Furlow 282* (MSC). OREGON. Curry Co.: Brookings, *Abrams & Benson 10711* (DS, RM); just back of seashore, 3 mi N of Brookings, *Bacigalupi 2323* (DS, NY, US). Josephine Co.: head of Bolan Creek, Siskiyou Mountains, *Bacigalupi et al. 3469* (JEPS, UC). Multnomah Co.: Corbett, *Matthews 54* (UC). WASHINGTON. Gray's Harbor Co.: rocky talus slopes by trail to Mt. Colonel Bob, Olympic Mts., *Thompson 7319* (WTU). King Co.: Seattle, *Piper s.n.,* June 26, 1889 (UC). Kittitas Co.: wooded slopes along Boulder Creek, *Thompson 10701* (WTU). Pierce Co.: Chinook Pass, Mount Rainier National Park, *Furlow 288* (MSC). Snohomish Co.: by alpine stream along Perry Creek Trail, Cascade Mts., *Thompson 14539* (NY, UC, WTU). Stevens Co.: along the E side of Columbia River near Canadian boundary, *Rogers 412* (DS, NY, UC, WTU). Whatcom Co.: boulder glacier moraine, Mt. Baker, *Eaton s.n.,* July 28, 1908 (WTU). WYOMING. Park Co.: S of Camp 14, *Rose 356* (US).

Alnus viridis ssp. *sinuata* is usually considered a separate species, *Alnus sinuata,* in current manuals, although Hultén (1944) treats it as a subspecies of *Alnus crispa.* In northeastern Asia (as far south as Japan) this subspecies is usually known as *A. kamtschatica.* Although this name is usually credited to Komorov, his combination is a later homonym of that of Kudo. The relationship of *A. kamtschatica* to *A. viridis* ssp. *sinuata* has not been studied in detail, but from the specimens seen, it appears that the two taxa are identical. In the area of Japan, ssp. *sinuata* apparently hybridizes with ssp. *maximowiczii* where the ranges of these taxa come together, just as it does with ssp. *crispa* in Alaska and adjacent regions (cf. Hultén, 1944).

Subspecies *sinuata* is often difficult to distinguish from ssp. *crispa* in herbarium material except on the basis of leaf morphology. Its foliage is usually much thinner, lighter (and more yellowish) green, and much more coarsely toothed, sometimes even approaching a triply-serrate condition. The largest known member of this taxon grows in Saddle Mountain State Park, Oregon and has a trunk circumference of about 40 cm (Dixon, 1961).

Alnus subg. **Clethropsis** (Spach) Regel

Alnus subg. *Clethropsis* (Spach) Regel, Bull. Soc. Nat. Mosc. **38**(3): 421. 1865; *Clethropsis* Spach, Ann. Sci. Nat. ser. 2, **15**: 183. 1841; *Alnus* b. *Clethropsis* (Spach) Endlicher, Gen. Pl. suppl. **2**, p. 28. 1842; *Alnus* sect. *Clethropsis* (Spach) Sargent, Silva of N. Amer. **9**: 68. 1896; *Alnus* subg. *Gymnothyrsus* sect. *Clethropsis* (Spach) Murai, Bull. Gov. For. Expt. Sta. Jap. **171**: 40. 1964. TYPE SPECIES: *Alnus nepalensis* D. Don (lectotype).

Trees or large shrubs with several erect trunks; twigs and young branches not differentiated into a system of long and short shoots; buds stalked, covered with 2 equal, stipular, valvate scales. Leaves single-toothed; venation semicraspedodromous to eucamptodromous. Pistillate inflorescences solitary or in racemose clusters in leaf axils along the branch on short, stout peduncles, the staminate catkins forming one or more racemose clusters at the apex of this branch, the lowest several usually subtended by leaves; inflorescences produced during the current growing season, anthesis occurring in late summer or early autumn (near the end of the growing season), fruit maturation occurring the following spring (beginning of the next growing season); staminate flowers with 4 stamens. Fruits lacking wings.

Alnus subg. *Clethropsis* occurs only in eastern Asia and eastern North America. It is distinct from the other segments of the genus, especially in its autumn-flowering habit and unique leaf venation. As discussed above, fossil leaves closely matching those of modern representatives of this subgenus have been found in parts of the world not now within the ranges of these modern species, including western North America.

Spach, in creating the genus *Clethropsis,* named two species, *C. nepalensis* and *C. nitida.* The following year, 1842, Endlicher placed this taxon in the genus *Alnus* and established *Alnus nepalensis* as the type (the only species mentioned). Endlicher did not specify the rank of his infrageneric taxon, the first author to do so being Regel in 1865.

Strangely, most treatments recognizing this subdivision of the genus have not included *Alnus maritima* in spite of its distinct affinities with the southern Asian species, placing it instead in subgenus or section *Gymnothyrsus* (= subgen. *Alnus*). Murai (1964) finally placed this species with its true relatives, but he considered the group only a section of the large subgenus *Gymnothyrsus.* Subgenus *Clethropsis* is probably derived from ancestors similar to present species of subg. *Alnus,* but it is distinct in the same fundamental ways as subg. *Alnobetula* and deserves subgeneric status.

10. **Alnus maritima** Muhlenberg ex Nuttall

Alnus maritima Muhlenberg ex Nuttall, North Amer. Sylva **1:** 50. 1842; *Alnus maritima* Muhlenberg, Obs. Bot. Pl. Amer. Sept. **1:** 193. 1807, unpublished manuscript; *Alnus maritima α typica* Regel, Bull. Soc. Nat. Mosc. **38**(3): 428. TYPE: *Muhlenberg specimen 477* (collected by Bartram?) without location or date (LECTOTYPE OF FURLOW, 1977, PH!).

Betula-alnus maritima Marshall, Arbust. Am., p. 20. 1785; *Alnus metoporina* Furlow, Ann. Mo. Bot. Gard. **63:** 381. 1977. TYPE: *Furlow 205,* Delaware, Sussex Co.: 4 mi. south of Milford, on the west shore of Hudson's Pond, September 14, 1970 (NEOTYPE, MSC!). Figure 61.

Narrow-crowned shrubs or trees up to 10 (–26) m in height; trunks usually several, erect, up to 15 (–35) cm in diameter; bark light gray, turning reddish-brown or brown in age, smooth or slightly rough, the lenticels obscured; young stems light red-brown to greenish-brown or brown, slightly to moderately lustrous, slightly to moderately glaucous, lightly to moderately resin-coated, not differentiated into long and short shoots, often with longitudinal ridges originating at the nodes; internodes glabrous to sparsely pubescent and sparsely to densely glandular; nodes very densely glandular; pubescence yellowish to brown; glands brownish to dark brown; lenticels of twigs circular to elliptic, 0.1–0.3 mm long and wide, whitish, usually inconspicuous; leaf scars 0.7–2 mm high, 1.5–2.5 mm wide, bundle scars inconspicuous. Buds obovoid to ellipsoid, slightly rounded to rounded at the apex, without resinous coating to heavily resin-coated; stalk 1–2 mm long, 1–1.5 mm in diameter, sparsely pubescent to velutinous, very densely glandular; body 2.5–5 mm long, 1.5–2 mm in diameter; scales 2 (sometimes apparently absent from apical buds), stipular, equal, valvate, often incompletely covering the underlying organs, glabrous to moderately villous, glandular, the pubescence and glands usually obscured by the resin coating. Leaves elliptic, oblong, or obovate; apex acute, obtuse, or rounded; base acute to cuneate; blade (3–) 4.5–8 (–9) cm long, (1.8–) 2–4 (–5) cm wide, dark to very dark green and dull above, light brown or green-brown and dull to moderately lustrous below, moderately coriaceous, somewhat sticky when young; margin flat, slightly to moderately thickened, bearing low, single, relatively distant ascending teeth, each enlarged below at the tip into a single gland, 3–5 per cm, 0.2–1 mm deep, regular; adaxial surface glabrous or sparsely pubescent, moderately to densely glandular; abaxial surface and veinlets glabrous, moderately to densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base moderately to densely villous; pubescence whitish, yellowish, or brownish; glands small to medium, yellowish or brownish. Lateral veins (6–) 7–11 (–13), 4–10 mm apart at mid-leaf, moderately to strongly ascending, sometimes branching once again, especially near the base, terminating in peripheral veins or, less frequently, in teeth at the margin; cross veins between the lateral veins poorly developed. Petioles (5–) 10–17 (–20) mm long, 0.6–1.5 mm in diameter, glabrous, moderately to densely glandular. Stipules oblong-elliptic or obovate, the apex acute to obtuse, 3–4 mm long, 0.5–1.2 mm wide, green, brown, or red-brown, glabrous to sparsely pubescent, the hairs yellowish, moderately glandular, the glands yellowish. Pistillate inflorescences solitary in leaf axils (2 to 4 per branch), produced during the current growing season, erect, ovate, at anthesis 3.5–4.5 mm long, 1.5–3 mm in diameter, on peduncles 5–7 mm long, 1–1.5 mm in diameter; staminate catkins borne in a single racemose cluster at the end of the branch bearing the pistillate inflorescences, the lowermost subtended by leaves, produced during the current growing season, pendent, at anthesis 2–6 cm long, 5–7 mm in diameter, on peduncles 2–16 mm long,

Figure 61. Representative specimen of *Alnus maritima* Muhlenberg ex Nuttall. Neotype of *Betula-alnus maritima* Marshall.

0.4–1 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these ovate to elliptic, the apex obtuse to rounded, ca. 1 mm long, 0.4–0.8 mm wide, the margin lined with small to medium-sized glands; stamens 4, opposite, separate from, and usually appearing much longer than the perianth, the filaments 0.2–0.7 mm long, the anthers 1.1–1.4 mm long and 0.9–1.1 mm in diameter, the thecae separate for 30–40% of their length. Infructescences ovoid (rarely ellipsoid), (12–) 17–24 (–28) mm long, 11–18 (–22) mm in diameter, on peduncles (3–) 7–10 mm long, 1.2–2.5 mm in diameter; scales 5.5–7 mm long, 6–7 mm wide at the apex, 1.5–2.2 mm wide at the base, the apex greatly thickened and reflexed, the terminal lobe-tip truncate to rounded, not extended. Fruits unwinged or narrowly wing-margined, dark brown, elliptic, 4–4.2 mm long, 2.5–2.7 mm in diameter; wing-margin 3–4 mm long, 0–0.2 mm wide; persistent styles 0.4–1 mm long. Figures 7B, 8B, 13C, 15F, 17D, and 61.

DISTRIBUTION AND HABITAT: Delaware and adjacent Maryland on the Delaware Peninsula; disjunct population in south-central Oklahoma. Found along the edges of ponds and small streams, often standing in water. Near sea level in Delaware and Maryland to about 175 meters in Oklahoma. Figure 62.

COMMON NAMES: Seaside alder, brook alder, Oklahoma alder.

REPRESENTATIVE SPECIMENS: **United States.** DELAWARE. Kent Co.: near mill ponds, Milford, *Canby s.n.*, in 1874 (NY). Sussex Co.: edge of mill pond near Georgetown, *Britton 16* (NY); on the shore of Record Pond off rt. 13 about 4 mi S of town, *Churchill s.n.*, Aug. 12, 1967 (MSC); 4 mi S of Milford on the W shore of Hudson's Pond, *Furlow 205* (MSC); Trap Pond State Park, along a small stream entering the E end of Trap Pond, *Furlow 248* (MSC); just S of Laurel on the N shore of Record's Pond, *Furlow 249* (MSC); along the muddy shore of Burton's Pond, Angola, *Proctor 3623* (DAO, MSC, NY, UC); 10 mi NW of Rehobeth, *Smith s.n.*, Sept. 2, 1935 (F, NY, RM, UC). MARYLAND. Wicomico Co.: Salisbury, *Canby 1956* (MSC); Quantico, near Salisbury, *Tidestrom 7398* (US). OKLAHOMA. Johnston Co.: 10 mi N of Tishomingo, *Furlow 349* (MSC); Pennington Creek, about 3 mi NE of Reagan, *Goodman 5980* (DAO, UC); along Pennington Creek at Devil's Den, *Nelson & Nelson 5863* (OKL, RM); along margins of Pennington Creek, *Palmer 39417* (F, NY, UC); Devil's Den, Pennington Creek, *Robbins 3265* (NY, UC, WTU); moist rocky banks of Blue River, 12 mi W of Wapanucka, *Waterfall 9258* (OKL). Pontotoc Co.: Sheep Creek, 1.5–2 mi SW of Hardin City, *Robbins 2795* (DAO, NY, WTU). Banks of Red River, Indian Territory, *Elihu Hall 612* (F, NY).

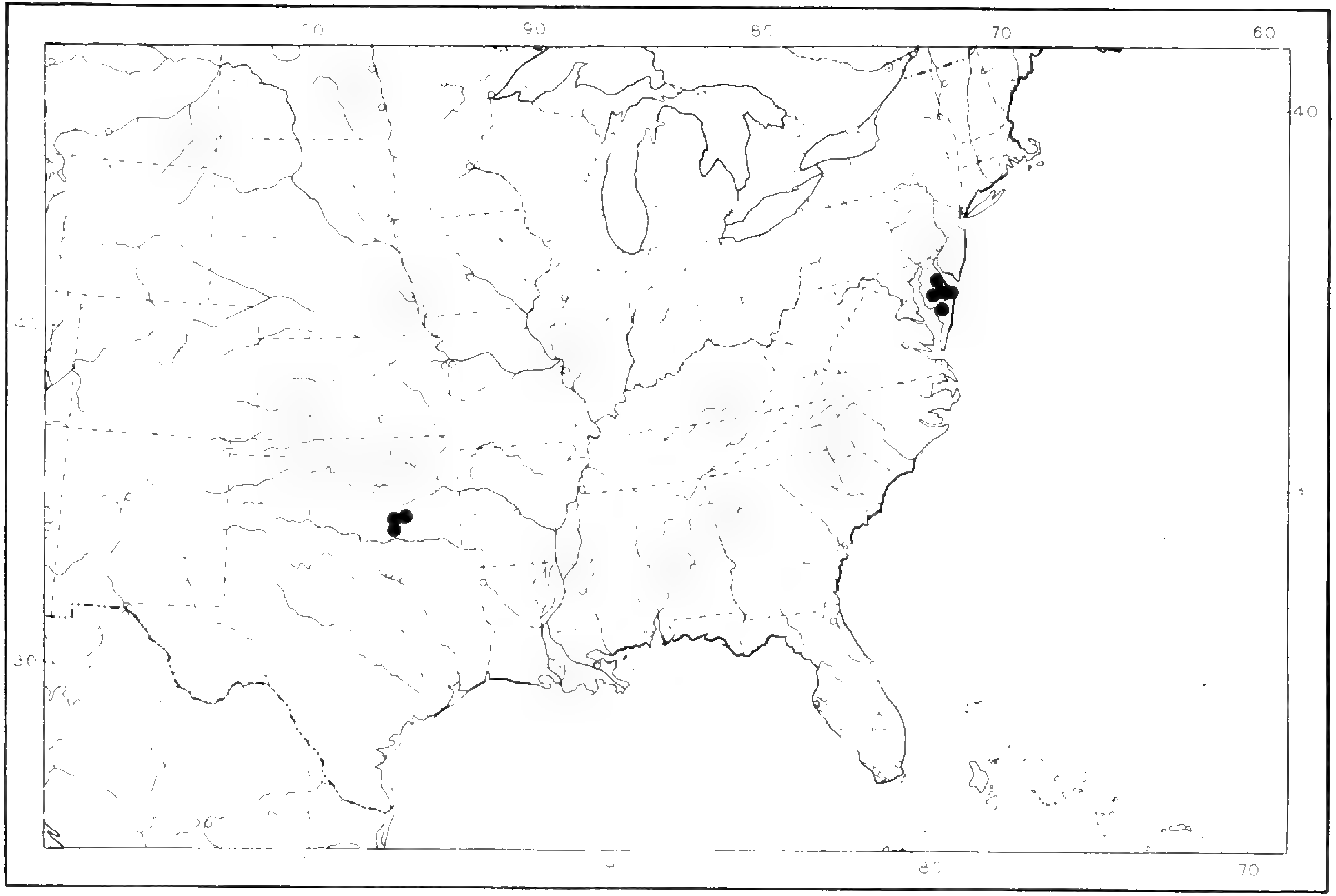


Figure 62. Distribution of *Alnus maritima* Muhlenberg ex Nuttall.

Humpfrey Marshall is usually cited as the original author of the epithet in Nuttall's combination, *Alnus maritima.* However neither Nuttall's protologue nor the unpublished manuscript of Muhlenberg, from which Nuttall obtained the name in the first place, makes reference to Marshall's binomial *Betula-alnus maritima.* There is no evidence that Marshall's and Nuttall's names were not derived independently for the same species and represent taxonomic, not nomenclatural, synonyms. In an earlier paper (Furlow, 1976), it was reported that Nuttall's combination, *Alnus maritima,* was illegitimate and had to be rejected, and a new name, *Alnus metoporina,* based on *Betula-alnus maritima* Marshall, was created to take its place. However this change was, in fact, not necessary according to the *International Code of Botanical Nomenclature* (Stafleu et al., 1972) and the new name has therefore been reduced to synonymy in the present treatment.

The type of *Alnus maritima* is the specimen labeled "477" in the Muhlenberg herbarium at the Academy of Natural Sciences of Philadelphia (Furlow, 1976). The actual collector of this specimen is not known. Muhlenberg (1807) begins the section of his manuscript dealing with the genus *Alnus* (which lists several species, including *Alnus maritima*) with the words *"Alnus bei Bartram",* which may indicate that the specimen itself was collected by Bartram, or it could mean something entirely different. Only a handful of authentic Bartram specimens are known with certainty to exist in the Muhlenberg herbarium (James A. Mears, personal communication).

In describing *Alnus maritima,* Nuttall (1842) made use of both the specimen just discussed and another collected by Charles Pickering along the eastern shore of Maryland (also at PH). Though the Pickering specimen has been somewhat better preserved, both demonstrate the essential diagnostic characteristics of *A. maritima* and are cited by Nuttall in his protologue. The former was selected as the lectotype because it is the original material upon which the name *Alnus maritima* was based by Muhlenberg.

Alnus maritima is easily distinguished from the other American species by its autumnal flowering (all of the others blooming in the spring), the color of its foliage (which is much darker than that of any of the others), the smoothness of the adaxial surface of the leaf blade, the more distantly serrulate leaf margin, the unique venation pattern of the leaves, and the larger infructescences (at least with respect to the taxa occurring north of Mexico). It occurs sympatrically with *A. serrulata* in both Delaware and Oklahoma, sometimes with individuals of the two species growing on the same pond shore or stream bank. Where they do occur together, however, *A. maritima* is usually found in much wetter stiuations, often actually standing in several inches of water, while *A. serrulata* is found higher on the bank.

Alnus maritima has the most restricted geographical range of all the North American species. The presence of related fossil species in the western United States and Canada shows that the subgenus was once much more widespread over the continent, but today it is found only in two small and widely-separated populations of this single species. For many years botanists have speculated about the origin of the very small population in southern Oklahoma. This question has not been totally resolved by the present work, but in light of the formerly more widespread range of the subgenus as a whole, the earliness of the first collections of the species in Oklahoma, and the significant morphological and chemical differences between the members of the two populations noted here, it seems probable that the southern populations represent an actual relict and were not introduced by humans.

Alnus maritima is the most specialized of the New World species in terms of vegetative and floral characters, as discussed above. The solitary and axillary pistillate inflorescences are interpreted as having originated from racemose clusters, as seen in the other species, by reduction. Other species of subg. *Clethropsis* do, in fact, have clusters of inflorescences rather than solitary ones. The autumn-blooming habit appears to have been derived from the spring-blooming habit seen in the subgenera *Alnus* and *Alnobetula*, as well as in most other broad-leafed, wind-pollinated tree taxa of the northern part of North America. It is proposed that this may have originated from the early anthesis of the flowers produced during the current growing season but which would otherwise not bloom until growth resumes the following season following dormancy.

The largest specimen of *Alnus maritima* known to exist is a cultivated tree in Rock Creek Park, Washington, D.C. This individual has a trunk circumference of about 1.2 m, a height of 26 m, and a crown spread of nearly 17 m (Dixon, 1961).

NAMED HYBRIDS

Alnus crispa (Aiton) Pursh × subsp. *hulteni* Murai *in* Trappe *et al.*, Biology of Alder, p. 35. 1968, not validly published (= *Alnus viridis* subsp. *sinuata* (Regel) Löve & Löve × *A. viridis* subsp. *crispa* (Aiton) Turrill).

Alnus × *fallacina* Callier, Fedde Repert. Sp. Nov. **10:** 232. 1911. (= *Alnus incana* subsp. *rugosa* (DuRoi) Clausen × *A. serrulata* (Aiton) Willdenow). TYPE LOCALITY: "Hab. Amer. Septentrion." (original material not seen).

Alnus × *ljungeri* Murai, Bull. Gov. For. Expt. Sta. Jap. **171:** 60. 1964, not validly published. (= *Alnus glutinosa* (Linnaeus) Gaertner × *A. rubra* Bongard).

UNCERTAIN AND EXCLUDED NAMES

Alnus americana hort. ex Hartig, Vollst. Naturgesh. Forstl. Kulturpfl., p. 337. 1851, not validly published. Possibly = *Alnus rubra* Bongard.

Alnus arguta β benthami Regel, Mem. Soc. Nat. Mosc. **13**(2): 151. 1861. *Nom. nud.*

Alnus arguta γ ovata Regel, Mem. Soc. Nat. Mosc. **13**(2): 152. 1861, *nom. subnud.* From the description and type locality ("Naulingo, Acatlan, Chiconquiaco, und Tabina in Peru") probably = *Alnus acuminata* Humboldt, Bonpland, & Kunth subsp. *acuminata* in part and subsp. *arguta* (Schlechtendal) Furlow in part.

Alnus × *aschersoniana* Callier, Jahresb. Schles. Ges. Vaterl. Kult. **64:** 82. 1891. This taxon is identified by Callier as equivalent to *Alnus autumnalis* × *incana* Schweinfurth ex Ascherson. The identity of *A. autumnalis* in the latter name is uncertain.

Alnus autumnalis hort. ex Hartig, Vollst. Naturgesh. Forstl. Kulturpfl., p. 337. 1851, not validly published. Possibly = *Alnus serrulata* (Aiton) Willdenow.

Alnus autumnalis hort. ex Petzold & Kirchner, Arb. Musc., p. 599. 1864, *pro syn.* Possibly = *Alnus maritima* Muhlenberg ex Nuttall.

Alnus auctumnalis × *incana* ex Schweinfurth ex Ascherson, Fl. Prov. Brandenb. **1:** 623. 1864. See *Alnus* × *aschersoniana* Callier, above.

Alnus × *fiekii* Callier, Jahresb. Schles. Ges. Vater. Cult. **64:** 83. 1891. See *Alnus* × *silesiaca* Fiek, below.

Alnus × *fiekii* var. *dressleri* Callier, Jahresb. Schles. Ges. Vater. Cult. **64:** 84. 1891. See *Alnus* × *silesiaca* Fiek, below.

Alnus × *fiekii* var. *silesiaca* Callier, Jahresb. Schles. Ges. Vater. Cult. **64:** 84. 1891. See *Alnus* × *silesiaca* Fiek, below.

Alnus glutinosa var. *autumnalis* Kuntze, Rev. Gen. Pl. **2:** 638. 1891. Possibly = *Alnus serrulata* (Aiton) Willdenow.

Alnus glutinosa var. *quercifolia* hort. ex Hartig, Vollst. Naturgesh. Forstl. Kulturpfl., p. 337, not validly published. Possibly = *Alnus rubra* Bongard.

Alnus hybrida Neumann ex Reichardt, Vehr. Zool.-Bot. Ges. Wein **4**(2): 267. 1854, *non* A. Braun *in* Reichenbach, Icon. Fl. Germ. **12:** 3. 1850. This plant is reported to be a hybrid between *A. glutinosa* and *A. rugosa,* however the latter does not occur naturally in Europe where this putative hybridization supposedly took place.

Alnus incana α Hooker, Fl. Bor. Amer. **1:** 157. 1838. Possibly = *Alnus incana* subsp. *rugosa* (DuRoi) Clausen.

Alnus incana β Hooker, Fl. Bor. Amer. **1:** 157. 1838. Possibly = *Alnus serrulata* (Aiton) Willdenow.

Alnus incana 2. *autumnalis* hort. ex Petzold & Kirchner, Arb. Musc., p. 599. 1864. Possibly = *Alnus maritima* Muhlenberg ex Nuttall.

Alnus incana α. glauca (Aiton) Aiton f., Hort. Kew. ed. 2, **5:** 259. 1813. See *Betula incana α glauca* Aiton.

Alnus jorullensis var. *η acuminata* f. *angustifolia* Winkler, Pflanzenreich **19**(4.61): 127. 1904.

Alnus jorullensis var. *η. acuminata* f. *macrocarpa* Winkler, Pflanzenreich **19**(4.61): 127. 1904.

Alnus jorullensis var. *liebmanni* Callier, Mitt. Deutsch. Dendr. Ges. **27:** 165. 1918. Possibly = *A. jorullensis* subsp. *lutea* Furlow.

Alnus latifolia Desfontaines, Cat. Pl. Hort. Par. ed. 3, p. 352. 1829. *Nom. nud.*

Alnus oblongata Willdenow, Sp. Pl. ed. 4, **4**(1): 335. 1805. See *Betula oblongata* Aiton, below.

Alnus oblongata α genuina Regel, Mem. Soc. Nat. Mosc. **13**(2): 174. 1861. Possibly = *Alnus serrulata* (Aiton) Willdenow.

Alnus oblongata β oblonga Regel, Mem. Soc. Nat. Mosc. **13**(2): 174. 1861. Possibly = *Alnus maritima* Muhlenberg ex Nuttall.

Alnus × *purpusi* Callier *in* Schneider, Ill. Handb. Laubh. **1:** 132. 1904. This hybrid supposedly is between *A. rugosa* and *A. tenuifolia.* The type (*Purpus 1887*) is from British Columbia, however, where *A. incana* subsp. *rugosa* does not occur.

Alnus rugosa × *incana* Callier *in* Schneider, Ill. Handb. Laubh. **1:** 132. 1904. The identity of *"Alnus rugosa"* in this hybrid is uncertain. Callier equates it with *A. autumnalis,* and the hybrid with *A. auctumnalis* × *incana* Schweinfurth ex Ascherson (see above).

Alnus serrulata pumila Demcker, Mitt. Deutsch. Dendr. Ges. **18:** 326. 1909, *nom. nud.* Possibly = *Alnus acuminata* subsp. *acuminata.*

Alnus × *silesiaca* Fiek *in* Fiek & Pax, Jahresb. Schles. Ges. Vater. Cult. **66:** 178. 1888. Supposedly = *Alnus serrulata* × *glutinosa,* but originally collected in Europe where *A. serrulata* does not occur naturally.

Alnus tomentosa Durand ex Kellogg *in* Peirce, Rept. Supt. U.S. Coast Surv., p. 324. 1869, *nom. nud.* Durand's specimen (no. 199) was not seen; the collecting site is listed as Sitka, so the species may be either *Alnus rubra* Bongard or *Alnus viridis* subsp. *sinuata* (Regel) Löve & Löve.

Alnus viridis var. *glabra* Chamisso, Linnaea **6:** 538. 1831. Possibly = *Alnus viridis* subsp. *sinuata* (Regel) Löve & Löve.

Alnus viridis var. *microphylla* Chamisso, Linnaea **6:** 538. 1831. Possibly = *Alnus viridis* subsp. *sinuata* (Regel) Löve & Löve.

Betula alnus var. *americana* Ludwig, Neuere Wilde Baumz., p. 8. 1783, *nom. nud.* The only description provided is "dwarf american alder" and "die amerikanische Eller mit glatten Blattern." Possibly = *Alnus incana* subsp. *rugosa* (DuRoi) Clausen.

Betula alnus var. *glutinosa* Ludwig, Neuere Wilde Baumz., P. 8. 1783, *nom. nud.* From the common name provided ("round-leaved A."), probably = *Alnus glutinosa* (Linnaeus) Gaertner.

Betula alnus var. *incana* Ludwig, Neuere Wilde Baumz., p. 8. 1783, *nom. nud.* Probably = *Alnus incana* (Linnaeus) Moench.

Betula alnus var. *rugosa* Ludwig, Neuere Wilde Baumz., p. 8. 1783, *nom. nud.* Probably = *Alnus incana* subsp. *rugosa* (DuRoi) Clausen.

Betula incana α glauca Aiton, Hort. Kew. **3:** 339. 1789. May = either *Alnus incana* subsp. *incana* or subsp. *rugosa.* This taxon is *not* cited by Michaux as the basis for his *Alnus glauca,* as is sometimes indicated by other authors.

Betula oblongata Aiton, Hort. Kew. **3:** 338. 1789. May = *Alnus glutinosa* (Linnaeus) Gaertner, *A. serrulata* (Aiton) Willdenow, or *A. maritima* Nuttall (*vide* the discussion of Regel, 1861, pp. 171–172).

Betula-alnus 6. *crispa* Weston, Bot. Univers. Hortul. **1:** 323. 1770, *nom. subnud.* Possibly = *Alnus viridis* subsp. *crispa* (Aiton) Turrill.

Betula-alnus glauca Marshall, Arbust. Am., p. 20. 1785, *nom. nud.* Probably = *Alnus incana* subsp. *rugosa* (DuRoi) Clausen.

Betula-alnus 1. *glutinosa* Weston, Bot. Univers. Hortul. **1:** 323. 1770, *nom. subnud.* Probably = *Alnus glutinosa* (Linnaeus) Gaertner.

Betula-alnus 4. *incana* Weston, Bot. Univers. Hortul. **1:** 323. 1770, *nom. subnud.* Probably = *Alnus incana* (Linnaeus) Moench.

Betula-alnus rubra Marshall, Arbust. Am., p. 20. 1785, *nom. nud.* This name probably refers to *Alnus serrulata* (Aiton) Willdenow. It was used as the basis of *Alnus rubra* Tuckerman, *non* Bongard, as a name for *A. serrulata.*

Betula-alnus 3. *rubra* Weston, Bot. Univers. Hortul. **1:** 323. 1770, *nom. subnud.* Possibly = *Alnus serrulata* (Aiton) Willdenow.

LITERATURE CITED

ABBE, E. C. 1935. Studies in the phylogeny of the Betulaceae. I. Floral and inflorescence anatomy and morphology. Bot. Gaz. **97:** 1–67.

______. 1938. Studies in the phylogeny of the Betulaceae. II. Extremes in the range of variation of floral and inflorescence morphology. Bot. Gaz. **99:** 431–469.

ACOSTA-SOLIS, M. 1939. Principal timbers used in the Sierra del Ecuador. Tropical Woods **57:** 3–5.

AITON, W. 1789. Hortus Kewensis. London. Vol. 3.

AITON, W. T. 1813. Hortus Kewensis, ed. 2. London. Vol. 5.

ANDERSON, E., & E. C. ABBE. 1934. A quantitative comparison of specific and generic differences in the Betulaceae. Jour. Arnold Arb. **15:** 43–49.

ASCHERSON, P. F. A. 1864. Flora der Provinz Brandenburgh. Berlin. Vol. 1.

______, & P. GRAEBNER. 1908–1913. Synopsis der Mitteleuropaischen Flora. Leipzig. Vol. 4.

AXELROD, D. I. 1939. A Miocene flora from the western border of the Mojave Desert. Carnegie Inst. Publ. 516, pp. 1–129.

______. 1952. A theory of angiosperm evolution. Evolution **6:** 29–60.

______, & P. H. RAVEN. 1972. Evolutionary biogeography viewed from plate tectonic theory. *In:* J. A. BEHENKE, Ed. Challenging Biological Problems. New York. Pp. 218–236.

BAILEY, I. W. 1911. The relation of the leaf trace to the formation of compound rays in the lower dictyledons. Ann. Bot. **25:** 225 241.

———. 1912. The evolutionary history of the foliar ray in the wood of the dicotyledons and its phylogenetic significance. Ann. Bot. **26:** 647 661.

BALL, P. W. 1964. *Alnus. In:* T. G. TUTIN, V. H. HEYWOOD, N. A. BURGES, D. H. VALENTINE, S. M. WALTERS, & D. A. WEBB, Eds. Flora Europaea. Cambridge. Vol. 1, p. 59.

BARTLETT, A. S., & E. S. BARGHOORN. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate and sea-level change). *In:* A. GRAHAM, Ed. Vegetation and Vegetational History of Northern Latin America. Amsterdam. Pp. 203 299.

BARTLETT, H. H. 1909. Notes on Mexican and Central American alders. Proc. Am. Acad. **44:** 609 612.

BENSON, L. 1962. Plant Taxonomy: Methods and Principles. New York. 494 pp.

BERRY, E. W. 1922. Late Tertiary plants from Jancocata, Bolivia. *In:* E. B. MATHEWS, Ed. Contributions to the Paleobotany of Peru, Bolivia, and Chile. The Johns Hopkins University Studies in Geology, No. 4, Baltimore. Pp. 207 221.

———. 1923. Tree Ancestors: a Glimpse into the Past. Baltimore. 270 pp.

———. 1926. Tertiary floras from British Columbia. Bull. Can. Geol. Surv. **42:** 91 116.

BOIVIN, B. 1967. Enumération des plantes du Canada. VII. Résumé statistique et regions adjacentes. Nat. Canad. **94:** 625 655.

BOND, G. 1956. Evidence for fixation of nitrogen by root nodules of alder (*Alnus*) under field conditions. New Phytol. **55:** 147 153.

———. 1963. The root nodules of non-leguminous angiosperms. *In:* P. S. NUTMAN, & B. MOSSE, Eds. Symbiotic Associations. London. Pp. 72 91.

———, W. W. FLETCHER, & T. P. FERGUSON. 1954. The development and function of the root nodules of *Alnus, Myrica,* and *Hippophae.* Plant and Soil **5:** 309 323.

BONGARD, H. G. 1833. Observations sur la vegetation de l'isle de Sitcha. Mem. Akad. Sci. St. Petersb. ser. 6, **2:** 119 178.

BOUBIER, A. M. 1896. Recherches sur l'anatomie systematique des Betulaceés-Corylaceés. Malpighia **10:** 349 436.

BRAUN, A. 1850. Amentaceae: Betulineae et Cupuliferae, Urticaceae, Aristolochiaceae, Laurineae, et Dipsaceae cum valerianeis. *In:* H. G. L. REICHENBACH. Icones Florae Germanicae et Helveticae. Lipseae. Vol. 12.

BRAUN, E. L. 1951. Plant distribution in relation to the glacial boundary. Ohio Jour. Sci. **51:** 139 145.

———. 1955. The phytogeography of unglaciated eastern United States and its interpretation. Bot. Rev. **21:** 297 375.

BREITUNG, A. J. 1957a. Annotated catalogue of the vascular flora of Saskatchewan. Am. Midl. Nat. **58:** 1 72.

———. 1957b. Plants of Waterton Lakes National Park, Alberta. Canad. Field-Nat. **71:** 39 71.

BRITTON, N. L. 1904. An undescribed species of *Alnus.* Torreya **4:** 124.

BROWN, D. M. 1941. The vegetation of Roan Mountain, a phytosociological and successional study. Ecol. Mon. **11:** 61-97.

BROWN, R. W. 1937. Additions to some fossil floras of the western United States. U.S. Geol. Surv. Prof. Paper 186-J.

CAIN, S. A. 1944. Foundations of Plant Geography. New York. 556 pp.

CALLIER, A. 1892. Uber die in Schlesien vorkommenden Formen der Gattung *Alnus*. Jahresbericht der Schlesischen Gesellschaft für Vaterländische Cultur **69**(2): 72-85.

______. 1904, 1912. Gattung *Alnus*. *In:* C. K. SCHNEIDER. Illustriertes Handbuch der Laubholzkunde. Jena. Vol. 1, pp. 119-136; vol. 2, pp. 857-891.

______. 1911. Diagnoses formarum novarum generis *Alnus*. Fedde Repert. Sp. Nov. **10:** 225-237.

______. 1918. *Alnus* Formen der europäischen Herbarien und Garten. Mitt. Deutsch. Dendr. Gesel. **27:** 39-185.

CAMP, W. H., & C. L. GILLY. 1943. The structure and origin of species. Brittonia **4:** 323-385.

CHAMBERLAIN, C. J. 1927. Hayfever in the Pacific North West. Ann. Otol. Rhinol. Laryngol. **36:** 1083-1092.

CHAMISSO, A. DE. 1831. De plantis in expeditione speculatoria Romanzoffiana observatis sisserere pergunt Ad. de Chamisso et D. de Schlechtendal. Arcticae, quae supersunt. Linnaea **6:** 528-592.

CHANEY, R. W. 1936. The succession and distribution of Cenozoic floras around the northern Pacific basin. *In:* Essays in Geobotany in Honor of W. A. Setchell. Berkeley. Pp. 55-85.

______. 1947. Tertiary centers and migration routes. Ecol. Mon. **17:** 143.

______. 1959. Miocene floras of the Columbia Plateau. Pt. I. Composition and Interpretation. Carnegie Inst. Publ. 617, pp. 1-134.

______, & D. I. AXELROD. 1959. Miocene floras of the Columbia Plateau. Pt. II. Systematic Considerations. Carnegie Inst. Publ. 617, pp. 135-237.

CHIBA, S. 1962. Studies on the breeding of *Betula* and *Alnus* species. (1) On the differences of morphological characters and chromosome numbers between *Alnus hirsuta* and *Alnus hirsuta* var. *microphylla*. Jour. Jap. For. Soc. **44:** 237-243.

CLARKSON, R. B. 1960. Notes of the distribution of *Alnus crispa* in eastern North America. Castanea **25:** 83-86.

CLAUSEN, R. T. 1949. Checklist of the vascular plants of the Cayuga Quadrangle 42°-43° N, 76°-77° W. Mem. Cornell Univ. Agr. Expt. Sta. **291:** 1-87.

CONTANDRIOPOULOS, J. 1964. Recherches sur la flore endemique de la corse et sur ses origenes. (II). Revue General de Botanique **71:** 361-384.

COON, N. 1963. Useful Plants for Healing. Great Neck, N.Y. 272 pp.

COOPER, W. S. 1923a. The recent ecological history of Glacier Bay, Alaska. I. The interglacial forests of Glacier Bay. Ecol. **4:** 93-128.

______. 1923b. The recent ecological history of Glacier Bay, Alaska. II. The present vegetation cycle. Ecol. **4:** 223-246.

______. 1931. A third expedition to Glacier Bay, Alaska. Ecol. **12:** 61-95.

______. 1939. A fourth expedition to Glacier Bay, Alaska. Ecol. **20:** 130-155.

CRACRAFT, J. 1975. Historical biogeography and earth history: perspectives for a future synthesis. Ann. Mo. Bot. Gard. **62:** 227 250.

CROCKER, R. L., & B. A. DICKSON. 1957. Soil development on the recessional moraines of the Herbert and Mendenhall glaciers, southeastern Alaska. Jour. Ecol. **45:** 169–185.

CROCKER, R. L., & J. MAJOR. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Jour. Ecol. **43:** 427 448.

CULPEPER, N. 1653. The Complete Herbal and English Physitian Enlarged. London. 398 pp.

CZEREPANOV, S. 1955. Systema generis *Alnus* Mill. S. Str. Generumque affinium. Notulae Systematicae ex Herbario Instituti Botanici Nomine V. L. Komarovi Academiae Scientiarum U.R.S.S. **17:** 90 105.

DALTON, D. A., & A. W. NAYLOR. 1975. Studies on nitrogen fixation by *Alnus crispa*. Am. Jour. Bot. **62:** 76–80.

DAVIS, G. L. 1966. Systematic Embryology of the Angiosperms. New York. 528 pp.

DEMCKER, R. 1909. Neue Gehölze. Mitt. Deutsch. Dendr. Ges. **18:** 323–326.

DIPPEL, L. 1892. Handbuch der Laubholzkunde. Berlin. Vol. 2.

DIXON, D. 1961. These are the champs. Am. Forests **67(1):** 40 46; 48 50.

DORMAN, F. 1924. Zur Kenntnis der Hautdrüsen und der Harzexkretion von *Alnus viridis*. Sitz-ber. Akad. Wien **133:** 585 612.

DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. Jour. Arnold Arb. **50:** 1–35.

DRESSLER, R. L. 1954. Some floristic relationships between Mexico and the United States. Rhodora **56:** 81 96.

DU RIETZ, G. E. 1930. The fundamental units of biological taxonomy. Sv. Bot. Tidskr. **24:** 333–428.

DUROI, J. P. 1771. Dissertatio Inauguralis Observationes Botanicas Sistens. Helmstadii. 62 pp.

EDLIN, H. L. 1964. A modern sylva or a discourse of forest trees. 11. Alder—*Alnus* spp. Quart. Jour. Forest. **58:** 302–310.

EHRHART, B. 1753. Oekonomische Pflanzen-Historie. Ulm. Vol. 2.

EHRHART, F. 1788. Beitrage zur Naturkunde. Hannover und Osnabruk. Vol. 2.

ENDLICHER, S. 1842. Genera Plantarum Secundum Ordines Naturales Deposita, supplementum secundum. Vindobonae. 114 pp.

ERDTMAN, G. 1969. Handbook of palynology. New York. 486 pp.

FERNALD, M. L. 1904a. The green alders of New England. Rhodora **6:** 162, 163.

______. 1904b. Synopsis of the Mexican and Central American species of *Alnus*. Proc. Am. Acad. **40:** 24 28.

______. 1907. Diagnoses of new spermatophytes from Mexico. Proc. Am. Acad. **43:** 61–68.

______. 1913. *Alnus crispa* (Ait.) Pursh var. *mollis* Fern. n. comb. Rhodora **15:** 44.

______. 1914. A cut-leafed alder. Rhodora **16:** 56.

______. 1945a. *Alnus crispa* (Ait.) Pursch, forma *stragula*. Rhodora **47:** 144.

______. 1945b. Eastern North American representatives of *Alnus incana*. Rhodora **47:** 333 361.

______. 1950. Gray's manual of botany, ed. 8. New York. 1632 pp.

Fiek, E., & F. Pax. 1888. Resultate dur Durchforschung der schlesischen Phanerogamenflora in Jahre 1888. Jahresbericht der Schlesischen Gesellschaft für Vaterländische Cultur **66:** 174–206.

Fleschner, M. D., C. C. Delwiche, & C. R. Goldman. 1976. Measuring rates of symbiotic nitrogen fixation by *Alnus tenuifolia*. Am. Jour. Bot. **63:** 945–950.

Forsaith, C. C. 1920. Anatomical reduction in some alpine plants. Ecol. **1:**124–235.

Fryxell, P. A. 1967. The interpretation of disjunct distributions. Taxon **16:** 316–324.

Furlow, J. J. 1976. Nomenclatural changes in *Alnus* (Betulaceae). Ann. Mo. Bot. Gard. **63:** 380–381. (Actual date of publication January 18, 1977.)

———. 1977. Betulaceae. *In:* W. Burger. Flora Costaricensis. Fieldiana: Botany **40:** 56–58.

Gaertner, J. 1790. De Fructibus et Seminibus Plantarum. Stutgardiae. Vol. 2, Pt. 1.

Gandoger, M. M. 1919. Sertum plantarum novarum. Bull. Soc. Bot. Fr. **66:** 216–233; 286–307.

Gillis, W. T. 1971. The systematics and ecology of poison-ivy and the poison-oaks (*Toxicodendron*, Anacardiaceae). Rhodora **73:** 72–159; 161–237; 370–443; 465–540.

Gleason, H. A. 1963. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. New York. Vol. 3, pp. 36, 37.

———, & A. Cronquist. 1963. Manual of the Vascular Plants of Northeastern United States and Adjacent Canada. New York. 810 pp.

Goldman, E. A. 1951. Biological investigations in Mexico. Smithsonian Institution Publ. 4017. 476 pp.

Graham, A. 1972a. Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America. *In:* A. Graham, Ed. Floristics and Paleofloristics of Asia and Eastern North America. Amsterdam. Pp. 1–18.

———. 1972b. Some aspects of Tertiary vegetational history about the Caribbean basin. Memorias de Symposia, I Congreso Latinoamericano V Mexicano de Botanica. Mexico, D.F. Pp. 97–117.

———. 1973. History of the arborescent temperate element in the northern Latin American biota. *In:* A. Graham, Ed. Vegetation and Vegetational History of Northern Latin America. Amsterdam. Pp. 301–314.

Gram, K., C. M. Larsen, C. S. Larsen, & M. Westergaard. 1942. Contributions to the cytogenetics of forest trees. II. *Alnus* studies. Kongelige Veterinaer-og Landbohojskole Aarsskrift. **1941:** 44–58.

Gray, A. 1842. Notes of a botanical excursion to the mountains of North Carolina. Am. Jour. Sci. **42:** 1–49.

Hall, J. W. 1952. The comparative anatomy and phylogeny of the Betulaceae. Bot. Gaz. **113:** 235–270.

Hammen, T. van der. 1972. Historia de la vegetacion y el medio ambiente del norte Sudamericano. Memorias de Symposia, I Congreso Latinoamericano V Mexicano de Botanica. Mexico, D.F. Pp. 119–134.

Hara, H. 1948. Notes on the mountain area of Central America. Jour. Jap. Bot. **22:** 6.

Harshberger, J. W. 1903. An ecological study of mountainous North Carolina. Bot. Gaz. **36:** 241–258; 368–383.

Hartig, T. 1851. Vollständige Naturgeschichte der Forstlichen Kulturpflanzen Deutschlands. Berlin. 584 pp.

Hawker, L. E. & J. Fraymouth. 1951. A re-investigation of the root-nodules of species of *Elaeagnus, Hippophae, Alnus,* and *Myrica,* with reference to the morphology and life histories of the causative organisms. Jour. Gen. Microbiol. **5:** 369–386.

Heilman, P. E. 1966. Changes in the distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. Ecol. **47:** 825–831.

Hemsley, W. B. 1882. Botany. *In:* F. D. Goodman & O. Salvin, Eds. Biologia Centrali-Americana. London. Vol. 55.

Heusser, C. J. 1960. Late Pleistocene Events of North Pacific America. New York. 308 pp.

Hickey, L. J. 1973. Classification of the architecture of dicotyledonous leaves. Am. Jour. Bot. **60:** 17–33.

Hill, J. 1756–1757. The British Herbal. London. 536 pp.

Hitchcock, C. L., A. Cronquist, M. Ownbey, & J. W. Thompson. 1964. Vascular Plants of the Pacific Northwest. Seattle. Vol. 2.

Hjelmqvist, H. 1948. Studies on the floral morphology and phylogeny of the amentiferae. Bot. Not. Suppl. **2**(1): 1–171.

Hoar, C. S. 1916. The anatomy and phylogenetic position of the Betulaceae. Am. Jour. Bot. **3:** 415–435.

Holmgren, P. K., & W. Keuken. 1974. Index Herbariorum. Part I. The Herbaria of the World, ed. 6. Utrecht. 397 pp.

Hooker, W. J. 1838. Flora Boreali-Americana. London. Vol. 2.

Hornemann, J. W. 1821. Forsög til en Dansk Oekonomisk Plantelaere in Kojobenhaven, ed. 3. Copenhagen. Vol. 1.

House, H. H. 1924. Annotated list of the ferns and flowering plants of New York State. New York State Mus. Bull. **254:** 1–759.

Hultén, E. 1928. On the American component in the flora of eastern Siberia. Sv. Bot. Tidskrift **22:** 220–229.

———. 1937a. Flora of the Aleutian Islands. Stockholm. 397 pp.

———. 1937b. Outline of the History of Arctic and Boreal Biota During the Quaternary Period; their Evolution During and After the Glacial Period as Indicated by the Equiformal Progressive Areas of Present Plant Species. Stockholm. 168 pp.

———. 1941–1950. Flora of Alaska and Yukon. Lunds Universitets Årsskrift, N.F., **37–45:** 1–1341.

———. 1963. Phytogeographical connections of the North Atlantic. *In:* A Löve & D. Löve, Eds. North Atlantic Biota and their History. New York. Pp. 45–72.

———. 1967. Comments on the flora of Alaska and Yukon. Arkiv för Botanik, ser. 2, **7**(1): 1–147.

———. 1971. The circumpolar plants. II. Dicotyledons. Kunglia Svenska Vetenskapsakademiens Handlingar, ser. 4, **13**(1): 1–463.

Humboldt, F. H. A. von, A. J. Bonpland, & C. S. Kunth. 1817. Nova Generis et Species Plantarum. Paris. Vol. 2.

Hurd, R. M. 1971. Annual tree-litter production by successional forest stands, Juneau, Alaska. Ecol. **52:** 881-884.

Hylander, N. 1957. On cut-leaved and small-leaved forms of *Alnus glutinosa* and *A. incana.* Sv. Bot. Tidskrift **51:** 437-453.

Iltis, H. H. 1966. The western element in the eastern North American flora and its phytogeographical implications. Am. Jour. Bot. **53:** 635.

Ives, J. D. 1963. Field problems in determining the maximum extent of pleistocene glaciation along the eastern Canadian seaboard — a geographer's point of view. *In:* A. Löve & D. Löve, Eds. North Atlantic Biota and their History. New York. Pp. 337-354.

Jaretzky, R. 1930. Zur Zytologie der Fagales. Planta **10:** 120-137.

Johannsen, D. A. 1940. Plant Microtechnique. New York. 523 pp.

Johnson, F. D. 1968a. Disjunct populations of red alder in Idaho. *In:* J. M. Trappe, J. F. Franklin, R. F. Tarrant, & G. M. Hansen, Eds. Biology of Alder. Portland. Pp. 1-8.

______. 1968b. Taxonomy and distribution of northwestern alders. *In:* J. M. Trappe, J. F. Franklin, R. F. Tarrant, & G. M. Hansen, Eds. Biology of Alder. Portland. Pp. 9-22.

Judd, W. S. 1978. Monograph of *Lyonia* (Ericaceae). Ph.D. dissertation. Harvard University. 811 pp.

Kelley, A. P. 1950. Mycotrophy in Plants. Waltham, Mass. 223 pp.

Kellogg, A. 1869. Report of Albert Kellogg, M.D., Aid United States Coast Survey, to George Davidson, Assistant United States Coast Survey on the Botany of Alaska. *In:* B. Peirce. Report of the Superintendent of the United States Coast Survey showing the Progress of the Survey During the Year 1867. 40th Congress, 2nd session. House Executive Document no. 275. Pp. 318-324.

Kjellman, F. R. 1883. Fanerog. Fran Vest-eskimaernas Land. *In:* A. E. Nordenskjold, Ed. Vega-Expeditiones Vetenskapliga i Akttagelser. Stockholm. Vol. 2.

Klečka, A., & V. Vukolov. 1935. Srounávací studie o mykorrhize dřevin (užitkových, okrasných a ovacných). Sbornik Ceskoslav Akad. Zemed. **10:** 443-457.

Koch, K. H. E. 1869-1873. Dendrologie, ed. 2. Erlangen. 3 vols.

Koch, W. D. J. 1837. Synopsis Florae Germanicae et Helveticae. Francofurti ad Moenum. Pt. 2.

Kodama, A. 1967. Karyological studies on root nodules of three species of *Alnus.* Bot. Mag. (Tokyo) **80:** 230-232.

Komorov, V. L. 1927-1930. Flora Peninsulae Kamtschatka. I. Cum Summario Lingua Britannica Expresso. 3 vols.

______. 1936. Flora S.S.S.R. Moskva-Leningrad. Vol. 5.

Kryshtofovich, A. N. 1929. Evolution of the Tertiary flora in Asia. New Phytol. **28:** 303-312.

Kuntze, O. 1891. Revisio Generum Plantarum. Wurzburg. Pp. 638-640.

Lamarck, J. B. A. P. M. de, & A. P. de Candolle. 1805. Flore Francaise, ed. 3. Paris. Vol. 3.

La Motte, R. S. 1952. Catalogue of the Cenzoic Plants of North America Through 1950. New York. 381 pp.

LANGE, J. 1871. Florae Danicae. Icones Plantarum Sponte Noscentium in Regno Daniae et in ducatibus Slesvici, Holsatiae, et Lauenburgiae. Hauniae. Vol. 16.

______. 1887. Conspectus florae Groenlandicae, pars secunda. Med. om Grönl. **3:** 280.

LAWRENCE, D. B. 1958. Glaciers and vegetation in southwestern Alaska. Am. Scient. **46:** 89 122.

LEDEBOUR, K. F. VON. 1850. Flora Rossica. Stuttgartiae. Vol. 3.

LEOPOLD, E. B., & H. D. MACGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. *In:* A. GRAHAM, Ed. Floristics and Paleofloristics of Asia and Eastern North America. Amsterdam. Pp. 147 200.

LEPAGE, E. 1950. Une variété nouvelle de l'*Alnus crispa* (Ait.) Pursh. Nat. Canad. **77:** 44 46.

LI, H. L. 1971. Floristic Relationships between Eastern Asia and Eastern North America. Philadelphia. 429 pp.

______. 1972. Eastern Asia-eastern North America species pairs in wide-ranging genera. *In:* A. GRAHAM, Ed. Floristics and Paleofloristics of Asia and Eastern North America. Amsterdam. Pp. 64 78.

LINNAEUS, C. 1753. Species Plantarum. Holmiae. Vol. 2.

______. 1759. Systema Naturae, ed. 10. Holmiae. Vol. 2.

LINNAEUS, C. 1871. Supplementum Plantarum Systematis Vegetabilum, ed. decimae tertiae. Brunsvigas. 467 pp.

LIVINGSTONE, D. A. 1955. Some pollen profiles from arctic Alaska. Ecol. **36:** 587 600.

LJUNGER, Å. 1959. Al-och alföradling. Skogen **46:** 115-117.

LODDIGES, C. 1826. The Botanical Cabinet. London. Vol. 12.

LOUDON, J. C. 1838. Arboretum et Fruticetum Britannicum. London. 8 vols.

LÖVE, A. 1954. Cytotaxonomical evaluation of corresponding taxa. Vegetatio **5-6:** 212 224.

______. 1959. Origin of the arctic flora. Publ. McGill Univ. Mus. **1:** 82 95.

______. 1967. The evolutionary significance of disjunctions. Taxon **16:** 324-333.

______, & D. LÖVE. 1965. Taxonomic remarks on some American alpine plants. Univ. Colo. Stds. Ser. Biol. **17:** 1-43.

______, & D. LÖVE. 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. Univ. Colo. Stds. Ser. Biol. **24:** 1 74.

______, & D. LÖVE. 1967. The origin of the North Atlantic flora. Aquilo Ser. Bot. **6:** 52 66.

LÖVE, D. 1959. The postglacial development of the flora of Manitoba: a discussion. Can. Jour. Bot. **37:** 547 585.

LUDWIG, C. F. 1783. Die Neuere Wilde Baumzucht in einem Alphabetischen und Systematischen Verzeichnisse Aufgestellt. Leipzig. 70 pp.

MACBRIDE, J. F. 1936. Flora of Peru, pt. 2. Field Mus. Natrl. Hist. Bot. Ser. **13:** 267, 268.

MARSHALL, H. 1785. Arbustum Americanum. Philadelphia. 174 pp.

MARTINEZ, M. 1959. Plantas Medicinales de México. México, D.F. 657 pp.

MASAMUNE, G. 1934. Plantae vasculares a Prof. I. Namikawa anno 1920 in Kamtschatka lectae, auctore Yushun Kudo. Jour. Jap. Bot. **10:** 487 526.

Masui, K. 1926. A study of the ectotrophic mycorrhiza of *Alnus*. Mem. Coll. Sci. Kyoto Imp. Univ. ser. B, **2:** 189–209.

Matuda, E. 1953. Plantas Asiaticas en México. Mem. Congr. Cient. Mex. IV Centenario Univ. Mex. **6:** 234–248.

Mayr, E. 1947. Ecological factors in speciation. Evolution **1:** 263–288.

McVaugh, R. 1952. Suggested phylogeny of *Prunus serotina* and other wide ranging phylads in North America. Brittonia **7:** 317–346.

McVean, D. N. 1953a. *Alnus* Mill. *In:* Biological flora of the British Isles. Jour. Ecol. **41:** 447–466.

———. 1953b. Regional variation of *Alnus glutinosa* (L.) Gaertn. in Britain. Watsonia **3:** 26–32.

———. 1955. Ecology of *Alnus glutinosa* (L.) Gaertn. II. Seed distribution and germination. Jour. Ecol. **43:** 61–71.

———. 1956a. Ecology of *Alnus glutinosa* (L.) Gaertn. III. Seedling establishment. Jour. Ecol. **44:** 195–218.

———. 1956b. Ecology of *Alnus glutinosa* (L.) Gaertn. IV. Root system. Jour. Ecol. **44:** 219–225.

Metcalfe, C. R., & L. Chalk. 1950. Anatomy of the Dicotyledons. Oxford. Vol. 2.

Michaux, A. 1803. Flora Boreali-Americana. Paris. 2 vols.

Michaux, F. A. 1813. Historie des Arbores Forestiers de l'Amerique Septentrionale. Paris. Vol. 3.

———. 1859. The North American Sylva. Philadelphia. Vol. 2.

Miller, P. 1754. The Gardner's Dictionery, Abridged, ed. 4. London.

———. 1759. The Gardner's Dictionery, ed. 7. London.

———. 1768. The Gardner's Dictionery, ed. 8. London.

Mirbel, C. F. B. de. 1827. Description de quelques especes nouvelles de la famille des amentacees. Mem. Mus. Nat. Hist. Nat. **14:** 462–474.

Mitchell, W. W. 1968. On the ecology of the Sitka alder in the subalpine zone of south-central Alaska. *In:* J. M. Trappe, J. F. Franklin, R. F. Tarrant, & G. M. Hansen, Eds. Biology of Alder. Portland. Pp. 45–56.

Moench, K. 1794. Methodus Plantas Horti Botanici et Agri Marburgensis. 780 pp.

Muhlenberg, H. 1807. Observationes Botanicae de Plantis Americae Septentrionalis. Unpublished manuscript. Library of the Academy of Natural Sciences of Philadelphia. Vol. 1.

Muller, C. H. 1940. New and otherwise noteworthy plants of the Southwest. Madroño **5:** 152–158.

Munz, P. A., & I. M. Johnston. 1925. Miscellaneous notes on plants of southern California. IV. Bull. Torr. Club. **52:** 221–228.

Murai, S. 1963. Phytotaxonomical and geobotanical studies on so-called genus *Alnus* in Japan (II). Comparative studies on all species, including shrubby species. Bull. For. Expt. Sta. Jap. **154:** 21–72.

———. 1964. Phytotaxonomical and geobotanical studies on gen. *Alnus* in Japan (III). Taxonomy of whole world species and distribution of each sect. Bull. Gov. For. Expt. Sta. Jap. **171:** 1–107.

______. 1968. Relationships of allied species between northwestern U.S.A. and Japan on the genus *Alnus*. *In:* J. M. Trappe, J. F. Franklin, R. F. Tarrant, & G. M. Hansen, Eds. Biology of Alder. Portland. Pp. 23 36.

Murray, J. A. H., H. Bradley, W. A. Craigie, & C. T. Onions, Eds. 1933. The Oxford English Dictionery. Oxford. 12 vols.

Neal, J. L., Jr., J. M. Trappe, K. C. Lu, & W. B. Bollen. 1968. Some ectotrophic mycorrhizae of *Alnus rubra*. *In:* J. M. Trappe, J. F. Franklin, R. F. Tarrant, & G. M. Hansen, Eds. Biology of Alder. Portland. Pp. 179 184.

Newton, M., B. A. El Hassan, & J. Javitkovski. 1968. Role of red alder in western Oregon forest succession. *In:* J. M. Trappe, J. F. Franklin, R. F. Tarrant, & G. M. Hansen, Eds. Biology of Alder. Portland. Pp. 73 84.

Nuttall, T. 1842. The North American Sylva. Philadelphia. Vol. 1.

Nyman, C. F. 1881. Conspectus Florae Europaeae. Orebro Sueciae. Pp. 671 672.

Opiz, P. M. 1839. Oekonomische Neuigkeiten und Verhandlungen 1839: 521–527.

______. 1852. Seznam Rostlin Kveteny Ceske. Prague. Vol. 10.

Persoon, C. H. 1805 1807. Synopsis Plantarum. Paris. 2 vols.

Petermann, W. L. 1849. Deutschlands Flora mit Abbildungen. Leipzig. 668 pp.

Petzold, E., & G. Kirchner. 1864. Arboretum Muscoviense. Gotha. 830 pp.

Philippi, R. A. 1895. Plantas nuevas Chilenas de las familias que corresponden al Tomo IV de la obre de Gay. Anal. Univ. Chile **91:** 514.

Pomeroy, K. B., & D. Dixon. 1966. These are the champs. Amer. Forests **72**(5): 14 35.

Porsild, A. E. 1939. Contributions to the flora of Alaska. Rhodora **41:** 199–254; 262 301; 441–483.

Poucques, M. L. de. 1949. Etudes caryologiques sur les Fagales. I. Le genre *Alnus*. Bull. Mus. Hist. Nat. Paris **21**(2): 147 152.

Pouzar, Z. 1964. Nomenclatural remarks on some generic names of Phanerogams validly published by Filip Maximillian Opiz. Preslia **36:** 337 342.

Pursh, F. 1814. Flora Americae Septentrionalis. London. 2 vols.

Raupe, H. M. 1936. Phytogeographic studies in the Athabaska-Great Slave Lake region. I. Catalogue of vascular plants. Jour. Arnold Arb. **17:** 241 315.

______. 1947. Some natural floristic areas in boreal America. Ecol. Mon. **17:** 221 234.

Raven, P. H. 1962. The systematics of *Oenothera* subgenus *Chylismia*. Univ. Calif. Publ. Bot. **34:** 1 122.

______. 1972. Plant species disjunctions: a summary. Ann. Mo. Bot. Gard. **58:** 234 246.

______, & D. I. Axelrod. 1972. Plate tectonics and Australasian paleobotany. Science **176:** 1379 1386.

______, & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Mo. Bot. Gard. **61:** 539 673.

Ray, J. 1682. Methodus Plantarum. Amsterdam. 166 pp.

Record, S. J., & R. W. Hess. 1943. Timbers of the New World. New Haven. 640 pp.

Regel, E. 1861. Monographische Bearbeitung der Betulaceen. Mem. Soc. Imp. Nat. Mosc. **13**(2): 59–187.

______. 1865. Bemerkungen uber die Gattungen *Betula* und *Alnus* nebst Beschreibung einiger neuer Arten. Bull. Soc. Imp. Nat. Mosc. **38**(3): 388 434.

———. 1868. Betulaceae. *In:* A. P. DE CANDOLLE, A. DE CANDOLLE, & C. DE CANDOLLE. Prodromous Systematis Naturalis Regni Vegetabilis. Paris. Vol. 16, pt. 2.

REHDER, A. 1927. Manual of Cultivated Trees and Shrubs. New York. 930 pp.

———. 1949. Bibliography of Cultivated Trees and Shrubs. Jamaica Plain, Mass. 825 pp.

REICHARDT, H. W. 1854. Verzeichniss allen von Herrn J. Ch. Neumann in Bohmen gesammelten Pflanzen. Verhandl. Zool. Bot. Ver. Wein **4:** 253 284.

REINERS, W. A., I. A. WORLEY, & D. B. LAWRENCE. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecol. **52:** 55–69.

RICHARDSON, J. 1823. Appendix No. VII. Botanical Appendix. *In:* J. FRANKLIN, Narrative of a Journey to the Shores of the Polar Sea in the Years 1819, 20, 21, and 22. London. Pp. 729–768.

RIDGWAY, J. E., & J. J. SKVARLA. 1969. Scanning electron microscopy as an aid to pollen taxonomy. Ann. Mo. Bot. Gard. **56:** 121 124.

RODRIQUES-BARRUECO, C., & G. BOND. 1968. Nodule endophytes in the genus *Alnus*. *In:* J. M. TRAPPE, J. F. FRANKLIN, R. F. TARRANT, & G. M. HANSEN, Eds. Biology of Alder. Portland. Pp. 185 192.

RUPRECHT, F. J. 1845. Beitrage zur Pflanzenkunde des Russichen Reiches. St. Petersburgh. Vol. 2.

RYDBERG, P. A. 1897. Rarities from Montana. Bull. Torr. Club **24:** 188 192.

RZEDOWSKI, J. 1965. Relaciones geograficas y posibles origenes de la flora de México. Boletin Soc. Bot. Méx. **29:** 121 177.

SARGENT, C. S. 1896, 1902. The Silva of North America. Boston. Vols. 9 and 14.

SCHALIN, I. 1968. Germination analysis of gray alder (*Alnus incana*) and black alder (*Alnus glutinosa*) seeds. *In:* J. M. TRAPPE, J. F. FRANKLIN, R. F. TARRANT, & G. M. HANSEN, Eds. Biology of Alder. Portland. Pp. 107–113.

SCHLECHTENDAL, D. F. L. VON. 1832. De plantis Mexicanis a G. Schiede M. Dre. collectis nuntium adfert D. F. L. de Schlechtendal. Linnaea **7:** 136–144.

SCHNEIDER, C. K. 1916. *Alnus*. *In:* C. S. SARGENT. Plantae Wilsonianae. Cambridge. Vol. 2, pp. 488–508.

SCHRANK, F. VON PAULA VON. 1789. Baiersche Flora. Munchen. 2 vols.

SCHUR, P. J. 1853. Verhandlungen und Mittheilungen des siebenburgischen Vereins fur Naturwissenschaften zu Hermannstadt **4:** 68.

SHARP, A. J. 1953a. Generic correlations in the flora of Mexico and eastern Asia. Jour. Tenn. Acad. Sci. **28:** 188.

———. 1953b. Notes on the flora of Mexico: world distribution of the woody dicotyledonous families and the origin of the modern vegetation. Jour. Ecol. **41:** 374 380.

———. 1972. The possible significance of some exotic distributions of plants occurring in Japan and/or North America. *In:* A. GRAHAM, Ed. Floristics and Paleofloristics of Asia and Eastern North America. Amsterdam. Pp. 61–64.

SMITH, H. H. 1923. Ethnobotany of the Menomini Indians. Bull. Publ. Mus. City of Milwaukee **4:** 1 174.

———. 1928. Ethnobotany of the Meskwaki Indians. Bull. Publ. Mus. City of Milwaukee **4:** 175 326.

———. 1932. Ethnobotany of the Ojibwe Indians. Bull. Publ. Mus. City of Milwaukee **4:** 327 525.

———. 1933. Ethnobotany of the firest Potawatomi Indians. Bull. Publ. Mus. City of Milwaukee 7: 1–230.

SMITH, J. H. G. 1968. Growth and yield of red alder in British Columbia. *In:* J. M. TRAPPE, J. F. FRANKLIN, R. F. TARRANT, & G. M. HANSEN, Eds. Biology of Alder. Portland. Pp. 273–286.

SPACH, A. E. 1841. Revisio Betulacearum. Ann. Sci. Nat. ser. 2, **15:** 182–212.

SPORNE, K. R. 1956. The phylogenetic classification of the angiosperms. Biol. Rev. Cambr. Phil. Soc. **31:** 1–29.

SPRENGEL, C. 1826. Caroli Linnaei, . . . Systema Vegetabilium, ed. 16. Gottingae. Vol. 3.

STAFLEU, F. A., C. E. B. BONNER, R. MCVAUGH, R. D. MEIKLE, R. C. ROLLINS, R. ROSS, J. M. SCHOPF, G. M. SCHULTE, R. DE VILMORIN, & E. G. VOSS, Eds. 1972. International Code of Botanical Nomenclature. Utrecht. 426 pp.

STANDLEY, P. C. 1920. Betulaceae. *In:* Trees and Shrubs of Mexico, Part 1. Contr. U.S. Nat. Herb. **23**(1): 167, 168.

———, & J. A. STEYERMARK. 1952. Betulaceae. *In:* Flora of Guatemala. Fieldiana: Botany **24**(3): 359–364.

STARKER, T. J. 1939. A new alder. Jour. For. **37:** 415, 416.

STEARN, W. L. 1973. Development of the amentiferous concept. Brittonia **25:** 316–333.

STEELE, F. L. 1961. Introgression of *Alnus serrulata* and *Alnus rugosa*. Rhodora **63:** 297–304.

STEENIS, C. G. G. J. VAN. 1957. Specific and infraspecific delimitation. Flora Malesiana ser. 1, **5**(3): clxvii-ccxxxiv.

TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Edinburgh. 310 pp.

TARRANT, R. F. 1968. Some effects of alder on the forest environment. *In:* J. M. TRAPPE, J. F. FRANKLIN, R. F. TARRANT, & G. M. HANSEN, Eds. Biology of Alder. Portland. P. 193.

TAYLOR, R. L., & G. A. MULLIGAN. 1968. Flora of the Queen Charlotte Islands. Pt. 2. Cytological Aspects of the Vascular Plants. Ottawa. 148 pp.

THORARINSSON, S. 1963. The Svinafell layers plant-bearing interglacial sediments in Oraefi, southeast Iceland. *In:* A. LÖVE & D. LÖVE, Eds. North Atlantic Biota and their History. New York. Pp. 337–389.

TIPPO, O. 1938. Comparative anatomy of the Moraceae and their presumed allies. Bot. Gaz. **100:** 1–99.

TISDALE, E. W., M. A. FOSBERG, & C. E. POULTON. 1966. Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia. Ecol. **47:** 517–523.

TORREY, J. 1859. Botany of the boundary. *In:* W. H. EMORY. Report on the United States and Mexico boundary survey made under the direction of the Secretary of the Interior. 34th Congress, 1st session. Senate Executive Document no. 135. Vol. 2, pp. 861–863.

TOURNEFORT, J. P. 1700. Institutiones rei herbariae, editio altera. Parisiis. Vol. 1.

TRAPPE, J. M. 1964. Mycorrhizal hosts and distribution of *Cenococcum graniforme*. Lloydia **27:** 100–106.

TUCKER, J. M. 1974. Patterns of parallel evolution of leaf form in New World oaks. Taxon **23:** 129–154.

TUCKERMAN, E. 1843. Observations on some interesting plants of New England. Am. Jour. Sci. ser. 2, **45:** 27 49.

TURRILL, W. B. 1962. *Alnus viridis* subsp. *crispa*. Curtis's Bot. Mag. **173:** 382.

UGOLINI, F. C. 1968. Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska. *In:* J. M. TRAPPE, J. F. FRANKLIN, R. F. TARRANT, & G. M. HANSEN, Eds. Biology of Alder. Portland. Pp. 115–140.

VANALSTINE, R. E. 1969. Geology and mineral deposits of the Poncho Springs NE quadrangle, Chaffee County, Colorado. U.S. Geol. Surv. Prof. Paper **626:** 1 52.

VAVILOV, N. I. 1951. The Origin, Variation, Immunity, and Breeding of Cultivated Plants. New York. 366 pp.

VILLARS, D. 1786, 1789. Historie des Plantes de Dauphine. Grenoble. Vols. 1 and 3.

VINES, R. A. 1960. Trees, Shrubs, and Woody Vines of the Southwest. Austin. 1104 pp.

WAHLENBERG, G. 1812. Flora Lapponica. Berolini. 550 pp.

WANSCHER, J. H. 1934. The basic chromosome number of the higher plants. New Phytol. **33:** 101 126.

WATSON, S. 1880. Botany of California. Boston. Vol. 2.

WESTON, R. 1770. Botanicus Universalis et Hortulanus. London. Vol. 1.

WETZEL, G. 1927. Chromosomenzahlen bei den Fagales. Berichte der Deutsch. Bot. Gesells. **45:** 251, 252.

——. 1928. Chromosomenstudien bei den Fagales. Berichte der Deutsch. Bot. Gesells. **46:** 212–214.

——. 1929. Chromosomenstudien bei den Fagales. Bot. Archiv **25:** 257 283.

WHERRY, E. T. 1960. Intermediate occurrences of *Alnus crispa*. Castanea **25:** 135.

WHITTAKER, R. H., & W. A. NIERING. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecol. **46:** 429–452.

WILLDENOW, K. L. 1805. Caroli a Linne Species Plantarum, ed. 4. Berolini. Vol. 4, pt. 1.

WILLIAMSON, R. L. 1968. Productivity of red alder in western Oregon and Washington. *In:* J. M. TRAPPE, J. F. FRANKLIN, R. F. TARRANT, & G. M. HANSEN, Eds. Biology of Alder. Portland. Pp. 287 292.

WINKLER, H. 1904. Betulaceae. Das Pflanzenreich **19**(4.61): 1 149.

WODEHOUSE, R. P. 1935. Pollen Grains. New York. 574 pp.

WOLFE, J. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño **20:** 83–110.

——. 1972. An interpretation of Alaskan Tertiary floras. *In:* A. GRAHAM, Ed. Floristics and Paleofloristics of Asia and Eastern North America. Amsterdam. Pp. 201–233.

——. 1973. Fossil forms of amentiferae. Brittonia **25:** 334 355.

——. 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. Ann. Mo. Bot. Gard. **62:** 264 279.

Wood, A. 1880. Class-book of Botany. New York. Pp. 649, 650.

Woodworth, R. H. 1929. Cytological studies in the Betulaceae. II. *Corylus* and *Alnus*. Bot. Gaz. **88:** 383 399.

______. 1930. Cytological studies in the Betulaceae. III. Parthenogenesis and polyembryony in *Alnus rugosa*. Bot. Gaz. **89:** 402 409.

______. 1931. Polyploidy in the Betulaceae. Jour. Arnold Arb. **12:** 206-217.

Worthington, N. P., R. H. Ruth, & E. E. Matson. 1962. Red Alder, its Management and Utilization. U.S. Dept. of Agriculture Misc. Publ. 881 Washington. 44 pp.

Zumaglini, A. M. 1849. Flora Pedemontana. Vol. 1.

DEPARTMENT OF BIOLOGY
CAPITAL UNIVERSITY
COLUMBUS, OHIO 43209

INDEX TO NAMES OF SPECIES AND INFRASPECIFIC TAXA

Alnaster alnobetulus (Ehrhart) Schweinfurth ex Ascherson = *Alnus viridis* (Villars) Lamarck & DeCandolle

Alnaster crispus (Aiton) Czerepanov = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnaster crispus (Aiton) Murai = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnaster crispus f. *mollis* (Fernald) Murai = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnaster crispus ssp. *sinuatus* (Regel) Murai = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve

Alnaster fruticosus (Ruprecht) Ledebour = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnaster kamtschaticus (Callier) Czerepanov = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve

Alnaster sinuatus (Regel) Czerepanov = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve

Alnaster viridis (Villars) Spach = *Alnus viridis* (Villars) Lamarck & DeCandolle

Alnobetula viridis (Villars) Schur = *Alnus viridis* (Villars) Lamarch & DeCandolle

Alnus acuminata Humboldt, Bonpland, & Kunth = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus acuminata ssp. *arguta* (Schlechtendal) Furlow

Alnus acuminata γ *ferruginea* (Humboldt, Bonpland, & Kunth) Regel = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus acuminata α *genuina* Regel = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus acuminata ssp. *glabrata* (Fernald) Furlow

Alnus acuminata δ *jorullensis* (Humboldt, Bonpland, & Kunth) Regel = *Alnus jorullensis* Humboldt, Bonpland, & Kunth ssp. *jorullensis*

Alnus acuminata β *mirbelii* (Spach) Regel = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus acuminata γ *spachii* Regel = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus acutissima (Winkler) Callier = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus alnobetula (Ehrhart) Hartig = *Alnus viridis* (Villars) Lamarck & DeCandolle

Alnus alnobetula (Ehrhart) K. Koch = *Alnus viridis* (Villars) Lamarck & DeCandolle

Alnus alnobetula var. ζ. *crispa* (Aiton) Winkler = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus alnobetula var. β. *fruticosa* (Ruprecht) Winkler = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus alnobetula a. *parvifolia* (Regel) Dippel = *Alnus viridis* ssp. *crispa* (Aiton) Turrill, in part

Alnus alnobetula var. θ. *parvifolia* (Regel) Winkler — see *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus alnobetula var. ϵ. *repens* (Hornemann) Winkler = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus alnobetula var. η. *stenophylla* Winkler = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve

Alnus alnobetula var. a. *typica* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill, in part

Alnus alnobetula var. *typica* f. *repens* (Hornemann) Winkler = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus alnus (Linnaeus) Britton = *Alnus glutinosa* (Linnaeus) Gaertner

Alnus alpina Villars = *Alnus viridis* (Villars) Lamarck and DeCandolle

Alnus americana (Regel) Czerepanov = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus americana hort. ex Hartig — see Excluded Names

Alnus americana hort. ex Petzold & Kirchner = *Alnus serrulata* (Aiton) Willdenow

Alnus argentea hort. ex Petzold & Kirchner = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus arguta (Schlechtendal) Spach = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow

Alnus arguta β *benthami* Regel — see Excluded Names

Alnus arguta var. *cuprea* Bartlett = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow

Alnus arguta α *genuina* Regel = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow

Alnus arguta γ *ovata* Regel — see Excluded Names

Alnus arguta δ *punctata* Regel = *Alnus acuminata* H.B.K. ssp. *acuminata*

Alnus arguta var. *subsericea* Bartlett = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow

Alnus × *aschersoniana* Callier — see Excluded Names

Alnus autumnalis hort. ex Hartig — see Excluded Names

Alnus autumnalis hort. ex Petzold & Kirchner — see Excluded Names

Alnus californica hort. ex Winkler = *Alnus rhombifolia* Nuttall

Alnus canadensis hort. ex Winkler = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus carpinifolia Desfontaines ex Spach = *Alnus serrulata* (Aiton) Willdenow

Alnus castaneifolia Douglas ex Hooker = *Alnus rubra* Bongard

Alnus castaneifolia Mirbel = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus communis Desfontaines ex Kuntze = *Alnus incana* ssp. *tenuifolia* (Nuttall) Bretung

Alnus crispa (Aiton) Pursh = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus crispa var. *elongata* Raup = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus crispa var. *harricanensis* Lepage = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus crispa × ssp. *hulteni* Murai — see Named Hybrids
Alnus crispa var. *mollis* (Fernald) Fernald = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus crispa f. *mollis* (Fernald) Murai = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus crispa ssp. *sinuata* (Regel) Hultén = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus crispa ssp. *sinuata* var. *laciniata* Hulten = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus crispa var. *sinuata* (Regel) Breitung = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus crispa f. *stragula* Fernald = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus densiflora Muller = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung
Alnus × *fallacina* Callier — see Named Hybrids
Alnus ferruginea Humboldt, Bonpland, & Kunth = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*
Alnus ferruginea var. *aliso* Lorenz & Hieronymus ex Winkler = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*
Alnus ferruginea var. *obtusifolia* Callier = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*
Alnus ferruginea var. a. *typica* Callier = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata* (in part), *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow (in part)
Alnus × *fiekii* Callier — see Excluded Names
Alnus × *fiekii* var. *dressleri* Callier — see Excluded Names
Alnus × *fiekii* var. *silesiaca* Callier — see Excluded Names
Alnus firmifolia Fernald = *Alnus jorullensis* Humboldt, Bonpland, & Kunth ssp. *jorullensis*
Alnus fruticosa Ruprecht = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus fruticosa var. *kamtschatica* (Callier) Komorov = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus fruticosa var. a. *typica* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus fruticosa var. *typica* f. *grandifolia* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus fruticosa var. *typica* f. *macrophylla* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus fruticosa var. *typica* f. *normalis* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus fruticosa var. *typica* f. *vulgaris* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus glabrata Fernald = *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow
Alnus glabrata var. *durangensis* Bartlett = *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow
Alnus glandulosa Sargent = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus glauca Michaux = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Alnus glutinosa (Linnaeus) Gaertner
Alnus glutinosa var. *autumnalis* Kuntze — see Excluded Names

Alnus glutinosa var. *quercifolia* hort. ex Hartig – see Excluded Names

Alnus glutinosa δ serrulata (Aiton) Regel = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen (in part), *Alnus rhombifolia* Nuttall (in part), *Alnus serrulata* (Aiton) Willdenow (in part)

Alnus glutinosa δ serrulata lusus d. *californica* Regel = *Alnus rhombifolia* Nuttall

Alnus glutinosa δ serrulata lusus a. *genuina* Regel = *Alnus serrulata* (Aiton) Willdenow

Alnus glutinosa δ serrulata lusus b. *obtusifolia* Regel = *Alnus serrulata* (Aiton) Willdenow

Alnus glutinosa δ serrulata lusus c. *rugosa* (DuRoi) Regel = *Alnus incana* ssp *rugosa* (DuRoi) Clausen

Alnus glutinosa var. *virescens* (Watson) Kuntze = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung

Alnus glutinosa (*vulgaris*) Persoon = *Alnus glutinosa* (Linnaeus) Gaertner

Alnus glutinosa — *α*: *vulgaris* Spach = *Alnus glutinosa* (Linnaeus) Gaertner

Alnus guatemalensis Gandoger = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow

Alnus hybrida Neumann ex Reichardt – see Excluded Names

Alnus incana (Linnaeus) Moench

Alnus incana α Hooker — see Excluded Names

Alnus incana β Hooker – see Excluded Names

Alnus incana β americana Regel = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus incana var. *ι. americana* (Regel) Winkler = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus incana 2. *autumnalis* hort. ex Petzold & Kirchner — see Excluded Names

Alnus incana α glauca (Aiton) Aiton f. — see Excluded Names

Alnus incana α glauca (Michaux) Regel = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus incana var. 3 *glauca* (Michaux) Loudon = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus incana var. *glauca* f. *tomphylla* Fernald = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus incana η rubra (Bongard) Regel = *Alnus rubra* Bongard

Alnus incana ssp. *rugosa* (DuRoi) Clausen

Alnus incana ssp. *rugosa* var. *occidentalis* (Dippel) Hitchcock = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung

Alnus incana var. *serrulata* (Aiton) Boivin = *Alnus serrulata* (Aiton) Willdenow

Alnus incana ssp. *tenuifolia* (Nuttall) Breitung

Alnus incana var. *tomophylla* (Fernald) Rehder = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus incana var. *virescens* Watson = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung

Alnus jorullensis Humboldt, Bonpland, & Kunth = *Alnus jorullensis* Humboldt, Bonpland, & Kunth ssp. *jorullensis*

Alnus jorullensis var. *acuminata* (Humboldt, Bonpland, & Kunth) Kuntze = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus jorullensis var. *acuminata* f. *angustifolia* Winkler — see Excluded Names

Alnus jorullensis var. *acuminata* f. *macrocarpa* Winkler – see Excluded Names

Alnus jorullensis var. *acuminata* f. *media* Winkler = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata* (in part), *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow (in part), *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow in part)

Alnus jorullensis ζ. *acutissima* Winkler = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus jorullensis β *castaneifolia* (Mirbel) Regel = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus jorullensis var. *exigua* Fernald = *Alnus jorullensis* ssp. *lutea* Furlow

Alnus jorullensis var. *ferruginea* (Humboldt, Bonpland, & Kunth) Kuntze = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus jorullensis var. *liebmanni* Callier — see Excluded Names

Alnus jorullensis ssp. *lutea* Furlow

Alnus jorullensis var. ε. *mirbelii* (Spach) Winkler = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus jorullensis α *typica* Regel = *Alnus jorullensis* Humboldt, Bonpland, & Kunth ssp. *jorullensis*

Alnus kamtschatica (Callier) Komorov = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve

Alnus kamtschatica (Regel) Kudo ex Masamune = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve

Alnus lanceolata Philippi = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus latifolia Desfontaines — see Excluded Names

Alnus latifolia Desfontaines ex Hartig = *Alnus serrulata* (Aiton) Willdenow

Alnus lindeni Regel = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus × *ljungeri* Murai — see Named Hybrids

Alnus macrophylla Desfontaines ex Spach = *Alnus serrulata* (Aiton) Willdenow

Alnus maritima Muhlenberg ex Nuttall

Alnus maritima hort. ex Spach = *Alnus serrulata* (Aiton) Willdenow

Alnus maritima hort. ex Wetzel = *Alnus rubra* Bongard

Alnus maritima α *typica* Regel = *Alnus maritima* Muhlenberg ex Nuttall

Alnus metoporina Furlow = *Alnus maritima* Muhlenberg ex Nuttall

Alnus mirbelii Spach = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus mirbelii var. *acutissima* (Winkler) Callier = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*

Alnus mitchelliana Curtis ex Gray = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus mollis Fernald = *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus noveboracensis Britton = *Alnus serrulata* (Aiton) Willdenow

Alnus oblongata (Aiton) Willdenow — see Excluded Names

Alnus oblongata hort. ex Winkler = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus oblongata α *genuina* Regel — see Excluded Names

Alnus oblongata β *oblonga* Regel — see Excluded Names

Alnus oblongifolia Torrey

Alnus obtusifolia Mertens ex Regel = *Alnus serrulata* (Aiton) Willdenow

Alnus occidentalis Dippel = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung
Alnus orbiculata Lopylaie ex Spach = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus oregona Nuttall = *Alnus rubra* Bongard
Alnus ovalifolia Bartlett = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow
Alnus ovata (Schrank) Loddiges = *Alnus viridis* (Villars) Lamarck & DeCandolle
Alnus ovata var. *repens* (Hornemann) Lange = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus ovata var. *repens* f. *macrophylla* Lange = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus ovata f. *repens* (Hornemann) Kjellman = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus pringlei Fernald = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow
Alnus × *purpusi* Callier — see Excluded Names
Alnus repens Wormskjold ex Hornemann = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus rhombifolia Nuttall
Alnus rhombifolia var. *bernardina* Munz & Johnston = *Alnus rhombifolia* Nuttall
Alnus rhombifolia var. *ovalis* Winkler = *Alnus rhombifolia* Nuttall
Alnus rhombifolia var. *typica* Callier = *Alnus rhombifolia* Nuttall
Alnus rubra Bongard
Alnus rubra Desfontaines ex Spach = *Alnus serrulata* (Aiton) Willdenow
Alnus rubra Tuckerman = *Alnus serrulata* (Aiton) Willdenow
Alnus rubra var. *pinnatisecta* Starker = *Alnus rubra* Bongard
Alnus rubra f. *pinnatisecta* (Starker) Rehder = *Alnus rubra* Bongard
Alnus rufescens Liebmann ex Hemsley = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata* (in part), *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow (in part)
Alnus rugosa (DuRoi) Sprengle = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Alnus rugosa var. *americana* (Regel) Fernald = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Alnus rugosa var. *americana* f. *hypomalaca* Fernald = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Alnus rugosa var. *americana* f. *tomophylla* Fernald = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Alnus rugosa var. γ. *obtusifolia* (Regel) Winkler = *Alnus serrulata* (Aiton) Willdenow
Alnus rugosa var. β. *serrulata* (Aiton) Winkler = *Alnus serrulata* (Aiton) Willdenow
Alnus rugosa var. α. *typica* Winkler = *Alnus serrulata* (Aiton) Willdenow
Alnus rugosa var. *typica* f. *emersoniana* Fernald = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Alnus serrulata (Aiton) Willdenow
Alnus serrulata α *genuina* Regel = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata — β: *macrophylla* Spach = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata γ *oblongifolia* (Torrey) Regel = *Alnus oblongifolia* Torrey
Alnus serrulata δ *obtusifolia* Regel = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata pumila Demcker — see Excluded Names
Alnus serrulata β *rugosa* (DuRoi) Regel = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen

Alnus serrulata var. *subelliptica* Fernald = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata var. *subelliptica* f. *emarginata* Fernald = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata var. *subelliptica* f. *mollescens* Fernald = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata var. *subelliptica* f. *nanella* Fernald = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata — α: *vulgaris* Spach = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata var. *vulgaris* Fernald = *Alnus serrulata* (Aiton) Willdenow
Alnus serrulata var. *vulgaris* f. *noveboracensis* (Britton) Fernald = *Alnus serrulata* (Aiton) Willdenow
Alnus × *silesiaca* Fiek — see Excluded Names
Alnus sinuata (Regel) Rydberg = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus sinuata var. b. *kamtschatica* (Callier) Callier = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus sinuata var. *stenophylla* (Winkler) Callier = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus sinuata var. a. *typica* Callier = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus sitchensis (Regel) Sargent = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus sitchensis var. b. *kamtschatica* Callier = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus sitchensis var. a. *typica* Callier = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus spachii (Regel) Callier = *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*
Alnus tenuifolia Nuttall = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung
Alnus tenuifolia var. b. *occidentalis* (Dippel) Callier = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung
Alnus tenuifolia var. a. *virescens* (Watson) Callier = *Alnus incana* ssp. *tenuifolia* (Nuttall) Breitung
Alnus tomentosa Durand ex Kellogg — see Excluded Names
Alnus tristis Wormskjold ex Regel = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus undulata Willdenow = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus undulata hort. ex Winkler = *Alnus serrulata* (Aiton) Willdenow
Alnus viridis (Villars) Lamarck & DeCandolle
Alnus viridis α Hooker = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis β Hooker = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus viridis var. *crispa* (Aiton) House = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis ssp. *crispa* (Aiton) Turrill
Alnus viridis var. *fernaldii* House = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis ssp. *fruticosa* (Ruprecht) Nyman = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis var. *glabra* Chamisso — see Excluded Names
Alnus viridis var. *microphylla* Chamisso — see Excluded Names
Alnus viridis β, *parvifolia* Regel = *Alnus viridis* ssp. *crispa* (Aiton) Turrill, in part
Alnus viridis var. *parvifolia* Sauter ex Winkler — see *Alnus viridis* ssp. *crispa* (Aiton) Turrill

Alnus viridis var. *repens* (Hornemann) Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis var. *repens* f. 1 *groenlandica* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis var. *repens* f. *typica* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis β sibirica Regel = *Alnus viridis* ssp. *crispa* (Aiton) Turrill, in part; = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve, in part
Alnus viridis β sibirica lusus a. *communis* Regel = *Alnus viridis* ssp. *crispa* (Aiton) Turrill, in part
Alnus viridis β sibirica lusus d. *kamtschatica* Regel = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus viridis β sibirica lusus b. *sitchensis* Regel = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus viridis β sibirica lusus c. *subglabra* Regel = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis var. *sibirica* (Regel) Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis var. *sibirica* lusus c. *glabra* Callier = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus viridis δ sinuata Regel = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Alnus viridis ssp. *sinuata* (Regel) Löve & Löve
Alnus viridis I. *typica* d. *repens* (Hornemann) Ascherson & Graebner = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Alnus vulgaris Hill = *Alnus glutinosa* (Linnaeus) Gaertner
Alnus washingtonia hort. ex Wetzel = *Alnus rubra* Bongard
Betula alnobetula Ehrhart = *Alnus viridis* (Villars) Lamarck & DeCandolle
Betula alnus Linnaeus = *Alnus glutinosa* (Linnaeus) Gaertner, in part; = *Alnus incana* (Linnaeus) Moench, in part
Betula alnus var. *americana* Ludwig — see Excluded Names
Betula alnus crispa (Aiton) Michaux = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Betula alnus α glutinosa Linnaeus = *Alnus glutinosa* (Linnaeus) Turrill
Betula alnus var. *glutinosa* Ludwig — see Excluded Names
Betula alnus β incana Linnaeus = *Alnus incana* (Linnaeus) Moench
Betula alnus var. *incana* Ludwig — see Excluded Names
Betula alnus (*rugosa*) DuRoi = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Betula alnus var. *rugosa* Ludwig — see Excluded Names
Betula alnus serrulata (Aiton) Michaux = *Alnus serrulata* (Aiton) Willdenow
Betula alpina (Villars) Borkhausen = *Alnus viridis* (Villars) Lamarck & DeCandolle
Betula arguta Schlechtendal = *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow
Betula crispa Aiton = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Betula glutinosa (Linnaeus) Linnaeus = *Alnus glutinosa* (Linnaeus) Gaertner
Betula incana (Linnaeus) Linnaeus f. = *Alnus incana* (Linnaeus) Moench
Betula incana α glauca Aiton see Excluded Names
Betula oblongata Aiton — see Excluded Names
Betula ovata Schrank = *Alnus viridis* (Villars) Lamarck & DeCandolle
Betula rugosa (DuRoi) Ehrhart = *Alnus incana* ssp. *rugosa* (DuRoi) Clausen
Betula serrulata Aiton = *Alnus serrulata* (Aiton) Willdenow
Betula viridis Villars = *Alnus viridis* (Villars) Lamarck & DeCandolle

Betula-alnus 6. *crispa* Weston — see Excluded Names
Betula-alnus glauca Marshall — see Excluded Names
Betula-alnus glutinosa Weston — see Excluded Names
Betula-alnus incana Weston see Excluded Names
Betula-alnus maritima Marshall = *Alnus maritima* Muhlenberg ex Nuttall
Betula-alnus rubra Marshall — see Excluded Names
Betula-alnus rubra Weston see Excluded Names
Duschekia crispa (Aiton) Pouzar = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Duschekia fruticosa (Ruprecht) Pouzar = *Alnus viridis* ssp. *crispa* (Aiton) Turrill
Duschekia ovata (Schrank) Winkler = *Alnus viridis* (Villars) Lamarck & DeCandolle
Duschekia sinuata (Regel) Pouzar = *Alnus viridis* ssp. *sinuata* (Regel) Löve & Löve
Duschekia viridis (Villars) Opiz = *Alnus viridis* (Villars) Lamarck & DeCandolle
Semidopsis viridis (Villars) Zumaglini = *Alnus viridis* (Villars) Lamarck & DeCandolle

A VASCULAR FLORA OF THE CARIBOU RANGE, NORTHWEST TERRITORIES, CANADA[1]

M. A. Jasieniuk and E. A. Johnson

Only in recent years has access to large areas of the Canadian western subarctic become possible to ecologists and botanists. Since 1972 we have been carrying on ecological investigations on the role of forest fires in a 105,000 sq km area of subarctic forest (Figure 1). The region extends from 60° N latitude north to tree line and from longitude 104° W to 112° W. It is called the Caribou Range because it serves as the primary wintering ground for the Beverley caribou population, the largest caribou population in Canada.

Only three other floristic reports deal with parts of this area: Harper (1931), Raup (1936), and Scotter (1966). Of these Scotter is the most pertinent. Because of the nature of our ecological research, collections reflect the uplands and peatlands with only cursory collections in aquatic and strand habitats. Figure 1 shows the locations in which collections were made; all transportation in the region is by boat or float equipped aircraft as there are no roads.

The Caribou Range is located on the Precambrian Shield and consists mainly of an Archaean crystalline basement with Proterozoic intrusives. The bedrock is covered to varying thicknesses by an assortment of glacial formed features. East of approximately longitude 109° W the landscape is covered with molded till with many extensive esker trains. West of longitude 109° W the till becomes thinner with much bedrock exposed.

Climatically the region has short cool summers and long cold winters. The mean January temperature at Fort Smith on the southern edge of the region is −26° C and mean July temperature is 17° C. The annual precipitation for the region is approximately 250 mm. Snow occurs first in early October and melts in May. Snow patches in protected locations can be found into July.

The Caribou Range includes small patches of tundra and parts of two forest sections in the Halliday classification (Rowe 1972), viz. from southwest to northeast, the Northwestern Transition (B.27) and the Forest-Tundra (B.32). These vegetation belts correspond

---

[1] This paper is dedicated to the memory of Prof. A. R. Hodgdon.

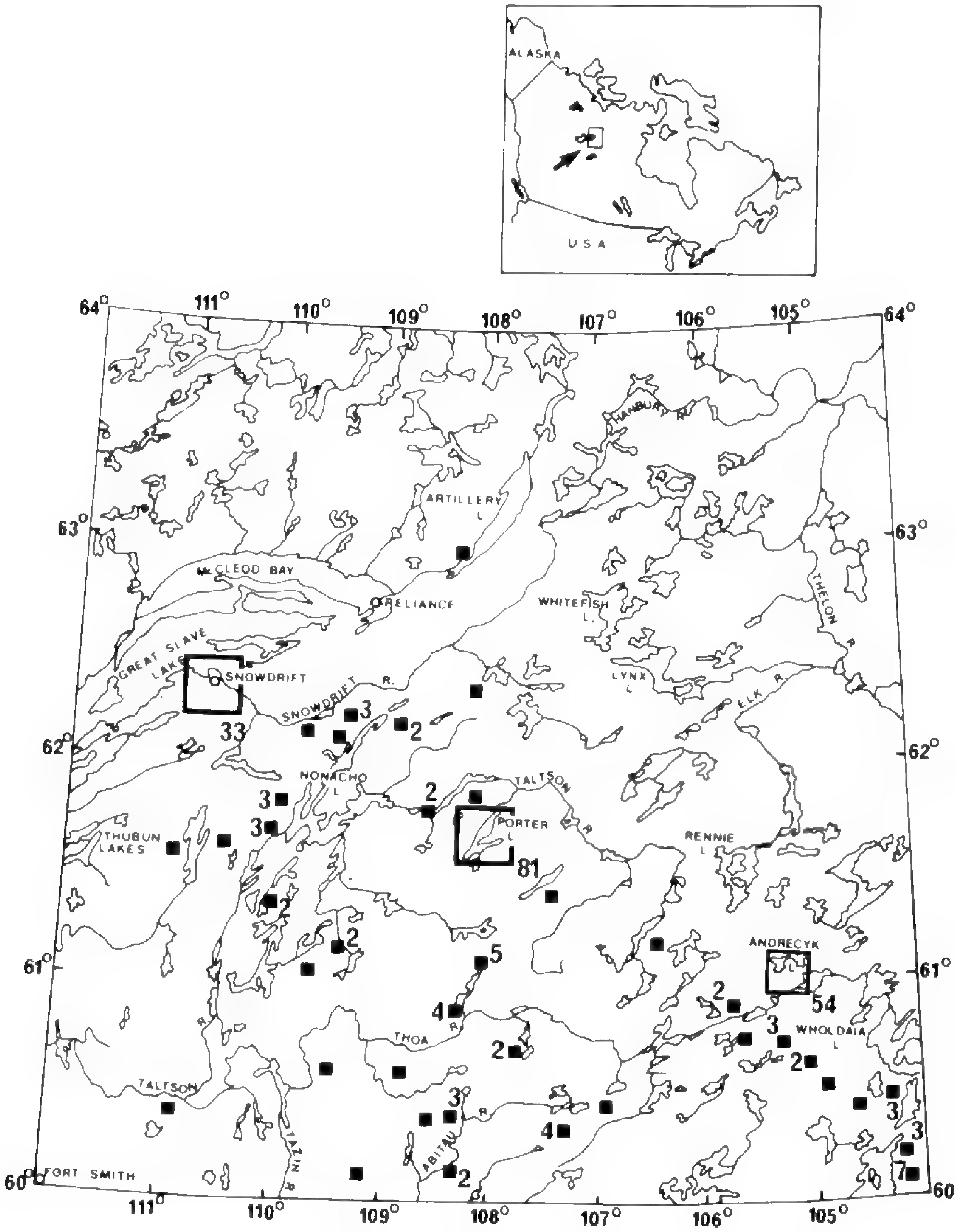


Figure 1. Map showing location and approximate number of collecting stations in the Caribou Range, N.W.T. Squares indicate one collection station in an area unless otherwise stated.

approximately to what Hustich (1949) and Hare (1950) recognized east of Hudson Bay as "Open Boreal Woodland" or "Taiga" and "Forest-Tundra Ecotone" or "Forest Tundra".

The general physiognomy of the vegetation in the Caribou Range is as follows: Upland sites are mostly dominated by closed or open forests of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). White spruce (*Picea glauca*) is a common component of forests on coarse-textured materials, for example on outwash sand gplains and esker ridges. It is also the prominent tree adjacent to moving water, reaching a large size on alluvium. It is very common on areas adjacent to Great Slave Lake. Aspen (*Populus tremuloides*) is not a conspicuous tree except in areas of pronounced relief in the south and west. White birch (*Betula neoalaskana* Sarg.), on the other hand, is common throughout the forested area and extends to the tundra.

Peatland sites are generally dominated by open forests of black spruce. Tamarack (*Larix laricina*) occurs infrequently with the black spruce. Treeless lichen-covered peat plateaus become more common and polygonally patterned towards tree line. Aquatic sphagna and/or sedges are common in wet depressions within these peatland sites. Meadows with *Carex* and *Eriphorum* also occur on mucky or peaty lake margins.

More detailed vegetation and floristic studies relevant to this region are Argus (1966), Maini (1966), Larsen (1971), Johnson and Rowe (1975), and Johnson (1975, 1977a,b). Nomenclature follows Hultén (1968) except in *Betula* which follows Dugle (1966) and in *Salix* which follows Argus (1973). Other species not found in Hultén follow the nomenclature of Moss (1959). Numbers in the annotated list are collection numbers of one of the authors (E.A.J.). All specimens cited here are deposited in the W. P. Fraser Herbarium, University of Saskatchewan. Coordinates are given for unnamed lakes. The lake locally known as Forestry Lake is near Andrecyk Lake. All other lakes can be located on National Topographic Surveys Maps of 1:250,000 scale.

ACKNOWLEDGMENTS

We should like to thank Northwest Lands and Forest Service, Fort Smith, N.W.T., particularly John Gilmour, Howard Gray, and

Eddy Powder for their co-operation in the field. Collections were undertaken with the help of R. Godwin, J. Haraldson, W. Harris, D. Johnson, S. Johnson, A. Lincoln, K. Traynor, and T. Trottier.

Taxonomic assistance was provided by N. A. Skoglund and V. L. Harms, University of Saskatchewan; J. H. Hudson, University of Saskatchewan (*Carex* and *Eriophorum*); and G. W. Argus, National Herbarium, Ottawa (*Salix*). We also thank V. L. Harms, J. W. Sheard, and N. A. Skoglund for helpful comments during the preparation of the manuscript. This work was supported in part by Dept. Indian and Northern Affairs, Canadian Forestry Service, and Canadian Wildlife Service contracts to J. S. Rowe. We are grateful to the Dept. of Biology and the Centre for Northern Studies and Research, McGill University for defrayal of publication costs. Collection and identification of plant specimens and preparation of the paper are solely the responsibility of the authors.

ANNOTATED LIST OF SPECIES

LYCOPODIACEAE

Lycopodium annotinum L. ssp. **annotinum.** Porter Lake — common in black spruce-lichen woodland, *610.* Forestry Lake — uncommon with *Alnus crispa, Betula glandulosa, 1224.*

Lycopodium complanatum L. Porter Lake uncommon in recently burned area, *617, 641.* Snowdrift — uncommon in white spruce woodland. Forestry Lake — common in black spruce-lichen woodland, *879;* recently burned area, *1289.*

Lycopodium obscurum L. var. **dendroideum** (Michx.) D.C. Eat. Porter Lake — rare on edge of sphagnum bog.

EQUISETACEAE

Equisetum arvense L. Common throughout area on wet sandy or peaty sites. Rutledge Lake, *1141.*

Equisetum fluviatile L. ampl. Ehrh. Common throughout area in protected sandy bays of lakes and rivers. Rutledge Lake, *1134.*

Equisetum scirpoides Michx. Porter Lake — common in moist feather moss forests. Snowdrift — common in moist black spruce, white spruce-lichen woodlands. Found on east-facing slope, *718.*

Equisetum silvaticum L. Common throughout area in moist upland and lowland sites and recently burned areas. Forestry Lake, *894*.

CRYPTOGRAMMACEAE

Cryptogramma crispa (L.) R. Br. var. **acrostichoides** (R. Br.) Clarke. Snowdrift — common in moist crevices of rock outcroppings, *745*. D'Aoust Lake — common on top of esker, *1030*.

ATHYRIACEAE

Cystopteris fragilis (L.) Bernh. Snowdrift — uncommon on rock outcroppings.

Woodsia ilvensis (L.) R. Br. Uncommon on rock outcroppings. Porter Lake, *656, 1064*. Snowdrift, *786*.

ASPIDIACEAE

Dryopteris fragrans (L.) Schott. Porter Lake — common in crevices of rock outcroppings and among boulders, *645, 1064*. Snowdrift.

Gymnocarpium dryopteris (L.) Newm. Rare in moist birch stand. Porter Lake.

Gymnocarpium robertianum (Hoffm.) Newm. Forestry Lake — rare in crevices of exposed bedrock in a recently burned lichen woodland, *881*.

POLYPODIACEAE

Polypodium vulgare L. var. **virginianum** (L.) Eaton. Uncommon on rock outcroppings. Snowdrift. Porter Lake, *634*.

PINACEAE

Pinus Banksiana Lamb. Common throughout area on sandy uplands and rocky ridges. Porter Lake, *608*.

Larix laricina (DuRoi) K. Koch. Uncommon throughout area in bog forests with black spruce. Forestry Lake, *888*.

Picea glauca (Moench) Voss. Common throughout area on coarse-textured materials of outwash plains and esker ridges and along streams. Porter Lake — common on esker, *896*. Forestry Lake — common on esker, *1232*. Rutledge Lake, *923*.

Picea mariana (Mill.) Britt., Sterns & Pogg. Common throughout area on mineral soil, rock outcroppings and peatlands. Porter Lake — common in lichen woodland, *609*.

CUPRESSACEAE

Juniperus communis L. ssp. **nana** (Willd.) Syme. Common throughout area on south-facing sandy or rocky slopes. Porter Lake — common with *Picea glauca, 600*.

Juniperus horizontalis Moench. Snowdrift — common on south-facing rock outcroppings, *721*.

TYPHACEAE

Typha latifolia L. Porter Lake – rare along edge of marsh with *Carex* spp.

SPARGANIACEAE

Sparganium angustifolium Michx. Common in water 2–4 feet deep. Snowdrift, *840*. Forestry Lake, *871*.

Sparganium minimum (Hartm.) E. Fries. Snowdrift – common in water 2–3 feet deep, *842*.

POTAMOGETONACEAE

Potamogeton alpinus Balb. Snowdrift — rare submerged in shallow water, *858*.

Potamogeton filiformis Pers. Snowdrift — rare in water 3 feet deep, *860*.

Potamogeton perfoliatus L. ssp. **Richardsonii** (Bennett) Hult. Snowdrift — common in 2–3 feet of water, *861*. Porter Lake, Forestry Lake — uncommon in shallow water.

JUNCAGINACEAE

Triglochin maritimum L. Rutledge Lake – uncommon along lakeshore, *1127.*

GRAMINEAE

Phalaris arundinacea L. Snowdrift — rare in shallow water along sandy shore, *854.*

Hierochloë alpina (Sw.) Roem. & Schult. Forestry Lake — common on sandy esker in white spruce-lichen woodland, *1243.*

Oryzopsis pungens (Torr.) Hitchc. Snowdrift – rare in sandy jack pine area, *766.*

Agrostis scabra Willd. Snowdrift — rare on moist slope, *777.* Forestry Lake — common in recently burned area, *1293.* D'Aoust Lake — uncommon in burned area top of esker, *1031.*

Calamagrostis canadensis (Michx.) Beauv. Snowdrift — common along lakeshore, *811;* uncommon in white spruce-lichen woodland on bedrock, *733.* Unnamed lake (60° 18′N, 107° 20′W) — common in recently burned area, *1274.*

Calamagrostis canadensis (Michx.) Beauv. ssp. **Langsdorffi** (Link) Hult. Common throughout area along lakeshores and in open upland forests. Forestry Lake, *876.*

Calamagrostis inexpansa Gray. Unnamed lake (60° 18′N, 107° 20′W) — common in recently burned area, *1292.*

Calamagrostis lapponica (Wahlenb.) Hartm. MacInnis Lake common on bedrock slope, *1033.*

Calamagrostis neglecta (Ehrh.) Gaertn., Mey. & Schreb. Common in recently burned upland areas. Siltaza Lake, *1016.* Porter Lake, *1041, 1067.* Forestry Lake, *1285.* Uncommon in wet depressions. Porter Lake, *952, 973.* Uncommon in black spruce-lichen woodland. Wholdaia Lake, *1282.*

Calamagrostis purpurascens R. Br. ssp. **purpurascens.** Snowdrift — common in white spruce and jack pine-lichen woodland, *729, 782.* Forestry Lake — uncommon on sandy ridge, *877.* D'Aoust Lake — uncommon in recent burn, *1054.* Alcantara Lake, *1296.*

Deschampsia caespitosa (L.) Beauv. ssp. **caespitosa.** Snowdrift — rocky sand shore, *812.*

Trisetum spicatum (L.) Richter ssp. **majus** (Vasey) Hult. Common in lichen woodland on bedrock. Porter Lake, *659.* Snowdrift, *696, 697, 833.*

Beckmannia erucaeformis (L.) Host. Snowdrift - rare on sandy shore with *Agrostis, 838.*

Poa alpigena (E. Fries) Lindm. Rare on exposed bedrock in lichen woodland. Snowdrift, *781.* Porter Lake, *665.*

Poa alpina L. Snowdrift — rare on recently burned exposed bedrock, *831.*

Poa glauca M. Vahl. Common throughout area on dry upland sites, moister slopes, burned areas. Porter Lake, *631, 642, 663.* Snowdrift, *700, 707.* Siltaza Lake, *1015.* D'Aoust Lake, *1052.* Forestry Lake, *1242.*

Glyceria borealis (Nash) Batchelder. Snowdrift — rare on sandy shore of river, *846.*

Festuca saximontana Rydb. Common throughout area on dry sandy areas and exposed bedrock. Snowdrift, *778, 779.* Forestry Lake. Porter Lake, *661.* D'Aoust Lake — uncommon on recently burned area on top of esker, *1032.*

Agropyron subsecundum (Link) Hitchc. Snowdrift — uncommon in open black spruce-lichen woodland, *794.*

Agropyron violaceum (Hornem.) Lange. Snowdrift — rare on exposed bedrock, *832.*

Hordeum jubatum L. Snowdrift — common in disturbed areas around settlement, *847.*

CYPERACEAE

Eriophorum angustifolium Honck. Porter Lake - common in *Sphagnum recurvum* bog pools with *Carex* spp., *897, 920, 977.*

Eriophorum brachyantherum Trautv. & Mey. Common throughout area in *Sphagnum riparium — S. recurvum* bog pools. Porter Lake, *962.* Forestry Lake, *1082, 1089.*

Eriophorum russeolum E. Fries. Common throughout area in bog pools of *Sphagnum recurvum* and *Carex* species. Porter Lake, *902, 962, 897, 966.* Forestry Lake, *1080, 1089.*

Eriophorum vaginatum L. ssp. **spissum** (Fern.) Hult. Forestry Lake — uncommon on lichen-covered peat plateau, *1082.*

Eriophorum vaginatum L. ssp. **vaginatum.** Porter Lake uncommon in *Sphagnum fuscum* bog forests with ericaceous shrubs, *1057.* Uncommon on *Sphagnum balticum, S. magellanicum* mounds, *963.*

Trichophorum caespitosum (L.) Hartm. Porter Lake uncommon with *Carex* sp. on collapsed palsa, *985.* Unnamed lake (60° 23′N, 108° 05′W) — common in sphagnum bog with *Chamaedaphne calyculata* and *Andromeda polifolia, 1253.*

Eleocharis palustris (L.) Roem. & Schult. Porter Lake — rare in slow moving water.

Carex aenea Fern. Common in recently burned black spruce-lichen upland forests. Porter Lake, *642.* Forestry Lake, *882.* Siltaza Lake, *1020.* Unnamed lake (61° 42′N, 108° 14′W), *1068.*

Carex albo-nigra Mack. Snowdrift — rare in open jack pine-lichen woodland on bedrock, *783.*

Carex aquatilis Wahlenb. Porter Lake — common in *Sphagnum fuscum* bog forests, *936, 945, 947, 948, 974, 984, 987, 1060.* Common in *Sphagnum recurvum* bog pool with *Carex* spp., *976.* Forestry Lake — common in *Sphagnum recurvum — S. riparium* bog pools with *Carex* spp., *1094, 1095.* Snowdrift — common on rocky sand shore, *810.*

Carex brunnescens (Pers.) Poir. Uncommon in recently burned areas. Unnamed lake (60° 42′N, 108° 14′W), *1069A.* Porter Lake, *1073.* Unnamed lake (60° 18′N, 107° 20′W), *1275.* Uncommon in black spruce upland forest. Flett Lake, *1279.*

Carex canescens L. Porter Lake — common in *Sphagnum recurvum* bog pools, *910.* Common in fen pool with brown mosses, *958.* Rare on collapsed palsa mound with *Scirpus caespitosis, 986.*

Carex capillaris L. Porter Lake — rare on exposed bedrock in open black spruce-lichen woodland, *660.*

Carex deflexa Hornem. Common in recently burned upland areas. MacInnis Lake, *1034*. Unnamed lake (60° 50′N, 110° 07′W), *1040*. Porter Lake, *1074*. Alcantara Lake, *1300*.

Carex foena Willd. Common throughout area on sandy eskers and recent upland burns. Porter Lake, *663*. Siltaza Lake, *1026*. D'Aoust Lake, *1062*. Forestry Lake, *1241*. Alcantara Lake, *1294, 1299*.

Carex gynocrates Wormsk. Porter Lake — common on treeless lichen-covered peat plateau, *913*.

Carex lasiocarpa Ehrh. Rutledge Lake – found in shallow water, *1138*.

Carex limosa L. Common in *Sphagnum recurvum* — *S. riparium* bog pools. Porter Lake, *907, 916, 925, 956, 960, 961, 965*. Forestry Lake, *1097*.

Carex magellanica Lam. Common throughout area in *Sphagnum riparium* — *S. recurvum* bog pools. Forestry Lake, *1090, 1093, 1096, 1200*. Common throughout area on *S. balticum, S. magellanicum* mounds with ericaceae. Porter Lake, *922, 964*. Found in fen pool with brown mosses. Porter Lake, *959*.

Carex norvegica Retz. Rutledge Lake — found along lakeshore, *1139*.

Carex praticola Rydb. Selwyn Lake — uncommon in recent burn, *1287*.

Carex rariflora (Wahlenb.) J. E. Sm. Forestry Lake — common in *Sphagnum riparium* and *S. recurvum* pools, *1083, 1214*.

Carex rostrata Stokes. Common in shallow water along lakes. Forestry Lake, *895, 1244*.

Carex rotundata Wahlenb. Common in *Sphagnum recurvum* bog pools on peat plateaus. Porter Lake, *905*. Forestry Lake, *1078, 1215*.

Carex saxatilis L. var. **major** Olney. Snowdrift — rare on rocky sand shore, *809, 814*. Rutledge Lake — found along lakeshore, *1140*.

Carex scirpoidea Michx. Snowdrift — uncommon in open white spruce-lichen woodland, *709*.

Carex supina Willd. ssp. **spaniocarpa** (Steud.) Hult. Snowdrift — uncommon in open jack pine-lichen woodland on bedrock, *784.*

Carex vaginata Tausch. Snowdrift — common in white spruce-lichen woodland, *698, 701, 710.* Porter Lake — uncommon in bog forest, *946.*

ARACEAE

Calla palustris L. Forestry Lake — uncommon in shallow water along a stream, *868.*

LEMNACEAE

Lemna trisulca L. Snowdrift — rare in bay of Great Slave Lake, *857.*

JUNCACEAE

Juncus arcticus Willd. Snowdrift — rare in shallow water and along lake shore.

Juncus filiformis L. Snowdrift — rare along sandy shore of Snowdrift River, *843.* Forestry Lake — uncommon on sandy beach, *1210.*

LILIACEAE

Tofieldia pusilla (Michx.) Pers. Porter Lake — rare in sphagnum bog with open black spruce, *647, 934.* Snowdrift — common in sphagnum bogs and moist slopes, *705.*

Allium schoenoprasum L. var. **sibiricum** (L.) Hartm. Snowdrift — uncommon on gravel shores of river and on sandbars, *765, 799.*

Smilacina trifolia (L.) Desf. Selwyn Lake — rare in moist area in black spruce woods, *885.* Forestry Lake — common in *Sphagnum recurvum* bog pools, *1091.*

ORCHIDACEAE

Cypripedium passerinum Richards. Snowdrift — common in moist areas on north-facing slopes with *Picea mariana* or *P. glauca, 823.*

Amerorchis rotundifolia (Banks) Hult. Snowdrift — common in moist areas on north-facing slopes with *Picea mariana* or *P. glauca.*

Platanthera obtusata (Pursh) Lindl. Snowdrift — common in moist areas on north-facing slopes with *Picea mariana* and *P. glauca, 703.*

Corallorrhiza trifida Châtelain. Snowdrift — rare in moist areas on north-facing slope with *Picea mariana* and *P. glauca, 704, 780.*

Calypso bulbosa (L.) Rchb. f. Snowdrift — uncommon in white spruce lichen-woodland, *715, 815.*

SALICACEAE

Populus balsamifera L. ssp. **balsamifera.** Porter Lake — rare on sandy beach. Snowdrift — common along sandy and rocky shore.

Populus tremuloides Michx. Porter Lake — rare on exposed bedrock in black spruce-lichen woodland, *653.* Snowdrift — uncommon on exposed bedrock slopes, *720.* Forestry Lake.

Salix alaxensis (Anderss.) Cov. var. **alaxensis.** Snowdrift — found on rocky sand beach, *836.*

Salix arctophila Cock. ex Heller. Porter Lake — found in open black spruce-lichen woodland on exposed bedrock, *651.* Found on *Sphagnum fuscum* hummocks with *Carex* spp., *933, 1059.*

Salix bebbiana Sarg. Common in recently burned areas. Porter Lake, *611, 635.* Sparks Lake, *1045.* Unnamed lake (60° 19′N, 107° 07′W), *1267.* Flett Lake, *1284A.* Alcantara Lake, *1295.* Found along lake shore. Unnamed lake (60° 10′N, 108° 30′W), *1258.* Found in black spruce-lichen woodland. Flett Lake, *1280.*

Salix glauca L. Common throughout area in recently burned areas. Porter Lake, *615, 1072.* Snowdrift, *807, 808.* Siltaza Lake, *1013, 1014, 1021.* Unnamed lake (61° 49′N, 110° 04′W), *1043.* Unnamed lake (60° 18′N, 107° 06′W), *1271, 1272.* Flett Lake, *1284B.* Alcantara Lake, *1298.* Found in black spruce, white spruce-lichen woodland. Snowdrift, *788.* Found in black spruce-feather moss forest. Porter Lake, *931.* Found in black spruce-glandular birch woodland. Sandy Lake, *1277.* Unnamed lake (60° 18′N, 107° 06′W), *1286.* MacInnis Lake, *1035.*

Salix myrtillifolia Anderss. Porter Lake — common in bog forest on *Sphagnum fuscum* hummocks with ericaceous shrubs and sedges, *949.*

Salix planifolia Pursh ssp. **planifolia.** Porter Lake found in depression with *Sphagnum recurvum* and sedges, *975.* Flett Lake — found in black spruce-birch-lichen woodland, *1283.*

Salix scouleriana Barr. Forestry Lake — rare in black spruce-birch forest, *1276.*

MYRICACEAE

Myrica gale L. var. **tomentosa** C.DC. Common throughout area along lake shores on peat or sand. Forestry Lake, *892, 1245.*

BETULACEAE

Betula glandulosa Michx. Common throughout area on upland spruce-lichen woodlands. Forestry Lake — common on esker with *Picea glauca, Stereocaulon paschale, Empetrum nigrum, 1234.* Porter Lake — common in recently burned area, *640.*

Betula neoalaskana Sarg. Porter Lake — common in open black spruce, white spruce-lichen woodland, *601, 603, 618, 625, 629, 672;* common in recently burned areas, *616, 636.* Forestry Lake — common on esker with *Picea glauca, Empetrum nigrum, Stereocaulon paschale, 1233.*

Betula papyrifera Marsh. Uncommon throughout area along streams and on upland mineral soils. Snowdrift — found in open black spruce-white spruce-lichen woodland, *789.*

Betula × sargentii Dugle. Snowdrift — found in open white spruce-lichen woodland, *690.*

Betula × uliginosa Dugle. Porter Lake — uncommon in recently burned area, *614;* uncommon in open black spruce-lichen woodland, *671.*

Alnus crispa (Ait.) Pursh. Common throughout area on upland mineral soils and peatland sites. Porter Lake *613, 652.* Snowdrift, *722.*

Alnus incana (L.) Moench. ssp. **tenuifolia** (Nutt.) Breitung. Snowdrift — uncommon along shoreline in sandy locations. Rare on moist uplands, *805*.

URTICACEAE

Urtica gracilis Ait. Snowdrift — rare around townsite, *862*.

SANTALACEAE

Geocaulon lividum (Richards.) Fern. Common throughout area on eskers and rock outcroppings. Porter Lake, *602*. Snowdrift, *692*. Forestry Lake, *1238*.

POLYGONACEAE

Rumex mexicanus Meisn. Snowdrift — uncommon along the Snowdrift River, *849*.

Polygonum achoreum Blake. Snowdrift common around townsite, *848*.

Polygonum viviparum L. Siltaza Lake — rare in bog forest, *1012*.

CHENOPODIACEAE

Chenopodium album L. Snowdrift — rare around townsite, *853*.

Chenopodium capitatum (L.) Aschers. Snowdrift — rare in disturbed areas near townsite and on burns, *821*.

CARYOPHYLLACEAE

Stellaria monantha Hult. Snowdrift — rare in open white spruce-lichen woodland on bedrock, *711*.

Minuartia dawsonensis (Britt.) Mattf. Snowdrift — uncommon in moist areas of white spruce-lichen woodland on bedrock, *712*.

Moehringia lateriflora (L.) Fenzl. Snowdrift — uncommon in open white spruce-lichen woodland on bedrock, *764*.

NYMPHEAECEAE

Nuphar variegatum Engelm. Common along streams and lakeshores in shallow water. Porter Lake. Forestry Lake, *887, 1087.* Unnamed lake (60°50′N, 110°07′W), *1036.*

RANUNCULACEAE

Aquilegia brevistyla Hook. Snowdrift — uncommon on rocky shore with *Populus balsamifera, 714.*

Anemone multifida Poir. Snowdrift — found in open white spruce-lichen woodland on bedrock, *713.*

Pulsatilla patens (L.) Mill. Common on south-facing slopes in lichen woodland. Porter Lake, Snowdrift, Whirlwind Lake.

Ranunculus lapponicus L. Porter Lake rare along stream with *Picea glauca* overstory.

Ranunculus reptans L. Snowdrift common along lakeshore, *801.* Forestry Lake — uncommon in wet peaty area, *1211.*

Ranunculus trichophyllus Chaix. var. **trichophyllus.** Forestry Lake — common in shallow water, *869.*

FUMARIACEAE

Corydalis aurea Willd. Snowdrift — uncommon in one-year old burn near townsite, *817.*

Corydalis sempervirens (L.) Pers. Common in dry lichen woodland on exposed bedrock slopes and disturbed area. Porter Lake, *649, 955.* Snowdrift, *772.*

CRUCIFERAE

Capsella bursa-pastoris (L.) Medic. Snowdrift — rare around townsite, *851.*

Draba aurea Vahl. Snowdrift — uncommon in recently burned area, *835;* rare in open white spruce-lichen woodland on bedrock, *732.*

Descurainia pinnata (Walt.) Britt. var. **brachycarpa** (Richards.) Fern. Snowdrift — rare around townsite, *864*.

Descurainia sophia (L.) Prantl. Snowdrift — rare around townsite, *852*.

Arabis arenicola (Richards.) Gelert. Alcantara Lake — rare in recent burn on sandy esker, *1297*.

Arabis Drummondii Gray. Snowdrift found in recently burned area, *834*.

Arabis Holboellii Hornem. Snowdrift — uncommon in lichen woodland with *Arctostaphylos uva-ursi*, *792*.

DROSERACEAE

Drosera anglica Huds. Porter Lake — uncommon in *Carex aquatilis* — aquatic sphagna bog pools, *991*.

Drosera rotundifolia L. Unnamed lake (60° 23′N, 108° 05′W) — common in *Sphagnum fuscum* bog forests, *1255*.

SAXIFRAGACEAE

Saxifraga aizoides L. Snowdrift — common on dry rock outcroppings with *Picea glauca*, *702*.

Saxifraga nivalis L. Snowdrift — uncommon growing in crevices in rock outcroppings, *744A*.

Saxifraga tricuspidata Rottb. Common on sandy eskers. Porter Lake, *638*, *996*. Forestry Lake, *1239*.

Parnassia Kotzebuei Cham. & Schlecht. Porter Lake — rare along rocky beach.

Parnassia palustris L. ssp. **neogaea** (Fern.) Hult. Snowdrift — uncommon along sandy-rock beach, *855*. Unnamed lake (60° 23′N, 108° 05′W) — common in sphagnum bog bordering lake growing with *Trichophorum caespitosum*, *Eriophorum*, *1254*. Rutledge Lake — uncommon along sandy shores, *1137*.

Ribes glandulosum Grauer. Uncommon on recently burned upland sites with *Betula papyrifera* and *Vaccinium vitis-idaea*. Porter Lake, *612*, Siltaza Lake, *1022*. Unnamed lake (60° 18′N, 107° 20′W), *1273*.

Ribes hudsonianum Richards. Porter Lake — uncommon along streams. Snowdrift — uncommon in recently burned areas with dense *Alnus* cover, *803*.

Ribes oxyacanthoides L. Porter Lake uncommon on dry rocky slopes and recently burned areas. Snowdrift — common on dry uplands.

Ribes triste Pall. Snowdrift — uncommon in recently burned area, *804*.

ROSACEAE

Amelanchier alnifolia (Nutt.) Nutt. Snowdrift — common on dry rock slopes, *723*. Conway Lake — common in sandy area, *1055*.

Rubus arcticus L. ssp. **acaulis** (Michx.) Focke. Uncommon in sphagnum bogs. Porter Lake, *930*. Unnamed lake (60° 23′N, 108° 05′W), *1256*.

Rubus chamaemorus L. Common throughout area in *Sphagnum fuscum* bogs. Forestry Lake, *891, 1248*. Porter Lake, *909, 1039*.

Rubus idaeus L. ssp. **melanolasius** (Dieck) Focke. Uncommon in recently burned areas on rocky slopes and bedrock areas. Siltaza Lake, *1053*. Snowdrift, *802, 806*.

Fragaria virginiana Duchesne ssp. **glauca** (S. Wats.) Staudt. Snowdrift — common in open areas on stony slopes and exposed bedrock with *Picea glauca, 731*.

Potentilla fruticosa L. Snowdrift — found in recently burned area, *819*.

Potentilla nivea L. Snowdrift — common in white spruce and jack pine-lichen woodlands on exposed bedrock, *728, 776*.

Potentilla norvegica L. Snowdrift — common on sandy shore of Snowdrift River, *844*. Porter Lake — uncommon in open black spruce-lichen woodland in sandy area, *675*.

Potentilla palustris (L.) Scop. Forestry Lake – common along edge of *Sphagnum riparium* — *Carex limosa* bog pool, *1092*. Rutledge Lake — common in moist areas along shore, *1136*. Snowdrift — uncommon in open white spruce-lichen woodland on bedrock, *735*.

Potentilla tridentata Ait. Unnamed lake (60° 04′N, 108° 30′W) — rare in boulder area near shore, *1259*.

Dryas Drummondii Richards. Snowdrift — rare on rock outcroppings, *795*.

Dryas integrifolia M. Vahl ssp. **integrifolia.** Snowdrift — common in open white spruce-lichen woodland on north-facing slope, *688*.

Rosa acicularis Lindl. Porter Lake — common on dry south-facing slopes of eskers with *Picea glauca* overstory. Snowdrift — common in white spruce-lichen woodland on exposed bedrock, *724*.

Prunus pensylvanica L. f. Snowdrift — rare in recently burned bedrock area, *796*. Alcantara Lake — uncommon on sandy esker with *Populus tremuloides* and *Pinus Banksiana, 1291*.

LEGUMINOSAE

Oxytropis splendens Dougl. Snowdrift — uncommon in open white spruce-lichen woodland on bedrock, *713*.

Hedysarum alpinum L. ssp. **americanum** (Michx.) Fedtsch. Snowdrift — common in white spruce-lichen woodland on exposed bedrock, *685*.

GERANIACEAE

Geranium Bicknellii Britt. Snowdrift — rare on one-year-old burn around townsite, *828*.

CALLITRICHACEAE

Callitriche verna L. emend. Lönnr. Forestry Lake — rare in shallow water at mouth of stream, *870*.

VIOLACEAE

Viola renifolia Gray var. **Brainerdii** (Greene) Fern. Porter Lake — rare along small stream in moist *Betula papyrifera* woods.

ELAEAGNACEAE

Shepherdia canadensis (L.) Nutt. Snowdrift — common in white spruce and black spruce-lichen woodlands, *790, 691*. Conway Lake, *1048*.

ONAGRACEAE

Epilobium adenocaulon Haussk. Snowdrift — rare on one-year old burn, *829*. Rutledge Lake — common in recently burned areas, *1142, 1143*.

Epilobium angustifolium L. ssp. **angustifolium.** Common throughout area in recently burned upland sites and rock outcroppings. Porter Lake — common on black spruce rock outcropping, *674;* common on beach ridge, *997*. Snowdrift — common in black spruce-white spruce-lichen woodland, *771*.

Epilobium glandulosum Lehm. Unnamed lake (60° 10′N, 108° 30′W) — uncommon in recently burned area on rocky slope with *Pinus Banksiana, Betula papyrifera, 1263*. Snowdrift — found in recently burned area, *829*.

Epilobium latifolium L. Common along sandy beaches and sandbars. Snowdrift. D'Aoust Lake, *1029*.

HALORAGACEAE

Hippuris vulgaris L. Common in shallow water. Forestry Lake, *866*. Porter Lake, *1118*.

UMBELLIFERAE

Cicuta Douglasii (DC.) Coult. & Rose. Rutledge Lake — found in shallow water along stream, *1144*.

Cicuta mackenzieana Raup. Rutledge Lake – found in shallow water along stream, *1145*.

CORNACEAE

Cornus canadensis L. Selwyn Lake — rare in moist black spruce woods, *884*. Conway Lake, *1049*.

PYROLACEAE

Pyrola asarifolia Michx. var. **asarifolia.** Conway Lake, *1050*.

Pyrola grandiflora Radius. Snowdrift — uncommon along rocky shoreline, *856*. Siltaza Lake — common in recently burned area, *1019*.

Pyrola minor L. Snowdrift — common in white spruce-lichen woodland, *695*.

Pyrola secunda L. ssp. **obtusata** (Turcz.) Hult. Snowdrift — common in moist areas of white spruce-lichen woodland, *726*. Conway Lake, *1051*.

Moneses uniflora (L.) Gray. Snowdrift — uncommon in black spruce-feather moss wood, *746*.

EMPETRACEAE

Empetrum nigrum L. Common throughout area on dry upland sites and sphagnum bogs. Porter Lake — common on southeast-facing slope of esker, *604*. Forestry Lake — common on esker, *1235*.

ERICACEAE

Ledum palustre L. ssp. **decumbens** (Ait.) Hult. Common throughout area in sphagnum bogs and dry upland sites. Forestry Lake — common in sphagnum bog forest, *893;* common in black spruce-feather moss forest, *1250*.

Ledum palustre L. ssp. **groenlandicum** (Oeder) Hult. Common throughout area in sphagnum bogs and upland sites. Porter Lake — common in white spruce and black spruce-lichen woodland, *606, 630, 998*. Forestry Lake — common in bog forest, *1249*.

Rhododendron lapponicum (L.) Wahlenb. Snowdrift — common in white spruce-lichen woodland, *689*.

Loiseleuria procumbens (L.) Desv. Forestry Lake — common in white spruce woods on esker, *1247*. Porter Lake — uncommon on open sandy ridges, *632;* rare on lichen covered peat plateau, *1075*.

Kalmia polifolia Wang. ssp. **polifolia.** Porter Lake — uncommon in sphagnum bogs, *904*.

Andromeda polifolia L. Common in moist areas in lichen woodland. Porter Lake, *669*. Snowdrift, *708*. Common in lichen covered bog forest. Porter Lake, *911*. Common in *Sphagnum recurvum - S. riparium* bog pool. Forestry Lake, *1246*.

Chamaedaphne calyculata (L.) Moench. Common throughout area in sphagnum bogs. Forestry Lake, *889, 1251.*

Arctostaphylos rubra (Rehd. & Wilson) Fern. Porter Lake — rare in black spruce-sphagnum bog, *670.* Snowdrift — common in black spruce-sphagnum bog, *699.*

Arctostaphylos uva-ursi (L.) Spreng. Common throughout area on dry upland sites. Porter Lake — common on southeast-facing slope, *607.* Forestry Lake — common on esker with *Picea glauca, Stereocaulon paschale, Empetrum nigrum, 1240.*

Vaccinium caespitosum Michx. Snowdrift — rare in black spruce-sphagnum bog.

Vaccinium myrtilloides Michx. Forestry Lake — common in recently burned upland areas, *1269.* Selwyn Lake — rare on recently burned upland, *883.*

Vaccinium uliginosum L. ssp. **alpinum** (Bigel.) Hult. Common throughout area on upland and peatland sites. Porter Lake — common in moist upland areas with *Picea mariana, 639, 664.* Snowdrift — common on north-facing bedrock slope, *693.* Forestry Lake — common on esker with *Picea glauca, Stereocaulon paschale, Empetrum nigrum, 1237.*

Vaccinium vitis-idaea L. ssp. **minus** (Lodd.) Hult. Common throughout area on upland and peatland sites. Porter Lake — common on southeast-facing esker slope and open lichen woodland, *605, 637, 970.* Forestry Lake — common on esker with *Picea glauca, Stereocaulon paschale, Empetrum nigrum, 1236.*

Oxycoccus microcarpus Turcz. Common throughout area in black spruce-sphagnum bogs. Porter Lake, *898.* Forestry Lake, *1252.* Common on recently burned bog forest. Porter Lake, *903.*

Oxycoccus palustris Pers. Rutledge Lake — rare in black spruce-sphagnum bog, *1128.* Forestry Lake — rare in *Sphagnum riparium* - *S. recurvum* bog mat, *1081.*

PRIMULACEAE

Androsace septentrionalis L. Snowdrift — uncommon on disturbed soil around townsite and on recent burns.

GENTIANACEAE

Menyanthes trifoliata L. Porter Lake uncommon in small *Sphagnum recurvum* pools with *Carex* and *Eriophorum, 899, 912.*

HYDROPHYLLACEAE

Phacelia Franklinii (R.Br.) Gray. Snowdrift — uncommon on disturbed areas around townsite, beaches and recent burns, *727, 830.* Unnamed lake — rare on recently burned rocky slopes with *Pinus Banksiana, Betula papyrifera, 1264.*

LABIATAE

Dracocephalum parviflorum Nutt. Snowdrift — rare in recently burned area, *818.*

SCROPHULARIACEAE

Veronica scutellata L. Rutledge Lake — found in shallow water, *1146.*

Castilleja Raupii Pennell. Snowdrift - common in white spruce-lichen woodland, *686.*

Pedicularis labradorica Wirsing. Snowdrift — common in moist areas of white spruce-lichen woodland, *706.* Porter Lake — uncommon in mineral-influenced bog forest, *932.*

OROBANCHACEAE

Boschniakia rossica (Cham. & Schlecht.) Fedtsch. Snowdrift — uncommon on moist upland areas with *Picea mariana* and *P. glauca, 725.*

LENTIBULARIACEAE

Pinguicula villosa L. Snowdrift — uncommon in sphagnum bogs with *Picea mariana, 736.* Porter Lake — common on *Sphagnum fuscum* hummocks, *971.*

Utricularia vulgaris L. ssp. **macrorhiza** (Le Conte) Clausen. Forestry Lake — uncommon in slow moving water with *Nuphar variegatum, 890.*

PLANTAGINACEAE

Plantago major L. var. **major.** Snowdrift — rare on disturbed areas around townsite.

RUBIACEAE

Galium boreale L. Snowdrift — uncommon in open lichen woodland and recently burned area, *769, 824.*

Galium trifidum L. Rutledge Lake found in moist places, *1147.*

Viburnum edule (Michx.) Raf. Rare on moist upland sites and along stream channels. Snowdrift — common in black spruce-white spruce-lichen woodland, *787.* Nonacho Lake — uncommon in white birch-black spruce woods, *1038.* Unnamed lake (60° 10′N, 108° 30′W) — uncommon along lakeshore in open jack pine woods, *1260.* Porter Lake — uncommon in recently burned area, *630.*

CAPRIFOLIACEAE

Linnaea borealis L. ssp. **borealis.** Common throughout area in feather moss forests. Snowdrift — common in white spruce-lichen woodland on bedrock, *719.*

CAMPANULACEAE

Campanula rotundifolia L. Unnamed lake (60° 10′N, 108° 30′W) — rare in recently burned boulder area, *1257.*

LOBELIACEAE

Lobelia Dortmanna L. Rutledge Lake rare in two feet of water, *1130.*

COMPOSITAE

Solidago decumbens Greene var. **oreophila** (Rydb.) Fern. Snowdrift — common on exposed bedrock, *773.* Unnamed lake (60° 04′N, 108° 30′W) in open jack pine-lichen woodland, *1261.*

Aster sibiricus L. Snowdrift — rare in recently burned lichen woodland on exposed bedrock, *820.*

Erigeron acris L. ssp. **politus** (E. Fries) Schinz & Keller. Siltaza Lake — rare in recent burn, *1023*. Snowdrift found around townsite, *863*.

Erigeron elatus Greene. Snowdrift — uncommon on sandy shores of Snowdrift River, *845*.

Antennaria rosea Greene. Snowdrift — uncommon on south-facing exposed bedrock slopes or sandy areas, *770*.

Achillea lanulosa Nutt. Snowdrift — common in open white spruce or jack pine-lichen woodland on exposed bedrock, *716, 775*.

Matricaria matricarioides (Less.) Porter. Snowdrift — rare in disturbed areas around townsite, *865*.

Artemisia borealis Pall. Snowdrift — uncommon in crevices in granite outcropping, *797*. D'Aoust Lake — uncommon in recently burned sandy area, *1056*.

Artemisia campestris L. Snowdrift — uncommon in open white spruce-lichen woodland on bedrock, *734*.

Petasites frigidus (L.) Franch. Snowdrift — rare in moist area under *Alnus crispa* in recent burn, *816*.

Petasites sagittatus (Banks) Gray. Rutledge Lake — rare in moist area along lakeshore, *1131*.

Arnica alpina (L.) Olin. Porter Lake — uncommon on exposed bedrock in open black spruce-lichen woodland, *648, 650*. Snowdrift — uncommon in recent burn, *826, 827*.

Arnica lonchophylla Greene. Snowdrift – common in open lichen woodland, *785*.

Senecio congestus (R.Br.) DC. Rutledge Lake uncommon along lakeshore, *1132*.

Senecio cymbalarioides Nutt. Snowdrift — common in open jack pine-lichen woodland on exposed bedrock and rocky sand shore, *774, 813*.

Senecio cymbalarioides Nutt. var. **borealis** (Torr. & Gray) Greenm. Snowdrift — common on bedrock, *730, 744b;* common in recently burned area, *825*. Unnamed lake (60°04′N, 108°30′W) found in open jack pine-lichen woodland, *1262*.

Senecio pauciflorus Pursh var. **fallax** Greenm. Porter Lake – found in black spruce-lichen woodland on bedrock, *666*.

Taraxacum ceratophorum (Ledeb.) DC. Porter Lake – found in black spruce-lichen woodland on bedrock, *654;* found on rocky shore of lake, *643*.

LITERATURE CITED

ARGUS, G. W. 1966. Botanical investigations in northeastern Saskatchewan; the subarctic Patterson-Hasbala Lake Region. Can. Field-Nat. **80:** 119 143.

______. 1973. The genus *Salix* in Alaska and the Yukon. Nat. Mus. of Can. Publ. in Bot. No. **2.**

DUGLE, J. R. 1966. A taxonomic study of western Canadian species in the genus *Betula*. Can. Jour. Bot. **44:** 929 1007.

HARE, F. K. 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. Geogr. Rev. **40:** 615 635.

HARPER, F. 1931. Some plants of the Athabaska and Great Slave Lake region. Can. Field-Nat. **45:** 97 107.

HULTÉN, E. 1968. Flora of Alaska and neighboring territories. Stanford University Press, Calif. 1008 pp.

HUSTICH, I. 1949. On the forest geography of the Labrador Peninsula: a preliminary synthesis. Acta Geogr. **10:** 1-63.

JOHNSON, E. A. 1975. The buried seed populations in the subarctic forest east of Great Slave Lake. Can. Jour. Bot. **53:** 2933-2941.

______. 1978a. A theory of fire recurrence in the western subarctic and its implications for vegetation change. Submitted.

______. 1978b. A theory of vegetation compositional change in the western subarctic. Submitted.

______, & J. S. ROWE. 1975. Fire in the wintering ground of the Beverley Caribou Herd. Amer. Midl. Nat. **94:** 1-14.

LARSEN, J. A. 1971. Vegetation of Fort Reliance, N.W.T. Can. Field-Nat. **85:** 147-178.

MAINI, J. S. 1966. Phytoecological study of sylvo-tundra at Small Tree Lake, N.W.T. Arctic **19:** 220-243.

MOSS, E. H. 1959. Flora of Alberta. University of Toronto Press. 546 pp.

RAUP, H. M. 1936. Phytogeographic studies in the Athabaska-Great Slave Lake Region. I. Catalogue of vascular plants. Jour. Arnold Arbor. **17:** 180 315.

ROWE, J. S. 1972. Forest Regions of Canada. Dept. of Envir., Can. For. Serv. Publ. No. **1300.**

SCOTTER, G. W. 1966. A contribution to the flora of the eastern arm of Great Slave Lake, Northwest Territories. Can. Field-Nat. **80:** 1 18.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF SASKATCHEWAN
SASKATOON, CANADA
S7N 0W0

Present Addresses:

M.A.J.
McGILL UNIVERSITY
DEPT. OF BIOLOGY
1205 McGREGOR AVE.
MONTREAL, CANADA
H3A 1B1

E.A.J.
DEPT. OF BIOLOGY
UNIVERSITY OF CALGARY
CALGARY, CANADA
T2N 1N4

BY-LAWS

OF

THE NEW ENGLAND BOTANICAL CLUB, Incorporated

(To repeal and replace all previous By-Laws)

ARTICLE I

NAME AND PURPOSE

Section **1.** The name of this corporation shall be The New England Botanical Club, Incorporated.

Section **2.** Its purpose shall be to promote the dissemination of local and general botanical information.

Section **3.** The Club shall be organized and operated exclusively for its educational and scientific purposes. No part of the property or net earnings of the Club shall inure to the benefit of any individual; and no part of the property of the Club shall be used directly or indirectly in carrying on propaganda, nor shall any substantial part of the activities of the Club consist of the carrying on of propaganda or otherwise attempting to influence legislation. The Club shall not participate in, nor intervene in, any political campaign on behalf of any candidate for public office, nor shall it publish or distribute any statements with respect thereto.

ARTICLE II

SEAL

The seal of the Club shall, subject to alteration by the Council, consist of a flat-faced circular die with the words "Massachusetts," "Organized 1895," and the name of the corporation cut or engraved thereon.

ARTICLE III

OFFICERS

Section **1.** The officers of the Club shall be a President, a Vice-President, a Curator of Vascular Plants, an Assistant Curator of Vascular Plants, a Curator of Nonvascular Plants, a Librarian, a

Corresponding Secretary, a Recording Secretary, a Treasurer, and three Councillors. The Councillors, other Officers above-named, and the Editor-in-Chief of *Rhodora* shall constitute the Council.

Section **2.** All officers shall be elected by ballot by a majority of those members voting at the annual meeting of the Club, and, except in the case of death, resignation, or removal, each officer shall hold his office until the next annual meeting after his election or until his successor is elected. Voting by proxy shall not be allowed.

Section **3.** If the office of any officer becomes vacant by reason of death, resignation, or removal, the Council may appoint a successor, who shall hold office until the next annual meeting or until his successor is elected.

ARTICLE IV

COUNCIL

Section **1.** The Council, six members of which shall constitute a quorum, shall have the management and control of the Club and of all its property and affairs, and shall direct the expenditure of its funds.

Section **2.** The Council shall authorize and approve, except as the Council may generally or in particular cases authorize the execution thereof in some other manner, all deeds, transfers and contracts; and all bonds or notes made or endorsed by the Club shall be signed by the Treasurer and countersigned by the President or the Vice-President. All deeds, transfers and contracts shall be signed by the President or in his absence by the Vice-President.

Section **3.** The Council may appoint and remove such other officers or agents as it may from time to time determine. It may appoint committees as it sees fit and may delegate to these committees such powers for such terms as the Council deems best, subject to the power of the Council to revoke any such appointment at any time.

Section **4.** The Council shall have the books and accounts of the Treasurer audited at least once a year by an Auditing Committee which it shall appoint.

ARTICLE V

DUTIES OF OFFICERS

Section **1.** The President and Vice-President shall perform the usual duties of their offices.

Section **2.** The Curator of Vascular Plants and the Curator of Nonvascular Plants shall have charge of the botanical collections of the Club. The Assistant Curator of Vascular Plants shall perform the duties of the Curator of Vascular Plants in the latter's absence.

Section **3.** The Librarian shall have charge of the books and manuscripts of the Club.

Section **4.** The Corresponding Secretary shall give notices of all meetings of the Club and of the Council. He shall conduct the correspondence of the Club and shall notify all persons elected to membership or to office of their election.

Section **5.** The Recording Secretary, who shall be the Clerk, shall be sworn before entering upon his duties as Recording Secretary, and as such he shall keep the minutes of all meetings of the Club and of the Council and such other records as the Council may direct.

Section **6.** The Treasurer shall, subject to the orders and supervision of the Council, collect and disburse the funds of the Club, and for this purpose he shall have power to endorse for deposit or collection, all funds, checks, drafts, etc., payable to the corporation or its order. He shall keep, or cause to be kept, accurate books of account, and shall make a report of the financial condition of the Club at each annual meeting, and at such other times as the Council may request.

ARTICLE VI

NOMINATING COMMITTEE

On or before December fifteenth of each year the President shall appoint a committee of three voting members — who shall not be officers — to nominate officers for the ensuing year. The report of this committee, which shall be filed with the Corresponding Secretary and open to inspection at least three weeks prior to the annual meeting, shall be incorporated in the call for the annual meeting.

Nothing herein shall restrict the right of members to offer nominations from the floor provided a notice listing such nominees and signed by not less than three voting members shall be filed with the Corresponding Secretary not later than ten days prior to the date of the meeting.

ARTICLE VII

MEMBERSHIP AND DUES

The classes of membership and the prerequisites of each class (except as provided by this Article), the dues of each class, and the subscription price of *Rhodora* shall be determined at appropriate intervals by the Council, subject to approval by the voting members. A proposal to alter existing regulations must be announced in the call for a meeting, must receive majority approval of the voting members present at the meeting and voting, and all members entitled to receive Club notices shall be notified of any alteration accepted. The classes of Active Members and Sustaining Members shall constitute the voting members, and one of these classes shall be open to all members.

ARTICLE VIII

ELECTION TO MEMBERSHIP

Section **1.** Nomination for membership stating the class of membership desired shall be made in writing to the Corresponding Secretary, endorsed by two members entitled to recommend new members, and shall be presented by the Corresponding Secretary to the Council at its next meeting. Favorable action by the Council on any such nomination shall constitute a recommendation of the candidate whose name shall then be placed before the Club for election at any regular meeting of the Club, provided that notice of such recommendation is sent in the call for such meeting.

Section **2.** All elections to membership shall be by ballot, and a simple majority shall elect to membership. Voting by proxy shall not be allowed.

Section **3.** Persons elected to membership shall, within thirty days after receiving notice of election, accept said election by paying to the Club such dues as may become payable by such person in accordance with the provisions of these By-Laws. A person elected to membership at a meeting subsequent to the annual meeting shall pay only his proportionate share of the current annual dues. Failure by any person elected to membership to comply with these provisions shall render such election void.

ARTICLE IX

TRANSFER OR TERMINATION OF MEMBERSHIP

Section **1.** Members who may wish to change from one class of membership to another may be so transferred only by action of the Council, and the only if all obligations to the Club have been discharged. Request for transfer of membership shall be made in writing to the Corresponding Secretary.

Section **2.** Resignations of membership may be made only in writing to the Corresponding Secretary. No resignation shall be accepted unless all indebtedness to the Club of the member resigning shall have been paid.

Section **3.** In the event of the death, resignation, or other termination of the membership of a member, all privileges shall cease.

Section **4.** The membership of any member whose dues shall remain unpaid for more than three months after same become payable may be terminated by the Council upon a majority vote of the members present. The membership of any member shall automatically terminate if his dues or other indebtedness to the Club remain unpaid for thirteen months after same become payable.

Section **5.** The Council may, by a two-thirds vote of its entire number, after notice and opportunity for hearing, suspend or expel any member for conduct unbecoming a member.

ARTICLE X

MEETINGS OF THE CLUB

Section **1.** The annual meeting of the Club shall be held on the first Friday in February of each year, unless otherwise ordered by the Council, and regular meetings shall be held monthly, except during July, August and September at such times as the Council may determine.

If the annual meeting is omitted by oversight or otherwise on the day herein provided therefor, a special meeting may be held in place thereof, and any business transacted or elections held at such meeting shall have the same effect as though transacted or held at the annual meeting.

Section **2.** Special meetings may be called by the President or by vote of the Council or by written request of any ten Voting Members given to the Corresponding Secretary. Every such call shall state the object for which the meeting is called.

Section **3.** Notice of all meetings shall be sent to all members who receive notices of the Club at least seven days before such meetings.

Section **4.** At any meeting of the Club fifteen voting members shall constitute a quorum for the transaction of business, except the amendment of the By-Laws.

ARTICLE XI

AMENDMENTS OF BY-LAWS

These By-Laws may be altered, amended, or repealed in the following manner. At any annual, regular, or special meeting of the Club by a two-thirds vote of the Voting Members present and voting, provided that no such action shall be taken at any meeting unless at least twenty Voting Members or two-thirds of the Voting membership (whichever is the smaller number) are present at the meeting, and unless the subject matter of the proposed alteration, amendment, or repeal has been given in the call for the meeting at which the alteration, amendment, or repeal is to be considered.

ARTICLE XII

FISCAL YEAR

The fiscal year of the Club shall end on the thirty-first day of December in each year.

ARTICLE XIII

DISSOLUTION

Should the Club be dissolved for any reason, the officers shall, after paying or making provision for payment of all of the liabilities of the corporation, distribute all assets, including all accrued income, to one or more scientific, educational, and/or literary organizations which qualify as exempt scientific, educational, and/or literary organizations under Section 501(c)(3) of the Internal Revenue Code of 1954 (or the corresponding provision of any subsequent United States Internal Revenue Law).

CERASTIUM CLAWSONII (CARYOPHYLLACEAE): A SYNONYM OF LINUM HUDSONIOIDES (LINACEAE)

RONALD L. HARTMAN

While preparing a treatment of the Caryophyllaceae for the forthcoming "Chihuahuan Desert Flora" (by M. C. Johnston, J. Hendrickson, and collaborators), I encountered the holotype of *Cerastium clawsonii* Correll (Figure 1). Preliminary observations of this unicate (TEXAS: **Brewster Co.,** McIntyre Ranch, 3 miles S of Alpine, *A. B. Clawson 29–173,* LL) suggested that it was very unusual for a member of the genus *Cerastium.* As Dr. Donovan Correll (1968) noted in the protologue, "it is totally unrelated to all other members of this genus in Texas." On closer inspection, this specimen, which Correll referred to *Cerastium* at the suggestion of Dr. Lyman B. Smith, proves not to be a member of the Caryophyllaceae, but is an immature individual of *Linum hudsonioides* Planchon of the Linaceae. It corresponds well with specimens of *L. hudsonioides* at the Lundell Herbarium (University of Texas at Austin) and agrees in all features available with the description of that species by Rodgers (1963). The most prominent characters are: leaves opposite near the base, alternate above, closely imbricate, linear with mucronate to aristate apices; sepals with conspicuous awns; styles 5, united to near the summit, with capitate stigmas. Unfortunately, fruits are lacking.

ACKNOWLEDGMENT

I wish to thank Dr. Correll for reviewing the manuscript and to acknowledge financial support in the form of a University Postdoctoral Fellowship from The Ohio State University, Columbus, Ohio.

LITERATURE CITED

CORRELL, D. S. 1968. Some additions and corrections to the flora of Texas — V. Wrightia **4:** 25–28.

ROGERS, C. M. 1963. Studies in Linum: L. imbricatum and L. hudsonioides. Rhodora **65:** 50–55.

BOTANY DEPARTMENT
AVEN NELSON BUILDING
UNIVERSITY OF WYOMING
LARAMIE, WYOMING 82071

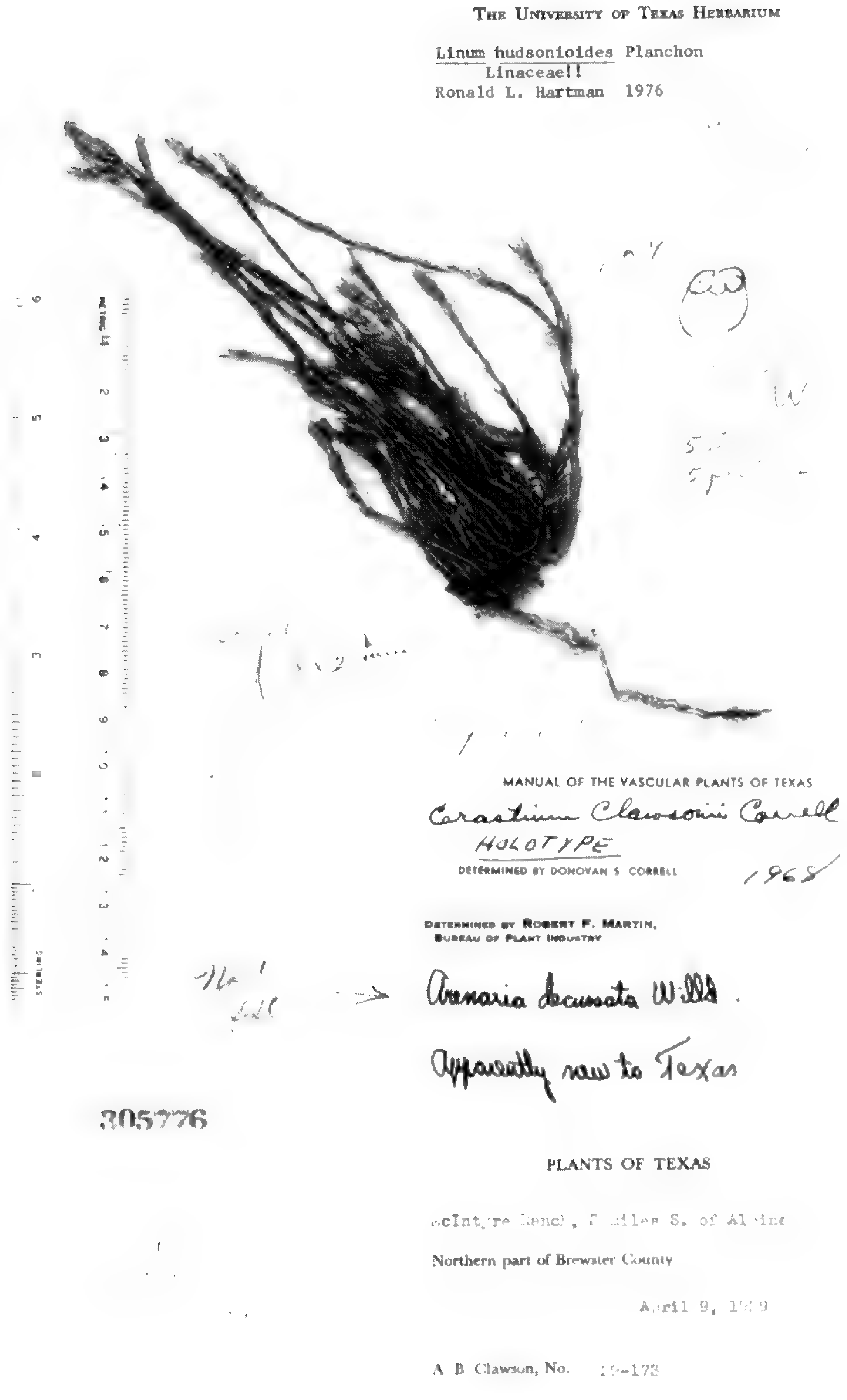


Figure 1. Photograph of holotype of *Cerastium clawsonii* Correll (LL).

LEDUM GROENLANDICUM REDISCOVERED IN CONCORD, MASSACHUSETTS

RAY ANGELO

In spite of 155 years of intense botanizing in Concord, Massachusetts, by such dedicated amateurs as Henry Thoreau and Richard J. Eaton, one of the largest bogs in the township has apparently been overlooked by all but one botanical enthusiast of the past. It seems, however, that this one (Minot Pratt) did not adequately convey his knowledge to future generations.

The bog is 1.1 km northeast of the juncture of the townships of Concord, Acton, Maynard, and Sudbury. On August 22, 1978, I entered this bog and within a short time came upon a small but apparently thriving colony of *Ledum groenlandicum* Oeder. This species is among the one dozen listed by the late Richard J. Eaton in his *A Flora of Concord* (1974) as having been extirpated in the township.[1]

The single station of *Ledum* known to Eaton and others was a small and curious roadside bog that also harbored the locally very rare *Arceuthobium pusillum* Peck parasitic on *Picea mariana* (Mill.) BSP. It was here that Henry Thoreau first found *Ledum* in Concord on February 4, 1858. This bog was gradually ruined by the drainage and brush-cutting operations of its farmer owners. (Eaton, 1935).[2]

In his manuscript "Plants of Concord" (1878) Minot Pratt noted that *Ledum* occurred in *two* bogs in the township, both in the southwest quarter of the town. The two bogs are evidently the well-known one and the overlooked one, both in the southwest quarter. Mr. Pratt, notorious for his introduction of plants into Concord,[3]

---

[1] *Chamaecyparis thyoides* (L.) BSP., also on this list, has since been found at two sites in the town.

EATON, R. J. 1974. A Flora of Concord.

[2] EATON, R. J. 1935. The waning of Arceuthobium at Concord, Massachusetts. Rhodora **37**: 413-414.

[3] HOSMER, A. W. 1899. On the plants introduced by Minot Pratt at Concord, Massachusetts. Rhodora **1**: 168-72.

PRATT, M. 1878. Plants of Concord.

does not indicate in his manuscript that he placed any *Ledum* in the town (as he indicates for other species). Consequently, the rediscovery of the second station maintains Concord at the southeastern limit of the range of *Ledum groenlandicum* in New England.

Other locally scarce species found in the bog are *Woodwardia virginica* (L.) Sm., *Larix laricina* (DuRoi) K. Koch, *Kalmia polifolia* Wang., and *Vaccinium oxycoccus* L. The prospect remains of finding a few of the orchid species thought to be extinct in the town.

CONCORD FIELD STATION
BEDFORD, MASSACHUSETTS 01730

NOTICE OF PUBLICATION

Harriman, Neil A. *An index to the vascular plants of Willdenow's* **Species Plantarum,** *Volumes I-V (1), 1797–1810.* Willdenow's *Species Plantarum,* edition 4 of Linnaeus' *Species Plantarum,* devotes 7,016 pages to the vascular plants. An alphabetical index (offset copy of computer printout) includes 16,092 entries to the species descriptions. There are no entries for the generic descriptions alone, since these will readily be found preceding the species descriptions.

The Index, paperbound, is offered for sale at cost, $3.00 postpaid, from the author at the address below. Please do not request billing.

Neil A. Harriman
Biology Department
University of Wisconsin-Oshkosh
Oshkosh, Wisconsin 54901

NOTICE OF PUBLICATION

Angelo, Ray. 1978. *Concord Area Shrubs.* Concord Field Station, Harvard University. 428 prints and illustrations, 128 pages. — This field guide, the first in the northeast to use leaf prints for identification, is designed for the rapid and reliable identification of nearly every wild shrub and woody vine likely to be encountered in eastern Massachusetts.

Additional features include directions for making leaf prints, an illustrated guide to shrubs in flower, and an annotated bibliography. Edibility (or inedibility) of every berry-like fruit is indicated. This book will serve well both as a reference work and as an introduction to the shrubs of eastern Massachusetts.

Copies of *Concord Area Shrubs* may be ordered (for $3.50 each) from:

Publications Department,
Museum of Comparative Zoology,
Harvard University,
Cambridge, MA 02138

Concord Area Trees is still available ($1.50 each).

VASCULAR PLANTS OF NORTH AMERICA NORTH OF MEXICO

The Flora North America project (FNA) was recently revitalized by the Man and Biosphere Program (MAB) as a binational effort between the United States and Canada to produce a conventional flora of the vascular plants of North America north of Mexico using traditional methods. Initial funding for the proposed five-volume work is being provided by the National Park Service of the Department of the Interior. The MAB/FNA Program Council plans to coordinate the research which will be necessary to produce a floristic publication of high scientific quality pertinent to national needs.

The Program Council has appointed an Editorial Subcommittee consisting of Dr. Reed C. Rollins, Chairman, Gray Herbarium of Harvard University; Dr. Howard S. Irwin of the New York Botanical Garden; and Dr. Roy L. Taylor of the University of British Columbia Botanical Garden. Dr. James L. Reveal of the University of Maryland has been appointed Editor. Their function will be to stimulate and coordinate the efforts of the botanical community in the writing of the flora. Toward this goal, the Editorial Subcommittee is currently working on a proposed format for the flora. Initial efforts will be toward the production of a volume treating the monocotyledonous plants, with a volume on the sympetalous dicotyledonous plants to follow next. The remaining three volumes will be worked on in the future.

Long-term funding for the flora project is being explored by the Program Council, chaired by Dr. Peter H. Raven of the Missouri Botanical Garden. It is hoped that the flora project will be completed by 1990.

Individuals wishing additional information or interested in contributing to the project, and in particular treatments of the monocots and sympetalous dicots should write to:

DR. JAMES L. REVEAL, EDITOR
MAB/FNA PROJECT
DEPARTMENT OF BOTANY
UNIVERSITY OF MARYLAND
COLLEGE PARK, MARYLAND 20742

Vol. 81, No. 825, including pages 1–150 was issued January 1, 1979.

ANNOUNCING A SYMPOSIUM

"RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND"

4, 5 May 1979

Auditorium D, Science Center, Harvard University, Cambridge

Friday Evening, May 4

KEYNOTE ADDRESSES

"Why some plants are naturally rare."
William H. Drury

"Rare plant management — after preservation, what?"
Susan P. Bratton & Peter S. White

Saturday Morning, May 5

KEYNOTE ADDRESS & SESSION I

"Rarity of plants; a population genetics viewpoint."
G. L. Stebbins

Session I: "Biology of endangered species."
Participants: *Richard B. Primack, J. R. Massey, L. W. Macior, Gregory J. Anderson, Rayond E. Graber.*

Saturday afternoon

SESSIONS II & III

Session II: Plant conservation concerns in the New England States.
Participants: Connecticut, *Leslie J. Mehrhoff;* Rhode Island, *George L. Church;* Massachusetts, *Katherine G. Field & Jonathan Coddington;* New Hampshire, *Garrett E. Crow & Irene M. Storks;* Maine, *Leslie M. Eastman;* Summary, *Richard W. Dyer.*

Session III: Conserving rare plants and their habitats.
Participants: *E. LaVerne Smith, Norton H. Nickerson, Harry R. Tyler, Steven C. Buttrick.*

For information/registration please contact:
Dr. Garrett E. Crow
Dept. of Botany and Plant Pathology
University of New Hampshire
Durham, New Hampshire 03824

sponsored by
The New England Botanical Club
In cooperation with the
United States Fish and Wildlife Service

RHODORA INDICES

Volumes 1-50 (1899-1948)

$10.00 per copy

This index consists of 415 double column pages arranged in two parts. Part I is an Index to Plant Names in the 50 volumes. Part II is an Index to Authors and Titles. Bound in paper wrapper.

Volumes 51-75 (1949-1973)

$20.00 per copy

This index consists of 287 double column pages arranged in two parts. Part I is an Index to Taxa Cited in the 25 volumes. Part II is an Index to Authors and Titles. Bound in paper wrapper.

Remittance should be made payable, in United States funds, to RHODORA. Please direct all orders to:

RHODORA
Botanical Museum
Oxford Street
Cambridge
Massachusetts 02138

RHODORA April, 1979 Vol. 81, No. 826

CONTENTS

ANNOUNCING A SYMPOSIUM

"RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND"

4, 5 May 1979
at Harvard University

Biology of Endangered Species

Plant Conservation Concerns in New England

Conserving Rare Plants and Their Habitats

Further information, contact:
Dr. Garrett E. Crow
Dept. of Botany and Plant Pathology
University of New Hampshire
Durham, New Hampshire 03824
Organized by the
New England Botanical Club

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 81 July, 1979 No. 827

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Conducted and published for the Club, by
ROLLA M. TRYON, Editor-in-Chief

RHODORA. — A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes, and single copies are available. For information and prices write RHODORA at address given below.

Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes, relating to the plants of North America, and floristically related areas, will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. All manuscripts should be submitted in duplicate, and must be double- (at least ⅜ of an inch) or triple-spaced throughout. Please conform to the style of recent issues of the journal. Extracted reprints, if ordered in advance, will be furnished at cost.

Address manuscripts and proofs to:
Russell R. Walton
Managing Editor, RHODORA
Harvard University Herbaria Building
22 Divinity Avenue
Cambridge, Mass. 02138

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Scirpus Longii Fernald

In New England, this rare species grows in a few marshes and wet meadows in central Connecticut and eastern Massachusetts.

Original artwork by Frances S. Chew

Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 81 July, 1979 No. 827

REVISION OF LIPOCHAETA (COMPOSITAE:HELIANTHEAE) OF THE HAWAIIAN ISLANDS

ROBERT C. GARDNER

Understanding patterns of speciation and phylogeny in plants involves gathering comparative data from available populations. These data, from such sources as morphology, cytology, and flavonoid chemistry, when considered together, can help indicate degrees of relationship among the taxa being investigated. Along these lines, to maximize the efficacy of such evolutionary studies, groups of plants are selected that appear to reflect a diversity of evolutionary trends. These tendencies are often more obvious in groups that (a) are isolated from extant presumptive relatives, and (b) are in regions with broad ranges of habitat diversity, yet in relatively small geographical areas. These criteria are especially fulfilled in taxa of oceanic islands. *Lipochaeta* DC. of the Hawaiian Islands was selected as a system for asking evolutionary questions.

Although the initial focus on *Lipochaeta* was evolutionary, it soon became evident that broad revisionary work needed to be done. This need was somewhat surprising, because the genus was revised recently by Sherff (1935). It was necessary, however, to develop a new revision of these Hawaiian plants before meaningful statements could be made regarding evolutionary relationships.

The following treatment is the result of four years of study including four months of field work in the Hawaiian Islands. Especially important to this investigation, and what we may hope has resulted in a more predictive system of classification, has been the observation and documentation of populational variation of most of the taxa in their natural habitats. In addition, over 2,400 herbarium specimens have been examined, including collections of the earliest botanical expeditions to the islands.

TAXONOMIC HISTORY

Robert Brown (1817) described the genus *Lipotriche*, based on plants collected by a Dr. Smith "on the banks of the Congo," Africa, without including any recognized species. In 1831, Lessing described the first two species of *Lipotriche;* one from Mexico, *L. gymnolomoides,* and the other from Hawaii, *L. australis.* At this point there were really three species of *Lipotriche;* the invalid species of Brown from Africa and the two from Mexico and Hawaii of Lessing. De Candolle (1836) validated the species based on the African collection of Smith, calling it *Lipotriche brownei.* He also moved *L. gymnolomoides* to *Perymenium,* and transferred Lessing's *Lipotriche australis* to a new genus, *Lipochaeta,* along with nine additional species from Mexico and Hawaii. Because the type species of *Lipochaeta* was based on *Verbesina lobata* Gaud. (1829), Lessing's name, *L. australis* is superfluous and must be replaced by *Lipochaeta lobata* (Gaud.) DC.

In de Candolle's treatment (1836) he included ten species: five were from the Americas (mainly Mexico), and the other five from the Hawaiian Islands. Nuttall (1841), recognizing that the American taxa differed from those of Hawaii, transferred the five Hawaiian taxa, plus three new species from Hawaii, out of *Lipochaeta* and into two new genera: *Microchaeta* with seven species, and *Schizophyllum* with one species [this latter generic name being a later homonym of *Schizophyllum* Fries (1831) and therefore re-named *Aphanopappus* by Endlicher (1842)]. Gray (1861), believing that all of de Candolle's American species of *Lipochaeta* belonged in *Zexmenia,* treated just those taxa from the Hawaiian Islands as belonging to *Lipochaeta.* He also placed the two genera of Nuttall in synonymy with *Lipochaeta.* In addition, he described four new species and transferred *Macraea laricifolia* Hook. f. of the Galapogos Islands to *Lipochaeta.* Bentham and Hooker (1873) accepted Gray's treatment, and also recognized two sections within *Lipochaeta: Microchaeta* and *Aphanopappus,* which were differentiated by features of the pappus. Harling (1962), re-elevated *L. laricifolia* to generic status as *Macraea laricifolia* Hook. f. This decision is accepted here and by Cronquist (1971).

Sherff (1933) described numerous new taxa of *Lipochaeta* and in 1935 revised the genus. In these and subsequent works by Sherff (1939, 1941, 1951, 1954, and 1960), Degener and Sherff (1940), Degener and Clay (1949), St. John (1959, 1972, and 1976b) more than 65 taxa have been described in some 33 species.

In the present treatment, *Lipochaeta* is recognized as endemic to the Hawaiian Islands and has two sections: Section *Lipochaeta* with nine taxa in six species and Section *Aphanopappus* which includes 18 taxa in 17 species.

GENERIC RELATIONSHIPS

Lipochaeta has traditionally (Gray, 1861; Bentham & Hooker, 1873; Sherff, 1935) been considered intermediate between *Wedelia* Jacq. and *Zexmenia* La Llave & Lexarza. In fact, de Candolle's (1836) original description included four species now recognized as belonging to *Zexmenia,* one species of *Wedelia,* and five *Lipochaetas.* Other workers (Gray, 1852; Bentham & Hooker, 1873; Jones, 1905) have recognized under various names, a "Wedelioid" section of *Zexmenia.* Becker (1972) has concluded that the species of this section represent a separate genus[1] very close to *Wedelia.* These "Wedelioid" taxa are characterized by involucral bracts in two series of approximately equal length, achenes with a neck or slight constriction, fragile awns, and variously developed wings along the angles of the achenes. These features are also typical of most species of *Wedelia* and *Lipochaeta.*

In a recent revision of the subtribal limits within the Heliantheae (Stuessy, 1977), a closer relationship between *Lipochaeta* and *Wedelia* has been indicated by the inclusion of both genera in the subtribe Ecliptinae. *Zexmenia,* on the other hand, has been placed in the subtribe Verbesininae near *Perymenium* and *Oyedaea,* a positioning with which I concur.

Further evidence suggesting a connection between *Lipochaeta* and *Wedelia* comes from cytological data. *Lipochaeta* is known as $x = 15$ (Solbrig, et al., 1972; Gardner, 1977a); *Wedelia* as $x = 11$, 12, and 15 (Solbrig, et al., 1972). The species complex to which

---

[1] Due to nomenclatural requirements (Becker, 1972; McVaugh, 1975), this genus must bear the name *Zexmenia,* and the species of the traditional grouping become known as *Lasianthaea* DC.

Lipochaeta is most similar morphologically (those features listed above) is the $x = 15$ group of *Wedelia*.

MORPHOLOGICAL AND TAXONOMIC CRITERIA

In the past, considerable emphasis has been placed on variations in leaf morphology as a basis for delimitation of taxa of *Lipochaeta*. In the present study, field observations of populational variation have indicated that caution is necessary in recognizing taxa, especially at the species level, on differences in leaf morphology. Two examples will illustrate the dubious utility of some of these features. (1) Sherff (1935) lists as the major distinction between *Lipochaeta rockii* var. *rockii* and var. *subovata*, leaves 3–5 parted in the former and coarsely dentate or incisely lobulate for the latter. Single specimens have been seen in the field (*Gardner 406*) with both kinds of leaves, and virtually every population of *L. rockii* observed showed a range of variation from almost entire to deeply five lobed. (2) The major difference between *L. profusa* and *L. alata* (Sherff, 1935) is that the former has sessile leaves with connate-perfoliate bases, while the latter has winged petioles, but no connate bases. After examining numerous specimens, both in the field and from pressed material, I found a morphological range from petiolate to connate-perfoliate leaf bases at least within a single population and occasionally on the same plant. From limited observations on plants grown in the greenhouse, it appears that the amount of leaf material produced at a node increases with the age of the specimen, i.e., first formed leaves are nearly petiolate, and later formed leaves become sessile with connate-perfoliate bases. This variability does not mean that leaf characteristics are totally useless for recognizing taxa; clearly, the thick, succulent leaves of *L. integrifolia* distinguish it from all other species of the genus, just as the ternately compound leaves of *L. tenuifolia* make it distinct. Although these and other vegetative features can be used to delimit some taxa (see key), most of the useful taxonomic characters in *Lipochaeta* are floral.

FLORAL FEATURES

Involucre. The number and series of involucral bracts is relatively constant throughout *Lipochaeta*. The phyllaries are produced in two series with four or five bracts in each whorl. However, differences in length, width, and shape of the phyllaries have been useful for differentiating between closely related taxa.

Chaff. The chaff is relatively uniform throughout the genus. Slight differences in texture exist, but these are difficult to describe in a meaningful way, and also tend to vary within taxa. Certain collections of *Lipochaeta succulenta* are atypical within the genus in having a slightly three-lobed (typically unlobed) chaff. However, this lobing does not appear to be correlated with any other consistent variation, and therefore is not regarded as taxonomically significant.

Ray Florets. The number of rays varies from four to as many as 16. This variation in number is useful in interpreting relationships among several taxa in Section *Aphanopappus* (e.g., *Lipochaeta fauriei, L. kamolensis, L. micrantha, L. remyi, L. subcordata, L. venosa,* and *L. waimeaensis*) that produce only four to six rays. Length and width of the ligule and length of the tube are also useful markers. The number of lobes per ligule, however, may vary from none to three on the same specimen, and thus is not considered useful in differentiating taxa.

Disc Florets. Approximately one-third of the species of *Lipochaeta* have four-lobed disc corollas and four anthers. The others are five-merous, as is typical of the Compositae (Gardner, 1977b). Without additional data from cytology and leaf flavonoid chemistry, the significance of this morphological difference cannot be appreciated, as indicated by Sherff's 1935 revision. It is now apparent, however, that the tetramerous Lipochaetas are tetraploid and synthesize flavones and flavonols, while the pentamerous taxa are diploid and produce only flavonols. This combination of characters is significant for sectional assignment. Section *Lipochaeta* is distinguished morphologically by tetramerous florets, and Section *Aphanopappus* hy pentamerous florets. Characters useful at the specific and subspecific levels are length of corollas, corolla lobes, and anthers.

Fruits. Diagnostic features of mature ray and disc achenes that are significant at the specific and varietal levels include fruit length and width and presence or absence of a corona and/or wings. These characters, however, are not useful for delimitation at the sectional level. Bentham and Hooker (1873), in recognizing two sections of

Lipochaeta, relied primarily on pappus features. Their section *Microchaeta* (=*Lipochaeta*) has prominent aristae, and section *Aphanopappus* has a rudimentary pappus or none. Sherff (1935) recognized these same sections and added a third, *Macraea* to accommodate *Lipochaeta laricifolia* (Hook. f.) A. Gray, of the Galapagos Islands; Harling (1962), has since re-elevated *L. laricifolia* to generic status as *Macraea laricifolia* Hook. f., this latter section being characterized by a corona. These sectional characters do not seem workable for two important reasons. First, variation in the pappus of some taxa (e.g., *L. connata* and *L. heterophylla*) ranges from a distinct corona as long as 2 mm to a few uneven scales. Numerous overlapping conditions, therefore, occur in this feature within the genus. Second, in early stages of fruit development, all Lipochaetas produce short (to 3 mm) pappus awns, and as the fruits mature the awns become increasingly less tightly attached. Specimens containing ripe fruits, therefore, often lack awns whether observed in the field or in the herbarium, and cannot be referred successfully to any of the sections. Thus, pappus variation is not used as a basis for assigning taxa at the sectional level in this treatment.

HYBRIDIZATION

Natural hybridization in *Lipochaeta* is uncommon. Although no hybrids have been detected during the present field studies, two examples can be mentioned that indicate its probable but infrequent occurrence. First, Degener and Sherff (1935) described × *L. procumbens* as a hybrid between *L. lobata* (a tetraploid) and *L. integrifolia* (a diploid). Pollen stainability (in lactophenol-aniline blue) in this plant is 2 per cent, no full achenes are present, and it has a leaf morphology intermediate between the two putative parents. In addition, it has been determined that the plant has an additive leaf flavonoid profile. In view of these data, it is probable that a sterile triploid has been formed. These plants were collected near Kaena Point, Oahu (*Degener, et al. 4187*), an area of sympatry for the parental taxa. Another possible hybrid is *L. intermedia* Degener and Sherff (placed in synonymy with *L. subcordata* in this treatment). Known from a single collection, *Meebold 4254*, this taxon was found on Hawaii in an area where both *L. subcordata* and *L. lavarum* occur. It is intermediate between the two species. The specimen does, however, have a pollen stainability of 90 per cent, and several full achenes.

LEAF FLAVONOID CHEMISTRY

The usefulness of flavonoid chemistry in determining degrees of relationship among plant taxa is well established (Turner & Alston, 1959; Alston & Turner, 1962; Levin, 1967; Crawford, 1974; Gardner, 1974; Giannasi, 1975). In the hope of gaining insight concerning the systematics of *Lipochaeta,* a chemical study was initiated.

Specimens of 16 of the 23 species of *Lipochaeta* were surveyed for flavonoid content. Population samples from throughout the morphological and geographical range of each taxon were examined (indicated by asterisks in the representative specimens). Voucher specimens for all personal collections are deposited in OS.

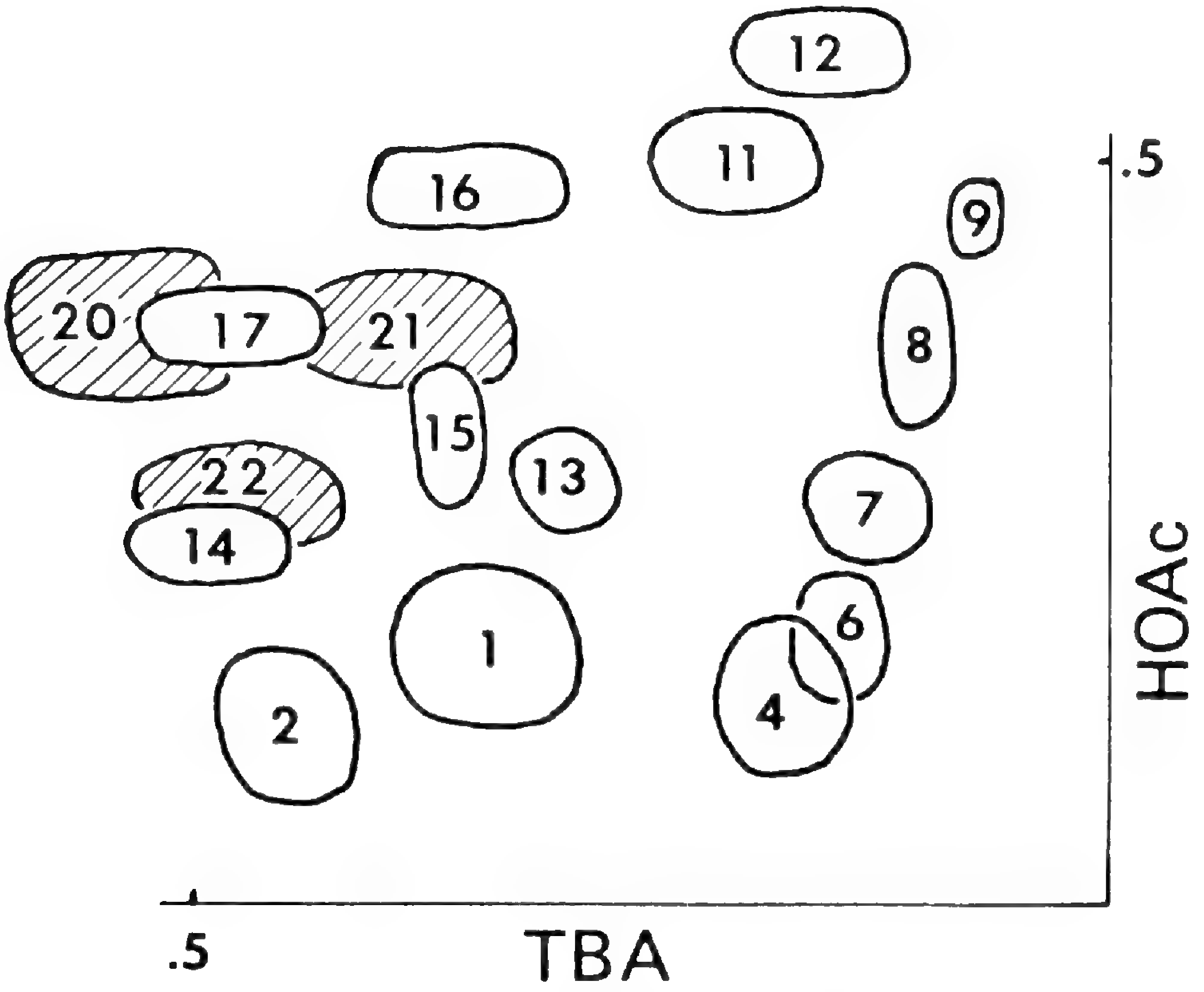


Figure 1. **Drawing of two dimensional paper chromatogram of *Lipochaeta* leaf extracts.** Hatching shows compounds of Section *Aphanopappus,* all others are characteristic of Section *Lipochaeta.*

Materials and Methods

The methods of Mabry et al. (1970) were followed for paper chromatography and spectral analyses except that fused sodium acetate was used. Extraction and isolation of compounds was achieved following the procedures of Bacon (1975). A single collection of each taxon was subjected to the bulk extraction methods, while all additional collections were surveyed using two dimensional paper chromatography. If the resultant chromatogram was judged to differ from those obtained with the mass samples the unique compounds were identified. If, however, the profiles were considered to be identical, no additional identification was done.

Intact leaves were taken from herbarium specimen packets and soaked for 24 hours in 85 per cent aqueous methanol. After extraction, the leaves were air dried and returned to the packets. The extract was concentrated under vacuum and checked for flavonoid content using thin layer chromatography (glass plates coated with PH-101 microcrystalline cellulose). Because of insufficiency of material, no compounds were identified, but rather the TLC profiles were compared with known paper profiles.

Results

Leaf flavonoid chemistry is useful for making sectional assignments in *Lipochaeta.* The species of Section *Lipochaeta* (tetraploid and four-merous) synthesize both flavones and flavonols, whereas the taxa of Section *Aphanopappus* (diploid and five-merous) produce only flavonols (Figure 1, Table 1). Considerable infrasectional similarity is also indicated. Although the utility of recognizing species, based on chemical constituents, in either section is weak, some patterns (primarily absence of compounds) are species-specific in the tetraploids (e.g., *L. succulenta, L. degeneri*).

PHYLOGENY

Phylogenetic relationships among the taxa are depicted in Figure 2; taxa below the dashed line are diploid, those above are tetraploid. Although the diploids are at least partially ancestral to the tetraploids, once formed the two sections have evolved independently.

Many of the taxa, e.g., *Lipochaeta ovata,* are known only from single collections, and it is estimated that at least one third of those

Table 1. **Major leaf flavonoid constituents of *Lipochaeta*.**

In the ratios, the first figure is the number of populations sampled and the second is the number of collections examined. Compounds in all samples tested are indicated by +; those absent from some populations are indicated by −. Compounds 1–7 are luteolin glycosides, 13–15 are apigenin glycosides, and 16–22 are quercetin glycosides.

		Compound	Flavones												Flavonols				
	Ratio	Number	1	2	4	6	7	8	9	11	12	13	14	15	16	17	20	21	22
Sect. *Lipochaeta*																			
L. rockii	(9:22)		+	+	+	+	+		−	−	−	−	−	−	+	+			
L. connata var. *acris*	(6:6)		+		+	+	+	+	−			+			+				
L. connata var. *connata*	(4:6)		+		+		−		−		−		+		+	+			
L. lobata var. *lobata*	(3:5)		+		+	+	+		−	+			+		+	+			
L. heterophylla	(6:11)		+	−	+	+	+	−	−		−	−	−		−	−			
L. succulenta	(5:6)		+		+	+							−						
L. degeneri	(1:1)		+							+	+								
Sect. *Aphanopappus*																			
L. tenuifolia	(1:1)																	+	
L. populifolia	(1:1)																+	+	
L. lavarum	(9:9)																	+	
L. integrifolia	(9:15)																	+	+
L. waimeaensis	(1:1)																	+	
L. micrantha var. *exigua*	(1:1)																	+	
L. kamolensis	(1:1)																+	+	+
L. subcordata	(1:1)																	+	
L. remyi	(1:1)																	+	
L. tenuis	(1:1)																	+	

species are extinct. It is believed that some of the extinctions are recent, e.g. *L. degeneri* was collected on Molokai in 1910 (*Rock 10288*), 1912 (*Forbes 59-Mo*) and 1928 (*Degener 4198*). A thorough search of the type locality in 1974 was unsuccessful in re-discovering the taxon.

Lipochaeta ovata, a diploid, is believed to be the most primitive species of the genus. It is similar to the close relative *Wedelia*, especially *W. biflora*, in habit (upright shrub, petiolate leaves to 7.5 cm long, 3.5 cm wide) and in characters of the mature achenes (smooth external surface, thickened pericarp, and lacking a pappus).

The diploids can be separated into two major groups (Figure 2). Group A is characterized by large headed taxa with mostly more than 30 disc florets per head. The habit of these taxa varies from coarse and upright (*Lipochaeta lavarum, L. populifolia, L. perdita, L. ovata*) to more delicate and decumbent (*L. dubia, L. tenuifolia, L. tenuis*) to succulent and prostrate (*L. integrifolia*). *Lipochaeta tenuifolia* has ternately compound leaves, which is atypical for the genus; some other species have leaves deeply dissected, but not truly compound.

Group B (Figure 2) is characterized by generally fewer ray and disc florets and smaller heads than group A. All are suffruiticose except *Lipochaeta remyi*, an herb. The remaining taxa show variations in growth habit similar to group A; upright (*L. bryanii, L. deltoidea, L. fauriei, L. subcordata, L. venosa*) or decumbent (*L. kamolensis, L. micrantha, L. waimeaensis*). *Lipochaeta deltoidea* has characters that tie it to each of the other subgroups and is therefore considered as the ancestral type for group B.

Lipochaeta deltoidea shows also a resemblance to *L. connata* var. *acris* (a tetraploid) through the vegetative features listed above. In addition, *L. deltoidea* has tuberculate achenes and purple paleae. These features are common throughout the tetraploids. *Lipochaeta connata* var. *acris* is a taxon from which all of the tetraploid species can be derived, except for *L. degeneri*. This species, unknown cytologically, is included in Section *Lipochaeta* based on floral morphology and leaf flavonoid chemistry, but its connection to the remaining tetraploids is obscure.

Many of the islands are characterized by certain tetraploid species that are unique to that island e.g.; Kauai, *Lipochaeta connata;* Oahu, *L. lobata;* Molokai, *L. rockii;* Lanai, *L. heterophylla*. One

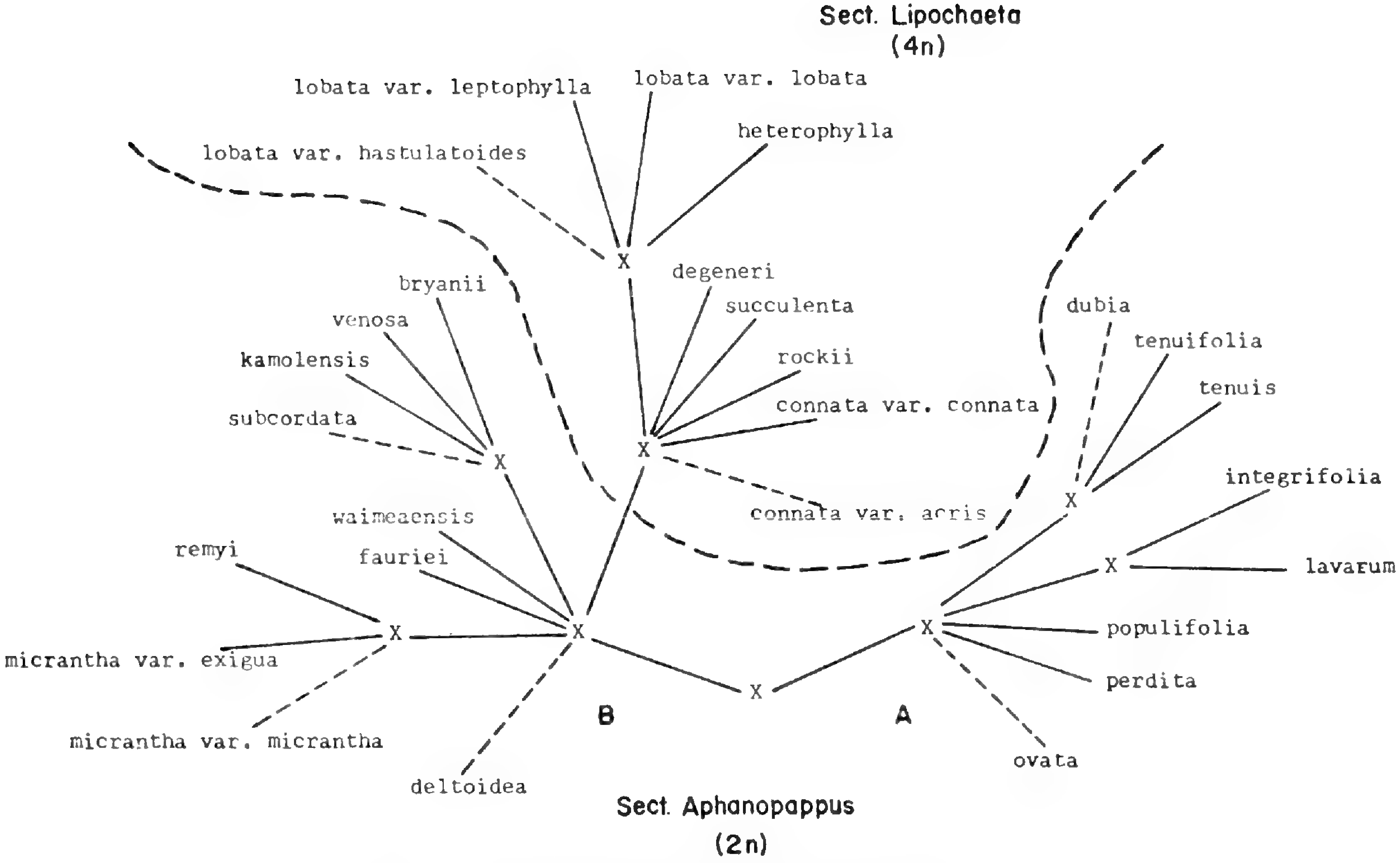


Figure 2. **Phylogenetic relationships among *Lipochaeta* taxa.**

taxon, however, *L. succulenta,* which may be dispersed by water, has been found on all of the major islands except Lanai.

TAXONOMIC TREATMENT

Lipochaeta DC.

Lipochaeta DC. Prodr. **5:** 610. 1836. Type species: *Lipochaeta lobata* (Gaud.) DC.

Microchaeta Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841. *nom. superfl.* Type species: *Lipochaeta lobata* (Gaud.) DC.

Schizophyllum Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 452. 1841. *nom. illegit.* non Fries. 1831. Type species: *Schizophyllum micranthum* Nutt. (=*Lipochaeta micrantha* (Nutt.) A. Gray).

Aphanoppaus Endl. Gen. Plantarum Suppl. **2:** 43. 1842. *nom. nov.,* based on *Schizophyllum micranthum* Nutt.

Plants suffruticose perennial or rarely annual; stems upright to 2 m tall, or arcuate-spreading or decumbent to prostrate and rooting along lower surface. Leaves opposite, simple or rarely ternately compound, petiolate, often with alate-margined petioles or sessile with connate-perfoliate bases, margin entire to pinnate-pinnatifid, on both surfaces glabrous to hispidulose. Heads solitary or in cymose clusters, terminal on stems and branches, pedunculate. Phyllaries in 2 equal or subequal series, 4 or 5 per series, green to tan and sometimes purple near base and along midrib. Ray florets carpellate, fertile; ligule yellow, divergent or reflexed, at apex entire to 3-dentate. Disc florets hermaphrodite, generally all fertile; corollas yellow, four- or five-merous. Achenes tuberculate or smooth, sometimes winged, with outer wall of mature achenes becoming thick, approximately doubling external size of fruit; pappus often of scales or forming a corona and also of deciduous awns, ray achenes 3-angled, disc achenes 2 or 4 angled. Paleae rigid, erect or arching over developing florets, sometimes purple near tip or along midrib.

KEY TO THE TAXA

a. Majority of disc florets in a single head with 4-lobed corollas (Section *Lipochaeta*). (b)
  b. Leaves to 2 cm long and 0.5 cm wide; ray florets 6 or fewer. 2. *L. degeneri*
  b. Leaves more than 2 cm long, more than 0.5 cm wide; ray florets more than 6. (c)

c. Leaves and stems fleshy in the field, stems often flattened on mounted specimens; ray ligules reflexed, to 6 mm long; mature achenes nearly smooth. .... 1. *L. succulenta*

c. Leaves subcoriaceous to herbaceous and stems suffruticose, rigid on mounted specimens; ray ligules divergent, more than 6 mm long; mature achenes tuberculate. (d)

d. Leaves entire, if rarely divided then outer phyllaries broadly ovate, broadly acute to rounded at apex and leaves petiolate; leaf vestiture strigulose to nearly glabrous. (e)

e. Outer phyllaries broadly acute to rounded at apex, if attenuate, then leaves lanceolate-linear; heads solitary or in 3 headed cymes. (f)

f. Leaves ovate; phyllaries broadly acute to rounded. (g)

g. Leaves sessile or short petiolate, bases not extending across node. .... 5a. *L. lobata* var. *lobata*

g. Leaves sessile, bases connate-perfoliate. .... 5b. *L. lobata* var. *hastulatoides*

f. Leaves lanceolate-linear; phyllaries attenuate. .... 5c. *L. lobata* var. *leptophylla*

e. Outer phyllaries acute to attenuate, if attenuate, then leaves ovate; heads in compound cymose clusters. (h)

h. Leaf bases connate-perfoliate. ... 6a. *L. connata* var. *connata*

h. Leaf bases narrowed to an alate margined petiole .... 6b. *L. connata* var. *acris*

d. Leaves divided or parted, if not divided than outer phyllaries acute and/or leaves sessile; leaf vestiture strigose to appressed hispidulose. (i)

i. Heads in compound cymose clusters; outer phyllaries narrowly ovate; leaves petiolate or sessile. .... 3. *L. rockii*

i. Heads in 3 headed cymes; outer phyllaries broadly ovate; leaves sessile. .... 4. *L. heterophylla*

a. Majority of disc florets in a single head with 5-lobed corollas (Section *Aphanopappus*). (k)

k. Plants annual, herbaceous. .... 10. *L. remyi*

k. Plants perennial, suffruticose. (l)

l. Stems decumbent or prostrate. (m)

m. Leaves appearing as six per node (ternately compound with sessile leaflets), leaflets pinnatifid, ultimate segments less than 3 mm wide. .... 7. *L. tenuifolia*

m. Leaves 2 per node, simple (some species with divided leaves, but not compound), ultimate segments more than 3 mm wide. (n)

n. Leaves thick and succulent; mature achenes nearly smooth. .... 23. *L. integrifolia*

n. Leaves herbaceous; mature achenes tuberculate. (o)

o. Leaves linear to narrowly elliptic, nearly entire, less than 1 cm wide. .... 12. *L. waimeaensis*

o. Leaves ovate to deltoid or divided, more than 1 cm wide. (p)

p. Ray florets 4 or 5, ligules less than 6.5 mm long. (q)

q. Ray ligules more than 2.5 mm long. .... 15a. *L. micrantha* var. *micrantha*
q. Ray ligules to 2.5 mm long. 15b. *L. micrantha* var. *exigua*
p. Ray florets 6–12, ligules more than 6.5 mm long. (r)
r. Leaves pinnatifid to pinnate-pinnatifid; ray florets 6. .... 19. *L. kamolensis*
r. Leaves entire or with 2 or 4 basal lobes, ray florets more than 6. (s)
s. Leaves deltoid, usually with 2 or 4 basal lobes. .... 8. *L. dubia*
s. Leaves ovate, not lobed basally. .... 9. *L. tenuis*
l. Stems arcuate spreading or upright. (t)
t. Achenes nearly smooth. (u)
u. Heads in compound cymose clusters; outer phyllaries less than 2.5 mm long. .... 11. *L. ovata*
u. Heads solitary or in 3-headed cymes; outer phyllaries more than 2.5 mm long. .... 21. *L. lavarum*
t. Achenes tuberculate. (v)
v. Ray ligules less than 7 mm long. (w)
w. Disc corollas more than 3.8 mm long; petioles narrowly alate margined. .... 14. *L. fauriei*
w. Disc corollas less than 3.5 mm long, and/or petioles not alate margined. (x)
x. Heads in compound cymose clusters; achenes with scales along upper, outer rim. .... 16. *L. subcordata*
x. Heads solitary or in 3-headed cymes; achenes with hairs along upper, outer rim or naked, but without scales. (y)
y. Outer phyllaries obtuse at apex; ray ligules less than 5 mm long. .... 17. *L. venosa*
y. Outer phyllaries attenuate at apex; ray ligules more than 5.5 mm long. .... 13. *L. deltoidea*
v. Ray ligules more than 7 mm long. (z)
z. Ray florets 5 or fewer. .... 20. *L. bryanii*
z. Ray florets more than 5. (aa)
aa. Leaves less than 4.5 cm long and less than 2.8 cm wide; disc corollas more than 3.5 mm long. .... 22. *L. perdita*
aa. Leaves more than 4.5 cm long and more than 2.8 cm wide; disc corollas less than 3.5 mm long. .... 18. *L. populifolia*

LIPOCHAETA SECTION LIPOCHAETA

Lipochaeta DC. section *Microchaeta* (Nutt.) Bentham and Hooker, Gen. Plantarum **2:** 372. 1873. *Microchaeta* Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841. *nom. superfl.* TYPE SPECIES: *Lipochaeta lobata* (Gaud.) DC.

Leaves with narrowly alate-margined petioles or broadly connate-perfoliate at the base. Majority of disc florets four-merous. Chromosome number, $n = 26$. Species numbers 1–6.

1. **Lipochaeta succulenta** (Hook. & Arn.) DC. Prodr. **5:** 611. 1836.

Verbesina succulenta Hook. & Arn. Bot. Beechey's Voyage. **87.** 1832. TYPE: Hawaii: Oneeheow [Niihau]: 1826–27, *G. T. Lay & A. Collie s.n.* (Holotype, K!). *Microchaeta succulenta* (Hook. & Arn.) Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841.

Lipochaeta lanceolata Nutt. Trans. Amer. Philos. Soc. **7**(n.s.): 451. 1841. TYPE: Hawaii: Oahu: near the sea, *Nuttall s.n.* (Holotype, BM!).

Lipochaeta australis Lessing var. *decurrens* A. Gray, Proc. Amer. Acad. Arts **5:** 129. 1861. TYPE: Hawaii: Kauai: 1838–42, *U. S. Exploring Expedition s.n.* (Lectotype chosen, US!). *Lipochaeta connata* (Gaud.) DC. var. *decurrens* (A. Gray) Hillebrand, Flora Hawaiian Islands. 206. 1888.

Lipochaeta connata (Gaud.) DC. var. *littoralis* Hillebrand, Flora Hawaiian Islands. 206. 1888. TYPE: Hawaii: Molokai: *W. Hillebrand s.n.* (Holotype, apparently destroyed, not at B).

Lipochaeta variolosa Léveillé, Repert. Spec. Nov. Regni Veg. **10:** 122. 1911. TYPE: Hawaii: Kauai: Wainiha, Jan 1910, *A. U. Faurie 1008* (Lectotype chosen, P!; isotypes, BISH!, G[2]!).

Lipochaeta succulenta (Hook. & Arn.) DC. var. *angustata* Sherff, Bot. Gaz. (Crawfordsville) **95:** 87. 1933. TYPE: Hawaii: Kauai: 1909, *C. N. Forbes s.n.* (Holotype, F!; isotypes, BISH!, F!).

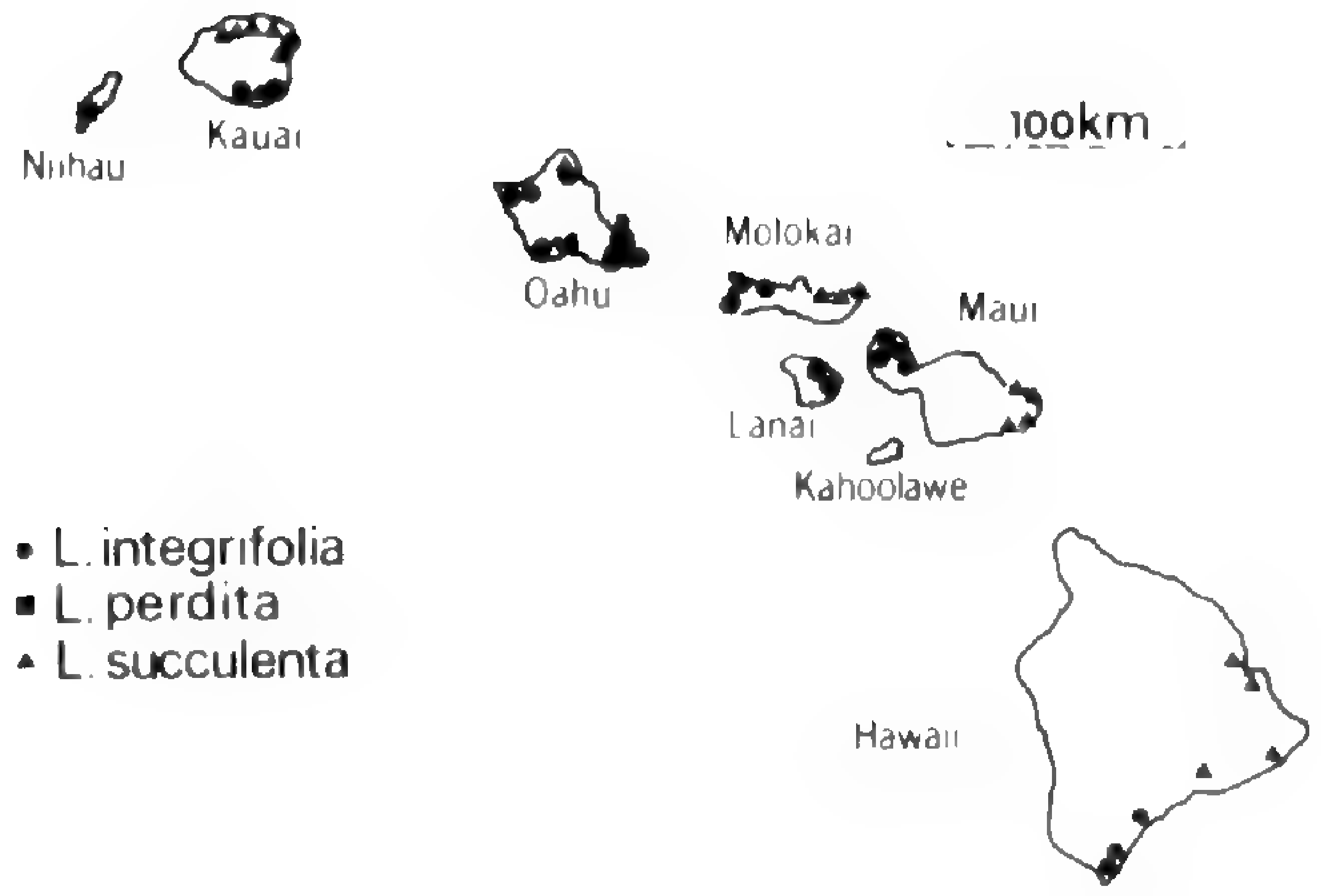
Lipochaeta succulenta (Hook. & Arn.) DC. var. *barclayi* Sherff, Bot. Gaz. (Crawfordsville) **95:** 87. 1933. TYPE: Hawaii: Atooi [Kauai]: in loam soil, hills, Jul 1837, *G. Barclay 1327* (Holotype, BM; photo of holotype, F!).

Suffruticose; stems decumbent, rooting along lower surface, to 1.5 m long. Leaves with narrowly alate margined petiloes 2–10 mm long; blades linear to elliptic-ovate, 6–12.5 (–14) cm long, (1–) 2–4 (–6.5) cm wide, entire to serrate, glabrous to strigulose.[1] Heads in simple or compound cymes. Outer phyllaries ovate, 3.2–5 mm long, 1.5–3.8 mm wide, acute, occasionally purple near apex, sparsely strigulose. Ray florets 9–15; ligules oval to oblong, (3.8–) 4.5–6 mm long, (1.3–) 2.3–3.3 mm wide; tube 1.2–1.5 (–1.8) mm long. Disc florets 25–40 (–50); corollas 3.1–3.7 mm long, lobes 0.9–1.2 mm long; anthers 1.3–1.5 mm long. Achenes nearly smooth, those of ray 2.3–2.7 mm long, 1.2–1.7 mm wide, with wings to 0.5 mm, those of disc 2.2–2.9 mm long, 1.1–1.4 mm wide, with wings to 0.6 mm; pappus of fused scales forming an uneven corona and with awns to 0.6 mm long. Paleae occasionally purple near apex.

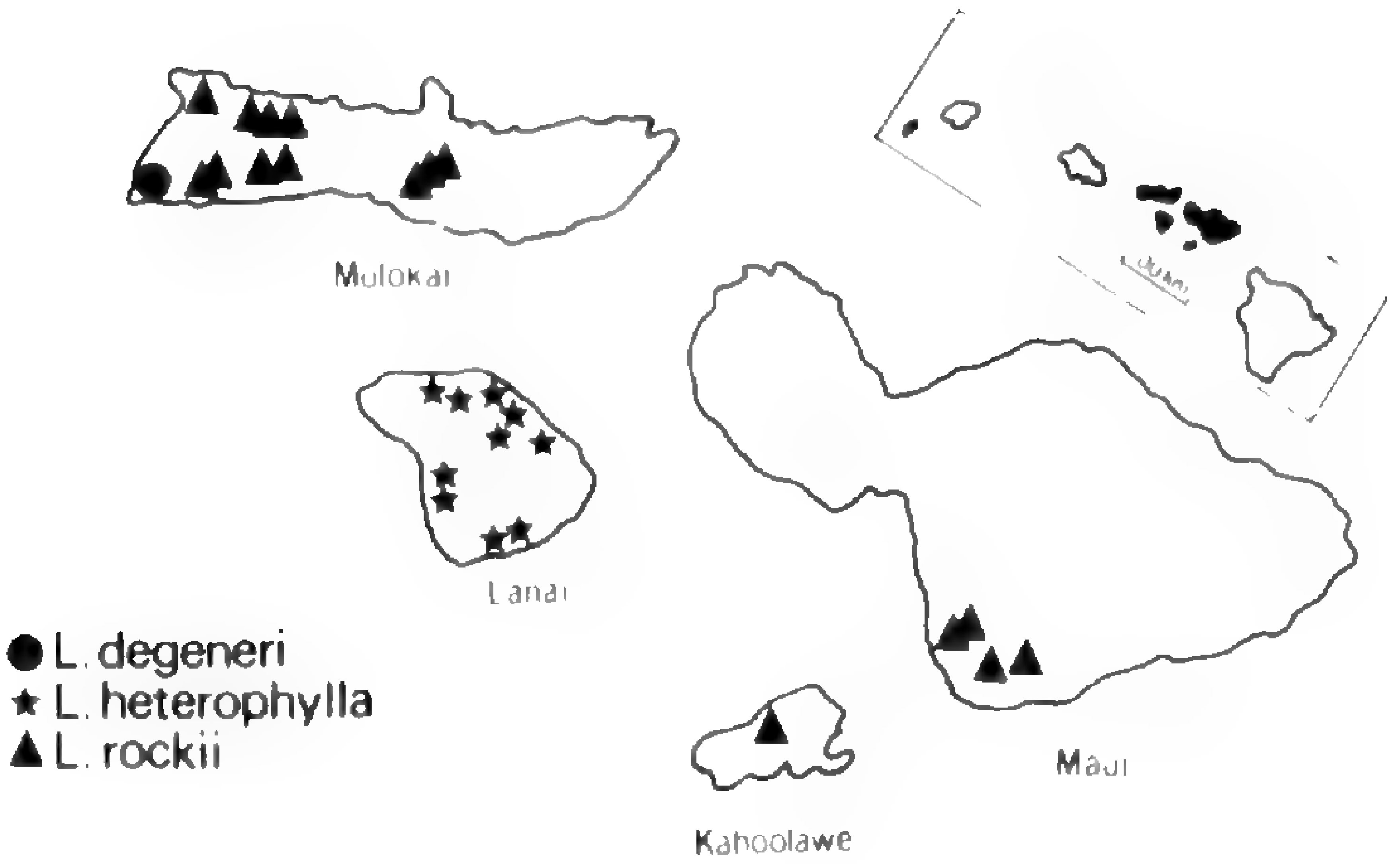
Known from all of the major islands except Lanai (Figure 3); generally near sea level to 100 m in coastal areas, but occasionally

---

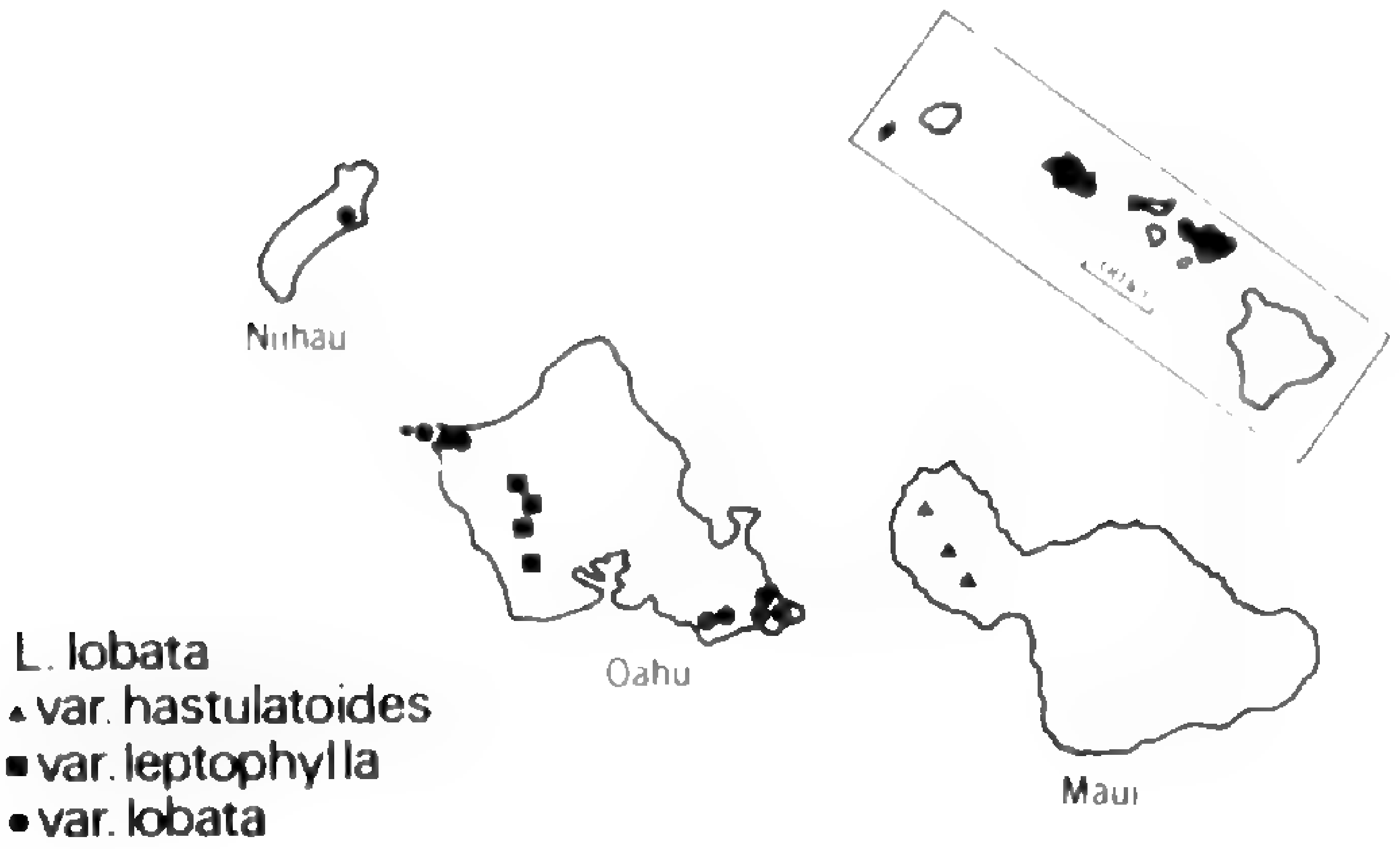
[1] Length and width of leaves at second node below the peduncles.



3



4



5

Figures 3–5. **Documented distributions of *Lipochaeta*.** 3. *L. integrifolia, L. perdita,* and *L. succulenta.* 4. *L. degeneri, L. heterophylla,* and *L. rockii.* 5. *L. lobata* var. *hastulatoides,* var. *leptophylla,* and var. *lobata.*

further inland and at higher elevations (200 m). Flowering throughout the year. Extant.[1]

Lipochaeta succulenta is similar to *L. connata* var. *acris* in several gross morphological features, but can be distinguished from the latter by the much shorter ray ligules; shorter and broader, smooth fruits; fleshy leaves; and ovate phyllaries. The achenes of this taxon have a very thick outer layer of cork which may facilitate flotation and thus serve in dispersal.

Sherff (1935) recognized four varieties of *Lipochaeta succulenta,* based almost entirely on variations in leaf shape and size. Variety *trifida* was distinguished by "commonly" trilobed leaves. Closer examination, especially of floral features, has shown it to be a large leaved variant of *L. rockii.* The extremes of the type specimens of the other three varieties recognized by Sherff (1935) intergrade to a large degree, and this character is most obvious when population samples are analyzed. In addition, observations of plants grown in the greenhouse indicate that differences in water availability and light levels can make considerable differences in leaf size and shape.

Representative specimens. HAWAII. **Hawaii:** Hilo Bay, *Brumaglin 4300* (F, NY), *Degener 4029* (GH, NY, US); S side of Hilo Bay, *Degener 18077* (NY); between Keaukaha and Leleiwii Pt, Puno,*Degener & Picco 31642* (MO, W); Hawaii National Park, *Fagerlind & Mitchell 1116* (BISH, NY); Hilo, *Hitchcock 14155* (BISH, US); Kalapaua, *Rock 13007* (BISH). **Kauai:** Hanalei, Makahoa Pt, *Degener 20507* (BISH, NY); Waiahuakua, *Degener & Ordonez 12612* (A, BISH, F, G, GH, MO, US); Haena-Kalalau Trail, *Gardner 284, 285** (OS); Anini Beach, *Gardner 289** (OS); S side of Moloaa Bay, *Gardner 354* (OS); N of Ka Lae Amana Pt, Moloaa Bay, *Gardner 356, 356A* (OS); Pakala Pt, *Gardner 357** (OS); S of light house, Kilauea Pt, *Gardner 358* (OS); Hanakapiai, *St. John, et al. 10870* (US). **Maui:** Keanae, *Degener & Degener 23645* (G, NY, W); near Kaapahu Bay, *Degener & Degener 25237* (BISH, F, G, K, MO, NY, W); Nahiku, *Degener & Degener 27564* (BISH, F); Kaapahu Bay, *Degener & Degener 27567* (BISH, F, NY); Hana, N side of Kauiki Head, *Degener et al. 12422* (A, BISH, F, MO, NY, US); *Degener & Murashize 19797* (BISH, NY, US); beach at Kipahula, *Forbes 274-M* (BISH, F); Kaapahu, *Forbes 1774-M* (BISH, US); Kahanu Gardens of Pacific Tropical Botanical Gardens, *Gardner 381** (OS); Kaapahu Bay, *Gardner 383*, 384** (OS). **Molokai:** Wailau Valley, *Degener & Nitta 4028* (BISH, CAS, DS, F, K), *4211* (F, G, GB, GH, K, MO, NY, UC, US, W); Manawai, *Forbes 396-Mo* (BISH, F, K, UC); Wailau Valley, *Forbes 522-Mo* (BISH, F); Pelekunu Valley, *Forbes 577-Mo* (BISH, F); W of Wailau Valley, *Fosberg 9657* (BISH); Wailau Valley, *Fosberg 9663* (BISH, DS, F, GH); Manawai,

---

[1] Because of the inclusion of nearly all of the taxa of *Lipochaeta* on the endangered species list for Hawaii (Fosberg & Herbst, 1975), comments will be made on the presumptive current status of each taxon.

Kahanami Ridge, *Fosberg 13393* (BISH, F); mouth of Halawa Valley, *Fosberg 13407* (F, GH, US); Kalaupapa, *Gardner 313* (OS). **Niihau:** no locality, *Remy 287* (GH, NY). **Oahu:** Kahuku, *Pearsall 100* (BISH).

2. **Lipochaeta degeneri** Sherff, Bot. Gaz. (Crawfordsville) **95:** 84. 1933. TYPE: Hawaii: Molokai: hot, arid boulder-covered plain near sea, SW point of island, 16 May 1928, *O. Degener 4198* (Holotype, F!; isotypes, A!, F!, G!, GH!, K!, MO!, US!, W[2]!).

Suffruticose, stems upright, to 30 cm tall. Leaves sessile, spatulate, 1.7–2 cm long, 0.3–0.4 cm wide, entire, sparsely strigulose. Heads solitary or in 2's or 3's. Outer phyllaries ovate, 3–3.8 mm long, 1.3–2.1 mm wide, acute, often purple near apex, strigulose. Ray florets about 6; ligules oblong, 3.6–4 mm long, 2–2.4 mm wide; tube 1–1.2 mm long. Disc florets about 15; corollas 2.7–3.3 mm long, lobes 0.6–0.7 mm long; anthers 1.2–1.5 mm long. Achenes tuberculate, those of ray 2.3–2.4 mm long, 1.1–1.5 mm wide, with wings to 0.4 mm, those of disc 2.7–3.2 mm long, 0.8–1.8 mm wide, with wings to 0.3 mm; pappus of scales to 0.2 mm long, fused at the base and with deciduous awns to 1 mm long. Paleae with a purple midrib and often purple near apex. Chromosome number unknown.

Known from three collections near the southwest point of Molokai (Figure 4), near sea level. Habitat information scarce except for "hot, arid, boulder-covered plain" (*Degener 4198*). Flowering May-Jun. Probably extinct.

Lipochaeata degeneri superficially resembles an upright *L. integrifolia.* Closer examination, however, shows that the leaves of the former are not succulent, the heads are few-flowered, and the achenes are winged and tuberculate. Its position within this section is unclear.

Representative specimens. HAWAII. **Molokai:** Ka Lae O Ka Laau, *Forbes 59-Mo* (F, US); *Rock 10288* (GH, NY, US, W); *Rock 14011* (UC).

3. **Lipochaeta rockii** Sherff, Bot. Gaz. (Crawfordsville) **95:** 100. 1933. TYPE: Hawaii: Molokai: Mapulou, 22 Mar 1910, *J. F. Rock 6156* (Holotype, GH!; isotypes, BISH!, F[3]!).

Lipochaeta forbesii Sherff, Bot. Gaz. (Crawfordsville) **95:** 83. 1933. TYPE: Hawaii: Maui: Nuu, S slope of Haleakala, 9 Mar 1920, *C. N. Forbes 1916-M* (Holotype, F!; isotypes, K!, NY!, UC!, US!).

Lipochaeta heterophylla A. Gray var. *malvacea* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 96. 1933. TYPE: Hawaii: Molokai: arid, rocky plain near Kolo, 5 Apr 1928, *O. Degener 4199* (Lectotype chosen, F!; isotypes, BISH! CAS!, F[4]!, G[2-frag.]!, GB!, MO[2]!, NY!, UC!, US!, W[2]!).

Lipochaeta kahoolawensis Sherff, Bot. Gaz. (Crawfordsville) **95:** 98. 1933. Type: Hawaii: Kahoolawe: 1851–1855, *J. Remy 269* (Holotype, P!).

Lipochaeta lobata (Gaud.) DC. var. *maunaloensis* Sherff, Bot. Gaz. (Crawfordsville) **95:** 93. 1933. Type: Hawaii: Molokai: Mauna Loa, Jun 1912, *C. N. Forbes 7-Mo* (Holotype, F!; isotype, BISH!).

Lipochaeta rockii Sherff var. *dissecta* Sherff, Bot. Gaz. (Crawfordsville) **95:** 101. 1933. Type: Hawaii: Maui: 1838–42, *U.S. Exploring Expedition s.n.* (Holotype, US!).

Lipochaeta rockii Sherff var. *subovata* Sherff, Bot. Gaz. (Crawfordsville) **95:** 101. 1933. Type: Hawaii: Molokai: 1851–1855, *J. Remy 270* (Holotype, P!).

Lipochaeta succulenta (Hook. & Arn.) DC. var. *trifida* Sherff, Bot. Gaz. (Crawfordsville) **95:** 87. 1933. Type: Hawaii: Molokai: Manawai, Aug 1912, *C. N. Forbes 397-Mo* (Lectotype chosen, F!; isotypes, BISH!, F[2]!, UC!).

Lipochaeta forbesii Sherff var. *sherffii* Degener & Clay, Flora Hawaiiensis, Fam. 344:Lip:Forb. 1949. Type: Hawaii: Maui: between Kepuni and Palaha Gulches, 25 Dec 1948, *O. Degener 19292* (Holotype, BISH!; isotypes, A!, B!, F[3]!, G!, GB!, NY[2]!, US!).

Lipochaeta lobata (Gaud.) DC. var. *makenensis* Degener & Sherff *In:* Sherff, Brittonia **12:** 174. 1960. Type: Hawaii: Maui: Makena, arid lava flow. 40 ft, 1 Apr 1959, *O. Degener, I. Degener, & W. Fleming 25133* (Holotype, F!; isotypes, BISH!, F[2]!, G!, UC!, W[2]!).

Lipochaeta scabra St. John, Pacific Sci. **30:** 40. 1976. Type: Hawaii: Hawaii: *D. Nelson s.n.* (Holotype, BM!).

Suffruticose, stems arcuate-spreading to upright, 0.5–1 m tall. Leaves with narrowly alate margined petioles 9–25 mm long or sessile with connate-perfoliate bases; blades ovate 4–7.3 (–10) cm long, 2.5–5 (–7.2) cm wide, nearly entire to deeply 3–5 divided, terminal segment lanceolate to obovate, entire to pinnatifid, appressed hispidulose on both surfaces. Heads in simple or compound cymes. Outer phyllaries ovate, (2.5–) 3–5.3 mm long, 1.5–2.5 mm wide, acute, appressed hispidulose. Ray florets 7–12; ligules oblong, (5–) 7–10 (–11.5) mm long, 2.3–4.3 mm wide, tube 1.3–2 mm long. Disc florets 20–45 (–55); corollas 2.8–3.5 (–4) mm long, lobes 0.7–1 (–1.2) mm long; anthers 1.3–1.7 mm long. Achenes tuberculate, those of ray 2.2–3.1 mm long, 1.1–2 mm wide, with wings to 0.5 mm, those of disc 2.1–3 mm long, 1–2 mm wide, with wings to 0.5 mm. Pappus of fused scales forming an uneven corona and with awns to 1.5 mm long. Paleae purple near apex.

Known from several localities from central to western Molokai, south-central Maui, and Kahoolawe 30–500 m (Figure 4). Often found in areas disturbed by erosion or along the margins of and out into "aa" lava flows. Flowering Dec-Jul. Extant, except possibly those from Kahoolawe.

With respect to leaf morphology, *L. rockii* is the most variable species in the genus. Most populations have plants that vary from nearly entire to deeply dissected five-lobed leaves. Occasionally an individual plant even shows this spectrum of variation (*Gardner 406*). The leaf bases also are variable, ranging from petiolate to sessile, and if sessile, then the bases are connate-perfoliate. Generally one finds that the plants in a particular population are either petiolate or they are sessile, but not plants of both types. This geographical separation of morphological types, suggests that with time perhaps additional differences will be accumulated such that distinct varieties might be recognized.

Lipochaeta scabra St. John is placed in synonymy here as it fits within the range of variation of *L. rockii* in all aspects. This early collection of David Nelson does represent a new record for *L. rockii,* previously known only from Molokai and Maui. As stated by St. John (1976b), this population is probably extinct.

Representative specimens. HAWAII. **Maui:** Makena, *Degener & Degener 30313* (A, BISH, G, NY, W); Hwy 31 to Makena, *Gardner 330** (OS); E of Ulupalakua, *Gardner 334** (OS); Hwy 31, 1.1 mi N of Makena, *Gardner 374* (OS); Hwy 31, 5.5 mi SE of Ulupalakua Ranch Office, *Gardner 378* (OS); Mahawao, *Hillebrand & Lydgate 135* (BISH). **Molokai:** Kakaaukuu Gulch, *Degener 22204* (BISH, F, G, MO, NY, UC, US, W); Waiele, *Degener 22207* (BISH, DS, F, G, K, MO, NY, UC, US, W); between airport and Homelani Cemetery, *Degener 22209* (BISH, F, G, K, MO, NY, US, W); Hwy 46, 5 mi W of Jct Hwy 46 and airport road, *Gardner 299A-F*, 399 A & B, 400 A & B* (OS); Kolo Rd, *Gardner 300-D** (OS); Moomomi Beach, *Gardner 301*, 303A* & B** (OS); S of Moomomi Beach, *Gardner 304A-C*, 305** (OS); road up Makakupoia, *Gardner 306*, 307*, 308** (OS); Rd to Kolo Wharf, *Gardner 402, 403, 404, 405* (OS); E of Kaunakakai, *Gardner 406, 407, 408, 409* (OS).

4. **Lipochaeta heterophylla** A. Gray, Proc. Amer. Acad. Arts **5:** 130. 1861. TYPE: Hawaii: Maui: W. Maui, 1838–42, *U.S. Exploring Expedition s.n.* (Holotype, US!).

Lipochaeta lobata (Gaud.) DC. var. *heterophylla* (A. Gray) Hillebrand, Flora Hawaiian Islands. 209. 1888. TYPE: Hawaii: Lanai: 1870, *W. Hillebrand s.n.* (Holotype, B; isotypes, BISH [frag]!, GH!, US!).

Lipochaeta peduncularis del Castillo, Florae Insularum Maris Pacifici. **72.** *t. 35.* 1888. TYPE: Hawaii: Lanai: 1851 1855, *J. Remy 267* (Holotype, P!).

Lipochaeta heterophylla A. Gray var. *molokaiensis* Sherff, Bot. Gaz. (Crawfordsville) **95:**96. 1933. TYPE: Hawaii: Molokai: W. end, 1910, *J. F. Rock 10287* (Holotype, F!; isotypes, BISH[2]!, GH!, UC!).

Suffruticose, stems arcuate-spreading, 0.5–1 m tall. Leaves sessile, with connate-perfoliate bases; blade narrowly to broadly elliptic, 4.5–6.5 (–9.5) cm long, 2–3.5 (–4.5) cm wide, scarcely serrate, occasionally with 2 basal lobes, on both surfaces appressed hispidulose. Heads in simple cymes. Outer phyllaries ovate 4–6.5 (–10) mm long, 2.5–4 (–4.5) mm wide, broadly acute, appressed hispidulose. Ray florets 8–12; ligules oblong, 8–12 mm long, 2–3.5 (–5) mm wide, tube (1.5–) 2–2.8 (–3.3) mm long. Disc florets (35–) 45–60; corollas (3.4–) 3.6–4.2 mm long, lobes 0.6–1 mm long; anthers (1.5–) 1.7–2 mm long. Achenes tuberculate, those of ray (2.2–) 2.6–3 mm long, 1.3–1.7 mm wide, with wings to 0.5 mm, those of disc (2.5–) 2.7–3.5 (–3.8) mm long, 1.1–1.5 mm wide, with wings to 0.6 mm. Pappus of fused scales forming an uneven corona and with awns to 1.3 mm long. Paleae often purple near apex.

Known from western Maui, Molokai, and numerous localities on Lanai (Figure 4), near sea level to 400 m. On dry open hillsides and along margins of lava flows. Flowering throughout the year. Extant on Lanai, probably extinct on Maui & Molokai.

Based on habit, Sherff (1935) recognized three varieties of this species: one being weak, scarcely erect (var. *heterophylla*), the second, robust, branches stronger (var. *molokaiensis*), and the third intermediate in these features (var. *malvacea*). Between the former two these differences intergrade frequently and make varietal delimitation unwarranted. Comparisons of floral characters show the latter taxon to be indistinguishable from *L. rockii*. *Lipochaeta heterophylla* is most closely related to *L. lobata* from which the former can be distinguished by broadly connate-perfoliate leaf bases.

Representative specimens. HAWAII: **Lanai:** Keomuku, *Degener 21995* (CAS, G, GB, NY, UC); Keomuku Hwy, _Gardner 314*, 315*_ (OS); near Poaiwa, _Gardner 316A* & B*_ (OS); Lapaiki Rd, _Gardner 318*, 319*_ (OS); Awalua Rd, _Gardner 320A & B*_ (OS); Naupaka Rd, _Gardner 321*_ (OS); Manele Bay, _Gardner 327A* & B*_ (OS); Hwy 44, 12 mi NE of Lanai City, *Gardner 386* (OS); Kuahua Gulch, *Degener & Degener 28741* (A, BISH, DS, F, G, MO, NY, UC, W); Point across Puu Pehe, Manele, *Hobdy 57* (BISH).

5. **Lipochaeta lobata** (Gaud.) DC. Prodr. **5:** 611. 1836.

Suffruticose, stems arcuate-spreading to decumbent, 0.5–1.5 m tall. Leaves with narrowly alate margined petioles 2–5 mm long or sessile with narrowly connate-perfoliate bases; blades lanceolate-linear to ovate, 4–9.7 cm long, 1–5.6 cm wide, scarcely serrate to serrate, occasionally with 2 or 4 basal lobes or with undulate margin, on both surfaces sparsely strigulose. Heads solitary or in 2's or 3's. Outer phyllaries oblong to lanceolate, 4.7–8.2 mm long, 1.7–4.7 mm wide, rounded to long attenuate, sparsely strigulose. Ray florets 8–15; ligules oblong, 7.5–11 mm long, 2.1–4.5 mm wide, tube 1.5–2.2 mm long. Disc florets 20–65; corollas 3.6–4.4 mm long, lobes 0.7–1 mm long; anthers 1.5–2 mm long. Achenes tuberculate, those of ray 2.5–3.2 mm long, 1.1–1.5 mm wide, with wings to 0.4 mm, those of disc 2.8–3.7 mm long, 1–1.3 mm wide, with wings to 0.5 mm. Pappus of fused scales forming an uneven corona and with awns to 1.5 mm long. Paleae purple near apex.

Known from numerous localities on Oahu, and from western Maui and Niihau (Figure 5), near sea level to 900 m. Flowering Oct.-July. All varieties probably extant.

Lipochaeta lobata, as recognized here, consists of three varieties. Variety *lobata* is the most common of the three, being found in the southeast and northwest corners of Oahu, in low coastal dune areas to a few hundred meters elevation, on shrubby, open hillsides. *Lipochaeta niihauensis* St. John, known only from the type specimen, also belongs in this variety.

Variety *leptophylla* is apparently restricted to the Waianae Range of western Oahu, (although certain collections of var. *lobata* from eastern Oahu approach var. *leptophylla*) where it occurs at several hundred meters elevation. It is distinguished by the generally lanceolate leaves, long, narrow phyllaries with attenuate to acuminate-aristate apices, and more numerous disc florets.

Variety *hastulatoides* occurs at middle elevations in the mountains of western Maui. Through this variety a connection between *Lipochaeta heterophylla* and *L. lobata* can be seen. Variety *hastulatoides* can be distinguished from var. *lobata* by the narrowly connate-perfoliate leaf bases, and ovate to oval blades and from var. *leptophylla* by the same characters plus the broad phyllaries.

5a. **Lipochaeta lobata** (Gaud.) DC. var. **lobata**

Lipochaeta lobata (Gaud.) DC. Prodr. **5:** 611. 1836. *Verbesina lobata* Gaud. *In:* L.C.D. de Freycinet (ed.), Voyage Autour de Monde, Botanique **4:** 464. 1829. TYPE: "In insulus Sandwicensibus," *C. Gaudichaud s.n.* (Holotype, P!; isotype, G!). *Lipotriche australis* Less. Linnaea **6:** 510. 1831. *nom.*

superfl., based on type of *Verbesina lobata* Gaud. *Microchaeta lobata* Gaud.) Nutt. Trans. Amer. Philos. Soc. **7**(n.s.): 451. 1841. *Lipochaeta australis* Less. var. *lobata* (Gaud.) A. Gray, Proc. Amer. Acad. Arts **5:** 129. 1861.

Verbesina hastulata Hook. & Arn. Bot. Beechey's Voyage **87.** 1832. TYPE: Hawaii: Oahu: 1826–27, *G. T. Lay & A. Collie s.n.* (Holotype, K!). *Lipochaeta hastulata* (Hook. & Arn.) DC. Prodr. **5:** 611. 1836. *Microchaeta lobata* (Gaud.) Nutt. var. *hastulata* (Hook. & Arn.) Nutt. Trans. Amer. Philos. Soc. **7**(n.s.): 451. 1841. *Lipochaeta lobata* (Gaud.) DC. var. *hastulata* (Hook. & Arn.) Sherff, Bot. Gaz. (Crawfordsville) **95:** 91. 1933.

Lipochaeta calycosa A. Gray, Proc. Amer. Acad. Arts. **5:** 130. 1861. TYPE: Hawaii: Oahu: 1838–42, *U.S. Exploring Expedition s.n.* (Holotype, GH!; isotype, US!).

Lipochaeta australis Less. var. *denticulata* Wawra, Beiträge zur flora der Hawi'schen Inseln **56**(n.s. 31): 77. 1873. TYPE: Hawaii: Oahu: 1868–71, *H. Wawra 2294* (Holotype, W!). *Lipochaeta lobata* (Gaud.) DC. var. *denticulata* (Wawra) Sherff, Bot. Gaz. (Crawfordsville) **95:** 92. 1933.

Lipochaeta aprevalliana del Castillo, Florae Insularum Maris Pacifici **71.** *t. 34.* 1888. TYPE: Hawaii: Oahu: 1851–1855, *J. Remy 272* (Holotype, P, apparently lost. The illustration is taken to be the holotype.). *Lipochaeta lobata* (Gaud.) DC. var. *aprevalliana* (del Castillo) Sherff, Bot. Gaz. (Crawfordsville) **95:** 92. 1933.

Lipochaeta lobata (Gaud.) DC. var. *albescens* Sherff, Bot. Gaz. (Crawfordsville) **95:** 92. 1933. TYPE: Hawaii: Oahu: Diamond Head, 28 Mar 1895, *A. A. Heller 2021* (Holotype, F!; isotypes, A!, GH!, K!, MO!, NY!, UC!, US!).

Lipochaeta niihauensis St. John, Pacific Sci. **13:** 188. 1959. TYPE: Hawaii: Niihau: Kii, among rocks on basalt knoll, 100 ft, 2 Apr 1949, *H. St. John 23664* (Holotype, BISH!).

Lipochaeta trilobata St. John, Pacific Sci. **30:** 42. 1976. TYPE: Hawaii: Hawaii: Mountain slope above Kealakekua, 1779, *D. Nelson s.n.* (Holotype, BM; photo of holotype, OS!).

Leaf blades ovate, 4–5.6 (–9.7) cm long, (1.5–) 2.2–5.6 cm wide, occasionally with 2 or 5 basal lobes or with undulate margin. Outer phyllaries oblong, (4–) 4.7–5.8 (–6.5) mm long; 2.3–4.7 mm wide, broadly acute to rounded. Ray florets 7.5–10 mm long. Disc florets 20–25.

Common around Kaena Pt and from Koko Head to Makapuu Pt on Oahu and at Kii on Niihau (Figure 5), near sea level to 100 m. Flowering Dec-Jul. Extant.

Lipochaeta trilobata St. John is placed in synonymy here as it falls within the range of variation of *L. lobata* var. *lobata*. St. John's type, collected by David Nelson, extends considerably the distribution of this variety, although it is doubtful that the population from which this collection was taken is extant.

Representative specimens. HAWAII. **Oahu:** Kaena Pt, *Degener 4177b* (BISH, DS, F, G, GB, GH, K, MO, NY, UC, US, W); S side of Manakuli Valley, *Degener, et al. 20836* (F, K, NY, US, W); Diamond Head Crater, *Fosberg 13884* (BISH, DS, F, GH); near Makapuu Pt, _Gardner 278*_ (OS); Kaena Pt, _Gardner 279A* & B*, 280*, 281*, 346, 347_ (OS); 0.2 mi from Diamond Head Rd on rd into crater, *Gardner 341* (OS); Hwy 72, 0.8 mi N of Hawaii-Kai Golf Course, *Gardner 350* (OS); Hwy 72, 0.7 mi N of Hawaii-Kai Golf Course, *Gardner 351* (OS).

5b. **Lipochaeta lobata** (Gaud.) DC. var. **hastulatoides** Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 93. 1933. TYPE: Hawaii: Maui: Pohakea Gulch, southernmost part of western Maui, 11 Jul 1927, *O. Degener 4305* (Lectotype chosen, F!; isotypes, F!, G!, GH!, K!, NY[2]!).

Leaf bases scarcely connate-perfoliate, blades ovate to oval, 3–6 cm long, 2–2.6 cm wide. Outer phyllaries ovate, 4.6–5.5 mm long, 3.1–4 mm wide, broadly acute to rounded. Ray florets 8.7–10.5 mm long. Disc florets 35–40. Chromosome number, unknown.

Known only from the mountains of Western Maui (Figure 5) to 700 m. Flowering Dec-Mar. Probably extant.

Representative specimens. HAWAII. **Maui:** Mauka of McGregor, *Degener 22034* (BISH, G, GB, NY, UC, US, W); Hanaula Rd, 1972, *Hobdy s.n.* (US); Lahainaluna, Kuia Ridge, *Pearsall 26* (BISH).

5c. **Lipochaeta lobata** (Gaud.) DC. var. **leptophylla** Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville), **95:** 92. 1933. TYPE: Hawaii: Oahu: Kolekole Pass, Waianae Mountains, 1–2 Feb 1915, *C. N. Forbes 2024-O* (Holotype, F!; isotypes, BISH! F[2]!, K!, NY!, UC!).

> *Lipochaeta lobata* (Gaud.) DC. var. *grossedentata* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville), **95:** 92. 1933. TYPE: Hawaii: Oahu: N of middle ridge between Puu Pane and Puu Kanaohanui, 10 Jun 1932, *O. Degener, K. K. Park, & W. Bush 4299* (Lectotype chosen, F!; isotypes, F!, K!).

Leaf blades lanceolate to lanceolate-linear, 5.7–7 cm long, 1–1.5 (–2.4) cm wide. Outer phyllaries ovate to lanceolate, 5–8.2 mm long, 1–3 mm wide, long attenuate to acuminate-aristate. Ray florets 10–11 mm long. Disc florets (20) 30–60. Chromosome number, unknown.

Known from the Waianae Range of Western Oahu (Figure 5), to 600 m. Flowering Oct-Jun. Probably extant.

Representative specimens. HAWAII. **Oahu:** NE of Puu Hapapa summit, *Degener & Hatheway 20976* (BISH); NE slope of Puu Hapapa, *Degener, et al. 12287* (A, F, G, GH, MO, NY, US).

6. **Lipochaeta connata** (Gaud.) DC. Prodr. **5:** 611. 1836.

Suffruticose, stems upright, 1–2 m tall. Leaves with alate margined petioles 6–30 mm long or sessile with connate-perfoliate bases; blades ovate to broadly elliptic, 8–19 cm long, 4–9.5 cm wide, on both surfaces strigulose. Heads in compound cymes. Outer phyllaries lanceolate to ovate, 3.5–6.5 mm long, 1.3–2.8 mm wide, attenuate to acute, usually purple near apex, strigulose. Ray florets 8–16; ligules oblong, 5–13 mm long, 2.3–4.8 mm wide, tube 1–2.4 mm long. Disc florets 20–45; corollas 3–5 mm long, lobes 0.8–1.3 mm long; anthers 1.4–1.8 mm long. Achenes tuberculate, those of ray 2.1–3 mm long, 1.1–1.7 mm wide, with wings to 0.5 mm, those of disc 2.5–3.3 mm long, 1–1.7 mm wide, with wings to 0.5 mm. Pappus of fused scales forming a corona or variously reduced and with awns to 1.6 mm long. Paleae usually purple near apex.

Known from several localities in the mountains and valleys of central, western, and northern Kauai, and from a few collections on western Maui (Figure 6), 50–710 m. Over a broad range of habitats from dry, open slopes to the margins of forested areas. Flowering throughout the year. Extant.

Lipochaeta connata represents a continuum of variation with respect to leaf morphology. Variety *acris* has narrowly alate margined petioles, with long narrow phyllaries, narrow ligules, generally more disc florets and longer lobes of the disc corollas. Variety *connata* has sessile leaves with connate-perfoliate leaf bases and shows considerable variation with respect to the amount of leaf material produced at the nodes, with leaf bases ranging from 5–50 mm wide at point of attachment to the stem. From observations on plants grown in the greenhouse, it has been shown that there is a gradual increase in the amount of leaf material produced at a node as the plant matures.

Most of the collections in this complex show various stages in the development of a corona on the achenes. Particularly striking are plants of var. *acris* in the Polihale Ridge-Hikimoe Valley region and also in the Hanakapiai area along the Kalalau Trail. In these specimens a well developed corona (in excess of 1 mm long) can be seen. From this extreme a reduction series has been observed, finally resulting in a few uneven scales around apex of the achene in var. *connata*.

6a. **Lipochaeta connata** (Gaud.) DC. var. **connata**

Lipochaeta connata (Gaud.) DC. Prodr. **5:** 611. 1836. *Verbesina connata* Gaud. *In:* L.C.D. de Freycinet (ed.), Voyage Autour de Monde, Botanique **4:** 464. 1829. TYPE: "In insulis Sandwicensibus," *C. Gaudichaud s.n.* (Holotype, P!). *Microchaeta connata* (Gaud.) Nutt. Amer. Philos. Soc. **7**(n.s.): 452. 1841.

Lipochaeta alata Sherff, Bot. Gaz. (Crawfordsville) **95:** 81. 1933. TYPE: Hawaii: Kauai: along Hanapepe River, near the Falls, 12 Jul 1895, *A. A. Heller 2563* (Holotype, F!; isotype, UC!).

Lipochaeta alata Sherff var. *acrior* Sherff, Bot. Gaz. (Crawfordsville) **95:** 82. 1933. TYPE: Hawaii: Kauai: 1840, *U.S. Exploring Expedition, s.n.* (Holotype, US!; isotype, GH!).

Lipochaeta alta Sherff var. *pulcrior* Sherff, nom. nud.

Lipochaeta profusa Sherff, Bot. Gaz. (Crawfordsville) **95:** 95. 1933. TYPE: Hawaii: [No island] Jan 1885, *Sinclair s.n.* (Holotype, K!).

Lipochaeta profusa Sherff var. *robustior* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 96. 1933. TYPE: Hawaii: Kauai: 2 mi from Kekaha, in lowlands, 18 Jul 1932, *O. Swezey 4185* (Holotype, F!; isotype, K!).

Leaves sessile, with connate-perfoliate bases. Outer phyllaries ovate, with acute apices. Disc florets 20–30; corolla lobes 0.8–1 mm long.

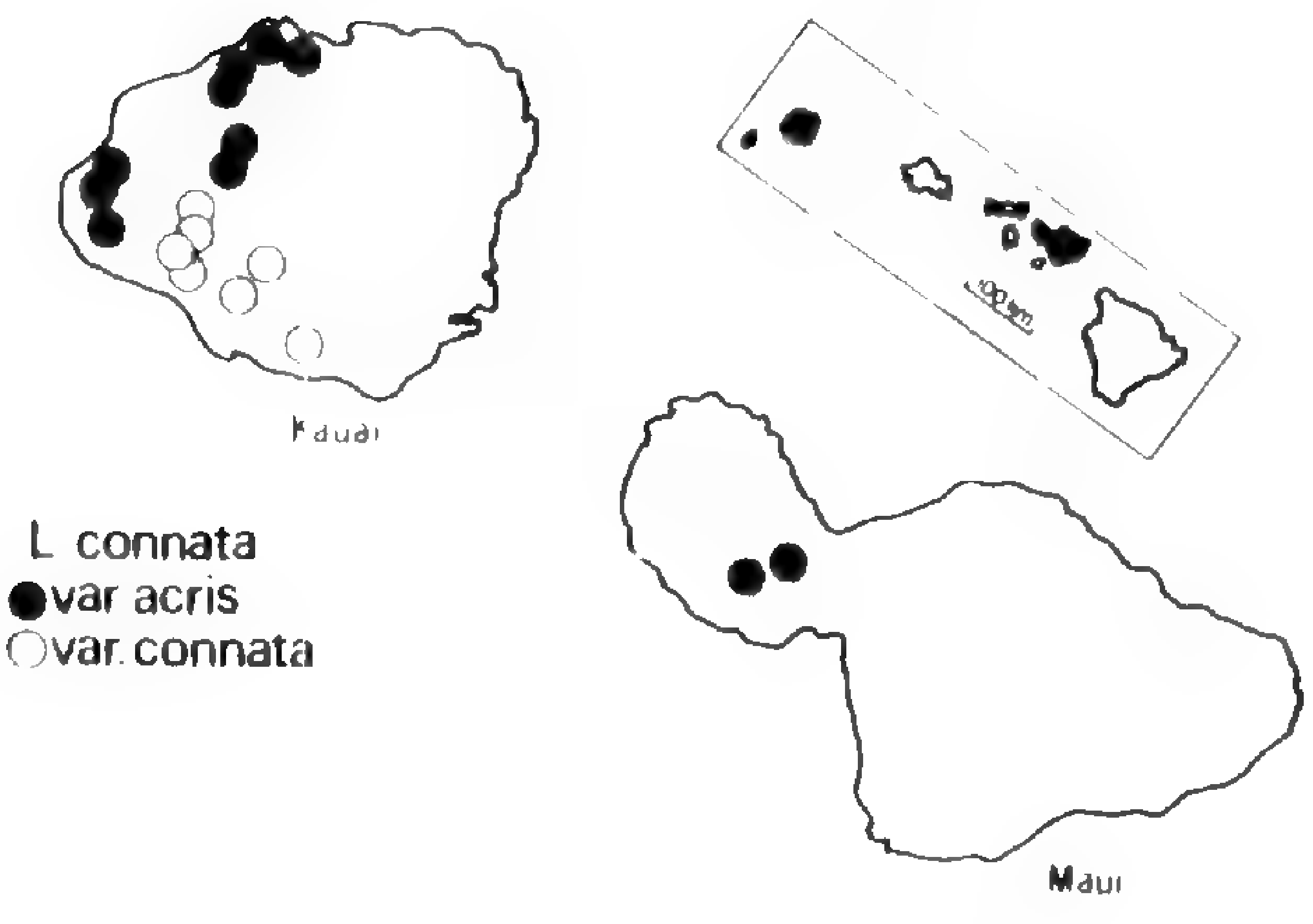
Common in the foothills of western Kauai (Figure 6), 70 to 400 m. Flowering Sep-Jul. Extant.

Representative specimens. HAWAII: **Kauai:** Waipao Valley, *Degener 20514* (BISH, GB, GH, NY); Waimea, *Faurie 1006, 1007* (A, G); Lawai Valley, *Gardner 294** (OS); N of Waimea, *Gardner 296** (OS); Hwy 55, N of Kekaha, *Gardner 359, 360A & B* (OS); Waimea Canyon Rim, 3 mi S of Jct Hwy 55, *Gardner 369* (OS); Kukui Trail, Waimea Canyon, *Gardner 370* (OS); Hanapepe River, near falls, *Heller 2563A* (F, G); by Waimea Canyon Rim Lookout, *Hobdy 39* (BISH); Olokele Canyon, *Skottsberg 1041* (BISH, GB).

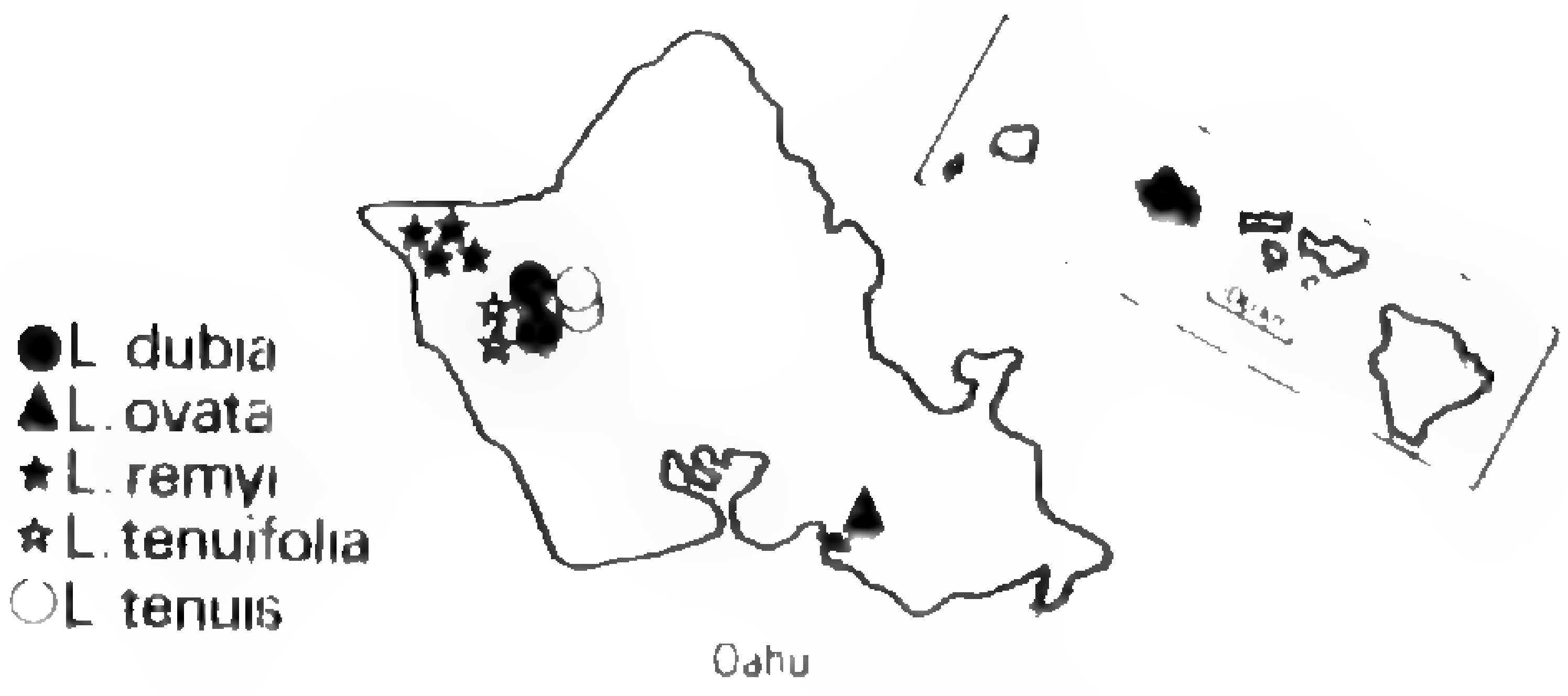
6b. **Lipochaeta connata** (Gaud.) DC. var. **acris** (Sherff) Gardner, comb. et stat. nov.

Lipochaeta acris Sherff, Bot. Gaz. (Crawfordsville) **95:** 83. 1933. TYPE: Hawaii: Kauai: Waimea, 2000–3000 ft, *Mann & Brigham 540* (Holotype, F!; isotypes, BISH!, G!, GH[2]!, MO!, NY!).

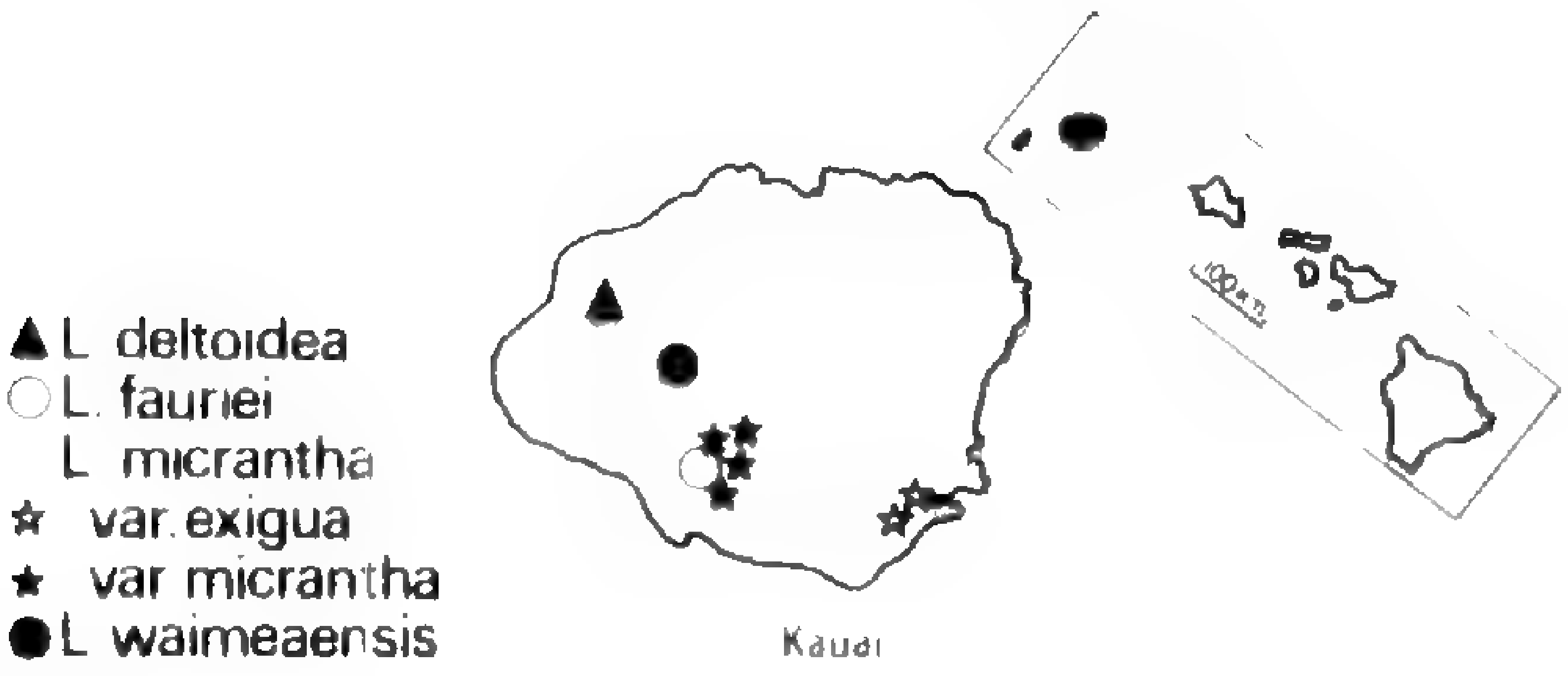
Lipochaeta lobata (Gaud.) DC. var. *incisor* St. John, Pacific Sci. **13:** 185. 1959. TYPE: Hawaii: Niihau: Kaaliwai, in thicket, 750 ft, 1–1.5 m tall, 29 Mar 1949, *H. St. John 23572* (Holotype, not located; isotype, BISH!).



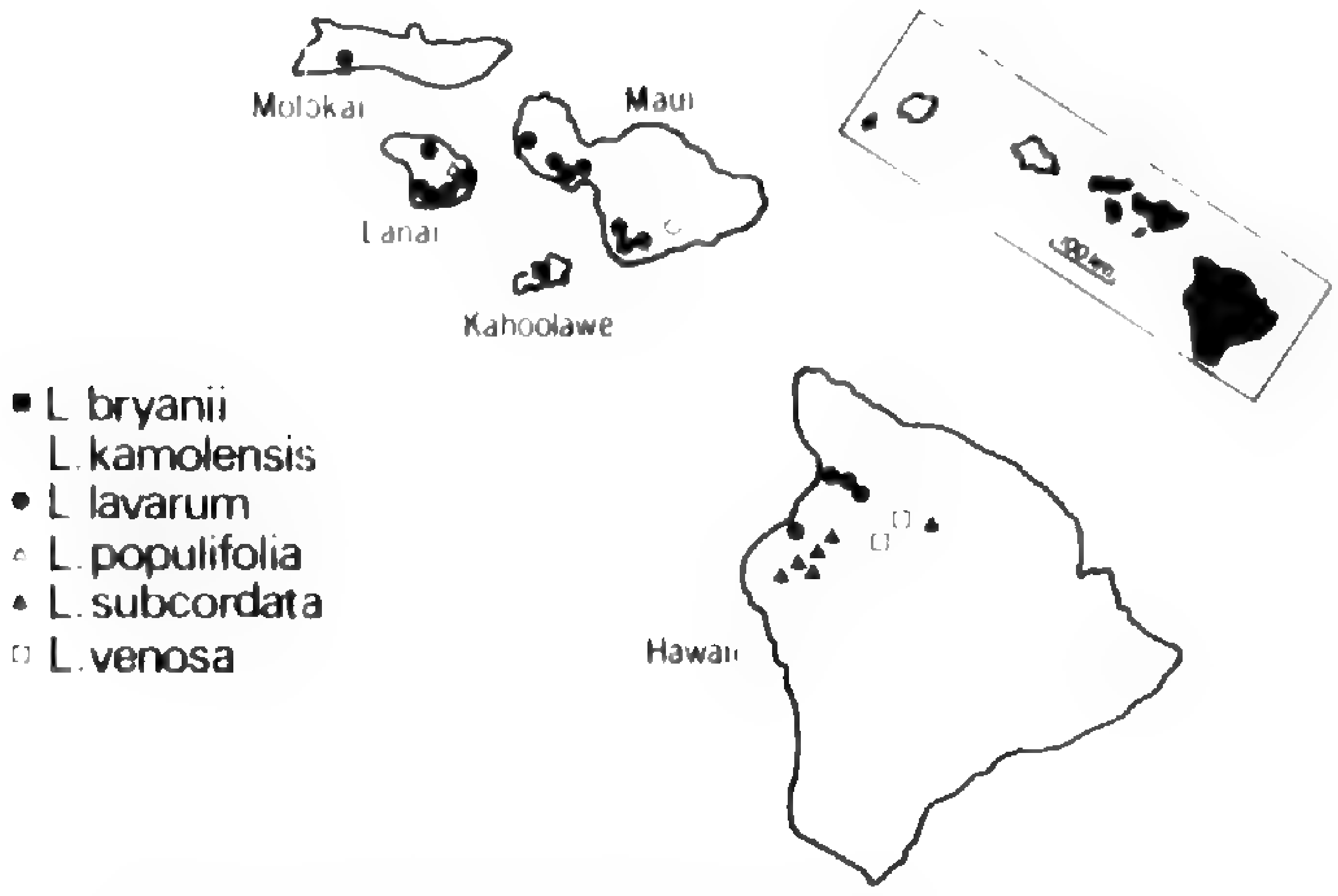
6



7



8



9

Figures 6-9. **Documented distributions of *Lipochaeta*.** 6. *L. connata* var. *acris* and var. *connata*. 7. *L. dubia, L. ovata, L. remyi, L. tenuifolia,* and *L. tenuis*. 8. *L. deltoidea, L. fauriei, L. micrantha* var. *exigua*, and var. *micrantha*, and *L. waimeaensis*. 9. *L. bryanii, L. kamolensis, L. lavarum, L. populiflolia, L. subcordata,* and *L. venosa*.

Leaves with alate margined petioles 6–30 mm long. Outer phyllaries lanceolate to ovate, with attenuate apices. Disc florets 25–45; corolla lobes 1–1.3 mm long.

Found along the northern and western valleys of Kauai, south central Kauai, Niihau, and western Maui (Figure 6), 20–400 m. Flowering throughout the year. Extant.

Representative specimens. HAWAII. **Kauai:** Kokee Stream between YMCA Camp & Waipoo Falls, *Degener 21489* (BISH, F, C, K, NY, UC, US, W); 100 ft E of Kalalau lookout (Kilohana), *Degener & Hatheway 20505* (BISH, NY); Haena-Kalalau Trail, *Gardner 286, 287*, 288* (OS); Waikapalae Wet Cave, *Gardner 291** (OS); Maniniholo Dry Cave, *Gardner 292** (OS); Polihale Ridge, *Gardner 364** (OS); Hikimoe Valley, *Gardner 365, 366** (OS); Waikapalae Wet Cave, *Gardner 371* (OS); Halemanu Stream near brink of Waimea Canyon, *Greenwell 21539* (F); Kaaweiki, *Hobdy 94* (US); Hanakapiai Valley *Hobdy 221* (US); **Maui:** Waliluku, Black Gorge, *Degener & Degener 23736* (BISH, NY, US, W); Olowalu Valley, *Forbes 2431-M* (NY); Olowalu Valley, ridge above Wailuku Poi, *Forbes 2451-M* (BISH, F); Black Gorge, *Gardner 376** (OS); W Maui, no date, *U.S. Exploring Expedition s.n.* (US); no locality, 1868–1871, *Wawra 2094* (W).

LIPOCHAETA SECTION APHANOPAPPUS (Endl.) Bentham and Hooker

Lipochaeta DC. section *Aphanopappus* (Endl.) Bentham and Hooker, Gen. Plantarum **2:** 372. 1873. *Aphanopappus* Endl. Gen. Plantarum Suppl. **2:** 43. 1842. *nom. nov.*, based on *Schizophyllum micranthum* Nutt.

Schizophyllum Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 452. 1841. *nom. illegit.* non Fries. 1831. TYPE SPECIES: *Schizophyllum micranthum* Nutt. = *Lipochaeta micrantha* (Nutt.) A. Gray.

Leaves petiolate (rarely alate margined). Majority of disc florets five-merous. Chromosome number, n = 15. Species numbers 7–23.

7. **Lipochaeta tenuifolia** A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. TYPE: Hawaii: Oahu: 1838–42, *U.S. Exploring Expedition s.n.* (Lectotype chosen, GH!; frag of holotype, BISH!).

Suffruticose, stems decumbent and rooting along lower surface, stem length unknown. Leaves sessile, ternately compound, leaflets 3–8.5 cm long, 1–3 cm wide, deeply dissected, ultimate divisions usually cut clear to midrib, sparsely strigulose. Heads solitary or 2. Outer phyllaries lanceolate, 5–7.5 mm long, 1–1.8 mm wide, attenuate, strigulose. Ray florets 8–10; ligules oblong, 8–11.5 mm long, 2.7–3.9 mm wide, tube 0.7–1 mm long. Disc florets 20–30;

corollas 2.7–3 mm long, lobes 0.7–0.9 mm long; anthers 1.3–1.5 mm long. Achenes tuberculate, those of ray 1.8–2.6 mm long, 1.2–1.5 mm wide, with wings to 0.3 mm, those of disc 1.8–2.4 mm long, 1.1–1.5 mm wide, with wings to 0.2 mm. Pappus of deciduous awns to 1 mm long. Paleae tan throughout.

Known from the central portion of the Waianae range, Oahu (Figure 7), 700–900 m. Flowering May. Extant.

Lipochaeta tenuifolia is most similar to *L. dubia* and *L. tenuis* from which the former can be distinguished by ternately compound, finely dissected leaves. *Lipochaeta tenuifolia* is the only member of the genus that has truly compound leaves. From studies of plants grown in the greenhouse, it has been shown, however, that if branches are cut back the leaves that develop first are not compound, but rather range from nearly entire to dissected.

Representative specimens. HAWAII. **Oahu:** Upper Makua Valley, *Degener, et al. 4174* (BISH, CAS, DS, F, G, GB, GH, K, MO, NY, UC, US, W); Makaha, *Gagne 640* (US); Makaha, Waianae, no date, *Hillebrand & Lydgate s.n.* (BISH): Kaala Mts, *Mann & Brigham 534* (BISH, F, G, GH, MO, NY, US).

8. **Lipochaeta dubia** Degener & Sherff *In:* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 580. 1939. TYPE: Hawaii: Oahu: NE slope of Puu Hapapa, among lantana and grasses, 7 May 1939, *O. Degener, E. Ordonez, & J. Foster 12331* (Holotype, F!; isotypes, A[2]!, F[2]!, GB! GH! MO!, NY! US!).

Lipochaeta minuscula Degener & Sherff *In:* Sherff, Bot. Leafl. No. **9:** 9. 1954. TYPE: Hawaii: Oahu: ridge N of Kolekole Pass, 15 Jun 1947, *M. Kerr 21660* (Lectotype chosen, BISH!).

Suffruticose, stems decumbent and probably rooting along lower surface, length unknown. Leaves with petioles 8–12 mm long, overall shape deltoid, but most leaves with 2 or 4 basal lobes and a long spatulate terminal segment; blades 2.4–4.4 cm long, 1–2.1 cm wide, entire to serrate, strigulose above, densely so below. Heads solitary or occasionally 2. Outer phyllaries lanceolate, 4.5–5.1 mm long, 1.2–2.1 mm wide, attenuate, strigulose. Ray florets 8–10; ligules oblong, 8.3–12 mm long, 3.5–4.3 mm wide, tube 1–1.2 mm long. Disc florets 30–45; corollas 3.2–3.4 mm long, lobes 0.8 mm long; anthers 1.5–1.7 mm long. Achenes tuberculate, those of ray 2.2–2.5 mm long, 1.7–1.9 mm wide, with wings to 0.3 mm, those of disc 2.3–2.6 mm long, 1.2–1.4 mm wide, with wings to 0.2 mm.

Pappus of deciduous awns to 1.4 mm long. Paleae often purple near apex. Chromosome number unknown.

Known from the central portion of the Waianae Range, Oahu (Figure 7). 700–900 m. Apparently on open slopes with lantana and grasses. Flowering Apr-Jun. Probably extant.

Lipochaeta dubia is most similar to *L. tenuis* with respect to floral features but can be distinguished by the basally lobed leaves of the former. *Lipochaeta minuscula* was collected in the same general vicinity as *L. dubia* and except for having leaves which are slightly smaller than most specimens of *L. dubia*, it is indistinguishable.

Representative specimens. HAWAII. **Oahu:** NE slope of Puu Hapapa, *Degener, et al. 12285* (A, F, G, MO, NY, UC, US), *12287* (F, G, NY, UC, US), *12290* (F, G, GH, NY, UC).

9. **Lipochaeta tenuis** Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfrodsville) **95:** 102. 1933. TYPE: Hawaii: Oahu: in the rain forest, Waianae Valley, up toward Puu Kaala, on lateral spur leading to summit ridge between Kaala and Kalena, 24 Apr 1932, *O. Degener, K. K. Park, & W. Bush 4258* (Lectotype chosen, F!; isotypes, F!, K!, MO!, NY!).

Lipochaeta tenuis Degener & Sherff var. *sellingii* Degerer & Sherff *In:* Flora Hawaiiensis, Fam. 344:Lip: Ten. 1940. TYPE: Hawaii: Oahu: NE slope of Puu Hapapa, in sunny stream-bed near contour trail, 3 Sep 1938, *O. Degener, O. H. Selling & E. Ordonez 12253* (Holotype, GB; isotypes, BISH!, F!, G!, MO!, NY!).

Suffruticose, stems decumbent, probably rooting along lower surface, stem length unknown. Leaves with petioles 8–17 mm long, ovate, 2.2–3.9 cm long, 1–1.9 cm wide, serrate, on both surfaces strigulose, most densely so below. Heads solitary or in 2's or 3's. Outer phyllaries lanceolate, 5–6.8 mm long, 1.1–2.2 mm wide, attenuate, strigulose. Ray florets 8–12; ligules oblong, 8.8–11.5 mm long, 3–4.5 mm wide, tube 1.1–1.4 mm long. Disc florets 40–60; corollas 3.2–3.5 mm long, lobe 0.7–1 mm long; anthers 1.3–1.4 mm long. Achenes tuberculate, those of ray 2.5–3 mm long, 1.5–2 mm wide, with wings to 0.3 mm, those of disc 2.5 mm long, 1.5 mm wide, with wings to 0.3 mm. Pappus of deciduous awns to 1.4 mm long. Paleae often purple at apex. Chromosome number unknown.

Known from the central portion of the Waianae range, Oahu (Figure 7), 700–900 m. Flowering Apr.-Sep. Probably extant.

Lipochaeta tenuis is most similar to *L. dubia*. The former is distinguished by unlobed leaves. The two varieties of *L. tenuis* of Degener and Sherff (1940) are identical except for minor differences in size of plant which are not here accorded formal recognition.

Representative specimens. HAWAII. **Oahu:** 0.75 mi S of Kolekole Pass, *Cranwell, et al. 3336* (GB); NE slope of Puu Hapapa, *Degener, et al. 12288* (A, BISH, F, G, GH, MO, NY, US), *12291* (BISH, F, GH, MO, NY, US), *12332* (BISH, F, G, K).

10. **Lipochaeta remyi** A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. TYPE: Hawaii: Oahu: 1851–1855, *J. Remy 260* (Holotype, GH!; frag of holotype, BISH!).

Annual herb, stems upright, 50–60 cm tall. Leaves with petioles (6–) 20–40 mm long, overall shape ovate, (1.3–) 3.4–7 cm long, (1–) 2.6–5 cm wide, dissected, ranging from cleft with scarcely noticable basal lobes to lobes which are cut clear to the midrib, on both surfaces strigulose. Heads solitary or in 2's or 3's. Outer phyllaries lanceolate, 3.5–5.3 (–7) mm long, 1.2–1.8 (–2.2) mm wide, attenuate, often purple near base, strigulose. Ray florets 5–8; ligules oval, 3–5 mm long, 1.7–3.5 (–4.2) mm wide, tube 0.6–1 mm long. Disc florets 20–30 (–35); corollas 2.5–2.9 mm long, lobes 0.3–0.5 mm long; anthers 1.2–1.4 mm long. Achenes tuberculate, those of ray 1.9–2.3 mm long, 1.1–1.6 mm wide, with wings to 0.3 mm, those of disc 1.9–2.4 mm long, 1–1.4 mm wide, with wings to 0.3 mm. Pappus of deciduous awns to 1.3 mm long. Paleae often purple near apex.

Known from numerous localities in the Waianae Range of northwestern Oahu (Figure 7), 30–200 m. Moist, often spring-fed hillsides, in the forest understory. Flowering Dec.-Jun. Extant.

Lipochaeta remyi is most closely related to *L. micrantha* of Kauai, from which the former can be distinguished by the annual, herbaceous growth habit and more numerous disc florets.

Representative specimens. HAWAII. **Oahu:** Kealia Trail, Kawaihapai, *Carlson 3828* (F); Kawaihapai, *Degener 18078* (GH, MO, NY, US); CCC Trail, Kawaihapai, *Degener, et al. 11032* (BISH, CAS, F, G, GH, MO, NY, US); Kawaihapai, *Forbes, et al. 1840-O* (BISH, F, NY, W); Kealia, Waianae Mts, *Fosberg & Fosberg 12859* (BISH, DS, F, GB, GH, UC); Kealia, *Gagne 647* (US); Kealia Trail, S of Dillingham Airstrip, *Gardner 349** (OS); Kealia, Waianae Mts, *Hosaka 1328* (BISH); Kaala Mts, *Mann & Brigham 533* (BISH, GH, MO, NY, US); Kaena Pt, *Pearsall 84* (BISH).

11. **Lipochaeta ovata** R. C. Gardner, sp. nov. Figure 10.
TYPUS: Hawaii: Oahu: Honolulu, 1852, *N. J. Anderson s.n.* (Holotype, GB!, photo of holotype, OS!).

Plantae suffruticosae; caules apparenter erecti, altitudines ignotae. Folia petiolis usque ad 21 mm longis, ovata usque elliptica, 7.5 cm longa, 3.3 cm lata, vix serrata, strigulosa apprime subtus et secus venas. Capitula cymis disposita. Phyllaria externa ovata, 2.3 mm longa, 2.8 mm lata, obtusa, strigulosa. Flosculi radii 7 vel 8; ligulae oblongae, 7 mm longae, 2.8 latae; tubi 1.2 mm longi. Flosculi disci circa 30; corollae 4.3 mm longae, lobis 0.8 mm longis; antherae 2.1 mm longae. Achenia laevia; achenia radii 2.2 mm longa, 1.7 mm lata, sine alis; achenia disci 2.4 mm longa, 1.6 mm lata, sine alis. Pappus ex aristis deciduis usque ad 0.4 mm longis compositis. Paleae penitus brunneolae. Chromosomatum numerus ignotus.

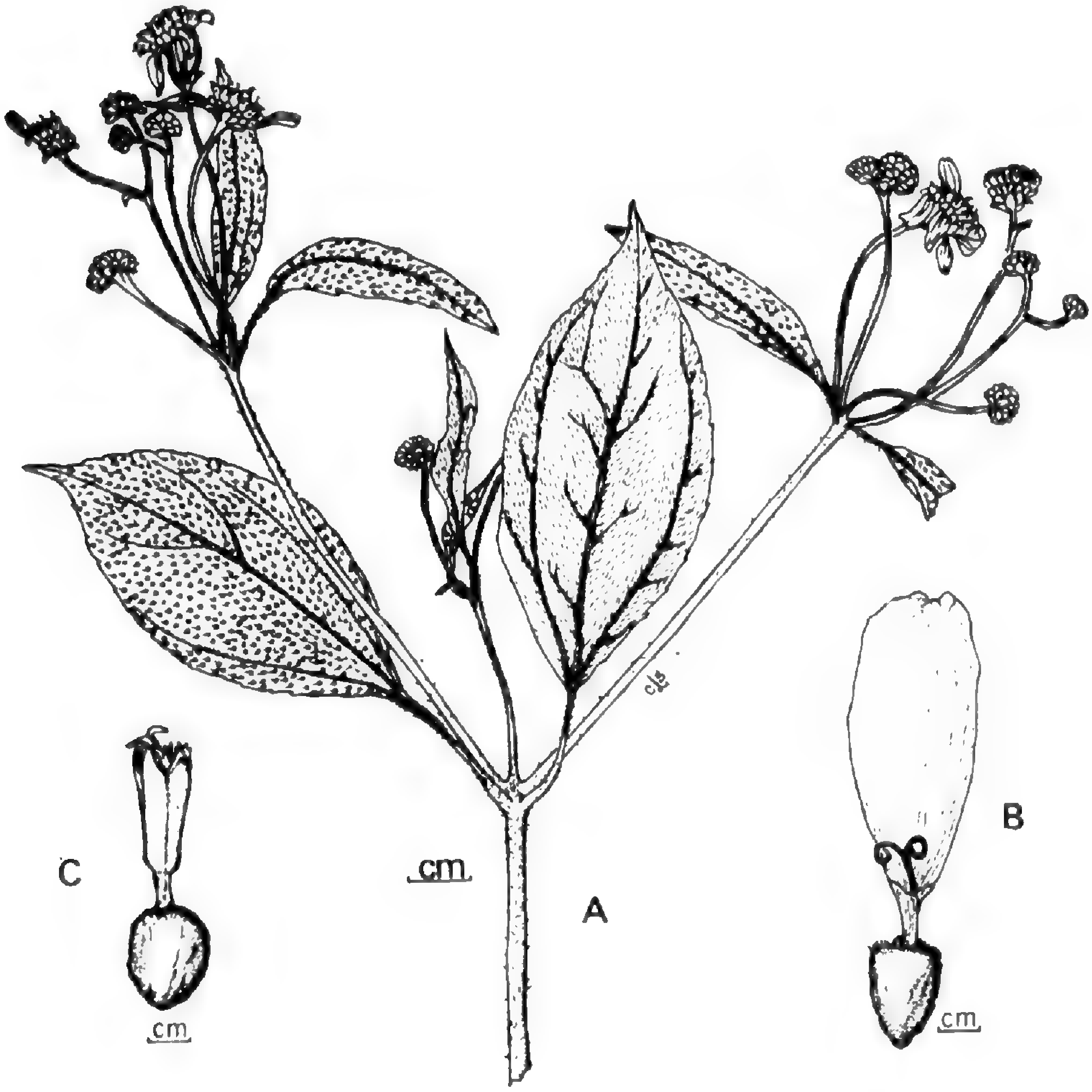


Figure 10. **Holotype of *Lipochaeta ovata*.** A, habit; B, ray floret and achene; C, disc floret and achene.

Known only from the type specimen, collected at Honolulu, Oahu (Figure 7). Habitat and flowering period unknown. Probably extinct.

Lipochaeta ovata is one of the least specialized members of this section. It is distinguished by its large leaves, compound cymose inflorescences, upright habit, and smooth achenes.

12. **Lipochaeta waimeaensis** St. John, Pacific Sci. **26:** 293. 1972. TYPE: Hawaii: Kauai: Waimea Canyon, upper slope of W side, 1200 ft, 17 Apr 1967, *R. W. Hobdy 101* (Holotype, BISH!).

Suffruticose, stems decumbent and rooting along lower surface, to 2 m long. Leaves with petioles 5–8 mm long, linear to narrowly elliptic, 4.7–5 cm long, 0.5–0.8 cm wide scarcely serrate, strigulose along major veins above, evenly strigulose below. Heads solitary or in 2's or 3's. Outer phyllaries lanceolate, 3–4 mm long, 1.5–2 mm wide, attenuate, often with the lower quarter purple, strigulose. Ray florets 4 or 5; ligules nearly oval, 3.2–3.5 mm long, 2.8–2.9 mm wide, tube 0.6–0.8 mm long. Disc florets 20–25; corollas 2.3–2.8 mm long, lobes 0.8–0.9 mm long; anthers 1.2–1.4 mm long. Achenes tuberculate, those of ray 2.2–2.5 mm long, 1.7–2.3 mm wide, with wings to 0.2 mm, those of disc 2.2–2.4 mm long, 1.2–1.6 mm wide, with wings to 0.1 mm. Pappus of scales fused at the base and with deciduous awns to 1 mm long. Paleae often purple near apex.

Known only from the type locality on the upper slope, west side of Waimea Canyon, Kauai (Figure 8), 350–400 m. Flowering Feb.-Apr. Extant.

Lipochaeta waimeaensis is most similar to *L. deltoidea* from which the former can be distinguished by fewer and smaller ray and disc florets and linear or narrowly elliptic leaves.

Representative specimens. HAWAII. **Kauai:** Waimea Canyon Rim, 3 mi S of Jct with Hwy 55, *Gardner 368** (OS); Waimea Heights Rd, *Hobdy 170* (US).

13. **Lipochaeta deltoidea** St. John, Pacific Sci. **26:** 291. 1972. TYPE: Hawaii: Kauai: lower Hikimoe Valley, 1800 ft, 18 Apr 1969, *R. W. Hobdy 102* (Lectotype chosen, BISH!; isotype BISH!).

Suffruticose, stems upright, to 40 cm tall. Leaves with petioles to 11 mm long, narrowly deltoid, 8.4 cm long, 4 cm wide, biserrate, on both surfaces strigulose. Heads in 2's or 3's. Outer phyllaries lanceolate, 4.8 mm long, 1.5 mm wide, attenuate, strigulose. Ray florets about 7; ligules oblong, 5.9 mm long, 3.4 mm wide, tube 1 mm long. Disc florets about 35; corollas 3.3 mm long, lobes 1.3 mm long; anthers 1.5 mm long. Achenes tuberculate, those of ray 2.5 mm long, 2 mm wide, with wings to 0.4 mm, those of disc 2.5 mm long, 1.5 mm wide, with wings to 0.2 mm. Pappus of numerous deciduous awns to 1.3 mm long. Paleae often purple near apex. Chromosome number unknown.

Known only from type locality, ca. 600 m, Hikimoe Valley, Kauai (Figure 8). Flowering Apr. Extant.

Lipochaeta deltoidea is an unspecialized member of the genus, and as mentioned previously, has characters in common with most of the taxa of group B (Figure 2). Because of this similarity, a form similar to *L. deltoidea* is considered to be ancestral to the Lipochaetas of this group.

14. **Lipochaeta fauriei** Léveillé, Repert. Spec. Nov. Regni Veg. **10:** 122. TYPE: Hawaii: Kauai: Holokele [Olokele?], Mar 1910, *A. U. Faurie 1012* (Holotype, not located; isotype, P!).

Suffruticose, stems apparently upright, height unknown. Leaves with alate margined petioles to 6 mm long; blades lanceolate, 7 cm long, 3 cm wide, serrate, sparsely strigulose. Heads in 2's or 3's. Outer phyllaries ovate, 4.5 mm long, 2.3 mm wide, acute, purple near base, strigulose. Ray florets about 6; ligules oblong, 4.2 mm long, 2.3 mm wide, tube 1.3 mm long. Disc florets about 30; corollas 3.9 mm long, lobes 0.8 mm long; anthers 1.8 mm long. Achenes unknown. Pappus unknown. Paleae tan throughout. Chromosome number unknown.

Known only from type collections gathered at Holokele, this taken to mean Olokele Canyon (Figure 8), south central Kauai. Habitat unknown. Flowering Mar. Probably extinct.

Lipochaeta fauriei is most similar to *L. deltoidea* from which the former can be distinguished by ovate phyllaries, smaller ray ligules and larger disc corollas.

15. **Lipochaeta micrantha** (Nutt.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861.

Suffruticose, stems decumbent and rooting along lower surface, to 2 m long. Leaves with petioles 8–22 mm long, overall shape deltoid, 2.1–9.7 cm long, 1.2–7.8 cm wide, entire to variously dissected, sparsely strigulose. Heads in 2's or 3's. Outer phyllaries ovate to lanceolate, 3.2–5.5 mm long, 1–3 mm wide, attenuate, often purple near base and along midrib, sparsely strigulose. Ray florets 4 or 5; ligules oval to oblong, 2.3–5.8 mm long, 1.4–3.5 mm wide, tube 0.7–1.4 mm long. Disc florets 5–9; corollas 2.7–3.1 mm long, lobes 0.4–0.7 mm long; anthers 1.2–1.5 mm long. Achenes tuberculate, those of ray 2.1–2.9 mm long, 1.5–1.8 mm wide, occasionally with wings to 0.2 mm, those of disc 2.2–2.6 mm long, 1–1.3 mm wide, without wings. Pappus of scales forming an uneven corona and with deciduous awns to 1.4 mm long. Paleae often purple near apex.

Two varieties are recognized here within *Lipochaeta micrantha.*

15a. **Lipochaeta micrantha** (Nutt.) A. Gray var. **micrantha**

Lipochaeta micrantha (Nutt.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. *Schizophyllum micranthum* Nutt. Trans. Amer. Philos. Soc. **7** (n.s.): 452. 1841. TYPE: Hawaii: Atooi [Kauai]: In shady woods near Kolao [Koloa], *T. Nuttall s.n.* (Holotype, BM!). *Aphanopappus nuttallii* Walpers, Repertorium Botanices Systematicae **2:** 620. 1843. *nom. superfl.*, based on type of *Schizophyllum micranthus* Nutt. *Aphanopappus micranthus* (Nutt.) Heller, Minnesota Bot. Stud. **1:** 915. 1897.

Leaves 2.1–9.7 cm long, 1.2–7.8 cm wide, dissected, ranging from incised or cleft to pinnate-pinnatifid. Ray ligules oval to ovate, 2.7–5.8 mm long, 1.7–3.5 mm wide, tube 0.9–1.4 mm long. Ray achenes 2.3–2.9 mm long, 1.6–1.8 mm wide, with wings to 0.5 mm. Disc achenes 2.5–2.6 mm long, 1.3 mm wide, without wings. Chromosome number, unknown.

Variety *micrantha* is known from several localities in Olokele and Hanapepe Valleys (Figure 8), south central Kauai, apparently in forest understory, and along canyon sides. Flowering June-Oct. Extant (John Fay, pers. comm.).

Representative specimens. HAWAII. **Kauai:** Olokele Canyon, *Degener & Wiebke 2143* (F, G, GB, GH, MO, NY, UC, US, W); Olokele Canyon, *Degener & Wiebke 2144* (F, GH, NY); Hanapepe Valley, *Forbes 304-K* (BISH, F); Hanapepe River, near falls, *Heller 2439* (F, GH, K, MO, NY, UC, US); Olokele Gulch, *Hitchcock 15239, 15244* (US); Hanapepe, *Mann & Brigham 536* (BISH, F, G, GH, MO, NY); no locality, Oct 1916, *Rock s.n.* (BISH); Olokele Canyon, *Skottsberg 1035* (BISH, GB); Koloa, no date, *U.S. Exploring Expedition s.n.* (NY); Olokele Canyon, Jul 1927, *Winne s.n.* (BISH).

15b. **Lipochaeta micrantha** (Nutt.) A. Gray var. **exigua** (Degener & Sherff) Gardner, comb. et stat. nov.

Lipochaeta exigua Degener & Sherff *In:* Sherff, Amer. J. Bot. **28:** 30. 1941. TYPE: Hawaii: Kauai: Grassy shrubby summit ridge, 0.71 mi SW of Hokunui, Nawiliwili, 8 Jan 1940, *O. Degener & E. Ordonez 12610* (Lectotype chosen, F!, isotypes, B!, E[2]!, G!, GH!, MO[2]! NY[3], UC[3]!, US[2]!).

Leaves to 3.1 cm long, 2.2 cm wide, many with 2 or 4 basal lobes, these occasionally cut clear to midrib, terminal segment elliptic. Ray ligules oblong, 2.3 mm long, 1.4 mm wide, tube 0.7 mm long. Ray achenes 2.1 mm long, 1.5 mm wide, without wings. Disc achenes 2.2 mm long, 1 mm wide, with wings to 0.2 mm.

Variety *exigua* is known from a few localities in the Haupu range of southeastern Kauai (Figure 8), 300–400 m, in grass and shrub areas. Flowering Jan.-July. Extant (John Fay, pers. comm.).

16. **Lipochaeta subcordata** A. Gray, Proc. Amer. Acad. Arts **5:** 130. 1861. TYPE: Hawaii: Hawaii: 1840, *U.S. Exploring Expedition s.n.* (Holotype, US, not located).

Lipochaeta flexuosa del Castillo, Florae insularum Maris Pacifici, **72.** *t. 35.* 1886. TYPE: Hawaii: Hawaii: 1851–1855, *J. Remy 265* (Holotype, P!).

Lipochaeta intermedia Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 102. 1933. TYPE: Hawaii: Hawaii: Huehue, Kona District, among lava, May 1932, *Meebold 4254* (Holotype, F!; frag of holotype, G!).

Suffruticose, stems upright to 3 m tall. Leaves with petioles 12–25 mm long, deltoid, (3.2–) 5–10 cm long, (2.4–) 3–4.8 cm wide, occasionally with 2 basal lobes, terminal segment cleft to biserrate, sparsely strigulose above, densely so below. Heads in compound cymes. Outer phyllaries ovate, 3.2–6 mm long, 1.5–2.3 mm wide, narrowly acuminate, often purple along midrib, strigulose. Ray florets 5–7; ligules oblong, (3–) 4–6.3 mm long, 2–3.8 mm wide, tube 0.7–1 mm long. Disc florets 11–20; corollas 2.5–3.4 mm long, lobes 0.5–0.9 mm long; anthers 1.1–1.5 mm long. Achenes tuberculate, often spotted with purple, and with a fringe of scales on upper outer rim, those of ray 1.9–2.5 mm long, 1.5–2 mm wide, with wings to 0.3 mm, those of disc 2.1–2.8 mm long, 1.1–1.7 mm wide, with wings to 0.2 mm. Pappus of scales forming an uneven corona and with deciduous awns to 1.5 mm long. Paleae often purple near apex.

Known from several localities on Hawaii, but mainly in the North Kona District (Figure 9), 600–1500 m. Flowering throughout the year. Extant.

Lipochaeta subcordata is most similar to *L. venosa* from which the former can be distinguished by the much larger, usually unlobed leaves, greater number of flower heads, and fewer disc florets. The taxa included in synonymy are minor variants, *L. flexuosa* having slightly more divided leaves and *L. intermedia* having slightly smaller leaves than typical. *Lipochaeta intermedia* is intermediate between *L. subcordata* and *L. lavarum* in vegetative features and is possibly of hybrid origin, however, pollen stainability (in lacto-phenol-analine blue) is 90 per cent and several full achenes are on the specimens.

Representative specimens. HAWAII. **Hawaii:** between Puuwaawaa & Huehue, *Degener 4214* (F, G, GB, GH, K, MO, NY, US, UC, W); Huehue, *Degener 21816* (BISH, CAS, G, GB, MO, NY, UC, US); 1801 lava flow, *Degener & Degener 27562* (BISH, F, G, K, MO, NY, UC, W); northern edge of 1859 lava flow, *Degener, et al. 19810* (BISH, F, G, GH, K, MO, NY, UC, US); Kohala Rd, near 1859 lava flow, *Fosberg 10169A* (BISH, DS, GH); N Kona District, Hwy 19, *Gardner 410** (OS); Kau, 1868, *Hillebrand s.n.* (GH, K); lava flows of Puuwaawaa, 9 Dec 1955, *Rock s.n.* (BISH); Puuokeanui Crater, *Rock 10049* (BISH, F, K, NY, UC, US).

17. **Lipochaeta venosa** Sherff, Bot. Gaz. (Crawfordsville) **95:** 100. 1933. TYPE: Hawaii: Hawaii: Waimea, at Nohonaohae Crater, Jun 1910, *J. F. Rock 8349* (Holotype, F!, isotypes. BISH[2]!, GH!, UC!).

Suffruticose, stems apparently arcuate-spreading, length unknown. Leaves with petioles 8–10 mm long, overall shape deltoid, 2.1–2.8 cm long, 1.5–1.9 cm wide, dissected, usually with 2 basal lobes, terminal segment incised or cleft, sparsely strigulose above, more densely so below. Heads solitary or 2. Outer phyllaries ovate, 5–5.5 mm long, 2.5–3.5 mm wide, obtuse, strigulose. Ray florets about 5; ligules oval, 3–4.8 mm long, 2–2.8 mm wide, tube 0.7–0.9 mm long. Disc florets 20–30; corollas 3–3.3 mm long, lobes 0.5–0.8 mm long; anthers 1.4–1.5 mm long. Achenes tuberculate, often spotted with purple, those of ray 2–2.4 mm long, 1.5–1.8 mm wide, with wings to 0.2 mm, those of disc 2–2.4 mm long, 1.4–1.5 mm wide, without wings. Pappus of deciduous awns to 0.7 mm long. Paleae often purple near apex. Chromosome number, unknown.

Known from two localities in the South Kohala District of northwestern Hawaii (Figure 9), 1000 m. Flowering May-June. Probably extant.

Lipochaeta venosa is most similar to *L. subcordata* from which the former can be distinguished by the much smaller, lobed leaves, fewer flower heads, and more disc florets.

Representative specimens. HAWAII. **Hawaii:** S. Kohala, Waimea, Puu Holoholoku, *Hosaka 2114* (BISH, K).

18. **Lipochaeta populifolia** (Sherff) Gardner, stat. nov.

Lipochaeta subcordata A. Gray var. *populifolia* Sherff, Bot. Gaz. (Crawfordsville) **95:** 91. 1933. TYPE: Hawaii: Lanai: Maunalei Valley, 18 Jun 1918, *G. C. Munro 670* (Holotype, F!; isotype, US!).

Suffruticose, stems upright, height unknown. Leaves with petioles to 28 mm long, deltoid, 7.5 cm long, 6 cm wide, biserrate, on both surfaces strigulose. Heads in 2's or 3's. Outer phyllaries ovate, to 5.5 mm long, 1.8 mm wide, obtuse, sparsely strigulose. Ray florets 7 or 8; ligules oblong, 9.3 mm long, 4 mm wide, tube 1.3 mm long. Disc florets about 45; corollas 3.3 mm long, lobes 1 mm long; anthers 1.5 mm long. Achenes tuberculate and with a fringe of scales on upper outer rim, those of ray 2.8 mm long, 2.5 mm wide, with wings to 0.3 mm, those of disc 2.8 mm long, 2.2 mm wide, without wings. Pappus of deciduous awns to 1.9 mm long. Paleae tan throughout. Chromosome number, unknown.

Known only from type specimens collected in Maunalei Valley, east central Lanai (Figure 9), ca. 100 m. Habitat unknown. Flowering June. Probably extinct.

Lipochaeta populifolia is a fairly unspecialized member of this section. Sherff (1935) described it as a variety of *L. subcordata,* without giving any explanation of why it belonged there. I cannot see a connection between the two unless it might be that both have rather large leaves. The two taxa are quite distinct in most other characters.

19. **Lipochaeta kamolensis** Degener & Sherff *In:* Sherff, Amer. J. Bot. **38:** 54. 1951. TYPE: Hawaii: Maui. Very rare, among lantana and grass on side of Kamole Gulch, southernmost central eastern Maui, 21 Dec 1948, *O. Degener, H. F. Clay & R. Bertram 19288* (Lectotype chosen, GH!; isotypes, BISH!, G[2]!, MO[2]!, NY!, UC!, US[2]!).

Suffruticose, stems decumbent and rooting along lower surface, to 3 m long. Leaves with petioles 13–17 mm long, overall shape deltoid, 4.3–6.5 cm long, 1.2–4.4 cm wide, basal lobes widely flaring, the lobes pinnatifid, remainder of leaf pinnatifid to pinnate-pinnatifid, on both surfaces strigulose, especially along veins. Heads solitary or 2. Outer phyllaries lanceolate, 6–6.8 mm long, 1.7–2.5

mm wide, attenuate, strigulose. Ray florets 6; ligules oblong, 8.5–9 mm long, 3.7–4 mm wide, tube 1.2–1.4 mm long. Disc florets about 15; corollas 3.3–3.4 mm long, lobes 0.5–0.7 mm long; anthers 1.4 mm long. Achenes tuberculate, those of ray 2.2 mm long, 1.9 mm wide, without wings, those of disc 2.1 mm long, 1.4 mm wide, without wings. Pappus of fused scales and with deciduous awns to 0.9 mm long. Paleae tan throughout.

Known only from Kamole Gulch, Maui (Figure 9), 240 m. Flowering Dec.-Feb. Extant.

The closest extant relative to *L. kamolensis* is probably *L. subcordata,* however, the former has diverged considerably from this taxon in the deeply dissected, pinnatifid to pinnate-pinnatifid leaves.

Representative specimens. HAWAII. **Maui:** Hwy 31, 11.8 mi SE of Ulupalakua Ranch Office, *Gardner 385** (OS).

20. **Lipochaeta bryanii** Sherff, Bot. Gaz. (Crawfordsville) **95:** 97. 1933. TYPE: Hawaii: Kahoolawe: on slope, amid pili grass, 300 m, 16 Feb 1931, *Bryan 736* (Holotype, BISH, not located; isotype, BISH!).

Suffruticose, stems upright, 30–50 cm tall. Leaves with petioles to 10 mm long, generally oblong, but often with 2 basal lobes, to 3.5 cm long, 1.4 cm wide, scarcely serrate, on both surfaces strigulose. Heads in compound cymose clusters. Outer phyllaries ovate, to 4 mm long, 2.5 mm wide, obtuse, sparsely strigulose. Ray florets 4 or 5; ligules oblong, 8.8 mm long, 3.3 mm wide, tube 0.8 mm long. Disc florets about 25; corollas 3.1 mm long, lobe to 0.5 mm long; anthers 1.5 mm long. Achenes tuberculate, those of ray 2.2 mm long, 2.2 mm wide, without wings, those of disc 2.3 mm long, 1.7 mm wide, without wings. Pappus of scales forming an uneven corona and with awns to 1 mm long. Paleae tan throughout. Chromosome number unknown.

Known only from the type specimens collected on Kahoolawe (Figure 9), 300 m. Habitat unknown except "amid pili grass." Flowering Feb. Probably extinct.

Lipochaeta bryanii is most similar to *L. subcordata* from which the former can be distinguished by much smaller leaves, broader phyllaries, more numerous disc florets, and tan phyllaries.

21. **Lipochaeta lavarum** (Gaud.) DC. Prodr. **5:** 611. 1836.

Verbesina lavarum Gaud. *In:* L.C.D. de Freycinet (ed.), Voyage Autour de Monde, Botanique **4:** 464. 1829. Type: "In insulis Sandwicensibus," *C. Gaudichaud s.n.* (Holotype, P!; isotypes, G[2]!). *Microchaeta lavarum* Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841.

Lipochaeta lavarum (Gaud.) DC. var. *hillebrandiana* Sherff, Bot. Gaz. (Crawfordsville) **95:** 89. 1933. Type: Hawaii: Maui: Lahaina, on rocks near sea, *Hillebrand s.n.* (Holotype, B, photo of holotype, F!).

Lipochaeta lavarum (Gaud.) DC. var. *longifolia* Sherff, Bot. Gaz. (Crawfordsville) **95:** 90. 1933. Type: Hawaii: Lanai: Maunalei Valley, 9 Mar 1915, *G. C. Munroe 202* (Holotype, BISH!; isotype, BISH!).

Lipochaeta lavarum (Gaud.) DC. var. *ovata* Sherff, Bot. Gaz. (Crawfordsville) **95:** 88. 1933. Type: Hawaii: Maui: Kahikinui, below crater, Nov 1910, *J. F. Rock 8674* (Holotype, GH!; isotypes, BISH[2]!, CAS!, F!, K!, NY!, UC!).

Lipochaeta lavarum (Gaud.) DC. var. *salicifolia* Sherff, Bot. Gaz. (Crawfordsville) **95:** 88. 1933. Type: Hawaii: Maui: near Lahaina, *E. Bishop s.n.* (Holotype, B, photo of holotype, F!).

Lipochaeta lavarum (Gaud.) DC. var. *skottsbergii* Sherff, Bot. Gaz. (Crawfordsville) **95:** 89. 1933. Type: Hawaii: Maui: 1833–36, *Bennett 43* (Holotype, B, photo of holotype, F!).

Lipochaeta lavarum (Gaud.) DC. var. *conferta* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 582. 1939. Type: Hawaii: Lanai: *H. Mann & W. T. Brigham 358* (Holotype, F!; isotypes, BISH[2]!, GH!, MO!, NY!, US!).

Lipochaeta lavarum (Gaud.) DC. var. *lanaiensis* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 582. 1939. Type: Hawaii: Lanai: Maunalei Gulch, Sep 1917, *C. N. Forbes 507-L* (Lectotype chosen, F!; isotypes, BISH!, F[2]!).

Lipochaeta lavarum (Gaud.) DC. var. *maneleana* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 583. 1939. Type: Hawaii: Lanai: on slopes above Manele, Jun 1913, *C. N. Forbes 288-L* (Lectotype chosen, F!; isotypes, BISH!, F!, NY[2]!, US!, W!).

Lipochaeta lavarum (Gaud.) DC. var. *stearnsii* Degener & Sherff *In:* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 581. 1939: Type: Hawaii: Lanai: Kapoho Canyon, 800 ft, June 1936, *H. Sterns 11050* (Holotype, F!; isotypes, F!, G!, GH!, MO!).

Suffruticose, stems upright, to 2 m tall. Leaves with narrowly alate margined petioles, 5–15 mm long; blades ranging from linear lanceolate to elliptic to subovate, (2.3–) 3–6.5 (–8) cm long, (0.6–) 0.8–1.5 cm wide, entire to serrate, strigulose above, densely so below. Heads solitary or in 2's or 3's. Outer phyllaries ovate to oblong, (3–) 3.8–6.5 mm long, 2–2.6 mm wide, acute to rounded at apex, strigulose. Ray florets 8–10; ligules oblong, (9–) 10–15 mm long, 4–6.2 mm wide, tube 1–2 mm long. Disc florets 40–60; corollas 3.2–4.1 mm long, lobes 0.8–1 mm long; anthers 1.6–2 mm long.

Achenes nearly smooth, often with a fringe of scales along upper outer rim, those of ray 2.2–2.8 (–3.2) mm long, 3 mm wide, with wings to 0.5 mm, those of disc 2.2–3 mm long, 1.6–2.3 mm wide, with wings to 0.2 mm. Pappus of scales forming an uneven corona and with awns to 1.5 mm long. Paleae tan throughout.

Known from numerous localities along the western and southern side of eastern Maui, around most of the southern half of Lanai and northwestern Hawaii (Figure 9), 20–520 m. Usually in dry, exposed areas often along margins of old "aa" or "pahoehoe" lava flows. Flowering throughout year. Extant.

Lipochaeta lavarum is a specialized member of this section. It is distinguished by the upright habit, relatively long and narrow leaves, long ligules and numerous disc florets. Sherff (1935, 1939) and Degener and Sherff (1939) recognized ten varieties based almost entirely on differences in leaf size. A comparison of the specimens reveals that considerable variation can be seen at the population level. Sherff (1935) in attempting to justifiy *Lipochaeta lavarum* var. *ovata* states (p. 57) "Indeed the cited cotype sheet has, besides two sprays of the ovate-leaved form, one spray with numerous smaller and narrower leaves hardly atypic for *L. lavarum.*" If one considers only the extremes, differences can be recognized, but all are tied together through a continuum of overlapping variation, which makes any attempt to recognize distinct varieties impracticable.

Representative specimens. HAWAII. **Hawaii:** between Kawaihae & Waimea, *Christensen & Christensen 27912* (F); mauka of Kawaihae, *Degener 4188* (BISH, CAS, DS, F, G, GH, MO, NY, UC, W); near Kona Village Resort, *Gardner 338** (OS); S of Waimea, *Gardner 339** (OS); no locality, *Remy 277* (GH). **Lanai:** S Lanai, *Degener 21986* (BISH, CAS, G, GB, K, MO, NY, UC, US, W); mauka of Hulopoe Bay, *Degener & Degener 28391* (BISH, F, G, GH, MO, NY, UC, W); lower Naio Gulch, *Degener, et al. 24161* (BISH, DS, G, K, MO, NY, US, W); Awehi Rd, *Gardner 317* (OS); Naupaka Rd, *Gardner 322* (OS); Puu Makani Rd, *Gardner 323** (OS); Kaunolu Rd, *Gardner 325*, 326* (OS); Malawea Rd, *Gardner 394* (OS); Anapuka Rd, *Gardner 395* (OS); Maunalei Rd, *Gardner 396** (OS); **Maui:** near McGregor, *Degener 4027* (DS, F, G, GB, GH, MO, NY, UC, US, W); Kanaio, *Degener 21975* (BISH, CAS, G, GB, K, MO, NY, UC, US); Papawai Pt, *Degener, et al. 25134* (BISH, F, G, K, MO, NY, UC, US, W); Lahaina *Forbes 2270-M* (A, BISH, F); E of Olowalu Store, *Gardner 331** (OS); E of Ulupalakua, *Gardner 335** (OS); Hwy 30, 0.6 mi E of road tunnel, *Gardner 372* (OS); Hwy 31, 4.8 mi SE of Ulupalakua Ranch Office, *Gardner 379** (OS); Mts of W Maui above Maalaea Bay, *Mann & Brigham 374* (F, NY); Ulupalakua. 27 Feb 1962, *Uehara s.n.* (BISH, US). **Molokai:** no locality, *Rock 10286* (BISH, F, GH).

22. **Lipochaeta perdita** Sherff, Bot. Gaz. (Crawfordsville) **95:** 99. 1933. TYPE: Hawaii: no island: no locality, 1788–1789, *D. Nelson s.n.* (Holotype, BM!).

Lipochaeta kawaihoaensis St. John, Pacific Sci. **13:** 181. 1959. TYPE: Hawaii: Niihau: Kawaihoa Pt., 300 ft, in dry tuff, head of steep gully, 31 Mar 1949, *H. St. John 23611* (Holotype, not located; isotype, BISH!).

Suffruticose, stems upright, to 1 m tall. Leaves with petioles 4–18 mm long, ovate to deltoid-ovate, 1.2–4 cm long, 0.7–2.8 cm wide, serrate, on both surfaces hispidulose. Heads solitary or in 3's. Outer phyllaries broadly or narrowly elliptic or lanceolate, 4–8 mm long, 3 mm wide, subacute, appressed hispidulose. Ray florets 6–9; ligules elliptic, 7–9 mm long, 4 mm wide, tube 1 mm long. Disc florets 80; corollas 4 mm long, lobes 0.8 mm long; anthers 1.8 mm long. Achenes tuberculate, often with brown spots, and with a fringe of scales on upper outer rim, those of ray 2.7–3.1 mm long, 1.9–2.7 mm wide, wings to 0.5 mm, those of disc 2.5 mm long, 1.7–2 mm wide, wings to 0.5 mm. Pappus of deciduous awns to 2.3 mm long. Paleae tan throughout. Chromosome number, unknown.

The only precise locality for this taxon is the collection of *St. John 23611,* near Kawaihoa Pt, Niihau, 100 m, in dry tuff (Figure 3). Flowering Mar. Probably extant.

These two names are put into synonymy with some reservation. David Nelson, who collected the type of *Lipochaeta perdita,* supposedly only went ashore on the island of Hawaii (St. John, 1976a). If that is the case, there is a wide disjunction in the distribution of *L. perdita,* however, St. John (1976) also states that Kauai was on the itinerary of Nelson's voyage. If Nelson did collect on Kauai, even if only briefly, the chances of finding this taxon there would not be so surprising. Another reason for questioning the reliability of this taxonomic decision is that the Nelson collection is in very poor condition. The ray florets and disc achenes are completely lacking, yet on the basis of the characters that can be measured, the two specimens are strikingly similar. St. John's conclusion that *L. kawaihoaensis* is most closely related to *L. lobata* is not acceptable. The latter taxon is known to be a tetraploid whereas the collection from Kawaihoa Pt, although unknown cytologically, is 5-merous and presumably a diploid.

23. **Lipochaeta integrifolia** (Nutt.) A. Gray, Proc. Amer. Acad. Arts **5:** 130. 1861.

> *Microchaeta integrifolia* Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841. TYPE: Hawaii: Atooi [Kauai]: *T. Nuttall s.n.* (Holotype, BM!).
>
> *Lipochaeta integrifolia* (Nutt.) A. Gray var. *argentea* Sherff, Bot. Gaz. (Crawfordsville) **95:** 84. 1933. TYPE: Hawaii: Maui: on sandy isthmus, *H. Mann & W. T. Brigham 371* (Holotype, F!; isotypes, BISH!, F!, G!, GH[2]!, MO!, NY!).
>
> *Lipochaeta integrifolia* (Nutt.) A. Gray var. *gracilis* Sherff, Bot. Gaz. (Crawfordsville) **95:** 85. 1933. TYPE: Hawaii: [No island] Sep-Oct 1836, *C. Gaudichaud 217* (Holotype, GH!; isotype, P!).
>
> *Lipochaeta integrifolia* (Nutt.) A. Gray var. *major* Sherff, Bot. Gaz. (Crawfordsville) **95:** 85. 1933. TYPE: Hawaii: Oahu: old lava flow back of Diamond Head, 8 Apr 1895, *A. A. Heller 2092* (Holotype, GH!; isotypes A!, BISH!, F!, G!, K[2]!, MO!, NY!, UC!, US!).
>
> *Lipochaeta integrifolia* (Nutt.) A. Gray var. *megacephala* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 86. 1933. TYPE: Hawaii: Oahu: Kaena Pt, in sand, 5 m, 14 Dec 1930, *E. Christophersen 1400* (Holotype, F!; isotype, BISH!).

Suffruticose, stems prostrate and rooting along lower surface, to 2 m long. Leaves with alate margined petioles 2–10 mm long; blades ranging from oblong to spatulate, (0.4–) 0.8–3 cm long, (0.2–) 0.4–1.2 cm wide, entire to scarcely serrate, on both surfaces densely strigulose. Heads solitary or in 2's or 3's. Outer phyllaries ovate to oblong, 3–3.6 mm long, 1.6–2.3 mm wide, rounded at apex, strigulose. Ray florets 8–10; ligules oval to oblong, 3.3–5.1 mm long, 2.5–4.3 mm wide, tube 0.7–1.2 mm long. Disc florets 30–50; corollas (2.4–) 2.7–3.6 mm long, lobes 0.6–0.9 mm long; anthers (1.2–) 1.4–1.6 mm long. Achenes nearly smooth, those of ray 2–2.5 mm long, 1.9–2.7 mm wide, without wings, those of disc 2.4–3 mm long, 1.7–2.7 mm wide, without wings. Pappus of deciduous awns to 1.2 mm long. Paleae tan throughout.

Known from several localities on all of the major islands (Figure 3), generally found near sea level to 20 or 30 m, but on Molokai it occurs along the pali near Hoolehua at 170 m. In exposed, windswept areas, usually prostrate over rocks and other vegetation and forming dense mats. Flowering throughout the year. Extant.

Lipochaeta integrifolia is a specialized member of this section. It is distinguished by thick succulent leaves and a mat forming habit. Sherff (1935) and Degener and Sherff (1935) recognized five varieties based on leaf and capitulum size. When one examines multiple collections made from a single population (e.g. *Gardner 298A-C*), a continuum of variation is seen in both leaf and head size. It is true that Oahu specimens tend to be a bit larger than those from Maui or Lanai, but because of intergradation, these size differences cannot be recognized formally.

Representative specimens. HAWAII. **Hawaii:** first aa lava flow NE of South Pt, *Degener 31583* (BISH); Punaluu, *Degener & Degener 30836* (A, BISH, G, K, NY, UC, W), *Gardner 336* (OS); South Pt, *Gardner 337 A & B* (OS), *Greenwell 19561* (BISH, F, NY); 1 2 mi S of South Pt light house, *Greenwell 20684* (BISH, G, US); Punaluu, *St. John, et al. 11317* (US); Kaalualu Bay, *Whistler W7* (BISH). **Kaohikaipu:** Waimanolo Bay, *Fosberg 14051* (BISH, F). **Kapapa:** Kanehoe Bay, *Fosberg & Egler 14028* (BISH, GH). **Kauai:** Kipu Kai, *Alexander & Kellogg 5332* (BISH, K, NY, UC, US), makai of Puu Keke, *Degener, et al. 27167* (BISH, F, G, NY, US, W); near Puu Keke, *Gardner 293** (OS); Kipu Kai, *Gardner 297A* & B** (OS); Ka Lae Amana Pt, Moloaa Bay, *Gardner 355* (OS). **Kure:** central plain, *Caum 14* (NY, US); no locality, *Lamoureux 1911* (A); E end, *Long 2243* (BISH, US). **Lanai:** Poaiwa, *Degener & Degener 28374* (A, BISH, DS, F, G, MO, NY), *Gardner 388* (OS); Limestone Pt, 31 Mar 1914, *Munro s.n.* (BISH), *Munro 143* (BISH),Munro 257 (BISH), *Munro 414* (BISH). **Laysan:** no locality, Apr 1903, *Bryan s.n.* (BISH, F). **Maui:** between Waihee Golf Course and Maunlani Cemetery, *Carlquist 2124* (BISH); Puu Ohai, SW of Honokahua Valley, *Cranwell, et al. 2735* (BISH, GB); Wailuku, *Degener 4203* (F, K, US); Honokohua, *Degener 12417* (A, F, MO, NY); between Wailuku & Waiehu, *Degener 19572* (BISH, F, G, NY); Kahakuloa, *Degener 21969* (BISH, CAS, G, GB, NY, UC, US); NE of Kaanapali, *Gardner 332** (OS); Hwy 34, 15.4 mi NW of jct Hwys 33 and 34, *Gardner 333** (OS); Hwy 30, 14 mi NE of Lahaina, *Gardner 373* (OS); between Kahului and Wailua, *Melville & Melville 1098* (K); **Mokulua:** N peak, *Long 1674* (US), *1676* (BISH, US), *Long 1745* (US). **Molokai:** Hoolehua Dump, W of Hoolehua, *Carlquist 2236* (BISH); near Moomomi, *Degener 4216* (F, GH); near Waiakanapo, *Degener 4216B* (F, G, GH, NY, UC); beach near Ka Lae Ka Ilio Ilio, *Forbes 615-Mo* (F); Moomomi sand dunes, *Fosberg & Fosberg 13439* (BISH, US); Hoolehua Dump, *Gardner 298A-C** (OS), *Gardner 401** (OS); Moomomi Beach, *Gardner 302* (OS); N of Laau Pt, *Gardner 309** (OS); Ilio Pt, *Gardner 311* (OS). **Oahu:** Makapuu Pt, 8 Apr 1923, *Degener s.n.* (F, GH, MO, NY); Makapuu Peninsula, Pyramid Rock, *Fosberg 10575* (BISH, F, GH); divide at head of Kalama Valley, *Fosberg 13615* (BISH, F, GH, US); Hanauma Bay, *Gardner 275A*, 275 POP** (OS); near Koko Head Shooting Range, *Gardner 276** (OS); Kaena Pt, N shore road, *Gardner 282*, 283*, 348** (OS); Blowhole, *Gardner 277A & B* (OS); Blowhole, Koko Crater, *St. John 10402* (BISH, K); Hanauma Bay Beach Park, *Van Royen 10195* (A, BISH, K, US). **Popoia:** no locality, *Forbes 2194-O* (F near Kailua, *Fosberg 10556* (BISH, F).

DOUBTFUL AND EXCLUDED NAMES

Lipochaeta amazonica Poeppig & Endlicher, Nov. Gen. et Sp. **3:** 49. *t. 256.* 1845. TYPE: "Crescit in insulis arenosis fluminis Amazonum inter Ega et Rio Negro," no date, collector unknown (Holotype, ?). The type has not been located, but the illustration is taken to be of the holotype = *Zexmenia.*

Lipochaeta asymetrica Léveillé, Feddes Repert. Spec. Nov. Veg. **10:** 122. 1911. TYPE: Hawaii: Oahu: Kaliki, Oct 1909, *A. U. Faurie 960* (Holotype, location not known) = *Bidens asymmetrica (Lé*veillé) Sherff, Bot. Gaz. (Crawfordsville) **81:** 49. 1926. *fide* Sherff (1926).

Lipochaeta costaricensis Benth. Genera Plantarum **2:** 373. 1873. *nom. nud.*

Lipochaeta fasciculata DC. Prodr. **5:** 610. 1836. TYPE: Mexico: 1832. *J. L. Berlandier 2134* (Holotype, G-DC; photo of Holotype, F!) = *Zexmenia fasciculata* (DC.) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald **306.** 1856. *fide* Jones (1905).

Lipochaeta goyazensis Gardner, London J. Bot. **7:** 406. 1848. TYPE: Brazil: near Villa de Arrayas, Mar-May 1840, *G. Gardner 3847* (Holotype, K; isotype, G; photo of isotype, F!) = *Zexmenia goyazensis* (Gardner) Benth. & Hook. Genera Plantarum **2:** 373. 1873. *fide* Jones (1905).

Lipochaeta hastata Kellogg, Proc. Calif. Acad. Sci. **2:** 106. 1836. TYPE: Cerros Island, *J. A. Veatch s.n.* (Holotype, UC) = *Verbesina hastata* Kellogg ex. Curran, Bull. Calif. Acad. Sci. **1:** 140. 1885. *fide* Sherff (1935).

Lipochaeta lantanifolia Schauer, Linnaea **19:** 729. 1847. TYPE: Mexico: "circa Zimapan," *Aschenborn 210* (Holotype, B?) = *Zexmenia lantanifolia* (Schauer) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald 306. 1856. *fide* Jones (1905).

Lipochaeta laricifolia (Hook. f.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. = *Macraea laricifolia* Hook. f. Proc. Linn. Soc. London **1:** 278. 1845. TYPE: Ecuador: Galapagos Islands, Charles Island, *C. Darwin s.n.* (Lectotype, CGE; syntype, [*Macrae s.n.*] G!, K!).

Lipochaeta lifuana Hochreutiner, Bull. New York Bot. Gard. **6:** 297. 1910. TYPE: Loyalty Islands, Lifu, *E. Vieillard 799* (Holotype, NY!; isotype, G!, NY[2]!, P!) = *Wedelia uniflora* (Forst.) Moore, J. Linn. Soc. Bot. **45:** 347. 1921. *fide* Moore (1921).

Lipochaeta longipes Benth. Genera Plantarum **2:** 373. 1873. *nom. nud.*

Lipochaeta DC. section *Macraea* Sherff, Bot. Gaz. (Crawfordsville) **95:** 77. 1935. TYPE SPECIES: *Lipochaeta laricifolia* (Hook. f.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861.

Lipochaeta macrocephala Hook. & Arn. Bot. Beechey's Voy. 436. 1841. TYPE: Mexico: Guerrero: Acapulco, *Hinds 1841* (Holotype, K) = *Zexmenia macrocephala* (Hook. & Arn.) Hemsley, Biologia Centrali-Americana, Bot. **2:** 137. 1881. *fide* Jones (1905).

Lipochaeta monocephala DC. Prodr. **5:** 610. 1836. TYPE: "Caribaeis: in horto Paris, culta" (Holotype, G-DC; photo of holotype, F!) = *Zexmenia monocephala* (DC.) Heynhold, Nomenclature ed. **1:** 863. 1840. *fide* Jones (1905).

Lipochaeta scaberrima Benth., J. Bot. (Hooker), **2:** 43. 1840. TYPE: British Guiana: Mount Roraima, 1839, *Schomburgk s.n.* (Holotype, K!; isotype, W; photo of isotype, F!) = *Oyedaea scaberrima* (Benth.) Blake, Contr. U.S. Natl. Herb. **20:** 414. 1921. *fide* Blake (1921).

Lipochaeta serrata (La Llave & Lexarza) DC. Prodr. **5:** 611. 1836. = *Zexmenia serrata* La Llave & Lexarza, Nov. Veg. Description. fasc. **1:** 13. 1824. TYPE: Mexico: San Jose del Corral, *La Llave s.n.* (Holotype: G-DC). *fide* Jones (1905).

Lipochaeta strigosa DC. Prodr. **5:** 610. 1836. TYPE: Mexico: "Oaxacana australi circa Tehuantepec," *Andrieux 313* (Holotype, G-DC; photo of holotype, F!) = *Zexmenia strigosa* (DC.) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald 306. 1856. *fide* Jones (1905).

Lipochaeta tagetiflora G. Don, *In:* Sweets Hort. Brit. ed. 3. 360. 1856. TYPE: cultivated from Mexico in 1828 (Holotype, ? not located at BM [R. Ross, in litt.] = *Zexmenia tagetiflora* D. Don, *In:* Sweets Hort. Brit. ed. 2. 309. 1830.

Lipochaeta texana Torrey & Gray, Flora North Amer. **2:** 357. 1842. TYPE: Texas: *Riddell s.n.* (Holotype, NY!) = *Zexmenia hispida* A. Gray, Synoptical Flora North Amer. **1:** 286. 1884. *fide* Jones (1905).

Lipochaeta umbellata DC. Prodr. **5:** 610. 1836. TYPE: Mexico: Cuernavaca, *J. L. Berlandier 1065* (Holotype, G-DC; photo of holotype, F!) = *Zexmenia ceanothifolia* (Wild.) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald 306. 1856.

Lipochaeta umbellata DC. var. *conferta* DC. Prodr. **5:** 610. 1836. TYPE: Mexico: Morelos: Cuernavaca, *J. L. Berlandier 1053* (Holotype, G-DC; photo of holotype, F!) = *Zexmenia ceanothifolia* (Wild.) Sch.-Bip. var. *conferta* (DC.) A. Gray ex Jones, Proc. Amer. Acad. Arts **41:** 155. 1905. *fide* Jones (1905).

ACKNOWLEDGMENTS

This research could not have been completed without the assistance of numerous people. I acknowledge especially the willingness to help, the encouragement, and direction offered by Dr. Tod F. Stuessy, my major professor. He served as principal investigator under the terms of the grant funded by the National Science Foundation. I also thank Dr. Sherwin Carlquist of the Rancho Santa Ana Botanical Garden for advice concerning the logistics of the field work and for reviewing the grant proposal.

Several people assisted me during the field work by acting as guides or by allowing access to their private land. Especially helpful were: Dr. John J. Fay, formerly of the Pacific Tropical Botanical Garden, Kauai; Mr. Noah Pekelo, of the Hawaii Department of Natural Resources; Mr. Akah Hodges, of Molokai Ranch, Molokai; the Hawaiian Homelands Commission, Molokai; and Mr. Robert Cushnie, of the Lanai Company, Lanai. Drs. Derryl Herbst, Lyon Arboretum, and John J. Fay provided me with living and pressed material for some of the taxa I did not locate while in the field.

I wish to thank the curators of the herbaria from which specimens were borrowed (A, B, BISH, CAS, DS, F, G, GB, GH, K, MO, NY. PH, UC, US, W). Without the support and field assistance of my wife, Pat, and without the ideas and suggestions of my fellow graduate students this research would have been much more difficult.

Appreciation is expressed to Drs. Jere N. Brunken, and Tod F. Stuessy for their comments on and criticisms of the manuscript, and to Carol Stuessy for preparing Figure 10.

Financial support for chemical supplies from Sigma Xi Grants-in-Aid of Research and for the field work from National Science Foundation grant GB-41175 is gratefully acknowledged.

LITERATURE CITED

ALSTON, R. E., & B. L. TURNER. 1962. New techniques in analysis of complex natural hybridization. Proc. Natl. Acad. U.S.A. **48:** 130 137.

BACON, J. D. 1975. The genus *Nerisyrenia* (Cruciferae): A chemosystematic and cytotaxonomic study. Ph.D. Dissertation: Univ. Texas, Austin.

BECKER, K. M 1972. Proposal to conserve the generic name 9216. *Zexmenia* A. Gray (1852) non La Llave and Lexarza (1824) Asteraceae. Taxon **21:** 712 715.

BROWN, R. 1817. Some observations on the natural family of plants called Compositae. Trans. Linn. Soc. London **12:** 76 142.

BENTHAM, G., & J. D. HOOKER. 1873. Genera Plantarum **2:** 370 374.

DE CANDOLLE, A. P. 1836. Prodromus Systematis Naturalis Regni Vegetabilis **5:** 610 611.

CRAWFORD, D. J. 1974. A morphological and chemical study of *Populus acuminata* Rydberg. Brittonia **26:** 74 89.

CRONQUIST, A. 1971. *In.* I. L. Wiggins and D. M. Porter, Flora of the Galápagos Islands. Stanford University Press.

DEGENER, O., & H. F. CLAY. 1949. Family 344. Flora Hawaiiensis. Patten Co., Honolulu.

———, & E. E. SHERFF. 1940. Family 344. Flora Hawaiiensis. Patten Co., Honolulu.

ENDLICHER, S. L. 1842. Genera Plantarum, Suppl. **2:** 43.

FOSBERG, F. R., & D. HERBST. 1975. Rare and endangered species of Hawaiian vascular plants. Allertonia **1:** 1 72.

GARDNER, R. C. 1974. Systematics of *Cirsium* (Compositae) in Wyoming. Madroño **22:** 239 265.

———. 1976. Patterns of adaptive radiation in *Lipochaeta* DC. (Compositae) of the Hawaiian Islands. Syst. Bot. **1:** 383 391.

———. 1977a. Chromosome numbers and their systematic implications in *Lipochaeta* (Compositae:Heliantheae). Amer. J. Bot. **64:** 810 813.

———. 1977b. Observations on tetramerous disc corollas in the Compositae. Rhodora **79:** 139 146.

GAUDICHAUD, M. C. 1826 1830. Botanique. *In.* L. C. D. de Freycinet (ed), Voyage Autour du Monde, **4.** Paris.

GIANNASI, D. E. 1975. The flavonoid systematics of the genus *Dahlia* (Compositae). Mem. New York Bot. Gard. **26**(2): 1 125.

GRAY, A. 1852. Plantae Wrightianae **I:** 113.

———. 1861. Characters of some Compositae in the United States South Pacific Exploring Expedition under Captain Wilkes, with observations by Asa Gray. Proc. Amer. Acad. Arts **5:** 114 146.

HARLING, G. 1962. On some Compositae endemic to the Galapagos Islands. Acta Horti Berg. **20:** 63 120.

HILLEBRAND, W. 1888. Flora of the Hawaiian Islands. Facsimile edition of 1888 ed. Hafner Publ. Co. New York and London. 1965.

JONES, W. W. 1905. A revision of the genus *Zexmenia.* Proc. Amer. Acad. Arts **41:** 143 167.

LESSING, C. F. 1831. Synanthereae Rich. *In*, A. de Chamisso & D. de Schlechtendal (eds.), De plantis in expeditione Romanzoffiana. Linnaea **6:** 83 170, 209 258 (addenda), 501 526 (continuatio).

LEVIN, D. A. 1967. Hybridization between annual species of *Phlox;* population structure. Amer. J. Bot. **54:** 1122 1130.

MABRY, T. J., K. R. MARKHAM, & M. B. THOMAS. 1970. The systematic identification of flavonoids. Springer-Verlag, New York.

MCVAUGH, R. 1975. Reports on proposals for conservation. Taxon **24:** 245.

NUTTALL, T. 1841. Descriptions of new species and genera of plants in the natural order of the Compositae, collected in a tour across the continent to the Pacific, a residence in Oregon, and a visit to the Sandwich Islands and Upper California, during the years 1834 and 1835. Trans. Amer. Philos. Soc. **7**(n.s.): 283 454.

SHERFF, E. E. 1933. New and otherwise noteworthy Compositae IX. Bot. Gaz. (Crawfordsville) **95:** 80 103.

———. 1935. Revision of *Tetramolopium, Lipochaeta, Dubautia,* and *Railliardia.* Bernice P. Bishop Mus. Bull. No. **135:** 1 136.

———. 1939. Some new and otherwise noteworthy Labiatae and Compositae. Field Mus. Nat. Hist., Bot. Ser. **17:** 577 612.

———. 1941. New or otherwise noteworthy plants from the Hawaiian Islands. Amer. J. Bot. **28:** 18 31.

———. 1951. Miscellaneous notes on new or otherwise noteworthy dicotyledonous plants. Amer. J. Bot. **38:** 54 73.

———. 1954. I. Further notes upon the flora of the Hawaiian Islands. Bot. Leafl. No. **9:** 2 10.

———. 1960. Some dicotyledonous plants recently collected in the Hawaiian Islands. Brittonia **12:** 170 175.

SOLBRIG, O. T., D. W. KYHOS, M. POWELL, & P. H. RAVEN. 1972. Chromosome numbers in Compositae VIII: Heliantheae. Amer. J. Bot. **59:** 869 878.

ST. JOHN, H. 1959. Botanical novelties on the Island of Niihau, Hawaiian Islands, Hawaiian plant studies 25. Pacific Sci. **13:** 156–190.

———. 1972. Plantae Hobdyanae Kauaienses. Hawaiian plant studies 31. Pacific Sci. **26:** 275 295.

———. 1976a. Biography of David Nelson, and an account of his botanizing in Hawaii. Pacific Sci. **30:** 1 5.

———. 1976b. New species of Hawaiian plants collected by David Nelson in 1779: Hawaiian Plant Studies 52. Pacific Sci. **30:** 7 44.

STUESSY, T. F. 1977. A revised subtribal classification of the Heliantheae. *In:* J. B. Harborne, V. H. Heywood, and B. L. Turner (eds.), The Biology and Chemistry of the Compositae. Academic Press, New York.

TURNER, B. L., & R. E. ALSTON. 1959. Segregation and recombination of chemical constituents in a hybrid swarm of *Baptisia laevicaulis* × *B. viridis* and their taxonomic implications. Amer. J. Bot. **46:** 678 686.

DEPARTMENT OF BIOLOGY
BAYLOR UNIVERSITY
WACO, TEXAS 76703

LIST OF TAXA OF LIPOCHAETA

1. *L. succulenta* (Hook. & Arn.) DC.
2. *L. degeneri* Sherff
3. *L. rockii* Sherff
4. *L. heterophylla* A. Gray
5. *L. lobata* (Gaud.) DC.
    5a. *L. lobata* var. *lobata*
    5b. *L. lobata* var. *hastulatoides* Degener & Sherff
    5c. *L. lobata* var. *leptophylla* Degener & Sherff
6. *L. connata* (Gaud.) DC.
    6a. *L. connata* var. *connata*
    6b. *L. connata* var. *acris*
7. *L. tenuifolia* A. Gray
8. *L. dubia* Degener & Sherff
9. *L. tenuis* Degener & Sherff
10. *L. remyi* A. Gray
11. *L. ovata* Gardner
12. *L. waimeaensis* St. John
13. *L. deltoidea* St. John
14. *L. fauriei* Leveille
15. *L. micrantha* (Nutt.) A. Gray
    15a. *L. micrantha* var. *micrantha*
    15b. *L. micrantha* var. *exigua* (Degener & Sherff) Gardner
16. *L. subcordata* A. Gray
17. *L. venosa* Sherff
18. *L. populifolia* (Sherff) Gardner
19. *L. kamolensis* Degener & Sherff
20. *L. bryanii* Sherff
21. *L. lavarum* (Gaud.) DC.
22. *L. perdita* Sherff
23. *L. integrifolia* (Nutt.) A. Gray

INDEX TO EXSICCATAE

Numbers in parentheses represent the taxa recognized in this study (see preceding list).

Alexander & Kellogg 5306(1), 5330(21), 5332(23), 5335(1).
Andersson s.n.(11)
Barclay 1327(1).
Bennett 43(21).
Bishop s.n.(21).
Bryan s.n.(23), 317(5a), 736(20).
Bush 9301(23).
Bush & Topping 3746(5a).
Carlquist 1689, 2124, 2236(23).
Carlson 3828(10).
Caum 14(23).

Christ s.n.(5a).

Christensen & Christensen 27842, 27843(16), 27912(21).

Christopherson s.n., 1368, 1400(23).

Cooke s.n.(23)

Cowan 793, 869(23).

Cranwell, et al. 2735, 2792(23), 3336(9), 3541(23), 3862(6b).

Crosby & Anderson 1550(23).

Degener s.n.(6a), s.n.(23), 2482(5a), 4027(21), 4029(1), 4177b(5a), 4188(21), 4189(16), 4198(2), 4199(3), 4202(21), 4203(23), 4210, 4212, 4213(3), 4214(16), 4216, 4216B(23), 4217(3), 4305(5b), 7454(23), 7455(5a), 12413, 12414, 12415(21), 12417(23), 18075(16), 18077(1), 18078(10), 19292(3), 19343(21), 19572(23), 20507(1), 20514(6a), 21489(6b), 21816(16), 21969(23), 21975, 21986(21), 21995, 21996(4), 22029(21), 22034(5b), 22176(21), 22204, 22207, 22209(3), 27286(23), 27348(6b), 27286, 31583(23).

Degener & Carroll 20601(5a).

Degener & Degener 23645(1), 23736(6b), 23891(1), 24069(10), 25237(1), 27562(16), 27564, 27567(1), 28374(23), 28391(21), 28397, 28398, 28399(4), 28400, 28401(21), 28402, 28444, 28702, 28741(4), 28742, 28744, 28745(21), 28759, 28770, 28783(4), 30313(3).

Degener, et al. 4174(7), 4175, 4176(5a), 4179(23), 4181(5a), 4258(9), 4299(5c), 10076, 10096, 10533(5a), 11032(10), 12228, 12253(9), 12285(8), 12287(5c), 12290(8), 12291(9), 12331(8), 12332(9), 12412(21), 12422(1), 19280(18), 19289(21), 19362(10), 19810(16), 20836(5a), 24161, 24166(21), 25133(3), 25134(21), 25159(1), 27167(23), 27168(6b), 27169(6a), 27171(6b), 27563(3).

Degener & Hansen 23978(6a).

Degener & Hatheway 20418, 20419, 20505(6b), 20516(6a), 20976(5c).

Degener & Murashize 19797(1).

Degener & Nitta 4028(1).

Degener & Ordonez 12610(15b), 12611(6a), 12612(1), 12613(6b), 12614, 12615(6a), 30836(23).

Degener & Park 4180, 4182(5a), 4186, 4187(10).

Degener & Picco 31642(1).

Degener & Tams 23760(21).

Degener & Weibke 2143, 2144(15a), 2146(6a).

Fagerlind & Mitchell 1116(1).

Fagerlind & Scottsberg 6477, 6635(6a), 6636(15a).

Faurie 1001, 1005(3), 1006, 1007(6a), 1008(1), 1012(14).

Forbes s.n.(1), 4-H(16), 7-Mo(3), 59-Mo(2), 71-K(1), 110-Mo, 220-Mo(3), 274-M(1), 288-L(21), 304-K(15a), 315-M(21), 396-Mo(1), 397-Mo(3), 507-L(21), 522-Mo, 577-Mo(1), 615-Mo(23), 617-Mo(3), 951-K(6b), 1507-O(23), 1617-O(5a), 1774-M(1), 1916-M(3), 1918-O(5a), 2015-M, 2020-M(21), 2024-O(5c), 2194-O(23), 2270-M(21), 2275-O(23), 2431-M, 2451-M(6b), 2451-O, 2476-O(5a).

Forbes, et al. 1840-O(10).

Forbes & Lake 2274-O(5a).

Fosberg 9657, 9663(1), 10169A(16), 10556, 10575(23), 10593(5a), 12561(21), 12792(1), 12911, 12929(23), 13393, 13407(1), 13545(5a), 13597(23), 13599(5a), 13615(23), 13616, 13884(5a), 14051(23), 14124(5a).

Fosberg & Daker 9138(23).

Fosberg & Egler 14208(23).

Fosberg & Fosberg 12859(10), 13150(5a), 13439(23).

Gagne 640(7), 647(10).

Garber & Forbes 141(5a).

Gardner 275A, 275POP, 276, 277A&B(23), 278, 279A&B, 280, 281(5a), 282, 283(23), 284, 285(1), 286, 287, 288(6b), 289(1), 290A&B(6a), 291, 292(6b), 293(23), 294, 295A&B, 296(6a), 297A&B, 298A-C(23), 299A-F, 300A-D, 301(3), 302(23), 303A&B, 304, 305, 306, 307, 308(3), 309, 311(23), 313(1), 314, 315, 316A&B(4), 317(21), 318, 319, 320A&B, 321(4), 322, 323, 324, 325, 326(21), 327A&B(4), 328, 329(21), 330(3), 331(21), 332, 333(23), 334(3), 335(21), 336, 337A&B(23), 338, 339(21), 341, 346, 347(5a), 348(23), 349(10), 350, 351(5a), 354(1), 355(23), 356, 356A, 357, 358(1), 359, 360A&B, 361(6a), 364, 365, 366(6b), 368(12), 369, 370(6a), 371(6b), 373(23), 374(3), 376(6b), 378(3), 379(21), 381, 383, 384(1), 385(18), 386, 387(4), 388(23), 389, 391, 392(4), 393, 394, 395, 396(21), 397(4), 399A&B, 400A&B(3), 401(23), 402, 403, 404, 405, 406, 407, 408, 409(3), 410(16).

Gaudichaud s.n.(5a), s.n.(6a), s.n.(21), 217(23).

Grant 7063(23).

Greenwell 19237, 19409(16), 19561(23), 19646(5a), 19652(23), 20684(23), 21539(6b).

Guppy s.n.(5a).

Hatheway 134(5a), 504(16).

Hatheway & Hess 119(5a).

Heller 2021(5a), 2092(23), 2439(15a), 2563, 2563A, 2787(6a).

Hendrickson 3996(1).

Herbst 757(23).

Hillebrand s.n.(4), s.n.(16), s.n.(21).

Hillebrand & Lydgate s.n.(7), 135(3).

Hitchcock 14155(1), 15239, 15244(15a).

Hobdy s.n.(5b), 39(6a), 57, 66(4), 79(1), 94(6b), 101(12), 102(13), 170(12), 221(6b).

Mann & Brigham 358(21), 359(4), 371(23), 374(21), 375(1), 533(10), 534(7), 536(15a), 540, 542(6b).

Meebold s.n., s.n., 4254, 20887(16).

Melviile & Melville 1098(23).

Munro s.n.(4), s.n., 2(23), 18(4), 25(21), 52(5a), 143(23), 202(21), 229(4), 275(23), 316, 327, 349(4), 393(3), 408(4), 414(23), 426(4), 502, 503, 504(4), 518(21), 519(4), 526(16), 537(4), 554(3), 670(18).

Neal s.n.(23)

Nelson s.n.(3), s.n.(5a), s.n.(22).

Nitta 7452(23).

Nuttall s.n.(1), s.n.(15a), s.n.(23).

Pearsall s.n.(23), 26(5b), 73(23), 84(10), 85, 86, 87(5a), 88(23), 100(1).

Pekelo 46(3).

Remy 245(15a), 255(23), 260(10), 265(16), 267(4), 269, 270(3), 272(5a), 277(21), 287(1).

Rock s.n.(5a), s.n.(6b), s.n.(15a), s.n.(16), 3066(5a), 6156, 6166(3), 6192, 7055(1), 8349(17), 8674(21), 10049(16), 10286(21), 10287(4), 10288(2), 10294(23), 10295(16), 10304, 12930(23), 13007(1), 14003, 14009, 14010(3), 14011(2), 14022(3), 17011(10), 17042(23), 17122(5a).

Seamster 30462(23).

Sinclair s.n.(6a).
Skottsberg 674(16), 960(6b), 1035(15a), 1041(6a).
Sterns 10885, 11050(21).
St. John 10402, 11317(23), 23611(22), 23572(6a), 23664(5a).
St. John & Christopherson 10527(5a).
St. John et al. 10870(1), 10897, 10907(6b), 22548(16), 23109(1).
St. John & Fosberg 13907(6b).
Stone 760, 825(6b), 1437(1), 1479, 1493(6b), 3419(6a), 3754(1).
Sweezey s.n.(23), 4184(6b), 4185(6a), 10305(5a).
Topping s.n., 3006(23), 3305(5a).
Topo 3281(10).
Ulhara s.n.(21).
U. S. Exploring Expedition s.n.(1), s.n.(3), s.n.(4), s.n.(5a), s.n.(6a), s.n., s.n.(6b), s.n.(7), s.n.(15a), s.n.(16).
Von Royen 10195, 10236(23).
Wawra 2294(5a).
Weber 506(5a).
Webster 1482(23).
Welch s.n.(5a).
Whistler W7(23).
Wichman & Skottsberg 2847(6b).
Wilbur 505, 637(23).
Wilson 59(23).
Winne s.n.(15a).

THE REPRODUCTIVE BIOLOGY OF PROBOSCIDEA LOUISIANICA (MARTYNIACEAE)

ANN PHILLIPPI[1] AND R. J. TYRL

Proboscidea louisianica (Mill.) Thellung, found in temperate North America, is the most widely distributed representative of the Martyniaceae. It can be found growing in disturbed soils and waste places from West Virginia to Illinois and Minnesota and southward to Georgia and Mexico. The fruits with their vicious claw-like appendages give the plant its common name, Devil's Claw. Devil's Claw is an erect or prostrate freely branched summer annual which grows 3–8 dm tall. The entire plant is covered with viscid, glandular hairs whose secretions give the plant a fetid odor. The lavender, pink, or almost white flowers are strongly scented, borne in racemes of 8–20 flowers at the summit of the stems and branches, and have yellowish and purplish mottling inside the throat. The four stamens are didynamous.

Sexual reproduction in the Martyniaceae is somewhat unusual. The stigma is composed of two flat, sensitive lobes which rapidly close when touched (Figure 1). The lobes reopen after stimulation provided that no pollen has been placed on the stigmatic surface. However, when compatible pollen touches the stigmatic surface the lobes generally remain closed. The sensitive stigma of *Proboscidea louisianica* has been superficially investigated by Anderson (1922) and Thieret (1976) and both observed that the pollinators caused the closing of the stigma as they entered the flower but before contact with the anthers occurred. These observations suggested that the stigma functions to decrease the possibility of self-pollination. Additionally, Thieret suggested that self-polination was "fruitless" since his experiments indicated that *P. louisianica* was not self-compatible. The sensitive stigma and the compatibility among closely related annual species in the genus *Proboscidea* (Hevly, 1976) suggest that the reproductive biology of *P. louisianica* is unusual and worthy of further study. Therefore, a detailed study of *P. louisianica* was undertaken in order to elucidate its reproductive biology.

---

[1] Present address: Kentucky Nature Preserves Commission, 407 Broadway, Frankfort, Kentucky 40601

STUDY AREA

In June of 1976, five populations of *Proboscidea louisianica* were located on the north shore of Lake Texoma in Marshall County, Oklahoma, approximately two miles west of the University of Oklahoma Biological Station (Phillippi, 1977). It was unknown at the time that Thieret (1976) had observed plants in the same general area in 1973. In the past this region was covered by alternating tallgrass prairies and blackjack-postoak forests generally described as "The Cross Timbers". The soils are fine sandy loam soils of the Miller series formed during the Upper and Lower Cretaceous (Bennet, et al., 1912). At present, row crops and pastures dominate the landscape. The populations, occurring in overgrazed pastures and at the edge of fields, are in typical habitats for *P. louisianica.*

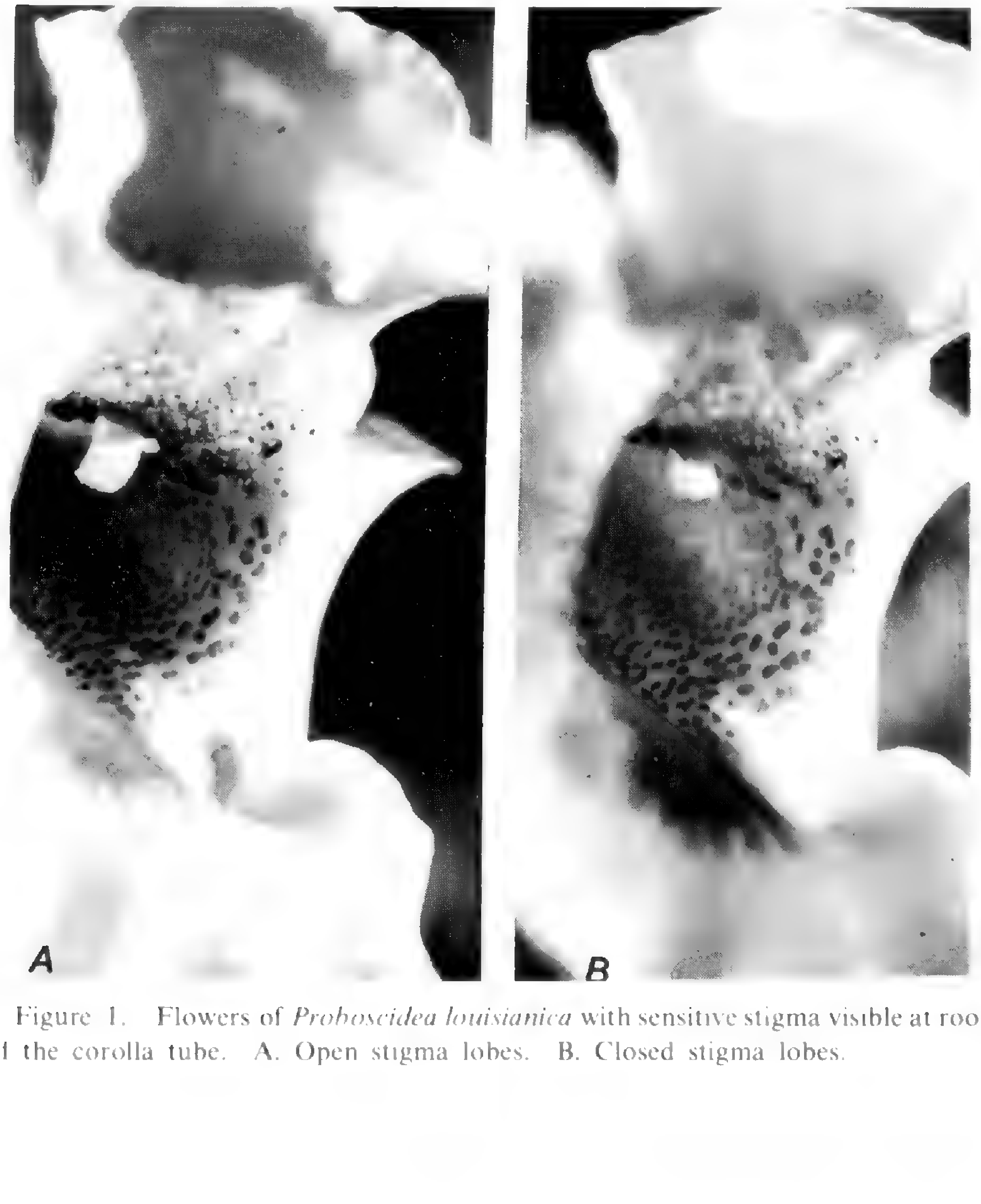


Figure 1. Flowers of *Proboscidea louisianica* with sensitive stigma visible at roof of the corolla tube. A. Open stigma lobes. B. Closed stigma lobes.

Collected insects were deposited in the Oklahoma State University Entomological Museum and the Snow Entomological Museum at the University of Kansas. Voucher specimens of *Proboscidea louisianica* have been placed in the Oklahoma State University Herbarium (OKLA). In each population, the phenology and fruit development of the plants, the insect visitors and their behavior, and the breeding system were examined.

PHENOLOGY

The observations of Anderson (1922) and Thieret (1976) are combined with ours to describe the phenological patterns of *Proboscidea louisianica*. Flowering commences in late May or early June. After a bud reaches approximately 1.5 cm in length, development proceeds rapidly until the corolla reaches a length of 3–6 cm the day before opening. The time of opening is variable, usually occurring before noon, but flowers can be found opening at any hour of the day. This observation is at variance with Thieret's (1976) who reports that flowers generally open in the afternoon, usually about 6:00 p.m. On the first day of anthesis, the corolla is pale yellow or yellowish white (color 1A2 or 1A3 according to the 1961 classification of Kornerup & Wanscher). Dark yellow (4A8) guidelines extend from the center of the lower lobe into the tube. Dark magenta (13F6) spots mark the tube and the bases of the lobes. Shortly before the corolla drops off, some two to three days after opening, the inner lobes are often tinged with pink (11A2 to 13A3). As described by Thieret, the opening takes three to six hours as the upper and lateral lobes gradually open and become somewhat reflexed. When fully open the corolla throat is directed slightly downward, due to a bending of the basal portion of the corolla tube. In each raceme, only one or two flowers are open at a time.

The stamen filaments remain short until just prior to anthesis when they elongate into the throat of the corolla. The four anthers are paired one set behind the other in the corolla roof directly below and behind the stigma lobes (cf. Figure 2 of Thieret). The anthers dehisce longitudinally shortly after flower opening commences. The large, sticky pollen grains, with an average diameter of 80 μ, are characterized by an exine that is irregularly thickened thus forming hexagonal surface patterns. The number of grains per anther was determined via direct observation and dilution-counting. Buds from the five populations were collected, killed and fixed in Carnoy's solution and then stained in Snow's alcoholic-carmine. Buds 1–1.5 cm long from five different plants were selected from each population. One anther was excised from the bud and dissected in 20 ml of tapwater to release the grains. A 0.2 ml subsample of this mixture was pipetted while the water was rapidly agitated to assure uniform dispersion of the grains. The subsample was transferred to microscope slides and the grains were counted. Any grains left in the pipette were also counted. Three counts were made from each anther. The average number of grains per anther was 10,396 (9,200 13,000). The number of pollen grains per ovule was 850. This ratio is low when compared to those of other entomophilous species (Pohl, 1937) and may reflect the large size of the individual grains.

Pollen fertility was also examined. Five flowers from five different plants from each population were collected on the first day of anthesis. Pollen from each flower was scraped onto two slides. The grains on one slide were immediately stained with lactophenol: aniline blue (80ml:.05gm) and the first 200 grains observed were scored as either fertile or infertile. Darkly stained spherical pollen was scored as fertile, while pollen irregular in shape or faintly stained was scored as infertile. Percent fertility for all populations ranged from 92 to 96 with no significant difference between populations. Pollen on the second slide was placed in full sunlight for 48 hours, stained, and observed as before. No significant difference was detected between the fertility of two-day old pollen and that of freshly shed grains, which suggests that the pollen remains viable throughout anthesis.

To determine the time of pollen germination after deposition on the stigma, ten flowers were emasculated and bagged the night prior to opening. The next morning at 9:00 a.m. the flowers were hand-pollinated with pollen from another plant. Stigmas were collected at one-hour intervals following pollination, and fixed in a mixture of chloroform:ethanol:glacial acetic acid (6:3:1) and observed with a binocular microscope following staining with safranin O - aniline blue. The first pollen grains germinated within one hour of pollination.

Pollen tube growth was examined for both selfed and outcrossed plants. On the afternoon before flower opening, 60 flowers were bagged, half of which were emasculated. The following day at 6:00

p.m. 30 flowers were manually self-pollinated while the 30 remaining emasculated flowers were pollinated with pollen from other plants. At six-hour intervals throughout flowering, three selfed and three outcrossed plants were collected, killed and fixed in a 6:100 mixture of 37% commercial formalin to 70% ethanol (Chandler, 1931). Using the technique described by Ramming et al. (1973) the pollen tubes were stained with 0.005% water soluble aniline blue in a 0.15 *M* solution of K_2HPO_4 at pH 8.65 and the intact style and stigma squashed and observed by fluorescence microscopy. The pollen tube walls fluoresced a bright yellow-green. Pollen tubes reached the apex of the ovary in less than six hours with no observable difference between the growth of tubes in selfed and outcrossed plants.

The style is tubular and terminates in the two-lobed stigma. The lower lobe, with an average length of 2.5 mm, is substantially longer than the upper, which averages 2.1 mm long. Numerous viscid papillae cover the inner surfaces of both lobes. The stigma is exserted approximately 5 mm beyond the distal end of the anthers.

Stigma receptivity was examined. Thirty flowers were emasculated and bagged the night before opening. Beginning at 6:00 a.m. the following day, three flowers were hand-pollinated with pollen from another plant. Three stigmas were collected one hour after pollination, and fixed in the formalin:ethanol mixture. Thereafter stigmas were collected and fixed at six-hour intervals for 54 hours, or throughout anthesis. The stigmas were stained in a one percent solution of safranin-aniline blue (1:1) and examined for germinated pollen. Pollen tubes were observed on all stigmas, indicating that the stigma is receptive throughout anthesis.

At the base of the ovary is a dark green ring of cells that secretes nectar throughout anthesis. Ovules per ovary average 50 (range of 36-73, sample size = 25). Fruit development is rapid. Within one week after the corolla is shed, the fruit is several centimeters long with a green, fleshy pericarp. A unilocular, loculicidal capsule, the fruit is differentiated into a basal body 2–3 cm thick and 5–10 cm long and an arcuately-curved beak 15–20 cm long. Approximately two months after flowering, the exocarp sloughs away and the hard endocarp splits from the apex to the base forming the two horns or claws that give the fruit its name (Mayberry, 1947). This bizarre fruit facilitates seed dispersal as it is readily entangled in the legs of herbivores, particularly cattle. Farmers, whose stock are tormented by the pain the fruit inflicts, describe the plant as a nuisance (Gardner, 1932).

INSECT VISITORS AND POLLINATION

Observations of the flowers of *Proboscidea louisianica* reveal adaptations for insect pollination (Baker and Hurd, 1968; Faegri & van der Pijl, 1971). The flowers are of the "gullet-type" and are characterized by the sexual organs positioned at the roof of the corolla so that pollen is deposited on the dorsal parts of the pollinator, and by a prominent landing platform. In addition, flowers of *P. louisianica* exhibit typical adaptations for bee pollination as the flowers are zygomorphic and mechanically strong, possess well-hidden nectar, have nectar guides, and are odoriferous.

During the summer months of 1976, observations and collections were made of the insects visiting *Proboscidea louisianica* blossoms. The behavior of insects alighting on the corollas was recorded. The insects were then collected, pinned, and labeled. Insects collected were examined for *P. louisianica* pollen. Every part of the insect where pollen was visible under a binocular scope was scraped, and the pollen transferred to a microscope slide. The pollen grains were then stained with safranin-aniline blue and identified. No attempt was made to quantify the amount of *P. louisianica* pollen in relation to other grains present. Insect visitors bearing *P. louisianica* pollen are listed in Table 1 (cf. Appendix C in Phillippi, 1977). Other visitors observed and/or collected but without pollen include butterflies, syrphid flies, fruit flies, and thrips; there is no indication that any of these visitors play a role in the pollination of *Proboscidea.*

Because of their behavior, the frequency of visits, and the number of individuals observed, two bee species are considered the major pollinators of *Proboscidea louisianica* in south-central Oklahoma. The first bee, *Melissodes communis* Cresson, was found foraging on *Proboscidea* at the beginning of the summer. As circumscribed by Mitchell (1960), *Melissodes* is a relatively large genus (>100 spp.) of moderately robust hairy bees. Members of this genus are regarded as important pollinators of native plants and crops. Laberge (1956) reports that *M. communis* is highly polylectic and prefers flowers of the Fabaceae and Lamiaceae, particularly members of the genera

Table 1

Insect visitors bearing *Proboscidea louisianica* pollen.
Classification according to Mitchell (1960).

Order Hymenoptera	Number of Individuals Collected	Number of Individuals Bearing Pollen
Family Apidae		
Bombus p. pennsylvanicus De G.[1]	15	14
Family Anthophoridae		
Melissodes communis Cresson[2]	25	21
Xenoglossa strenua (Cresson)[2]	9	7
Centris lanosa Cresson[2]	2	2
Anthophora walshii Cresson[2]	1	1
Melissodes sp.[2]	1	1
Family Megachilidae		
Megachile montivaga Cresson[3]	2	2
Family Halictidae		
Lasioglossum (*Evylaeus*) sp.[2]	2	2

[1] Identified by Dr. H. E. Milliron, New Martinsville, West Virginia.
[2] Identified by Dr. Charles D. Michener, University of Kansas.
[3] Identified by Dr. T. B. Mitchell, North Carolina State University.

Melilotus and *Medicago*. In addition, this species was collected from *P. louisianica* by Robertson (1928) and by Thieret (1976).

During the course of this study as many as five to ten *Melissodes communis* females were seen foraging simultaneously in the large populations of *Proboscidea louisianica*. No distinctive flight pattern was observed and flower visitation appeared random. These insects also showed no apparent preference for the younger, light yellow flowers or the older, pink flowers. When entering the flower, the bee lands on the lower lobe of the corolla and moves into the corolla tube. Occasionally it may turn upside down while inside the corolla so that pollen is deposited both ventrally and dorsally.

Only females, 12–16 mm long, were captured and of the 25 individuals collected, pollen of *Proboscidea louisianica* was found on the head, thorax, abdomen, and scopae of twenty-one. Pollen is a rich source of food, especially protein, and is used in nourishing the larvae. The bees were also observed utilizing the nectar, probably for individual maintenance (Faegri & vand der Pijl, 1971).

Melissodes communis was observed and collected primarily in June, July and early August. Thereafter, these bees were only rarely seen. According to Laberge (1956) *M. communis* is most abundant from the end of June through August, but can be collected from March to September. The abrupt decrease of *M. communis* cannot be explained adequately, as *Proboscidea* was still in full bloom and there was no substantial increase in flowering of other plants that might have attracted the bees. *Melissodes communis* is thus believed to be a major pollinator of *P. louisianica.* The geograhic extent of this specific relationship awaits further collections from other populations of *P. louisianica* throughout its range.

In June, July and early August, *Mellisodes communis* was the only regular visitor to *Proboscidea.* In early August the number of *M. communis* visits decreased; at the same time, workers of *Bombus pennsylvanicus pennsylvanicus* De G. began visiting *P. louisianica.* Although visiting *Sloanum rostratum, Monarda punctata,* and *Helianthus annuus* which occurred among the populations of *P. louisianica,* this large bumblebee had not previously been observed landing on *Proboscidea.* It became the major pollinator throughout the remainder of *Proboscidea's* flowering season, which ended in early September. *Bombus p. pennsylvanicus* is distributed throughout northern Mexico, the United States, and southern Canada.

The bumblebee approaches the flower, lands on the lower lobe, and moves as far into the corolla as it is able. Pollen of *Proboscidea louisianica* was identified on 14 of the 15 individuals, being collected from the dorsal portions of the head and thorax as well as in the scopae. The bumblebees were also observed utilizing nectar. *Bombus pennsylvanicus* individuals were observed visiting *Solanum rostratum* and *Monarda punctata* as well as *P. louisianica.* This is to be expected since a colony is active throughout the growing season because of the overlapping generations of adults; the bees exploit a wide variety of plant species as they become seasonally available (Heinrich, 1976).

Solanum rostratum and *Monarda punctata* came into bloom later than *Proboscidea louisianica;* perhaps it was these species that at first attracted *Bombus pennsylvanicus* into the populations of Devil's Claw, during which time the bumblebee began "minoring" (Oster and Heinrich, 1976) on *P. louisianica,* then eventually "majoring" on it. The first pollinator's decline is unexplained at this point. No acts of aggression were observed between *Mellisodes communis* and *B. pennsylvanicus* and according to Heinrich (1976) it is "unlikely that [bumblebee] colonies can seize, hold or defend territories . . . they do not give any sign of intolerance of [other species] while foraging under natural conditions."

Both putative pollinators remove almost all of the pollen from the anthers of each flower. Observations of 25 newly opened flowers on two occasions (n = 50) revealed that all of the flowers were visited at least once before noon of the first day of anthesis. Pollen grains were packed in the scopae and on the head and thorax of *Bombus* and the head, thorax, and abdomen of *Melissodes.* Kraai (1962) suggests that pollen packed in the scopae does not play a role in pollination as viability is quickly diminished. The entrance of both bees into the corolla invariably stimulated the sensitive stigma to close so that its receptive surfaces were no longer exposed. The lower stigma lobe hangs down into the mouth of the corolla and comes into contact with the head, thorax, or abdomen of the entering visitor and at that time pollen from another plant is deposited on the stigma. When the pollen dusted bee exits the corolla there is little chance that self-pollination will occur, since the lobes of the stigma are closed. These observations are at variance with Thieret's (1976), who reported infrequent insect visits and the lack of pollen deposition on the stigmas of many flowers. This difference in observation can perhaps be attributed to our more intensive study and to the population dynamics of *Melissodes* and *Bombus.*

THE SENSITIVE STIGMA

The sensitive stigma is not unique to the Martyniaceae but has been described from species in the Bignoniaceae (Burck, 1902; Newcombe, 1922), Lentibulariaceae (Hildebrand, 1869), Acanthaceae (Morren, 1839; Trelease, 1882) and the Scrophulariaceae (Henderson, 1841; Burck, 1902). In most cases, an insect pollinator serves as the stimulating agent; however, Elrod (1904) observed hummingbirds fulfilling this role in *Campsis radicans* (L.) Seeman. The external morphologies of the stigmas are generally similar, and consist of two obovate to oblanceolate lobes which diverge at varying angles from 90° to nearly 360°, prior to stimulation and closing. In one genus of the Acanthaceae, *Strobilanthes*, the sensitive stigma consists of a slender style that tapers at its apex to form the stigma. In this case, the stigma and style quickly straighten and recurve upon stimulation so as to press the stigma closely against the lower lobe (Trelease, 1882).

Another common attribute of these sensitive bilobed stigmas is that the lobes reopen after stimulation, provided that no pollen has been deposited on the stigmatic surface (Newcombe, 1922). However, when compatible pollen touches the stigmatic surface the lobes generally remain closed. The sensitive stigma has been generally considered to function to decrease the possibility of self-pollination. However, Burck (1902) found that the sensitive stigma of *Torenia fournieri* (Scrophulariaceae) functioned to increase the possibility of self-pollination. Burck (1902), Lloyd (1911), and Brown (1913) investigated the response mechanism and concluded that water withdrawal from the lobes was responsible for the stigmatic closure. Newcombe (1922) confirmed their findings and, in addition, gathered evidence which suggested that an enzyme or other chemical substance in the pollen maintained closure.

Heckel first described the sensitive stigma of *Proboscidea louisianica* in 1874. Rain or a water droplet would close the stigma momentarily, which reopened in five to ten minutes. Sand dusted over the lobes, as well as blowing on the lobes, would also cause temporary closure. The stigma is sensitive to very slight stimulations and can readily be closed by pulling a human hair across the lobes. Observations concerning fatigue of the stigma agree with those of Brown (1913) and Thieret (1976). The first stimulation of the stigma at the beginning of anthesis requires five to ten minutes to reopen. On the 5th, 6th, or 7th stimulation, reopening generally requires 25–45 minutes, stimulation after that requires up to two hours.

Observations during the present study suggest that the stigma of *Proboscidea louisianica* functions primarily to decrease the possibility of self-pollination. The stigma may also serve to protect the germinating pollen physically.

THE BREEDING SYSTEM

In order to determine the nature of the breeding system in *Proboscidea louisianica,* different modes of reproduction were tested using standard techniques. All plants in each population were numbered. Fifty flowers at approximately the same stage of development were randomly selected in each treatment. Fruit set was checked one month later. Modes of reproduction tested and the methods employed were:

Controls: In order to estimate the percent fruit set under natural conditions, flowers were marked with a piece of fluorescent ribbon, but otherwise undisturbed.

Anemophily: Flowers were emasculated before pollen dehiscence, nylon stocking securely tied around the blossom and adjusted so that the stigma was exposed to the wind. The nylon stocking served to exclude insects but not air-borne pollen.

Agamospermy: Flowers were emasculated while still in the bud and bagged to prevent pollen from reaching the stigma.

Intrapopulational Xenogamy: Buds were emasculated and bagged. At early anthesis stigmas were hand pollinated with the pollen from another plant in the same population and then re-bagged.

Interpopulational Xenogamy: Buds in population A were emasculated and bagged. While the bagged flowers were in early anthesis flowers from population C were collected, placed in separate four-dram vials, and the pollen was transferred to the stigmas of the bagged flowers in population A. Flowers were then re-bagged. Reciprocal crosses were made.

Natural Autogamy: Flowers were bagged while still in bud to test for natural self-fertilization.

Artificial Autogamy: Flowers were bagged while in the bud. During early anthesis, stigmas were manually self-pollinated and re-bagged.

The results of these crosses are summarized in Table 2. As expected, wind pollination is not part of the breeding system of *Proboscidea louisianica* as the flowers lack the structural modifica-

Table 2

Percent fruit set under experimental conditions.
No significant differences among populations at 5% level, population results pooled.

Mode of reproduction tested for	Number of flowers	Percent fruit set
Controls	42	52
Anemophily	46	0
Agamospermy	75	1
Intrapopulational Xenogamy	47	83
Interpopulational Xenogamy	49	78
Natural Autogamy	48	4
Artificial Autogamy	47	57

tions generally associated with anemophily (Faegri & van der Pijl, 1971). *Proboscidea* also does not appear to be agamospermous; the one fruit occurring in population A was most likely due to an error in technique. Twenty-five additional flowers were tested in that population, none of which set fruit.

Intrapopulational and interpopulational crosses were equally successful. There was no significant difference between these two modes of reproduction ($p > .5$)*. However, a significant difference was observed between these crosses and the control percent fruit set ($p < .02$), but this was most likely due to the extensive predation of control flowers by lepidopteran larvae that foraged on *P. louisianica* throughout the summer. Bagged flowers utilized in the crossing experiments were protected somewhat from this predation.

Natural autogamy, in the absence of biotic pollinators, does not play a significant role in the reproduction of *P. louisianica* as indicated by the 4% fruit set. On the other hand, the taxon is self-compatible (57%) when manually self-pollinated. The previously

---

*All values of p refer to the t-test.

described spatial relationship of the essential organs and the exclusion of biotic pollinators are responsible for the lack of natural selfing. In addition, there seems to be an internal isolating mechanism partially preventing self-fertilization. There was a significant difference ($p < .05$) in fruit set between artificially selfed and outcrossed plants. As previously mentioned, a comparison of pollen tube growth between selfed and outcrossed plants did not reveal any differences. There was no distinguishable difference in the autogamous fruits either during development or in the number of seeds set per fruit ($p > .5$) (Table 3). Furthermore, there was no significant difference ($p > .5$) in the percent germination of the seeds from selfed or outcrossed fruits (Table 4). It is suggested that the barrier is prezygotic, perhaps a failure of the pollen tubes to penetrate the embryo sac consistently.

Cytological studies of *Proboscidea* began with investigations by Anderson (1922) who described the development of the flower, sporogenesis, and gametogenesis. Chromosome counts of $2n = 30$ were made by Martini (1939) and Perry (1924) which are confirmed. Buds were collected, killed and fixed in chloroform: 95% ethanol: glacial acetic acid (6:3:1), bulk stained in Snow's alcoholic-carmine, and dissected anthers squashed in Hoyer's medium. Meiotic con-

Table 3

Seeds per fruit in selfed versus outcrossed fruits from populations A and C.

	Population		
Selfed	A	C	A & C
Number of fruit	4	10	14
Number of seeds	249	427	676
Average number of seeds/fruit	62.25	42.7	46.8
Outcrossed			
Number of fruit	5	15	20
Number of seeds	266	636	902
Average number of seeds/fruit	53.25	42.4	45.0

Table 4

Percent germination of selfed versus crossed seeds from populations A and C[1].

	Population		
Selfed	A	C	A & C
Number of seeds	249	427	676
% germination	57	6	25
Crossed			
Number of seeds	266	636	902
% germination	40	8	18

[1] Normal fruit development requires approximately eight weeks. Germination of seeds from eight week old fruits or older is 75%. Fruits of populations A and C were collected early (six and three weeks respectively) because of extensive rodent and insect predation.

figurations of 70 microsporocytes from 26 plants from all 5 populations were analyzed. Pairing and disjunction of the chromosomes is quite regular with 15 bivalents at Metaphase I. Chiasmata number and position is fairly constant with 52% of the bivalents characterized by one terminal chiasma, 35% by two terminal, 10% by one interstitial and one terminal, and 3% by one interstitial chiasma. Fifteen dyads were observed consistently in Anaphase I. Cytokinesis is post-meiotic.

SUMMARY

A detailed study of five populations of *Proboscidea louisianica* in south-central Oklahoma was undertaken to determine its breeding system, phenological patterns, and principal pollinators. Major findings are that:

1. *Proboscidea louisianica* is an outcrosser capable of autogamy. The sensitive bilobed stigma is the mechanism that facilitates xenogamy. A pre-zygotic barrier to self-fertilization is hypothesized to exist.

2. Of the eight insect taxa utilizing pollen of *P. louisianica* two, *Melissodes communis* and *Bombus pennsylvanicus pennsylvanicus,* are considered major pollinators.

Possessing attributes favoring both genecologic flexibility and fitness, *Proboscidea louisianica* is adapted for dispersal and occurrence in disturbed habitats. This is a common characteristic of autogamous plants, as Stebbins (1958) demonstrated. It is conceivable that before rangeland was fenced, there was considerable long-distance dispersal of the Devil's Claw fruits by large herbivores. At present, the fruits of *P. louisianica* are thought to be dispersed by certain agricultural practices (Gardner, 1932). Self-compatibility makes it possible for a single plant to reproduce and start a population.

Perpetual self-fertilization does have its disadvantages. Continued inbreeding tends to reduce heterozygosity, recombination, variability, and therefore the evolutionary potential of a species. On the other hand, outcrossing promotes genetic recombination and thus genetic diversity which is likely to lead to ecologic diversity. Therefore, a plant such as *Proboscidea louisianica* whose reproductive mechanisms encompass both cross- and self-fertilization is likely to be successful in invading new habitats.

ACKNOWLEDGMENTS

We thank Drs. William Drew, Charles Michener, H. E. Milliron, and T. B. Mitchell for their assistance in identifying the insects collected. This paper is based on a thesis submitted to Oklahoma State University in partial fulfillment of the requirements for the masters degree.

LITERATURE CITED

Anderson, F. 1922. The development of the flower and embryogeny of *Martynia louisianica*. Bull. Torrey Bot. Club **49:** 141–157.

Baker, H. G., & P. H. Hurd, Jr. 1968. Intrafloral ecology. Ann. Rev. Ent. **13:** 385–414.

Bennett, F., C. Lounbury, R. T. Avon Burke, A. T. Sweet, & P. O. Wood. 1912. Soil Survey of Grayson County, Texas. U.S.D.A. Field Operations of the Bureau of Soils. 1909. Government Printing Office, Washington, D.C.

Brown, W. H. 1913. The phenomenon of fatigue in the stigma of *Martynia*. Philippine Jour. Sci. Bot. **8:** 197–201.

Burck, W. 1902. On the irritable stigmas of *Torenia Fournieri* and *Mimulus luteus* and on the means to prevent the germination of foreign pollen on the stigma. Kon. Akad. van Wetenschap. Amsterdam, Proc. Sec. Sci. **4:** 184 194.

Chandler, C. 1931. A method for staining pollen tubes within the pistil. Stain Technol. **6:** 25.

Elrod, M. N. 1904. Botanical Notes. Indiana Acad. Sci. Proc. **1903:** 119.

Faegri, K., & van der Pijl. 1971. The Principles of Pollination Ecology. Pergamon, Oxford.

Gardner, A. 1932. A new noxious weed, The Devil's Claw. Jour. Dept. Agric. W. Aust. **9:** 129 131.

Heckel, E. 1874. Du mouvement dans les stigmates bilabies des Scrophularinees des Bignoniacees et de Sesamees. Comptes rendus de l'Academie des sciences. *In:* The significance of the behavior of sensitive stigmas I. 1922. F. C. Newcombe. Amer. J. Bot. **9:** 99 120.

Heinrich, B. 1976. Bumblebee foraging and the economics of sociality. Amer. Scientist **64:** 384 395.

Henderson, J. 1841. On the structure of the stigma in *Mimulus* and *Diplacus*. Ann. and Mag. of Nat. Hist. **6:** 51 52.

Hevly, R. H. 1976. Personal communication of unpublished research.

Hildebrand, F. 1869. Wietere Beobachtungen uber die Bestaubungsverhaltnisse an Bluten. *Utricularia vulgaris*. Bot. Zeit. **27:** 505. *In:* Significance of the behavior of sensitive stigmas II. F. C. Newcombe. 1924. Amer. Jour. Bot. **11:** 85 93.

Kornerup, A., & J. H. Wanscher. 1961. Reinhold Color Atlas. Reinhold Pub. Corp., New York.

Kraai, A. 1962. How long do honeybees carry germinable pollen on them? Euphytica **11:** 53 56.

LaBerge, W. A. 1956. A revision of the bees of the genus *Melissodes* in North and Central America. Part I. (Hymenoptera, Apidae) Univ. Kan. Bull. **37,** p. 1053.

Lloyd, F. E. 1911. Certain phases of the behavior of the stigma lips in *Diplacus glutinosus* Nutt. Plant World **14:** 257.

Martini, E. 1939. Ricerche Embriologiche sulle Martyniaceae. Nuovo Giornale Botanico Italiano. *In:* Chromosome Atlas. 1955. C. D. Darlington & A. P. Wylie. George Allen and Unwin Ltd, London.

Mayberry, Marshall W. 1947. *Martynia louisiana* Mill, an anatomical study. Kansas Acad. Sci. **50:** 164 171.

Mitchell, T. B. 1960, 1962. Bees of the eastern United States, vols. **1-2.** Tech. Bull. Nos. 141 152. North Carolina Agric. Expt. Sta.

Morren, C. 1839. Recherches sur le mouvement et l'anatomie du style *Goldfussia anisophylla*. Academie Royale des science, Des lettres et des beau-arts de Belgique, Brussel, 12. *In:* Significance of the behavior of sensitive stigmas. II. F. C. Newcombe. 1924. Amer. J. Bot. **11:** 85 93.

Newcombe, F. C. 1922. Significance of the behavior of sensitive stigmas I. Amer. J. Bot. **9:** 99 120.

Oster, G., & B. Heinrich. 1976. Why do bumblebees "major"?: A mathematical model. Ecol. Monogr. **46:** No. 2.

Perry, B. A. 1942. Genetic and cytological studies on the Euphorbiaceae, Martyniaceae, and Malvaceae. Vir. Univ. Abst. **1942:** 43–47.

Phillippi, A. 1977. The reproductive biology of *Proboscidea louisianica* (Martyniaceae). Masters thesis, Oklahoma State University, Stillwater, Oklahoma. 32 p.

Pohl, F. 1937. Die Pollenerzeugung der Windblutter. Beih. bot. Zbl. **56,** 365 470. *In:* The principles of pollination ecology. K. Faegri & L. van der Pijl. 1971. Pergamon, Oxford.

Ramming, D. W., H. A. Hinrichs, & P. E. Richardson. 1973. Sequential staining of callose by aniline blue and lacmoid for fluorescence and regular microscopy on durable preparation of the same specimen. Stain Technol. **48:** 133 134.

Robertson, C. 1928. Flowers and insects. Science Press, Lancaster, Pa.

Stebbins, G. L. 1958. Longevity, habitat, and release of genetic variability in higher plants. Cold Spring Harbor Symp. Quantitative Biol. **23:** 365–378.

Thieret, J. W. 1976. Floral biology of *Proboscidea louisianica* (Martyniaceae). Rhodora **78:** 169 179.

Trelease, W. 1882. On the structures which favor cross-fertilization in several plants. Proc. Boston Soc. of Nat. Hist. **21:** 410–437.

OKLAHOMA STATE UNIVERSITY
SCHOOL OF BIOLOGICAL SCIENCES
STILLWATER, OKLAHOMA 74074

NECTARIES OF CERTAIN ARCTIC AND SUB-ARCTIC PLANTS WITH NOTES ON POLLINATION

DOROTHY E. SWALES

The nectaries, stamens, and pistils of the most common genera and species of seventeen Arctic and sub-Arctic families were studied from living material at Frobisher Bay, Resolute, Inuvik, and Tuktoyaktuk, N.W.T., and at Keno Hill, Dawson City, and Whitehorse, Y.T.

The study was initiated by the growing interest in the pollination of arctic plants, and importance of self-pollination, apomixis, and polyploidy in areas where weather conditions often reduce the numbers and activity of pollinating insects. There is a singular lack of detailed information on the position and type of nectaries and the mechanics of self- and cross-pollination in Nearctic plants.

The theory that nectaries in the primitive families usually occur on the outside whorl, and migrate to the base of the style in the most advanced, was evaluated in the seventeen arctic families, as well as the adaptations of the flower to facilitate either cross- or self-pollination.

An account of nectar and nectaries in the arctic flowers would be incomplete without reference to the type of insects involved in pollination in the areas where the field work was undertaken. Insects were collected from individual flowers in the relatively few species which were visited freely by them. Insect names were added to plant species' discussion, along with some data collected by others in a much more severe weather area further north, Ellef Ringnes Is., where the insects crawled rather than flew to their nectar food source, playing a part in the survival of the 49 species of flowering plants recorded there.

POLYGONACEAE

Two species of this family are circumpolar, and are very common in our Arctic, *Oxyria digyna* and *Polygonum viviparum*. The first is wind-pollinated, producing copious pollen from four stamens (rarely six), later trapped by the fimbriate red stigmas with branches 0.48–0.52 mm. No vestigial nectary was found. Pollen grains were found scattered all over the inflorescence in some specimens.

Polygonum viviparum has a well-developed nectary, and yielded 0.155 mg of sugar in the nectar per flower per day at Churchill, and 0.095 mg, with sugar concentrations of 18–31% at Lake Hazen (Hocking, 1968). Knuth (1909) lists a variety of insects visiting this species in Europe, although it is listed as apomictic (Fryxell, 1957). The flower spikes at Frobisher Bay had flowers at the tip and bulbils lower down, the bulbils seen to be germinating while still attached to the parent plant on July 4, 1976, an adaptation for quick establishment of new plants. There were well-filled trigonous achenes in the flowers examined there, although they are sometimes sterile. On the exposed shore of the Beaufort Sea at Tuktoyaktuk, July 12, 1965, there were large stands of dwarf *P. viviparum* which bore bulbils only, this species being increasingly viviparous as the climate deteriorates.

The hermaphroditic flowers examined had a greenish band on the petaloid calyx at the base of the filaments, changing to either purple or beige in the thickened glandular nectary ring immediately surrounding the ovary. Four stamens were attached to the perianth segments in the green band, and four were swollen at the base and embedded in the glandular tissue. The swellings fitted neatly into the three concave sides of the achene, stamens three and four compressed to fit together in one concavity (Plate 1, Figure 1).

The nectary was unique among all arctic species studied, perhaps closest to those in the Caryophyllaceae, but more primitive in the irregular disposition of the stamens.

Savile's statement that some species retain a pattern attractive to insects after becoming apomictic (1972) applies fully to *Polygonum viviparum.*

CARYOPHYLLACEAE

The Caryophyllaceae have six genera widely distributed in the arctic. Four of these, *Arenaria, Cerastium, Sagina,* and *Stellaria,* have small white flowers, each with a polysepalous calyx allowing it to open widely and expose the nectar to the visits of small flies. Two genera, *Lychnis* and *Silene,* have flowers of purplish shades and a gamosepalous calyx forming a tube concealing the nectar. In the Alps bees and syrphids with long probosces are known to visit them freely to suck nectar (Knuth, 1908), but in the eastern Canadian

Arctic they seem to attract few insects of any kind (Kevan, 1972b; Hocking, 1968).

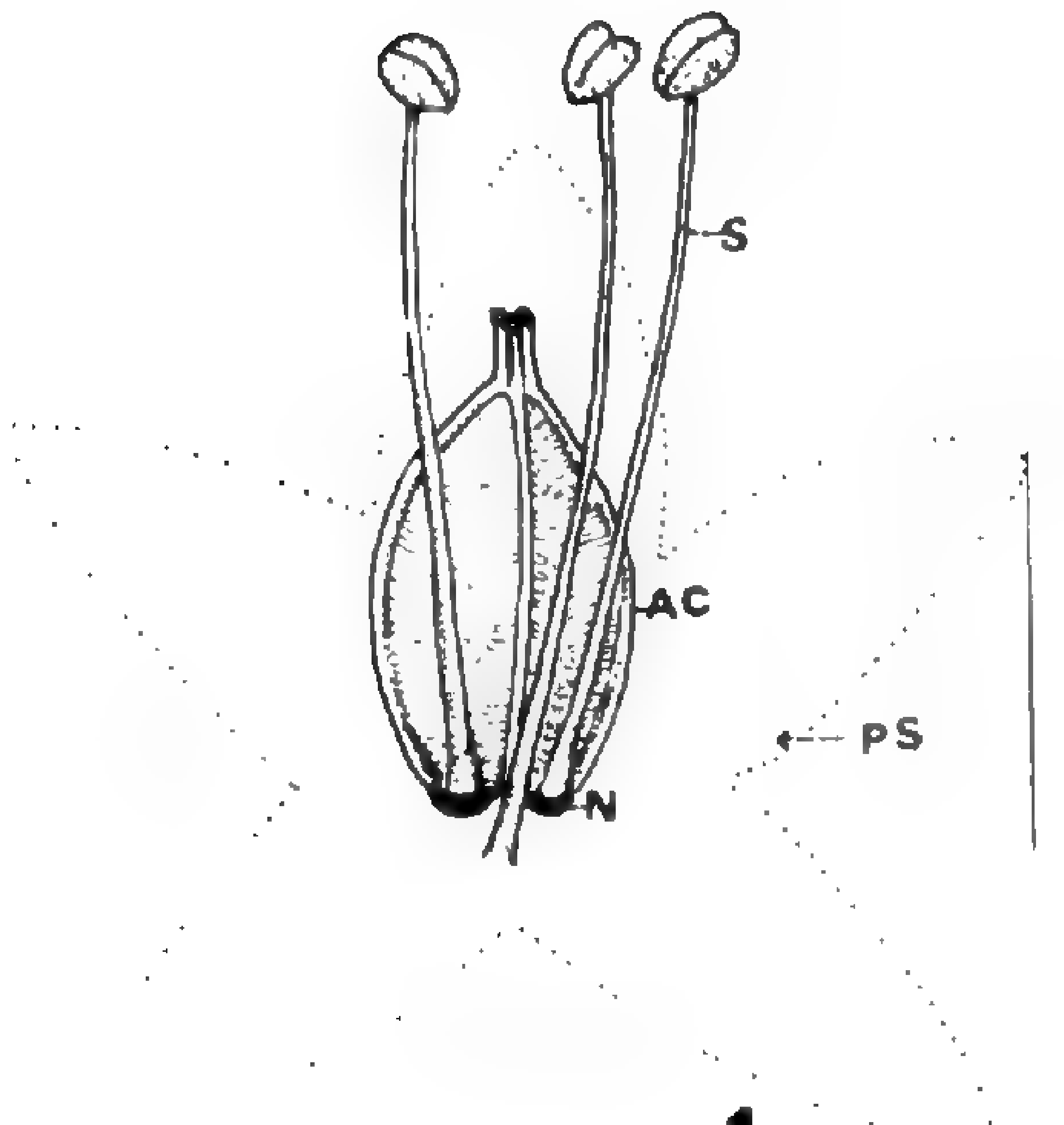
Members of the first group, *Cerastium alpinum* and *Stellaria longipes,* were among the most visited flowers at Frobisher Bay in 1964. Savile (1972) pointed out that appreciable hybridization occurs between members of the four Arctic species of the *Stellaria longipes* complex. Flies probably play an active pollinating role in both *Cerastium* and *Stellaria.* I collected *Lasiops subrostratus* Zett., *Hylema* (Paregle) *radicum* (L.), (Muscidae), and *Protophormia terrae-novae* (R.-D.) (Calliphoridae) on *Cerastium alpinum; Hylema* sp., *Spilogona* (R.-D.) *imitatrix* (Mall.), (Muscidae), on *Stellaria longipes;* and *Boloria polaris* Bdv., (Nymphalidae) on *Silene acaulis.*

The nectaries of the Caryophyllaceae are associated with the base of the stamens. I examined *Cerastium alpinum, C. arcticum, Stellaria crassifolia, S. humifusa, S. longipes, Arenaria laricifolia, A. physodes,* and *A. peploides* in the field, and all had a yellow, or yellowish-green, nectary partially surrounding the base of every second stamen, the outer ones opposite the sepals (Plate 1, Figure 2). Sometimes, as in *A. peploides,* the nectary was wide enough to touch the adjacent stamen (the one opposite the petals), so there appeared to be nectariferous tissue between every stamen.

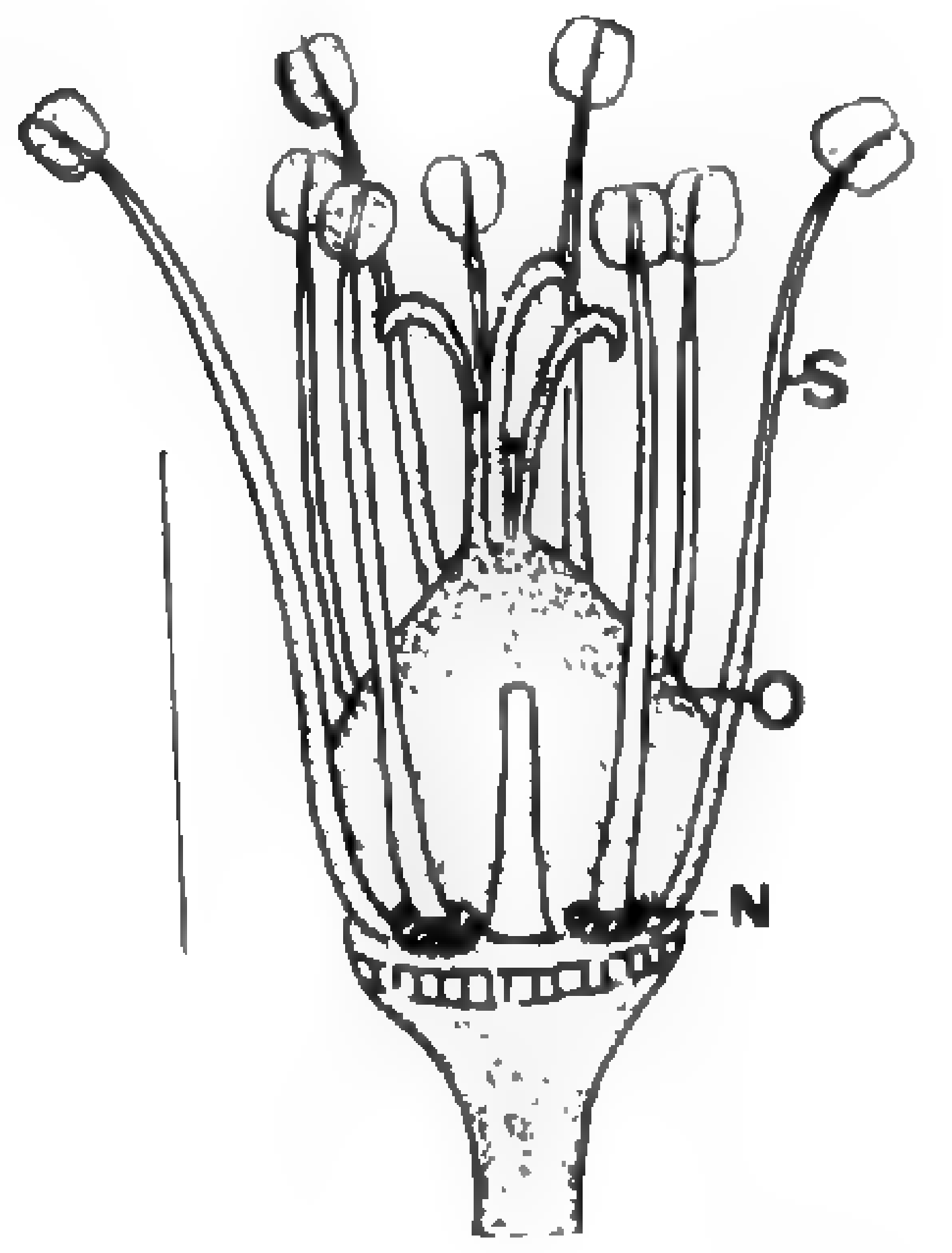
The flowers tend to be protandrous; the outer, nectary-bearing stamens elongate and dehisce before the stigmas are receptive, and before the inner whorl elongates, allowing a brief time for cross-fertilization to take place. As they age, the stigmas curl outwards towards the anthers and the inner whorl of stamens mature, allowing for self-pollination.

In *Lychnis* and *Silene* the stamens are fused with the claws of the petals to form a short tube around the carpophore, or stalk, of the ovary. In *L. affinis,* this band was easily pulled off with forceps, the upper yellow swollen part of the nectariferous band being free from the carpophore and the lower green portion adhering loosely to it (Plate 1, Figures 5 & 6). Every stamen had contributed a nectary, rather than every second one, as in the polysepalous flowers examined.

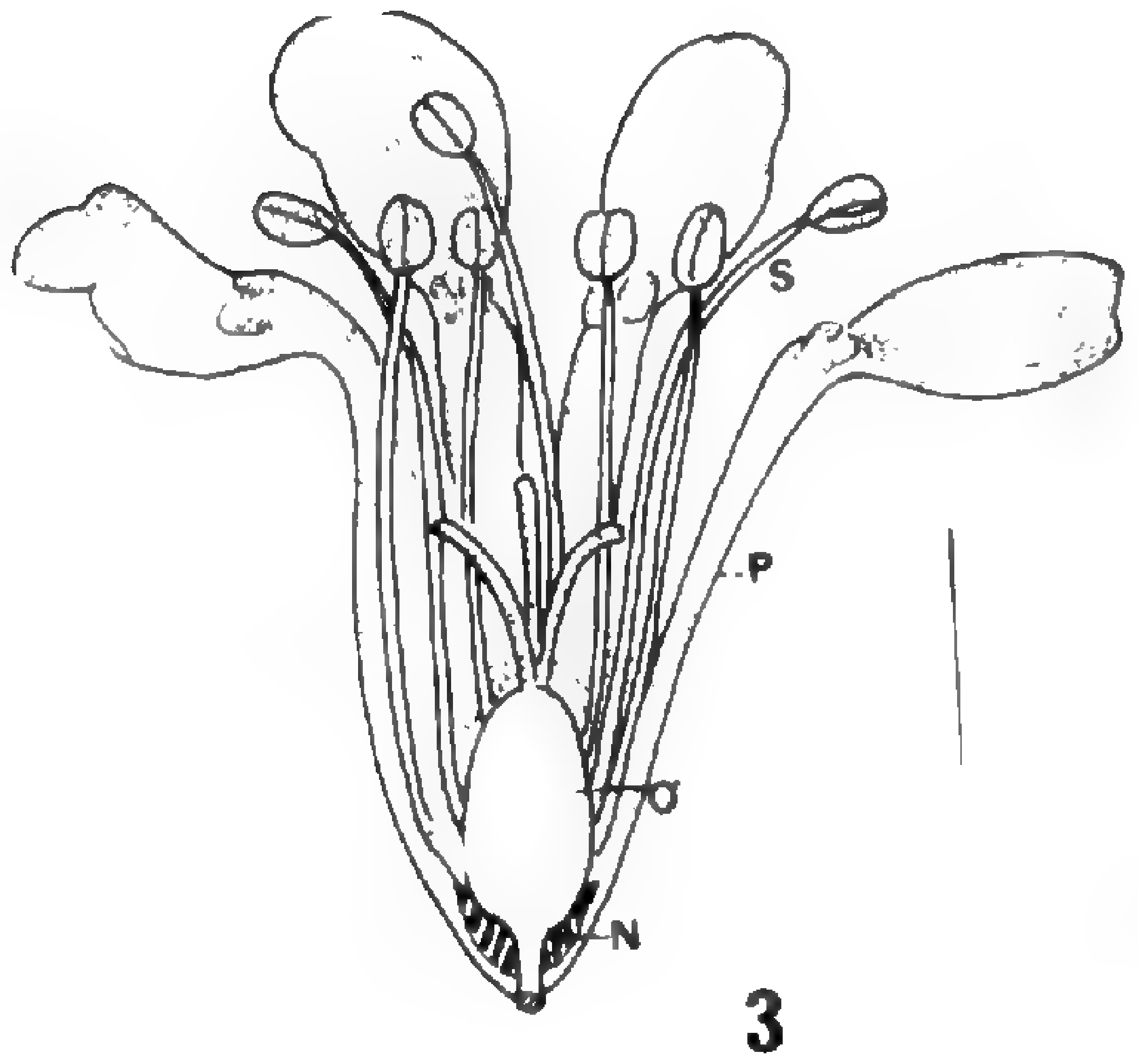
Silene acaulis also had a continuous yellowish nectary band, but when a petal was pulled off, with its fused stamen, the individual part separated readily from the rest of the band (Plate 1, Figure 4).



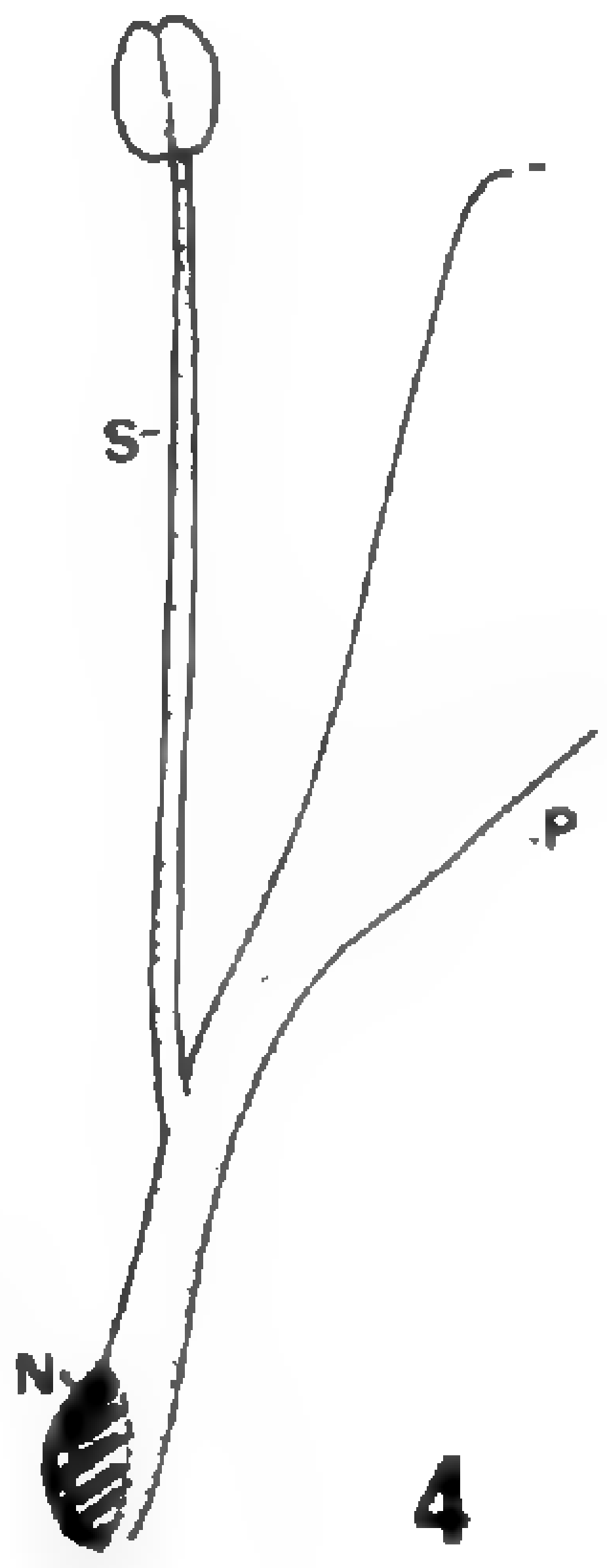
1



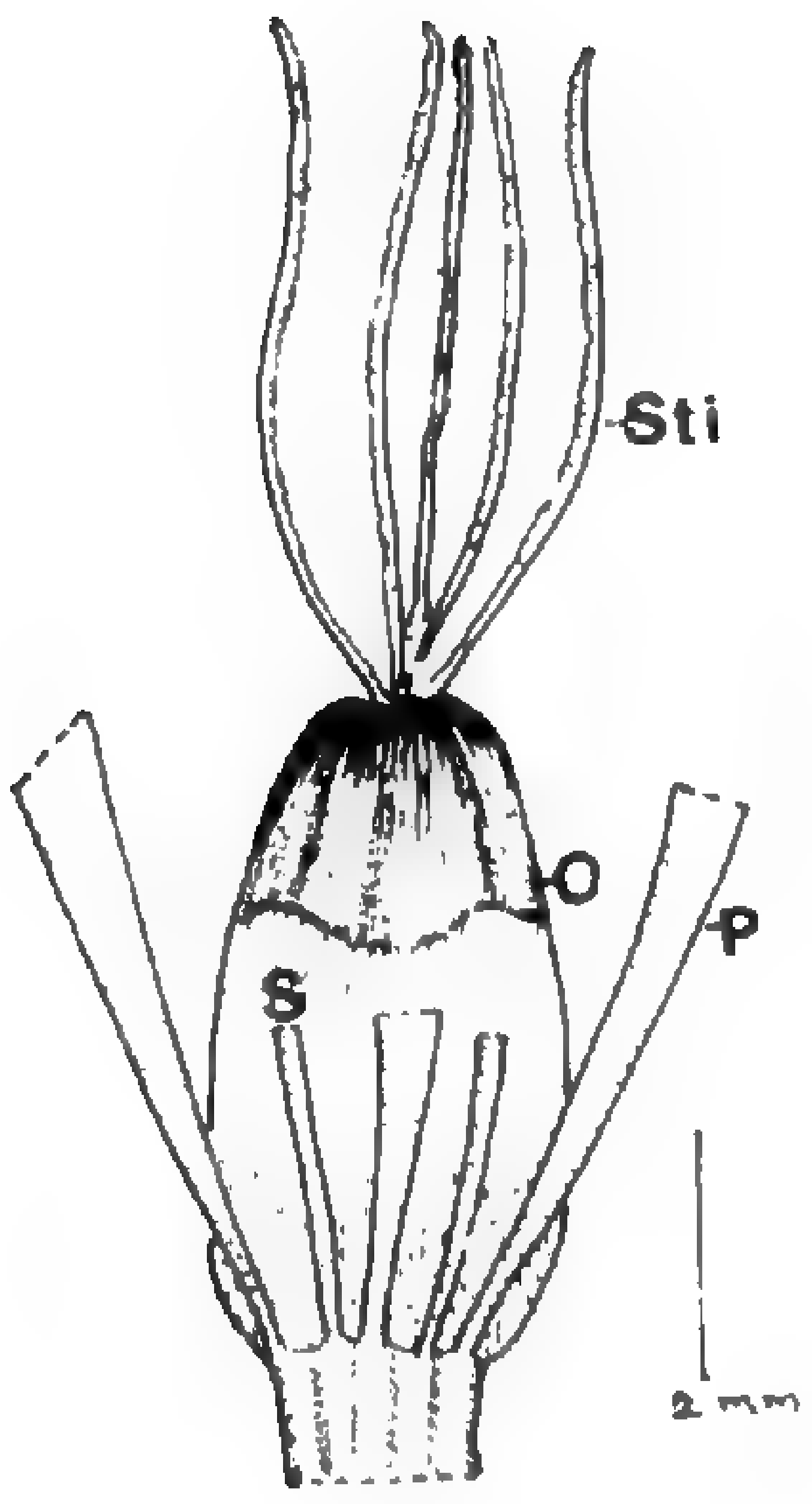
2



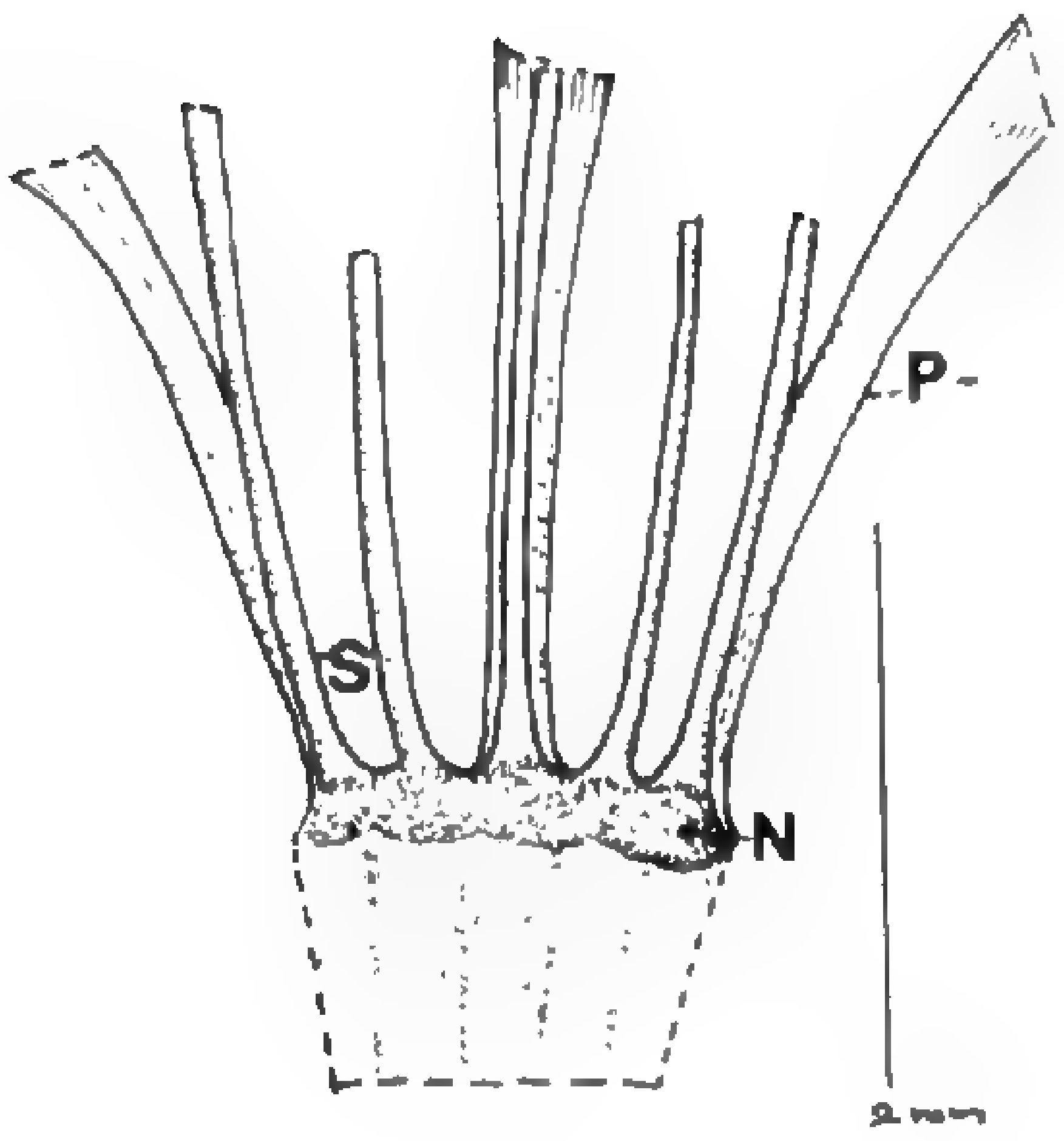
3



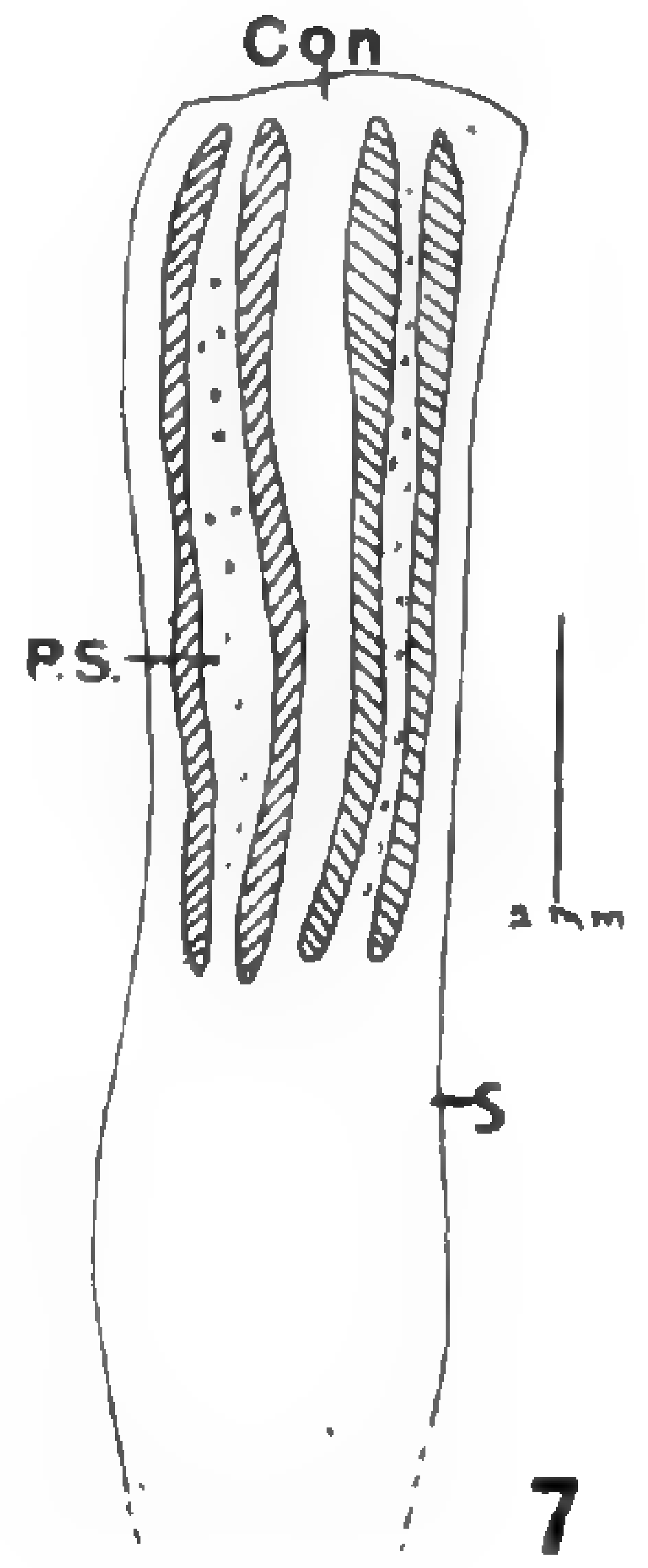
4



5



6



7

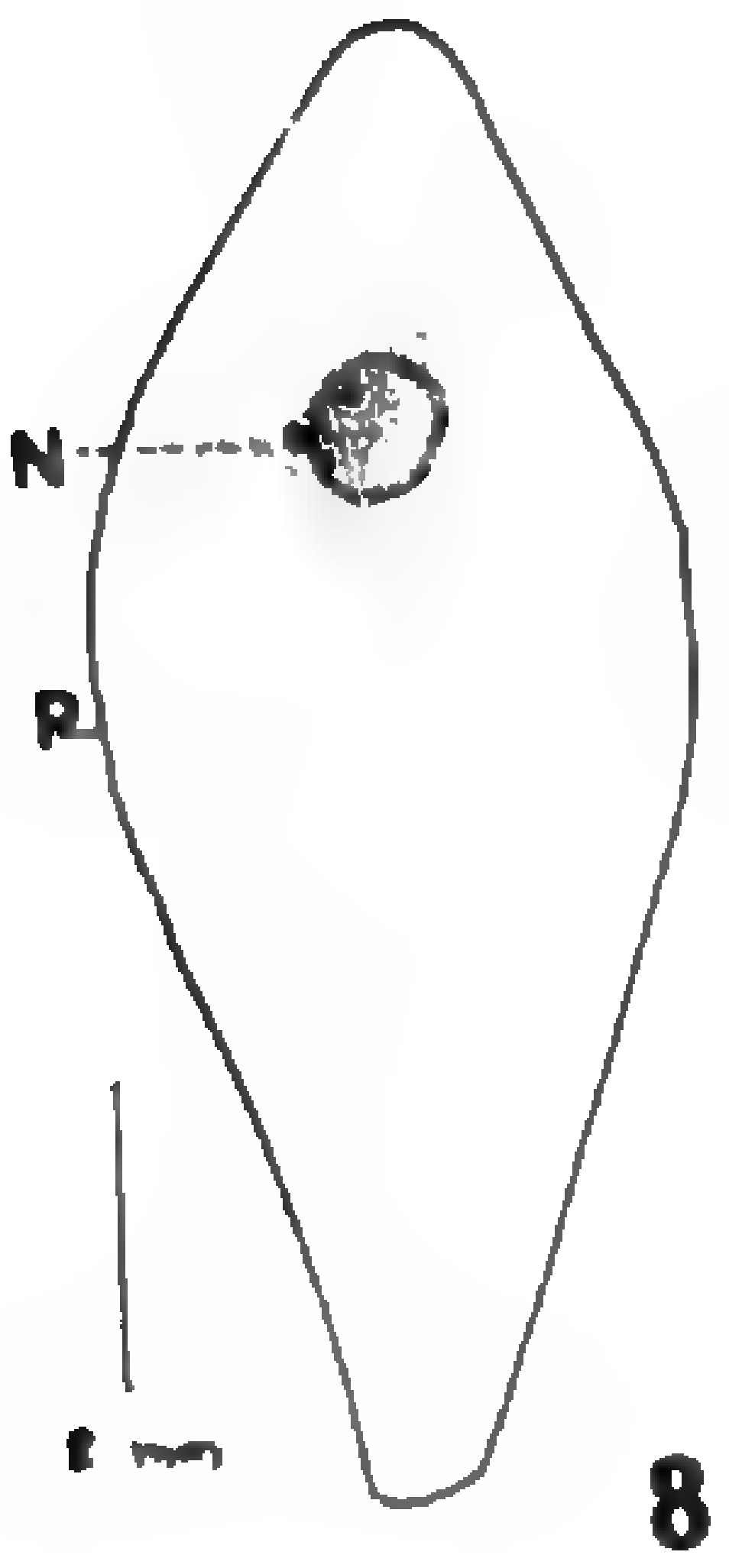
This species has three kinds of flowers, one hermaphroditic, and two unisexual types, from the partial suppression of either stamens or carpels. All three types were found at Frobisher Bay, and the extent of the suppression noted. In pistillate flowers the ovary measured 2.5 mm in height, but fleshy vestigial stamens were present, measuring 0.6–1.3 mm, either completely lacking any signs of anthers, or rarely having them represented by a slight enlarging and roughening of the top of the filaments. The typical nectariferous band was present. In staminate flowers both whorls of stamens were well developed and there were vestigial ovaries, measuring 1.4–1.5 mm in height. The stigmas had papillae measuring only 0.06 mm, obviously not receptive, although ovules were seen in the ovary. Again the nectariferous band was well developed. The hermaphroditic flowers were strongly protandrous, starting off with the male stage, with long stamens, later becoming bisexual.

NYMPHAEACEAE

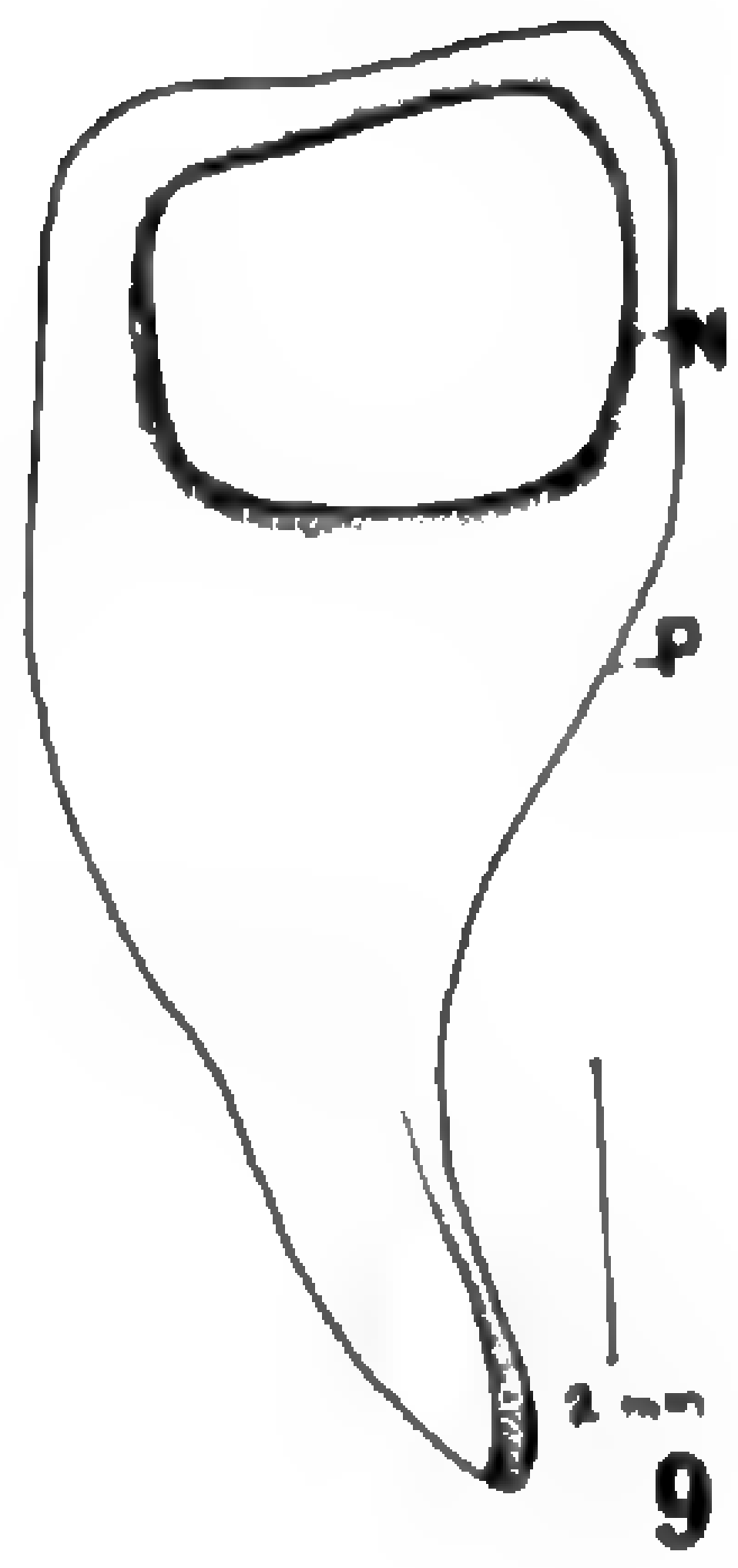
Nuphar and *Ranunculus* of the order Ranales share the primitive character of having nectaries if the form of pits in their petals, *Nuphar* on the under side of the petal next the sepals, and *Ranunculus* on the upper side next the stamens. The mechanism of pollination, however, differs markedly. In *Nuphar* a visiting insect lands on the wide platform formed by the fused stigmas of a multicarpellate ovary. The flowers are slightly protogynous, as the stigmas are fully mature when the stamens start to dehisce centripetally. The broad, flat stamens are first pressed against the ovary under the over-hanging stigma platform, but bend away from it as they mature, the anther curling slightly downwards, so that self-fertilization would seem to be improbable. Nectar collects in the angle between the petals and sepals and the nectar-seeking insect

---

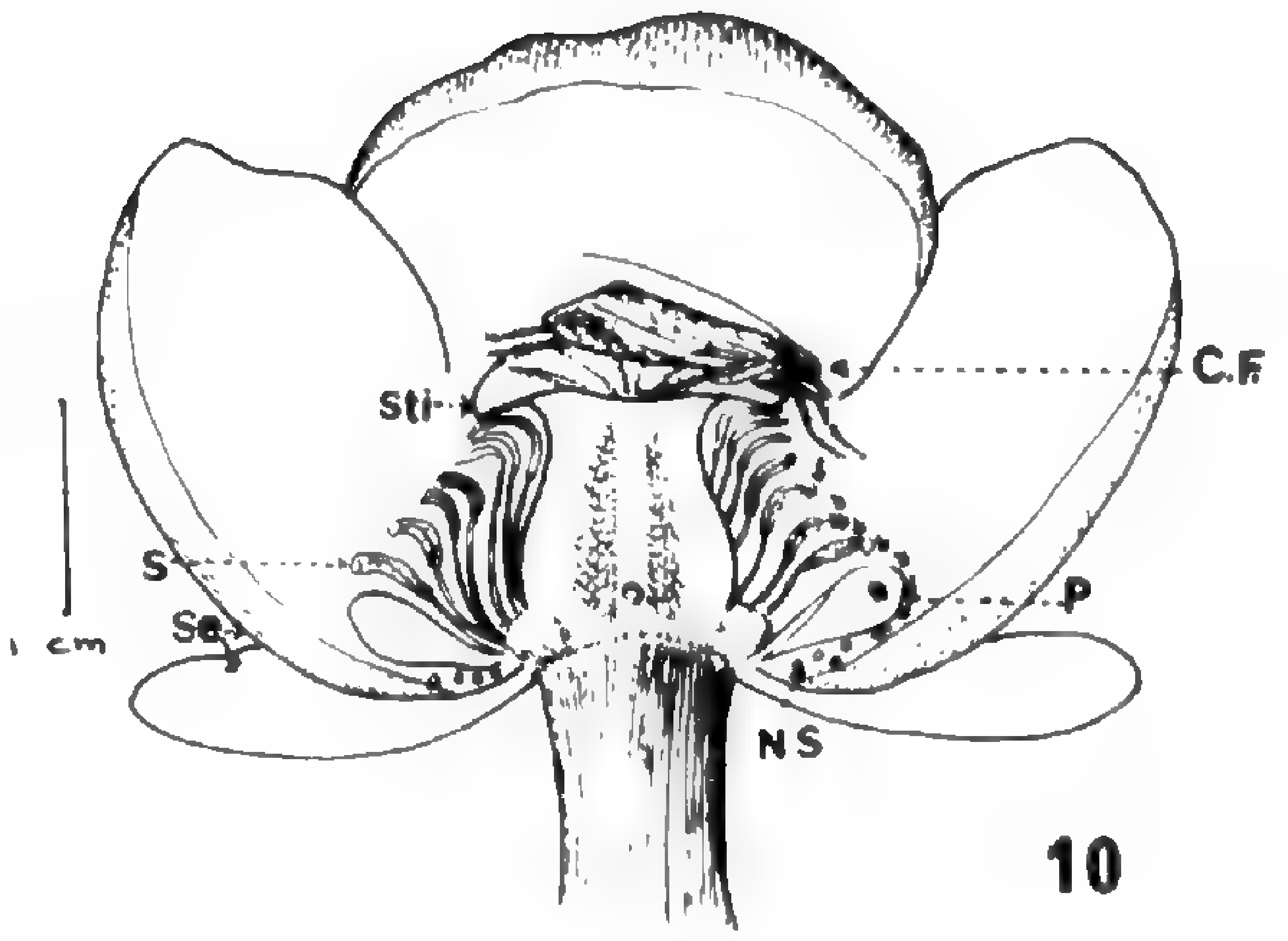
Plate 1, Figures **1–7.** **1,** *Polygonum viviparum* L. Achene, with two inner stamens and one outer shown; **2,** *Stellaria humifusa* Rottb. Yellowish-green, horseshoe-shaped nectary at base of stamens opposite sepals; **3 & 4,** *Silene acaulis* L. var. *exscapa* (All.) DC.; 3, Longitudinal section through hermaphroditic flower in male stage. Yellowish nectaries fused to base of petals, forming a band around carpophore; 4, Single petal with inner nectary; **5 & 6,** *Lychnis affinis* Fries; 5, Pistil with basal band around carpophore; 6, Segment of band removed to show free marginal nectariferous section, and lower section formerly adhering to ovary stipe; **7,** *Nuphar variegatum* Engelm. Laminar stamen. O, Ovary. STI, Stigma. AC, Achene. S, Stamen. CON, Connective. P, Petal. PS, Perianth Segment. N, Nectary. Line equals 2 mm.



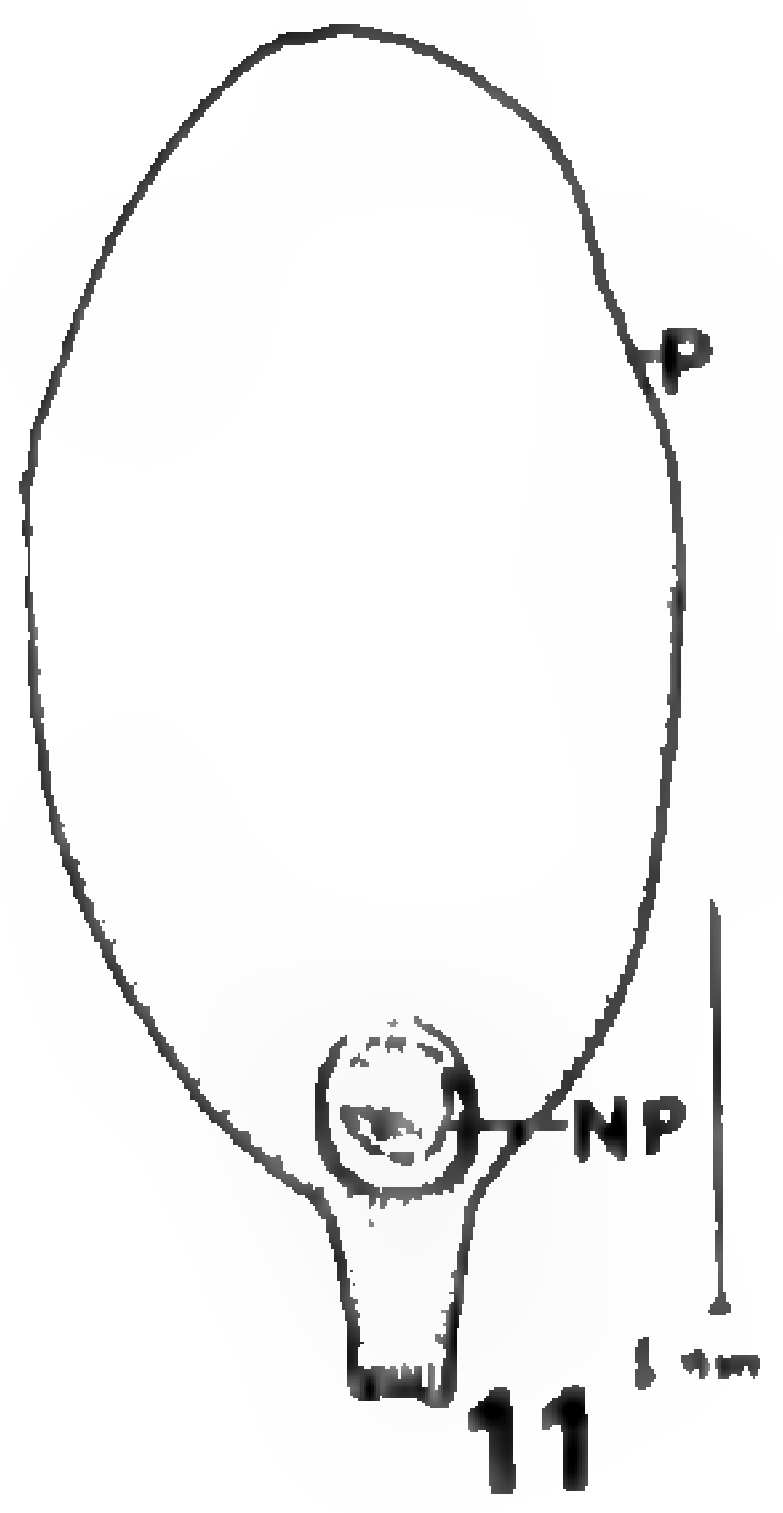
8



9

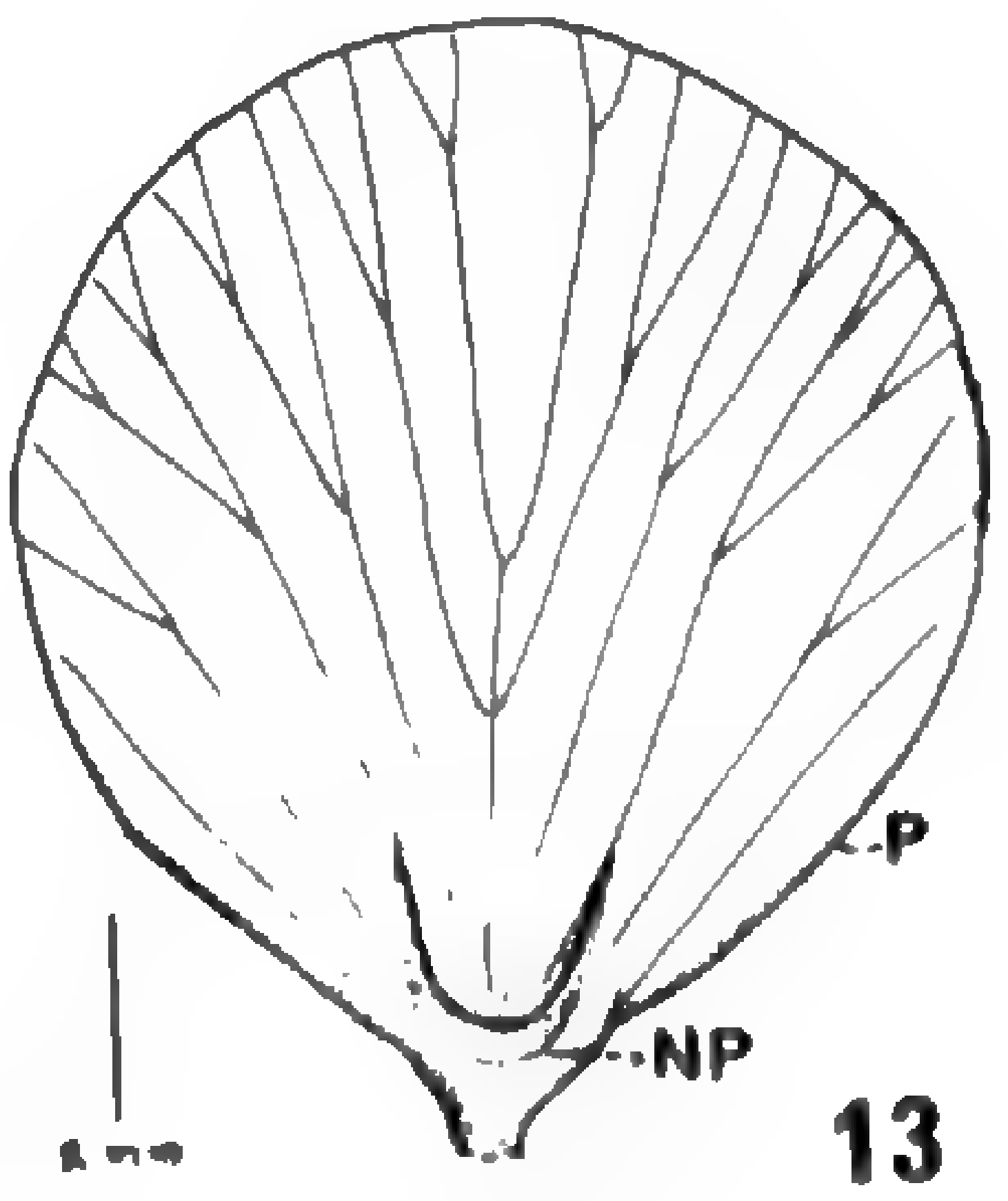


10

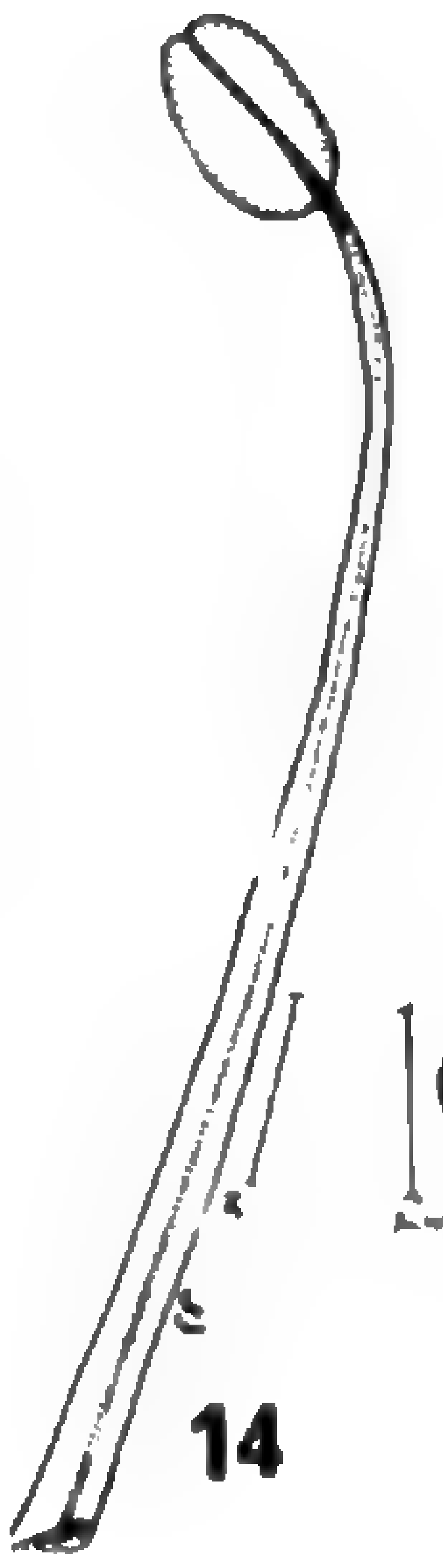


11

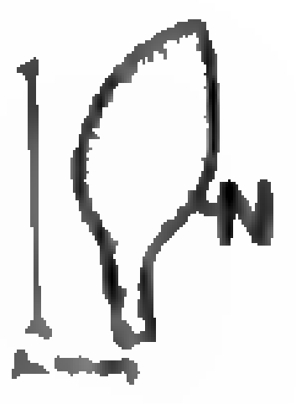
12



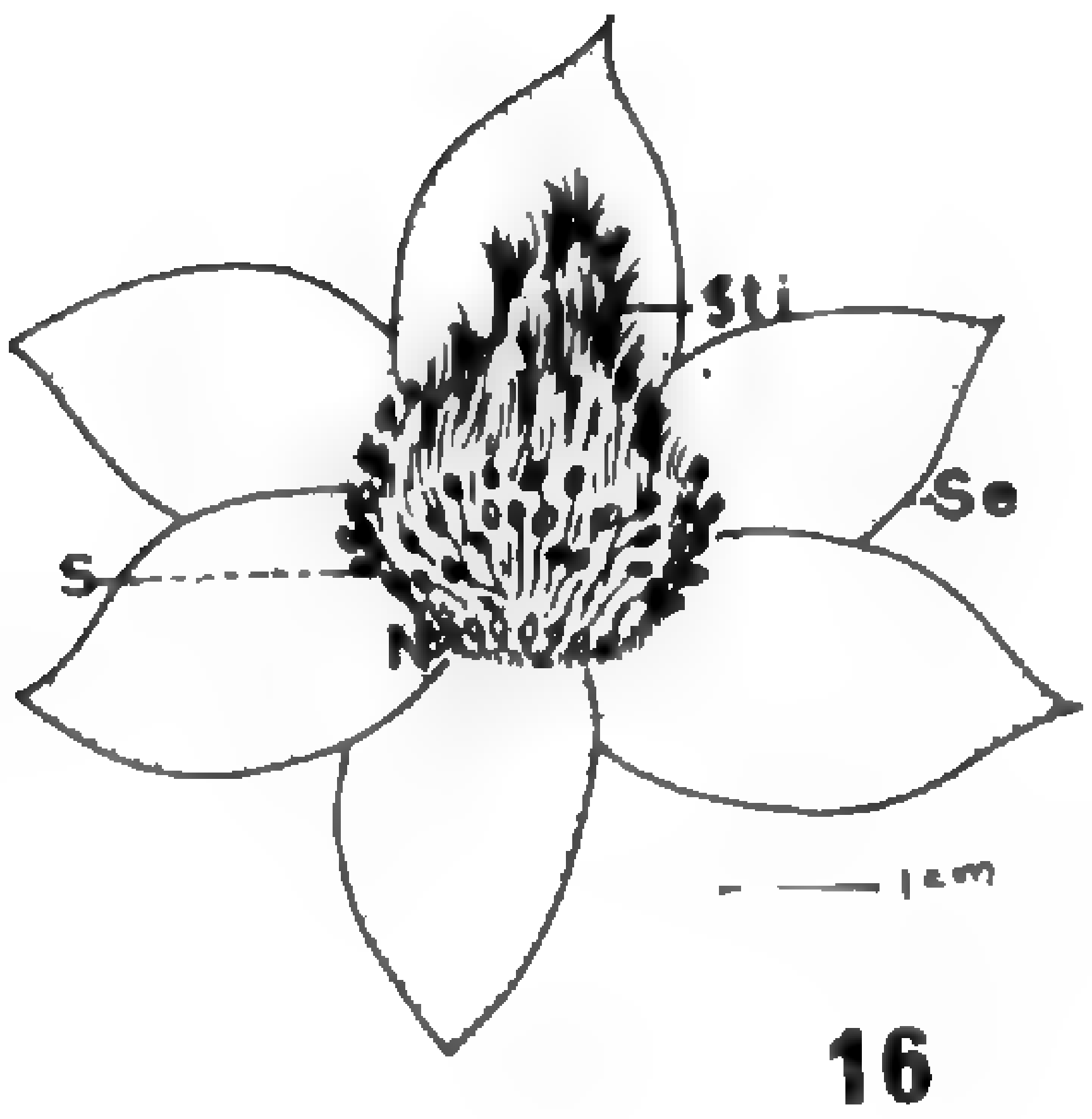
13



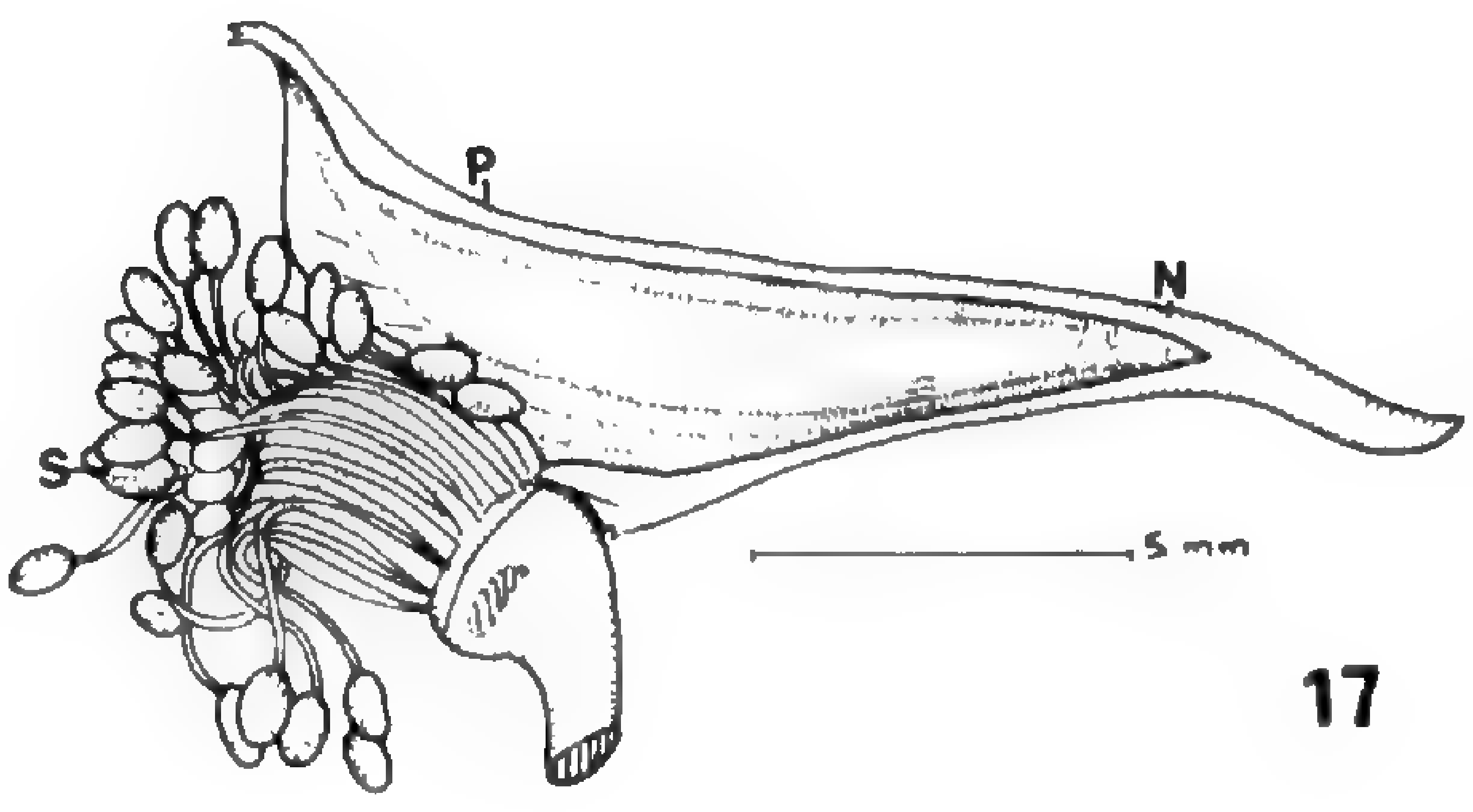
14



15



16



17

slips down an oblique slide some 14 mm long, over numerous powdery anthers, collecting pollen on his ventral surface (Plate 2, Figure 10).

Nuphar polysepalum Engelm. is widely distributed in Alaska and the Yukon, and sporadically along the lower MacKenzie River and as far east as the Anderson River (Hultén, 1968; Cody & Porsild, 1968). It was common on Shell and Hidden Lakes at Inuvik in 1965, and I found a large Caddis Fly, *Agrypnia straminea* Hagen (Phryganidae) on one flower. He was hairy on head, thorax, wing veins, and the tibia and tarsus. All parts of his body, even the smooth abdomen, were covered with the large, spiny pollen grains of this species. There was no doubt that this insect functioned as a pollinating agent (Plate 2, Figure 10).

Nuphar variegatum Engelm. is a more southern species, but occurs on the eastern flank of the Mackenzie Valley and in the Great Bear Lake corridor to the Alberta border (Cody & Porsild, 1968) as well as throughout Labrador to the tree line (Hultén, 1968). In both species the yellow sepals are large and the petals inconspicuous, about one-third as long as the sepals, but bearing nectar pits of very varied size near, or at, the tips. The pits may be as small as 1 mm and as wide as 3.5 mm, and secrete nectar copiously. (See Plate 2, Figures 8 & 9). No further collections could be made because of lack of a boat, but Phryganidae and Muscidae have been recorded on *Nuphar luteum* Sm. in Europe (Knuth, 1908), and could reasonably be expected to be pollinating agents in northern Canada.

Plate 2, Figures **8–17.** **8–10,** *Nuphar polysepalum* Engelm; 8 & 9, Under side of petal showing variation. Stamen as in *N. variegatum;* 10, Longitudinal section of flower with caddis fly, *Agrypnia straminea* Hagen (Phryganidae) on stigma, arrows show route to nectar. Outer stamens dehiscing, inner ones still appressed to style; **11 & 12,** *Ranunculus hyperboreus* Rottb; 11, Petal with minute nectary pit; 12, Enlargement of nectary pit; **13,** *Ranunculus pedatifidus* Sm. Petal with nectary pit; **14–16,** *Anemone patens* (L.) ssp. *multifida* Pritzel (=*Pulsatilla patens* L.) Mill; 14, Normal stamen; 15, Stamen modified as nectary; 16, Flower showing outer stamens modified as nectary glands; **17,** *Delphinium glaucum* L. Internal view of one of the two petals modified as nectaries. N, Nectary. NP, Nectary Pit. NS, Nectar Storage. S, Stamen. P, Petal. SE, Sepal. STI, Stigma. CF, Caddis Fly. Line equals 2 mm except in Figure 11 equals 1 mm, in Figure 17, 5 mm, and in Figures 10 & 16, equals 1 cm.

RANUNCULACEAE

Some genera of the northern Ranunculaceae produce no nectar, *Thalictrum* and non-plumose Anemones. The large-flowered *Anemone narcissiflora,* common on Keno Hill, Y.T., was dry, but with abundant pollen to attract pollen-eating insects. Most genera of this family are nectar producing and show unusual variation in nectary types, from simple circular pits at the base of petals in *Ranunculus hyperboreus,* to elaborately modified petals in *Aconitum* and *Delphinium.*

Ranunculus acris, apomictic in Spitzbergen (Polunin, 1959) but principally cross-pollinated according to Fryxell (1957), is now introduced as far north as Fort Smith in the N.W.T. (personal communication, W. J. Cody). This species, and *R. abortivus,* which occurs in the Mackenzie Mts. (Cody & Porsild, 1968) and in the Yukon (Hultén, 1968), have nectary pits at the base of each petal, covered by an upward-directed fleshy scale. *Ranunculus pedatifidus* has a crescent-shaped depression, with a slight infolding of the petal tissue above it at the two sides, suitable for storing minute quantities of nectar (Plate 2, Figure 13). *Ranunculus nivalis* has a pit 0.8 mm wide with a thickened petal ridge beneath it. *Ranunculus hyperboreus* has a minute pit surrounded by a circular ridge on petals as small as 0.3 mm. It is below the size likely to attract insects, and is listed by Fryxell (1957) as possibly apomictic (Plate 2, Figures 11 & 12).

The stamens in *Ranunculus* move away from the pistils as they mature, and the anthers dehisce laterally, allowing pollen to fall on both petals and filaments, to be picked up easily by short-tongued insects seeking pollen or nectar. Hocking (1968) found no nectar in *R. hyperboreus,* and although I saw no nectar on *R. nivalis* in the field there appeared to be dried nectar at the base of petals on some herbarium specimens.

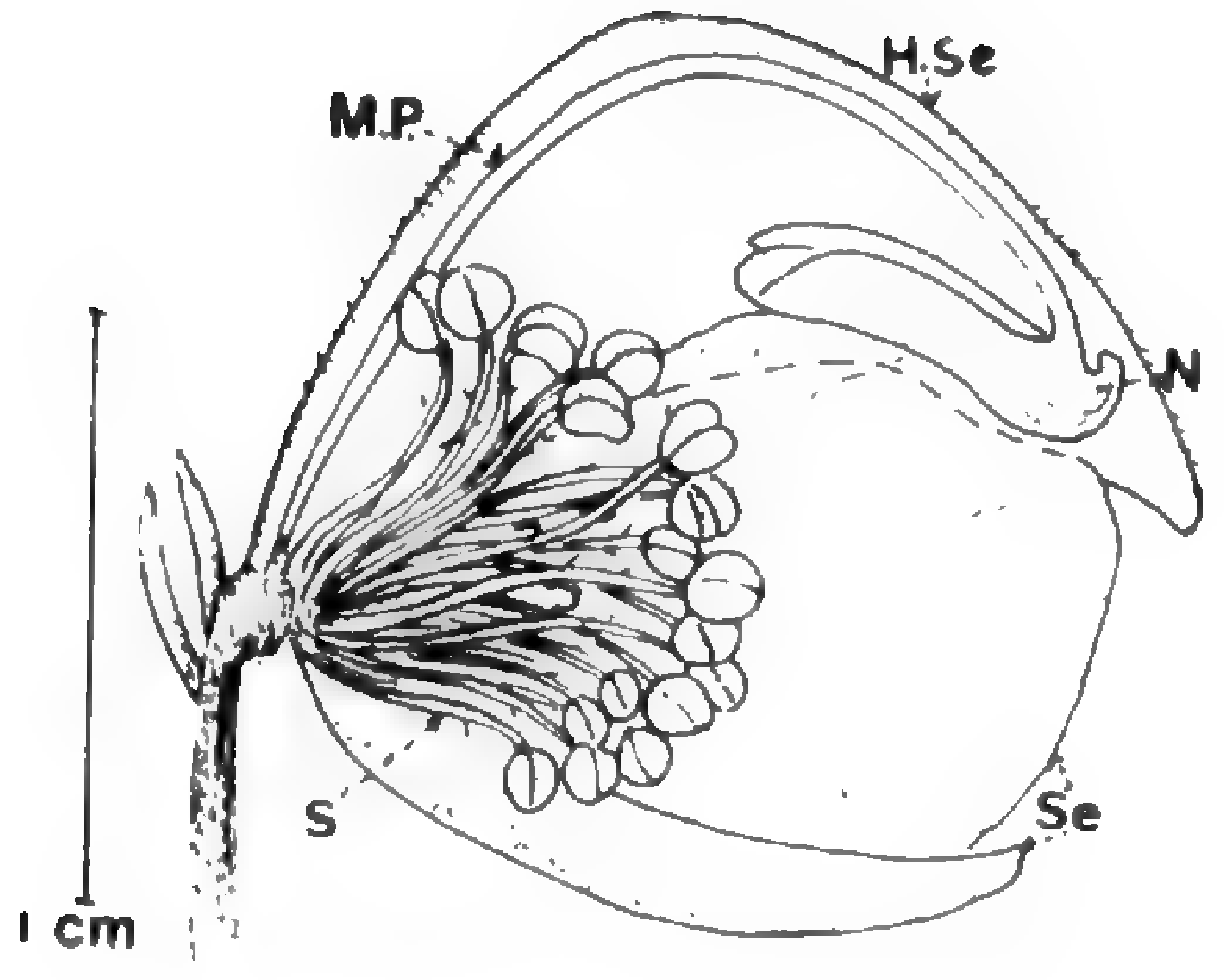
Pulsatilla is recognized as a genus separate from *Anemone* by some authors, based on its possession of long plumose styles. Yuzapchuk, in the Flora of the U.S.S.R. (V. L. Komorov, ed., Vol. VII, 1937) lists 26 Asiatic and European species of *Pulsatilla,* 24 of which have the outer stamens adapted as nectaries. Only one of these, *P. patens* (L.) Mill., (=*Anemone patens* L.) reaches Canada It was in bloom July 12, 1965, at Tuktoyaktuk, N.W.T., and the outermost 12–14 stamens were reduced from the normal 7–13 mm length, with cream-coloured anthers, to amber-coloured stalked nectaries 2 mm (or slightly more) in length (Plate 2, Figures 14–16). The large flowers, attractive to bees, are protogynous at first, stigmas projecting well beyond the longest stamens, so that cross-pollination at an early stage would seem likely.

The side of a small stream at Keno Hill, Y.T., yielded *Aconitum delphinifolium,* in the flowers of which the two petals were modified to two independent, long-stalked nectaries. The stalk had a channel some 9 mm long, followed the curve of the upper hooded sepal and ended in a purplish receptacle for nectar, open at the distal end like a trough, and closed at the proximal end within and near the tip of the hood (Plate 3, Figures 18–21). The closed dilated end has fleshy walls which secrete the nectar. The two lateral sepals were marked with dark veins acting as nectar guides, and an opening 7 mm wide was left for the entrance of insects between the hood and the two lower boat-shaped sepals. *Bombus frigidus* Sm. and *Bombus polaris* Curt. were seen to enter the opening readily, and passed over the stamens in an upside-down position, in order to insert the proboscis down the stalk channel to the nectar receptacle. The protandrous stamens, as in *Delphinium,* completely hid the immature pistils until the pollen was discharged, making cross-pollination obligate.

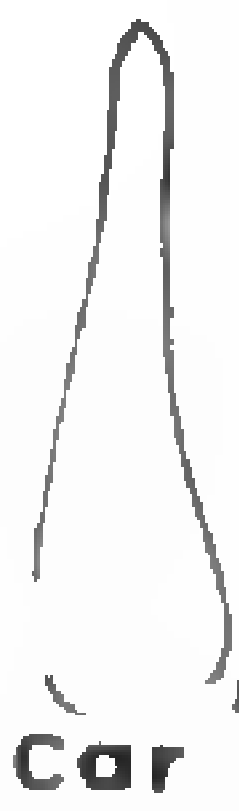
Dawson City, Y.T., was my source of *Delphinium glaucum.* In this blue flower the two petals were less completely modified than in the above, and fitted neatly into the spur of the upper sepal. Each had an open inner side which fitted together to form a channel posterior to the stamens (Plate 2, Figure 17) and into which a *Bombus* could push its head, extending its proboscis to reach the nectar secreted by the thickened petal wall within the spur. The nectary ended in a solid tip 4 mm long. Both protandrous genera, *Aconitum* and *Delphinium* are confined to areas in which bumblebees occur, as they require insects with long probosces to reach the nectar and accomplish cross-pollination.

CRUCIFERAE

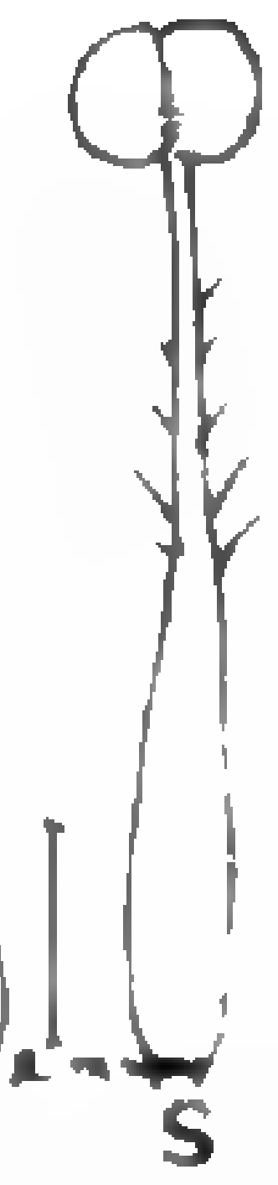
A very limited number of arctic Cruciferae have flowers large enough to attract insects in spite of the fact they are borne in corymbs or racemes. *Parrya nudicaulis, Cardamine pratensis, Arabis alpina,* and *Erysimum pallasii* are among the largest, and the



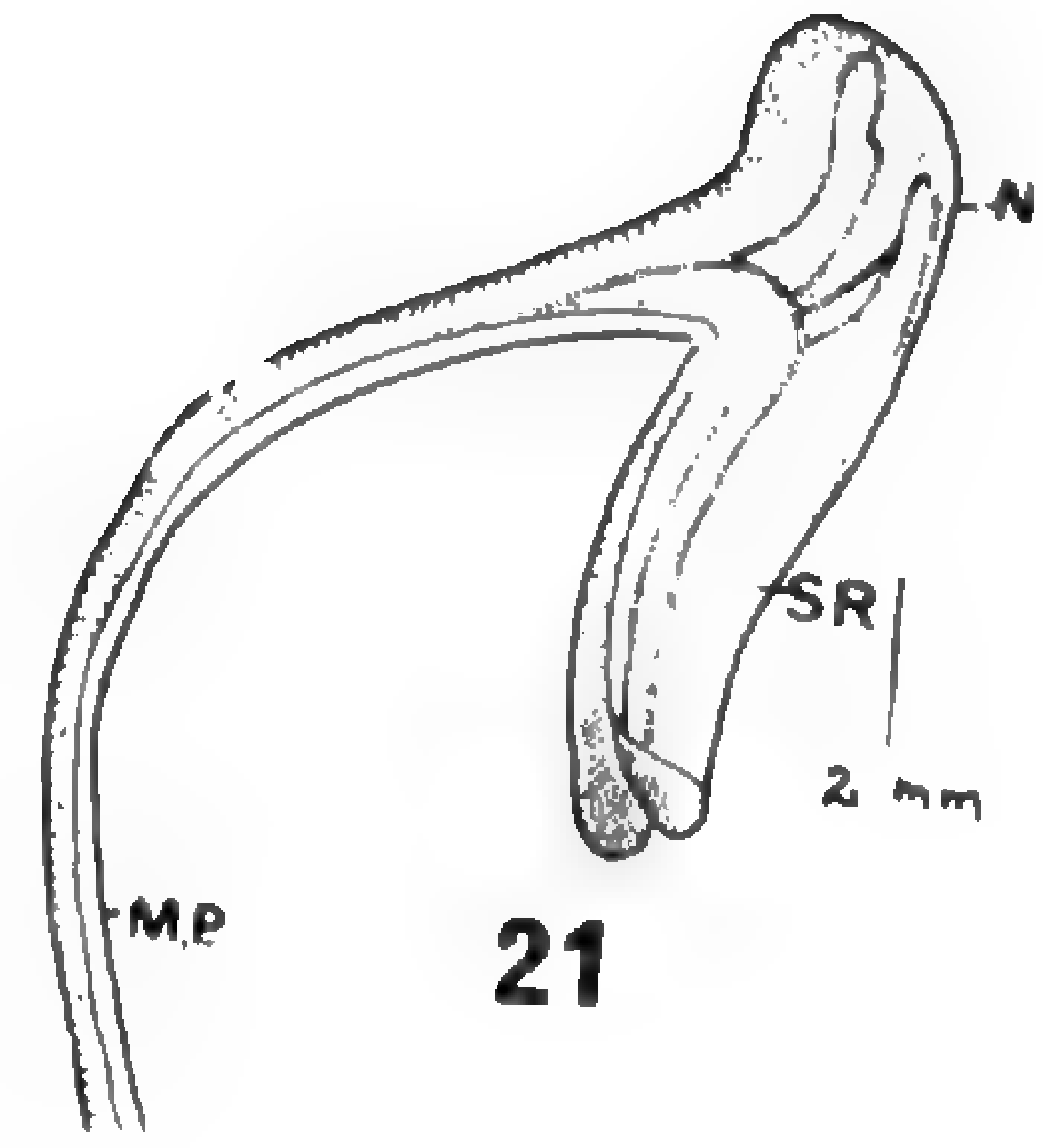
18



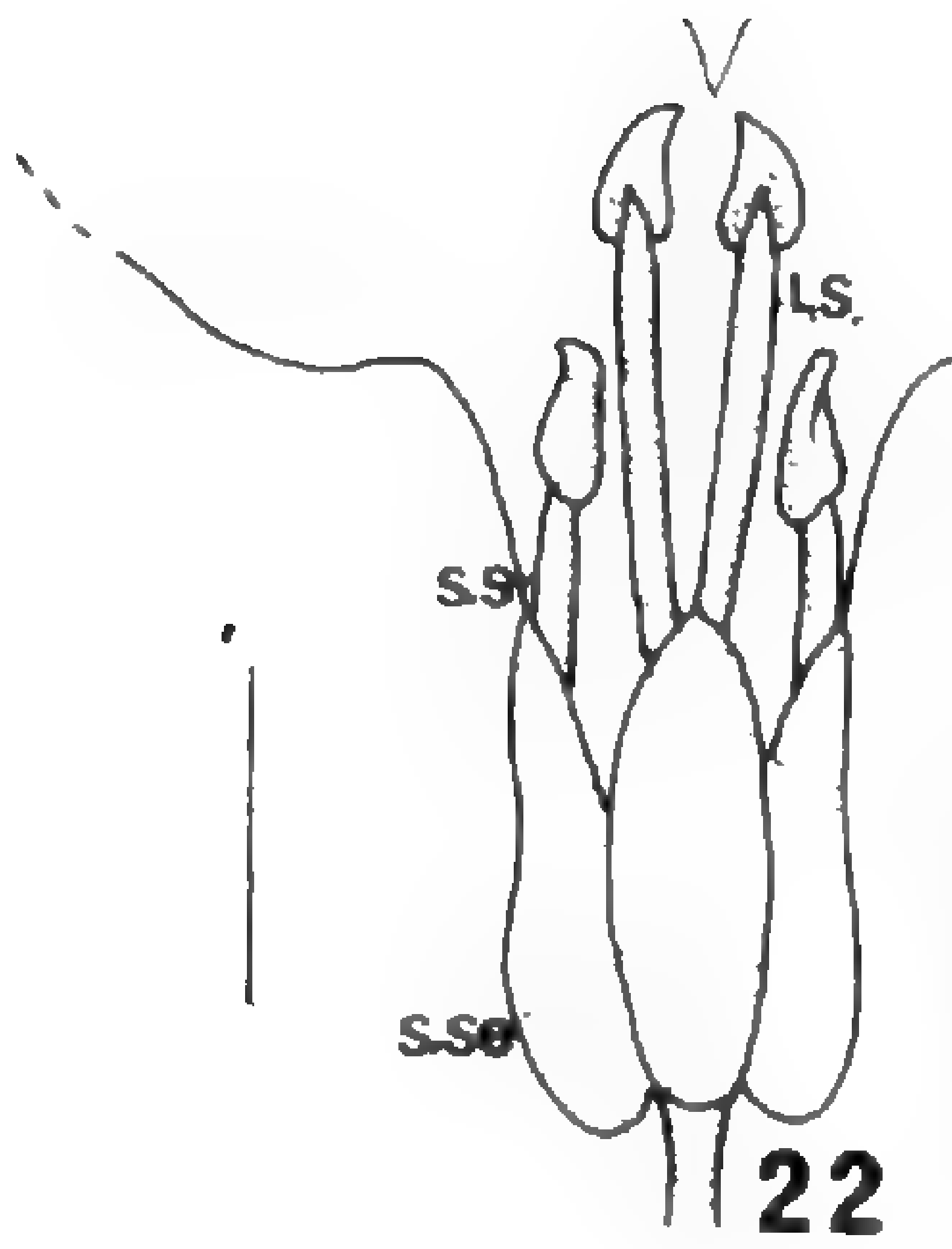
19



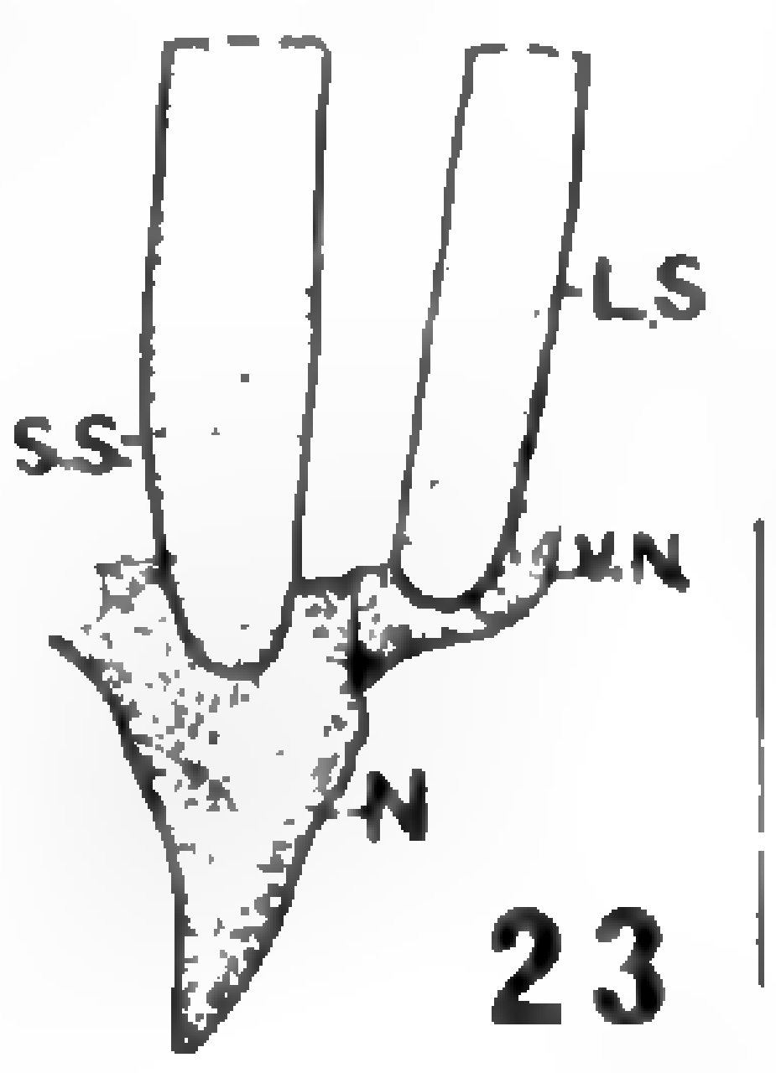
20



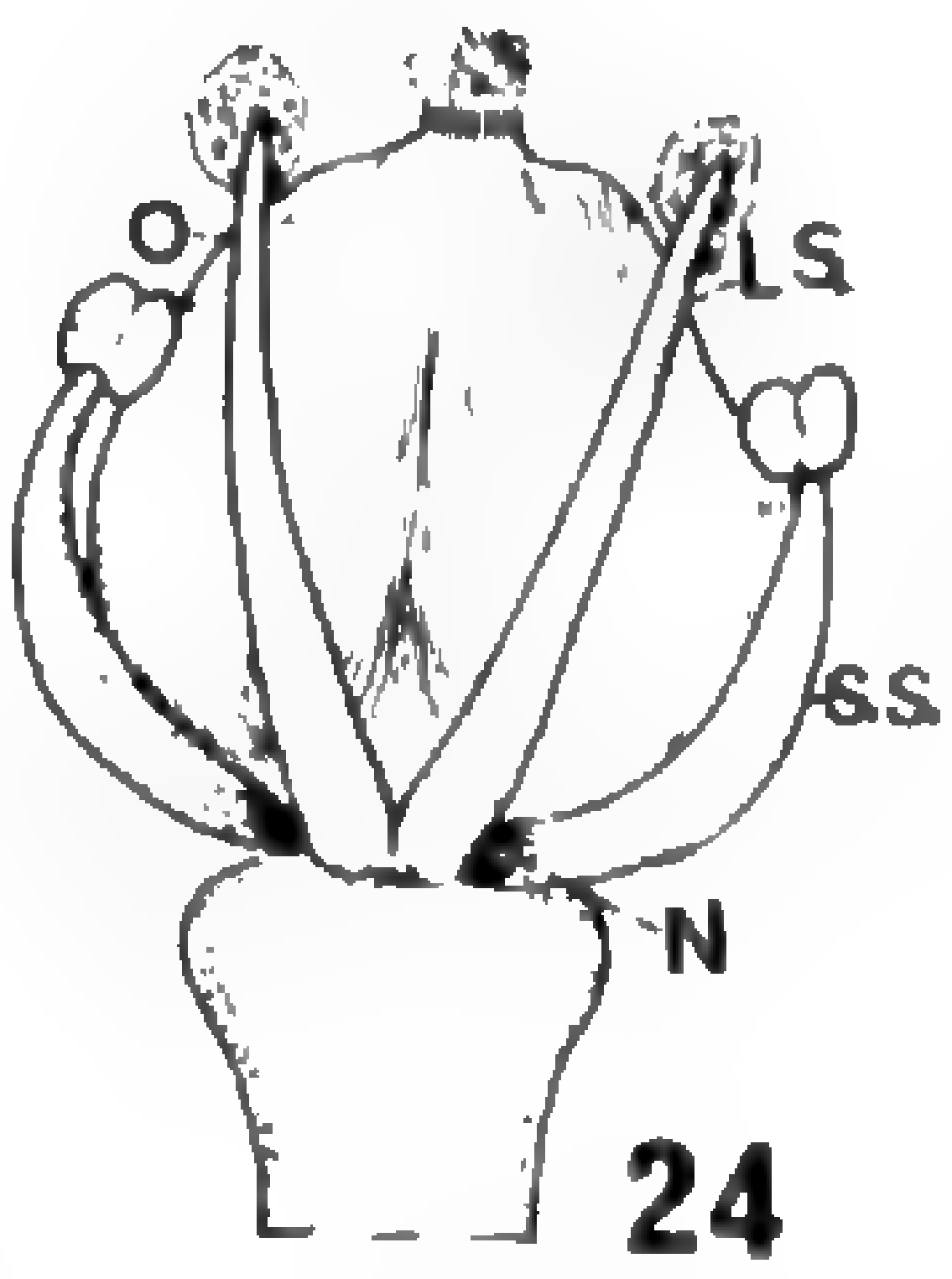
21



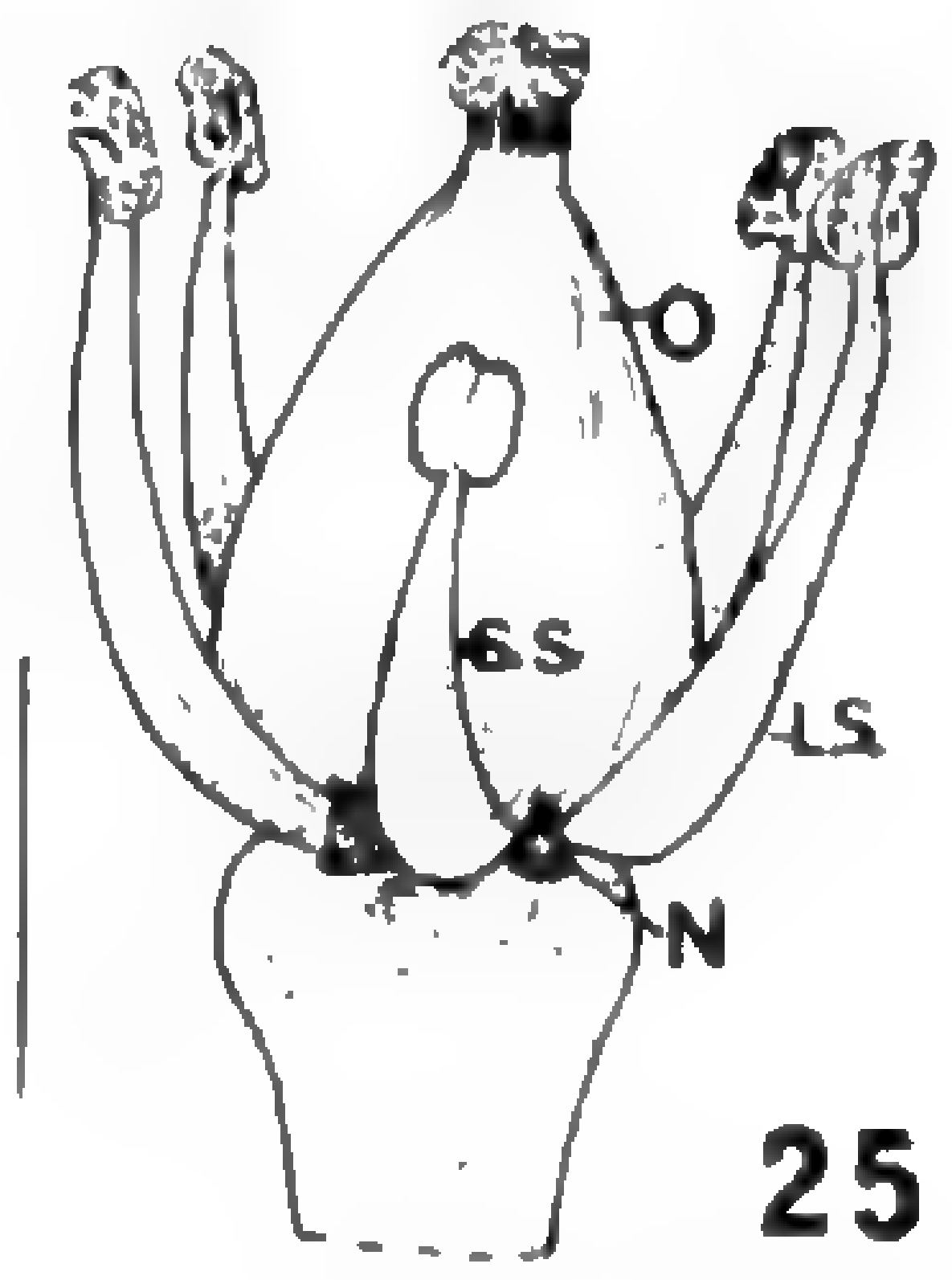
22



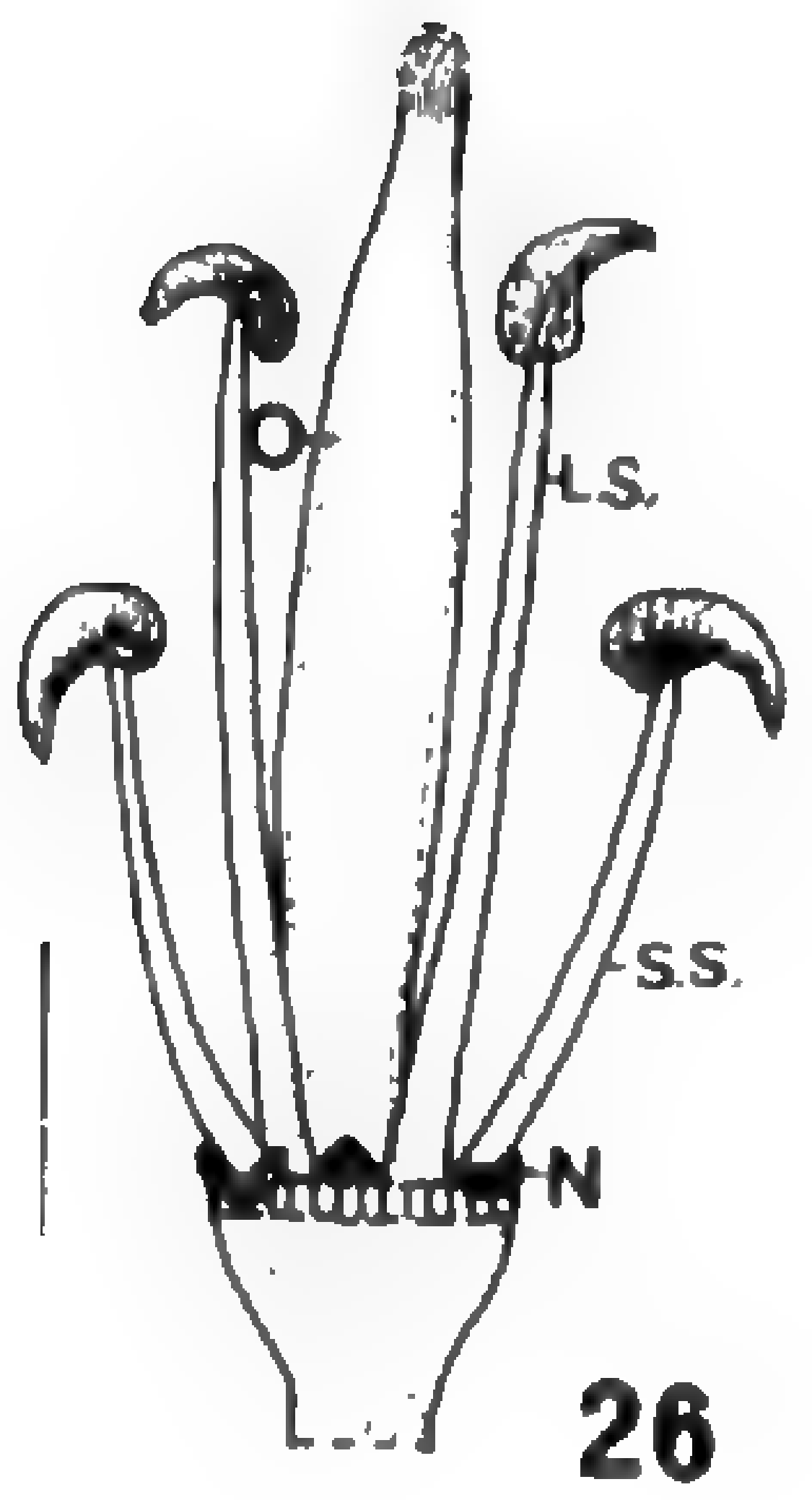
23



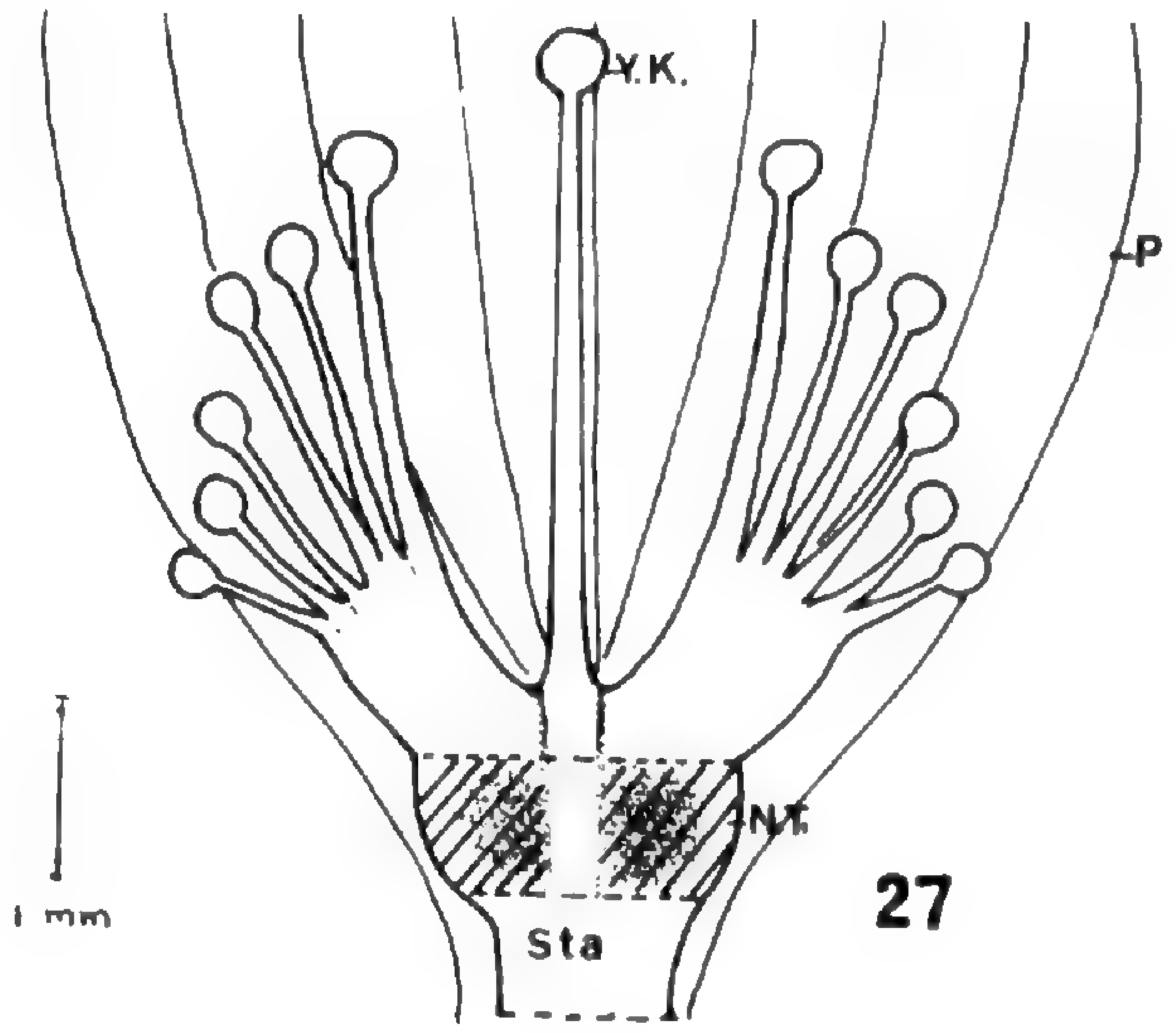
24



25



26



27

first three are probably apomictic. The sweet-scented *Erysimum pallasii* is self-fertilized. Many of the smaller ones, *Lesquerella arctica,* and at least six of our northern Drabas are capable of self-fertilization. Mulligan (1966; and Mulligan & Findlay, 1970) discovered that one of his experimental ones, *Draba oligosperma,* and also *Erysimum inconspicuum,* were apomictic. He adds that, given good weather, some out-crossing occurs in the Drabas and probably in other self-compatible Cruciferae.

In spite of the possible reduction or loss of functional significance of nectaries in arctic Cruciferae, nectaries are present in all species at the base of the short stamens. They contrast in colour from the staminal filament (ex. yellow filament and green nectaries in *Draba nivalis*) and vary in shape and size from species to species. *Cochlearia officinalis* has a very small wart-like nectary on either side of the short stamens (Plate 3, Figures 24–25), the Drabas have somewhat larger warts, *Parrya arctica* has nectaries like flat triangles, and *Arabis alpina* (Plate 3, Figures 22 & 23), a single conspicuous green flap beneath the short stamens connected laterally to a nectariferous ridge at the base of the long stamen next to it. *Cardamine pratensis* has a single horseshoe-shaped nectary around each short stamen, open on the side next the ovary (Plate 3, Figure 26), *Erysimum cheiranthoides* the same type, but open on the outside. The long stamens, too, may have nectaries between their bases, a triangular one in *C. pratensis* (Plate 3, Figure 26), a flat vestigial one in *E. cheiranthoides,* or they may be missing entirely,

---

Plate 3, Figures **18–27. 18–21,** *Aconitum delphinifolium* DC.; 18, Section through flower, stamens hiding immature carpels; 19, Carpel; 20, Stamen; 21, Petal modified as nectary; **22 & 23,** *Arabis alpina* L.; 22, Saccate lateral sepals modified to store nectar; 23, Ear-like nectary at base of short stamen, vestigial nectary at base of long stamen; **24 & 25,** *Cochlearia officinalis* L.; 24, Median view showing stamens closely appressed to ovary; 25, Lateral view showing small wart-like nectaries at each side of short stamen; **26,** *Cardamine pratensis* L. (Apomictic in Arctic, not necessarily obligate, Fryxell, 1957). Anthers discharged, ovary elongating. Horseshoe-shaped nectary outside short stamens, conical nectary glands between long stamens; **27,** *Parnassia palustris* L. Staminode with short stalk, broadening into a thicker green band, the nectary, and then a blade with nine to many capitate filaments. MP, Modified Petal. SR, Storage Receptacle. HSe, Hooded Sepal. N, Nectary. VN, Vestigial Nectary. S, Stamen. STA, Staminode. YK, Yellow Knob. NT, Nectariferous Tissue. SS, Short Stamen. LS, Long Stamen. CAR, Carpel. O, Ovary. Line in Figure 18 equals 1 cm; in Figure 27, 1 mm; in Figures 19–26, 2 mm.

as in the Drabas. The numerous variations in nectaries of the Cruciferae of Europe are well illustrated by Hegi (1958).

The cruciform shape of the corollas in the family does not attract insects for basking, lacking the warmth found in sunshine within the cup-shaped forms of *Dryas* or *Stellaria*. As well, many bloom very early in the season when weather conditions preclude much insect activity. It is probable that many are self-pollinated in the Arctic. Few insect visitors to the white-flowered Cruciferae were noted by Kevan (1972) at Lake Hazen, or by me at Frobisher Bay.

Although the flowers of Cruciferae in general are slightly protogynous, the anthers of the young flowers may be above the stigma and capable of dropping pollen on it as they dehisce, or if below it, usually elongate and brush against the stigmas at maturity, producing self-pollination. Mulligan and Findlay (1970) noted the stigma of *Draba* was receptive some five and a half hours before the long stamens grew to its level, and discharged their pollen. The short stamens elongate later, giving still another chance for selfing.

SAXIFRAGACEAE

The genus *Saxifraga* is represented by 14 species in the Arctic Archipelago (Porsild, 1964), some reaching the northern limit of land. My studies have been primarily on the variation in position of the ovary, from superior to partly or wholly inferior, and the changes in the relative position and type of the nectary, with some observations on the movement of stamens.

The records in the floras on the position of the ovary vary greatly, partly due, in protandrous species, to the gradual upward growth of the ovary as the stamens dehisce, and the stage at which it was described. For example, Hitchcock *et al.* (1961) noted that the ovary of *Saxifraga cernua* was one-quarter inferior at anthesis, less so at maturity; Hegi (1961) said it was one-third inferior, and Komorov (1939) that it was half inferior. My own observations agreed with Hitchcock. I made longitudinal sections of mature flowers of the species studied, noting the percentage of ovule-bearing tissue above and below the point of attachment of the stamens, finding some variation between populations.

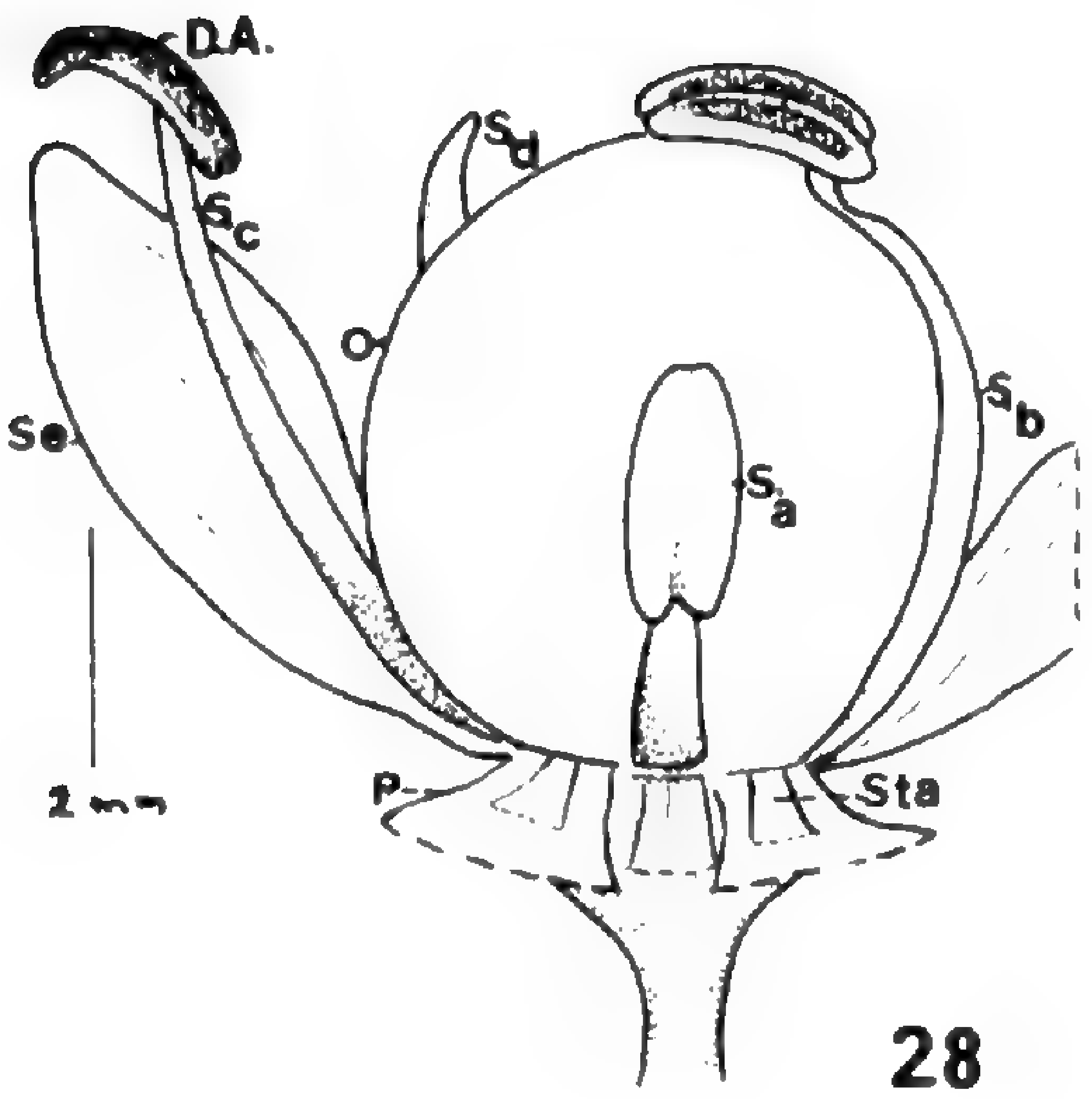
In *Saxifraga* the nectary is either in the form of a band at the base of the ovary (with the nectar exposed in open-type flowers, and half-concealed when the petals remain close to the stamens and ovary), or in the form of an epigynous disk on the top of inferior ovaries, where it is exposed and easily reached by short-tongued insects.

The nectary band in species with superior, or nearly superior, ovaries (ex. *Saxifraga davurica, S. foliolosa, S. hirculus,* and *S. cernua*) is not marked by any swelling, but merely by a change of colour or texture, the commonest being a change from a green or purplish ovary to a yellow-green nectary band, or sometimes from a purple ovary to a narrow green band, the nectary always with a shiny smooth surface. The colours of ovary and nectary may vary with the habitat, but the two can be distinguished easily in freshly-picked specimens.

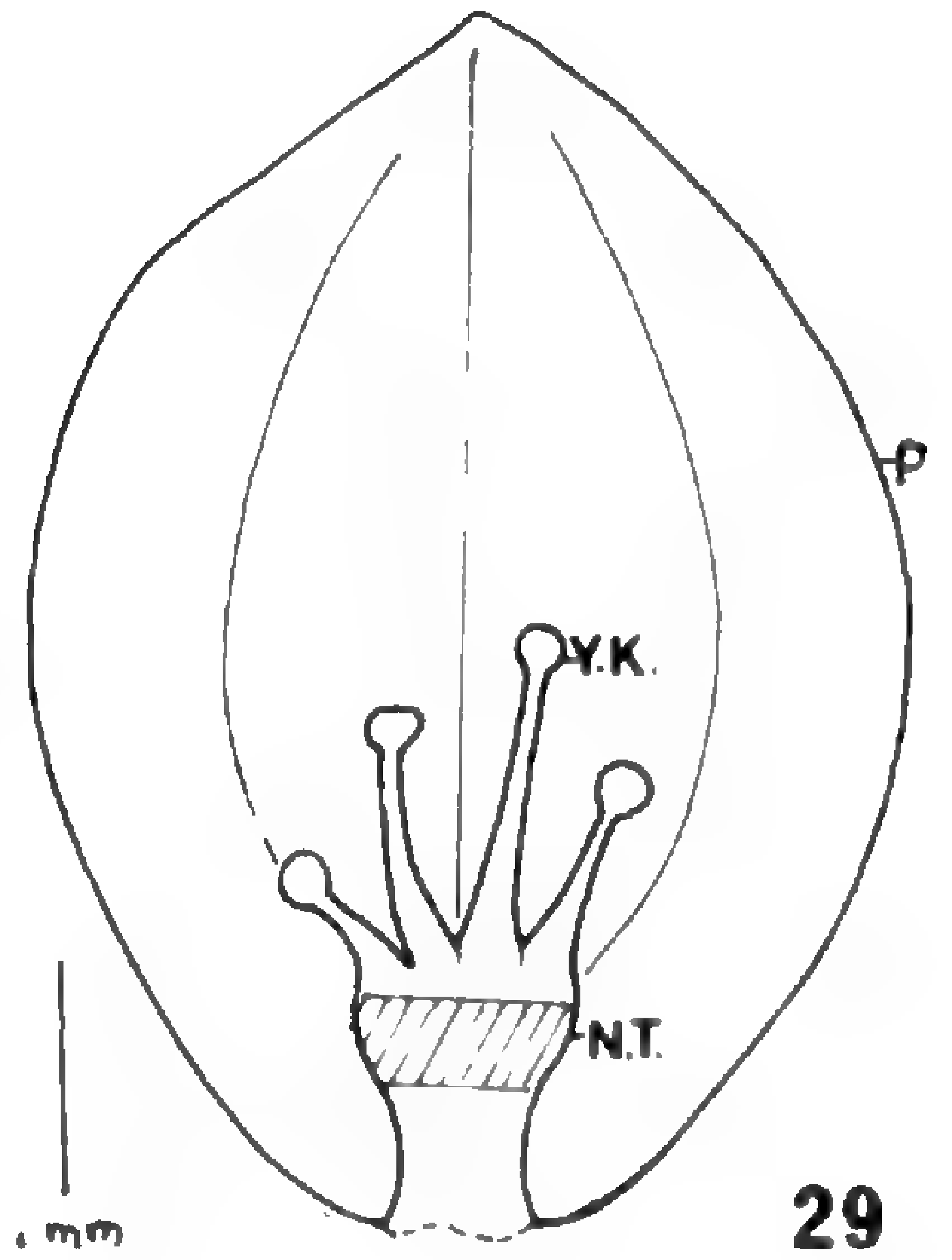
At Frobisher Bay, no free nectar was noted in *Saxifraga rivularis,* a species with about a one-third inferior ovary, and no distinctive nectary band was seen, although there was a slightly yellower colour at the base. It seemed as though this small species with inconspicuous flowers would not be attractive to insects and was self-pollinated.

The nectaries of *Saxifraga* species with partly inferior ovaries, such as *S. aizoides, S. hieracifolia,* and *S. nivalis* are conspicuous as more or less swollen bands, usually of a more yellow colour than the ovary.

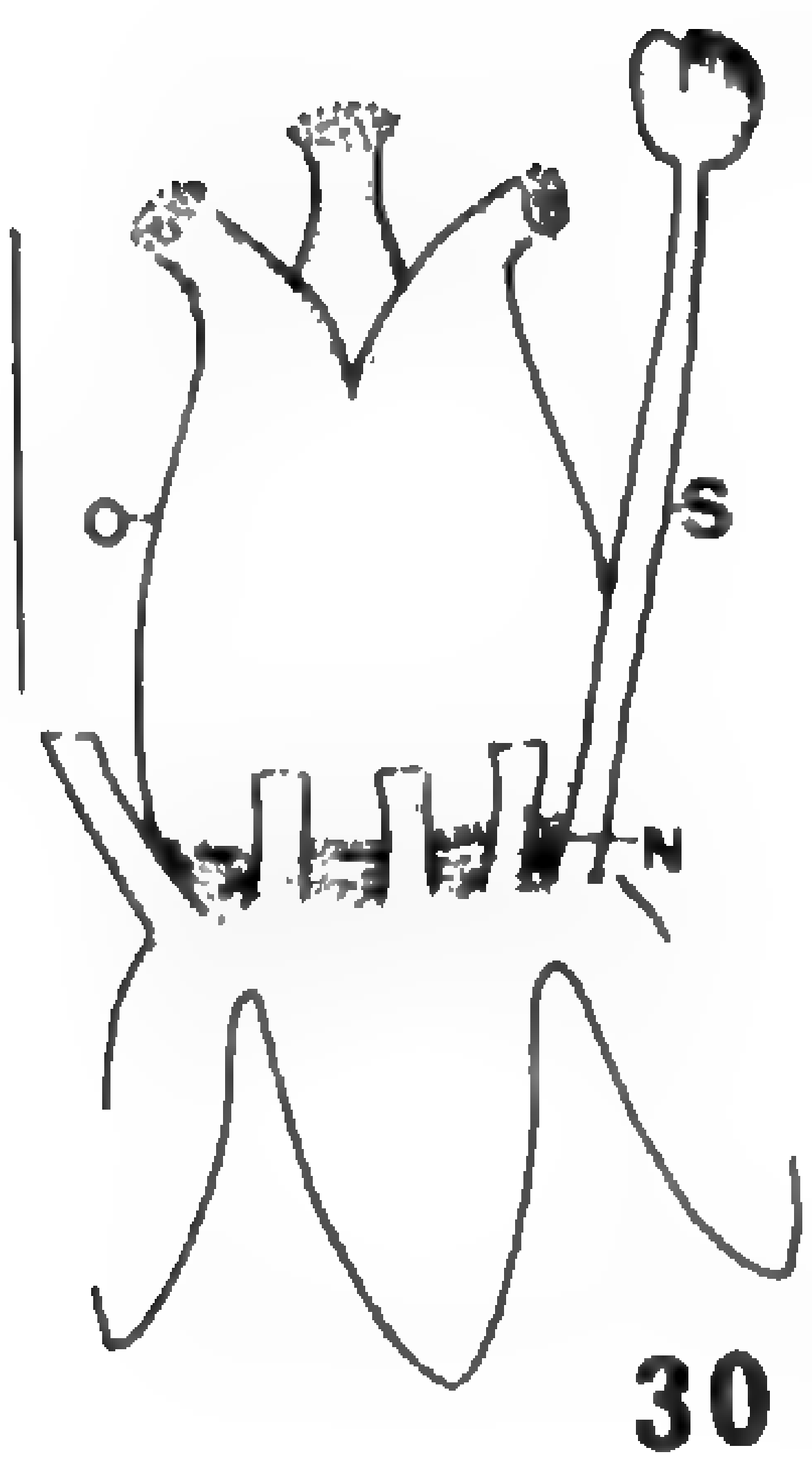
Saxifraga oppositifolia, slightly protogynous (Savile, 1972), has a purplish ovary, slightly inferior at anthesis and almost superior in fruit, changing to a brilliant flame colour in its lowest 0.3–0.5 mm. The bright coloured tissue continued among the bases of the filaments and was secreting abundant nectar in all plants examined from Stefansson I., Baillie Hamilton I., and Resolute between July 7 and 14, under weather conditions precluding insect flight (Plate 4, Figure 31). Normally, the flower is bell-shaped with petals 6–9 mm long, and has concealed nectar most readily obtained by insects with long probosces, but a second form, with mauve rather than magenta petals and a more open flower, was present at Resolute, and noted by Savile (1964) on Ellef Ringnes. By its form it was suited to visits from smaller insects. Kevan (pers. comm.) found that over-wintered Calliphoridae, the Blow Flies, went immediately to *S. oppositifolia* as soon as they became active at Lake Hazen, no doubt effecting cross-pollination. Savile found 30 males of a Chironomid, *Lymnophyes* sp., on this saxifrage on Ellef Ringnes in 1960, and McAlpine collected the Muscid *Spilogona obsoleta* (Mall.) on the same species and island two years later (McAlpine, 1965b) indicating possible



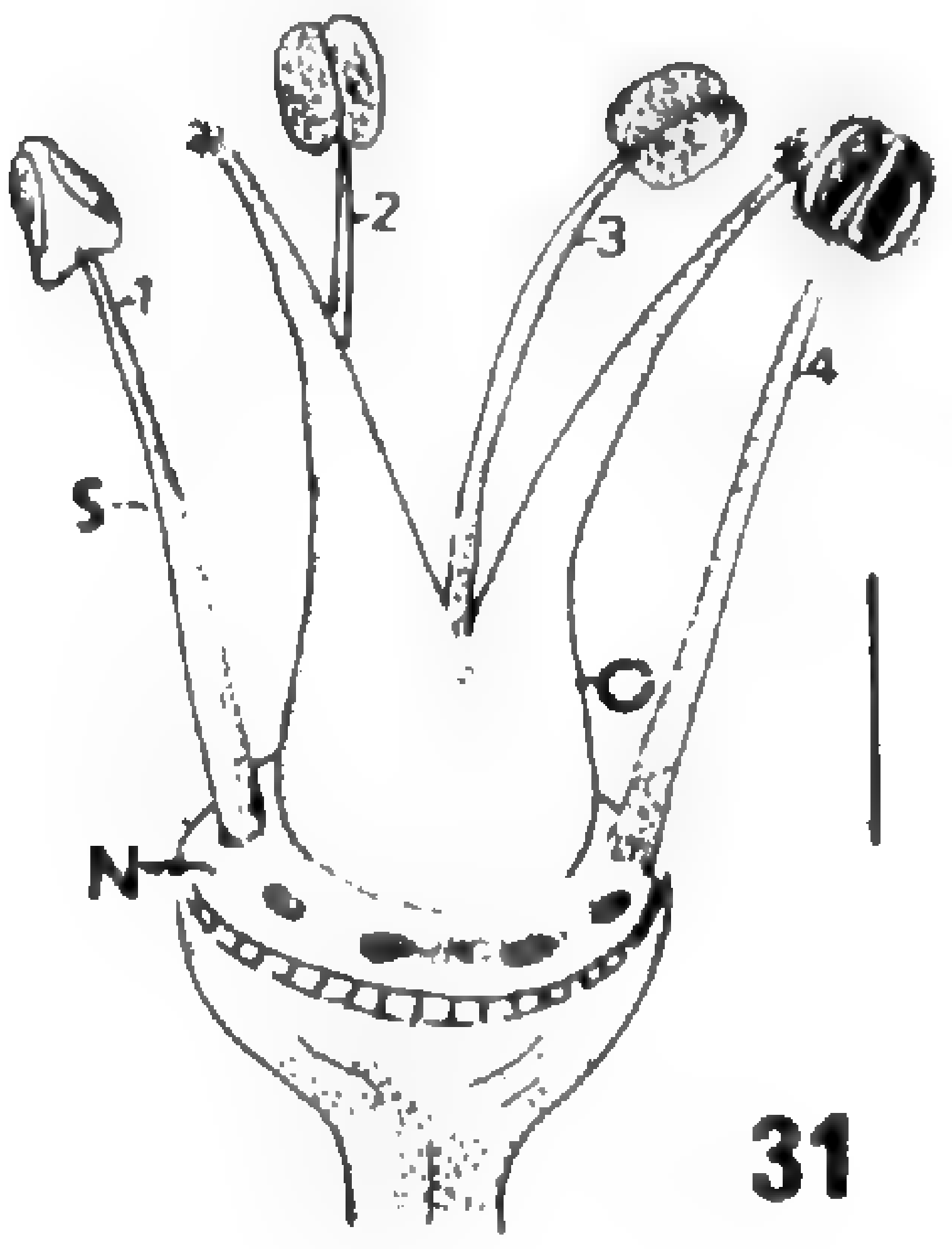
28



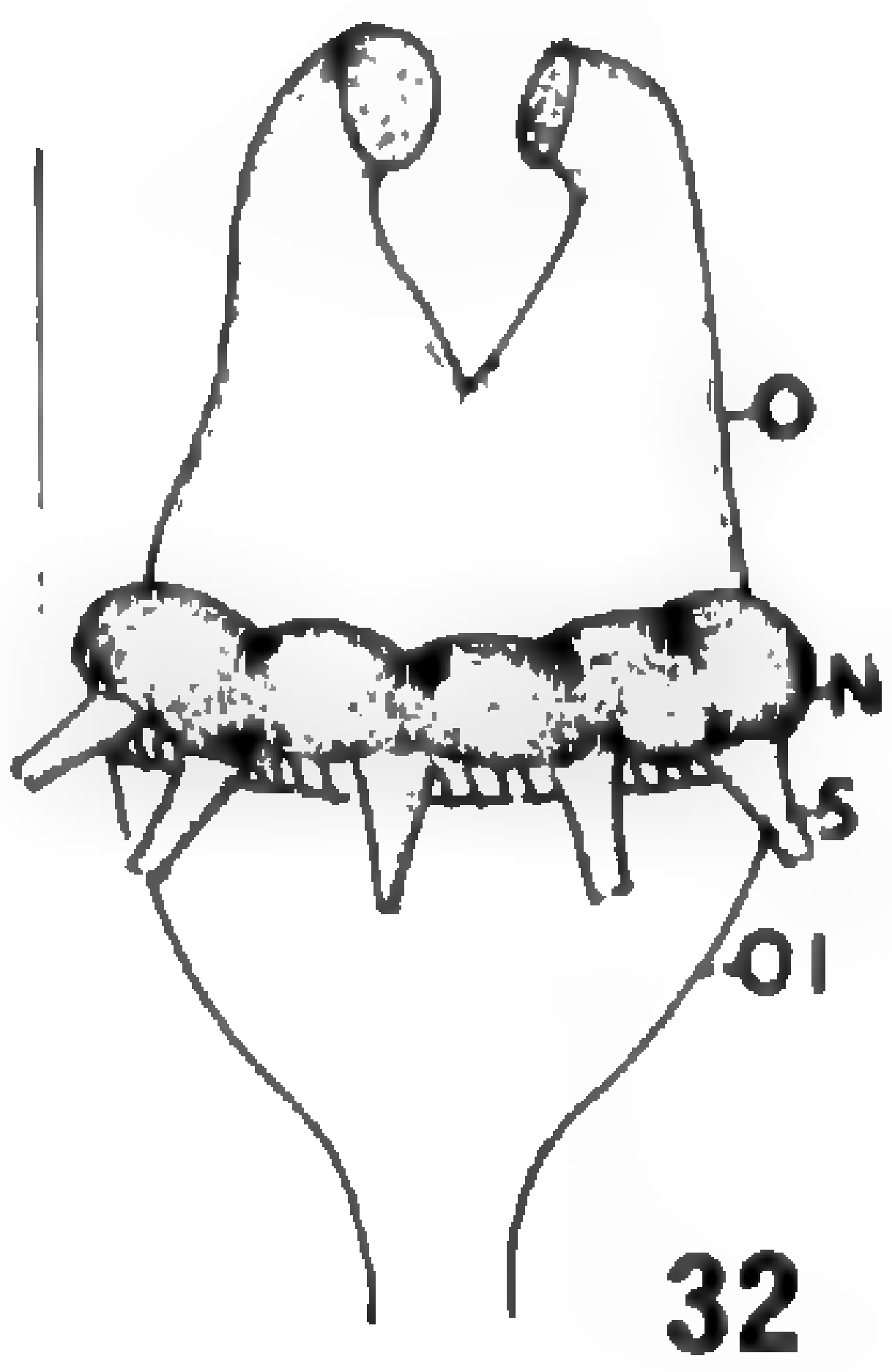
29



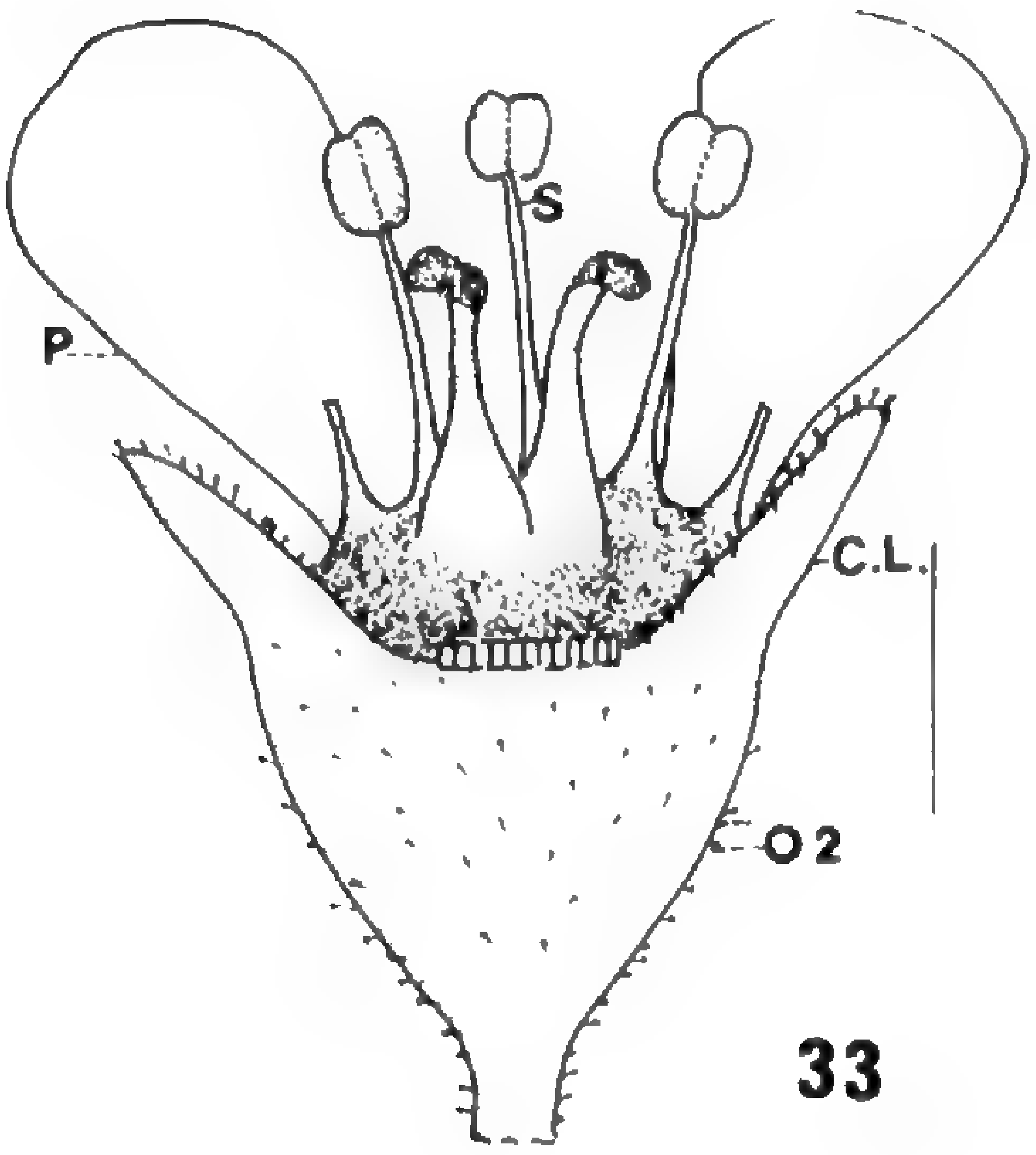
30



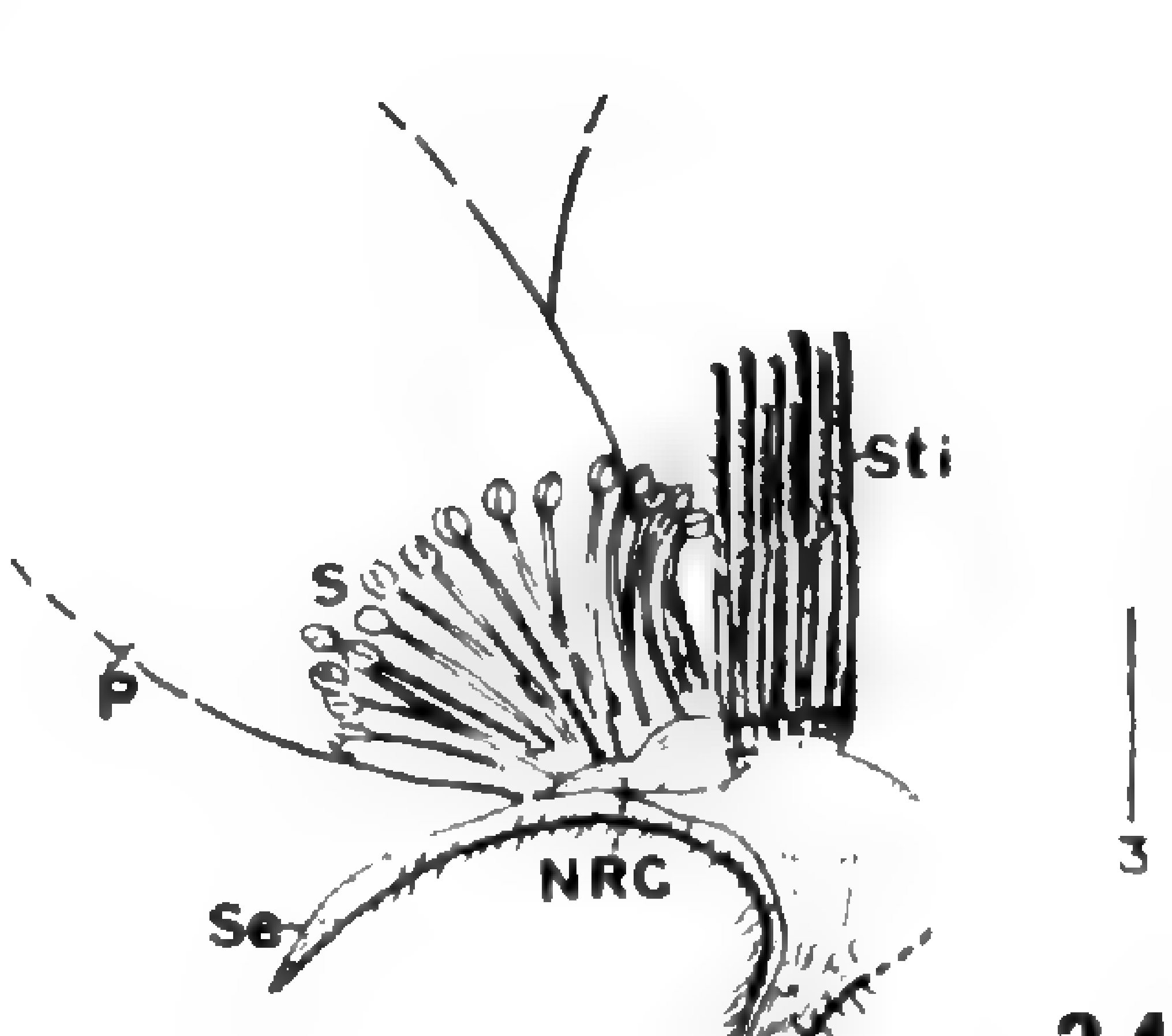
31



32



33



34

pollination activity within individual flowers by small flies, whose movement from flower to flower was restricted by weather. There are no Apidae on Ellef Ringnes, and probably none at Resolute (no specimens of bumblebees from there are in the D.A.O. insect collection). Kevan (1972) found autogamous seed production in *S. oppositifolia* at Lake Hazen was less than 10%. Savile (1964) credited *Bombus polaris* and *B. hyperboreus* with active pollination there and thought the bees responsible for the many genetic forms of colour and petal shape on *S. oppositifolia* at Lake Hazen.

There were few remains of 1975 capsules at Resolute in 1976, indicating little successful pollination in the previous year. Other species of *Saxifraga,* with uncrowded flowers and relatively exposed nectar, no doubt can be pollinated by flies. McAlpine (1965b) found the Muscid *Spilogona sanctipauli* (Mall.) strongly attracted to *Saxifraga caespitosa,* on Ellef Ringnes Is., but self-pollination is possible in the later stages.

Staminal Movements. Notes were made in the field on the staminal movements in *Saxifraga caespitosa, S. rivularis,* and *S. oppositifolia* (Plate 4, Figure 31). At first the position of the stamens was upright and close to the petals. Then the stamens elongated slightly and bent

---

Plate 4, Figures **28–34**. **28,** The male stage of *Parnassia* flower, with successive positions of stamens: Sa, immature; Sb, filament elongated, mature anther over undeveloped stigma; Sc, anther discharged and stamen moved outwards; Sd, anther deciduous; DA, dehisced anther; **29,** *Parnassia kotzebuei* Cham. Petal with opposite staminode. Blade with four to six capitate filaments; **30,** *Saxifraga davurica* Willd. (Keno Hill, Y.T.). Carpels, usually three, occasionally two. Both numbers can occur on the same plant. Nectary a non-swollen glistening yellowish or reddish-purple band on pale green ovary; **31,** *Saxifraga oppositifolia* L. Nectariferous tissue of bright flame colour, or pale in form with mauve flowers. Stamen no. 1 dehisced and returned to original position; stamen no. 2, in early position by corolla; stamen no. 3, moving towards centre of flower; stamen no. 4, dehiscing by stigma; **32,** *Saxifraga aizoides* L. Nectary a conspicuous yellowish swollen, somewhat lobed band on greenish ovary. Lobing due to pressure of staminal filaments; **33,** *Saxifraga caespitosa* L. Nectary a broad yellow epigynous disc, the nectariferous tissue extending among the bases of the filaments. In *S. aizoon* the nectary differs in remaining within the staminal ring; **34,** *Dryas integrifolia* M. Vahl. Nectariferous tissue lining shallow receptacle cup. O, Ovary. O1, Half-inferior Ovary. O2, Inferior Ovary. STI, Stigma. S, Stamen (developmental stages: a, b, c, d). DA, Dehisced Anther. STA, Staminode. NT, Nectariferous Tissue. YK, Yellow Knob. NRC, Nectariferous Receptacle Cup. P, Petal. SE, Sepal. CL, Calyx Lobe. Line in Figure 29 equals 1 mm; in Figures 28, 30–33, 2 mm; in Figure 34, 3 mm.

towards the stigma, dehiscing as they reached the centre of the flower. The spent stamens moved back towards the corolla. Usually several stamens were in motion at once, one having reached and often touched the stigma, another bending towards it, and several dehisced and undehisced stamens pressing against the corolla. Variations in this pattern were frequent. One flower of *S. oppositifolia* from Baillie Hamilton I. had all stamens bending towards the stigma, and all dehisced; another had the two styles bending towards the petals and touching a dehiscing anther there; still another had the two long styles crossing and bending towards the stamens. In one flower, from Stefansson I., the stigmas were 2 mm higher than the anthers, even though two anthers had dehisced, and chances for self-pollination seemed nil. In most flowers the anthers reached the same height as the stigmas before dehiscence. Knuth (1908) remarks, "Failing insect visits, self-pollination frequently takes place in *S. oppositifolia*".

PARNASSIACEAE

Parnassia. This genus occurs on the mainland in Canada except for a single record, of *Parnassia kotzebuei,* on the southern coast of Baffin Island (Porsild, 1964). I found *P. kotzebuei* and *P. palustris* (both markedly protandrous) on the bank of a small stream at Keno Hill, Y.T., the former almost finished flowering and the latter at its peak. In this genus only the five stamens alternating with the petals produce pollen, the other five opposite the petals having been modified into scale-like staminodia. Each staminodium has a short basal stalk, either whitish or transparent in colour, followed above by a slightly thickened greenish band, the nectary, then a broadened blade terminated by capitate filaments (Plate 3, Figure 27). The two species can be distinguished readily by the form of the staminodium, that of *P. kotzebuei* measuring from 0.4 0.6 mm wide, and bearing four to six filaments (Plate 4, Figure 29), that of *P. palustris* measuring 1.8 2.5 mm wide, with nine to many filaments (Plate 3, Figure 27). The capitate knobs at the ends of the filaments in the former were slightly tinged with yellow, those of the latter were a bright transparent gold colour, very attractive to insects. The stamens move to a position over the sessile immature stigma one by one, and dehisce upwardly, so that any insect climbing over the staminodium to reach the nectar would automatically touch the anther which had reached the centre of the flower and become dusted with its pollen (Plate 4, Figure 28). The successive ripening of anthers allows more time for cross-pollination, should poor weather prevent insect flight on certain days.

ROSACEAE

The genera *Dryas* and *Potentilla* are found in every latitude of land above the Arctic Circle in Canada. *Dryas integrifolia* depends largely upon visits from flies for seed production (Kevan, 1972b), but *Potentilla* sp. may be apomictic (Fryxell, 1957). Davis and Heywood (1963) noted that both reduced and unreduced embryo sacs may occur side by side in the same population of *Potentilla,* and occasionally it may reproduce sexually. *Rubus chamaemorus,* widespread in the low arctic, is one of the few dioecious dicot species in the north, and must depend entirely upon insect pollination for seed set.

All three genera have perigynous flowers with shallow cup-shaped receptacles lined, between the stamens and carpels, with shining, often yellow or flame coloured, nectariferous tissue. The nectar can be reached easily by small or short-tongued insects, although *Dryas* and *Potentilla* are also visited by northern bumblebees (Milliron, 1973), (Plate 4, Figure 34).

Among unusually small flowers of *Dryas integrifolia* at Frobisher Bay there were a few purely staminate ones. However, they contained dark-coloured vestigial pistils 0.5 mm long. The staminate flowers of *Rubus chamaemorus* contained no vestigial pistils, but the pistillate flowers had vestigial stamens 1.4–1.8 mm compared with the functional ones on the staminate flower, which measured 5.0–7.0 mm.

Although *Potentilla* may not require insect visits for seed production, abundant nectar was found at the base of the stamens in *P. anserina* when picked on the banks of the Klondike River near Dawson City, and in fresh specimens of *P. hyparctica* from Melville I. Hocking (1968) noted *Potentilla* sp. at Lake Hazen produced 123 gm total sugar per hectare, with a maximum sugar concentration of 80%.

The stamens of both *Dryas* and *Potentilla* tend to move outwards towards the petals as they dehisce, and the anthers to turn laterally so that pollen may fall on petals, staminal filaments, and, as the inner stamens dehisce, on stigmas as well. Pollen was noted scattered on styles, filaments, petals and sepals in *P. anserina*. Self-pollination could take place in an older flower of *Dryas*, or pollen contact on the stigma may stimulate seed formation in an apomictic *Potentilla*. Faegri and van der Pijl (1966) note that many apomicts need pollination to start the development of seed, even if fertilization does not seem to occur, possibly through the production of hormones and auxins.

Dryas integrifolia was one of the most insect-visited flowers at Frobisher Bay, partly for basking (Kevan, 1973), and partly for pollen and nectar. McAlpine (1965a) made careful notes on insect visitors to *Dryas* at Lake Hazen, and Mosquin and Martin at Melville I. (1967), to which I add the species I collected from individual flowers at Frobisher Bay: *Rhamphomyia* sp. (Empidae), *Amauronematus* sp. (Tenthredinidae), *Peleteria aenea* Staeg. (Tachinidae), *Eupogonomyia groenlandica* Lundback, *Hydrophora alaskensis* Mall., *Hylema (Paregle) radicum* (L.), *Lasiops subrostratus* (Zett.), *Limosia* sp., *Spilogona imatatrix* (Hall), *Spilogona sactipauli* (Mall.), (Muscidae).

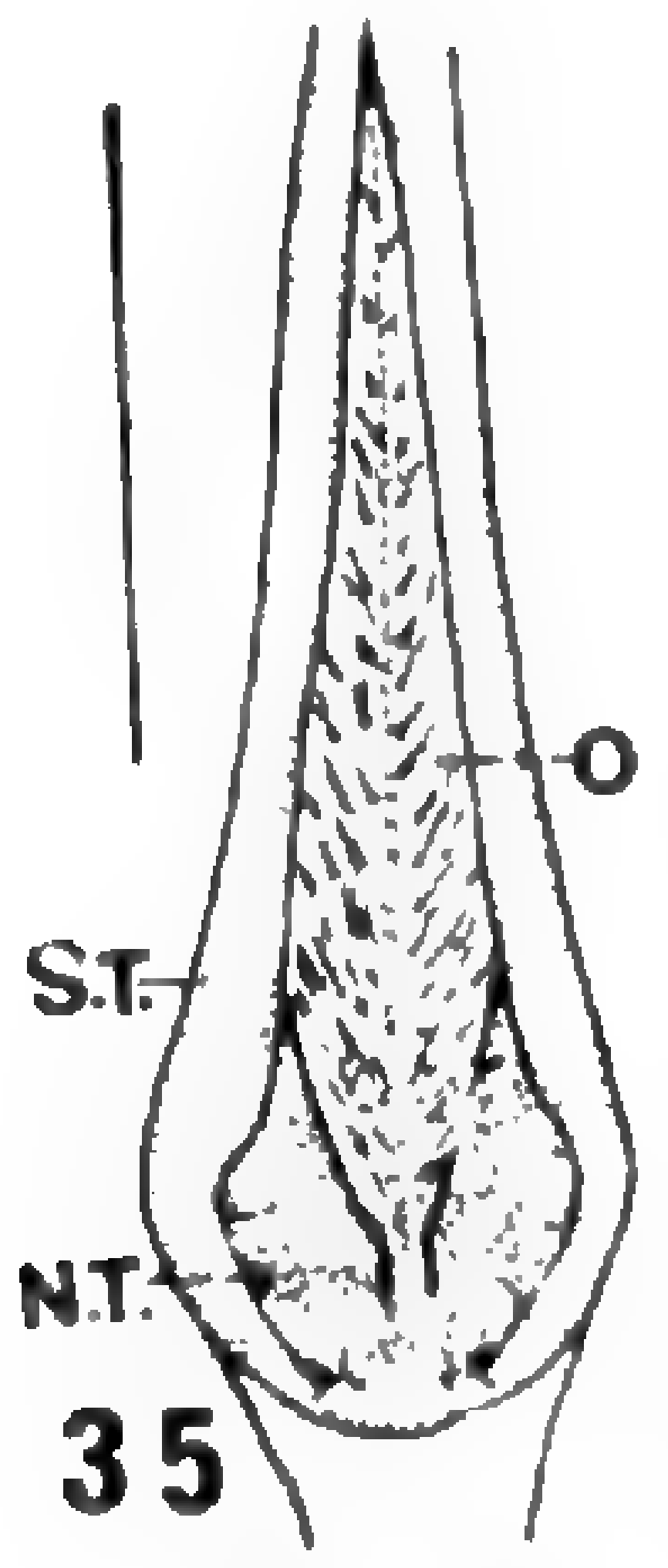
The Potentillas were visited by bumblebees, *Potentilla hyparctica* by *Bombus hyperboreus* Schon. at Frosbisher Bay, and *P. palustris* by *Bombus frigidus* Sm., *B. jonellus* (Kby.) and *B. sylvicola* Kby., at Inuvik. McAlpine (1965a) recorded Syrphidae feeding on the pollen grains of *P. chamissonis*, and Calliphoridae on its nectar at Lake Hazen.

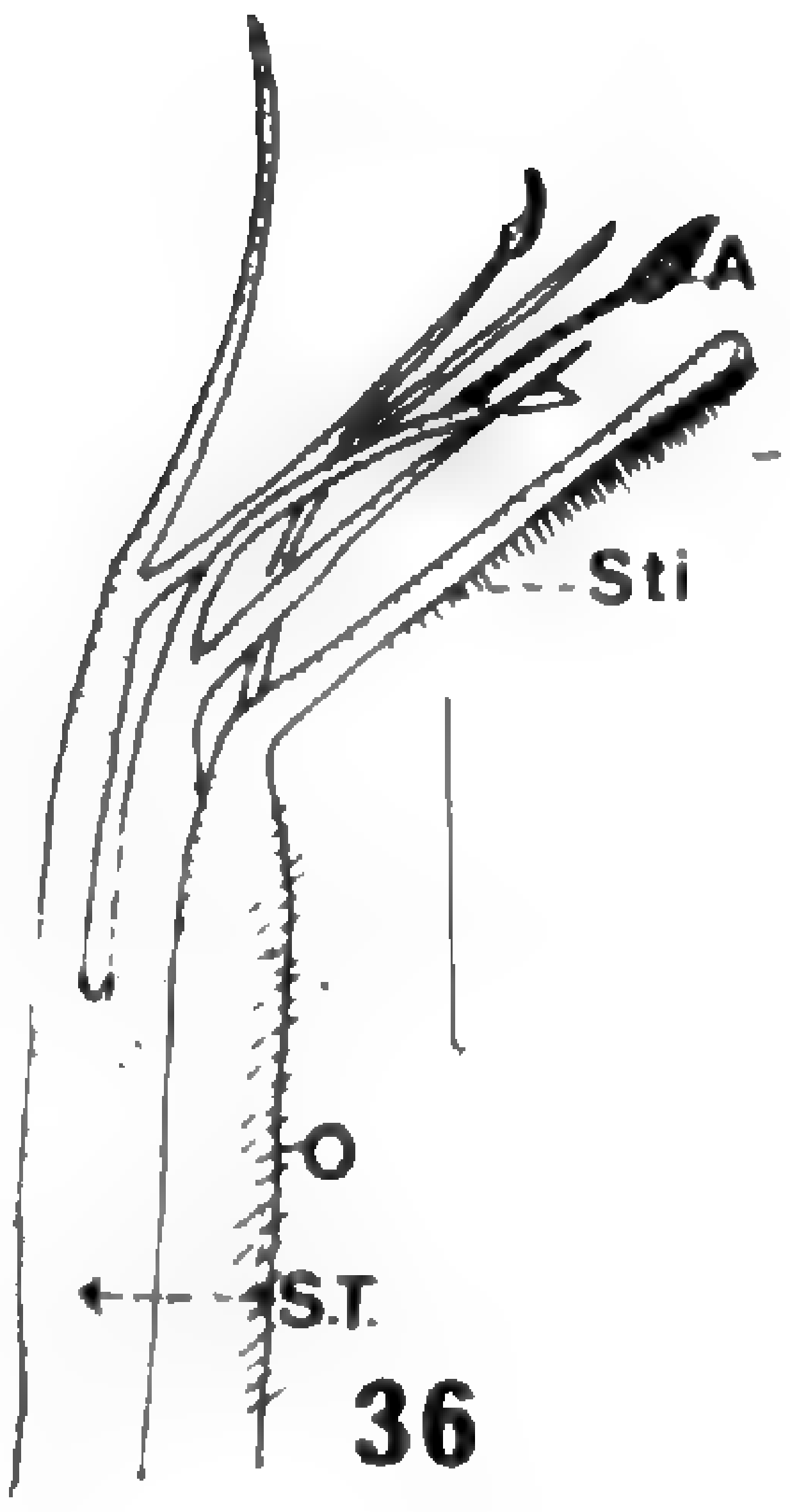
FABACEAE

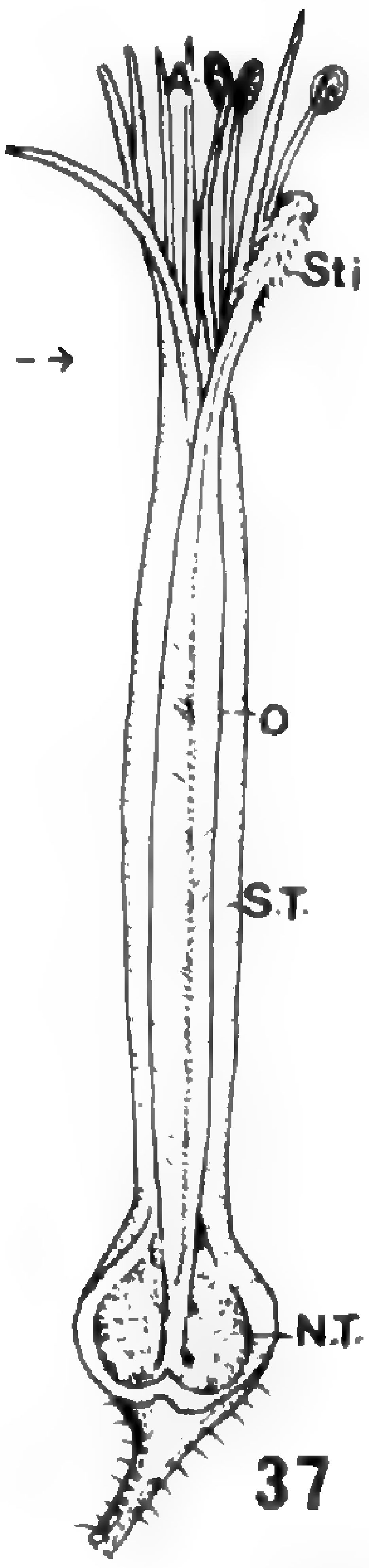
The nectar-secreting tissue of the two commonest arctic genera, *Oxytropis* and *Astragalus*, as well as *Lathyrus*, from Great Whale River on the Hudson Bay, were examined under a dissecting microscope. These genera have no obvious nectar glands, unlike some of the Phaseoleae which have collar-shaped nectaries (Waddle & Lersten, 1973), but the thickened membranous base of the nine fused filaments, and the top of the receptacle are lined with shiny secretory tissue (Plate 5, Figures 35 & 37). The tenth stamen is free from the membrane, leaving a slit through which a bee can push his proboscis to reach the nectar. The monadelphous genus *Lupinus*, common along the Mackenzie River above the Arctic Circle, has all ten stamens fused, and no slit left for the entrance of a proboscis. It produces pollen only, no nectar.

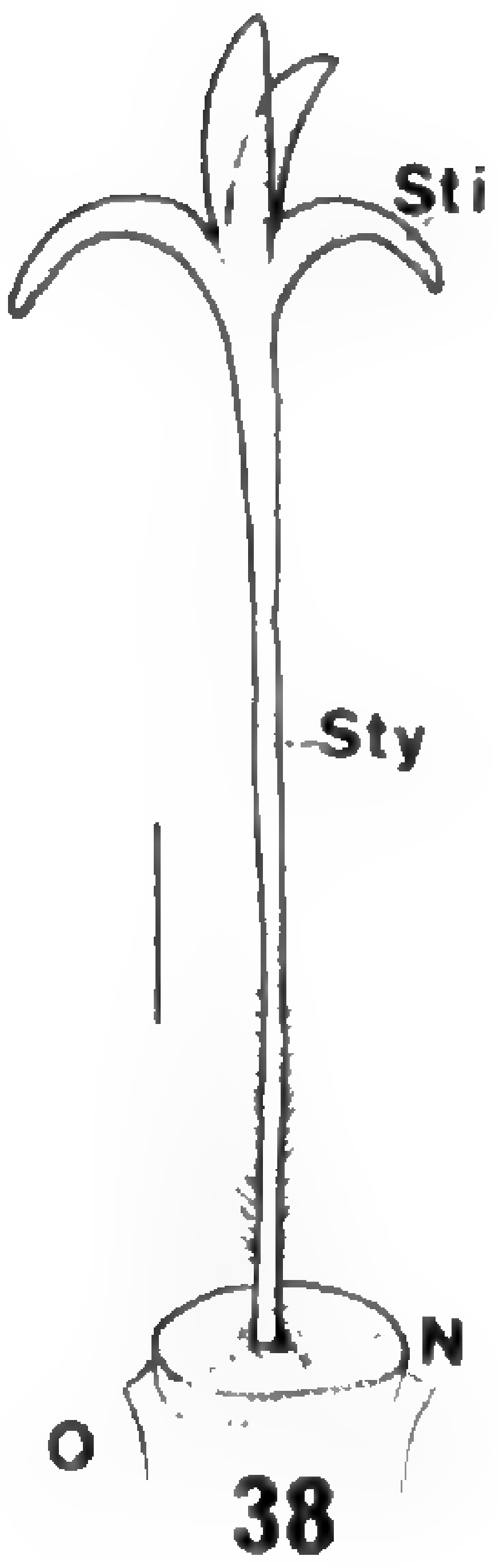
Insect pollination of our arctic legumes must be confined to *Bombus,* or insects heavy enough to depress the keel and free the stigma and stamens. In order to estimate the chances of stamens and stigma coming in contact mechanically, I depressed the keels of *Oxytropis podocarpa* and *O. maydelliana* with forceps and the stigma and stamens sprang instantly into sight. In *O. podocarpa,* one anther was touching the stigma, the others slightly behind the receptive part. Although the tissue around the stipe of the ovary was shiny and glandular, there was no free nectar apparent. In *O. maydelliana* the stigma projected beyond the anthers in some cases; in others the anthers, with a peculiar fuzzy appearance, completely surrounded it. The basal chamber was very wet with nectar, and even the glabrous base of the ovary was damp, although probably not in itself secretory. Laboratory examination of the anthers showed them to be full of germinating pollen grains. The germ tubes reached a maximum length of 72 microns, sufficient to penetrate the stigma next to the anther. The germination of pollen *in situ* in *O. maydelliana* was first spotted in 1964 at Frobisher Bay, and further seen in fresh material brought in from Hooper I., N.W.T., in 1975 and finally noticed again at Frobisher Bay in 1976. My first reaction in 1964 was that some freak of weather had caused the pollen to germinate abnormally, but it seems that at least one strain of *O. maydelliana* has an adaptation to secure self-pollination, necessitated by the few insect visitors it receives. D.B.O. Savile remarked (personal communication) that it is far more abundant at many arctic sites than most legumes, indicating a successful selfing mechanism. In Frobisher Bay I saw only one visitor to its flower, *Bombus sylvicola* Kby., compared to dozens from both *B. sylvicola* and *B. polaris* Curt. to the fragrant, purple *Astragalus alpinus* growing beside it. Mosquin and Martin (1967) noticed on Melville I. the same difference between *Oxytropis arctica* and *A. alpinus,* the latter apparently being unusually attractive to bees.

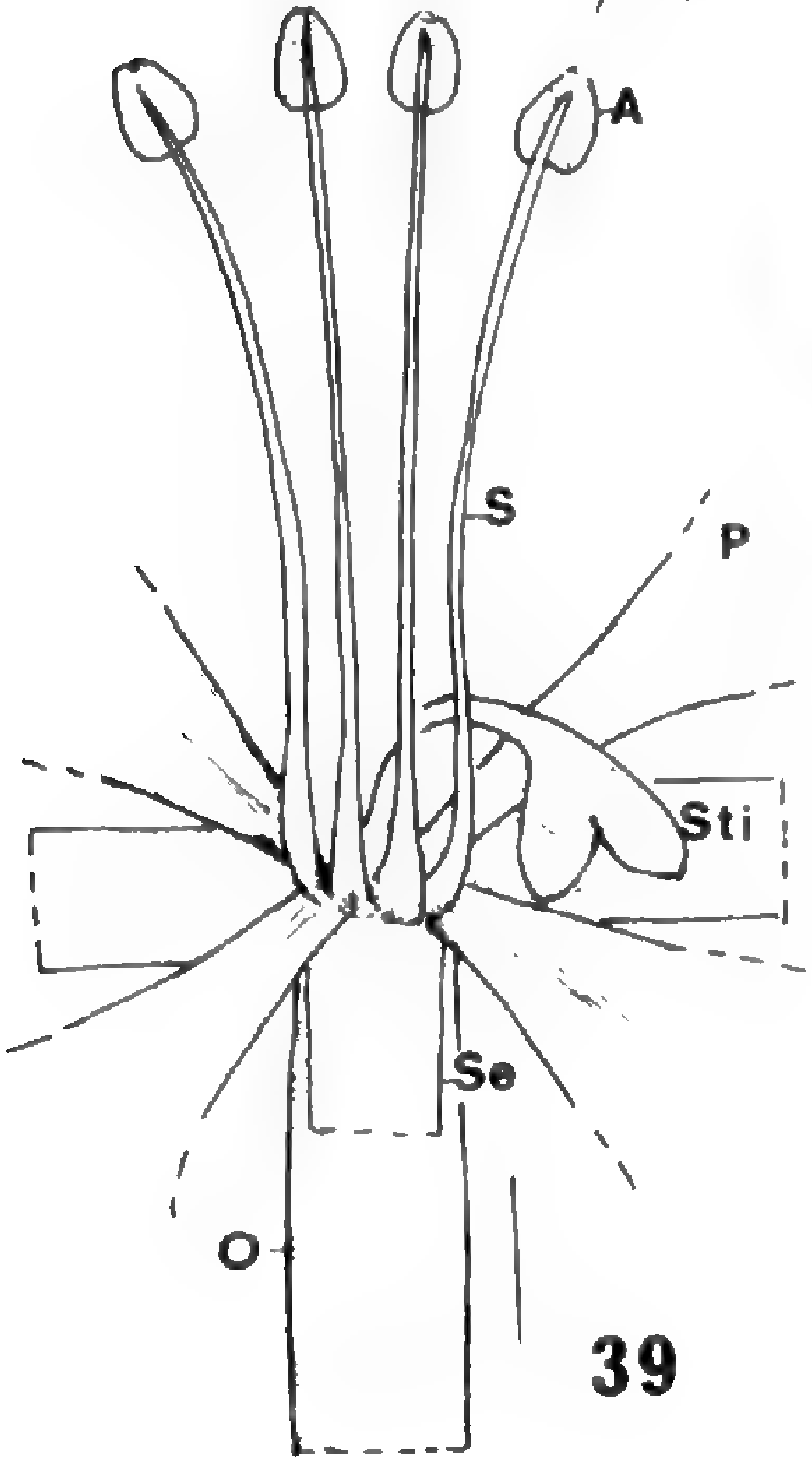
According to Fryxell, perennial legumes of the low latitudes are normally self-incompatible (1957). Clapham, Tutin, and Warburg (1962) state *Astragalus alpinus* is usually cross-pollinated by bees, as well as *Oxytropis.* At Frobisher Bay in 1964 both *Oxytropis maydelliana* and *A. alpinus* freely produced well-filled pods, indi-

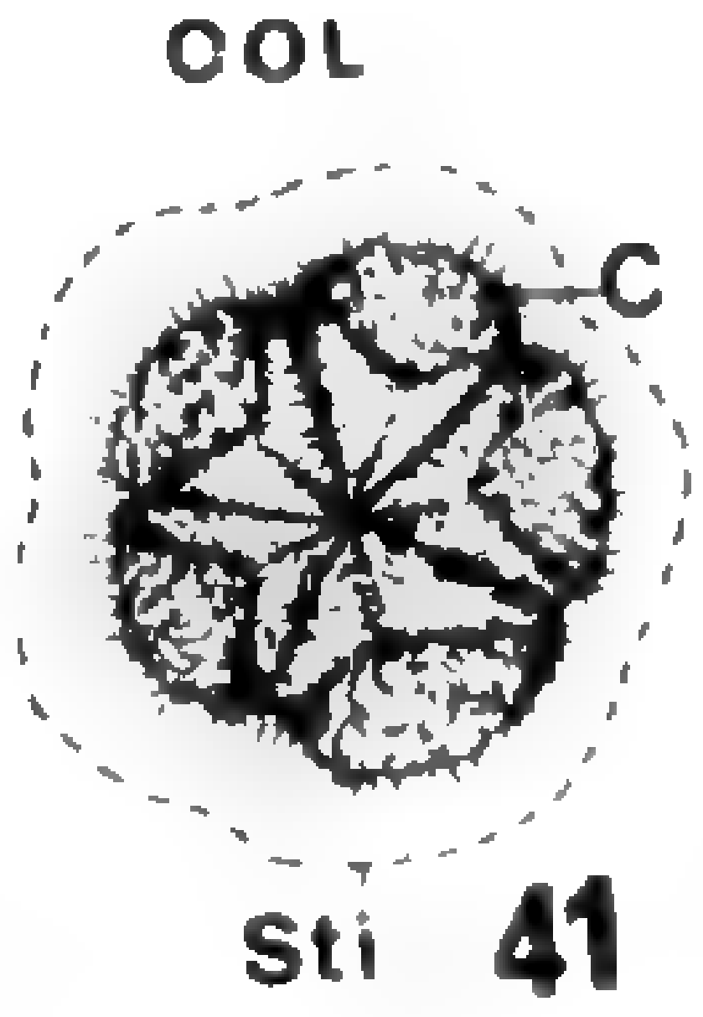

35


36

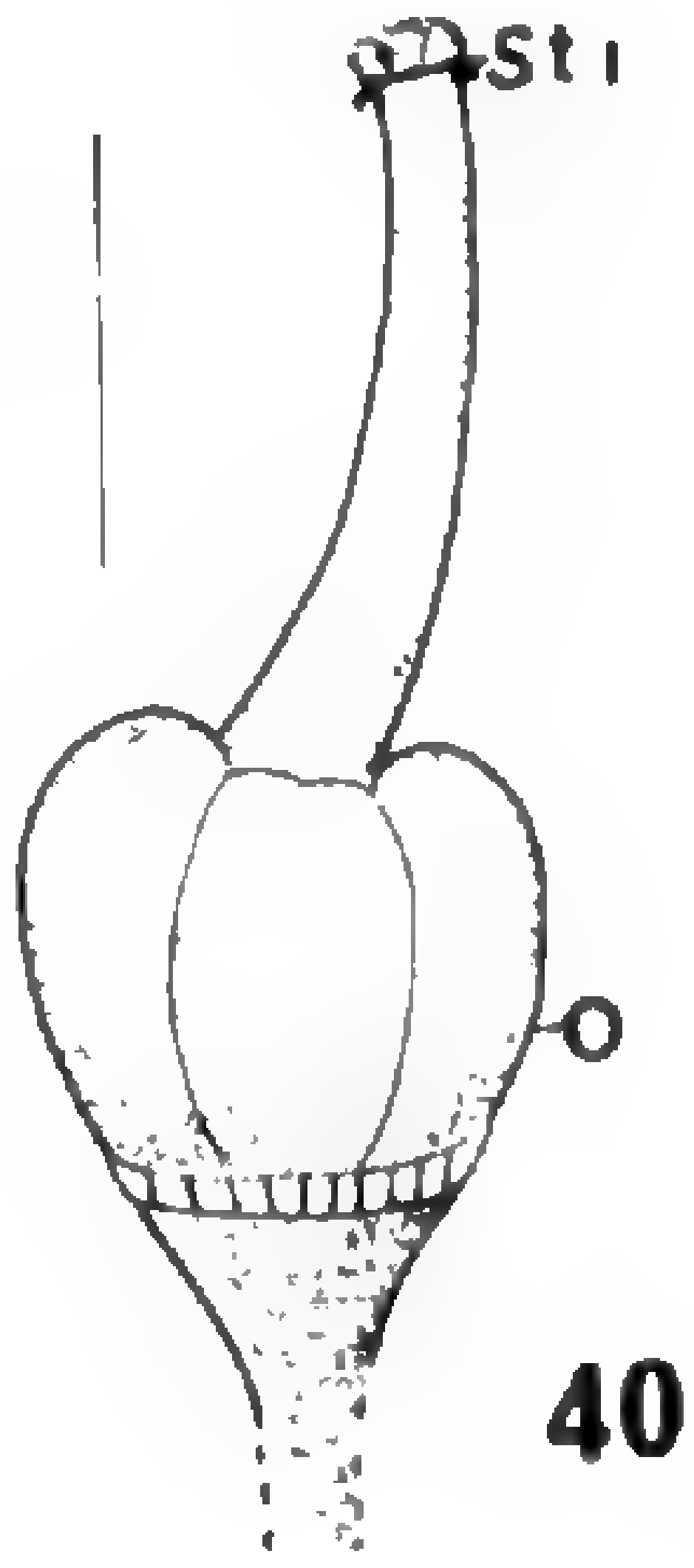

37

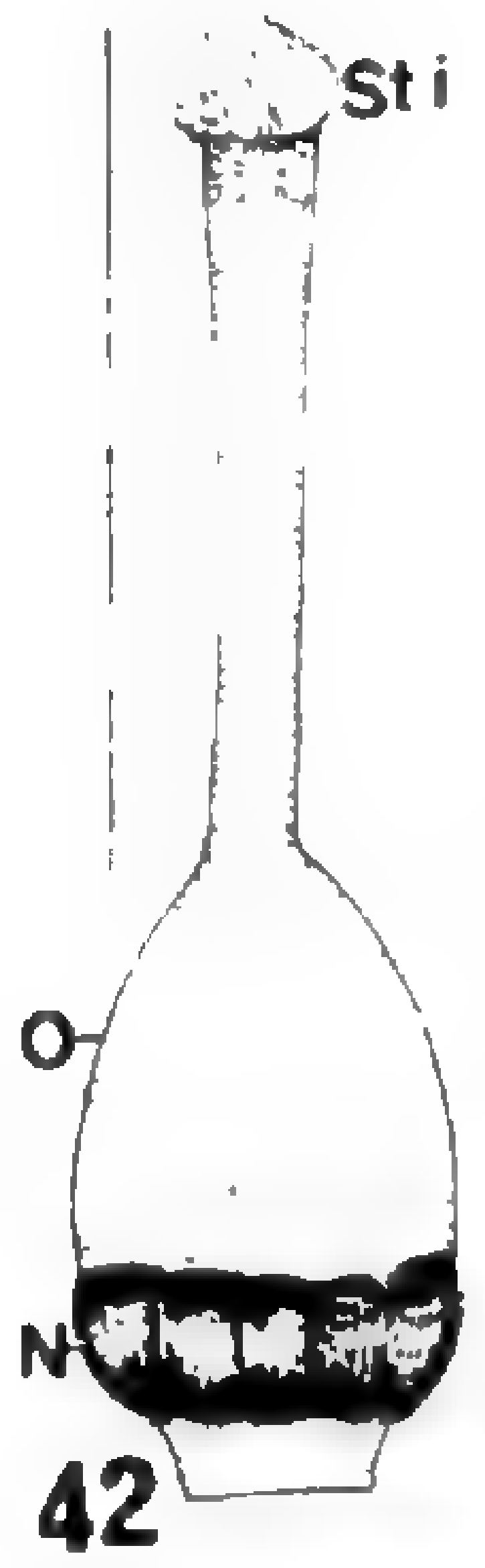

38

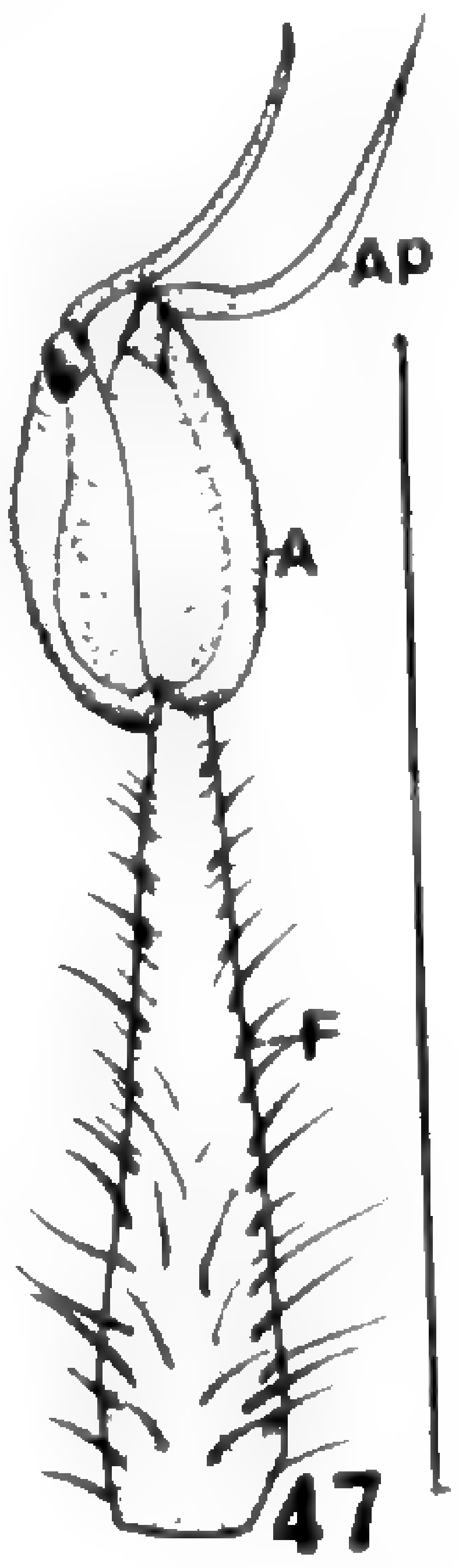

39

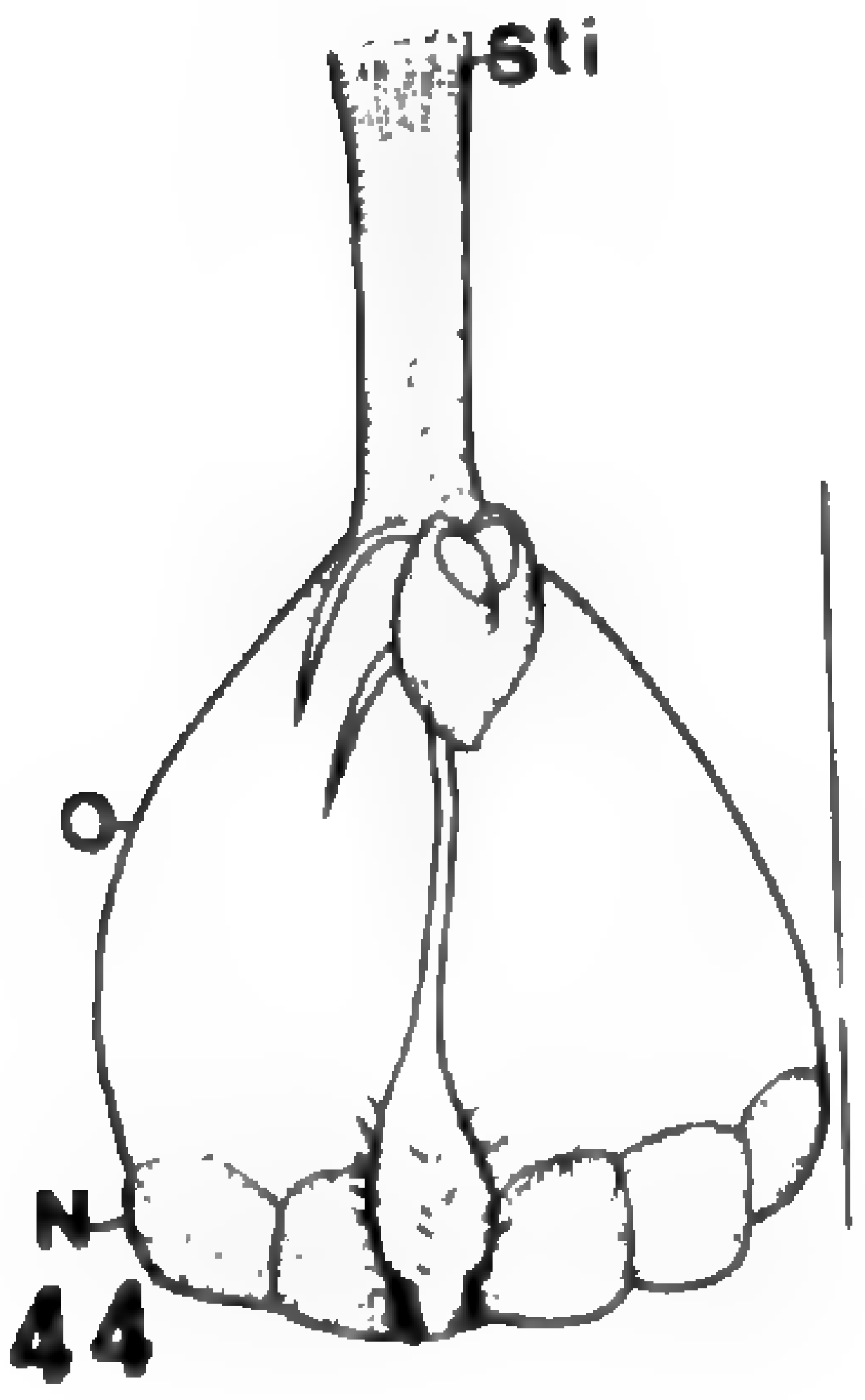

41

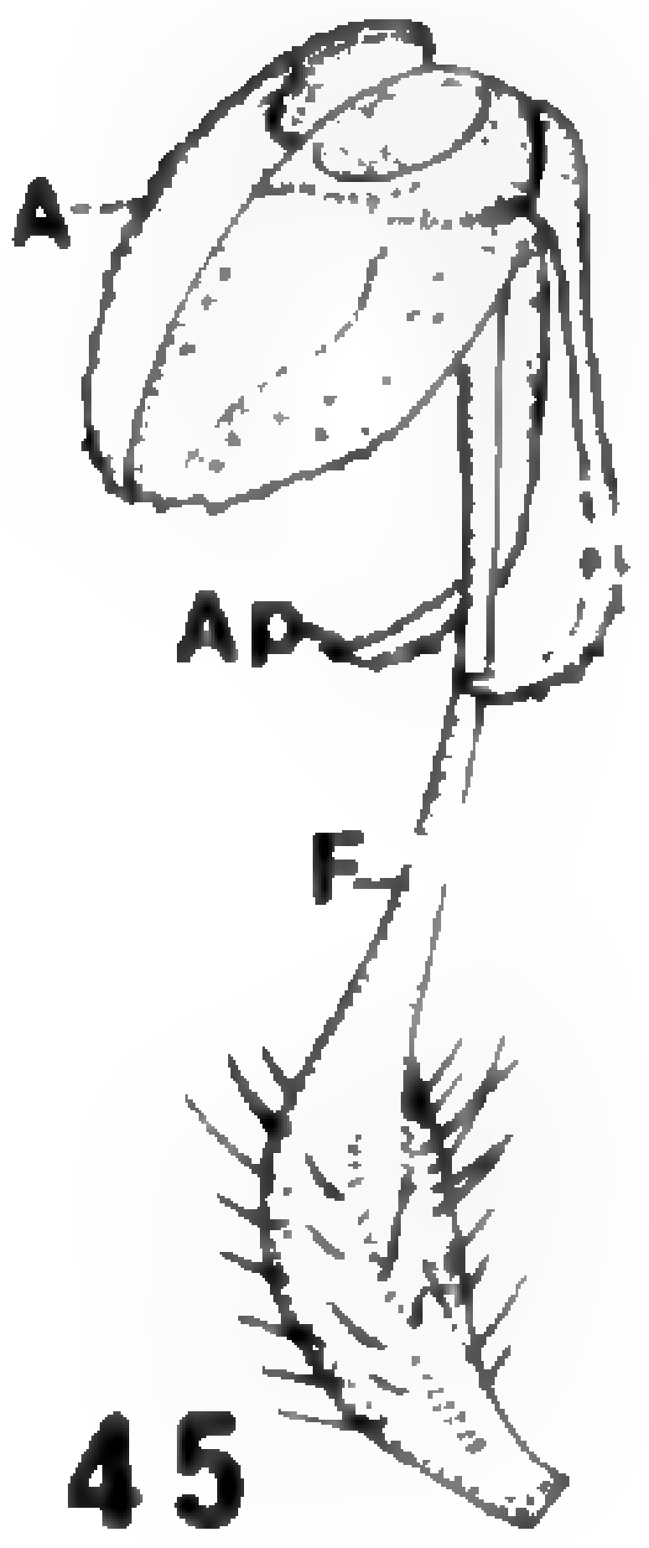

43

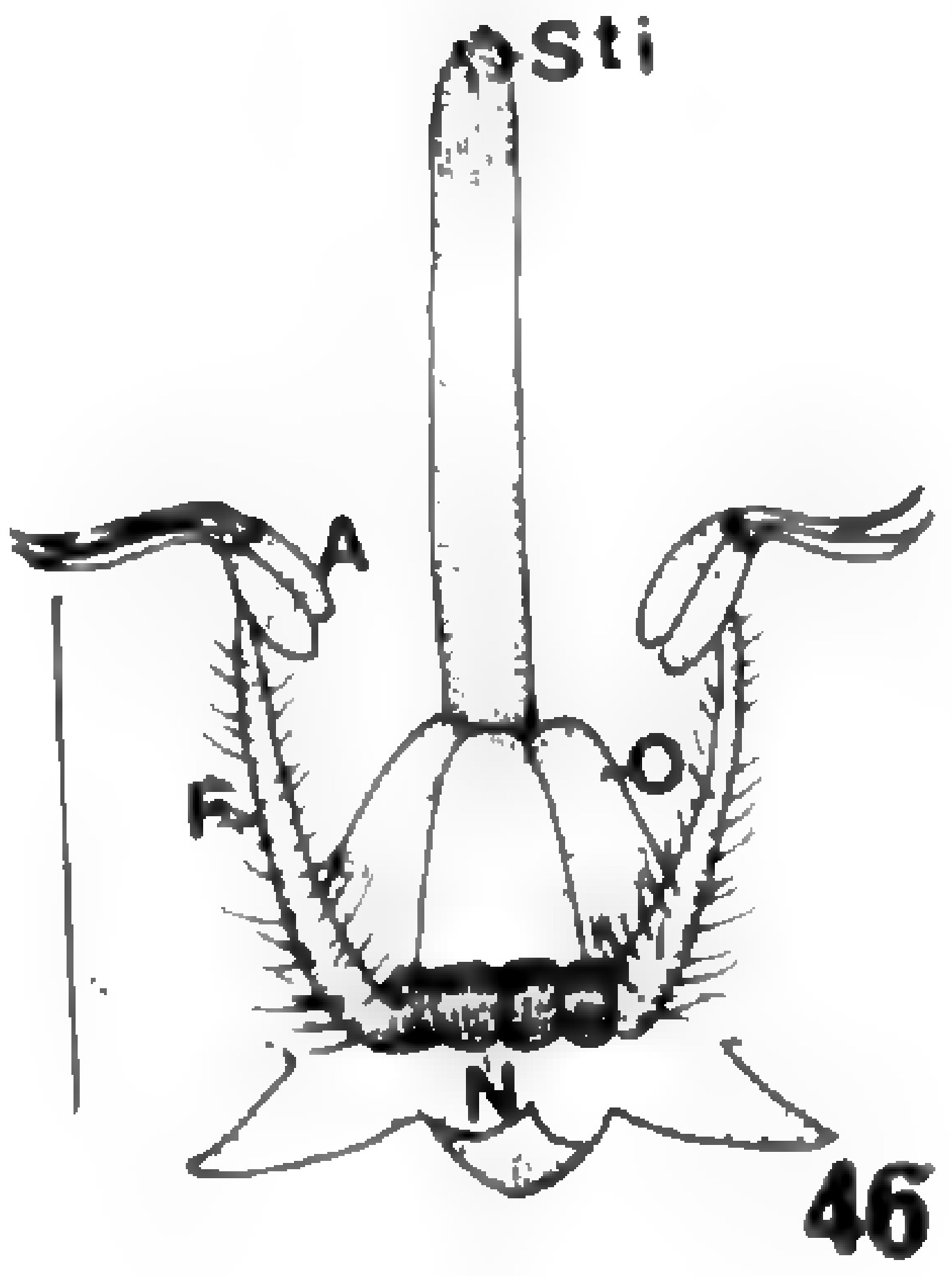

40


42


47


44


45


46

cating that the former (without insect visitors) must have been self-compatible.

ONAGRACEAE

One genus only is listed for the Arctic Achipelago, *Epilobium* (Porsild, 1964). Two large and showy species are common, the territorial flower of the Yukon, *E. angustifolium,* which barely reaches the eastern islands, and *E. latifolium,* which extends to the northern limit of land at latitude 83° on Ellesmere I.

Epilobium angustifolium is a classical example of protandry, and cross-pollination by insects must be the usual method of fertilization. In the young flowers the style is curved downwards, the stigma lobes closed, while the stamens are upright in the process of dehiscing. The visiting bee must land on the anthers first when the flowers are in this condition and it normally proceeds upwards on the raceme, visiting still younger flowers, so pollination may not occur until it flies to another inflorescence. In older flowers the style straightens and elongates beyond the anthers, the stigma lobes open, and the bee lands on the stigma first, depositing pollen gathered previously from younger flowers. I examined an inflorescence on

---

Plate 5, Figures **35–47.** *Note:* The tenth, or free, stamen in Fabaceae removed before drawings made. **35,** *Astragalus alpinus* L. Lower half of ovary and staminal tube. Shiny nectariferous tissue at base of split tube formed by nine fused filaments; **36 & 37,** *Lathyrus maritimus* (L.) Bigel. (Great Whale River); 36, Lateral view, showing proximity of anthers to the stigma; 37, Ventral view of staminal tube with basal nectariferous tissue. Anthers deciduous; **38,** *Epilobium angustifolium* L. (Markedly protandrous). Nectary a green epigynous disc on purple inferior ovary. Style markedly curved in staminate stage, elongated and straight in the pistillate stage shown in drawing; **39,** *Epilobium latifolium* L. (Slightly protandrous). Semi-diagrammatic drawing showing protective enlarged bases of four of the stamens, and fleshy, curved glabrous style and stigma. Epigynous nectary hidden inside filaments; **40 & 41,** *Pyrola grandiflora* Rad.; 40, Pistil, with 5-lobed ovary, no nectary; 41, Stigma seen from above, with five sticky cones above collar; **42 & 43,** *Arctostaphylos alpina* (L.) Spreng.; 42, Nectary a slightly lobed band at base of shiny green ovary. Stigma larger than in *A. uva-ursi;* 43, Stamen with enlarged pubescent base fitting in between scallops of nectary; **44 & 45,** *Arctostaphylos uva-ursi* (L.) Spreng.; 44, Nectary a torulose band; 45, Stamen anther with long appendages decorated with transparent peg-like thickenings; **46 & 47,** *Andromeda polifolia* L.; 46, Nectary a torulose band at base of lobed ovary; 47, Stamen. O, Ovary. STY, Style. STI, Stigma. COL, Stigmatic Collar. C, Stigmatic Cone. S, Stamen. F, Filament. A, Anther. AP, Anther Appendage. ST, split Staminal Tube. N, Nectary. NT, Nectariferous Tissue. Line equals 2 mm, except 3mm in Figure 36.

the banks of the Klondike River, Y.T., and found the lowest four flowers had elongated styles, with open lobes, anthers fading; the next three had shorter styles, and stigmas closed, with anthers actively discharging pollen. Above that, the raceme bore flower-buds only. The succession of changes in the flower is illustrated well by von Marilaun (1895).

There is a green, fleshy, slightly concave nectary on the upper end of the purplish, inferior ovary, which produces nectar with a high concentration of sugar, 77% (Hocking, 1968). The nectar is protected from rain by the bending of the broadened bases of the filaments over the nectary to form a covering cone. Above the cone, which continues for some 1.6 4 mm, the style has hairs up to 0.5 mm, acting as a deterrent both to raindrops and to insects too small to be useful for pollination (Plate 5, Figure 38).

Bee visitors were numerous and of eight different species, as follows: *Bombus frigidus* Sm., *B. jonellus* Kby., *B. lucorum* (L.), *B. mixtus* Cr., and *B. sylvicola* Kby., collected at Inuvik from individual flowers; *B. bifarius nearcticus* Handl., *B. frigidus, B. mixtus* and *B. pleuralis* Nyl., collected as above, at Dawson City, Y.T., *B. frigidus, B. occidentalis* Grm., and *B. sylvicola,* collected at Keno Hill, Y.T., at 914 metres altitude. As well, Syrphidae were common visitors to *Epilobium angustifolium* at Inuvik: *Eristalis bardus* (Say), *Helophilus groenlandicus* (O. Fab.), and *H. obscurus* Lw. Homoptera and Hemiptera were recovered from the inflorescence by sweeping, but they were probably getting sap from the flower tissue and not greatly involved in carrying pollen. The hairs were minute on those collected and little or no pollen was present on their bodies.

Epilobium latifolium is not markedly protandrous. The style remains curved and lower than the anthers even in older flowers, and lacks the hairs seen in *E. angustifolium.* The nectary is similar, green and concave, protected by the enlarged flat bases of the filaments (Plate 5, Figure 39). Hocking (1968) found it capable of producing up to 3.5 mg of sugar per flower per day at Churchill, well above the other species he tested. At least six observers have seen bees visit this species and I saw one bee, unidentified, at Frosbisher Bay on Aug. 2, 1975, in exceptionally warm weather. I did not see any bees visit it during the cool summer of 1964, but saw three butterflies, *Colias* spp., the Syrphidae, *Helophilus borealis* Staeg., the Muscidae, *Egle.* sp., and *Lasiops subrostratus* Zett., a

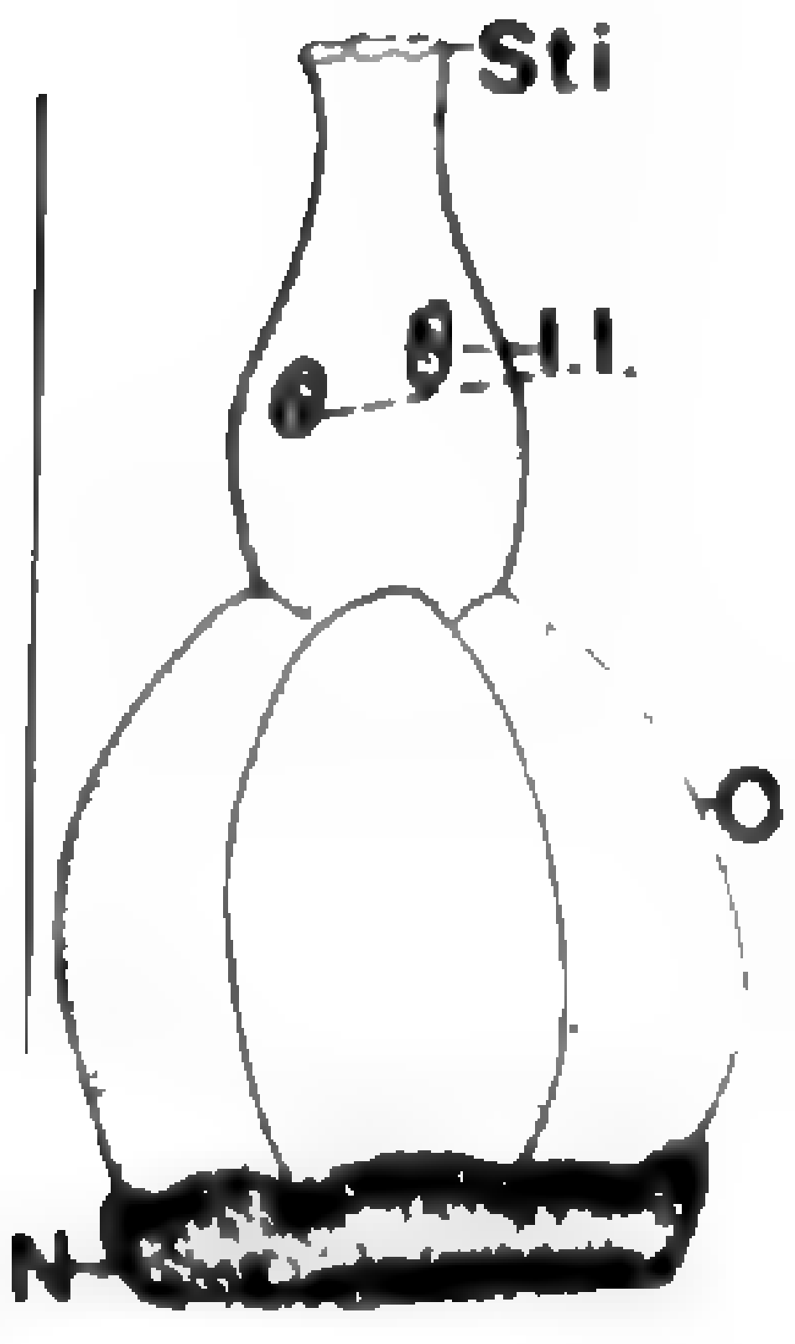
Heliomisidae, *Neoleria prominens* (Beck), and innumerable *Protophormia terrae-novae* (R-D) of the Calliphoridae. The last were crawling over the flowers and were covered with pollen, so were probably active pollinating agents. The pollen grains of *Epilobium* tend to stick together with viscin threads, so it is doubtful if they fall readily onto the stigmas below, to effect self-fertilization.

ERICACEAE

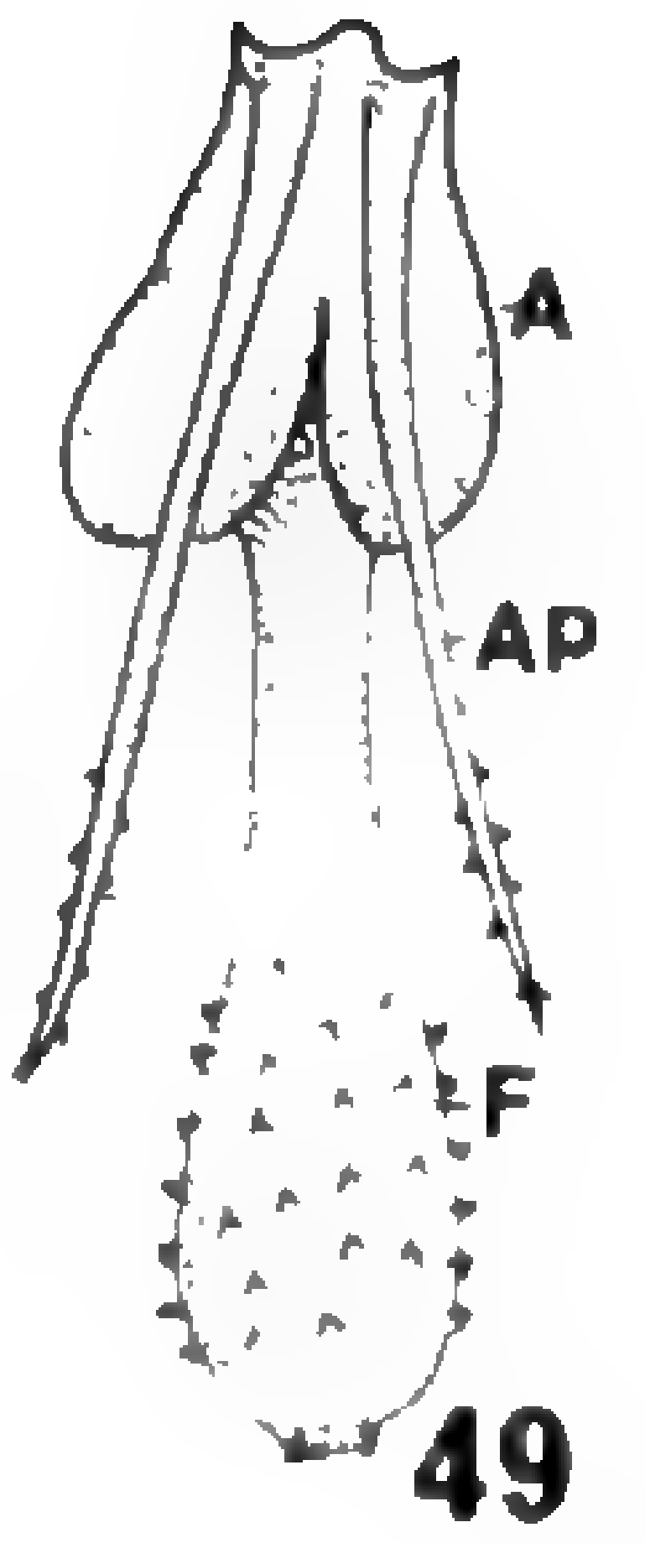
Porsild (1964) lists seven genera in the Canadian Arctic Archipelago, many species possessing urceolate corollas and drooping flowers particularly suited to pollination by bees. One with an open flower, *Kalmia,* has an explosive mechanism for liberating the pollen, which normally is triggered by the movements of a heavy-bodied insect probing for nectar. The anthers are held in hollows of the corolla by bowed filaments under tension, and at a touch they are released, and send a shower of pollen onto the visiting insect.

Most of the Ericaceae are autogamous, according to Fryxell (1957) (although some *Vaccinium* species are known to be obligate out-crossers), but the distribution of the family in the arctic seems to reflect the local bee population. *Cassiope tetragona* is an exception, being distributed in most of the Queen Elizabeth Islands. Kevan (1972) found it to set seed well under insect excluders, but other ericaceous species seem to disappear in the islands where bees are absent or rare.

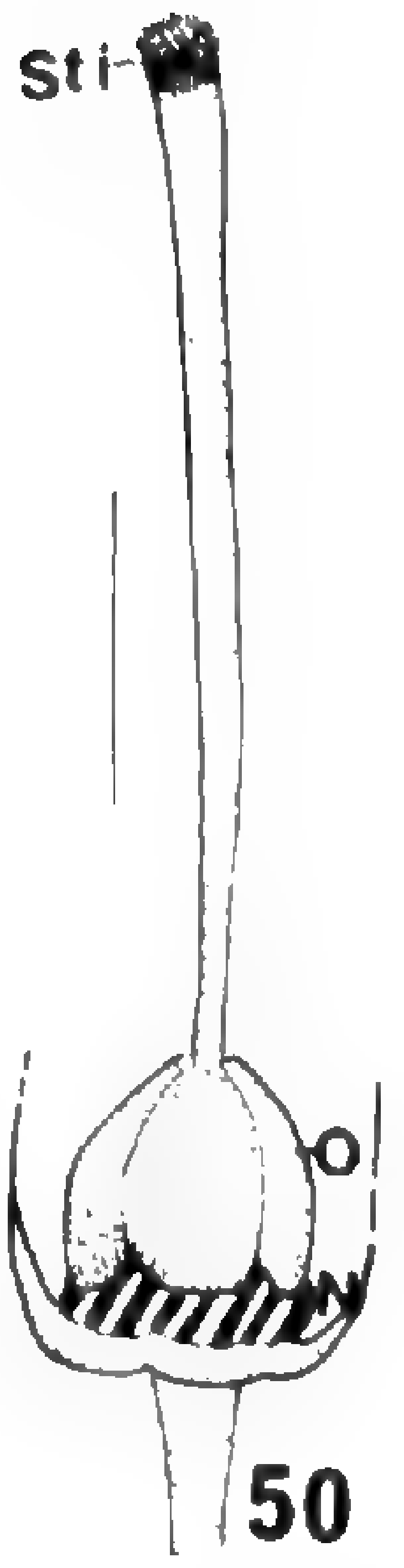
The flowers of all species studied, except *Pyrola grandiflora,* were found to have the attraction to insects of actively secreting nectaries. The anthers of a number had appendages which act as trip hammers when touched, shaking pollen over the visitors (Plate 5, Figures 43–47). Many specimens of the sweet-scented *P. grandiflora* were examined in the field at Frobisher Bay without finding a trace of nectar or nectaries, although Clapham *et al.* (1962) say nectar in *Pyrola* is secreted by the base of the petal. The stigma was unique, composed of five wet glistening cones (Plate 5, Figures 40–47). The fluid present seemed more than necessary to ensure pollen grains sticking to it, and was a possible attractant. The whole of the short, fleshy, yellowish-green style of *Cassiope hypnoides* was sticky to the touch and frequently bore holes made by insect larvae, perhaps the oviposition sites of a moth (Plate 6, Figure 48). It was not clear what advantage, if any, such a style had for the plant. There are devices,



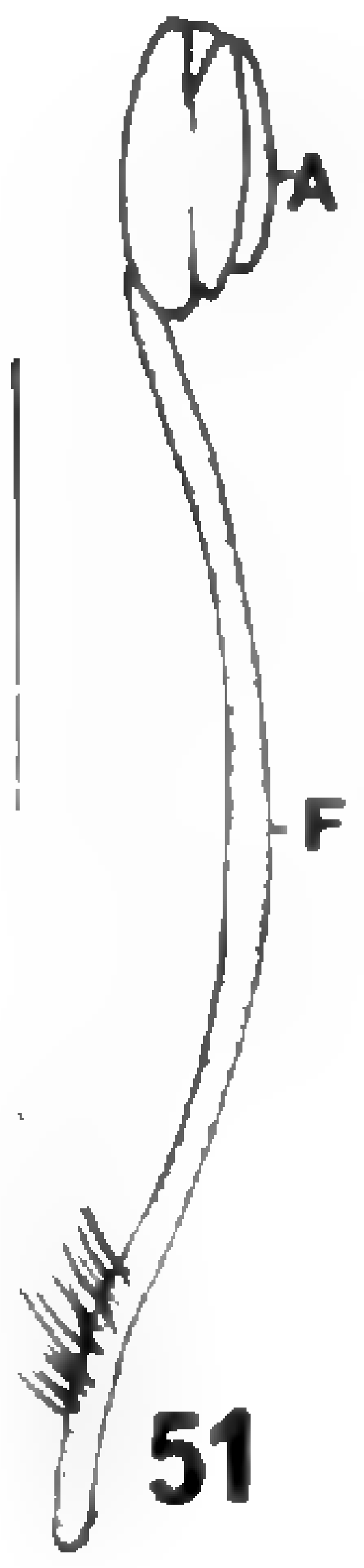
48



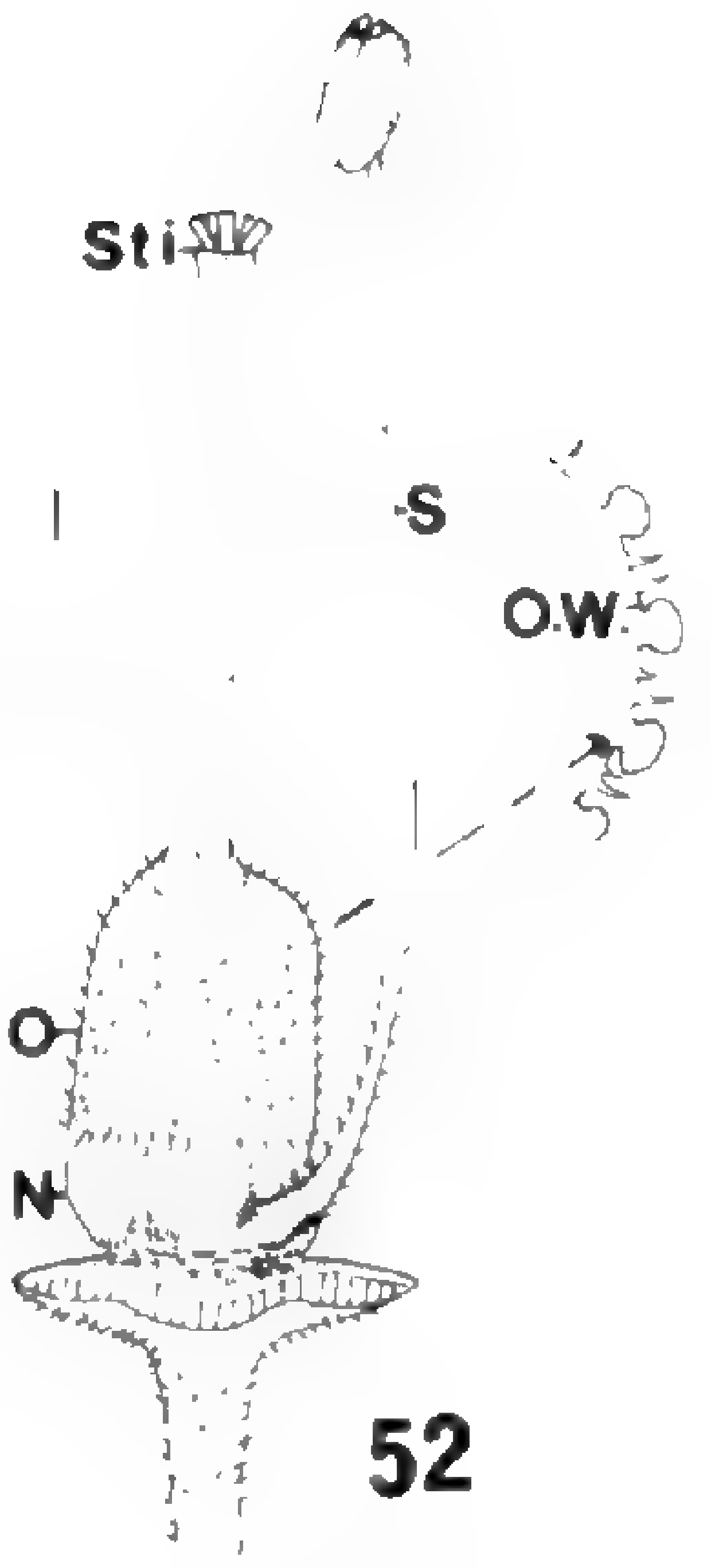
49



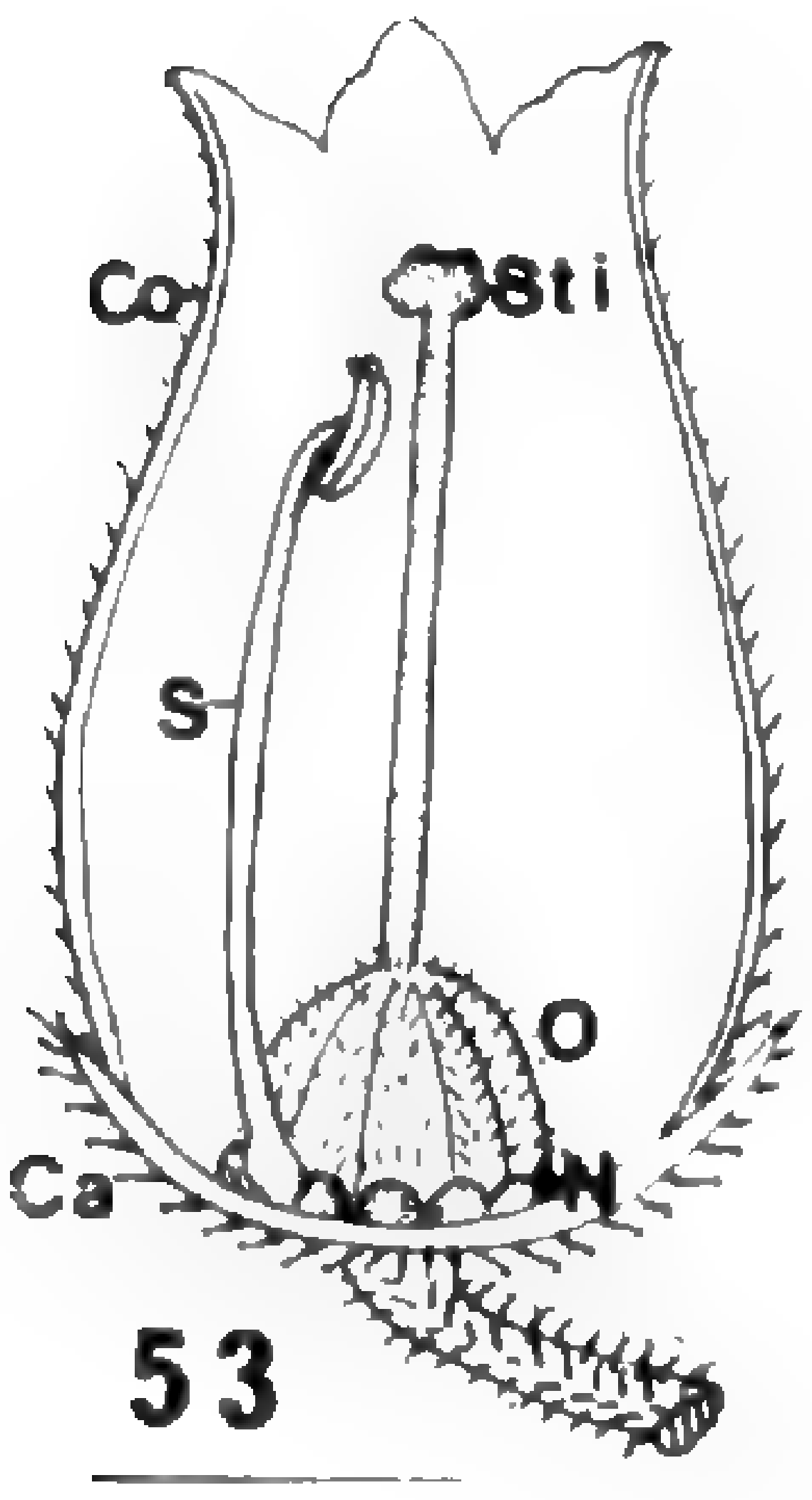
50



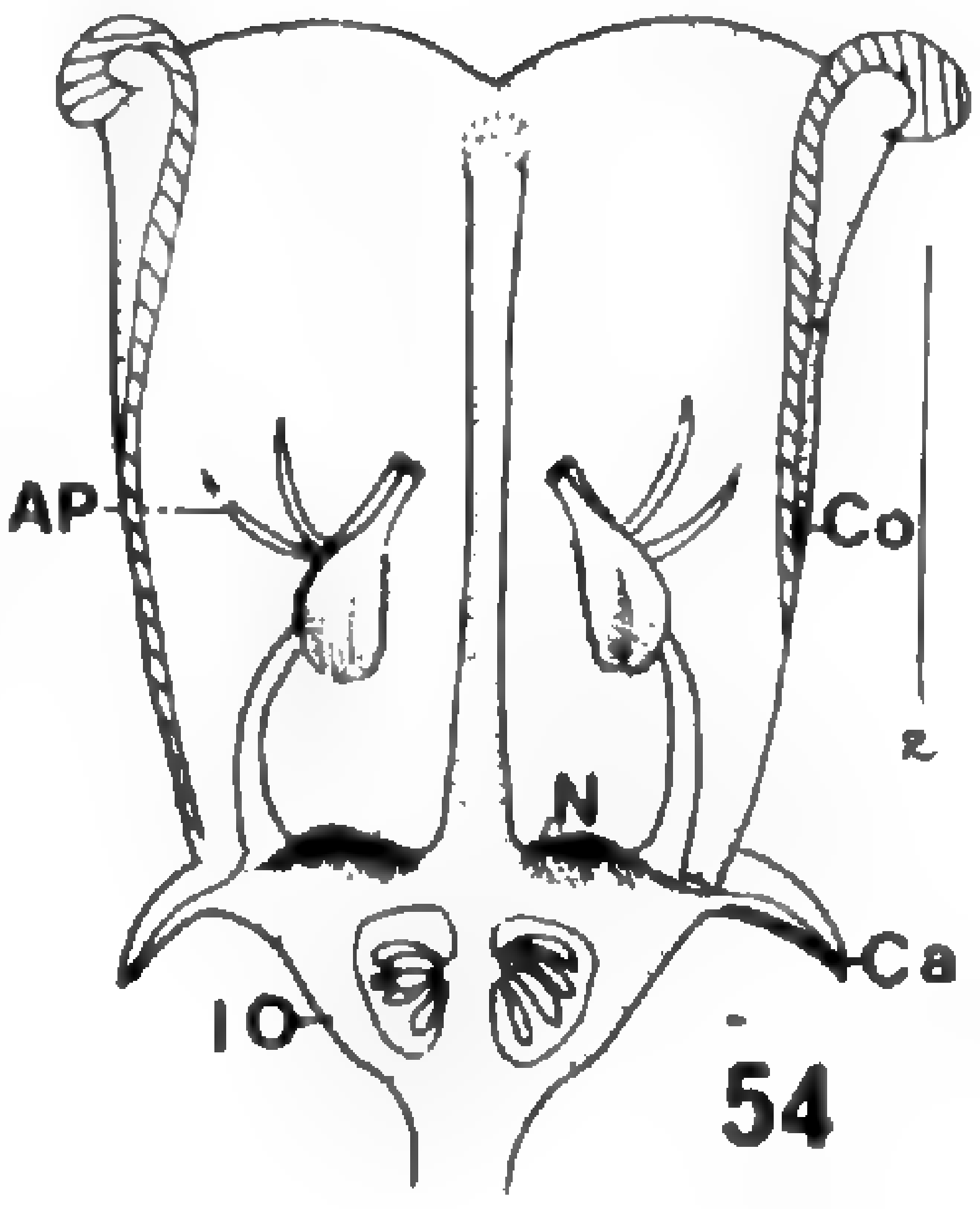
51



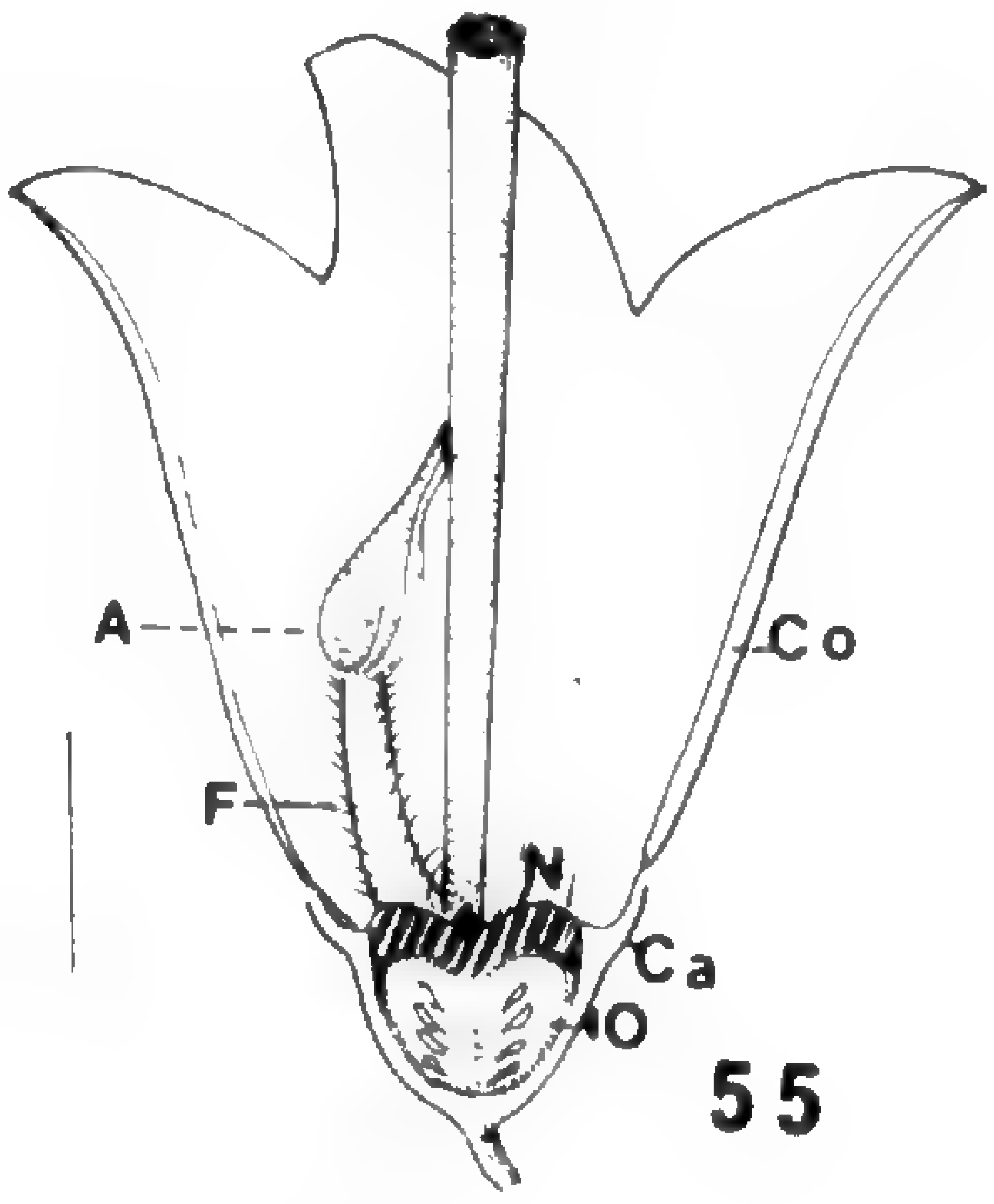
52



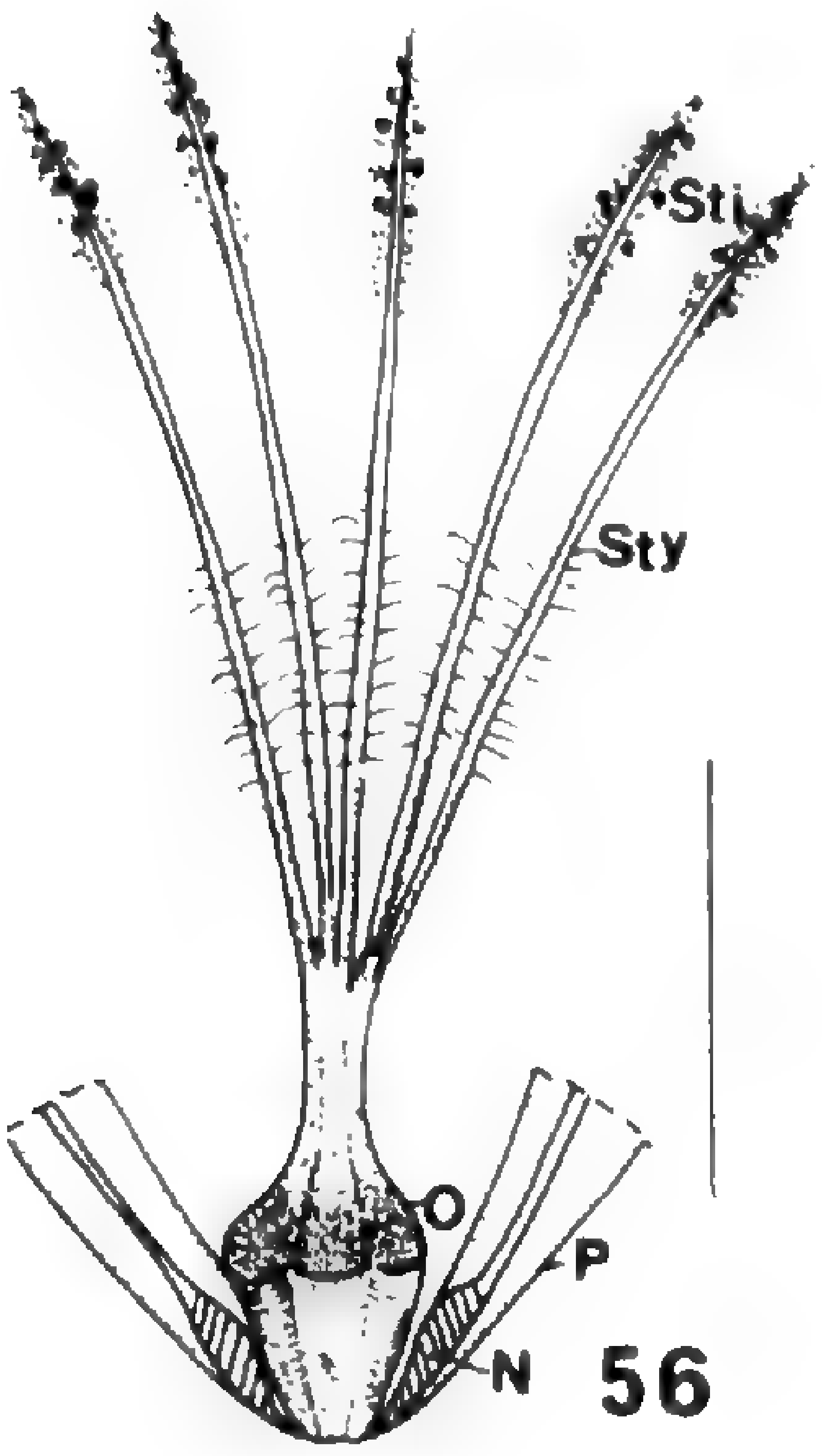
53



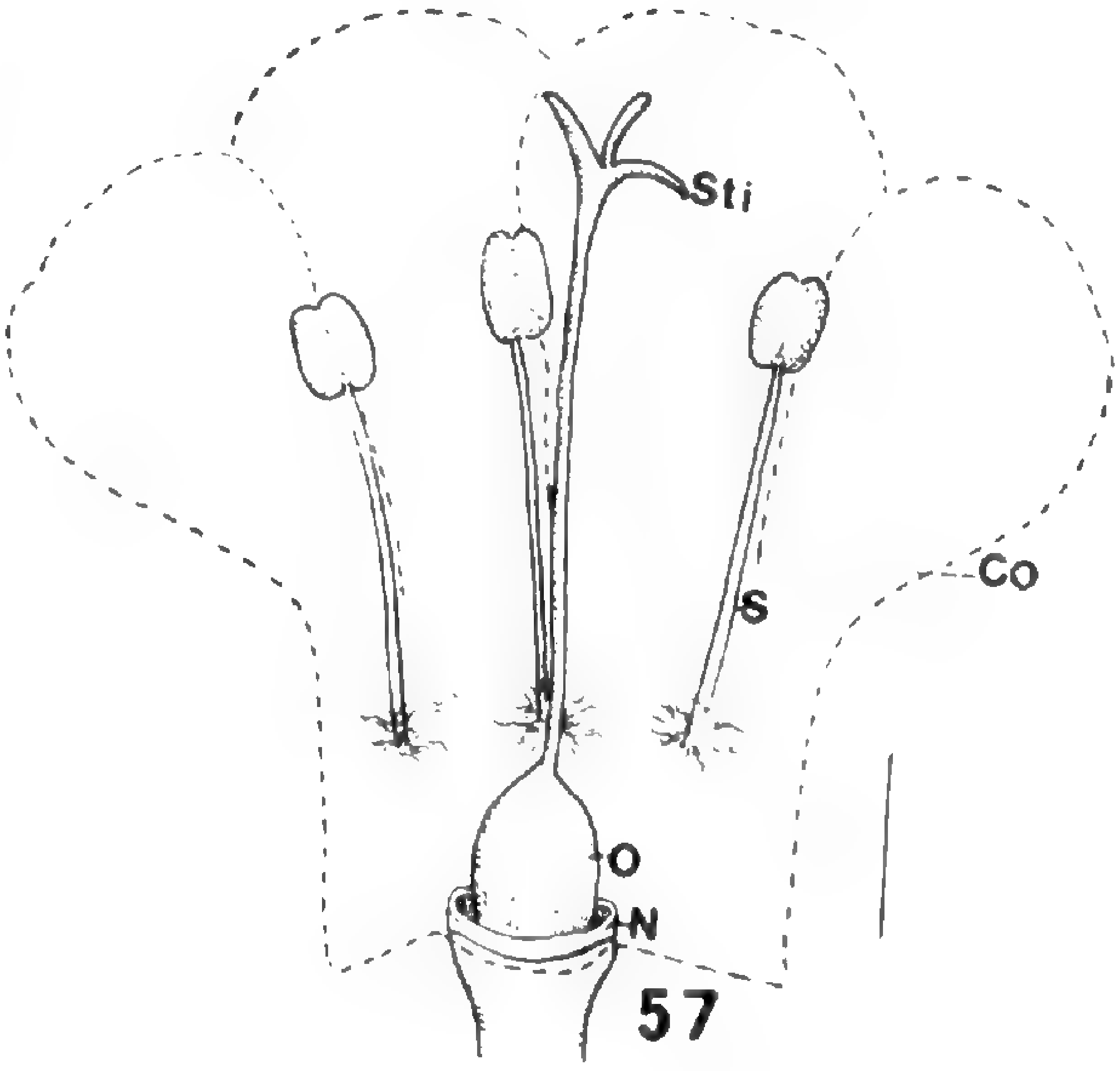
54



55



56



57

such as hairs on the filaments (*Andromeda, Ledum, Kalmia*) (Plates 5 & 6) or tangled hairs within the corolla (*Arctostaphylos, Andromeda*) to prevent small non-pollinating insects from reaching the nectar.

It is probable that some cross-pollination takes place in the arctic in flowers so well adapted to it, and known to have bee and other flower visitors. On the other hand, self-pollination would be physically easy when the stigma is above the level of the anthers in nodding or pendulous flowers such as *Andromeda, Arctostaphylos,* and *Cassiope.* The pollen would simply fall by gravity to the stigma on a windy day. In the umbellate flowers of *Ledum* the stigma is below the level of the anthers, but the flower is upright and pollen would be shaken down onto the stigma with wind movement (Plate 6, Figure 52).

Nectaries. The species with superior ovaries bear a shiny nectariferous band at the base of each ovary, varying from 0.3–1.0 mm in depth, and swollen between the bases of the filaments, often giving it a scalloped or torulose appearance (Plate 5, Figures 42, 44 & 46; Plate 6, Figures 48–53). The band is readily seen because it is always of a slightly different shade from the ovary, usually a darker green. In *Vaccinium* spp., with inferior ovaries, the nectary occurs as a thin, shiny, fleshy epigynous disc, its thickness evident in a longitudinal section of the flower (Plate 6, Figures 54 & 55).

Plate 6, Figures **48–57. 48 & 49,** *Cassiope hypnoides* (L.) Don; 48, Slightly scalloped nectary at base of 5-lobed ovary; 49, Stamen (1.5 mm) with long appendages, decorated with sharp peg-like projections; **50 & 51,** *Kalmia polifolia* Wang; 50, Nectary band green; 51, Stamen with flat filament; **52,** *Ledum groenlandicum* Oeder. Nectary of indefinite swellings at base of ovary. At right, details of ovary wall; **53,** *Phyllodoce coerulea* (L.) Bab. Nectary a green glabrous scalloped band at base of greenish-yellow ovary with glandular hairs. *Note:* Although the *Vaccinium* species illustrated had eight stamens each, most were removed to prevent cluttering of drawings. **54,** *Vaccinium uliginosum* L. Longitudinal section of flower. Nectary an epigynous disc; **55,** *Vaccinium vitis-idaea* L. Longitudinal section of flower. Nectary an epigynous disc; **56,** *Armeria maritima* (Miller) Willd. Nectary a yellowish swelling at base of staminal filament fused to petal; **57,** *Polemonium pulcherrimum* Hook. Corolla opened to show 4 of the 5 lobes, and 3 of the 5 stamens. Nectary a dark-green cup-like rim at base of a light green ovary. O, Ovary (superior). IO, Inferior Ovary. OW, Ovary Wall, greatly enlarged. STY, Style. STI, Stigma. II, Insect Injury. S, Stamen. F, Filament. A, Anther. AP, Anther Appendage. CO, Corolla. P, Petal. CA, Calyx. N, Nectary. Line equals 2 mm.

PLUMBAGINACEAE

Armeria maritima (Mill.) Willd. ssp. *labradorica* (Wallr.) Hult. is a widely distributed species along the coasts, rarely inland. Although the European race has both "cob" and papillate stigmas and is self-incompatible, the North American race, presumably derived from it, has only papillate stigmas and is self-compatible (Baker, 1959). All Frobisher Bay plants examined had papillate stigmas, but retained the texture and colour of the dimorphic race attractive to insects.

There was a swollen yellowish nectary below the point at which the stamen was attached to each of the five petals. Nectar collected in the space between the petals and ovary, 7 mm below the tip of the flower, protected from rain and the invasion of small, non-pollinating insects by long hairs on the lower part of the style branches (Plate 6, Figure 56). As the flowers were slightly protandrous, insect visitors would become powdered with pollen before the five stigma branches opened, leading to possible cross-pollination. In older flowers the stigmas diverged, and the anthers were seen to bend inwards at right angles to the filament, so that a foraging insect would touch both stigma and anthers on the same visit, making self-pollination possible in this self-compatible race.

POLEMONIACEAE

The pleasant-scented *Polemonium acutiflorum* and the mephitic *P. pulcherrimum* are common in the Yukon and continue into Alaska, *P. acutiflorum* to well above the Arctic Circle, and *P. pulcherrimum* mainly south of it, as far as the mountain ranges of California.

The two species were studied at Dawson City, Y.T., June 23–28, 1969. Both had blue to purple campanulate corollas, with darker, purple veins converging towards the base, acting as insect guidelines to the nectary, a dark green cup-like rim at the bottom of the lighter-green ovary, thicker in *Polemonium acutiflorum* than in *P. pulcherrimum*. The stamens were attached to the corolla 2–4 mm from the base, in a tangle of white hairs 0.54–0.59 mm long, outgrowths of both the filaments and the corolla. Insects were further attracted to the nectary by the whitish throat in *P. acutiflorum* and the striking yellow one in *P. pulcherrimum* (Plate 6, Figure 57).

Ekstam reported *Polemonium caeruleum* L. to be protogynous to homogamous in Novaya Zemlya (Knuth, 1909), but in the early flowering stage of both the Dawson species, the anthers dehisced while the stigma lobes were still closed, making them protandrous, and suited to cross-pollination. The stigmas were usually on a higher level than the anthers, occasionally opposite, so in the next, homogamous, stage, self-pollination might take place, particularly if the flower became horizontal, or drooped as it aged, more frequent in *P. acutiflorum.*

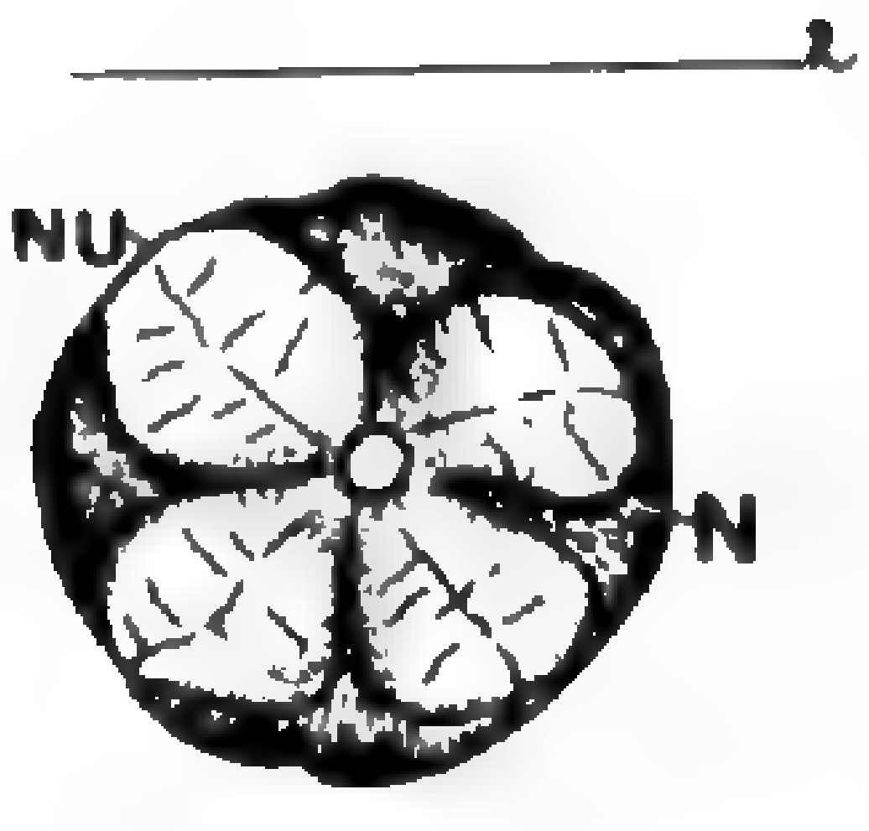
A strong proboscis would be needed to penetrate the tangle of hairs above the nectary and Knuth (1909) records bees and flies visiting the European species. I made no observations on their insect visitors, due to lack of time, but *Bombus* spp. were common along the Yukon River.

The corollas of *Polemonium acutiflorum* at Dawson City were thickly covered with short-stalked yellow glands 0.139–0.163 mm in diameter. The flowers at Keno Hill had only occasional yellow glands, and they were missing in Lac Laberge specimens. Kluane Lake plants had flat white hairs on the margins and backs of the petals. *Polemonium pulcherrimum* had very few, or no, glands on the corolla. It would be interesting to know if these clones would be consistent in the production of glands and hairs under varying conditions, and whether they had any effect on insect visits. They were not described in the floras listed.

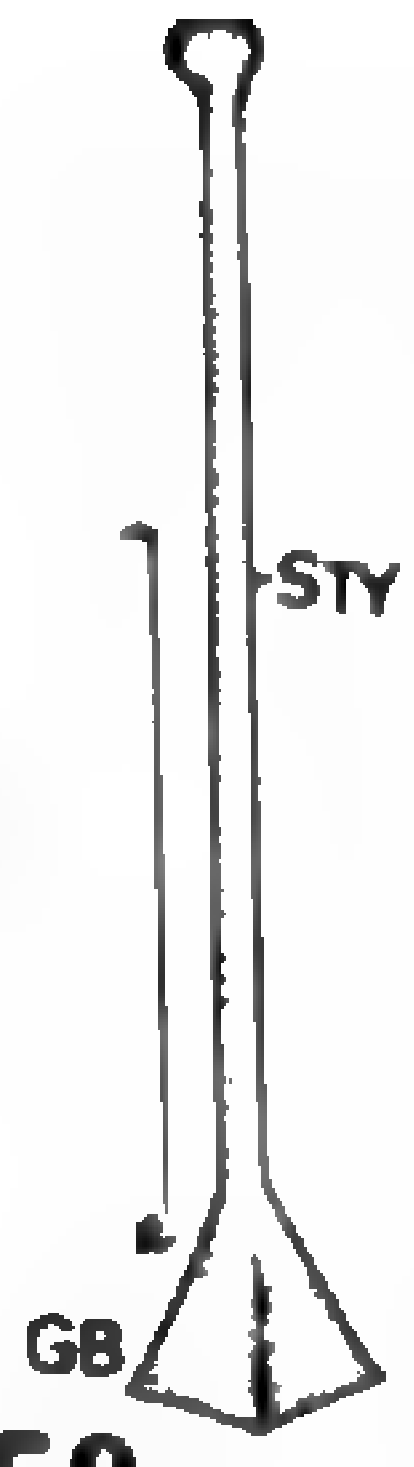
BORAGINACEAE

Mertensia maritima, of gravel beaches, is the only species of the Boraginaceae found commonly in the Arctic. Other genera are known in the western sub-arctic mainland, of which I collected *Myosotis alpestris* at Whitehorse and *Amsinckia menziesii* at Dawson City in the Yukon. *Mertensia maritima* was studied at Frobisher Bay, from Ikaluit Beach.

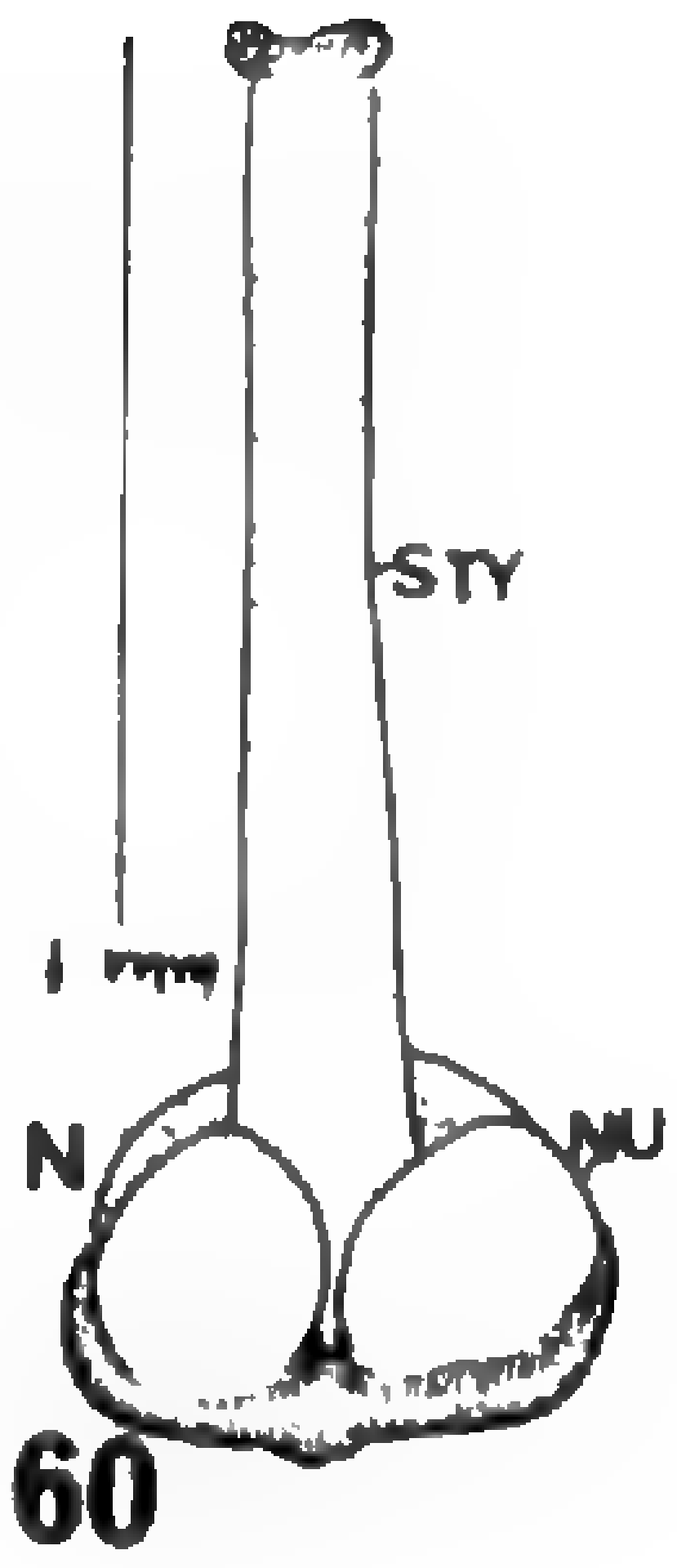
There is much uniformity in the size of flowers, the type of nectary, and the position of anthers and stigmas in the northern Boraginaceae. The introrse stamens are attached to the corolla near the top of the tube by very short filaments, 0.5 mm in *Myosotis* to 1.2 mm in *Mertensia,* and intermediate in *Amsinckia.* The filaments tend to bend away from the corolla in the later stages, bringing the top or the bottom of the anther opposite the stigma, and close to it.



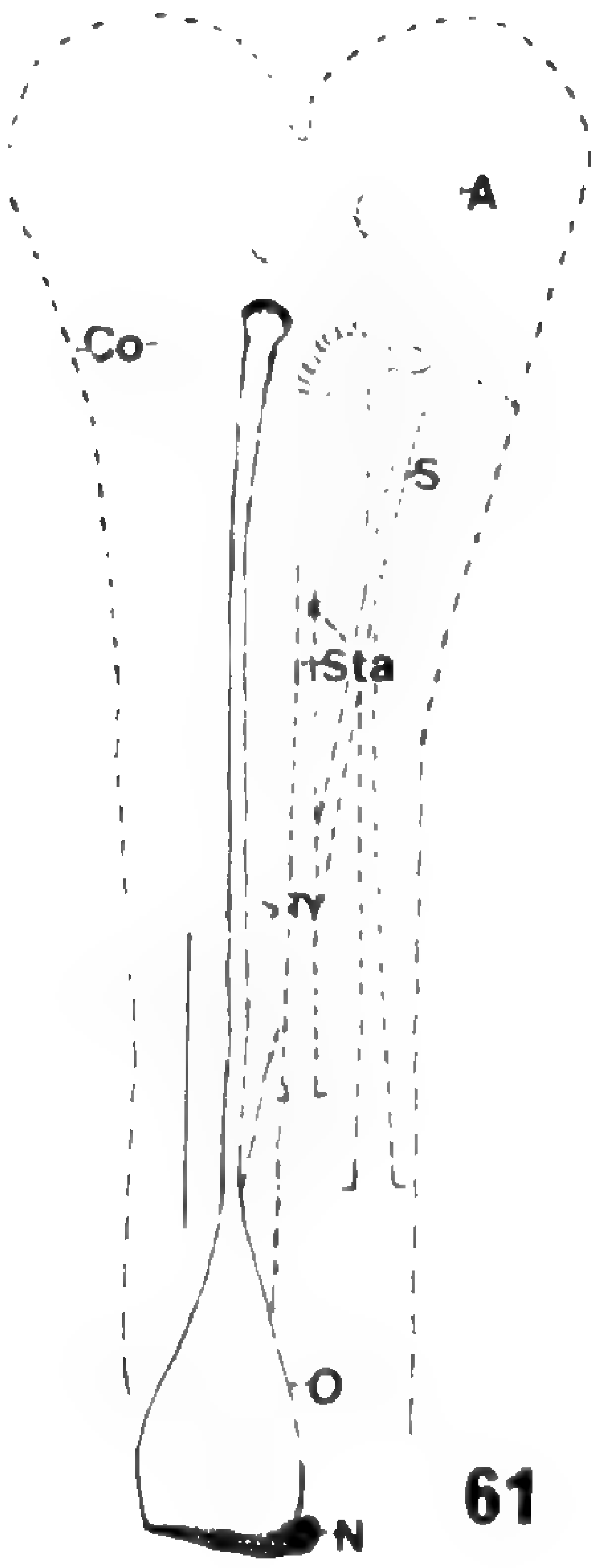
58



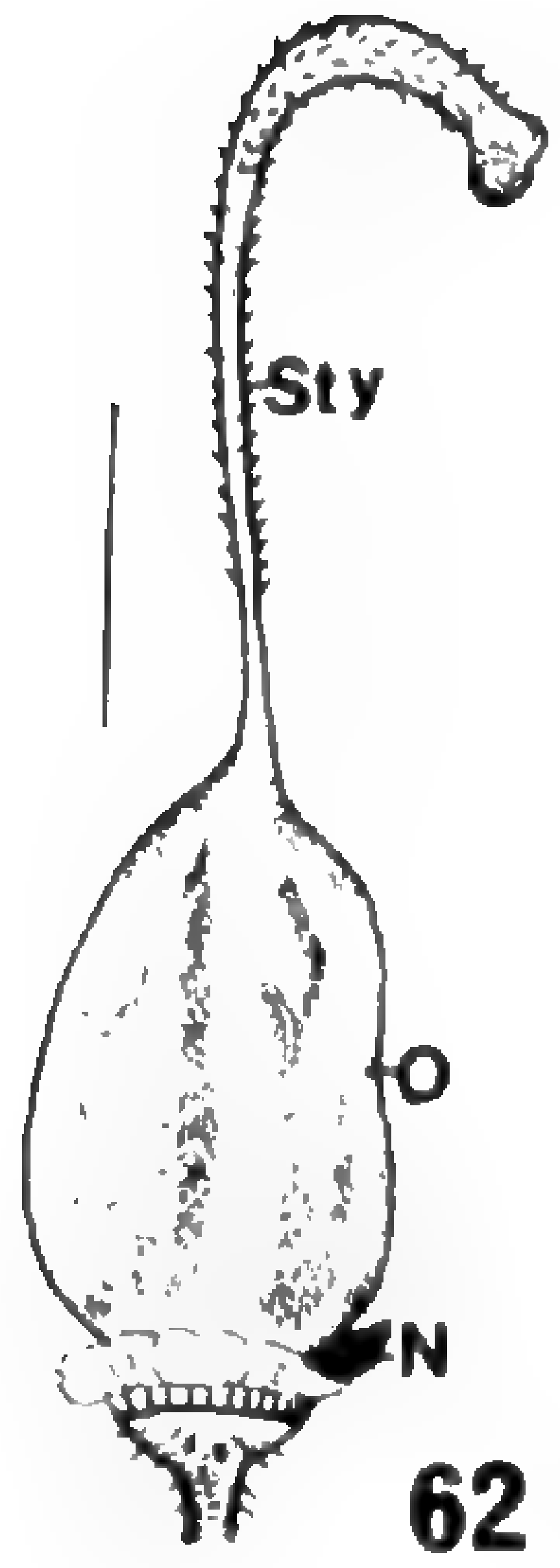
59



60

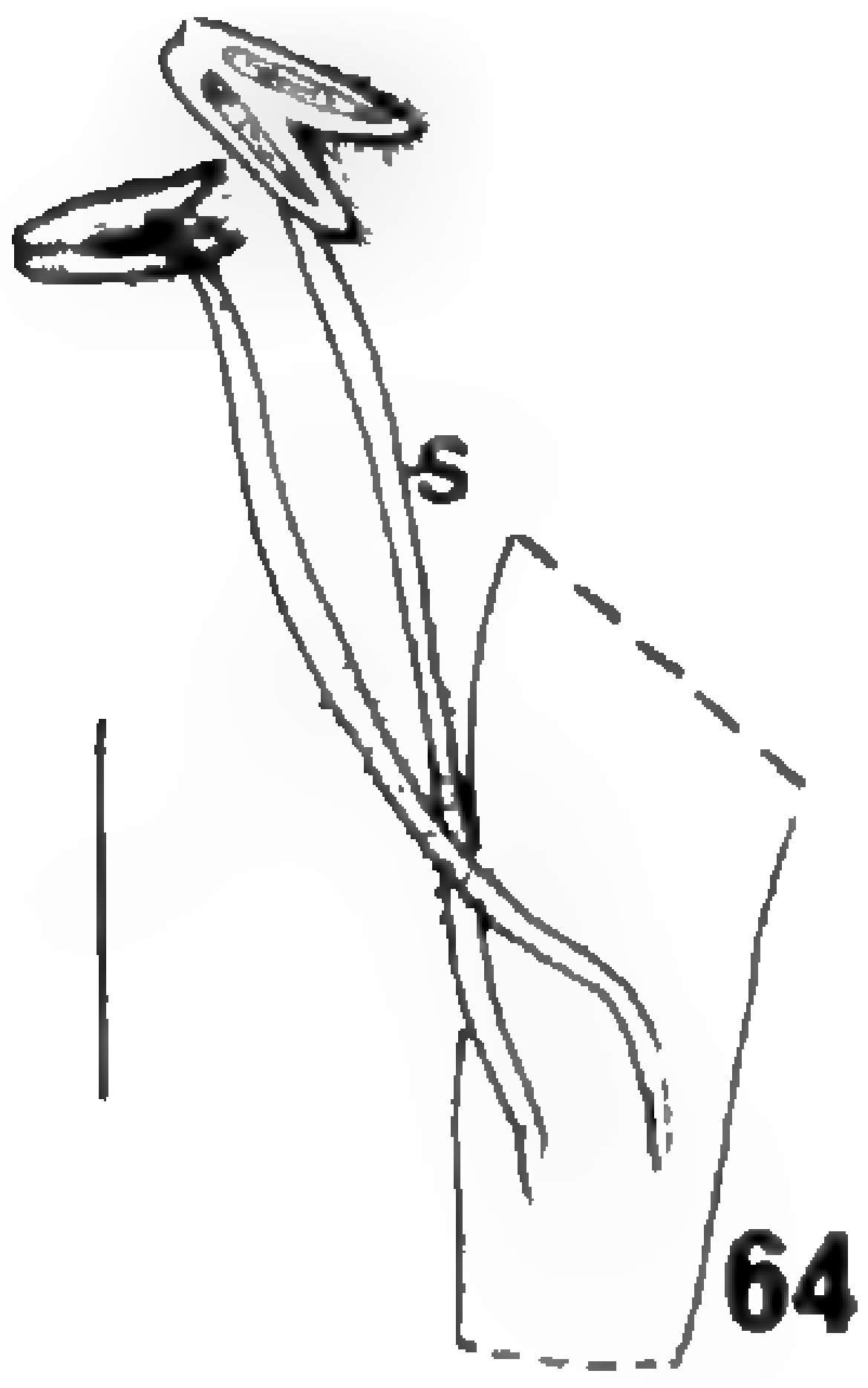


61

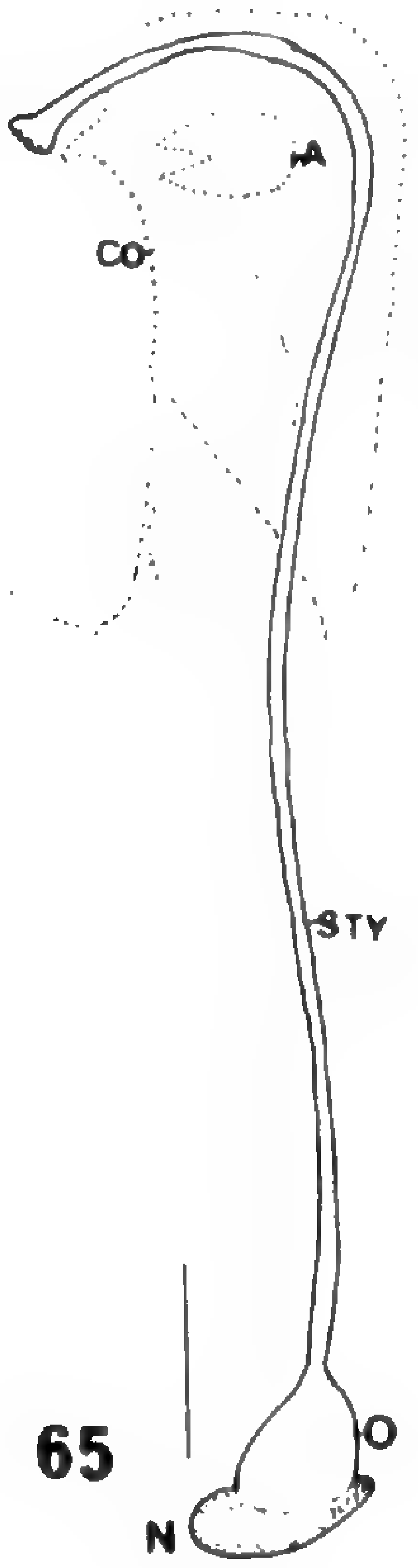


62

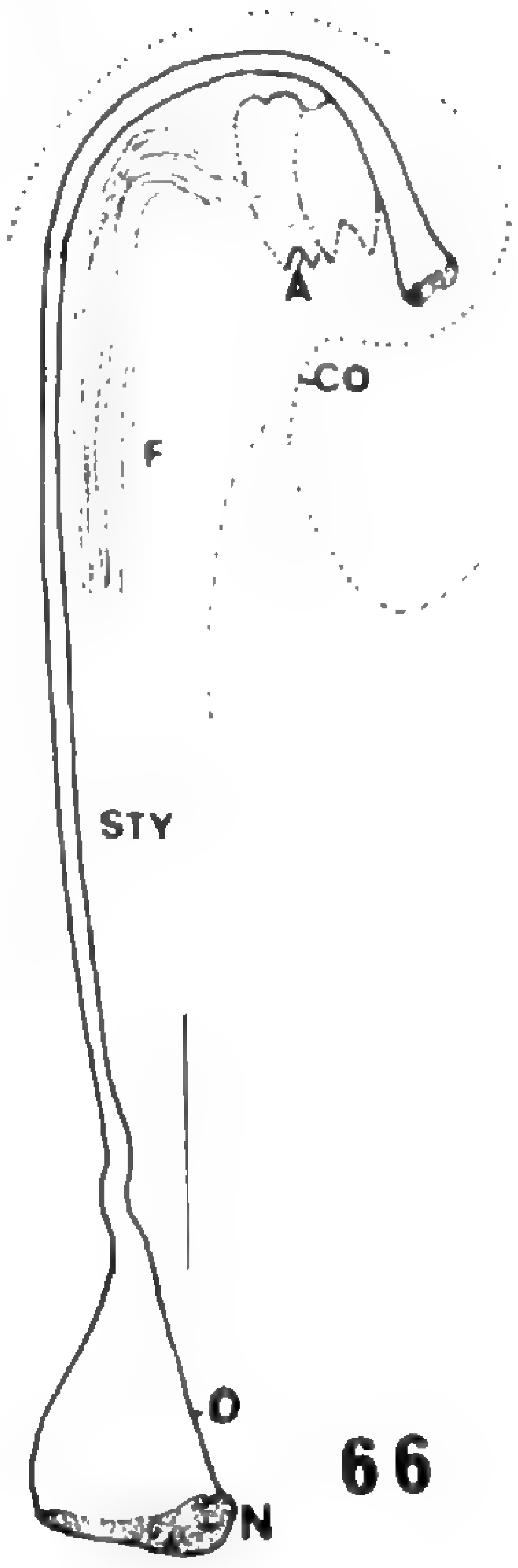
63



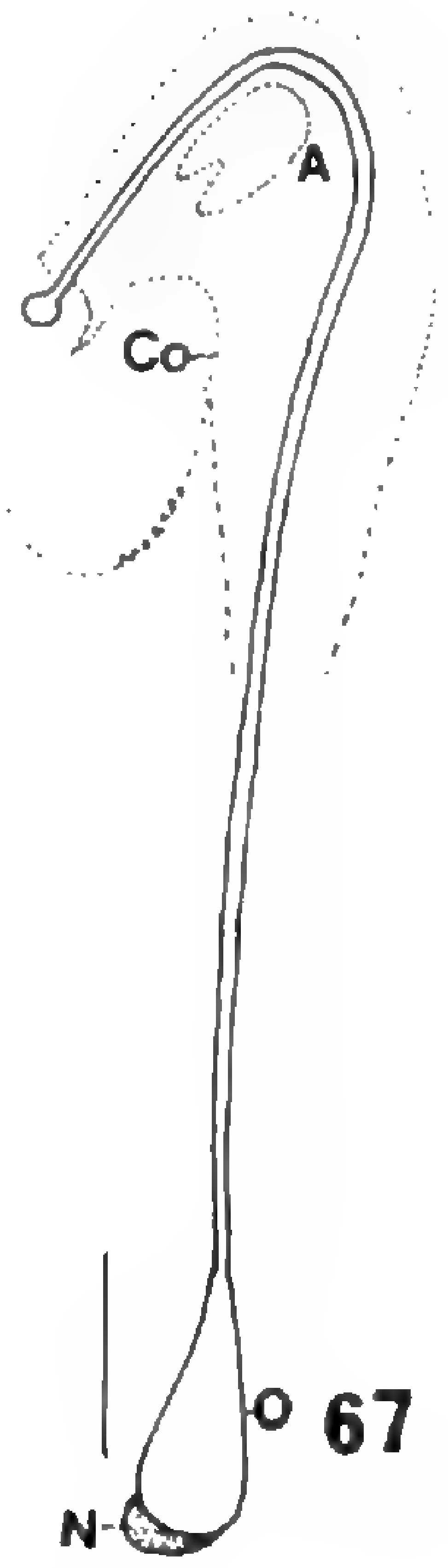
64



65



66



67

The corolla tube is not more than 2–3 mm wide, the limb expanded to a varying degree in the three species, but the throat is further narrowed in *Myosotis* by scales. Under this condition one side of the proboscis of a bee would touch the anther, the other the stigma, when inserted into the flower.

The style ends in an elongated pyramid-shaped gynobase in *Amsinckia* (Plate 7, Figure 59), with four membraneous wings radiating to the outside of the ovary in *Mertensia,* in both species allowing for lateral attachment of the nucules in the concavities between the "rays". The style of *Myosotis* widens only slightly between the nucules, which are attached basally (Plate 7, Figure 60). Beneath the ovary in all three genera is a somewhat irregular, fleshy, nectary ring, yellowish in *Mertensia* and *Myosotis* and a darker green than the nucules in *Amsinckia.*

The nectaries in these small flowers secrete scanty nectar and are visited very little by insects, although Knuth (1909) records bees, Lepidoptera and Syrphids visiting *Myosotis* in Europe. The close proximity of the anthers and stigmas in the later stages of the flower suggests that self-pollination is usual in these species in the Arctic.

Plate 7, Figures **58–67.** **58 & 59,** *Amsinckia menziesii* (Lehm.) Nels. & Macbr. (Dawson City); 58, Nucules and nectary from above. Nectary a dark green fleshy disc; 59, Pyramid-shaped gynobase, the nucules removed from the concavities; **60,** *Myosotis alpestris* R. W. Schmidt. Nectary an irregular ring beneath nucules, enlarging slightly between them; **61,** *Penstemon procerus* Dougl. Nectary a soft yellow disc at base of green ovary. Upper pair of stamens attached to corolla above lower stamens. Staminode opposite anthers of lower stamens, attached to corolla above both pairs of fertile stamens, with club-shaped enlarged tip, pubescent on one side; **62–64,** *Rhinanthus crista-galli* L. (Great Whale River); 62, Pistil showing nectary and basal corolla "frill"; 63, Enlargement of corolla frill and nectary gland; 64, Pair of anthers (normally apposed and attached by connective at the proximal end) pulled apart to show dehisced pollen sacs; **65–67 & 68** (Plate 8), *Pedicularis,* General note: The dotted lines outline the upper lip, or galea, and show the position of the anthers of the stamens opposite the point the proboscis of the visiting insect enters to release the pollen sprinkling mechanism; 65, *Pedicularis arctica* R.Br. Pistil showing asymmetric nectary at base of ovary; 66, *Pedicularis hirsuta* L. Pistil with well-developed asymmetric nectary, and filaments markedly coiled for increasing tension; 67, *Pedicularis labradorica* Wirsing. Pistil with small asymmetric nectary. N, Nectary. NU, Nucule. GB, Gynobase. O, Ovary. STY, Style. S, Stamen. STA, Staminode. A, Anther. CO, Corolla. Line equals 2 mm, except 1 mm in Figure 60.

SCROPHULARIACEAE

The Scrophulariaceae are particularly well represented in the arctic by the genus *Pedicularis*, with 16 species in Alaska (Hultén, 1968) and 8 in the arctic islands (Porsild, 1964). Other less common (sub-arctic) genera I have collected include *Castilleja, Lagotis*, and *Penstemon* in the Yukon, and *Rhinanthus* in Labrador. The long, tubular, and usually bilabiate corollas of the arctic and sub-arctic species are particularly adapted for pollination by *Bombus* spp. and the larger Syrphidae, such as *Helophilus borealis*.

The nectar of these genera is concealed, secreted by nectaries of varied form at the base of the ovary, either as asymmetrical discs, or single glands (Plate 7, Figures 61-63 and Plate 8, Figure 68). *Rhinanthus* has a cone-shaped fleshy gland on the side of the ovary below the terminal curve of the style. Nectar seems to be copiously produced and dries on the delicate base of the corolla so that a frill of tissue, strengthened by the sugar deposits, is left when the corolla is pulled off by hand. This frill was evident at the base of the capsules in herbarium specimens, collected in fruit, in which the corolla had dropped off naturally (Plate 7, Figures 62 & 63).

Penstemon gormanii and *P. procerus* had small soft nectary discs of rather indefinite shape, differing in colour from the ovary, and wet with nectar in the latter species, when picked at Whitehorse, Y.T. (Plate 7, Figure 61). *Pedicularis* had firm asymmetrical discs, thicker on the side below the curvature of the style, and usually of a different shade from the ovary, and easily distinguished. The nectary of *Pedicularis flammea* was smaller than that of the other species studied, and may be functionless in this species, found to be autogamous, and stated to be nectarless, by MacInnes (1972). Macior (1970) noted that *P. lanceolata* in Colorado was nectarless.

Pollination in *Pedicularis* has been studied experimentally through the artificial exclusion of insects by MacInnes (1972) and Kevan (1972b) in the Canadian Arctic, by Sprague (1962) in California, and by Macior (1970, 1973, 1975) in California, Colorado, and Washington. Sprague said the flowers of *P. crenulata* were limitedly self-compatible, and autogamy occurred rarely. Macior found the California species had obligate dependence on insects for fruit production and that no species in Colorado were self-pollinating, including *P. sudetica*. Our northern species seem to have evolved towards autogamy. Mosquin and Martin (1967) saw no bees visiting *P. arctica* and *P. sudetica* in Melville I., and thought they must be autogamous there, although Savile saw bees visiting *P. arctica* on Somerset Island, a bit further south (1959).

MacInnes (1972) found *Pedicularis lapponica* totally dependent on insects, *P. labradorica* and *P. sudetica* only partially dependent and *P. flammea* wholly independent of insects for seed production. Kevan (1972b) found *P. capitata* and *P. arctica* dependent on insects, although 7% of the plants of the latter were able to produce capsules under an insect excluder. *Pedicularis hirsuta* and *P. lanata* are structurally well suited to selfing, and have produced seeds vigorously in Spitzbergen where there are no bees (Knuth, 1909). The genus is usually homogamous.

Correlation between exsertion of stigma outside of corolla and insect pollination. A correlation of possible significance was noted between the exsertion of the style in *Pedicularis* and the experimental results on the need of different species for insects. The style was conspicuous outside the corolla of *P. capitata,* slightly less conspicuous in *P. sudetica* and with a short exsertion in *P. labradorica.* All these are dependent or partially dependent on insects, the most completely dependent being *P. capitata,* with the longest exsertion. The style is enclosed in the galea in *P. flammea* and *P. hirsuta,* known to be mainly autogamous. *Pedicularis lanata,* known to be self-pollinated in Spitzbergen (Knuth, 1909), usually has the style within the hood, but occasionally the stigma projects slightly on the lower older flowers of the spike.

Mechanics of pollination in *Pedicularis* and *Rhinanthus*. The "sprinkling apparatus" of the sub-family Rhinanthoideae, to which these two genera belong, is well known (von Marilaun, 1895). The lower lip of the bilabiate corolla serves as a landing platform for the bee. Of interest is the fact that the heads of *Bombus polaris* and *B. sylvicola,* known pollinators of *Pedicularis* (MacInnes, 1972) measure 1.0–1.3 mm more from side to side than in depth (measured in personally collected specimens), and that the lower lip of most of our arctic *Pedicularis* species is oblique (noted in *P. arctica, P. hirsuta,* and *P. lapponica*), lower on the left side than on the right so that the bee is tilted on its landing platform and its head automatically enters the very narrow slit of the galea by its narrower dimension. The pressure of the bee on the lip and galea distends the slit laterally. The lower end of the galea has papillae on its margin, hazardous to the sensitive proboscis, so the bee inserts it at the top end where its head will brush against the stigma, depositing on it any pollen grains it may have collected from other flowers.

The four stamens are arranged in pairs, the anthers pressing tightly against one another to form potential pouches. When the pollen sacs dehisce, they discharge the pollen into the pouch, where it is held by the tension of curved staminal filaments in *Pedicularis* (Plate 7, Figures 65–67; Plate 8, Figure 68) or stiff flat filaments in *Rhinanthus* (Plate 7, Figures 62–64). At the touch of the bee's proboscis the tension is released in *Pedicularis*, the anthers spring apart, and a shower of pollen falls on the bee's head and the anterior part of its thorax.

I tested the mechanism by sticking a dissecting needle into the top of the galeal slit in freshly picked *Pedicularis arctica, P. hirsuta,* and *P. flammea.* In all three species the touch of the needle triggered an instant shower of pollen, which scattered over the inside of the galea.

Self-pollination with aging of the flower. As the flower of *Pedicularis* ages it tends to move to a horizontal or lower position, so that released pollen may fall by gravity onto stigmas now below the anthers and autogamy may take place. If the sprinkling mechanism is not released by the touch of an insect, the pollen will fall eventually as the pairs of anthers become flaccid and no longer press firmly against one another.

No explosive mechanism in *Penstemon*. *Penstemon,* a protandrous genus, belongs to a different sub-family, the Antirrhinoideae, in which the anthers discharge their pollen gradually. The mouth of the narrow, dark blue corolla of *P. procerus* is only 2–3 mm wide, and the bee's proboscis is guided to the purple anthers over a glabrous palate between two patches of white hairs on the lower lip. The base of the ovary was wet with nectar from a soft yellowish nectary when the plant was picked at Whitehorse, Y.T. The blue corolla of *P. gormanii,* with a reddish-purple tinge, measured 2.8 cm long by 1.8 cm wide, but the throat was protected from the entrance of small non-pollinating insects by copious long white hairs. *Bombus* spp. were the effective pollinators, aided by purple lines on a whitish corolla background, leading to the narrow pale green nectary at the base of a darker green ovary.

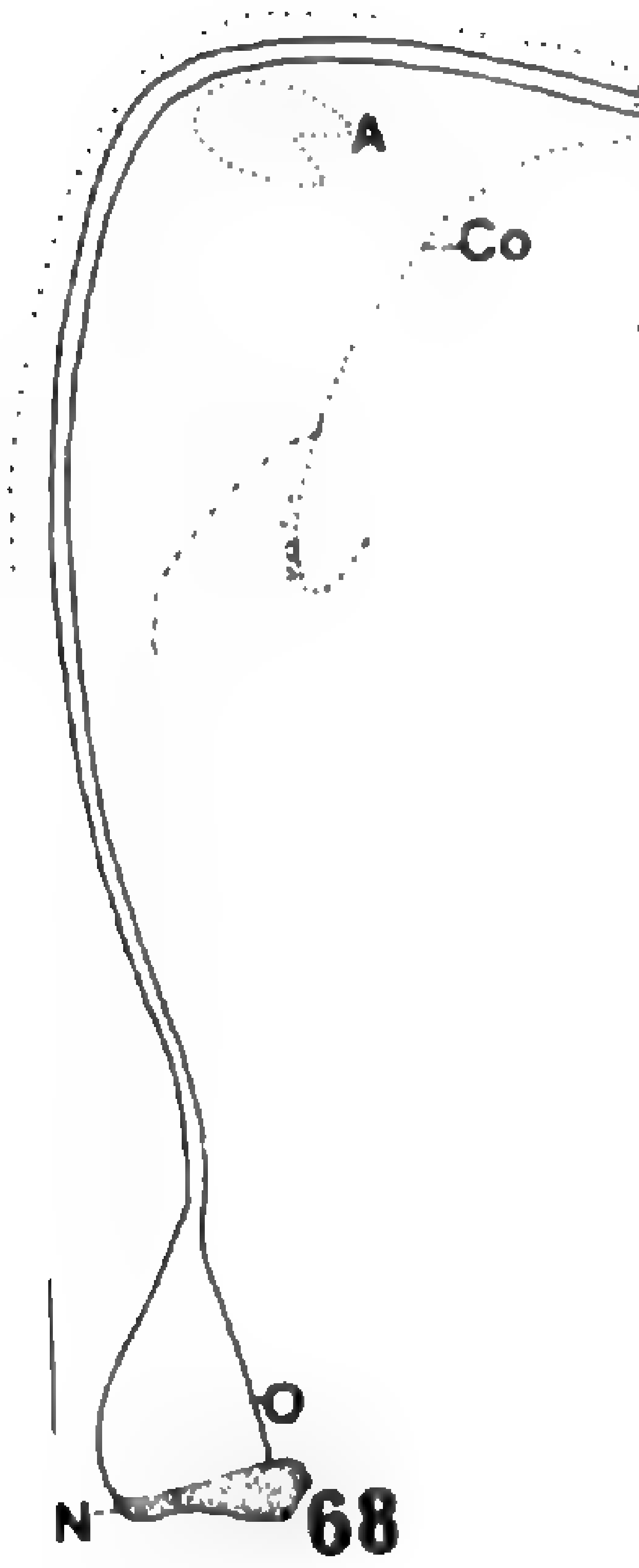
The hairy staminode, a modified fifth stamen, was below the stigma and the long pair of stamens in both species of *Penstemon* at Whitehorse. However, examination of herbarium material showed that in *P. gormanii* the staminode elongated even beyond the corolla in age. It is possible it had some function in carrying pollen grains past the stigma to pollinate a flower lacking insect visitors.

CAMPANULACEAE

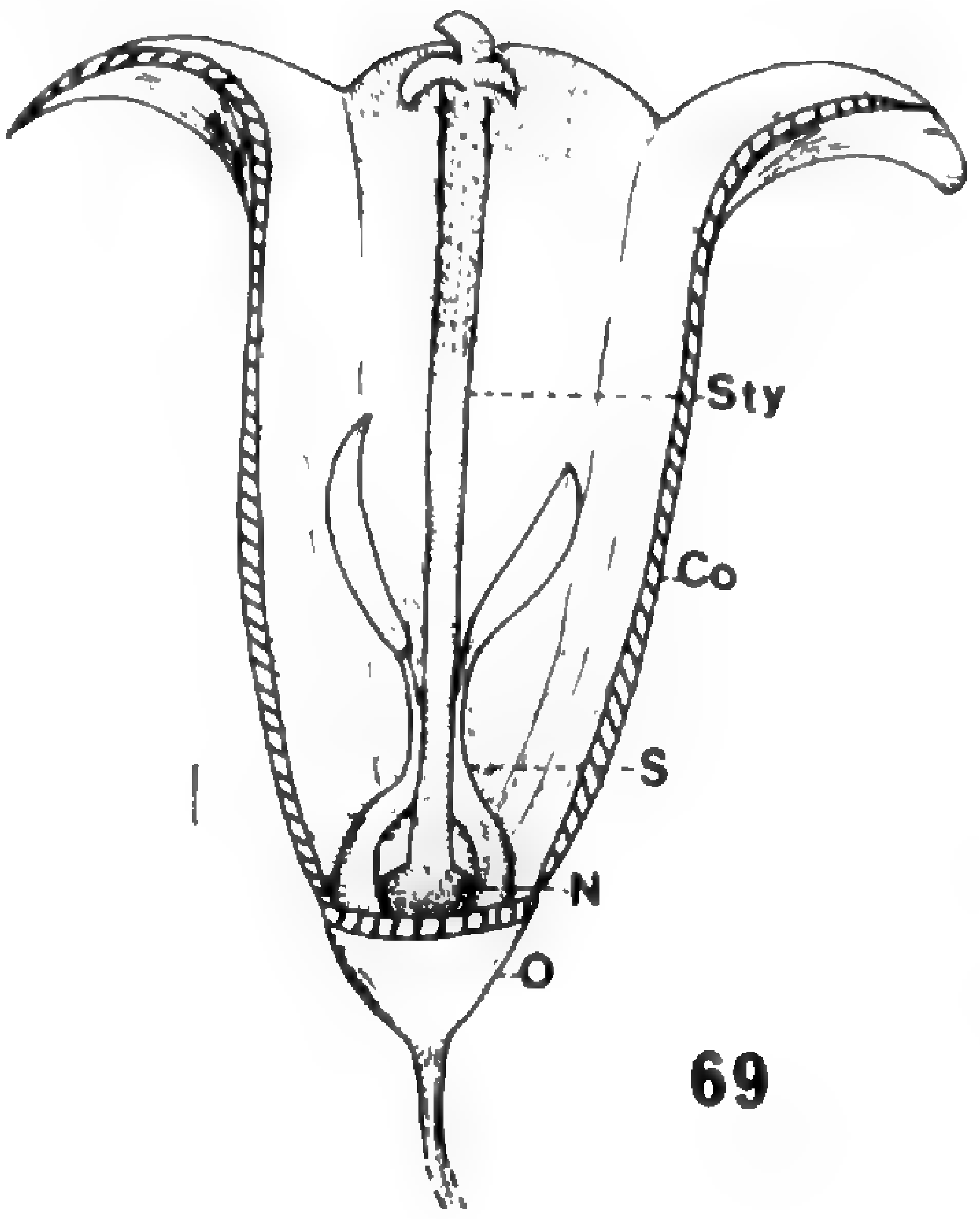
Campanula is the only genus of the Campanulaceae to reach the arctic, and the pollination mechanism and nectaries of three arctic and two sub-arctic species were studied. All had bell-shaped flowers, *C. rotundifolia, C. lasiocarpa,* and *C. uniflora* with shallow-lobed corollas, *C. scouleri* deeper lobes, and *C. aurita* with lobes four-fifths of its length. The structure influences the type and size of insects able to enter. The size of the corolla mouth varied from 0.6–1 mm in *C. uniflora,* up to 2 cm in large specimens of *C. rotundifolia* and *C. lasiocarpa* giving ample room for large Hymenoptera (Plate 8).

In all species the nectary is in the form of a fleshy yellow epigynous disc at the base of the style. It is covered by the triangular bases of the five stamens, firmly held together by marginal interlocking hairs, requiring a stout proboscis to penetrate. The style is glabrous in the lower part, but densely pubescent for a substantial part of the upper end. In the young stages the stigma lobes are tightly closed, and surrounded by the anthers which form a tube. The flower is strongly protandrous and the anthers discharge introrsely onto the hairy part of the style. Once the anthers are empty the style elongates carrying its load of pollen upward, and the stamens shrivel to the bottom of the corolla. Then the stigma lobes open and become receptive. Any bee entering the bell at this stage must brush against the stigma, and, as it probes for nectar, would have its coat powdered with pollen. The method is an ingenious one for ensuring cross-pollination, but should insects fail to visit, self-pollination is possible in the last stages of the flower, when the stylar branches curl backwards and touch the hairy pollen-dusted style.

In *Campanula aurita,* which I collected at Dawson City in the Yukon, the corolla lobes curled backwards so that short-tongued

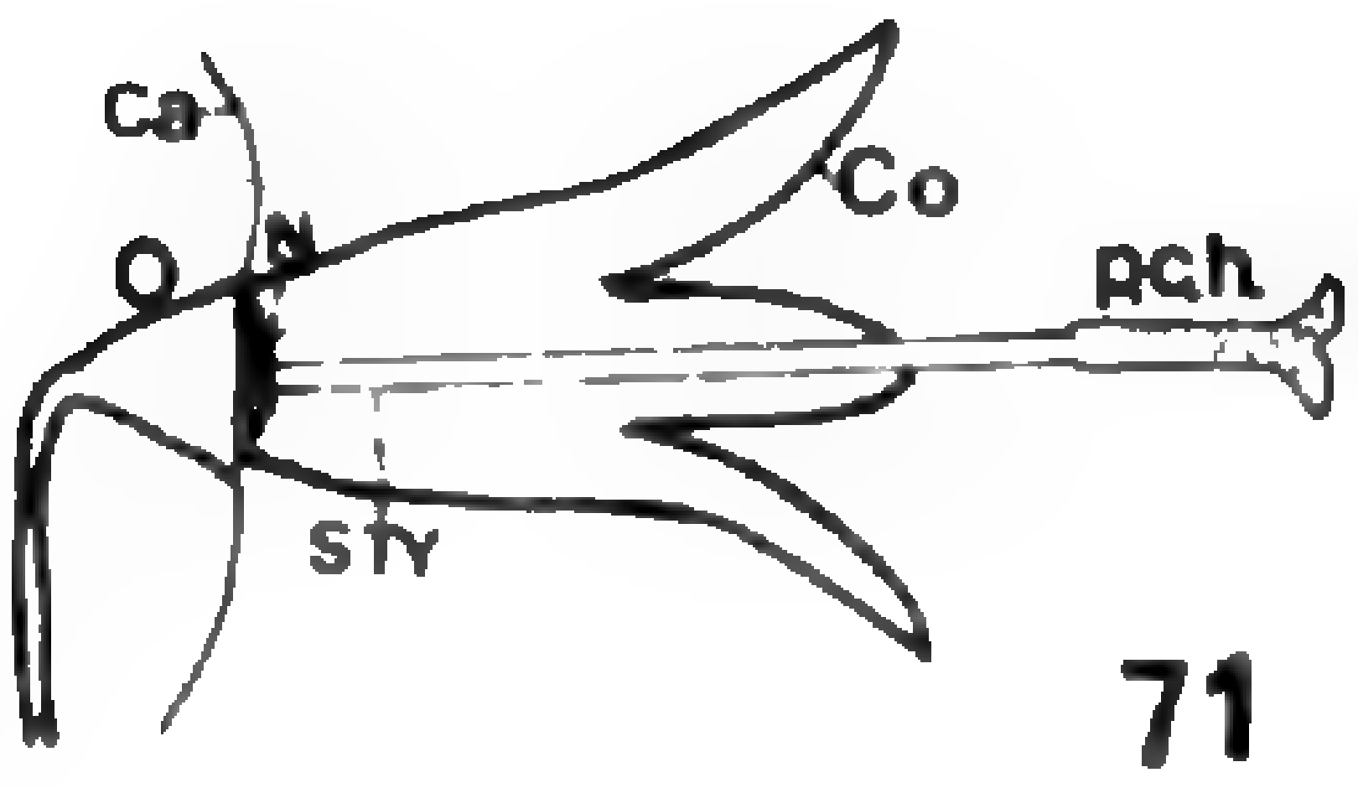


68

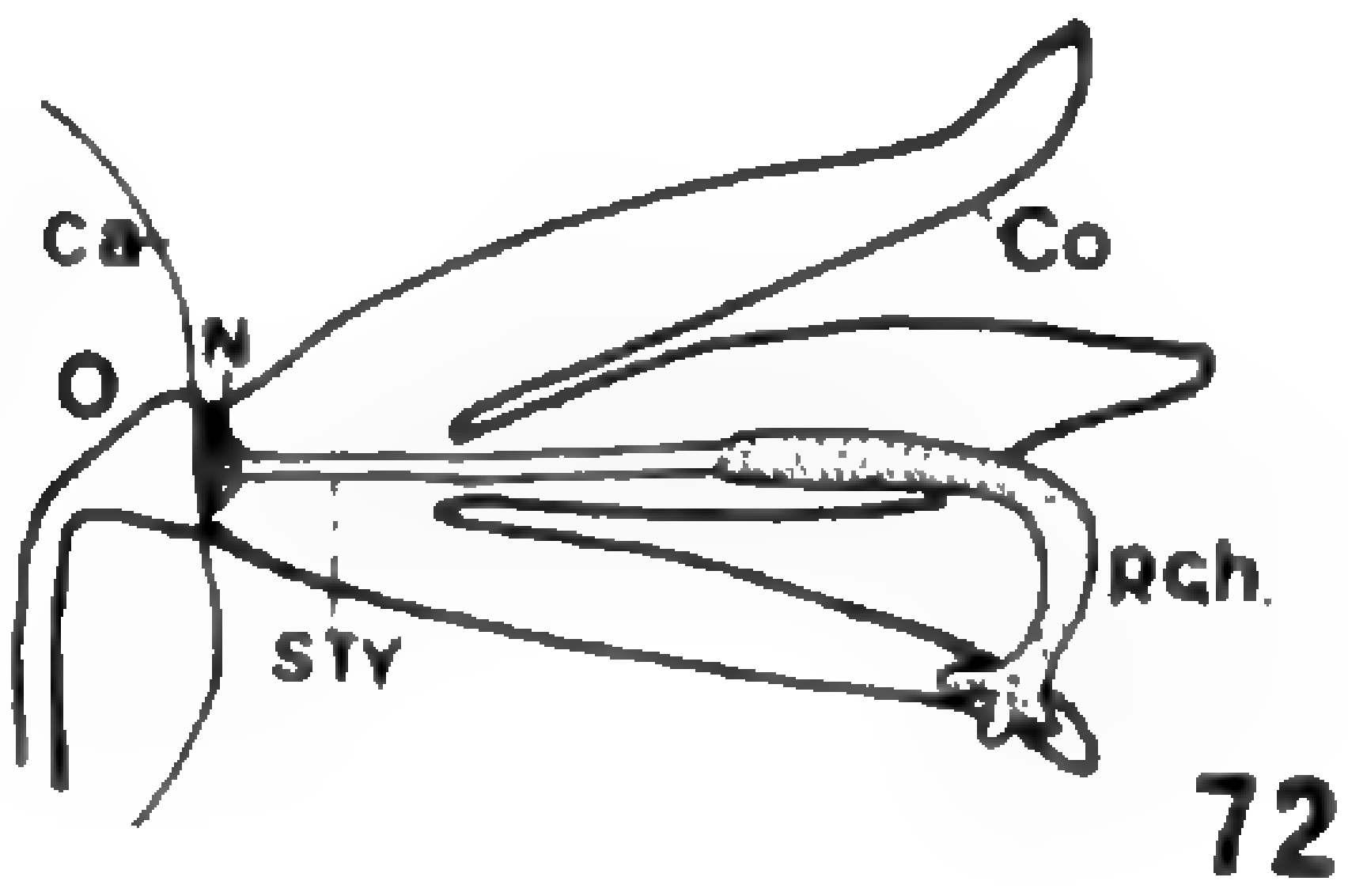


69

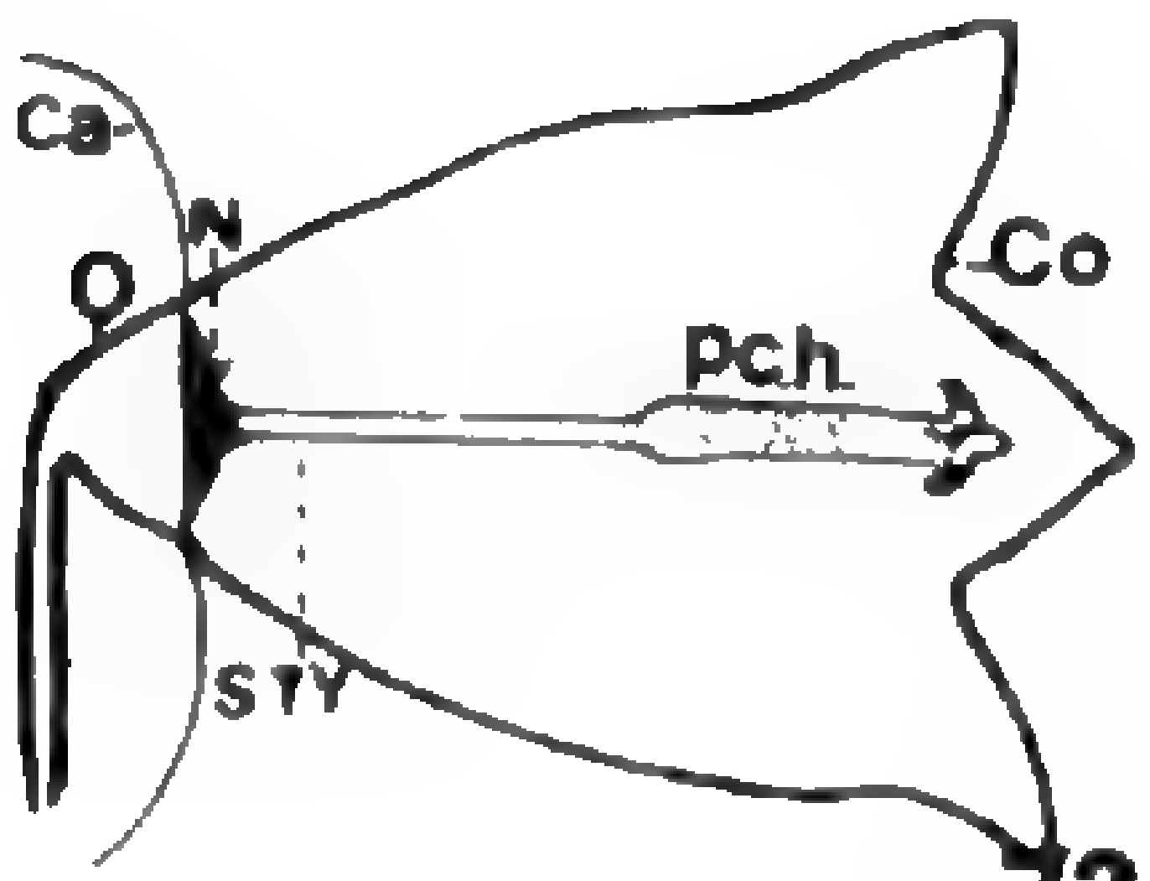
70



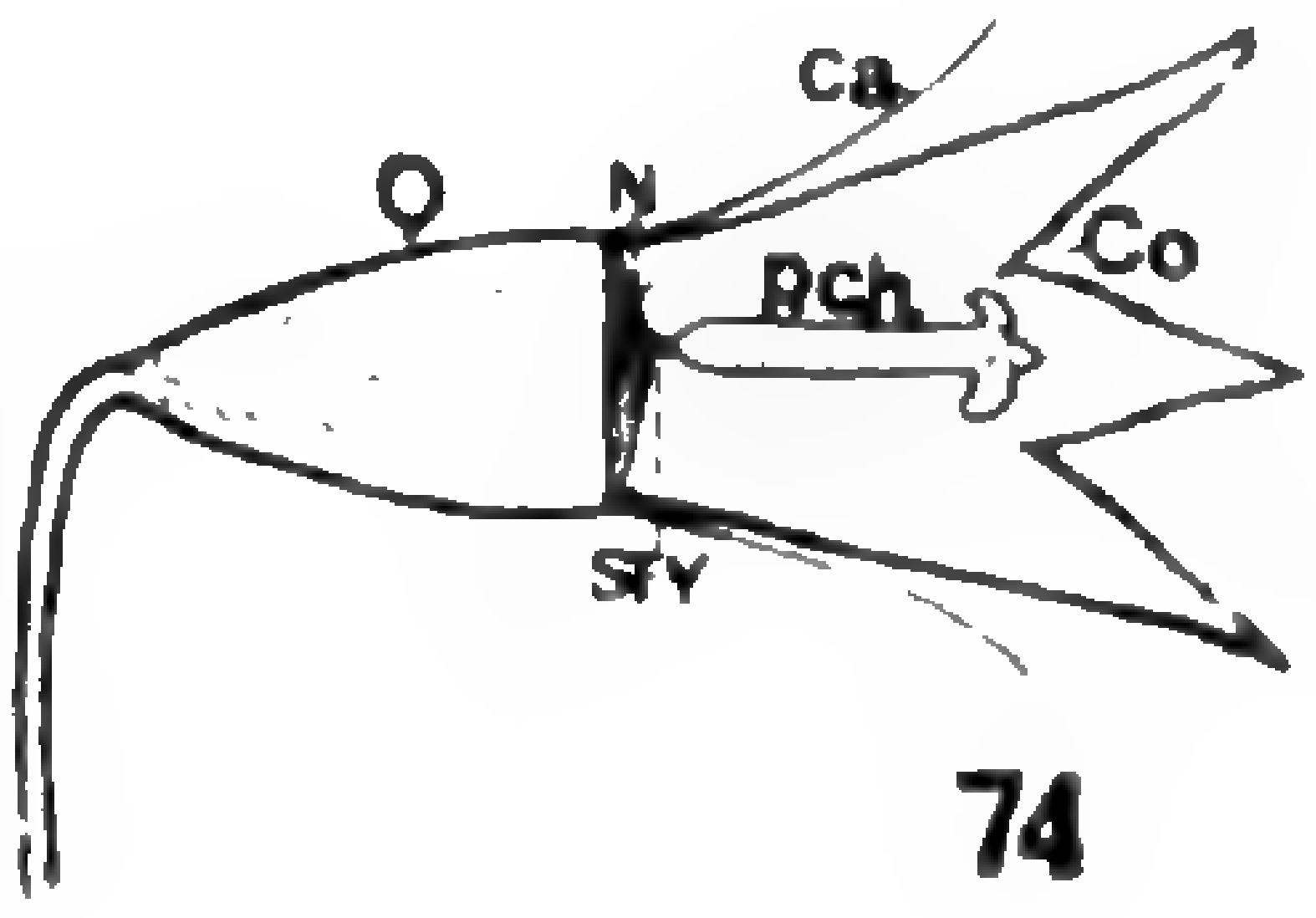
71



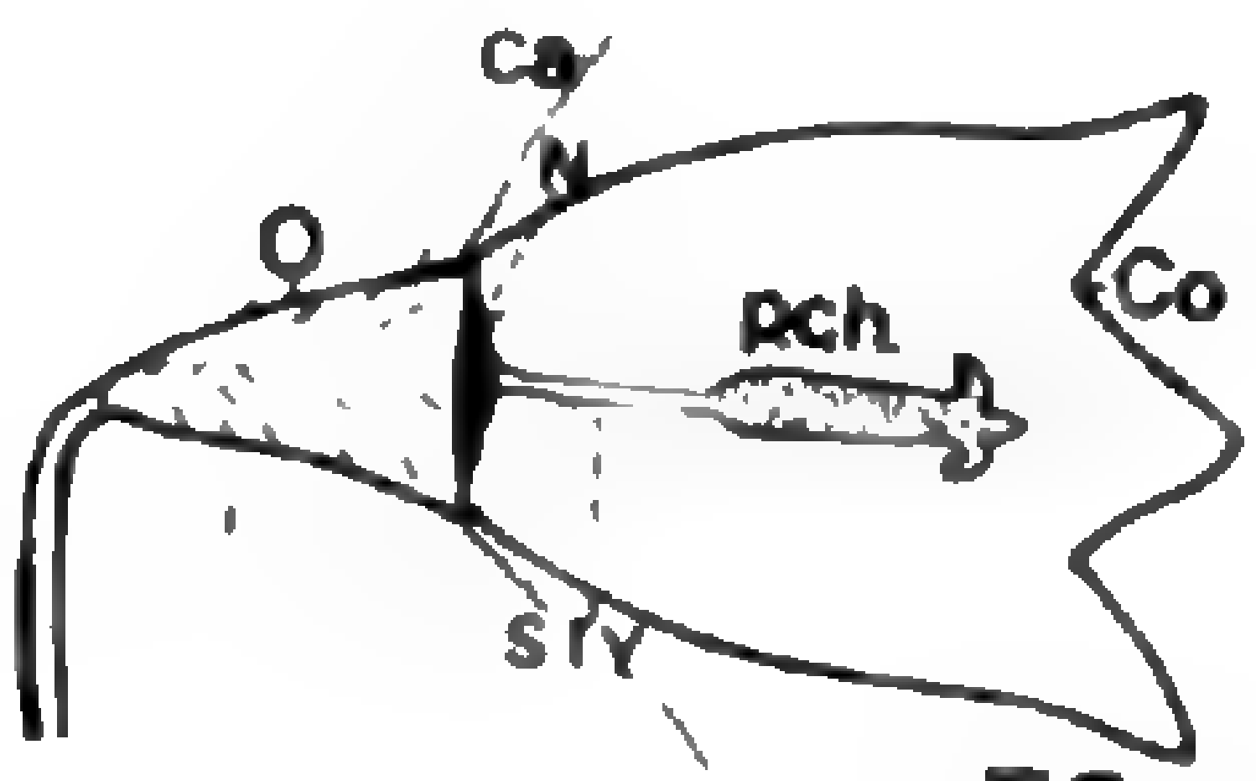
72



73



74



75

insects could reach the bottom of the bell, and if strong enough, could penetrate between the staminal bases to the nectar. The relative length of pubescent and glabrous parts of the style varied greatly between species, and could be used as an additional character to distinguish between them (Plate 8).

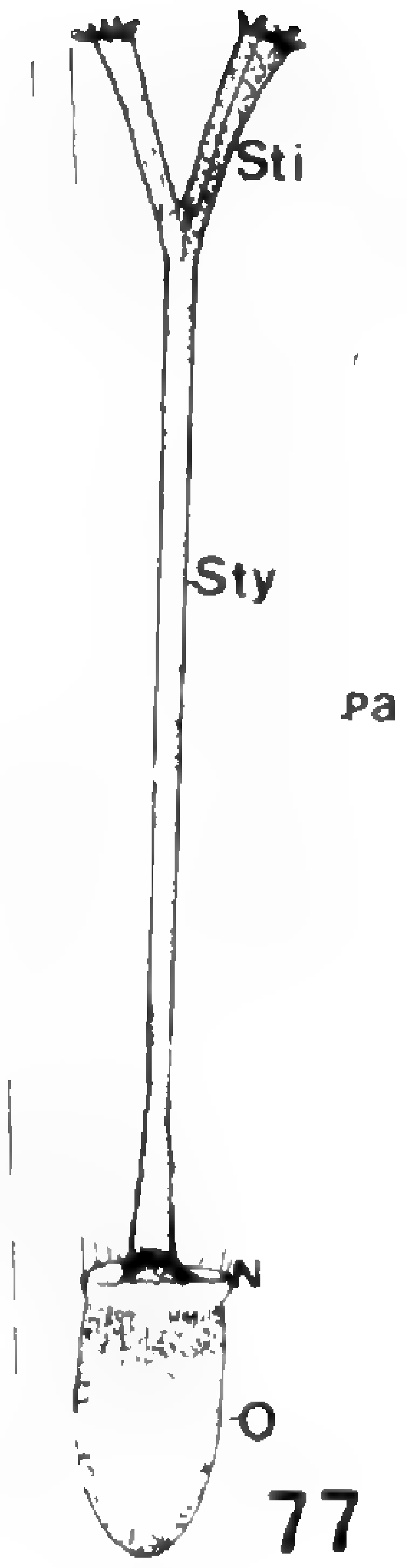
ASTERACEAE

The nectaries of the Asteraceae occur as small swellings at the base of the style which fit neatly within the narrow tube of the corolla. If the nectar is copious, it may rise in the tube so that shorter-tongued insects may reach it. However, long-tongued insects of the Hymenoptera, and members of the Lepidoptera are the usual successful nectar seekers in the Asteraceae. The genus *Achillea* is exceptional in having short corollas (2–3 mm long in *Achillea borealis* at Inuvik) so that flies are its main pollinators.

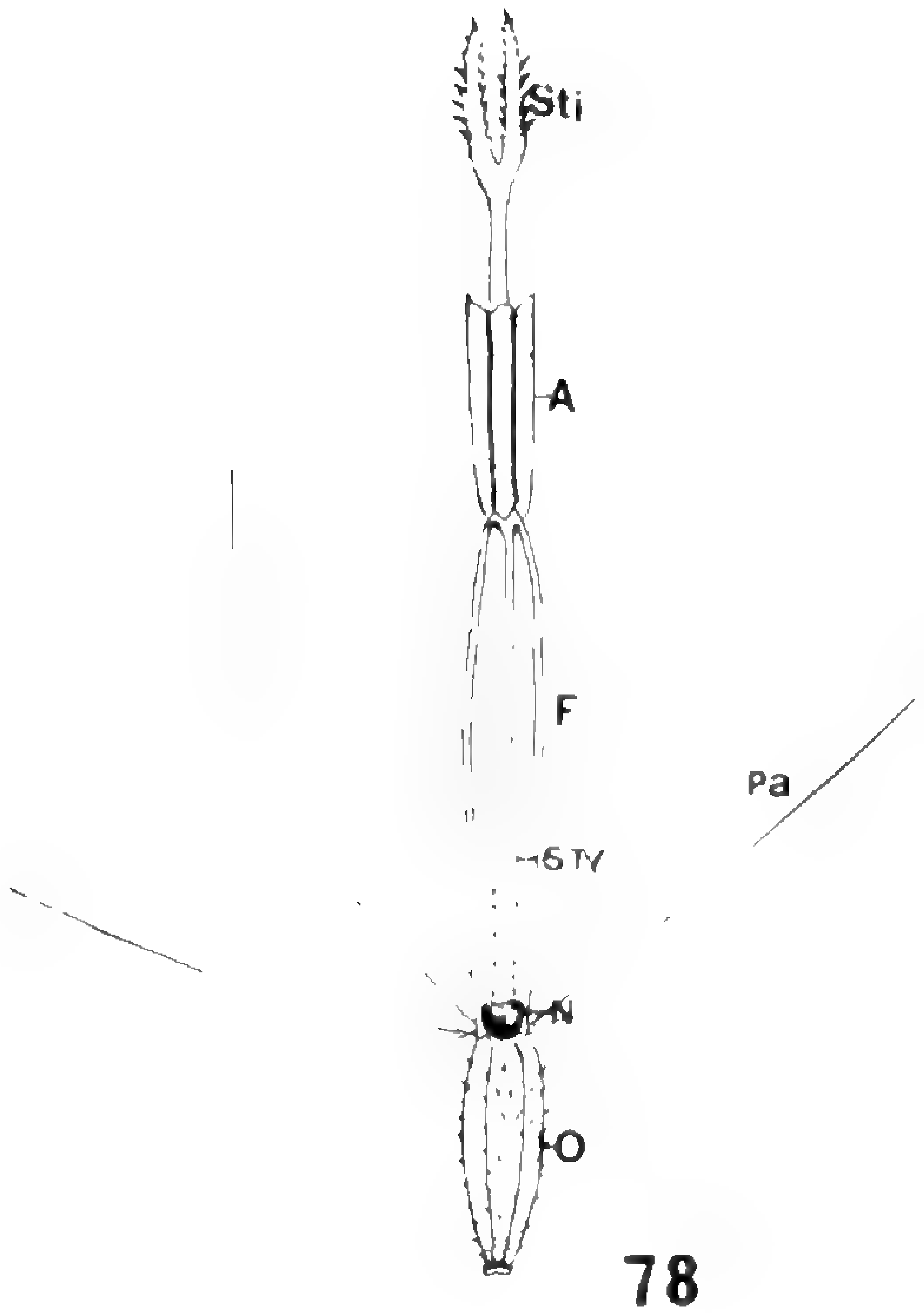
The length of the disc florets varies with latitude and habitat, but most arctic Asteraceae fall within the range of *Senecio congestus* and *S. lugens,* 5 mm at Inuvik, *Solidago multiradiata,* 6 mm, and *Arnica alpina,* 8 mm at Dawson City, all requiring long-tongued insects to reach the nectar. The width of the corolla at the base varied from 0.3–0.5 mm. A very narrow tube was noted in *Petasites palmatus* from Great Whale River, in which the tube of the ligulate flowers was only 0.25 mm wide. Butterflies are known to favor sucking nectar out of a narrow tube and are attracted to this family.

Plate 8, Figures **68–75. 68,** *Pedicularis lapponica* L. Pistil with conspicuous asymmetric nectary at base of ovary; **69 & 70,** *Campanula rotundifolia* L.; 69, Longitudinal section through the protandrous flower in pistillate stage. Anthers dehisced, stamens shrinking. Nectary epigynous; 70, Stamen with broad base and protective interlocking marginal hairs; **71–75,** Diagrammatic drawings of five northern species of *Campanula* in pistillate phase. The lobing, and depth and width of corolla, indicate probable size and type of insects adapted for their pollination; 71, *Campanula scouleri* Hook (Alaska). Corolla length 10–15 mm, corolla mouth 8–12 mm. Stigmas frequently 2-lobed, sometimes 3-lobed; 72, *Campanula aurita* Greene (Dawson City). Corolla length 10–13 mm, corolla mouth 15 mm. Style often curved in older flowers; 73, *Campanula rotundifolia* L. (Frobisher Bay). Corolla length 15–30 mm, corolla mouth 15–20 mm; 74, *Campanula uniflora* L. (Frobisher Bay). Corolla length 5–15 mm, corolla mouth 6–10 mm; 75, *Campanula lasiocarpa* Cham. (Dawson City). Corolla length 15–32 mm, corolla mouth 10–24 mm. N, Nectary. O, Ovary. STY, Style. P.C.H., pollen-collecting hairs. S, Stamen. A, Anther. CO, Corolla. CA, Calyx. Line equals 2 mm.

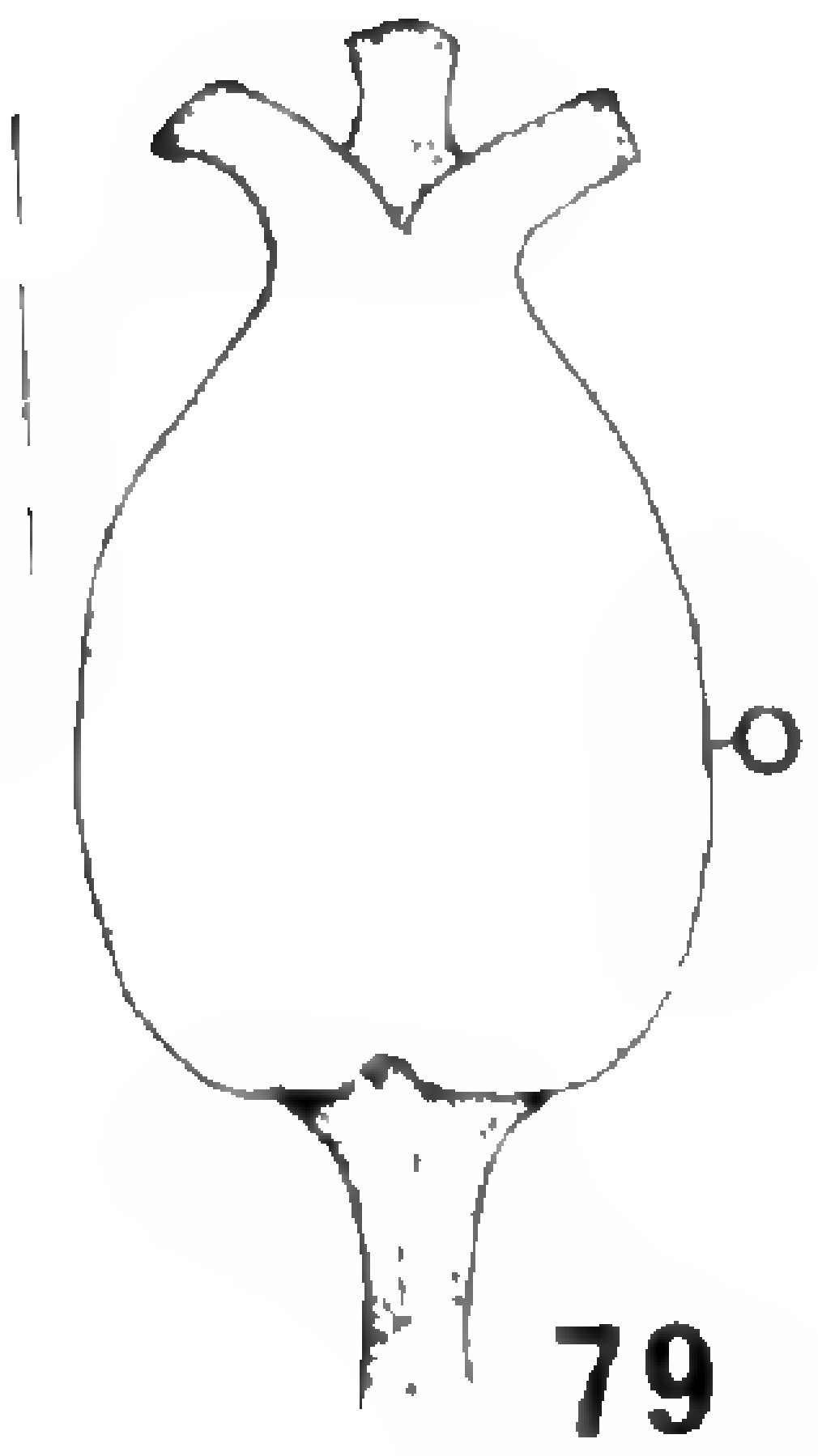
76



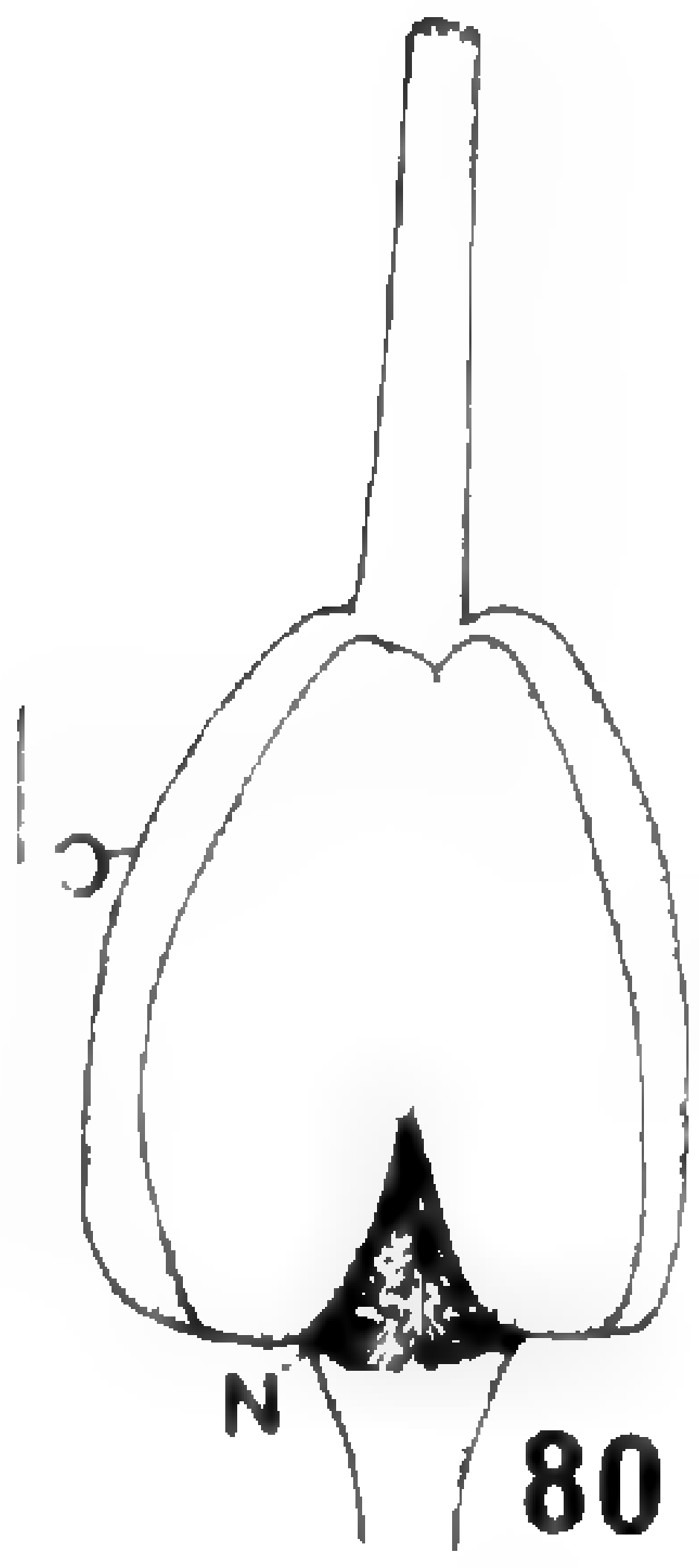
77



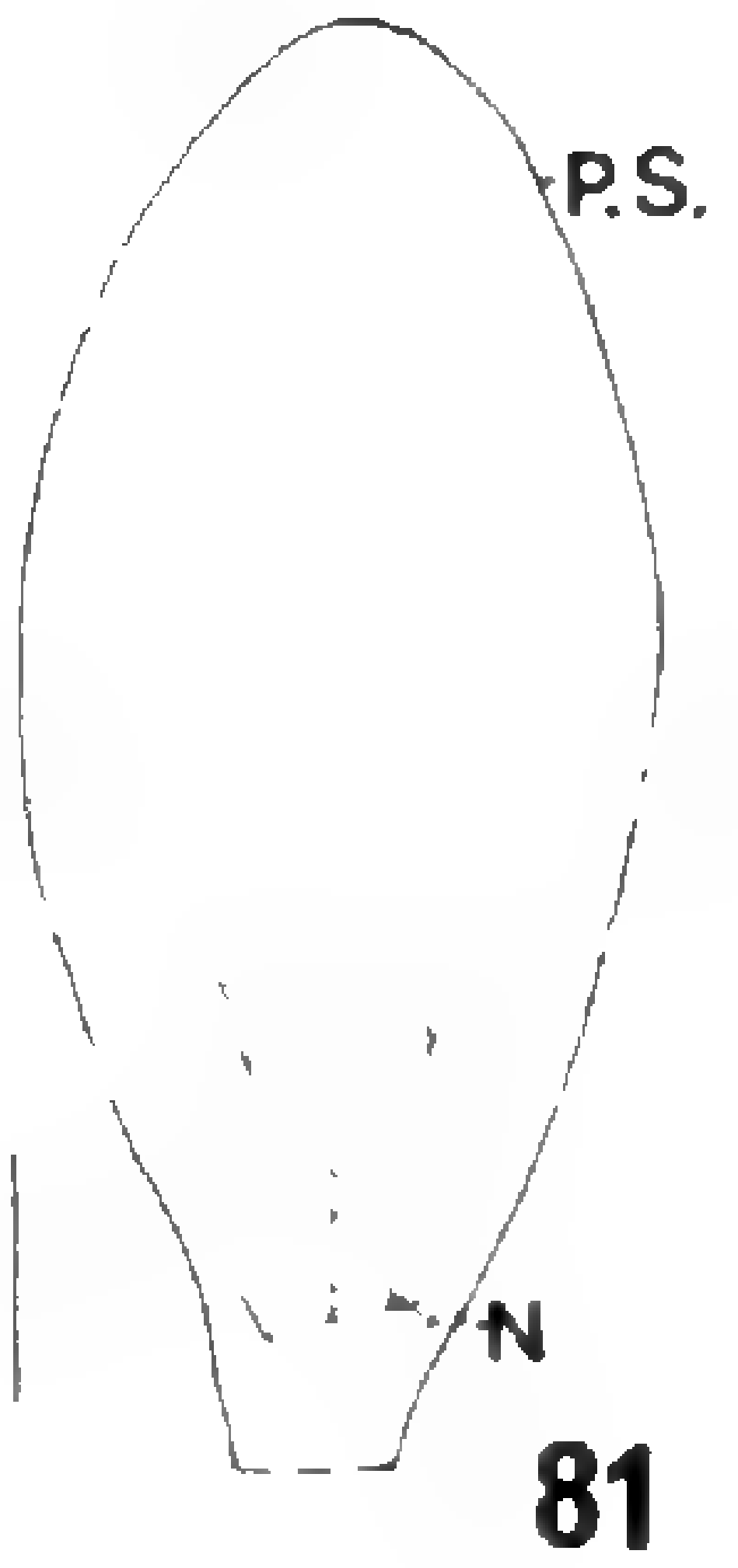
78



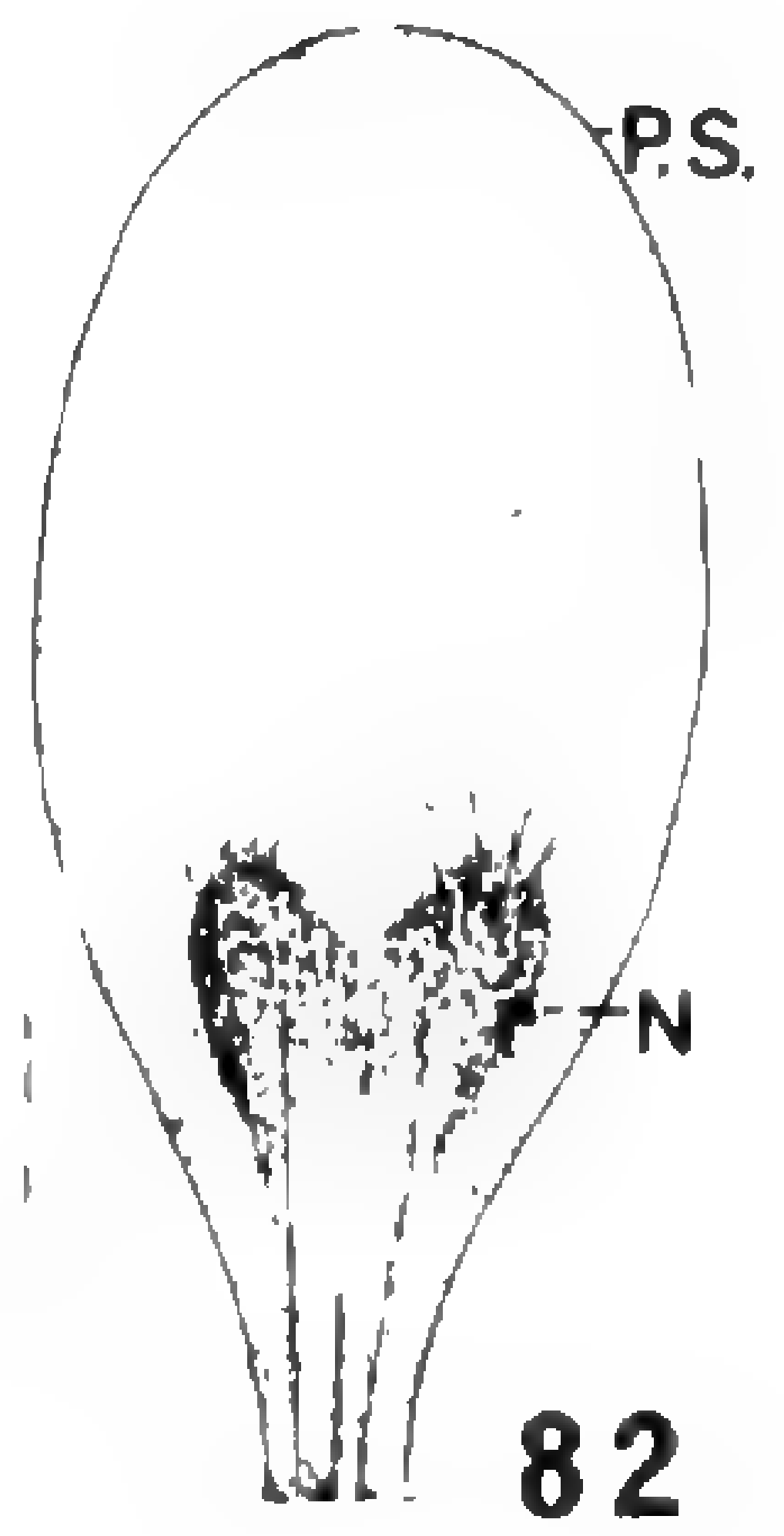
79



80



81



82

In the Asteraceae pollen is pushed up to the mouth of the corolla and beyond by the growing style, after the five cohering anthers have discharged introrsely within the corolla. At this stage the stigma lobes are pressed against each other and are variously adapted by epidermal outgrowths to carry the pollen upward. In *Solidago multiradiata* the stigma lobes are marginally and internally beset with oblique upward-pointing papillae, longest at mid-point (0.06 mm), becoming shorter towards the narrow tip, down to as little as 0.036 mm. In *Arnica alpina* the inner surface of the stigma lobes was fairly smooth with rounded cells, the outer slightly rougher, with small oblique papillae. The enlarged tip had a tuft of one-celled hairs well suited for brushing the pollen from the corolla tube to the mouth. In *Senecio lugens* the inner and outer surfaces of the stigma lobes were covered with upward pointing, but closely appressed, papillae, and the blunt tips had a tuft of hairs from 0.072–0.096 mm long, adapted to carry pollen upwards (Plate 9, Figures 76–78).

The stigma lobes then diverge, the inner surfaces becoming receptive, and, as the flower ages further, they curl downwards until they are able to touch pollen sticking to their own style, or on a neighbouring floret, ensuring pollination in self-compatible flowers, should cross-pollination not have taken place through the agency of insects.

I collected insects on *Senecio congestus* and *S. lugens* at Inuvik, both species attractive to insects through copious pollen lying on the

---

Plate 9, Figures **76–82.** **76,** *Arnica alpina* (L.) Olin. Style pulled from ovary, leaving round epigynous nectary surrounding its base; **77,** *Senecio lugens* Richardson. Nectary a small ring-like epigynous swelling around base of style. The blunt tip of stigma branches with a tuft of upward and outward pointing papillae about 0.06 mm long; **78,** *Solidago multiradiata* Ait. Nectary a small epigynous swelling around base of style. Stigma branches sharp pointed, the surface with outer and inner upward-pointing papillae, longest 0.06 mm, becoming shorter, 0.036 mm, towards tip; **79,** *Tofieldia pusilla* (Michx.) Pers. Nectar exuded between incompletely fused partitions of tricarpellary ovary; **80,** *Allium schoenoprasum* L. Nectary three septicidal pits (0.47–0.54 mm wide, 0.3 mm deep) at base of ovary. Nectar secreted copiously; **81,** *Lloydia serotina* (L.) Reichenb. Nectary a dark yellow ridge of nectariferous tissue at base of each of the six whitish tepals; **82,** *Zygadenus elegans* Pursh. Nectary an obcordate gland. Present on all six tepals. N, Nectary. O, Ovary. STY, Style. SH, Stigma. F, Filament. A, Anther. PA, Pappus. PS, Perianth Segment. Line equals 2 mm.

disc flowers. *Senecio lugens* was visited by the syrphids *Scaeva pyrastri* (L.), *Syrphus* sp., and the apid, *Bombus sylvicola* Kby. *Senecio congestus* was visited by the syrphids *Eristalis bardus* (Say), *Helophilus obscurus* Lw., and *Syrphus bigelowii* Cn., and the apids, *Bombus sylvicola* Kby., *B. frigidus* Sm., *B. jonellus* (Kby.), *B. mixtus* Cr., and *B. lucorum* (L.). The bees are listed in order of proboscis length, and probably all but the workers of *Bombus lucorum*, with glossae only 2.85 mm, could reach the nectaries. All could gather pollen freely. One species of butterfly, *Colias hecla* L. (Pieridae) was seen sucking nectar from *Senecio congestus*.

LILIACEAE

Only one species of Liliaceae, *Tofieldia pusilla*, occurs in the Canadian Arctic Archipelago (Porsild, 1964), but it is widely distributed on the mainland across northern Canada, along with *Allium schoenoprasum* var. *sibiricum*. *Zygadenus elegans* occurs west of the Hudson Bay in the N.W.T., and *Lloydia serotina* west of the Mackenzie River (Cody & Porsild, 1968; Hultén, 1968). I found *Lloydia* on Keno Hill in the Yukon.

Nectar is secreted between the incompletely fused partitions of the syncarpous ovary in *Tofieldia* and by septicidal pits in *Allium*. *Tofieldia* is the most primitive type because of "the absence of septal glands, with epithelial lining of the intercarpellary spaces unlike those of higher sub-families" (Eames, 1964). I could see no slits or external canal openings by microscopic examination, but the three carpels pulled free from one another at the distal end of the ovary with a slight pressure from a dissecting needle, indicating a very fragile connation between them through which nectar could be exuded.

The greenish-white perianth segments and the stamens of *Tofieldia pusilla* were about the same height, 1.5 mm, the latter closely appressed to the shorter ovary. At Frobisher Bay the whole inflorescence was only 3.5 mm long, and the combination of small size and dull colour did not seem to attract insects to the flowers. The relative position of stigmas and anthers, and the fact the anthers dehisce introrsely, suggest self-fertilization takes place in this species (Plate 9, Figure 79).

Allium schoenoprasum had three septicidal pits at the base of the ovary sutures, measuring 0.47–0.54 mm wide and 0.3 mm deep. Nectary is produced freely in these and collects between the ovary and the inner whorl of stamens. The shining mauve papery perianth, and the many flowers in a compact umbel, have a strong attraction for bees and other insects, important for seed-set, as Fryxell (1957) lists it as self-incompatible (Plate 9, Figure 80).

The perianth segments of *Zygadenus elegans* and *Lloydia serotina* open widely in sunshine, exposing the nectary at the base of each tepal. The former has a conspicuous obcordate nectary, about 3 mm wide by 2 mm deep, on a greenish background. The green is replaced by white towards the tip and margins of the tepal and the gland is raised above its surface 0.8 mm at its upper end (Plate 9, Figure 82).

In *Lloydia serotina* the nectary is a dark yellow horizontal ridge at the base of the tepal (Plate 9, Figure 81), and purplish veins on a whitish background serve as nectar guides for insect visitors. Both species are slightly protandrous and are pollinated by flies and short-tongued Hymenoptera. The position of the anthers, higher than the stigmas in *Zygadenus,* and about opposite in *Lloydia* would allow for self-pollination in the later stages.

NECTARIES IN ARCTIC AND SUB-ARCTIC SPECIES. SUMMARY

POLYGONACEAE: Swollen base of inner stamens embedded in nectariferous ring on petaloid sepals, *Polygonum viviparum.* NYMPHAEACEAE: Small to large irregularly-shaped pits on underside of petals, *Nuphar.* CARYOPHYLLACEAE: Swelling around base of outer row of stamens opposite sepals and occasionally at side of inner row, polysepalous Caryophyllaceae, *Arenaria, Cerastium, Stellaria.* Fused with base of petals, forming ring around carpophore, gamosepalous Caryophyllaceae, *Lychnis, Silene.* RANUNCULACEAE: Simple small pits, open or covered with a scale, upper side of petals, *Ranunculus.* Two greatly modified petals, *Delphinium, Aconitum.* CRUCIFERAE: Basal swellings on sides or partly surrounding short stamens, occasionally developed by long stamens. SAXIFRAGACEAE: Band of different colour and texture from ovary, *Saxifraga cernua, S. davurica, S. foliolosa, S. hirculus.* Band slightly swollen, *S. aizoides, S. hieracifolia, S. nivalis, S. rivularis.* Concave band between ovary and stamens, *S. oppositifolia.* Epigynous disc, *S. aizoon* and *S. caespitosa*. PARNASSIACEAE: Thickened band on each staminode. ROSACEAE: Receptacle cup, tissue lining cup between stamens and carpels, *Dryas, Potentilla, Rubus*. FABACEAE: (Diadelphous). Nectariferous tissue lining base of membrane formed by nine stamens and top of receptacle, *Astragalus, Lathyrus, Oxytropis*. ONAGRACEAE: Fleshy epigynous disc, *Epilobium angustifolium, E. latifolium*. ERICACEAE: Swollen, often torulose band at the base of ovary, *Andromeda, Arctostaphylos, Cassiope, Kalmia, Phyllodoce, Rhododendron*. Epigynous disc, *Vaccinium*. PLUMBAGINACEAE: Swollen base of each stamen below fusion of stamen and petal, *Armeria maritima*. POLEMONIACEAE: Fleshy concave rim surrounding base of ovary, *Polemonium acutiflorum, P. pulcherrimum*. BORAGINACEAE: Flat cushion beneath gynobase, thicker between nucules, *Amsinckia, Myosotis*. SCROPHULARIACEAE: Asymmetrical swelling at base of ovary, *Castilleja, Pedicularis*. Single prominent curved gland at one side of base of ovary, *Rhinanthus*. CAMPANULACEAE: Epigynous disc, *Campanula*. ASTERACEAE: Very small swelling around base of style, *Arnica, Senecio, Solidago*. LILIACEAE: Base of tepals, *Lloydia, Zygadenus*. Nectar secreted between carpels, exuding at septa, *Tofieldia*, or secreted in three septal pits, *Allium*.

PHYLOGENETIC TREND IN NECTARIES

Fahn (1967) considers the phylogenetic trend in nectaries to be acrocentripetal and he is supported by Radford *et al.* (1974) who state, "As evolutionary advancement occurs the nectaries migrate to the inner floral parts and in the pistil from the base of the ovary to the base of the style".

The above summary agrees in part with Fahn's theory but there are notable variations even within the same family. In Ranunculaceae there are perigonial nectaries in *Ranunculus* and *Aconitum* and staminodial in *Anemone patens;* in Liliaceae nectar is secreted by the ovary in *Tofieldia* and *Allium*, and by distinct nectaries on the tepals in *Lloydia* and *Zygadenus*. In a family such as the Ericaceae, which achieves epigyny in the genus *Vaccinium*, there is an inevitable upward movement of ovary nectaries. Generally speaking, the trend is towards the centre of the flower and upwards in the more highly evolved families.

POLLINATING INSECTS

Nectar may be reached readily by small, short-tongued insects in most open, polypetalous, polysepalous, actinomorphic arctic flowers. They are prevented from reaching the nectar in many of the larger gamopetalous flowers by devices such as copious hairs on the staminal filaments, or on the inside of the corolla itself, and by the hiding of the nectaries under enlarged filament bases. Zygomorphic flowers such as *Aconitum, Delphinium,* and the Faboideae, require heavy-bodied insects with strong probosces to penetrate to the nectar. They depend on bumblebees to such an extent that they disappear in northern areas where such insects are missing or rare.

CROSS-POLLINATION AND SELF-FERTILIZATION

A number of arctic and subarctic species are apomictic (Fryxell, 1957; Mulligan, 1966; Mulligan & Findlay, 1970; Mosquin & Hayley, 1966), and they as a rule do not require insect visits in order to set seed. Those cross-fertilized by necessity are the dioecious species (e.g., *Rubus chamaemorus*), or the protandrous species in which the anthers dehisce before the stigmas are receptive, (e.g., *Campanula, Parnassia, Polemonium acutiflorum, P. pulcherrimum* — last two at Dawson City). Protogyny seemed to be of short duration in the species studied, soon changing to homogamy in *Anemone patens, Dryas integrifolia,* and *Draba* species. Many arctic species are slightly protogynous, *Lloydia serotina, Allium schoenoprasum,* and the Caryophyllaceae, for example. The gap between the time of ripening of anthers and stigma allows a short period for cross-pollination. A large percentage of northern plants are homogamous, Ericaceae, Fabaceae, and *Pedicularis* among them, all with many species known to be self-fertile.

Some of the commonly found adaptations for selfing in mature flowers noted in arctic and sub-arctic species:

1. Flowers change in position from partly upright to drooping, allowing pollen to fall on stigma by gravity (*Pedicularis*).
2. Stigma branches move outwards towards the anthers (Caryophyllaceae and *Armeria maritima*) or curl downwards to touch pollen (Asteraceae, *Campanula* species).
3. Stamens elongate as the flower matures, becoming level with the stigmas (*Draba* species).

4. The stamens move towards the stigmas until contact is made (*Saxifraga oppositifolia*).

5. Stamens twist so that anthers scatter pollen on stigmas and filaments, or the flowers close in dull weather, making contact with stigmas or scattered pollen (*Potentilla* species).

As a result of flower stigma and stamen movements, self-compatible species have additional chances for pollination in an area where insect activity may be very low.

The possibility of wind pollination in entomophilous arctic plants has not been considered, lacking data on the numbers and types of pollen grains in the air. Proctor and Yeo (1975) found it of some importance in Great Britain.

ACKNOWLEDGEMENTS

My sincere thanks go to Mr. Richard Hill, Director of the Inuvik Research Laboratory, who provided me with space and a microscope in the laboratory in 1965, as well as to Mr. George Hobson, Director of the Polar Continental Research Project, who brought in living material from various islands of the High Arctic while I was enjoying their hospitality at Resolute in 1976.

The insects I collected were identified, and some plant identifications checked, by staff members of the Biosystematics Research Institute in Ottawa, Canada. Dr. D. B. O. Savile read the manuscript and made constructive suggestions, for all of which I am deeply appreciative.

The illustrations were drawn by C. C. Hsiung of the Lyman Entomological Museum at Macdonald College, based on my field sketches, augmented by microscopic examinations in the laboratory of the McGill University Herbarium.

ADDENDUM: RECORDS OF SCENTS OF ARCTIC FLOWERS, 1976

SALICACEAE: *Salix arctica*, scent of clover, Frobisher Bay. CARYOPHYLLACEAE: *Cerastium alpinum*, honey scent, Frobisher Bay; *C. arcticum*, mild sweet scent, Resolute. CRUCIFERAE: *Parrya arctica*, strong pleasing scent, Resolute. SAXIFRAGACEAE: *Saxifraga cernua*, no scent, Resolute. ROSACEAE: *Dryas integrifolia*, no scent, Frobisher Bay. FABACEAE: *Astragalus alpinus*, honey scent, Frobisher Bay; *Oxytropis podocarpa*, very strong pleasant scent, Frobisher Bay. ERICACEAE: *Arctostaphylos alpina*, no scent, Frobisher Bay; *Cassiope tetragona*, resinous scent, Frobisher Bay; *Rhodendron lapponicum*, slight spicy fragrance, Frobisher Bay. SCROPHULARIACEAE: *Pedicularis arctica*, light, pleasant scent, Norway I., off Banks Is.; *Pedicularis flammea*, no scent, Frobisher Bay; *Pedicularis lanata*, faint sweet scent, Devon I.

LITERATURE

Anderson, J. P. 1959. Flora of Alaska. 543 pp. Iowa State University Press.

Baker, H. G. 1959. The contribution of autecological and geneological studies to our knowledge of the past migrations of plants. Amer. Natur. **93:** 255–272.

Clapham, A. R., T. G. Tutin, & E. F. Warburg. 1962. Flora of the British Isles, 2nd. ed. 1269 pp. University Press, Cambridge.

Cody, W. J., & A. E. Porsild. 1968. Checklist of vascular plants of the continental Northwest Territories, Canada. 102 pp. Plant Research Inst., Ottawa, Ont.

Davis, P. H., & V. H. Heywood. 1963. Principles of angiosperm taxonomy. 558 pp. Oliver and Boyd, Edinburgh and London.

Eames, Arthur J. 1947. Morphology of the angiosperms. 510 pp. McGraw-Hill Book Co.

Faegri, K., & L. van der Pijl. 1966. The principles of pollination ecology. 248 pp. Pergamon Press, N.Y.

Fahn, A. 1967. Plant anatomy (trans. from the Hebrew). 534 pp. Pergamon Press, N.Y.

Fryxell, P. A. 1957. Mode of reproduction in higher plants. Bot. Rev. **23:** 135–233.

Gillett, John M. 1963. The gentians of Canada, Alaska and Greenland. Publ. 1180: 1–99. Res. Branch, Can. Dept. of Agric., Ottawa, Ont.

Hegi, Gustav. 1958. Illustrierte Flora von Mitteleuropa, Band IV_1 (includes Cruciferae). 1961. Band IV_2 (includes Saxifragaceae).

Hitchcock, C. Leo, Arthur Cronquist, Marion Ownbey, & J. W. Thompson. 1955–1969. Vascular plants of the Pacific Northwest, Parts 1–5. Univ. of Washington Press, Seattle.

Hocking, B. 1968. Insect-flower associations in the high arctic, with special reference to nectar. Oikos, Vol. **19**(2): 359–388.

Hultén, Eric. 1968. Flora of Alaska and neighbouring territories. 1008 pp. Stanford Univ. Press, Stanford, California.

Kevan, Peter G. 1972a. Floral colours in the high arctic with reference to insect-flower relations and pollination. Canad. J. Bot. **50**(11): 2289–2316.

______. 1972b. Insect pollination of high arctic flowers. J. Ecol. **60:** 831–847.

______. 1973. Flowers, insects and pollination ecology in the Canadian high arctic. Polar Record **16:** 667–674.

______. 1977. High Arctic insect-flower relations: the interrelationships of arthropods and flowers at Lake Hazen, Ellesmere Island, Northwest Territories, Canada. Ph.D. thesis, Dept. of Entomology, University of Alberta, Edmonton, Alberta, Canada.

Knuth, P. E. O. 1908–1909. Handbook of flower pollination, based on Hermann Müller's "The fertilization of flowers by insects". Vols. II and III. Clarendon Press, Oxford.

Komorov, V. L. (editor). 1937 & 1939. Flora of the U.S.S.R. Vol. VII, 1937, (Ranunculaceae); Vol. IX, 1939, (Saxifragaceae). Translated from the Russian by the Israel Program for Scientific Translation, Jerusalem, 1970–71.

Marilaun, Anton Kerner von. 1895. The natural history of plants. Translated from the German by F. W. Oliver. Vol. II, 1–983.

MacInnes, K. L. 1972. Reproduction in arctic populations of *Pedicularis* (Scrophulariaceae). Unpublished Ph.D. thesis, Dept. of Biology, University of Western Ontario.

Macior, Lazarus Walter. 1970. The pollination ecology of *Pedicularis* in Colorado. Amer. J. Bot. **57:** 716–728.

______. 1973. The pollination ecology of *Pedicularis* in Colorado. Amer. J. Bot. **57:** 716–728.

______. 1975. The pollination ecology of *Pedicularis* in the Sierra Nevada Mountains of California. Abstract of paper given at meetings of Bot. Soc. of Am. at Oregon State University, Corvallis.

Milliron, H. E. 1973. A monograph of the western hemisphere bumblebees (Hymenoptera) Apidae; Bombinae. Memoirs of the Ent. Soc. of Canada, Ottawa, No. **89:** 1–237.

Mosquin, T., & D. E. Hayley. 1966. Chromosome numbers of some Canadian arctic plants. Canad. J. Bot. **44:** 1209–1218.

Mosquin, T. 1966. Reproductive specialization as a factor in the evolution of the Canadian flora. *In:* The evolution of Canada's flora, edited by S. L. Taylor and R. A. Ludwig. 137 pp. Univ. of Toronto Press.

Mosquin, Theodore, & J. E. H. Martin. 1967. Observations on the pollination biology of plants on Melville Island, N.W.T., Canada. Can. Field Nat. **81:** 201–205.

McAlpine, J. F. 1964. Arthropods of the bleakest barrenlands: composition and distribution of the arthropod fauna of the northwestern Queen Elizabeth Islands. Can. Ent. **96:** 127–129.

McAlpine, J. F. 1965a. Observations on anthophilous Diptera at Lake Hazen, Ellesmere Is. Can. Field Nat. **79:** 247–252.

McAlpine, J. F. 1965b. Insects and related terrestrial invertebrates of Ellef Ringnes Is. Arctic **18:** 73–102.

Mulligan, G. A. 1964. Chromosome numbers of the family Cruciferae. Canad. J. Bot. **42:** 1509–1519.

______. 1966. Chromosome numbers of the family Cruciferae. Canad. J. Bot. **44:** 309–319.

______. & Judy N. Findlay 1970. Sexual reproduction and agamospermy in the genus *Draba*. Can. Jour. Bot. **48:** 269–270.

Polunin, N. 1959. Circumpolar arctic flora. 514 pp. Clarendon Press, Oxford.

Porsild, A. E. 1964. Illustrated flora of the Canadian Arctic Archipelago. Bull. No. **146,** Nat. Museum of Canada.

Proctor, Michael, & Peter Yeo. 1975. The pollination of flowers. 418 pp. Collins, St. James Place, London.

Radford, A. E., W. C. Dickison, J. R. Massey, & C. Ritchie Bell. 1974. Vascular plant systematics. 891 pp. Harper and Row publishers, New York.

Savile, D. B. O. 1959. The botany of Somerset Island, District of Franklin. Canad.J. Bot. **37:** 959–1002.

______. 1961. The botany of the north-western Queen Elizabeth Islands. Canad. J. Bot. **39:** 909–942.

______. 1964. General ecology of the vascular plants of the Hazen Camp area. Arctic **17:** 237–258.

———. 1972. Arctic adaptations of plants. Monograph No. 6, Res. Branch, Can. Dept. of Agric., Ottawa, Ont.

SPRAGUE, E. F. 1962. Pollination and evolution in *Pedicularis* (Scrophulariaceae). Aliso **5:** 181 209.

SWALES, DOROTHY E. 1966. Species of insects and mites collected at Frobisher Bay, Baffin Is., 1964, and Inuvik, N.W.T., 1965, with brief ecological and geographical notes. The Annals of the Entomological Society of Quebec **11:** 189 199.

WADDLE, ROBERTA M., & NELS R. LERSTEN. 1973. Morphology of discoid floral nectaries in Leguminosae, especially the tribe Phaseoleae (Papilionoideae). Phytomorphology **23:** 152 161.

WILLIS, J. R. Rev. ed. by A. K. Airy Shaw 1973. Flowering plants and ferns. 245 pp. University Press, Cambridge.

DEPARTMENT OF PLANT SCIENCE
MACDONALD COLLEGE OF McGILL UNIVERSITY
STE. ANNE DE BELLEVUE, QUEBEC, CANADA H0A 1C0

PHYSOSTEGIA GODFREYI (LAMIACEAE), A NEW SPECIES FROM NORTHERN FLORIDA

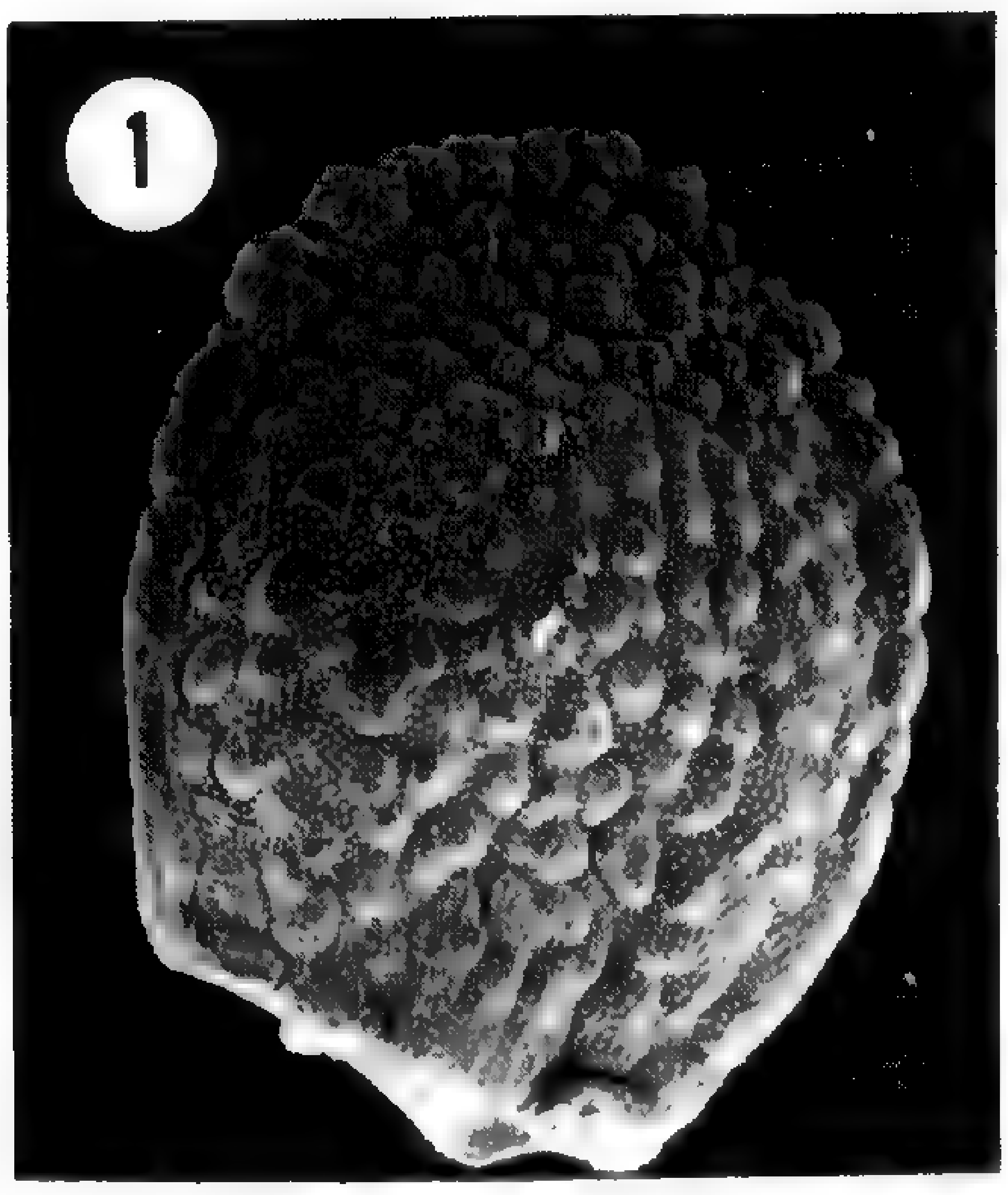
PHILIP D. CANTINO

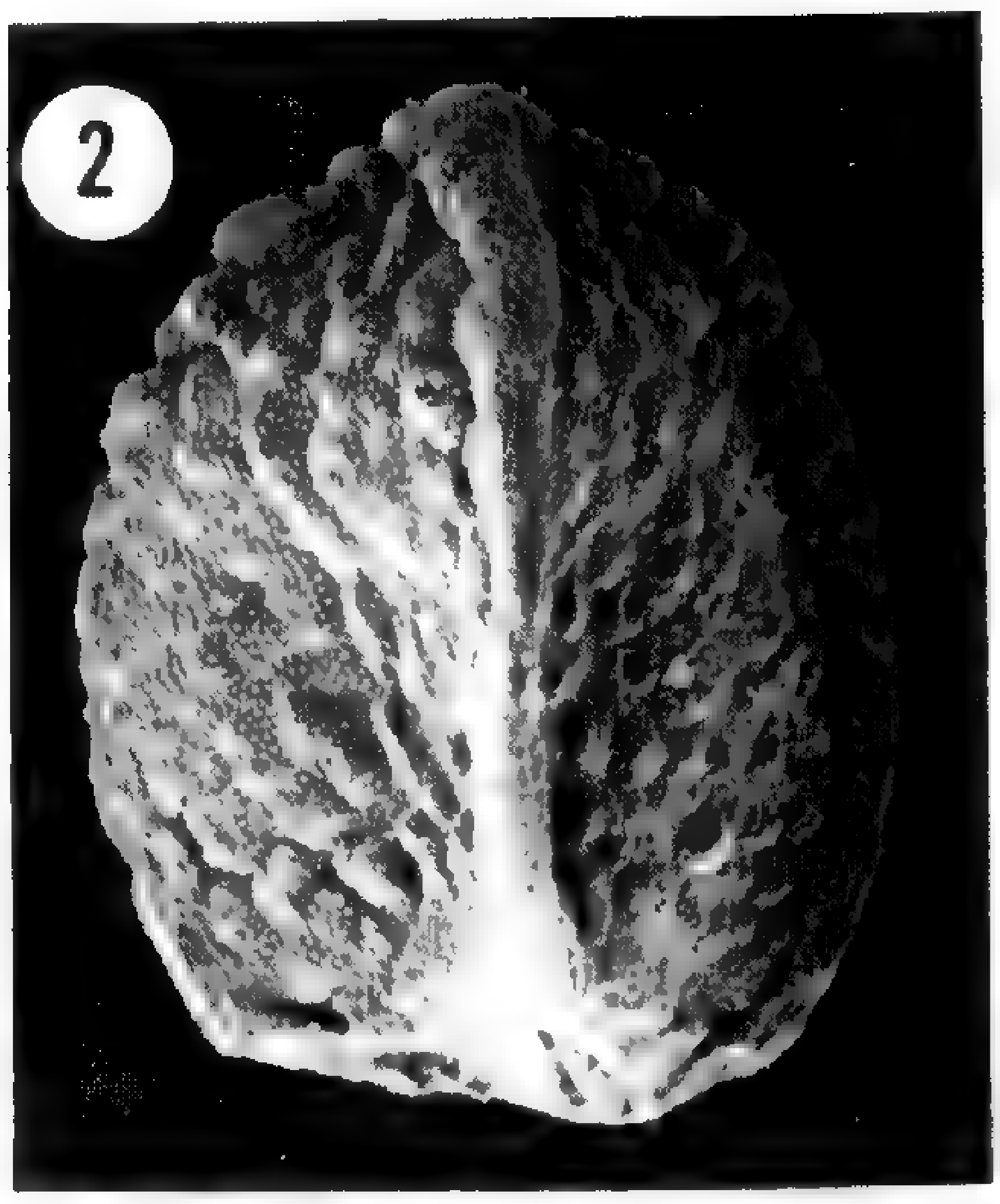
The populations of *Physostegia* that occur in moist pine savannas west of the Ochlockonee River in the Florida "Panhandle" resemble most closely *P. purpurea* (Walt.) Blake, having in common with that species linear to oblanceolate leaves and entire to bluntly serrate leaf margins, a combination of characters unique within the genus, as well as sharing other similarities in the rhizome, inflorescence, and overall habit. In addition these populations and *P. purpurea* occur in similar habitats but are allopatric or possibly narrowly sympatric. However the plants from west of the Ochlockonee River possess several characteristics that easily distinguish them from *P. purpurea*, including one that occurs nowhere else in the genus.

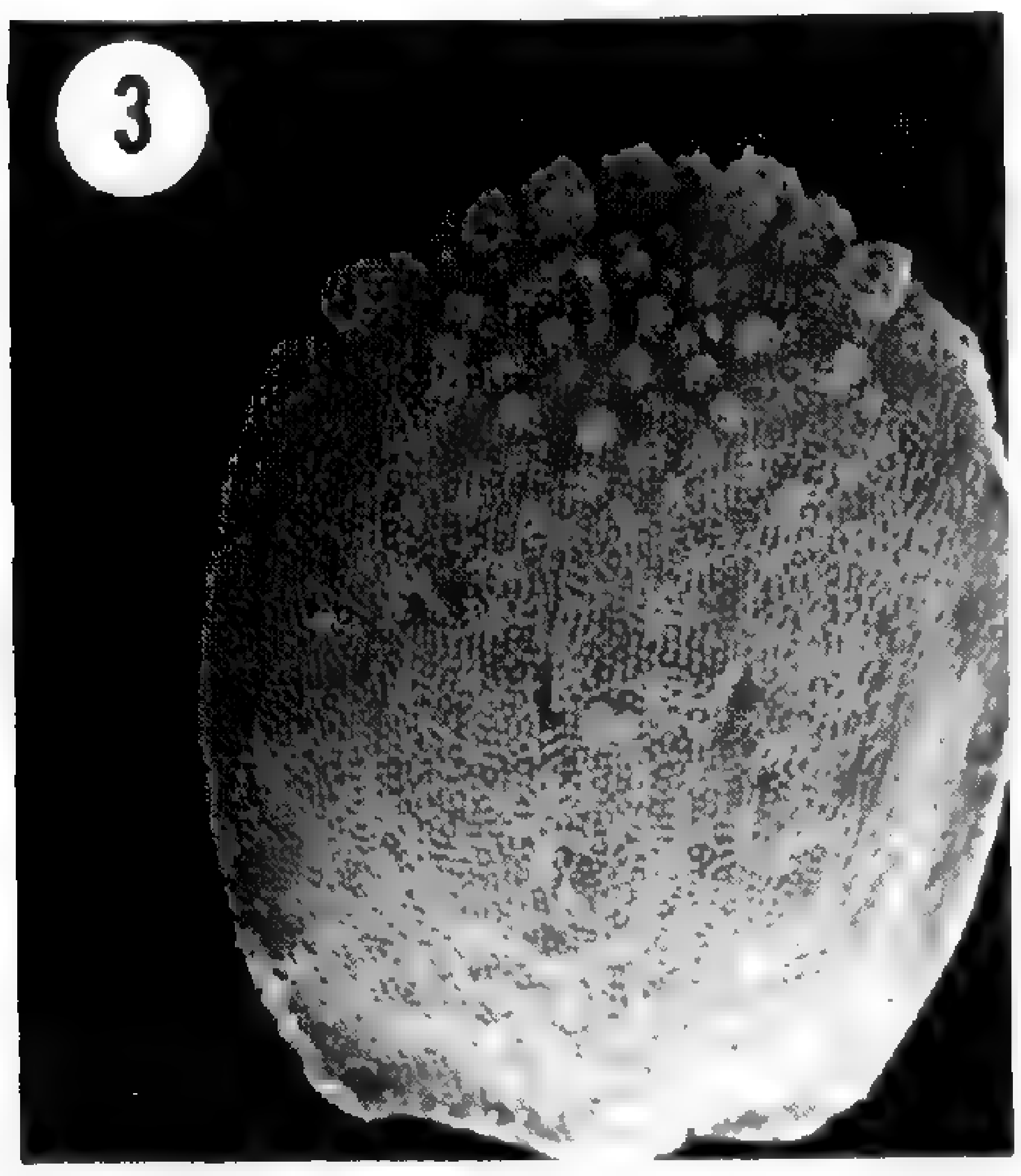
In the course of a systematic study of the genus as a whole, to be published at a later date, I have found that the species of *Physostegia* are distinguishable on the basis of combinations of characters very few of which are unique to any particular species. The possession of a unique character by the Panhandle plants, in addition to several other characters that are not unique within the genus but which distinguish them from their most similar relatives, warrants their recognition at the species level. Indeed, when *Physostegia* is viewed as a whole, this new species is among the most distinctive in the genus.

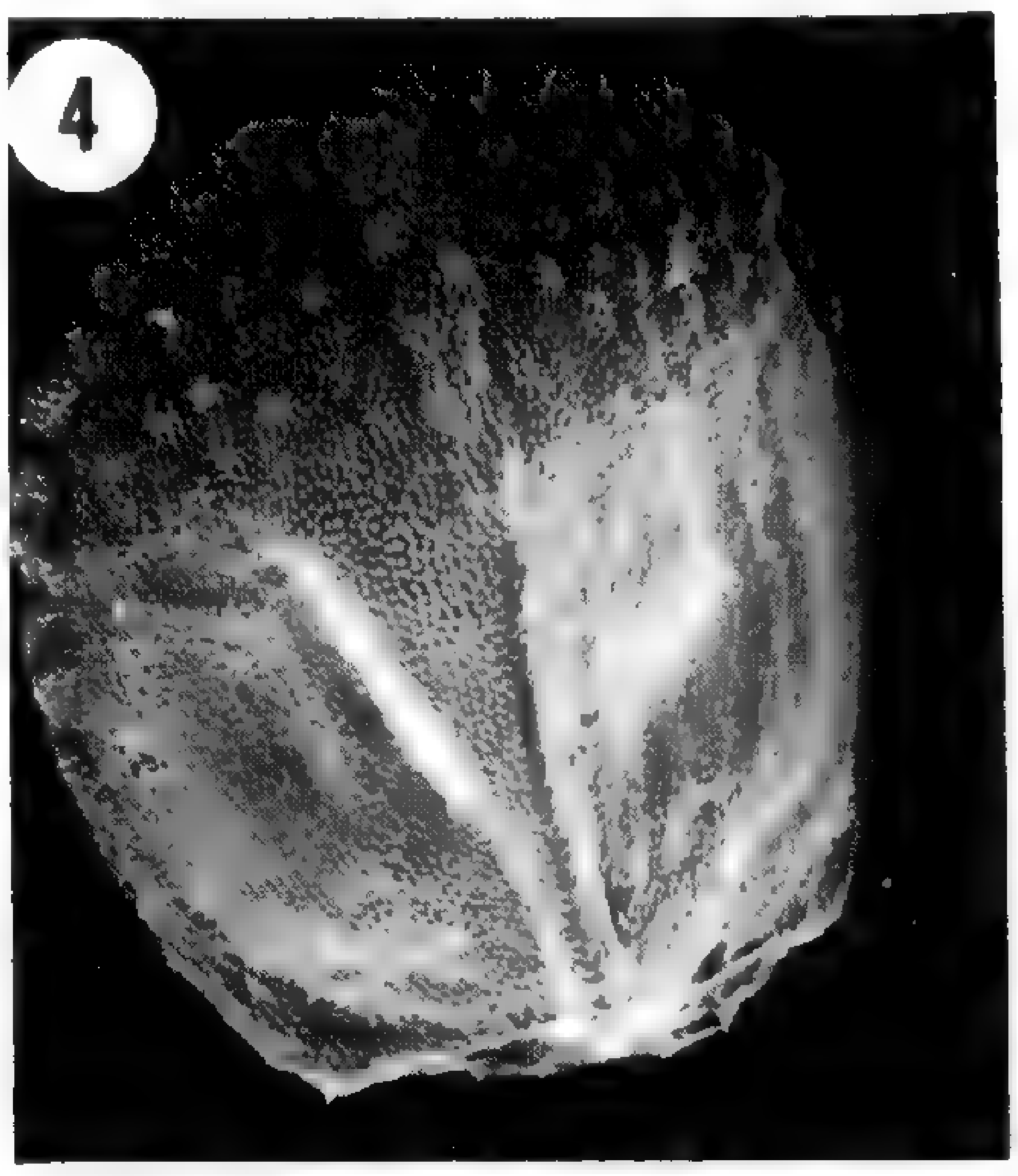
I am naming the new species *Physostegia godfreyi* in honor of Dr. Robert K. Godfrey of Florida State University, whose extensive field work has been instrumental in furthering our botanical knowledge of the region where this species is endemic. The type collection of the species is his, as are many of the other existing specimens.

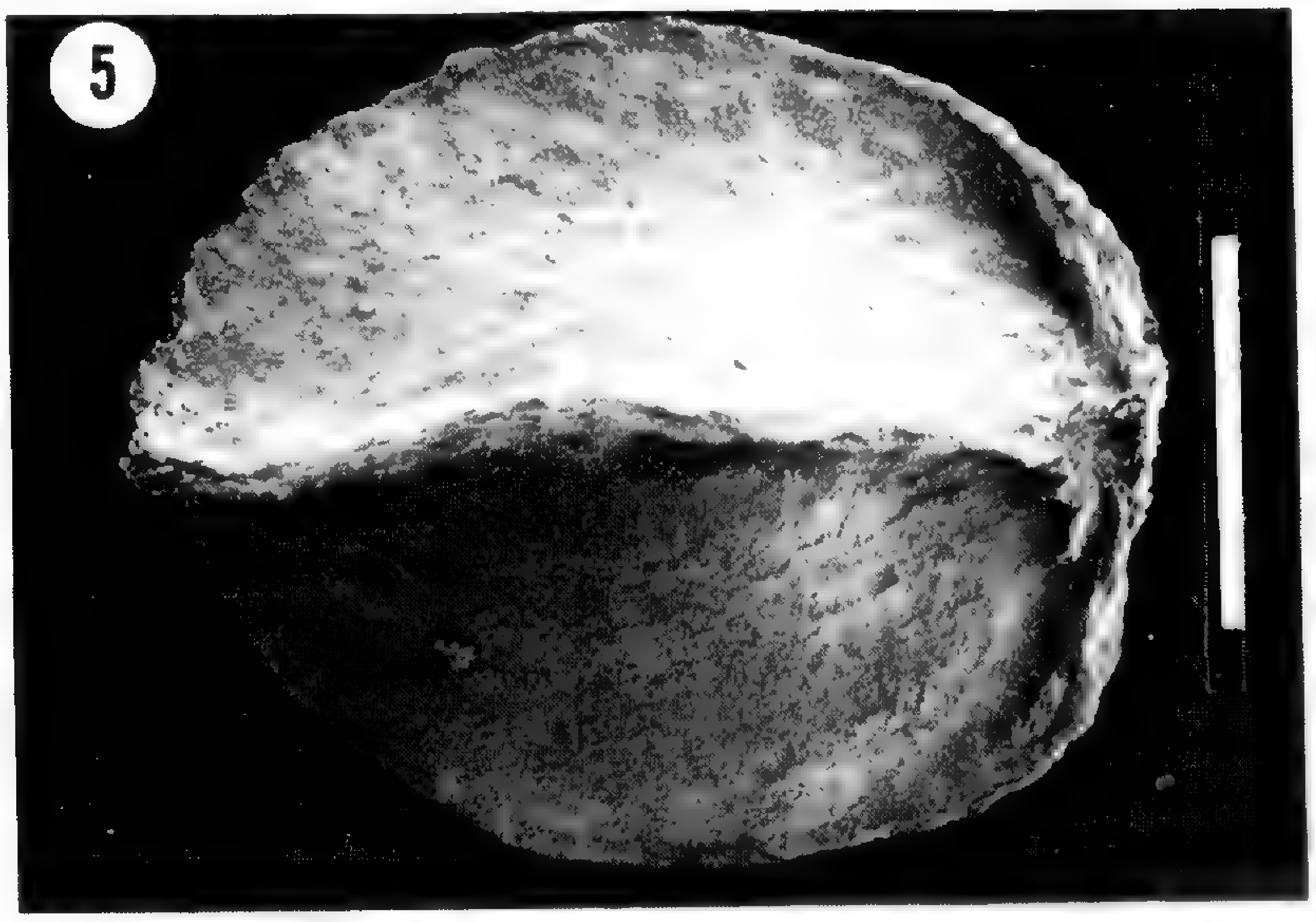
The nutlets of *Physostegia godfreyi*, in addition to being the smallest in the genus (1.7–2.0 mm long), are usually warty over part or all of their surface (Figures 1–4). All other species have smooth nutlets (Figure 5). Secondly, *P. godfreyi* possesses minute stalked glands on the calyx and rachis of the inflorescence (Figures 6 & 7), a character that is found elsewhere in the genus but not in *P. purpurea*, the only species with which it could be confused. Thirdly,


1


2


3


4


5

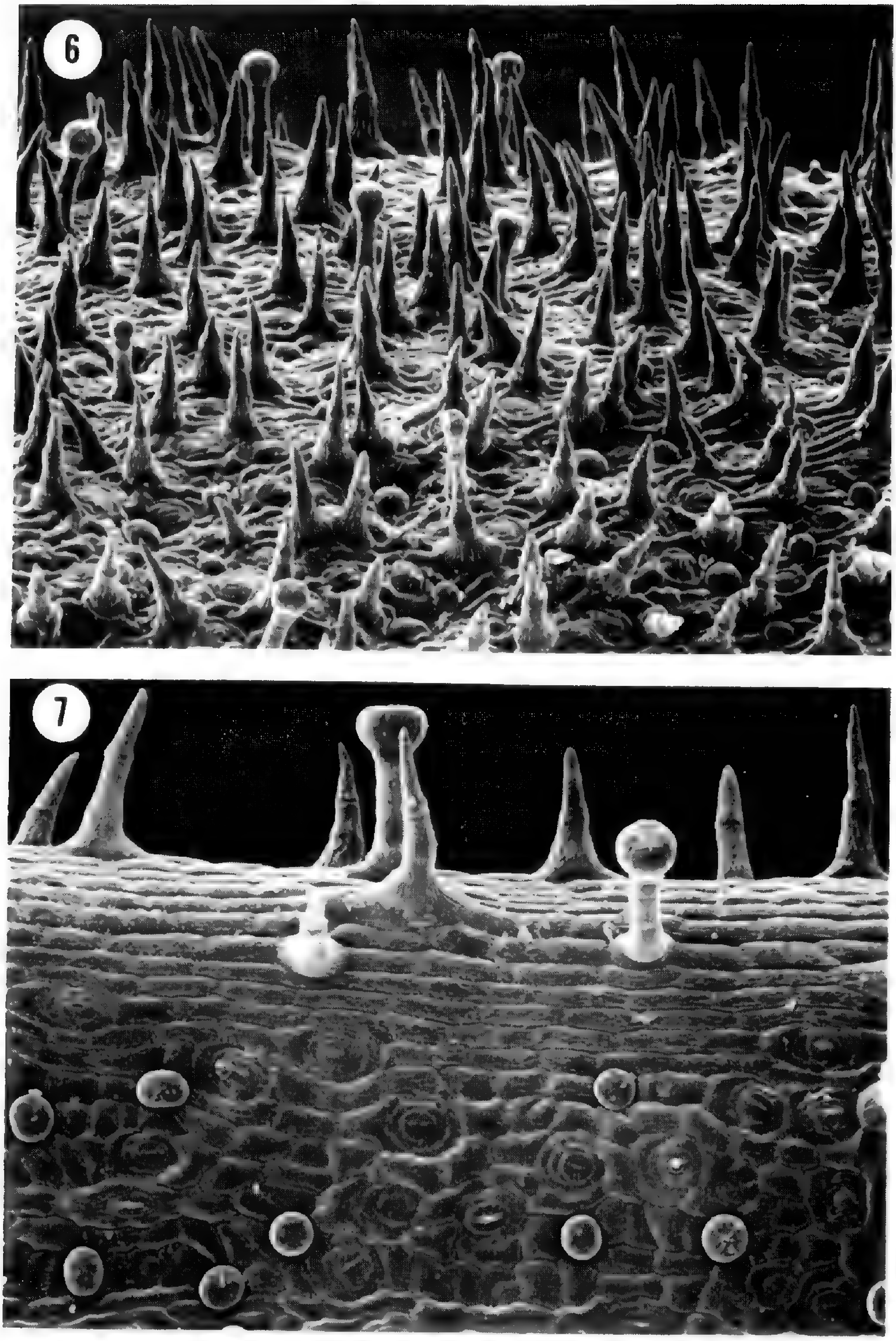
its flower size and leaf shape fall at the extremes of the range of variation of these characters in *P. purpurea.* In parts of Georgia and northern Florida *P. purpurea* has flowers as small as those of *P. godfreyi* (11–23 mm) but usually has less elongate leaves. In far southern Florida (Lee and Collier Counties) some individuals of *P. purpurea* have the nearly linear leaves of *P. godfreyi* but have much larger flowers. Thus although *P. purpurea* is exceptionally variable in both flower size and leaf shape, the combination of small flowers and linear or nearly linear leaves that characterizes *P. godfreyi* is infrequent in *P. purpurea.*

The warty nutlet surface, although unique to *Physostegia godfreyi,* is not an entirely reliable character and the degree of its expression is somewhat variable. There are a few specimens from Bay County that have smooth or only very faintly warty nutlets. Of the specimens with conspicuously warty nutlets, some have the wartlike projections over the whole surface (Figures 1 & 2), while others are warty only near the apex of the nutlet (Figures 3 & 4). It is worth noting that although *P. godfreyi* and *P. purpurea* may come into contact at one point along the Ochlockonee River (see below), the section of the range of *P. godfreyi* where plants with smooth nutlets occur is relatively far from the possible point of contact with *P. purpurea.* Thus it is unlikely that smooth nutlets have arisen in *P. godfreyi* through recent hybridization and introgression. All specimens of *P. godfreyi,* including those with smooth nutlets, have stalked glands on the calyx and rachis of the inflorescence, and all have the distinctive combination of small flowers and linear to nearly linear leaves.

One collection, *F. H. Sargent 11004* from just east of the Ochlockonee River in Wakulla County, is problematical. I have seen two specimens of this collection. One of them (WIS) has the warty nutlets and glandular calyx of *P. godfreyi,* while the second one (GH) has the smooth nutlets and eglandular calyx of *P. purpurea.* The shape of the leaves and length of the flowers are similar on the two specimens and are within the range of overlap of

---

Figures 1–5. Nutlets of *Physostegia godfreyi* and *P. purpurea,* showing difference in size and surface sculpturing (S.E.M. photographs). White bar in Figure 5 = 1 mm (all photos at same magnification). Figures 1 & 2. *P. godfreyi. R. K. Godfrey, et al. 53473* (GH). Figures 3 & 4. *P. godfreyi. R. K. Godfrey 57086* (Isotype; USF). Figure 5. *P. purpurea. D. W. Buden 45* (WIS).



Figures 6 & 7. Stalked glands of *Physostegia godfreyi*. The parts photographed (S.E.M.) were taken from a greenhouse plant grown from rhizomes of *P. Cantino 1054* (GH). The noncapitate trichomes and sessile glands visible here are found throughout *Physostegia*. **6.** Surface of calyx (100×). **7.** Rachis of raceme (160×).

the two species in these characters. There is no evidence that either specimen is a hybrid. It is possible that this is a mixed collection that includes specimens from several localities accidentally combined under one collection number. In this regard it is worth noting that there is, in the herbarium of the University of Wisconsin, an unnumbered Sargent specimen of *P. godfreyi* that was collected in Liberty County on the same date as were the Wakulla County specimens. Since it is similar in general aspect to the two specimens of *Sargent 11004,* it is quite possible that Sargent inadvertently mixed one specimen from the Liberty County site with his collection from Wakulla County. As is evident from the distribution map of the two species (Figure 8), the site of Sargent's Wakulla County collection is much closer to other localities where *P. purpurea* has been collected than to any collection sites of *P. godfreyi.*

It is, on the other hand, quite possible that the species are indeed growing together at the collection site of *Sargent 11004.* I searched the site during July of 1977 but failed to find any *Physostegia.* However some of the roadsides in the area had been mowed shortly before my visit. While mowing does not kill the plants, it does make them exceedingly difficult to spot; thus further study of the site would be worthwhile. I have examined about 30 other specimens of *P. purpurea* from Wakulla County and none of them has either the glandular calyx or the warty nutlets of *P. godfreyi.* Similarly none of the specimens of *P. godfreyi* from the part of its range near populations of *P. purpurea* has the eglandular calyx or smooth nutlets of the latter species. Thus if hybridization is occurring in a local zone of contact, it appears not to be resulting in introgression.

With the exception of the basal rosette, the following description and key are based entirely on dried herbarium specimens. Because of their somewhat fleshy nature, the leaves shrink considerably in drying, and it is in the width measurements that this change is most noticeable. Since leaf width and the ratio of leaf length to width are among the distinctive characters of *Physostegia godfreyi,* it should be borne in mind that live plants will have wider leaves and a lower ratio of leaf length to width than is stated in the description. The flowers also average several millimeters longer on live plants.

Herbarium specimens rarely include the basal leaves because they normally fall off before anthesis. The description of the basal leaves is based on one dried specimen (*R. K. Godfrey et al. 53473*) and

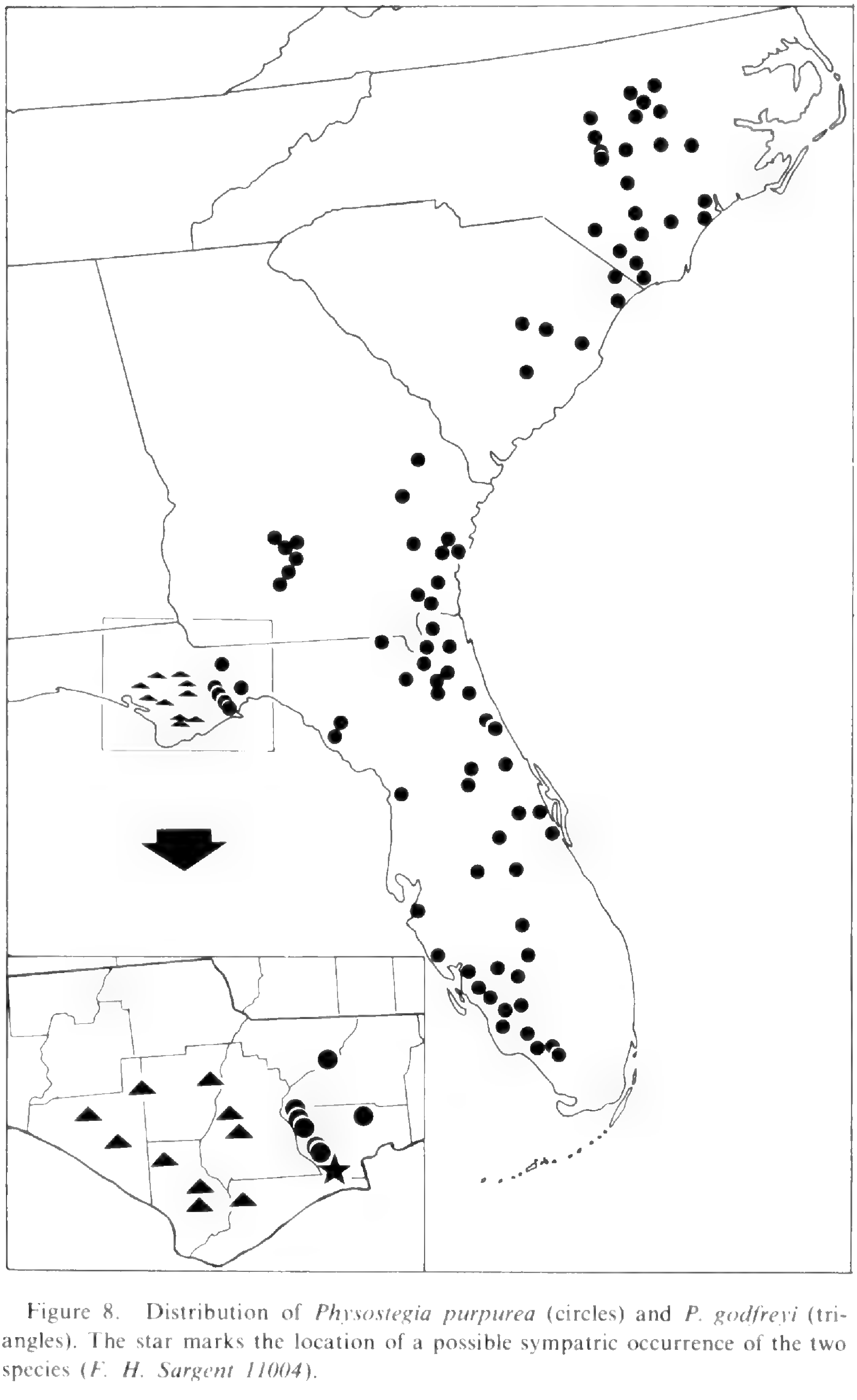


Figure 8. Distribution of *Physostegia purpurea* (circles) and *P. godfreyi* (triangles). The star marks the location of a possible sympatric occurrence of the two species (*F. H. Sargent 11004*).

several live plants grown from rhizomes collected near the type locality.

KEY TO DISTINGUISH **P. godfreyi** AND **P. purpurea**

Calyx and rachis of inflorescence puberulent and bearing minute stalked glands; nutlets 1.7–2.0 mm long, usually warty over part or all of surface; flowers (on dried specimens) 11–23 mm long; mostly west of Ochlockonee River in Florida Panhandle. .... *P. godfreyi* Cantino

Calyx and rachis of inflorescence puberulent but lacking stalked glands; nutlets 2.0–3.1(–3.6) mm long, smooth; flowers (on dried specimens) 15–34 mm long; North Carolina to Florida, not occurring west of Ochlockonee River in Florida. .... *P. purpurea* (Walt.) Blake

Physostegia godfreyi Cantino, sp. nov.

Herba perennis erecta ad 110 cm alta, plerumque infra inflorescentiam non ramosa. Rhizoma 1–10 cm longum, plerumque non ramosum. Folia rosulae basalis plerumque ante anthesin decidua. Folia caulina inferna et media glabra, firma, aliquanto succulenta; lamina linearis vel peranguste elliptica, peranguste oblonga, oblanceolata, vel raro lanceolata, saepe aliquanto falcata, (1.2–)1.5–6.5(–7.5) cm longa, (1.5–)2–6(–9) mm lata, marginibus integris, repandis, vel sparse dentatis, dentibus obtusis vel acutis. Folia caulina inferna plerumque in petiolum decrescentia; folia caulina media sessilia. Folia caulina superna sessilia, magnopere deminuta, plerumque bracteas simulantia. Racemi 1–3(–5), erecti, 5–23 cm longi, apicem versus puberuli, basi subglabri, glandes stipitatas ubique sparsim ferentes. Flores 11–23 mm longi, rare positi, calycibus post anthesin plerumque non imbricatis; pedicellus 0.5–2.0 mm longus, dense puberulus, plerumque glandes stipitatas aliquot ferens. Calyx sub anthesi tubulari-campanulatus, puberulus, glandes stipitatas ferens, tubo 3.0–5.5 mm longo, dentibus triangularibus, 0.6–1.8 mm longis. Corolla pallide rosea, extus villosa vel glabra, tubo calyce 2–3plo longiore, labio superno integro, 3 lobis labii inferni integris vel emarginatis. Nucula 1.7–2.0 mm longa, trigona, lateribus convexis, plerumque undique el saltem apicem versus verrucosa.

HERBARIUM OF FLORIDA STATE UNIVERSITY
TALLAHASSEE
PLANTS OF FLORIDA

COUNTY: GULF June 18, 1958

Physostegia veroniciformis Small

Wet pine flatwoods, and in shallow water of ditches, 7 miles S of Wewahitchka.

Collected by R. K. Godfrey, No. 57086

Figure 9. Holotype of *Physostegia godfreyi* Cantino.

TYPE COLLECTION. Florida. Gulf County: wet pine flatwoods, and in shallow water of ditches, 7 miles south of Wewahitchka, 18 June 1958, *R. K. Godfrey 57086*. HOLOTYPE: GH (Figure 9); ISOTYPES IA, USF, FSU.

ADDITIONAL SPECIMENS EXAMINED. Florida. **Bay County:** 5 miles north of Youngstown, *R. Kral 15648* (VDB); Between West Bay and Vicksburg, *R. K. Godfrey & J. N. Triplett, Jr. 59818* (LL); Lynn Haven, *C. Billington 12* (US). **Calhoun County:** 5 miles west of Bloutstown, *R. Kral 2467* (VDB); 4 miles west of Blountstown, *R. K. Godfrey et al. 53473* (GH). **Franklin County:** 6 miles south of Sumatra, *R. Kral & R. K. Godfrey 15058* (VDB). **Gulf County:** south of Wewahitchka, May 1928, *J. K. Small s.n.* (USF, NY, NCU); Wewahitchka, *D. Demaree 50379* (NCU); 10 miles north of Port St. Joe, *M. Meagher 389* (USF); 12 miles west of Wewahitchka, 29 May 1972, *R. K. Godfrey 71370* (NCU); 7.4 miles south of Wewahitchka, *P. Cantino 1053* (GH); 15 miles northeast of Port St. Joe, 14 June 1955, *E. S. Ford & E. West s.n.* (GH). **Liberty County:** 11.5 miles north of Sumatra, *R. K. Godfrey & J. N. Triplett, Jr. 59747* (LL, NCU); 10 miles south of Bristol, 23 June 1950, *F. H. Sargent s.n.* (WIS). **Wakulla County:** 4 miles west of Sopchoppy, *F. H. Sargent 11004* (WIS).

ACKNOWLEDGMENTS

I am grateful to Dr. Reed C. Rollins, Dr. Carroll E. Wood, Jr., and Mr. Michael Donoghue for reading and criticizing the manuscript, to Dr. Elizabeth A. Shaw for her aid in the preparation of the Latin description, and to Dr. Norton G. Miller for advice on the preparation of material for scanning electron microscopy. The S.E.M. photographs were obtained through the assistance of Mr. Edward Seling, using the facilities of the Harvard University Museum of Comparative Zoology.

GRAY HERBARIUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

BOOK REVIEW: THE FLORA OF CAPE COD

Svenson, Henry K. & Robert W. Pyle. *The Flora of Cape Cod,* An annotated list of the Ferns and Flowering Plants of Barnstable County, Massachusetts. v + 139 pp. 1979. The Cape Cod Museum of Natural History, Brewster, Massachusetts. (Price $4.95)

This catalog of species constitutes an authoriatative checklist of the flora of Barnstable County; Cape Cod and Barnstable County are identical geographic areas. It represents extensive coverage for a region that has lacked adequate treatment for too long a time. John M. Fogg Jr.'s "Flora of the Elizabeth Islands" (Rhodora 32, 1930), Frank C. MacKeever's "Plants of Nantucket" (University of Massachusetts Press, 1968) and other lists from the area have preceded this catalog of species, but none of these overlaps it except in a general way, and the floras of adjacent areas are by no means identical with that of Cape Cod.

Not only will this annotated list serve as a foundation for other botanists and naturalists to build on and perhaps add to, but also on a land mass suffering a double attack by sea and by man it can serve as an historical document listing many plants whose days on this particular land form must surely be numbered.

The plant families, genera and species are listed as in M. L. Fernald's *Gray's Manual of Botany,* 8th edition, 1950, and where there are common or colloquial names these are given also, followed by a brief statement of habitat, frequency, and often locality. There is a complete index to the Latin names and a somewhat shorter index to colloquial names, since some plants lack common names. Only those plants growing without benefit of cultivation are listed in this checklist. The authors used the herbarium of the New England Botanical Club, other herbaria, and their own knowledge of the Cape flora in assembling this list.

I find this flora a welcome and useful addition to the botanical literature of New England. It is a very complete listing, including some 1500 plant species and varieties. The two authors with their long experience in botanical work and in botanizing on Cape Cod are eminently qualified to produce such a flora. It is a well made book with durable flexible covers and sewn-bound signatures, something usually found only in hard-cover books; it should stand up to hard use in the field. I am grateful for this extremely well done flora; I wish only that it had appeared years ago.

WESLEY N. TIFFNEY
CURATOR, GEORGE M. GRAY HERBARIUM & MUSEUM
MARINE BIOLOGICAL LABORATORY
WOODS HOLE, MASSACHUSETTS 02543

NOTICE OF PUBLICATION

Gentry, Howard S. 1978. *The Agaves of Baja California.* Occasional Papers of The California Academy of Sciences, no. 130. 119 pp., Frontis. & 62 figs, 11 tables. This is a systematic and economic account of the Genus *Agave* in Baja California and adjacent areas of the Gulf of California. Four new species, eight other new taxa, total taxa 23. Keys, distribution maps, line drawings, and photographs. Notes on modern and historical economic uses.

Available from Scientific Publications Department, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118 for $8 plus postage (and tax, if applicable).

NOTICE OF PUBLICATION

G. W. Corrivault & P. Morisset — *Le Naturaliste Canadien, Index*. 352 pp., 1979, Les Presses de l'Université Laval, Quebec G1K 7P4. Price: $10.00 can. — The first part is an author and title index to the 2504 papers published in volumes 1–100 (1868–1973) of Le Naturaliste Canadien. The second part is a topical index with possibly 75,000 entries, covering volumes 55 to 100 (1929–1973). All plant, animal and mineral taxa are indexed, as are also a wide variety of topics, mainly by key words appearing in titles. Topics indexed are all cross-referenced to the author and title index. New taxa and other taxonomic innovations are underlined. Biographical papers are traceable by the name of the biographee even when his name does not appear in a paper title. Common names are cross-referenced to Latin names. Junior authors are cross-referenced to their senior authors. Indices to volumes earlier than 55 already exist. An index to vols. 1–20 will be found at the end of vol. 20 and an index to vols. 21–54 appears at the end of vol. 54. A cumulated author index for vols. 1–82 was published at the beginning of vol. 83.

Although the subject index does not cover all 100 volumes, this reference volume should be of special interest to botanists because nearly all of the botany published in the Naturaliste Canadien has appeared during the more recent period. The data in more than 500 botanical papers is retrievable through this index, including some 8,000 different plant names and about 700 botanical taxonomic innovations.

Vol. 81, No. 826, including pages 151–290, was issued Apr. 13, 1979.

The Proceedings of the Symposium

"RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND"

4, 5 May 1979

which was sponsored by
The New England Botanical Club
in co-operation with the
U.S. Fish and Wildlife Service
will be published as the January 1980 issue (No. 829, Vol. 80)

RHODORA

Non-subscribers, as well as those members who want extra copies, may order from:

NEBC Symposium
Department of Botany and Plant Pathology
Nesmith Hall
University of New Hampshire
Durham, N. H. 03824

Make checks payable to: **NEBC Symposium**

PRICES: $6.50 for orders received before Dec. 31, 1979
$8.00 for orders received after Jan. 1, 1980

Please include Zip Code in your return address, with the number of copies desired and the amount enclosed.

RHODORA **July, 1979** **Vol. 81, No. 827**

CONTENTS

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 81 October, 1979 No. 828

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Conducted and published for the Club, by
ROLLA M. TRYON, Editor-in-Chief

RHODORA. — A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes, and single copies are available. For information and prices write RHODORA at address given below.

Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes, relating to the plants of North America, and floristically related areas, will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. All manuscripts should be submitted in duplicate, and must be double- (at least ⅜ of an inch) or triple-spaced throughout. Please conform to the style of recent issues of the journal. Extracted reprints, if ordered in advance, will be furnished at cost.

Address manuscripts and proofs to:
Russell R. Walton
Managing Editor, RHODORA
Harvard University Herbaria Building
22 Divinity Avenue
Cambridge, Mass. 02138

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Scirpus Longii Fernald

In New England, this rare species grows in a few marshes and wet meadows in central Connecticut and eastern Massachusetts.

Original artwork by Frances S. Chew

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

Vol. 81 October, 1979 No. 828

SYNOPSIS AND POLLEN MORPHOLOGY OF VERNONIA (COMPOSITAE: VERNONIEAE) IN THE NEW WORLD

SAMUEL B. JONES, JR.

The tribe Vernonieae was recognized by Cassini (1817, 1819) and delimited by Lessing (1829, 1831a & b). Lessing's organization was used by de Candolle (1836) to form the basis of his classification. The next major reorganization was that of Bentham (1873) and Bentham and Hooker (1873). In 1894, Hoffman made a few rearrangements, but his treatment is essentially the same as Bentham's. Smaller, but important, contributions have been made by several workers who have examined and classified portions of the tribe on a limited geographical basis, e.g. Schultz-Bipontinus (1861, 1863), Baker (1873), Gleason (1906, 1922), Ekman (1914), and Cabrera (1944).

The tribe has over 1,450 species and about 70 genera, with ca. 37 genera being monotypic. *Vernonia,* the largest genus in the tribe, with ca. 900 to 1,000 species, is predominately tropical. Four to five hundred species of *Vernonia* are native to the New World with about the same number in Africa and southeast Asia. *Vernonia* forms the central core of the Vernonieae with the smaller genera appearing to radiate from it. Although the importance of *Vernonia* to the classification of the tribe is clear, there has been no comprehensive reevaluation of the genus since de Candolle (1836) and Bentham (1873). Subsequent changes in its classification generally have been restricted to limited geographic areas. The current delimitation of sections, subsections, series, etc., of *Vernonia* is nebulous and many are clearly artificial (Smith, 1971).

Vernonia presents an impressive array of leaf and stem morphology, habit, and ecological preference, demonstrating the tremendous diversification that has occurred during its evolution. The habit of *Vernonia* varies widely. Some species are annuals; others are perennial herbs, shrubs, or trees. The plants range in size from acaulescent perennials ca. 4 cm tall to trees reaching 30 m in height. They inhabit a wide array of habitats. A few species grow in marshy or wet soil, others in very dry places. Some Vernonias inhabit cloud forests, additional ones are adapted to grassland-fire habitats. In spite of this radiation, many of the reproductive features of *Vernonia* have remained remarkably constant. In addition to the diversification, parallelism is rampant when species grow in similar habitats.

Since evolution of the group has often caused species relationships to become obscured, it is difficult to arrange phylogenetic groupings and construct a classification. In addition, since the genus is so large and accommodates so much variation and parallelism, subdivisions of the genus above the rank of species have been difficult to circumscribe fully. To achieve a higher level of clarity, additional characters must be used to aid in developing an improved classification. Both Gleason (1923) and Cabrera (1944) have pointed out the possible value of inflorescence types as a character in *Vernonia.*

Figures 1–3 show generalized representative inflorescences of *Vernonia* in the New World. **1f, 2c, 2e, 2f, & 2g** follow Cabrera (1944), and **2d** follows Gleason (1923). All are drawn or redrawn from herbarium material. The presence or absence of bracteal leaves subtending the heads is significant.

Another such character is external pollen morphology (Fig. 4). Workers such as Wodehouse (1928), Smith (1969), Jones (1970), Kingham (1976), and Keeley and Jones (1977) have demonstrated the variability and usefulness of pollen features of Vernonieae. In the last few years, evidence from two additional sources has been accumulating slowly, i.e., natural plant products (Mabry, et al., 1975) and chromosome numbers (Jones, 1977). It seems likely that new evidence from pollen morphology, chemosystematics, and cytotaxonomy, when combined with evidence from gross morphology, can be used to improve the classification of *Vernonia.*

The present investigation is based upon some 16 years experience in the genus and includes field work in the United States, Mexico, and Brazil, along with greenhouse and garden studies. In addition, two months were spent in England at K and BM. During the past several years, the pollen grains of over 600 species of *Vernonia* were acetolyzed by the procedure of Erdtman (1966) and prepared for

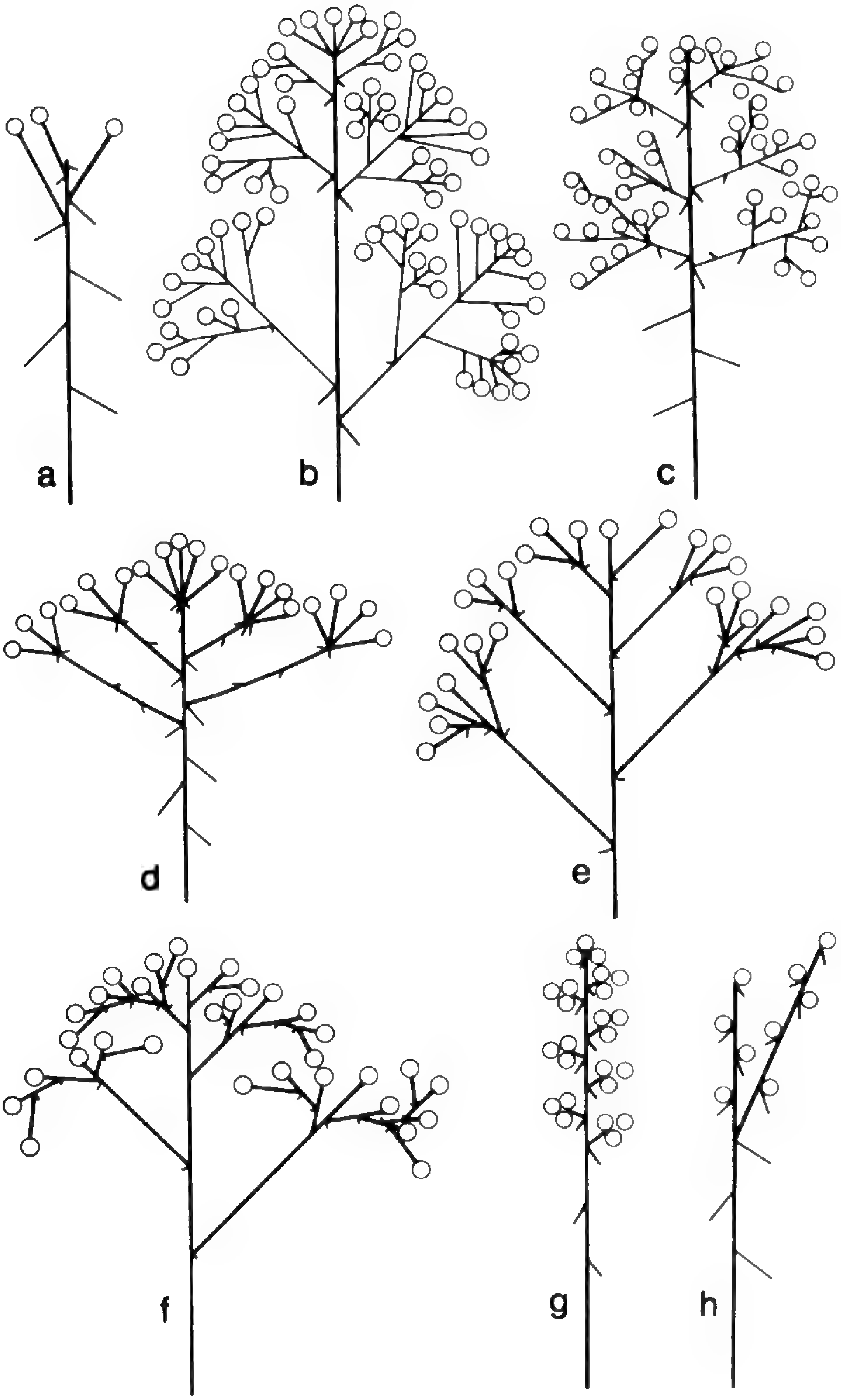


Figure 1. Generalized representative inflorescences of *Vernonia* in the New World. 1f follows Cabrera (1944).

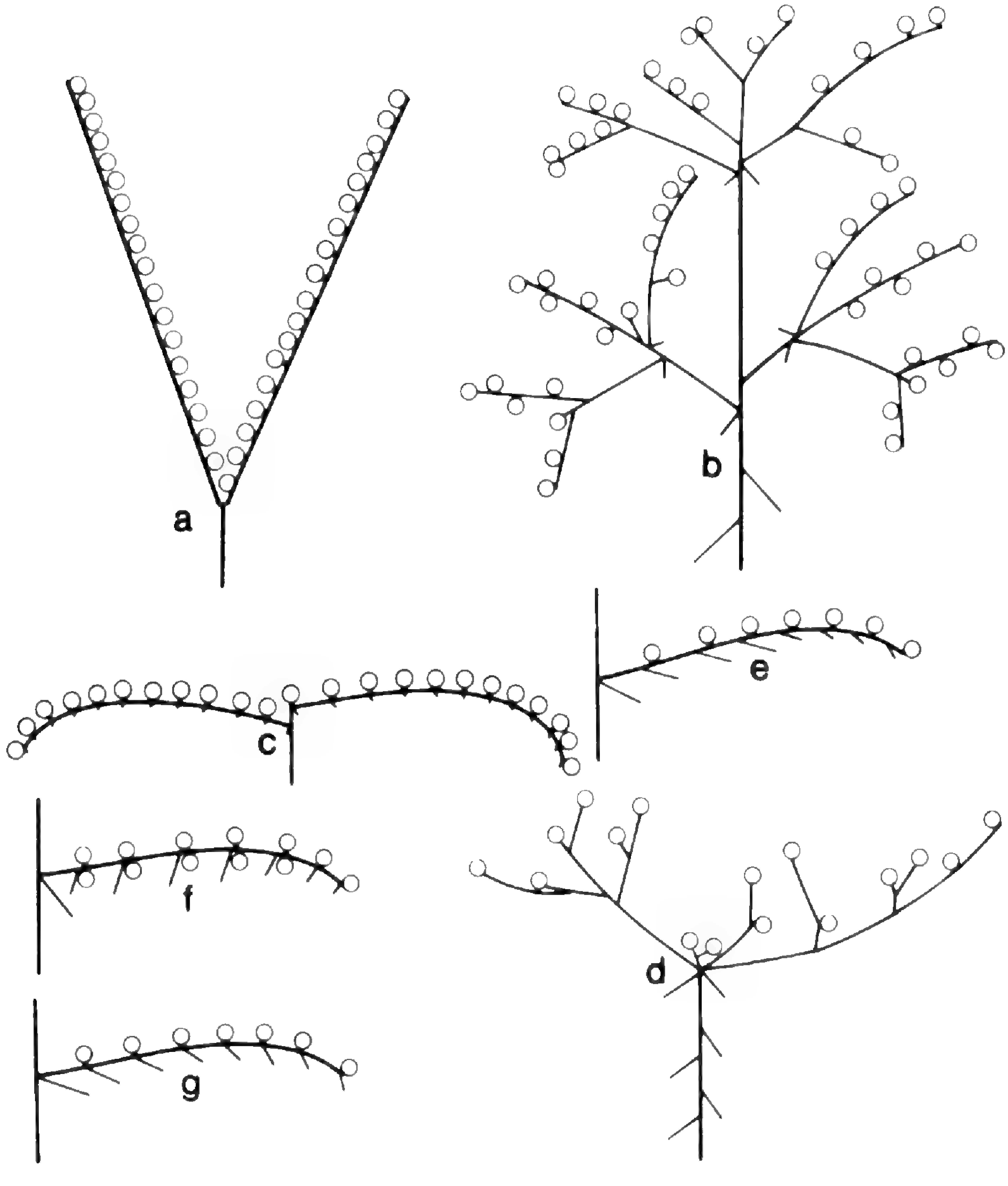


Figure 2. Generalized representative inflorescences in *Vernonia* in the New World. 2c, e, f, & g follow Cabrera (1944). 2d follows Gleason (1923).

light microscopy by mounting whole grains in glycerin jelly on glass slides and staining them lightly with methyl green. Acetolyzed grains were prepared for scanning electron microscopy (SEM) as previously described by Jones (1970). Light microscopy supplemented by SEM was used to determine the pattern of the grains. Names of the species cited in the paper are those taken from labels unless an obvious error was detected. In such cases, the sheets were annotated.

Once the pollen type had been determined, attempts were made to develop phylogenetic groupings using other available data. In the process, it became apparent that the best approach was to report the results of the pollen study in conjunction with a synoptic treatment. Four types of pollen grains are known from the New World Vernonias (Fig. 4). In addition, two other types of pollen grains not known from the New World are found in the Old World. The results are then summarized here, but due to the size of the genus this paper treats only the New World Vernonias, which are recognized as belonging to a subgenus erected on morphological, chemical, and cytological grounds. The New World Vernonias have chromosome numbers based on $n = 17$, whereas $n = 9$ and 10 in the Old World (Jones, 1977). Likewise, the sesquiterpene lactones of the New World Vernonias are similar to but differ from those found in the Old World (Mabry, et al., 1975). The Old World species will be treated in a second paper.

The major goal of the effort was to develop a classification which reflects evolution. Furthermore, the development of phylogenetic units provides workable-sized groups of species for taxonomic

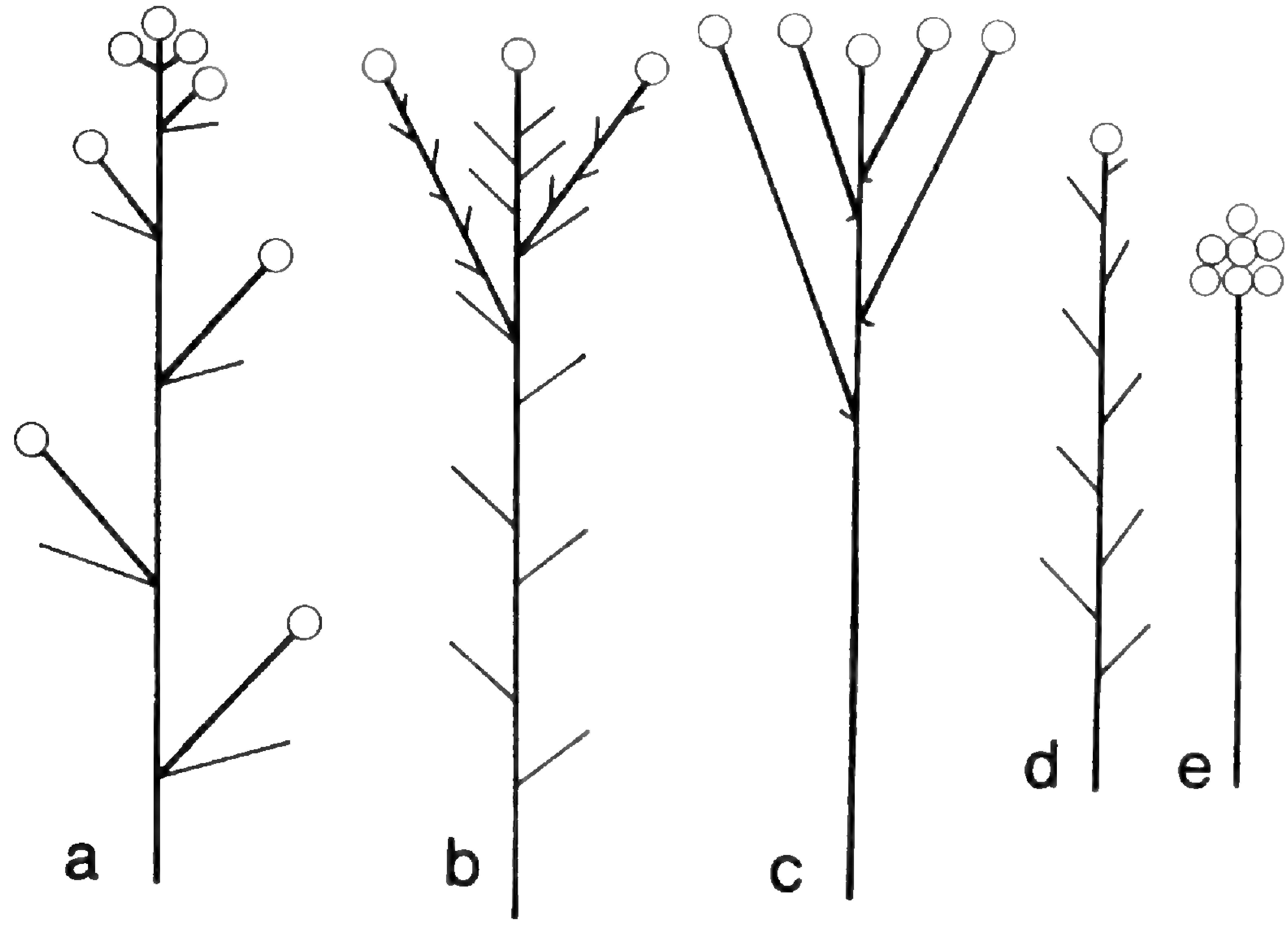


Figure 3. Generalized representative inflorescences of *Vernonia* in the New World.

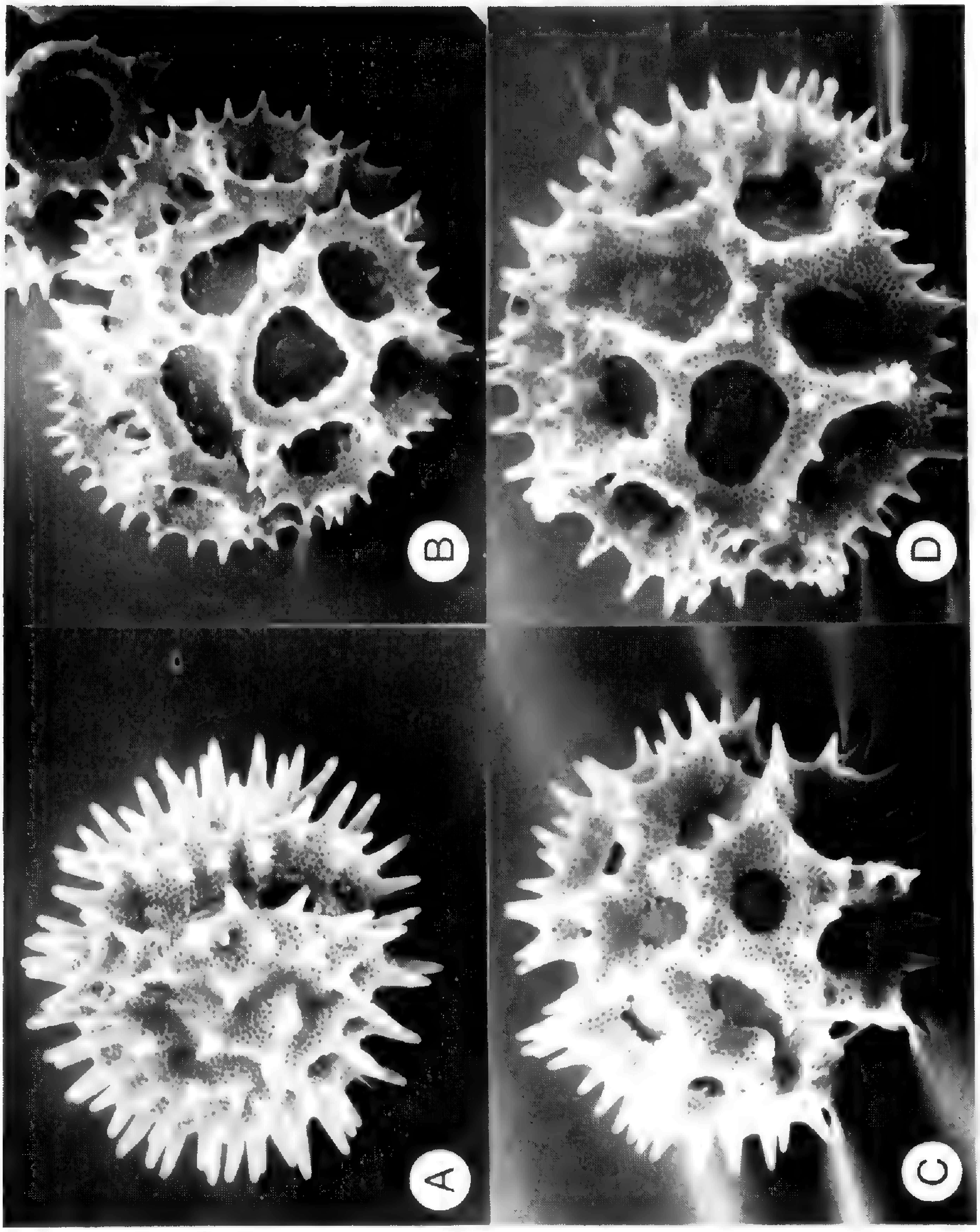


Figure 4. Pollen types A, B, C, and D of *Vernonia* from the New World. Type A: *V. barkerii*, equatorial view, diameter of grain ca. 44 μm. Type B: *V. ammophila*, polar view, diameter of grain ca. 66 μm. Type C: *V. canescens*, polar view, diameter of grain ca. 44 μm. Type D: *V. eremophylla*, equatorial view, diameter of grain ca. 56 μm. Types A, B and C were described in Keeley and Jones (1977). Type D has a ridge surrounding the germinal pore, and therefore, lacks a germinal furrow. Type A is regarded as primitive and types B, C, and D as derived. Spines are sometimes reduced to almost absent in types B and C.

revision. Undoubtedly, with additional study, some groups presented here will have to be redefined. Until an effort is made to develop a new classification, the genus will stand in the arrangements of the 1800s.

SYNOPSIS OF CLASSIFICATION OF THE NEW WORLD VERNONIAS:

Vernonia
  Subgenus *Vernonia*
    Section *Leiboldia*
    Section *Hololepis*
    Section *Vernonia*
      Subsection *Noveboracenses*
      Subsection *Eremosis*
      Subsection *Polyanthes*
      Subsection *Buxifoliae*
      Subsection *Chamaedrys*
      Subsection *Stenocephalum*
      Subsection *Nudiflorae*
        Series *Nudiflorae*
        Series *Brevifoliae*
        Series *Verbascifoliae*
        Series *Subulatae*
      Subsection *Scorpioides*
        Series *Scorpioides*
        Series *Macrolepidae*
        Series *Remotiflorae*
        Series *Flexuosae*
        Series *Aureae*
        Series *Canescentes*
        Series *Foliatae*
        Series *Sagraeanae*
        Series *Arborescentes*
        Series *Pallescentes*

Subgenus **Vernonia.** TYPE SPECIES: *Vernonia noveboracensis* (L.) Willd.

Herbaceous perennials to shrubs and small trees; inflorescences highly variable, forming complex patterns often based upon a scorpioid-cymose design sometimes greatly reduced, in others very large (Figs. 1, 2 & 3); heads with 1 to numerous florets; involucres usually campanulate, phyllaries usually tightly appressed; pappus usually in two series, and occasionally subequal; corollas reddish-purple to pinkish or whitish, never bright blue nor yellow in color.

Geographical distribution: from Manitoba, Canada and the eastern United States, Mexico, and the West Indies south into Argentina. Most abundant in southern Brazil and the mountains of Mexico, Central America, and the Andes.

Chemistry: the new world species thus far examined all contain the glaucolide type of sesquiterpene lactone.

Chromosome numbers: based upon $n = 17$.

Pollen types: A, B, C, and D (Fig. 4).

Section **Leiboldia** (Schlecht.) Benth. & Hook. Gen. Pl. **2:** 228. 1873.

Leiboldia Schlecht. Linnaea **19:** 742. 1847. TYPE SPECIES: *Vernonia leiboldiana* Schlecht.

Shrubs or small trees; leaves elliptic to lanceolate or obovate; inflorescences terminal, of a few heads, often arranged in the axils of foliage leaves (see Fig. 1a); heads large and with numerous florets; phyllaries lanceolate to semi-foliaceous; pappus bristles subequal in several series; corollas with tubes twice as long as the lobes.

Geographical distribution: mountains of southern Mexico into Central America.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia arctioides Less., MÉXICO: Oaxaca, *Smith 4495* (US). **V. corae** Standl. & Steyerm., GUATEMALA: San Marcos, *Williams, et al. 25943* (NY). **V. mexicana** Less., MÉXICO: Puebla, *Sharp 45806* (NY).

Section **Hololepis** (DC.) DC. Prodr. **5:** 16. 1836.

Hololepis DC. Ann. Mus. Nat. Hist. Paris **16:** 190. 1810. TYPE SPECIES: *Vernonia pedunculata* (DC.) DC.

Woody shrubs; leaves ovate, coriaceous above, tomentose beneath; inflorescences of single heads borne in axils of upper foliage leaves (see Fig. 1a); heads large, with numerous florets, phyllaries in two distinct series, the outer ovate and leaf-like, the inner smaller and lanceolate; pappus of subequal bristles; corolla lobes twice the length of the tube; achenes glabrous, faintly ribbed.

Geographical distribution: in the state of Minas Gerais, Brazil.

Pollen type: A. Pollen grains were examined from the following specimen:

Vernonia pedunculata DC., BRAZIL: Minas Gerais, *Irwin, et al. 30242* (NY).

Section **Vernonia** TYPE SPECIES: *Vernonia noveboracensis* (L.) Willd.

Section *Lepidaploa* (Cass.) DC. Prodr. **5:** 26. 1836.
Section *Stenocephalum* (Sch.-Bip.) Benth. & Hook. Gen. Pl. **2:** 230. 1873.
Section *Trianthaea* Spach. Hist. Veg. Phan. **10:** 39. 1841.
Section *Critoniopsis* (Sch.-Bip.) Benth. & Hook. Gen. Pl. **2:** 230. 1873.
Section *Eremosis* (DC.) Benth. & Hook. Gen. Pl. **2:** 231. 1873.

Shrubs, small trees, herbaceous perennials, rarely annuals; pappus usually in two distinct series.

Geographical distribution: from extreme southern Canada south into Argentina. The greatest number of species are found in southern Brazil, the West Indies, Mexico and the eastern United States.

Chemistry: sesquiterpene lactones of a glaucolide type.

Chromosome numbers: a series based on $n = 17$, with $n = 17$, 34, 51, and 68.

Pollen types: A, B, C, and D.

Subsection **Noveboracenses** Ekman, Ark. Bot. **13**(15): 95. 1914. TYPE SPECIES: *Vernonia noveboracensis* (L.) Willd.

Herbaceous perennials, sometimes becoming slightly woody at base; leaves highly variable; inflorescences corymbose to paniculate (see Figs. 1b, 1d, 2d); heads of 10 to 60 florets; phyllaries small, outer greatly reduced; pappus bristles in two series, outer pappus often scale-like; achenes usually ribbed.

Geographical distribution: much of the eastern United States, and into southern Manitoba, Canada, southward to southern Mexico.

Chemistry: sesquiterpene lactones glaucolide-A, B, F, and marginata.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia acaulis (Walt.) Gleason, UNITED STATES: Georgia, *Duncan 12029* (GA). **V. alamanii** DC., MÉXICO: Michoacan, *Jones 22407* (GA). **V. angustifolia** Michx., UNITED STATES: Alabama, *Kral 28542* (GA). **V. arkansana** DC., UNITED STATES: Arkansas, *Demaree 59216* (GA). **V. autumnalis** McVaugh, MÉXICO: Jalisco, *McVaugh 25476* (GA). **V. baldwini** Torr., UNITED STATES: Oklahoma, *Jones 15850* (GA). **V. bealliae** McVaugh, MÉXICO: Jalisco, *McVaugh 10331* (NY). **V. blodgettii** Small, UNITED STATES: Georgia, *Jones 1099* (GA). **V. cronquistii** S. B. Jones, MÉXICO: Guerrero, *Cronquist 11226* (GA). **V. fasciculata** Michx., UNITED STATES: Iowa, *Urbatsch 33* (GA). **V. flaccidifolia** Small, UNITED STATES: Georgia, *Urbatsch 99* (GA). **V. gigantea** (Walt.) Trel., UNITED STATES: Georgia, *Urbatsch 125* (GA). **V. glauca** (L.) Willd., UNITED STATES: Georgia, *Holder 1929* (GA). **V. greggii** Gray, MÉXICO: Nuevo Leon, *Chapman 82* (GA). **V. karvinskiana** DC., MÉXICO: Oaxaca, *Jones 21669* (GA). **V. larsenii** King & Jones, UNITED STATES: Texas, *Demaree 58832* (GA). **V. lettermanni** Engelm., UNITED STATES: Arkansas, *Jones 15838* (GA). **V. liatroides** DC., MÉXICO: México, *Jones 22389* (GA). **V. lindheimeri** Gray & Engelm., UNITED STATES: Texas, *Jones 15877* (GA). **V. marginata** (Torr.) Raf., UNITED STATES: Oklahoma, *Jones 17670* (GA). **V. missurica** Raf., UNITED STATES: Arkansas, *Jones 15831* (GA). **V. noveboracensis** (L). Michx., UNITED STATES: Georgia, *Jones 1201* (GA). **V. oaxacana** Sch.-Bip. ex Klatt, MÉXICO: Oaxaca, *Jones 21670* (GA). **V. pulchella** Small, UNITED STATES: Georgia, *Jones 1085* (GA). **V. serratuloides** H.B.K., MÉXICO: Najavit, *Hennen 238* (GA). **V. texana** (Gray) Small, UNITED STATES: Mississippi, *Jones 17657* (GA).

Subsection **Polyanthes** Ekman, Ark. Bot. **13**(15): 89. 1914. TYPE SPECIES: *Vernonia baccharoides* H.B.K.

Woody shrubs to suffrutescent perennials; inflorescences paniculate to corymbose to semi-scorpioid cymose (see Figs. 1b, 1c, 1d, & 1f); heads usually medium sized with ca 15–25 florets; phyllaries usually small and tightly imbricate; achenes usually ribbed.

Geographical distribution: southern Mexico south through Central America and down the Andes into Brazil.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia aschenborniana Schauer, MÉXICO: Veracruz, *Ventura A. 5040* (NY). **V. baccharoides** H.B.K., PERU: San Martín, *Belshaw 3242* (F). **V. bakerana** Britt., BOLIVIA, *Buchtien 1546* (NY). **V. crotonides** Sch.-Bip., BRAZIL: Minas Gerais, *Irwin, et al. 29689* (NY). **V. deppeana** Less., MÉXICO: Jalisco, *McVaugh 22912* (NY). **V. discolor** Less., BRAZIL, *Lanna 1823* (GA). **V. ferruginea** Less., BRAZIL: Mato Grosso, *Ratter & de Castro 117* (NY). **V. fulta** Griseb., ARGENTINA: Tafi, *Sás 174* (NY). **V. havanensis** DC., CUBA, *Barker & Abarco 3721* (US). **V. hieracioides** Griseb., CUBA, *Morton & Acuna 3120* (US). **V. jubifera** Rusby, BOLIVIA, *Bang 1554* (NY). **V. menthaefolia** (Poepp.) Less., CUBA, *Wright (1860 64) 2792* (MO). **V. oppositifolia** Less., BRAZIL, *Sobrinho 1817* (GA). **V. pacchensis** Benth. var. *tambillensis* Hieron., PERU: Piura, *Hutchinson & Wright 6690* (MO). **V. patens** H.B.K., PERU: San Martín, *McDaniel 14232* (GA). **V. petiolaris** DC., BRAZIL, *Lejo 16117* (NY). **V. polyanthes** (Spreng.) Less., BRAZIL: Minas Gerais, *Williams & Assis 8010* (GA). **V. polylepsis** Sch.-Bip., PERU: Cuzco, *Vargas 2038* (MO). **V. rubriramea** Mart. ex DC., BRAZIL: Minas Gerais, *Pires 57961* (NY). **V. ruficoma** Schlecht. ex Mart., BOLIVIA, *Williams 1410* (NY). **V. sordidopapposa** Hieron., PERU: Cuzco, *Vargas C. 15495* (NY). **V. stellaris** Llave & Lex., COSTA RICA, *Molina R., et al. 18006* (NY). **V. suaveolens** H.B.K., ECUADOR: Cañar, *Prieto P-76* (NY). **V. trichoclada** Gleason, PERU: Cuzco, *Vargas 6083* (F).

Subsection **Eremosis** (DC.) S. B. Jones, *stat. nov.*

Monosis DC., Section *Eremosis* DC. Prodr. **5:** 77. 1836. TYPE SPECIES: *Vernonia salicifolia* (DC.) Sch.-Bip. (*Monosis salicifolia* DC.).
Critoniopsis Sch.-Bip. Pollichia **20/21:** 430. 1863.
Section *Critoniopsis* (Sch.-Bip.) Benth. & Hook. Gen. Pl. **2:** 230. 1873.

Shrubs or small trees; inflorescences large, paniculate (see Figs. 1b & 1d); heads sessile, subsessile, or sometimes pedicellate, few (1–16) flowered; phyllaries in several series, inner usually deciduous; pappus of bristles, outer pappus shorter, variable, and sometimes lacking.

Geographical distribution: Sierra Madre Orientale and Occidentale of Mexico south through Central America, then along the Andes into Brazil.

Chemistry: sesquiterpene lactones glaucolide-A, B, C, D, E, F, G, and H.

Chromosome number: $n = 17$.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia baadii (McVaugh) Jones, MÉXICO: Michoacan, *Hinton, et al. 13651* (NY). **V. barbinervis** Sch.-Bip. ex Seem., MÉXICO: Sinaloa, *Jones 22530* (GA). **V. bogotana** Cuatr., COLOMBIA: Cundinamarca, *Fosberg & Villareal 20575* (NY). **V. glandulata** Cuatr., COLOMBIA: Del Norte de Santander, *Fosberg 19154* (NY). **V. gurigaseusis** Britt., BOLIVIA, *Rusby 1732* (NY). **V. leiocarpa** DC., MÉXICO: Chiapas, *Jones 21675* (GA). **V. littoralis** Brandeg., MÉXICO, *Moran 5760* (NY). **V. obtusa** Blake, MÉXICO: San Luis Potosi, *Cronquist 11274* (GA). **V. pallens** Sch.-Bip., MÉXICO: Michoacan, *McVaugh 22556* (NY). **V. paniculata** DC., MÉXICO: Michoacan, *Jones 22401* (GA). **V. pycnantha** Benth., ECUADOR, *Espinosa 1572* (NY). **V. salicifolia** (DC.) Sch.-Bip., MÉXICO: México, *Jones 20571* (GA). **V. shannoni** Coult., GUATEMALA: Totonicapán, *Williams, et al. 22913* (NY). **V. steetzii** Sch.-Bip., MÉXICO: Jalisco, *Jones 20583* (NY). **V. tarchonanthifolia** (DC.) Sch.-Bip., MÉXICO: Oaxaca, *Cronquist 10908* (GA). **V. triflosculosa** H.B.K., MÉXICO: Oaxaca, *Jones 21671* (GA). **V. uniflora** Sch.-Bip., MÉXICO: México, *Jones 22390* (GA).

Subsection **Buxifoliae** Ekman, Ark. Bot. **13**(15): 22. 1914. TYPE SPECIES: *Vernonia buxifolia* (Cass.) Less.

Series *Aggregatae* Gleason. Bull. New York Bot. Gard. **4:** 190. 1906.

Woody, rigid shrubs; leaves coriaceous; inflorescences terminal and cymose, of few (3–5) heads (see Figs. 1b & 1g); heads small with ca 10 florets; achenes glabrous with 8–9 ribs.

Geographical distribution: A distinct subsection from Hispaniola.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia barkeri Ekman, HISPANIOLA, *Ekman 7351* (US). **V. buxifolia** (Cass.) Less., HISPANIOLA, *Ekman 3391* (GH). **V. tuerckheimii** Urban, HISPANIOLA, *Keeley & Keeley 1489* (GA).

Subsection **Chamaedrys** Cabrera, Darwiniana **6:** 307. 1944. TYPE SPECIES: *Vernonia chamaedrys* Less.

Subsection *Nitidulae* Cabrera, Darwiniana **6:** 347. 1944.

Fruticose perennials to shrubs; inflorescences cylindrical, compact, thyrsoid-paniculate (see Figs. 1b, 1g, & 1e); heads numerous, medium sized with 10–20 florets; phyllaries tightly imbricated in several series.

Geographical distribution: from Peru south to Argentina, but centered in southern Brazil. A well marked and distinctive subsection.

Chromosome number: $n = 17$.

Pollen types: A and B. Pollen grains were examined from the following specimens:

(TYPE A) **Vernonia chamaedrys** Less., BRAZIL: Paraná, *Hatschback 31764* (NY). **V. chaquensis** Cabrera, ARGENTINA: Mburucuyá, *Peterson 1708* (NY). **V. crassa** Ekman ex Malme, BRAZIL: Paraná, *Lindemann & De Haas 2452* (NY). **V. cuneifolia** Gardn., BRAZIL: Paraná, *Lindemann & DeHaas 5537* (NY). **V. flex** Chod., PARAGUAY, *Hassler 3800* (NY). **V. florida** Gardn., BRAZIL: Paraná, *Hatschbach 30290,* (NY). **V. gochnatioides** Hook. & Arn. ex DC. URAGUAY: Colonia, *Cabrera 3882* (NY). **V. jalcana** Cuatr., PERU: Amazônas, *Hutchinson & Wright 5515* (MO). **V. laxa** Gardn., PARAGUAY, *Hassler 9136* (NY). **V. montevidensis** (Spring) Ekman, ARGENTINA, *Rodriguex 37* (NY). **V. mucronulata** Less., BRAZIL: Minas Gerais, *Williams & Assis 1486* (GA). **V. nitidula** Less., BRAZIL: Paraná, *Hatschbach 22424* (NY). **V. oligactoides** Less., BRAZIL: Paraná, *Dusén 9680* (NY). **V. oligolepis** Sch.-Bip., BRAZIL: Paraná, *Dusén 9192* (NY). **V. puberula** Less., BRAZIL: Paraná, *Hatschbach 20081* (NY). **V. quinqueflora** Less., BRAZIL: Santa Catarina, *Reitz & Klein 9702* (NY). **V. rigiophylla** Sch.-Bip. ex Baker in Mart., BRAZIL: Paraná, *Reiss 43A* (NY). **V. squamulosa** H. & A., ARGENTINA: Tucumán, *Sás 93* (NY). **V. viscidula** Less., BRAZIL: Minas Gerais, *Pieres 57938* (NY).

(TYPE B) **Vernonia myrsitnitis** Ekman, BRAZIL: Goiás, *Ana 519* (NY). **V. pycnostachya** DC., BRAZIL: Minas Gerais, *Irwin, et al., 27655* (NY). **V. rosea** Mart. ex DC., BRAZIL: São Paulo, *Brade 20635* (NY). **V. tomentella** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 20341* (NY). **V. vepretorum** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 22619* (NY).

Subsection **Stenocephalum** (Sch.-Bip.) S. B. Jones, *stat. nov.*

Stenocephalum Sch.-Bip. Pollichia **20/21:** 385. 1863. TYPE SPECIES: *Vernonia apiculata* Mart. ex DC.

Annuals or herbaceous perennials; leaves densely white pubescent beneath; heads cylindric, elongate, small with 4–12 florets, sessile, sometimes clustered or arranged in axils of leaves (see Figs. 2f & 2g); phyllaries apiculate; achenes pubescent.

Geographical distribution: Mexico south to and centered in southern Brazil, sometimes weedy.

Chromosome number: n = 17.

Pollen type: C. Pollen grains were examined from the following specimens:

Vernonia apiculata Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 26921* (NY). **V. hexantha** Sch.-Bip. ex Baker in Mart., PARAGUAY, *Hassler 9825a* (NY). **V. jucunda** Gleason, MÉXICO: Chiapas, *Breedlove & Raven 13724* (NY). **V. megapotamica** Spreng., ARGENTINA: Mburucuyá, *Petersen 1380* (NY). **V. tragiaefolia** DC., BRAZIL São Paulo, *Brade 5711* (NY).

Subsection **Nudiflorae** Cabrera, Darwiniana **6:** 353. 1944. TYPE SPECIES: *Vernonia nudiflora* Less.

Herbaceous perennials, sometimes woody at base, rarely annuals; leaves linear to elliptic or lanceolate; inflorescences corymbose-paniculate to reduced and few-flowered; heads small to medium sized or sometimes large.

Geographical distribution: southern Brazil to Argentina.

Series **Nudiflorae** S. B. Jones, *ser. nov.*

Herbae perennes vel raro suffrutices; caules simplices vel raro ramosi; folia linearia vel lanceolata; inflorescentiae corymboso-paniculatae vel diminutae; capitula 10–25 flosculis. TYPE SPECIES: *Vernonia nudiflora* Less.

Herbaceous perennials, sometimes slightly woody at base; leaves frequently linear, sometimes elliptic or lanceolate; inflorescences corymbose-paniculate or reduced (see Figs. 1b, 1c, 1e, 1f, 3a, & 3e); heads small to medium sized with 10–25 florets.

Geographical distribution: southern Brazil south into Argentina.

Chemistry: Sesquiterpene lactones glaucolide-A and B.

Chromosome number: n = 17.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia amplexicaulis Fries, ARGENTINA: Jujuy, *Venturi 5218* (NY). **V amygdalina** Lam., BRAZIL: Goiás, *Irwin, et al. 17827* (NY). **V. brasiliana** Druce., BRAZIL, *Bunting 3343* (GA). **V. densiflora** Gardn., BRAZIL: Paraná, *Hatschbach 16239* (NY). **V. echioides** Less., BRAZIL: Paraná, *Hatschbach 30991* (NY). **V. incana** Less., ARGENTINA: Empedrado, *Pederson 9613* (NY). **V. lorentensis** Hieron., ARGENTINA: Mburucuyá, *Petersen 1442* (NY). **V. marianna** Mart., BRAZIL: Minas Gerais, *Irwin, et al. 28388* (NY). **V. missionis** Gardn., BRAZIL: Minas Gerais, *Macedo 2346* (NY). **V. nudiflora** Less., URUGUAY, *Millot 11362* (GA). **V. pseudo-linearifolia** Hieron., PARAGUAY, *Hassler 3654* (NY). **V. scabra** Pers., BRAZIL: Goiás, *Irwin, et al. 17793* (NY). **V. scapigera** Baker ex. Mart., BRAZIL: Minas Gerais, *Irwin, et al. 28085a* (NY). **V. tweedieana** Baker ex. Mart., PARAGUAY: Guairé, *Pedersen 10094* (NY). **V. westiniana** Less., BRAZIL: São Paulo, *Filho 75-1* (GA).

Series **Brevifoliae** (Cabrera) S. B. Jones, *stat. nov.*

Subsection *Brevifoliae* Cabrera. Darwiniana **6:** 303. 1944. TYPE SPECIES: *Vernonia brevifolia* Less.

Herbaceous perennials; leaves usually linear but sometimes elliptic to ovate; inflorescences greatly reduced, sometimes corymbose (see Figs. 3a, 3b, 3c, & 3d); heads relatively few to typically solitary.

Geographical distribution: southern Brazil south into Argentina.

Chromosome number: $n = 17$. Series *Brevifoliae* is very closely related to series *Nudiflorae.*

Pollen types: B and D. Pollen grains were examined from the following specimens:

(TYPE B) **Vernonia compactiflora** Mart. ex Baker in Mart., BRAZIL: Distrito Federal, *Irwin, et al. 13155* (NY). **V. erythrophila** DC., BRAZIL: Distrito Federal, *Irwin, et al. 10064* (NY). **V. graminifolia** Gardn., BRAZIL: Minas Gerais, *Irwin, et al. 28405* (NY). **V. grandiflora** Less., PARAGUAY, *Hassler 4341* (NY). **V. hypochaeris** DC., BRAZIL: Paraná, *Lindeman & de Haas 2526* (NY). **V. intermedia** DC., URUGUAY, *Rosengurtt B-2401* (NY). **V. psilophylla** DC., BRAZIL: Minas Gerais, *Irwin, et al. 28090* (NY). **V. sessilifolia** Less., BRAZIL: Paraná, *Hatschbach 15959* (NY).

(TYPE D) **Vernonia brevifolia** Less., BRAZIL: Paraná, *Lindeman & de Haas 3091* (NY).

Series **Verbascifoliae** S. B. Jones, *ser. nov.*

Herbae perennes vel suffrutices; inflorescentiae diminutae; capitula magna, 40–80 flosculis; phyllaria magna. TYPE SPECIES: *Vernonia verbascifolia* Less.

Herbaceous perennials, sometimes becoming woody at base; leaves tomentose and often conspicuously whitish beneath; inflorescences often greatly reduced with few heads, sometimes branched and having several heads (see Figs. 1f, 1g, 1h, 3a, 3b, 3c, & 3d); heads large and conspicuous with 40 to 80 florets; phyllaries relatively large, often tightly overlapping.

Geographical distribution: southern Brazil south to Argentina.

Chromosome number: $n = 17$.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia argentea Less., BRAZIL,*Loëfgrun 16103* (NY). **V. argyrophylla** Less., BRAZIL: Minas Gerais, *Jones 22665* (GA). **V. asteriflora** Mart., BRAZIL: Paraná, *Hoehne 23391* (NY). **V. buddleiaefolia** Mart. ex DC., BRAZIL: Goiás, *Irwin, et al. 25019* (NY). **V. farinosa** Baker in Mart., BRAZIL: Minas Gerais, *Irwin, et al. 23247* (NY). **V. flavescens** Glaziou, BRAZIL: Goiás, *Anderson 10287* (NY). **V. floccosa** Gardn., BRAZIL: Goiás, *Anderson 10117* (NY). **V. lorentzii** Hieron., ARGENTINA: Federación, *Pedersen 4720* (NY). **V. mollissima** D. Don ex Hook. & Arn., PARAGUAY, *Hassler 9227a* (NY). **V. monocephala** Gardn., BRAZIL: Goiás, *Irwin, et al. 24711* (NY). **V. secunda** Sch.-Bip. ex Baker in Mart., BRAZIL: Distrito Federal, *Irwin, et al. 15459* (NY). **V. venosissima** Sch.-Bip. ex Baker in Mart., BRAZIL: Distrito Federal, *Irwin, et al. 15642* (NY). **V. verbascifolia** Less., BRAZIL: Minas Gerais, *Irwin, et al. 19668* (NY). **V. warmingiana** Baker in Mart., BRAZIL: Minas Gerais, *Irwin, et al. 25490* (NY).

Series **Subulatae** S. B. Jones, *ser. nov.*

Herbae annuae vel perennes; caules diffusi vel infirme ramosi inflorescentiae corymboso-paniculatae vel diminutae; capitula pusilla, 10–20 flosculis; phyllaria lanceolata. TYPE SPECIES: *Vernonia subulata* Baker.

Annuals or herbaceous perennials, diffuse or weakly branched; leaves relatively small, linear-lanceolate to elliptic-lanceolate; inflorescences corymbose-paniculate to reduced and sparingly branched (see Figs. 1b & 3a); heads relatively small with 10–20 florets; phyllaries narrowly lanceolate.

Geographical distribution: southern Brazil. A rather well marked series.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia holosericea Mart. ex DC., BRAZIL: Goiás, *Anderson 10284* (NY). **V. pungens** Gardn., BRAZIL: Distrito Federal, *Santos 11353* (NY). **V. schwenkiaefolia** Mart. ex DC., BRAZIL: Goiás, *Anderson 10425* (NY). **V. stricta** Gardn. in Hook., BRAZIL, *Warming 1863-65* (NY). **V. subulata** Baker, BRAZIL: Minas Gerais, *Irwin, et al. 27943* (NY). **V. virgulata** Mart. ex. DC., BRAZIL: Distrito Federal, *Irwin & Soderstrom 6097* (NY).

Subsection **Scorpioides** Ekman. Ark. Bot. **13**(15): 86. 1914. TYPE SPECIES: *Vernonia scorpioides* (Lam.) Pers.

Inflorescences cymose-scorpioid; heads sessile or nearly so, with or without bracteal leaves.

Geographical distribution: Mexico, Central America and the West Indies south into Argentina.

Chromosome numbers: based on $n = 17$.

Series **Scorpioides** S. B. Jones *ser. nov.*

Frutices vel parvae arbores; inflorescentiae cymoso-scorpioideae; capitula parva, 10–20 flosculis sessilibus, bracteis foliaceis nullis. TYPE SPECIES: *Vernonia scorpioides* (Lam.) Pers.

Shrubs to small trees; inflorescences conspicuously cymose-scorpioid (see Figs. 2a, 2b, & 2c); heads small, sessile or nearly so, crowded on the inflorescence branches, bracteal leaves absent, with ca. 10–20 florets.

Geographical distribution: From Mexico and the West Indies south into Argentina.

Pollen types: A & D. Pollen grains were examined from the following specimens:

(TYPE A) **Vernonia cainarachensis** Hieron., PERU: Loreto, *Hutchinson, et. al. 6043* (MO). **V. diffusa** Less., BRAZIL: *Belém 1881* (NY). **V. ignobilis** Less., BRAZIL: Minas Gerais, *Gardner 4766* (NY). **V. megaphylla** Hieron., PERU: San Martín, *Belshaw 3423* (NY). **V. scorpioides** (Lam.) Pers., PERU: La Libertad, *Sagástegui & Suarez 2636* (GA).

(TYPE D) **Vernonia brachiata** Benth., COSTA RICA: San Jóse, *Skutch 2525* (NY); morphologically very similar to **V. cainarachensis** which has type A pollen; perhaps best placed here for now.

Series **Macrolepidae** Benth. & Hook. Gen. Pl. **2:** 229. 1873. TYPE SPECIES: *Vernonia chamaepeuce* Sch.-Bip.

Series *Macrocephalae* Benth. & Hook. Gen. Pl. **2:** 229. 1873.
Subsection *Sellowianae* Cabrera, Darwiniana **6:** 306. 1944.
Subsection *Laurifoliae* Cabrera, Darwiniana **6:** 350. 1944.

Herbaceous perennials, sometimes slightly woody; inflorescences often greatly reduced with a few large heads, scorpioid-cymose to spike-like, or sometimes paniculate to scorpioid-cymose with many relatively large heads (see Figs. 1f, 2b, 2d, 2g & 3a); heads large with 40 to 80 florets; phyllaries various, sometimes highly developed or modified.

Geographical distribution: Centered mainly in southern Brazil and extending south into Argentina.

Chromosome number: n = 17.

Pollen type: A. Pollen grains were examined from the following specimens:

Vernonia arachniolepsis Ekman & Dusén ex Malme, BRAZIL: Rio Grande do Sul, *Rambos 51790* (NY). **V. bardanoides** Less., BRAZIL: Distrito Federal, *Irwin, et al. 13110* (NY). **V. carduoides** Baker ex Mart., BRAZIL: Goiás, *Irwin, et al. 14308* (NY). **V. chamaepeuces** Sch.-Bip. ex Baker in Mart., BRAZIL: Goiás, *Irwin, et al. 1674a* (NY). **V. eriolepsis** Gardn., BRAZIL: Paraná, *Hatschbach & de Haas 14523* (NY). **V. ixiamesis** Rusby, BOLIVIA, *Gardenas 2017* (NY). **V. lacunosa** Mart., BRAZIL: Minas Gerais, *Irwin, et al. 24693* (NY). **V. lappoides** Baker in Mart., BRAZIL: Goiás, *Irwin, et al. 13745* (NY). **V. laurifolia** DC., BOLIVIA, *Rusby 1617* (NY). **V. macrophylla** Less., BRAZIL: Minas Gerais, *Barreto 1461* (NY). **V. mansoana** Baker, BRAZIL: Mato Grosso, *Irwin, et al. 16542* (NY). **V. niederleinii** Hieron., BRAZIL: Paraná, *Hatschbach 21585* (NY). **V. onopordoides** Baker in Mart., BRAZIL: Goiás, *Irwin, et al. 13210* (NY). **V. pulverulenta** Baker in Mart., BRAZIL: Mato Grosso, *Ratter, et al. 1528* (NY). **V. radula** Mart. ex DC., BRAZIL: Minas Gerais, *Claussen 1804* (NY). **V. riedelii** Sch.-Bip. ex Baker in Mart., BRAZIL, *Pohl s.n. 1950* (NY). **V. sellowii** Less., PARAGUAY, *Hassler 9910* (NY). **V. westermanii** Ekman, BRAZIL: Paraná, *Dusén 16400* (NY). **V. zuccariniana** Mart. ex DC., BRAZIL: Mato Grosso, *Irwin, et al. 17315* (NY).

Series **Remotiflorae** (Cabrera) S. B. Jones, *stat. nov.*

Subsection *Remotiflorae* Cabrera, Darwiniana **6:** 311. 1944. TYPE SPECIES: *Vernonia remotiflora* Rich.

Herbaceous perennials, sometimes slightly woody at the base; inflorescences cymose-scorpioid, with conspicuous foliaceous bracts (see Figs. 1e, 2e, 2f, 2g, & 3d); heads sessile or short-pedicellate, variously arranged on the branches.

Geographical distribution: Southern Brazil south into Argentina.

Chromosome numbers: n = 17, 34, 51, 68.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia ammophila Gardn., BRAZIL: Goiás, *Irwin, et al. 31800* (NY). **V. brevipetiolata** Sch.-Bip. ex Mart., BRAZIL, *Hoehne 19101* (NY). **V. cordigera** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 28283* (NY). **V. coriacea** Less., BRAZIL: Minas Gerais, *Irwin, et al. 27494* (NY). **V. cuiabensis** Baker in Mart., BRAZIL: Mato Grosso, *Irwin, et al. 16013* (NY). **V. dorsiventralis** Chod., PARAGUAY, *Hassler 3127* (NY). **V. elegans** Gardn., BRAZIL: Goiás, *Irwin, et al. 15201* (NY). **V. glabrata** Less., PARAGUAY, *Hassler 8117a* (NY). **V. hoveaefolia** Gardn., BRAZIL, *Gardner 3792* (NY). **V. laevigata** Mart., BRAZIL: Distrito Federal, *Irwin, et al. 11211* (NY). **V. ligulaefolia** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 28162* (NY). **V. linearis** Spreng., BRAZIL: Distrito Federal, *Irwin, et al. 26566* (NY). **V. obscura** Less., BRAZIL, *Hoehne 16089* (NY). **V.**

obtusata Less., BRAZIL: Goiás, *Irwin, et al. 24246* (NY). **V. octandra** Sch.-Bip., BRAZIL, *Pohl 1588* (NY). **V. remotiflora** Rich., SURINAME, *Maguire, et al. 54252* (NY). **V. rubricaulis** H. & B., ARGENTINA, *Ochoa 1969-58* (GA). **V. rugulosa** Sch.-Bip. ex Baker in Mart., BRAZIL, *Pohl 2909* (NY). **V. saltensis** Hieron., ARGENTINA: Trancas, *Schreiter 7419* (NY). **V. squarrosa** Less., BRAZIL: São Paulo, *Mimura 286* (NY). **V. syncephala** Sch.-Bip., BRAZIL, *Hoehne 155* (NY). **V. tarijensis** Hieron., ARGENTINA: Orán, *Cabrera 4154* (NY). **V. valenzuelae** Chod., ARGENTINA, *Rodriguey 15* (NY). **V. veniea** Rich., BRAZIL, *Martus 238* (NY).

Series **Flexuosae** (Cabrera) S. B. Jones, *stat. nov.*

Subsection *Flexuosae* Cabrera, Darwiniana **6:** 329. 1944. TYPE SPECIES: *Vernonia cognata* Less.

Subsection *Echioides* Cabrera, Darwiniana **6:** 327. 1944.

Herbaceous perennials, stems usually unbranched to the inflorescence; inflorescences often reduced, bracteal leaves reduced or absent, heads arranged along the branches of the inflorescence (see Figures 2d, 2g, 3a, & 3b); heads numerous to more typically few, sessile; phyllaries lanceolate, apex acuminate-aristate; pappus usually white, sometimes straw-colored; achenes pubescent.

Geographical distribution: Southern Brazil south into Argentina.

Chromosome numbers: n = 17, 34.

Pollen types: C, D. Pollen grains were examined from the following specimens:

(TYPE C) **Vernonia buchtieni** Gleason, BOLIVIA: Santa Cruz, *Steinbach 5286* (NY). **V. cognata** Less., BRAZIL: São Paulo, *Jones 22625* (GA). **V. desertorum** Mart. ex DC., BRAZIL: Mato Grosso, *Argent 6729* (NY). **V. flexuosa** Sims, URUGUAY: Santa Clara, *Gallinal, et al. 2914* (NY). **V. herbacea** (Vell.) Rusby, BRAZIL: Distrito Federal, *Sucre 756* (NY). **V. lepidifera** Chod., PARAGUAY, *Hassler 8241* (NY). **V. obovata** Less., BRAZIL, *Gardner 3255* (NY). **V. platensis** Less., PARAGUAY, *Archer 4750* (NY). **V. propingua** Hieron., PARAGUAY, *Hassler 8637* (NY). **V. sceptrum** Chod., PARAGUAY, *Hassler 8095* (NY). **V. senencionea** Chod., PARAGUAY, *Hassler 8316* (NY). **V. simplex** Less., BRAZIL: Mato Grosso, *Harley & Souza 10163* (NY). **V. tricholepsis** DC., PARAGUAY, *Hassler 5651* (NY).

(TYPE D) **Vernonia barbata** Less., BRAZIL, *Pohl 3025* (NY). **V. dura** Mart., BRAZIL: Mato Grosso, *Irwin, et al. 17436* (NY). **V. oxylepsis** Sch.-Bip. ex Baker in Mart., BRAZIL: São Paulo, *Leuderwaldt 16228* (NY).

Series **Aureae** S. B. Jones, *ser. nov.*

Herbae perennes vel interdum suffrutices; inflorescentiae scorpioideo-paniculatae interdum multum diminutae; bracteae foliaceae plerumque praesentes sed saepe multum diminutae; capitula

10–25 flosculis; phyllaria acuta usque longiacuminata. TYPE SPECIES: *Vernonia aurea* Mart. ex DC.

Herbaceous perennials, sometimes becoming shrubby; inflorescences scorpioid-paniculate, sometimes greatly reduced, bracteal leaves usually present but often greatly reduced (see Fig. 2g); heads medium sized with 10–25 florets; phyllaries acute to long-acuminate.

Geographical distribution: Southern Brazil. Not an especially well marked morphological series but many were also grouped together by Baker (Fl. Brasil **6**(2): 58. 1873).

Pollen type: D. Pollen grains were examined from the following specimens:

Vernonia arenaria Mart. ex DC., BRAZIL: Amazônas, *Prance, et al. 2700* (NY). **V. aurea** Mart. ex DC., BRAZIL: Bahia, *Irwin, et al. 14595* (NY). **V. eremophila** Mart. ex DC., BRAZIL: Distrito Federal, *Irwin & Soderstrom 5939* (NY). **V. fruticulosa** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 27705* (NY). **V. grisea** Baker, BRAZIL: Amazônas, *Pires, et al. 5322* (NY). **V. hirtiflora** Sch.-Bip. ex Baker in Mart., BRAZIL, *Pohl 3282* (NY). **V. subcordata** Gardn. ex Hook., BRAZIL: Minas Gerais, *Irwin, et al. 28384* (NY).

Series **Canescentes** S. B. Jones, *ser. nov.*

Suffrutices vel raro herbae perennes; folia subtus pilosa; inflorescentiae scorpioideae, bracteis foliaceis grandis vel reductis; capitula mediocria 10–12 flosculis; phyllaria acuta. TYPE SPECIES: *Vernonia canescens* H.B.K.

Shrubs or very rarely herbaceous perennials; leaves softly pilose beneath; inflorescences scorpioid (see Figs. 1f, 2a, 2b, 2f, & 2g); heads medium sized, with 10–20 florets; bracteal leaves large or reduced.

Geographical distribution: Southern Mexico and Central America across northern South America and south along the Andes into Brazil. This series appears closely related to series *Scorpioides*.

Chemistry: glaucolide-B.

Chromosome number: $n = 17$. Pollen types: B & C. Pollen grains were examined from the following specimens:

(TYPE B) **Vernonia costata** Rusby, PERU: Cuzco, *Vargas 14495* (US). **V. coulonii** Sch.-Bip. ex Baker in Mart., BRAZIL: Distrito Federal, *Irwin & Soderstrom 5204* (NY). **V. deflexa** Rusby, BOLIVIA, *Williams 1444* (NY). **V. densipaniculata** Rusby, BOLIVIA, *Buchtien 1533* (NY). **V. geminata** Less., BRAZIL, *Gardner 790* (NY). **V. helvphila** Mart., BRAZIL, *Hoehne 16068* (NY). **V. micrantha** H.B.K., COLOMBIA, *Sneidern 1559* (NY).

(TYPE C) **Vernonia araguensis** Badillo, VENEZUELA: Aragua, *Steyermark & Agostini 24* (NY). **V. araripensis** Gardn., GUYANA, *coll. ign. WB235* (NY). **V. canescens** H.B.K., PANAMA: Canal Zone, *Dressler 3425* (GA). **V. corrientensis** Ekman, PARAGUAY, *Hassler 2850* (NY). **V. cotoneaster** Less., VENEZUELA: Bolívar, *Wurdack 34412* (NY). **V. glandulosa** Badillo, VENEZUELA, *Foldats 2874* (NY). **V. gracilis** H.B.K., COLOMBIA: Atlántico, *Dugand & Jaramillo 2719* (NY). **V. lilacina** Mart. ex DC., BRAZIL: Minas Gerais, *Irwin, et al. 20649* (NY). **V. miersiana** Gardn., BRAZIL: Mato Grosso, *Irwin, et al. 16983* (NY). **V. mollis** H.B.K., GUATEMALA: Alta Verapaz, *Steyermark 44039* (NY). **V. muricata** DC., BRAZIL: Santa Catarina, *Reitz & Klein 6521* (NY). **V. pari** Badillo, GUYANA, *Tate 306* (NY). **V. phyllostachya** Gleason, MÉXICO, *Arsène 1913* (NY). **V. pseudomollis** Gleason, PERU: Cuzco, *Vargas 412* (F). **V. salzmanni** DC., PERU: Santa Ana, *Cook & Gilbert 1466* (US). **V. tricephala** Gardn., TRINIDAD, *Britton & Broadway 2421* (NY). **V. virens** Sch.-Bip. ex Baker in Mart., BRAZIL: Mato Grosso, *Hunt & Ramos 5977* (NY).

Series **Foliatae** (Benth. & Hook.) S. B. Jones, *stat. nov.*

Subseries *Foliatae* (Benth. & Hook.) Gen. Pl. **2:** 229. 1873. TYPE SPECIES: *Vernonia agyropappa* Buek.

Shrubs, often scandent; leaves tending to be coriaceous, apex acute to long acuminate; inflorescences lax, of few to many spreading scorpioid-cymes (see Figures 2a, 2b, 2c, & 2e); heads may or may not be subtended by a bracteal leaf.

Geographical distribution: Mexico south through Central America into Peru.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia agyropappa Buek, COSTA RICA, *Lems 5050* (NY). **V. ehretiaefolia** Benth., VENEZUELA: Bolívar, *Maguire & Wurdack 33939-A* (NY). **V. lehmannii** Hieron., COLOMBIA: Antioquia, *Barkley & Gutiérrez V. 1413* (NY). **V. myriocephala** DC., PERU: Junin, *Killip & Smith 26099* (NY). **V. polypleura** Blake, MÉXICO: Chiapas, *Mutuda 2067* (NY). **V. schiedeana** Less., BRITISH HONDURAS: Belize, *Dwyer, et al. 180* (NY). **V. seemanniana** Steetz in Seem., COSTA RICA: San José, *Skutch 4112* (NY). **V. tortuosa** (L.) Blake, MÉXICO: Veracruz, *Beaman 5623* (GA). **V. trilectorum** Gleason, COLOMBIA: Santander, *Killip & Smith 15374* (NY).

Series **Sagraeanae** (Ekman) S. B. Jones, *stat. nov.*

Subsection *Sagraeanae* Ekman. Ark. Bot. **13**(15): 11. 1914. TYPE SPECIES: *Vernonia sagraeana* DC.

Small shrubs; leaves membranaceous; inflorescences cymose-scorpioid, cymes elongate, with large bracteal leaves (see Figs. 1f, 2b, & 2g); heads rather large; involucres campanulate; achenes glabrous.

Geographical distribution: West Indies. A very natural series.

Pollen type: B. Pollen grains were examined from the following specimens:

Vernonia aronifolia Gleason, CUBA, *Shafer 13514* (F). **V. ekmanii** Urban, HAITI, *Ekman 5351* (US). **V. purpurata** Gleason, CUBA, *Ekman 9375* (NY). **V. sagraeana** DC., CUBA, *Ekman 10327* (GH). **V. sprengeliana** Sch.-Bip., HISPANIOLA, *Ekman 11618* (US). **V. viminalis** Gleason, CUBA, *Wright 285* (US). **V. wrightii** Sch.-Bip., CUBA, *Ekman 3370* (US).

Series **Arborescentes** (Ekman) S. B. Jones, *stat. nov.*

Subsection *Arborescentes* Ekman. Ark. Bot. **13**(15): 27. 1914. TYPE SPECIES: *Vernonia arborescens* (L.) Sw.

Mostly small shrubs; inflorescences cymose-scorpioid, cymes elongate or greatly reduced (see Figs. 1e, 2f, & 2g); foliaceous bracteal leaves.

Geographical distribution: West Indies. Appears closely related to other series of subsection *Scorpioides* from South America.

Chromosome number: $n = 17$.

Pollen types: B & C with a few species having a grain intermediate between B. and C. Pollen grains were examined from the following specimens:

(TYPE C) **Vernonia acuminata** Less., JAMAICA, *Howard & Proctor 13371* (GA). **V. albicaulis** Pers., ST. KITTS, *Proctor 18501* (US). **V. arborescens** (L.) Sw., ST. VINCENT, *Smith & Smith 359* (GH). **V. arbuscula** Less., BAHAMAS, *Wight 70* (F). **V. commutata** Ekman, CUBA, *Clemente 668* (NY). **V. complicata** Wright ex Griseb., CUBA, *Britton 2225* (F). **V. desiliens** Gleason, CUBA, *Alain & Figuiera 4792* (NY). **V. fructicosa** (L.) Sw., HISPANIOLA, *Ekman 2251a* (NY). **V. harrisii** S. Moore, JAMAICA, *Proctor 2168* (TEX). **V. leptoclada** Sch.-Bip., CUBA, *Shafer 8408* (F). **V. orbicularis** Alain, CUBA, *Webster 3873* (GH). **V. pineticola** Gleason, CUBA, *Ekman 10286* (GH). **V. segregata** Gleason, CUBA, *Acunae 12799* (US). **V. sericea** Rich., HISPANIOLA, *Leonard 8096* (US). **V. stenophylla** Less., CUBA, *Ekman 4050* (US). **V. urbaniana** Ekman ex Urban, CUBA, *Ekman 10083* (F). **V. verticillata** Proctor ex Adams, JAMAICA, *Keeley & Keeley 1250* (GA).

(TYPE B) **Vernonia borinquensis** Urban, PUERTO RICO, *Heller 4391* (F).

(TYPE B-C) **Vernonia pluvialis** Gleason, JAMAICA, *Maxon 9786* (NY). **V. trinitatis** Ekman, TRINIDAD, *Keeley & Keeley 1946* (GA).

Series **Pallescentes** (Ekman) S. B. Jones, *stat. nov.*

Subsection *Pallescentes* Ekman. Ark. Bot. **13**(15): 88. 1914. TYPE SPECIES: *Vernonia pallescens* Gleason.

Erect shrub; leaves membranaceous; inflorescences scorpioid-cymose, cymes elongate and sometimes dichotomously branched (see Fig. 2a); pappus bristles of outer series filiform and subequal with inner series.

Geographical distribution: St. Vincent in the West Indies.

Pollen type: C. Pollen grains were examined from the following specimen:

Vernonia pallescens Gleason, B.W.I.: St. Vincent, *Howard & Howard 18011* (GH).

ACKNOWLEDGEMENTS

My sincere thanks and appreciation go to Mr. Charles Jeffrey, Dr. Tod F. Stuessy, and Dr. Rogers McVaugh for their helpful suggestions during the course of the study. I am grateful to the herbaria cited herein for making the materials available for study. The technical assistance is acknowledged of: John Tanner, Bob Grese, Rick Gardini, Marcia Stefani, Oliver Ware, and Nancy Coile. The typescript was prepared by Katie Bishop and Carla Stewart.

The SEM was done at the University of Georgia Electron Microscopy Laboratory. The research was supported by grants from the National Science Foundation (DEB74-23127-A01).

LITERATURE CITED

BAKER, J. G. 1873. Compositae. I. Vernoniaceae. *In:* K. F. P. von. Martius, ed. Flora Brasiliensis **6**(2): 6 179.

BENTHAM, G. 1873. Notes on the classification, history, and geographical distribution of Compositae. J. Linnean Soc. **13:** 335 577.

______. & J. D. HOOKER. 1873. Vernonieae. Genera Plantarum **2:** 227 231.

CABRERA, A. L. 1944. Vernonieas Argentinas (Compositae). Darwiniana **6:** 19 379.

CANDOLLE, A. P. DE. 1836. Prodromus **5:** 15 66.

CASSINI, H. 1817. Apercu des genres nouveaux formés par M. Henri Cassini dans la famille des Synanthérées. Bull. Scient. Soc. Phil. **4:** 66.

______. 1819. Sur la famille des Synathérées contenant les caractéres des tribus. J. Phys. Chim. Hist. Nat. Arts **88:** 190 204 (cf. pp. 203 204).

EKMAN, E. L. 1914. West Indian Vernonieae. Ark. Bot. **13**(15): 1 106.

ERDTMAN, G. 1966. Pollen morphology and plant taxonomy. Angiosperms. Hafner, New York.

GLEASON, H. A. 1906. A revision of the North American Vernonieae. Bull. New York Bot. Gard. **4:** 144 243.

______. 1922. Vernonieae. N. Am. Flora **33:** 52 95.

______. 1923. Evolution and geographical distribution of the genus *Vernonia* in North America. Amer. J. Bot. **10:** 187 202.

HOFFMAN, O. 1894. Vernonieae. *In:* A. Engler & K. Prantl., eds. Die naturlichen Pflanzenfamilien **4**(5): 120 129.

JONES, S. B. 1970. Scanning electron microscopy of pollen as an aid to the systematics of *Vernonia*. Bull. Torrey Bot. Club **97:** 325 335.

———. 1977. Vernonieae Systematic Review. *In:* V. H. Heywood, et al. (eds.). The Biology and Chemistry of the Compositae. Academic Press. London.

KEELEY, S. C. & S. B. JONES. 1977. Taxonomic implications of external pollen morphology to *Vernonia* (Compositae) in the West Indies. Amer. J. Bot. **64:** 576 584.

KINGHAM, D. L. 1976. A study of the pollen morphology of tropical African and certain other Vernonieae (Compositae). Kew Bull. **31:** 9 26.

LESSING, C. F. 1829. De Synanthereis Herbarii regii berolinensis dissertationes, I. Vernonieae, Linnaea **4:** 240 356.

———. 1831a. De synthereis dissertatio quarta. Linnaea **4:** 240 288; 295 339.

———. 1831b. De Synanthereis Herbarii regii berolinensis dissertationes, IV. Vernoniearum mantissa. Linnaea **6:** 624 721.

MABRY, T. J., Z. ABDEL-BASET, W. G. PADOLINA, & S. B. JONES. 1975. Systematic implications of flavonoids and sesquiterpene lactones in species of *Vernonia* Biochem. Syst. Ecol. **2:** 185 192.

SCHULTZ-BIPONTINUS, C. H. 1861. Cassiniaceae uniflorae, oder Verzeichniss der Cassiniaceen mit 1-bluthigen kopfchen. Jber. Pollichia **18/19:** 157 190.

———. 1863. *Lychnophora* Martius und einige benachbarte Gattungen. Jber. Pollichia **20/21:** 321 439.

SMITH, C. E. 1969. Pollen characteristics of African species of *Vernonia*. J. Arnold Arbor. **50:** 469 477.

———. 1971. Observations on Stengelioid species of *Vernonia*. USDA Agr. Handbook No. **396.** U. S. Gov. Printing Office, Washington, D. C.

WODEHOUSE, R. P. 1928. The phylogenetic value of pollen grain characters. Ann. Bot. **42:** 891 934.

DEPARTMENT OF BOTANY
THE UNIVERSITY OF GEORGIA
ATHENS, GA 30602

SYSTEMATICS OF ZALUZANIA (ASTERACEAE:HELIANTHEAE)

JOHN S. OLSEN

Zaluzania is a small genus of herbaceous perennials and woody shrubs confined to Mexico, with one taxon disjunct, known only from Ecuador. Members of the genus occupy habitats ranging from 1700 meters altitude in the xeric north central plains to 4000 meters in the mesic mountainous regions of Hidalgo, Mexico, and of Ecuador (Figures 1 & 2). There are no common names for the genus, although two individual taxa have local names; *Z. triloba* is commonly called "hierba amargosa" and *Z. augusta* is called "caxtidani", "cenicillo", "hierba blanca", or "limpia tunas" (Standley, 1926). The genus is usually weedy, with negligible commercial value; however, *Z. triloba* has been shown to produce an antitumor sesquiterpene lactone, zaluzanin C (Jolad et al., 1974).

The present study was undertaken to clarify the taxonomic and phylogenetic relationships among the taxa. Data from cytology, flavonoid chemistry, palynology, geography, and ecology were utilized toward this goal.

GEOGRAPHY AND ECOLOGY

The range of the genus *Zaluzania* covers all of central Mexico, south into Oaxaca and Guerrero, with one taxon in Ecuador. Rzedowski (1973) includes *Zaluzania* in his list of genera primarily concentrated in the dry regions of Mexico, but which are not restricted by the aridity limits. Also included in the list are other Helianthoid genera, *Flourensia, Parthenium,* and *Encelia.* The range of *Zaluzania* is bounded on the west by the Sierra Madre Occidental and stretches eastward into the state of Vera Cruz.

Zaluzania is primarily a summer or fall blooming genus, mostly confined to middle altitudes (1650–2700 meters), commonly occurring in scrub vegetation. Only *Z. megacephala* var. *megacephala* and *Z. sodiroi* occur above 3200 meters. Two of the taxa are wholly xerophytic, the herbaceous *Z. megacephala* var. *coahuilensis* and the shrubby *Z. mollissima,* both being confined to the Chihuahuan Desert flora. Several other species frequent the desert regions, but other populations of the same species are adapted to the more mesic

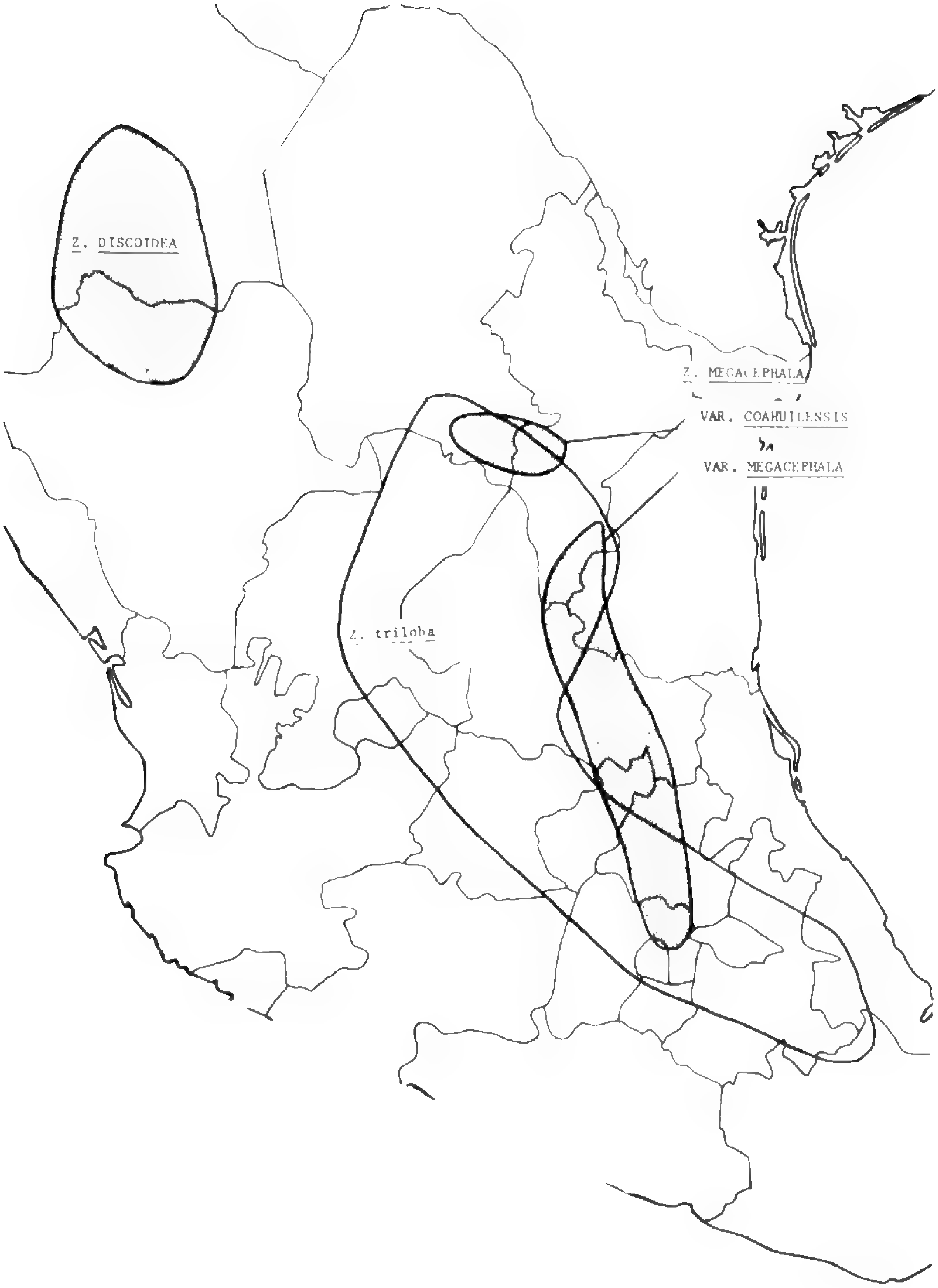


Figure 1. Geographic distribution of the herbaceous members of *Zaluzania*.

central and western areas. *Zaluzania triloba* and *Z. augusta* are typical of this type. Both extend into the Chihuahuan Desert on the north, but also occur in the Valley of Mexico on the south and into Puebla and Vera Cruz on the east. *Zaluzania triloba* is always found growing in the shade of shrubs or cacti in the desert areas. In central Mexico (Guanajuato), *Z. augusta* var. *augusta* often becomes an ecological dominant, at least in terms of biomass. It is frequently seen covering rocky limestone hills, and where it occurs in the Chihuahuan Desert, it is confined to the mountains, where it grows associated with *Agave*. *Zaluzania discoidea* and *Z. pringlei* occupy mountainous regions in more mesic areas. *Zaluzania pringlei* occurs on limestone hills in Morelos and Guerrero. *Zaluzania discoidea* occurs in Durango and adjacent areas, being especially prominent in areas disturbed by farming. The remaining taxa, *Z. subcordata* and *Z. montagnifolia,* occur in the limestone hills of Puebla, Vera Cruz and Oaxaca.

No pollinators have been identified for any *Zaluzania* taxon, but both beetles and bees have been observed on the flowers. Large grasshoppers have also been observed feeding on the leaves of *Z. augusta* and *Z. montagnifolia.*

TAXONOMIC HISTORY

The genus *Zaluzania* (Asteraceae:Heliantheae) was established in 1807 by Persoon, based on *Anthemis triloba* Ort., a plant widespread in Mexico. In 1816, the genus *Ferdinanda* Lag. was described, including two species, one of which was *F. augusta,* now *Zaluzania augusta.* Kunth described the genus *Chrysophania* in 1832 with *C. fastigiata* as the type species. Since *C. fastigiata* is synonymous with *Z. augusta,* the genus *Chrysophania* passes into synonymy. Robinson and Greenman (1899) retained *Ferdinanda* as a subgenus of *Zaluzania* as did Sharp (1935), the latter relegating 12 taxa to it.

The genus *Hybridella,* based on *Anthemis globosa* Ort., was described by Cassini in 1821. This was treated as a subgenus of *Zaluzania* by Robinson and Greenman (1899) and by Sharp (1935) who included within it two species and one variety.

Zaluzania was treated by Schultz-Bipontinus in 1861 and 1864. In his final assessment of the genus, he included 12 species, six of which

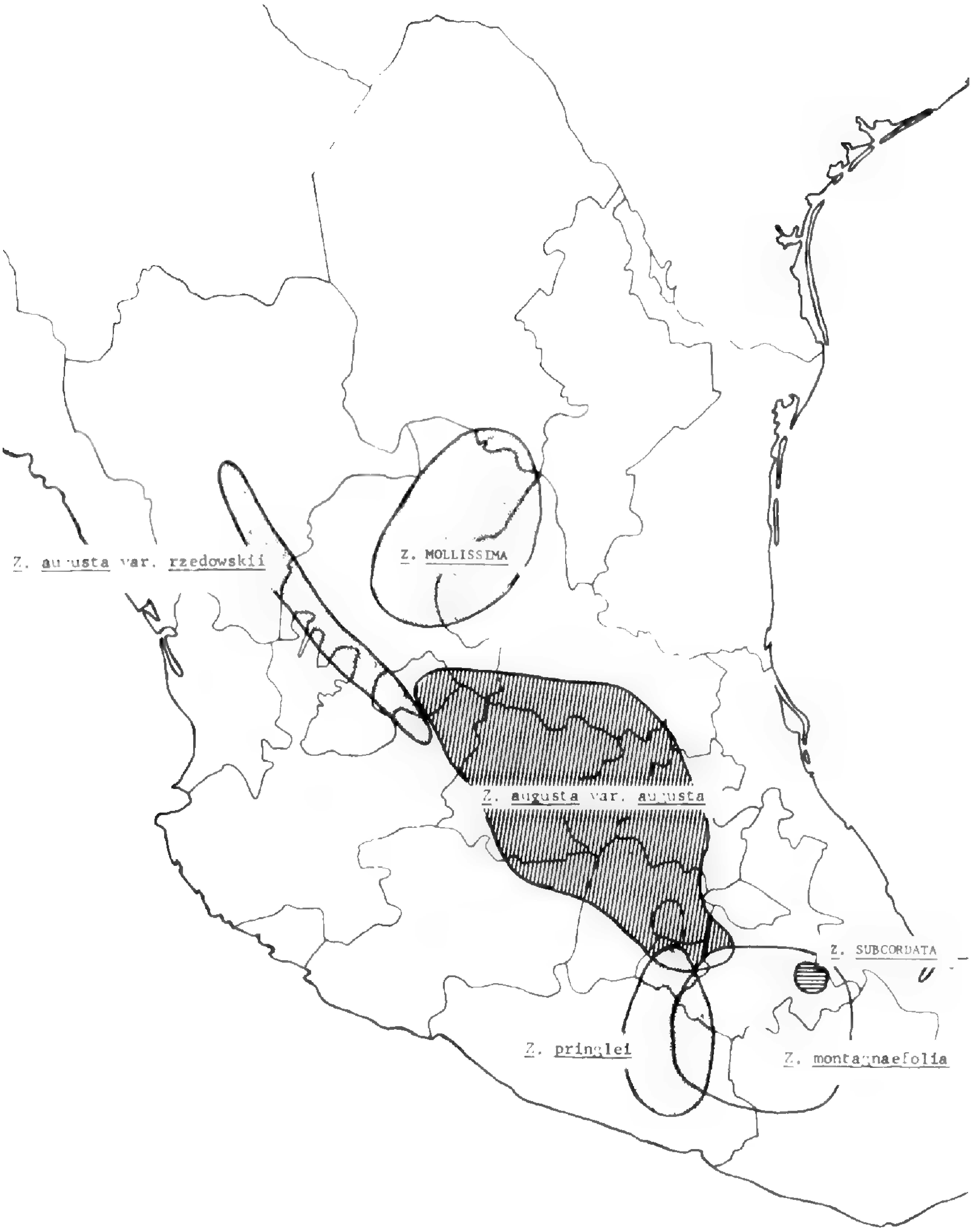


Figure 2. Geographic distribution of the shrubby members of *Zaluzania*, exclusive of *Z. sodiroi*, which is restricted to Ecuador.

are now retained in *Zaluzania*, three referred to *Viguiera*, two to *Hybridella*, and one to *Calea*. Robinson and Greenman published a revision of *Zaluzania* in 1899 in which they recognized 12 species and one variety. Hieronymus (1900) described three new *Zaluzania* taxa from Ecuador, thus extending the range of *Zaluzania* considerably. Sharp (1935) reduced these new taxa to one species, *Z. sodiroi,* and recognized *Zaluzania* as consisting of 14 species and one variety.

More recently, Rzedowski (1968) found *Zaluzania robinsonii* Sharp to be synonymous with the earlier *Aiolotheca parthenioides* DC., thereby making necessary the combination *Z. parthenioides.* McVaugh (1972) added an additional taxon by describing *Z. augusta* var. *rzedowskii. Monactis subdeltoidea,* described by Robinson in 1911 from Ecuadorian material, has been shown to be synonymous with *Z. sodiroi* (Robinson, 1976).

Zaluzania, as recognized in the present treatment, consists of 11 taxa (nine species and two varieties). Table 1 presents a comparison of the present arrangement with the arrangements of Robinson and Greenman (1899) and Sharp (1935). The present system differs from previous ones in several ways. Subgenus *Hybridella,* with its three taxa, has been removed from *Zaluzania* and resurrected to generic rank (Olsen, 1977a) based on differences in habit, morphology and cytology. *Zaluzania grayana,* because of its sterile ray florets and chromosome number of $n = 17$, has been removed from the genus and positioned in the series *Pinnatilobatae* of *Viguiera;* however, it is seemingly also closely related to *Heliomeris* (sensu Yates, 1967) and additional study might suggest a position in this taxon. Finally, *Z. parthenioides* is considered to be conspecific with *Z. triloba.*

GENERIC RELATIONSHIPS

Zaluzania is a homogeneous assemblage of closely knit taxa. Its recognition as a valid genus has not been questioned since its inception. The major taxonomic controversy has been its subtribal position within the tribe Heliantheae.

Persoon (1807) originally placed *Zaluzania* near *Pascalia* and *Spilanthes* (sect. *Acmella*) in the Verbesininae. Cassini (1821) believed that it was misplaced here and put it in his Heliantheae — Milleriees with the genera *Eleutheranthera, Sigesbeckia, Jaegeria, Guizotia,* and *Hybridella.* Of the five latter taxa, *Hybridella* has been moved to a position near *Heliomeris* of the subtribe Helianthinae (Olsen, 1977a); *Eleutheranthera, Sigesbeckia,* and *Jaegeria* were placed in the Verbesininae by Hoffman (1894). Torres (1968) pointed out the close relationship between *Jaegeria* and *Sabazia* of

Table 1
Comparison of Recent Taxonomic Dispositions of Zaluzania Taxa

ROBINSON AND GREENMAN (1899)	SHARP (1935)	OLSEN (1977)
ZALUZANIA	ZALUZANIA	ZALUZANIA
subg. **Ferdinanda**	subg. **Ferdinanda**	
Z. triloba	*Z. triloba*	*Z. triloba* (incl. *Z. robinsonii*)
	Z. robinsonii	
Z. grayana	*Z. grayana*	
Z. coulteri	*Z. cinerascens* (=*coulteri*)	*Z. megacephala* var. *megacephala*
Z. megacephala	*Z. megacephala*	var. *coahuilensis*
Z. discoidea	*Z. discoidea*	*Z. discoidea*
Z. augusta	*Z. augusta*	*Z. augusta* var. *augusta*
		var. *rzedowskii*
Z. mollissima	*Z. mollissima*	*Z. mollissima*
Z. asperrima	*Z. montagnifolia*	*Z. montagnifolia*
var. *montagnifolia*		
	Z. pringlei	*Z. pringlei*
	Z. sodiroi	*Z. sodiroi*
	Z. subcordata	*Z. subcordata*
Z. resinosa		
subg. **Hybridella**	subg. **Hybridella**	HYBRIDELLA (as genus)
Z. globosa	*Z. globosa*	*H. globosa* var. *globosa*
Z. myriophylla	var. *myriophylla*	var. *myriophylla*
Z. anthemidifolia	*Z. anthemidifolia*	*H. anthemidifolia*
	GREENMANIELLA	GREENMANIELLA
	G. resinosa	*G. resinosa*
		Viguiera triloba (=*Z. grayana*)

the Galinsoginae. The position of *Guizotia* is more controversial, its placement being problematical (Baagøe, 1974; Turner & Powell, 1978); in my opinion it is not related to *Zaluzania*.

Bentham (1873) placed *Zaluzania* in the Verbesininae, suggesting that its closest affinities are to the genera *Sabazia* and *Gymnolomia*. As indicated above, *Sabazia* and *Jaegeria* are clearly related. *Sabazia* presumably belongs to the Galinsoginae (Longpre, 1970; Urbatsch & Turner, 1975), along with *Tridax* (Powell, 1965) which would indicate ties to the Galinsoginae for *Zaluzania*.

The situation for *Gymnolomia* is much less clear. Blake (1918), in his monograph of the genus *Viguiera*, reduced *Gymnolomia* from the 30-odd species known to Bentham to only four; he related the latter to *Aspilia* in the Verbesininae. The transferred epappose taxa were distributed among *Viguiera*, *Tithonia* and *Hymenostephium*.

Robinson and Greenman (1899) made no statements about the generic relationships of *Zaluzania*, but Sharp (1935) placed *Zaluzania* in the Verbesininae noting that "The relationships of *Zaluzania* are with the *Viguiera* complex, but its exact ancestral stock is somewhat in question. Evidence at present points to affinities with a *Viguiera-Gymnolomia* type of ancestor." In short, *Zaluzania* has been related to two quite different subtribes, the Galinsoginae and the Verbesininae.

Stuessy (1978) made some major rearrangements in the subtribal taxonomy of the Heliantheae. He recognized the Verbesininae as distinct from the Helianthinae (containing *Viguiera*) and also erected several new subtribes. *Zaluzania* is placed in one of his new subtribes, the Neurolaeninae, a segregate of the Galinsoginae. Along with *Zaluzania*, the subtribe includes *Bebbia*, *Clappia*, *Dyscritothamnus*, *Greenmaniella*, *Pseudoclappia*, *Schistocarpha*, *Varilla*, and *Neurolaena* itself. This assemblage is characterized by alternate leaves, phyllaries of unequal length (increasing inwards), lanceolate paleae, and setose pappus. Turner and Powell (1978) would fragment Steussy's Neurolaeninae into two subtribes, the Neurolaeninae and the Varillinae; including in the latter, *Clappia*, *Pseudoclappia*, *Varilla*, and *Dyscritothamnus*. To this may be added *Bebbia* (Whalen, 1977).

Stuessy referred to the "obvious generic ties . . ." which "exist between *Calea* of the Galinsoginae and *Zaluzania* . . ." of the Neurolaeninae, but felt that inclusion of *Zaluzania* within the

Galinsoginae would result in the expansion of this subtribe beyond the useful limits of, at least his, subtribal concept.

Zaluzania, by my own interpretation, does not fit at all well with the other genera of the Neurolaeninae as circumscribed by Stuessy. It typically is epappose, the phyllaries are nearly equal or decrease in length inwardly and the paleae are not lanceolate, but oblanceolate and trifid. If the Neurolaeninae are ruled out as close relatives, the position of *Zaluzania* is either in the Helianthinae (sensu Stuessy), where Sharp placed it near *Viguiera,* or in the Galinsoginae, where Stuessy placed it near *Calea* and Bentham near *Sabazia.* In my opinion, *Zaluzania* is best placed in the subtribe Helianthinae.

While most of the taxa in the subtribe Helianthinae have neuter ray florets, at least four (*Balsamorhiza, Chromolepis, Vigethia,* and *Wyethia*) have fertile rays (Stuessy, 1978), as does *Zaluzania.* The inflorescence of *Zaluzania* is somewhat more crowded than others in the Helianthinae, but otherwise it fits quite well. The alternate leaves (although occasionally opposite below in the shrubby taxa), black anthers, and lack of glandular pubescence on the corolla tubes clearly distinguish *Zaluzania* from the Galinsoginae.

Calea, with only about 15% of its 85 taxa counted, is multibasic with chromosome numbers of $n = 15, 16, 17, 18, 19,$ and 24 (Beaman & Turner, 1962; Dejong & Longpre, 1963; Keil & Stuessy, 1975; Powell & Cuatrecasas, 1970; Powell & King, 1969; Powell & Turner, 1963[1]; Solbrig et al., 1972; Turner, Ellison & King, 1961; Turner, Powell & King, 1962; Turner, Powell & Watson, 1973), which indicates probable ancestral base numbers of $x = 8$ and 9, with the others derived through aneuploidy. *Viguiera* has chromosome numbers of $n = 12, 17, 18,$ and 32 (Butterwick, 1975; Gupta, Agarwal, & Srivastava, 1972; Heiser, 1963a & b; Heiser & Smith, 1955; Jones, 1970; Powell & Sikes, 1970; Solbrig et al., 1972; Turner & Ellison, 1960; Turner & Flyr, 1966; Turner & King, 1964; Turner, Beaman & Rock, 1961; Turner, Powell & Cuatrecasas, 1967; Turner, Powell & Watson, 1973). Chromosome numbers on a base of $x = 18$ are known in *Viguiera* only in series *Dentatae.*

Chromatographic data indicate that of the various infrageneric taxa of *Viguiera,* the series *Grammatoglossae* shows the closest

---

[1] *C. urticifolia* is erroneously printed as $n = 9$ in the table from Powell and Turner, 1963. Examination of the voucher (*Johnston 4797,* LL) shows the actual number to be $n = 19$ with a camera lucida drawing appended to the voucher.

approach to *Zaluzania* in its flavonoid profiles. *Calea* taxa examined present entirely different profiles.

Morphologically, series *Grammatoglossae* differs from *Zaluzania* in having, generally, larger and fewer heads, the pales only rarely trifid, and the ray florets all sterile. Cytological knowledge of this 11-species series is limited to three species, all exhibiting $n = 17$. The geographic range of series *Grammatoglossae* overlaps that of *Zaluzania,* but also extends further west into Nayarit. Series *Grammatoglossae* shows a tendency for the tube of the disc corolla to become expanded to form a cap over the achene. This character has previously been considered one of the distinguishing characters of *Zaluzania* (Sharp, 1935). Its presence in series *Grammatoglossae,* while not supporting the distinction, is further indication of the relationship between the two groups.

In short, based on chromosomal, morphological, geographical and chemical data, I believe that *Zaluzania* is best positioned in the Helianthinae, where it is most closely related to *Viguiera.* I would place its connections with section *Chloracra,* possibly with series *Grammatoglossae.*

CYTOLOGICAL STUDIES

Prior to the onset of the present study, chromosome reports were available for only four species of *Zaluzania: Z. augusta* ($n = 18$; Turner & Flyr, 1966), *Z. megacephala* ($n = 16$; Turner, Beaman & Rock, 1961), *Z. montagnifolia* ($n = 18$; Powell & Turner, 1963), and *Z. triloba* ($n = 18$; Powell & Turner, 1963; Turner & Johnston, 1961). Since then, Keil and Stuessy (1975) have reported a count of $n = 17$ for *Z. grayana* (here transferred to *Viguiera*) and Strother (1976) has reported an additional count of $n = 18$ for *Z. triloba.* I have obtained counts of all of these taxa and first reports of five others (Table 2). Vouchers of all counts are deposited in the Lundell Herbarium of the University of Texas (LL).

Chromosome numbers have been determined for over 200 individuals from 60 populations. *Zaluzania* would appear to be monobasic ($x = 18$), with two stabilized polyploid taxa in the genus; however, the series of chromosome numbers present in *Zaluzania* ($n = 18$, 27, & 36) suggests that the ancestral base number for the genus was $x = 9$. This number is one of the presumed base numbers for the Heliantheae as a whole (Stuessy, 1978) and it is possible that *Zaluzania* arose from an $x = 9$ taxon with stabilization occurring at

Table 2

Chromosome numbers in Zaluzania

TAXON	*n*	LOCALITY
		MEXICO
augusta var. *augusta*	18	**Guanajuato.** 35 mi NE of Guanajuato on Hwy 110 to Dolores Hidalgo. *Olsen 271.*
	18	**Guanajuato.** 6 mi NE of Dolores Hidalgo on Hwy 110. *Olsen 272.*
	18	**Hidalgo.** Along exit road to Tula off Hwy 57. *Olsen 244.*
	18	**Hidalgo.** 10 mi E of Hidalgo-Queretaro border on Hwy 45. *Olsen 284.*
	18	**Hidalgo.** 2.5 mi N of Pachuca on Hwy 105 to Real del Monte. *Olsen 286.*
	18	**Queretaro.** Hwy 57, 2 mi SE of San Juan del Rio. *Olsen 242.*
	18	**Queretaro.** ca 8 mi from Hwy 57 on Hwy 45 to Pachuca. *Olsen 243.*
	18	**Queretaro.** 6 mi S of Vizarron on Hwy 120. *Olsen 283.*
augusta var. *rzedowskii*	18	**San Luis Potosi.** 40 mi S of San Luis Potosi on Hwy 57. *Olsen 274.*
discoidea	18	**Chihuahua.** 15 mi E of Cuauhtemoc on Hwy 16. *Olsen 259.*
megacephala var. *megacephala*	18	**Hidalgo.** Road to El Chico, ca 4.5 mi N of Pachuca on Hwy 105. *Olsen 288.*
	18	**Hidalgo.** El Chico, road near La Ventura. *Olsen 289.*
mollissima	27	**Zacatecas.** Concepcion del Oro. *Olsen 297.*
	27	**Zacatecas.** 5 mi W of Concepcion del Oro on road to Mazapil. *Olsen 300.*

Table 2 (cont.)

TAXON	*n*	LOCALITY
		MEXICO:
mollissima	27	**Zacatecas.** Top of mountain on W side side of dirt road to Cadros; ca 16 mi N of Rosario. *Olsen 330.*
	27	**Zacatecas.** ca 2 mi E of Cedros on gravel road to Mazapil. *Olsen 331.*
	27	**Zacatecas.** 2 mi E of Mazapil on road to Concepcion del Oro. *Olsen 332.*
montagnifolia	18	**Puebla.** On Hwy 150d to Orizaba. *Olsen 245.*
	18	**Puebla.** ca 4 mi S of Esperanza on Mex 28 to Tehuacan. *Olsen 246.*
	18	**Puebla.** 4 mi S of Esperanza. *Olsen 247.*
	18	**Puebla.** 10 mi N of Tehuacan on Hwy 150. *Olsen 248.*
	18	**Puebla.** 16 mi N of Tehuacan on Hwy 190 to Puebla. *Olsen 249.*
		ECUADOR:
sodiroi	18	**Pichincha.** 6.5 km S of Quito on Pan American Hwy. *Olsen 435.*
	18	**Pichincha.** N of Machachi on Pan American Hwy. *Olsen 485.*
		MEXICO
subcordata	ca 36	**Puebla.** 7 mi N of Esperanza on road to Ciudad Serdan. *Olsen 291.*
triloba	18	**Coahuila.** Hwy 4 at General Cepeda. *Olsen 306.*
	18	**Hidalgo.** ca 10 mi S of Ixmiquilpan. *Dillon 674.*

Table 2 (cont.)

TAXON	*n*	LOCALITY
		MEXICO:
triloba	18	**Hidalgo.** Junction of Hwy 45 and 85. *Olsen 285.*
	18	**Nuevo Leon.** 27 mi E of San Roberto Junction on Hwy 60 to Linares. *Olsen 340.*
	18	**Queretaro.** On Hwy 120, 29 mi N of Cadereyta. *Olsen 241.*
	18	**Queretaro.** 40 mi SW of Jalpan on Hwy 120. *Olsen 282.*
	18	**San Luis Potosi.** 11 mi S of Matehuala on Hwy 57. *Olsen 217.*
	18	**San Luis Potosi.** 18 mi W of San Luis Potosi on Hwy 49 toward Zacatecas. *Olsen 219.*
	18	**San Luis Potosi.** El Catorce. *Olsen 233.*
	18	**San Luis Potosi.** 15 mi S of Matehuala on Hwy 57. *Olsen 234.*
	18	**San Luis Potosi.** Along side of Hwy 57, 55 mi S of Matehuala. *Olsen 235.*
	18	**San Luis Potosi.** On Hwy 57 intersection with road to Guadalcazar. *Olsen 236.*
	18	**San Luis Potosi.** ca 20 mi N of San Luis Potosi on Hwy 57. *Olsen 237.*
	18	**San Luis Potosi.** ca 9 mi N of San Luis Potosi on Hwy 57. *Olsen 238.*
	18	**San Luis Potosi.** Just W of San Luis Potosi on Hwy 49. *Olsen 239.*
	18	**San Luis Potosi.** 6 mi E of San Luis Potosi on Hwy 70. *Olsen 240.*
	18	**San Luis Potosi.** 40 mi S of San Luis Potosi on Hwy 57. *Olsen 273.*

Table 2 (cont.)

TAXON	*n*	LOCALITY
		MEXICO:
triloba	18	**San Luis Potosi.** 4 mi E of San Luis Potosi on Hwy 70 toward Rio Verde. *Olsen 275.*
	18	**Zacatecas.** West end of Guadelupe on Hwy 49. *Olsen 220.*
	18	**Zacatecas.** 8 mi S of Fresnillo, on Hwy 45. *Olsen 250.*
	18	**Zacatecas.** 9 mi S of Fresnillo. *Olsen 263.*
	18	**Zacatecas.** 51 mi NE of Zacatecas on Hwy 54. *Olsen 294.*
	18	**Zacatecas.** 80 mi NE of Zacatecas on Hwy 54. *Olsen 295.*
	18	**Zacatecas.** 108 mi NE of Zacatecas on Hwy 54. *Olsen 296.*
	18	**Zacatecas.** Concepcion del Oro. *Olsen 298.*
	18	**Zacatecas.** 33 mi N of Fresnillo on Hwy 49. *Olsen 326.*
	18	**Zacatecas.** 15 mi N of junction Hwy 49 and 54 on road to Saltillo. *Olsen 328.*
	18	**Zacatecas.** 2 mi N of Rosario on dirt road to Cedros. *Olsen 329.*

the tetraploid level, hence the extant base of $x = 18$. It is also likely that ancestral polyploidy (hexaploidy and octoploidy) is responsible for the seemingly triploid *Z. mollissima* ($n = 27$) and the seemingly tetraploid *Z. subcordata* ($n = 36$), as is discussed below.

Zaluzania triloba, Z. augusta var. *augusta, Z. augusta* var. *rzedowskii, Z. montagnifolia, Z. megacephala* var. *megacephala, Z.*

sodiroi, and *Z. discoidea* all uniformly show $n = 18$ (although an $n = 16$, presumably erroneous, count has been reported for *Z. megacephala*) with the majority of the counts coming from the two most widespread taxa, *Z. triloba* and *Z. augusta* var. *augusta.* Meiosis is regular with consistently good pairing; in fact, no meiotic irregularity was seen in the configurations examined, including those of the polyploids.

Zaluzania mollissima ($n = 27$) is a robust shrub frequenting the rocky limestone slopes in the vicinity of Concepcion del Oro and Cedros, Zacatecas and, indeed, is known to occur only in this narrowly restricted bolson region. The occurrence of good bivalent pairing in this taxon is the strongest evidence in favor of an $x = 9$ base chromosome number for the genus. Assuming the base of $x = 9$, *Z. mollissima* would be a hexaploid. If $x = 18$ were the original base number, meiosis of the 54 chromosomes would have required autosyndesis of one set of 18 to give the observed 27II, or in other words, non-homologous chromosomes would be pairing during meiosis. If $x = 9$ were the ancestral condition, autosyndesis would reflect pairing of homologous chromosomes.

Morphologically, the two polyploids are nearest to diploid *Zaluzania augusta.* These three taxa are shrubby, have entire leaves with a soft woolly pubescence on the lower surface, and a pappus on the ray florets. *Zaluzania augusta* has the broadest geographic range of any species in the genus (Figure 2), and is the only ecological dominant (in terms of biomass) in the genus, occupying lower elevations and more mesic areas than either of the two polyploids. It seems likely that the morphological similarities exhibited by these three taxa would be best explained if they had all been derived from the same ancestral diploid stock, a *Z. augusta*-like ancestor. The polyploids, *Z. mollissima* and *Z. subcordata* therefore, would be interpreted as apoendemic taxa (Stebbins, 1971), narrowly restricted polyploid taxa, related to and possibly derived from a more widely distributed diploid.

In summation, the following points can be made from the cytological observations:

1. Although two of the 11 taxa remain to be counted, the extant base chromosome number for the genus is $x = 18$, with an $x = 9$ ancestral number strongly suggested.

2. The polyploid taxa are believed to be apoendemic entities.

3. The diploid *Zaluzania augusta* probably played a role in the production of the two polyploid taxa, although this conclusion is based only upon circumstantial evidence.

PALYNOLOGY

The primary reason for initiating a light microscope pollen survey in *Zaluzania* was to determine whether pollen size or aperture number correlates positively with ploidal level in the genus.

Table 3 summarizes the pollen data obtained for *Zaluzania*. The pollen grains are echinate and nearly spherical, varying in diameter from 22.5–30.0 microns. The spines are prominent and conical, ranging from 2.5–6.3 microns in length. All grains examined are uniformly three-apertured with long tapering colpi.

Grain size is not consistently correlated with ploidal level in the genus, and in fact is rather similar in all 11 taxa. The smallest grains are found in *Zaluzania augusta* var. *rzedowskii,* with *Z. pringlei, Z. augusta* var. *augusta* and *Z. subcordata* only slightly larger. The largest grains are found in *Z. sodiroi,* with *Z. discoidea, Z. triloba* and *Z. mollissima* only slightly smaller.

Polyploidy, especially if recent, often results in the increase in size of the individual cells, including pollen grains (Stebbins, 1950); however, the polyploid taxa *Z. mollissima* and *Z. subcordata* do not produce significantly larger grains than the diploid taxa. This suggests that the polyploids are of ancient origin, being now completely diploidized.

Of greater interest than just the size of the grains is the length of the spines. Spine length is to some extent correlated with pollination mechanism. Wodehouse (1945) states that there is a general trend for reduction in spine length, going from an entomophilous condition to an anemophilous condition, the entomophilous condition usually being considered primitive in the angiosperms (Cronquist, 1968). While all *Zaluzania* taxa are believed to be entomophilous, a trend from long spines to short spines does fit with other morphological data, suggesting that the very short spines (about 2.5 microns) found in the rayless, herbaceous taxon, *Z. discoidea* are derived, while the long spines (4.5–6.3 microns) found in the shrubby taxa, *Z. montagnifolia* and *Z. augusta* and the polyploids are more primitive.

Table 3

Measurements of acetolyzed Zaluzania pollen (in microns)

TAXON	POLAR DIAMETER	EQUATORIAL DIAMETER	SPINE LENGTH
Z. augusta			
var. *augusta*	24.5	22.0	4.7
var. *rzedowskii*	22.5	20.0	5.0
Z. discoidea	27.5	27.5	2.5
Z. megacephala			
var. *coahuilensis*	26.3	25.0	3.8
var. *megacephala*	25.1	23.0	5.0
Z. mollissima	27.5	26.3	5.0
Z. montagnifolia	25.3	22.1	6.3
Z. pringlei	22.7	22.1	3.8
Z. sodiroi	30.0	26.0	4.9
Z. subcordata	23.8	24.0	5.6
Z. triloba	27.5	26.9	4.9

There is no absolute difference in spine length between the herbaceous taxa and the shrubby taxa. In general, however, the pollen of the herbaceous members of the genus have shorter spines than pollen from the shrubs.

PHYLOGENY

In constructing a phylogenetic arrangement of taxa, it is always difficult to determine primitive versus advanced morphological states. This is certainly the case in *Zaluzania;* consequently, many of the assumptions are based on familiarity with the taxa and their distributions. To give a visual representation of my views, the Wagner Divergence Index (Wagner, 1961; Whiffen & Bierner, 1972) has been employed. Divergence index values are listed in Table 4.

Character	**Primitive**	**Advanced**
1. chromosome number	$n = 18$	$n = 27, 36$
2. flavonoids	glycosides	aglycones, absent
3. habit	shrub	herbaceous perennial, small trees
4. heads	many, small	few, large
5. leaf margins	entire, crenate	dentate, toothed
6. leaf pubescence	hirsute, pustulate	tomentose
7. pappus on the ray floret	present	absent
8. pollen	long spines	short spines
9. roots	no tubers	tubers

Figure 3 represents the tree derived from these characters. There is an obvious split between the shrubby taxa centering around *Zaluzania augusta* and *Z. montagnifolia* and the herbaceous perennial taxa centering around *Z. megacephala.* The shrubby taxa can be further subdivided into two groups. One is the coarsely pubescent, epappose group of three taxa, *Z. montagnifolia, Z. pringlei* and *Z. sodiroi.* The other is the densely soft-pubescent, larger headed group with a pappus on the ray florets, consisting of *Z. augusta, Z. mollissima,* and *Z. subcordata.*

Zaluzania augusta var. *augusta* is the extant taxon possessing the greatest number of primitive characters. This wide-ranging shrubby taxon occupies a region probably near the geographical center of dispersal for the genus. It is suggested that the ancestral *Zaluzania* originated in the region of the Mexican Plateau, occurring in submesic areas, habitats presently inhabited by *Z. augusta* var. *augusta.* This is supported by Rzedowski (1973), who states that the Mexican xerophytic flora (of which *Zaluzania* is today a part) derived from ancestors of neotropical or general tropical affinities and not from a southwestern United States flora pushed southward. The ancestral stock probably arose as a stabilized tetraploid derivative from an $x = 9$ line which also gave rise to *Viguiera.* With the uplifting of the Sierra Madre Oriental (Oligocene) and the subsequent increasing aridity of its western slopes (until Pleistocene, Maldonado-Koerdell, 1964), the environments suitable for *Zaluzania* moved to the west, causing ancestral *Zaluzania* to move with them. The peripheral

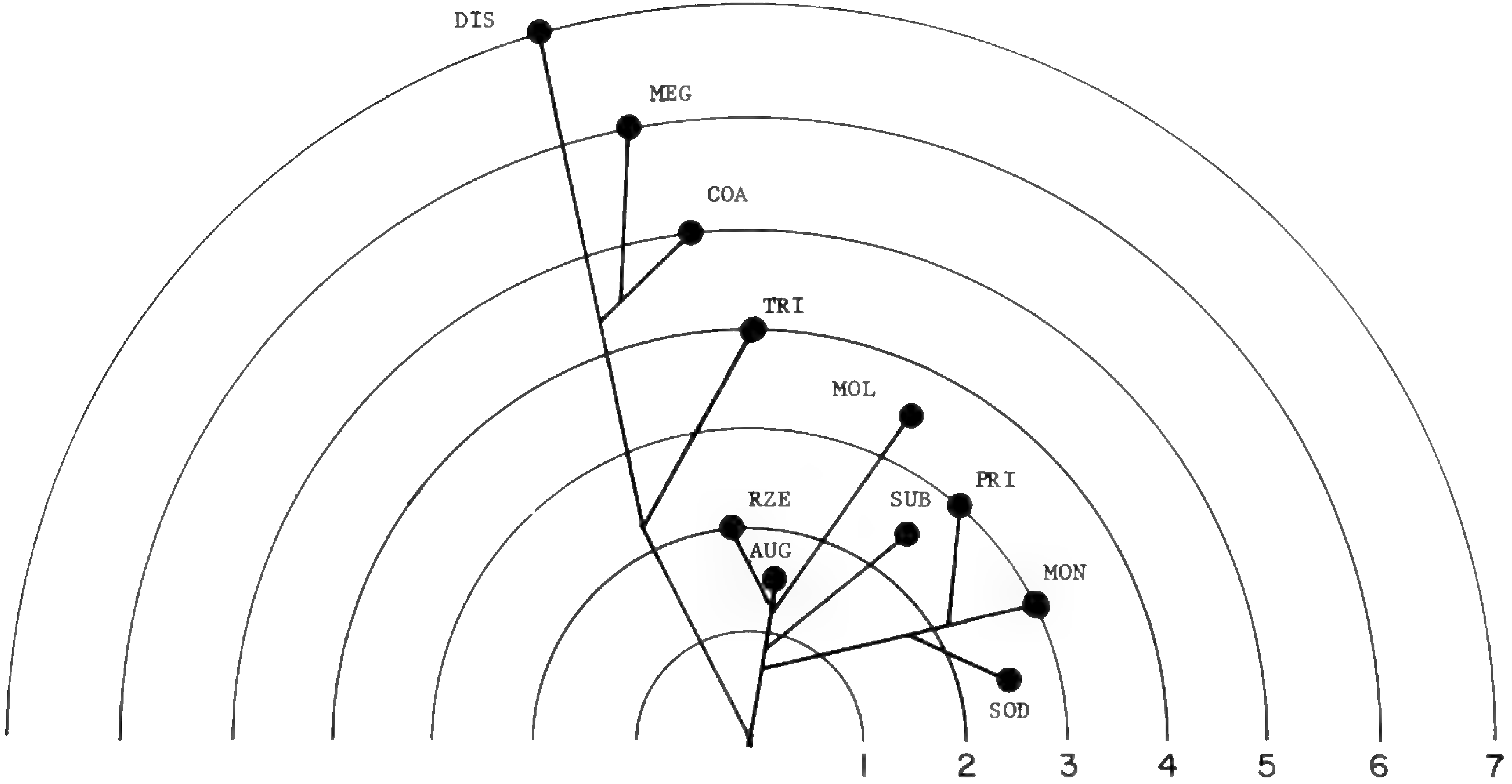


Figure 3. Relationships between *Zaluzania* taxa, indicated by divergence index values.

populations to the east which were pre-adapted to the arid conditions and presumably already isolated by polyploidy were left behind, where they are today represented by the apoendemic element, *Z. subcordata.*

Zaluzania montagnifolia inhabits the more mesic sites to the south of *Z. augusta.* This taxon is very woody in the south of its range, but this is viewed as a secondary adaptation and therefore a derived character (Carlquist, 1966 & 1976). This tendency is a common occurrence in the Asteraceae and reflects an adaptation of a more xeric element to mesic conditions (Carlquist, 1975). Radiation and evolution of this taxon probably gave rise to *Z. pringlei* to the south and west. It is also suggested that the Ecuadorian element, *Z. sodiroi,* could have arisen via chance introduction from *Z. montagnifolia* stock.

To the north and west, the Sierra Madre Occidental was being uplifted (Pliocene-Pleistocene, Axelrod, 1958; Johnson, 1968). This caused the movement of more arid conditions southward into Mexico. Presumably, evolution took place in response to this increasing aridity. The pre-adapted northern polyploid *Zaluzania mollissima,* already isolated chromosomally from *Z. augusta,* remained in the arid limestone hills to the north (Zacatecas) and is also best considered an apoendemic element.

The herbaceous perennials presumably arose from shrubby ancestors concurrently with the split of *Zaluzania augusta* var. *rzedowskii* from *Z. augusta* var. *augusta.* The similarity in flavonoid chemistry (Olsen, 1977b) of this variety and the herbaceous perennials suggests an origin from a common ancestor. These elements are all on the perimeter of the present range of *Z. augusta,* with *Z. megacephala* var. *megacephala* occupying very moist habitats in Tamaulipas and Hidalgo, *Z. megacephala* var. *coahuilensis* inhabiting the more xeric rocky hills of Coahuila; and *Z. augusta* var. *rzedowskii* occupying mesic areas in Zacatecas and Durango, south into Jalisco. *Zaluzania discoidea* to the north (in Durango and Chihuahua) inhabits disturbed areas along roadsides.

The widespread *Zaluzania triloba* occupies xeric sites in central and northern Mexico, but its relationships are uncertain. I have placed it in the herbaceous perennial line based on floral morphology; however, its sesquiterpene lactone chemistry (Yabuta et al., 1978) and flavonoid chemistry (Olsen, 1977b) are unique in the genus.

Table 4

Divergence index values for Zaluzania taxa

TAXON	1	2	3	4	5	6	7	8	9	TOTAL
Z. *augusta*										
var. *augusta*	0.0	0.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.5
var. *rzedowski*	—	0.0	0.0	0.5	0.0	1.0	0.5	0.0	0.0	2.0
Z. *subcordata*	1.0	0.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	2.5
Z. *sodiroi*	—	0.5	0.0	0.0	1.0	0.0	1.0	0.0	0.0	2.5
Z. *montagnifolia*	0.0	0.5	0.5	0.0	1.0	0.0	1.0	0.0	0.0	3.0
Z. *pringlei*		0.5	0.0	0.0	1.0	0.0	1.0	0.5	0.0	3.0
Z. *mollissima*	1.0	0.5	0.0	1.0	0.0	1.0	0.0	0.0	0.0	3.5
Z. *triloba*	0.0	1.0	1.0	0.0	1.0	0.0	1.0	0.0	0.0	4.0
Z. *megacephala*										
var. *coahuilensis*	—	0.0	1.0	1.0	0.5	0.5	1.0	0.0	1.0	5.0
var. *megacephala*	0.0	0.0	1.0	1.0	0.5	1.0	1.0	0.5	1.0	6.0
Z. *discoidea*	0.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	7.0

Zaluzania grayana is transferred here to *Viguiera*. The $n = 17$ chromosome number (Keil & Stuessy, 1975) and sterile ray florets are not known in *Zaluzania*. A list of some of the characters separating *Viguiera triloba* (Gray) Olsen (*Z. grayana*) from *Zaluzania* is presented below.

Zaluzania	**Viguiera triloba**
$n = 18, 27, 36$	$n = 17$
rays fertile; ligules short (except in *Z. mollissima*) and not showy	rays sterile; ligules long and showy
leaves not papery textured; pubescence hirsute to woolly	leaves thin and papery; pubescence sparse
involucre not spreading; inner series becoming scarious (at least along the margins)	involucre spreading; inner series strictly herbaceous

It has been suggested (H. Robinson, pers. comm.) that *Viguiera triloba* does indeed belong in *Zaluzania* because of the unique expansion of the disc corolla in these taxa to form a cap over the achene. Further examination of this character, however, has shown that the expansion referred to is also found in *Viguiera*, although not to the extent seen in *Zaluzania*. Several taxa in *Viguiera* series *Maculatae* and *Grammatoglossae* have the fleshy cap over the achene. Since this one character is not a consistent distinguishing feature, *V. triloba* is believed to belong in *Viguiera*, where the characters noted above would indicate its affinities to be.

ACKNOWLEDGMENTS

This study is based in part on a dissertation submitted in partial fulfillment of the Ph.D. requirements at the University of Texas at Austin. I am grateful to Dr. B. L. Turner for initially suggesting this problem and for his advice, discussions, and encouragement which made its completion possible. I am also grateful to Dr. T. J. Mabry for his discussions and support of several of my field trips. Dr. M. C. Johnston provided the Latin description. I also thank Dr. A. M. Powell, Dr. Ron Hartman, Dr. Dan Difeo, Dr. Charles Bohnstedt, Dr. Ken Becker, Sam Sikes, Scott Lewis, Meredith Lane and Linda Escobar for assistance and companionship on collecting trips.

Funds provided through a Dissertation Improvement Grant from NSF (DEB 76-09353) and through Sigma Xi supported some of the field work involved in this study.

Curators of the following herbaria are acknowledged for loans received: ARIZ, ASU, F, GH, LL, MEXU, MICH, NMC, NY, UC, and US.

TAXONOMIC TREATMENT

Zaluzania Persoon, Syn. Plant. **2:** 473. 1807.
Ferdinanda Lag., Gen. Sp. Nov. Pl. **31.** 1816.
Chrysophania Kunth ex Less., Syn. Gen. Comp. **224.** 1832.

Herbaceous or shrubby perennials to 4m in height. Stems glabrous below to tomentose above, 1 to many from a woody caudex (roots in herbaceous perennials usually with fleshy tubers). Leaves entire to tripartite; blades cordate, ovate, or lanceolate-elliptic in outline, sessile or attenuate if petiole present, hirsute to lanate below, pustulate to lanate above, hairs simple. Inflorescence corymbose, peduncles to 10 cm in length. Heads usually radiate (one species strictly discoid), 1.0–3.1 cm in diameter, including the rays. Involucre 2–3 seriate, the bracts herbaceous, linear-lanceolate, pubescent, the inner series glabrate and chartaceous. Receptacle conical. Chaff present, the pales oblanceolate in outline, trifid at the apex, enclosing the disc florets. Ray florets, when present, 4–10, pistillate and fertile, yellow (white in one species); style branches linear, enclosed in the tube or well exserted. Disc florets 40–100, hermaphroditic and fertile, yellow (white in one species); base of the corolla tube usually expanded to form a cap over the achene; style branches short, flat, stigmatic lines indistinct, appendage acute. Anthers sagittate at base; pollen echinate, polar diameter 22.5–30.0 microns, equatorial diameter 20.0–27.5 microns, spines 2.5–6.3 microns in length. Ray achenes 3-angled in cross section, black, glabrous or pubescent along the angles; pappus of 2–4 scales, or absent. Disc achenes black, 4-angled in cross section, glabrous; pappus absent. Base chromosome number $x = 18$.

TYPE SPECIES: *Zaluzania triloba* (Ort.) Pers.

KEY TO THE SPECIES

a. Herbaceous perennials .... b.
  b. Leaves tripartite, sometimes more highly dissected; pubescence hirsute. .... 1. *Z. triloba*
  b. Leaves undivided; pubescence tomentose to lanate. .... c.
    c. Heads discoid. .... 2. *Z.discoidea*
    c. Heads radiate. .... 3. *Z. megacephala*
a. Shrubs. .... d.
  d. Leaf margins entire; ray florets with a pappus of 2-4 awns. .... e.
    e. Heads more than 2 cm wide (including the rays)... 4. *Z. mollissima*
    e. Heads less than 1.5 cm wide (including the rays). .... f.
      f. Leaves cordiform; ligules less than 5 mm in length; disc corolla tube expanded to cap the achene. ....5. *Z. subcordata*
      f. Leaves ovate-lanceolate to ovate; ligules more than 5 mm in length; disc corolla tube not inflated to cap the achene. ..6. *Z. augusta*
  d. Leaf margins serrate; ray florets epappose. .... g.
    g. Heads (usually discoid) white; ray florets (if present) white. .... 7. *Z. pringlei*
    g. Heads radiate; yellow. .... h.
      h. Pubescence of upper leaf surface pustulate; throat of the disc and ray corollas weakly pubescent; plants of Mexico. .... 8. *Z. montagnifolia*
      h. Pubescence of upper leaf surface not pustulate; throat of the disc and ray corollas glabrous; plants of Ecuador..... 9. *Z. sodiroi*

1. **Zaluzania triloba** (Ort.) Pers., Syn. Plant. **2:** 473. 1807.

Anthemis triloba Ort., Desc. Pl. Rar. **72.** 1798. TYPE: MA. (Isotype, L; Photograph of Isotype, MO!).

Athemis sinuata LaLlave & Lexarza, Nov. Veg. Desc. **1:** 26. 1825. Type not designated; described from the vicinity of Los Remedios and San Angel, Mexico.

Acmella trilobata Spreng., Linn. Syst. Veg. **3:** 591. 1826. Based upon *Anthemis triloba* Ort.

Aiolotheca parthenioides DC., Prodr. **5:** 508. 1836. TYPE: G-DC *Berlandier 1341*. MEXICO: San Luis Potosi. Hacienda de la Encarnacion. Dec., 1827. (Phototypes, F!, LL!; Isotype, GH!).

Zaluzania robinsonii W. M. Sharp, Ann. Missouri Bot. Gard. **22:** 105. 1935. TYPE: MO! *Lloyd 124*. MEXICO: Zacatecas. Hacienda de Cedros. Aug., 1907. (Isotypes, LL!, UC!).

Zaluzania parthenioides (DC.) Rzedowski, Brittonia **20:** 166. 1968.

Herbaceous perennials to 1 m in height. Stems 1 to several from a woody caudex, usually striate; puberulent below to hirsute above. Roots without fleshy tubers. Leaves tripartite, becoming more highly dissected. Upper leaves 1.8–3.0 cm long, 1.4–2.1 cm wide; lower leaves 6.3–7.5 cm long, 4.2–5.5 cm wide; pubescence of the upper surface strigose, lower surface strigose to hirsute; petioles up to 1.5 cm in length. Peduncles 0.5–1.2 cm long, hirsute to tomentose. Heads 0.8–1.4 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate, outer series 2.5–3.0 mm long, 0.7–1.1 mm wide, inner series becoming trifid, equal in length, but broader. Pales oblanceolate in outline, trifid. Ray florets 8–10, ligules yellow, 3-lobed, 3.1–4.2 mm long, 2.5–3.5 mm wide; throat pubescent, styles well exserted from the tube. Disc florets about 75, yellow, corolla 1.8–2.2 mm long, 1.3–1.6 mm wide; throat minutely pubescent. Ray achenes hairy along the angles and the summit, 1.0–2.1 mm long, 0.3–0.6 mm wide; pappus absent. Disc achenes 1.0–1.3 mm long, 0.5–0.6 mm wide. (Figure 4).

Representative Specimens. MEXICO. **Aguascalientes:** shrub covered, nearly treeless mountainsides about 20 km E of Rincon de Romos, road to Asientos, between Cerro Altamira and Cerro de San Juan, *McVaugh 23744*, (MICH); Ladera N del Cerro San Juan, 5 km al E de Tepezala, *Rzedowski 25008* (MICH). **Coahuila:** 5 mi S of Saltillo, *Barkley 16037* (F, LL); In low places along the roadside in *Larrea* association, 6 mi N of Saltillo, *Cronquist 9840* (GH, LL, MICH, NY); Road from Saltillo S to Concepcion del Oro, Carneros Pass, *Johnston 7285* (GH); 1 mi N of Carneros, *Johnston & Graham 4189c* (MICH); La Encantada, 9 mi W of Saltillo, *Mears 32410* (LL); Highway 4 at General Cepaeda, *Olsen 306* (LL); Near Saltillo, *Palmer 360* (F, GH, MO, NY, UC, US); Parras, *Palmer 435* (GH, MO, NY, UC, US); Carneros Pass, *Pringle 2402* (F, GH, LL, MICH, MO, NY, UC, US); Carneros Pass, 21 mi S of Saltillo, *Shreve 8549* (ARIZ, MICH, US). **Federal District:** Vicinity of Rancho del Flores near San Pablo, 15 mi S of Mexico City, *Happ 294* (MO); Santa Maria Astahuacan, delegacion de Ixtapalapa, *Rzedowski 27867* (MICH). **Guanajuato:** San Luis de la Paz, *Kenoyer 2325* (GH). **Hidalgo:** 17 mi W of Tulancingo at village called Jalapilla, along Hwy, *Bierner & Turner 124* (LL); ca 10 mi SE of Ixmiquilpan, *Dillon 674* (LL); Pachuca, *Fisher 35245* (ARIZ, F, LL, MO, NY, US); Zimapan, *Hartweg 329* (NY); Junction Hwy 45 and 85, *Olsen 285* (LL); Sierra de Pachuca, *Pringle 9481* (F, GH, MEXU, MO, US); Calcareous mesas near Zontecomate Station, *Pringle 13093* (ARIZ, F, GH, LL, MICH, US); Near Tula, *Rose 8325* (GH, US); Hill-slopes behind Hacienda Tetlapayac, 12 km E of Apan, *West FF-8* (MICH). **Mexico:** Las Cruces, Hwy to Toluca, *Matuda 19227* (MEXU). **Nuevo Leon:** Near Casablanca, *Barkley 16016* (F, LL); 27 mi S of San Roberto Junction along Hwy 56, *Bierner & Turner 98* (LL, NY). **Oaxaca:** Al NE de Cuicatlan, *Miranda 4694* (MEXU). **Puebla:** 37 mi SE of Tehuacan and 2.5 mi N of Teotitlan, *Cronquist & Sousa 10384* (MEXU); Along rt 150, ca 20 mi NW of Tehuacan, *King 2639* (LL, MICH, UC, US). **Queretaro:** Del Ciervo of San Juan, *Altamirano s.n.*, 27 Aug 1905 (US); On Hwy 120, 29 mi N of Cadereyta, *Olsen 241* (LL); 40 mi SW of Jalpan on Hwy 120, *Olsen 282* (LL). **San Luis Potosi:** Matehuala a Rio Blanco, *Berlandier 3170* (MO); San Luis Potosi, *Fisher 136* (GH, US); 3 mi W of Ciudad del Maiz, *Johnston & Graham 4442* (LL, MEXU); 11 mi S of Matehuala on Hwy 57, *Olsen 217* (LL); 18 mi S of junction at

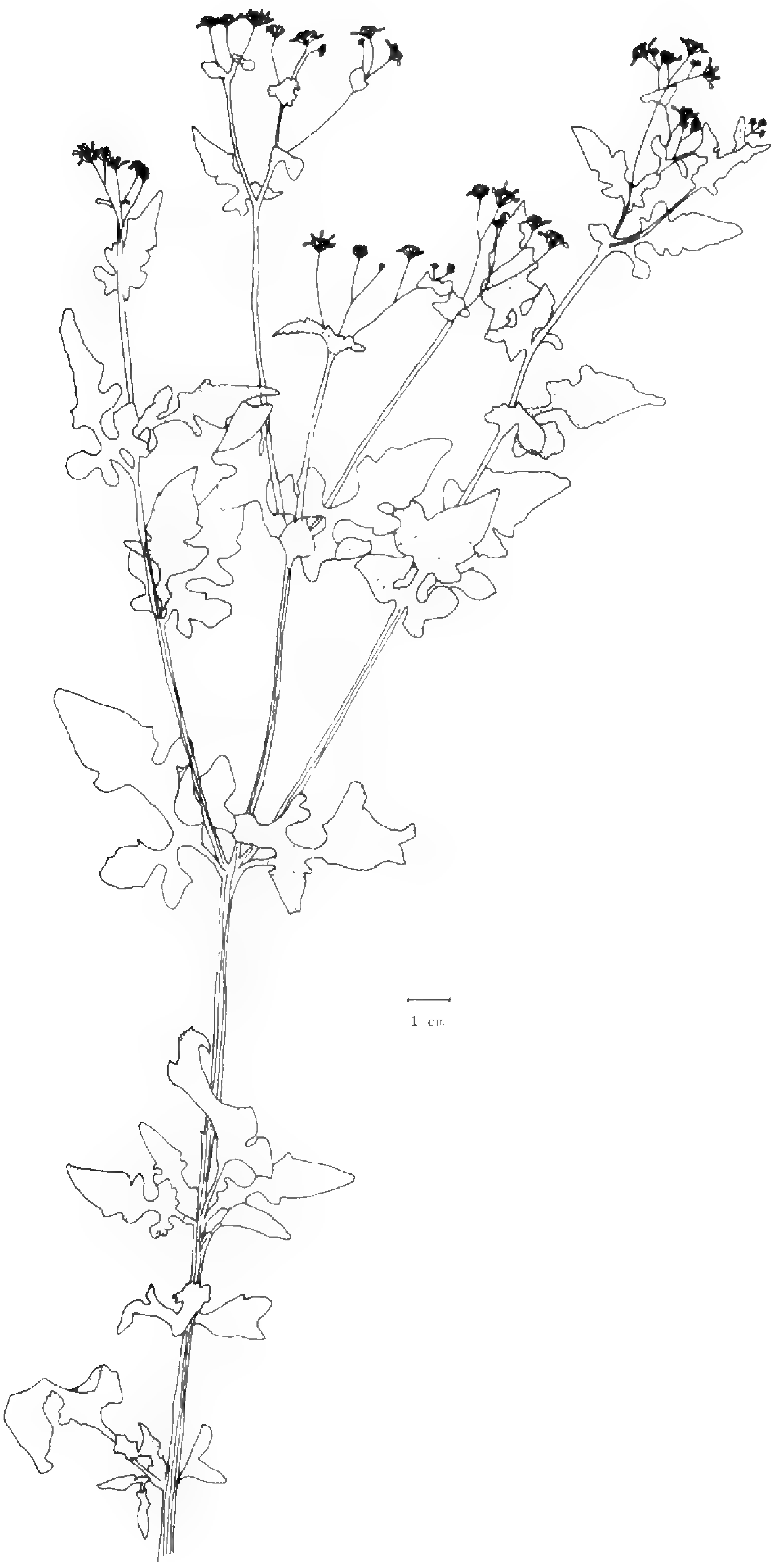


Figure 4. *Zaluzania triloba,* habit tracing.

Huizache on Hwy 57, 68 mi S of Matehuala, *Olsen 218* (LL); 18 mi W of San Luis Potosi on Hwy 49 toward Zacatecas, *Olsen 219* (LL); El Catorce, *Olsen 233* (LL); 40 mi S of San Luis Potosi on Hwy 57, *Olsen 273* (LL); 4 mi E of San Luis Potosi on Hwy 70 toward Rio Verde, *Olsen 275* (LL); Vanegas, *Pennell 17510* (GH, MEXU, US); Los Charcos, *Pringle 4026* (MICH); Along arroyo running through shrubs 25 mi NE of San Luis Potosi, *Waterfall 15707* (US). **Tamaulipas:** Near town of Miquihauana, *Stanford, Retherford & Northcraft 820* (ARIZ, GH, MO, NY, UC). **Vera Cruz:** Orizaba, *Botteri 843* (US); Justo Sierra, Municipio de Perote, *Ventura 4007* (LL, MICH). **Zacatecas:** In open thorn scrub communities dominated by *Acacia* and tree *Opuntias*, 20 mi SE of Zacatecas, *Cronquist 10533* (MEXU, MICH, NY, US); 34 air mi WNW of Concepcion del Oro, 9.2 mi W of Cedros, *Henrickson 6344b* (LL); West end of Guadalupe, Hwy 49, *Olsen 220* (LL); 8 mi S of Fresnillo on Hwy 45, *Olsen 250* (LL); 51 mi NE of Zacatecas on Hwy 54, *Olsen 294* (LL); Concepcion del Oro, *Olsen 298* (LL); Cactus savanna 21 mi S of Santa Maria de Manon, *Shreve 8627* (ARIZ, MICH, US); about 70 mi N of Zacatecas on road to Saltillo, *Strother 1116* (UC).

Zaluzania triloba (commonly called 'hierba amargosa') occurs at altitudes of 1500–2800 m. It is sympatric with two other *Zaluzania* species, *Z. augusta* and *Z. mollissima,* and is most commonly found in association with *Larrea tridentata* and species of *Acacia, Flourensia, Jatropha, Opuntia, Verbesina* and *Viguiera.*

Zaluzania triloba has been treated as two species by various authors, but close inspection of the morphological variation in the group does not support this splitting. Sharp (1935) separated *Z. robinsonii* from *Z. triloba* on the basis of pubescence, leaf dissection, head diameter, and stem striation. Rzedowski (1968) accepted Sharp's species, but noted it to be synonymous with the earlier *Aiolotheca parthenioides,* hence the name *Z. parthenioides* (DC.) Rzedowski.

Based upon examination of the material concerned and extensive field work on *Zaluzania triloba* from throughout its range, I conclude that the characters used to separate these taxa intergrade completely. Indeed, within the same population, plants found growing in the sun usually have the characters attributable to *Z. triloba,* while plants found growing in the shade have the characters attributable to *Z. parthenioides.* Both growth forms are diploid and both are found throughout the range of the taxon.

2. **Zaluzania discoidea** Gray, Proc. Amer. Acad. **21:** 388. 1886. TYPE: GH! *Pringle 309.* MEXICO: **Chihuahua.** Rocky hills near Chihuahua, 19 Oct 1885 (Isotypes: F!, LL!, NY!, US!).

Herbaceous perennials to 2 m in height. Stems single, arising from a woody caudex, unbranched until the inflorescence, pubescent along the entire length. Roots with fleshy tubers. Leaves cordate to ovate, the margins serrate to undulate, glandular, upper leaves 1.6–5.8 cm long, 0.6–2.5 cm wide; lower leaves 7.0–15.7 cm long, 6.3–15.3 cm wide; pubescence of the upper surface strigose, lower surface tomentose; petioles 0.2–2.2 cm in length. Peduncles 0.3–2.4 cm in length, densely pubescent. Heads discoid, 0.3–1.0 cm in diameter. Involucre 2–3 seriate, the bracts elliptical, outer series 3.9–4.2 mm long, 1.8–2.2 mm wide; inner series slightly longer and narrower. Pales oblanceolate, trifid, 3.4–3.6 mm long, 1.0–1.2 mm wide. Disc florets ca 75, corolla yellow, 2.5–3.6 mm long, 1.5–2.0 mm wide, throat pubescent. Achenes 1.8–2.0 mm long, 0.7–0.9 mm wide. (Figure 5.)

REPRESENTATIVE SPECIMENS. MEXICO. **Chihuahua:** Majalca, *LeSueur Mex-143* (ARIZ, LL); 63 mi W of Parral on road to El Vergel, *Correll & Gentry 22871* (LL); Parral and vicinity, Rio San Juan Valley along road from Parral, *Gentry, Correll, & Arguelles 18088* (US); 15 mi E of Cuauhtemoc on Hwy 16, *Olsen 259* (LL); Mountains near Chihuahua, *Pringle 1110* (LL, MEXU, MO, NY, UC). **Durango:** El Oro to Guanecevi, *Nelson 4727* (US); along road between Cerro Prieto and La Providencia, *Nelson 4970* (NY, US).

Zaluzania discoidea occurs on rocky clay soils among rolling hills at elevations of 1900–2200 m. It is most commonly found in disturbed areas along fenced fields, but also occurs in open wooded areas and grasslands. Taxa commonly found in association with *Z. discoidea* include species of *Machaeranthera, Quercus* and *Zinnia,* as well as many grasses.

Gray (1886) believed *Zaluzania discoidea* to be closely related to *Z. augusta* and *Z. mollissima.* It does not appear, however, to be very close to the latter, a shrubby taxon with long ray florets and lanceolate leaves. The ovate, densely pubescent leaves, erect unbranched habit and compact inflorescence of *Z. discoidea* do suggest a close relationship with *Z. augusta.* In any event, *Z. discoidea* is clearly related to the other herbaceous perennial taxa, these forming a closely knit phyletic group. On total characters, it is most closely related to *Z. megacephala,* the latter differing primarily in being radiate.

Figure 5. *Zaluzania discoidea*, habit tracing.

3. **Zaluzania megacephala** Sch.-Bip., Flora **44:** 563. 1861. (Typification and synonymy cited under varietal names.)

Herbaceous perennials to 1.5 m in height. Stems 1, or less commonly 2, from a woody caudex, unbranched until the inflorescence, reddish in color, glabrous at base to densely pubescent at the inflorescence. Roots with fleshy tubers. Leaves lanceolate-elliptic to ovate, the margins glandular-serrulate or serrate; upper leaves 3.5–7.5 cm long, 1.0–4.7 cm wide; lower leaves 6.6–13.0 cm long, 3.0–8.0 cm wide; pubescence of the upper surface strigose to tomentose, lower surface densely tomentose. Petioles 0.5 cm long or less. Peduncles 1.0–5.0 cm long, pubescent. Heads 1.4–2.7 cm in diameter (including the rays). Involucre 2–3 seriate, the bracts linear lanceolate in the outer series, apex truncate in the inner series; outer series 3.5–6.7 mm long, 0.7–2.5 mm wide, inner series shorter and broader. Pales 3.7–4.2 mm long, 1.2–2.5 mm wide. Ray florets 8–10, yellow, 4.2–14.0 mm long, 2.4–6.0 mm wide; throat pubescent with a few ascending hairs; style branches very short, not extending from the tube. Disc florets ca 75, yellow; corolla 1.6–3.4 mm long, 0.7–2.4 mm wide; throat sparsely pubescent. Ray achenes glabrous to sparsely pubescent, 0.8–2.6 mm long, 0.4–1.0 mm wide; pappus absent. Disc achenes 1.5–3.1 mm long, 0.4–1.0 mm wide.

KEY TO THE VARIETIES

a. Leaves ovate (rarely ovate-elliptic); margins serrulate; upper surface usually tomentose. .... 3a. var. *megacephala* (Figure 6)

a. Leaves lanceolate-elliptic (rarely ovate-elliptic); margins serrate; upper surface strigose. .... 3b. var. *coahuilensis* (Figure 7)

3a. **Zaluzania megacephala** Sch.-Bip. var. **megacephala** (Figure 6).

Zaluzania megacephala Sch.-Bip., Flora **44:** 563. 1861. TYPE: B, *Ehrenberg 462.* MEXICO: **Hidalgo:** Real del Monte, w/o date. (Phototype, GH!).

Zaluzania cinerascens Sch.-Bip., Flora **47:** 219. 1864. TYPE: B, *Ehrenberg 346.* MEXICO: **Hidalgo:** Mineral del Monte, w/o date. (Isotype, GH!; Phototype, GH!).

Zaluzania coulteri Hemsl., Diagn. Sp. Nov. **33.** 1879. TYPE: K, *Coulter 350.* MEXICO: **Hidalgo.** Real del Monte, w/o date. (Isotype, GH!).

REPRESENTATIVE SPECIMENS. MEXICO. **Federal District:** Sierra de Guadalupe, *Balls 5602* (US). **Hidalgo:** Sierra de Pachuca, ridge ca 2 km S of Real del Monte, *Beaman 2743* (GH); El Chico, *Lyonnet 387* (GH, MO, NY, US); Real del Monte, *Matuda 21659* (NY); Camino de Chico, *Matuda 25630* (MEXU, NY); Zimapan, *Moore & Wood*

Figure 6. *Zaluzania megacephala* var. *megacephala*, habit tracing.

44817 (NY); Road to el Chico, ca 4.5 mi N of Pachuca on Hwy 105, *Olsen 288* (LL); El Chico, road near La Ventura, *Olsen 289* (LL); Bosque de Encinos, *Paray 3218* (MEXU); Sierra de Pachuca, *Pringle 6956* (F, GH, MICH, MO, NY, UC, US), *Pringle 9997* (F, GH, MO, NY), *Pringle 13784* (ARIZ, GH, LL, MICH, US); Cerro de las Ventanas, 6 km al N de Pachuca, *Rzedowski 23025* (LL, MICH); El Bordo, 4 km N of Pachuca, *Rzedowski 24299* (F, LL, MICH); 3 km E del Cerro de las Ventanas, *Rzedowski 26824* (ARIZ, LL, MICH, US); Real del Monte, above Pachuca, *Sharp 44608* (NY); Oak forests near Real del Monte, above Pachuca, *Sharp 441086* (NY). **Nuevo Leon:** Cerro Potosi, east slope, *McGregor 361* (NY); E side of Cerro Linadero, *Meyer & Rogers 2905* (GH, MO, US); Cieneguillas to Puerto Santa Ana, about 15 mi SW of Galeana, *Mueller 909* (F, GH, LL, MICH); Cieneguillas, Pablillo, SE of Galeana, *Pennell 17094* (GH). **Queretaro:** 12 km al SW de Pinal de Amoles, sobre la carretera a Vizarron, *Rzedowski 27833* (F, MICH, NY). **Tamaulipas:** 4 km W of Miquihauana in canyon with luxuriant vegetation, *Stanford, Retherford, & Northcraft 673* (ARIZ, GH, MO, NY); 3 mi N of Miquihauana in pine forest, *Stanford, Lauber, & Taylor 2422A* (NY, US), *Stanford, Lauber, & Taylor 2434* (LL, NY, US).

This taxon has long gone under the name *Zaluzania cinerascens.* Schultz-Bipontinus gave only a very sketchy description of *Z. megacephala,* an Ehrenberg collection from Hidalgo. For some reason, he described a second species, *Z. cinerascens,* from other collections at the same locality (made by the same collector). Unfortunately, neither Robinson and Greenman (1899) nor Sharp (1935), in their revisionary studies of the genus, examined the types concerned and consequently did not recognize that the two names applied to the same taxon. Instead, they applied *Z. megacephala* to those populations around Saltillo, which as noted below are undescribed, and applied *Z. cinerascens* to those populations from Hidalgo, typified by *Z. megacephala,* a name which must be applied to the Hidalgo populations if these are to be recognized as distinct.

While the two recognized population groups are morphologically distinct and occupy different geographic regions, the characters distinguishing them are relatively trivial compared with those distinguishing other specific taxa; consequently, the populations concerned are recognized as only varietally distinct.

Variety *megacephala* is a high montane element, occurring primarily in the damp, pine-oak forests of eastern Mexico, at elevations above 3100 m.

3b. **Zaluzania megacephala** Sch.-Bip. var. **coahuilensis** Olsen, *var. nov.* TYPE: LL! *Pringle 10076.* Mountains near General Cepeda, 6500 ft, 7 Oct 1905 (Isotypes: F!, GH!, MO!, NY!, UC!, US!).

A varietate typica foliis lanceolato-ellipticis (raro ovato-ellipticis) margine serratis supra strigosis differt. (Figure 7).

REPRESENTATIVE SPECIMENS. MEXICO. **Coahuila:** La Casita, *Kenoyer & Crum 3016* (MICH); Cañon and elevated portions of Sierra Madre, 14 leagues S of Saltillo, *Palmer 734* (F, GH, NY, US); High summits near Carneros Pass, *Pringle 2398* (GH, MEXU, MICH, MO, NY, UC, US). **Durango:** El Salto (Aserrederos), *Pennell 18521* (NY, US). **Nuevo Leon:** Upper W slope of la Sierra de la Cebolla, Municipio de Rayonnes, *Mueller 2908* (GH, LL).

This taxon is also found in grassy pine-oak forests, but the habitats are typically lower and drier than those typifying *Zaluzania megacephala* var. *megacephala.* One collection, *Pennell 18521,* from Durango, appears to be far out of range for this taxon. Its location suggests *Z. augusta* var. *rzedowskii,* but leaf pubescence and epappose ray florets show it to be *Z. megacephala* var. *coahuilensis.*

Zaluzania megacephala is most closely related to *Z. discoidea.* Both are erect herbaceous perennials with compact, corymbose inflorescences. They differ primarily in characters of leaf pubescence, and *Z. discoidea* is obviously eradiate.

4. **Zaluzania mollissima** Gray, Proc. Amer. Acad. **15:** 35. 1880. TYPE: GH! *Parry & Palmer 445.* MEXICO. San Luis Potosi: Vicinity of San Luis Potosi, Aug 1878 (Isotypes: F!, MO!, NY!, US!).

Perennial shrubs to 2.5 m in height. Stems glabrous at base to tomentose above. Roots without fleshy tubers. Leaves lanceolate-elliptic, tending to become three lobed, margins entire; upper leaves 1.6–2.8 cm long, 0.6–0.8 cm wide; lower leaves 4.2–7.5 cm long, 1.4–2.0 cm wide; pubescence of the upper surface tomentose, lower surface lanate. Petioles less than 1.0 cm in length, pubescent. Heads 2.2–3.5 cm in diameter (including the rays). Involucre 3-serriate, the bracts lanceolate; outer series 3.3–3.6 mm long, 1.0–1.3 mm wide, inner series slightly longer. Pales oblanceolate, weakly trifid, 3.8–4.2 mm long, 1.3–1.6 mm wide. Ray florets 8–10, ligules yellow, 3-lobed, 10.7–11.4 mm long, 3.8–4.2 mm wide, throat pubescent, styles well exserted from the tube. Disc florets ca 50, corolla yellow, 2.3–2.7 mm long, 1.8–2.4 mm wide; throat glabrous. Ray achenes glabrous, 1.9–2.3 mm long, 0.8–1.1 mm wide; pappus of 2 scales or absent. Disc achenes 2.4–2.8 mm long, 0.6–0.9 mm wide. (Figure 8).

Figure 7. *Zaluzania megacephala* var. *coahuilensis*, habit tracing.

Figure 8. *Zaluzania mollissima*, habit tracing.

REPRESENTATIVE SPECIMENS. MEXICO. **Coahuila:** In valley 15 km W of Concepcion del Oro, just within Coahuila border, *Stanford, Retherford, & Northcraft 515a* (ARIZ, GH, MO, NY, UC). **San Luis Potosi:** Penasco, *Rzedowski 3442* (F, US); San Miguel, *Schaffner 767(342)* (MICH, NY, US). **Zacatecas:** 1 mi W of Concepcion del Oro along road to the main mine, *Henrickson 6252* (LL); 13.1 road miles W of Concepcion del Oro on road to Mazapil, *Henrickson 6293* (LL); ca 12 air miles NE of Estacion Camacho, 2 mi W of Pico de Teyra, *Henrickson 13398* (LL); 5 mi S of Majoma, *Johnston 7392* (GH, US); 2.5 km E of Mazapil on Hwy. Concepcion del Oro, *Johnston, Wendt, & Chiang 11544* (LL); In relatively wet places, vicinity of Cedros, *Kirkwood s.n.*, May 1908 (F); Hills near Cedros, *Lloyd 32* (GH); Zacatecas, *Lloyd 129* (LL, MO, US); Rocky cliff, Charcas-Vanegas road, *Lundell 5734* (ARIZ, LL, US); Concepcion del Oro, *Olsen 297* (LL); 5 mi W of Concepcion del Oro on road to Mazapil, *Olsen 300* (LL); 12 mi S of Cedros on dirt road, *Olsen 330* (LL); 7 mi E of Cedros on road to Mazapil, *Olsen 331* (LL); 2 mi E of Mazapil on road to Concepcion del Oro, *Olsen 332* (LL); Concepcion del Rio, *Palmer 314* (LL, MO, NY, UC, US); Open limestone slopes, *Pennell 17415* (MEXU, MICH, NY, US); 5 mi S of Rancho Mahoma, *Shreve 8579* (ARIZ, MICH, UC); Stony bajada near San Rafeal between Cedros and Camacho, *Shreve 9385* (ARIZ, MICH, UC).

Zaluzania mollissima is a frequent shrub on rocky limestone slopes and along cliffs; it is also found on sandy clay soils in open disturbed areas of the Chihuahuan Desert. It is sympatric with *Z. triloba* and occurs within a few miles of *Z. augusta* var. *augusta.* Common associates include: *Larrea tridentata* and species of *Acacia, Atriplex, Euphorbia* and *Opuntia.*

As pointed out earlier, *Zaluzania mollissima* is most closely related to *Z. augusta* and *Z. subcordata,* as evidenced by their pappose ray florets, entire, densely pubescent leaves and shrubby habit. The most distinguishing characteristic of this taxon is its long ray florets (more than 1 cm), not seen in any other *Zaluzania* taxon. It is suggested that the triploid *Z. mollissima* is an apoendemic element in the genus, derived from a *Z. augusta*-like ancestor.

5. **Zaluzania subcordata** W. M. Sharp, Ann. Missouri Bot. Gard. **22:** 111. 1935. TYPE: MO!. *Purpus 2580.* MEXICO: **Puebla.** On rocky hills of Esperanza, Aug 1907 (Isotypes: F!, GH!, MEXU!, NY!, UC!, US!).

Perennial shrubs to 3 m in height. Stems glabrous at base to tomentose above. Roots without fleshy tubers. Leaves cordiform, margins entire to minutely crenate; upper leaves 1.8–3.1 cm long, 0.6–1.4 cm wide; lower leaves 5.5–6.0 cm long, 2.4–3.4 cm wide;

pubescence of the upper surface tomentose, lower surface lanate; petioles 0.5–1.4 cm in length, densely pubescent. Peduncles 0.7–1.8 cm long, pubescent. Heads 1.1–1.2 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate, outer series 3.3–3.7 mm long, 1.5–1.7 mm wide; inner series slightly shorter and broader. Pales oblanceolate, weakly trifid, 3.2–3.5 mm long, 0.6–0.9 mm wide. Ray florets 8–10, ligules yellow, 3-lobed, 4.8–5.1 mm long, 4.2–4.5 mm wide; throat glabrous, style branches well exserted. Disc florets ca 40, yellow, corolla 2.5–2.9 mm long, 1.4 1.7 mm wide; throat pubescent. Ray achenes with a few hairs along the ridges; 1.7–1.9 mm long, 0.5–0.6 mm wide; pappus of two small awns or scales. Disc achenes 1.4–1.8 mm long, 0.5–0.7 mm wide. (Figure 9).

REPRESENTATIVE SPECIMENS. MEXICO. **Puebla:** Esperanza, *Arsene 7093* (US); Below Atzizintls (San Antonio), *Balls 5318* (GH, UC, US); 7 mi N of Esperanza on road to Ciudad Serdan, *Olsen 291* (LL); Hills about Esperanza, *Pittier 452* (US); Atzitzuilta, *Purpus 2790* (UC); In the vicinity of San Luis Tultitlanapa, near Oaxaca, *Purpus 3027* (ARIZ, F, MO, NY, UC, US); Coxcaltan, *Purpus 4121* (UC). **Vera Cruz:** Mt. Orizaba, *Seaton 286* (F, NY, US).

Zaluzania subcordata is restricted to the rocky limestone hills in southeastern Puebla and adjacent Vera Cruz. It is interpreted as an apoendemic element and is most closely related to *Z. augusta* and *Z. mollissima*.

6. **Zaluzania augusta** (Lag.) Sch.-Bip. Flora **44:** 562. 1861. (Typification and synonymy cited under varietal names.)

Perennial shrubs to 3 m in height. Stems glabrous at base to puberulent above. Roots without fleshy tubers. Leaves ovate to ovate-lanceolate, apex rounded or acute, margins entire or glandular crenate; upper leaves 1.2–1.8 cm long, 0.2–0.6 cm wide; lower leaves 4.2–7.5 cm long, 1.7–4.0 cm wide; pubescence of the upper surface hirsute to tomentose, lower surface lanate; petioles up to 1.0 cm in length. Peduncles 1.0–2.3 cm in length, puberulent. Heads 0.8–1.5 cm in diameter (including the rays). Involucre 2–3 seriate; the bracts lanceolate, outer series 3.0–3.3 mm long, 0.7–0.8 mm wide; inner series nearly equal in length, but slightly broader. Pales 3.5–3.7 mm long, 0.5–0.8 mm wide. Ray florets 8 10, ligules yellow, 2–3 lobed, 5.0–6.3 mm long, 2.5–3.0 mm wide; throat glabrous;

Figure 9. *Zaluzania subcordata,* habit tracing.

styles well exserted from the tube. Disc florets ca 50, corolla yellow, 2.5–2.8 mm long, 1.0 1.2 mm wide; throat glabrous. Ray achenes glabrous, 1.4–1.8 mm long, 0.6–0.8 mm wide; pappus of several (usually 4) scales or absent. Disc achenes 1.8–2.0 mm long, 0.6–0.8 mm wide.

KEY TO THE VARIETIES

a. Surface of the leaf dark green above, gray beneath; leaf apex acute; ligules 2-lobed; pappus of the ray florets of 4 scales; pales glutinous. .... 6a. var. *augusta* (Figure 10)

a. Surface of the leaf gray on both sides; leaf apex rounded; ligules usually 3-lobed; pappus of the ray florets reduced to 2 scales or absent; pales pubescent. .... 6b. var. *rzedowskii* (Figure 11)

6a. **Zaluzania augusta** (Lag.) Sch.-Bip. var. **augusta**

Ferdinanda augusta Lag., Gen & Sp. Nov. Pl. **31**. pl. 2. 1816. No type designated and herbarium at MA was destroyed. Photograph at GH! taken by Blake in 1925 of specimen he believed may have been seen by Lagasca, now deposited at P.

Anthemis lutescens La Llave & Lexarza, Nov. Veg. Desc. **1:** 26. 1824. MEXICO: **Federal District.** Guadalupe Mountains. *Cervantes s.n.,* w/o date. Description only, no specimens cited.

Chrysophania fastigiata Kunth ex Less., Syn. Gen. Comp. **224.** 1832. TYPE: P. *Humboldt s.n.,* w/o date. MEXICO: **Hidalgo.** Actopan.

Ferdinanda lutescens (La Llave & Lexarza) DC., Prodr. **5:** 553. 1836. Microfiche, G-DC!

Zaluzania angusta Sch.-Bip., *in* Hemsl. Biol. Centr. Am. Bot. **2:** 159. 1881. An orthographic variant of the original Lagasca name.

Zaluzania augusta var. *augusta,* while very common over much of its range, often becomes dominant in parts of Guanajuato and Queretaro where it frequently covers the low limestone hills. It can be found at elevations of 1500–2500 m on dry open slopes, upon stone-walled hedgerows between cultivated fields and on rocky limestone outcrops generally. Associated taxa include *Acacia, Agave, Jatropha, Mimosa, Opuntia* and *Prosopis.*

It is not unusual to find var. *augusta* heavily grazed by grasshoppers and other insects which consume the leaves late in the growing season, but there is generally no insect damage to the young plants at other times.

Variety *augusta* is a highly variable taxon, especially in its leaf morphology. Leaf shape varies from small, elliptic leaves with entire margins to large, nearly triangular leaves with crenate margins. (Figure 10).

Representative Specimens. mexico. **Aguascalientes:** Hwy to Ojuelos, Jalisco 9 mi E of Aguascalientes, *McVaugh & Koelz 69* (mich); 15 km al NE de Aguascalientes, sobre la carretera a Loreto, *Rzedowski 25095* (ll, mich). **Federal District:** Valley de Teotihuacan, *Conzatti 3413* (mexu); Sierra de Guadalupe, *Miranda 572* (mexu); Lomas de Chapultepec, *Miranda & Barkley 16M954* (f, ll); Hills near Mexico, *Pringle 7415* (mo). **Guanajuato:** San Luis de la Paz limite de los Estados Guanajuato y San Luis Potosi, *Hernandez 132* (mexu); Frequent in Satae, *Kenoyer 1705* (ny); 35 mi E of Guanajuato on Hwy 110 to Dolores Hidalgo, *Olsen 271* (ll); 6 mi NE of Dolores Hidalgo on Hwy 110, *Olsen 272* (ll). **Hidalgo:** 2.5 mi W of Huichapan, *Cronquist 9617* (gh, ll, mich, mo, ny, us); 2 km al NW de Tepeapulco, *Jimenez 226* (asu, mich); Zimapan, *Kenoyer A168* (f); 7 km al NE de Pachuca sobre

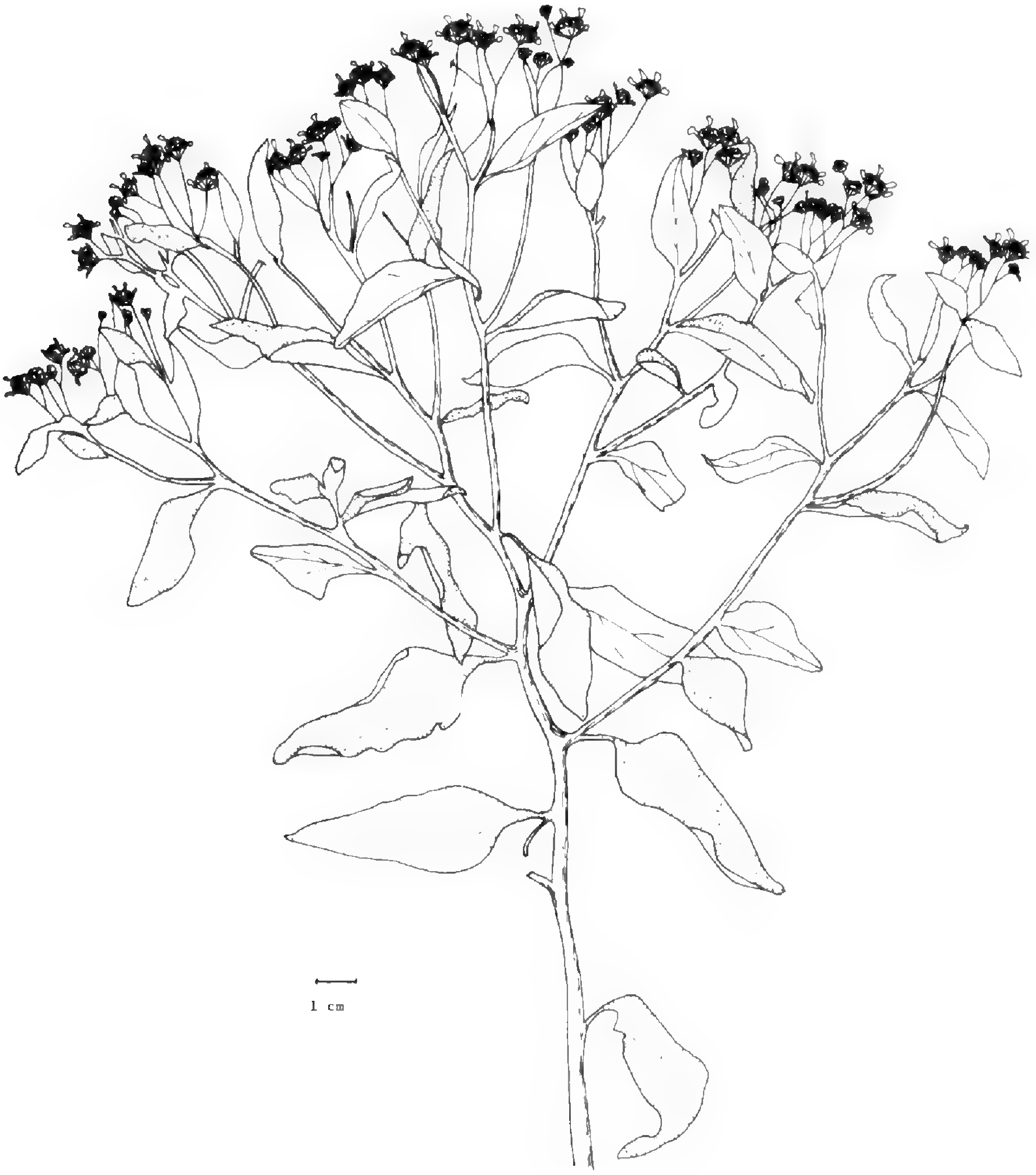


Figure 10. *Zaluzania augusta* var. *augusta*, habit tracing.

la carretera Pachuca-Mineral del Chico, *Moreno 162* (MICH, NY); 10 mi E of Hidalgo-Queretaro border on Hwy 45, *Olsen 284* (LL); 2.5 mi N of Pachuca on Hwy 105 to Real del Monte, *Olsen 286* (LL); Hills near Tula, *Pringle 9996* (F, GH, LL, MO, NY, US); Pachuca, *Purpus 1539* (F, GH, MO, NY, UC); Cerro Banxu, 4 km al N de Orizabita, *Quintero 3134* (MICH); Between Pachuca and Real del Monte, *Rose & Painter 6675* (NY, US); San Gregorio, municipio de San Tepeapulco, *Rzedowski 16965* (US); Huichapan, *Steyermark 52280* (F); W slopes of Cerro Chulco, near Rancho Los Voladores, 5 km SW of Apan, *West C-21* (MICH). **Jalisco:** Between Lagos de Morena and Aguascalientes, *Templeton 802e* (NY). **Mexico:** Vertiente E del Cerro Gordo, cerca San M. de las Piramides, *Cisneros 255* (MICH); 53 mi NW of Mexico City and 54 mi SE of San Juan del Rio, *Cronquist 10522* (LL, NY, US); Polotitlan, *Matuda 26371* (MEXU, NY); Sierra de Guadalupe, *Matuda 29525* (NY); Rio Hondo Canyon, *Pringle 3144* (F, GH, MICH, MO, NY, UC, US); Lecheria, *Pringle 13091*(F, GH, MICH, MO, NMC, US); Near Guadalupe, Valley of Mexico, *Rose & Painter 7278* (US); 2 km al W de Tlalnepantla, *Rzedowski 15854* (MICH); Laderos orientalis del Cerro Gordo, ca de San Martin de las Piramides, *Rzedowski 18834* (LL, MEXU, MICH). **Michoacan:** Dry west facing slopes in former *Acacia-Opuntia* thorn scrub above Rancho las Cerquillas at km 11 on Mex Hwy 120, halfway between Uruetaro and Alvaro Obregon ca 22 km NE Morelia, *Iltis & Cochrane 249* (US). **Morelos:** Xochitepec, *Lyonnet 844* (LL). **Queretaro:** Entre Cadereyta and Vizarron, *Altamirano 1652* (US); Cerro de las Campanas, *Arsene 10065* (F, GH, MO, US); 10 km al N de Queretaro, sobre la carretara a San Luis Potosi, *Crespo 345* (MICH); Cadereyta, *Kelly 669 & 669a* (UC); Hwy 57, 2 mi SE of San Juan del Rio, *Olsen 242* (LL); 8 mi from Hwy 57 on Hwy 45 to Pachuca, *Olsen 243* (LL); 6 mi S of Vizarron on Hwy 120, *Olsen 283* (LL); 4.7 mi N of Queretaro on Rt 57, *Rock M433* (LL). **San Luis Potosi:** 40 mi S of San Luis Potosi on Hwy 57, *Olsen 274* (LL); 2 km E de San Jose Alberquerque, municipio de Santa Maria del Rio, *Rzedowski 8431* (LL).

6b. **Zaluzania augusta** (Lag.) Sch.-Bip. var. **rzedowskii** McVaugh, Contr. Univ. Mich. Herb. **9:** 464. 1972. TYPE: MICH! *McVaugh 17673*. MEXICO: **Zacatecas:** Rocky oak covered hill ca 25 km E of Huejuquilla el Alto near the road between Valparaiso, Zacatecas and Mezquitic, Jalisco. 4–5 Sep 1958.

REPRESENTATIVE SPECIMENS. MEXICO. **Durango:** 87 km N of Durango, *Cronquist 10775* (GH, LL, MEXU, MICH, NY, US); 2–4 mi W of Nombre de Dios *Gentry 8437* (GH, MICH, UC). **Guanajuato:** Steep rocky hills ca 10 km SW of Leon, road to San Francisco del Rincon, *McVaugh 24275* (MICH). **Jalisco:** Near village of Arroyos del Agua, 10 km NW of Huejuquilla del Alto, *Feddema 2377* (LL, MICH, MO, NY); ca 11 mi SE of Lagos de Moreno, near Hwy to Leon, *McVaugh 13246* (MICH, US); Arroyos del Agua, 10 km NW de Huejuquilla, *Rzedowski 17629* (ARIZ, LL, MICH, NY). **Zacatecas:** 15 mi by road E of Huejuquilla del Alto on road leading from San Antonio to N-S road from Valparaiso to Mexquitic, Jalisco, *Anderson & Laskowski 3623* (MICH, NY).

Variety *rzedowskii* differs from var. *augusta* primarily in leaf characters, as noted in the key. It occurs primarily on clay soils,

Figure 11. *Zaluzania augusta* var. *rzedowskii,* habit tracing.

stony pastures, and high shrub grasslands at elevations of 1500–2000 m. Associated taxa include *Bursera, Quercus,* and cacti.

Populations of var. *rzedowskii* from the northern part of its range are typically erect and unbranched, as opposed to the shrubby habit of the more southern populations. This unbranched habit makes these populations resemble superficially the herbaceous perennial taxa, *Zaluzania megacephala* and *Z. discoidea,* although the pappus and pubescent pales of var. *rzedowskii* serve to distinguish readily between them. The convergence in habit seen in these taxa may represent a similar response to external factors such as moisture or exposure; alternatively, it may reflect a common genetic component linking the shrubby taxa with the herbaceous perennial taxa.

One questionable collection, *Cronquist 10775,* has been tentatively assigned to this variety. The pubescence of the upper leaf surface is not whitish as typically found in this taxon and the ligules are only 2-lobed, but the geographic locality (N of Durango), ray pappus of two scales and the pubescent pales suggest placement in var. *rzedowskii.*

7. **Zaluzania pringlei** Greenm., Proc. Amer. Acad. **39:** 101. 1903. TYPE: GH! *Pringle 8710.* MEXICO: **Morelos.** Limestone hills near Jojutla. 18 Oct 1902 (Isotypes: F!, MO!, NY!, UC!, US!).

Perennial shrubs to 3 m in height. Stems glabrous at base becoming puberulent above. Leaves elliptic to ovate, margins glandular-crenate; upper leaves 2.5–3.7 cm long, 0.8–1.5 cm wide, lower leaves 7.4–7.9 cm long, 3.4–3.6 cm wide; pubescence of the upper surface pustulate, lower surface hirsute; petioles 0.5–2.2 cm in length. Peduncles 0.5–1.3 cm long, puberulent. Heads 0.7–1.6 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate; outer series 3.0–3.2 mm long, 1.2–1.3 mm wide, inner series nearly equal. Pales 3.2–3.3 mm long, 1.6–1.7 mm wide. Ray florets present or absent, 1–5, ligules white, 4.5–4.8 mm long, 3.0–3.3 mm wide; throat pubescent, style branches well exserted from the tube. Disc florets ca 50, corolla white, 2.4–2.6 mm long, 2.0–2.4 mm wide; throat pubescent. Ray achenes glabrous, 1.3–1.5 mm long, 0.5–0.7 mm wide, pappus absent. Disc achenes 1.9–2.2 mm long, 0.5–0.8 mm wide. (Figure 12).

Figure 12. *Zaluzania pringlei*, habit tracing.

REPRESENTATIVE SPECIMENS. MEXICO. **Guerrero:** Steep calcareous, brushy E slope, overlooking N end of Chilpancingo, *Cronquist 9718* (LL, MEXU, MICH, NY); 8 mi N of Chilpancingo on Hwy 95 to Acapulco, *Olsen 395* (LL); 3 mi N of Chilpancingo, *Olsen 396* (LL). **Morelos:** 10 km N de Tehuxtla, *Gomez-Pompa 1070* (MEXU). **Puebla:** Along the Pan American Hwy, about 17 road mi SE of Acatlan and about 3 mi SE of Petlacingo, *Cronquist 9696* (GH, LL, MICH, MO, NY, US); Calcareous rocky hills 20 25 km SE of Acatlan, *McVaugh 24001* (MICH).

Zaluzania pringlei is a frequent shrub on calcareous brushy slopes at elevations of 1000 1600 m. It typically is found in subtropical deciduous forests associated with *Acacia, Bursera, Eysenhardtia,* and cacti.

Greenman (1903), presumably because of its usual discoid nature, believed it most closely related to *Zaluzania discoidea.* In my opinion, *Z. pringlei* is allied more closely to the shrubby taxa centering around *Z. montagnifolia,* as evidenced by its ovate, pustulate (on the upper surface), glandular-crenate leaves, shrubby habit, and geographic range. It is clearly distinguished from the latter taxon by floral characters, especially its white corollas.

8. **Zaluzania montagnifolia** (Sch.-Bip.) Sch.-Bip., Flora **44:** 563. 1861. TYPE: P. *Muller 293.* MEXICO: **Vera Cruz:** Between Veracruz and Orizaba. 1857 (Phototype, F!, Fragment, F!).

Ferdinanda montagnaefolia Sch.-Bip., Koch's Berl. Allgem. Gartenz. **179.** 1858.

Zaluzania asperrima Sch.-Bip. var. *asperrima,* Flora **47:** 218. 1864. TYPE: P. *Liebmann 544.* MEXICO: **Puebla:** Chapulco. Oct 1841 (Isotype GH!; Phototypes F!, GH!, NY!).

Zaluzania asperrima Sch.-Bip. var. *montagnaefolia* (Sch.-Bip.) Rob. & Greenm., Proc. Amer. Acad. **34:** 532. 1899.

Perennial shrubs to 4 m in height. Stems glabrous at base becoming hirsute above. Roots without fleshy tubers. Leaves elliptic to ovate, margins crenate, may be glandular, decurrent along the petiole; upper leaves 2.4–4.6 cm long, 1.1–1.7 cm wide, lower leaves 7.4–9.3 cm long, 3.6 4.7 cm wide; pubescence of the upper surface pustulate, lower surface puberulous to tomentose; petioles 1.0–2.0 cm in length. Peduncles 0.9–2.3 cm in length. Heads 1.5–2.0 cm in diameter (including the rays). Involucre 2–3 seriate, the bracts lanceolate, 4.0–4.2 mm long, 1.4–1.6 mm wide, the inner series slightly shorter and broader. Pales 3.4 3.5 mm long, 1.4–1.6 mm wide. Ray florets 6–10, ligules yellow, 6.6–6.9 mm long, 4.5 4.8 mm wide; throat minutely pubescent, style branches well exserted from the tube. Disc florets ca 50, corolla yellow, 2.5–2.7 mm long, 1.7–2.1

mm wide; throat pubescent. Ray achenes glabrous, 1.8–2.0 mm long, 0.4–0.7 mm wide; pappus absent. Disc achenes glabrous, 1.4–1.7 mm long, 0.5 0.8 mm wide. (Figure 13).

REPRESENTATIVE SPECIMENS: MEXICO. **Guerrero:** 9 mi W of Chilpancingo on road to lumber town of Olmiltemi, *Anderson & Laskowski 4347* (F, GH, MICH, MO); 9 mi W of Chilpancingo, *Cronquist 9716* (GH, LL, MICH, MO, US); ca 15 mi SE of Tonatico, *Webster & Brackon 16200* (F, MICH). **Morelos:** Tepozatlan-Chalci, *Paray 1712* (MEXU). **Oaxaca:** Mex. Hwy 190, 25 mi SE of Oaxaca, ca 1 mi S of road to Mitla, *Anderson & Laskowski 4197* (F, GH, MICH); Cerro de Frujano, distrito del Centro, *Conzatti 2317* (F); Cuesta de Huauchilla, Distrito de Wochixtlan, *Conzatti 4253* (US); Magdelena Feitfrac, Distrito de Tlacolula, *Conzatti 4601* (US); Talatlaco, *Conzatti 4812* (LL); 8 mi S of Ejutla and 47 mi S of Oaxaca, *Cronquist & Sousa 10441* (GH, LL, MICH, US); Monte Alban, near Oaxaca, *Pringle 4928* (GH, MEXU, MICH, MO, NY, UC, US); Monte Alban, cerca de la ciudad de Oaxaca, *Rzedowski 19279* (LL, MICH); Monte Alban, near Oaxaca city, *Smith 612(631)* (LL, MICH, MO, NY, UC, US). **Puebla:** 10 km by road S of Esperanza on road to Morelos Canada and Tehuacan, *Anderson & Anderson 5320* (MICH); 31 mi NW of Tehuacan, *Cronquist & Sousa 10378* (GH, LL, MEXU, MICH, US); Tehuacan, *Holway 5347* (GH); Open fields along rt 150, ca 1 mi N of Tehuacan, *King 2645* (LL, MICH, UC, US); Along Hwy 150d to Orizaba, *Olsen 245* (LL); ca 4 mi S of Esperanza on Mex 28 to Tehuacan, *Olsen 246* (LL); 4 mi S of Esperanza, *Olsen 247* (LL); 10 mi N of Tehuacan, *Olsen 248* (LL); 16 mi N of Tehuacan on Hwy 190 to Puebla, *Olsen 249* (LL); ca 30 mi S of Esperanza along Mex 28 to Tehuacan, *Olsen 365* (LL); Along Hwy 125, ca 3 mi S of Acatepec, *Olsen 367* (LL); In the vicinity of San Luis Tultitlanapa, near Oaxaca, *Purpus 2530* (GH, MO, NY, UC, US); Barrancas near Tlanisloltepec, *Purpus 3823* (GH, MO, NY, UC, US); Rocky soils, Tlacuilaltepec, *Purpus 3824* (GH, MO, NY, UC, US); Tehuacan, *Purpus 5610* (F, MO, UC); Near Tehuacan, *Rose & May 5947* (US); 2 km al SE of Tehuacan sobre la carretera a Caxcatlan, *Rzedowski 28154* (MICH). **Vera Cruz:** 3 mi NE of Acultzingo, *Cronquist & Sousa 10352* (GH, LL, MICH, US); Orizaba, *Kenoyer A173* (F).

Zaluzania montagnifolia is a locally common shrub in south-central and southeastern Mexico at elevations of 1500–2200 m. It is relatively low and spreading in the northern part of its range, becoming taller and less highly branched to the south. *Zaluzania montagnifolia* occurs on dry calcareous soils, frequently along rocky hillsides. Associated taxa include: *Acacia, Agave, Bursera, Juniperus, Pinus, Prosopis,* and *Quercus.*

Zaluzania montagnifolia is the central element in a group of shrubby, epappose taxa. It is most closely related to *Z. pringlei* and *Z. sodiroi,* as evidenced by its vegetative morphology, habit and distribution; however, it is easily distinguished from the former by its yellow florets, and from the latter by its pustulate upper leaf surface.

Figure 13. *Zaluzania montagnifolia,* habit tracing.

9. **Zaluzania sodiroi** Hieron., *In* Engl. Bot. Jahrb. **29:** 35. 1900. TYPE: B. *Sodiro 31/1.* ECUADOR: Arid inter-Andean hills, w/o date (Phototype, F!; Isotype fragment, US!).

Zaluzania nonensis Hieron., *In* Engl. Bot. Jahrb. **29:** 36. 1900. TYPE: B. *Sodiro 31/2.* ECUADOR: Near Nono, in silvis subandinis, w/o date (Phototype F!, NY!).

Zaluzania quitensis Hieron., *In* Engl. Bot. Jahrb. **29:** 37. 1900. TYPE: B. *Sodiro 31/3.* ECUADOR: In hills near Quito, w/o date (Phototype F!, NY!; Isotype fragment, US!).

Monactis subdeltoidea Robinson, Proc. Amer. Acad. **47:** 210. 1911. TYPE: B. *W. Jameson 162.* ECUADOR: on the banks of the Machangara River, near Quito, 2750 m, 21 Jan 1856 (Isotype fragment, US!).

Kingianthus sodiroi (Hieron.) H. Robinson, Phytologia **38:** 415. 1978.

Perennial shrubs to 3 m in height. Stems puberulent at base to tomentose above. Roots without fleshy tubers. Leaves ovate, margins glandular-dentate, upper leaves 2.9–4.7 cm long, 0.6–1.5 cm wide, lower leaves 7.6–11.5 cm long, 3.7–6.7 cm wide; pubescence of the upper surface hirsute, lower surface tomentose; petioles 0.5–1.9 cm in length. Peduncles 0.3–1.0 cm long, tomentose. Heads 1.1–1.5 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate, outer series 2.9–3.5 mm long, 1.0–1.4 mm wide, inner series longer with the same width. Ray florets 8–10, ligules yellow, 6.2–6.5 mm long, 3.2–3.5 mm wide; throat glabrous, style branches well exserted from the tube. Disc florets ca 20, corolla yellow, 2.7–3.1 mm long, 1.0–1.3 mm wide; throat glabrous. Ray achenes glabrous, 2.7–3.1 mm long, 0.6–0.8 mm wide; pappus absent. Disc achenes glabrous, 1.8–2.0 mm long, 0.6–0.7 mm wide. (Figure 14).

REPRESENTATIVE SPECIMENS. ECUADOR: Vicinity of Quito, Cotocollao, *Asplund 6116* (NY, US); Machachi, *Asplund 6246* (NY, US); North rim of the valley of the Rio de Canar, between Tambo and Suscal, *Camp & Giler E-2785* (US); Entre la Magdelena y Chillogallo, *Firmin 140* (US); Hacienda S. Gridro, entro la Magdelena y Chillogallo, *Firmin 471* (LL, US); Quito, *Holway & Holway 948* (US); In coll. y Chimbia, prp. Quito, *Mille 568* (MO); Guapalo, roadside E of Quito, *Olsen & Escobar 419* (LL); In roadside waste areas across from Administration de Aduanas, Pan American Hwy km 6.5, *Olsen & Escobar 435* (LL); Along Pan American Hwy N of Machachi, *Olsen & Escobar 485* (LL); Ficoa, near Ambato, *Pachano 134* (US); Quito, *Sodiro 568* (NY); Entre Pangala y Alao, Prov. Chimborazo, *Solis 7591* (F); Valle Seco del Pedregal, cord. Oriental, *Solis 8439* (F); De Cunchibama a Tangaleo, Prov. Tungurahua, *Solis 8594* (F); Chimbacalle, Quito, *Solis 10104* (F); Shanshipamba, Prov. Imbabura, *Solis 14254* (F); Shanshipamba, Pena Blanca, *Solis 14448* (F); Magotilla-Magota, Prov. Pichincha, *Solis 16514* (F); Valley of Lloa, about 6 km WSW of Quito overlooking the Rio Cinto, *Ugent & Ugent 5594* (US).

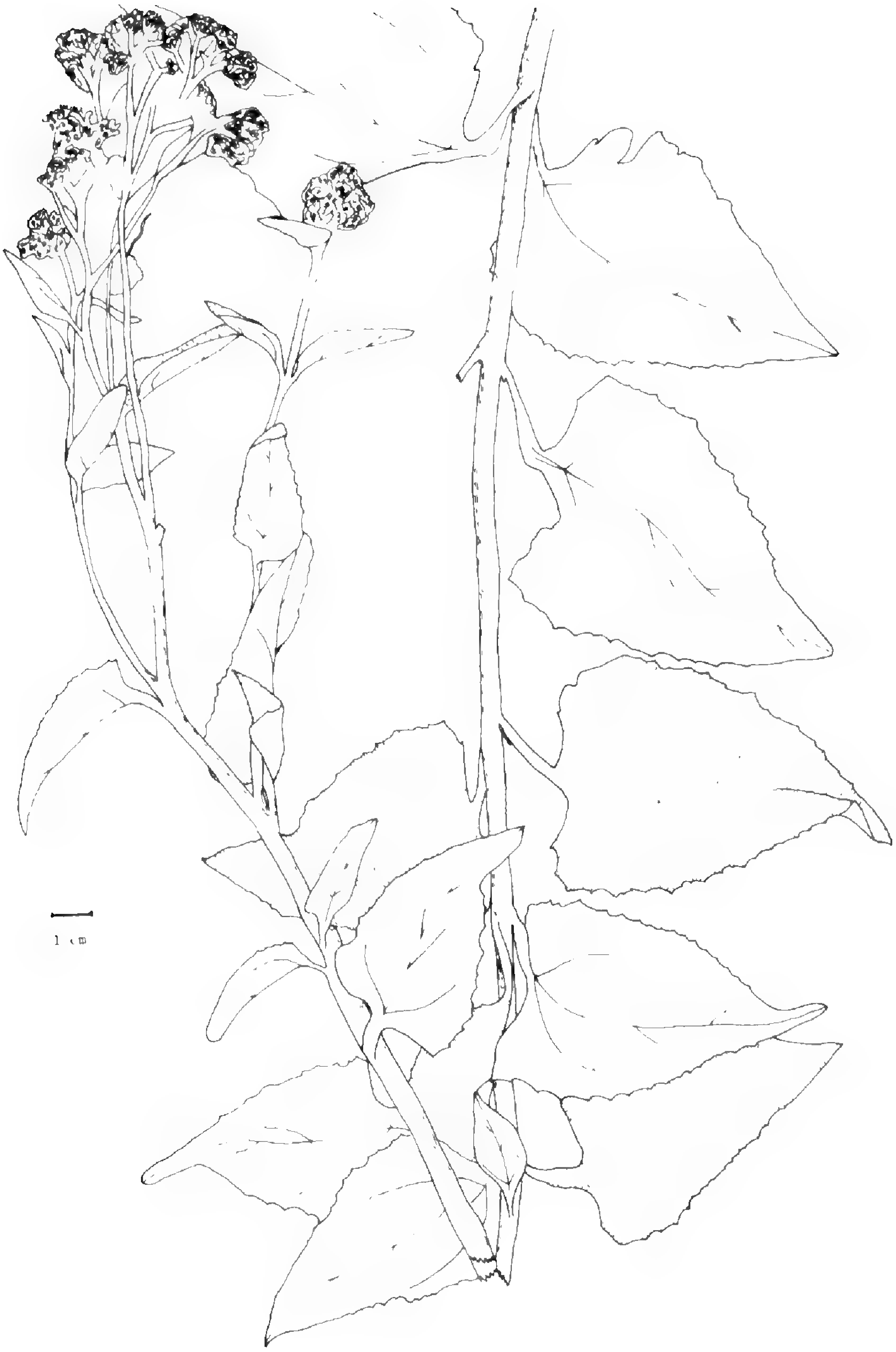


Figure 14. *Zaluzania sodiroi*, habit tracing.

Zaluzania sodiroi occurs as a roadside shrub in the high grasslands of Ecuador at elevations of 2300–3200 m. Associated taxa include: *Castilleja, Passiflora, Rumex, Senecio, Solanum,* and bamboo.

Zaluzania sodiroi presumably arose as a chance introduction into Ecuador, probably from a *Z. montagnifolia*-like ancestor. *Z. sodiroi* differs from other *Zaluzania* taxa in producing one unusual flavonoid compound (Olsen, 1977) as well as the usual set of glycosides. On paper chromatograms, this compound has previously only been seen in *Calea;* however, the floral morphology and alternate leaves in *Z. sodiroi* clearly distinguish it from *Calea.*

The recently published monotypic genus *Kingianthus* (Robinson, 1978), erected to house *Zaluzania sodiroi,* is certainly not sufficiently distinct to warrant exclusion from *Zaluzania.* Robinson believes this taxon related to *Monactis* rather than to *Zaluzania,* based on his interpretation of micromorphological characters. In my opinion, the taxon in question is correctly placed in *Zaluzania.* The $n = 18$ chromosome number and the *Zaluzania* flavonoid pattern (Olsen, 1977) clearly distinguish it from *Monactis* ($n = 30$ and a very different flavonoid pattern) and strongly support its inclusion in *Zaluzania.*

EXCLUDED TAXA

Zaluzania, Comm. ex Gaertn. f. Fruct. **3:** 74. 1805. Name invalid when published.
  =*Bertiera* Aubl. Pl. Gui. **1:** 180. 1775. Rubiaceae.

Zaluzania anthemidifolia Rob. & Greenm. Proc. Amer. Acad. **34:** 531. 1899.
  =*Hybridella anthemidifolia* (Rob. & Greenm.) Olsen, Madrono **24:** 29. 1977.

Zaluzania ensifolia Sch.-Bip. Flora **47:** 216. 1864.
  =*Viguiera ensifolia* Blake, Contr. Gray Herb. **54:** 58. 1918.

Zaluzania globosa (Ort.) Sch.-Bip. var. **globosa,** Flora **44:** 564. 1861.
  =*Hybridella globosa* (Ort.) Cass. var. *globosa,* Dict. Sci. Nat. **22:** 86. 1821.

Zaluzania globosa var. **myriophylla** (Sch.-Bip.) Sharp, Ann. Missouri Bot. Gard. **22:** 103. 1935.
  =*Hybridella globosa* var. *myriophylla* (Sch.-Bip.) Olsen, Madrono **24:** 29. 1977.

Zaluzania grayana Rob. & Greenm. Proc. Amer. Acad. **34:** 531. 1899.
  =VIGUIERA TRILOBA (Gray) Olsen, *comb. nov.*
    Gymnolomia triloba Gray, Proc. Amer. Acad. **17:** 217. 1882. TYPE: GH! *Lemmon 846.* Arizona. Mountains of southern Arizona, south of Rucker's Valley. 1881.
    Zaluzania grayiana Rob. & Greenm. Proc. Boston Soc. Nat. Hist. **29:** 104. 1899. An orthographic variant.

Zaluzania indica Reinw. ex Blume, Mus. Bot. Lugd. Bat. **1:** 239.
=*Geniostoma rupestre* Forst., Char. Gen. **24:** 12. 1776. Loganiaceae.
Zaluzania oppositifolia Sch.-Bip., Flora **44:** 562. 1861.
=*Calea scabrifolia* Benth. & Hook., Gen. Pl. **2:** 391. 1873.
Zaluzania pinnatilobata Sch.-Bip., Flora **47:** 219. 1864.
=*Viguiera pinnatilobata* (Sch.-Bip.) Blake, Contr. Gray Herb. **54:** 95. 1918.
Zaluzania resinosa S. Wats., Proc. Amer. Acad. **21:** 388. 1886.
=*Greenmaniella resinosa* (Watson) Sharp, Ann. Missouri Bot. Gard. **22:** 141. 1935.
Zaluzania squarrosa Sch.-Bip., Flora **47:** 216. 1864.
=*Viguiera squarrosa* (Sch.-Bip.) Blake, Proc. Amer. Acad. **49:** 376. 1913.

LITERATURE CITED

AXELROD, D. I. 1958. Evolution of the Madro Tertiary geoflora. Bot. Rev. **24:** 433 509.

BAAGØE, J. 1974. The genus *Guizotia* (Compositae). A taxonomic revision. Bot. Tidsskr. **69:** 1-39.

BEAMAN, J. H., & B. L. TURNER. 1962. Chromosome numbers in Mexican and Guatemalan Compositae. Rhodora **64:** 271-276.

BENTHAM, G. 1873. Notes on the classification, history and geographical distribution of Compositae. Jour. Linn. Soc., Bot. **13:** 335-577.

BLAKE, S. F. 1918. A revision of the genus *Viguiera*. Contr. Gray Herb. **54:** 1 205.

BUTTERWICK, M. L. 1975. A systematic treatment of series *Pinnatilobatae* of *Viguiera*. M.A. Thesis, The University of Texas at Austin.

CARLQUIST, S. 1966. Wood anatomy of Compositae: A summary, with comments on factors controlling wood evolution. Aliso **6:** 25 44.

———. 1975. Ecological strategies of xylem evolution. The University of California Press, Berkeley, Los Angeles and London.

———. 1976. Tribal relationships and phylogeny of the Asteraceae. Aliso **8:** 465 492.

CASSINI, A. 1821. Dict. Sci. Nat. **22:** 86. (Reproduced in R. M. KING and H. D. DAWSON, 1975, Cassini on Compositae. **1:** 454. Oriole Editions, Inc. Sentry Press, New York.

CRONQUIST, A. 1968. The evolution and classification of flowering plants. Houghton-Mifflin Co. Boston.

DEJONG, D. C. D., & E. K. LONGPRE 1963. Chromosome studies in Mexican Compositae. Rhodora **65:** 225 240.

GUPTA, P. K., D. K. AGARWAL, & A. K. SRIVASTAVA. 1972. Further cytological investigations in Indian Compositae. Cytologia **37:** 581 593.

HEISER, C. B. 1963a. Artificial intergeneric hybrids of *Helianthus* and *Viguiera*. Madrono **17:** 118 127.

———. 1963b. Numeracion cromosomica de plantas ecuatorianas. Ciencia y Nat. (Quito) **6:** 2-6.

———, & D. M. SMITH. 1955. New chromosome numbers in *Helianthus* and related genera (Compositae). Proc. Indiana Acad. Sci. **64:** 250 253.

HIERONYMUS, G. 1900. Plantae ecuadorensis II. Engl. Bot. Jahrb. **29:** 35 37.

Hoffmann, O. 1894. *In:* Engler and Prantl, Die Naturlichen Pflanzenfamilien **4:** 233–234.

Jolad, S. D., R. M. Wiedhopf, & J. R. Cole. 1974. Tumor-inhibitory agent from *Zaluzania robinsonii* (Compositae). Jour. Pharm. Sci. **63:** 1321-1322.

Jones, S. B. 1970. Chromosome numbers in Compositae. Bull. Torrey Bot. Club **97:** 168–174.

Johnson, A. W. 1968. The evolution of desert vegetation in western North America. *In:* Desert Biology. C. W. Brown, Jr., Ed. Academic Press.

Keil, D. J., & T. F. Stuessy. 1975. Chromosome counts of Compositae from the United States, Mexico and Guatemala. Rhodora **77:** 171–195.

Kunth, C. S. 1832. Syn. Gen. Comp.

Longpre, E. K. 1970. The systematics of the genera *Sabazia, Selloa* and *Tricarpha* (Compositae). Publ. Mus. Michigan State Univ., Biol. Ser. **4:** 283–384.

Maldonado-Koerdell, M. 1964. Geohistory and Paleogeography of Middle America. Handbook of Middle Amer. Indians **1:** 3–32.

McVaugh, R. J. 1972. Compositarum Mexicanarum Pugillus. Contr. Univ. Michigan Herb. **9:** 359–484.

Olsen, J. 1977a. Re-establishment of the genus *Hybridella* (Asteraceae:Heliantheae). Madrono **24:** 29–36.

______. 1977b. Systematic studies in the genus *Zaluzania* (Asteraceae:Heliantheae). Ph.D. Dissertation, The University of Texas at Austin.

Persoon, C. H. 1807. Syn. Plant. **2:** 473.

Powell, A. M. 1965. Taxonomy of *Tridax* (Compositae). Brittonia **17:** 47–96.

______, & J. Cuatrecasas. 1970. Chromosome numbers in the Compositae, Colombian and Venezuelan species. Ann. Missouri Bot. Gard. **57:** 374–379.

______, & R. M. King. 1969. Chromosome numbers in the Compositae: Colombian species. Am. Jour. Bot. **56:** 116–121.

______, & S. Sikes. 1970. Chromosome numbers of some Chihuahuan Desert Compositae. Southw. Nat. **15:** 175–186.

______, & B. L. Turner. 1963. Chromosome numbers in the Compositae. VII. Additional species from the southwestern United States and Mexico. Madroño **17:** 128–140.

Robinson, B. L., & J. M. Greenman. 1899. Revision of the genera *Montanoa, Perymenium* and *Zaluzania*. Proc. Amer. Acad. Sci. **34:** 507–534.

Robinson, H. 1976. Studies in the Heliantheae (Asteraceae). VII. Notes on the genus *Monactis*. Phytologia **34:** 33–45.

______. 1978. Studies in the Heliantheae (Asteraceae). XI. A new Genus *Kingianthus*. Phytologia **38:** 415–416.

Rzedowski, J. 1968. Nota sobre la identidad de los generos *Aiolotheca* DC. y *Tonalanthus* T. S. Brandegee (Compositae). Brittonia **20:** 166–168.

______. 1973. Geographical relationships of the flora of Mexican dry regions. *In:* A. Graham, ed., Vegetation and vegetational history of northern Latin America. Elsevier Scientific Publishing Co. New York.

Schultz-Bipontinus, C. H. 1861. Uber die Gattung *Zaluzania* Persoon, eine historische-kritische Untersuchung. Flora **44:** 553–565.

______. 1864. Ueber die Gattung *Zaluzania* Pers. Flora **47:** 216–220.

Sharp, W. M. 1935. A critical study of certain epappose genera of the Heliantheae:Verbesininae of the natural family Compositae. Ann. Missouri Bot. Gard. **22:** 51–153.

Solbrig, O. T., D. W. Kyhos, M. Powell, & P. H. Raven. 1972. Chromosome numbers in Compositae VIII: Heliantheae. Amer. J. Bot. **59:** 869–878.

Standley, P. C. 1926. Trees and Shrubs of Mexico. Contr. U. S. Natl. Herb. **23:** 1313–1721.

Stebbins, G. L. 1950. Variation and evolution in plants. Columbia University Press, New York and London.

______. 1971. Chromosomal evolution in higher plants. Addison-Wesley Pub. Co. Reading, Mass.

Strother, J. L. 1976. Chromosome studies in Compositae. Amer. J. Bot. **63:** 247–250.

Stuessy, T. F. 1978. A revised subtribal classification of the Heliantheae. *In*, V. H. Heywood, J. B. Harborne, & B. L. Turner, eds. The Biology and Chemistry of the Compositae. Academic Press, London.

Torres, A. M. 1968. Revision of *Jaegeria* (Compositae:Heliantheae). Brittonia **20:** 52–73.

Turner, B. L., J. H. Beaman, & H. F. L. Rock. 1961. Chromosome numbers in the Compositae V. Mexican and Guatemalan species. Rhodora **63:** 121–130.

______, & W. L. Ellison. 1960. Chromosome numbers in the Compositae I. Meiotic chromosome counts for 25 species of Texas Compositae including 6 new generic reports. Texas J. Sci. **12:** 146–151.

______, ______, & R. M. King. 1961. Chromosome numbers in the Compositae IV. North American species, with phyletic interpretations. Am. Jour. Bot. **48:** 216–223.

______, & D. Flyr. 1966. Chromosome numbers in the Compositae X. North American Species. Am. Jour. Bot. **53:** 24–33.

______, & M. C. Johnston. 1961. Chromosome numbers in the Compositae III. Certain Mexican species. Brittonia **13:** 64–69.

______, & R. M. King. 1964. Chromosome numbers in the Compositae VIII. Mexican and Central American species. Southw. Naturalist **9:** 27–39.

______, & A. M. Powell. 1978. Disposition of genera in the dismantled polyphyletic tribe Helenieae (Asteraceae). *In:* V. H. Heywood, J. B. Harborne, and B. L. Turner, Eds., The biology and chemistry of the Compositae. Academic Press, London.

______, ______, & J. Cuatrecasas. 1967. Chromosome numbers in Compositae XI. Peruvian species. Ann. Missouri Bot. Gard. **54:** 172–177.

______, ______, & R. M. King. 1962. Chromosome numbers in the Compositae VI. Additional Mexican species. Rhodora **64:** 251–271.

______, ______, & T. R. Watson. 1973. Chromosome numbers in Mexican Asteraceae. Am. Jour. Bot. **60:** 592–597.

Urbatsch, L. E., & B. L. Turner. 1975. New species and combinations in *Sabazia* (Heliantheae:Galinsoginae). Brittonia **27:** 348–354.

Wagner, W. H. Jr. 1961. Problems in the classification of ferns. Recent Advances Bot. **1:** 841–844.

Whalen, M. 1977. Taxonomy of *Bebbia* (Compositae:Heliantheae). Madroño **24:** 112–123.

Whiffin, T., & M. W. Bierner. 1972. A quick method for computing Wagner trees. Taxon **21:** 83–90.

Wodehouse, R. P. 1945. Hayfever Plants: Their appearence, distribution, time of flowering and their role in hayfever with special reference to North America. Chronica Botanica Co. Waltham, Mass.

Yabuta, G., J. S. Olsen, & T. J. Mabry. 1978. Sesquiterpene lactones from the genus *Zaluzania* (Compositae:Heliantheae). Rev. Latinoamer. Quim. **9:** 83 85.

Yates, W. F. Jr. 1967. Taxonomic studies in the genus *Heliomeris* (Compositae). Ph.D. Dissertation, Indiana University.

DEPARTMENT OF BOTANY
SOUTHWESTERN AT MEMPHIS
MEMPHIS, TENNESSEE
38112

ANNOTATED LIST OF THE FERNS AND FERN ALLIES OF ARKANSAS[1]

W. Carl Taylor and Delzie Demaree

Records of ferns and fern allies in Arkansas date back to the travels and collections of Nuttall (1821, 1835). In 1835, Nuttall reported 23 species of pteridophytes from the Arkansas Territory. Lesquereux (1860) recorded 35 species for the state as part of a geological survey. Harvey (1881) compiled an annotated list of Arkansas ferns with notes on the ranges and habitats of 40 taxa. In a list of Arkansas plants, Branner and Coville (1891) included 45 species of ferns and fern allies.

Buchholz (1924) made deletions from and additions to the lists of Harvey and Branner and Coville to arrive at 46 species and 3 varieties of pteridophytes for Arkansas. Buchholz's study was immediately followed by Palmer's (1924) report of two new species for the state. These additions were incorporated in a supplement ot the Arkansas plants by Buchholz and Palmer (1926) which lists 15 pteridophytes. Scully (1937, 1939) produced two papers describing the ferns and fern allies found in and around Hot Springs National Park.

The most recent account of the Arkansas pteridophytes was written by Moore (1940). It includes an annotated list of 67 species and lesser taxa. Moore (1941) also published a paper entitled "Some Noteworthy Fern Communities of Arkansas" which contains lists of species found in five different localities within the Interior Highlands. The latest, statewide, compilatory list available on all Arkansas vascular plants is by Smith (1978). This work includes distribution maps for 70 ferns and fern allies.

Since the early 1940's, thousands of voucher specimens have been added to herbaria and taxonomic research has resulted in a number of nomenclatural changes. Over a dozen additional taxa have been discovered in the state including those reported by Chandler (1941), Moore (1947, 1950, 1951), Wagner (1962), Bowers and Redfearn (1967), Farrar and Redfearn (1968), Tucker (1971), Thomas (1976), and Buck (1977). These additions and changes make it desirable to provide an up-to-date account of the Arkansas pteridophytes.

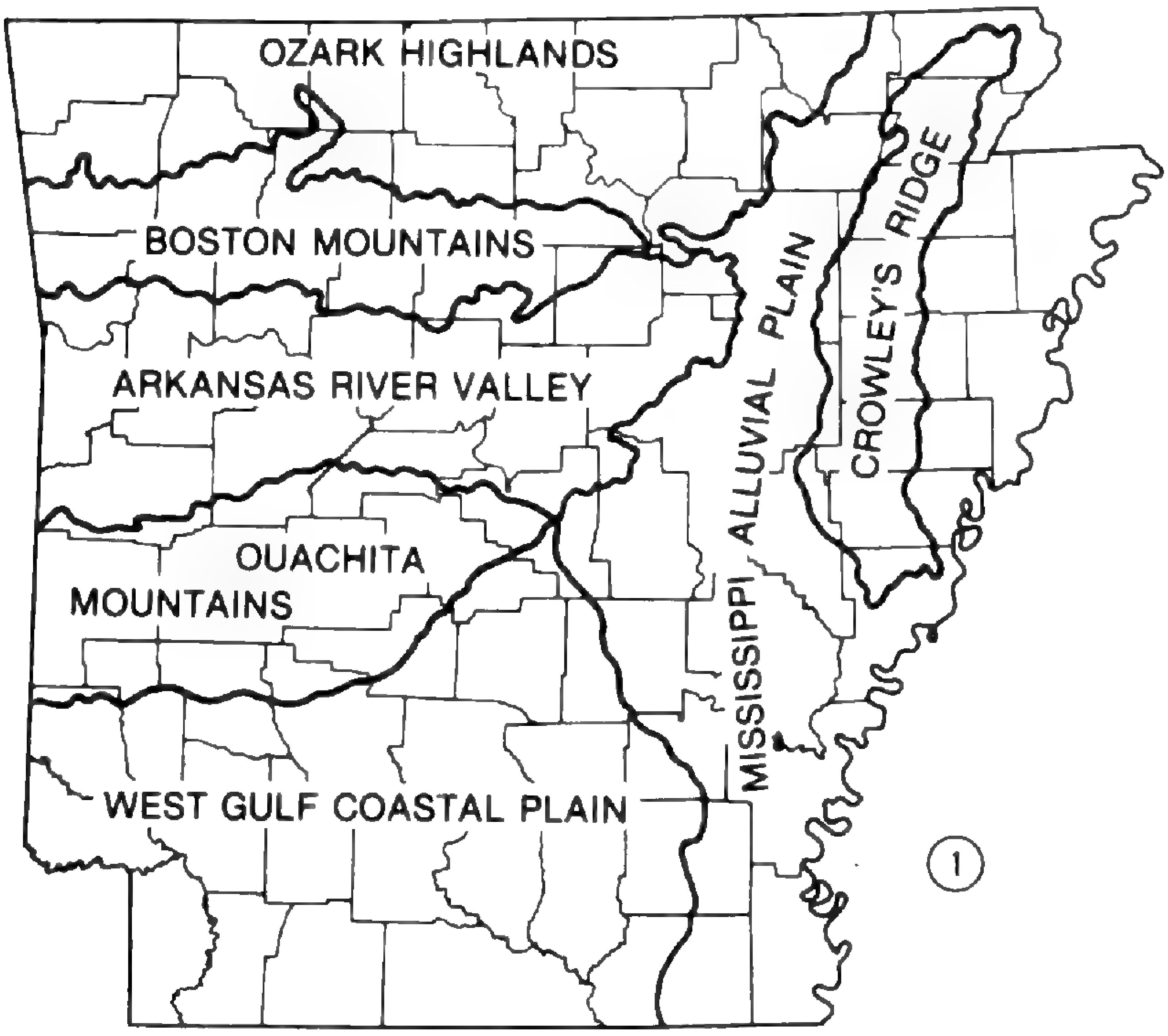
---

[1] Research supported in part by National Science Foundation grant DEB75-16333.

TABLE 1. **List of Herbaria Examined**[2]

(APCR)	Arkansas Polytechnic College Russellville, Arkansas
(ARKSU)	Arkansas State University Jonesboro, Arkansas
(F)	Field Museum of Natural History Chicago, Illinois
(HXC)	Hendrix College Conway, Arkansas
(MO)	Missouri Botanical Garden St. Louis, Missouri
(MEM)	Memphis State University Memphis, Tennessee
(NLU)	Northeast Louisiana University Monroe, Louisiana
(NY)	New York Botanical Garden Bronx, New York
(PH)	Academy of Natural Sciences Philadelphia, Pennsylvania
(SIU)	Southern Illinois University Carbondale, Illinois
(SMS)	Southwest Missouri State University Springfield, Missouri
(SMU)	Southern Methodist University Dallas, Texas
(UARK)	University of Arkansas Fayetteville, Arkansas
(UCA)	University of Central Arkansas Conway, Arkansas
(US)	Smithsonian Institution Washington, D.C.

[2] Abbreviations mostly after Holmgren and Keuken (1974).


OZARK HIGHLANDS
BOSTON MOUNTAINS
ARKANSAS RIVER VALLEY
OUACHITA MOUNTAINS
WEST GULF COASTAL PLAIN
MISSISSIPPI ALLUVIAL PLAIN
CROWLEY'S RIDGE

①


BENTON
CARROLL
BOONE
MARION
BAXTER
FULTON
RANDOLPH
CLAY
WASHINGTON
MADISON
NEWTON
SEARCY
IZARD
SHARP
LAWRENCE
GREENE
STONE
CRAIGHEAD
MISSISSIPPI
CRAWFORD
FRANKLIN
JOHNSON
POPE
VAN BUREN
CLEBURNE
INDEPENDENCE
JACKSON
POINSETT
SEBASTIAN
LOGAN
CONWAY
FAULKNER
WHITE
WOODRUFF
CROSS
CRITTENDEN
YELL
PERRY
ST FRANCIS
SCOTT
PULASKI
LONOKE
PRAIRIE
MONROE
LEE
POLK
MONTGOMERY
GARLAND
SALINE
PHILLIPS
HOT SPRING
GRANT
JEFFERSON
ARKANSAS
HOWARD
PIKE
SEVIER
CLARK
DALLAS
CLEVELAND
LINCOLN
DESHA
LITTLE RIVER
HEMPSTEAD
NEVADA
OUACHITA
CALHOUN
BRADLEY
DREW
MILLER
LAFAYETTE
COLUMBIA
UNION
ASHLEY
CHICOT

②

The sequence of families and genera listed in this paper follows Crabbe, Jermy, and Mickel (1975). Lesser taxa are arranged alphabetically under the genus. Synonyms that have been applied to Arkansas material are given in brackets. Data gathered from personal collections and specimens contained in the herbaria listed in Table I were used to develop habitat descriptions and distribution maps for the various taxa.

Arkansas can be divided into several physiographic regions based on differences in topography, geology, soil associations, and forest types (Foti, 1974). In Figure 1, the Interior Highlands are divided into the Ozark Highlands, the Boston Mountains, the Arkansas River Valley, and the Ouachita Mountains, while the Gulf Coastal Plain Lowlands are divided into the West Gulf Coastal Plain, the Mississippi Alluvial Plain, and Crowley's Ridge. Many species of Arkansas pteridophytes show distribution patterns which correspond to these physiographic regions. These regions are mentioned when they are useful in characterizing distribution patterns.

A representative specimen is cited for each county in which the species, hybrid, or infraspecific taxon has been collected (see Figure 2 for map of Arkansas counties). Dot maps, which depict the cited specimens, are included near the end of this paper.

Remarks on some doubtful and excluded taxa follow the annotated list.

ANNOTATED LIST OF ARKANSAS PTERIDOPHYTA

LYCOPODIACEAE

1. **Lycopodium appressum** (Chapm.) Lloyd & Underw., Bull. Torrey Bot. Club 27: 153. 1900. [*Lycopodium inundatum* var. *bigelovii* Tuckerm.; *Lycopodium inundatum* var. *appressum* Chapm.]

Moist to wet, sandy, disturbed soil along streams and railroad tracks, at edges of lakes, in open pine woods, waste ground, and sandy bogs; West Gulf Coastal Plain.

Clark Co.: *Taylor 2172* (SIU). Hempstead Co.: *D. Moore 490062* (UARK). Ouachita Co.: *Taylor 2627* (SIU). Saline Co.: *Young 1513* (UCA). Union Co.: *D. Moore 6264* (APCR).

2. **Lycopodium lucidulum** Michx., Fl. Bor. Am. 2: 284. 1803.

North-facing, shaded, sandstone outcrops in the Boston Mountains.

Franklin Co.: lower talus slope; Spy Rock Hollow; sect. 20, T12N, R26W; *Redfearn 21148* (SMS). Madison Co.: tributaries to Mulberry Creek; sect. 1–12, T13N, R24–25W; *Redfearn 18553* (SMS). Newton Co.: narrow ravine along upper reaches of Terrapin Branch; sect. 26, T14N, R23W; *Redfearn & Weber 27493* (SMS).

SELAGINELLACEAE

3. **Selaginella apoda** (L.) Spring (as "apus") in Mart., Fl. Bras. 1(2): 119. 1840. [*Lycopodium apodum* L.; *Diplostachyum apodum* (L.) Beauv.; *Selaginella apoda* (L.) Fern.]

Moist to wet, usually shaded, sandstone and shale outcrops, low meadows, seepage areas, and sandy or clayey soils along stream banks.

Ashley Co.: *Taylor 1874* (SIU). Clark Co.: *Redfearn 24404* (SMS). Cleburne Co.: *Babb 1023* (ARKSU). Drew Co.: *Demaree 17899* (MO). Faulkner Co.: *Taylor 2008* (SIU). Garland Co.: *Taylor 2557* (SIU). Greene Co.: *D. Moore 480681* (UARK). Hempstead Co.: *D. Moore 56128* (UARK). Hot Spring Co.: *Taylor 936* (SIU). Howard Co.: *Iltis 680* (UARK). Little River Co.: *D. Moore 50021* (UARK). Logan Co.: *Taylor 1044* (SIU). Montgomery Co.: *D. Moore 430154* (UARK). Perry Co.: *Issacs 3319* (UCA). Polk Co.: *J. Moore 3145* (UCA). Pope Co.: *D. Moore 520759* (UARK). Randolph Co.: *Taylor 2665* (SIU). Sevier Co.: *D. Moore 510094* (UARK). Union Co.: *Taylor 2631* (SIU). Van Buren Co.: *Johnson 292* (HXC). Washington Co.: *French 269* (UARK).

4. **Selaginella eclipes** Buck, Can. J. Bot. 55: 366. 1977.

Moist to wet, usually shaded, calcareous rock outcrops; Ozark Highlands and Boston Mountains.

Benton Co.: *D. Moore 321202* (UARK). Crawford Co.: *Taylor 1096* (SIU). Franklin Co.: *Redfearn 23699* (SMS). Fulton Co.: *Redfearn 26438* (SMS). Izard Co.: *Taylor 1268* (SIU). Madison Co.: *Redfearn 18857* (SMS). Marion Co.: *D. Moore 350165* (UARK). Newton Co.: *Taylor 2690* (SIU). Searcy Co.: *Redfearn 14273* (SMS). Stone Co.: *D. Moore 450810* (UARK). Washington Co.: *Callicott s.n.* (UARK).

5. **Selaginella riddellii** Van Eselt., Contr. U.S. Nat. Herb. 20: 162. 1918. [*Selaginella arenicola* subsp. *riddellii* (Van Eselt.) Tryon]

Sandy, open soil.

Nevada Co.: roadside along Hwy. 24; ca. 0.3 mi. E of Bluff City; *Taylor 2747* (SIU). Ouachita Co.: hillside; ca. 0.5 mi. N of Chidester Baptist Church, Chidester and dumping ground along Hwy. 368; ca. 1.7 mi. W of jct. Hwys. 24 & 368; *Taylor 2743* (SIU). Pike Co.: outcrops along Little Missouri River; NW¼ sect. 6, T5S, R27W; *Roberts & Bradford s.n.* (UARK). Pope Co.: sandstone bluffs above Arkansas River; Norristown Mountain, Russellville; *Tucker 6563* (SMU).

6. **Selaginella rupestris** (L.) Spring, Flora 21: 149, 182. 1838. [*Lycopodium rupestre* L.]

Exposed, sandstone outcrops.

Baxter Co.: *Tucker 6809* (APCR). Benton Co.: *D. Moore 350203* (MO). Carroll Co.: *Haas 1516* (UCA). Cleburne Co.: *Babb 1580* (ARKSU). Conway Co.: *J. Moore 1097*

(UARK). Independence Co.: *Demaree 59791* (SMU). Izard Co.: *Demaree 32518* (MO). Marion Co.: *Redfearn 08163* (SMS). Newton Co.: *D. Moore 32490* (UARK). Pope Co.: *Redfearn 26772* (SMS). Searcy Co.: *D. Moore 350160* (MO).

ISOETACEAE

7. **Isoetes butleri** Engelm., Bot. Gaz. 3: 1. 1878.

Seasonally moist to wet calcareous soil pockets on limestone glades and dolomite, calcareous shale, or chalk outcrops.

Carroll Co.: *Bush 1350* (MO). Little River Co.: *D. Moore 50040* (UARK). Madison Co.: *Haas 1519* (UCA). Newton Co.: *Taylor 1228* (SIU). Polk Co.: *J. Moore 3147* (UCA). Pulaski Co.: *Harper 17* (PH). Sebastian Co.: *D. Moore 490016* (UARK). Sharp Co.: *Hartsoe 333* (SMU). Stone Co.: *D. Moore 470698* (UARK). Washington Co.: *D. Moore 53186* (UARK). Yell Co.: *Buchholz s.n.* (UARK).

8. **Isoetes melanopoda** Gay & Dur., Bull. Soc. Bot. Fr. 11: 102. 1864.

Seasonally moist to wet woods, meadows, fields, margins of ponds, roadside ditches, and thin soil depressions on sandstone, shale, or igneous rock outcrops.

Arkansas Co.: *D. Moore 510225* (UARK). Baxter Co.: *J. Moore 5677* (UCA). Benton Co.: *D. Moore 400259* (UARK). Cleburne Co.: *Taylor 1011* (SIU). Conway Co.: *Demaree 23119* (MO). Faulkner Co.: *Taylor 2006* (SIU). Fulton Co.: *D. Moore 330226* (UARK). Garland Co.: *Palmer 24921* (UARK). Grant Co.: *Locke 2513* (UARK). Independence Co.: *D. Moore 450503* (APCR). Izard Co.: *Taylor 2117* (SIU). Johnson Co.: *D. Moore 380015* (UARK). Logan Co.: *Taylor 1043* (SIU). Madison Co.: *D. Moore 32320* (UARK). Marion Co.: *D. Moore 390302* (UARK). Newton Co.: *D. Moore 350181* (UARK). Polk Co.: *J. Moore 3147* (UCA). Pope Co.: *Taylor 2703* (SIU). Pulaski Co.: *Demaree 18801* (MO). Saline Co.: *D. Moore 480157* (UARK). Van Buren Co.: *Johnson 296* (HXC). Washington Co.: *Palmer 24755* (MO).

The pale-based form, *Isoetes melanopoda* f. *pallida* (Engelm.) Clute, is often found growing with the typical black-based form.

EQUISETACEAE

9. **Equisetum arvense** L., Sp. Pl. 2: 1601. 1753.

Sandy or gravelly stream banks and roadsides.

Benton Co.: *D. Moore s.n.* (UARK). Fulton Co.: *Demaree 26821* (SMU). Newton Co.: *Smith 3180* (UARK). St. Francis Co.: *Demaree 22154* (NY). Stone Co.: *D. Moore 450615* (UARK). Washington Co.: *D. Moore 490105* (UARK).

10. **Equisetum** × **ferrissii** Clute, Fern Bull. 12: 22. 1904. [*Equisetum laevigatum* var. *elatum* Engelm.; *Equisetum hiemale* var. *intermedium* A. A. Eat.; *Equisetum laevigatum* auct. non A. Br.: Schaffner; *Equisetum hyemale* var. *affine* × *E. laevigatum* Hauke]

Moist, sandy or calcareous soils along stream banks, railroad tracks, and roadsides.

Baxter Co.: *D. Moore 450742* (UARK). Benton Co.: *D. Moore 400255* (UARK). Fulton Co.: *D. Moore 330167* (UARK). Independence Co.: *Thomas 9056* (NLU). Izard Co.: *Taylor 1272* (SIU). Jefferson Co.: *Locke 978* (UARK). Marion Co.: *D. Moore 480731* (UARK). Newton Co.: *D. Moore 650* (UARK). Phillips Co.: *Demaree 15219* (SMU). Pulaski Co.: *Merrill 513* (UARK). Stone Co.: *D. Moore 451190* (UARK).

11. **Equisetum hyemale** L. var. **affine** (Engelm.) A. A. Eat., Fern Bull. 11: 111. 1903. [*Equisetum praealtum* Raf.; *Equisetum robustum* A. Br. ex Engelm; *Equisetum hiemale* var. *robustum* (A. Br.) A. A. Eat.; *Equisetum hyemale* var. *elatum* (Engelm.) Morton; *Equisetum hyemale* var. *pseudohyemale* (Farw.) Morton]

Sandy or gravelly stream banks, roadside ditches, fence rows, edges of lakes, or generally disturbed, moist soil.

Arkansas Co.: *D. Moore 480644* (UARK). Baxter Co.: *Demaree 23551* (SMU). Benton Co.: *Demaree 4631* (UARK). Carroll Co.: *Leonard 59* (UARK). Craighead Co.: *Demaree 30294* (PH). Cross Co.: *Demaree 3759* (UARK). Drew Co.: *D. Moore s.n.* (UARK). Faulkner Co.: *Haas 1503* (UCA). Fulton Co.: *D. Moore 470255* (UARK). Garland Co.: *Taylor 2559* (SIU). Hempstead Co.: *Buchholz 438* (UARK). Lafayette Co.: *Loche s.n.* (UARK). Lawrence Co.: *Carter 352* (UARK). Lee Co.: *Taylor 1188* (SIU). Marion Co.: *D. Moore 480731* (UARK). Mississippi Co.: *Bowers s.n.* (MEM). Montgomery Co.: *Taylor 2610* (SIU). Newton Co.: *D. Moore 32463* (UARK). Perry Co.: *Johnson 62* (HXC). Phillips Co.: *Taylor 1190* (SIU). Polk Co.: *McWilliam s.n.* (UARK). Pope Co.: *Tucker s.n.* (APCR). Pulaski Co.: *Demaree 8567* (NY). Randolph Co.: *Riggs s.n.* (UARK). St. Francis Co.: *Demaree 7230* (UARK). Searcy Co.: *Clark 104* (HXC). Sharp Co.: *Demaree 26448* (SMU). Stone Co.: *Taylor 2900* (SIU). Washington Co.: *D. Moore 450851* (UARK).

OPHIOGLOSSACEAE

12. **Botrychium biternatum** (Sav.) Underw., Bot. Gaz. 22: 407. 1896. [*Osmunda biternata* Sav.; *Botrychium tenuifolium* Underw.; *Botrychium obliquum tenuifolium* (Underw.) Gilbert; *Botrychium dissectum* var. *tenuifolium* (Underw.) Farw.]

Moist to dry, open woods, thickets, and low wet areas.

Cleburne Co.: *Johnson 398* (HXC). Cleveland Co.: *Miller 764* (UARK). Columbia Co.: *D. Moore 420478* (UARK). Conway Co.: *J. Moore 1233* (UARK). Craighead Co.: *Watkins s.n.* (UARK). Cross Co.: *Lowman 260* (HXC). Drew Co.: *Palmer 44224* (MO). Faulkner Co.: *Johnson 470* (HXC). Franklin Co.: *Barber 420* (UARK). Garland Co.: *Taylor 2862* (SIU). Grant Co.: *Demaree 87193* (SMU). Hempstead Co.: *Palmer 8980* (MO). Hot Spring Co.: *D. Moore 400085* (UARK). Independence Co.: *Thomas 34313* (NLU). Jefferson Co.: *Locke 1216A* (UARK). Lincoln Co.: *Thomas 34392* (NLU). Little River Co.: *D. Moore 5621* (UARK). Logan Co.: *Pyle 557* (UARK). Lonoke Co.: *Clark 673* (HXC). Montgomery Co.: *Taylor 2219* (SIU). Newton Co.: *Johnson 463* (HXC).

Perry Co.: *Johnson 133* (HXC). Polk Co.: *Taylor 2548* (SIU). Pope Co.: *Johnson 289* (HXC). Pulaski Co.: *Merrill 1217* (UARK). Saline Co.: *D. Moore 50171* (UARK). Sevier Co.: *D. Moore 401102* (UARK). Union Co.: *Taylor 2640* (SIU). Van Buren Co.: *Johnson 100* (HXC). Washington Co.: *Hartsoe 370* (SMU). White Co.: *Thomas 34166* (NLU). Yell Co.: *Demaree 67357* (SIU).

13. **Botrychium dissectum** Spreng., Anleit. Gewachse 3: 172. 1804. Two varieties are recognized in the state.

13a. **Botrychium dissectum** Spreng. var. **dissectum** [*Botrychium lunarioides* var. *dissectum* Gray; *Botrychium obliquum* var. *dissectum* (Spreng.) Prantl; *Botrychium dissectum* var. *typicum* Clausen]

Newton Co.: mesic ravine in Lost Valley State Park; *Thompson 907* (SMS). Washington Co.: low, open woods near Farmington; *D. Moore 300309* (MO).

13b. **Botrychium dissectum** Spreng. var. **obliquum** (Muhl.) Clute, Fern Bull. 10: 76. 1902. [*Botrychium obliquum* Muhl.; *Botrychium lunarioides* var. *obliquum* (Muhl.) Gray; *Botrychium ternatum* var. *obliquum* (Muhl.) D. C. Eat.]

Rich, moist, open woodlands and thickets.

Faulkner Co.: *Taylor 2606* (SIU). Howard Co.: *Kellogg s.n.* (MO). Montgomery Co.: *J. Moore & McWilliam s.n.* (UARK). Newton Co.: *D. Moore 350391* (UARK). Polk Co.: *D. Moore 510021* (UARK). Van Buren Co.: *Demaree 4755* (UARK). Washington Co.: *D. Moore 330309* (UARK).

14. **Botrychium lunarioides** (Michx.) Sw., Syn. Fil., 172. 1806. [*Botrypus lunarioides* Michx.; *Botrychium fumarioides* Willd.; *Botrychium ternatum* var. *lunarioides* D. C. Eat.]

Cemeteries and church yards in the West Gulf Coastal Plain.

Howard Co.: County Line Missionary Baptist Church Cemetery; off Hwy. 24, ca. 5 mi. W of Nashville; *Thomas 28147* (NLU). Lafayette Co.: Forest Grove Baptist Church Cemetery; off Hwy. 53, ca. 1 mi N of Walker Creek; *Thomas 34005* (NLU). Sevier Co.: Coulter Memorial Garden; off Hwy. 71, Locksburg; *Thomas 28139* (NLU). Union Co.: Olive Branch Methodist Church Yard; off Hwy. 7, ca. 4.5 mi. SE of New Caledonia; *Taylor 2638* (SIU).

15. **Botrychium virginianum** (L.) Sw., Journ. Bot. Schrad. 1800 (2): 111. 1801. [*Osmunda virginiana* L.: *Osmundopteris virginiana* (L.) Small]

Moist to dry woodlands and thickets.

Ashley Co.: *Taylor 1875* (SIU). Baxter Co.: *Taylor 2675* (SIU). Benton Co.: *Taylor 1124* (SIU). Boone Co.: *Demaree s.n.* (UARK). Carroll Co.: *Palmer 4443* (MO). Clark Co.: *Taylor 2178* (SIU). Clay Co.: *Hartsoe 374* (SMU). Cleburne Co.: *Babb 338* (ARKSU). Conway Co.: *J. Moore 1086* (UARK). Craighead Co.: *Richards 5332* (ARKSU). Crawford Co.: *Moore 710233* (UARK). Crittenden Co.: *Browne 62123* (MEM).

Dallas Co.: *Taylor 1133* (SIU). Faulkner Co.: *Haas 1496* (UCA). Franklin Co.: *D. Moore 300251* (UARK). Garland Co.: *Palmer 24553* (MO). Greene Co.: *Demaree 3932* (SMU). Hempstead Co.: *Bush 1364* (NY). Hot Spring Co.: *D. Moore 451096* (UARK). Howard Co.: *McSwain 43E77* (UARK). Independence Co.: *Demaree 26732* (SMU). Izard Co.: *Matthews 125* (ARKSU). Jefferson Co.: *Locke 2231* (UARK). Johnson Co.: *D. Moore 450257* (UARK). Lawrence Co.: *Taylor 2596* (SIU). Lee Co.: *Taylor 1183* (SIU). Logan Co.: *Haas 1495* (UCA). Lonoke Co.: *Clark 672* (HXC). Madison Co.: *D. Moore 460146* (UARK). Marion Co.: *Taylor 1234* (SIU). Montgomery Co.: *Taylor 2838* (SIU). Nevada Co.: *D. Moore 450105* (UARK). Newton Co.: *D. Moore 32504* (UARK). Phillips Co.: *Taylor 2829* (SIU). Pike Co.: *Lindley & Lindley s.n.* (UARK). Polk Co.: *Lodewyks 195* (MO). Pope Co.: *Taylor 1207* (SIU). Pulaski Co.: *Redfearn 25934* (SMS). Randolph Co.: *Taylor 2100* (SIU). St. Francis Co.: *Demaree 4349* (NY). Searcy Co.: *Taylor 1852* (SIU). Sharp Co.: *Demaree 27719* (SMU). Stone Co.: *Taylor 1262* (SIU). Union Co.: *D. Moore 68109* (UARK). Van Buren Co.: *Taylor 2566* (SIU). Washington Co.: *D. Moore 50008* (UARK). White Co.: *Johnson 456* (HXC).

16. **Ophioglossum crotalophoroides** Walt., Fl. Caroliniana, 256. 1788. [*Ophioglossum bulbosum* Michx.; *Ophioglossum pusillum* Nutt.; *Ophioglossum vulgatum* var. *crotalophoroides* (Walt.) D. C. Eat.]

Sandy, open soil in lawns, meadows, cemetery yards, pastures, and roadsides.

Ashley Co.: *Thomas 27300* (NLU). Bradley Co.: *Thomas 27912* (NLU). Calhoun Co.: *Lawson 256* (NLU). Clark Co.: *Lawson 74* (NLU). Cleveland Co.: *Thomas 43991* (NLU). Columbia Co.: *D. Moore 5771* (UARK). Dallas Co.: *Lawson 226* (NLU). Drew Co.: *Thomas 26904* (NLU). Faulkner Co.: *Taylor 2009* (SIU). Hempstead Co.: *D. Moore 53155* (UARK). Hot Spring Co.: *Thomas 34114* (NLU). Howard Co.: *D. Moore 5772* (UARK). Independence Co.: *Thomas 38584* (NLU). Jackson Co.: *Thomas 34217* (NLU). Jefferson Co.: *Thomas 34132* (NLU). Lafayette Co.: *Thomas 34006* (NLU). Lincoln Co.: *Thomas 34141* (NLU). Little River Co.: *Thomas 27954* (NLU). Miller Co.: *Thomas 34011* (NLU). Nevada Co.: *D. Moore 450039* (UARK). Newton Co.: *Thompson 1015* (SMS). Ouachita Co.: *Taylor 2625* (SIU). Polk Co.: *Thomas 34106* (NLU). Pulaski Co.: *Thomas 34377* (NLU). Randolph Co.: *Thomas 34239* (NLU). Sevier Co.: *Taylor 2641* (SIU). Union Co.: *Taylor 2629* (SIU). White Co.: *Thomas 34159* (NLU).

17. **Ophioglossum engelmannii** Prantl, Ber. Deutsch Bot. Ges. 1: 351. 1883. [*Ophioglossum vulgatum* f. *engelmannii* (Prantl) Clute; *Ophioglossum vulgatum* var. *engelmannii* (Prantl) Clute]

Seasonally moist to wet calcareous soils on limestone glades, in open woods, and on chalk outcrops.

Baxter Co.: *Palmer 14333* (MO). Benton Co.: *Palmer 17199* (MO). Boone Co.: *Demaree s.n.* (UARK). Carroll Co.: *D. Moore 350435* (MO). Faulkner Co.: *Taylor 2010* (SIU). Fulton Co.: *D. Moore 520391* (UARK). Garland Co.: *Haas 1492* (UCA). Hempstead Co.: *Palmer 5376* (MO). Independence Co.: *Thomas 8926* (NLU). Izard Co.: *Taylor 2107* (SIU). Little River Co.: *D. Moore 50036* (UARK). Madison Co.: *D. Moore 450406* (UARK). Marion Co.: *D. Moore 520332* (APCR). Pulaski Co.: *D.*

Moore 330069 (UARK). Randolph Co.: *Taylor 2086* (SIU). Sharp Co.: *D. Moore 520382* (UARK). Stone Co.: *Taylor 1259* (SIU). Washington Co.: *Palmer 23300* (MO).

18. **Ophioglossum nudicaule** L. f. var. **tenerum** (Mett. ex Prantl) Clausen, Mem. Torrey Bot. Club 19: 146. 1938. [*Ophioglossum tenerum* Mett. ex Prantl]

Cemeteries and church yards in the West Gulf Coastal Plain.

Ashley Co.: Carter Cemetry; off Hwy. 82, ca. 1 mi. W of jct. Hwys. 81 and 82 and Antioch Methodist Church Cemetery; off Hwy. 81, ca. 3 mi. S of jct. Hwys. 81 and 82; *Thomas 27903* (NLU). Hempstead Co.: Shover Springs Baptist Church Cemetery; off Hwy. 32, Shover Springs; *Thomas 27951* (NLU). Nevada Co.: White's Chapel Baptist Church Yard; ca. 3 mi. E of Hwy. 53 and Bodcaw; *Thomas 27947* (NLU). Union Co.: Harper Springs Cemetery; S of Hwy. 129 and Huttig; also Cemetery in pine woods along Hwy. 275, ca. 5 mi. S of Strong; *Taylor 2630* (SIU).

19. **Ophioglossum petiolatum** Hook., Exotic Flora 1: 56. 1823. [*Ophioglossum floridanum* E. P. St. John]

Cemeteries and yards; West Gulf Coastal Plain and Mississippi Alluvial Plain.

Dallas Co.: Oakland Cemetery, Fordyce; *Thomas 27918* (NLU). Jefferson Co.: yard beside bldg. at Pine Bluff Arsenal; sect. 20, T4S, R10W; *Thomas 44091* (NLU). Union Co.: Olive Branch Methodist Church Yard; ca. 0.5 mi. off Hwy. 7, ca. 4.5 mi. SE of New Caledonia; *Taylor 2637* (SIU). White Co.: Antioch Union Church Yard; off Hwy 31, Antioch; *Thomas 34184* (NLU).

20. **Ophioglossum vulgatum** L. var. **pycnostichum** Fern., Rhodora 41: 494. 1939.

Moist, open woods, alluvial woodlands, and swamps.

Arkansas Co.: *Kellogg s.n.* (MO). Ashley Co.: *Thomas 34123* (NLU). Clay Co.: *Hartsoe s.n.* (UARK). Craighead Co.: *Richards 6209* (ARKSU). Cross Co.: *Clark 683* (HXC). Drew Co.: *Thomas 34129* (NLU). Grant Co.: *D. Moore 50095* (UARK). Hempstead Co.: *Kellogg s.n.* (MO). Howard Co.: *D. Moore 5680* (UARK). Independence Co.: *Thomas 38606* (NLU). Izard Co.: *J. Moore 5680* (UCA). Jackson Co.: *Richards 6197* (ARKSU). Jefferson Co.: *Locke 1734* (UARK). Little River Co.: *D. Moore 5620* (UARK). Pike Co.: *Lindley and Lindley s.n.* (NLU). Poinsett Co.: *Kellogg s.n.* (MO). Polk Co.: *J. Moore 3140* (UCA). Pulaski Co.: *Lowman s.n.* (HXC). Union Co.: *Thomas 35321* (NLU).

OSMUNDACEAE

21. **Osmunda cinnamomea** L., Sp. Pl. 2: 1066. 1753.

Swamps, marshes, moist woods, seepage slopes, wet depressions, stream banks, edges of lakes, around springs, and on wet rock ledges.

Bradley Co.: *Locke 2026* (UARK). Benton Co.: *Demaree 4885* (UARK). Calhoun Co.: *Demaree 16908* (SMU). Clark Co.: *Taylor 2182* (SIU). Clay Co.: *Rosen 99* (HXC).

Cleburne Co.: *Babb 281* (ARKSU). Cleveland Co.: *Demaree 23309* (MO). Columbia Co.: *Taylor 1898* (SIU). Conway Co.: *D. Moore s.n.* (UARK). Crawford Co.: *D. Moore 710288* (UARK). Cross Co.: *D. Moore 420368* (UARK). Drew Co.: *Demaree 28816* (SMU). Faulkner Co.: *Johnson 490* (HXC). Franklin Co.: *Hartsoe s.n.* (UARK). Garland Co.: *Taylor 2560* (SIU). Grant Co.: *Taylor 2724* (SIU). Greene Co.: *Demaree 26659* (SMU). Hempstead Co.: *Bush 5724* (MO). Hot Spring Co.: *Palmer 8103* (MO). Howard Co.: *McSwain 43E126* (UARK). Independence Co.: *Johnson 301* (HXC). Izard Co.: *Demaree 24435* (SMU). Jefferson Co.: *Demaree 24054* (SMU). Lafayette Co.: *Fassett 20907* (F). Logan Co.: *D. Moore 480082* (UARK). Lonoke Co.: *Clark 666* (HXC). Madison Co.: *Davis 1499* (UARK). Montgomery Co.: *Taylor 2207* (SIU). Nevada Co. *D. Moore 450091A* (UARK). Newton Co.: *Redfearn 27509* (SMS). Ouachita Co.: *D. Moore 4505* (UARK). Perry Co.: *Robertson s.n.* (APCR). Pike Co.: *Demaree 9543* (MO). Polk Co.: *D. Moore 480559* (UARK). Pope Co.: *D. Moore 350368* (UARK). Pulaski Co.: *Taylor 2541* (SIU). Saline Co.: *Haas 1489* (UCA). Sevier Co.: *D. Moore 400181* (UARK). Stone Co.: *D. Moore 450520* (UARK). Union Co.: *Taylor 1155* (SIU). Van Buren Co.: *Palmer 25175* (MO).

Osmunda cinnamomea f. *frondosa* (Torr. & Gray) Britton, which differs from the typical form in having sterile pinnae toward the base of the fertile frond, was collected by E. J. Palmer (MO *945740*) from a sandy, open woods near Malvern, Hot Spring County.

22. **Osmunda claytoniana** L., Sp. Pl. 2: 1066. 1753.

Pope Co.: Alder thicket above a persistent spring, 0.9 mi. W. of Pelsor; *D. Moore 4191* (UARK). Stone Co.: around natural opening of Blanchard Springs Caverns; *Taylor 1251* (SIU).

23. **Osmunda regalis** L. var. **spectabilis** (Willd.) Gray, Man., 600. 1856. [*Osmunda spectabilis* Willd.]

Swamps, marshes, moist woods, seeps, wet depressions, stream banks, edges of lakes, and around springs.

Benton Co.: *Plank s.n.* (NY). Bradley Co.: *Locke 1091* (UARK). Calhoun Co.: *Demaree 22108* (MO). Clark Co.: *Taylor 2183* (SIU). Clay Co.: *Richards 5046* (ARKSU). Cleburne Co.: *Taylor 1025* (SIU). Cleveland Co.: *Taylor 1140* (SIU). Columbia Co.: *Taylor 1158* (SIU). Conway Co.: *J. Moore 928* (UARK). Craighead Co.: *Demaree 5056* (UCA). Crawford Co.: *D. Moore 710286* (UARK). Dallas Co.: *Taylor 2734* (SIU). Drew Co.: *Demaree 22417* (MO). Faulkner Co.: *D. Moore 55236* (UARK). Franklin Co.: *Barber s.n.* (UARK). Garland Co.: *Palmer 24949* (MO). Grant Co.: *Taylor 2726* (SIU). Greene Co.: *Demaree 4065* (SMU). Hempstead Co.: *Taylor 1178* (SIU). Hot Spring Co.: *Demaree 14784A* (SMU). Howard Co.: *McSwain 43E127* (UARK). Independence Co.: *Johnson 304* (HXC). Jefferson Co.: *Demaree 24300* (MO). Johnson Co.: Redfearn 23839 (SMS). Lawrence Co.: *Wheeler 54* (F). Logan Co.: *D. Moore 480041* (UARK). Lonoke Co.: *Clark 667* (HXC). Montgomery Co.: *Taylor 2208* (SIU). Nevada Co.: *D. Moore 450091* (UARK). Newton Co.: *Johnson 465* (HXC). Ouachita Co.: *Demaree 16846* (MO). Pike Co.: *Demaree 9539* (MO). Poinsett Co.: *Pyle 588* (UARK). Polk Co.: *Palmer 12625* (MO). Pope Co.: *D. Moore 350369* (UARK). Pulaski Co.: *Taylor 2542* (SIU). Saline Co.: *Haas 1485* (UCA). Stone Co.: *Thomas 8355* (NLU). Union Co.: *Taylor*

1157 (SIU). Van Buren Co.: *D. Moore 350438* (UARK). Washington Co.: *Hite 29* (UARK). Yell Co.: *Buchholz 1088* (UARK).

Osmunda regalis var. *spectabilis* f. *anomala* (Farw.) Harris, which differs from typical plants in having sterile pinnules borne in the fertile segment of the frond, has been collected in Clay, Green, Polk and Washington Counties.

ADIANTACEAE

24. **Cheilanthes alabamensis** (Buckl.) Kunze, Linnaea 20: 4. 1847. [*Pteris alabamensis* Buckl.]

Limestone or dolomite outcrops; primarily Ozark Highlands.

Baxter Co.: *Taylor 2674* (SIU). Benton Co.: *Palmer 24739* (MO). Boone Co.: *Palmer 6905* (MO). Carroll Co.: *Leonard 115* (UARK). Garland Co.: *Engelmann s.n.* (MO). Independence Co.: *Thomas 7720* (NLU). Izard Co.: *Demaree 3264* (UARK). Newton Co.: *Taylor 1219* (SIU). Searcy Co.: *Taylor 2583* (SIU). Stone Co.: *D. Moore 470697* (UARK). Washington Co.: *Taylor 1111* (SIU).

25. **Cheilanthes castanea** Maxon, Proc. Biol. Soc. Wash. 32: 111. 1919.

Baxter Co.: rock outcrops; Norfork; *D. Moore 451026* (UARK).

26. **Cheilanthes feei** Moore, Ind. Fil., 38. 1857. [*Cheilanthes lanuginosa* Hook.]

Limestone, dolomite, or calcareous sandstone outcrops; primarily Ozark Highlands.

Baxter Co.: *Taylor 2681* (SIU). Benton Co.: *Demaree 4975* (UARK). Boone Co.: *Palmer 6906* (MO). Carroll Co.: *Trelease 4/20799* (MO). Garland Co.: *Letterman s.n.* (MO). Izard Co.: *Demaree 17038* (MO). Marion Co.: *D. Moore 410522* (UARK). Newton Co.: *D. Moore 350103* (UARK). Searcy Co.: *D. Moore 350150* (UARK). Stone Co.: *Tucker 6904* (APCR). Washington Co.: *Demaree s.n.* (SMU).

27. **Cheilanthes lanosa** (Michx.) D. C. Eat. in Torr., Rep. U. S. and Mex. Bound. Surv. 2: 234. 1859. [*Nephrodium lanosum* Michx.; *Adiantum vestitum* Spreng.; *Cheilanthes vestita* (Spreng.) Sw.]

Sandstone, shale, dolomite, chert, novaculite, and occasionally limestone outcrops; chiefly Interior Highlands.

Baxter Co.: *Taylor 1844* (SIU). Benton Co.: *Taylor 1118* (SIU). Carroll Co.: *Palmer 4454* (MO). Clark Co.: *Taylor 2189* (SIU). Cleburne Co.: *Taylor 1023* (SIU). Conway Co.: *Tucker 3509* (APCR). Crawford Co.: *D. Moore 710221* (UARK). Faulkner Co.: *Taylor 2607* (SIU). Franklin Co.: *Taylor 1127* (SIU). Fulton Co.: *Palmer 29131* (MO). Garland Co.: *Taylor 2227* (SIU). Greene Co.: *Richards 5489* (ARKSU). Howard Co.: *Kellogg s.n.* (MO). Independence Co.: *Thomas 16443* (NLU). Izard Co.: *Palmer 35550* (MO). Johnson Co.: *Taylor 1091* (SIU). Lawrence Co.: *Taylor 2594* (SIU). Logan Co.:

Palmer 24191 (UARK). Madison Co.: *Redfearn 26788* (SMS). Marion Co.: *Johnson 91* (HXC). Montgomery Co.: *D. Moore 32975* (UARK). Perry Co.: *Owens s.n.* (US). Polk Co.: *J. Moore 3148* (UCA). Pope Co.: *Snider 23* (APCR). Pulaski Co.: *Buchholz 576* (UARK). Saline Co.: *Demaree 23017* (MO). Scott Co.: *D. Moore 430135* (UARK). Searcy Co.: *Taylor 1238* (SIU). Sebastian Co.: *Taylor 2718* (SIU). Stone Co.: *Taylor 2125* (SIU). Van Buren Co.: *Johnson 102* (HXC). Washington Co.: *Taylor 1113* (SIU). White Co.: *Demaree 26934* (SMU). Yell Co.: *Taylor 1198* (SIU).

28. **Cheilanthes tomentosa** Link, Hort. Berol. 2: 42. [*Cheilanthes lanosa* sensu Fern., Gray's Man. Bot., ed. 8: 47. 1950, non Eaton (1859)]

Sandstone, shale, dolomite, limestone, chert, and novaculite outcrops; Interior Highlands.

Baxter Co.: *D. Moore 451021* (UARK). Benton Co.: *Demaree 2911* (SMU). Boone Co.: *D. Moore 490379* (UARK). Cleburne Co.: *Taylor 1026* (SIU). Conway Co.: *D. Moore 480368* (UARK). Crawford Co.: *Palmer 26423* (UARK). Faulkner Co.: *Taylor 2601* (SIU). Franklin Co.: *Palmer 8140* (MO). Garland Co.: *Harvey 83* (MO). Hot Spring Co.: *Demaree 16534* (SMU). Howard Co.: *Kellogg s.n.* (MO). Izard Co.: *Demaree 3285* (SMU). Logan Co.: *Palmer 23207* (UARK). Marion Co.: *Johnson 98* (HXC). Montgomery Co.: *Demaree 34158* (SMU). Newton Co.: *D. Moore 32488* (UARK). Perry Co.: *Redfearn 24134* (SMU). Pike Co.: *Roberts 27* (UARK). Polk Co.: *J. Moore 3139* (UCA). Pope Co.: *D. Moore 520746* (UARK). Pulaski Co.: *Palmer 22990* (UARK). Scott Co.: *D. Moore 430134* (UARK). Searcy Co.: *D. Moore 350152* (UARK). Sebastian Co.: *Taylor 2716* (SIU). Stone Co.: *D. Moore 470747* (UARK). Washington Co.: *Taylor 1114* (SIU). Yell Co.: *Taylor 4369* (SIU).

29. **Notholaena dealbata** (Pursh) Kunze, Am. Journ. Sci. II. 6: 82. 1848. [*Cheilanthes dealbata* Pursh; *Pellaea dealbata* (Pursh) Prantl]

Limestone and dolomite outcrops; Ozark Highlands.

Baxter Co.: *Palmer 5951* (MO). Benton Co.: *Palmer 3790* (MO). Carroll Co.: *Palmer 4538* (MO). Madison Co.: *Nelson 10861* (MO). Washington Co.: *Taylor 1109* (SIU).

30. **Pellaea atropurpurea** (L.) Link, Fil. Sp. Hort. Berol., 59. 1841. [*Pteris atropurpurea* L.; *Allosorus atropurpureus* (L.) Presl]

Limestone, dolomite, or calcareous sandstone outcrops; most common in the Ozark Highlands.

Baxter Co.: *Taylor 1842* (SIU). Benton Co.: *Demaree 2908* (SMU). Boone Co.: *Palmer 6904* (MO). Carroll Co.: *Palmer 4424* (MO). Cleburne Co.: *Taylor 1020* (SIU). Conway Co.: *J. Moore 1262* (UARK). Franklin Co.: *Barber 448* (UARK). Fulton Co.: *Demaree 5370* (UARK). Garland Co.: *Taylor 2225* (SIU). Hot Spring Co.: *Demaree 15567* (SMU). Independence Co.: *Trelease s.n.* (MO). Izard Co.: *Taylor 1270* (SIU). Lawrence Co.: *Taylor 1789* (SIU). Madison Co.: *Taylor 1995* (SIU). Marion Co.: *Taylor 1231* (SIU). Newton Co.: *Taylor 1217* (SIU). Polk Co.: *J. Moore s.n.* (UARK). Pope Co.: *D. Moore 52074* (UARK). Randolph Co.: *Taylor 1802* (SIU). Searcy Co.: *Taylor 1242* (SIU). Sebastian Co.: *Taylor 2719* (SIU). Sharp Co.: *Taylor 1809* (SIU). Stone Co.: *Taylor 1247* (SIU). Van Buren Co.: *Palmer 25171* (UARK). Washington Co.: *Taylor 1112* (SIU).

An aberrant form of *P. atropurpurea* in which the pinnae or ultimate segments repeatedly fork was collected by D. M. Moore near West Fork, Washington County. Moore's specimens (MO *1860929,* UARK *340687*) are referable to *Pellaea atropurpurea* f. *cristata* (Trel.) Clute.

31. **Pellaea glabella** Mett. ex Kuhn, Linnaea 36: 87. 1869. [*Pellaea atropurpurea* var. *bushii* Mack. & Bush; *Pellaea atropurpurea* f. *glabella* (Mett. ex Kuhn) Clute]

Limestone, dolomite, or calcareous sandstone outcrops; chiefly in the Ozark Highlands.

Baxter Co.: *Taylor 1841* (SIU). Benton Co.: *D. Moore 4000284* (UARK). Carroll Co.: *D. Moore 410184* (UARK). Faulkner Co.: *Lane 241* (UARK). Garland Co.: *Engelmann s.n.* (MO). Izard Co.: *Taylor 1271* (SIU). Marion Co.: *Demaree s.n.* (SMU). Newton Co.: *Taylor 2697* (SIU). Sharp Co.: *Johnson 485* (HXC). Stone Co.: *Taylor 2898* (SIU).

32. **Adiantum capillus-veneris** L., Sp. Pl. 2: 1096. 1753. [*Adiantum modestum* Underw.; *Adiantum tricholepis* f. *glabrum* Clute]

Moist to wet calcareous rock outcrops; principally Ozark Highlands and Boston Mountains.

Benton Co.: *Palmer 2940* (MO). Carroll Co.: *D. Moore 410188a* (UARK). Crawford Co.: *Moore 710274* (UARK). Franklin Co.: *Barber 2011* (UARK). Garland Co.: *Engelmann 19* (MO). Hot Spring Co.: *Demaree 19856* (MO). Izard Co.: *Taylor 1269* (SIU). Logan Co.: *D. Moore 480076* (UARK). Madison Co.: *Nelson 10873* (MO). Marion Co.: *Palmer 5985* (MO). Newton Co.: *Taylor 1218* (SIU). Pope Co.: *D. Moore 520755* (UARK). Searcy Co.: *Taylor 1239* (SIU). Stone Co.: *Taylor 1250* (SIU). Van Buren Co.: *Palmer 24203* (UARK). Washington Co.: *Palmer 23906* (MO).

33. **Adiantum pedatum** L., Sp. Pl. 2: 1095. 1753.

Moist, shaded, rich woods, primarily Interior Highlands and Crowley's Ridge.

Baxter Co.: *Taylor 2682* (SIU). Benton Co.: *Demaree 4592* (SMU). Boone Co.: *Demaree s.n.* (UARK). Carroll Co.: *Palmer 4547* (MO). Clay Co.: *Richards 4402* (ARKSU). Cleburne Co.: *Demaree 30509* (SMU). Conway Co.: *Demaree 22793* (SMU). Craighead Co.: *Alliston 15* (ARKSU). Crawford Co.: *Taylor 1093* (SIU). Crittenden Co.: *Demaree 61080* (SMU). Cross Co.: *Lowman 344* (HXC). Faulkner Co.: *Demaree s.n.* (MO). Franklin Co.: *Johnson 527* (HXC). Fulton Co.: *Demaree 5372* (NY). Garland Co.: *Trelease s.n.* (MO). Hot Spring Co.: *Palmer 26589* (UARK). Independence Co.: *Demaree 17097* (MO). Izard Co.: *Matthews 91* (ARKSU). Johnson Co.: *D. Moore 450265* (UARK). Lee Co.: *Taylor 1186* (SIU). Logan Co.: *Palmer 24158* (MO). Madison Co.: *Key 265* (SMS). Marion Co.: *Palmer 4777* (MO). Montgomery Co.: *Taylor 2215* (SIU). Newton Co.: *Taylor 1221* (SIU). Perry Co.: *Demaree 35477* (SMU). Phillips Co.: *Demaree 19221* (SMU). Polk Co.: *Taylor 1067* (SIU). Pope Co.: *Taylor 1202* (SIU). Pulaski Co.: *Johnson 122* (HXC). St. Francis Co.: *Demaree 21539* (MO). Saline Co.: *Demaree 23987* (SMU). Searcy Co.: *Taylor 2572* (SIU). Sevier Co.: *D. Moore 410371*

(UARK). Stone Co.: *Taylor 1253b* (SIU). Van Buren Co.: *Taylor 2565* (SIU). Washington Co.: *Taylor 1102* (SIU). White Co.: *Johnson 457* (HXC). Yell Co.: *Buchholz 1077* (NY).

34. **Pteris multifida** Poir. ex Lam., Encyc. Bot. 5: 714. 1804. [*Pycnodoria multifida* (Poir. ex Lam.) Small]

Garland Co.: Northwest facing limestone tufa at the base of Hot Springs Mountain, Hot Springs National Park; *Taylor 2708* (SIU).

HYMENOPHYLLACEAE

35. **Trichomanes boschianum** Sturm ex Bosch, Nederl. Kruidk. Arch. 5(2): 160. 1861.

Under moist, overhanging sandstone outcrops.

Cleburne Co.: ca. 1.5 mi. NE of Greers Ferry Dam; sect. 5, T10N, R9W; *Taylor 1013* (SIU). Madison Co.: 6.5 mi. SE of Pettigrew; sect. 1, T13N, R25W; *Clark 1400* (MO).

36. **Trichomanes petersii** Gray, Am. Jour. Sci. II. 15: 326. 1853.

Pope Co.: side of sandstone boulder in narrow drainage ravine running to Indian Creek; ca. 3 mi. SW of Pelsor, sect. 16, T12N, R20W; *Redfearn 21508* (SMS). Stone Co.: calcareous sandstone ledge along North Sylamore Creek; sect. 25, T169, R12W; *Taylor 2897* (SIU).

POLYPODIACEAE

37. **Polypodium polypodioides** (L.) Watt var. **michauxianum** Weatherby, Contr. Gray Herb. 124: 31. 1939. [*Acrostichum polypodioides* L.; *Polypodium incanum* sensu auct., non Sw. (1788); *Polypodium ceteraccinum* Michx; *Marginaria polypodioides* (L.) Tidest.]

On rocks or as an epiphyte on trees, especially oaks and elms.

Arkansas Co.: *Taylor 1867a* (SIU). Ashley Co.: *Taylor 1873b* (SIU). Baxter Co.: *Taylor 1848* (SIU). Bradley Co.: *Taylor 1145* (SIU). Calhoun Co.: *Johnson s.n.* (HXC). Carroll Co.: *Palmer 4528* (MO). Clark Co.: *Taylor 2179* (SIU). Clay Co.: *Hartsoe 376* (SMU). Cleburne Co.: *Taylor 1024* (SIU). Cleveland Co.: *Taylor s.n.* (SIU). Columbia Co.: *Taylor 1165* (SIU). Conway Co.: *Demaree 24962* (SMU). Craighead Co.: *Taylor 2882* (SIU). Crawford Co.: *Redfearn 24556* (SMS). Cross Co.: *Palmer 31658* (MO). Dallas Co.: *Taylor 2731* (SIU). Desha Co.: *Johnson s.n.* (UARK). Drew Co.: *Taylor 1149* (SIU). Faulkner Co.: *Taylor 2013* (SIU). Franklin Co.: *J. Moore s.n.* (APCR). Fulton Co.: *Demaree 5284* (UARK). Garland Co.: *Taylor 2196* (SIU). Grant Co.: *Taylor 2728* (SIU). Hempstead Co.: *Taylor 1179* (SIU). Hot Spring Co.: *Demaree 21194* (SMU). Howard Co.: *McSwain 43E66* (UARK). Independence Co.: *Demaree 17098* (SMU). Izard Co.: *Taylor 2138* (SIU). Jefferson Co.: *Locke 761* (UARK). Johnson Co.: *Johnson 54* (HXC). Lawrence Co.: *Taylor 1791* (SIU). Lee Co.: *Demaree 37378* (SMU). Lincoln Co.: *Demaree 13739* (SMU). Little River Co.: *Taylor 2149* (SIU). Logan Co.: *Palmer 24152* (MO). Lonoke Co.: *Buchholz s.n.* (UARK). Madison Co.: *Taylor 2001*

(SIU). Marion Co.: *Taylor 1836* (SIU). Miller Co.: *Taylor 1911* (SIU). Mississippi Co.: *Metcalf 645* (US). Monroe Co.: *Taylor 2832* (SIU). Montgomery Co.: *Taylor 1076* (SIU). Nevada Co.: *Taylor 2747* (SIU). Newton Co.: *Moore & Demaree 6386* (UARK). Ouachita Co.: *Taylor 2628* (SIU). Perry Co.: *Demaree 27056* (SMU). Pike Co.: *Demaree 9507* (SMU). Poinsett Co.: *Demaree 28624* (SMU). Polk Co.: *Taylor 2549* (SIU). Pope Co.: *Redfearn 23888* (SMS). Pulaski Co.: *Demaree 8467* (SMU). Randolph Co.: *Taylor 2096* (SIU). St. Francis Co.: *Johnson 486* (HXC). Saline Co.: *Aingworth s.n.* (UARK). Scott Co.: *Taylor 2714* (SIU). Searcy Co.: *Emig 85* (MO). Sebastian Co.: *Taylor 2722* (SIU). Sevier Co.: *Culwell 3239* (UCA). Sharp Co.: *Demaree 26281* (SMU). Stone Co.: *Demaree 59388* (SMU). Union Co.: *Taylor 2633* (SIU). Van Buren Co.: *Palmer 25188* (MO). Washington Co.: *Demaree 2742* (SMU). White Co.: *D. Moore 451040* (UARK). Woodruff Co.: *Johnson 479* (HXC). Yell Co.: *Taylor 2622* (SIU).

38. **Polypodium virginianum** L., Sp. Pl. 2: 1085. 1735. [*Polypodium vulgare* var. *virginianum* (L.) Eat.; *Polypodium vulgare* var. *americanum* Hook.]

Usually shaded, sandstone outcrops; chiefly Ozark Highlands and Boston Mountains.

Benton Co.: *D. Moore 410014* (UARK). Cleburne Co.: *Babb 186* (ARKSU). Franklin Co.: *Johnson 526* (HXC). Logan Co.: *Taylor 1042* (SIU). Madison Co.: *Taylor 2002* (SIU). Marion Co.: *D. Moore 480728* (UARK). Newton Co.: *Palmer 27090* (UARK). Pope Co.: *Taylor 1214* (SIU). Searcy Co.: *Demaree 51919* (SMU). Stone Co.: *Taylor 2901* (SIU). Washington Co.: *Harvey 77* (MO).

DENNSTAEDTIACEAE

39. **Dennstaedtia punctilobula** (Michx.) Moore, Ind. Fil., 307. 1857. [*Nephrodium punctilobula* Michx.; *Dicksonia punctilobula* (Michx.) Gray]

Crevices and ledges of moist, shaded, sandstone outcrops.

Logan Co.: near summit on N side of Magazine Mountain; *Taylor 1046* (SIU). Stone Co.: Blanchard Springs and City Rock Bluff across the White River from Calico Rock; *D. Moore 390311* (F).

40. **Pteridium aquilinum** (L.) Kuhn in Decken, Reisen Ost-Afr. 3: 11. 1879. [*Pteris aquilina* L.]

Open woods, cut-over and burned-over areas, thickets, old fields, roadsides. Two varieties are recognized in the state.

40a. **Pteridium aquilinum** var. **latiusculum** (Desv.) Underw. ex Heller, Cat. N. Am. Pl., 17. 1909. [*Pteris latiuscula* Desv.; *Pteridium latiusculum* (Desv.) Fries]

This variety is found with greater frequency in the northern third of the state.

Boone Co.: *Demaree s.n.* (UARK). Calhoun Co.: *Demaree 22104* (MO). Carroll Co.: *D. Moore 410188* (UARK). Clay Co.: *Richards 5353* (ARKSU).

Cleburne Co.: *Smith 1488* (UARK). Columbia Co.: *D. Moore 420448* (UARK). Conway Co.: *D. Moore 480371* (UARK). Craighead Co.: *Pyle 589* (UARK). Crawford Co.: *D. Moore 710281* (UARK). Dallas Co.: *Taylor 1138* (SIU). Garland Co.: *Bragg 131* (MO). Grant Co.: *Taylor 2727* (SIU). Greene Co.: *Richards 5494* (ARKSU). Hempstead Co.: *Bush 1045* (MO). Hot Spring Co.: *Palmer 26597* (UARK). Independence Co.: *Thomas 14926* (NLU). Izard Co.: *Taylor 2134* (SIU). Jefferson Co.: *Locke 1030* (UARK). Johnson Co.: *Wright 930* (UARK). Lawrence Co.: *Demaree 31002* (SMU). Lincoln Co.: *Demaree 19185* (MO). Logan Co.: *Pyle 332* (UARK). Lonoke Co.: *Clark 679* (HXC). Marion Co.: *Smith 1420* (SMU). Miller Co.: *Taylor 1916* (SIU). Montgomery Co.: *Taylor 1078* (SIU). Newton Co.: *Taylor 2701* (SIU). Perry Co.: *Demaree 35633* (SMU). Pike Co.: *Taylor 2904* (SIU). Polk Co.: *Taylor 1071* (SIU). Pope Co.: *Taylor 1206* (SIU). Prairie Co.: *Demaree 22307* (MO). Pulaski Co.: *Bailey s.n.* (UARK). Saline Co.: *D. Moore 300068* (UARK). Sevier Co.: *D. Moore 401105* (UARK). Stone Co.: *Taylor 1256* (SIU). Union Co.: *Taylor 1152* (SIU). Van Buren Co.: *Palmer 25176* (UARK). Washington Co.: *Taylor 1157* (SIU). Yell Co.: *Demaree 15935* (SMU).

40b. **Pteridium aquilinum** var. **pseudocaudatum** (Clute) Heller, Cat. N. Am. Pl., 12. 1909. [*Pteris aquilina* var. *pseudocaudata* Clute]

This variety is the more commonly encountered taxon in the West Gulf Coastal Plain.

Ashley Co.: *Taylor 1890* (SIU). Benton Co.: *D. Moore 450891* (UARK). Bradley Co.: *Demaree 23878* (SMU). Calhoun Co.: *Demaree 16616* (SMU). Clark Co.: *Taylor 2181* (SIU). Cleveland Co.: *Taylor 1139* (SIU). Columbia Co.: *Taylor 1169* (SIU). Conway Co.: *Clark 45* (HXC). Crawford Co.: *D. Moore 50283* (UARK). Cross Co.: *Johnson 440* (HXC). Dallas Co.: *Demaree 19048* (SMU). Drew Co.: *Taylor 1148* (SIU). Faulkner Co.: *Buchholz 988* (UARK). Fulton Co.: *Taylor 2668* (SIU). Garland Co.: *Taylor 2860* (SIU). Grant Co.: *Demaree 16564* (SMU). Greene Co.: *Demaree 26697* (SMU). Hempstead Co.: *D. Moore 480477* (APCR). Hot Spring Co.: *Taylor 2859* (SIU). Howard Co.: *Demaree 9952* (SMU). Independence Co.: *Thomas 7778* (NLU). Jefferson Co.: *Demaree 19457* (SMU). Johnson Co.: *Demaree 20213* (SMU). Lee Co.: *Holmes 81* (SMU). Lincoln Co.: *Demaree 19185* (SMU). Little River Co.: *Taylor 2162* (SIU). Lonoke Co.: *Demaree 8406* (SMU). Marion Co.: *Demaree 29322* (SMU). Miller Co.: *Demaree 24486* (SMU). Montgomery Co.: *Taylor 2220* (SIU). Nevada Co.: *Taylor 2749* (SIU). Perry Co.: *Wright P701* (UARK). Pike Co.: *Taylor 2171* (SIU). Polk Co.: *Demaree 15695* (SMU). Prairie Co.: *Demaree 22307* (SMU). Pulaski Co.: *Taylor 2540* (SIU). Randolph Co.: *Taylor 2101* (SIU). Saline Co.: *Demaree 8545* (SMU). Union Co.: *Hoiberg 326* (SMU). Van Buren Co.: *Wherry s.n.* (PH). Washington Co.: *French s.n.* (APCR). White Co.: *Demaree 26892* (SMU). Yell Co.: *Demaree 20584* (SMU).

THELYPTERIDACEAE

41. **Thelypteris kunthii** (Desv.) Morton, Contr. U. S. Nat. Herb. 38: 53. 1967. [*Thelypteris normalis* (C. Chr.) Moxley]

Ashley Co.: roadside in lumbered pine forest; timber access road SE of Lake Georgia-Pacific; sects. 22 and 35, T17S, R9W; *Johnson 281* (HXC).

42. **Thelypteris noveboracensis** (L.) Nieuwl., Amer. Midl. Nat. 1: 226. 1910. [*Polypodium noveboracense* L.; *Aspidium noveboracense* (L.) Sw.; *Dryopteris noveboracensis* (L.) Gray]

Moist, rocky soils of woods and thickets along streams; chiefly Ouachita Mountains.

Cleburne Co.: *Johnson 393* (HXC). Garland Co.: *D. Moore 6278* (APCR). Montgomery Co.: *Taylor 1084* (SIU). Pike Co.: *Taylor 2903* (SIU). Polk Co.: *D. Moore 410261* (UARK). Pulaski Co.: *Johnson 112* (HXC). Saline Co.: *D. Moore 480154* (UARK).

43. **Thelypteris palustris** Schott, Gen. Fil. t. 10. 1834. [*Acrostichum thelypteris* L.; *Aspidium thelypteris* (L.) Sw.; *Dryopteris thelypteris* (L.) Gray]

Low, marshy areas around ponds and lakes and along streams. Two varieties are recognized in the state.

43a. **Thelypteris palustris** var. **haleana** Fern., Rhodora 31: 34. 1929. [*Dryopteris thelypteris* var. *haleana* (Fern.) Weatherby]

Bradley Co.: cypress swamp near Warren; *Demaree 19445* (SMU). Drew Co.: among grasses and sedges in swamp near Wilmar; *Demaree 24624* (SMU).

43b. **Thelypteris palustris** var. **pubescens** (Laws.) Fern. [*Dryopteris thelypteris* var. *pubescens* (Laws.) Weatherby]

Ashley Co.: *Johnson 276* (HXC). Bradley Co.: *Demaree 19445* (MO). Drew Co.: *D. Moore 420048* (UARK). Greene Co.: *D. Moore 480685* (UARK). Hempstead Co.: *D. Moore 480353* (UARK). Izard Co.: *Johnson 422* (HXC). Lawrence Co.: *Taylor 1794* (SIU). Little River Co.: *Palmer 8359* (MO). Polk Co.: *J. Moore & McWilliams s.n.* (UARK). Sharp Co.: *Wade 167* (UARK). Washington Co.: *Henbest 16* (UARK).

44. **Thelypteris torresiana** (Gaud.) Alston, Lilloa 30: 11. 1960.

Ashley Co.: roadside at edge of field; timber access road, W of Crossett, sect. 9, T18S, R9W and roadside in lumbered pine forest; timber access road SE of Lake Georgia-Pacific, sect. 22, T17S, R9W; *Johnson 283* (HXC).

45. **Phegopteris hexagonoptera** (Michx.) Fee, Gen. Fil. 243. 1850–52. [*Polypodium hexagonopterum* Michx.; *Dryopteris hexagonoptera* (Michx.) C. Chr.; *Thelypteris hexagonoptera* (Michx.) Weatherby]

Moist, sandy soil on slopes and in ravines of rich woods; Interior Highlands, West Gulf Coastal Plain, and Crowley's Ridge.

Ashley Co.: *Taylor 1877* (SIU). Benton Co.: *D. Moore 410010* (UARK). Bradley Co.: *Demaree 21022* (MO). Carroll Co.: *Palmer 4471* (MO). Clark Co.: *Taylor 2176* (SIU).

Clay Co.: *Bush 2616* (MO). Cleburne Co.: *Smith 1494* (UARK). Conway Co.: *Tucker 7157* (APCR). Craighead Co.: *Demaree 3576* (MO). Cross Co.: *Palmer 31663* (UARK). Drew Co.: *Palmer 44223* (SMU). Faulkner Co.: *Buchholz 946* (UARK). Franklin Co.: *Johnson 521* (HXC). Garland Co.: *Palmer 29210* (UARK). Greene Co.: *Demaree 4002* (SMU). Hempstead Co.: *Bush 5713* (NY). Hot Spring Co.: *Wherry s.n.* (PH). Howard Co.: *McSwain 43E80* (UARK). Independence Co.: *Demaree 17080* (SMU). Izard Co.: *Thomas s.n.* (NLU). Jefferson Co.: *Stewart 20* (UARK). Johnson Co.: *Redfearn 18929* (SMS). Lawrence Co.: *Taylor 1793* (SIU). Lee Co.: *Taylor 1185* (SIU). Logan Co.: *Palmer 23236* (MO). Madison Co.: *Key 267* (SMS). Marion Co.: *Johnson 92* (HXC). Montgomery Co.: *Taylor 1075* (SIU). Newton Co.: *Taylor 1220* (SIU). Perry Co.: *Demaree 20145* (MO). Phillips Co.: *Taylor 1190a* (SIU). Pike Co.: *Redfearn 24472* (SMS). Poinsett Co.: *Emig 58* (MO). Polk Co.: *Taylor 1066* (SIU). Pope Co.: *Taylor 1203* (SIU). Pulaski Co.: *Haase s.n.* (NY). St. Francis Co.: *Demaree 7234* (UARK). Saline Co.: *Palmer 10549* (MO). Searcy Co.: *Taylor 2582* (SIU). Stone Co.: *Taylor 1254* (SIU). Union Co.: *Taylor 1153* (SIU). Van Buren Co.: *Palmer 24291* (UARK). Washington Co.: *Taylor 1103* (SIU). White Co.: *Johnson 460* (HXC).

ASPLENIACEAE

46. **Asplenium bradleyi** D. C. Eat., Bull. Torrey Bot. Club 4: 11. 1873. [*Asplenium* × *stotleri* Wherry]

Sandstone and novaculite outcrops; chiefly Interior Highlands.

Baxter Co.: *Culwell 3188* (UCA). Benton Co.: *D. Moore 41096* (UARK). Boone Co.: *Redfearn 23716* (SMS). Cleburne Co.: *Johnson 468* (HXC). Conway Co.: *D. Moore 470468* (UARK). Franklin Co.: *Redfearn 21149* (SMS). Garland Co.: *D. Moore 46-092* (UARK). Greene Co.: *Demaree 26704* (SMU). Independence Co.: *Coville 161* (US). Izard Co.: *Demaree 23437* (SMU). Johnson Co.: *Redfearn 23834* (SMS). Logan Co.: *Haas 135* (MO). Madison Co.: *Taylor 2004* (SIU). Montgomery Co.: *Johnson 180* (HXC). Newton Co.: *Taylor 2699* (SIU). Perry Co.: *Redfearn 23982* (SMS). Polk Co.: *D. Moore & McWilliams 56197* (UARK). Pope Co.: *Taylor 1216* (SIU). Pulaski Co.: *Hasse s.n.* (NY). Saline Co.: *Redfearn 24325* (SMS). Searcy Co.: *Redfearn 23721* (SMS). Stone Co.: *Taylor 2902* (SIU). Van Buren Co.: *Demaree 4757* (SIU). Washington Co.: *D. Moore 340680* (UARK). Yell Co.: *Taylor 4368* (SIU).

47. **Asplenium × ebenoides** R. R. Scott, Gardener's Monthly 7: 267. 1865. [*Asplenium platyneuron* × *Camptosorus rhizophyllus* Slosson; × *Asplenosorus ebenoides* (R. R. Scott) Wherry]

Johnson Co.: shaded boulder face along road to campground; Haw Creek Falls Recreation Area; W of Fort Douglas; *Johnson 79028* (HXC). This hybrid has been reported from Crawford County along Lee Creek (Moore, 1940) but voucher material has not been located.

48. **Asplenium × kentuckiense** McCoy, Amer. Fern J. 25: 104. 1936. [*Asplenium pinnatifidum* × *platyneuron* Wagner]

Benton Co.: growing near both parents on a sandstone outcrop; ca 1 mi. W of old Elkhorn Tavern, Pea Ridge National Military Park; *D. Moore 430114* (MO).

49. **Asplenium pinnatifidum** Nutt., Gen. 2: 251. 1818.

Crevices of sandstone and novaculite outcrops; Interior Highlands.

Benton Co.: *Taylor 1123* (SIU). Cleburne Co.: *Johnson 435* (HXC). Garland Co.: *Taylor 2704* (SIU). Independence Co.: *D. Moore 61118* (UARK). Izard Co.: *Johnson 79054* (HXC). Van Buren Co.: *Johnson 437* (HXC).

50. **Asplenium platyneuron** (L.) Oakes ex D. C. Eat., Ferns N. Amer. 1: 24. 1878. [*Asplenium ebeneum* Ait.]

Moist to dry, rocky woods, hillsides, ravines, thickets, rock outcrops, stream banks, and roadsides. Three varieties are recognized in the state.

50a. **Asplenium platyneuron** var. **bacculum-rubrum** (Featherm.) Fern., Rhodora 38: 304. 1936.

Boone Co.: *Haas 2798* (UCA). Cleburne Co.: *Taylor 1017b* (SIU). Johnson Co.: *Taylor 1087* (SIU). Lee Co.: *McDaniel 804* (UARK). Polk Co.: *Taylor 1061* (SIU). Pulaski Co.: *Palmer 23002* (UARK). Stone Co.: *Taylor 1248* (SIU). Van Buren Co.: *Nelson 482* (SIU).

50b. **Asplenium platyneuron** var. **incisum** (Howe ex Peck) B. L. Robins., Rhodora 10: 29. 1908. [*Asplenium ebeneum* var. *incisum* Peck; *Asplenium ebeneum* var. *serratum* E. S. Miller; *Asplenium platyneuron* var. *serratum* (E. S. Miller) BSP.]

Baxter Co.: *Taylor 2677* (SIU). Benton Co.: *D. Moore 460177* (UARK). Carroll Co.: *Palmer 6351* (MO). Clark Co.: *Taylor 2175* (SIU). Clay Co.: *Taylor 2661* (SIU). Cleveland Co.: *Taylor 2736* (SIU). Conway Co.: *Demaree 23122* (SMU). Craighead Co.: *Demaree 3523* (NY). Crawford Co.: *Taylor 1126* (SIU). Cross Co.: *Akers 20* (HXC). Garland Co.: *Palmer 23106* (MO). Greene Co.: *Richards 5488* (ARKSU). Hempstead Co.: *Palmer 10512* (MO). Howard Co.: *McSwain 43E69* (UARK). Jackson Co.: *Richards 6203* (ARKSU). Lee Co.: *McDaniel 804* (ARKSU). Marion Co.: *Palmer 4747* (MO). Montgomery Co.: *Taylor 2843* (SIU). Nevada Co.: *D. Moore 420470* (UARK). Newton Co.: *Taylor 2700* (SIU). Phillips Co.: *Palmer 25162* (UARK). Pike Co.: *Johnson 177* (HXC). Polk Co.: *Taylor 2850* (SIU). Pulaski Co.: *Wheeler 50* (F). Randolph Co.: *Taylor 2087* (SIU). Saline Co.: *Demaree 23031* (SMU). Sharp Co.: *Demaree 27732* (SMU). Stone Co.: *Johnson 74* (HXC). Washington Co.: *Buchholz s.n.* (US). White Co.: *Johnson 217* (HXC).

50c. **Asplenium platyneuron** var. **platyneuron.**

Ashley Co.: *Demaree 16368* (SMU). Baxter Co.: *Taylor 1828* (SIU). Benton Co.: *Taylor 1120* (SIU). Boone Co.: *Demaree s.n.* (UARK). Calhoun Co.: *Demaree 22666* (MO). Carroll Co.: *Palmer 4527* (MO). Clark Co.: *Taylor 2192* (SIU). Clay Co.: *Bush 2646* (MO). Cleburne Co.: *Demaree 30305* (SMU). Cleveland Co.: *Taylor 1017* (SIU). Conway Co.: *Demaree 23122* (MO).

Crawford Co.: *Redfearn 23642* (SMS). Cross Co.: *Demaree 19631* (MO). Dallas Co.: *Taylor 1137* (SIU). Drew Co.: *Demaree 24348* (MO). Faulkner Co.: *Taylor 2609* (SIU). Franklin Co.: *Palmer 8160* (MO). Fulton Co.: *Taylor 2667* (SIU). Garland Co.: *Taylor 2193* (SIU). Greene Co.: *Demaree 26688* (SMU). Hempstead Co.: *Bush 1452* (US). Hot Spring Co.: *Demaree 15610* (SMU). Howard Co.: *Kellogg s.n.* (MO). Independence Co.: *Demaree 17067* (MO). Izard Co.: *Taylor 2136* (SIU). Jefferson Co.: *Locke 1223* (UARK). Johnson Co.: *Taylor 1089* (SIU). Lawrence Co.: *Taylor 1787* (SIU). Lee Co.: *Demaree 37381* (SMU). Little River Co.: *Johnson 475* (HXC). Logan Co.: *Taylor 1032* (SIU). Lonoke Co.: *Clark 665* (HXC). Madison Co.: *Taylor 2005* (SIU). Marion Co.: *Taylor 1230* (SIU). Miller Co.: *Taylor 1172* (SIU). Montgomery Co.: *Taylor 1073* (SIU). Nevada Co.: *D. Moore 420464* (UARK). Newton Co.: *Taylor 1224* (SIU). Ouachita Co.: *Hoiberg 351* (SMU). Perry Co.: *Demaree 54546* (SMU). Phillips Co.: *Palmer 25165* (MO). Pike Co.: *Demaree 9766* (SMU). Polk Co.: *Taylor 1059* (SIU). Pope Co.: *Taylor 1204* (SIU). Pulaski Co.: *Demaree 17347* (MO). Randolph Co.: *Taylor 1800* (SIU). Saline Co.: *Demaree 23021* (MO). Scott Co.: *Taylor 1058* (SIU). Searcy Co.: *Taylor 1853* (SIU). Sebastian Co.: *Taylor 2721* (SIU). Sevier Co.: *Taylor 2164* (SIU). Sharp Co.: *Taylor 1819* (SIU). Stone Co.: *Taylor 1257* (SIU). Union Co.: *Taylor 1163* (SIU). Van Buren Co.: *Redfearn 16862* (SMS). Washington Co.: *Taylor 1105* (SIU). White Co.: *D. Moore 451039* (UARK). Yell Co.: *Taylor 1192* (SIU).

The striking, deeply dissected *Asplenium platyneuron* f. *hortonae* (Davenp.) L. B. Smith is a sporadic, sterile plant. It was collected in Arkansas from a mossy, rock ledge on Petit Jean Mountain, Conway County by D. M Moore (D. Moore 480355 UARK).

51. **Asplenium resiliens** Kunze, Linnaea 18: 331. [*Asplenium parvulum* Mart. & Gal.]

Limestone, dolomite, and chert outcrops; primarily Ozark Highlands.

Baxter Co.: *Taylor 1840* (SIU). Benton Co.: *Demaree 4654* (F). Boone Co.: *Palmer 6907* (MO). Carroll Co.: *Palmer 29314* (MO). Garland Co.: *Engelmann 10* (MO). Independence Co.: *Demaree 28594* (SMU). Izard Co.: *Demaree 17039* (SMU). Johnson Co.: *Johnson 79033* (HXC). Lawrence Co.: *Taylor 1788* (SIU). Madison Co.: *Haas 1437* (UCA). Marion Co.: *Palmer 43872* (MO). Newton Co.: *Taylor 2698* (SIU). Randolph Co.: *Demaree 26813* (SMU). Searcy Co.: *Taylor 1243* (SIU). Sharp Co.: *Demaree 26434* (SMU). Stone Co.: *Taylor 1244* (SIU). Washington Co.: *Demaree 2797* (UARK).

52. **Asplenium rhizophyllum** L., Sp. Pl. 2: 1078. 1753. [*Camptosorus rhizophyllus* (L.) Link]

Moist, shaded, limestone and sandstone outcrops; chiefly Ozark Highlands and Boston Mountains.

Baxter Co.: *Taylor 1849* (SIU). Benton Co.: *Demaree 4616* (SMU). Carroll Co.: *Haas 1453* (UCA). Conway Co.: *Johnson 195* (HXC). Crawford Co.: *Redfearn 21086* (SMS). Franklin Co.: *Johnson 520* (HXC). Fulton Co.: *Wheeler 50* (F). Independence Co.: *Thomas 8494* (SMU). Izard Co.: *Barr s.n.* (UARK). Johnson Co.: *Redfearn 23826* (SMS). Lawrence Co.: *Taylor 1785* (SIU). Logan Co.: *Pyle 286* (APCR). Madison Co.: *Taylor 1994a* (SIU). Marion Co.: *D. Moore 380727* (UARK). Newton Co.: *Taylor 2696* (SIU). Pope Co.: *Taylor 1213* (SIU). Randolph Co.: *Demaree 26812* (SMU). Searcy Co.: *Taylor 2574* (SIU). Sharp Co.: *Demaree 25922* (SMU). Stone Co.: *Taylor 1246* (SIU). Van Buren Co.: *Palmer 24292* (UARK). Washington Co.: *Henbest 14* (UARK).

—. **Asplenium ruta-muraria** L., Sp. Pl. 2: 1079. 1753. [*Asplenium cryptolepis* Fern.]

Asplenium ruta-muraria was first reported from Arkansas in the list of Nuttall (1835). Lesquereux (1860) recorded this species from "limestone cliffs." Harvey (1881) also included *A. ruta-muraria* in his list, stating that he had specimens from Lesquereux said to have been collected in northeast Arkansas. Although no specimens have been located to confirm its presence in the state, *A. ruta-muraria* is included here on the basis of the above reports.

Asplenium ruta-muraria has been collected from a number of counties in southeast Missouri plus Stone, Ozark, Howell, Oregon, and Ripley Counties which border Arkansas to the north. In Missouri, *A. ruta-muraria* is found on north- and east-facing limestone outcrops (Steyermark, 1963, p. 30). Similar sites occur in the Ozark Highlands of Arkansas and field work in this region should yield specimens.

53. **Asplenium trichomanes** L., Sp. Pl. 2: 1080. 1753. [*Asplenium melanocaulon* Willd.]

Moist rock outcrops; Interior Highlands.

Baxter Co.: *Taylor 2685* (SIU). Benton Co.: *Taylor 1117* (SIU). Boone Co.: *Demaree 3246* (NY). Carroll Co.: *Palmer 5615* (MO). Cleburne Co.: *Palmer 6952* (MO). Conway Co.: *Demaree 23123* (MO). Crawford Co.: *Taylor 1098* (SIU). Faulkner Co.: *Buchholz 995* (UARK). Franklin Co.: *Taylor 1128* (SIU). Fulton Co.: *Palmer 14691* (MO). Garland Co.: *Palmer 23105* (UARK). Howard Co.: *Kellogg s.n.* (MO). Independence Co.: *Demaree 17099* (MO). Izard Co.: *Demaree 3275* (UARK). Johnson Co.: *Redfearn 23847* (SMS). Logan Co.: *Taylor 1031* (SIU). Madison Co.: *Davis 1503* (UARK). Marion Co.: *Taylor 1232* (SIU). Montgomery Co.: *J. Moore 3154* (UCA). Newton Co.: *Redfearn 23102* (SMS). Perry Co.: *Redfearn 24135* (SMS). Polk Co.: *J. Moore s.n.* (UARK). Pope Co.: *Robinette 2789* (UCA). Pulaski Co.: *Owens s.n.* (US). Sebastian Co.: *Taylor 2720* (SIU). Stone Co.: *D. Moore 450518* (UARK). Van Buren Co.: *Taylor 2561* (SIU). Washington Co.: *Demaree 3007* (UARK). White Co.: *Johnson 453* (HXC). Yell Co.: *Taylor 1194* (SIU).

54. **Onoclea sensibilis** L., Sp. Pl. 2: 1062. 1753.

Moist to wet soil along margins of streams and lakes, in meadows, woods, roadside ditches, and around springs.

Ashley Co.: *Taylor 1888* (SIU). Benton Co.: *Pyle s.n.* (UARK). Bradley Co.: *Demaree 23832* (SMU). Calhoun Co.: *Hoiberg 307* (SMU). Clark Co.: *Demaree 21920* (SMU). Clay Co.: *Demaree 4140* (NY). Cleburne Co.: *Babb 977* (ARKSU). Columbia Co.: *Johnson 33* (HXC). Conway Co.: *J. Moore 5* (UARK). Craighead Co.: *Demaree 7038* (SMU). Crawford Co.: *Taylor 1095* (SIU). Cross Co.: *D. Moore 420380* (UARK). Faulkner Co.: *Spencer 52* (HXC). Garland Co.: *Palmer 24933* (UARK). Franklin Co.: *Davis 444* (UARK). Greene Co.: *Demaree 26661* (SMU). Hempstead Co.: *Taylor 1175* (SIU). Independence Co.: *Johnson 500* (HXC). Johnson Co.: *Redfearn 23828* (SMS). Lawrence Co.: *Taylor 2595* (SIU). Lee Co.: *Davis 331* (ARKSU). Little River Co.: *Taylor 2141* (SIU). Marion Co.: *Thomas 16197* (SMU). Montgomery Co.: *Taylor 2210* (SIU). Nevada Co.: *D. Moore 410340* (UARK). Newton Co.: *Redfearn 27519* (SMS). Ouachita Co.: *Demaree 61376* (SMU). Perry Co.: *J. Moore 3318* (UCA). Phillips Co.: *Palmer 25128* (UARK). Pike Co.: *Demaree 9974* (MO). Poinsett Co.: *Demaree 3671* (SMU). Polk Co.: *J. Moore 3150* (ARKSU). Pope Co.: *Redfearn 17341* (SMS). Pulaski Co.: *Johnson 114* (HXC). St. Francis Co.: *Lowman 372* (HXC). Saline Co.: *Demaree 53157* (SIU). Searcy Co.: *Taylor 2577* (SIU). Sevier Co.: *Johnson 150* (HXC). Union Co.: *Taylor 1160* (SIU). Van Buren Co.: *Haas 1477* (ARKSU). Washington Co.: *Buchholz 1010* (UARK). White Co.: *Johnson 210* (HXC). Woodruff Co.: *Johnson 442* (HXC).

Onoclea sensibilis f. *obtusilobata* (Schkuhr) Gilb., with fronds somewhat intermediate in form between normal sterile and fertile fronds, was collected by F. L. Harvey without location (UARK *13*) and by D. M. Moore at Crowley's Ridge State Park, Greene County (*D. Moore 480680* UARK).

55. **Athyrium filix-femina** (L.) Roth subsp. **asplenioides** (Michx.) Hulten, Kgl. Sv. Vet. Akad. Handl. 8: 178. 1962. [*Nephrodium asplenioides* Michx.; *Athyrium asplenioides* (Michx.) A. A. Eat.; *Asplenium asplenioides* (Michx.) Chapm.; *Athyrium filix-femina* var. *asplenioides* (Michx.) Farw.]

Moist woodlands, stream banks, marshy areas around ponds and lakes, roadsides.

Ashley Co.: *Taylor 1876* (SIU). Benton Co.: *Buchholz s.n.* (UARK). Bradley Co.: *Locke 547* (UARK). Calhoun Co.: *Demaree 22107* (MO). Carroll Co.: *Palmer 3813* (NY). Clark Co.: *Taylor 2177* (SIU). Clay Co.: *Rosen 90* (UARK). Cleburne Co.: *Taylor 1014* (SIU). Columbia Co.: *Taylor 1167* (SIU). Conway Co.: *Demaree 37230* (SMU). Craighead Co.: *Demaree 3569* (MO). Crawford Co.: *Moore 710287* (UARK). Cross Co.: *Palmer 31665* (UARK). Dallas Co.: *Miller 682* (UARK). Drew Co.: *Demaree 22101* (SMU). Faulkner Co.: *Buchholz s.n.* (UARK). Franklin Co.: *D. Moore 340684* (UARK). Garland Co.: *Taylor 2555* (SIU). Grant Co.: *Taylor 2723* (SIU). Greene Co.: *Demaree 26695* (SMU). Hempstead Co.: *Taylor 1177* (SIU). Hot Spring Co.: *Palmer 26592*

(UARK). Howard Co.: *D. Moore 410263* (UARK). Independence Co.: *Demaree 17099* (SMU). Izard Co.: *Demaree 23512* (SMU). Jefferson Co.: *Demaree 24069* (MO). Johnson Co.: *D. Moore 450275* (UARK). Lawrence Co.: *Demaree 520965* (SIU). Little River Co.: *Palmer 8353* (MO). Logan Co.: *Taylor 1038* (SIU). Lonoke Co.: *Clark 663* (HXC). Madison Co.: *Davis 1504* (UARK). Miller Co.: *Palmer 10530* (MO). Montgomery Co.: *Taylor 1072* (SIU). Nevada Co.: *Bush 694* (MO). Newton Co.: *D. Moore 480752* (UARK). Ouachita Co.: *D. Moore 490652* (UARK). Perry Co.: *J. Moore 6616* (UCA). Phillips Co.: *Palmer 25146* (UARK). Pike Co.: *Taylor 2169* (SIU). Poinsett Co.: *Demaree 3667* (SMU). Polk Co.: *Taylor 1069* (SIU). Pope Co.: *Robinette 2795* (UCA). Pulaski Co.: *Demaree 8899* (SMU). St. Francis Co.: *Clark 613* (HXC). Saline Co.: *Demaree 23034* (MO). Union Co.: *Taylor 1160* (SIU). Van Buren Co.: *Palmer 24294* (MO). Washington Co.: *Hite 23* (UARK). White Co.: *Johnson 458* (HXC).

The narrow blade form of subsp. *asplenioides,* which has "the blade narrowed below so as to approach an elliptic outline," has been distinguished as f. *ellipticum* by Wherry (1948) and has been collected from a number of counties in the state. However, in Arkansas it appears that this form is scarcely justifiable for fronds assignable to f. *ellipticum* may be found in nearly every population of subsp. *asplenioides.* Elliptical blades have been noted particularly in juvenile plants and in early, spring foliage.

The striking, highly dissected f. *subtripinnatum* Butters, which has pinnules that are deeply cut into oblong segments, was collected in Pike County by D. Demaree (F *1420306*). Additional collections from Harrisburg, Poinsett County; Pelsor, Pope County; and Grassy Lake, Hempstead County have been reported by Moore (1940).

56. **Athyrium pycnocarpon** (Spreng.) Tidest., Elys. Marianum 1: 36. 1906. [*Asplenium angustifolium* Michx.; *Asplenium pycnocarpon* Spreng.; *Diplazium angustifolium* (Michx.) Butters; *Diplazium pycnocarpon* (Spreng.) Broun]

Rocky slopes and ravines in moist, rich woods; primarily Ozark Highlands and Boston Mountains.

Benton Co.: *Demaree 4494* (SMU). Carroll Co.: *Palmer 3813* (US). Cleburne Co.: *Babb 1596* (ARKSU). Crawford Co.: *Taylor 1097* (SIU). Franklin Co.: *Davis 1357* (UARK). Independence Co.: *Thomas 8568* (NLU). Johnson Co.: *Redfearn 18927* (SMS). Marion Co.: *D. Moore 410516* (UARK). Newton Co.: *Taylor 2694* (SIU). Phillips Co.: *Clark 446* (HXC). Pope Co.: *Tucker 3545* (APCR). Searcy Co.: *D. Moore 350149* (UARK). Stone Co.: *Graham 373* (APCR). Van Buren Co.: *Palmer 24302* (UARK). Washington Co.: *Palmer 27037* (MO).

57. **Athyrium thelypterioides** (Michx.) Desv., Mem. Soc. Linn. Paris 6: 266. 1827. [*Asplenium acrostichoides* Sw.; *Asplenium thelypterioides* Michx.; *Diplazium acrostichoides* (Sw.) Butters]

Moist, rich woods; near streams and on shaded slopes.

Hot Spring Co.: *Redfearn 24143* (SMS). Johnson Co.: *Johnson 47* (HXC). Logan Co.: *D. Moore 420124* (SMU). Madison Co.: *Davis 1506* (UARK). Phillips Co.: *Akers 42* (HXC).

58. **Cystopteris bulbifera** (L.) Bernh., Neu. Journ. Bot. Schrad. 1(2): 10. 1806. [*Polypodium bulbiferum* L.]

Moist, shaded outcrops of limestone, dolomite, calcareous sandstone and shale; primarily Ozark Highlands.

Baxter Co.: *D. Moore 510522* (UARK). Benton Co.: *Demaree 4897* (F). Carroll Co.: *D. Moore 58218* (UARK). Fulton Co.: *Wheeler 13* (F). Howard Co.: *Kellogg s.n.* (MO). Independence Co.: *Thomas 8302* (NLU). Johnson Co.: *Redfearn 23832* (SMS). Madison Co.: *Palmer 24796* (MO). Marion Co.: *Palmer 4780* (MO). Newton Co.: *Taylor 2693* (SIU). Pope Co.: *Key 383* (SMS). St. Francis Co.: *Johnson 441* (HXC). Searcy Co.: *Taylor 2579* (SIU). Sharp Co.: *Demaree 26436* (SMU). Stone Co.: *Taylor 2899* (SIU). Van Buren Co.: *Palmer 25192* (MO). Washington Co.: *Palmer 27033* (MO).

59. **Cystopteris protrusa** (Weatherby) Blasdell, Mem. Torrey Bot. Club 21: 41. 1963. [*Cystopteris fragilis* var. *protrusa* Weatherby]

Moist, shaded, humus-rich, loam soils of woodlands; Interior Highlands and Crowley's Ridge.

Benton Co.: *Demaree 6517* (UARK). Craighead Co.: *Richards 6346* (ARKSU). Crawford Co.: *Taylor 1100* (SIU). Franklin Co.: *Johnson 528* (HXC). Garland Co.: *D. Moore 480192* (UARK). Hot Spring Co.: *Palmer 29708* (UARK). Johnson Co.: *Johnson 48* (HXC). Logan Co.: *Taylor 1047* (SIU). Newton Co.: *D. Moore 480225* (UARK). Phillips Co.: *Lowman 98* (HXC). Polk Co.: *Taylor 1065* (SIU). Searcy Co.: *D. Moore 350143* (UARK). Sharp Co.: *Demaree 27712* (SMU). Stone Co.: *D. Moore 510354* (UARK). Van Buren Co.: *Johnson 152* (HXC). Washington Co.: *Hite 24* (UARK). White Co.: *Johnson 221* (HXC).

60. **Cystopteris tennesseensis** Shaver, Journ. Tenn. Acad. Sci. 25: 107. 1950. [*Cystopteris fragilis* f. *simulans* Weatherby; *Cystopteris fragilis* var. *simulans* (Weatherby) McGregor; *Cystopteris fragilis* var. *tennesseensis* (Shaver) McGregor]

Moist, shaded outcrops of sandstone, limestone, dolomite, and shale; Interior Highlands.

Baxter Co.: *Taylor 2679* (SIU). Benton Co.: *Taylor 1122* (SIU). Conway Co.: *J. Moore 1089* (SMU). Fulton Co.: *Wheeler 39* (UARK). Independence Co.: *Thomas 7753* (NLU). Izard Co.: *Taylor 1267* (SIU). Johnson Co.: *Redfearn 23833* (SMS). Logan Co.: *Pyle 280* (APCR). Madison Co.: *Key 270* (SMS). Marion Co.: *Taylor 1235* (SIU). Newton Co.: *Redfearn 23479* (SMS). Pope Co.: *D. Moore 520756* (UARK). Randolph Co.: *Demaree 26816* (SMU). Scott Co.: *Demaree 58499* (UARK). Searcy Co.: *Taylor 1240* (SIU). Stone Co.: *Taylor 1245* (SIU). Van Buren Co.: *Demaree 4753* (UARK). Washington Co.: *Haas 1471* (UCA).

61. **Woodsia obtusa** (Spreng.) Torr., Cat. Pl. in Geol. Rep. N. Y., 195. 1840. [*Polypodium obtusum* Spreng.]

Well drained, rocky or sandy soils of woodlands, rock outcrops, along roadsides and fence rows, occasionally on old rock walls.

Baxter Co.: *Taylor 1829* (SIU). Benton Co.: *Taylor 1121* (SIU). Boone Co.: *D. Moore 490380* (UARK). Calhoun Co.: *Demaree 22105* (SMU). Carroll Co.: *Palmer 4537* (MO). Clark Co.: *Taylor 2190* (SIU). Clay Co.: *Demaree 30417* (SMU). Cleburne Co.: *Taylor 1018* (SIU). Cleveland Co.: *Taylor 2737* (SIU). Columbia Co.: *Thomas 27931* (NLU). Conway Co.: *Demaree 23115* (SIU). Crawford Co.: *Taylor 1099* (SIU). Cross Co.: *Richards 3946* (ARKSU). Faulkner Co.: *Taylor 2011* (SIU). Franklin Co.: *Taylor 1129* (SIU). Fulton Co.: *Taylor 2666* (SIU). Garland Co.: *Taylor 2232* (SIU). Greene Co.: *Hess 1132* (SMU). Hempstead Co.: *Bush 5711* (MO). Hot Spring Co.: *Demaree 16539* (SMU). Howard Co.: *McSwain 43E70* (UARK). Independence Co.: *Demaree 27150* (SMU). Izard Co.: *Taylor 2137* (SIU). Jefferson Co.: *Locke 1224* (UARK). Johnson Co.: *Taylor 1088* (SIU). Lawrence Co.: *Taylor 1786* (SIU). Lee Co.: *Demaree 37377* (SMU). Little River Co.: *Johnson 474* (HXC). Logan Co.: *Taylor 1033* (SIU). Madison Co.: *Taylor 1997* (SIU). Marion Co.: *Taylor 1229* (SIU). Miller Co.: *Taylor 1910* (SIU). Montgomery Co.: *Taylor 1081* (SIU). Newton Co.: *D. Moore 480228* (UARK). Ouachita Co.: *Demaree 63771* (SIU). Perry Co.: *Demaree 27051* (SMU). Pike Co.: *Taylor 2170* (SIU). Polk Co.: *Hoiberg 560* (SMU). Pope Co.: *Taylor 1200* (SIU). Pulaski Co.: *Demaree 17375* (MO). Randolph Co.: *Taylor 1081* (SIU). St. Francis Co.: *Demaree 22149* (SMU). Saline Co.: *Demaree 23042* (SMU). Scott Co.: *Taylor 2715* (SIU). Searcy Co.: *Taylor 1241* (SIU). Sebastian Co.: *Taylor 2712* (SIU). Sharp Co.: *Taylor 1817* (SIU). Stone Co.: *Taylor 1249* (SIU). Van Buren Co.: *Wherry s.n.* (PH). Washington Co.: *Taylor 1115* (SIU). White Co.: *Demaree 26902* (SMU). Yell Co.: *Taylor 1193* (SIU).

62. **Woodsia scopulina** D. C. Eat. var. **appalachiana** (T. M. C. Taylor) Morton, Amer. Fern J. 40: 224. 1950. [*Woodsia appalachiana* T. M. C. Taylor]

Logan Co.: ledges of sandstone outcrops and talus on north side, near summit of Magazine Mountain; *Taylor 1045* (SIU).

63. **Polystichum acrostichoides** (Michx.) Schott, Gen. Fil. pl. 9. 1834. [*Nephrodium acrostichoides* Michx.; *Aspidium acrostichoides* (Michx.) Sw.]

Rich, rocky, wooded slopes and ravines, along stream banks, and in alluvial woods; nearly throughout the state.

Arkansas Co.: *Wherry s.n.* (PH). Ashley Co.: *Taylor 1878* (SIU). Baxter Co.: *D. Moore 450747* (UARK). Benton Co.: *D. Moore 460154* (UARK). Boone Co.: *Demaree s.n.* (UARK). Bradley Co.: *Demaree 21025* (UARK). Carroll Co.: *Bush 15424* (UARK). Clark Co.: *Taylor 2174* (SIU). Clay Co.: *Demaree 27019* (SMU). Cleburne Co.: *Taylor 1021* (SIU). Cleveland Co.: *Locke 2268* (UARK). Columbia Co.: *Johnson 35* (HXC). Conway Co.: *Demaree 22791* (MO). Craighead Co.: *Demaree 3493* (SMU). Crawford Co.: *Taylor 1094* (SIU). Cross Co.: *Palmer 31660* (UARK). Dallas Co.: *Taylor 1134*

(SIU). Drew Co.: *Palmer 44222* (SMU). Faulkner Co.: *Buchholz 929* (UARK). Franklin Co.: *Johnson 519* (HXC). Fulton Co.: *Wheeler 40* (F). Garland Co.: *Taylor 2194* (SIU). Grant Co.: *Taylor 2725* (SIU). Greene Co.: *Demaree 4009* (NY). Hempstead Co.: *Bush 1651* (NY). Hot Spring Co.: *Palmer 26575* (MO). Howard Co.: *McSwain 43E65* (UARK). Independence Co.: *Demaree 17068* (MO). Izard Co.: *Taylor 2135* (SIU). Jefferson Co.: *Demaree 24084* (MO). Johnson Co.: *D. Moore 450264* (UARK). Lawrence Co.: *Taylor 1792* (SIU). Lee Co.: *Taylor 1184* (SIU). Logan Co.: *Taylor 1034* (SIU). Lonoke Co.: *Clark 680* (HXC). Madison Co.: *Taylor 1996* (SIU). Marion Co.: *Taylor 1236* (SIU). Miller Co.: *Taylor 1173* (SIU). Montgomery Co.: *Taylor 1074* (SIU). Nevada Co.: *D. Moore 420463* (UARK). Newton Co.: *Taylor 1222* (SIU). Ouachita Co.: *Demaree 16844* (MO). Perry Co.: *Taylor 2852* (SIU). Phillips Co.: *Taylor 1189* (SIU). Pike Co.: *Demaree 9419* (SMU). Poinsett Co.: *D. Moore 31057* (APCR). Polk Co.: *Taylor 1068* (SIU). Pope Co.: *Taylor 1205* (SIU). Prairie Co.: *Taylor 1182* (SIU). Pulaski Co.: *Merrill 1425* (UARK). St. Francis Co.: *Demaree 22156* (MO). Saline Co.: *Palmer 8442* (MO). Scott Co.: *Taylor 1056* (SIU). Searcy Co.: *Taylor 1851* (SIU). Sevier Co.: *Brinkley 349* (F). Sharp Co.: *Schmitt 11* (ARKSU). Stone Co.: *Taylor 1252* (SIU). Union Co.: *Taylor 1154* (SIU). Van Buren Co.: *Taylor 2563* (SIU). Washington Co.: *Taylor 1104* (SIU). White Co.: *Johnson 455* (HXC). Yell Co.: *Taylor 1196* (SIU).

Fronds of *Polystichum acrostichoides,* which bear pinnae that are coarsely serrate to lobed and that sometimes have scattered sori extending to the tips of the lower pinnae, have been recognized as f. *incisum* (Gray) Gilb. Specimens bearing these variously cut pinnae and scattered sori have been noted from a number of collections in the state.

64. **Dryopteris celsa** (W. Palmer) Small, Ferns Southeastern States, 284. 1938. [*Dryopteris goldiana* var. *celsa* W. Palmer]

Moist to wet, shaded, rocky humus around seeps near streams in rich woods.

Lawrence Co.: York Springs; ca. 3.5 mi. S of Imboden; *Marshall 9* (US). Montgomery Co.: along Forest Service Road 43; ca. 0.7 mi. S of jct. with Hwy. 8; *Taylor 2845* (SIU). Polk Co.: valley of Big Fork Creek on north side of Missouri Mountain; along Forest Service Road 38; ca. 2 mi. S of Big Fork and along Forest Service Road 216; ca. 1 mi. N of Big Fork; *D. Moore 520840* (US).

65. **Dryopteris × leedsii** Wherry, Bartonia 21: 2. 1942.

Van Buren Co.: moist, wooded, rocky slope below northwest-facing bluffs; along the west bank of the Middle Fork of the Little Red River; ca. 0.5 mi. SW of Shirley; sect. 25, T12N, R13W; *Taylor 2597* (SIU).

66. **Dryopteris marginalis** (L.) Gray, Man. 632. 1848. [*Polypodium marginale* L.; *Aspidium marginale* (L.) Sw.; *Nephrodium marginale* (L.) Michx.; *Thelypteris marginalis* (L.) Nieuw.]

Rich, rocky slopes and ravine woods, exposed or shaded outcrops; Interior Highlands.

Baxter Co.: *Taylor 2689* (SIU). Benton Co.: *Taylor 1119* (SIU). Boone Co.: *Redfearn 12376* (SMS). Cleburne Co.: *Palmer 6964* (MO). Conway Co.: *Demaree 22792* (MO). Crawford Co.: *Redfearn 21082* (SMS). Faulkner Co.: *Buchholz 950* (UARK). Franklin Co.: *Stephens 10582* (NY). Garland Co.: *Taylor 2195* (SIU). Hot Spring Co.: *Demaree 19033a* (NY). Independence Co.: *D. Moore 450510* (UARK). Izard Co.: *Taylor 2132* (SIU). Johnson Co.: *Redfearn 18920* (SMS). Logan Co.: *Taylor 1039* (SIU). Madison Co.: *Taylor 1999* (SIU). Marion Co.: *D. Moore 41052* (UARK). Montgomery Co.: *Taylor 1085* (SIU). Newton Co.: *Redfearn 23587* (SMS). Perry Co.: *Johnson 481* (HXC). Pike Co.: *Demaree 9486* (SMU). Polk Co.: *Taylor 1060* (SIU). Pope Co.: *Taylor 1212* (SIU). Pulaski Co.: *Demaree 8477* (MO). Searcy Co.: *Spessard 149* (HXC). Scott Co.: *Taylor 271* (SIU). Sebastian Co.: *Palmer 33287* (NY). Stone Co.: *D. Moore 450610* (UARK). Van Buren Co.: *Taylor 2562* (SIU). Washington Co.: *Redfearn 14818* (SMS). White Co.: *Johnson 216* (HXC). Yell Co.: *Taylor 1195* (SIU).

Two luxuriant forms of *Dryopteris marginalis* have been collected in Arkansas. Forma *tripinnatifida* (Clute) Weatherby, which has pinnules that are deeply lobed, has been found in Montgomery County at Camp Albert Pike along the Little Missouri River (*Taylor 1085* SIU). Forma *elegans* (J. Robinson) F. W. Gray, with the pinnules pinnatifid, long, and overlapping the pinnules of adjacent pinnae, has been collected from Magnet Cove, Hot Spring County (*Demaree 19033a* NY).

67. **Dryopteris spinulosa** (O. F. Muell.) Watt, Can. Nat. II 3: 159. 1867. [*Polypodium spinulosum* O. F. Muell.; *Aspidium spinulosum* (O. F. Muell.) Sw.; *Dryopteris austriaca* var. *spinulosa* (O. F. Muell.) Fiori; *Dryopteris carthusiana* (Villars) H. P. Fuchs]

Stone Co.: rich, moist humus on a limestone outcrop sloping toward the entrance of Rowland Cave; ca. 1 mi. N of Fifty-six; *Taylor 2894* (SIU).

BLECHNACEAE

68. **Lorinseria areolata** (L.) Presl, Epim. Bot. 72. 1851. [*Acrostichum areolatum* L.; *Woodwardia angustifolia* J. Smith; *Woodwardia areolata* (L.) Moore]

Moist to wet woods, along streams, marshy areas, roadside ditches, occasionally on sandstone outcrops; primarily Ouachita Mountains and West Gulf Coastal Plain.

Bradley Co.: *Demaree 18381* (MO). Cleburne Co.: *Johnson 436* (HXC). Clark Co.: *Taylor 2180* (SIU). Columbia Co.: *Taylor 1170* (SIU). Conway Co.: *Culwell 3328* (UCA). Crawford Co.: *D. Moore 66121* (APCR). Cross Co.: *Richards 3963* (ARKSU). Dallas Co.: *Taylor 2733* (SIU). Drew Co: *D. Moore 420045* (UARK). Franklin Co.: *Barber 1026* (UARK). Garland Co.: *Taylor 2556* (SIU). Grant Co.: *Demaree 57196* (SIU). Hempstead Co.: *Taylor 1176* (SIU). Hot Spring Co.: *D. Moore 440088* (UARK).

Howard Co.: *McSwain 43E128* (UARK). Independence Co.: *Johnson 302* (HXC). Izard Co.: *Demaree 22436* (MO). Jefferson Co.: *Demaree 24294* (SMU). Logan Co.: *D. Moore 510073* (UARK). Lonoke Co.: *Clark 662* (HXC). Madison Co.: *Taylor 4274* (SIU). Miller Co.: *Taylor 1908* (SIU). Montgomery Co.: *Taylor 1079* (SIU). Nevada Co.: *Pule 587* (UARK). Ouachita Co.: *D. Moore 490668* (UARK). Perry Co.: *J. Moore 6603* (UCA). Pike Co.: *Taylor 2910* (SIU). Poinsett Co.: *Pyle 587* (UARK). Polk Co.: *Taylor 2552* (SIU). Pope Co.: *Tucker 16079* (APCR). Pulaski Co.: *Demaree 8478* (SMU). Saline Co.: *Haas 1435* (UCA). Stone Co.: *Tucker 3581* (APCR). Union Co.: *Demaree 19408* (SMU). Yell Co.: *Taylor 4367* (SIU).

A frond of *Lorinseria areolata* collected in Pike County by D. Demaree (*Demaree 9785* HXC) has the blade abnormally expanded so that it is more or less intermediate between a fertile and sterile frond. This intermediate condition has been described as f. *obtusilobata* by Waters (1903, p. 128).

69. **Woodwardia virginica** (L.) J. Smith, Mem. Acad. Turin 5: 411. 1793. [*Blechnum virginicum* L.; *Anchistea virginica* (L.) Presl]

Low, wet, sandy soil of woodlands; chiefly West Coastal Plain.

Cleveland Co.: *Taylor 1141* (SIU). Columbia Co.: *Taylor 1166* (SIU). Garland Co.: *D. Moore 410418* (UARK). Hempstead Co.: *D. Moore 56179* (UARK). Hot Spring Co.: *D. Moore 440081* (UARK). Jefferson Co.: *Locke 1309* (UARK). Nevada Co.: *D. Moore 490643* (UARK). Saline Co.: *D. Moore 410434* (UARK). Union Co.: *D. Moore 410335* (UARK).

MARSILEACEAE

70. **Marsilea uncinata** A. Br., Flora 22: 304. 1839. [*Marsilea vestita* var. *uncinata* (A. Br.) Baker]

Margins of ponds, small streams and swamps in the Arkansas River Valley and the Mississippi Alluvial Plain.

Arkansas Co.: edge of pond; Arkansas Post National Memorial; *Taylor 1863* (SIU). Chicot Co.: muddy flat inside levee near small stream; Refuge Plantation; ca. 0.3 mi. S of Hwy. 82; *McDaniel 20043* (SIU). Crawford Co.: in water along edge of swamp; "old government ditch" near W end of Vine Prairie Lake; ca. 3 mi. SW of Mulberry; *Barber s.n.* (APCR). Pulaski Co.: a small pond in the Arkansas River bottoms below Little Rock; near Sevier's farm; *Engelmann 33* TYPE (MO).

71. **Marsilea vestita** var. **mucronata** (A. Br.) Baker, J. Bot. 24: 279. 1886. [*Marsilea mucronata* A. Br.]

Bradley Co.: temporary pools in hard pan of open, savanna like area; ca. 7 mi. SE of Warren; *Demaree 18969* (MO).

72. **Pilularia americana** A. Br., Monatsb. Kon., Akad. Wiss. Berlin 1863, 435. 1864.

Margins of lakes; Interior Highlands.

Conway Co.: Cedar Lake and Bailey Lake; *Taylor 2883* (SIU). Faulkner Co.: Beaverfork Lake; *J. Moore 6608* (UCA). Garland Co.: Lake Hamilton; *D. Moore 480532* (UARK). Logan Co.: Cove Lake; *D. Moore 490427* (UARK). Sebastian Co.: near Ft. Smith; *Nuttall 180* TYPE (MO). Washington Co.: Lake Wedington; *D. Moore 480774* (MO).

AZOLLACEAE

73. *Azolla mexicana* Presl, Abh. Bohm. Ges. Wiss. 3: 150. 1845.

Floating on still waters of lakes, ponds, creeks, and ditches or occasionally stranded along their desiccated margins.

Arkansas Co.: *Taylor 1858* (SIU). Chicot Co.: *Taylor 1869* (SIU). Conway Co.: *Johnson 478* (HXC). Crittenden Co.: *Taylor 2822* (SIU). Drew Co.: *Demaree 17625* (SMU). Faulkner Co.: *Engelmann 127* (MO). Hempstead Co.: *Taylor 1180* (SIU). Jefferson Co.: *Locke 2133* (UARK). Lawrence Co.: *McNalty 652* (ARKSU). Phillips Co.: *Richards 4793* (ARKSU). Pulaski Co.: *Engelmann 126* (MO). St. Francis Co.: *McDaniel 1097* (NY). Washington Co.: *D. Moore 4184* (UARK).

DOUBTFUL AND EXCLUDED TAXA

Asplenium montanum Willd.

Small (1938) included Arkansas in the range he gave for *A. montanum.* No voucher specimens have been found to support the occurrence of this species in Arkansas.

Athyrium filix-femina subsp. **angustum** (Willd.) Clausen
[*Athyrium angustum* (Willd.) Presl]

Scully (1939) reported *A. angustum* from Hot Springs National Park. The isolated occurrence of this northern taxon in southern Arkansas is doubtful. No specimens have been found to support its presence in the state.

Azolla caroliniana Willd.

On the basis of vegetative characters and the occurrence of septate glochidia (when reproductive structures are present), all the Arkansas material of *Azolla* has been identified as *A. mexicana.*

Botrychium multifidum var. **silaifolium** (Presl) Broun

Moore (1940) listed this plant from "low woods, St. Francis River and Hempstead County." The presence of this northern taxon in Arkansas is untenable. No specimens have been found to support such a listing for Arkansas.

Cheilanthes eatoni Baker

Branner and Coville (1891) reported this plant "in clefts in the rocks at Mountain Park, Big Rock, near Little Rock." Coville's specimen of *C. eatoni* has been found to be *C. tomentosa* (Buchholz, 1924).

Cystopteris fragilis (L.) Bernh.

All of the Arkansas specimens that have been identified as *C. fragilis* or *C. fragilis* var. *mackayi* Laws. are either *C. protrusa* or *C. tennesseensis.*

Dryopteris clintoniana var. **australis** Wherry [*D.* × *australis* (Wherry) Small]

The listing of this taxon in Arkansas (Moore, 1940) is based on a misidentification. Specimens bearing this name are referable to *D.* × *leedsii.*

Dryopteris cristata (L.) Gray

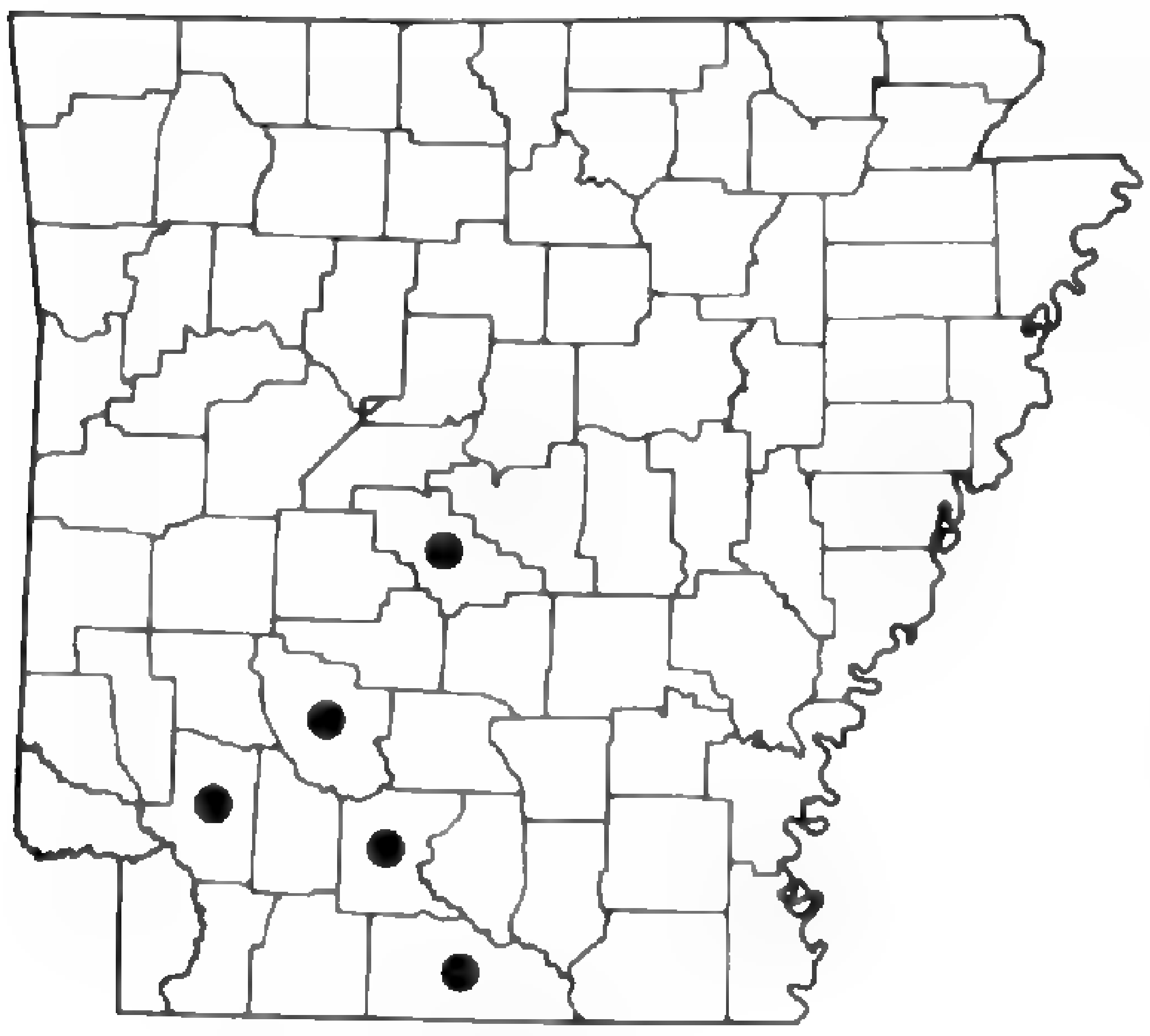
Reports of this species in Arkansas apparently are founded on misidentifications. *Dryopteris cristata* has been maintained in all Arkansas pteridophyte lists since Lesquereux (1860) reported it in "swamps and woods". Moore (1940) also described this species as occurring in the "swamps of southeastern Arkansas." *Dryopteris cristata* is a northern species with a circumboreal distribution and reports as far south as "southeastern Arkansas" are extremely dubious (Thomas, Wagner, and Mesler, 1973). Repeated searches for Arkansas voucher specimens of this plant have been unsuccessful.

Equisetum laevigatum Engelm. [*E. kansanum* Schaffner]

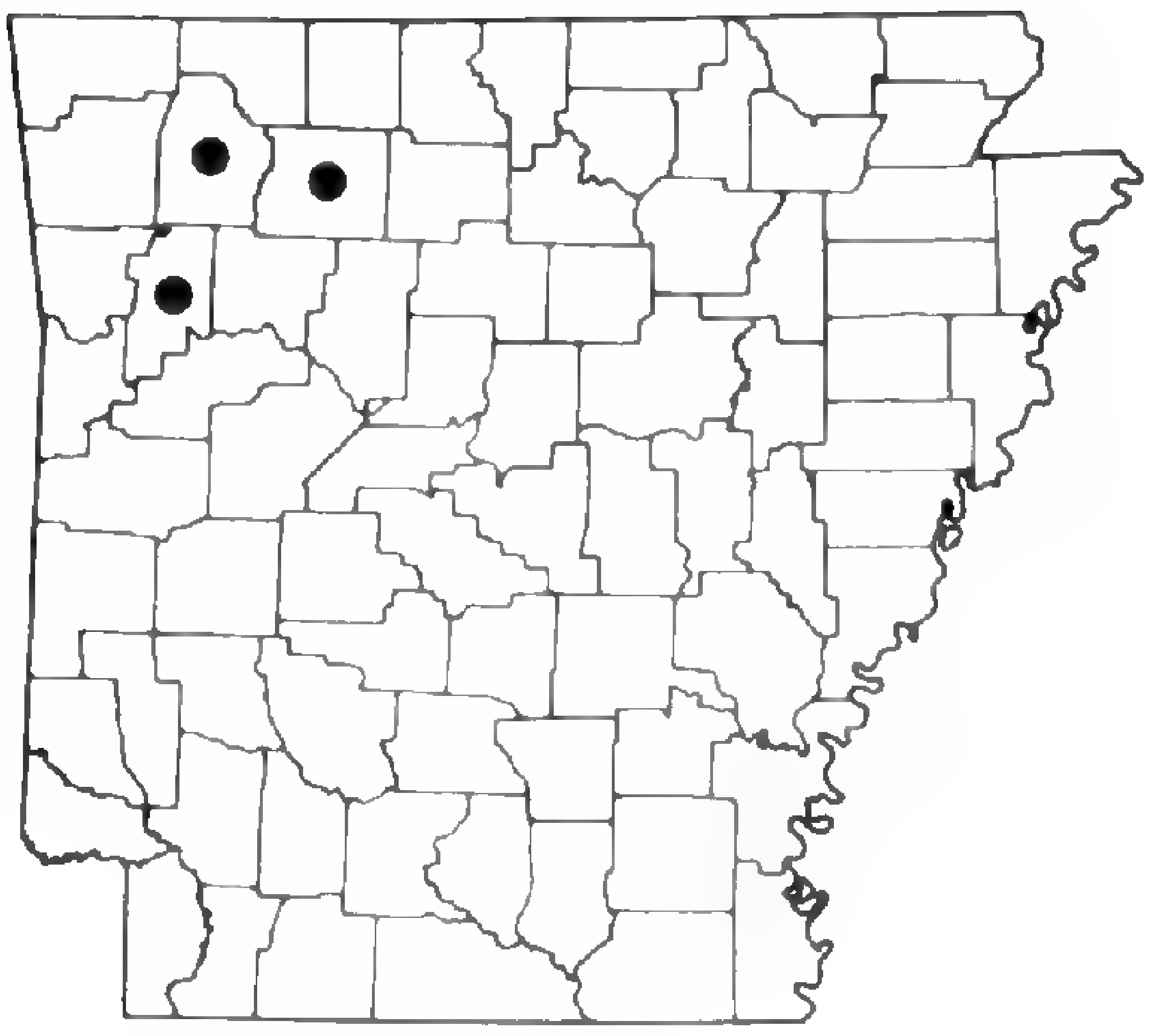
Moore (1940) reported this species from Newton and Faulkner Counties. All specimens that have been examined from Arkansas, and identified as *E. laevigatum,* are referable to either *E. hyemale* var. *affine* or *E.* × *ferrissii.*

Pteridium aquilinum subsp. **caudatum** (L.) Bonap. [*Pteris aquilina* var. *caudata* (L.) Link]

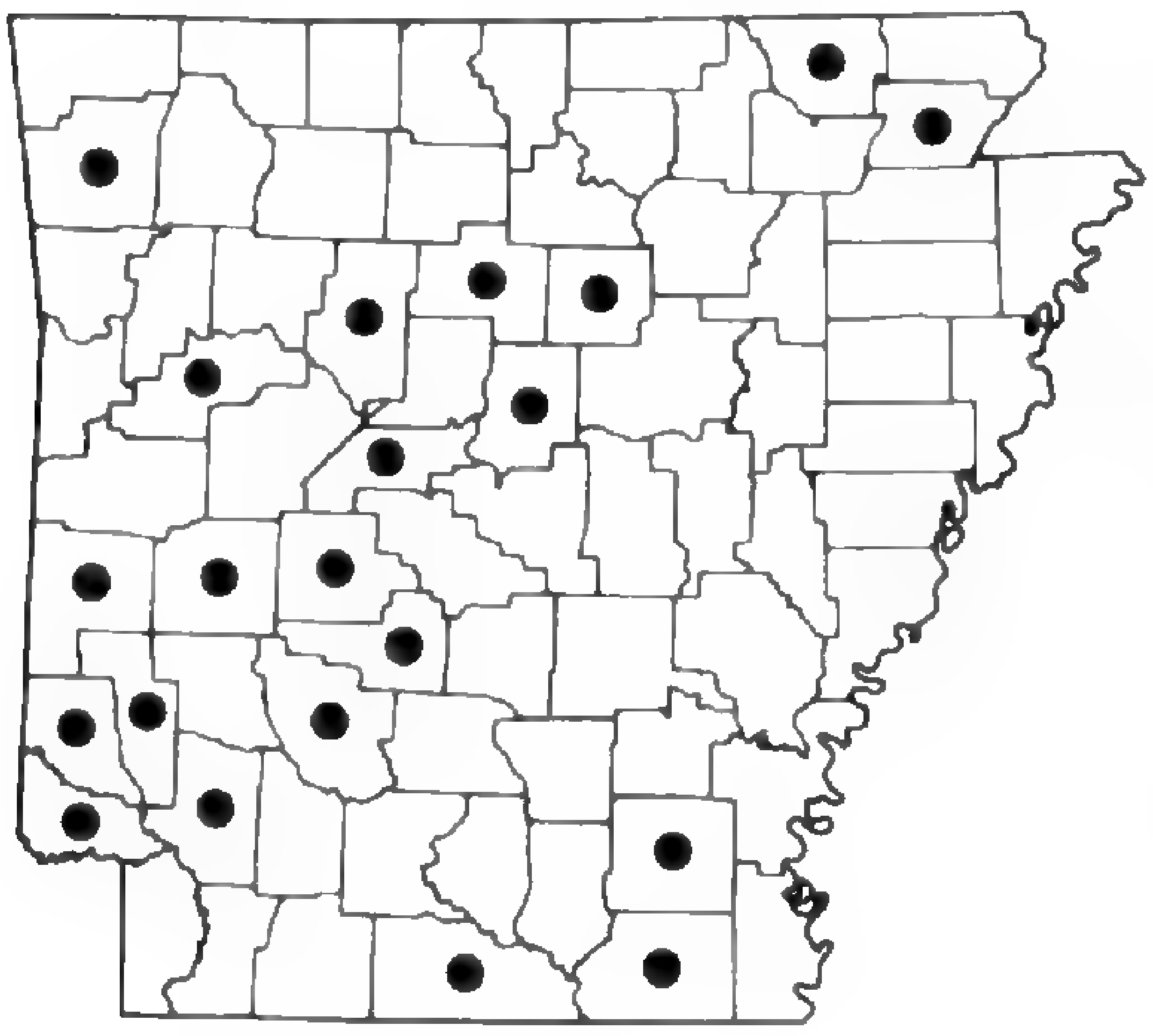
Harvey (1881) listed this taxon as ". . . found all over the southern part of the state . . ." apparently confusing it with var. *pseudocaudatum.* Subspecies *caudatum,* a more southern taxon, is known from the West Indies, Florida, Mexico, Central America, and the coastal regions of northern South America (Tryon, 1941).



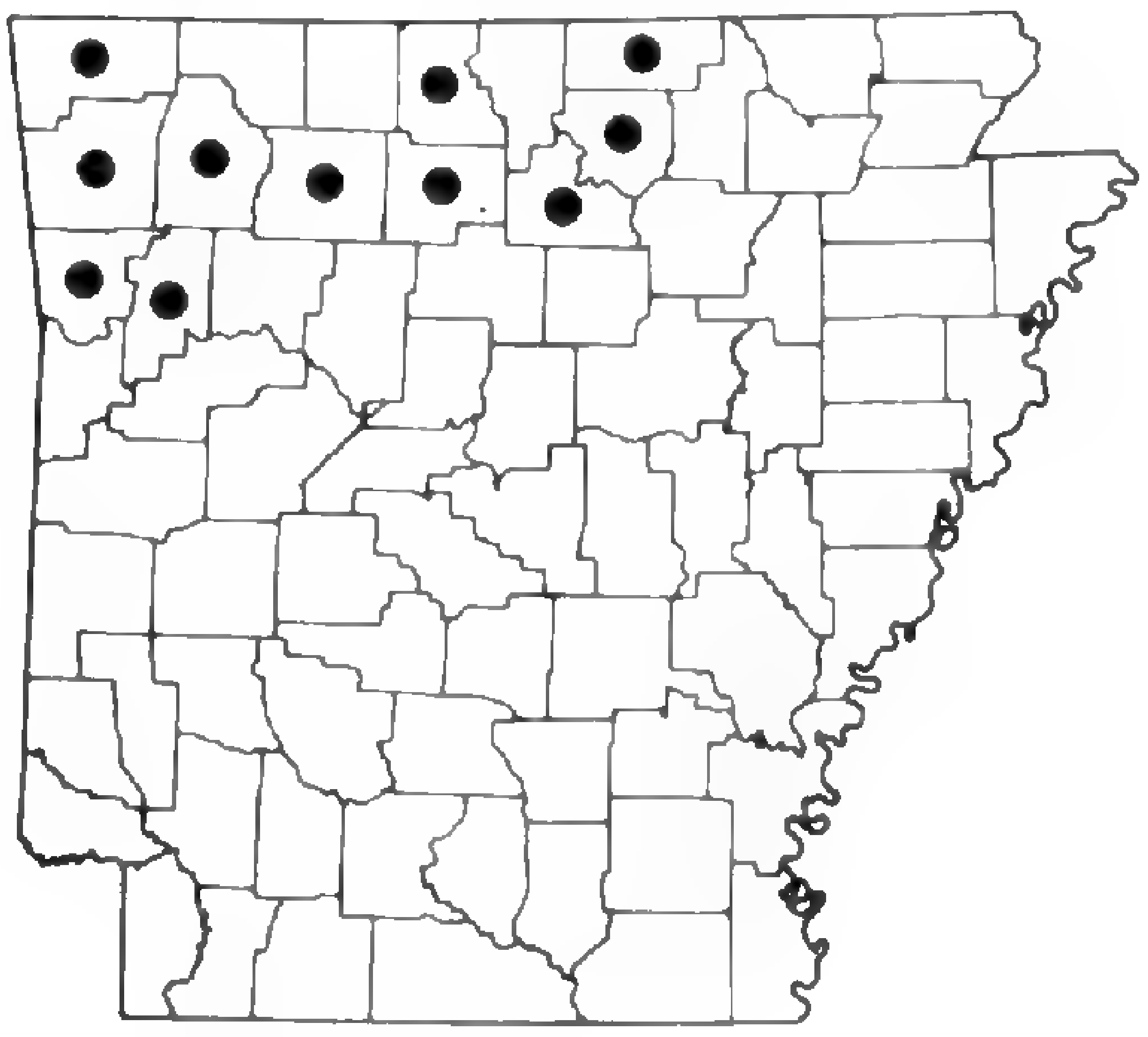
1. *Lycopodium appressum*



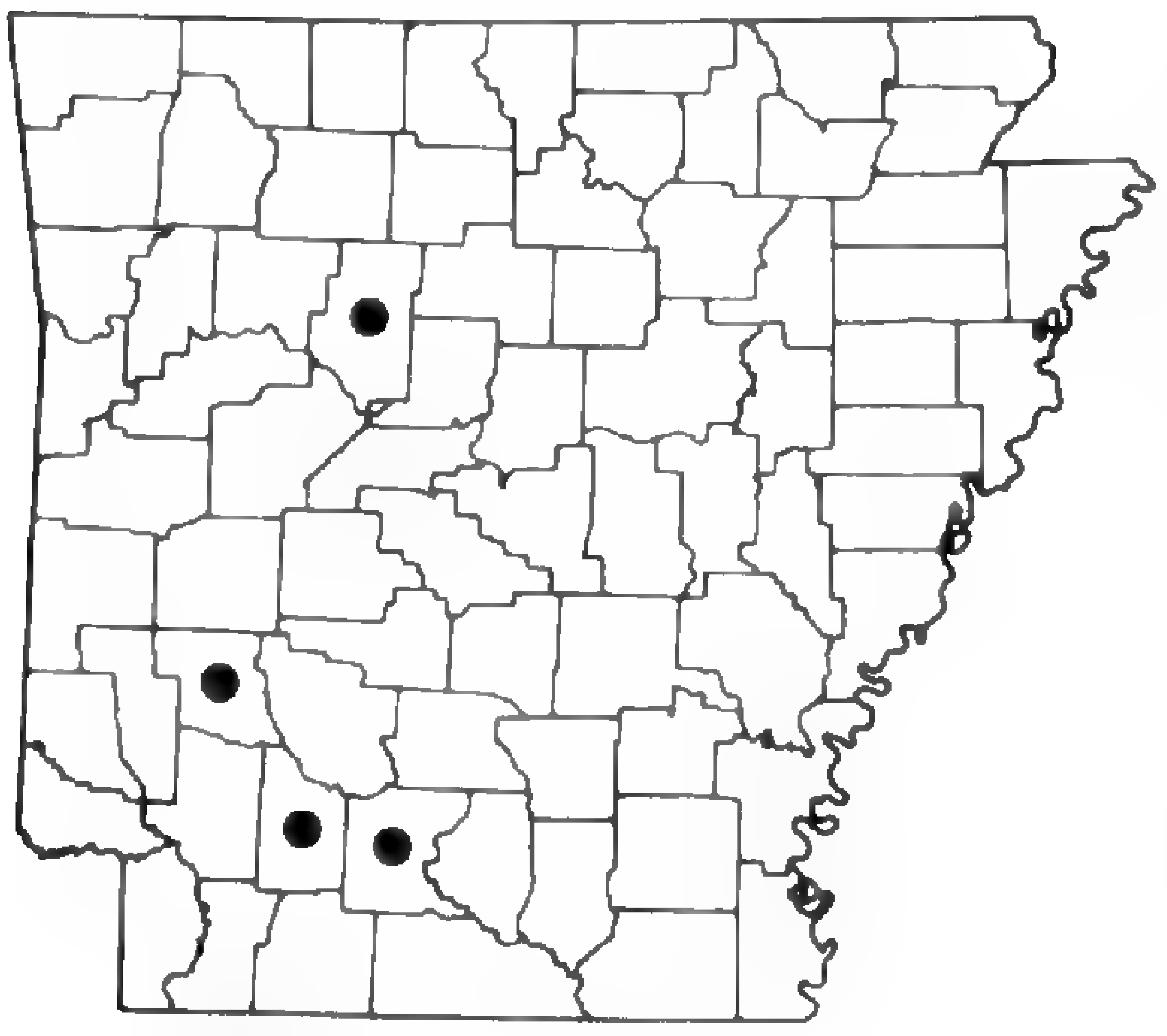
2. *Lycopodium lucidulum*



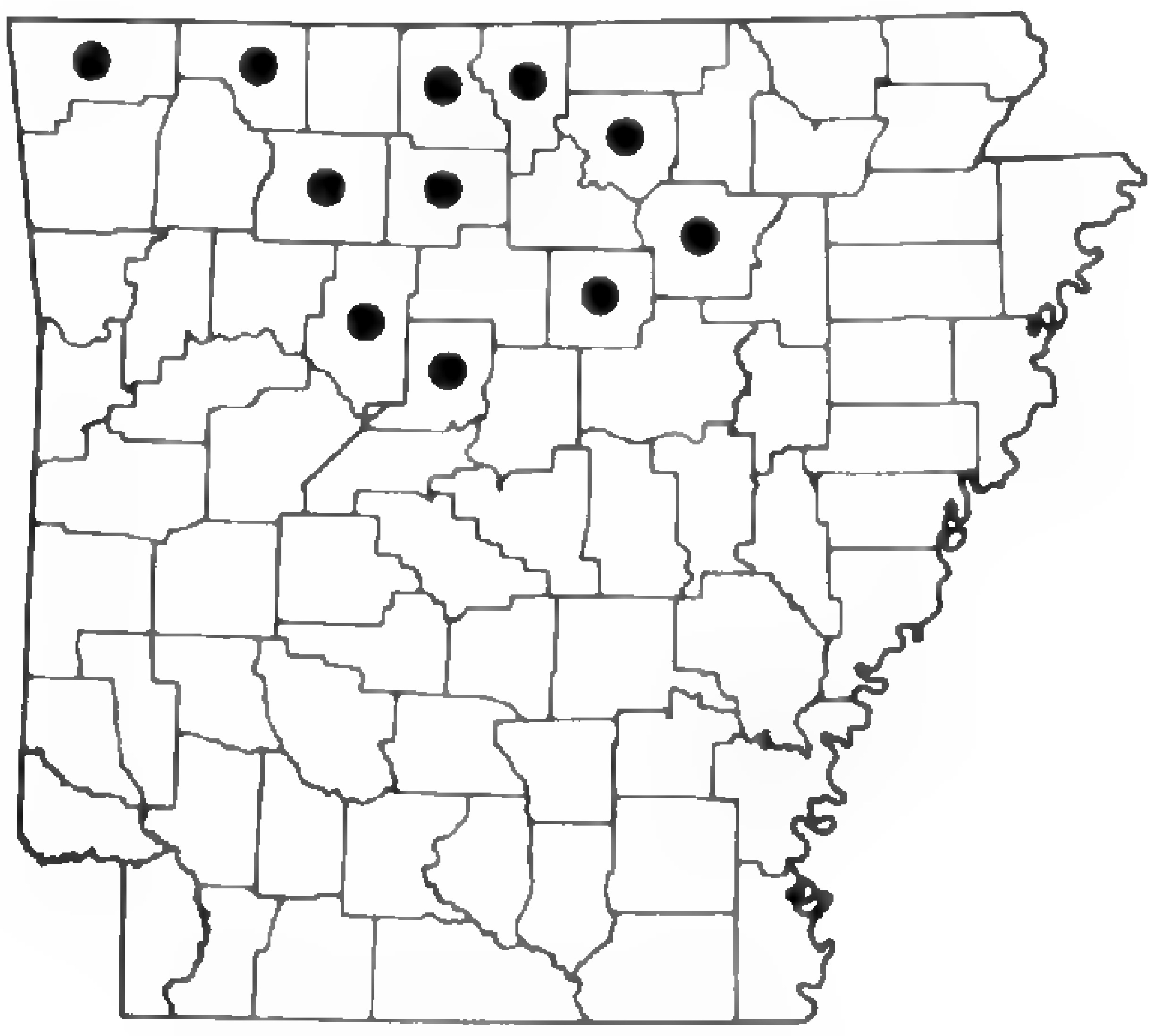
3. *Selaginella apoda*



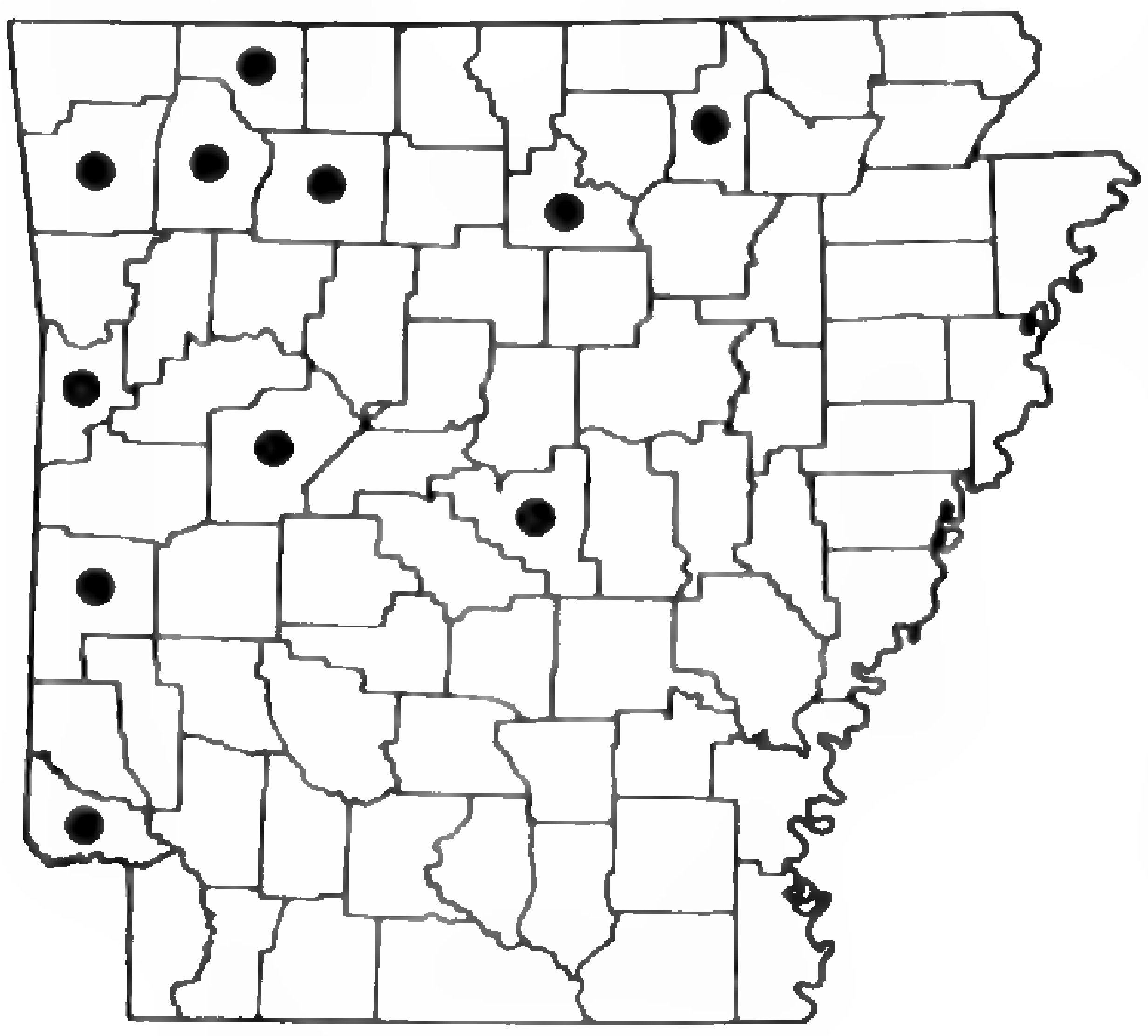
4. *Selaginella eclipes*



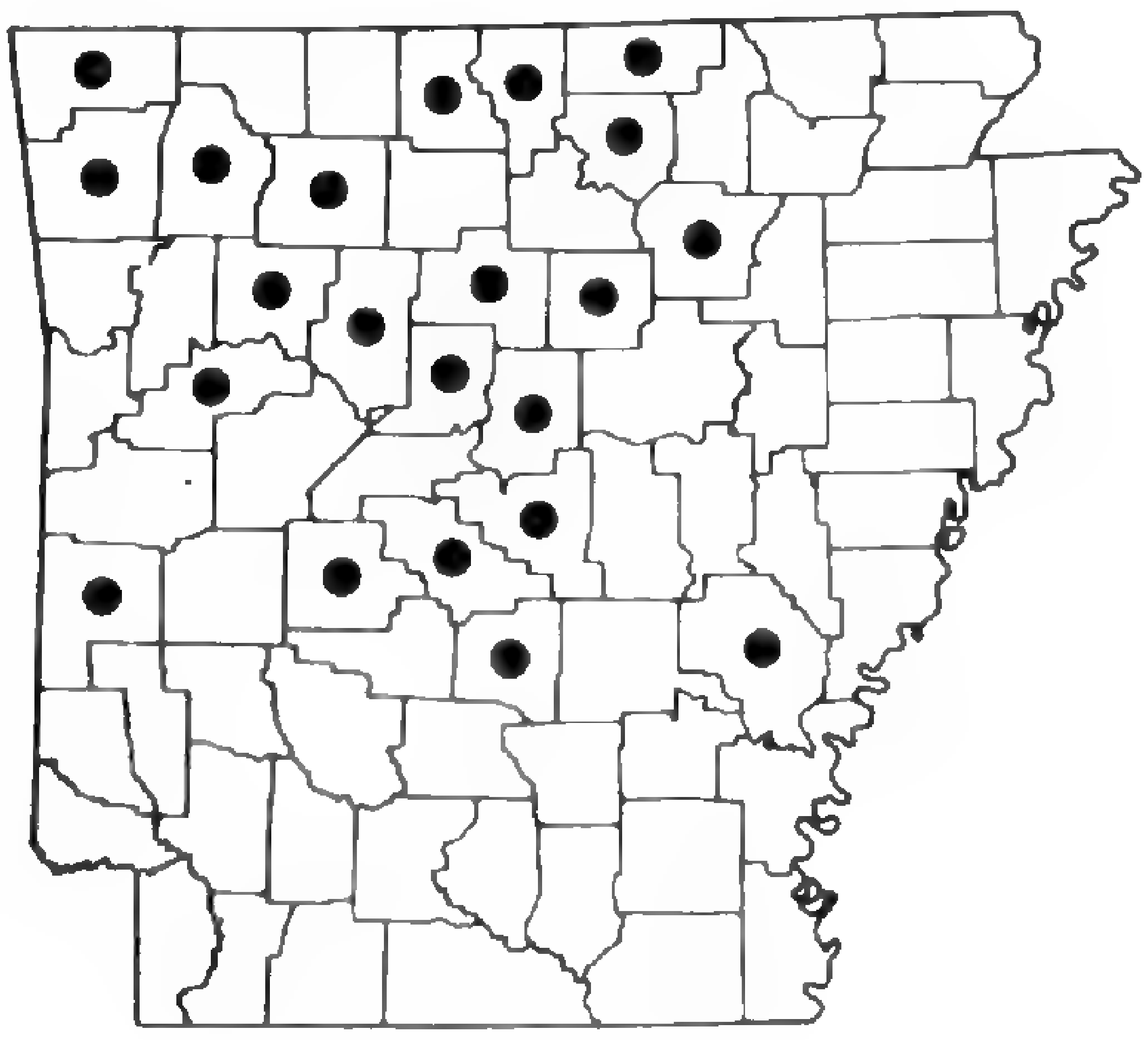
5. *Selaginella riddellii*



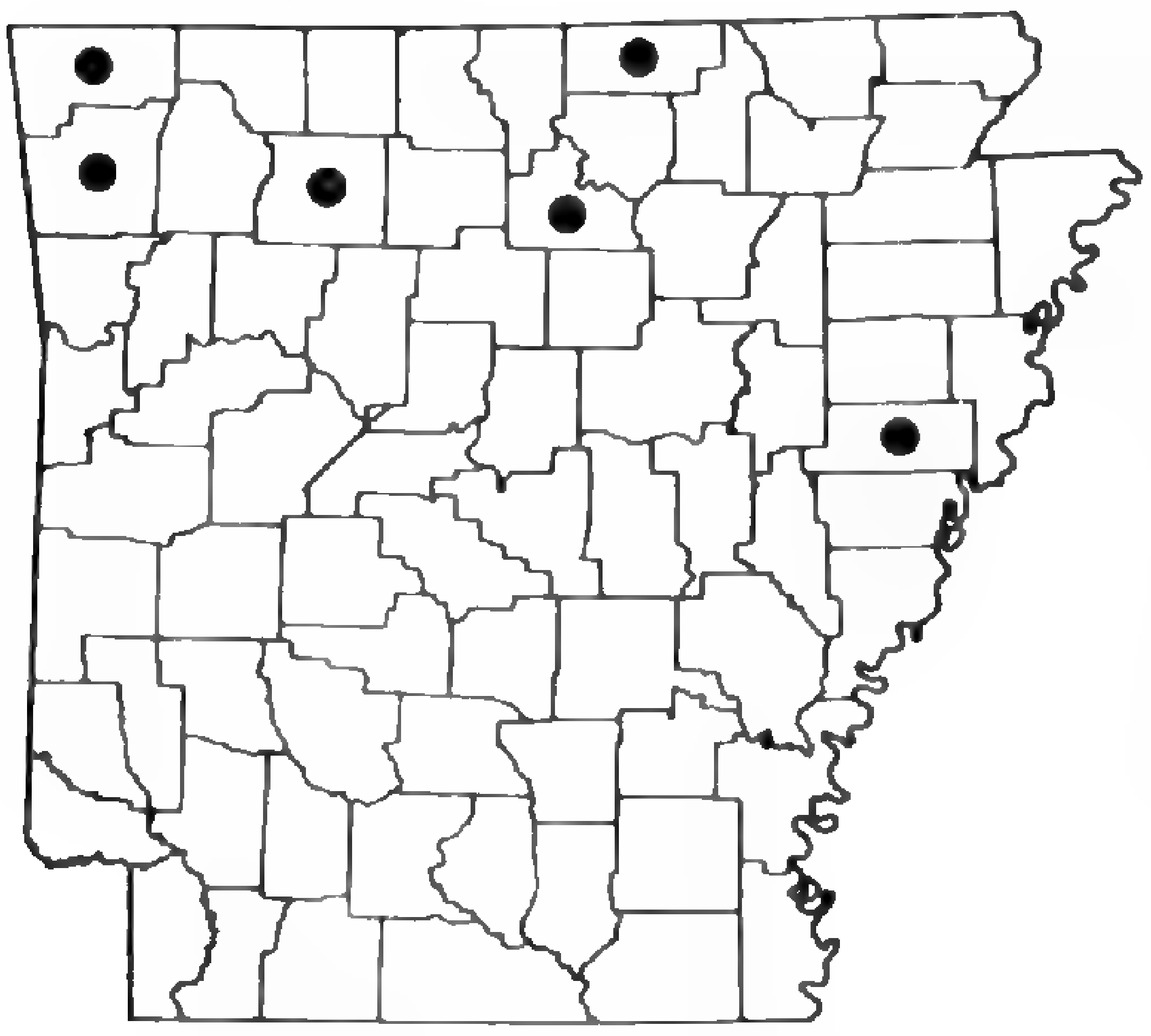
6. *Selaginella rupestris*



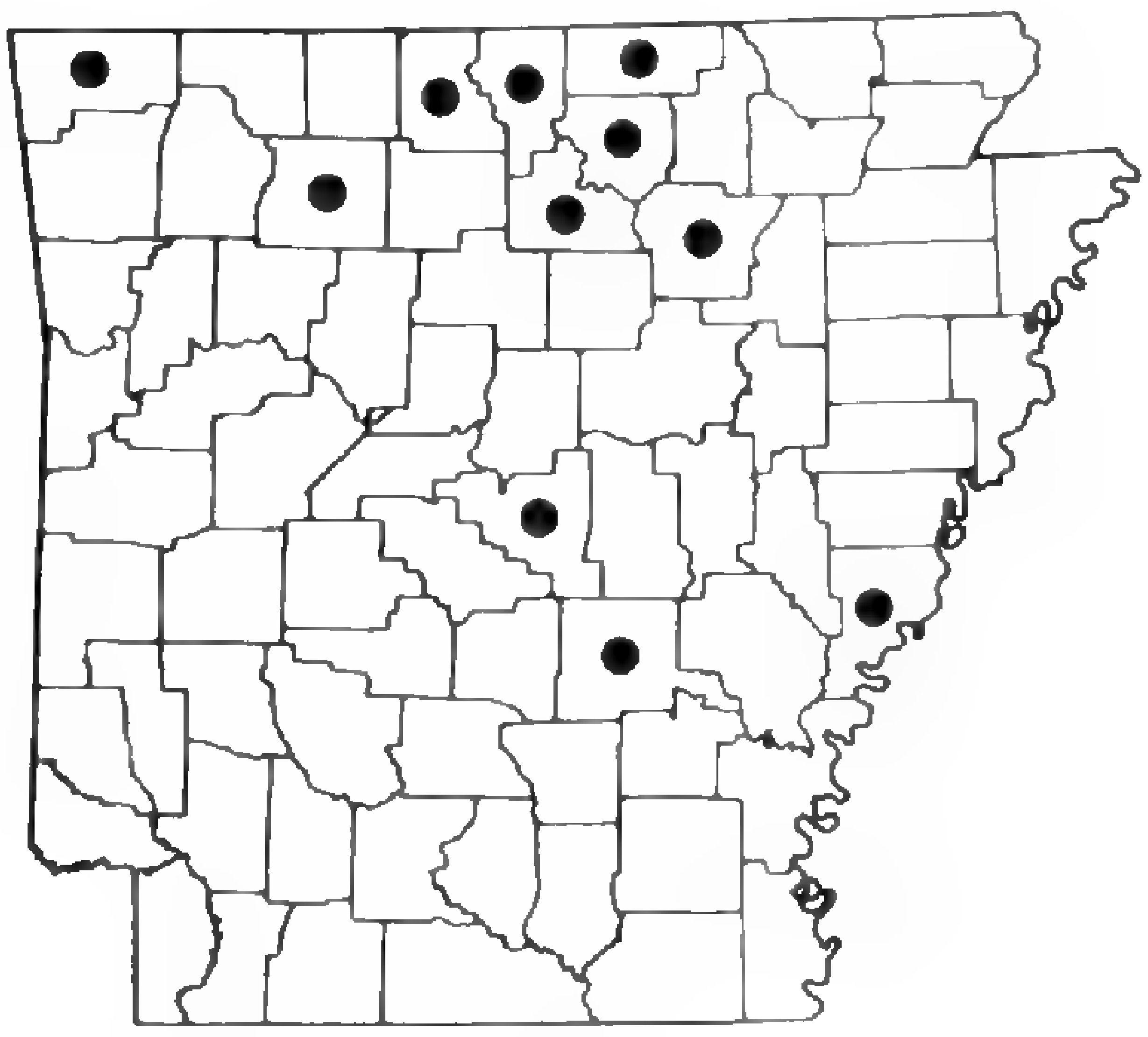
7. *Isoetes butleri*



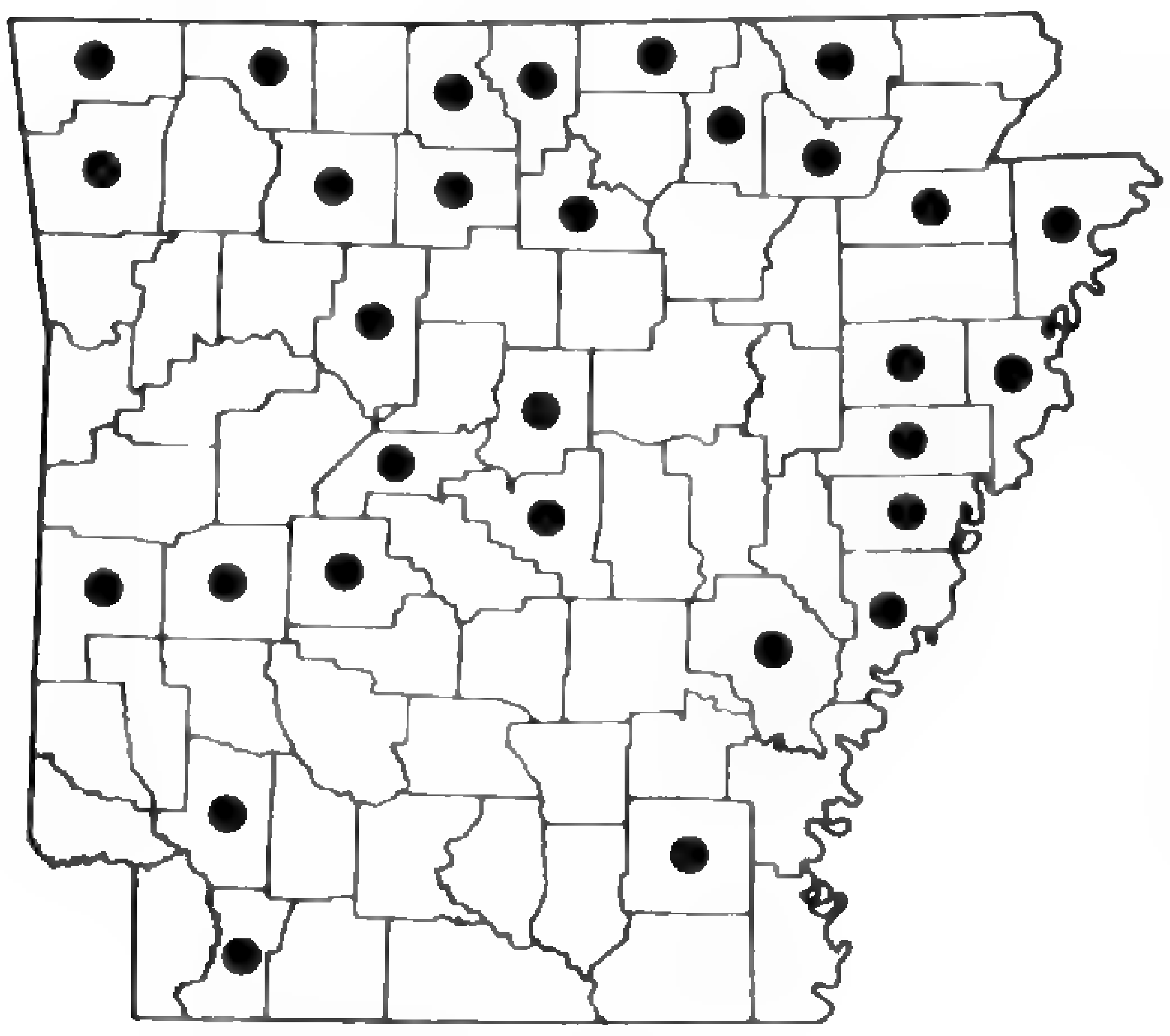
8. *Isoetes melanopoda*



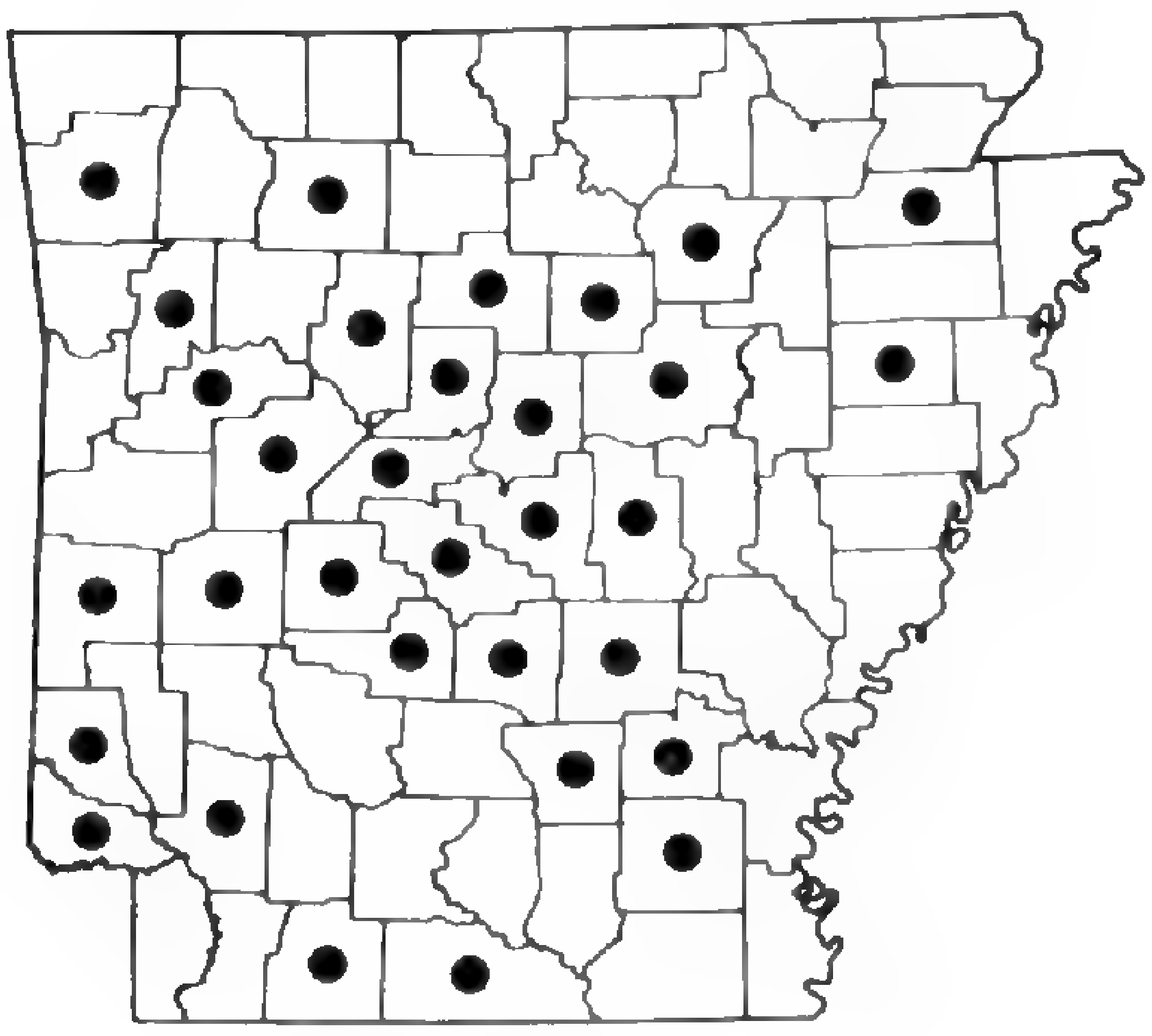
9. *Equisetum arvense*



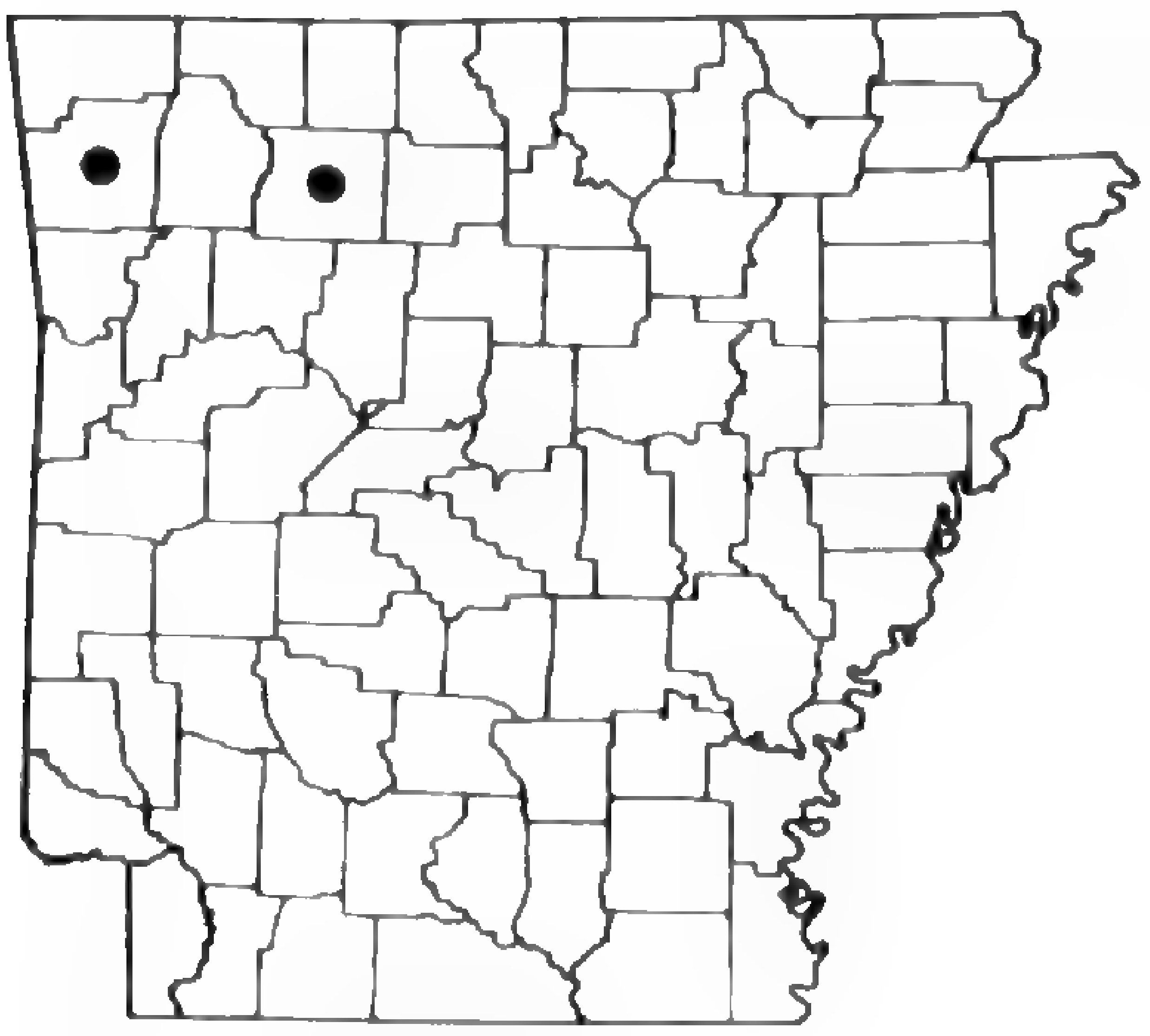
10. *Equisetum X ferrissii*



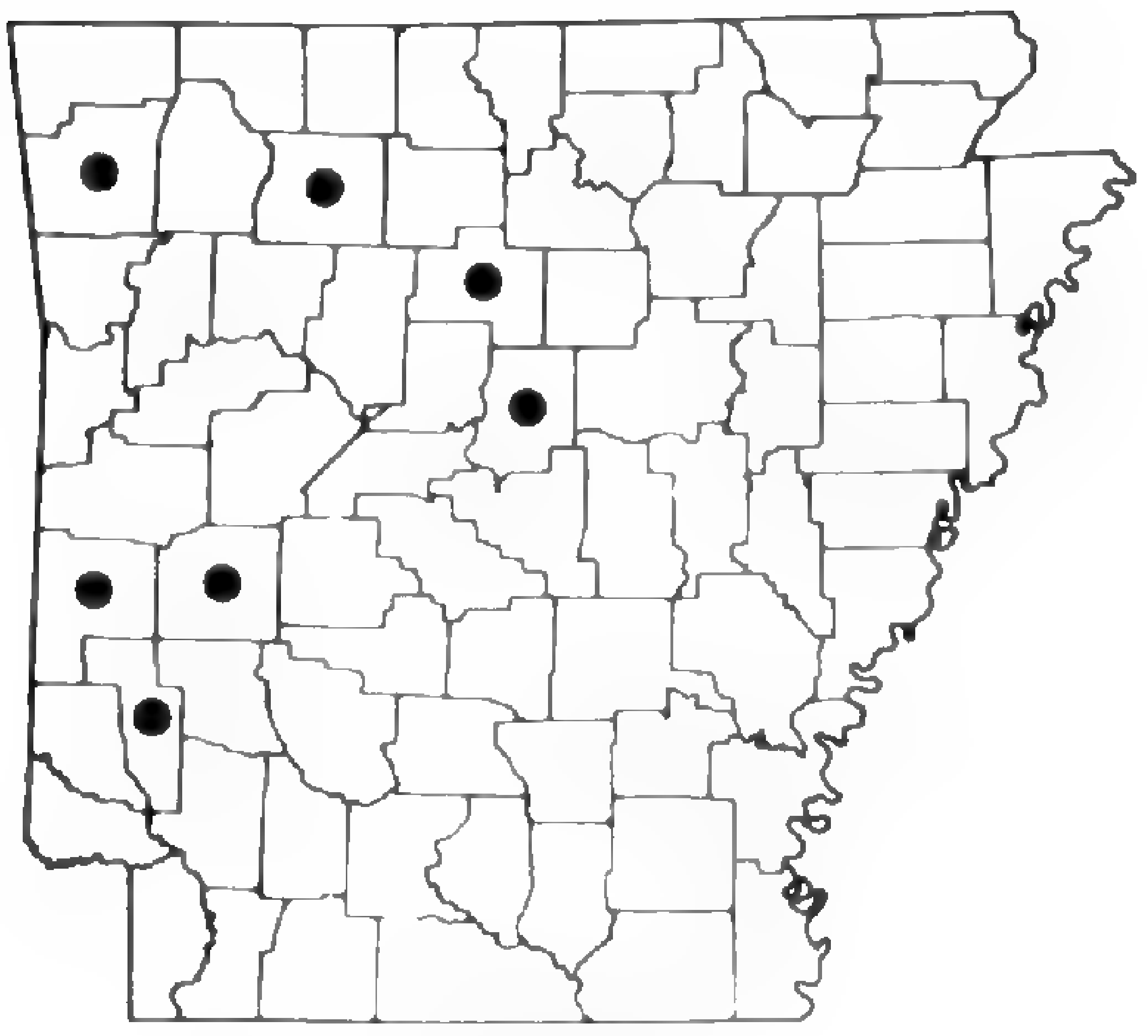
11. *Equisetum hyemale* var. *affine*



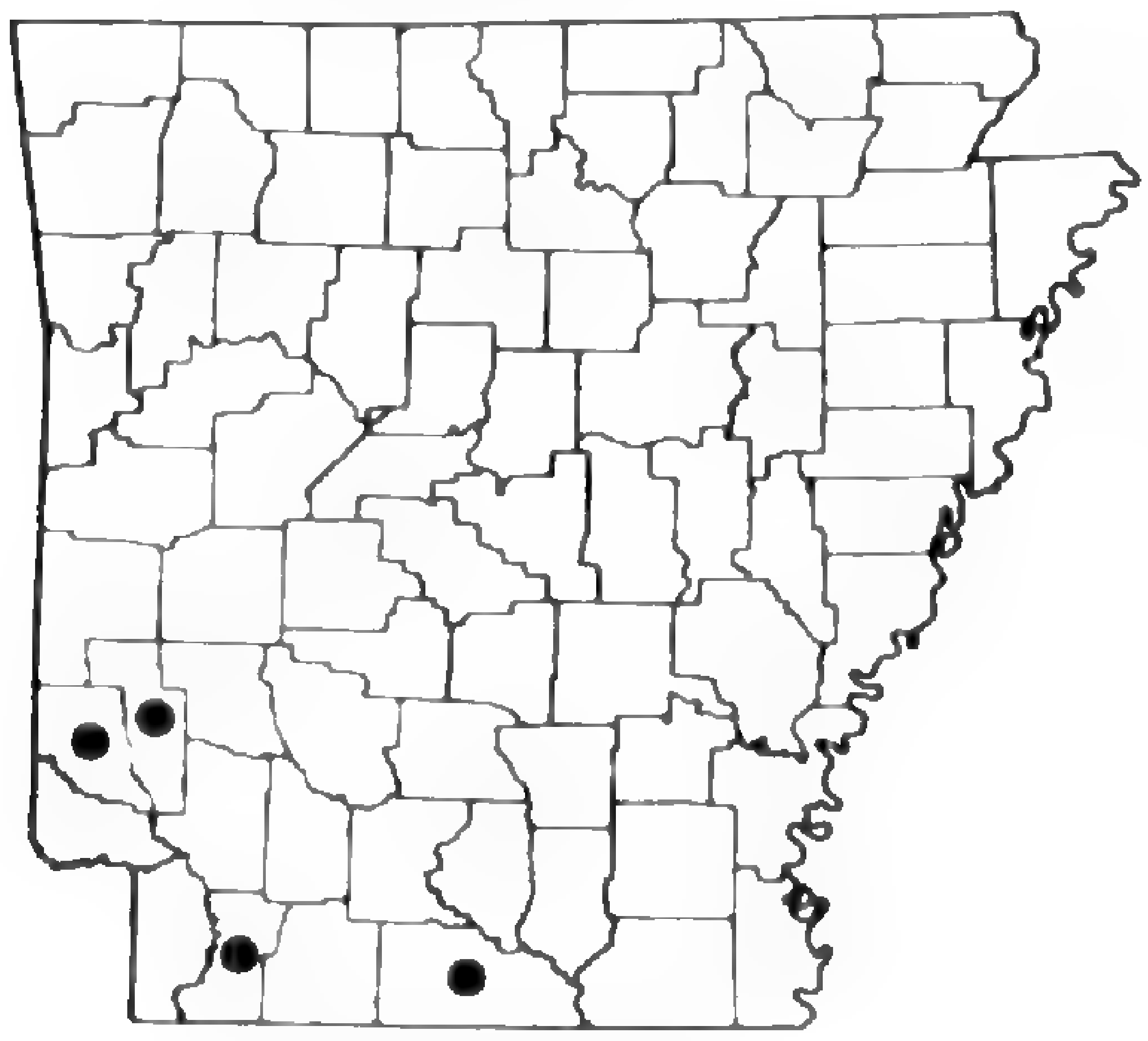
12. *Botrychium biternatum*



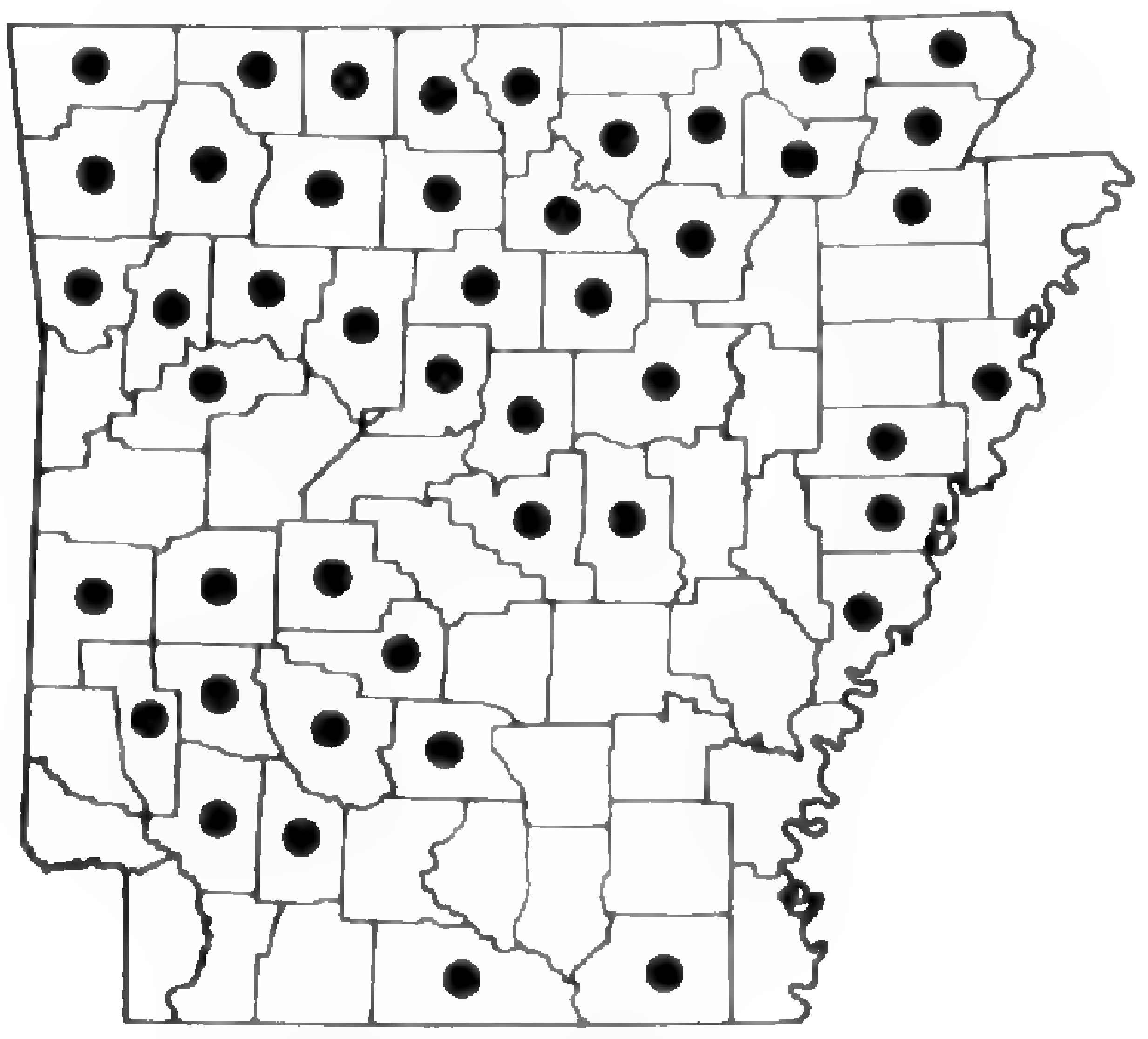
13a. *Botrychium dissectum* var. *dissectum*



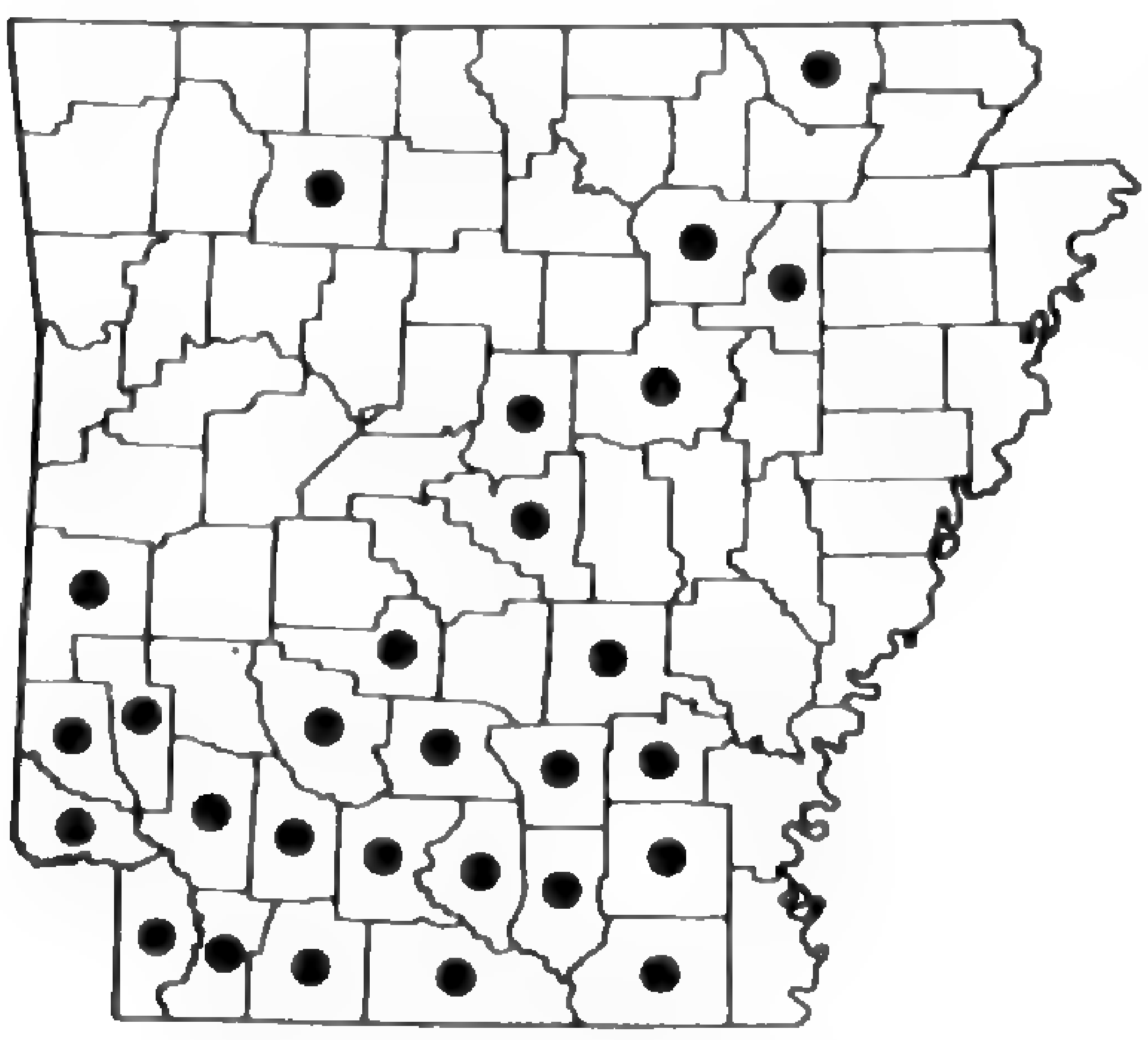
13b. *Botrychium dissectum* var. *obliquum*



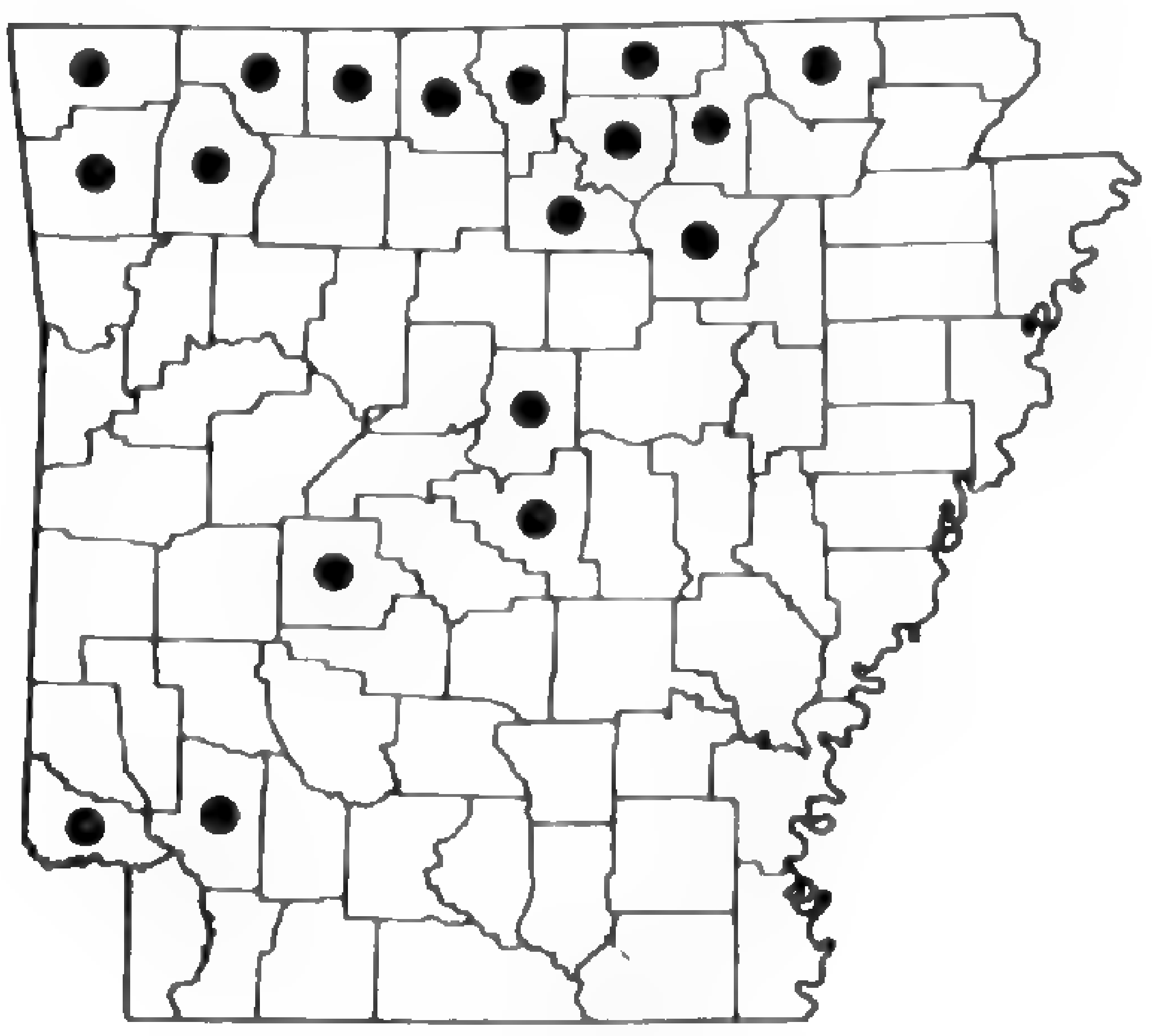
14. *Botrychium lunarioides*



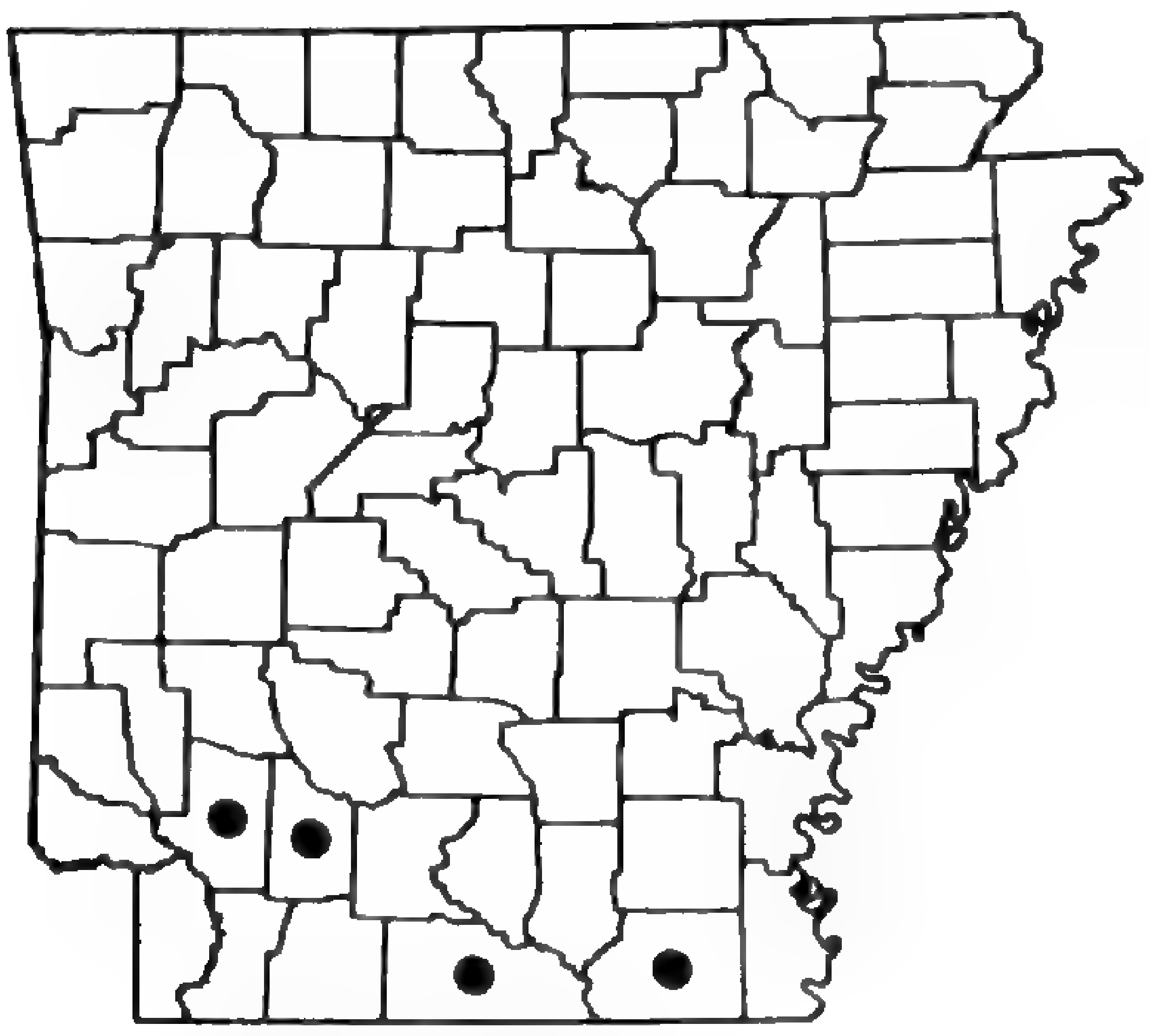
15. *Botrychium virginianum*



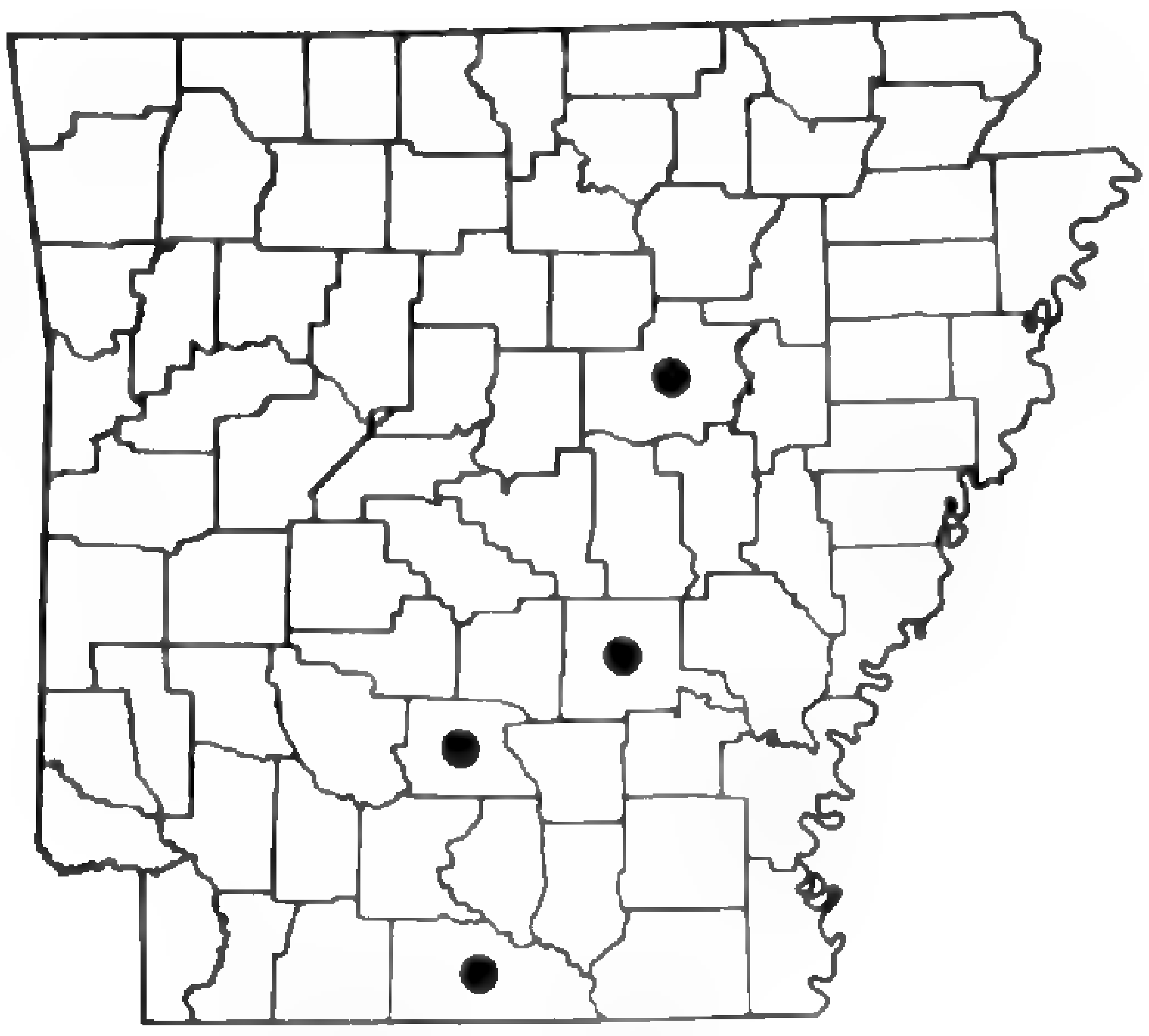
16. *Ophioglossum crotalophoroides*



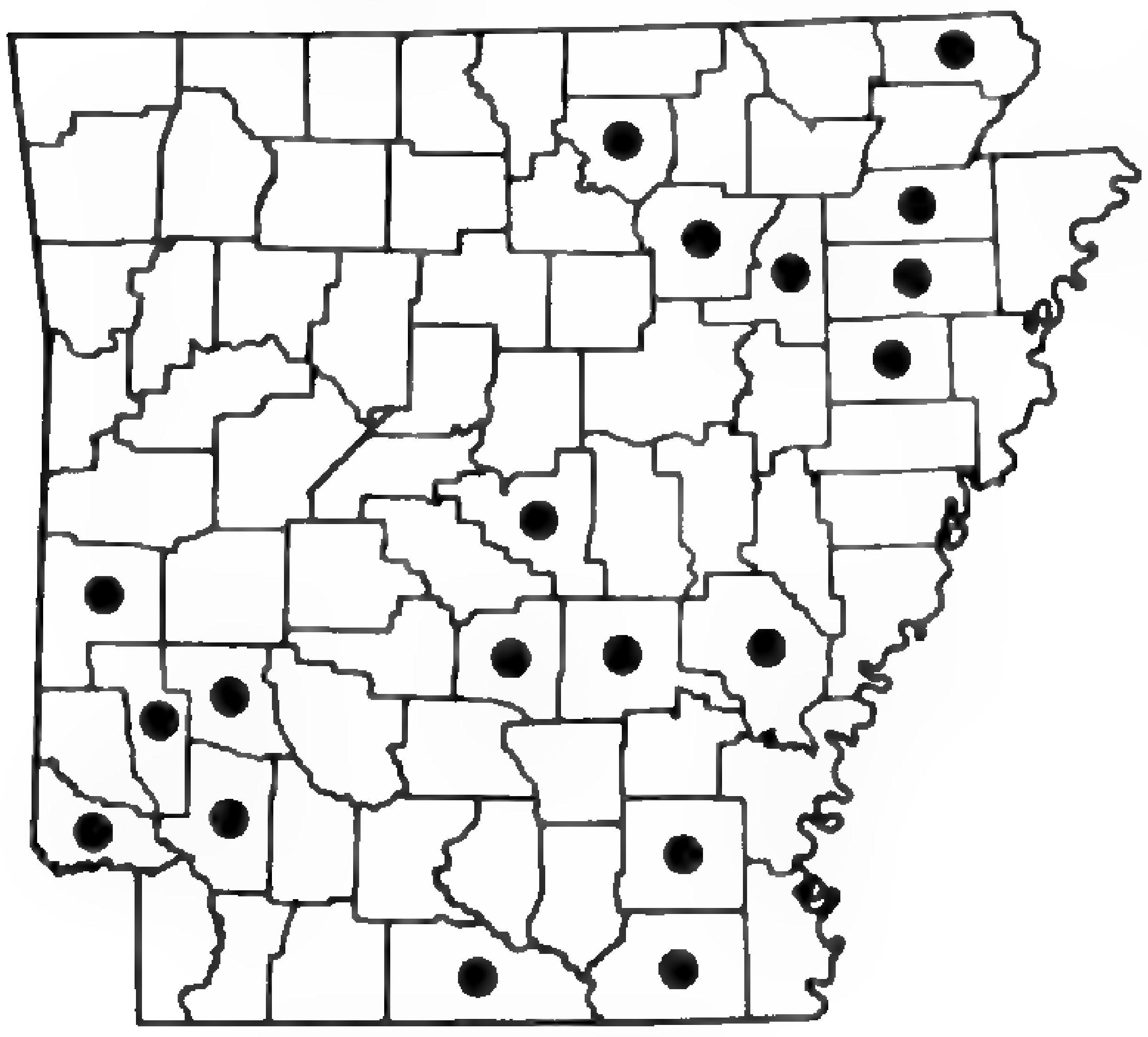
17. *Ophioglossum engelmannii*



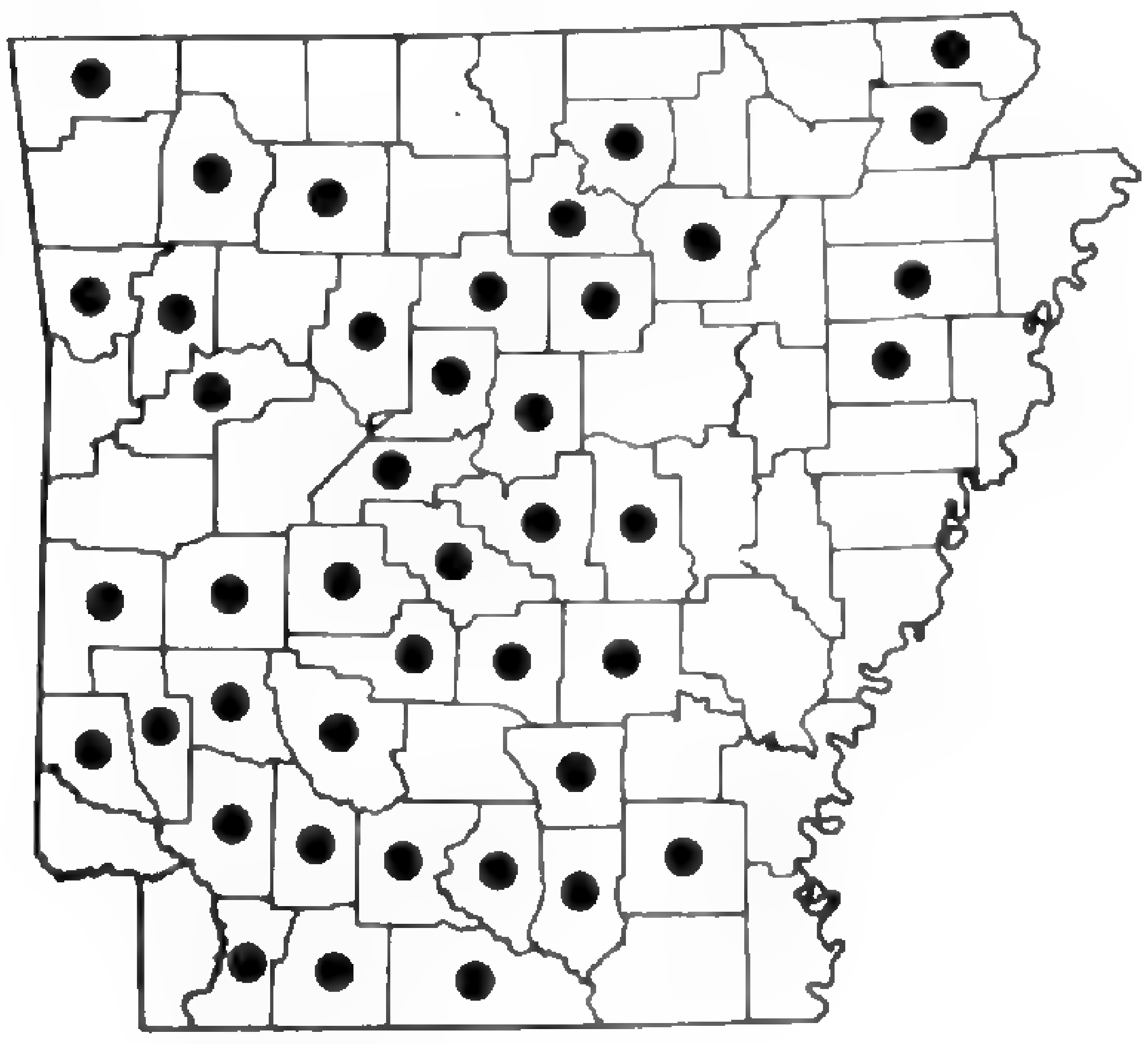
18. *Ophioglossum nudicaule* var. *tenerum*



19. *Ophioglossum petiolatum*

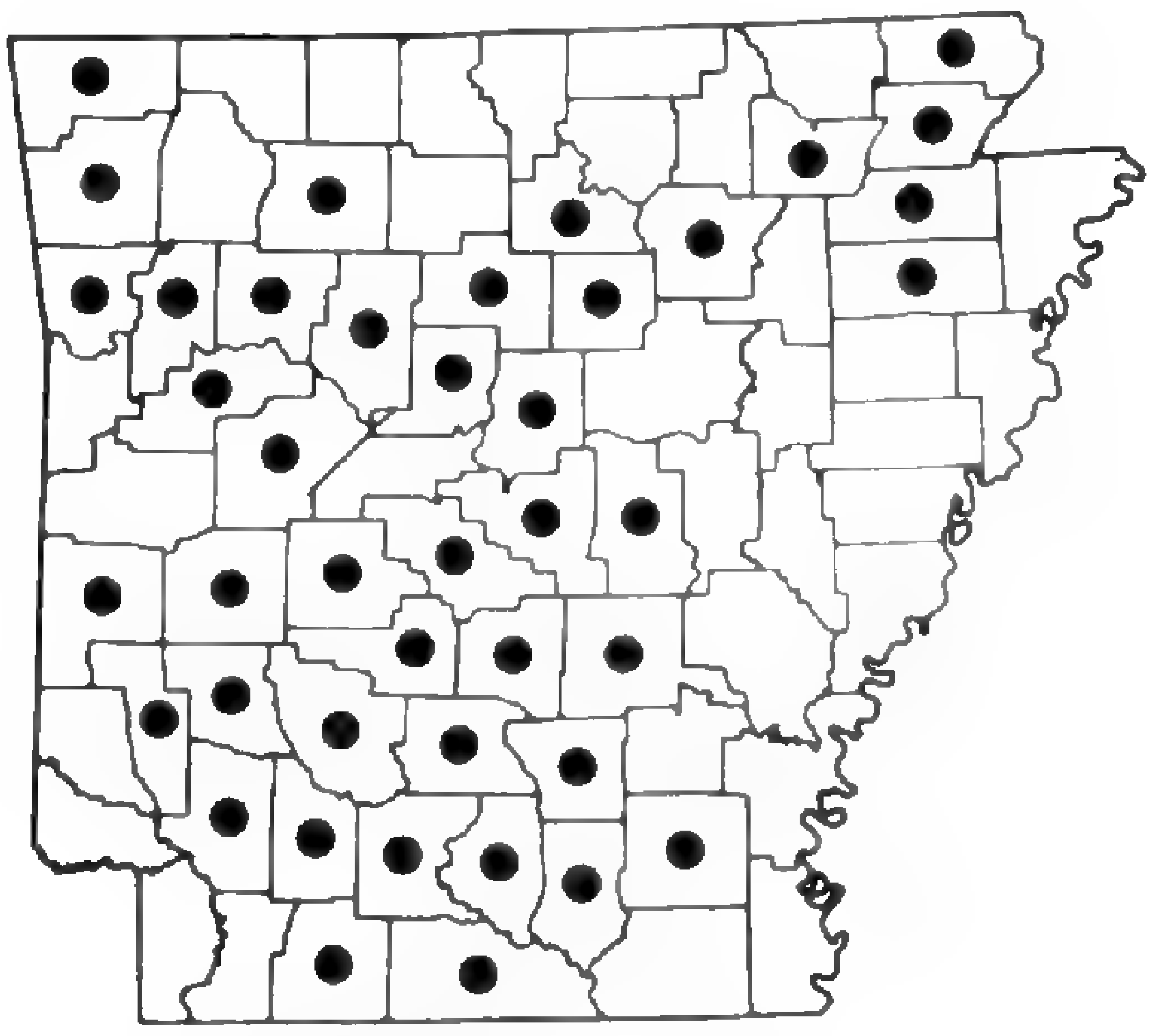


20. *Ophioglossum vulgatum* var. *pycnostichum*

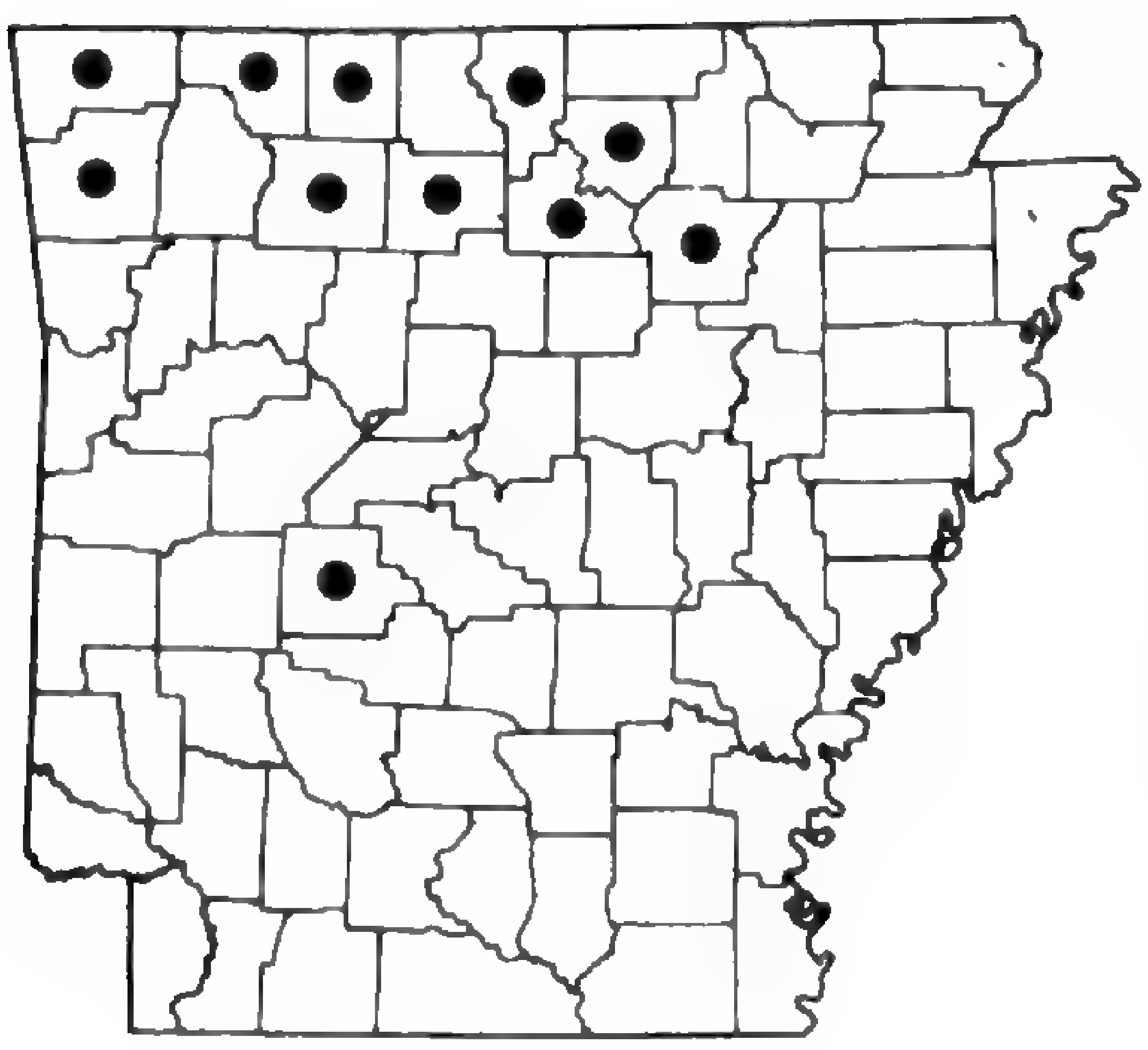


21. *Osmunda cinnamomea*

22. *Osmunda claytoniana*

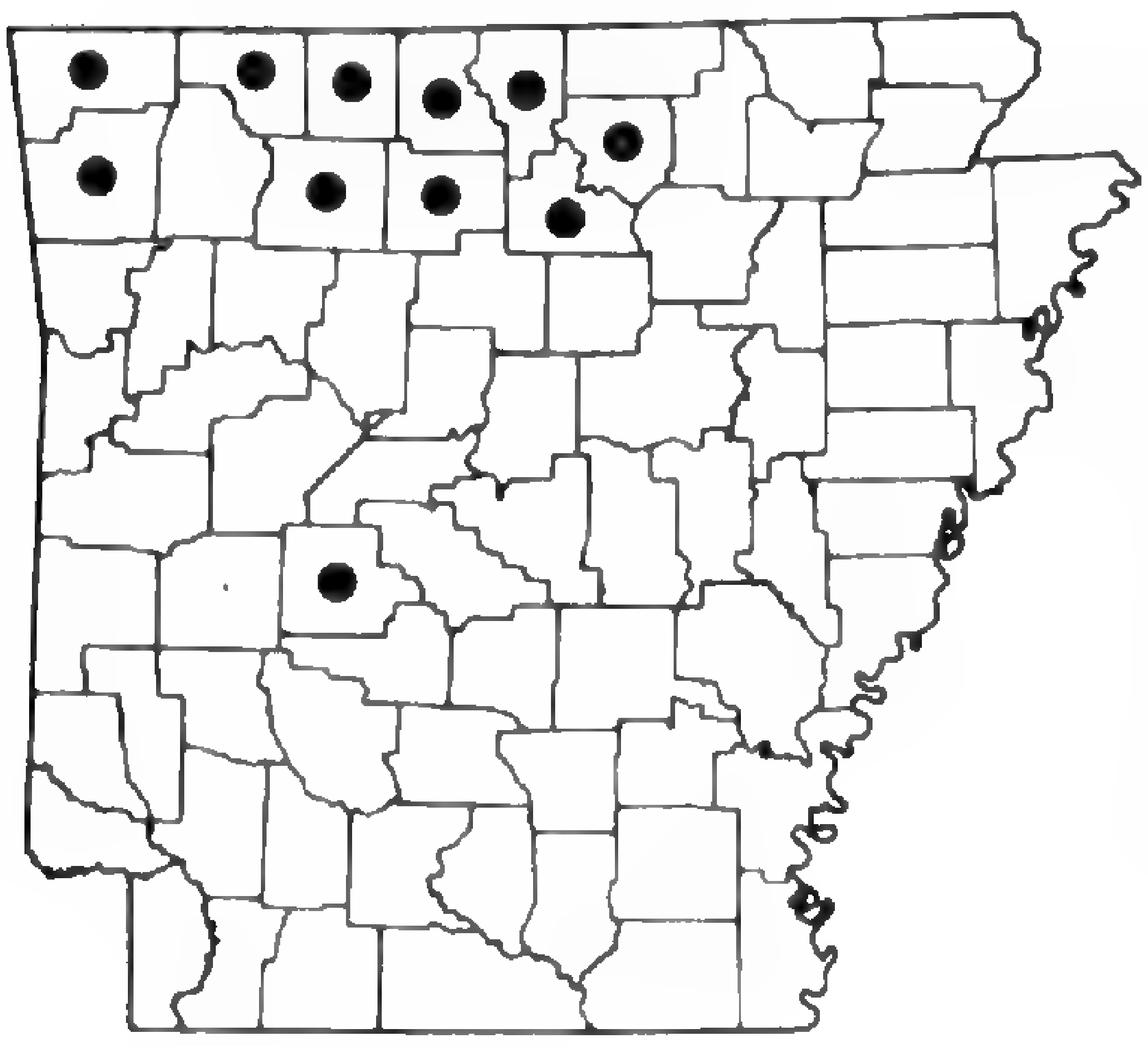


23. *Osmunda regalis* var. *spectabilis*

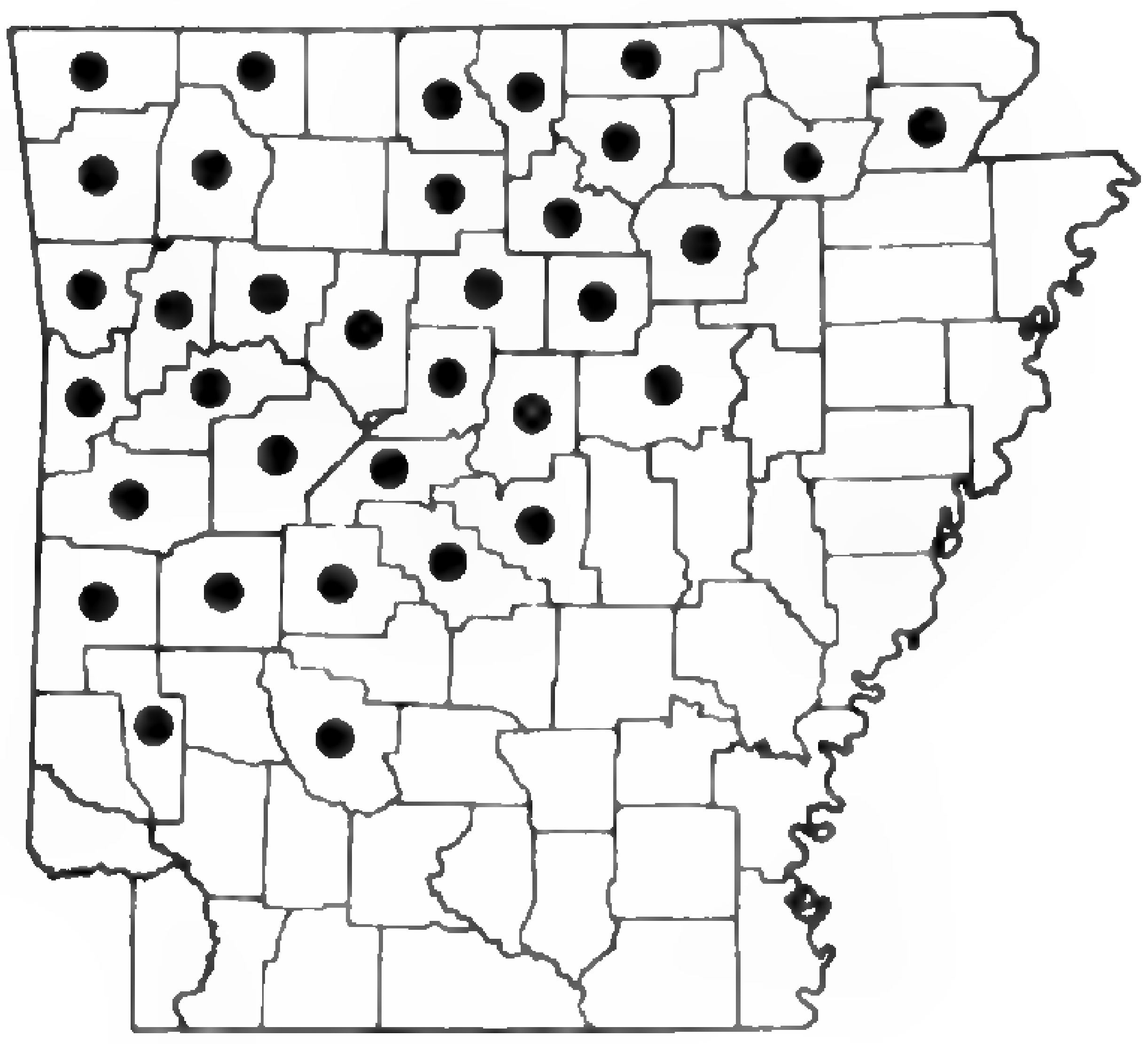


24. *Cheilanthes alabamensis*

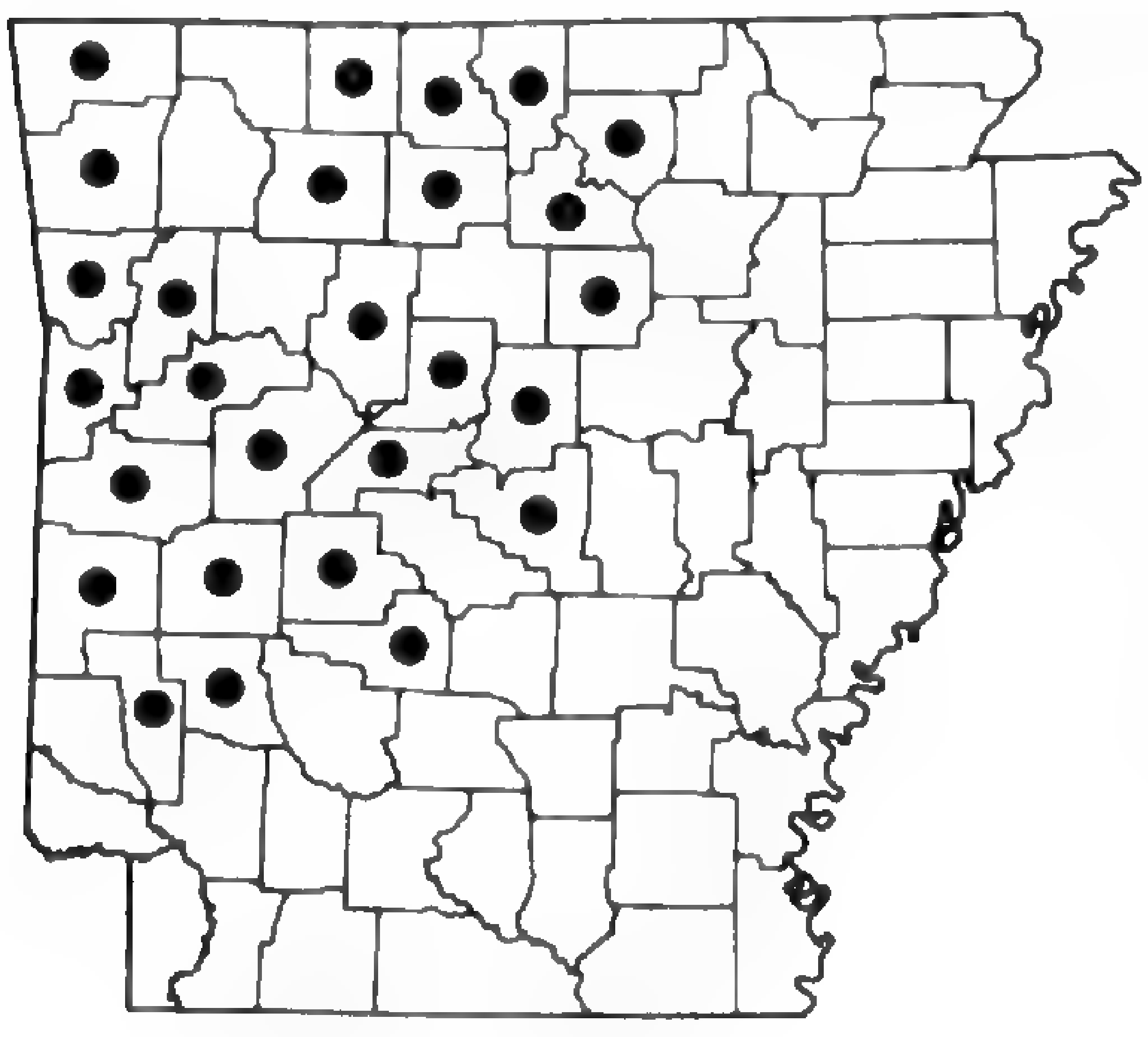
25. *Cheilanthes castanea*



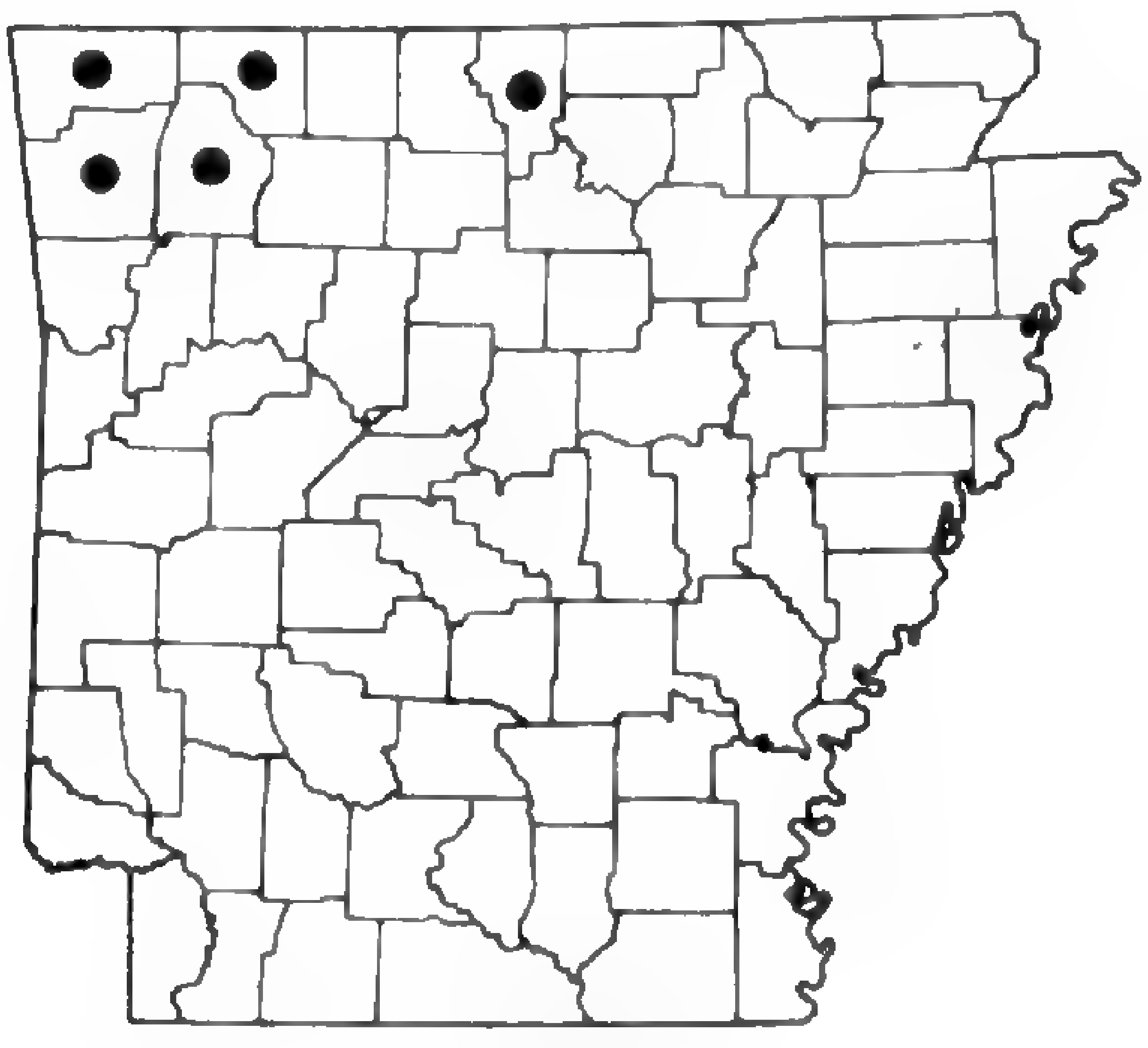
26. *Cheilanthes feei*



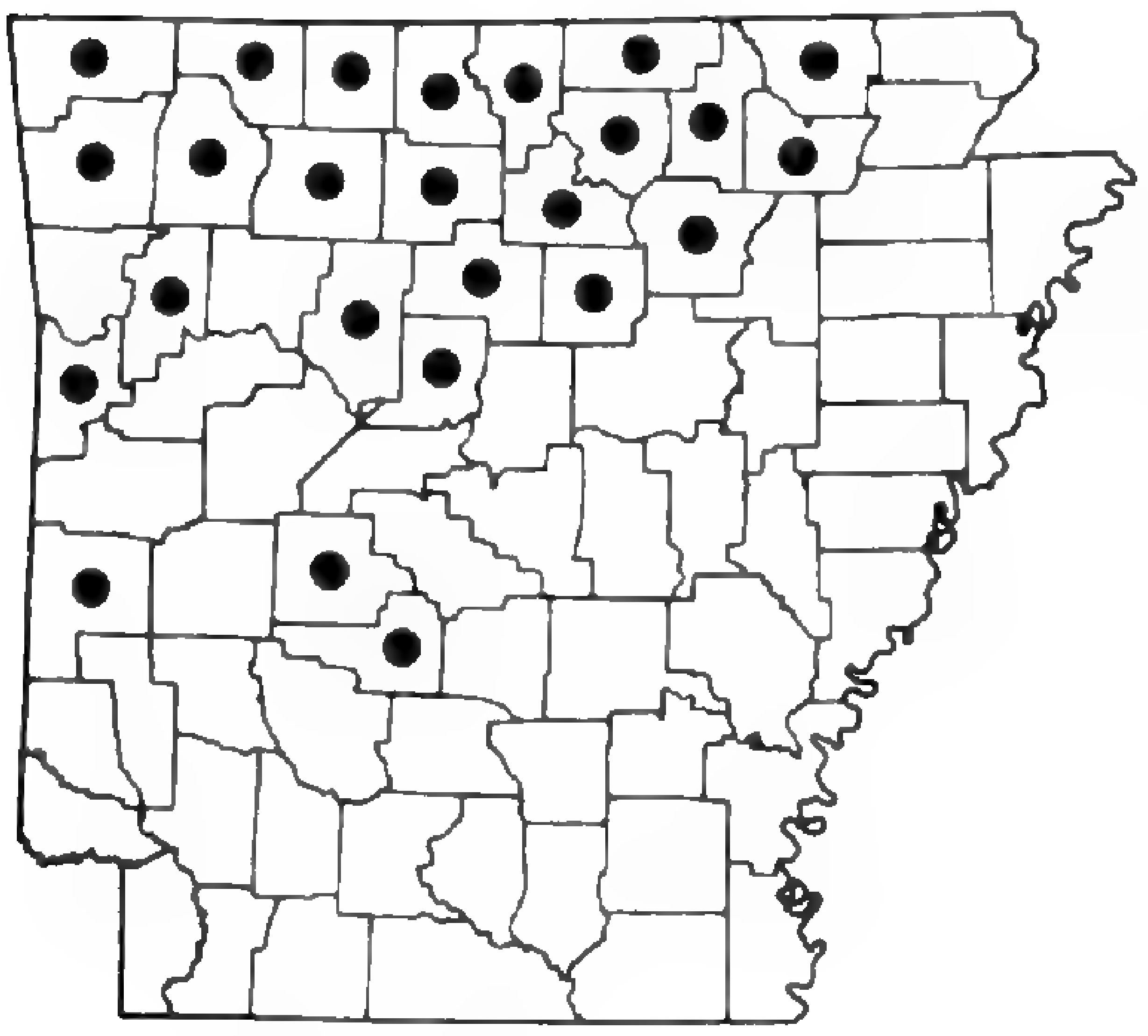
27. *Cheilanthes lanosa*



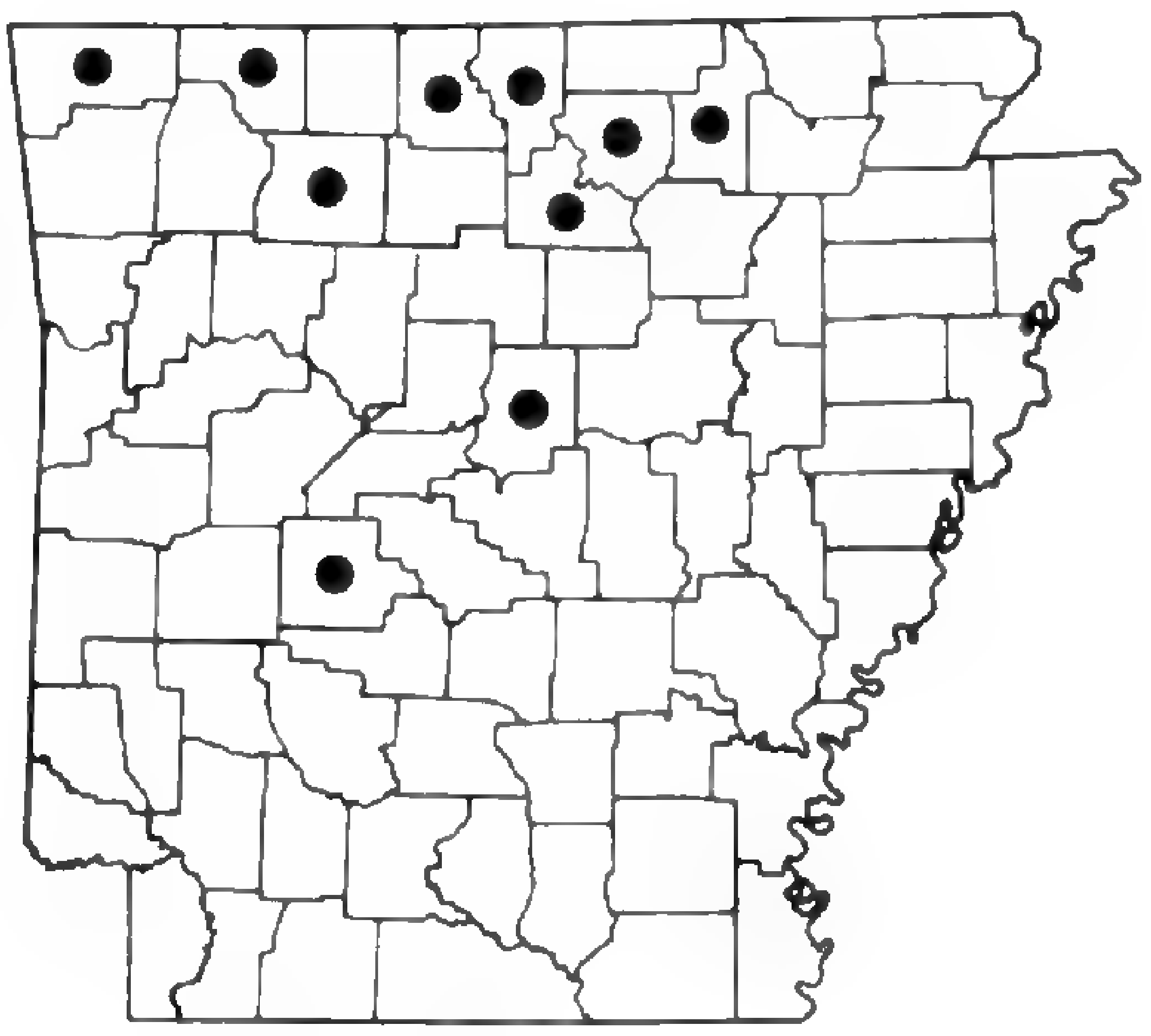
28. *Cheilanthes tomentosa*



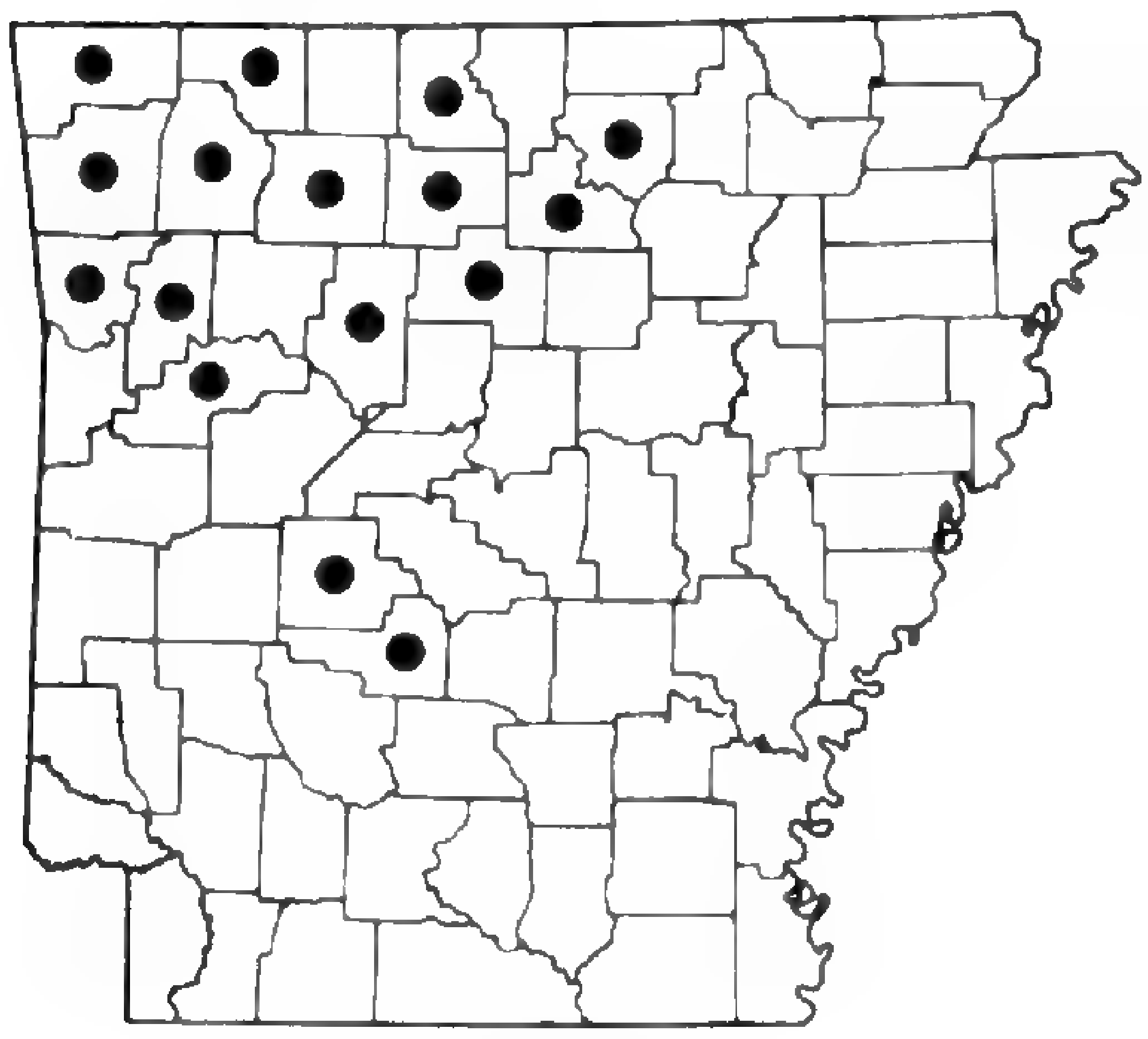
29. *Notholaena dealbata*



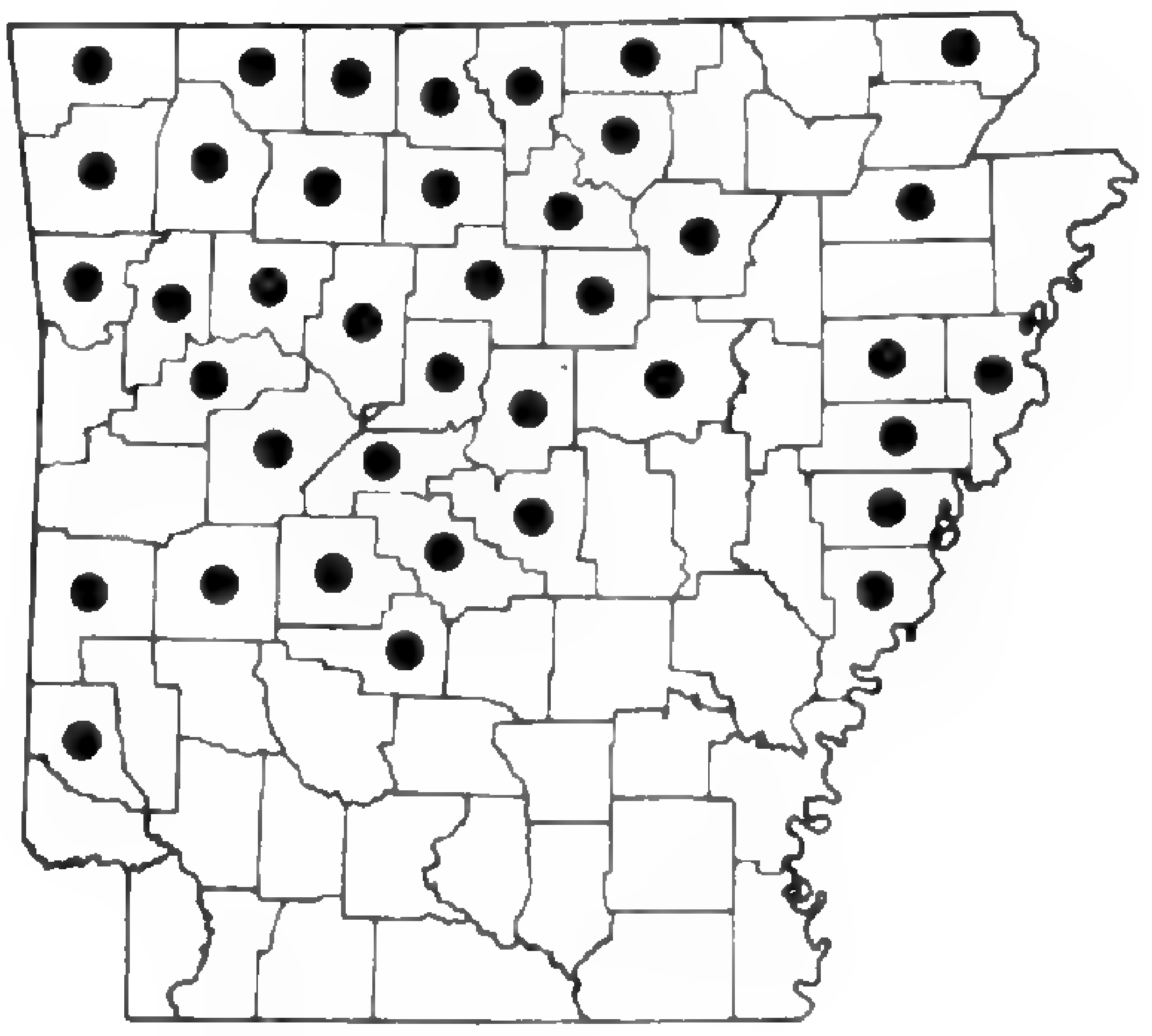
30. *Pellaea atropurpurea*



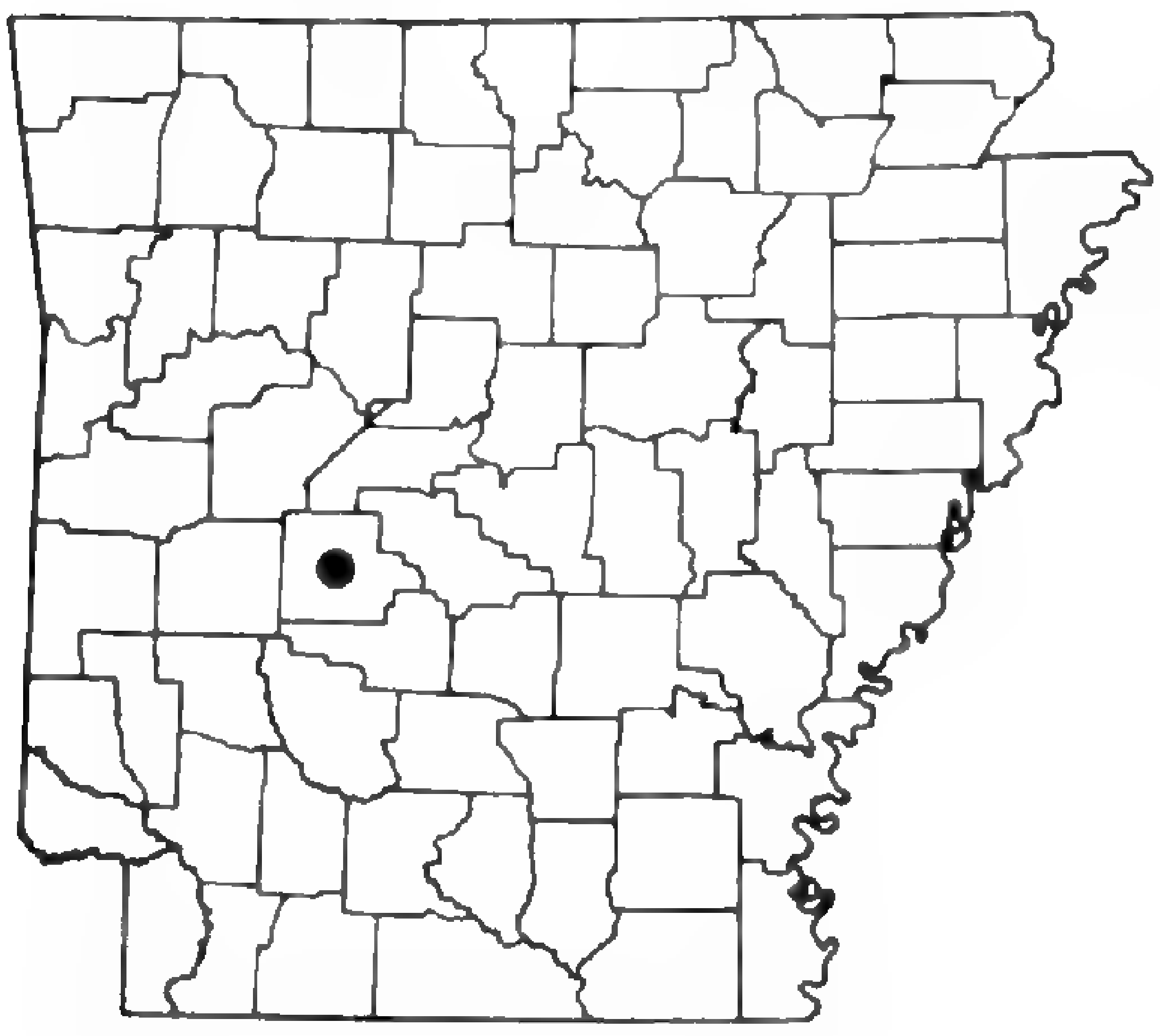
31. *Pellaea glabella*



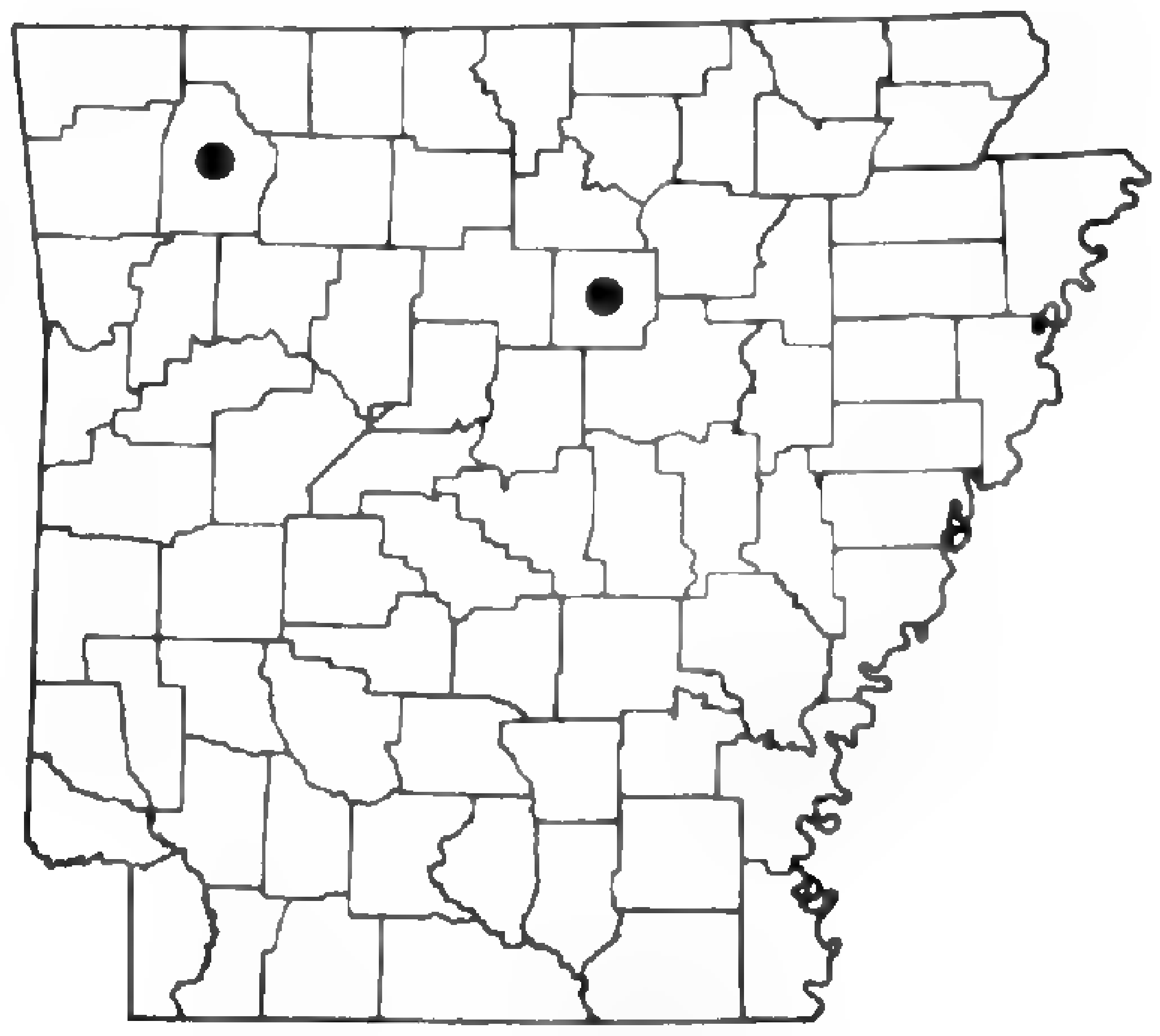
32. *Adiantum capillus-veneris*



33. *Adiantum pedatum*

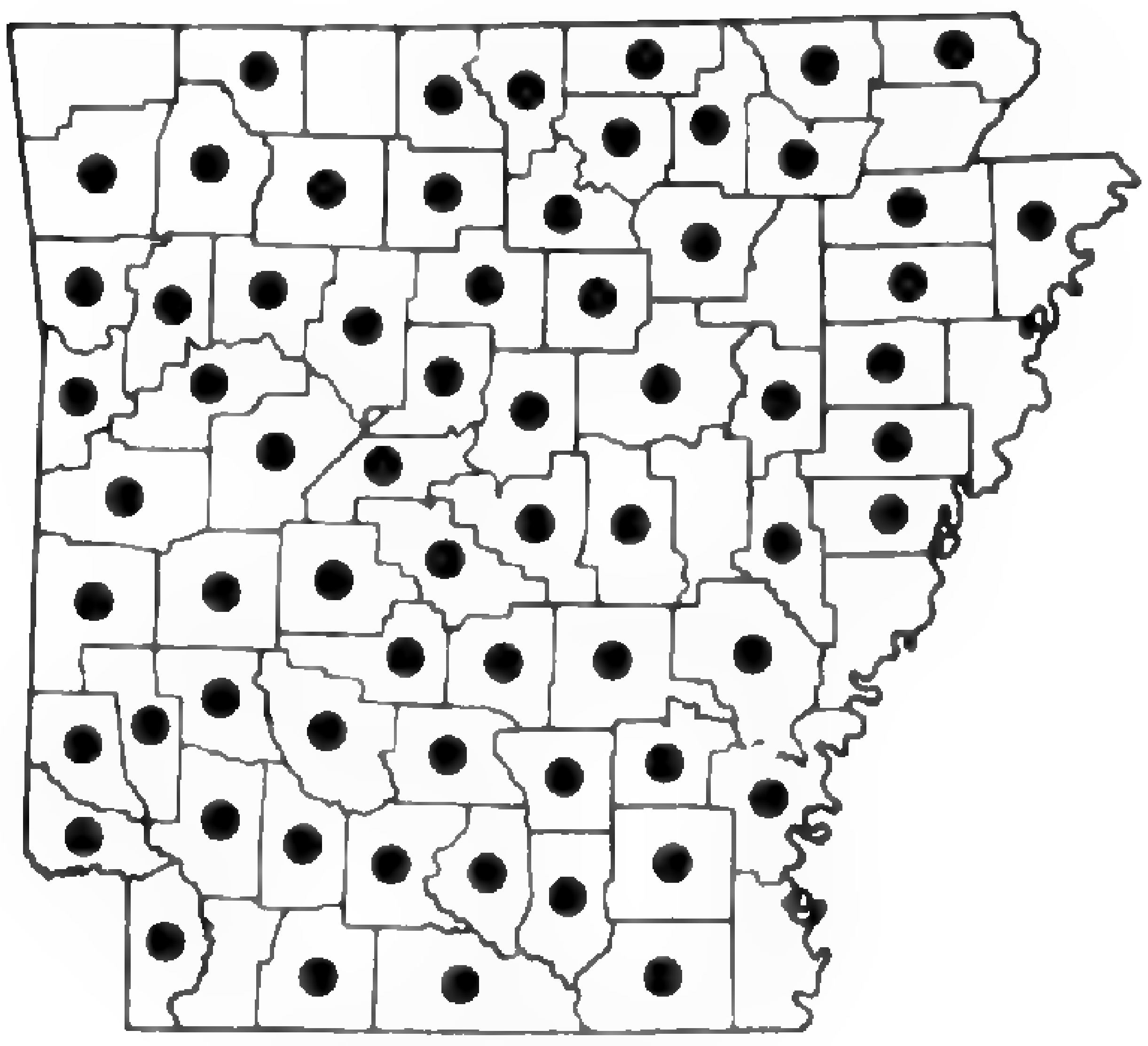


34. *Pteris multifida*

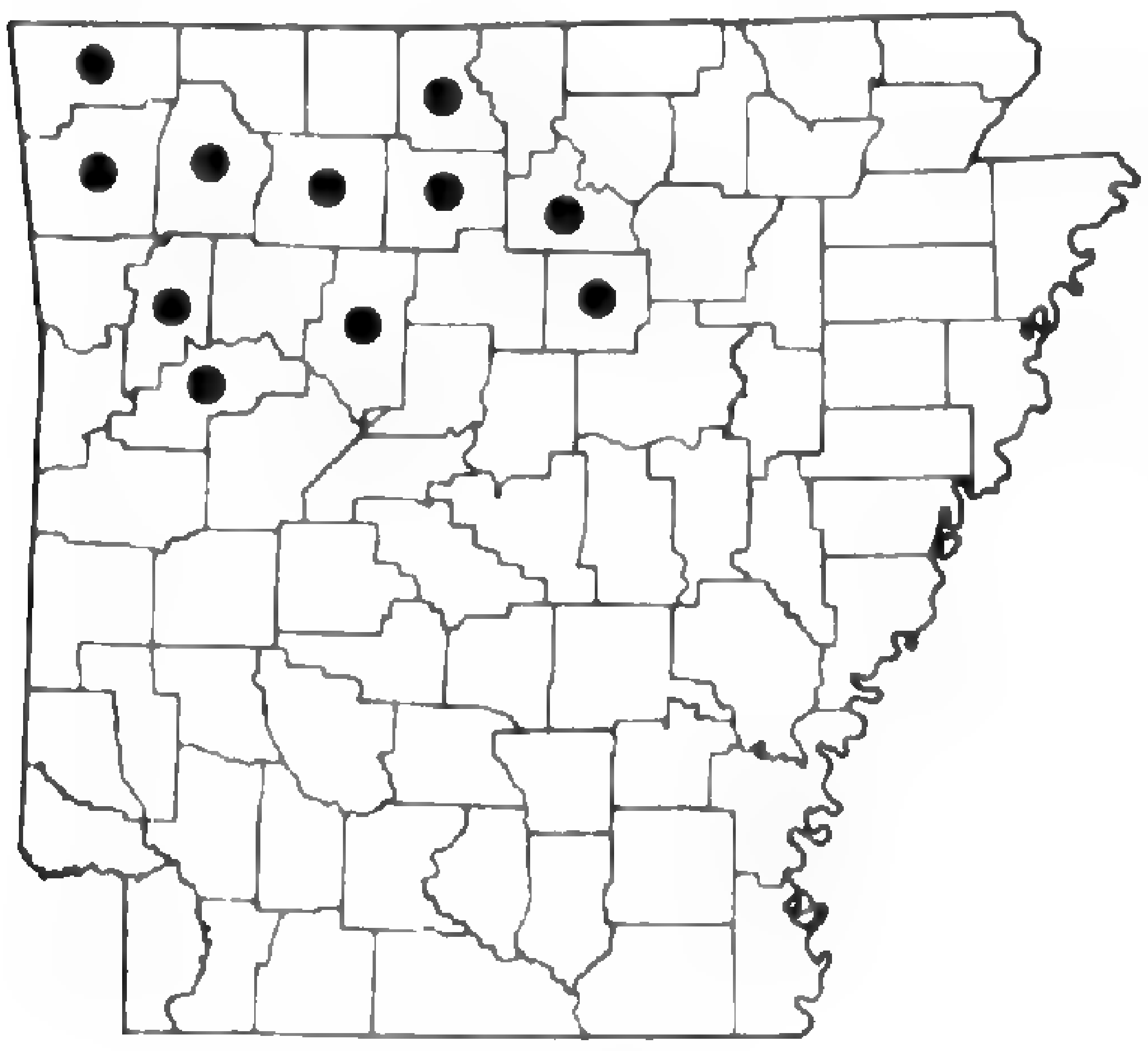


35. *Trichomanes boschianum*

36. *Trichomanes petersii*

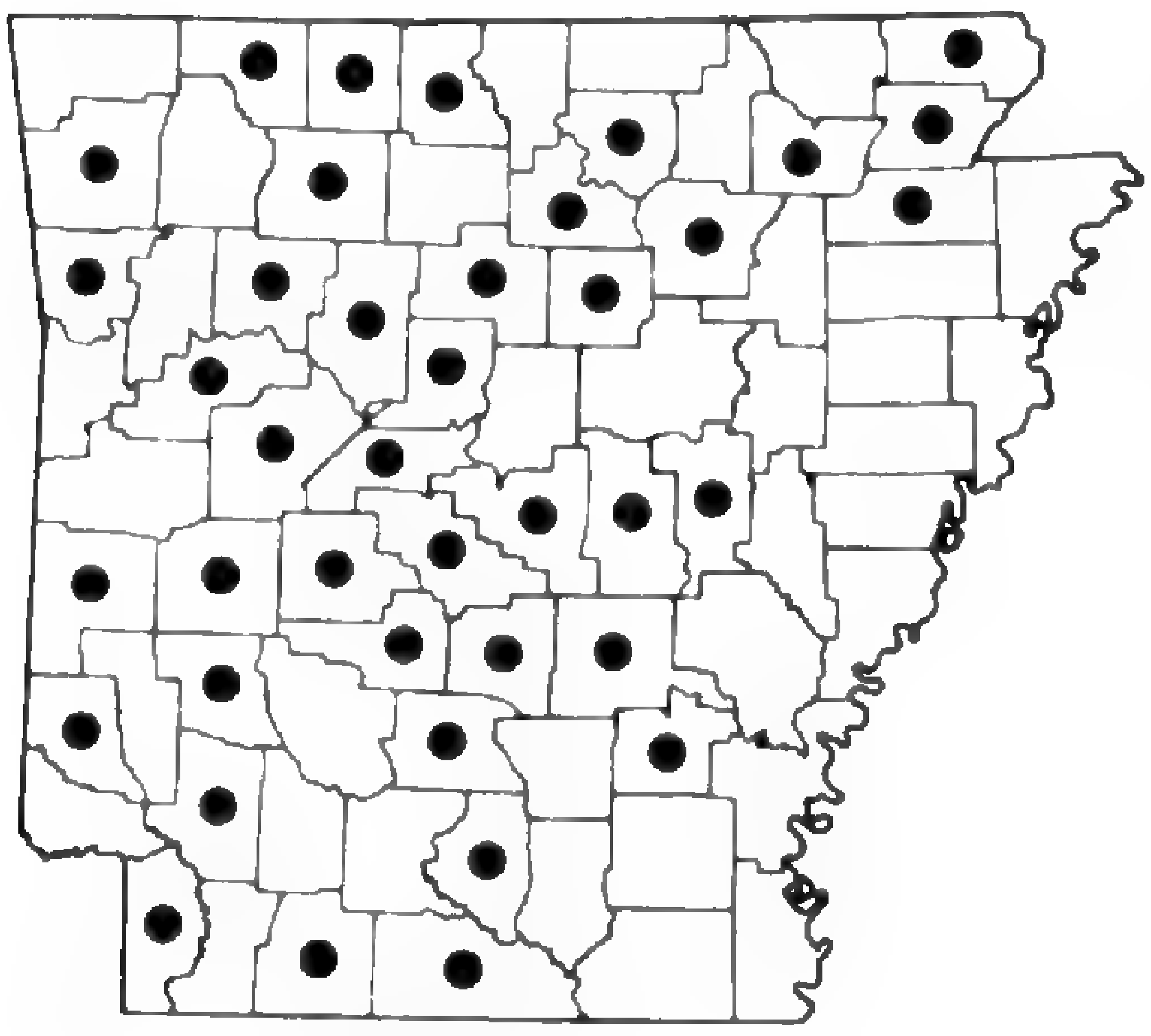


37. *Polypodium polypodioides* var. *michauxianum*

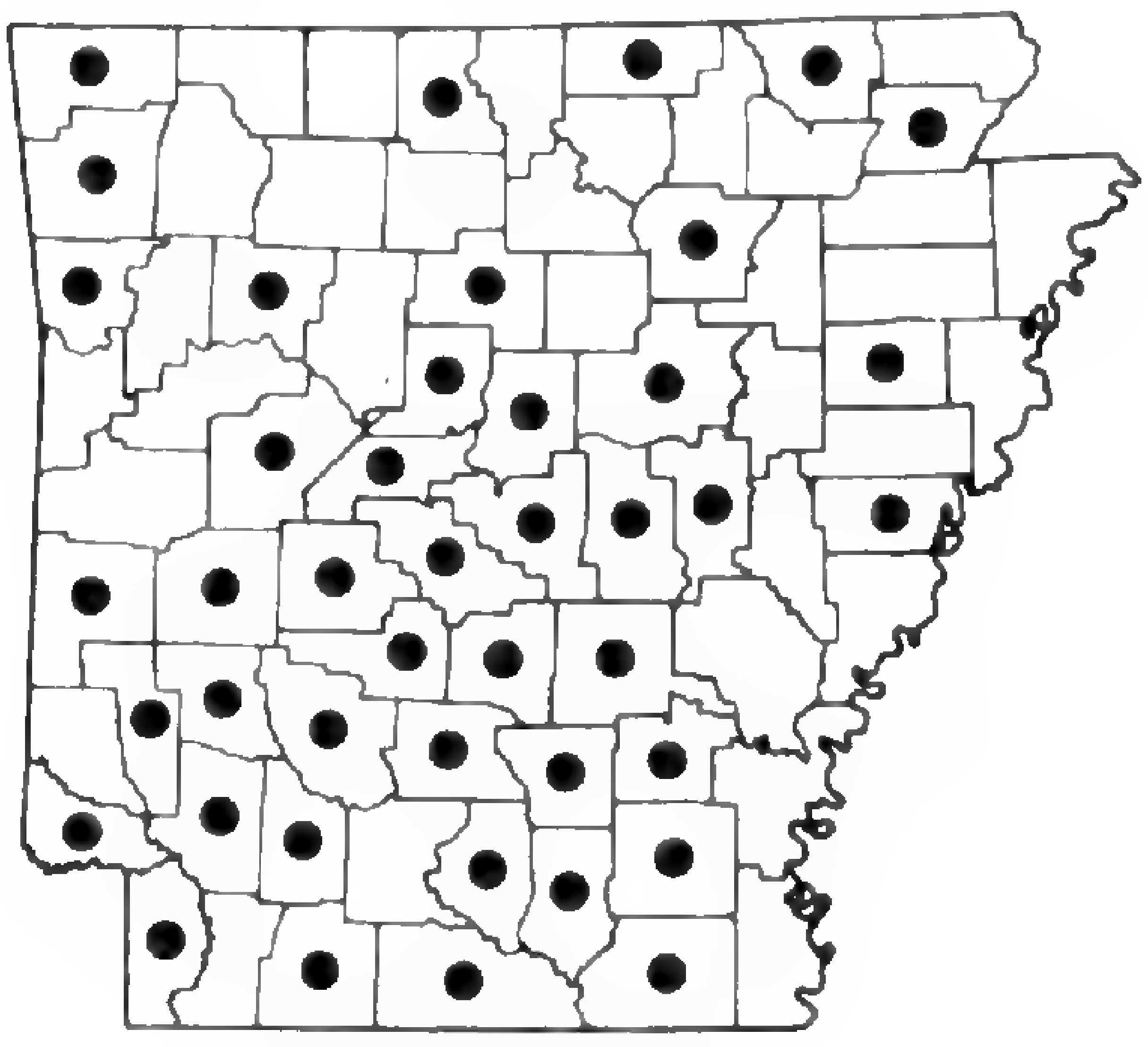


38. *Polypodium virginianum*

39 *Dennstaedtia punctilobula*

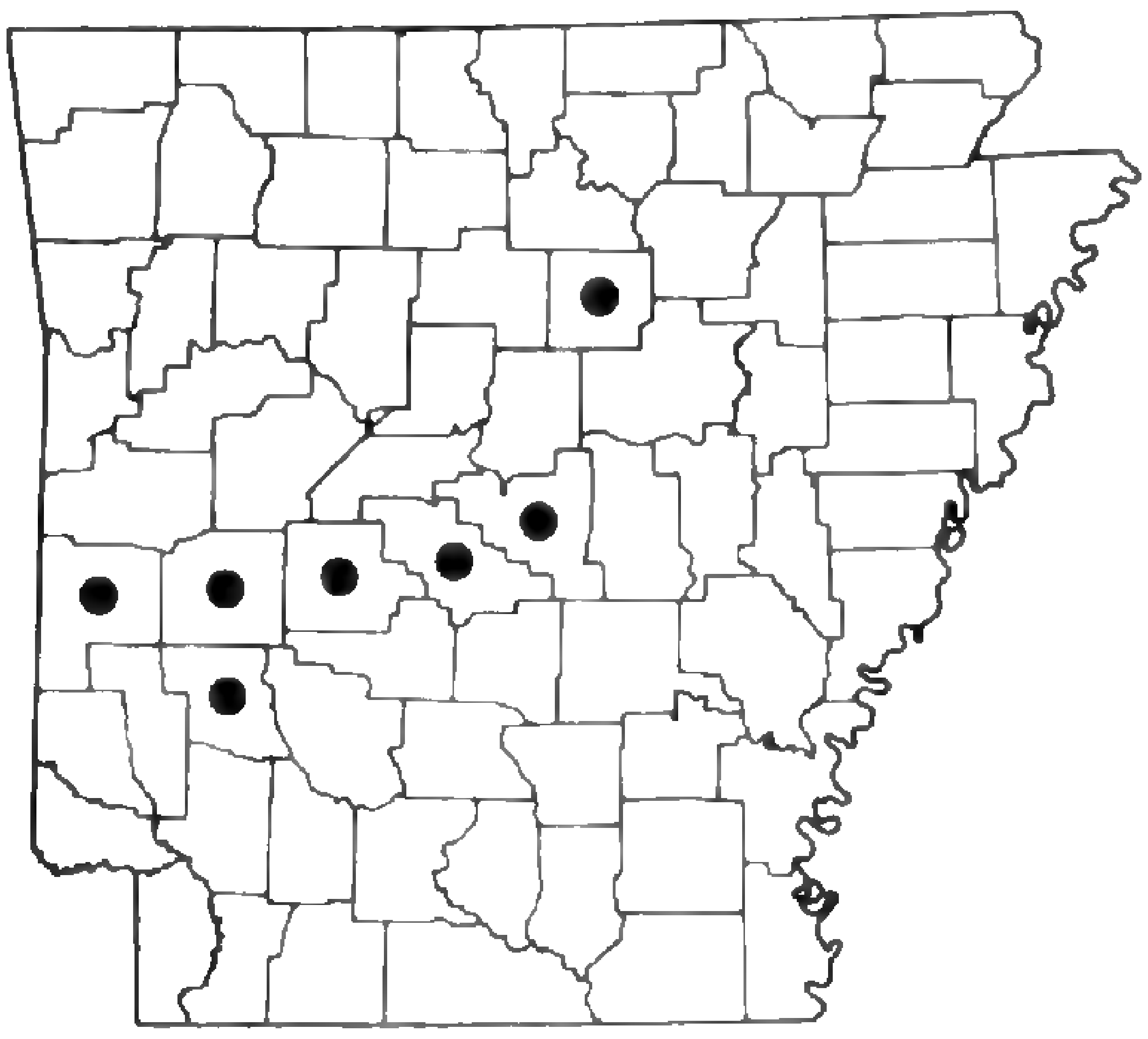


40a *Pteridium aquilinum* var. *latiusculum*

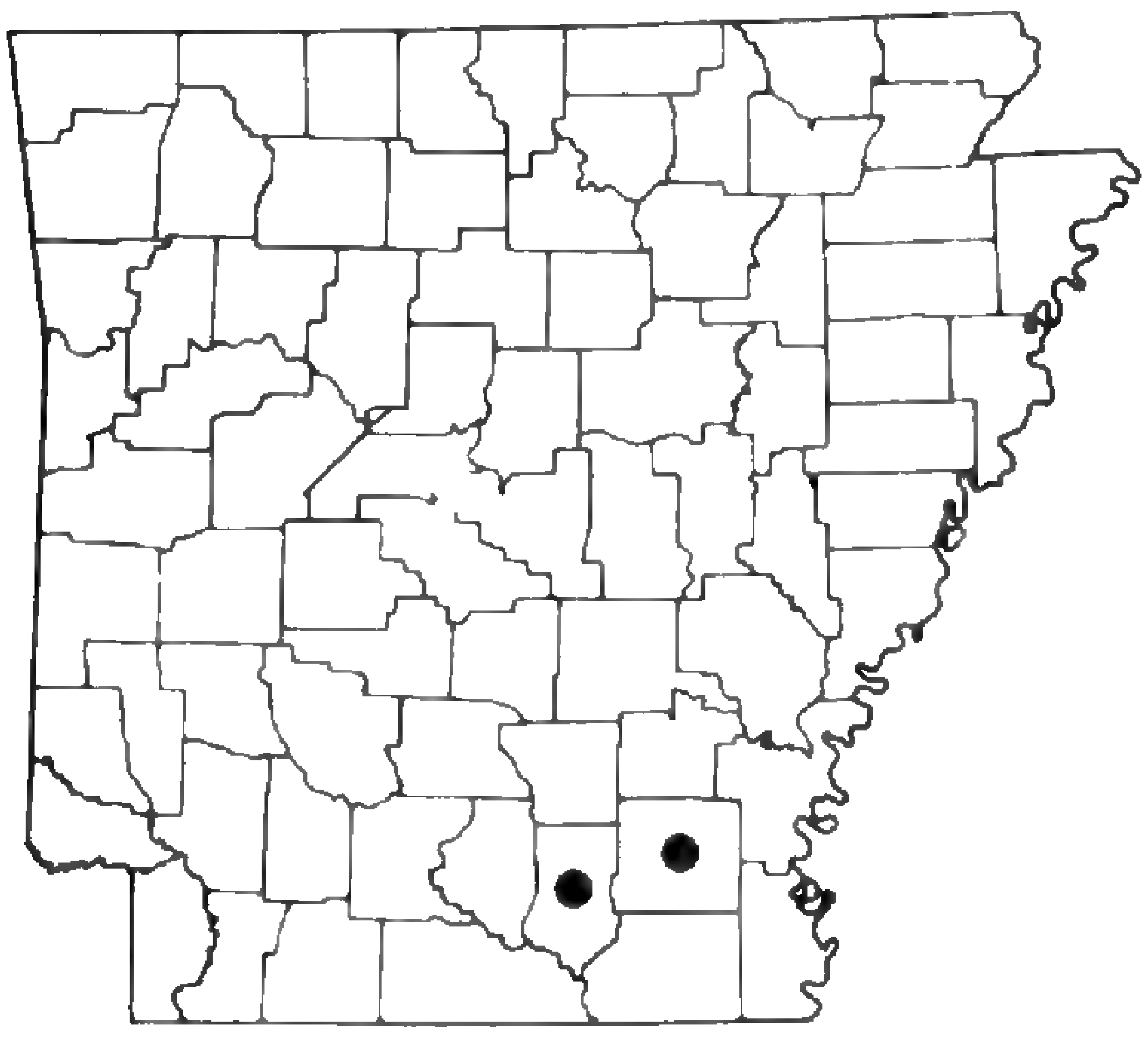


40b *Pteridium aquilinum* var. *pseudocaudatum*

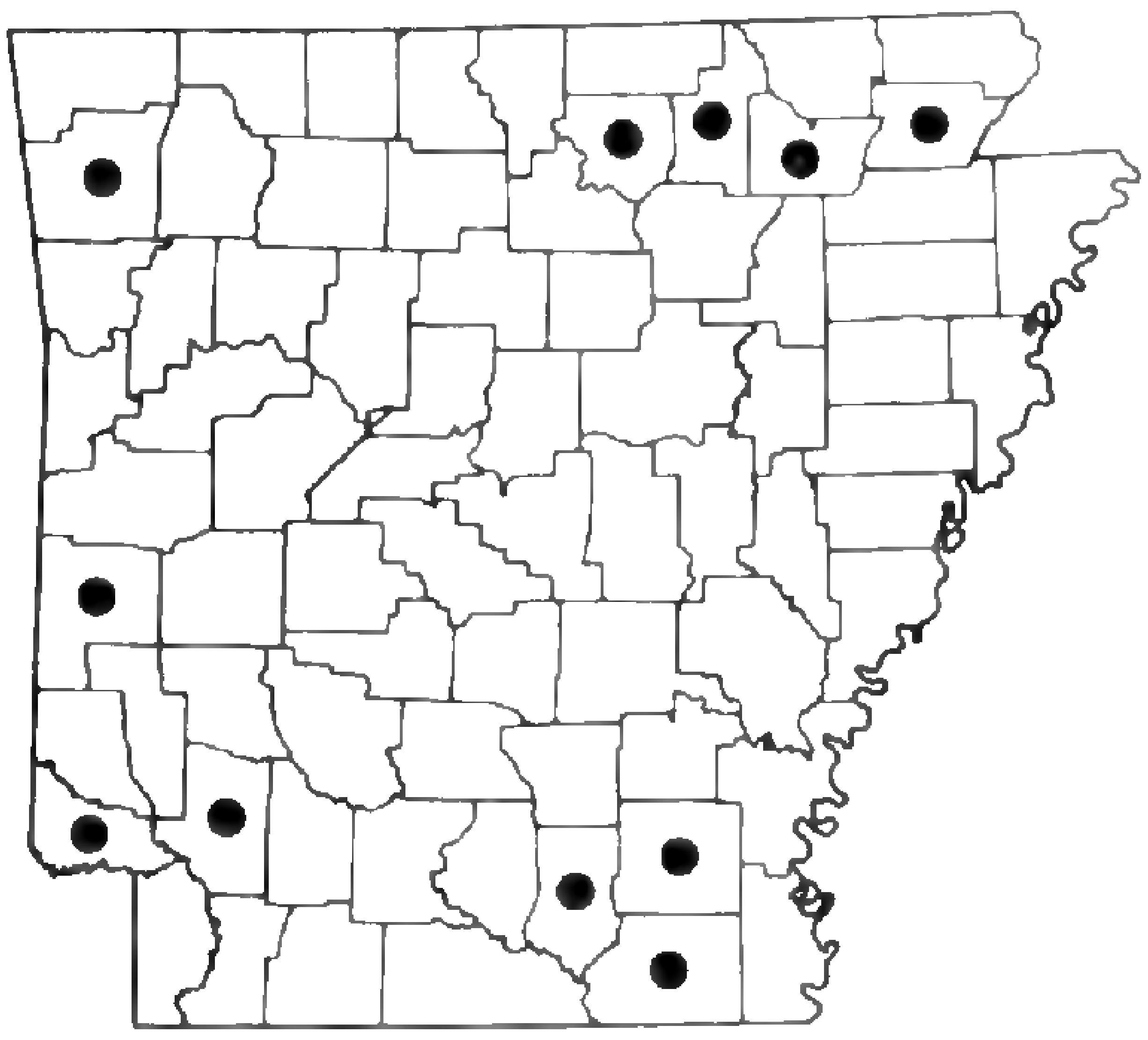
41. *Thelypteris kunthii*



42. *Thelypteris noveboracensis*

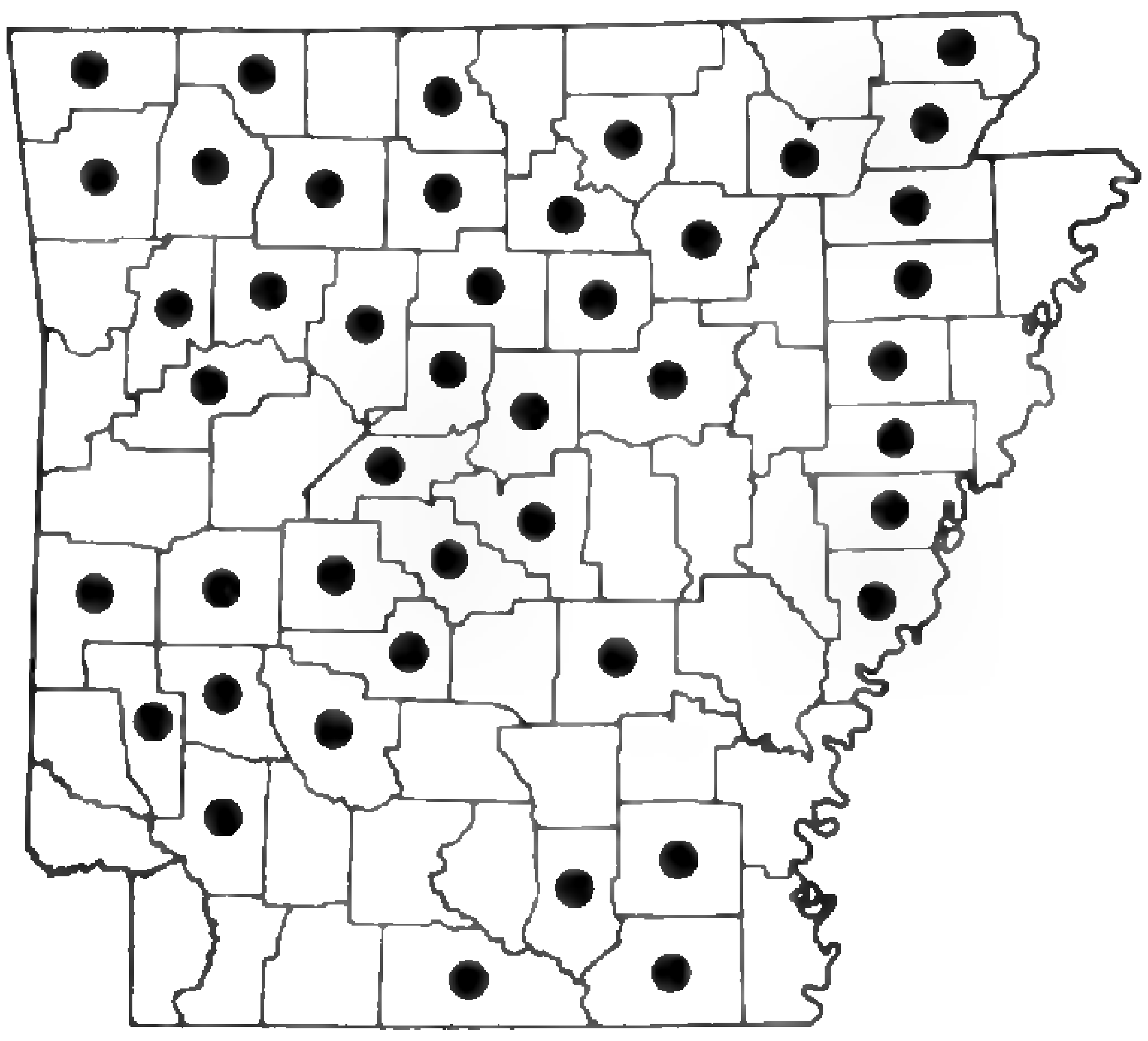


43a. *Thelypteris palustris* var. *haleana*

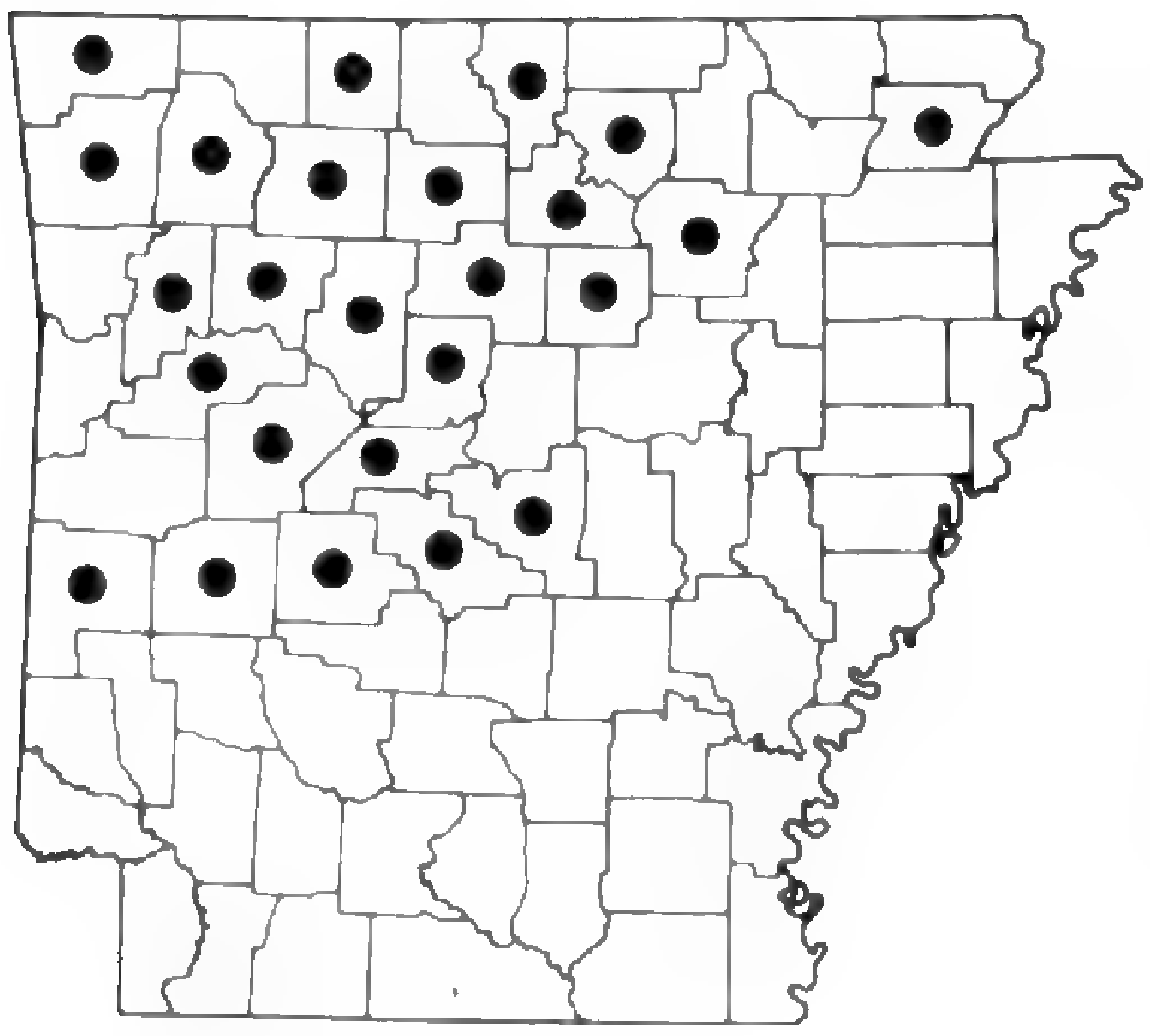


43b *Thelypteris palustris* var. *pubescens*

44. *Thelypteris torresiana*

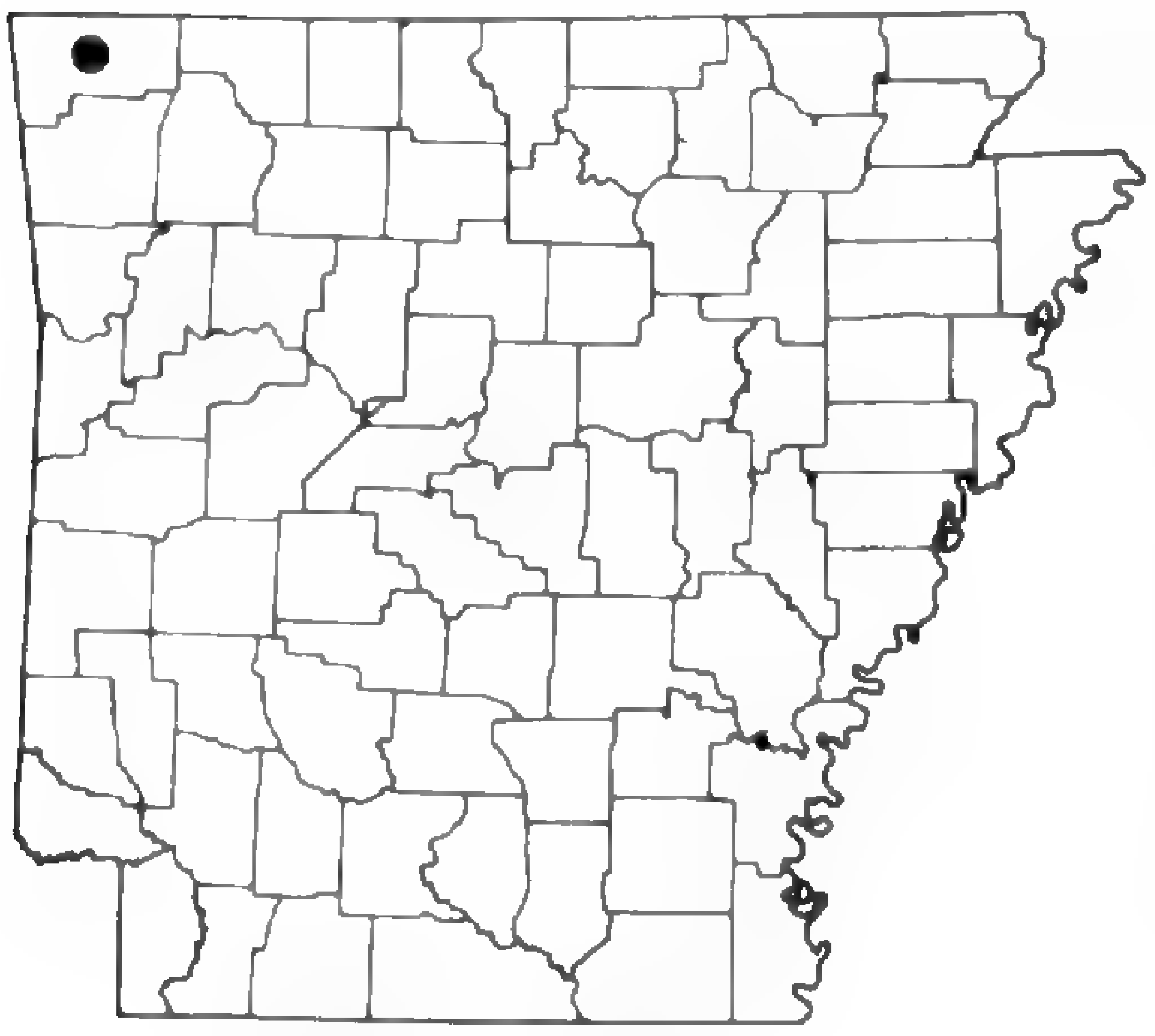


45. *Phegopteris hexagonoptera*

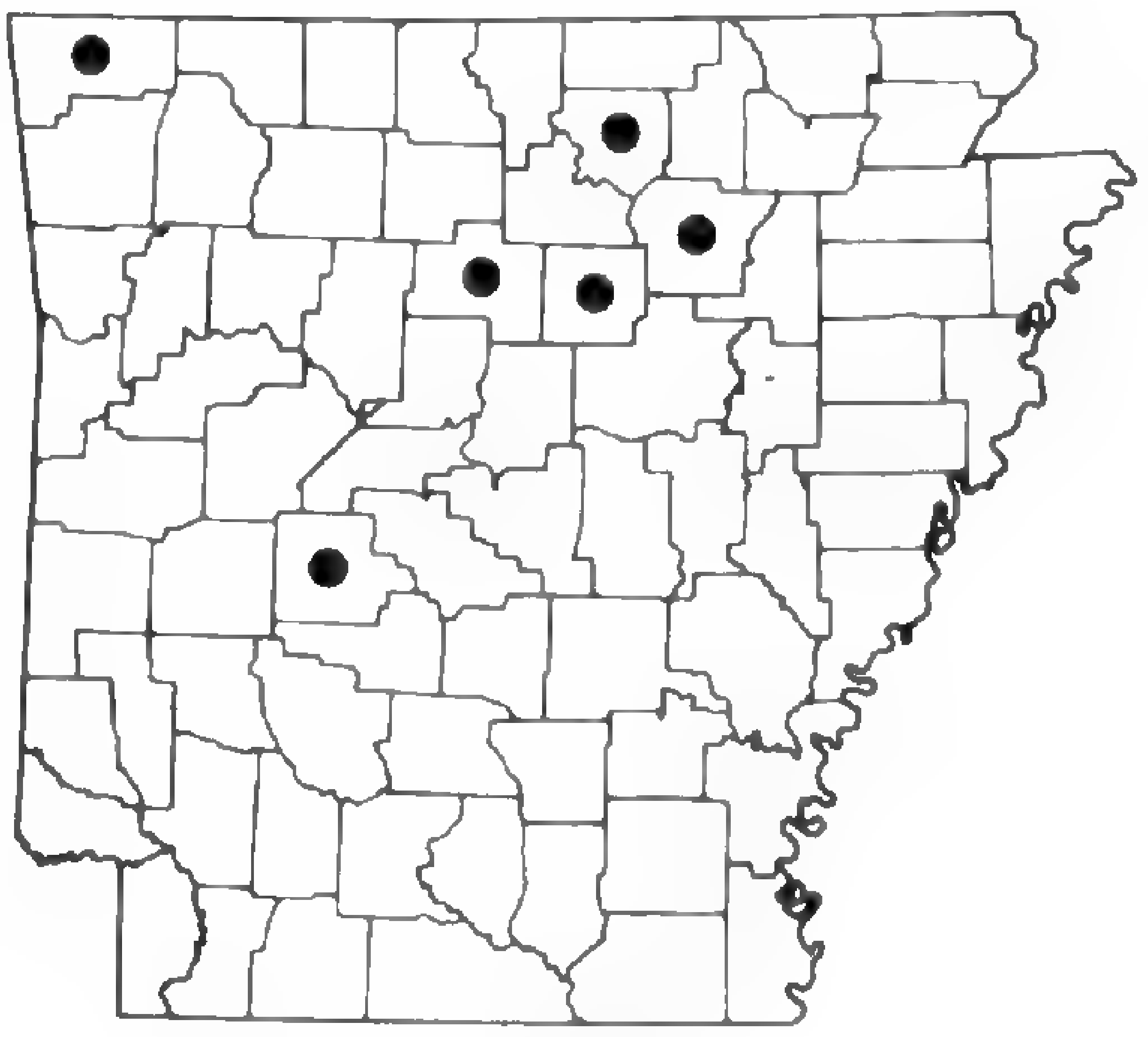


46. *Asplenium bradleyi*

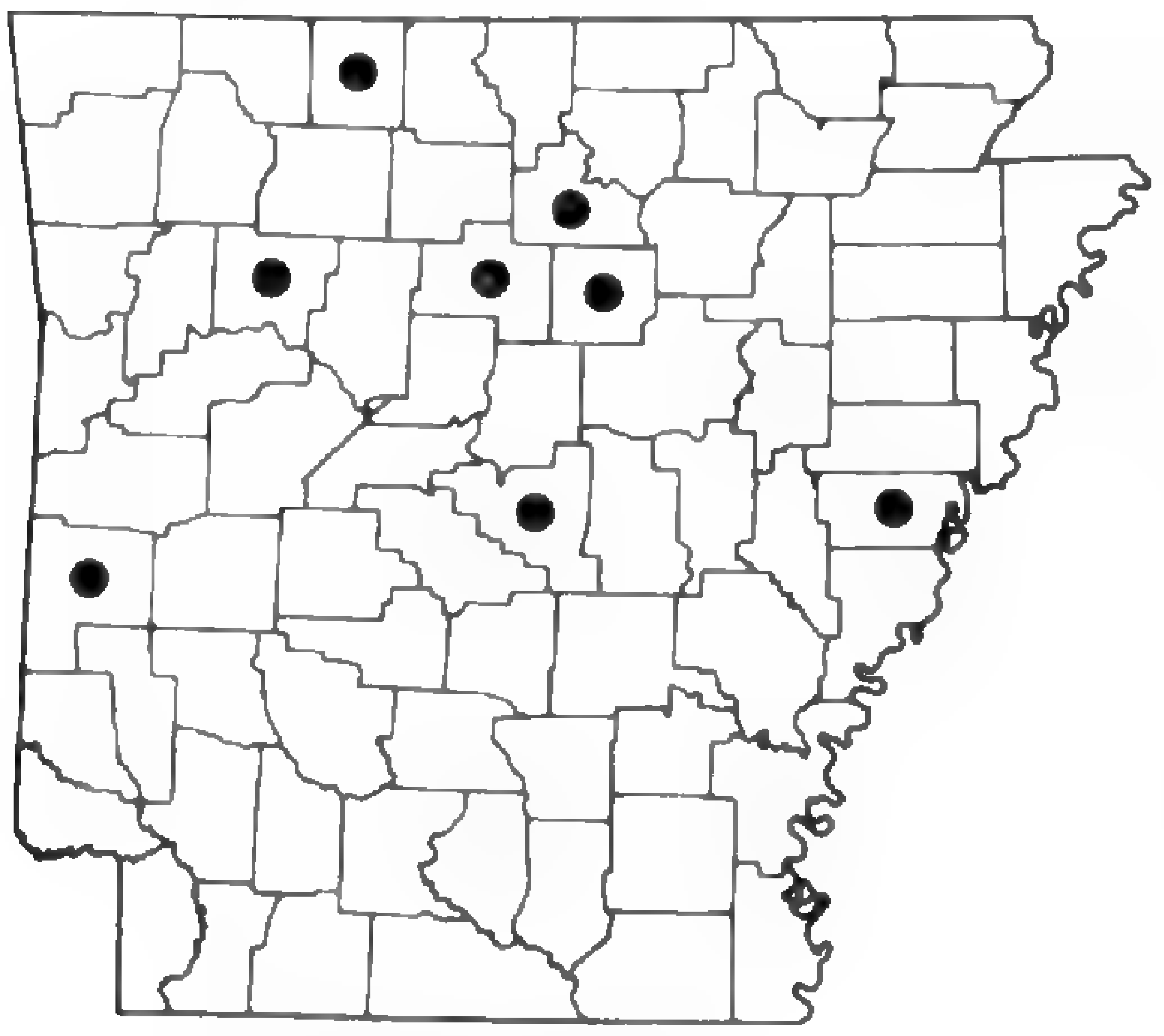
47. *Asplenium X ebenoides*



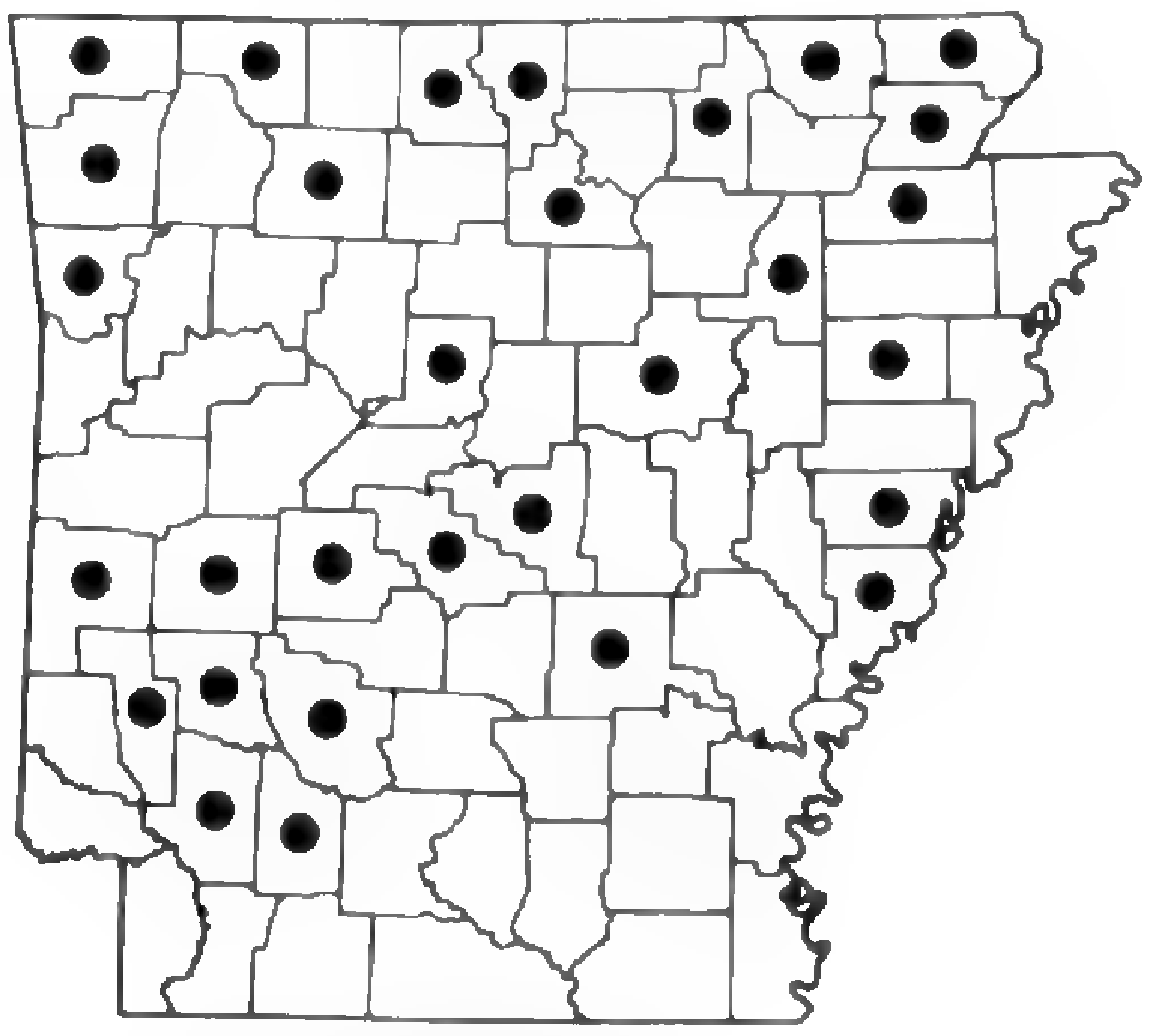
48. *Asplenium X kentuckiense*



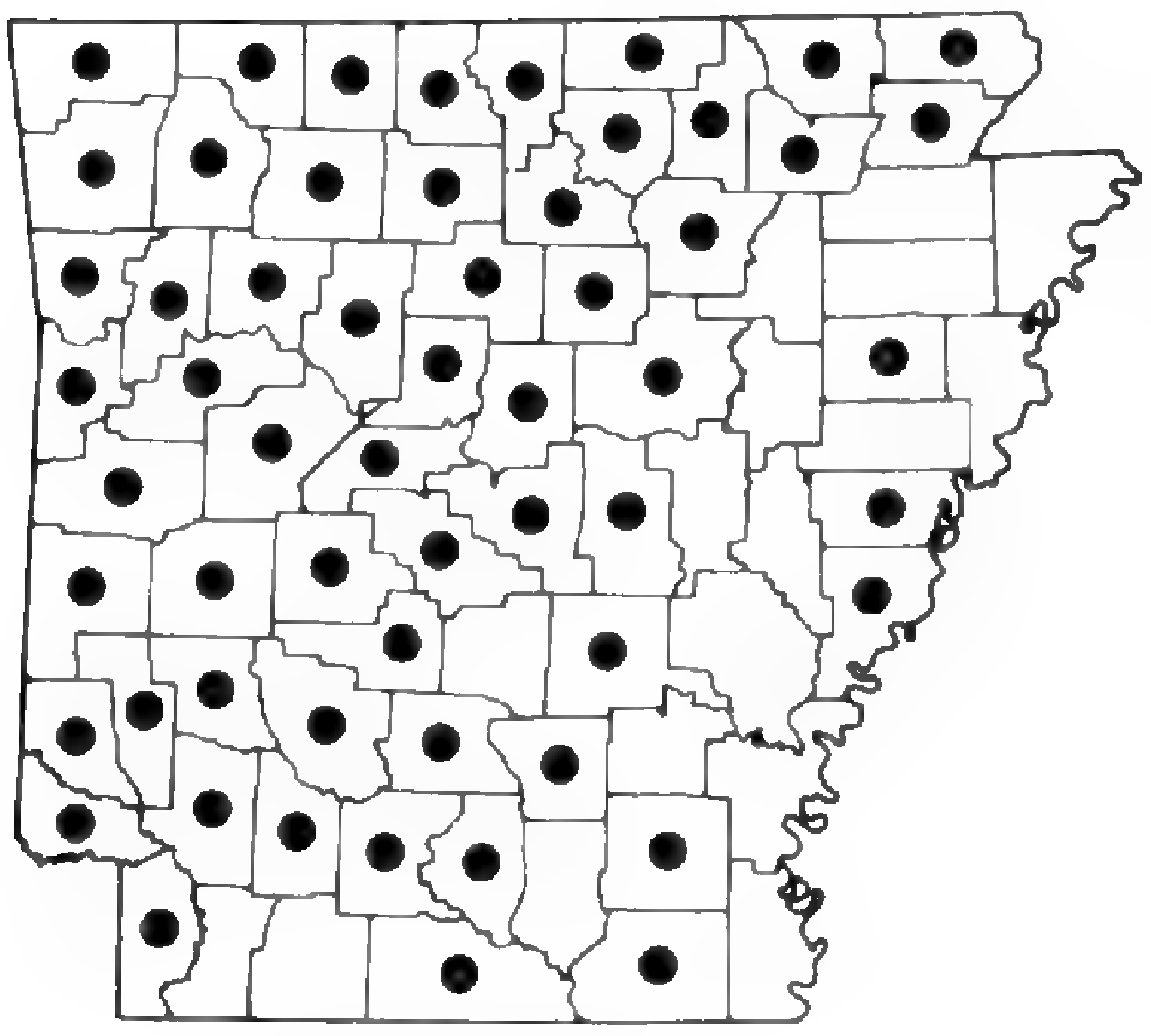
49. *Asplenium pinnatifidum*



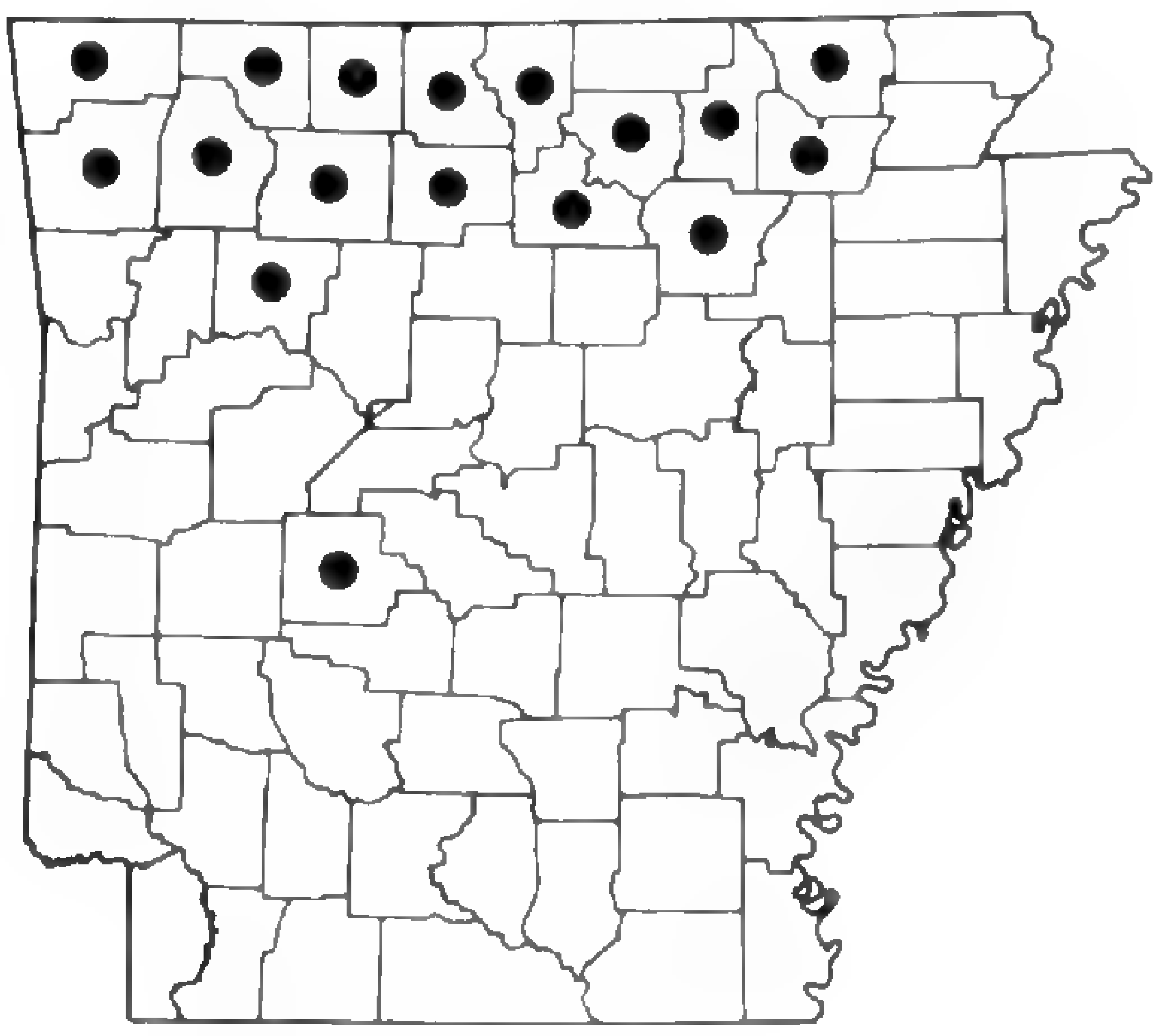
50a. *Asplenium platyneuron*
var. bacculum-rubrum



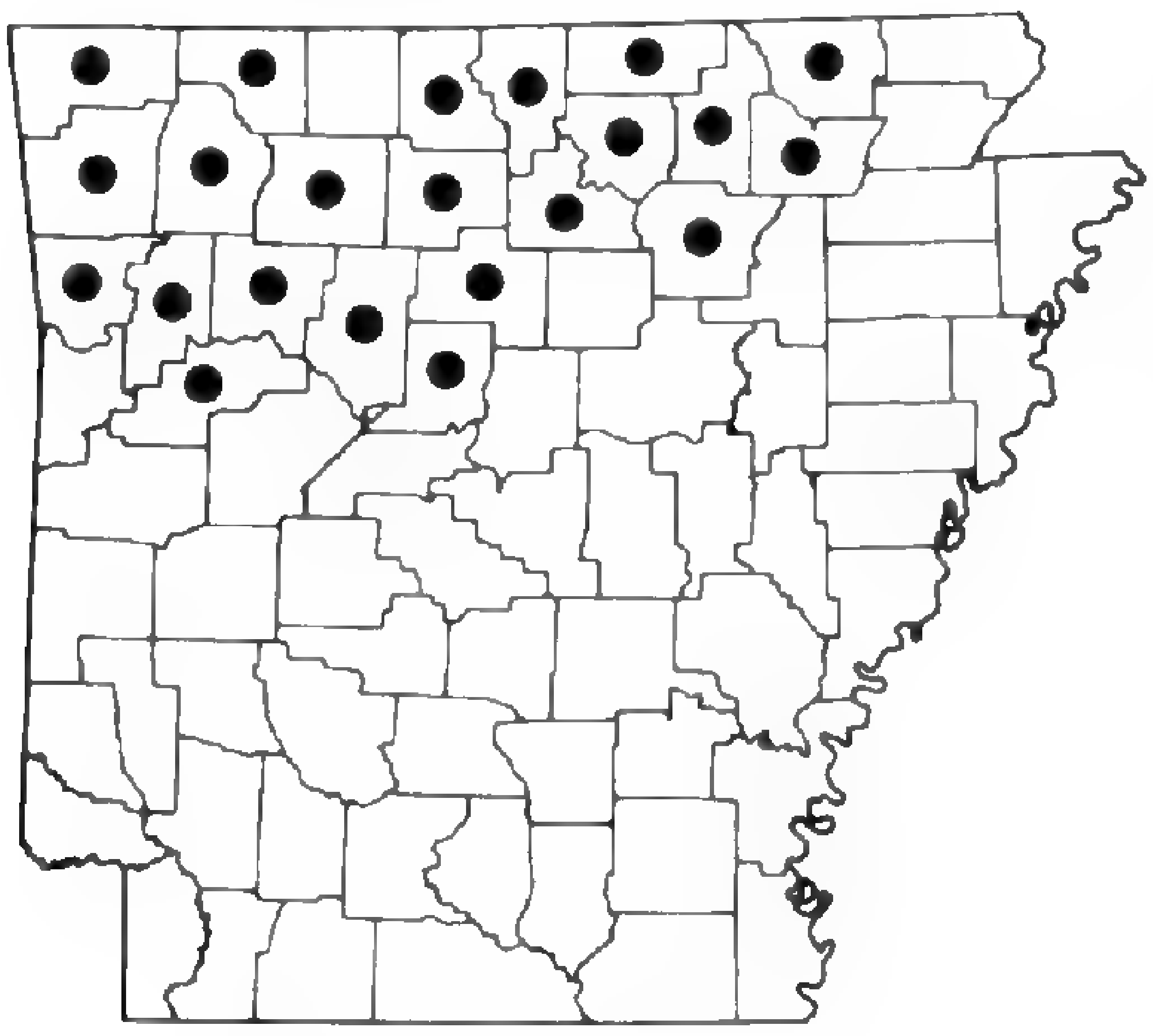
50b. *Asplenium platyneuron*
var. incisum



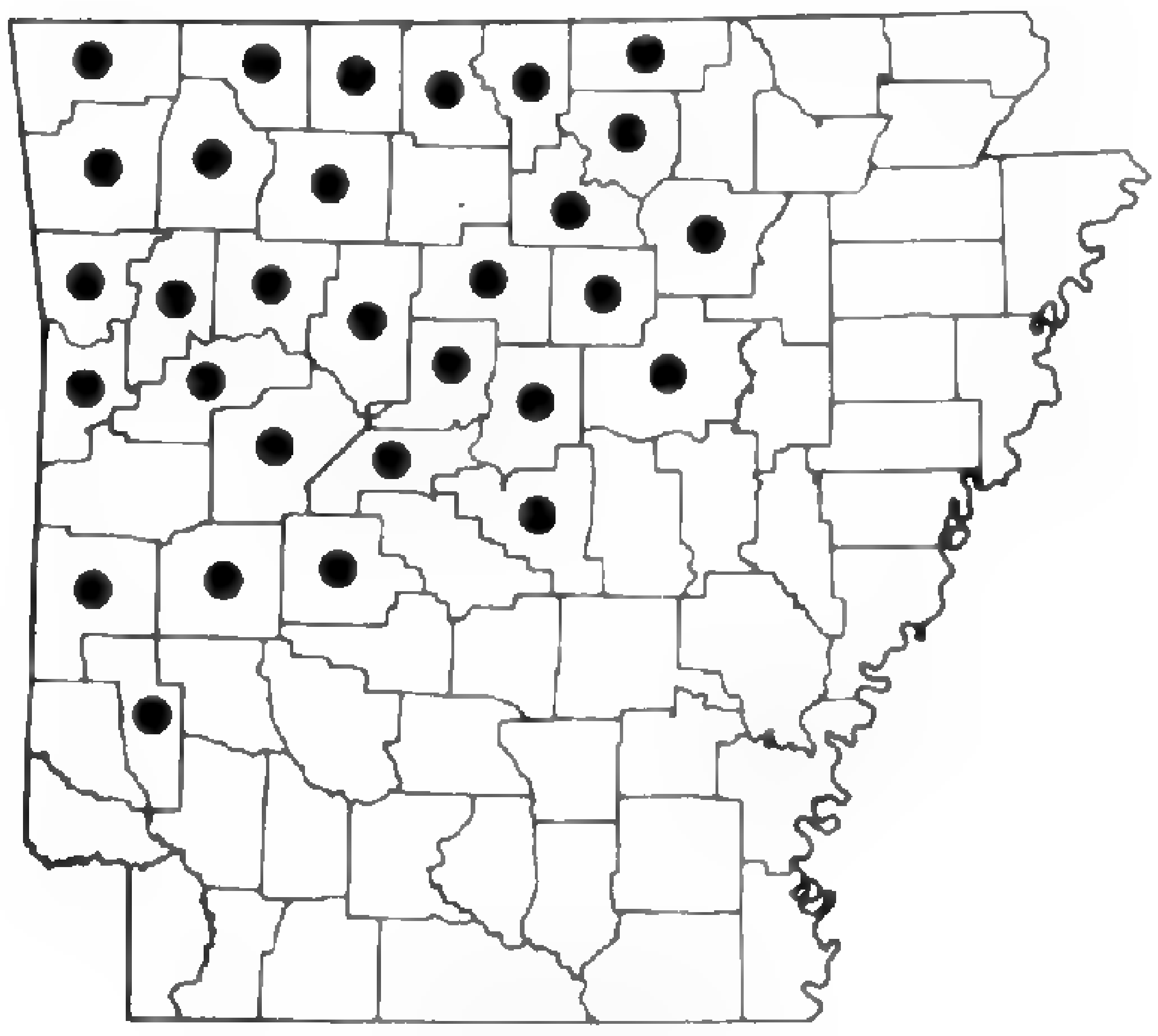
50c *Asplenium platyneuron* var. *platyneuron*



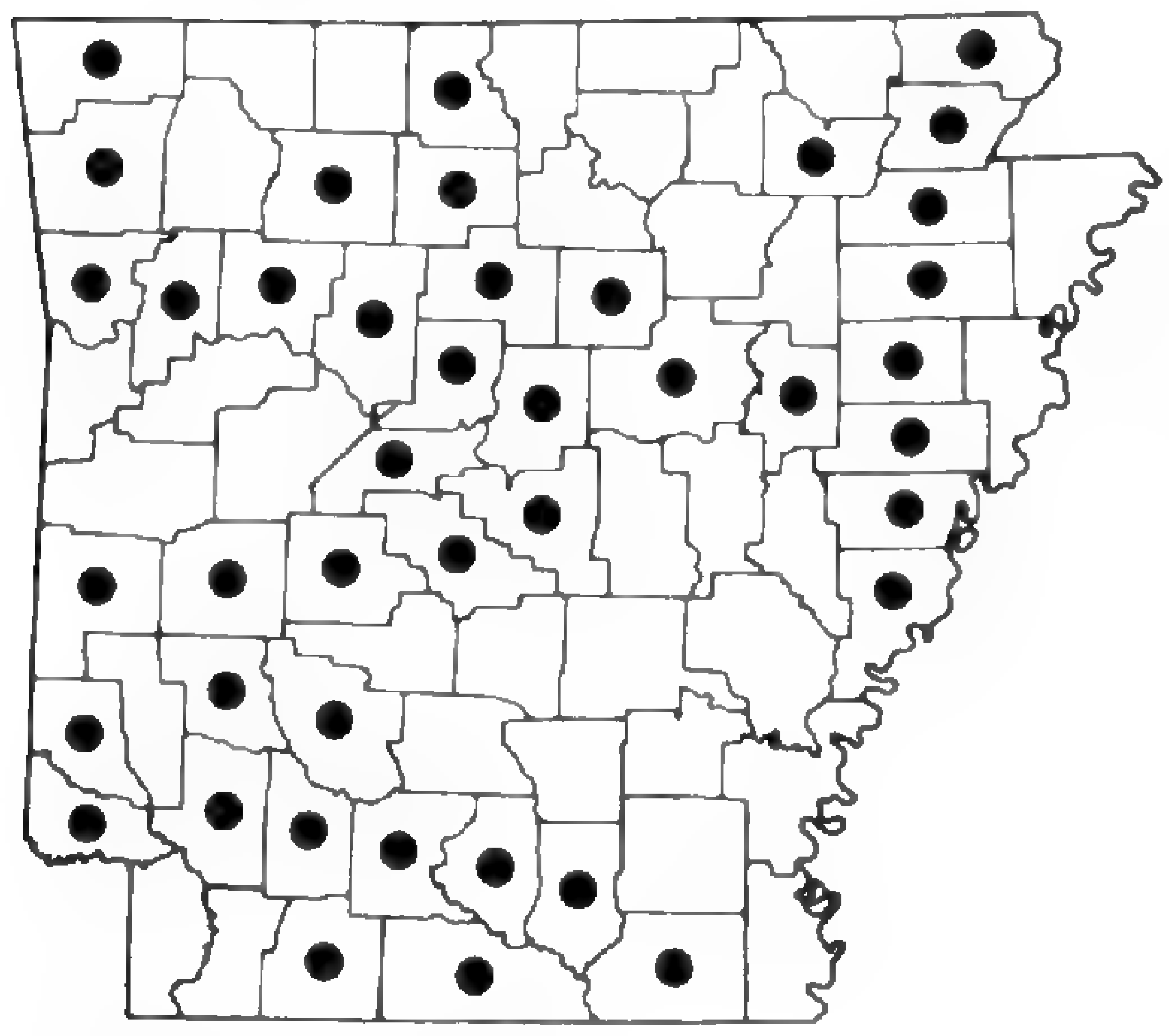
51. *Asplenium resiliens*



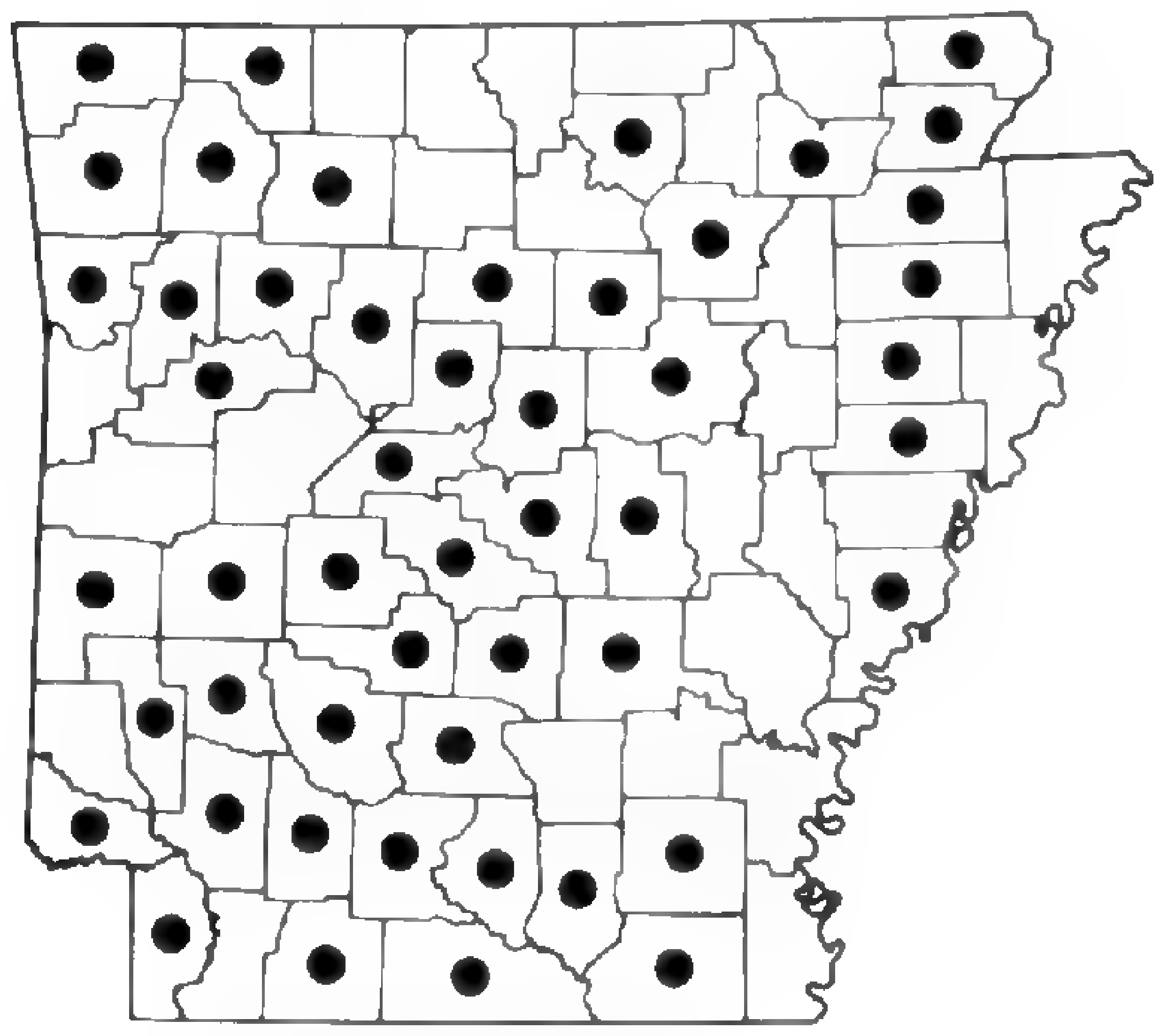
52. *Asplenium rhizophyllum*



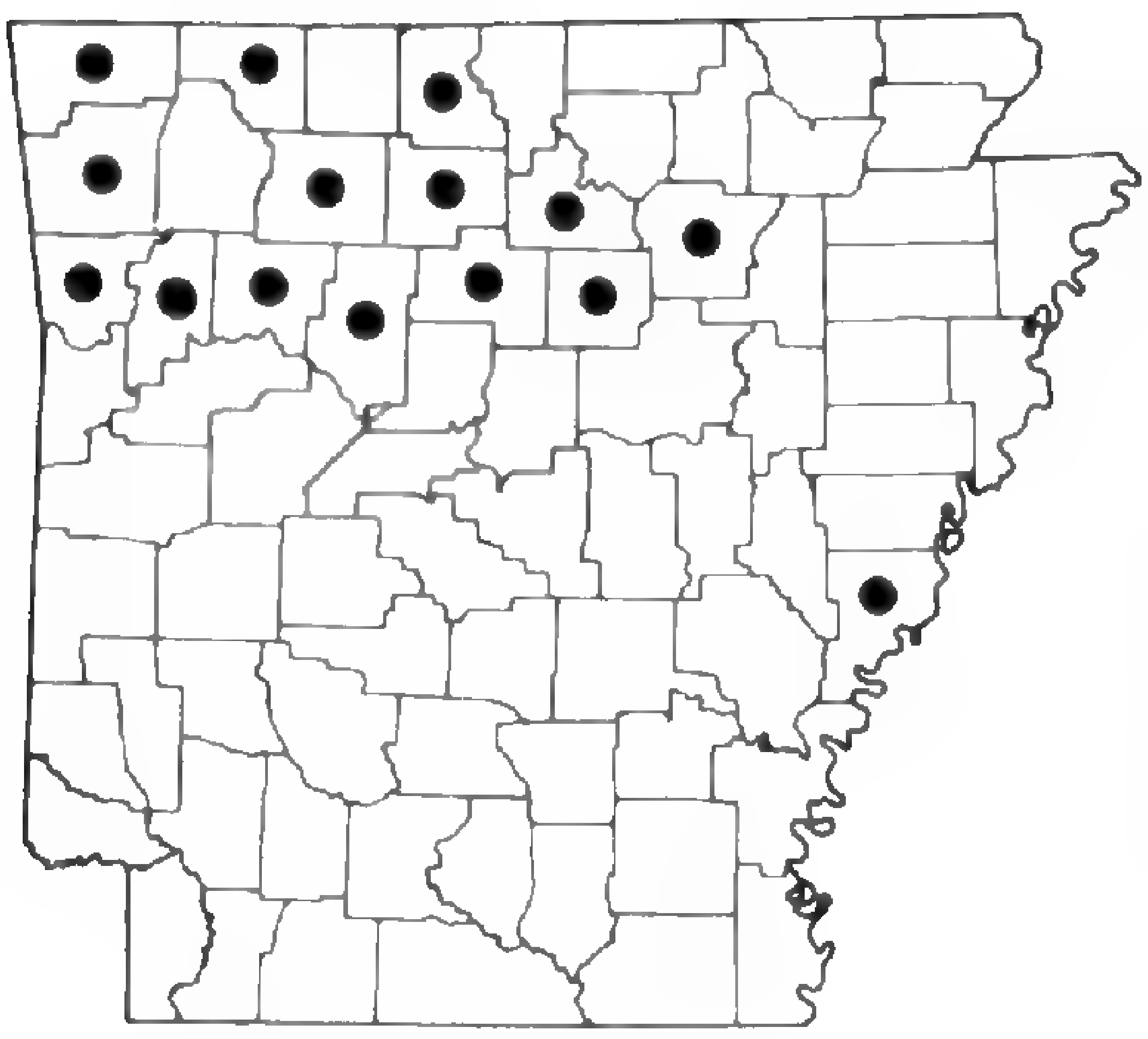
53. *Asplenium trichomanes*



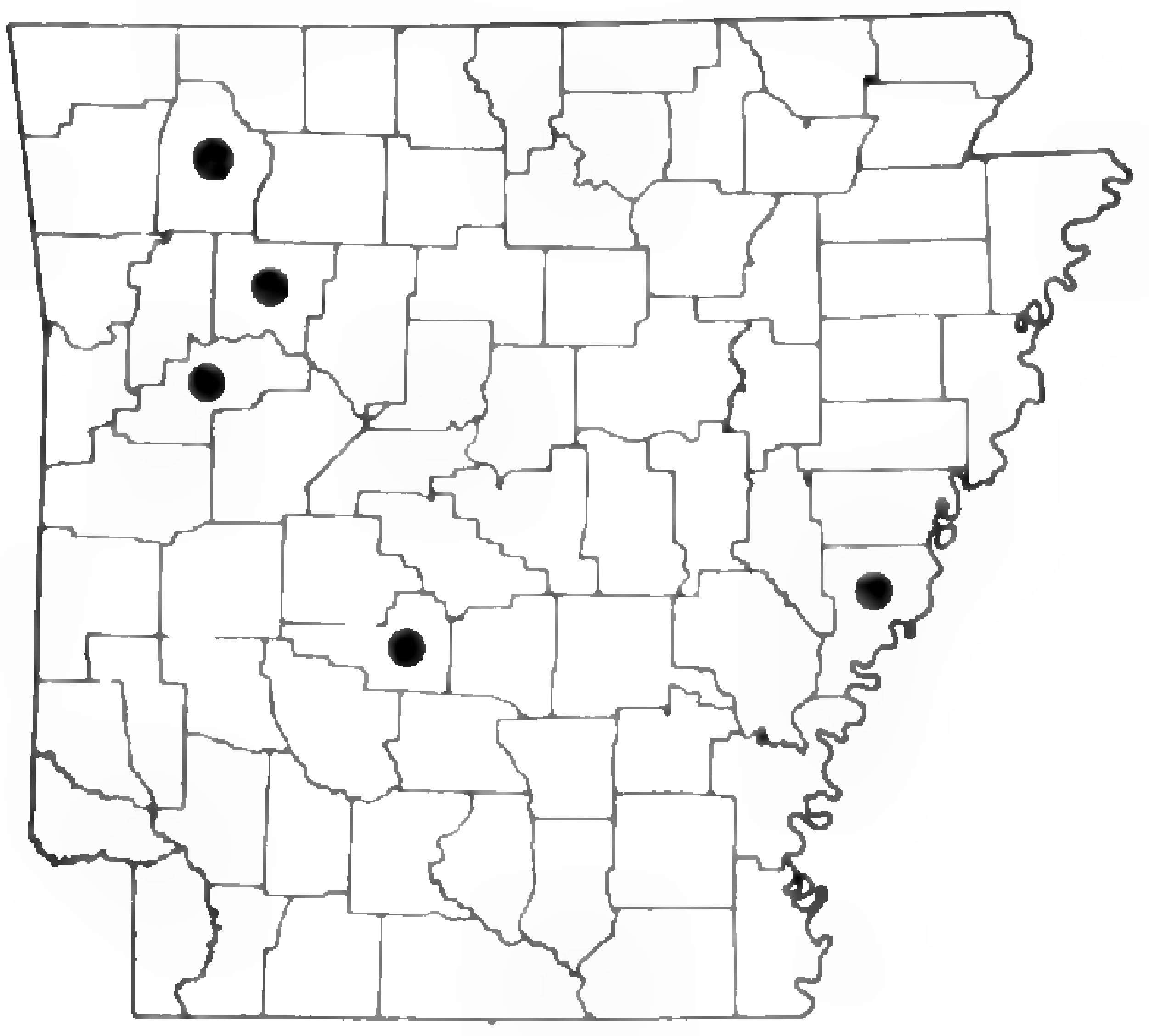
54. *Onoclea sensibilis*



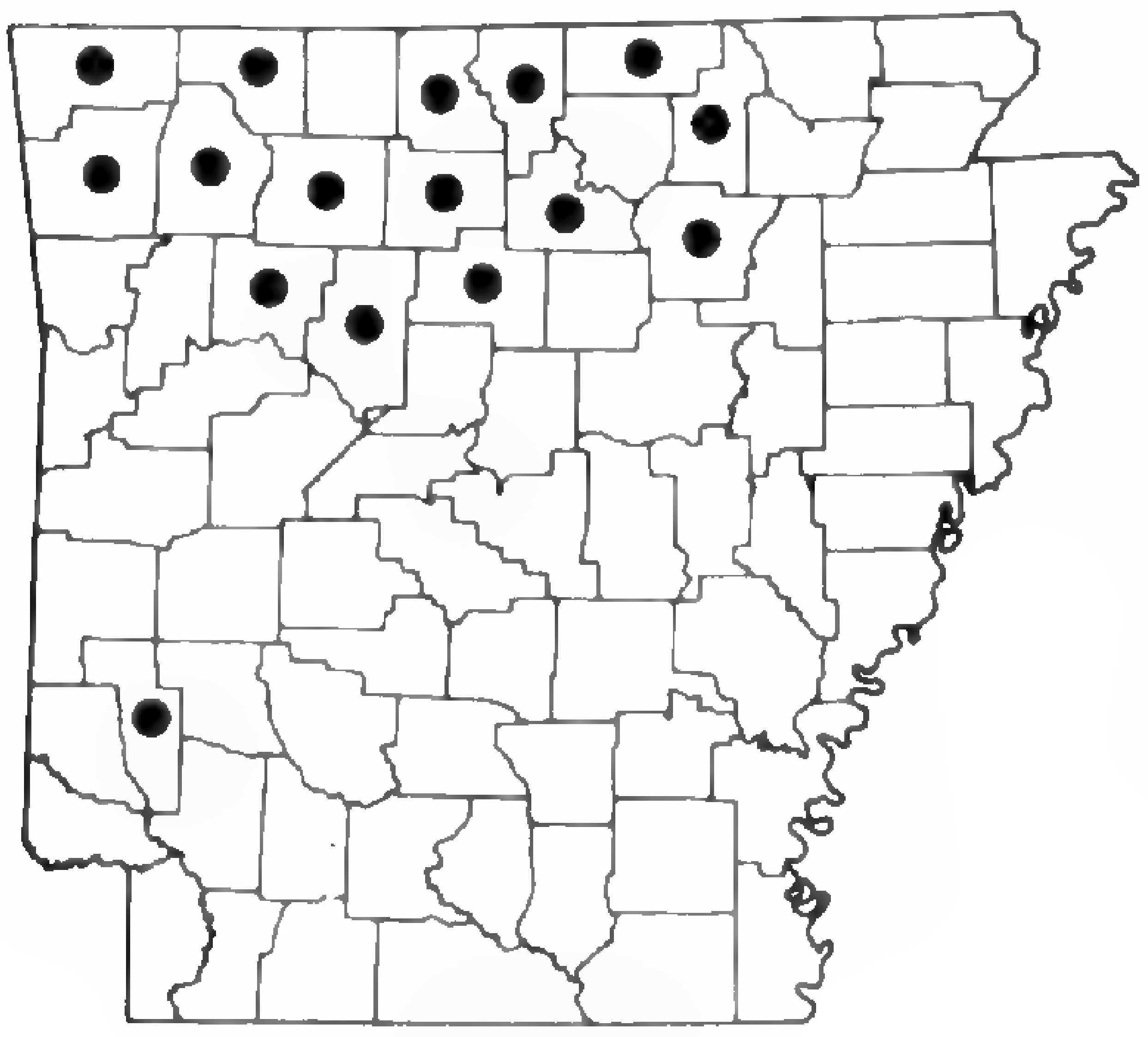
55. *Athyrium filix-femina* subsp. *asplenioides*



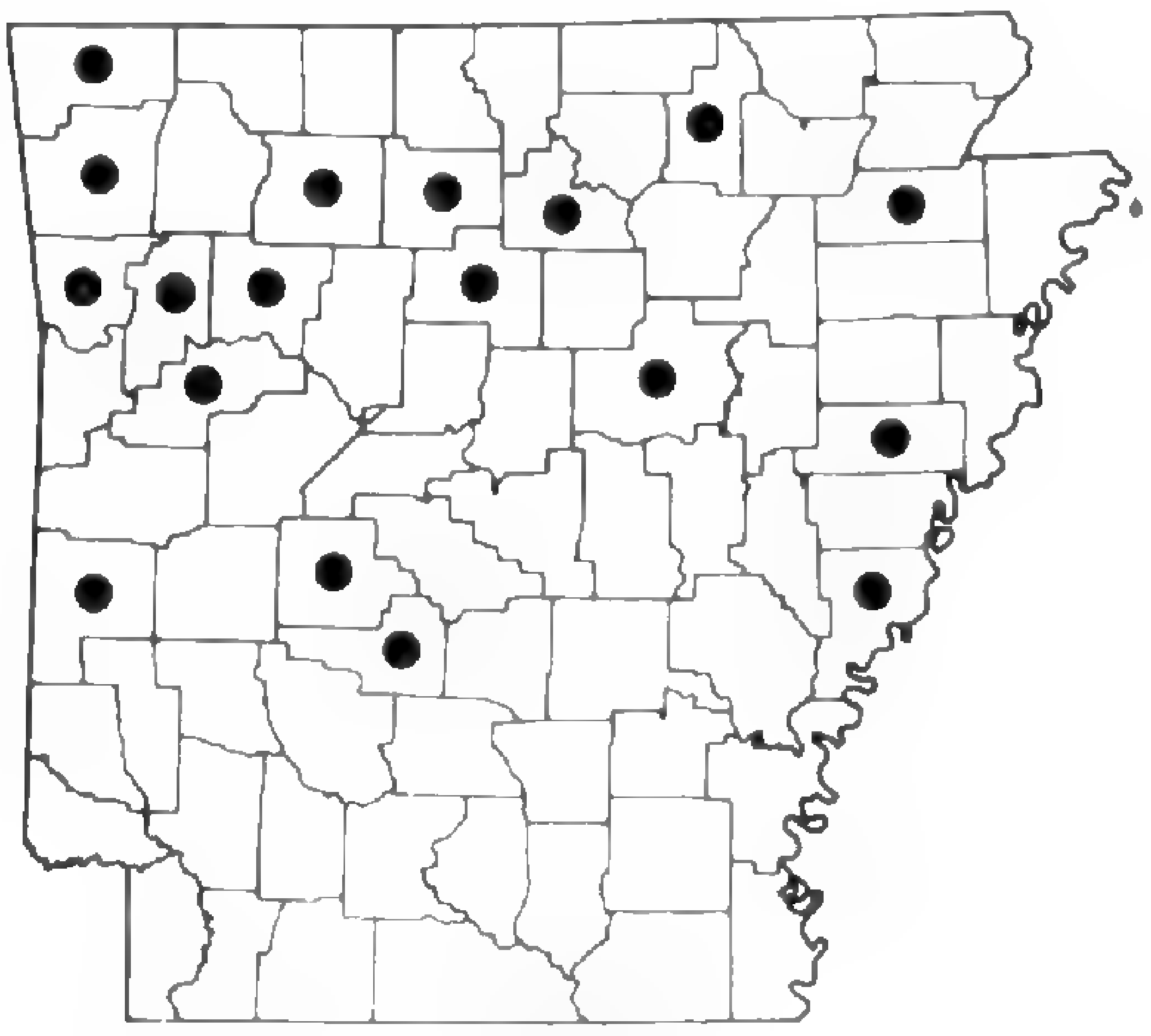
56. *Athyrium pycnocarpon*



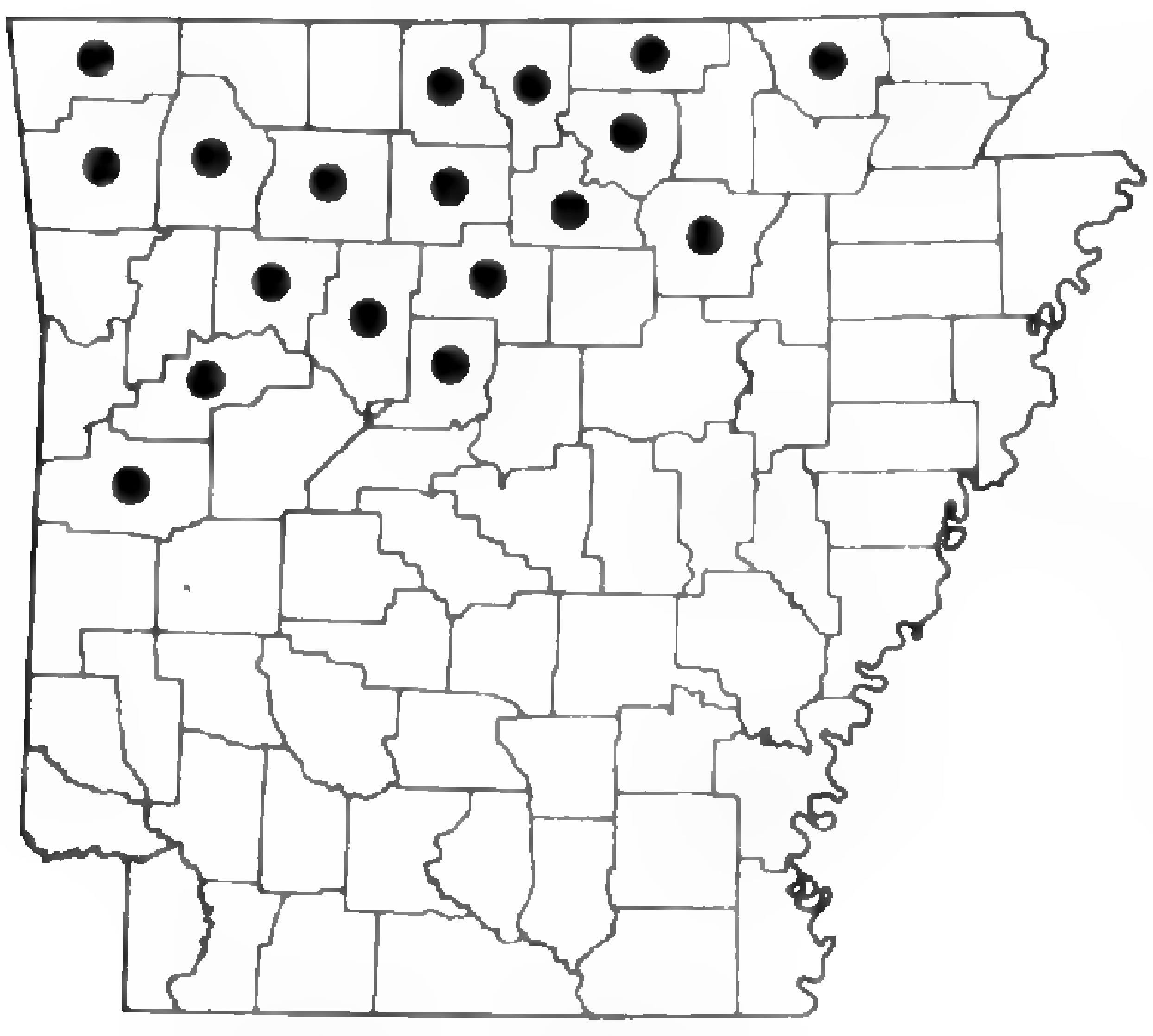
57. *Athyrium thelypterioides*



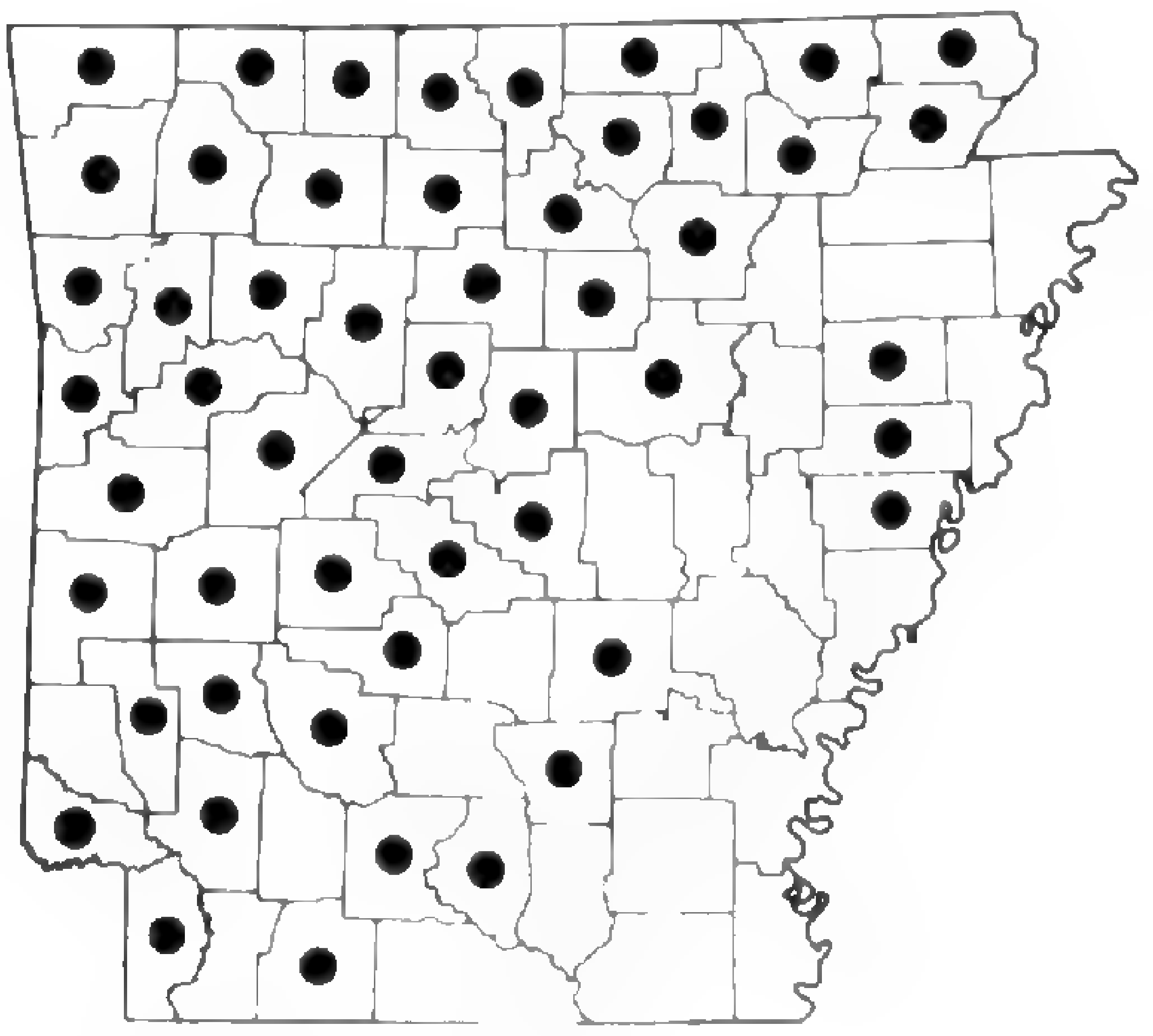
58. *Cystopteris bulbifera*



59. *Cystopteris protrusa*

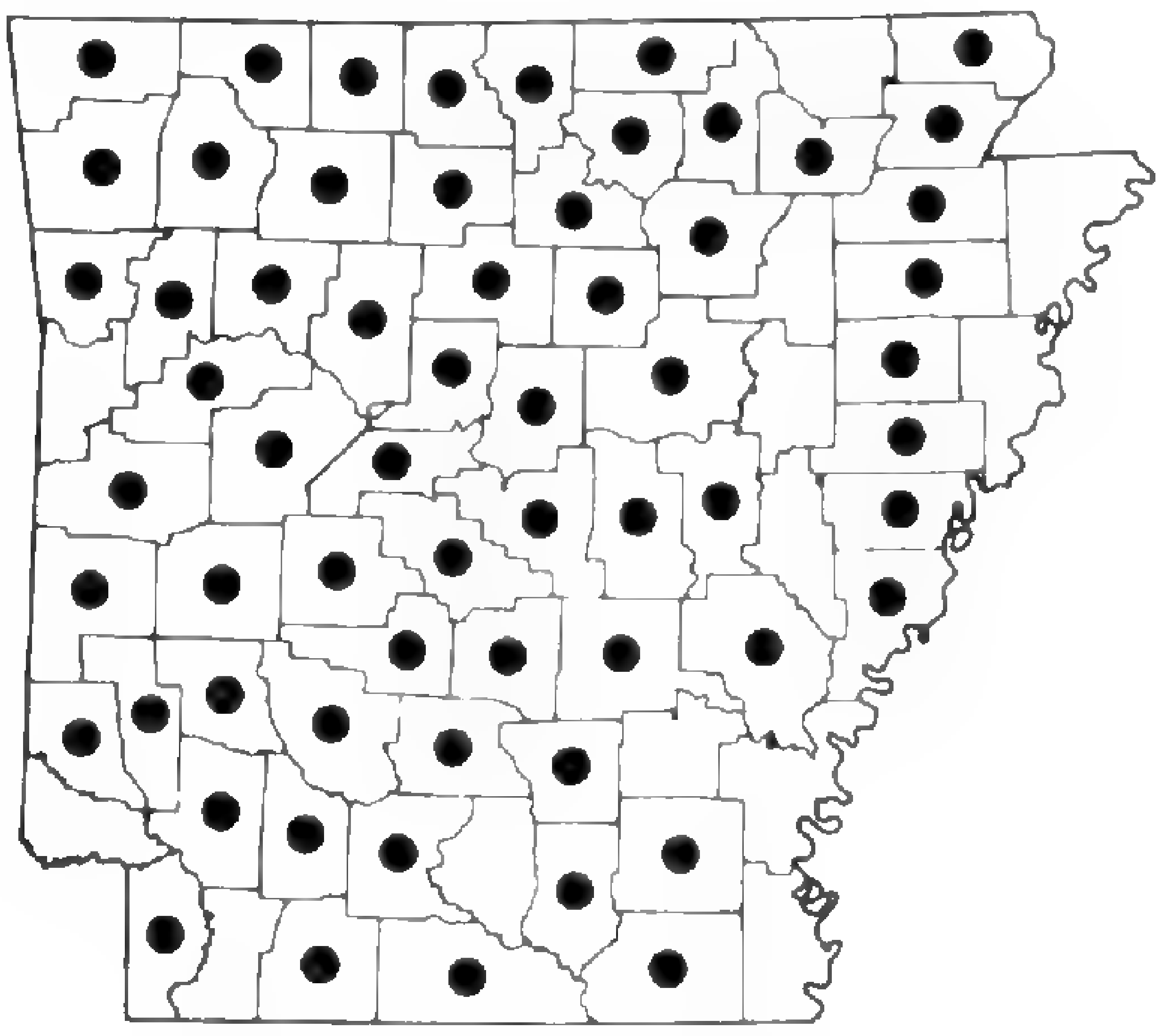


60. *Cystopteris tennesseensis*

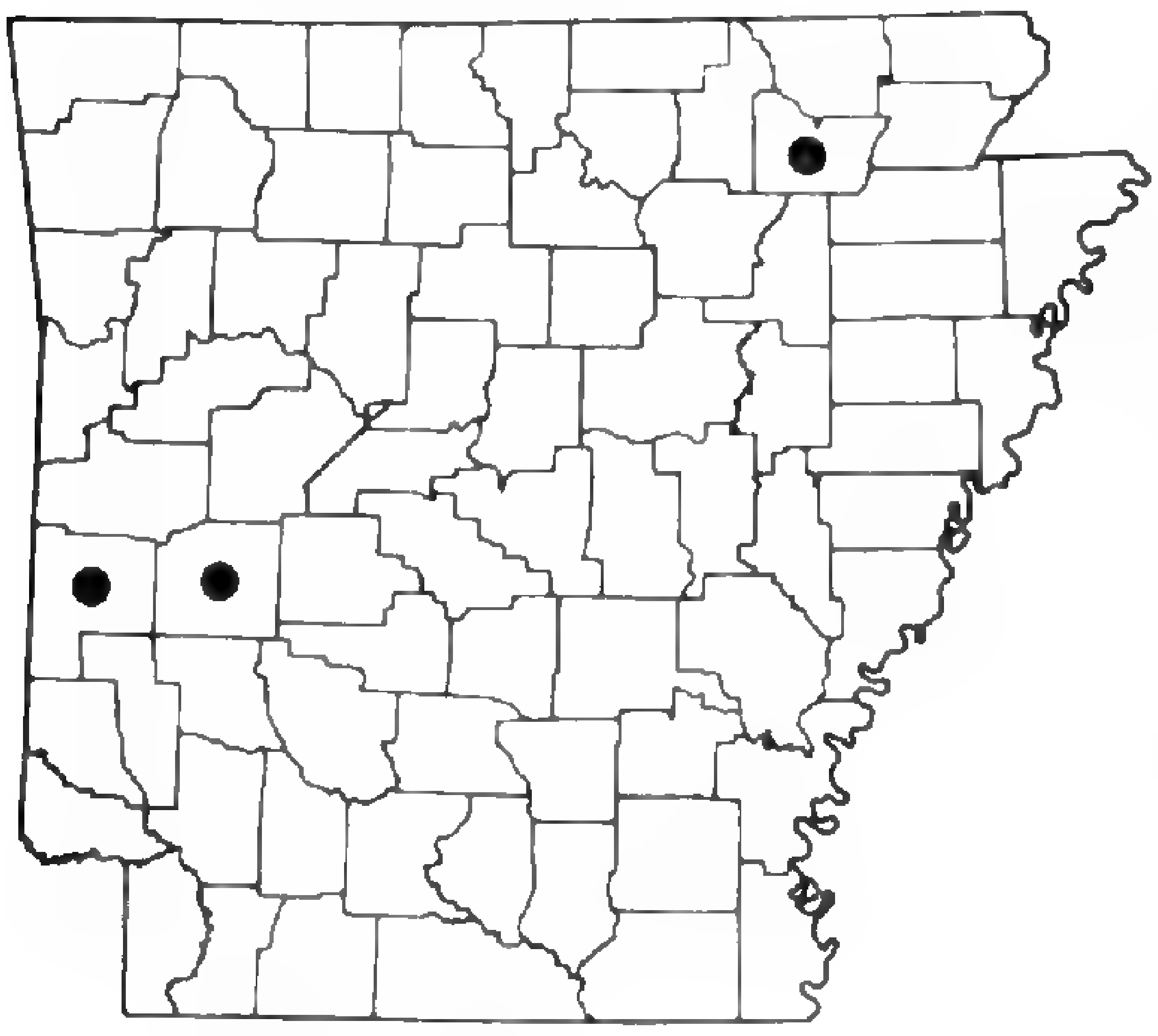


61. *Woodsia obtusa*

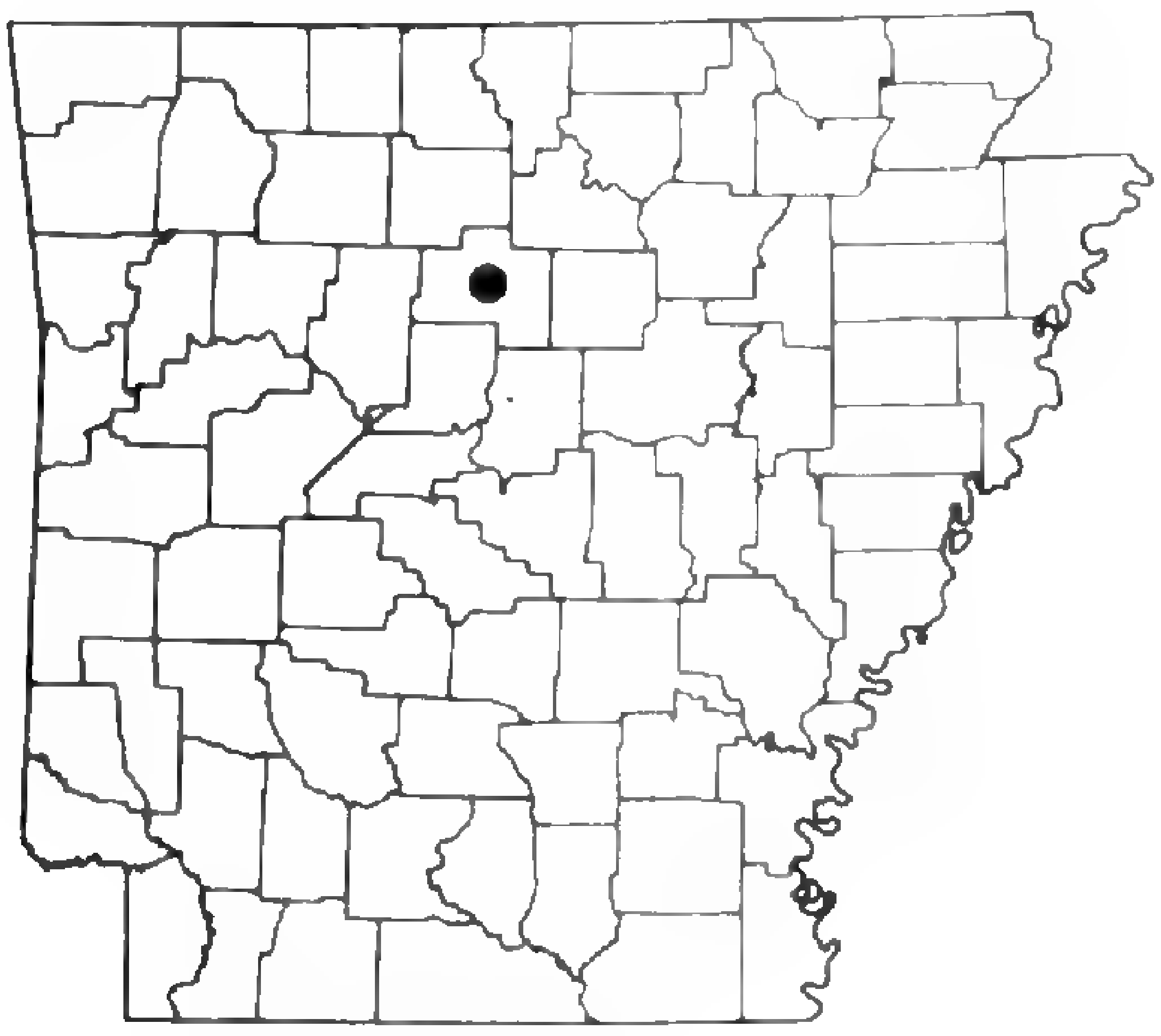
62. *Woodsia scopulina* var. *appalachiana*



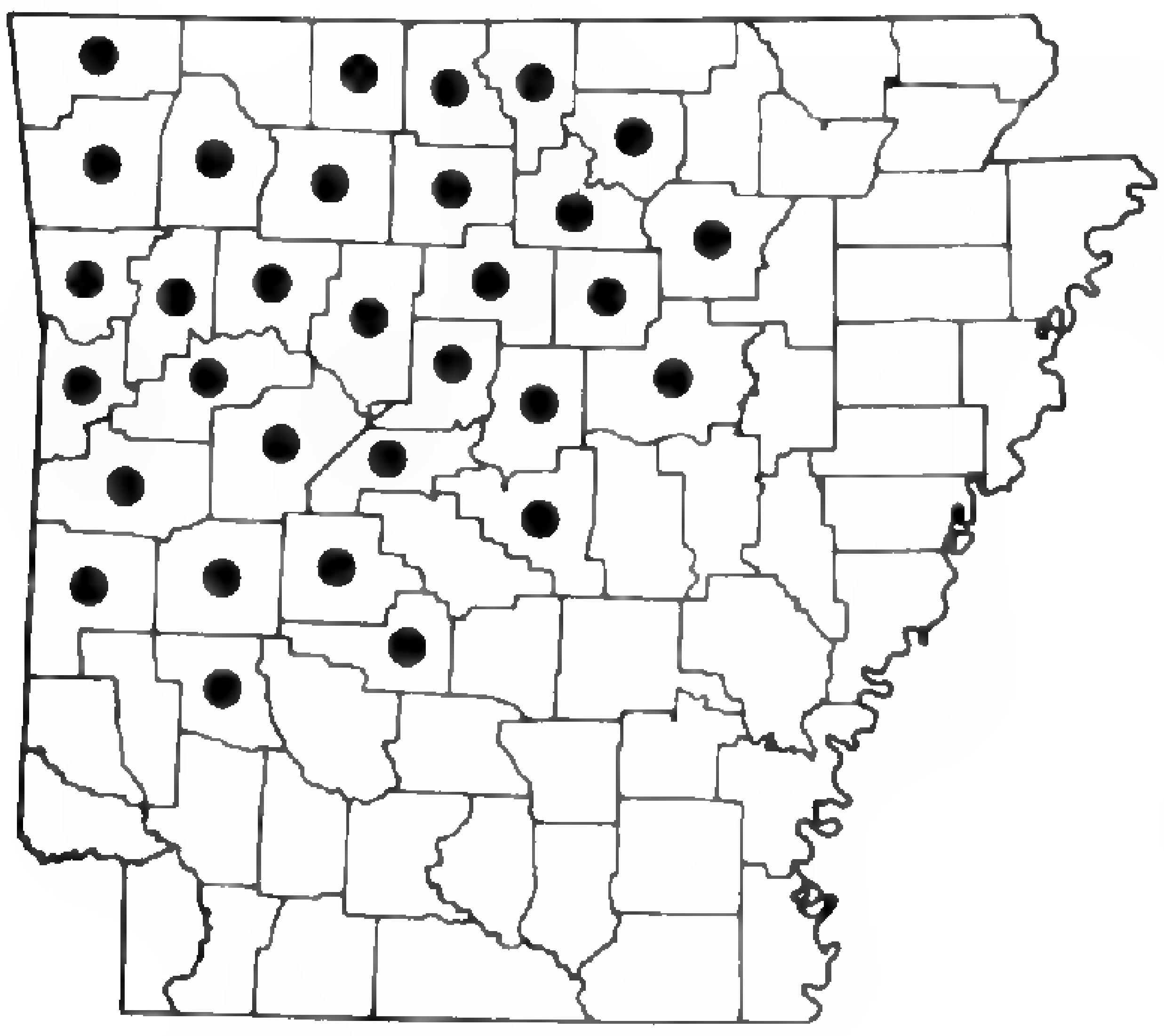
63. *Polystichum acrostichoides*



64. *Dryopteris celsa*

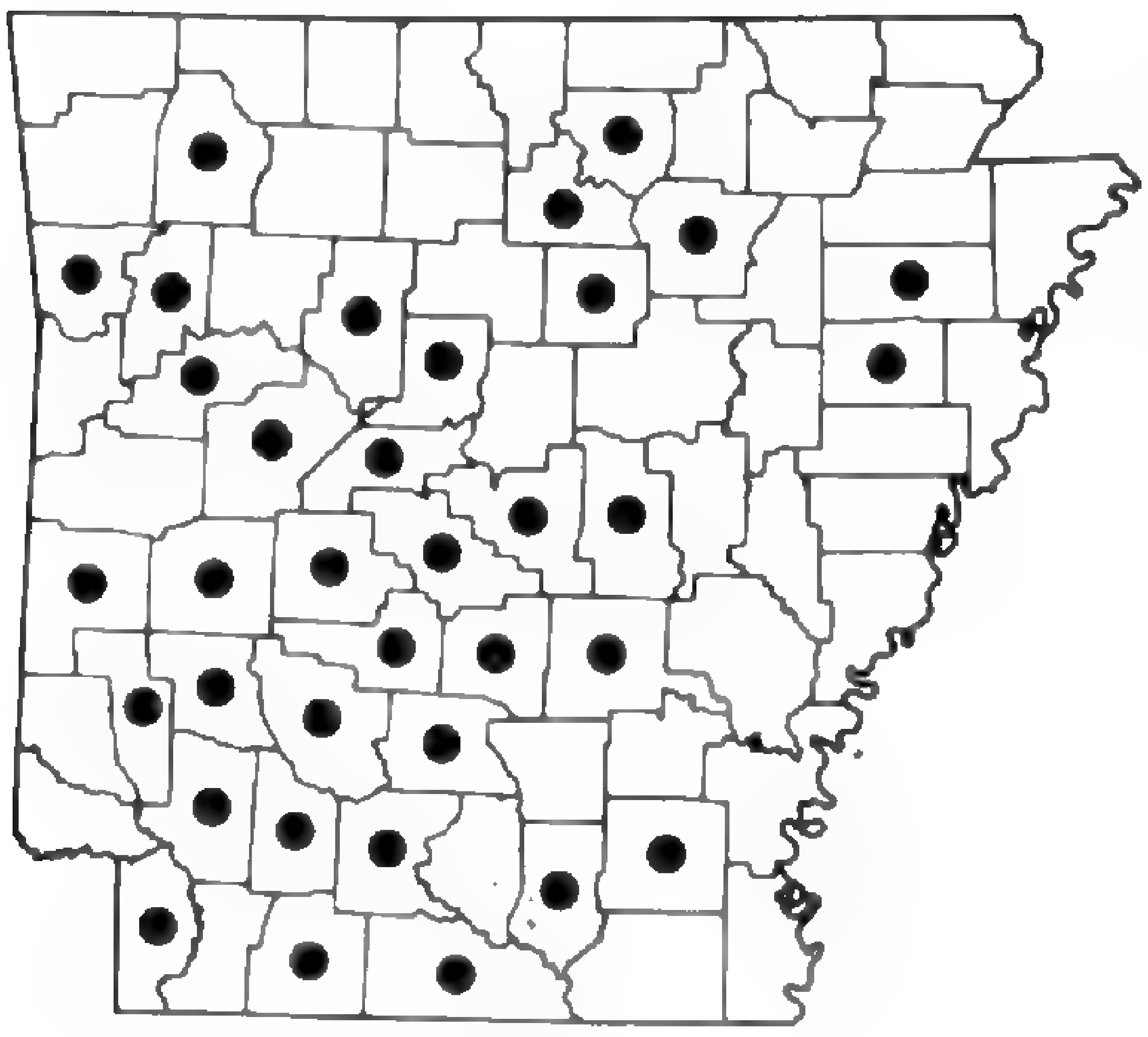


65. *Dryopteris X leedsii*

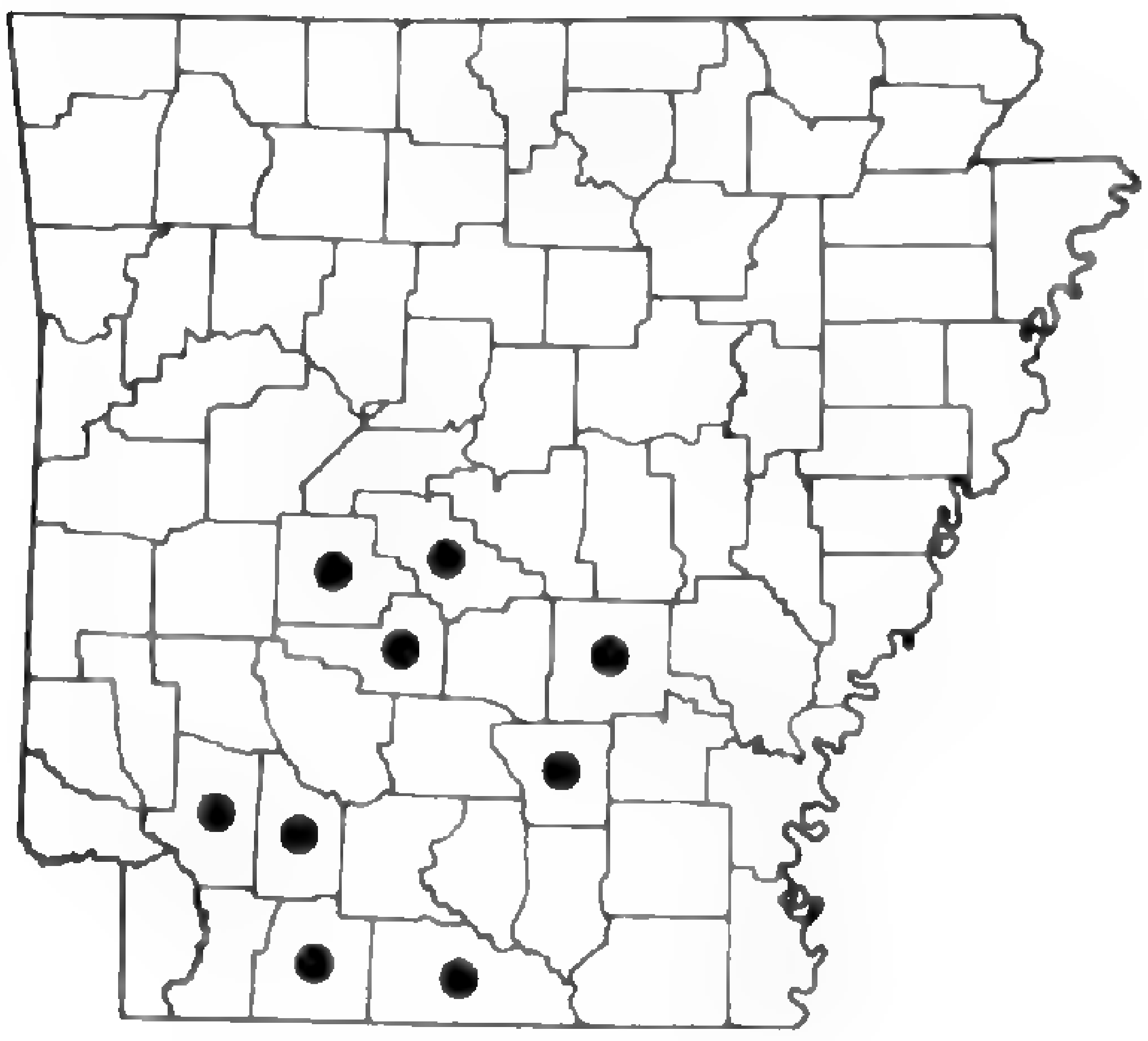


66. *Dryopteris marginalis*

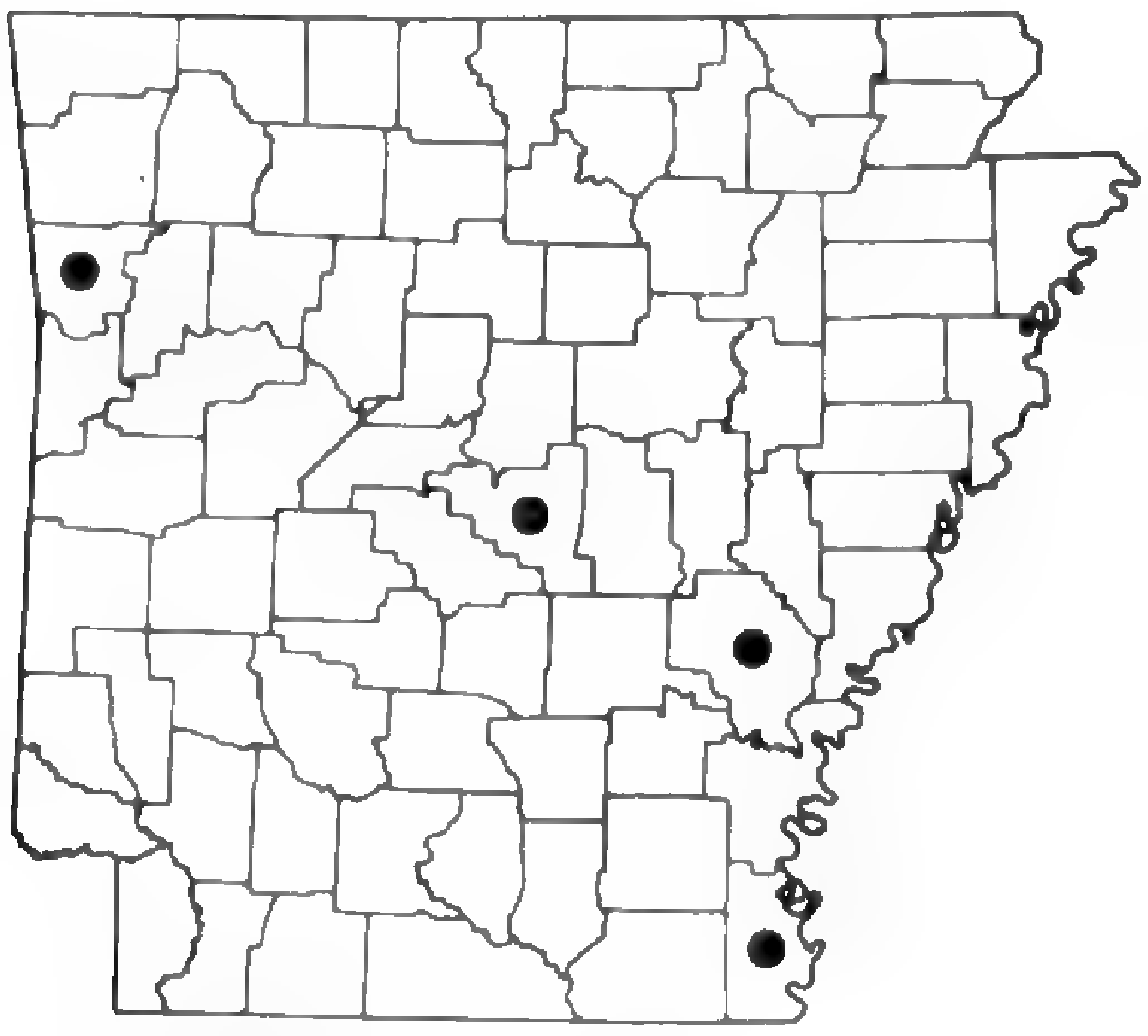
67. *Dryopteris spinulosa*



68. *Lorinseria areolata*

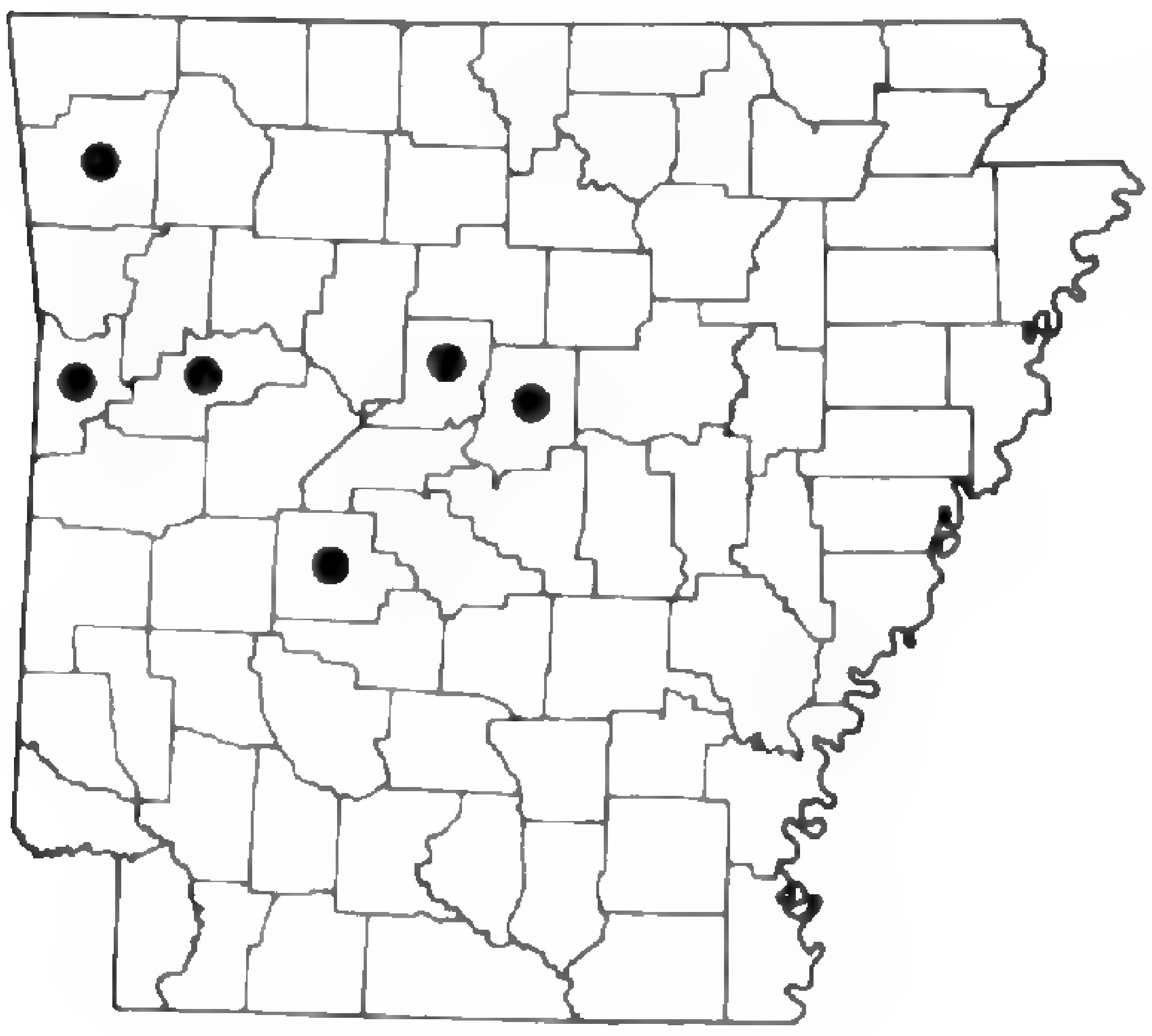


69. *Woodwardia virginica*

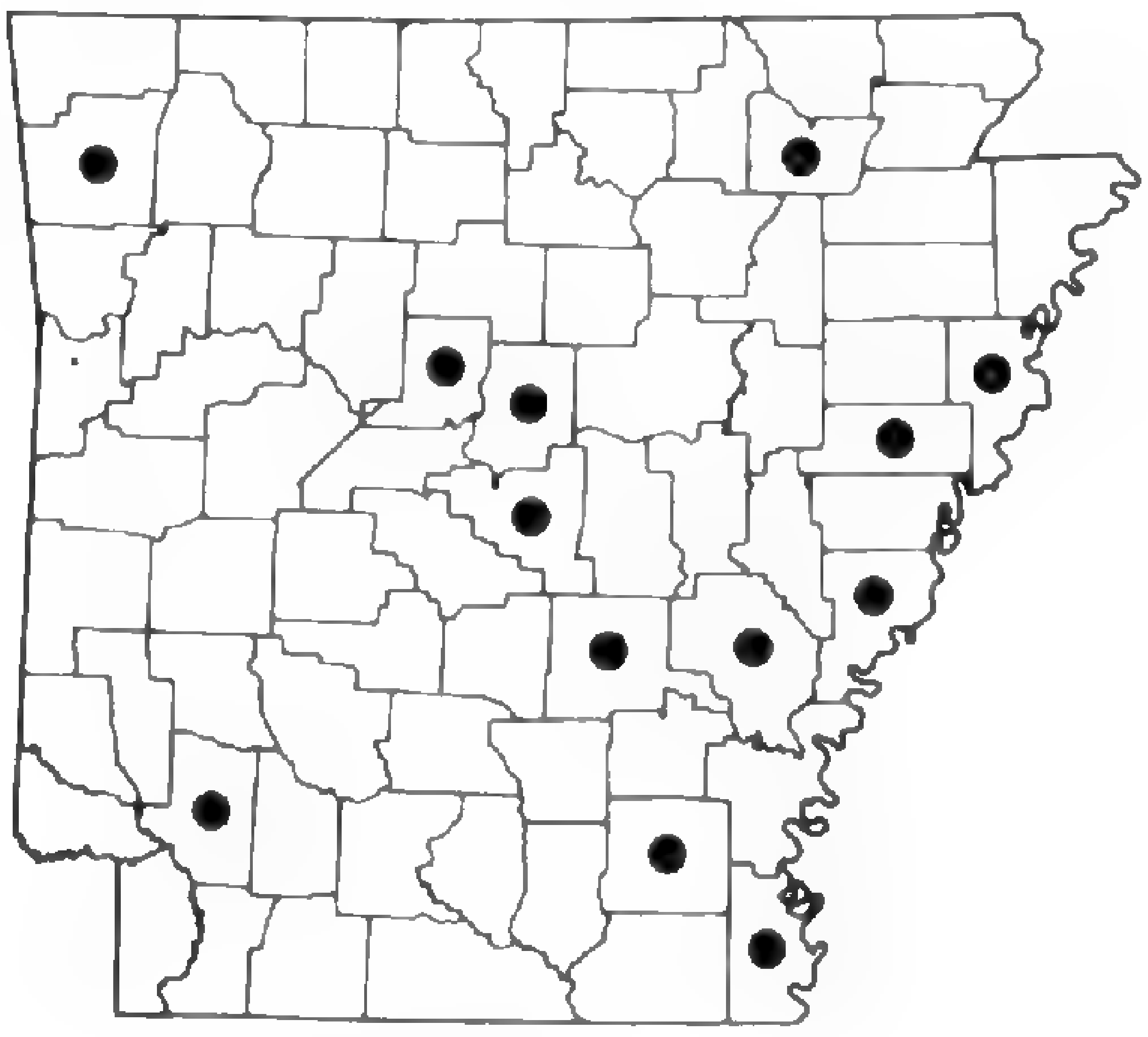


70 *Marsilea uncinata*

71. *Marsilea vestita*
var *mucronata*



72. *Pilularia americana*



73. *Azolla mexicana*

ACKNOWLEDGMENTS

We wish to express our gratitude to the many persons who have offered us assistance during the course of this study. Without their help this work would not have been possible. Thanks are due to Dr. Edward T. Browne, Jr., Dr. George T. Clark, Ms Beverly Gerdeman, Dr. Richard L. Hauke, Mr. David Johnson, Dr. James S. Key, Mr. Douglas Ladd, Dr. David B. Lellinger, Dr. William F. Mahler, Dr. Dan Marsh, Dr. Sidney McDaniel, Ms Aileen McWilliam, Dr. Robert H. Mohlenbrock, Dr. Dwight M. Moore, Dr. Jewel E. Moore, Mr. Ronald W. Pearman, Dr. Paul L. Redfearn, Dr. E. Leon Richards, Dr. Clarence B. Sinclair, Dr. Edwin B. Smith, Dr. Paul Somers, Dr. Robert G. Stolze, Dr. Jerry L. Taylor, Dr. R. Dale Thomas, Mr. Ralph L. Thompson. Dr. Gary Tucker, Dr. Warren H. Wagner, Jr., and Dr. Wallace Weber. We are also indebted to those unnamed individuals who have rescued our automobile on several occasions when we thought it was hopelessly lost in the mire. To have been blessed with the help and encouragement of so many, we are indeed fortunate.

LITERATURE CITED

Bowers, F., & P. L. Redfearn, Jr. 1967. *Lycopodium lucidulum* in the Boston Mountains of Arkansas. Amer. Fern J. **57:** 91–92.

Branner, J. C., & F. W. Coville. 1891. A. list of the plants of Arkansas. *In:* Annual Report of the Geological Survey of Arkansas for 1888. Vol. IV. Press Printing Co., Little Rock.

Buchholz, J. T. 1924. Notes on Arkansas pteridophyta. Amer. Fern J. **14:** 33–38.

———, & E. J. Palmer. 1926. Supplement to the catalogue of Arkansas plants. Trans. Acad. St. Louis **25:** 91–155.

Buck, William R. 1977. A new species of *Selaginella* in the *S. apoda* complex. Canad. J. Bot. **55:** 366–371.

Chandler, A. 1941. *Pteris multifida* in Arkansas. Amer. Fern J. **31:** 112.

Crabbe, J. A., A. C. Jermy, & J. T. Mickel. 1975. A new generic sequence for the pteridophyte herbarium. Fern Gaz. **11:** 141–162.

Farrar, D. R., & P. L. Redfearn. 1968. *Trichomanes petersii* in the Boston Mountains of Arkansas. Amer. Fern. J. **58:** 32–33.

Foti, T. L. 1974. Natural divisions of Arkansas. pp. 11–34 *In:* Arkansas Department of Planning, Arkansas Natural Area Plan. Little Rock.

Harvey, F. L. 1881. Classified list of the ferns of Arkansas with notes on the geographical range and habitat of the species. Bot. Gaz. **6:** 188–190, 213–215.

Holmgren, P. K., & W. Keuken. 1974. Index Herbariorum. Part I. The Herbaria of the World. 6th ed. Oosthoek, Scheltema, and Holkema, Utrecht, Netherlands.

Lesquereux, L. 1860. A catalogue of the plants of Arkansas. *In:* D. D. Owen. Second Report of a Geological Reconnoissance of the Middle and Southern

Counties of Arkansas Made During the Years 1859 and 1860. C. Sherman & Son, Printers. Philadelphia.

MOORE, D. M. 1940. Arkansas pteridophyta. Amer. Fern J. **30:** 105–119.

———. 1941. Some noteworthy fern communities of Arkansas. Amer. Fern. J. **31:** 63–71.

———. 1947. Further notes on Arkansas pteridophytes. Proc. Arkansas Acad. **2:** 69–70.

———. 1950. A new fern record for Arkansas. Proc. Arkansas Acad. **3:** 33–34.

———. 1951. Some new records for the Arkansas flora. Proc. Arkansas Acad. **4:** 61–63.

NUTTALL, T. 1821. Journal of Travels into the Arkansas Territory During the Year 1819 with Occasional Observations on the Manners of the Aborigines. Thomas H. Palmer, Philadelphia.

———. 1835. Collections towards a flora of the territory of Arkansas. Trans. Am. Phil. Soc. **5:** 139–160.

PALMER, E. J. 1924. Two interesting ferns from Arkansas. Amer. Fern J. **14:** 39–41.

SCULLY, F. J. 1937. Ferns of Hot Springs National Park and vicinity. Amer. Fern J. **27:** 59–62.

———. 1939. Ferns of Hot Springs National Park and vicinity. Natural History Journal No. **5.** Hot Springs National Park.

SMALL, J. K. 1938. Ferns of southeastern states. Science Press, Lancaster, Pennsylvania.

SMITH, E. B. 1978. An atlas and annotated list of the vascular plants of Arkansas. University of Arkansas, Fayetteville, Arkansas.

STEYERMARK, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames.

THOMAS, R. D. 1976. The distribution and habitats of seven species of Ophioglossaceae in the southern United States. (Abstr.) page 44 *In:* Botanical Society of America Abstracts of Papers. Allen Press, Inc., Lawrence, Kansas.

———, W. H. WAGNER, JR., & M. R. MESLER. 1973. Log fern (*Dryopteris celsa*) and related species in Louisiana. Castanea **38:** 269–274.

TRYON, R. M. 1941. A revision of the genus *Pteridium*. Rhodora **43:** 1–31, 37–67.

TUCKER, G. E. 1971. *Selaginella arenicola* ssp. *riddellii* in Arkansas. Sida **4:** 275.

WAGNER, W. H., JR. 1962. *Trichomanes boschianum* in Arkansas. Amer. Fern. J. **52:** 84–85.

WATERS, CAMPBELL E. 1903. Ferns. Henry Holt and Company, New York.

WHERRY, E. T. 1948. Remarks on the American Lady Ferns. Amer. Fern J. **38:** 155–158.

W.C.T.
DEPARTMENT OF BOTANY
MILWAUKEE PUBLIC MUSEUM
MILWAUKEE, WI 53233

D.D.
109 SOUTH AVENUE
HOT SPRINGS, AR 71901

THE DISTRIBUTION OF PINUS BANKSIANA LAMB. IN NEW ENGLAND AND NEW YORK

HENRY I. BALDWIN

THE NATURAL RANGE OF PINUS BANKSIANA

The range has been described in general terms by Sargent (1897), Bell (1897), and many others. Schoenike (1976) pointed out that jack pine has a southeast-northwest range of 4185 km in a belt up to 1600 km in width. It occurs over 23 degrees of latitude and 67 degrees of longitude. Fernald (1911, 1950) and Rudolf (1958) traced the northern limit from Nova Scotia and northern Quebec to the Northwest Territories at Lat. 65° in the McKenzie River Valley, and the southern boundary from Central Maine west to the Lake States, central Manitoba, Alberta, to northeastern British Columbia. Halliday and Brown (1943) published a map showing details of the range in Canada and suggested that the northern boundary is not limited by rainfall, but that it may be by temperature. Jack pine ceases to be found several hundred miles south of the northern tree limit, namely at the 14° C. July isotherm. Mirov (1967) stated that jack pine occurs in areas of warm to cool summers, very cold winters and low rainfall. It occurs farther north than any other pine. Critchfield and Little (1966) provided a more up-to-date map of the range. Schoenike (1962) surveyed the range in Minnesota.

Within such a wide range, provenance studies have shown clearly the existence of local races that are part of the continuum of clinal variation associated with climatic gradients. These have been reported by Rudolph et al. (1957), Williams and Beers (1959), Holst and Yeatman (1961), Schoenike (1962 & 1976, loc. cit.), Mergen and Worrall (1965), and Yeatman (1974).

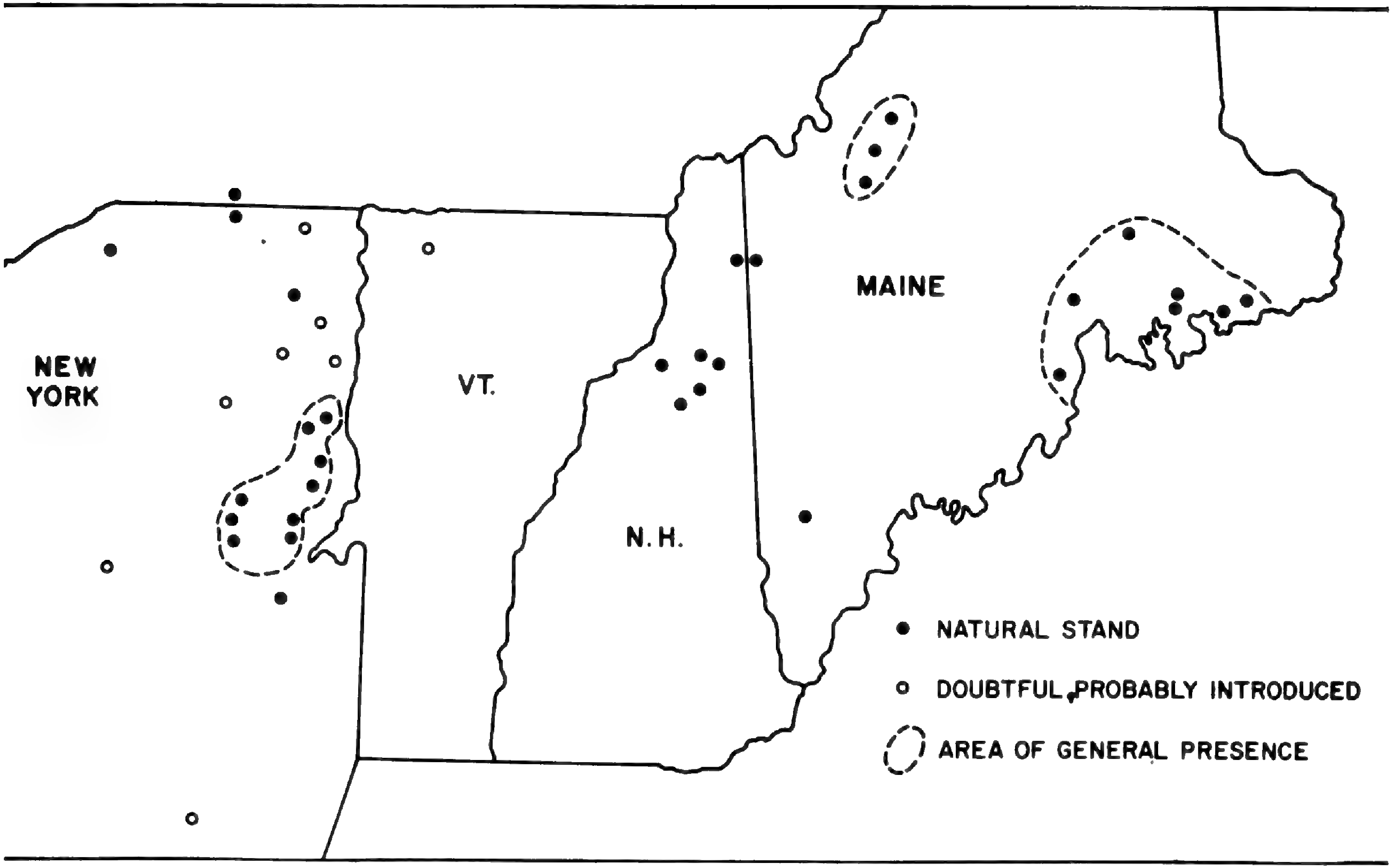
RANGE OF PINUS BANKSIANA IN THE NORTHEASTERN UNITED STATES

Range delimits the area within which naturally occurring trees are found. Fernald (1911, loc. cit.) defined the southern limit as a "line running from the east side of Penobscot Bay to the Rangeley Lakes, thence with a slight dip southward at the western edge of the White Mountains, and (then) across northern Vermont." The Vermont natural stands were thought to be extinct. The New York southern boundary probably would be a line from southern Essex County to northern St. Lawrence Co. The northern boundary would run through Clinton Co. to the northern tip of St. Lawrence Co. In New England the northern line might run from Jonesboro, Maine northwesterly to Jackman, and thence to Rangeley Lakes, and west across the central White Mountains. Steele and Hodgdon (1968) characterized the occurrence of jack pine as "infrequent in northern and central Maine, rare in northern New Hampshire and Vermont, usually on ledges".

Report of outliers beyond this narrow belt have been found so far to be introduced trees. The most famous was the report by Harshberger (1914) of jack pine on Nantucket Island, refuted by Bicknell (1916) who showed that the trees were planted along with many other exotics as early as 1847 and 1888. Jack pine reproduces naturally from planted mother trees ("established escapes") and this may account for some of the reports and herbarium records from outside its natural range. Bramble (1946) described a case in Pennsylvania where jack pine reproduced abundantly following a fire that destroyed a mixed plantation containing a small proportion of jack pine. Weatherby et al. (1926) referred to jack pine as a local species in New England, with 5 stations on the coast of Maine, the Dead River Valley (Me.), Lake Umbagog, Thornton, N.H. and the headlands of Lake Champlain, "all, it will be noted, at low elevations".

The natural range was determined from (1) published accounts, (2) herbarium records, and (3) on the ground examination. It was difficult to separate introduced or "established escapes" from truly natural indigenous populations. Lowland and southern stations were suspected of consisting of introduced trees. Trees growing on high mountain ledges or rocky lake shores are unlikely to have been brought in by man. Where there is no convincing evidence of origin, no firm decision can be made. No records of natural stands in Connecticut or Rhode Island have been found. The investigation was made chiefly from 1958 to 1961. The present recorded distribution is shown in Fig. 1.

Figure 1. Stations for *Pinus Banksiana* Lamb. in New England and New York.


NEW YORK
VT.
N. H.
MAINE
● NATURAL STAND
○ DOUBTFUL, PROBABLY INTRODUCED
AREA OF GENERAL PRESENCE

NEW YORK

Many of the general range maps (e.g. Hough, 1936; Munns, 1938; Little, 1971) showed all of northern New York in the range of jack pine. Actually it is limited essentially to Essex and Clinton counties and is very spotty in occurrence. Sargent (op. cit.) mentioned the Adirondacks, but he was evidently generalizing. Little (1953) and Rudolf (op. cit.) stated that it occurred up in the Adirondack Mountains to 610 m. Hough (op. cit.) included a picture of a jack pine in Essex County. Blakeslee and Jarvis (1911) traced the range through northern New York. Sears (1881) probably first pinpointed the locations at Altona, followed by Peck (1898) and House (1924). Littlefield (1928) gave detailed descriptions of natural jack pine stands. He described an interesting mixture of *Pinus Banksiana, P. rigida,* and *P. resinosa* near the village of Clintonville, Essex County. He termed jack pine quite common elsewhere in the Ausable River valley from Ausable Forks to Upper Jay. This is not far from the well-known stand in Wilmington. Pratt and Littlefield (1938) reported the discovery in 1931 of a group of jack pines on a sandy knoll on the east bank of Deer River in the Town of Brasher, St. Lawrence Co. This was within a mile of the Brasher Iron Works at an elevation of 73 m, 80 km west and northwest from the nearest stations in Altona and Wilmington. It was formerly thought to be limited to the counties mentioned, but Littlefield (1960) enumerated other stations such as New Russia on the Bouquet River, Wainwright Mt. and the northern spur of Poke-O-Moonshine Mt. at 457 m, all in Essex County. In Clinton County he reported it at Flat Rock near Schuyler Falls and Altona. A new station near Ellenburg Depot on both sides of the Canadian boundary was reported to Pratt and Littlefield in a personal communication from Frére Marie-Victorin (University of Montreal). This location was subsequently visited and reported by Littlefield (1960, 1962).

Sears (op. cit.) made some interesting observations on jack pine in New York. He called it quite a rare tree in New York, with "seldom more than four or five growing within 10 miles of each other". . . . "Solitary ones are more common." . . . "As to size, they are seldom over 8 feet high, although one was found in Altona 15 feet high and 8 inches in diameter, but this tree was partially decayed."

"This tree is known as the unlucky tree by the inhabitants. The more observant ones call it a cross between a pine and a spruce. It is considered dangerous to pass within 10 feet of its limbs, and more so to women than to men. It is equally dangerous to cattle. So that whatever ill befalls a man, his family or his cattle, if there is one of these trees on his land, it must be destroyed — burned down by wood being piled around it — for no one would venture to cut it down." This was also quoted by Sargent (op. cit., p. 149). No one has suggested this superstition as a reason for the rarity of jack pine, or its presumed disappearance from places where it formerly grew.

VERMONT

Older range maps show the range of *Pinus Banksiana* covering northern Vermont (Hough, op. cit.; Munns, op. cit.), some almost one-half the state. However natural stands appear to have been very rare. Sargent (op. cit.) stated that about 1860 a small grove was found near Ferrisburg in Addison County by Rowland E. Robinson of Ferrisburg. Blakeslee and Jarvis (loc. cit.) reported jack pine at Monkton and Starksboro, Addison Co. and at Fairfax in Franklin County. A few trees were found at each station on rocky slopes and on sandy soil. The same stations were listed by Burns and Otis (1899, 1916–1924). Little (1953, op. cit.) and Rudolf (op. cit.) state that it was local in occurrence in Vermont. Seymour (1969) listed only Farfax in Addison County. Schoenike (personal communication, 1959) was unable to locate any of the stations in Vermont. Recently, Little (1971, op. cit.) showed on his range map crosses indicating that he believed jack pine to be extinct in Vermont. However, Professor H. W. Vogelmann of the University of Vermont reported to me that one of his students had brought in a specimen on March 31, 1977 from a stand near Hygate Center, east of Swanton on Route 78. I visited this station in May 1978 and found several small groups of jack pines from small saplings to trees 30 years old. I interviewed several residents of the area, and concluded that all the jack pines had originated from a 50-year mixed conifer plantation that contained a few jack pines.

MAINE

This species is much more widely distributed and more common in Maine than in other Northeastern states. Rand (1889a, 1889b) reported it on the coast. Hyland (1946) called it "frequent locally, and rather plentiful on barren, sandy or rock soils in central and eastern Maine, and apparently absent from other sections." Blakeslee and Jarvis (loc. cit.) reported it from Traveller Mts. and Grand Lake. Fernald (1911, loc. cit.) described the southern limit as a line running from the east side of Penobscot Bay to the Rangeley Lakes. Peirson (1951) gave the most southern point as Ossipee Mt. in Waterboro. Coburn (1920) gave detailed descriptions of large stands near Attean Lake. Seymour (1969, loc. cit.) mentioned Orrington, Heron Lake and Jonesport, and Ogden et al. (1948) listed seven counties where it is found. Norton (1913) found it on the coast and on islands and Pike and Hodgdon (1963) found it on Great Wass Island.

MASSACHUSETTS

A number of specimens collected in Massachusetts are to be found in herbaria. Many of these were found in the vicinity of Boston, and either are noted by the collector as coming from planted trees, or are suspected of being non-indigenous. The late Dr. Stuart K. Harris collected from a number of places in the state. In his Flora of Essex County, he listed *Pinus Banksiana* under "species exclusae" because it was probably introduced. Other noteworthy collections include a specimen in the herbarium at Clark University from Uxbridge, described by the collector as coming from "a large colony, from seedlings to large trees; both sides of the Quaker Highway, possibly an established escape". The University of Massachusetts herbarium contains one from Deerfield, "Pole Swamp Road, below the shack". The long-standing conclusion by Fernald and others that *Pinus Banksiana* was limited to northern New England and New York casts doubt on these reports from southern New England. However, they demonstrate that jack pine becomes established easily where the habitat is congenial. Russell R. Walton has recently told me of several small stands on Martha's Vineyard. These were probably introduced originally, but now have escaped and become established.

At the invitation of Mrs. Mary Walker of Concord, Mass., I visited the so-called Smith Grant area in Southern Winchendon; there are several hundred jack pines growing in an area of about 5 acres around a cranberry bog and on adjacent eskers and hillsides. The pines range from small saplings to trees which are 50 ft high, 12″ in diameter, and about 50 years old. There are also some stunted, crooked, branchy trees. How the seed reached the area is a mystery;

Mr. Lambert, of the Mass. Conservation Department, suggests that it might have blown from a plantation on the Otter Brook State Forest, but why pine did not colonize intervening areas cannot be explained.

NEW HAMPSHIRE

Jack pine is the rarest natural pine, occurring in several isolated mountain stations in the White Mountains and along the shores and on some islands in Umbagog Lake. Discovery of jack pine seems to have been recorded earlier than in most other states. Huntington (1884) reported: "There was also found on Welch Mountain the gray scrub pine *Pinus Banksiana*. This thought to be farther south than any point where it has been previously seen." Following this, Sargent (loc. cit.) mentioned Welch Mountain as the only station in New Hampshire as did Fernald (1919): "In New Hampshire the species is only on Welch Mountain, a sterile granite mass south of the syenitic Franconia Range."

Welch Mountain, Waterville, 790 m

This is not only the largest assemblage of jack pines so far discovered in New Hanpshire, but the earliest reported. Pychowska (1891) wrote "My sister, Miss Edith W. Cook, found sundry stunted specimens of *Pinus Banksiana* on the mountain top August 9, 1881." Miss Cook was an active botanist in the White Mountains at that time. It is significant that she found only "sundry stunted specimens" indicating that there were very few trees there. Foster (1931–1946), a citizen of Waterville, wrote of jack pine: "On Welch Mountain, Waterville, there are low clumps of it near the summit." Perhaps Foster was referring to conditions he saw on an early ascent. He was an active climber, and must have climbed Welch Mountain many times. The population increased with passage of time. Jenks (1934) stated that Edward W. Littlefield had told him that the pine had spread from the few trees seen by Cook and by Littlefield in 1923 to a large stand at that time. By 1950 the whole upper part of the mountain had become abundantly sprinkled with jackpine wherever a crack in the rocks afforded a root hold. This may be taken as evidence that the number of trees and the area occupied have increased. The cause may lie in the fact that the mountain offers so much bare area for exploitation. There are as yet few competitors. Spruce has taken over the sheltered hollows, along with some white pine, but jack pine is not hindered elsewhere. The entire summit and the eastern and southern flanks of the mountain down to the top of the steep cliffs on the eastern side are now covered by this species. There is an almost pure stand of jack pine on the summit where it was first reported.

The mountain must have been swept by a severe fire many years ago that completely destroyed all soil. Thomas Starr King (1862), probably referring to observations several years previously, refers (page 94) to Welch Mountain as "being nearly destitute of forest covering, and showing large masses of bare quartz (sic.); it presents very beautiful and striking harmonies of the grays and neutral hues of blue and white and at sunrise and sunset exhibits proportional increase of splendor."

The only fires of record are one in 1933, and possibly one in 1923. Revegetation after the original fire is still progressing rapidly as demonstrated by young spruce and white pine on the rocks of nearby Dickey Mountain. Many of the older jack pine on Welch Mountain are leaning or have prostrate stems, possibly felled by the 1938 hurricane, since they are slanted toward the northwest. These have remained alive because part of the root system remained in the soil or cracks in the rock, and now side branches have grown into erect trees. Cones are still borne on twigs in contact with the bare granite, or slightly above it. These may be subject to high temperatures in summer, high enough, it may be, to open the cones and release seeds more plentifully than before. Schoenike (1959 personal communication) sampled 20 trees on Welch Mountain and found that they were predominantly of the open cone type, common in southern populations as shown by Schoenike (1976, op. cit.).

Dickey Notch, Thornton 520 m

While following the open rocky ledge southwest from the top of Dickey Mountain on October 8, 1958, I discovered a single tree on the edge of the cliff above Dickey Notch. It was a small tree about 20 years old and may have originated from seed blown from Welch Mountain over a mile to the east. It is noteworthy that no jack pine was found in the intervening area, nor on Dckey Mountain or on the ledges to the westward. (Baldwin 1961)

Bog Pond, Lincoln, 750 m

On July 11, 1975, Mr. Frederic L. Steele's son discovered one tree "about 13 years old in a swampy area under the power line and south of a shack". (Steele, personal communication, 1977). Specimens are in Mr. Steele's private herbarium.

Carter Ledge, Mt. Chocorua, Albany, 700 m

The trees occur in a limited area of open ledge about 1.6 ha in extent. Bare granite ledges slope rather steeply to the southwest. The trees seem to have been discovered August 31, 1935 by Arthur C. Comey. The following day Alexander Lincoln collected specimens. Comey (1936) published an account of the station with a photo taken by Lincoln. It appears that jack pine became established here after a fire over 100 years ago consumed all the original soil. Some of the trees grew in cracks in bare rock on the summit ridge; a few were mingled with red spruce and white pine on a thin duff soil that accumulated on the bedrock.

About 100 trees were found in the area; most were bent, depressed and crooked, typical of timberline trees in exposed locations. Some were once erect but had become bent by ice and snow. The only straight specimens were on the ridge top mixed with spruce. One of these measured 15 cm at breast height and showed 65 annual rings at that point in 1958. A deformed and nearly prostrate tree near the top of the ledge was 20 cm in diameter and had 45 rings. Nearby a tree about 1.5 m high had 27 rings at the stump. This suggests that it takes a long time to reach breast height (1.3 m) on this adverse site. If jack pine invaded the area soon after the fire, it has evidently reproduced actively since. There were numerous small seedlings in cracks in the rock. On the other hand it is questionable if the species is now increasing, since red spruce and other trees and shrubs are encroaching on the pine. Away from the open ledge jack pines were already overtopped by spruce.

Mt. Webster, Hart's Location (Three separate stations)

This great west-facing wall rises abruptly above Crawford Notch and extends more than two miles north and south. There are smooth steep slides and equally steep talus slopes of more recent origin. The intermediate areas support stands of small spruce trees, paper birch and other northern hardwoods.

Station 1, 915 m This single tree was discovered by Steele and Lincoln (Steele 1954) on November 13, 1953, the first found in this area. Crossing the Saco River considerably upstream from the Willey Site they followed a steep couloir almost to the top of the ridge. Descending slightly they saw a single tree on the slope above and to the northwest of them. It was about 5 m high and the trunk was ellipsoidal in cross section just above the ground level with diameters 9–14 cm. There was no other vegetation in the area.

Station 2, 900 m While looking for this tree in October 1961, I found an "island" of vegetation about 5 × 7 m, halfway up the cliff on a very steep slide. This contained five jack pines 5–15 cm in diameter at breast height. One was apparently very old with a prostrate stem, bent down by avalanches, from which a curiously deformed branch of elliptical cross section supported long creeping branches spreading over the rock. Associated plants on this "island" were an interesting mixture of northern and southern taxa: *Vaccinium Vitis Idaea* var *minor, Potentilla tridentata, Ledum groenlandicum,* and northern trees; also warm site or southern species *Cornus alternifolia, Quercus rubra, Tsuga, Juniperus, Arctostaphylos, Rubus,* and *Thalictrum.*

Station 3, 976 m Searching the slope farther south, I found a rather large stand near the summit of the cliffs south of a newly formed avalanche gully of talus, across from the Willey Site State Park. I estimated the stand to contain no less than 500 trees (Baldwin, 1961, op. cit.). Increment cores taken at stump height showed that the trees ranged from 70 to 96 years old. Trees were 15–30 cm at breast height and 3.7–12 m high.

Lake Umbagog, Errol, Coos County, 380 m

This has been a favorite collecting ground for botanists, but few have identified the place of collection accurately. Hodgdon and Steele (1958) describe the area of jack pine as "the vicinity of Lake Umbagog; all New Hampshire stations are on ledges". Many collectors were uncertain whether they were in New Hampshire or Maine. As on Welch Mountain, Schoenike (1959, personal communication) found 45% of the trees at Umbagog to be of the open-cone type and 20% closed-cone types.

Tyler Point. The most northern tree on the lake (and in New Hampshire as a whole) was one tree on the northern promontory, on a ledge at high water mark. This was on the south side of the point. No trees were found on the west facing shore; but to the south of Tyler Point, on a small rocky arm about midway from the state line to the point, I found a considerable colony of 75 to 100 trees. These were mostly young trees; the oldest and largest, nearly 30 cm in diameter, had been blown down and were prostrate, but still alive. Branches were growing erect and bearing cones. There was charcoal on a dead basal branch, and evidence of fire on stumps in the forest back from the shore. Many seedlings less than 30 cm high were growing in cracks in the bare pink granite.

Schoenike (1959, personal communication) reported finding a few scattered jack pines growing on a low east-facing sandy slope about 4.8 km north of Upton, Maine. He writes: "South of Camp Gordon and inland is the largest stand I saw, perhaps several hundred trees up to 40 cm d.b.h. and 18 m tall, quite dense, but not reproducing. This extends from near the lake shore up a hill to perhaps 120 m or more inland. It can be reached by trail on the Maine side of the lake."

Tidswell Point. The shore opposite the island near the tip of the point, southwesterly to the state line, was well populated with scattered jack pines, some of considerable size. Some trees were inland 15 m or more, but most were directly on the shore. This was the largest area containing jack pine that was found, and the only place on the lake where jack pines were present on a west exposure. On the south shore of a bay opposite the island nearest the point proper was a stand growing in marshy lowland. The soil was sand and the pines were being overtopped by paper birch. The greater size and age of trees along this shore suggest that this station may have been a seed source for colonization of the outlying groups of trees farther north on the lake.

Bear Island. This island of about 2 ha is heavily wooded with white pine, red spruce, hemlock, northern white cedar, and paper birch. The shores are low and marshy with a dense scrubby fringe of *Myrica gale, Spiraea latifolia, Cornus stolonifera, Viburnum dentatum, Viburnum cassinoides,* and *Alnus rugosa.* On the south shore, growing among these shrubs on wet sandy soil, were seven jack pines about 15–20 cm d.b.h. and 4.5–6 m high. They bore cones of several years, but no younger trees could be found. No age determination was made, but probably none of the trees exceeded 50 years, and most appeared one-half that. There was no evidence of fire on the island, which was uninhabited.

Metallak Island. This is the northernmost island where jack pine was found. Less than 0.8 ha, it has been extensively altered by man and contains the ruins of a large building that burned many years ago. Eleven huge white pines and one red oak form an impressive ring in the center. There were two pine stumps and two oak stumps in the same grove, the latter cut by beaver. White pine and northern white cedar formed a thicket around the shore, and in the southwest corner of the island were fourteen 20-year old jack pines in an area about 4 × 15 m. The jack pines are not on ledge, but growing in old sod land with shrubs such as low bush blueberry, meadowsweet, and speckled alder. One dead jack pine was also found. The radial growth rate of the living trees was 6 annual rings 2.5 cm. A few of the pines appeared to have been defoliated, possibly by sawflies.

Lone Pine Island. This is the name I have used to designate a small island south of Bear Island and west of Blake Island. It is about 18 m in diameter with one very large white pine in the exact center of the island. Its roots have been washed bare and eroded by ice but are anchored securely in crevices of the ledge forming the island. Surrounding the large white pine were 44 jack pines varying in size and age from 2-year seedlings to 15 cm d.b.h. and about 50 years old. The largest jack pine, nearly prostrate, with the base of the trunk decayed on the upper surface, was over 100 years old. Branches had grown erect into what appear like separate trees. This tree may be the immediate progenitor of the other trees on the island, although seeds may have blown or drifted from the mainland. Jack pine here was growing in pine humus, not directly on open ledge. The other vegetation of this island consisted of one white spruce, several small white cedars and red maples, and ericaceaous shrubs.

Islands Southwest of Tidswell Point. These contained numerous jack pines, apparently fairly young and growing on the south shores and under larger white pines. Two large jack pines are on the southernmost island. They measured 33 cm and 43 cm d.b.h. and were approximately 110 and 150 years old respectively. On the mainland opposite these was one jack pine 66 cm in diameter and about 137 years old. These trees may have antedated the large forest fires that swept the mainland, burned stumps remaining as evidence.

Other Islands. Blake Island and the one east of it were examined and no jack pine found. The same was true of Black Island, Big Island and the islands associated with it.

The West Shore. Only one tree has so far been found on the west shore north of Sargent Cove and in the Town of Errol.

Islands near the state line opposite Sargent's Cove. Numerous jack pines 15–20 cm d.b.h. were observed on the shore but not investigated further. It is possible that some of these may be in the Town of Cambridge.

DISCUSSION

FACTORS AFFECTING THE DISTRIBUTION OF PINUS BANKSIANA

Irregular or disjunct distribution has always puzzled plant geographers. Plants are certainly limited by extreme environments. Northern extension of trees is prevented by short growing seasons and insufficient heat to ripen seed. Since jack pine is a northern tree some authors have postulated that high temperature limits its southern migration, but it seems to thrive when planted far south of its natural range. Jack pine inhabits the hottest and driest sites, often bare rock ledges where summer temperatures must be high. This habit may be attributed more to lack of competition. It is found on the driest and most sterile soils in northern Canada where it becomes established in pure stands following fire. However fire is not necessary for the perpetuation of jack pine ecotypes having a high percentage of open cones. These types release some seeds in the fall when cool temperatures prevail. In these trees, repeated wetting and drying has more to do with seed release than temperature. Bare mineral soil occasioned by fire is not a prerequisite for germination and survival. Exposed loose duff is a poor seedbed since it dries out quickly. However, damp organic matter can provide a satisfactory substrate.

Hutchinson (1918) considered temperature one limiting factor but concluded that soil conditions must be the real cause restricting the presence of jack pine. Fernald (1919, op. cit.) presented evidence that *Pinus Banksiana* is absent from limestone areas and is found only in acid habitats. Schoenike (1962, op. cit.) found no jack pine on heavy clay, bogs, or hardwood types in Minnesota. Pease (1921) confirmed Fernald's observations but pointed out that jack pine was actually found on a wide variety of sites. Halliday and Brown (op.

cit.) stated that jack pine reaches its maximum size on basic soils in western Canada and is found on limestone in Manitoba, the Bruce Peninsula and Manitoulin Island. Stebbins (1935) also found jack pine and red pine in Ontario, where he was impressed by the contrast between boreal and southern types of the same association. This was made even more remarkable by the presence of calciphiles and acid-loving plants, both equally at home. Possibly jack pine limestone ecotypes have developed in these cases. But there is general agreement that jack pine is found on barren, sandy and rocky soil probably because it is best able to compete with other species there. Jack pine has outgrown red pine and scotch pine (*Pinus sylvestis* L.) where all were planted together on sterile sand and gravel. The same controlling effect of site can be seen in swamp-enduring species and those tolerating salt, alkali, or acidity. Such species tend to be uncommon with disjunct distribution, since suitable sites are irregularly distributed. Griggs (1940) concluded that (1) a species is rare because it cannot compete, (2) rare species occupy habitats in early stages of succession, and (3) rare plants have disrupted ranges that were once continuous. They tend to be slowly dying out. Nothing could better describe the distribution of *Pinus Banksiana.* Past climatic changes and migration following glacial retreat are probably important factors in disjunct distribution, especially of pioneer species. Why it is found on some sites and absent from closely adjoining and apparently equal habitats defies explanation. Palmgren (1929) reasoned that chance, as expressed in the ecological history of a particular site, and the occurrence of a major disturbance are ecological factors to be considered.

A second noteworthy fact is that the great majority of trees found in both New York and New Hampshire are rather young, younger than any recorded fires that denuded the mountains where they occurred in New Hampshire, or overgrown pasture land where they are most abundant in New York. Exceptions are a few large old trees on the shore of Lake Umbagog. If Brewster found jack pine on Metallak Island in 1896 as the herbarium specimen indicates, why did we find only 20-year old trees in 1958 on the same place? Probably the older trees were blown down and burned.

The migratory history of jack pine has been thoroughly surveyed by Yeatman (1967). He concluded that during the late Wisconsin jack pine was forced south along with other boreal plants and survived in one central refugium in the Appalachian highlands. He cited authors who reported jack pine fossil deposits from the glacial period as far south as South Carolina. With the retreat of the continental ice, jack pine was among the early pioneer species in post-glacial forests on outwash sands and gravels, as well as on exposed ledges on the high mountains. As more shade-tolerant trees invaded the soils protected by jack pine, only lightning fires ensured reproduction of jack pine on most sites. It is of interest that a lightning-caused forest fire occurred in 1953 on Mt. Webster not far from the jack pine stations there. The role of fire was more important in eliminating competition than in cone-opening. Later advance of mesophytic forests eliminated jack pine from all but a few stations in the northeast. With continued absence of competition from tolerant species such as on rocky situations of low fertility, jack pine can be self-perpetuating indefinitely with or without fire. Where these conditions do not obtain it is likely to become extinct in its remaining outposts.

ACKNOWLEDGMENTS

I wish to thank the curators of the following herbaria for supplying lists of voucher sheets in their collections: A, BU, CUW, GH, HNH, MAINE, MASS., NEBC. NHA, NY, NYS, US, VT, and YU. Copies of herbarium records have been deposited at NEBC and NHA. They may also be obtained from the author. I am especially indebted to Dr. C. W. Yeatman, Petawawa Forest Experiment Station, Ontario; Mr. Frederic L. Steele; and Mr. Alexander Lincoln, Jr. for reviewing the manuscript and many helpful suggestions; also to Mr. E. W. Littlefield for details and revision of the description of New York stations.

LITERATURE CITED

Baldwin, H. I. 1961. Exploring for Jack Pine in New Hampshire. Society for the Protection of New Hampshire Forests, Forest Notes **72:** 33-44.

Bell, R. 1897. The geographical distribution of forest trees in Canada. Scottish Geographical Magazine **13:** 281-296.

Bicknell, E. P. 1916. *Pinus Banksiana* on Nantucket. Rhodora **18:** 241-242.

Blakeslee, A. F., & C. D. Jarvis. 1911. New England trees in winter. Bull. **69,** Storrs Agri. Expt. Sta., Storrs, Conn.

Bramble, W. C. 1946. Natural reproduction of Jack Pine in Pennsylvania. Jour. For. **44:** 204.

Burns, G. P., & C. H. Otis. 1899. Trees of Vermont. Vt. Agri. Expt. Sta. Bull. **73.**

———. 1916 1924. Trees of Vermont. Vt. Agri. Expt. Sta. Bull. **194.**

Coburn, L. H. 1920. Flora of Birch Island in Attean Pond. Rhodora **22:** 129.

Comey, A. C. 1936. Jack Pine on Mt. Chocorua. Appalachia **21:** 116 117.

Critchfield, W. E., & E. L. Little. 1966. Geographic distribution of the pines of the world. U. S. Dept. Agri. Misc. Pub. **991.** Wash. 97 pp.

Fernald, M. L. 1911. Review of Harshberger: Phytogeographic survey of North America. Rhodora **13:** 213 224.

———. 1919. Lithological factors limiting the ranges of *Pinus Banksiana* and *Thuja occidentalis.* Rhodora **21:** 41 67.

———. 1950. Gray's Manual of Botany, 8th ed. American Book Co., N.Y. 1632 pp.

Foster, J. H. 1931 1946. Trees and Shrubs of New Hampshire, 3rd. ed. Soc. Protection of N. H. For. Concord. 117 pp.

Griggs, R. F. 1940. The ecology of rare plants. Bull. Torrey Bot. Club **67:** 575 593.

Halliday, W. & H. Brown. 1943. Distribution of some important forest trees in Canada. Ecology **24:** 353 372.

Harshberger, J. W. 1914. *Pinus Banksiana* on Nantucket. Rhodora **16:** 184.

Hodgdon, A. R., & F. L. Steele. 1958. The woody plants of New Hampshire. N. H. Agri. Expt. Sta. Bull. **447,** Univ. N. H.

Holst, M. J. & C. W. Yeatman. 1961. A provenance study of *Pinus Banksiana* Lamb. Recent Advances in Botany **II:** 1612 1616. Univ. of Toronto Press.

Hough, R. B. 1936. Handbook of Trees of The Northern States and Canada. Lowville, N. Y., 464 pp.

House, H. D. 1924. Report of the State Botanist. N. H. State Museum Bull. **254.**

Huntington, J. H. 1884. Report of the Councillor of Natural History, Autumn 1881. Appalachia **3** (1882 1884): 65.

Hutchinson, A. H. 1918. Limiting Factors in relation to specific ranges of tolerance of forest trees. Bot. Gaz. **66:** 465 493.

Hyland, F. 1946. The conifers of Maine. Maine Ext. Ser. Bull. **345.** Orono, Me.

Jenks, P. R. 1934. Jack pine on Welch Mt. Appalachia **20:** 280.

King, Thomas Starr. 1862. The White Hills. Crosby & Nichols, Boston. 403 pp.

Little, E. L. 1953. Checklist of Native and Naturalized Trees of the U. S. USDA Handbook **41.**

———. 1971. Atlas of United States Trees. Vol. 1. USDA Misc. Pub. **1146.**

Littlefield, E. W. 1928. An uncommon association of pines in northern New York. Rhodora **30:** 199 231.

———. 1960. Jack Pine: poor relation or pioneer. N. Y. State Conservationist **Apr.-May:** 4 7.

———. 1962. Jack Pine. Science News **2**(2): 3. Science Pub. of Canada, Montreal.

Mergen, F., & J. Worrall. 1965. Effect of environment and seed source on mineral content of Jack Pine seedlings. For. Sci. **11:** 393 400.

Mirov, N. T. 1967. The Genus Pinus. Ronald Press, N. Y. 602 pp.

Munns, E. N. 1938. The distribution of important forest trees of the U. S. USDA Misc. Pub. **287.** Washington, D.C.

NORTON, A. H. 1913. Some noteworthy plants from the islands and coast of Maine. Rhodora **15:** 137.

OGDEN, E. C., F. H. STEINMETZ, & F. HYLAND. 1948. Checklist of the vascular plants of Maine. Josselyn Botanical Society of Maine Bull. **8.**

PALMGREN, A. 1929. Chance as an element in plant geography. Proc. Int. Congress of Plant Sciences **I:** 591 602. Ithaca, N. Y.

PEASE, A. S. 1921. Gray Pine and Arbor Vitae. Rhodora **23:** 247 249.

PECK, C. H. 1898. Report of the State Botanist. N. Y. State Museum Mem. **5:** 257.

PIERSON, H. B. 1951. Forest trees of Maine. Maine For. Ser., Augusta, Me. 88 pp.

PIKE, R. B., & A. R. HODGDON. 1963. Notes on Great Wass Island, Maine. Rhodora **65:** 285.

PRATT, W. F., & E. W. LITTLEFIELD. 1938. Western extension of the range of *Pinus Banksiana* in New York. Rhodora **40:** 241-242.

PYCHOWSKA, L. G. 1891. Two letters on *Pinus Banksiana.* Bull. Torrey Bot. Club **18:** 150.

RAND, E. L. 1889a. *Pinus Banksiana* on the coast of Maine. Bull. Torrey Bot. Club **16:** 294 295.

______. 1889b. *Pinus Banksiana* on Mt. Desert Island. Rhodora **1:** 135 136.

RUDOLPH, P. O. 1958. Silvical characteristics of Jack Pine (*Pinus Banksiana*) Station Paper **61.** Lake States For. Expt. Sta., St. Paul, Minn.

RUDOLPH, T. D., W. S. LIBBY, & S. S. PAULEY. 1957. Jack Pine variation and distribution in Minnesota. Minn. For. Notes **58,** Univ. Minn., St. Paul, Minn.

SARGENT, C. S. 1897. Silva of North America **II:** 147.

SCHOENIKE, R. E. 1962. The distribution of Jack Pine in Minnesota. Paper **4762,** Univ. Minn. Agri. Expt. Sta. Sch. of Forestry Special Pub. **1.**

______. 1976. Geographical variation in Jack Pine (*Pinus Banksiana*) Agri. Expt. Sta. Univ. of Minn. 47 pp. Tech. Bull. **304-1976** Forestry Series 21.

SEARS, J. H. 1881. Notes on the forest trees of Essex, Clinton, and Franklin counties, New York. Bull. of the Essex Institute **13:** 174 178.

SEYMOUR, F. C. 1969. The Flora Of New England. Chas. E. Tuttle, Rutland, Vt. 596 pp.

STEBBINS, G. L., JR. 1935. Some observations on the flora of the Bruce Peninsula, Ontario. Rhodora **37:** 63 74.

STEELE, F. L. 1954. Notes on two New Hampshire trees. Rhodora **56:** 204.

______., & A. R. HODGDON. 1968. Trees and shrubs of northern New England. Soc. for the Pro. of N.H. For., Concord, N. H. 132 pp.

WEATHERBY, C. A., C. H. KNOWLTON, & R. C. BEAN. 1926. First report of the Committee on Floral Areas. Preliminary lists of New England plants. Rhodora **28:** 43 45.

WILLIAMS, R. D., & T. W. BEERS. Seed source affects the height growth of planted Jack Pine. Sta. Note **137,** Central States For. Expt. Sta. USDA.

YEATMAN, C. W. 1967. Biogeography of Jack Pine. Can. J. Bot. **45:** 2201 2211.

______. 1974. Jack Pine genetics program at Petawawa For. Exp. Sta. 1950-1970. Pub. **1331** Dept. Environ. & Canadian For. Ser.

HILLSBORO, N. H. 03244

HETEROSTYLY IN MITCHELLA REPENS (RUBIACEAE)

CHRISTINE R. KEEGAN[1], ROBERT H. VOSS,
AND KAMALJIT S. BAWA

Heterostyly in its broadest sense refers to a morphological property of some plants whereby flowers on individuals of the same species have stamens and styles of two or three different lengths. In the simpler form, distyly, some flowers have long stamens and short styles, while others have short stamens and long styles. Darwin (1897) referred to long-styled flowers as "pins" and to short-styled flowers as "thrums"; Hildebrand in 1867 had already proposed that the reciprocal placement of stamens and styles on different flowers facilitated cross-pollination by insects.

Heterostyly commonly follows either of two evolutionary pathways (Vuilleumier, 1967; Bir Bahadur, 1968), one leading to dioecy and subdioecy, and the other leading to homostyly and self-compatibility. Indeed, for *Mitchella repens*, a trailing herbaceous perennial common in North American temperate forests, all three conditions (heterostyly, dioecy, and homostyly) have been reported.

Darwin (1897) described specimens of *Mitchella repens* sent to him by the American botanist Asa Gray as being heterostylous and self-incompatible. He detailed the results of controlled pollinations he performed on individuals of both morphs — those he referred to as "legitimate" crosses [pin (P) × thrum (T) and T × P] resulted in a high level of fertilization, while "illegitimate" crosses (P selfed, P × P, T selfed, T × T) gave few fruits, and fewer seeds per fruit: ". . . Thus the two legitimate unions are more fertile than the two illegitimate, according to the proportion of flowers which yielded berries, in the ratio of 100 to 20; and according to the average number of contained seeds as 100 to 47." It is not possible to ascertain from Darwin's work if the incompatibility was sporophytically or gametophytically determined.

Thomas Meehan (1868) reported that a population of *Mitchella repens* in Pennsylvania, while morphologically heterostylous, was functionally dioecious: ". . . the pistil in the one case is not perfect,

---

[1] Present address: Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138.

and in the other the anthers are mere rudiments, without a trace of pollen. The two forms are truly male and female plants."

Ganders (1975) described a case of homostylous *Mitchella repens* intermixed with a population of heterostyles in Maryland. Controlled pollinations indicated that the homostylous flowers were functionally thrums, and self-incompatible, in contrast to most cases of homostyly derived from heterostyly (Ernst, 1955). "Legitimate" crosses (P × T, P × H, T × P, H × P) gave 93% fruit set, while only 7% of the "illegitimate" crosses (T × T, T selfed, P × P, P selfed, H × H, H selfed, T × H, H × T) produced fruits.

In light of these varying descriptions of *Mitchella repens'* floral morphology and compatibility relations, we decided to study the breeding system of a heterostyled population in northeastern Massachusetts. We had three objectives:

1) To verify the presumed incompatibility system and determine its type (sporophytic or gametophytic).
2) To measure degrees of "maleness" and "femaleness" of the two morphs, differences in which would demonstrate the progression from heterostyly to dioecy.
3) To examine pollen flow in relation to the dispersion of pins and thrums, which frequently are patchily distributed.

MATERIALS AND METHODS

Mitchella repens is a trailing evergreen perennial common in North American temperate forests from Newfoundland south to Florida and west to Texas and Minnesota. Its white or pink flowers, with four-lobed corollas, occur in terminal pairs with the ovaries of each pair united. Thus, each pair of flowers produces one fruit, a bright red berry with a maximum of 8 seeds. Sometimes smaller, 4-seeded fruits occur; these are probably the result of pollination of only one flower. All flowers on a particular plant are of the same morph.

Our field work was done at the Estabrook Woods of Harvard University in Concord, Massachusetts. The *Mitchella* we sampled grew under predominantly white pine-red maple canopies in a pine needle litter of about 2 cm. depth. Our sample areas were covered almost exclusively by *Mitchella repens*, but this species commonly grows intermixed with such woodland species as *Pteridium aquilinum*, *Dryopteris* spp., *Coptis groenlandica*, *Aralia nudicaulis*, *Trientalis borealis* and *Vaccinium* spp.

In order to see if the plants are self-compatible and to determine the nature of the incompatibility system, we brought unopened flowers to the laboratory and did controlled pollination of all six possible types:

1) Pin × thrum
2) Thrum × pin
3) Pin selfed
4) Pin × pin
5) Thrum selfed
6) Thrum × thrum

The total number of plants used for the controlled pollinations was 15. All flowers which opened on a plant, usually 2 4, were used, for a total of 45 crosses.

Flowers were left overnight after pollination, and the following afternoon we detached the styles, fixed them and stained them with aniline blue using the techniques described by Martin (1958). After treatment in this manner, pollen tubes fluoresce under ultraviolet light. We examined each style under a microscope equipped with an ultraviolet light source to determine the extent of pollen tube growth.

Our measurements of "maleness" and "femaleness" were based on the fact that bisexual flowers often differ in the proportions of their gametes which they transmit to the next generation via pollen and ovules, and thus, sexuality is a quantitative, not a qualitative property (Lloyd, 1979a). In populations of heterostylous self-incompatible plants, the number of ovules fertilized is an indication of the "femaleness" of pins and the "maleness" of thrums, while the number of thrum ovules fertilized is a measure of "femaleness" of thrums and "maleness" of pins (Lloyd, 1979b). In order to quantify gender in *Mitchella repens,* we marked 95 pins in 5 plots and 191 thrums in 6 plots, each of which was approximately 0.25 m^2 in area, and after the fruits had developed, we counted the number of fruits produced and the number of seeds per fruit for each morph.

In order to study the relationship of plant dispersion to pollen flow, we marked pins and thrums in homogeneous and heterogeneous plots, and subsequently observed fruit set in each morph as a function of proximity to the other morph. We also collected open flowers from several homogeneous and heterogeneous patches in order to examine the styles for differential pollen tube growth.

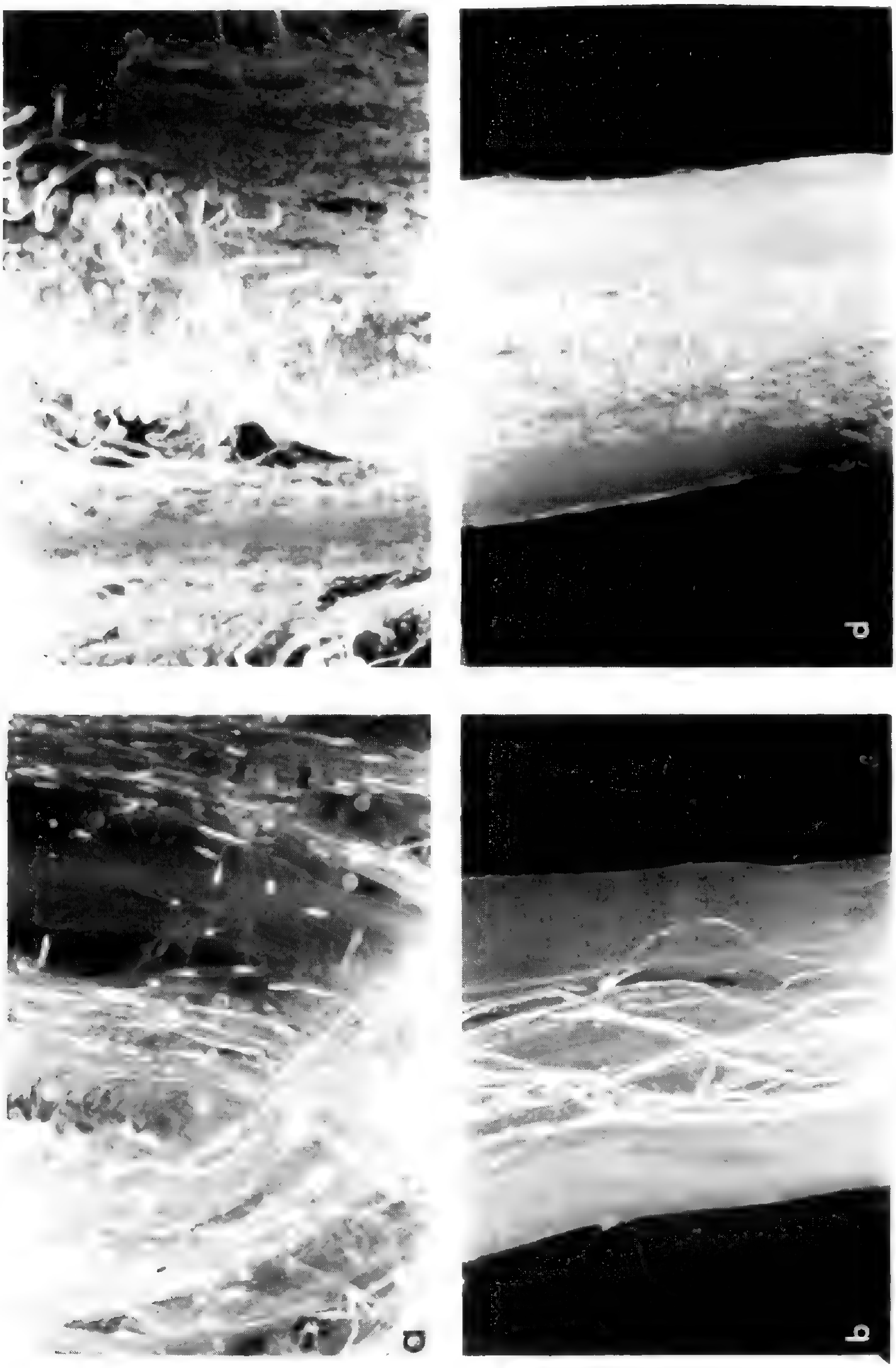


Figure 1. Photomicrographs of pollen tube growth in *Mitchella repens* (× 630). **a.** Normal pollen tube growth in stigma and **b.** style in a compatible pollination. **c.** Inhibition of pollen tube growth in stigma, idicative of sporophytic incompatibility. **d.** Absence of pollen tube growth in style in an incompatible cross.

RESULTS

Controlled pollinations indicate that heteromorphic crosses are compatible and homomorphic crosses are highly incompatible. Microscopic examination of stained styles with a UV light source disclosed extensive pollen tube growth down the stylar tissue in heteromorphic crosses, and either failure of pollen to germinate or early inhibition of pollen tube growth in homomorphic crosses (Table 1; Fig. 1). Hence, our population of *Mitchella repens* appears, as Darwin's did, to be both heterostylous and self-incompatible. In addition, the incompatibility appears to be sporophytically determined (see Discussion).

The number of fruits produced by each morph as well as the number of seeds per fruit indicate that there is no sexual differentation between pins and thrums. Of the marked pins, 96.8% produced fruits, while 96.3% of the thrums fruited (Table 2). The average number of seeds produced in pins was 6.7 ± 1.5, and that in thrums was 6.9 ± 1.4 out of a possible maximum of 8. A Mann-Whitney U-test for large sample sizes discloses no significant difference between the morphs in the number of seeds set per fruit ($t = 0.771$).

Because fruit production in homomorphic patches was nearly 100%, it appeared that pollen flow as influenced by plant dispersion was of negligible importance in effecting ovule fertilization. This finding obviated the necessity of examining styles from homogeneous patches for differential pollen tube growth.

DISCUSSION

A simple examination of our *Mitchella repens* samples indicates that we are not dealing with a morphologically dioecious species as

Table 1. Success of controlled pollinations as evidenced by presence or absence of pollen tubes

	No. of crosses	Pollen tubes present	Pollen tubes absent
Pin × Thrum	14	14	0
Thrum × Pin	9	9	0
Pin × Pin	2	0	2
P selfed	5	0	5
Thrum × Thrum	8	0	8
T selfed	7	0	7

Table 2. Fruit production and seed set in open-pollinated plots

	No. of flower pairs	No. and (%) of fruits	Seeds per fruit
Pins	95	92 (96.8)	6.7 ± 1.5
Thrums	191	184 (96.3)	6.9 ± 1.4

described by Meehan; neither pins nor thrums have pistils or anthers which could be termed rudimentary. Our controlled pollinations verified that indeed, pins and thrums are functionally perfect. Furthermore, all legitimate crosses were compatible and all illegitimate crosses were incompatible (Table 1); thus, *Mitchella repens* is self-incompatible in this region. These results are consistent with those of Darwin and Ganders, although they both reported some seed set from illegitimate crosses (Darwin, 1897; Ganders, 1975). However, our incompatibility studies were based on a rather small sample size (although comparable to that of Darwin), and additional sampling will be necessary before definitive conclusions can be made. If Meehan's finding of a dioecious population of *Mitchella repens* is confirmed, then this species will represent the only case in which both self-incompatible heterostyly and dioecy have been documented.

The barrier to pollen tube growth in *Mitchella repens* is in the stigmatic tissue, as illustrated in Figure 1. This is an indication that the incompatibility is sporophytic, as is usually the case in distylic plants (Pandey, 1970). However, to the best of our knowledge, this is the first demonstration of the association between the sporophytic incompatibility system and heterostyly based on actual observations of the pollen-stigma interaction.

Although the nearly 100% fruit production in homogeneous and heterogeneous patches indicates that dispersion has no marked influence on fertilization, this does not necessarily imply that pollen flow is independent of plant dispersion. It is possible that flowers in homogeneous patches are receiving less pollen than those in heterogeneous patches, but the difference is not great enough to reduce seed set. It is also possible that plants in the two types of patches transmit different amounts of pollen; our methods could not detect these differences. Even though dispersion does not appear to be a critical factor in fruit production, it would be desirable to examine the patterns of individual pollinator behavior (probably bumblebees) to determine the actual flow of pollen through a population.

SUMMARY

By performing controlled pollinations, we determined that *Mitchella repens* is heterostylous and perfectly self-incompatible in northeastern Massachusetts, with no evidence of evolution towards dioecy. Incompatibility was found to be sporophytically controlled, with the barrier to pollen tube growth in the stigmatic tissue.

A superficial investigation of pollen flow revealed no significant relationship between pollen flow and the dispersion of pins and thrums.

ACKNOWLEDGEMENTS

We thank John Ebersole for constructive criticism. RHV was a participant in the NSF Undergraduate Research Program in 1978. (Grant #SMI 76 83985).

LITERATURE CITED

Bir Bahadur. 1968. Heterostyly in Rubiaceae: a review. J. Osmania Univ. (Science), Golden Jubilee Special Volume.

Darwin, C. 1897. The different forms of flowers on plants of the same species. Murray, London.

Ernst, A. 1955. Self-sterility in monomorphic *Primulas*. Genetica **27**: 391 448.

Ganders, F. 1975. Fecundity in distylous and self-incompatible homostylous plants of *Mitchella repens* (Rubiaceae). Evol. **29**: 186-188.

Hildebrand, F. 1867. Die Geschlecter-Vertheilung bei den Pflanzen. Engelman, Leipzig.

Lloyd, D. 1979a. Quantitative methods for describing the sex (gender) of plants. In prep.

———. 1979b. Evolution towards dioecy in heterostylous populations. Plant Syst. & Evol. **131**: 71 80.

Martin, F. 1958. Staining and observing pollen tubes in the style by means of fluorescence. Stain Tech. **34**: 125 128.

Meehan, T. 1868. *Mitchella repens*, L., a dioecious plant. Proc. Acad. Nat. Sci. of Phil. **1868**: 183 184.

Pandey, K. 1970. Time and site of the S-gene action, breeding systems and relationships of incompatibility. Euphytica **19**: 364 372.

Vuilleumier, B. 1967. The origin and evolutionary development of heterostyly in the angiosperms. Evol. **21**: 210 226.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF MASSACHUSETTS
BOSTON, MASSACHUSETTS
02125

NEW COMBINATIONS IN THE EASTERN SPECIES OF HEUCHERA (SAXIFRAGACEAE)

Elizabeth Fortson Wells[1]

During a recent revision of the eastern North American species of *Heuchera* (Wells, in press), taxonomic decisions were made that necessitate three new nomenclatural combinations. One new species formerly treated as a variety of *H. americana* L. is recognized, and two taxa formerly recognized as species are reduced to varietal rank. For clarity and bibliographical convenience, these new combinations are validated and briefly explained here. Drawings, distribution maps, and fuller discussion of these entities are presented in the revisionary paper (Wells, in press).

1. **Heuchera caroliniana** (Rosendahl, Butters, and Lakela) Wells, *comb. nov.*

Heuchera americana L. var. *caroliniana* Rosendahl, Butters, and Lakela, Minn. Stud. in Pl. Sci. **2:** 59. 1936. Type: *A. A. Heller 10278*. In meadows near Faith, Rowan Co., North Carolina, May 27, 1911. (Holotype, MO).

Heuchera caroliniana resembles *H. americana* L. in possessing small flowers with a short calyx 2.8 4.5 mm long from the base of the ovary to the tip of the calyx lobes. The calyces of *H. americana* measure between 2.9 and 7.2 mm long. However, a number of important differences in floral characters separate the two species. At anthesis, the stamens in *H. caroliniana* flowers are exserted 0.2 to 1.5 mm beyond the calyx, and the styles vary from barely included (up to 0.7 mm shorter than the calyx) to barely exserted (up to 1.1 mm exserted beyond the calyx). In *H. americana* flowers the stamens are exserted 3 to 5 mm beyond the calyx, and the styles extend 2.6 to 6.4 mm beyond the calyx. The shape of the calyx is subhemispherical in *H. caroliniana* but urceolate to campanulate in *H. americana*. The free hypanthium on the adaxial side, from the lowest point in either of the two sinuses flanking the adaxial sepal

---

[1] Present address: Department of Biological Sciences, The George Washington University, Washington, D.C. 20052.

lobe to the point at which the hypanthium becomes free of the ovary wall, ranges from 1.3 to 2.5 mm long in *H. caroliniana* and from 0.6 to 1.5 mm long in *H. americana.*

Heuchera caroliniana also resembles *H. pubescens* Pursh in the degree of exsertion of reproductive parts relative to the length of the calyx, although the calyces of *H. pubescens* are much longer, ranging from 8.7 to 13.2 mm long. All three species are similar vegetatively and in ecological requirements.

Rosendahl et al. (1936), based on a small number of herbarium specimens available to them, recognized this entity as a variety of *Heuchera americana.* They regarded its floral characters as "so peculiar that it may be necessary eventually to separate it as a distinct species" (Rosendahl et al., 1936). The decision to recognize *H. caroliniana* as a species is based on field observations and examination of herbarium specimens from every county throughout and adjacent to its range.

Heuchera caroliniana is restricted to a long narrow band in the Piedmont of North Carolina and South Carolina. *Heuchera americana* occurs in counties adjacent to the range of *H. caroliniana* but is not sympatric except along the periphery. Intergradation between these two species is very infrequent.

2. **Heuchera americana** L. var. **hispida** (Pursh) Wells, *comb. nov.*

Heuchera hispida Pursh, Fl. Am. Sept. **1:** 188. 1814. TYPE: *F. Pursh s. n.* High mountains between Fincastle and the Sweet Springs and some other similar places. Craig Co., Virginia. (authentic specimen of Pursh, PH).

This taxon is intermediate between *Heuchera americana* var. *americana* and *H. pubescens* Pursh, and intergrades with both entities in most of its morphological attributes. It is distinguished from *H. americana* var. *americana* (calyx length 2.9–5.5 mm) by its relatively larger flowers with longer calyces (calyx length 5.7–8.8 mm) and free hypanthia and by its larger, fimbriate-margined petals, and from *H. pubescens* (calyx length 8.7–13.2 mm) by its long-exserted stamens and smaller flowers with shorter free hypanthia and petals. Its geographical distribution is in the mountains of Virginia and West Virginia where the ranges of *H. americana* var. *americana* and *H. pubescens* overlap. It appears to be the result of natural hybridization between *H. americana* var. *americana* and *H. pubescens.* Artificial hybrids between these two entities are fertile and resemble the naturally occurring plants of *H. americana* var. *hispida*. Furthermore, populations of *H. americana* var. *hispida* exhibit greater intrapopulational morphological variability than do either *H. americana* var. *americana* or *H. pubescens* in regions remote from the area of range overlap. The increased variability suggests genetic segregation following hybridization.

This taxon is reduced to varietal rank under *Heuchera americana* because of the intergradation of morphological characters, fertility of artificial hybrids, and difficulty of distinguishing specimens belonging to it from those of *H. americana* var. *americana*. *Heuchera pubescens* is maintained at the specific level because it is strikingly different from *H. americana* var. *americana* in floral characters and is confined to a cooler climatic region, the Ridge and Valley Province of Pennsylvania, Virginia, and West Virginia.

3. **Heuchera parviflora** Bartling var. **puberula** (Mackenzie & Bush) Wells, *comb. nov.*

Heuchera puberula Mackenzie & Bush, Rept. Mo. Bot. Gard. **16:** 103. 1905. TYPE: *B. F. Bush s. n.* Monteer, Missouri. July 27, 1899. (HOLOTYPE, NY).

Heuchera puberula f. *glabrata* Steyermark, Rhodora **51:** 117. 1949. TYPE: *Julian A. Steyermark 66615*. North-facing base of limestone bluffs, T 27 N, R 6 W, Shannon Co., Missouri. October 2, 1948. (HOLOTYPE, F).

This variety resembles *Heuchera parviflora* Bartling var. *parviflora* very closely, except for having shorter pubescence on the petioles, peduncles, and leaves, and entire, scale-like bracts subtending the floral branches. Except for a few populations in central Kentucky, the variety is restricted to Arkansas and Missouri. It was described by Mackenzie and Bush (1905) as a distinct species, but it is so similar to *H. parviflora* var. *parviflora* in every detail including flower size and shape, which they considered sources of important differences, that it is treated as a variety of *H. parviflora* here.

ACKNOWLEDGEMENT

I would like to express my appreciation to S. A. Spongberg for his careful reading of the manuscript.

LITERATURE CITED

MACKENZIE, K. K., & B. F. BUSH. 1905. New plants from Missouri. Rept. Mo. Bot. Gard. **16:** 102 108.

ROSENDAHL, C. O., F. K. BUTTERS, & OLGA LAKELA. 1936. A monograph on the genus *Heuchera*. Minn. Stud. in Pl. Sci. **2**: 1–180.

WELLS, E. F. (in press). Revision of the genus *Heuchera* (Saxifragaceae) in eastern North America.

DEPARTMENT OF BOTANY
UNIVERSITY OF BRITISH COLUMBIA
VANCOUVER, BRITISH COLUMBIA
CANADA V6T 1W5

CYPRIPEDIUM REGINAE REDISCOVERED IN NEW HAMPSHIRE

FRANCES E. BRACKLEY

Cypripedium reginae Walt., the Showy Lady Slipper, reported from only one station in New Hampshire, was last collected there in 1891. The site under consideration, the Bottomless Pit in Hanover (Grafton County) near the Lebanon town line, has changed from an open water bog earlier in this century (J. Poole, pers. comm.) to a *Picea mariana* shrub community at the present time. Since conditions in the bog have changed to the extent that it no longer supports an orchid population, *Cypripedium reginae* was considered "possibly extinct" in the state (Storks & Crow, 1978).

During the course of field work for my Orchid Flora of New Hampshire project this summer, I was directed by Frederic L. Steele to Scott Fitzpatrick, a naturalist working at Lost River Reservation in Woodstock, N.H. Mr. Fitzpatrick remembered seeing the Showy Lady Slipper in Lyme, N.H. and furnished directions to the site. On June 20, 1979, I visited the site and found a population of over 200 plants in full flower. The station is a rather ordinary swampy area with *Osmunda cinnamomea, Onoclea sensibilis,* and *Saxifraga pennsylvanica* growing in abundance.

On that same date I also visited the town of Lisbon, and was shown a large clump of *Cypripedium reginae* growing in a garden. The plants were said to have been transplanted from a swamp in the same town. The actual site of the swamp is a highly guarded secret, and it wasn't until July 6, 1979 that I received permission to be escorted to the site, a large *Thuja* swamp located on private property. Although the majority of the plants had finished flowering, the remaining display was still quite impressive. *Habenaria hyperborea, Monesis uniflora,* and *Pyrola secunda* were also quite abundant under the *Thuja*.

Despite the fact that the owner's wife has received a large annual bouquet of "swamp orchids" for the past 20 years, the station should be quite safe from exploitation under the present ownership.

Voucher specimens were taken from both sites and are deposited in the Hodgdon Herbarium at the University of New Hampshire (NHA). I am indebted to Fred Steele who directed me to both of the contacts. Should anyone have knowledge of any other locations for rare New Hampshire orchids, I would greatly appreciate the information. The confidentiality of specific sites is assured. Perhaps other "extinct" orchids are waiting to be rediscovered in New Hampshire.

LITERATURE CITED

STORKS, I. M. & G. E. CROW. 1978. Rare and Endangered Vascular Plant Species in New Hampshire. New England Botanical Club, in cooperation with the U.S. Fish and Wildlife Service. (Newton Corner, Mass.)

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE 03824

NOTICE OF PUBLICATION

HODGINS, JAMES L. 1978. *A Guide to the Literature on the Herbaceous Vascular Flora of Ontario.* Botany Press, 90 Wolfrey Ave., Toronto, Ontario M4K 1K8. 73 pp. Spiral-bound. $4.00 per copy.

The *Guide,* designed to aid access to the botanical literature on Ontario, includes listings of books and journal articles, an index of checklists and surveys, a compiled provisional checklist for the Province, and sources for useful maps. Nearly half of the volume is a list of journal articles on Ontario taxa (*not* including the grasses or sedges). Other sections list books or articles on phytogeography, ecology, botanical history, horticulture, and the human uses of plants. Two small maps showing vegetational and political divisions are presented.

NOTICE OF PUBLICATION: REVISED CONNECTICUT CHECKLIST

DOWHAN, JOSEPH J. 1979. Preliminary Checklist of the Vascular Flora of Connecticut (Growing Without Cultivation). x + 176 pp. State Geological and Natural History Survey/The Natural Resources Center, Dept. of Environmental Protection.

This volume is a major step toward the development of a revised, up-dated, and annotated State Flora. Pocket sized and sturdily paper bound, it is designed as a guide and as an impetus to the collection of field information on the status of Connecticut plants. The Checklist provides an up-to-date list of vascular plants known presently (or reported in the past) which grow without cultivation. (Some special cases of non-persistent species and of woody species persisting around old homesites are included in one brief appendix; certain problematical taxa are in another.) Nomenclature is based on "Gray's Manual" but has been up-dated extensively by reference to many recent revisions. Where a name has changed, a brief synonymy is given and the appropriate reference indicated. Common names are also listed.

Included are: an index to scientific names (Families and Genera); a bibliography of 82 references, manuals, guides, and revisions; a listing and a small map of Connecticut's "eco-regions".

Copies are available from the Department of Environmental Protection, State Office Building, Hartford, Conn. 06115. Price: $2.00 (Conn. residents please add $0.14 tax).

Changes, additions, and observations are actively encouraged. Please send such information to: Conn. Geol. & Nat. Hist. Survey, Dept. of Environmental Protection, State Office Building, Hartford 06115.

BOOK REVIEW: AQUATIC AND WETLAND PLANTS OF SOUTHEASTERN UNITED STATES

Godfrey, Robert K., & Jean W. Wooten. *Aquatic and Wetland Plants of Southeastern United States. Monocotyledons.* ix + 712 pp. 1979. The University of Georgia Press, Athens, Georgia. (Price $30.00)

This volume is an outstanding contribution on a group of plants that are receiving much attention today. It is intended for use by botanists, ecologists, college students and government agencies. The geographical range encompasses North Carolina to Arkansas and south, abutting the range of Correll and Correll's *Aquatic and Wetland Plants of the Southwest* (Stanford University Press).

The format is identical to that of the Southwest manual with an artificial key to the taxa. Each family and genus is accompanied by complete, well-written keys that are easy to follow. Each species treatment contains a description, habitat information, and complete range. Full page line drawings accompany many of the species. Also included is an introduction consisting of a description of the format, distribution of the plants, taxonomic coverage, habitat and environmental perspectives. A glossary of terms, list of references, and separate indexes to common and scientific names complete the volume.

The coverage of aquatics is extensive, including many "marginal" aquatic plants which may occur in damp areas for short periods. The problem of determining the extent of coverage is difficult when dealing with vascular aquatic plants; a greater coverage is definitely preferred to an inadequate one. Godfrey admits to the omission of plants which are of rare or local occurence or not found in any abundance. An example is the omission of *Potamogeton tennesseensis.* Such obvious aquatics should have been included no matter how uncommon.

A few of the line drawings reproduced poorly. These are too dark to show any detail. The majority are excellent indicating many of the important diagnostic characteristics. Nomenclature is updated with such problem genera as the southern *Sagittaria* and *Xyris* clarified.

The volume is excellent. It fills a real taxonomic gap in the south-east and provides the needed means of identification for both the botanist and layman. The many introduced species in the south have provided for greatly expanding ranges of nuisance species. This book belongs in the library of every aquatic biologist regardless of their region of botanical interest. I eagerly await the volume on the dicots.

C. BARRE HELLQUIST
DEPARTMENT OF BIOLOGY
BOSTON STATE COLLEGE
BOSTON, MASSACHUSETTS 02115

The Proceedings of the Symposium

"RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND"

4, 5 May 1979

which was sponsored by
The New England Botanical Club
in co-operation with the
U.S. Fish and Wildlife Service
will be published as the January 1980 issue (No. 829, Vol. 80)
RHODORA

Non-subscribers, as well as those members who want extra copies, may order from:

NEBC Symposium
Department of Botany and Plant Pathology
Nesmith Hall
University of New Hampshire
Durham, N. H. 03824

Make checks payable to: **NEBC Symposium**

PRICES: $6.50 for orders received before Dec. 31, 1979
$8.00 for orders received after Jan. 1, 1980

Please include Zip Code in your return address, with the number of copies desired and the amount enclosed.

Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

VOLUME 81

1979

The New England Botanical Club, Inc.
Botanical Museum, Oxford Street, Cambridge, Mass. 02138

INDEX TO VOLUME 81

New scientific names are printed in **bold face**

Volume 81, No. 827, including pages 291–424, was issued July 31, 1979.

U.S. POSTAL SERVICE

STATEMENT OF OWNERSHIP, MANAGEMENT AND CIRCULATION

(Required by 39 U.S.C. 3685)

1. TITLE OF PUBLICATION RHODORA

A. PUBLICATION NO.

2. DATE OF FILING Sept.20,1979

3. FREQUENCY OF ISSUE Quarterly

A. NO. OF ISSUES PUBLISHED ANNUALLY Four

B. ANNUAL SUBSCRIPTION PRICE $20.00

4. LOCATION OF KNOWN OFFICE OF PUBLICATION *(Street, City, County, State and ZIP Code) (Not printers)*

c/o Botanical Museum,Oxford Street, Cambridge,Mass. 02138

5. LOCATION OF THE HEADQUARTERS OR GENERAL BUSINESS OFFICES OF THE PUBLISHERS *(Not printers)*

c/0 Botanical Museum, Oxford Street, Cambridge,Mass. 02138

6. NAMES AND COMPLETE ADDRESSES OF PUBLISHER, EDITOR, AND MANAGING EDITOR

PUBLISHER *(Name and Address)*

New England Botanical Club,Inc.,Botanical Museum, Oxford Street,Cambridge,Mass.02138

EDITOR *(Name and Address)*

Prof. Rolla M. Tryon, 22 Divinity Ave.,Cambridge,Mass.02138

MANAGING EDITOR *(Name and Address)*

Russell R. Walton, 22 Divinity Ave.,Cambridge,Mass. 02138

7. OWNER *(If owned by a corporation, its name and address must be stated and also immediately thereunder the names and addresses of stockholders owning or holding 1 percent or more of total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address, as well as that of each individual must be giving. If the publication is published by a nonprofit organization, its name and address must be stated.)*

NAME	ADDRESS
NO STOCKHOLDERS	

8. KNOWN BONDHOLDERS, MORTGAGEES, AND OTHER SECURITY HOLDERS OWNING OR HOLDING 1 PERCENT OR MORE OF TOTAL AMOUNT OF BONDS, MORTGAGES OR OTHER SECURITIES *(If there are none, so state)*

NAME	ADDRESS
NONE	

9. FOR COMPLETION BY NONPROFIT ORGANIZATIONS AUTHORIZED TO MAIL AT SPECIAL RATES *(Section 132.122, PSM)*

The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes *(Check one)*

☒ HAVE NOT CHANGED DURING PRECEDING 12 MONTHS

☐ HAVE CHANGED DURING PRECEDING 12 MONTHS

(If changed, publisher must submit explanation of change with this statement.)

10. EXTENT AND NATURE OF CIRCULATION	AVERAGE NO. COPIES EACH ISSUE DURING PRECEDING 12 MONTHS	ACTUAL NO. COPIES OF SINGLE ISSUE PUBLISHED NEAREST TO FILING DATE
A. TOTAL NO. COPIES PRINTED *(Net Press Run)*	875	925
B. PAID CIRCULATION 1. SALES THROUGH DEALERS AND CARRIERS, STREET VENDORS AND COUNTER SALES	None	None
2. MAIL SUBSCRIPTIONS	846	852
C. TOTAL PAID CIRCULATION *(Sum of 10B1 and 10B2)*	846	852
D. FREE DISTRIBUTION BY MAIL, CARRIER OR OTHER MEANS SAMPLES, COMPLIMENTARY, AND OTHER FREE COPIES	16	16
E. TOTAL DISTRIBUTION *(Sum of C and D)*	862	868
F. COPIES NOT DISTRIBUTED 1. OFFICE USE, LEFT OVER, UNACCOUNTED, SPOILED AFTER PRINTING	13	57
2. RETURNS FROM NEWS AGENTS	None	None
G. TOTAL *(Sum of E, F1 and 2—should equal net press run shown in A)*	875	925

11. I certify that the statements made by me above are correct and complete.

SIGNATURE AND TITLE OF EDITOR, PUBLISHER, BUSINESS MANAGER, OR OWNER

Herman R. Sweet, Treasurer

12. FOR COMPLETION BY PUBLISHERS MAILING AT THE REGULAR RATES *(Section 132.121, Postal Service Manual)*

39 U. S. C. 3626 provides in pertinent part: "No person who would have been entitled to mail matter under former section 4359 of this title shall mail such matter at the rates provided under this subsection unless he files annually with the Postal Service a written request for permission to mail matter at such rates."

In accordance with the provisions of this statute, I hereby request permission to mail the publication named in Item 1 at the phased postage rates presently authorized by 39 U. S. C. 3626.

SIGNATURE AND TITLE OF EDITOR, PUBLISHER, BUSINESS MANAGER, OR OWNER

Herman R. Sweet, Treasurer

PS Form
Aug. 1978 3526 *(Page 1)*

(See instructions on reverse)

RHODORA **October, 1979** **Vol. 81, No. 828**

CONTENTS