

A REVISION OF NORTH AMERICAN MELANTHIUM L.

(LILIACEAE)

by
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ABSTRACT

Title of Thesis: A revision of North American Melanthium L. (Liliaceae)

Norlyn L. Bodkin, Doctor of Philosophy, 1978

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Melanthium L. (Liliaceae) is a genus of perhaps eight species with the four species of North America distributed from central Iowa eastward to southern New York, south to northern Florida and eastern Texas. The type species, M. virginicum L., is found over this entire range growing commonly in swamps, marshes and bogs. Melanthium latifolium Desr., found mostly on rich wooded slopes, and M. parviflorum (Michx.) S. Wats. located at higher elevations, occur mainly in the mid-Appalachian mountains. Melanthium woodii (Robbins ex Wood) Bodkin, comb. nov., is known from rich deciduous slopes of the Ozark Plateaus where it is very local and rare, and from five small disjunct populations in three eastern states.

The major decision made in this treatment is the maintenance of Melanthium as distinct from the heterogeneous genus Veratrum L. on the basis of leaf size and shape, inflorescence, features of the tepalular glands and claws, adnation of stamens to tepals and general habit of the plants.

The numerous synonyms associated with the name Melanthium are treated and either included under that genus, or excluded and assigned to their proper genera.

The four (tentatively) Asian species, all of southwestern China, are not discussed due to a paucity of recent material.

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INTRODUCTION

Melanthium L. (Liliaceae) is a genus of temperate herbaceous plants found in small, local populations throughout the Eastern Deciduous Forest Biome. The genus is most closely related to Veratrum L. and it has been submerged either totally or in part, in this genus by some authors. This concept is hereby rejected and Melanthium is defined as consisting of four species distributed from southern New York westward to central Iowa, south to eastern Texas and northern Florida. Although the range extends westward to Iowa and Texas, the major populations of three of its species are in the Appalachian Mountains. The fourth, rare species is sparsely distributed over the Ozark Plateau with five additional small disjunct populations known in three eastern states. The type species, M. virginicum L. is the most widespread and occurs sympatrically with the other three. None of the species is abundant in any area and, in my opinion, the Ozarkian species, M. woodii is endangered as defined by the Endangered Species Act of 1973. Plants of the genus are found in a broad spectrum of habitats ranging from sphagnum bogs to rich mesic slopes, but each species is adapted to a specific set of environmental factors, and thus, commonly restricted to a particular ecosystem type.

The present revision is involved with the taxonomy of the genus, and the morphological and geographical characters of the species. To accomplish this the literature pertinent to Melanthium was thoroughly reviewed and the past treatments of the genus analyzed. An extensive study of more than one thousand herbarium specimens was supplemented by six years of field investigations on the Appalachian populations. The field work was invaluable from the standpoint of gaining familiarity

with the general aspects of the genus, its taxonomic and ecological relationships with other closely related taxa, as well as other biological aspects unattainable in the herbarium. The study of herbarium specimens is an integral part of any revision but the opportunity to observe the plants growing in their native habitats throughout the seasons provided a broader understanding of all aspects of the species. Thus, plants were observed from the time of emergence in early March to mature fruit production and seed fall in December. Anatomical and cytological studies were done and the evidences used to support the taxonomic treatment. The numerous synonyms associated with the name Melanthium are treated and either placed under that genus, or excluded and assigned to their proper genera. Although the present revision is regional, treating only the North American species, there are four closely related species in eastern Asia, presently treated in the genus Veratrum, which appear to belong to Melanthium. Future revisionary research will treat these taxa.

The institutions whose herbaria were visited, consulted, or whose collections were borrowed include:

Academy of Natural Sciences, Philadelphia.....	(PH)
Bebb Herbarium, University of Oklahoma, Norman.....	(OKL)
British Museum (Natural History), London.....	(BM)
Carnegie Museum of Natural History, Pittsburgh.....	(CM)
Eastern Illinois University, Charleston.....	(EIU)
Gray Herbarium, Cambridge.....	(GH)
Illinois State University, Normal.....	(ISU)
James Madison University, Harrisonburg.....	(JMUH)
Linnean Society, London.....	(LINN)

Longwood College, Farmville, VA.....	(FARM)
Lynchburg College, Lynchburg.....	(LYN)
Missouri Botanical Gardens, St. Louis.....	(MO)
Museum National d'Histoire Naturelle, Laboratoire, Paris.....	(P,P-LA,P-MX)
New York Botanical Gardens, Bronx.....	(NY)
North Carolina State University, Raleigh.....	(NCSC)
Royal Botanic Gardens, Kew.....	(K)
Southern Illinois University, Carbondale.....	(SIU)
Southwest Missouri State University, Springfield.....	(SMS)
State University of Iowa, Eames.....	(ISC)
United States National Arboretum, Washington, D.C.....	(NA)
United States National Herbarium, Washington, D.C.....	(US)
University of Georgia, Athens.....	(GA)
University of Illinois, Urbana.....	(ILL)
University of Maryland, College Park.....	(MARY)
University of North Carolina, Chapel Hill.....	(NCU)
University of Tennessee, Knoxville.....	(TENN)
University of Wisconsin, Madison.....	(WIS)
West Virginia University, Morgantown.....	(WVA)

The abbreviations given in parentheses for each herbarium are according to Holmgren and Keuken (1974) and are used hereafter in the interest of brevity.

Although the group treated here is small, the problems associated with the taxonomy and nomenclature were many. In the past the taxonomy was that of uncertainty or indecision based mainly on personal choice without substantial data or justifications for delimiting the taxa.

Names which could not be typified were used, and although questioned, the names continued to be used. Few efforts were made to correct the nomenclature. Morphological structures were not studied thoroughly and generic placements were based on superficial observations. Diagnostic keys in modern use are overtly contradictory in that the generic key will not key out certain species, and in many cases included erroneous descriptions and confusing illustrations. Concentrated field studies of native populations and ecological complexes previous to this revision were non-existent.

The decision made in this treatment to maintain the genus Melan-thium as distinct from the heterogeneous genus Veratrum is based on thorough taxonomic research. Whether the judgements and reasoning used here are accepted will be determined over time, but accepted or not, this research provides for the first time the proper scientific name for each species, clear descriptions, operative diagnostic keys, and a justifiable generic concept.

TAXONOMIC HISTORY

The hundred years between 1650-1750 involved an intense scientific movement in Europe. The original Fellows of the Royal Society, including Sir John Clayton, Issac Newton, Robert Boyle, Martin Lister, Christopher Wren, John Ray and many other enthusiasts, established sound scientific foundations for the Society and for scientific investigation. When John Ray was elected to membership in 1667, his inspiration along with that of Nehemiah Grew, brought botany into focus as one of the Society's favorite subjects. Over the years the interest of this group had a great and lasting influence on the growth of botanical science (Berkeley, 1963). It was within this frame of scientific thought that the New World exploration brought many interesting and new plants to the research centers in Europe. John Clayton (grandson of Sir John Clayton) came to America in 1720, and while living and working in Gloucester County, Virginia, collected plants extensively, sending them back to the great herbaria of Europe. Among his plants was the first known collection of a species in the genus Melanthium. Melanthium virginicum, collected by John Clayton in Virginia and sent to Gronovius in Holland, was included in Gronovius' (1739) Flora Virginica. Although this is of no nomenclatural significance today, it was destined to become so when Linnaeus, after studying the Clayton collections, among others, included M. virginicum in Species plantarum (Linnaeus, 1753).

Linnaeus (1742) first recognized the genus Melanthium in his Genera plantarum where he included a brief discussion of a pistillate flower. The genus was considered again in 1754, with a more detailed

description of a bisexual flower corresponding to the characteristics which, since that time, have been commonly associated with Melanthium (Linnaeus, 1754). These descriptions were based on observations of the genus by Clayton in Virginia. In the first edition of Genera plantarum (Linnaeus 1737), the name Melanthium Malp., is listed as a synonym under Nigella Tourn., a member of Ranunculaceae, and based upon a wholly different plant.

In Species plantarum Linnaeus (1753) described two species of Melanthium, M. virginicum and M. sibiricum, the two being separated by characteristics of their petals, "ungviculatis" and "sessilibus", respectively. The clawed petal condition evident in M. virginicum became one of the important characteristics used in delimiting the genus. Melanthium virginicum was the name applied to the North American species collected by Clayton, and later by Kalm, in Virginia. The other species was collected by Johann Georg Gmelin in Siberia. Gmelin, a German botanist and geographer, employed by the Russian government, collected in Siberia from 1733 to 1743. Linnaeus acquired the Siberian plants through a circuitous route involving Gmelin's assistant, Georg Steller, who was in trouble with the Russian government and Grigorii Demidov, who finally sent the plants to Linnaeus. For some reason Linnaeus thought it desirable to conceal the origin of this material and he marked it with cryptic signs (Stearn, 1957; Savage, 1945).

Of these two species which initially composed the genus Melanthium, the American species, M. virginicum, became the type of the genus as designated by Britton and Brown in 1913. The other Linnaean species, M. sibiricum, was eventually transferred to the

closely related genus, Zigadenus Michx., by Gray (1837).

A brief digression is in order here to point out that close relationships have been commonly recognized between Melanthium, Zigadenus and Veratrum L. It is important to note here that Linnaeus distinguished between Melanthium and Veratrum, a separation which has been accepted in all major treatments with the exception of Zimmerman's (1958). With the erection of Zigadenus by Michaux (1803), it has been the practice to keep this taxon apart from Melanthium although there have been considerable differences of opinion as to what other taxa should be placed in it.

Linnaeus later included three other species in the genus Melanthium, two from Africa, the other from India. He proposed M. capense in Species plantarum (Linnaeus 1762) based on a collection from the Cape of Good Hope. Melanthium punctatum was described in one of the dissertations on rare African plants and was included in Linnaeus' (1764) Amoenitates academicae. These species have punctate petals and hooded leaves and were transferred to the African genus Androcymbium Willd. in the early 1800's. The last Melanthium mentioned by Linnaeus was M. indicum published in Mantissma plantarum (Linnaeus 1771), the plant apparently coming from India ("Tranquebaria"). This species has been transferred to the genus Iphigenia Kunth. Linnaeus' son proposed four names under his father's genus, also from African collections. Approximately 28 new species or combinations were made under Melanthium between 1762 and 1879 from plants occurring in Africa, mostly from the Cape of Good Hope. This is more than one third of all the names ever used under this genus.

With such acceptance of a vast assemblage of different species

from all parts of the world, and the associated proliferation of names, it is understandable that botanists would attempt to narrow the concept of the genus both morphologically and geographically. A prevalent view was to split the Old World forms from the New World forms. When Willdenow (1803) published Leimanthium, he was dividing Melanthium by proposing the Linnaean name for the Old World species and Leimanthium for the New World species. Rafinesque (1836) suggested the same idea when he erected the genus Evonyxis. Although their nomenclatural combinations were to prove to be superfluous, the ideas for delimiting the species in Melanthium (sen. lat.) were established.

Thunberg's Dissertationes academicae entitled, "Dissertatio Botanico de Melanthio," defended 13 December 1797, was the first comprehensive treatment of Melanthium species known or at least recognized by Thunberg up to that date. The dissertation written by Thunberg and publicly defended by one of his students, as was the custom at that time, included a genus description and listed 20 species with their distinguishing characters, including four new species. Thunberg's concept was extremely broad including in the genus a diverse assemblage of species from throughout the world. The new species that he recognized exhibited characters very close to Veratrum, in fact, many Veratrum species are listed in synonymy under his new Melanthium combinations. The confusion and questionable placement of species between these two genera, as noted throughout this thesis, had an early beginning in Thunberg's work and has continued to the present time.

In Willdenow's (1799) Species plantarum fourteen species of Melanthium are treated. This treatment included a diverse assemblage

of species with world wide distribution: three North American species, one Siberian, eight from the Cape of Good Hope, one each from Tranquebaria and Tierra del Fuego. This treatment, like Thunberg's, permitted diverse morphological characters and wide geographical distribution. It is likely that Willdenow when writing this edition of the Linnean works first realized that the genus had become unwieldy and was prompted to erect, in 1808, his genus Leimanthium for the New World forms. Other botanists were soon to follow his reasoning and further delimit the genus.

In Sprengel's (1830) edition of Linnaeus' Genera plantarum the genus was treated in the sense of the original author. Insertion of the stamens on the claws of the tepals was an important addition in the description which has proven to be one of the definitive characteristics by which the genus is delimited. Melanthium was not treated in de Candolle's (1823-1873) Prodromus nor was the closely related Veratrum. Jussieu (1789) in Genera plantarum lists Melanthium with a very brief description including characters commonly associated with the genus. Veratrum was held distinct in this treatment. Endlicher (1836) placed Melanthium in synonymy under Zigadenus. Veratrum was held separate in this treatment of Melanthaceae. Bentham and Hooker (1883) gave a detailed description of the genus and indicated that the genus consisted of three North American species. Melanthium and Veratrum were held distinct.

Engler and Prantl (1887) treated six genera in the tribe Veratreae, holding Melanthium and Veratrum separate. Only M. virginicum is listed with a geographical range in the North American Atlantic States. Leimanthium Willd. is listed in synonymy. It is

conceivable that Engler and Prantl, recognizing Willdenow's New World Leimanthium, chose to use Melanthium, the correct name for the genus. Why no other Melanthium species is included is not known. In an incomplete monograph on Liliaceae by Krauss (1930) Melanthium was treated as in Die natuerlichen pflanzenfamilien (Engler & Prantl 1887). Veratrum was broadened and included V. parviflorum, V. woodii and V. intermedium.

Although not a taxonomic treatment in a strict sense, an article by Gates (1917), A systematic study of the North American Melanthaceae from a genetic standpoint, is one of the few comprehensive works on the group. Supposed evolution and phylogeny are presented. Melanthium is held distinct from Veratrum and includes the two commonly recognized species, M. virginicum and M. latifolium plus M. monoicum Walt. which is presently considered a synonym of M. virginicum. Gates concluded that "Zigadenus has clearly led to Melanthium, and Melanthium to Veratrum through the loss of the glands on the perianth segments." It was Gates belief that Veratrum parviflorum was "entangled with Melanthium" and "stands intermediate between two genera." Assuming that there is a total absence of tepal glands in this species, Gates placed it in Veratrum. In this study as in numerous others, the glandular condition led to uncertainties in generic distinctions. Baker (1879), in one of his many papers in attempting to monograph the genera and species of Liliaceae, treats under the suborder "Colchicaceae," 39 genera and 150 species which included Melanthium. The two commonly recognized species, M. virginicum and M. latifolium were included with no significant changes in the treatments of these species from that of the original authors. Baker also treated nine

species of Veratrum, including V. parviflorum, V. woodii and V. intermedium. Curiously, under V. parviflorum he lists M. monoicum Walt. as a synonym.

Melanthium has been included in a considerable number of floristic treatments during the last 150 years. In addition to the importance of diagnostic keys, descriptions and distributions, these treatments are of interest here in the nomenclatural disposition of M. parviflorum; whether it is treated under Melanthium or under Veratrum. Most such works should be approached with some skepticism, in the case of Melanthium, since many are unreliable in use of good diagnostic characters, operative diagnostic keys, thorough descriptions and representative illustrations. An example is Gray's Manual (Fernald, 1950) in which the generic key uses the presence of tepal glands in Melanthium to distinguish it from Veratrum, and then in the species key uses the absence of glands to separate M. parviflorum from the other two species. In another widely used floristic work, Britton and Brown Illustrated Flora (Gleason, 1952), the flower illustrations do not match with the vegetative illustrations within the species. Both of these floras indicate that in the closely related Veratrum no glands occur on the tepals which is simply incorrect. The glandular condition has been one of the sources of confusion in delimitation of these genera.

The early floristic treatments (Torrey 1824, 1826; Gray 1848; Chapman 1860; Small 1903; Britton & Brown 1913) included the family Melanthaceae (Melanthiaceae in Small) in which Melanthium was treated and the species therein listed. All of these floras included M. virginicum and only Chapman omitted M. latifolium. Small and Britton

and Brown used the M. latifolium while the others listed used the name M. hybridum. In addition, Torrey recognized M. glaucum Nutt. and M. dioicum Walt., and Small included his M. dispersum. In the closely related Veratrum, Chapman was the first to include V. parviflorum and V. intermedium. Small's treatment of Veratrum included V. parviflorum and V. woodii and V. intermedium while Britton and Brown listed V. parviflorum and V. woodii.

In the sixth edition of Gray's Manual (Watson & Coulter, 1889) and in subsequent editions, Melanthium parviflorum is used. Watson (1879) gives no explanations for this name in any of his works. The New Britton and Brown (Gleason, 1952) retains the generic alignment of the previous edition but uses the name M. hybridum.

State floras (Strausbaugh & Core, 1970 ; Radford, Ahles & Bell 1964; Steyermark 1962) add nothing new to the taxonomic/nomenclatural treatments of Melanthium. Once again the questions lie in the placement of M. parviflorum.

The most significant treatment in the later history of Melanthium came about indirectly in Zimmerman's Monograph of Veratrum (1958) in which he submerged Melanthium in that genus. As indicated throughout this dissertation, close relationships between Veratrum and Melanthium have been recognized almost from the origin of the two generic concepts. Placement of species in the two genera become a matter of arbitrary choice. Seldom were reasons given for placement, and where explanations were given they were without substantial knowledge of the entities involved. An example of this is the continual misconception of absence of tepal glands in M. parviflorum and based on this, its placement in Veratrum.

Zimmerman's monographic work on Veratrum is most comprehensive, and while incomplete in the nomenclatural aspects of such monographic research, he presented strong arguments for his delimitation of taxa. Pubescent inflorescences and winged seeds were used as unifying characteristics of Veratrum although there are exceptions within some of the taxa.

Due to the relationship of Zimmerman's research and my treatment of Melanthium herein, a brief synoptic outline of his Veratrum classification is presented here.

Veratrum (Zimmerman, 1958)

Section: Alboveratrum Loes. f.

Stem stout, leafy to the inflorescence; rhizomes thick, elongated; tepal glands marginal, often confluent at the base, dark, little thickened; tepal margins usually erose to denticulate; anthers usually persistent into fruit; style bases ascending, remaining together in fruit; seeds broadly winged.

<u>V. viride</u>	E United States; E Canada
<u>album</u>	Central Europe to Turkey and the Caucasus
<u>articum</u>	Skandinavia to N Central Siberia
<u>misae</u>	N Central Siberia to W Alaska
<u>asiaticum</u>	Central to SE Siberia; Manchuria; Korea; N China
<u>dahuricum</u>	C Siberia to Manchuria
<u>puberlum</u>	C & SW China
<u>chenkowense</u>	C China
<u>dolichopetalum</u>	Korea

<u>grandiflorum</u>	Korea; Quelpaert; Japan
<u>alpestre</u>	N Japan
<u>oxysepalum</u>	Kamchatka; Kurile Islands
<u>attuense</u>	Attu Island
<u>eschscholtzii</u>	S Alaska to Idaho & N California
<u>jonesii</u>	W Idaho; E Washington; E Oregon
<u>tenuipetalum</u>	Colorado; New Mexico
<u>caudatum</u>	W Washington; W Oregon
<u>californicum</u>	California & Idaho south to Mexico
<u>insolitum</u>	W Oregon; N California
<u>stamineum</u>	Japan

Section: "Meloveratrum"

Stem slender; largest leaves basal, pubescent; root stout; bulb large; rhizome short, distinct; tepal glands on each side of midrib, each gland thickened near the center of the tepal; tepal margins deeply fimbriate; anthers soon deciduous; style bases ascending, remaining together in fruit; seeds wingless.

V. fimbriatum California

Section: Fuscoveratrum Loes. f.

Stem stout to slender; leaves reduced upward; rhizome often wanting; tepal glands confluent into a single area extending to the margins over the basal $2/5 - 1/2$ of the tepal; tepal margins entire; anthers fugacious; style bases strongly diverging, far apart in fruit; seeds winged.

V. nigrum E Asia; E & SE Europe

japonicum E Asia

<u>maximowiczii</u>	E Asia
<u>longebracteatum</u>	E Asia
<u>reymondianum</u>	E Asia
<u>maackioides</u>	E Asia
<u>coreanum</u>	E Asia
<u>maackii</u>	E Asia
<u>oblongum</u>	E Asia
<u>kiulingianum</u>	E Asia
<u>schindleri</u>	E Asia
<u>chingianum</u>	E Asia
<u>minutiflorum</u>	E Asia
<u>formosanum</u>	E Asia
<u>atroviolaceum</u>	E Asia

Section: "Telandrium"

Stem slender to delicate; leaves mostly basal; rhizomes reduced; tepal glands distinctly two, one on each side of the midrib; tepal margins entire to undulate, bases narrowed to attenuate; filaments inserted on the basal portion of the tepals; anthers fugacious; style bases strongly diverging, far apart in fruit; seeds winged.

<u>V. shanense</u>	SW China
<u>anticleoides</u>	Sachalia & adjacent Siberia
<u>taliense</u>	SW China
<u>cavaleriei</u>	SW China
<u>mengtzeanum</u>	SW China
<u>virginicum</u>	E United States

<u>hybridum</u>	E United States
<u>parviflorum</u>	E United States
<u>woodii</u>	E United States

Zimmerman's submersion of Melanthium in Veratrum is the most severe treatment of the genus. This was done on the basis of two characters common to both genera, pubescence and seed shape. Although these characters are used as the unifying basis for Veratrum there are exceptions to both features in the genus. In section "Telandrium" the inflorescence of V. anticleoides is wholly glabrous and in section "Meloeveratrum" V. fimbriatum has wingless seeds. Here are exceptions to major characters in Veratrum, characters used to justify generic changes.

There are many variable and exceptional characters displayed by the components of Veratrum as delimited by Zimmerman. The glands of section Alboveratrum are so unique that Zimmerman admitted "that a good case could be made for treating this section as a separate genus." Veratrum fimbriatum varies so greatly in tepal shape, tepal glands and seed shape that it alone is placed in a section. Species of section Fuscoveratrum are closely allied to those in section "Telandrium."

"Telandrium," the section in which the Melanthium species are included, is a heterogenous section including species with the unique tendency in Veratreae, for the stamens to be adnate to the tepals. Other characteristics shared by species in this section are, attenuation of tepals toward their bases, two distinct and separate non-marginal tepal glands (except in Veratrum shanense) and a geographic range coinciding with the two main refugia of ancient

temperate Arcto-Tertiary floras, eastern Asia and eastern United States.

Zimmerman (1958) indicated that his sectional classification of Veratrum is tenuous and states that after the monograph was written another system of classification was erected, which is composed of two sections and five subsections. A later paper (Kupchan et al., 1961), of which Zimmerman was one of the authors, did not incorporate this new system.

The history of the genus Melanthium, as circumscribed here, began with the Linnean species, M. virginicum in 1753. The next species added was M. latifolium Desr. in 1797 followed closely by M. parviflorum, first described as Veratrum parviflorum by Michaux in 1803, and transferred by Watson in 1879. The final species, V. woodii, was described by Wood in 1848 and is transferred to Melanthium herein. The major problems in the history of the genus are problems of generic placement owing to the close association with Veratrum.

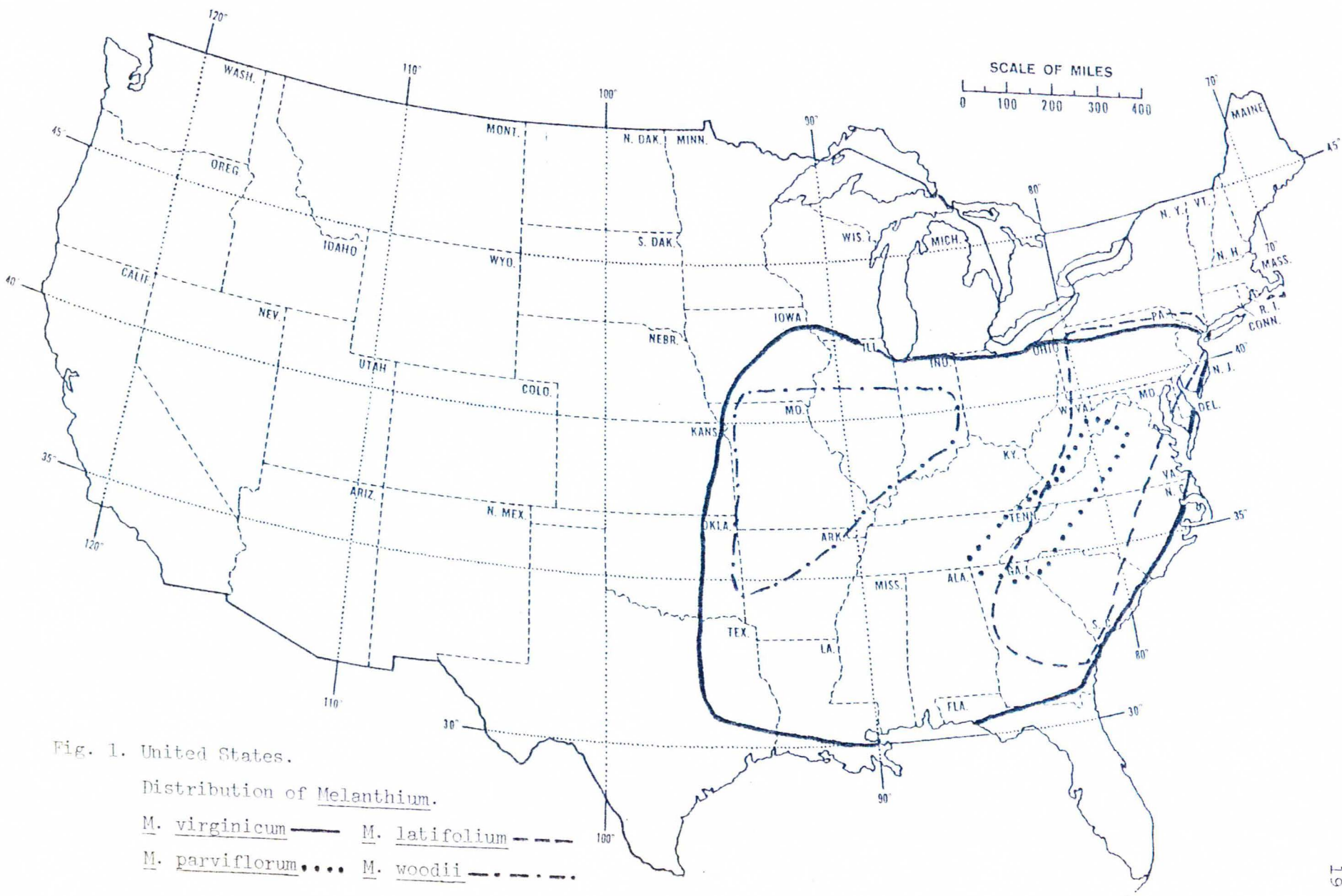
DISTRIBUTION AND ECOLOGY

In North America the distribution of Melanthium extends from central Iowa eastward to southern New York, south to northern Florida and eastern Texas (Fig. 1). The type species, M. virginicum, is found over this entire range and grows sympatrically with the other three species. A specimen of M. virginicum from Robertson County, Texas, is the western most collection found in this study. The most northern collection examined was M. virginicum from Allamakee County, Iowa. This species was collected along the Atlantic Coast from Suffolk County, on Long Island, New York, south to Chatham County, Georgia. Coastal populations, however, are not frequent.

Melanthium latifolium has the second widest distribution of the four species (Fig. 1). This species occurs mainly in the mid-Appalachian Mountains with the northern limit of the range in Fairfield County, Connecticut, and the southern limit in Burke County, Georgia. Major populations of this species are in the mountains of West Virginia, Virginia and North Carolina.

The most restricted species in terms of its range is Melanthium parviflorum. This species grows on the crests and higher slopes of the mid-Appalachian Mountains from Hardy County, West Virginia, south to Clay County, North Carolina (Fig. 1). Although the range is narrow, the number of plants per population is the greatest of the New World Melanthium species.

Melanthium woodii is distributed mainly in the Ozark Plateaus (popularly called the Ozark Mountains) and the southern section of the Central Lowlands (Fig. 1). It occurs mainly in Missouri, Illinois, and



Indiana, with disjuncts in three more eastern states. Zimmerman (1958) included Montgomery County, Ohio, in the distribution of the species, but this was based on plants "cultivated at Dayton" (Herb. Morgan 2515 - ISC). The most northeastern population located in this study was from Franklin County, Indiana.

Disjunct populations occur east of the Ozark Range in Polk County, North Carolina, Clay, Dekalb and Walker counties, Georgia, and Gadsden County, Florida. The assumption that these populations are native disjunct populations is not without question. Zimmerman (1958) reported that both Freeman and Wherry "thought the Polk County population to be native." Zimmerman lists a Freeman collection (53280 - WIS) from this site. The population contained approximately 85 plants in 1953 but was reduced to 31 by 1956, when the usual three to four plants failed to flower. Radford, Ahles and Bell (1964) do not include this species in their Manual of the Vascular Flora of the Carolinas.

Of the Georgia disjuncts only the Eggert specimen (MO) collected in Dekalb County in 1897 was studied. The specimen is non-flowering but is unquestionably Melanthium woodii. Zimmerman (1958) reported a vegetative specimen (Duncan and Hardin 15968 - GA) from Walker County but questions its identification (possibly M. hybridum). He also reported the other Georgia specimens (Thorne 4925 - ISC, and Thorne 6995 - GA) from Clay County.

Chapman (1860) reported Melanthium woodii (as M. intermedium) from "middle Florida" apparently intending to indicate near the middle of the State's northern boundary because the herbarium specimen (Chapman s.n. - GH) collected in 1836 is from Gadsden County, Florida.

Little information could be obtained from taxonomists in the areas in which these disjunct populations occur as to whether the herbarium specimens are representative of native and currently existing populations of Melanthium woodii (Radford, 1978; Hardin, 1978; Ahles, 1978, per. comm.).

The difficulties in locating populations of Melanthium species emphasizes the current lack of knowledge of floristic botany and certainly discredits the ideas of more quantitative botanists that studies of the temperate flora are exhausted with little need of future investigation. In groups such as Melanthium, where population size is very small, continuing field studies afford excellent opportunities to study what appears to be declining populations of a primitive group of angiosperms. In surveying collection dates of 277 herbarium specimens of Melanthium virginicum less than 20 percent were collected in the past three decades. Over 30 percent were collected prior to 1900. The same trend exists in the collection of the other species with only seven percent of the M. woodii sheets studied having been collected in the past 20 years. The largest number of collections were in the 1930's. Over 38 percent of the M. woodii specimens examined were collected in that decade. The relatively few collections of the past decade is due, in part, to less floristic research. This trend could be related to gradually diminishing populations of Melanthium, especially of the rare species, M. woodii.

The Melanthium species are primarily plants of the Eastern Deciduous Forest Biome, and although not abundant, differ in flowering time and stature from the other herbaceous plants of the ground cover. This is especially true of the large, light colored inflorescences of

M. virginicum and M. latifolium. The dense, darkly shaded woodland habitats are often interrupted by the tall, graceful, creamy-white panicles of bunchflower in late July, long after the conspicuous flowers of the spring flora have disappeared. Melanthium is found in most associations of the Eastern Deciduous Forest Biome, being most common in Oak-Hickory, Mixed Mesophytic and Beech-Maple associations of the mid-Appalachians and infrequent in the pine subclimaxes along the eastern coast and the boreal zones of the higher Appalachian Mountain crests. In the western range, where only M. virginicum and M. woodii occur, prairie areas are frequent but the deep coves, ravines and gorges afford favorable habitats for mesophytic communities; sugar maple, white oak and red oak are abundant. The contrast is pronounced between the open xeric plateau forest of low-statured trees, beneath which is a sparse herbaceous layer containing xeric prairie species, and the comparatively luxuriant cove and gorge forests with mesophytic undergrowth. Such mesophytic sites provide a suitable habitat for Melanthium. In the forest-prairie transition zones west of the Interior Highlands in Texas, Oklahoma, western Missouri, eastern Kansas and southern Iowa, the sparse Melanthium populations are confined to valley and ravine slopes.

Although the range of Melanthium is rather wide, the habitat type is narrow. Melanthium virginicum is most commonly found in bogs, marshes, swamps, seepage areas adjacent to streams or other such high organic, water-laden soils. The other three species most frequently grow on moist, rich slopes under a deciduous canopy. The ecological complexes of the species are somewhat altitudinally segregated with M.

virginicum in the lowlands, M. latifolium and M. woodii on the slopes and M. parviflorum on or near the mountain crests. However, M. latifolium and M. parviflorum populations overlap in some areas. Mixed populations were found at Peaks of Otter and Elliot Knob, in Virginia. Melanthium parviflorum grows at the highest elevations with many specimens being collected in the high mountainous areas of western North Carolina and eastern Tennessee. A specimen (collector unknown 4756 - US) from the spruce-fir zone on the upper slopes of Mt. Mitchell, elevation 6684 ft. (2037 m), the highest point east of the Mississippi River, represents the highest collection site known. The canopy of Picea rubens and Abies fraseri with underlying Rhododendron catawbiense in dense thickets are associates of M. parviflorum, atypical of the usual deciduous floristic complexes.

A population of Melanthium virginicum, in an ecosystem typical of this species, located in the northern Massanutten Mountains of Virginia, was studied most thoroughly. The habitat known as Mudhole Bog, is in Powell's Fort Valley, Shenandoah County, Virginia. The small mountain valley is at an elevation of 1500 ft. (458 m). Technically, the habitat is not a true bog although certain bog characteristics are present such as a low pH (5.0) and Sphagnum forming deep, black, peaty soil. The spring-fed area is poorly drained providing the sphagnum mat with ample water throughout the year. The 10000 sq. m. bog contains approximately 120 plants of Melanthium. Over five growing seasons that this population was studied an average of 20 plants per season produced flowers.

The bog is composed of flora greatly varying from the surrounding regional forest type, a xeric Oak-Hickory Association. The bog canopy

includes Fraxinus nigra (a northern species, reaching the southern limit of its range at this station), Liriodendron tulipifera, Acer rubrum, Quercus alba and Pinus strobus. Lower strata includes Viburnum acerifolium, Dirca palustris, Alnus serrulata, Physocarpus opulifolius, Lindera benzoin, Cornus florida and Kalmia latifolia. Some herbaceous associates of Melanthium virginicum making up the dense ground cover are Amianthium muscitoxicum, Orontium aquaticum, Chamaelirium luteum, Dodecatheon meadia, Trautvetteria caroliniensis, Caltha palustris, Thalictrum polygamum, Habenaria lacera, Pogonia ophioglossoides, Cypripedium acaule, Galium asprellum, Agrimonia pubescens, Chelone glabra, Lobelia puberula and L. cardinalis, Polygonum sagittatum, Senecio aureus, Cirsium muticum and Chrysogonum virginianum. Very tall clumps of Osmunda cinnamomea and O. regalis form a dense ground cover. Onoclea sensibilis, Thelypteris noveboracensis and Polystichum acrostichoides are common. The bog's unique floristic composition is further emphasized by the presence of Ophioglossum vulgatum and Isoetes engelmannii, two extremely rare plants in this region.

The tall, graceful Melanthium virginicum with basal leaves embedded in the dense bog ground cover produces an inflorescence of creamy-white flowers in mid-summer which is in striking contrast to the other herbaceous associates. This species is not abundant, the local populations are small, and like this Massanutten population, it is often found associated with other rather rare species growing in interesting and unique botanical complexes.

Melanthium latifolium was observed in the field at Stony Man Mountain, the second highest point (elev. 4010 ft. - 1225 m) in Shenandoah National Park, in the Blue Ridge Mountains of Virginia. The population

of approximately 50 plants is located below the crest on a north-east facing slope under an Oak-Hickory canopy. Over a five year observation period only seven plants produced flowering stalks. Three of these were in 1974 when an insect infestation defoliated the canopy. Data are not sufficient to support any hypothesis about the effect of light on flowering in this species.

The floristic complex on Stony Man Mountain is typical of the Oak-Hickory Association. Quercus rubra, Q. prinus, Q. velutina, Carya glabra, and C. tomentosa, make up the canopy. Associates in this stratum are Robinia pseudoacacia, Betula lutea and occasionally Acer rubrum. Stump sprouts of Castanea dentata are abundant. The lower strata woody forms include Acer pensylvanicum and A. spicatum, Nyssa sylvatica, Hamamelis virginiana, Menziesia pilosa, Rubus odoratus and Kalmia latifolia. Some herbaceous associates of Melanthium latifolium are Amianthium muscitoxicum, Silene stellata, Zizia aptera, Dioscorea villosa, Eupatorium rugosum, Aster divaricatus and A. microphyllus, Solidago arguta, S. curtissii and S. hispida, and finally Hieracium paniculatum. The few flowering stalks of M. latifolium emerge above a dense cover of Dennstaedtia punctilobula. This slope habitat is typical of the rocky, well-drained soil in which M. latifolium is most commonly found. Although the soil appears dry the numerous and deeply penetrating roots are located well within a moist rhizosphere.

Two mid-Appalachian populations of Melanthium parviflorum were studied, one on Reddish Knob, elev. 4397 ft. (1340 m), Augusta County, Virginia, in the Shenandoah Mountain range, and the second on North Mountain, elev. 4400 ft. (1341 m), Pendleton County, West Virginia. The ecological complexes are very similar to the ones in which M.

latifolium is found. The canopy is typical of the regional Oak Forest. The shrub layer at Reddish Knob contains some woody associates, Pyrus americana, Virburnum acerifolium, Corylus americana and C. cornuta, not seen at the other Melanthium habitats studied in the field. The constant associate, Amianthium muscitoxicum along with Campanula americana, Disporum langinosum, Aster acuminatus, Eupatorium rugosum and E. purpureum, and Prenanthes trifoliata form the ground cover. Dennstaedtia punctilobula, Thelypteris noveboracensis, Dryopteris spinulosa, D. marginalis, Polystichum acrostichoides and Polypodium virginianum compose a heavy ground cover. On North Mountain, Betula papyrifera, found in one of its most southern stands, is the canopy species associated with a large population of M. parviflorum.

The Virginia population of Melanthium parviflorum at Elliot Knob, elev. 4460 ft. (1363 m), in Augusta County, is in the spruce zone on the mountain crest. The small population is sheltered by Picea rubens and a dense shrub layer of Kalmia latifolia. The environmental factors are harsh as evidenced by the krumholtz vegetation.

Although numerous attempts to locate populations of Melanthium woodii were made, I was unsuccessful in finding a single population with plants producing flowers. As a result, field studies were not done. Herbarium specimen labels and botanists contacted in attempts to locate this rare plant describe its habitat as moist, rich, north-facing slopes under deciduous canopies. In the Ozark Plateaus such habitats are most commonly along river bluffs and ravines.

The rich forests of the mid-Appalachians support the largest populations of Melanthium. If herbarium specimens produce valid

distribution data, the center of distribution of M. virginicum, M. latifolium and M. parviflorum is in the tristate area of West Virginia, Virginia and North Carolina. Approximately the same numbers of each species have been collected in each of these three states. Most specimens of M. woodii observed were collected in Missouri and Illinois. Figures 2 - 26 show the county distributions of Melanthium in each state based on known herbarium specimens.



Fig. 2. Alabama. Distribution of Melanthium.

M. virginicum ●

M. parviflorum ▲

M. latifolium ■

M. woodii ○

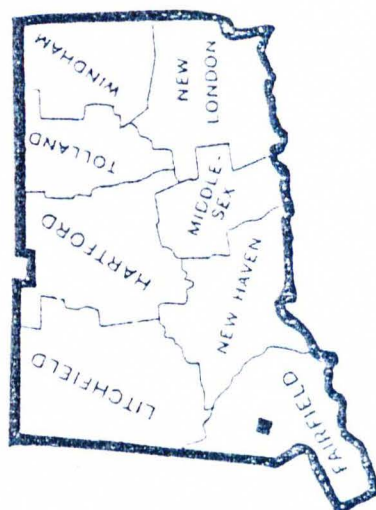


Fig. 4. Connecticut. Distribution of Melanthium.

<u>M. virginicum</u>	●	<u>M. latifolium</u>	■
<u>M. parviflorum</u>	▲	<u>M. woodii</u>	○

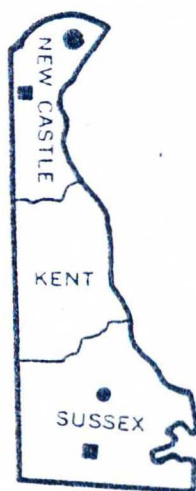


Fig. 5. Delaware. Distribution of Melanthium.

<u>M. virginicum</u>	●	<u>M. latifolium</u>	■
<u>M. parviflorum</u>	▲	<u>M. woodii</u>	○

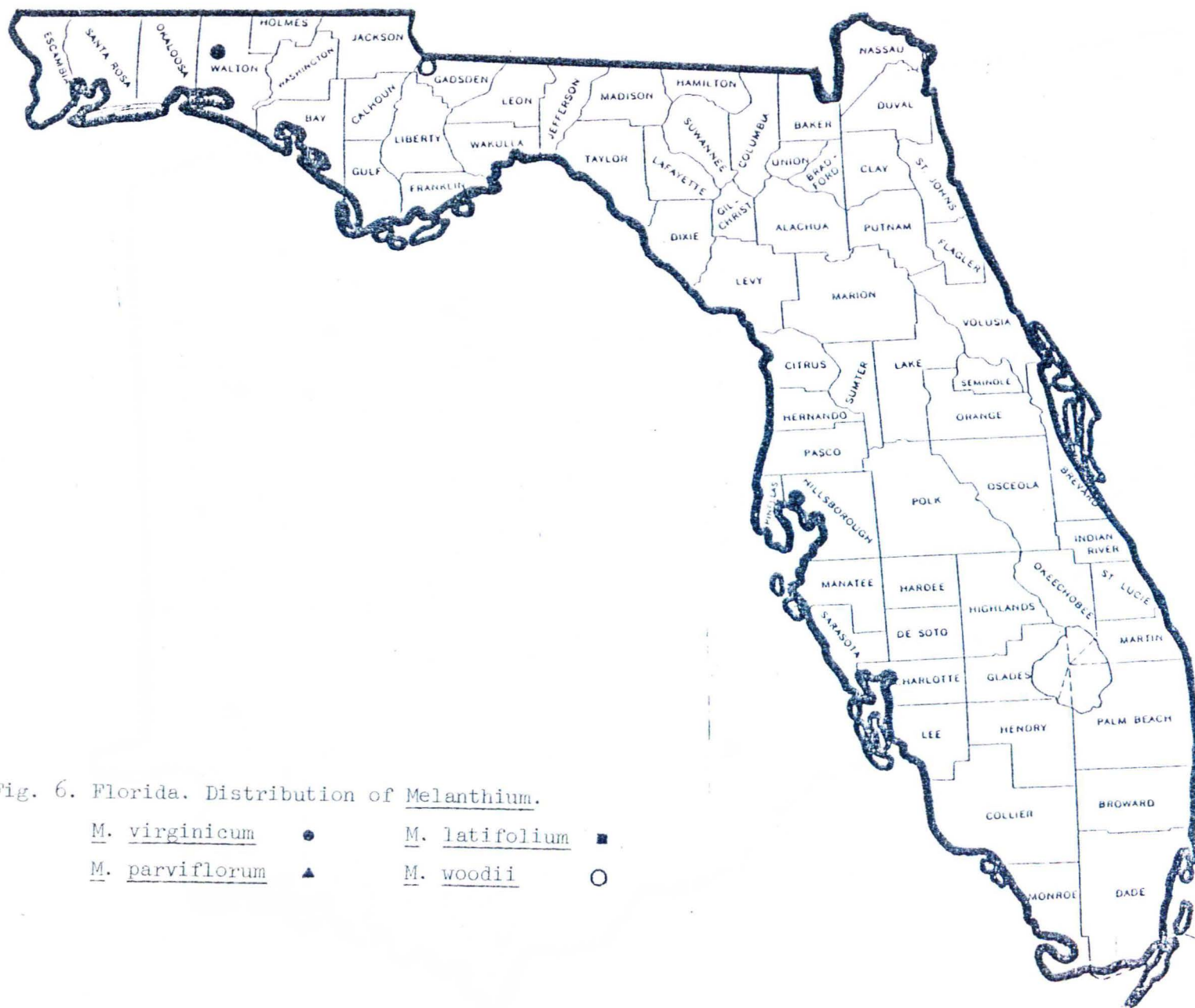


Fig. 6. Florida. Distribution of *Melanthium*.

M. virginicum ● *M. latifolium* ■
M. parviflorum ▲ *M. woodii* ○



Fig. 7. Georgia. Distribution of Melanthium.

<u>M. virginicum</u>	●	<u>M. latifolium</u>	■
<u>M. parviflorum</u>	▲	<u>M. woodii</u>	○

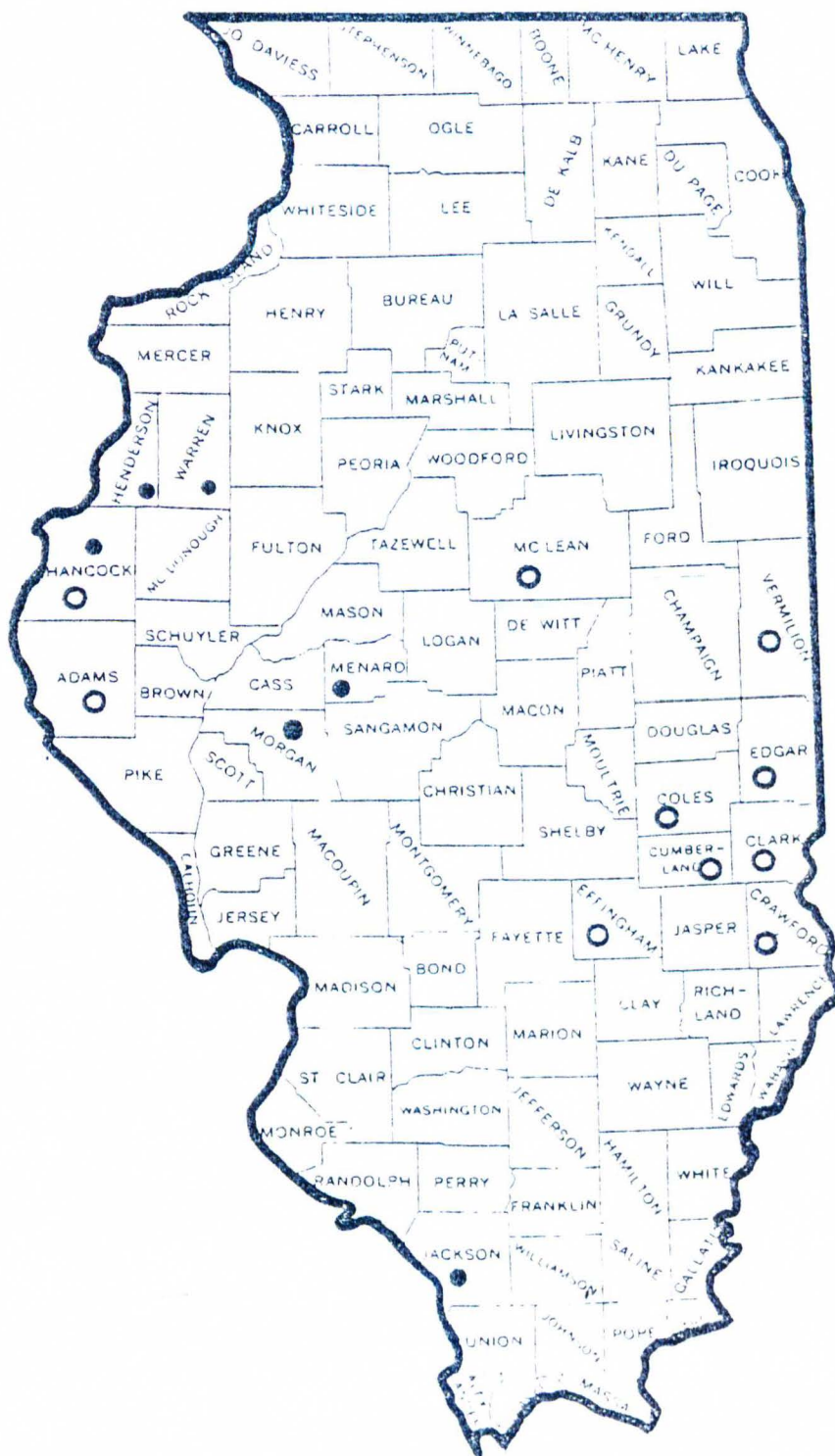


Fig. 8. Illinois. Distribution of Melanthium.

<u>M. virginicum</u>	●	<u>M. latifolium</u>	■
<u>M. parviflorum</u>	▲	<u>M. woodii</u>	○

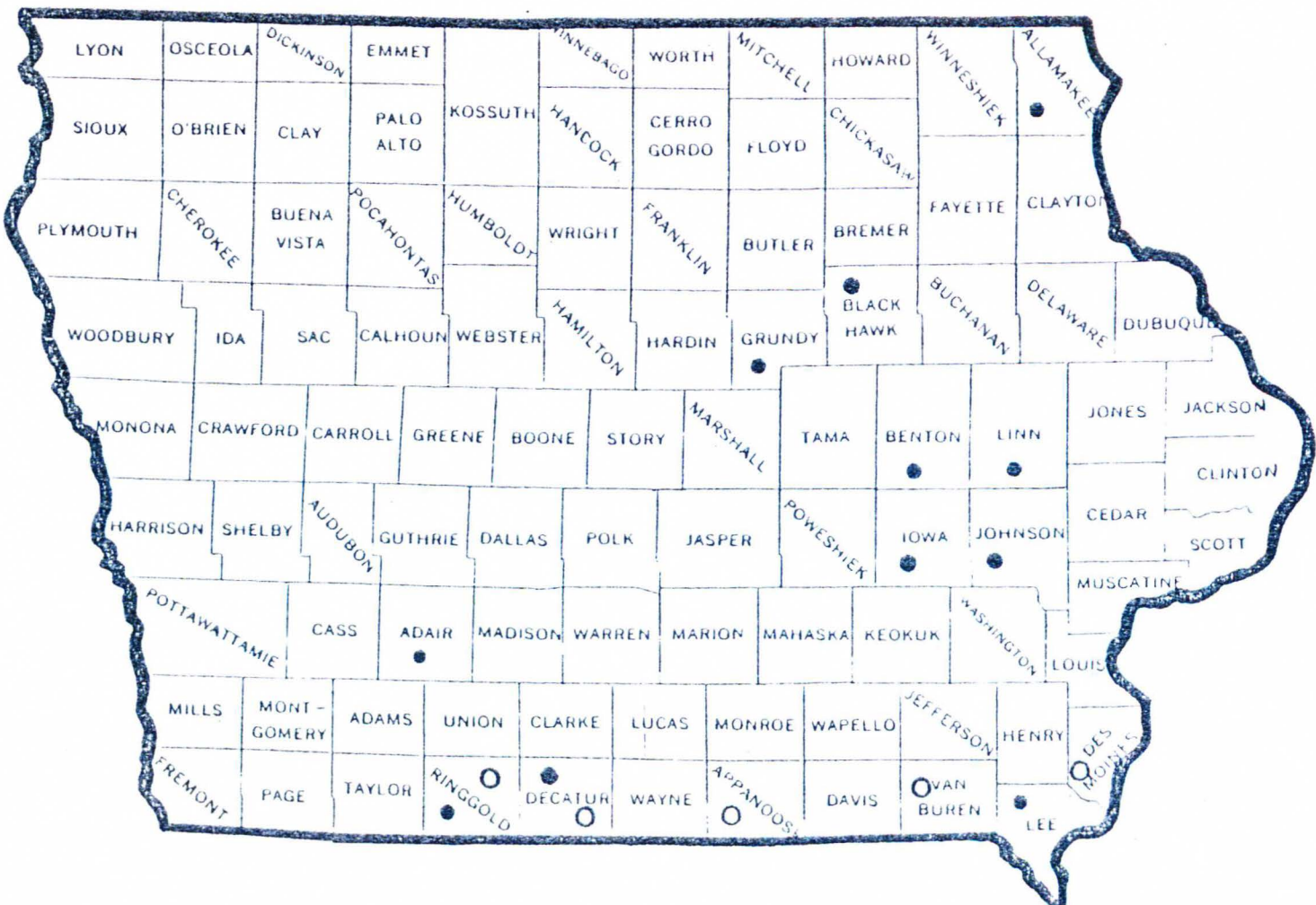


Fig. 9. Indiana. Distribution of Melanthium.

<u>M. virginicum</u>	●	<u>M. latifolium</u>	■
<u>M. parviflorum</u>	▲	<u>M. woodii</u>	○

FIG. 10. Iowa. Distribution of *Melanthium*.

M. virginicum ●
M. latifolium ■
M. parviflorum ▲
M. woodii ○



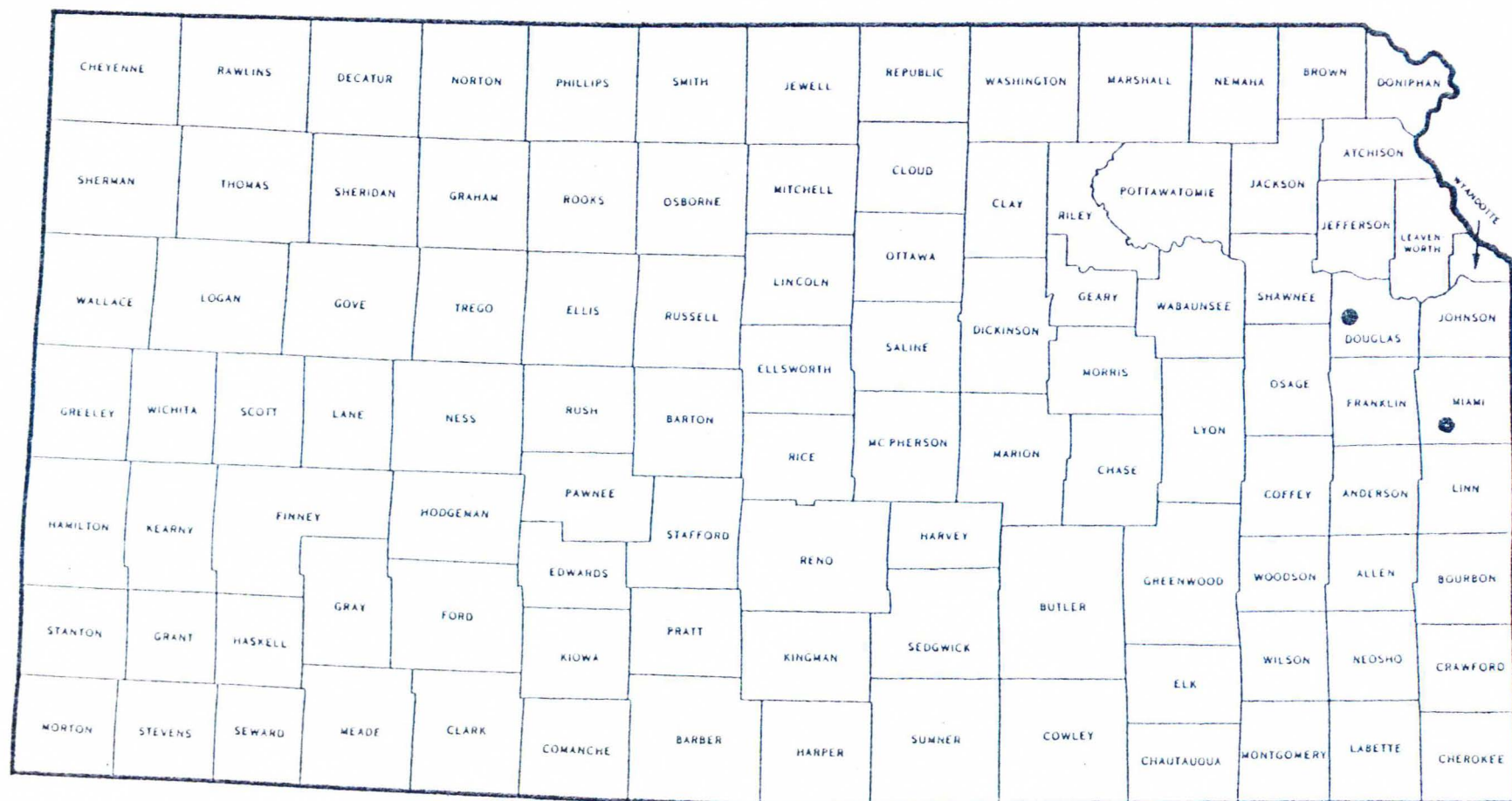


Fig. 11. Kansas. Distribution of *Melanthium*. *M. virginicum* ● *M. latifolium* ■ *M. parviflorum* ▲
M. woodii ○

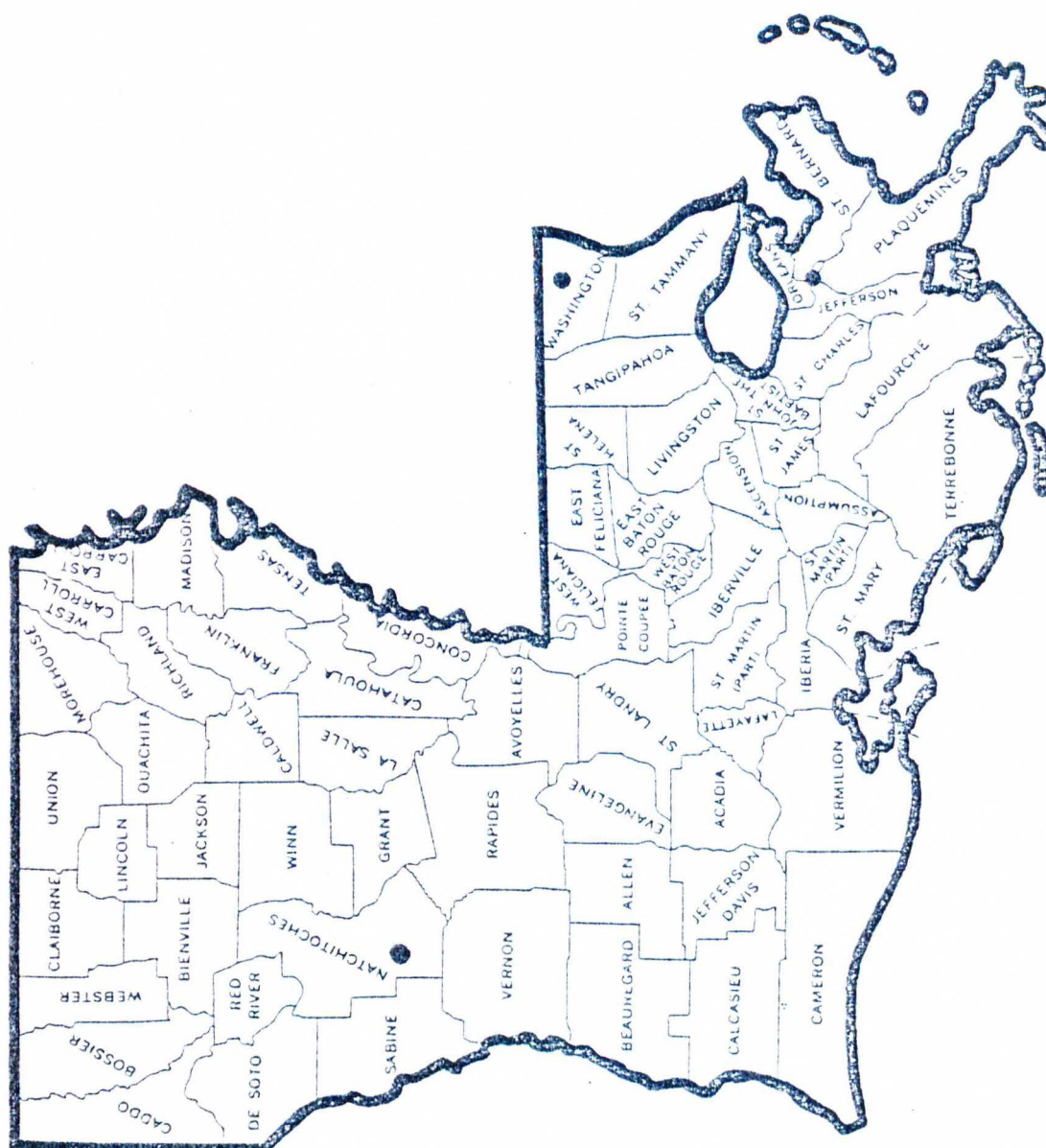


Fig. 12. Louisiana. Distribution of Melanthium.

M. virginicum ●

M. latifolium ■

M. parviflorum ▲

M. woodii ○

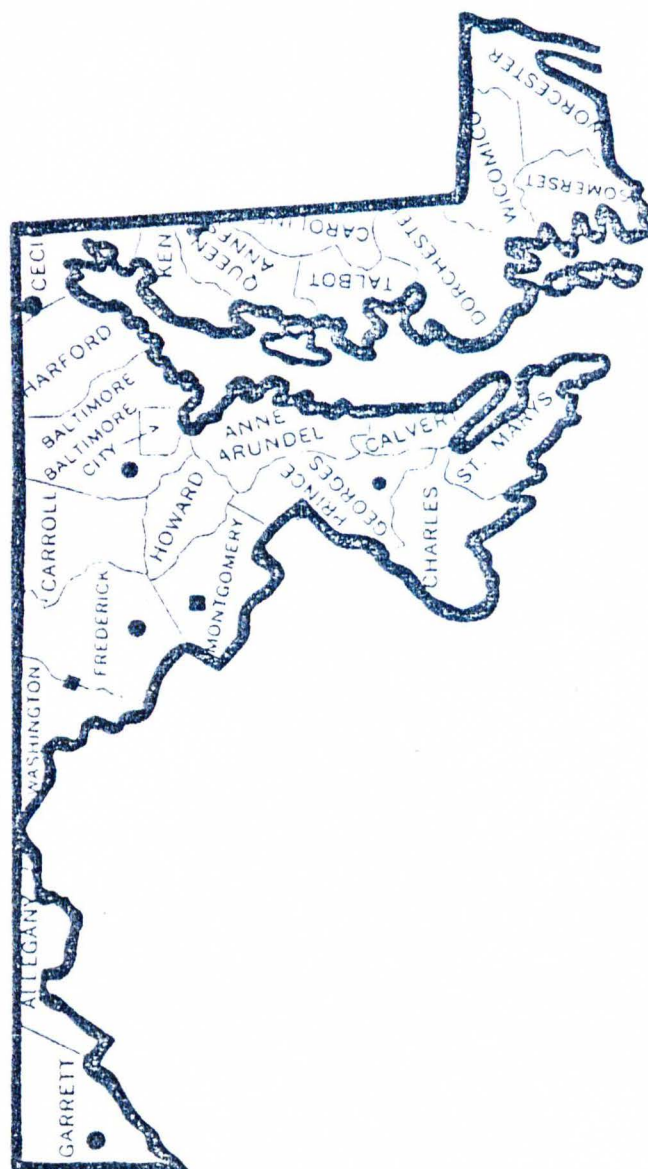


Fig. 13. Maryland. Distribution of *Melanthium*.

<i>M. virginicum</i>	●	<i>M. latifolium</i>	■
<i>M. parviflorum</i>	▲	<i>M. woodii</i>	○

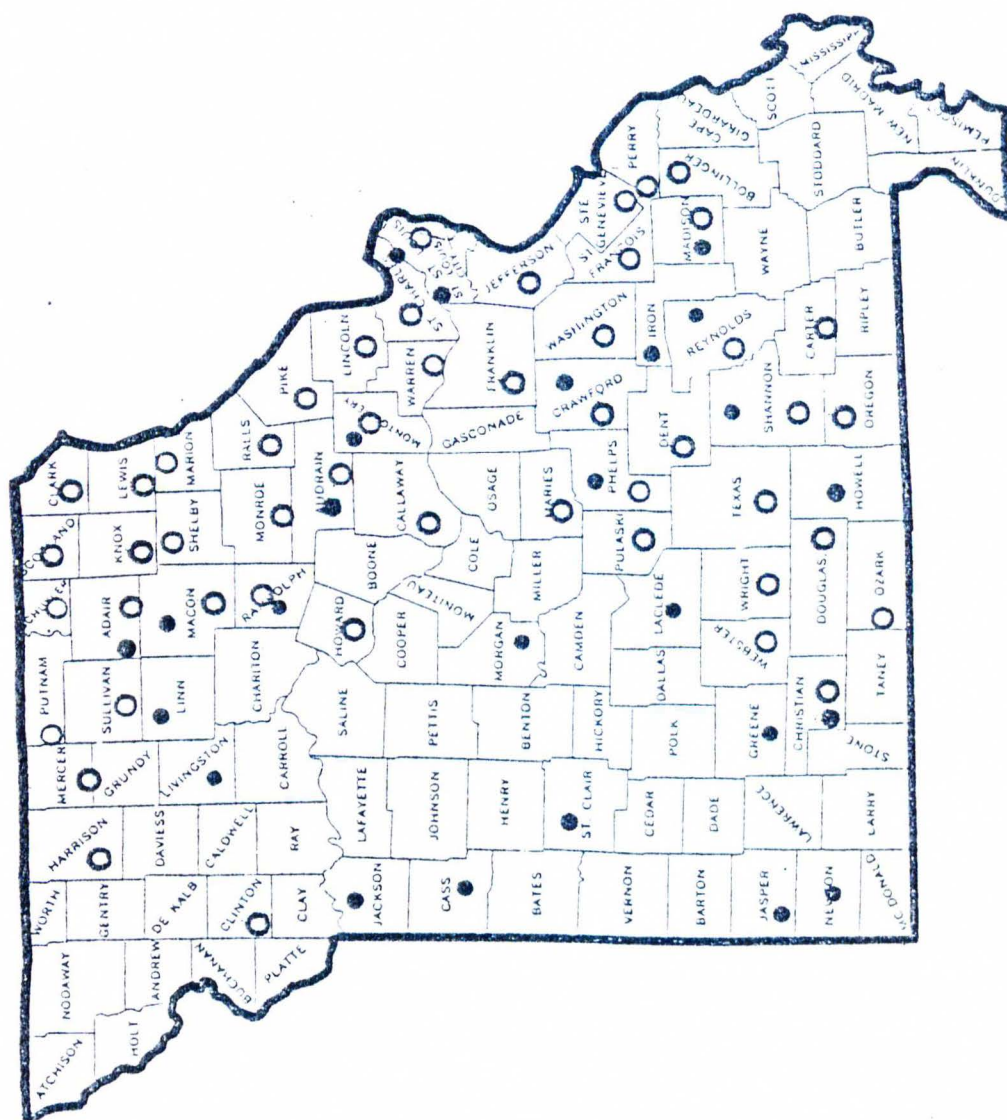


Fig. 15. Missouri. Distribution of Melanthium.

<u>M. virginicum</u>	●	<u>M. latifolium</u>	■
<u>M. parviflorum</u>	▲	<u>M. woodii</u>	○

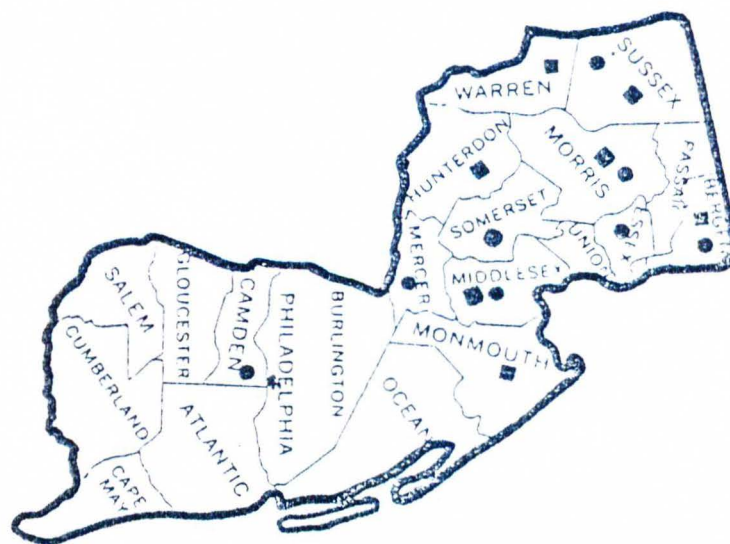


Fig. 16. New Jersey. Distribution of *Melanthium*.

M. virginicum ●

M. latifolium ■

M. parviflorum ▲

M. woodii ○

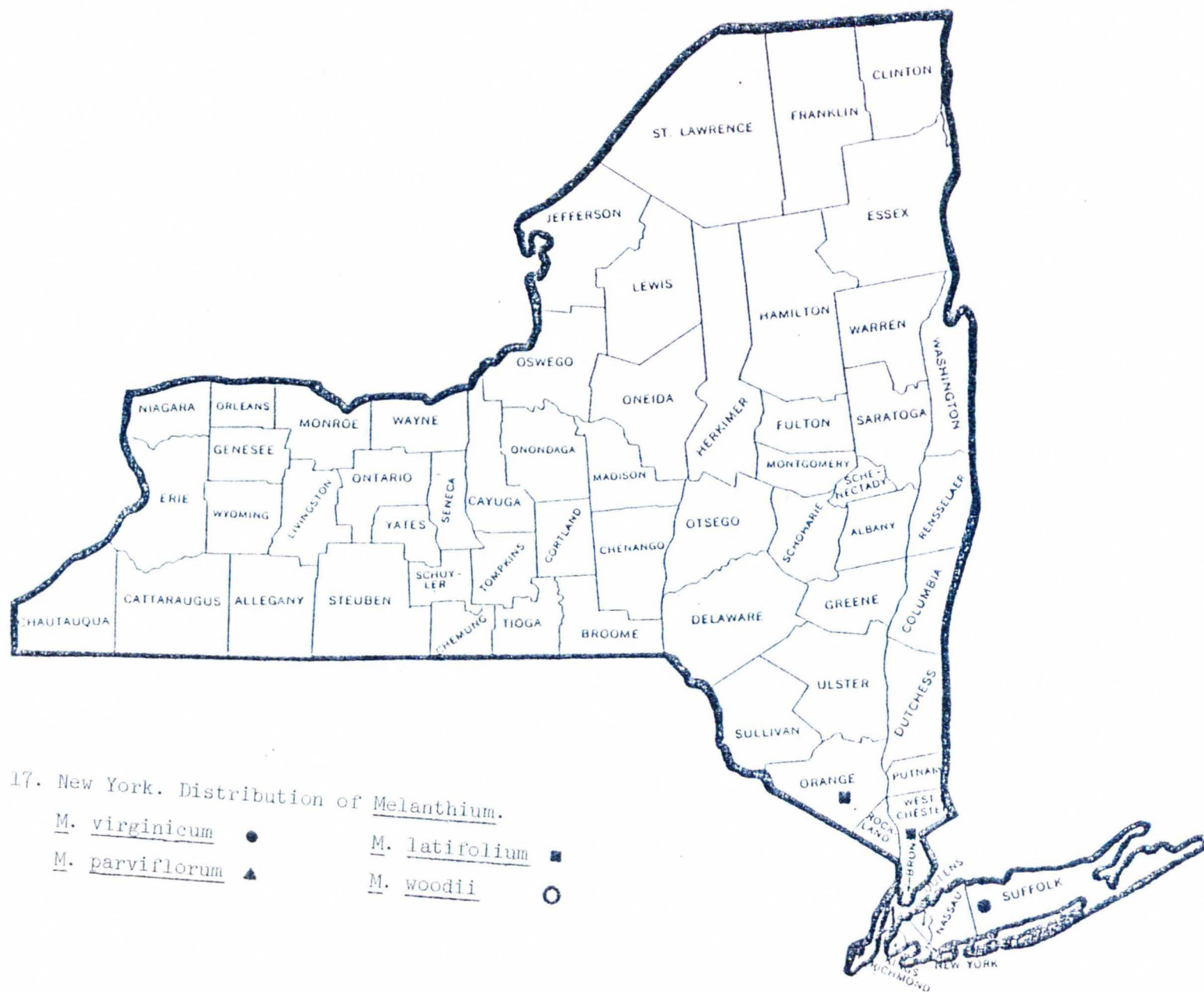


Fig. 17. New York. Distribution of *Melanthium*.

M. virginicum ●

M. latifolium ■

M. parviflorum ▲

M. woodii ○

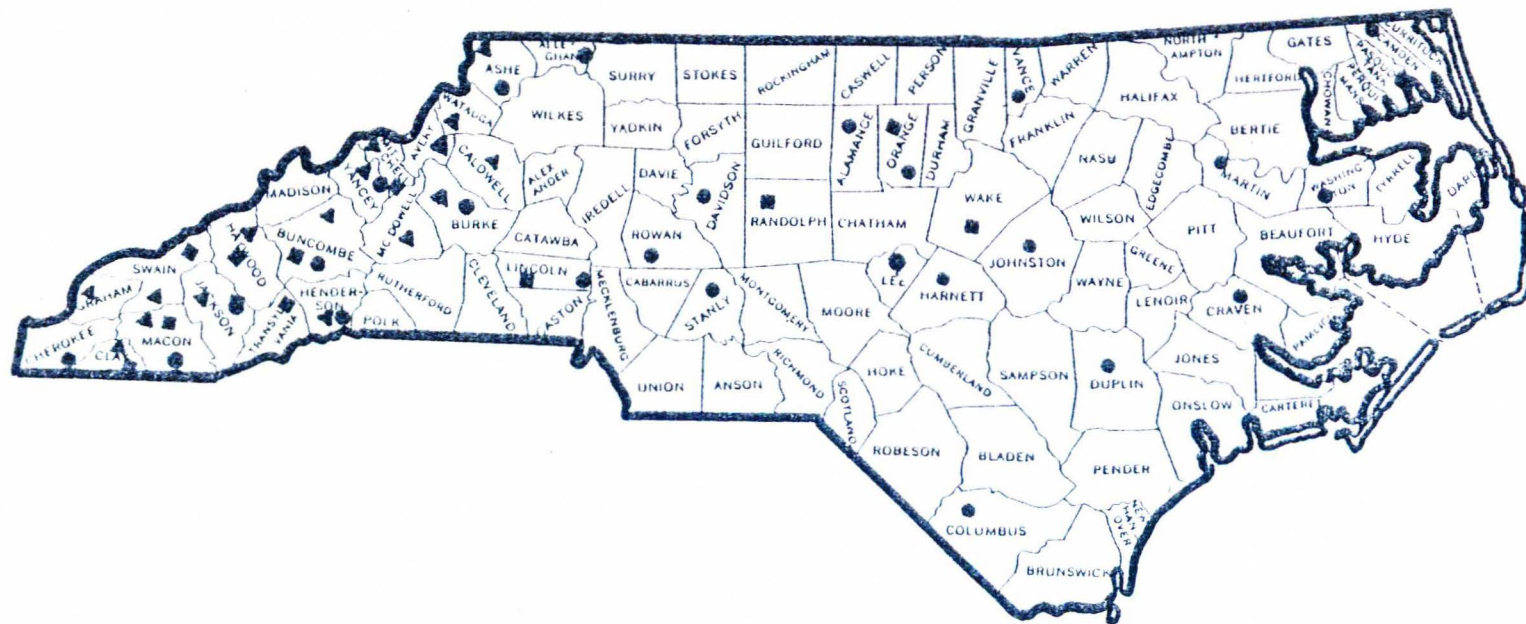


Fig. 18. North Carolina. Distribution of Melanthium.

M. virginicum ●

M. latifolium ■

M. parviflorum ▲

M. woodii ○

<u>M. virginicum</u>		<u>M. latifolium</u>	
<u>M. parviflorum</u>		<u>M. woodii</u>	





Fig. 20. Oklahoma. Distribution of Melanthium.

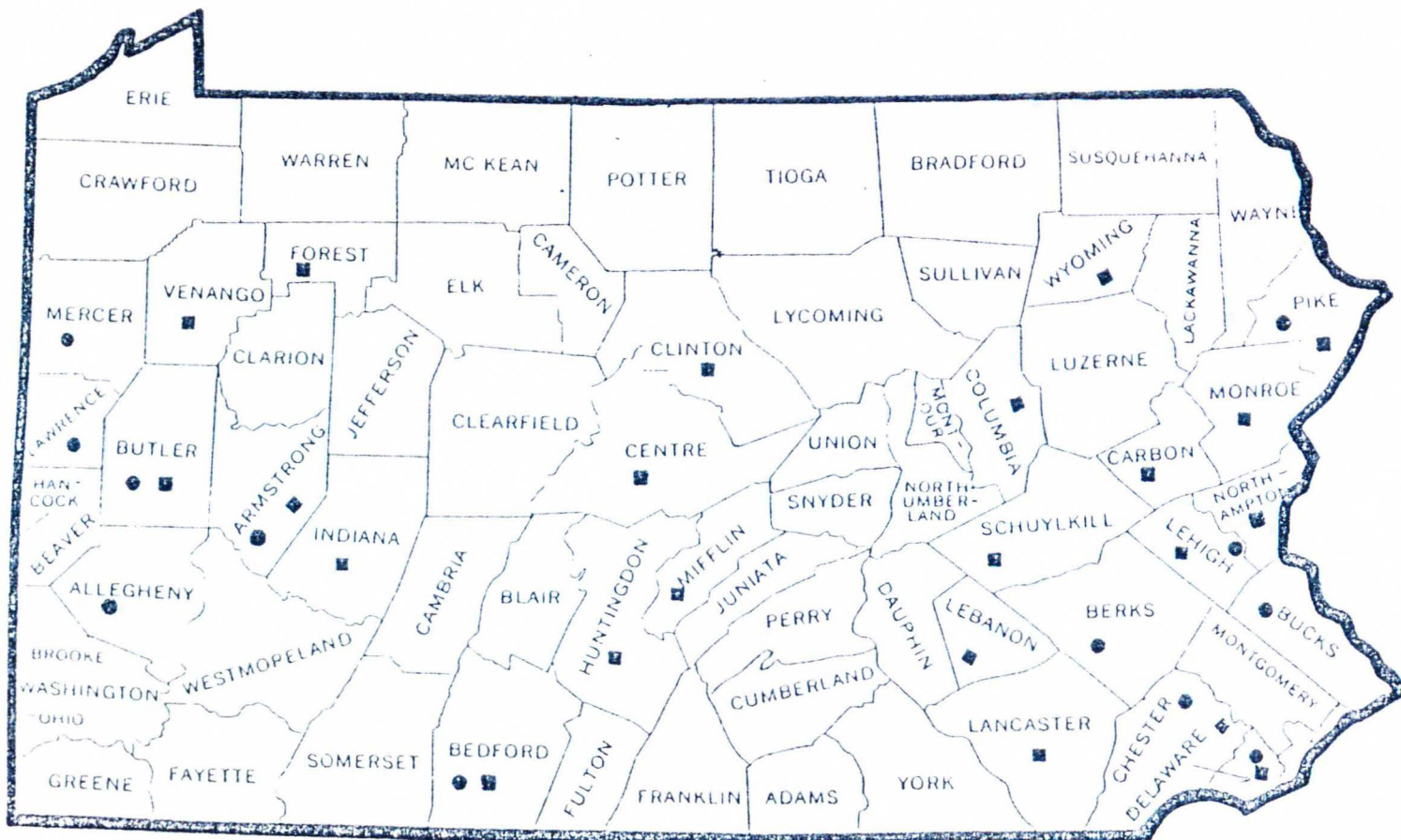
M. virginicum ●

M. parviflorum ▲

M. latifolium ■

M. woodii ○

<u>M. virginicum</u>	●	<u>M. latifolium</u>	■
<u>M. parviflorum</u>	▲	<u>M. woodii</u>	○



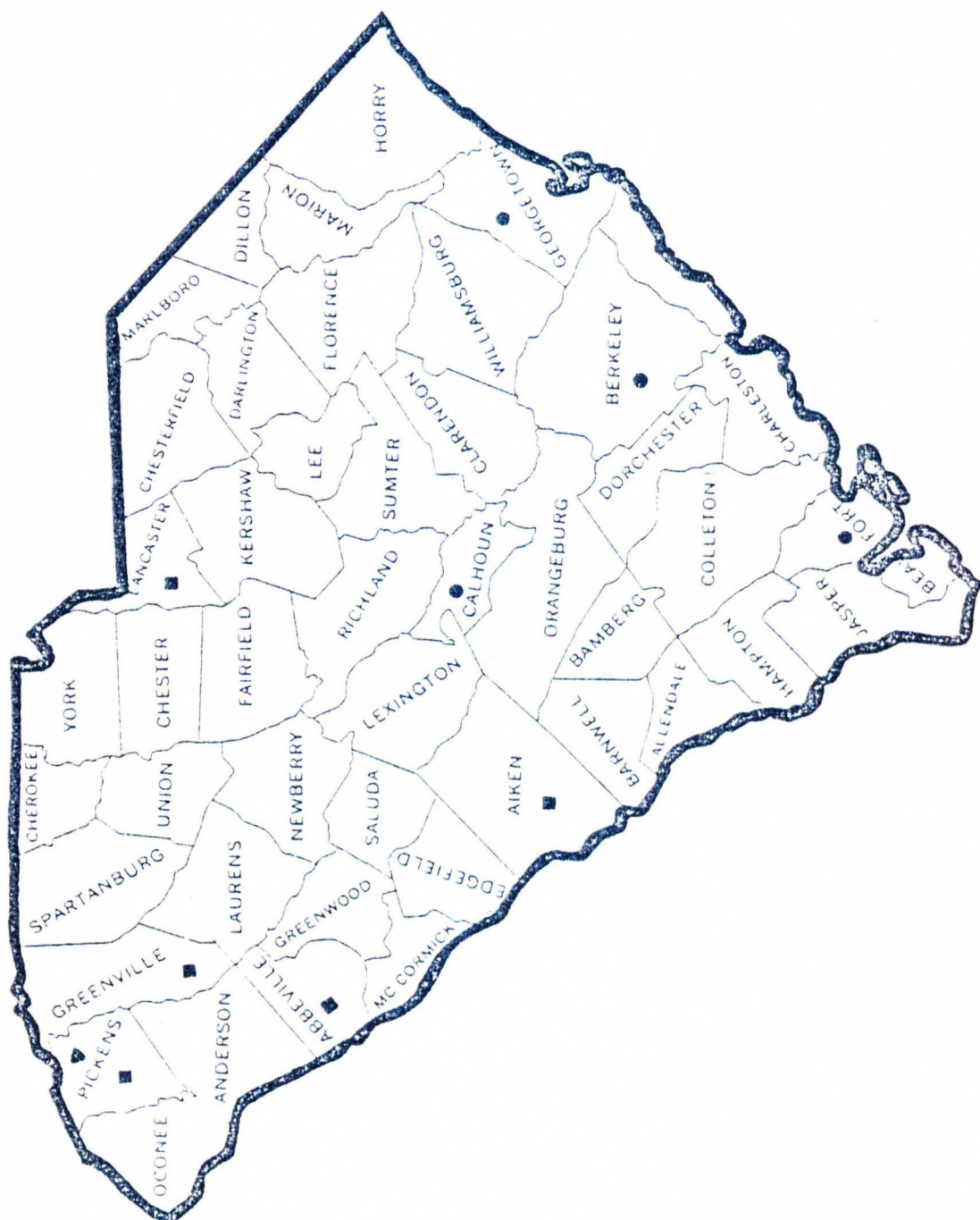


Fig. 22. South Carolina. Distribution of Melanthium.

M. virginicum •

M. latifolium ■

M. parviflorum ▲

M. woodii ○

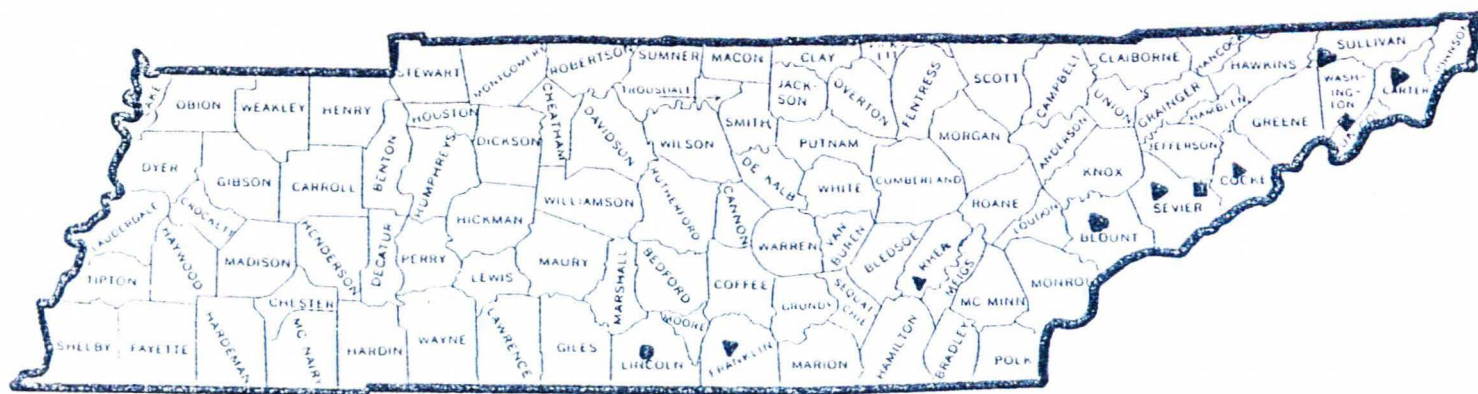


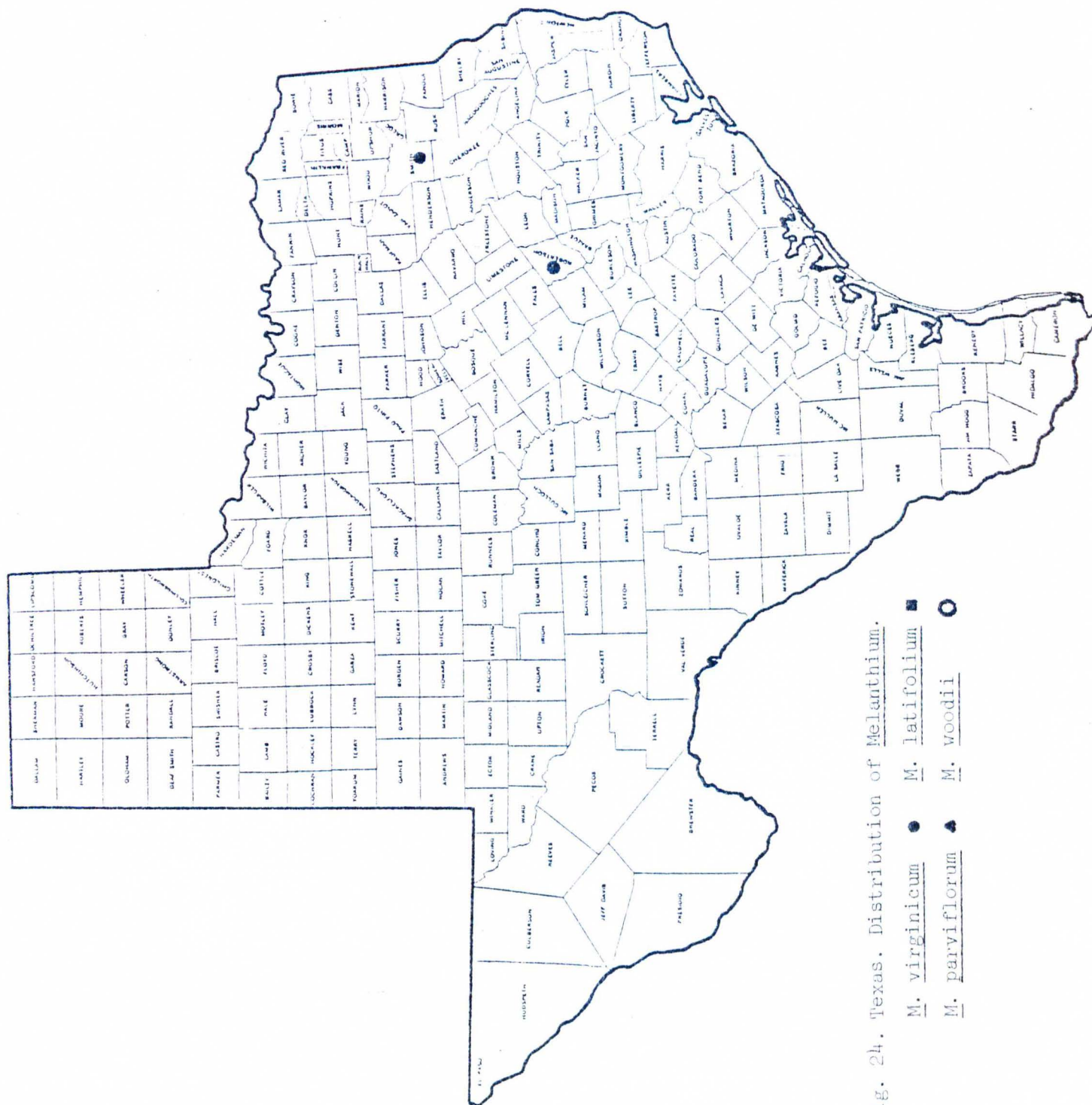
Fig. 23. Tennessee. Distribution of Melanthium.

M. virginicum ●

M. latifolium ■

M. parviflorum ▲

M. woodii ○



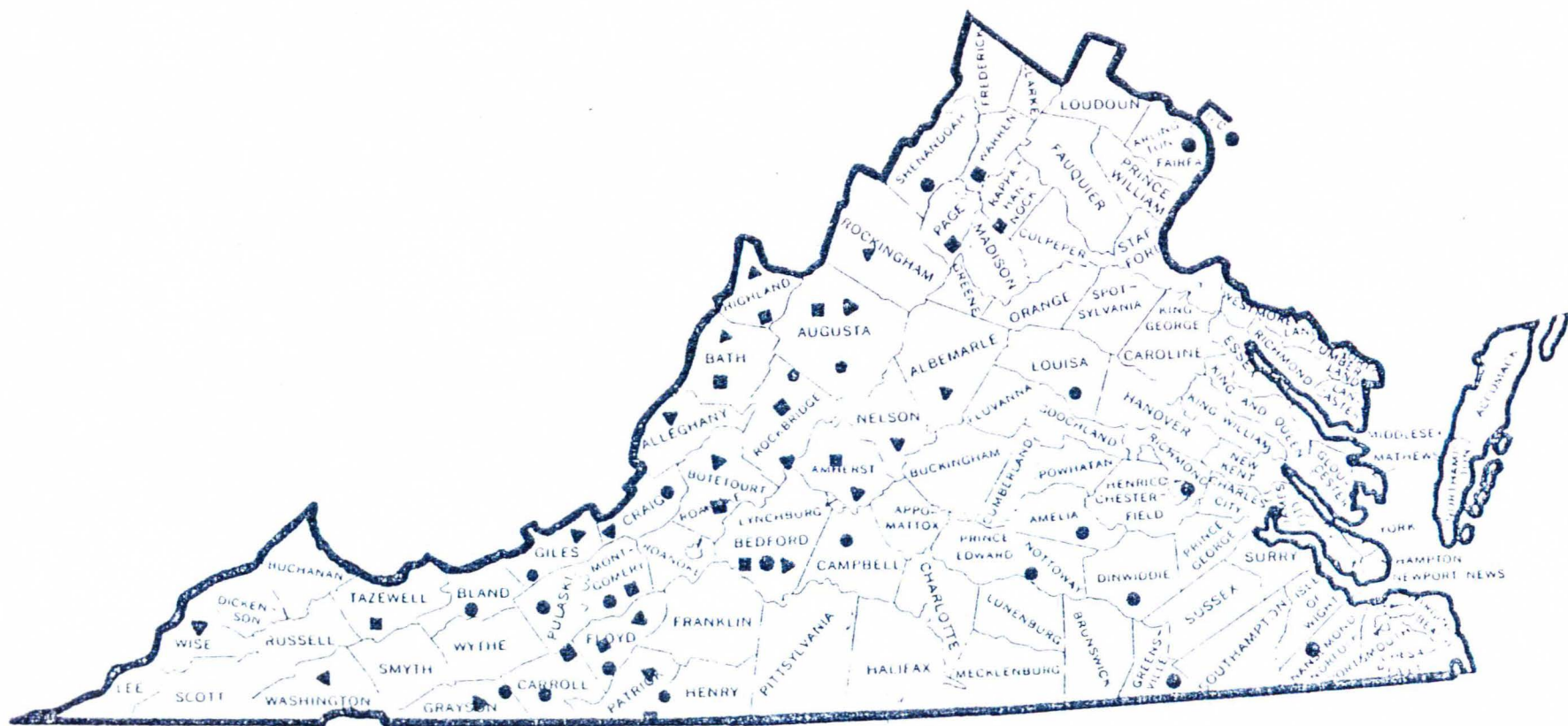


Fig. 25. Virginia. Distribution of Melanthium.

M. virginicum ●

M. latifolium ■

M. parviflorum ▲

M. woodii ○



Fig. 26. West Virginia. Distribution of *Melanthium*.

<i>M. virginicum</i>	●	<i>M. latifolium</i>	■
<i>M. parviflorum</i>	▲	<i>M. woodii</i>	○

MORPHOLOGY, ANATOMY AND CYTOLOGY

The species of Melanthium exhibit a range of variation in many morphological characters, the character states of which are useful at the infrageneric level. Taxonomy, in so far as it is concerned with variation in organisms and their classification, deals with characters which provide the taxonomic evidence for natural classification in the Adansonian sense and a large part of the evidence for phylogenetic classification. Although it is organisms which are classified, it is their characters which provide the evidence used in classification or more strickly speaking, it is our knowledge of them at any time that is classified (Davis & Heywood, 1963). Ideally it should be knowledge of all attributes but since each individual possesses thousands of potential characters, practical limitations impose a restriction on the numbers used. The number of characters used is determined by the choice and thoroughness of the investigator. Correlation weighting of characters is practiced by most taxonomists using the "good" characters which are reliable and constant.

In this study as in most monographic and revisionary works, exomorphology, anatomy and cytology are the prime taxonomic evidences used in delimiting the taxa. For the most part, morphological characters serve to separate taxa, but the question of tepal glands or the absence of these glands in the Melanthium/Veratrum complex is best served in the questionable species by anatomical means. Practically every treatment distinguishing between these two genera has involved the tepal glands as qualitative and quantitative characters. Taxa bearing the glands have traditionally been placed in Melanthium while

those without glands are assigned to Veratrum. Taxonomists making this distinction have been overtly inaccurate. Too often the assumption is made that angiosperm morphology is adequately known and this is seemingly a problem with taxonomists working with the Veratrum/Melanthium species. The glands in some species are not morphologically evident but if examined anatomically there is no question as to their presence. There is no a priori reason why any inconspicuous character should be inherently less important than some more obvious feature. More specific discussion of the glandular characters is given later in this section.

Habit

The general habit aspect of Melanthium is more nearly comparable to the habits of Zigadenus, Amianthium, Stenanthium and Tolfeldia than to Veratrum, the genus in which some Melanthium taxa are often submerged. The tall graceful Melanthium species with mainly basal leaves and terminal panicles are strikingly different from the stouter, leafly-stemmed North American Veratrum species (Figs. 27,28,29,30 and 31). Although habit is given little attention as a valid character, it is obvious here that it would improve our taxonomy. In fact, there would be no difficulty in using only vegetative characters in distinguishing between the North American Melanthium and Veratrum.

Vegetative Axes

The underground vegetative axis of Melanthium consists of a bulb under which is a very short, much reduced, erect rhizome. Roots arise from the peripheral area of the bulb at the junction with the rhizome (Fig. 32). There are often two series of lateral roots which are radially segmented and branch distally. The bulb is vertical and is composed of

Fig. 27. Melanthium virginicum L.

General characteristics. X 1/2.

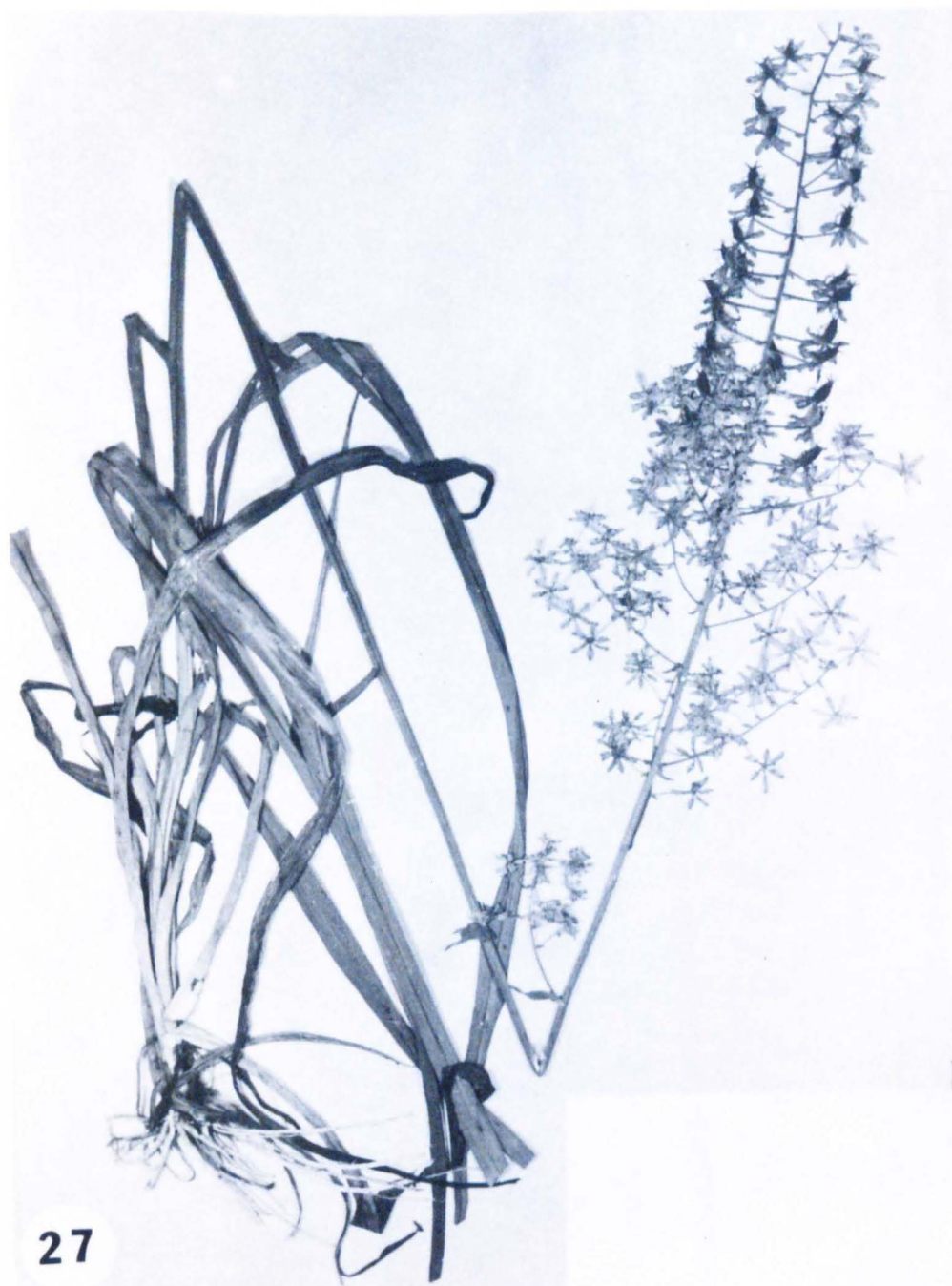


Fig. 28. Melanthium latifolium Desr.

General characteristics. X 1/2.



Fig. 29. Melanthium parviflorum (Michx.) S. Wats.

General characteristics. X 1/2.



Fig. 30. Melanthium woodii (Robbins ex Wood) Bodkin
General characteristics. X 1/2.



University of Wisconsin Herbarium, Madison.
VICTOR W. B. BARKER
Det. James H. Loomis 1936 - 37

Fig. 31. Veratrum viride Ait.

General characteristics. X 1/2.



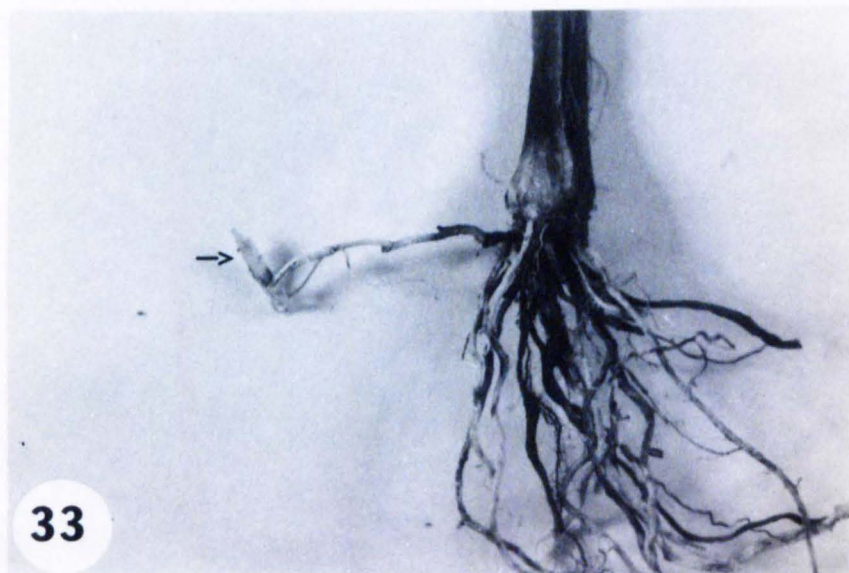
31

Fig. 32. Melanthium virginicum L.

Note short, erect, reduced rhizome. X 1.

Fig. 33. Stenanthium gramineum (Ker) Morong

Note horizontal rhizome bearing a bud. X 1.



the thickened bases of the basal leaves which are attached to the apex of the rhizome. The fleshy portion of the bulb is enclosed in fibrils, these being the remains of the fibrovascular tissue of the previous year's leaves which forms a tough hollow tube surrounding the bulb.

The linear to obovate leaves of Melanthium are mainly basal; the cauline leaves, being much reduced, give the inflorescence a subscapose appearance. The development of leaves begins in late summer and fall when short, fleshy scales form on the inner bulb. The next summer the scales elongate into aerial leaves which wither by early fall. The underground portions composing the bulb may live for another year or two, later becoming thin, dry and finally fibrillose. The outermost 1-3 leaves of each year's growth do not develop blades and are termed proleaves. The basal leaves of all species have closed sheaths; the upper reduced cauline leaves are clasping. Leaves are glabrous throughout the genus except for some sparse pubescence on the margins of the sheaths in M. virginicum.

The leaves, although different in shape among the various species of Melanthium, have the same general aspects relative to placement on the stem, progressive reduction in size upward, and distribution along the stem axis. The narrowing of the blades to canaliculate bases in Melanthium parviflorum and M. woodii gives the leaves a stalked appearance but not to a petiolate degree. The green leaves of M. parviflorum have a bluish tint above and are pale below, color traits which vary from the green leaves of the other three species. The leaves in this species are also plicate (Fig. 35). The leaves of all four species become apically necrotic rather early in each growing season. The leaves are conspicuously nerved with the center nerve in each leaf raised abaxially

Fig. 34. Melanthium parviflorum (Michx.) S. Wats.

Flowering stalk browsed by Virginia white-tailed deer.
X 1/16.

Fig. 35. Melanthium parviflorum (Michx.) S. Wats.

Young plicate leaves. X 1/16.



as a very fine midrib.

Inflorescence

The upper stem axis is terminated by the inflorescence. The inflorescence of Melanthium is a panicle or more definitely, a compound raceme bearing polygamous flowers. The terminal raceme bears mostly bisexual flowers, the flower size increasing progressively downward to the first secondary raceme. The secondary racemes increase in length downward to about the middle of the branched portion of the inflorescence. Rarely, the lower flowers on the longer secondary racemes are replaced by tertiary racemes. The lower secondary racemes are often wholly staminate. Each pedicel and axis of the secondary racemes is bracteate.

A major character which is used to distinguish Melanthium from the closely related genera, Zigadenus and Stenanthium, is the pubescence of the inflorescence. The trichomes on Melanthium are mostly dendritic and occur singularly or in dense appressed tufts. This type of vestiture is best described as floccose. The axes of the inflorescence is rather densely floccose and some scattered trichomes occur on the bracteoles and tepals. Zigadenus and Stenanthium are glabrous.

The inflorescences of the Melanthium species are open, not crowded, as in Veratrum viride (Figs. 27,28,29 and 30 best show this characteristic). The inflorescence of M. parviflorum is the most slender of any of the species with the greatest development in M. virginicum. Well developed plants of this latter species may have over 200 flowers in the inflorescences, the terminal raceme with up to 45 and the larger secondary racemes bearing approximately 25 flowers.

The perianth of each species is composed of six nearly uniform

segments. Due to this uniformity the term tepals is employed. The outer series is slightly broader in all species with Melanthium virginicum and M. latifolium having the outer three segments slightly shorter. Of all floral characters the greatest variation occurs in tepal characteristics between the four species. The tepals provide excellent diagnostic characteristics which have proven to be reliable and constant. The shape of the tepals, their clawed or attenuate bases, margins, color, glandular nature, and the adnation of the stamens to their bases are all prime diagnostic characters. The abrupt claws and the truncate blades of M. virginicum and M. latifolium distinguish these species readily from M. parviflorum and M. woodii whose tepal bases are gradually attenuate (Figs. 36,37,38 and 39). The distinct claws and truncate blades not only separate these species within Melanthium but are excellent intergeneric characters. No other genus in Veratreae approaches the degree of development for a clawed tepal as found in these two species. The definitely undulate margin of M. latifolium is peculiar to this species, as the margins of the other species are entire.

The color of the tepals ranges from a very showy, creamy-white in Melanthium virginicum to light yellow in M. latifolium, or green in M. parviflorum to dark purplish-brown in M. woodii. The light colored inflorescences greatly contrast with other herbaceous plants in the forested habitats typical of these species. In addition to the light color some M. latifolium flowers emit a sweet musky odor, the only species in which this characteristic was noted.

The presence (or supposed absence) of glands on the tepals has been one of the most utilized and in some cases the most misunderstood

Fig. 36. Melanthium virginicum L.

Flower showing clawed tepals, truncate tepal blades, tepal glands and adnation of stamens to tepals. X 4.

Fig. 37. Melanthium latifolium Desr.

Flowers showing clawed tepals, orbicular tepal blades with undulate margins, tepal glands and adnation of stamens to tepals. X 3.

Fig. 38. Melanthium parviflorum (Michx.) S. Wats.

Flowers showing attenuated tepal bases. Glands are not evident on this specimen. X 3.

Fig. 39. Melanthium woodii (Robbins ex Wood) Bodkin

Flowers showing gradually attenuated tepal bases. Glands are not evident on this specimen. X 3.



36



37



39



38

character of the genus. Although Linnaeus did not include this character in his original description of M. virginicum, the character was commonly included in descriptions from the 1780's to the present time.

The glands on Melanthium virginicum and M. latifolium are very conspicuous, raised and succulent, oblong in the former and obcuneate in the latter (Figs. 36 and 37). The glands lie one on each side of the midrib and diverge apically. In each of these species the gland arises near the base of the claw, extends upward along the claw, passing the truncated base of the tepal blade and flaring laterally onto the tepal blade giving the glands a stalked appearance. The glands are 1.5 - 2.2 mm long in M. virginicum and slightly shorter in M. latifolium. In each species the glands glisten (in vivo) and are nectariferous.

Due to the importance of the tepal glands in the taxonomy of this genus, cross sections of the tepals through the glandular areas were prepared by the paraffin method and studied histologically. According to Fahn (1952) knowledge of the anatomy of nectaries is rather scant in most angiosperms. No studies of the anatomy of glands in Melanthium have been previously reported.

The anatomy of the glands is essentially the same in Melanthium virginicum and M. latifolium. The glands are raised above the surface of the tepal to a height equal to the thickness of the tepal. Each gland is somewhat lobed bilaterally (Figs. 41-47). Histologically, the secretory tissue consists of subepidermal, small, closely packed cells, with dense cytoplasmic content. The epidermal cells of the glands are very regular, cuboidal, nonvacuolar, compacted and strongly contrast with the papillose cells of the non-glandular tepal epidermis.

Fig. 40. Melanthium virginicum L.

Cross section of tepal segment with gland showing
general anatomy. X 45.

Fig. 41. Melanthium virginicum L.

Cross section of tepal gland showing histology. X 115.

Fig. 42. Melanthium virginicum L.

Cross section of Epidermis and subdermal region of a
tepal gland. X 250.

Fig. 43. Melanthium virginicum L.

Cross section of epidermis adjacent to tepal gland
showing papillose cells. X 250.

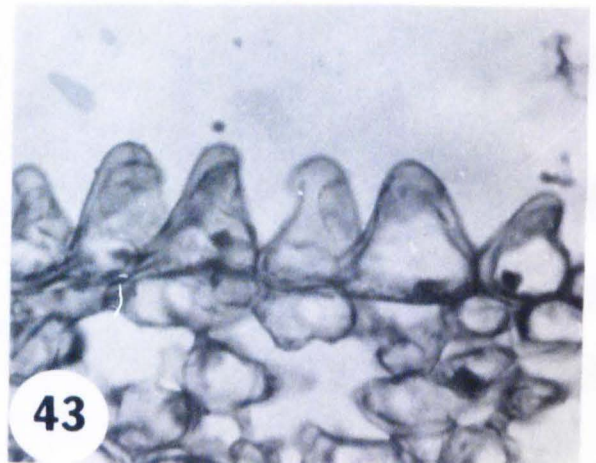
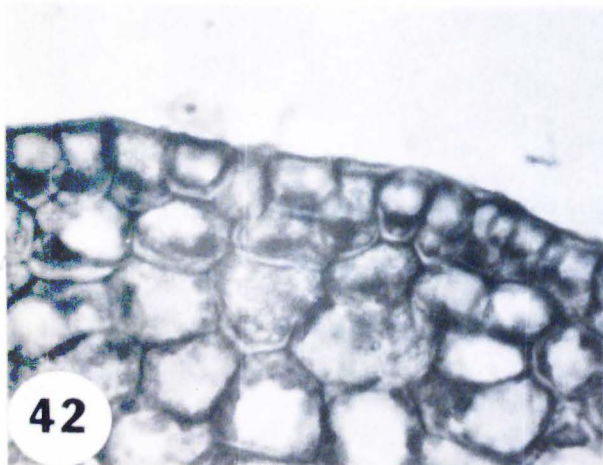
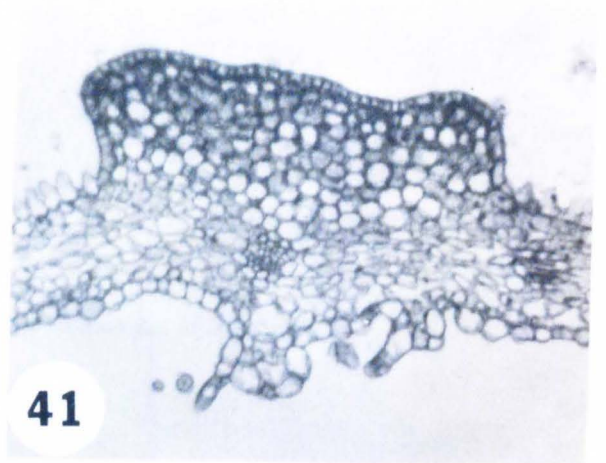
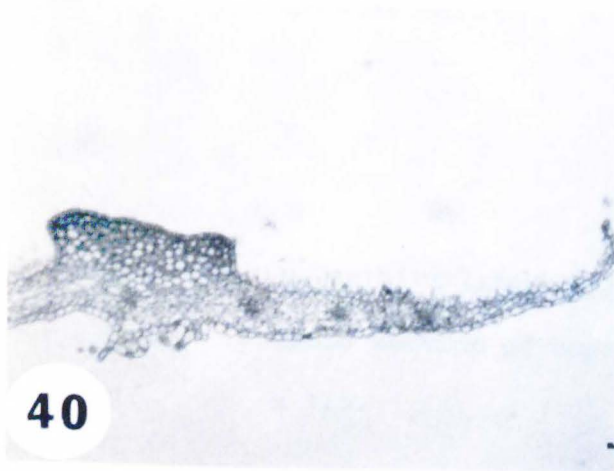


Fig. 44. Melanthium latifolium Desr.

Cross section of tepal segment with gland showing general anatomy. X 90.

Fig. 45. Melanthium latifolium Desr.

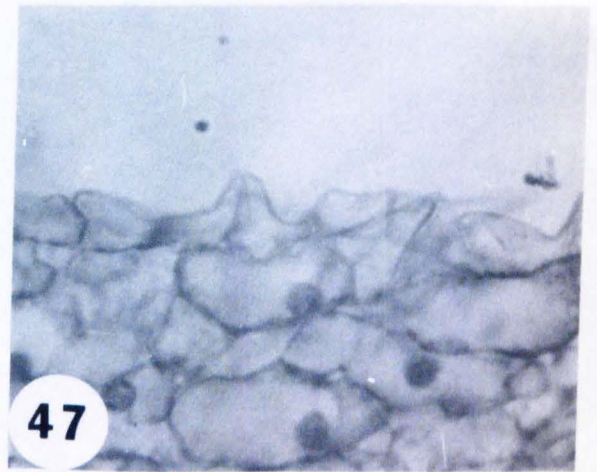
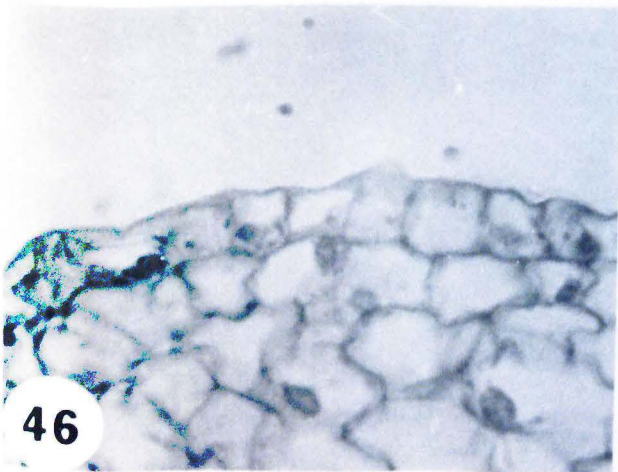
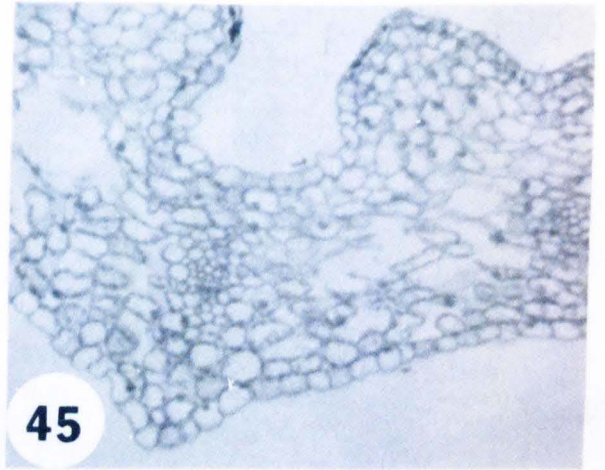
Cross section of tepal glands showing histology.
x 115.

Fig. 46. Melanthium latifolium Desr.

Cross section of epidermis and subdermal region of tepal glands. X 490.

Fig. 47. Melanthium latifolium Desr.

Cross section of epidermis adjacent to tepal gland showing papillose cells. X 490.



Eames (1961) reports, in a general discussion of nectaries, that a cuticle over glands is commonly thin and some are non-cuticular. Very little cuticle material was observed over the glands or other surfaces of the tepals in Melanthium. It is possible that if a cuticle existed, it was partially dissolved in the slide preparation. No stomates occur in the glandular epidermis so that it is assumed that exudation of nectar is directly through the epidermal cells. Vascular bundles in the tepal segments beneath each gland are not in greater number than in other parts of the tepal.

The anatomy of the tepals outside the glandular areas is typical monocotyledonous foliar anatomy, with the exception of the papillose epidermal cells. These cells contain large basal vacuoles. The mesophyll is nondifferentiated, spongy, with rather large air spaces and contains parallel vascular bundles. The lower epidermis is not papillose, contains few stomates and has occasional multicellular projections, possibly trichomes.

Melanthium parviflorum has been described by most taxonomists as non-glandular, and for this reason has been assigned to Veratrum. Studies indicating a non-glandular condition are simply inaccurate. It is possible that those authors, expecting large, succulent glands, as found in M. virginicum and M. latifolium, did not examine the tepal segments thoroughly. Although the glands are not readily evident on young tepals, in later stages the glandular area appears as a diffuse, darkened surface that is slightly raised and occupying approximately 1/4 of the base of the tepal. The midrib is obscure as is the division of the glandular area into two definite glands, but apical lobing at the top of the glandular area suggests the presence of two glands.

The glandular area in some older plants observed in the later part of the growing season become whitened on the surface (Fig. 48). This white glaucous covering is most likely due to the surface exudate from the underlying glandular tissue. Tepals preserved in FAA show a pronounced browning of the glandular area (Fig. 49).

Tepal sections of Melanthium parviflorum cut through the glandular area and examined histologically show slightly raised tissue regions on either side of the center of the tepal (Figs. 50, 51, and 52). In these elevated areas the subdermal cells are scarcely more dense in cytoplasmic content than other surrounding cells. The epidermal cells appear similar to those of M. virginicum and M. latifolium in being dense, regular and compacted. Few papillose epidermal cells occur along the upper epidermis as would be expected since the glandular area covers a greater proportion of the tepal surface (Fig. 51). The contention that there are no tepal glands in Melanthium parviflorum cannot be supported and the placement of this species in Veratrum based on that supposition cannot be supported.

The tepal glands of Melanthium woodii are somewhat intermediate in appearance between the raised, succulent glands of M. virginicum and M. latifolium and the more diffuse glands of M. parviflorum. The glandular area of M. woodii is weakly divided into two obtuse areas, one on either side of the midrib, extending apically from the base for approximately 1/3 the length of the tepal. The dark colored glands are somewhat obscured by the dark purplish-brown background of the tepal. The glands are neither succulent nor nectariferous. Due to the lack of flowering and availability of fresh material, no sectioning of M. woodii tepals and histological studies were undertaken.

Fig. 49. Melanthium parviflorum (Michx.) S. Wats.

Tepal gland preserved in FAA showing the darkened
glandular area. X 4.

Fig. 48. Melanthium parviflorum (Michx.) S. Wats.

Older flowers with tepals showing the discolored
glandular areas. X 4.

**49****48**

Fig. 50. Melanthium parviflorum (Michx.) S. Wats.

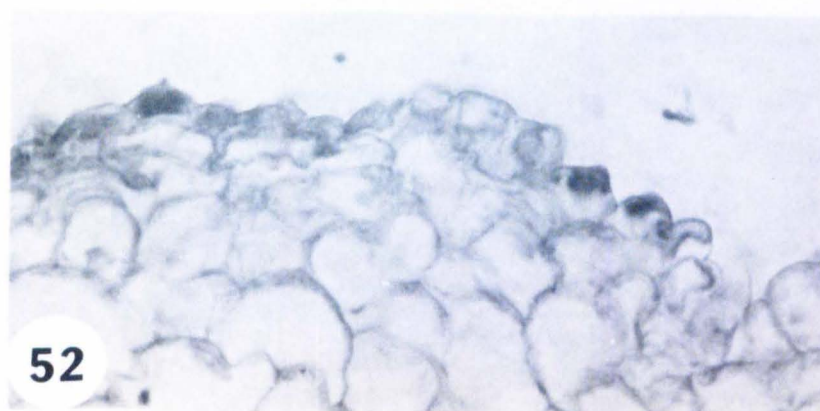
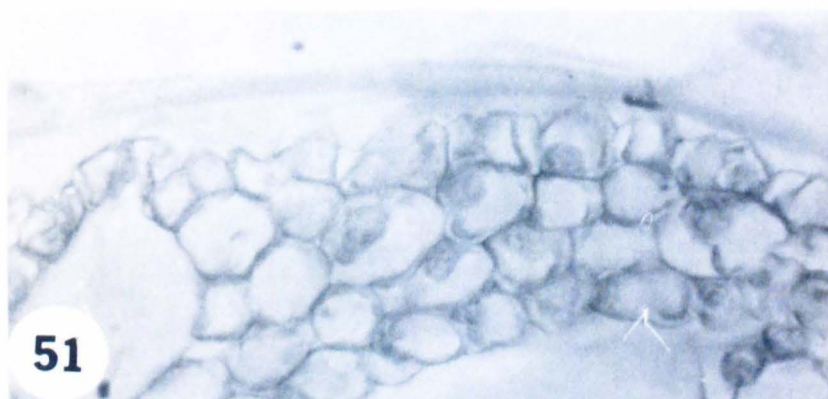
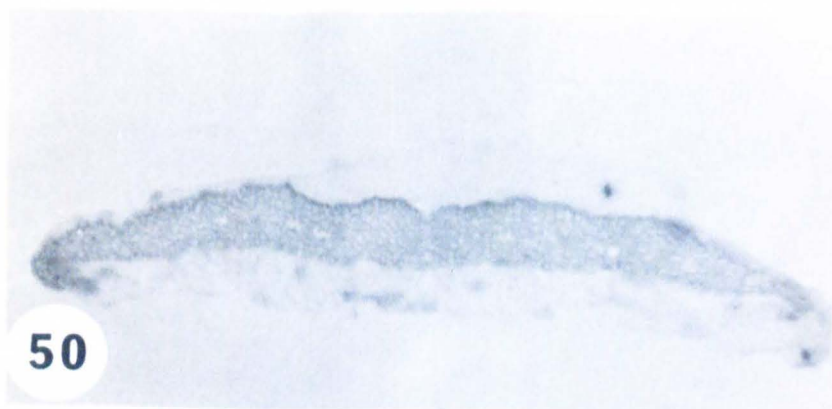
Cross section of tepal showing slightly raised
glandular areas. X 45.

Fig. 51. Melanthium parviflorum (Michx.) S. Wats.

Cross section showing papillose epidermal cells in
non-glandular areas. X 1000

Fig. 52. Melanthium parviflorum (Michx.) S. Wats.

Cross section showing dense epidermal cells of the
glands. X 1000.



The tepal glands of the Melanthium species are quite unlike the V-shaped marginal glands of the North American Veratrum species. In fact, the marginal V-shaped glands of Veratrum sect. Aboveratrum Loes. f. are unique among all genera of the tribe Veratreae. In addition to other significantly varying characters the glandar differences between Melanthium and Veratrum support this generic separation.

The adnation of the six stamens to the bases of the tepals in Melanthium is unique, occurring only in this genus of Veratreae. Zimmerman's (1958) unpublished sectional name "Telandrium" was chosen to denote this characteristic. The character is an outstanding diagnostic character at both the intergeneric and infrageneric levels. The species of Melanthium may be arranged in a series based on their increasing degree of stamen adnation to the tepals, beginning with M. woodii and proceeding through M. parviflorum, M. latifolium to M. virginicum, in which adnation reaches a point at or above the middle of the tepal claw (Figs. 36,37,38 and 39).

The anthers of Melanthium are most commonly described as extrorse although it is the apical excurving of the young filaments that cause the lines of dehiscence to appear outward. The young anthers are better described as apical which is unique to the tribe Veratreae. The anthers are subglobose with a groove or line of dehiscence which extends far down each side. The anther opens similar to the opening of two jaws with the halves of the anthers folding back until they are in one plane, somewhat flat or slightly reflexed, forming a peltate structure. This plate-like structure with masses of pollen on the surface is mostly apical but may be slightly tilted outward. The

anthers fall from the filaments within a few days after pollen release, but the curved filaments persist through fruit production.

The pistil is 3-carpellate with divergent styles (Fig. 53). The strongly diverging style bases are excellent generic characters separating Melanthium and Veratrum in North America. However, Veratrum sect. Fuscoveratrum Loes. f., with species occurring in east Asia and Europe also have divergent styles, and these species are closely related to Melanthium. In addition to the diverging styles, the style bases are situated apart at the top of the trigonous ovary. The stigmatic surfaces are not distinct. Features of the ovaries and styles are uniform in Melanthium with the exception of infrequently occurring red ovaries in M. latifolium. The placentation is axile with ovules in two rows in each carpel.

Fruit and Seeds

The mature fruit is a capsule which dehisces septicidally at the apices of the carpels. The numerous seeds are compressed and broadly winged which is one of the unifying characters of Melanthium. Zimmerman (1958) used winged seeds (and pubescent inflorescences) as a major distinguishing character in establishing his section "Telandrium" which is treated here, in part, as the genus Melanthium (sen. str.).

Chromosome Numbers

Using microsporocytes, and the acetocarmine smear technique (Radford et al., 1974), a chromosome count of $n=8$ was obtained for Melanthium virginicum, M. latifolium, and M. parviflorum. The count for the latter species agrees with that previously reported by Zimmerman (1958). Numbers of Veratrum are generally $n=16$ (Bolkhovskikh et al.,

Fig. 53. Melanthium virginicum L.

Carpels with divergent styles. X 4.



1969) with only few species having $n=8$. These include such eastern Asia species as V. japonicum, V. longibracteatum, V. maackii, V. maximowiczii, and V. formosanum, and the widespread European and northern Asia species, V. nigrum (Bolkhovskikh et al., 1969; Moore, 1973). Still, such species as V. album of Europe, and V. maximowiczii and V. nigrum, are polyploids, with numbers ranging from $n=8$ to as high as $n=32$. The eastern North American species, V. viride, is $n=16$ (Löve & Löve, 1966).

The chromosomes in Melanthium are large, conspicuous and may be counted in a number of different stages, my most definite counts being in telophase I (Figs. 54,55, and 56).

Due to the lack of flowering material the chromosome count of Melanthium woodii was attempted from root tips. No countable stages were obtained.

Other Anatomical Studies

Although the anatomical studies of the tepals done herein are significant and contribute to the solution of some of the taxonomic problems, other anatomical investigations added little evidence supporting the delimitation of taxa.

Cross sections of stems, roots and leaves of the Melanthium species were prepared by the paraffin method and examined. The studies yielded no taxonomically meaningful evidences aiding infra-generic delimitation. No detailed studies of the anatomy of Melanthium are known. Cross sections of M. virginicum stem, root and leaf are presented here (Figs. 57,58 and 59). Epidermal peels showing the arrangement of the subsidiary and guard cells of the stomates are often

Fig. 54. Melanthium virginicum L.

Chromosome smear. n= 8. X 960.

Fig. 55. Melanthium latifolium

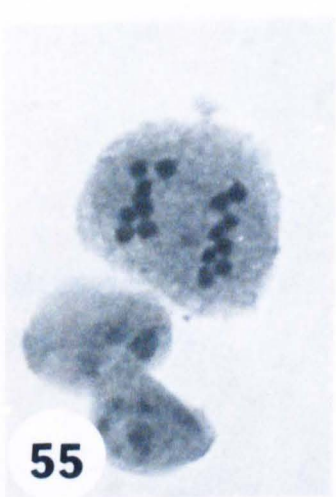
Chromosome smear. n= 8. X 880.

Fig. 56. Melanthium parviflorum

Chromosome smear. n= 8. X 880.



54



55



56

Fig. 57. Melanthium virginicum L.

Cross section of stem. X 45.

Fig. 58. Melanthium virginicum L.

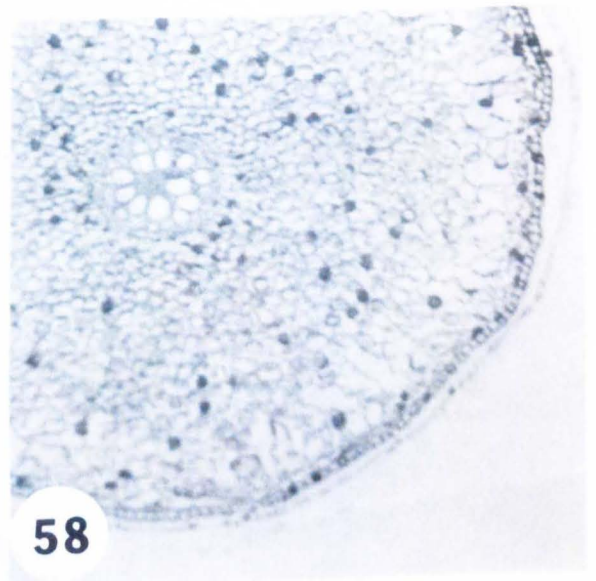
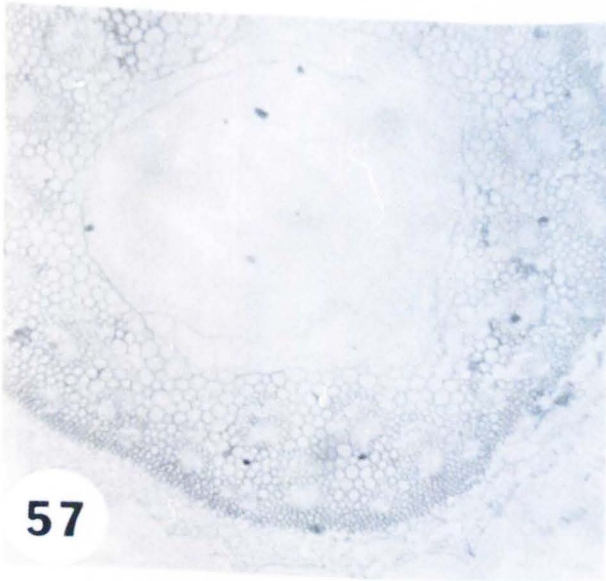
Cross section of root. X 35.

Fig. 59. Melanthium virginicum L.

Cross section of leaf. X 50.

Fig. 60. Melanthium virginicum L.

Epidermal peel showing tetracytic stomatal type. X 560.



taxonomically significant. All Melanthium species have four subsidiary cells, two lateral and two terminal, the tetracytic stomatal type, characteristic of many monocotyledons (Fig. 60).

REPRODUCTION

When this revision of Melanthium was first delimited, reproductive studies and crossing experiments were thought advisable and were included in the research plans. The majority of herbarium specimens examined in the early stages of this project contained large inflorescences with many flowers bearing nectariferous tepals and some with large capsules containing numerous seeds leading to the preliminary assumption that reproductive studies could be easily conducted.

To facilitate crossing experiments 25 bulbs of each of the Appalachian species were transplanted from their native habitats to a plot near the James Madison University greenhouse. The plants were carefully transplanted with some natural habitat soil and mulch.

The first season after transplanting one Melanthium parviflorum produced a flowering stalk, all others remaining vegetative.¹ Field studies of populations in their natural and undisturbed habitats soon confirmed the infrequency of flowering and it was realized that crossing experiments would not be possible within the time limits of this research. Flower production is more common in populations of M. virginicum and M. parviflorum than in M. latifolium and M. woodii. Based on my observations, less than 20% of the Melanthium plants in the Appalachian populations produce flowers each year.

The floral structures and behavior suggests sexual reproduction; many flowers, brightly colored tepals bearing nectariferous glands (in Melanthium virginicum and M. latifolium), insects visiting flowers

¹The James Madison University experimental plot was ultimately destroyed by the indiscriminate use of a bulldozer in preparation for an addition to the Infirmary.

and the production of large capsules with many seeds lead to this assumption. The unique incurving of older stamens in M. virginicum and M. latifolium toward the pistil might achieve self-pollination. Insects collected from the flowers of M. virginicum, M. latifolium, and M. parviflorum were tumbling flower beetles (Mordella sp.) and black flies (Simulium sp.). Black flies are biting flies and are not considered pollinators (Borror & DeLong, 1971). Although the bodies of the beetles are hairy, no copious amount of pollen was present. Zimmerman (1958) reports the attraction of flies to M. woodii but does not confirm them as pollinators.

Seed germination studies were totally unsuccessful. Many factors of germination were altered yielding no germination although some dissected seeds contain embryos. Seeds were tested for viability with 2,3,5-triphenyl tetra-zolium chloride. Only a faint and delayed (after 24 hours) color change occurred in this test. Evidence for seed viability in Melanthium using this chemical is inconclusive.

It is possible that in Melanthium, like some east Asian species and the closely related Stenanthium, that although flowers are produced, reproduction is mostly vegetative. Stenanthium produces elongated rhizomes which form buds (Fig. 33). The subterranean structures of Melanthium and Stenanthium are very similar. Repeated attempts to find buds on rhizomes of Melanthium have failed. It is possible that in removing the deeply buried roots and rhizomes of Melanthium, that if buds occur they were broken off. It is quite probable that with careful excavation of the subterranean structures, buds will be found.

TAXONOMY

MELANTHIUM L.

Melanthium L., Sp. Pl. 339. 1753; Gen. Pl. ed. 5, 151. 1754; non Medicus 1789 (= Nigella L.). LECTOTYPE: M. virginicum L., Sp. Pl. 339. 1753 (vide Britt. & Br., 111. Fl. N. U. S. ed. 2, 1:493. 1913). -- Leimanthium Willd., Ges. Naturf. Freunde Berlin Mag. 2:24. 1808, nom. illeg. superfl. a posteriori. -- "Leimanthemum" Ritg., Schiften Ges. Beford. Gesamnten Naturwiss. Marburg 2:130. 1830, nom. ined., orth. var. -- Evonyxis Raf., Fl. Tellur. 2:29. 1836, nom. illeg. superfl. a posteriori.

Perennial rhizomatous herbs with bulbous stems and sheathing leaves. Roots cylindric, diffuse, distally branching. Rhizomes vertical. Bulbs stout, the outer portions consisting of leaf bases from previous years, the innermost of these thin, dry and scaly, the outermost fibrillose with the persistent fibrils investing the bulbs. Stems erect. Leaves mostly basal, sublinear, elliptic, oblanceolate or obovate, narrowed to canaliculate stalks, tapering to acute apices, sometimes plicate, mostly glabrous. Cauline leaves few, progressively reduced upward. Bracts clasping, linear to subulate. Inflorescences terminal, compound racemose or paniculate, floccose; lateral racemes progressively longer downward to the middle of the inflorescence, thence progressively shorter. Flowers of the distal raceme bisexual, progressively larger downward, the lower flowers staminate. Perianth hexamerous, slightly adnate to the base of the ovary; tepals basally connate, unguiculate or attenuate toward the base, apically acute

to obtuse, relatively smaller in staminate flowers; glands 2 on each tepal, sub-basal, one to either side of the midvein, very prominent to obscure. Stamens 6, adnate to the tepal bases; anthers appearing extrorse but more or less apical; filaments becoming strongly arcuate inward, subglobose to reniform, persistent in fruit. Pistil compound, trimerous; ovary trilocular, the placentation axile in two rows per locule; styles 3, distinct. Fruit capsular, septicidal. Seeds compressed, broadly winged.

In North America, the species of Melanthium are distributed from central Iowa to southern New York, south to northern Florida and eastern Texas (Fig. 1).

According to article 10, in the Code, Britton and Brown's (1913) choice of Melanthium virginicum (instead of M. sibiricum) as the type species of Linnaeus' Melanthium is to be followed. For this reason, the generic names Leimanthium Willd. and Evonyxis Raf. are superfluous as they specifically include M. virginicum. Both Willdenow and Rafinesque subscribed to the widely held view that in splitting the very heterogenous assemblage of species in Melanthium the original Linnean name should be reserved for the Old World members of the assemblage. The New World M. virginicum and related species would therefore require a new or different generic name, hence the introduction of Leimanthium and Evonyxis.

The name "Leimanthemum," attributed to Ritgen (1830), is also often cited as a synonym of Melanthium. This is not a validly published name, but merely an orthographic variant of Leimanthium. For etymological reasons, Ritgen suggested that Leimanthium might better

be spelled "Leimanthemum." He did this in a purely discursive footnote to his treatment under Willdenow's generic name. For nomenclatural purposes, Ritgen's variant is an unpublished name and has no standing.

The major decision that had to be made in this treatment was whether or not to maintain the genus Melanthium or to submerge the genus into the large heterogenous genus Veratrum. The decision made here is to maintain Melanthium as valid, and include in it three traditionally recognized species of the eastern United States, and add a fourth, Veratrum woodii. This treatment of the genus Melanthium establishes a well defined group justified on morphological characters and its geographical distribution. From the standpoint of tradition, and practicality, at least in part, this treatment is equally acceptable to any other, and in my judgement, forms the most natural system of classification. It is certainly beyond reason to include species as diverse in significant taxonomic characters as seen in North American species of Melanthium and Veratrum in the same genus. To this time, Zimmerman (1958) is the only one to have suggested such a merger.

The taxonomic characters used in delimiting Melanthium are similar in kind and overall magnitude as those used to separate other genera of Liliaceae. Major characters of Melanthium and other closely related genera are presented in Table 1. In the tribe Veratreae, the closely related genera, Stenanthium, Zigadenus, and Veratrum are separated by characters which are essentially equal in magnitude to the characters Zimmerman (1958) used to transfer Melanthium to Veratrum. These include such common characters as the pubescent inflorescence and

Table 1. Major Characters of Melanthium and Closely Related Eastern North American Genera of Liliaceae

GENUS	CHARACTERS						
	Stem	Leaves	Inflorescence	Tepals	Stamens	Seeds	Chromosomes
<u>Melanthium</u>	Delicate Pubescent	Narrow Mostly basal Glabrous	Panicle Open	Clawed or attenuate Glandular	Adnate to tepals Anthers fugacious	Winged	$\underline{x} = 8$
<u>Veratrum</u>	Stout Pubescent	Broad Cauline Pubescent	Panicle Closed	Without claws Glandular	Free Anthers persistent	Winged	$\underline{x} = 8$
<u>Zigadenus</u>	Delicate Glabrous	Narrow Mostly basal Glabrous	Panicle Open	Without claws Glandular	Free	Wingless	$\underline{x} = 11$
<u>Stenanthium</u>	Delicate Glabrous	Narrow Mostly basal Glabrous	Panicle Open	Without claws Non-glandular	Free	Wingless	$\underline{x} = 8$
<u>Amianthium</u>	Delicate Glabrous	Narrow Mostly basal Glabrous	Raceme Closed	Without claws Non-glandular	Free	Wingless	unk.
<u>Tofieldia</u>	Delicate Pubescent	Narrow Mostly basal Pubescent	Raceme Closed	Without claws Non-glandular	Free	Wingless	$\underline{x} = 15$

broadly winged seeds. Zimmerman's treatment is the most thorough, and severe, involving Melanthium. This monographic work on the genus Veratrum is indeed, extensive and in some of the treatment strong arguments are presented for the delimitation of taxa. As is generally the case in classification schemes, however, there are no totally definitive characters that present taxonomic evidence for delimiting all taxa. There is the exception in most classification systems, and this, of course, is nothing new in the problematical world of subjective and interpretative taxonomy. Often there is no comfortable and simplified position based on objective facts which present everything as black or white, or right or wrong, and therefore the taxonomic pigeon hole is rarely absolute.

In this revision it was not only necessary to understand the criteria and concepts used traditionally to delimit Melanthium, but also the basis for delimiting Veratrum since the major question involves recognition of one or both of these genera. The system of Zimmerman (1958) was presented in the latter part of taxonomic history (see page 13). Reference to that summary of sectioning will aid understanding the subsequent discussion.

Zimmerman (1958) delimited Veratrum from Stenanthium and Zigadenus on the basis of the pubescent inflorescence and character of the seed, and his assignment of Melanthium virginicum, M. latifolium (called M. hybridum by Zimmerman) and M. parviflorum to Veratrum was based mainly on these two characters. Melanthium virginicum, M. latifolium and M. parviflorum share many features in common with Veratrum species but this is also true for Stenanthium and Zigadenus as well. The

use of winged seeds as a major unifying character in Veratrum is not without exception. In his section "Melovertatrum,"¹ V. fimbriatum has essentially wingless seeds although it is suggested that the wings fail to keep pace with the development of massive endosperm. Here is an exception to a major character in Veratrum, and a character which was used elsewhere to justify a generic change. A number of characters in "Melovertatrum" are shared by the other three sections of Veratrum, namely, with Albovertatrum Loes. f. stout roots, large bulb, free fibrils, distinct rhizome, large, broad, pubescent leaf blades, fringed white tepals and centrally attached styles; with Fuscovertatrum Loes. f., fugacious anthers and leaf shape sequence; and finally with "Telandrium" large, paired, thickened, nectariferous tepal glands. Zimmerman indicated that the glands of "Telandrium" reach "a degree of specialization seen also in the partially united glands of Zigadenus section "Anticlea" and the paired glands of Z. glaberrimus."

Considerable attention has been given to the tepal gland characters in this complex. Speculation as to possible evolutionary trends in Veratreae have been based on suggested reductional series of the glands. Supposed pollination has been based on the glands. The glands have been used in modern diagnostic keys in attempts to delimit taxa where the character has little diagnostic value. In section Albovertatrum the glandular area is a conspicuous V-shaped region extending along the margins of the narrowed basal third of the tepal, neither thickened nor succulent. In Fuscovertatrum the glands are confluent into a single area sometimes slightly thickened and fleshy covering the proximal 2/5 -

¹Zimmerman's unpublished sectional names are used, here as a matter of convenience. It does not imply acceptance nor rejection of these names.

3/5 of the tepal. In "Melovertum" the glands are paired with the two large fleshy lobes occupying most of the proximal half of the tepal on both sides of the midrib. The glands in "Telandrium" vary from distinctly two, one on each side of the midrib, to a very small single area (in Veratrum shanense), or very obscure (in Melanthium parviflorum). The most unique glands occur in Albovertum and Zimmerman (1958) goes so far as to suggest that this section might be treated as a distinct genus based on glandular structure. This suggestion is significant here, and with the development of other character concepts, profoundly affected the generic treatment in this revision.

Floccose pubescence of the inflorescence is a common feature of all sections, but only the leaves in Albovertum are significantly hairy. A few pilose hairs occur on the veins and margins of "Melovertum" and a little pubescence exists on the closed sheaths of Fuscovertum. "Telandrium" leaves are essentially glabrous.

Tepal shape varies widely in the sections. In Albovertum they are large, lanceolate to broadly elliptic, sometimes marginally toothed, and little narrowed at the base. Fuscovertum contains tepals that are oblong and in some species broadly so with bases that are less narrowed than in Albovertum. In "Melovertum" the tepals are obovate to rhombic, narrowed at the base, and with the margins deeply fimbriate. In "Telandrium" the tepals are oblanceolate to elliptic or obovate. A major difference in the tepals in this section from those in other sections is the extreme attenuation of the bases, especially in the four species occurring in the eastern United States, two being narrowly attenuate, two abruptly clawed to the point of sub-auriculation.

An exceptionally consistent character, the adnation of stamen to tepal, is unique in "Telandrium." In fact, this is Zimmerman's (1958) reason for the choice of the name for the section. Not only is this adnation unique to this section but also to all of the tribe, Veratreae.

As is generally the case, past authors working with this group of plants have paid little attention to habit. Perhaps this is because it is much easier to recognize habit than to describe it and, also, it is difficult if not impossible to assess from herbarium specimens. Habit as a part of a plant's concept can only be acquired in the field. There is no doubt that greater attention to characters other than those pertaining to flowers and fruits would in many cases improve and simplify our taxonomy.

The stout and coarse habit of the eastern, Veratrum viride (sect. Alboveratrum) is in sharp contrast to the more delicate and graceful Melanthium species. Only in Alboveratrum do the large stems bear broad leaves from the base to the inflorescence. The other sections have mostly basal to subbasal leaves with the cauline leaves sequentially reduced to the inflorescence. This is so striking in the eastern North American species that the plants appear scapose.

Geographically the most widespread of the sections is Alboveratrum which is circumboreal. Fuscoveratrum species are restricted primarily to eastern Asia, although there is one species in Europe. "Meloveratrum" occurs only in California. "Telandrium" is found in southwest China and the eastern United States.

The classification merging the genus Melanthium with Veratrum is, at best, very tenuous. Zimmerman's (1958) sectional classification of

Veratrum is tenuous, and he admitted it as so. Too many variable and exceptional characters are displayed by the components of Veratrum (sensu lato) for this classification to be justified.

It is concluded here, in view of the unique characters of the section "Telandrium" that the retention of Melanthium is justified. This treatment involves only the eastern North American species, of the genus namely, M. virginicum, M. latifolium, M. parviflorum and M. woodii. It is further proposed that other taxa in the section "Telandrium" with equal justification could be placed in Melanthium. Those southwest China species of "Telandrium" are not treated here but will be given consideration in future work. In fact, a case could be made for the transfer of the Fuscoveratrum species to Melanthium due to the close alignment with "Telandrium." Due to the strikingly different characters in Alboveratrum, from general habit to gland type, it is suggested that only this Section remain as Veratrum. Zimmerman stated that "because the glands of Alboveratrum are unique among the Veratreae a good case could be made for treating it as a separate genus." It is proposed here that this section constitute the genus Veratrum and that the other sections be generically transferred. "Meloveratrum" has wingless seeds and could be treated as another genus with justifications.

The complex of correlated characters by which Melanthium is herein differentiated from Veratrum include adnation of stamens to tepals, concave attenuation of tepals toward their bases, two separate non-marginal glands on the tepals (obscure in M. parviflorum) and glabrous leaves. Melanthium can be quite easily distinguished on a more casual basis by habit. The eastern North American Veratrum is a stout plant

with broad leaves from the base to the inflorescence. The Melanthium species are more delicate with narrow leaves that are mostly basal.

In summary, the major differences are:

<u>Melanthium</u>	<u>Veratrum</u>
Stem delicate	Stem stout
Bulb vertical	Bulb at an angle
Rhizome reduced	Rhizome thick often elongated
Leaves narrow	Leaves broad
Leaves mostly basal	Leaves to the inflorescence
Large leaves mostly glabrous	Large leaves somewhat pubescent
Inflorescence open	Inflorescence closed
Inflorescence axes floccose	Inflorescence axes densely pubescent
Tepals usually glabrous	Tepals pubescent
Tepal glands on each side of the midrib (obscure in <u>M. parviflorum</u>)	Tepal glands marginal and v-shaped
Tepal blade margins entire or undulate	Tepal blade margins erose
Filaments adnate to the tepals	Filaments not adnate to the tepals
Anthers fugacious	Anthers persistent
Style bases mostly diverging	Style bases ascending

The following key differentiates Melanthium from Veratrum in eastern North America.

1. Tepal bases narrowly attenuate to abruptly clawed with two distinct and separate non-marginal glands, one on either side of the midrib (macroscopically obscure in

M. parviflorum); stamens adnate to the tepals;
 style bases strongly divergent from one another;
 leaves glabrous; tall perennial herbs with
 elongate sheathing leaves, much reduced toward
 the inflorescence; inflorescences open and
 appearing delicate and flexible

..... Melanthium

1. Tepal bases contracted, each with a conspicuous
 V-shaped glandular area extending along the
 margins; stamens free; style bases ascending,
 not markedly divergent from one another; leaves
 pubescent; tall coarse perennial herbs with
 large broad leaves from the base to the inflor-
 escence, little reduced upward; inflorescences
 closed and appearing stout and rigid.

..... Veratrum

The North American species of Melanthium may be treated as fol-
 lows.

Key to Species

1. Tepals clawed or abruptly attenuate basally,
 the base of the blade sub-auriculate and truncate;
 basal leaves linear to narrowly oblanceolate.
 2
2. Tepal blades entire, abruptly auriculate to
 somewhat hastate, ovate to obovate-oblong, acute,
 claws flat to slightly involute, 1/5 - 1/4 the

length of the tepals; stamens inserted at
or above the middle of the claws.

..... 1. M. virginicum

2. Tepal blades strongly undulate, orbicular-
deltoid, shortly acuminate, claws involute,
2/5 the length of the tepals; stamens
inserted at or below the middle of the
claws.

..... 2. M. latifolium

1. Tepals very gradually attenuate to the base;
leaves broadly oblanceolate to broadly obovate.

.....3

3. Tepal glands obscure, the tepals greenish-
yellow to olive-green, rhombic-oblanceolate,
acute to subacuminate; young ovary glabrous;
filament bases barely 1/3 as wide as the
tepals at point of insertion; Southern
Appalachian Mountains.

.....3. M. parviflorum

3. Tepal glands obvious, very dark, obcuneate,
extending to the base of the tepal, the
tepals maroon to purplish to chocolate-
brown, oblanceolate, obtuse; young ovary
pubescent; filament bases 1/2 or more as
wide as the tepals at point of insertion;
Ozark Mountains and highly localized small
populations in Florida, Georgia and North
Carolina.

..... 4. M. woodii

1. MELANTHIUM VIRGINICUM L.

Melanthium virginicum L., Sp. Pl. 339. 1753. Types: "Virginia,"

1747-49, Kalm s.n. LECTOTYPE: LINN (! photo). "Virginia,"

s.d., Clayton 422. POSSIBLE SYNTYPES: BM (2, ex Herb.

Gronov.) (! photos). -- Helonias virginica (L.) Ker-Gawl.

in Sims, Bot. Mag. 25:985. 1805. -- Leimanthium virginicum

(L.) Willd., Ges. Naturf. Freunde Berlin Mag. 2:24. 1808.

-- Veratrum virginicum (L.) Ait., Hort. Kew. ed. 2, 5:426.

1813. -- Evonyxis virginica (L.) Raf., Fl. Tellur. 2:29.

1836. -- Zigadenus virginicus (L.) Kunth (erroneously attrib.
to Endl.) Enum. Pl. 4:195. 1843.

Melanthium monoicum Walt., Fl. Carol. 125. 1788. Type: United

States. South Carolina: Georgetown Co.: 12 mi N of

Georgetown, 25 Jun 1939, Godfrey & Tryon 110. NEOTYPE: NY!

-- Leimanthium monoicum (Walt.) Sweet, Hort. Brit. 429.

1826. -- Evonyxis monoica (Walt.) Raf., Fl. Tellur. 2:29.

1836.

Melanthium polygamum Desr. ex Lam., Encycl. Meth. Bot. 4:25. 1797.

Type: United States: "Carolina," s.d., Fraser s.n. HOLOTYPE:

P-LA (! photo).

Melanthium laetum Kinnet ex Kunth, Enum. Pl. 4:195. 1843, nom.

inval., pro. syn.

Melanthium dispersum Small, Bull. Torrey Bot. Club 25: 606. 1898.

Type: United States. Florida: Walton Co.: In woods, summer

1885, Curtiss s.n. HOLOTYPE: NY!

Tall herbs with large linear, mainly basal leaves and terminal panicles of greenish-white to cream-colored polygamous flowers. Roots 8 - 20, ca. 2 mm diameter, white, segmented, distally branching, arising radially from a bulb. Rhizome reduced, brown, 0.5 - 2 cm long, 0.5 - 1.8 cm diameter. Bulb erect, 0.6 - 2.5 cm diameter; fibrils brown, anastomosed, stiff, excurrent. Stem 6 - 20 dm tall, the terminal 1/4 - 1/3 floriferous. First leaves 2, hidden by fibrils, not persistent. Later leaves linear, mainly basal, 30 - 80 cm long, 0.6 - 3.2 cm wide, green through flowering, glabrous; bases equitant with sheaths closed; tips long attenuated; cauline leaves few, reduced upward, clasping. Inflorescence an open panicle of simple racemes, 13 - 80 cm long, axes floccose, hairs white; terminal raceme 10 - 26 cm long, the axis 1 - 3 mm diam. at the base; secondary racemes 2 - 11, up to 22 cm, spreading and ascending, their basal portions naked; tertiary racemes infrequent. Bracteoles ovate to subulate, green to brown, 2 - 4 mm long, densely flocculent over abaxial sides and margins. Pedicels spreading, ascending, 5 - 20 mm long. Tepals greenish-white to cream-colored, often turning dark reddish-purple in age, spreading, becoming reflexed, 5.5 - 13 mm long, 2.2 - 6 mm wide, the basal 1/5 - 1/4 clawed, 0.5 - 1.2 mm wide; blade abruptly auriculate to somewhat hastate, ovate to obovate-oblong; margins entire; tip acute, 8 - 12 nerved, flocculent, at least on the outer series. Tepal glands 2, basal, on each side of the midrib, much thickened apically, oblong to oblong-ovate, parallel to the midrib with a slight divergence at the apex, yellowish-green, glistening (in vivo), nectariferous. Stamens 6, 1/2 - 2/3 as long as the mature tepals; filaments inserted at or above the middle of the claw, 0.7 - 2.5 mm from the base of the ovary, at first curving

outward but soon (2 - 5 days after anthesis) curving strongly inward to the pistil; anthers 0.9 mm diameter, opening soon, fugacious. Ovaries trigonous, slenderly columnar to ovoid, superior and nearly free from the perianth, moderately pubescent to glabrous; styles 1.5 - 3.5 mm long, spreading, apically recurved, persistent in fruit, turning inward in age. Mature fruit a capsule, 10 - 18 mm long, 6 - 10 mm wide, ovoid to ellipsoid, light to dark brown, glabrate to glabrous, dehiscing distally. Mature seeds winged, 5 - 8 mm long, 2.5 - 4 mm wide, tan to pale yellow.

Common name: Bunchflower.

Distribution: Eastern United States from southern New York to Iowa, south to northern Florida and eastern Texas (Fig. 1). Bogs, marshes, savannas, wet woods and meadows. Local. June - August.

Representative Specimens: ALABAMA: Dallas: Black Belt s. of Selma, 11 Jun 1950, Crawford 1167 (WVA). Lee: Auburn, 1897, Earle & Baker s.n. (NY). FLORIDA: Walton: 1886, Curtiss s.n. (GH). GEORGIA: Charlton: e. of Folkston, sphagnous bog, 12 Aug 1902, Harper 1506 (GH). Colquitt: U.S. 319 s. of Colquitt-Tift Co. line, 3 Jul 1960, Browne 2544 (NCU). Early: s. of Hilton, boggy swamp, 25 Aug 1948, Thorne & Muenscher 8590 (GH). Lowndes: n. of Valdosta, 6 Jun 1930, Bright 4855 (CM). SOUTH CAROLINA: Berkeley: sw. of Moncks Corners, swampy woods, 11 Aug 1939, Godfrey & Tryon 1403 (NY), Calhoun: Halfway Swamp Creek on S.C. 267 se. of Lone Star, 3 Jul 1957, Ahles & Haesloop 30268 (NCU). NORTH CAROLINA: Alamance: w. of Burlington, 28 Jun 1927, Wiegand & Manning s.n. (GH). Alleghany: jct. of N.C. 18 & Co. Rt. 1416, 26 Jul 1968, Leonard, Radford & Moore 1858 (WVA). Ashe: Bog, 2 Aug 1961, Radford 17594 (NCU). Craven: near Tuscarora, 12 Aug 1949, Godfrey 49888 (GH). Mitchell:

Alder Marsh nw. of Spruce Pine on N.C. 26, 23 Jul 1961, Ahles & Gupton 53875 (NCU). VIRGINIA: Shenandoah: Mudhole Bog, Massanutten Mountain, 10 Jul 1947, Artz 618 (US); Mudhole Bog, Massanutten Mountain, 18 Jul 1977, Bodkin 77101 (JMUH). Bland: Marsh n. of Mechanicsburg, 28 Jun 1966, Harvill 14243 (NCU). Campbell: Timber Lake, 10 Jul 1966, Freer 4275 (NCU). Greensville: Three Creek n. of Emporia, 15 Jul 1938, Fernald & Long 8667 (GH). Henrico: Marsh w. of Elko Station, 14 Jul 1967, Harvill & Stevens (NCU). Montgomery: Blacksburg, s.d., Murrill s.n. (NY). Louisa: Swampy streamside e. of Louisa, 4 Sep 1971, Stevens 4337 (FARM). WEST VIRGINIA: Greenbrier: Meadow Creek Mt. 5 mi. from Lake Sherwood, 22 Jul 1959, Clarkson 2758 (WVA). Hardy: Lost River, 17 Aug 1928, W.V.U. Bot. Exped. s.n. (WVA). Mercer: Swamp near Athens, 18 Jul 1930, Berkley s.n. (MO). Pocahontas: Woods near hemlock forest, Jul 1969, Hinkle s.n. (WVA). Webster: Second Glade Meadow, 15 Jul 1890, Millspaugh 563 (WVA). PENNSYLVANIA: Allegheny: Branch of Bull Creek, 5 Aug 1900, Shafer s.n. (CM). Bedford: 2 mi. w. of Everett, 17 May 1941, Berkheimer 2430 (CM). Berks: 2 mi. e. of Fleetwood, 5 Jul 1942, Berkheimer 3272 (MO). Butler: Ribold Station, 11 Aug 1928, Bright 745 (WVA); Pike: 2.5 mi. e. of Porters Lake, 5 Jul 1938, DePue 135 (C). NEW JERSEY: Camden: 4 Jul 1906, Bartram s.n. (US). Bergen: 1862, Eaton s.n. (MO). Morris: Morristown, 1889, Parker s.n. (GH). MARYLAND: Cecil: 1890, Brinton s.n. (GH). INDIANA: Vigo: Terre Haute, May 1893, Underwood s.n. (NY). Cass: Bog 3 mi. w. of Hoovers, 22 Jun 1946, Friesner s.n. (MO). Randolph: Cabin Creek, bog n. of Modoc, 7 Jul 1945 Friesner 19218 (NY). ILLINOIS: Jackson: 0.2 mi. n. of Big Muddy River bridge, 10 Jun 1941, McCree s.n. (MO). Menard: Ahtens, 1861, Hall s.n. (GH). Morgan: Jul 1886, Milligan s.n. (US). IOWA: Black Hawk: 8 Jul

1929, Burk s.n. (MO). Decatur: 14 Jul 1897, Fitzpatrick s.n. (MO).
 Ringgold: Near Bentonport, Aug 1920, Graves 1824 (US). MISSOURI: Adair:
 Between Clay & Adair, 29 Jun 1933, Palmer & Steyermark s.n. (MO).
 Audrain: 9 mi. w. of Mexico, 29 Jun 1941, Steyermark 40608 (GH).
 Christian: 1 mi. e. of Christian, 22 Jul 1968, Redfearn 24530 (NCU).
 Iron: Arcadia, 27 Jun 1920, Palmer 18099 (GH). Jackson: Little Blue
 Tank, 26 Jun 1898, MacKenzie 173 (NY). Jasper: Near Orongo, 19 Jun
 1930, Palmer 36612 (GH). KANSAS: Douglas: 6 mi. w. of Lawrence, 27
 Jun 1960, McGregor 15760 (US). Miami: Between Olathe & Pleasanton, 18
 Jun 1929, Rydberg & Imler 49 (NY). ARKANSAS: Hempstead: 4 Sep 1916,
Palmer s.n. (MO). OKLAHOMA: Pushtamaha: Bog at Antlers, 17 Jul 1915,
Palmer 8327 (NY). LOUISIANA: Washington: Bog ne. of Franklinton, 29
 Jun 1938, Correll 9194 (NY). MISSISSIPPI: Attala: Natchez Trace
 Parkway, 28 Jun 1948, McDougall 1693 (US). Covington: 1.5 mi. se. of
 Mt. Olive, 11 Jul 1950, Webster & Wilbur 3306 (NY). George: Swamp,
 16 Jun 1953, Demaree 33420 (US). TEXAS: Robertson: Bog near Newbaden,
 16 Jun 1943, Barkley 13042 (MO).

Published Illustrations: In Gleason (1952), the rendering of habit is excellent but the important characters of the tepals are poorly illustrated. The drawing does not show the abruptly clawed tepals nor the correct gland structure. Strausbaugh & Core (1970). Radford et al. (1968), the tepal shape is not correctly illustrated.

Melanthium virginicum was first described by Linnaeus in his Species plantarum (1753). Linnaeus probably saw at least two collections prior to that. He cited Gronovius' "Melanthium foliis linearibus integerrimis longissimis, floribus paniculatis" (Flora Virginica, 59, 1739) in his Genera plantarum, ed. 2, (1742) and again in 1753. It

is quite possible that Linnaeus saw Clayton's material from Virginia in Gronovius' herbarium when he visited Holland. Two such sheets, apparently duplicates, are now at BM. The other collection that Linnaeus studied was that of Peter Kalm, now at LINN. It was collected in Virginia by Kalm and sent to Linnaeus. The 1753 description corresponds with these syntype collections as to all characters mentioned. The brief description of clawed petals, long linear, entire leaves, and flowers in a panicle are characters clearly evident on the Kalm sheet. One Clayton sheet contains no basal leaves, just the upper stem and panicle, while the other is complete with the lower part of the terminal raceme in full fruit. There are no fruit characters mentioned in Linnaeus' description.

It was Linnaeus' custom prior to 1753 to number specimens in accord with the species numbers which appeared in his Species plantarum. The Kalm sheet of Melanthium virginicum is clearly marked "1," corresponding to that species in Species plantarum. It is most reasonable that M. virginicum be lectotypified on the Kalm specimen, since that is the one most surely linked to the Linnean protologue.

Ker-Gawler apparently regarded Linnaeus' Melanthium and Helonias, both published in 1753, as cogenetic, recognizing M. virginicum under the latter generic name. He suggested that there was also little reason to hold Veratrum separate, but did not make any actual transfers in that regard. The combination Leimanthium virginicum was published by Willdenow in 1808. Willdenow attempted to segregate the Old World species of Melanthium L. from the New World forms. To Willdenow, Linnaeus' genus was characterized by M. sibiricum, which was significantly different from M. virginicum (M. sibiricum was transferred

to Zigadenus in 1837 by Asa Gray). He established Leimanthium to accommodate the segregated New World species, L. virginicum ("in Virginia"), along with two other species, L. laetum ("American boreali") and L. pallidum ("in Carolina"). Leimanthium pallidum, which included in synonymy both M. phalangioides Desr. (1797) and M. racemosum Michx. (1803), was superfluous when published and is typified in this work on the Desrousseaux name.

Aiton submerged all of Melanthium, as well as several other related genera, in Veratrum, adopting a broad view of the latter. In that connection he made the new combination V. virginicum.

The genus Evonyxis was described by Rafinesque in 1836. He felt that the genus Melanthium required a "radical reform" and stated that "the very name, black flower, does not apply." In his abrupt action he abandoned Melanthium in favor of his superfluous name, Evonyxis, under which he made the combination E. virginica and E. monoicum.

Kunth also thought that the Old World and New World species of traditional Melanthium should be segregated in different genera. He retained the name Melanthium for the Old World Species and transferred the New World species to Zigadenus. He erroneously attributed the combination Z. virginicus to Endlicher, who, in fact, did not make the combination, but only implied that it should be done.

Melanthium monoicum was described by Walter in 1788. As nearly as can be determined by his very brief diagnosis, Walter's specimen had mostly staminate flowers on the lower inflorescence axes and pistillate flowers above on the terminal raceme. Previous descriptions did not specifically make this distinction. Walter apparently distinguishes this species from M. virginicum on the basis of differing

sexual distributions within the inflorescence. However, M. virginicum displays great variability in this regard, regularly including the particular pattern Walter thought distinctive. There is no evidence to support the segregation of M. monoicum from M. virginicum.

No authentic material of M. monoicum is known to exist. As Walter's herbarium has changed hands a number of times before it was finally purchased by the British Museum (Natural History), this may account for the mediocre condition of many of his specimens relating to the Flora caroliniana as well as the absence of others. Walter gave the herbarium to John Fraser, whose son gave it to the Linnean Society, which kept it until 1863 when it was sold to the Museum (Stafleu, 1967). For neotypification of Walter's name I have chosen a collection which best fits the protologue and comes from the area where Walter collected. The neotype is the Godfrey and Tryon specimen cited above.

The name Melanthium monoicum has also been erroneously attributed to Pursh. He used it in his Flora americanae septentrionalis (1814), very clearly citing Walter after the description. There is a Pursh collection at Kew with a label which reads "Melanthium monoicum Walt." in Pursh's hand. He obviously knew that this was a Walter name and had no intention of publishing a new name. However, the sheet is interesting. There are discordant elements mounted under the same tape; one is M. virginicum, the other M. parviflorum. The collection site on the sheet is given as Peaks of Otter, Virginia, a known location for both species.

Melanthium polygamum was described by Desrousseaux in 1797. The holotype specimen at P-LA was collected by Fraser in "Carolina." There

are two labels on the sheet, "melanthium polygamum Dict." and "Melanthium virginicum l.?", in different hands. In the description, M. monoicum Walt. is cited as a questionable synonym. The Fraser specimen was young when collected and shows little sexual differentiation in the different parts of the inflorescence. Desrousseaux, aware of the sexual characters described by Walter for M. monoicum, discussed the apparent differences in his M. polygamum. The continuous range of variation in these characters within M. virginicum includes the specific pattern described for M. polygamum, which like M. monoicum is actually not distinct from Linnaeus' species.

Melanthium laetum is an invalid herbarium name taken by Kunth from a specimen in the Berlin Herbarium annotated as such by Kinnet. Kunth cited it as a synonym only, under his Zigadenus virginicus.

Melanthium dispersum was described by Small in 1898 and is based on a collection by Curtiss in Walton County, northwest Florida, in the summer of 1885. Another Curtiss sheet of M. dispersum is at GH and the annotation slip by Zimmerman is marked "isotype" and "1885." This is incorrect; this specimen was collected in 1886, and is therefore, not a duplicate of the original material, as clearly evident from the date of collection in Curtiss' own hand on the specimen label itself. Small indicated that M. dispersum is "near to M. virginicum" but that the habit is different, the leaves longer, the panicle broader with no prolonged main axis, the pedicels stouter, and the claws shorter. His description is similar to Walter's for M. monoicum, as noted by Gates (1917). The 1885 specimen at NY does have a much reduced terminal raceme, reduced to the point that it looks to have been injured. The Curtiss specimen of 1886 from the same location has a terminal raceme

more typical of M. virginicum.

Walter is often erroneously cited as author of Melanthium virginicum. In his "Flora caroliniana" he listed seven species: M. virginicum, hybridum, monoicum, muscaetoxicum, spicatum, dioicum and racemosum. Of the seven, only M. virginicum does not appear in italics, his conventional way of indicating a new species. Walter certainly intended to indicate M. virginicum as already treated by Linnaeus. He did not cite any authority but this practice was not uncommon at that time. Walter was simply listing and discussing an existing name along with his descriptions of new species which he considered properly placed in the genus.

Many of the biological aspects of Melanthium virginicum are not known at present. Little has been done and what is suggested is quite speculative. Progressive series of development have been suggested for tepal shape, gland reduction and stamen adnation (Kupchan, 1961).

The reproductive biology of this complex is little known from pollination to embryo development. As indicated previously, this is with good reason. Sexual reproduction in some populations rarely occurs. With the peculiarities of flowering, crossing experiments have not been done and unless years are available for such a study it is unlikely that it will be attempted. It is conceivable that reproduction by asexual means occurs frequently through budding of underground root-stocks. This has been found to occur in the closely related Stenanthium where rhizomes form buds some distance from the parent plant (Utech, pers. comm.) (Fig. 33). Some related groups of plants reproduce primarily in this manner although flowers are produced in abundance. In such cases, still, there is little seed-set.

It is reasonable to suggest that the "main line" of evolution in this group is presently represented by Melanthium virginicum. This species is the most widespread of the four and is sympatric with the other three. It has adapted to the diverse regional differences that exist from the Great Plains to the Coastal Plains. However, actual habitat differences are not as great as the geography would suggest. This species is most adapted to the water-laden soils of bogs, swamps, marshes and other highly organic soils at lower elevations. If evolutionary success is equated with population size and distribution, this species is the most successful of the four. From my observation of populations in the mid-Appalachians over a seven year period from 1971 to 1978, M. virginicum appears to be the most stable in plants per population and in the number of plants per population which produce flowers. The lowlands habitat of this species is probably somewhat more sheltered and subject to fewer climatic stresses on the average than are the mountain slope and crest habitats of the other species.

The major characteristics of Melanthium virginicum are quite constant throughout its range. An exception to this is tepal color. The tepals are more intensely cream-colored to yellow in some of the more western specimens examined (Reverchon 4032 from Texas, GH; Steyermark 40491 from Missouri, GH). The general habit of some plants to the western side of the range is more coarse and less graceful than that of the eastern plants. The panicles are stouter and more closed. One Kansas specimen (McGregor E317, GH) is beyond the normal limits of variation, with a very stout closed panicle, the axes of which are densely pubescent and large tepals that are vivid yellow. The

vestiture and tepal width (8 mm) also exceed the normal range of variation. There is diversity in plant size, inflorescence shape, and tepal shape, but without consistent geographic trends. These variations could be interpreted as environmentally induced. There is little variation in the amount of adnation of filament to claw, certainly a trait more fully under genetic control.

Melanthium virginicum is different from the other three species in having long, linear to narrowly oblanceolate leaves which are long-attenuate, narrowly clawed tepals with a blade that is abruptly auriculate to somewhat hastate and entire margined, stamens with filaments inserted at or above the middle of the claws, and tepal glands which are very thick, succulent and oblong to oblongovate. Although there is no reason to confuse any of the Melanthium species, M. latifolium approximates M. virginicum in some characters. The leaves of M. latifolium are wider and oblanceolate the tepals are abruptly clawed, but the very strikingly orbicular-deltoid blades with strongly undulate margins and folded tips are distinctive. The symmetry and preciseness of the tepal arrangement in M. latifolium suggests the exact regularity of spokes in a wheel (Fig. 28). This characteristic is consistent, obvious in the field, and easily preserved in pressed material. The tepal glands in this species are not as well developed but are obvious and obcuneate.

There is a habitat difference between these two species. Melanthium virginicum occurs in very moist or wet locations such as bogs, marshes, and in seepage areas along streams, while M. latifolium is found on more mesic slopes. In the mid-Appalachians no populations of these species observed in the field were overlapping and herbarium

studies yield no evidence to the contrary. Populations of these species are very localized and habitat specific. In fact, there is an interesting topographic situation in all four species. M. virginicum is mostly found in wet habitats at the lower elevations, the Appalachian M. latifolium and the Ozark M. woodii commonly grow on mesic slopes, while M. parviflorum is most frequently found on the crests of mountains or immediately below.

The clawed tepals in M. virginicum separate this species from M. parviflorum and M. woodii, the latter two having gradually attenuated bases. The leaves of these more mountainous species are much wider. The tepals of M. virginicum often turn from cream-colored to dark reddish-purple in age, then resembling the young tepals of M. woodii in color.

2. MELANTHIUM LATIFOLIUM Desr.

Melanthium latifolium Desr. in Lam., Encycl. Meth. Bot. 4:25.

1797. Type: Without data. HOLOTYPE: P-LA (! photo).

Melanthium racemosum Michx., Fl. Bor.-Amer. 2:251. 1803,

non Walt., Fl. Carol., 125. 1788. Type: United States:

"Carolina," Yellow Mountain (actually Mt. Mitchell, near Asheville, North Carolina, on the Tennessee border), 23

Jun 1789, Michaux s.n. HOLOTYPE: P-MX (! photo). ISO-

TYPE: P (ex Herb. Richard)!

Melanthium hybridum Walt., misappl. See under Excluded Taxa and Dubious names.

Tall herbs with large oblanceolate, mainly basal leaves and terminal panicles of greenish-white to light yellow polygamous flowers. Roots 7 - 18, ca. 2 mm diameter, white, segmented, distally branching, arising radially off the bulb. Rhizome reduced, brown, 0.5 - 1.5 cm long, 0.5 - 1 cm diameter. Bulb erect, 0.6 - 1.7 cm diameter; fibrils brown, anastomosed, stiff, excurrent. Stem 5 - 16 dm tall, the terminal 1/4 - 1/2 floriferous. First leaves 2, hidden by fibrils, non persistent. Later leaves narrowly oblanceolate, mainly basal, 20 - 55 cm long, 1 - 7.2 cm wide, green through flowering, glabrous; bases canaliculate 1/3 the length of the blade with sheaths closed; tips acute; cauline leaves few, reduced upward, clasping. Inflorescence an open panicle of simple racemes, 17 - 72 cm long, floccose, the hairs white to tan; terminal raceme 4 - 38 cm long, axis 1 - 3 mm diameter at the base; secondary racemes 7 - 18, up to 20 cm long, spreading and ascending, their basal portions 1/4 - 1/3 naked; tertiary racemes common. Bracteoles ovate to subulate, green to purplish brown,

2 - 6 mm long, densely floccose on the bases and margins. Pedicels spreading, ascending, 7 - 17 mm long. Tepals greenish-white to light yellow, green in age, spreading, becoming reflexed, 3 - 8 mm long, 2 - 4.8 mm wide, the basal 2/5 a linear involute claw, 0.3 - 6.9 mm wide; blade abruptly orbicular-deltoid; margins strongly undulate; tip shortly acuminate, 7 - 15 nerved, abaxially flocculent on the outer series. Tepal glands 2, basal, one on each side of the midrib, thickened apically, broadly obcuneate, diverging apically, yellowish, glistening (in vivo), nectariferous. Stamens 6, 1/2 - 2/3 as long as the tepals; filaments inserted at or below the middle of the claw, 0.4 - 1 mm from the base of the ovary, at first curving outward but later curving strongly inward to the pistil; anthers 0.7 mm diameter, opening soon, fugacious. Ovaries trigonous, ovoid, superior and nearly free from the perianth, moderately pubescent to glabrous; styles 1.7 - 3 mm long, spreading apically recurved, persistent in fruit, turning inward in age. Mature fruit a capsule, 12 - 19 mm long, 7 - 12 mm wide, ellipsoid-oblong, light brown, glabrate to glabrous, dehiscent distally. Mature seeds winged, 7.5 - 9 mm long, 4 - 4.5 mm wide, tan to pale yellow.

Common name: Crisped Bunchflower.

Distribution: Eastern United States mainly in the Appalachian Mountains from Connecticut to southwestern Pennsylvania, south to Georgia and eastern Tennessee (Fig. 1). Mesic wooded slopes. Local. July - August.

Representative Specimens: GEORGIA: Burke: Marl bluff on McBean Creek, 25 Jul 1967, Bozeman & Logue 10869 (NCU). SOUTH CAROLINA: Abbeville: Mixed deciduous forest near Mountain Lake, 5.5 mi. s. of Abbeville, 29 Jun 1957, Radford 25960 (NCU). Lancaster: Along Flat Creek, 16 Jul 1961, Williamson & Ahles 1264 (NCU). Pickins: Clemson College Woods,

8 Oct 1906, House s.n. (MO). NORTH CAROLINA: Clay: Buck Creek n. of Glade Gap, 31 Jul 1957, Terrell 3189 (NCU). Haywood: Near crest of Mt. Pisgah, 8 Aug 1951, Fox 5183, (GH). Macon: Highlands on Cowee Bald, 4 Aug 1938, Coker s.n. (NCU). Orange: South side of Apple's Pond, 27 Sep 1936, Warren s.n. (NCU). Transylvania: 5 mi. ne. of Wagon Road Gap, 18 Jul 1957, Freeman 57591A (NCU). VIRGINIA: Augusta: West slope of Elliot Knob, 19 Jul 1937, Allard 3268 (CM). Page: Passmaquoddy Trail at Skyland, Skyline Drive, Shenandoah National Park, 10 Aug 1974, Bodkin 74110 (JMUH). Bedford: Peaks of Otter, 27 Jul 1871, Curtiss s.n. (MO). Montgomery: 2 mi. se. of Ellet, 17 Aug 1960, Kral 11144 (NCU). Highland: Middle Mt., 25 Aug 1974, Stevens 9652 (FARM). Rockbridge: Rocky Mount., 12 Aug 1947, Freer s.n. (GH). WEST VIRGINIA: Greenbrier: Meadow Creek Mt., 22 Jul 1959, Clarkson 2806 (WVA). McDowell: Anawalt, 1 Aug 1961, Music s.n. (WVA). Pocahontas: Frost, 23 Jul 1927, W.V.U. Bot. Exped. s.n. (WVA). Randolph: Huttonsville, 11 Jun 1939, Hutton s.n. (WVA). MARYLAND: Montgomery: Southwest of Chevy Chase, 11 Jul 1909, Steele s.n. (GH). PENNSYLVANIA: Lehigh: Vicinity of Allentown, 22 Jul 1900, Dowell 846 (GH). Bedford: 1 mi. sw. of Breezwood, 23 Jul 1946, Berkheimer 7530 (CM). Butler: 1925, Millory s.n. (CM). Mifflin: Juniata Gorge e. of Lewistown, 17 May 1921, Jennings s.n. (CM). Monroe: Hogback Mt., 1 Jul 1918, Bartram s.n. (NY). NEW YORK: Orange: Jul 1859, Austin s.n. (NY). CONNECTICUT: Fairfield: Greenwich, 1869, Palcott s.n. (GH). NEW JERSEY: Monmouth: Mount Pleasant Hills, 27 May 1919, Long 20879 (GH). Sussex: Stokes State Forest, 17 Jul 1937, Chrysler s.n. (NY). Warren: Near Millbrook, 23 Jul 1918, Bartram s.n. (GH). TENNESSEE: Sevier: Surgarland Mts., Elkmont, s.d., Jennison 2778 (TENN). Published Illustrations: In Gleason (1952), the illustra-

tion of the flower to the lower right of the stem lacks tepal glands. The leaf habit is shown very well, especially the canaliculate base. The flower under the name M. hybridum and the fruit at the lower left are those of Veratrum viride. Strausbaugh & Core (1970), the tepals are poorly illustrated with no details of these critical characters in this species. Radford et al. (1964), the leaf placement in the illustration suggests a cauline tendency which is incorrect. The illustration of the tepal is misleading as to shape and the glands are not shown.

Melanthium hybridum Walt. which has been traditionally used for this taxon is a misapplied name. References have been made to this erroneous application (Watson, 1879 and Gates, 1918) but the formal and proper nomenclatural changes necessitated by this recognition have not been forthcoming. Only one modern taxonomic treatment, Britton and Brown's (1913) Illustrated Flora of the Northern United States and Canada uses M. latifolium Desr., with M. hybridum listed as a questionable synonym. The New Britton and Brown (1952) lists M. hybridum Walt. and includes no synonyms. Watson recognized M. latifolium in his treatment of three species of Melanthium and questioned Walter's name stating "the identity of Walter's M. hybridum is doubtful."

Melanthium hybridum was described by Walter in Flora caroliniana in 1788. There are insoluble problems in typifying this ambiguous name, ones relating to both the unassociable original description and the lack of any authentic type material. Walter's description does not fit the species which has been traditionally called M. hybridum. The description is brief and states, "petalis plicato-undulatis immaculatis, floribus masculis et foemineis mixtis." The word "immaculatis" is the source of trouble, the other parts of the description fitting the

species to which the name has usually been applied. By "immaculatis" Walter, with no doubt, was referring to the glandular condition on the tepals. He knew of the presence of glands in M. virginicum referred to in his description of that species on the same page and immediately preceeding his description of M. hybridum. This characteristic is also quite evident in traditional M. hybridum, and it is inconceivable that Walter would have overlooked it. In later descriptions under the name M. hybridum others invariably described the tepals as "maculatis." This was the case even when some later writers, such as Pursh and Elliot, cited Walter and certainly must have noted the differences in their descriptions.

Pursh's description of Melanthium hybridum is often cited in reference to this doubtfully named species. He stated "petalis subrotundis unguiculatis plicato-undulatis vix maculatis, extus hirsutus." Glands are included, yet he cites Walter. Elliot (1817) in A sketch of the botany of South Carolina and Georgia includes "glandulis coalitis" in his description of M. hybridum (the name is often attributed to Elliot but he clearly cited Walter). Only in Nuttall's (1818) Genera of North American plants is there a description under the name M. hybridum which indicates lack of glands. However, the remainder of the description also does not correlate with Walter's, so there are questions as to what species, irrespective of name, Nuttall was describing. The characteristics he described are closer to M. parviflorum. The problem here is one of nomenclature. The name M. hybridum cannot be typified and must be considered ambiguous and, in this context, misapplied. (See further under "Excluded Taxa and Dubious Names.")

Nuttall is sometimes credited with the combination M. hybridum,

but erroneously so. In his treatment of the genus he asterisked only one species, M. glaucum (now Zigadenus glauca), thereby indicating it to be new. The other species, including M. hybridum were thus not treated as new. Nuttall did fail to cite Walter in connection with M. hybridum, but it is still quite certain he did not regard it as new.

The next priorable name for this species is Melanthium latifolium, published by Desrousseaux (1797) in Lamarck's Encyclopedie methodique. Botanique. The description is very thorough and includes the characteristics commonly attributed to M. hybridum. Desrousseaux cited a Virginia collection by John Fraser. The symbol "v.v." is included at the end of the description, meaning he saw live material. A specimen at P-LA is labeled "Melanthium latifolium Dict." (the "Dict." is a common contemporary reference to Lamarck's Encyclopedie) and consists of two fragments of the panicle. There is no information on the sheet to indicate that it is a Fraser collection, nor any data as to collection site or date. However, Desrousseaux' description of the critical characters of the flowers, such as pubescent panicles and clawed orbicular petals with undulate margins and glands, represents precisely the common concept of M. hybridum. On the basis of this detailed description, which correlates exactly with the specimen at P-LA, and the near certainty that it is associated with Desrousseaux' original description, it seems justified to consider it the holotype of M. latifolium.

Lamarck's own copy of the Encyclopedie is at Paris. According to his marginal annotation in this copy, Melanthium latifolium is the same as M. racemosum Michx., a later synonym of M. hybridum Walt.

Melanthium racemosum was described by Michaux (1814) in Flora boreali-americana. The type sheet indicates that the specimen was gathered at "Yellow Mountain," a site, according to Ewan (1974) which is near Asheville, North Carolina, on the Tennessee border. Ewan also states that Yellow Mountain is now called Mt. Mitchell, and Michaux collected there on June 23rd., 1789. The description, which is very brief, corresponds with the specimens so labelled M. racemosum at P-MX. This specimen is complete and corresponds with M. latifolium in all characters. Melanthium racemosum is here lectotypified on the specimen at P-MX. The orbicular tepals with undulate margins leaves no questions as to the inaccuracy of this synonymy, although some authors have referred the name to M. virginicum.

Melanthium latifolium is very close to M. virginicum in many critical characters. It is reasonable to speculate that this species could have been derived from M. virginicum. The leaves of M. latifolium are more expanded, which could be a response to movement into the shaded slope habitat from the more open areas where M. virginicum typically grows. The clawed tepals could have become regressed in size and in this process become strongly undulated along the margins. The raised oblong glands of M. virginicum may have flattened and spread apically to form the characteristic obtuse glands of M. latifolium. With tepal reduction, from whatever cause, came less adnation of the filaments to the claws. Other changes would have included reduction in stem height, less frequent flowering, and flowering later in the growing season.

There is little variation within Melanthium latifolium throughout its range. The most notable variations are in size, especially of the

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There is little variation within Melanthium latifolium throughout its range. The most notable variations are in size, especially of the

tepals. There is no particular pattern to this variation relative to any consistent geographical or environmental factors. One small population at Big Meadows, Shenandoah National Park, Virginia, containing 22 plants, showed variation in ovary color. Three of the six plants that were flowering in 1978 had deep purplish-red ovaries. The other three had ovaries which were the usual brown. This pronounced variation is striking in the field and is seemingly retained in sicco (Bodkin 78110, JMUH). The purplish-red ovaries were slightly more pubescent than the typical forms. There is an occasional occurrence of red pigment in the bracteoles and in the trichomes on some racemes in the species as a whole, but this Virginia population is the only one known to have definite purplish-red ovaries. A sweet musky odor was associated with these particular flowers, the only time an odor has been noted in any Melanthium species.

An interesting and possible relationship between the amount of light and flowering response was observed in another Shenandoah National Park population of Melanthium latifolium. The canopy forest was defoliated during a heavy insect infestation in May 1974. Only three plants flowered this year out of approximately 50 in the population, and all three were in higher light intensity areas under the defoliated trees. No plants flowered under the undisturbed canopy. However, there is not enough data to support any general hypothesis about the effects of light intensity on flowering in this species. In view of the flowering habits of this species, adequate data is not likely to be accumulated. Over a five year period the population mentioned above had three plants flowering the first year, two the second, two the third and none in the final two years.

Melanthium latifolium is strikingly different from the other species in the genus in the habit or general appearance of the flowers. The regularity or symmetry in the arrangement of the blades at the ends of the claws suggests a hub with spokes each terminated by a wheel (Fig. 28). This habit, although difficult to describe, is distinctive. The tepal claw is narrower in this species (0.3 mm) than in M. virginicum, but it does not appear as such because the expanded orbicular blade of the tepal is also smaller. The orbicular blade with short acuminate reflexed tip is constant and quite different from those found in other species.

The large oblanceolate leaves of Melanthium latifolium are similar to the leaves of M. woodii, and narrower than those of M. parviflorum. Although sterile specimens can be identified using only foliar characters, caution should be used due to the wide range of variation. Some identification problems are eliminated on the basis of provenance due to the mostly allopatric distribution of M. latifolium and M. woodii (there are disjunct populations of the latter in North Carolina and Georgia, where the two are thus sympatric).

Melanthium latifolium varies greatly from M. parviflorum and M. woodii in its abruptly clawed tepals, the latter having gradually attenuated tepal bases. Tepal color is also quite different: greenish-white to yellow in M. latifolium, pale green in M. parviflorum, and purplish-brown in M. woodii.

Melanthium latifolium and M. parviflorum sometimes grow in overlapping populations. However, M. latifolium is more often found lower on the slopes while M. parviflorum is found toward or on the crests. The general range for M. latifolium is 1000 - 5500 ft. (305-1677 m) and

for M. parviflorum 2500 - 6684 ft. (762-2037 m). Both species are found most commonly on slopes in rich, moist soil under a deciduous forest canopy.

Like the other species in the genus, Melanthium latifolium exhibits definitive characteristics and is clearly differentiated from each of the others.

3. MELANTHIUM PARVIFLORUM (Michx.) S. Wats.

Melanthium parviflorum (Michx.) S. Wats., Proc. Amer. Acad. Arts

14:276. 1879, based on Veratrum parviflorum Michx., Fl.
Bor.-Amer. 2:250. 1803. Type: United States: "excelsis
montibus Carolinae," July s.d., Michaux s.n. HOLOTYPE:

P-MX (! photo).

Tall herbs with broadly oblanceolate to broadly obovate, mainly basal leaves and terminal panicles of pale green polygamous flowers. Roots 8 - 20, ca. 2 mm diameter, white, segmented, distally branching, arising radially off the end of the bulb. Rhizome reduced, brown, 0.6 - 3 cm long, 0.5 - 1.2 cm diameter. Bulb erect, 1 - 1.6 cm diameter; fibrils dark brown, anastomosed, stiff, excurrent. Stem 5 - 15 dm tall, the terminal 2/3 - 4/5 floriferous. First leaves 2, partly hidden by fibrils, persistent. Later leaves broadly oblanceolate to broadly obovate, slightly plicate, mainly basal, 17 - 35 cm long, 4.5 - 12.5 cm wide, green with a bluish tint, paler abaxially, glabrous; bases canaliculate approximately 1/3 the length of the blade with sheaths closed; tips obtuse to submucronate; cauline leaves few reduced upward, clasping. Inflorescence an open panicle of simple racemes, 25 - 100 cm long, slender, axes floccose, hairs white; terminal raceme 10 - 44 cm long, axis 1 - 3 mm diameter at the base, secondary racemes 6 - 22, up to 24 cm long, spreading and ascending, occasionally perpendicular to the axis their basal portions naked; tertiary racemes rare, sometimes replacing the first flower on the lower secondaries. Bracteoles subulate, dark green, 2 - 4 mm long, densely floccose abaxially, basally, and on the margins. Pedicels spreading nearly

perpendicular from the axis, 5.5 - 11 mm long. Tepals pale green to olive-green, spreading, little reflexed in fruit, 5 - 9 mm long, 1.3 - 3 mm wide; blade narrowly rhombic oblanceolate, gradually attenuate to a narrow stalk; margins entire, tip acute to subacuminate, 5 - 8 nerved, abaxially flocculent near the base. Tepal glands 2, obsolete and very obscure (sometimes obvious only as a slight discoloration on the basal 1/4 of the tepal). Stamens 6, 1/3 - 1/2 as long as the tepals; filaments inserted on base of tepals, 0.4 mm from the base of the ovary, curving outward, base little broadened, barely 1/3 as wide as the tepal at insertion, anthers 0.5 mm diameter, opening soon, fugacious. Ovaries trigonous, ovoid, superior, nearly free from the perianth, glabrous; styles 1 - 1.5 mm long, strongly divergent to reflexed, apically recurved in age, the tips turned inward in age. Mature fruit a capsule, 10 - 18 mm long, 7 - 10 mm wide, oblong-elliptic, dark brown, glabrous, dehiscent distally. Mature seeds winged, 7.5 - 10 mm long, 3.5 - 4.5 mm wide, pale brown to pale yellow.

Common name: Mountain Bunchflower.

Distribution: Eastern United States mainly in the mid-Appalachian Mountains from West Virginia to northern Georgia (Fig. 1). Rich, moist, wooded mountain crests and higher slopes, mostly above 2600 ft. (800 m), in deciduous forests. July - August.

Representative Specimens: WEST VIRGINIA: Hardy: North Mt. n. of Wolf Gap, 21 Jul 1969, Stevens 1227 (WVA). Pendleton: North Mt. w. of Franklin, 4 Aug 1932, Core 4325; North Mt., 26 Jul 1978, Bodkin 78102 (JMUH). Pocahontas: Marlinton, 27 Jun 1933, Strausbaugh s.n. (WVA). Greenbrier: Alvon, near Camp Wood, 29 Jun 1949, McCauley s.n. (NCU). Summers: Burgers Springs, 7 Aug 1933, Weldon 509 (WVA). VIRGINIA: Rockingham:

Crest of Shenandoah Mt., 2 mi. n. of Reddish Knob, 15 Jul 1973, Bodkin
7360 (JMUH); Skidmore Fork, 3 Aug 1968, Harvill & Stevens 20073 (FARM).
 Augusta: Summit of Elliot Knob, 4 Jul 1937, Allard 3148 (US); Elliot
 Knob, 3 Aug 1978, Bodkin 78104 (JMUH). Highland: Upper Back Creek, 25
 Jul 1971, Stevens 3885 (FARM). Allegheny: McGraw Gap near Clifton Forge,
 14 Jul 1973, Stevens 7313 (FARM). Bedford: Peaks of Otter, Sep 1872,
Curtiss s.n. (MO). Botetourt: Blue Ridge Mts. between Big Marsh and
 Fallingwater Cascades, 12 Sep 1966, Freer & Ramsey 473 (NCU). Giles:
 Potts Mt., 19 Aug 1903, Steele 28 (GH). Grayson: Point Lookout Mt. near
 Independence, 1 Jun 1976, Stevens 12701 (FARM). Patrick: Blue Ridge
 Mts., Upper Rock Castle Creek, 17 Jun 1976 Stevens 12931 (FARM).
 Floyd: Buffalo Mt. 18 June 1976, Stevens 12937 (FARM). Nelson: Three
 Ridges, 3 Jul 1975, Stevens 10929 (FARM). Wise: High Knob, 6 Jun 1968,
Harvill 18461 (FARM). NORTH CAROLINA: Avery: 4 Jul 1924, Woods 9284
 (WVA). Buncombe: Pisgah Mt., 30 Jul 1898, Herb. Biltmore 4756c (US).
 Burke: Jonas Ridge, Aug 1933, Hunnewell 12773 (GH). Clay: Buck Creek,
 U.S. 64 w. of Black Gap, 21 Aug 1956, Radford 16224 (GH). Haywood:
 Half Acre Ridge near Cove Creek Gap, 15 Jun 1955, Hardin 739 (GH).
 Macon: Rainbow Springs, 1 Aug 1935, Correll 3514 (GH). Watauga: 2 mi.
 e. of Blowing Rock, 1 Aug 1922, Randolph 1151 (GH). TENNESSEE: Carter:
 Roan Mt., 15 Sep 1884, Smith s.n. (GH). Sevier: Mt. LeCoute, 21 Aug
 1940, Fox s.n. (WVA). Sullivan: Bluff Mt., 28 Aug 1897, Kearney 919
 (US). Blount: Jul 1900, Ferris s.n. (MO). SOUTH CAROLINA: Pickens:
 Round Top Mt., s.d., Correll 6702 (NA). GEORGIA: Rabun: Mill Creek
 above Tate City, 25 Jul 1948, Cronquist 5555 (GH). Towns (?): Brass-
 town Bald, 15 Jul 1908, Howell 411 (US).

Published Illustrations: In Gleason (1952), the leaf apices should be more abruptly narrowed and the tepal shape is not accurate. In Strausbaugh & Core (1970), the illustration is accurately representative.

Watson's Melanthium parviflorum is based on a Michaux (1803) name, Veratrum parviflorum, which was described in Flora boreali-americana. Michaux collected this plant in the "high mountains of Carolina," as stated in the original article. In all characters the description agrees with the specimen at P-MX. Michaux also collected M. virginicum and M. latifolium in his travels through the Appalachians, the latter species described by him as M. racemosum but treated herein as a synonym of M. latifolium.

Confusion has existed over M. parviflorum for a century - whether to include it in Melanthium or in Veratrum. Watson made the transfer to Melanthium in 1879. In this treatment he simply proposed M. parviflorum, placing V. parviflorum in synonymy, giving no explanation for the transfer. This action is characteristic of the manner in which this entity has often been treated, as simply a matter of almost arbitrary choice. The reason most taxonomists place M. parviflorum under Veratrum is the apparent lack of tepal glands. The glands are macroscopically obscure, and thus not conspicuous as in the other species of Melanthium. However, there is abundant anatomical evidence of glands (Figs. 50 and 52) and in some plants macroscopic "areas" represent the reduced glandular structures.

Gray (1862), in his First lessons in botany, recognized Veratrum parviflorum, but later adopted Melanthium parviflorum (Gray 1887). The first five editions of Gray's manual of botany (1848-1868) treated

the taxon under Veratrum. Sereno Watson and John Coulter's 6th edition of the Manual (1889) adopted the Watson combination, and this has been maintained in subsequent revisions (1908, 1950). Strausbaugh and Core (1970) also recognized M. parviflorum. Small (1903), Gleason (1952, 1963) and Radford (1968) report this species as V. parviflorum.

On the basis of the various distinctions between these two genera, as previously discussed, I am including this species in Melanthium. The major reasons are: adnation of filaments to tepals, open panicle, glabrous tepals, entire tepal margins, fugacious anthers, the mainly basal oblanceolate to obovate leaves and the delicate stem habit. All these characteristics are in abrupt contrast to those of the sympatric North American Veratrum, V. viride Ait.

The apparent affinities of M. parviflorum support its placement in this genus. There are a series of lesser developed (or reduced) characteristics in this species. The most striking involves glandular structure. Zimmerman (1958) suggested that M. parviflorum is at the end of a reduction series involving the tepal glands. He further reported an intermediate position in degree of stamen adnation. Whether position in these apparent morphological series correlates with position in some phylogenetic series of species is speculative. It could be further suggested that there was a reduction in tepal size accompanied by the gland reduction and less adnation. Other apparent morphological series involve flower color and complexity of the inflorescence. The inflorescence of M. parviflorum is very slender with small flowers.

In contrast to these apparent reductions in relation to other species, the leaves in Melanthium parviflorum are relatively greatly

developed, especially in width. I concur with the well-expressed opinion of Zimmerman (1958) that "the wide leaves, it may be surmised, are associated with a history which has permitted these American species to remain physiologically, if not morphologically, unchanged since Tertiary time. V. parviflorum (M. parviflorum) ranks among the most uniform and distinct conservative Appalachian forest species. It appears that a continuity, through time, of the undisturbed, closed, mesic forest habitat to which it is adapted has, at one and the same time, made it unnecessary to evolve in order to survive, and made it impossible for variants to survive which might have spread beyond the Appalachian refugium." Melanthium parviflorum does, in fact, seem well adapted to its habitat. The populations are large, compared with other Melanthium species, and there is a relatively large number of plants per population which produce flowers each year.

An interesting aspect of this species was observed frequently in field studies. Virginia white tailed deer (Odocoileus virginiana) browse on the young inflorescences. The deer eat the entire inflorescence leaving only the stalk below the flowers (Fig. 34). In some populations in the Shenandoah Mountains of Virginia over 50 percent of the inflorescences were pruned by deer. This is even more curious in view of the high alkaloid content of the Veratrae (Kuphan, 1961).

Melanthium parviflorum is most similar to M. woodii. It is reasonable to suggest an immediate common ancestry, the latter having become separated as an Ozarkian disjunct. Both species grow on mesic slopes under deciduous canopies and have the combination of rather primitive broad leaves and small flowers in an open inflorescence. Melanthium parviflorum is the only species of the genus to combine

broad basal leaves with narrow pale green tepals. The leaves are somewhat plicate, adaxially tinted a bluish-green and paler abaxially. The inflorescence appears rigid and stiff owing to the more perpendicular arrangement of secondary racemes on the main axis as well as the ascending pedicels on the terminal raceme.

Melanthium parviflorum and M. woodii both have tepal bases that are gradually attenuate, and not abruptly clawed as in M. virginicum and M. latifolium. The tepals of M. parviflorum are smaller than those of M. woodii and are the only tepals in the genus which are basically green and not showy. The habit of the flower, which is similar in arrangement to M. latifolium, is one of delicate symmetry in the shape and spacing of the six perianth segments.

Melanthium parviflorum is sympatric with M. virginicum and M. latifolium in the mid-Appalachians, but allopatric with M. woodii, the latter species centered in the Ozarks. Although some taxonomists have considered M. parviflorum to be intermediate between Melanthium and Veratrum, the inclusion of V. woodii in Melanthium produces an apparently natural four species complex and there is no reason to suggest an intermediate position for M. parviflorum. According to this alignment, only one Veratrum, V. viride, occurs in eastern North America. This species is without question phylogenetically remote from all Melanthium species.

4. MELANTHIUM WOODII (Robbins ex Wood) Bodkin

Melanthium woodii (Robbins ex Wood) Bodkin, comb. nov., based on
Veratrum woodii Robbins ex Wood, Classbook ed. 2, 557. 1848.

Type: United States. Indiana: Green Co.: deep woods, August
 s.d., Wood s.n. HOLOTYPE: GH!

Veratrum intermedium Chapm., Fl. S. U.S. 489. 1860. Type: United
 States. Florida: Gadsden Co.: Without location, 1836, Chapman
s.n. LECTOTYPE: GH!

Tall herbs with large oblanceolate, mainly basal leaves and terminal panicles of maroon to purplish to chocolate brown polygamous flowers. Roots 8 - 20, ca. 2 mm diameter, white, segmented, distally branching, arising radially off the end of the bulb. Rhizome reduced, brown, 1.5 - 2 cm long, 0.5 - 1 cm diameter. Bulb erect, 1 - 1.6 cm diameter; fibrils dark brown, anastomosed stiff, excurrent. Stem 7 - 15 dm tall, the terminal 1/2 - 2/3 floriferous. First leaves 2 - 3, hyaline, partly hidden by fibrils, not persistent. Later leaves oblanceolate, mainly basal, 19 - 36 cm long, 3 - 10 cm wide, green beyond flowering, glabrous; bases canaliculate. Approximately 1/3 the length of the blade with sheaths closed; tips mostly obtuse, sometimes tapering and acute; cauline leaves few, reduced upward, clasping. Inflorescence an open panicle of simple racemes, 30 - 60 cm long, slender, the axes floccose, hairs white; terminal raceme 10 - 40 cm long, axis 1 - 2 mm diameter at the base; secondary racemes 6 - 12, up to 22 cm long, spreading and ascending, their basal portions naked, tertiary racemes rare. Bracteoles lanceolate to subulate, green to brownish, 2 - 6 mm long, floccose abaxially, proximally and marginally. Pedicels spreading, ascending, 2 - 11 mm long. Tepals maroon to purplish to chocolate brown on adaxial

side, green on the abaxial surface, spreading and ascending, 5 - 10 mm long, 1.8 - 4 mm wide, blade oblanceolate, occasionally obovate, gradually attenuate to the base, margins entire, tip obtuse, 9 - 18 nerved, flocculent on the abaxial surfaces and margins. Tepal glands 2, basal, on each side of the midrib, little thickened apically, obcuneate, paralleling midrib, dark purple to nearly black, non-glistening, not nectariferous. Stamens 6, $2/3$ to as long as the tepals; filaments, adnate to the base of the tepal 0.3 mm from the ovary, base broadened, $1/2$ or more as wide as the tepal at insertion, anthers 0.7 mm diameter, opening at anthesis, fugacious. Ovaries conic-ovoid, slightly adnate to the base of the perianth, finely tomentose, becoming glabrate; styles 1.6 - 4 mm long, spreading and ascending, recurved, directed inward later in mature fruit, tips recurved outward. Mature fruit a capsule, 18 - 25 mm long 10 - 15 mm wide, oblong-ellipsoid, light brown, often retaining sparsely scattered clusters of hairs, distally dehiscent. Mature seeds winged, 8 - 13 mm long, 4 - 6 mm wide, pale brown to pale yellow.

Common name: Ozark Bunchflower, Wood's False Hellebore.

Distribution: Southern Iowa east to eastern Indiana, south to Arkansas and adjacent Oklahoma with disjunct populations in Polk County, North Carolina, Walker, DeKalb, Clay and Early counties, Georgia and Gadsden County, Florida (Fig. 1). Rich, moist deciduous forests. Local and infrequent. July - August.

Representative Specimens: ARKANSAS: Logan: Magazine Mt., 9 May 1942, Demaree 22864 (MO). MISSOURI: Callaway: Bluffs along Stinson Creek, 10 Sep 1937, Steyermark s.n. (MO). Carter: Along Big Barren Creek, 10 Aug 1972, Marvin s.n. (MO). Christian: Along Sevan Creek, 6 Jul

1937, Steyermark s.n. (MO). Clinton: Cameron, Aug 1937, Ree s.n. (MO). Clark: Along Des Moines River, 30 May 1941, Steyermark s.n. (MO). Douglas: Along Indian Creek 3.5 mi. ne. of Topaz, 19 Jul 1937, Steyermark s.n. (MO). Franklin: Bank of Indian River, 15 Sep 1935, Schrenk s.n. (MO). Jefferson: Stoney Hills, 11 Jul 1891, Eggert s.n. (MO). Pulaski: 24 Aug 1937, Steyermark s.n. (MO). Maries: East side of Gasconade River, 13 Oct 1935, Steyermark s.n. (MO). Ralls: 2 mi. s. of Spalding, 4 Sep 1937, Steyermark s.n. (MO). Shelby: 29 Jun 1933, Steyermark & Palmer s.n. (MO). Shannon: North of Akers Ferry, 13 Sep 1975, Redfearn s.n. (SMS). Lewis: Along Middle Fabius River, 2 Sep 1937, Steyermark s.n. (MO). ILLINOIS: Hancock: 1842, Mead s.n. (MO). McClean: Along river at Funks Grove, 5 May 1951, Ahles 3670 (ILL). Vermillion: Kickapoo State Park, 18 Apr 1948, Jones 17772 (ILL). Adams: Along Burton Creek, 17 Jun 1946, Evers 1420 (ILL). Effingham: Southeast of Watson, 9 Aug 1955, Evers 48187 (ILL). Clark: Rocky Branch, 16 Jul 1967, Ebinger 7361 (EIU). Crawford: East of Stoy, 13 Aug 1972, Phillippel 1946 (EIU). OKLAHOMA: LeFlore: Vicinity of Page, 9 Sep 1913, Stevens s.n. (MO). IOWA: Ringgold: Bentonsport, Aug 1920, Graves s.n. (MO). INDIANA: Green: s.d. Wood s.n. (GH). FLORIDA: Gadsden: 1837, Chapman s.n. (MO). Aspalaga (?) May 1898, Chapman s.n. (MO).

Published Illustrations: In Gleason (1952), the tepal shape is not well illustrated with little attenuation toward the base. Tepal glands are not shown.

When Wood published the name Veratrum woodii and the accompanying description, he cited Robbins as author. There has been some confusion as to whether Robbins should be cited "in Wood" or "ex Wood." There is no indication or acknowledgement that Robbins actually wrote the

description, so the correct citation is Robbins ex Wood. The description is thorough and agrees in all characters with the holotype at GH.

Chapman (1860) erected Veratrum intermedium to include the southeastern populations (Florida and later Georgia and North Carolina) whose plants he felt had longer pedicels and more open racemes. He indicated that the more loosely flowered inflorescence allied this species as closely with Melanthium parviflorum as with V. woodii. However, Chapman did note the darker tepals and pubescent ovaries which characterize V. woodii. Watson (1879) also noted its apparent relationship to V. woodii. Zimmerman (1958) considered this species to be a minor geographic variant of V. woodii, tending to be taller and more branched and to have long pedicels and internodes. Comparative studies made in this investigation lead to the same conclusion. These characteristics are within the limits of variation for V. woodii. Some Missouri plants have longer pedicels than any of the southeastern plants. Southeastern variation in tepal color and ovary pubescence are also well within the overall range elsewhere exhibited in V. woodii. Veratrum intermedium is here lectotypified on Chapman's specimen at GH.

In consequence of the revised generic distinction of Melanthium from Veratrum previously discussed, a new combination, M. woodii, is here made. This species is most closely related to M. parviflorum. The distinct basal tepal glands, oblanceolate, mostly basal leaves, open inflorescence, and delicate stem habit are in stark contrast to the corresponding characteristics of Veratrum viride, which represents that genus within the range of Melanthium as here delimited.

It is probable that Melanthium woodii was derived from the wider ranging M. parviflorum or its immediate progenitor. The latter

species is centered in the Appalachians and it is possible that a small peripheral southwestern population became isolated in the Ozarkian range and diverged morphologically. Based on the very small populations of M. woodii (often of no more than 10 plants) and the frequency with which the plants are found only in the vegetative state, this species is not as successful in its ecological adaptation as is M. parviflorum. In the drier Ozarkian range, M. woodii appears to be a relict, growing mainly on north-facing slopes. In those habitats there is enough moisture to support its growth but not enough to support a potentially excluding dense layer of other competing herbs and shrubs.

In attempting to locate populations of Melanthium woodii containing plants in flower, I contacted a number of floristic botanists familiar with the localized distribution of the species. From 1974 through 1978, not a single flowering plant could be located (Demaree, Redfearn, Ebinger, Sheviak, Mohlenbrock and Ladd, per. comm.). Vegetative reproduction and infrequency of flowering have received some previous attention. Deam (1940) reported that the rhizome in this species forks and when the connection rots away two clones will result. He indicated that a given plant flowers once in four or five years. Zimmerman (1958), from personal communication with Steyermark in 1956, reported that "in most years few or no flowering plants can be found; that in a flowering year, only about one plant in 10 flowers."

The most obvious differences by which Melanthium woodii can be distinguished from any of the other species of the genus are the purplish-red tepals and tomentose young ovaries. As in the other species of Melanthium, the ovaries become glabrate in age. There is some occurrence of anthocyanin in the older tepals of M. virginicum

and in the variation reported for the ovaries of M. latifolium, but neither species exhibits the combined intensity and constancy of such coloring found in M. woodii.

EXCLUDED TAXA AND DUBIOUS NAMES

Melanthium aspericaule Poir. in Lam., Encycl. Meth. Bot. Suppl. 3:628.

1814. Type: "Carolina," 1798-1800, Bosc s.n. HOLOTYPE: P-LA,
not seen. = Tofeldia racemosa (Walt.) BSP.

Melanthium biglandulosum Bertol., Mem. Reale Accad. Sci. Inst. Bologna
2: 316. 1850. Type: unknown.

Gates (1917), as well as Index Kewensis (Jackson 1895), treat
this as a synonym of M. virginicum. However, as described by
Bertoloni it cannot be M. virginicum or any other species of
Melanthium. Bertoloni's plant was glabrous and had a fleshy
rhizome, characteristics entirely at variance with those of
Melanthium. The identity of M. biglandulosum is problematic.

Melanthium densum Desr. in Lam., Encycl. Meth. Bot. 4:26. 1797. A new
name for Veratrum luteum L., non M. luteum Thunb. (1784) =
Chamaelirium luteum (L.) A. Gray.

Melanthium dioicum Walt., Fl. Carol. 126. 1788. Type: North
America, s.d. collector unknown. LECTOTYPE: BM (Herb. Walter,
p. 71, right, below center, "Melanthium" s.n., ! photo) =
Chamaelirium luteum (L.) A. Gray.

Melanthium glaucum Nutt., Gen. N. Amer. Pl. 232. 1818. = Zigadenus
glaucus (Nutt.) Nutt.

Melanthium hybridum Walt., Fl. Carol. 125. 1788, nom. dubium. Type:
Unknown. Leimanthium hybridum (Walt.) Sweet, Hort. Brit. 429.
1827. -- Zigadenus hybridus (Walt.) Kunth (attrib. to Endl.),
Enum. Pl. 4:196. 1843.

There is apparently no extant authentic material of this entity.

Walter's Herbarium, now at BM, contains no specimen which can be linked with his *Melanthium hybridum* and, as discussed in the text under *M. latifolium*, his description cannot be matched with any known species of *Melanthium* or related genera. Its long-standing and widespread application to the North American species here recognized as *M. latifolium* is clearly erroneous and, failing future discovery of authentic material, application of the name must remain dubious.

Melanthium laetum Ait., Hort. Kew. 1:488. 1789, nom. dubium. Type: Not located, apparently based on a garden specimen introduced into England in 1770 from North America by George W. Earl of Coventry.

Gates (1917) equated this with *Amianthium muscitoxicum* (Walt.) A. Gray. Aiton's diagnosis is not sufficient for unambiguous identification of his species.

Melanthium luteum (L.) Willd., Ges. Naturf. Freunde Berlin Mag. Neusten Entdeck. Gesammten Naturh. 2:23. 1808, non *M. luteum* Thunb. (1784). = *Chamaelirium lateum* (L.) A. Gray.

Melanthium muscitoxicum Walt., Fl. Carol. 125. 1788, (as "*muscaetoxicum*"). = *Amianthium muscitoxicum* (Walt.) A. Gray. Type: Not located.

No material associable with this name could be found in Walter's Herbarium at BM.

Melanthium myocotonum J. F. Gmel., Syst. Nat. ed. 13, 1:587. 1791, a superfluous substitute for *M. muscitoxicum* Walt. = *Amianthium muscitoxicum* (Walt.) A. Gray.

Melanthium nuttallii (A. Gray) D. Dietr. (attrib. to Hooker), Syn. Pl. 2:1206. 1840, based on *Amianthium nuttallii* A. Gray. = *Zigadenus*

nuttallii (A. Gray) S. Wats.

Melanthium phalangioides Desr. in Lam., Encycl. Meth. Bot. 4:27. 1797,

a superfluous name for Anthericum subtrigynum Jacq. (1791). =

Amianthium muscitoxicum (Walt.) A. Gray.

Melanthium racemosum Walt., Fl. Carol. 126. 1788, non Roth (1821).

Type: North America: Location unknown, s.d., collector unknown.

LECTOTYPE: BM (Herb. Walter, p. 71, "375 Melanthium?", ! photo).

= Tofieldia racemosa (Walt.) BSP.

Melanthium spicatum Walt., Fl. Carol. 125. 1788, non Burm.f. (1768).

Type: North Americas, s.c., collector unknown. LECTOTYPE: BM

(Herb. Walter, p. 71, top right, "Melanthium" s.n., ! photo). =

Xerophyllum asphodeloides (L.) Nutt.

Melanthium striatum Hill, Veg. Syst. 16:56, +. 58. 1770. Type: Not

located, apparently based on a garden specimen. = ? Amianthium

muscitoxicum (Walt.) A. Gray.

Melanthium virens Thunb., Diss. Melanth. 9. 1797, based on Veratrum

viride Ait., non M. viride L.f. (1781). = Veratrum viride Ait.

Melanthium virescens Willd. ex Kunth, Enum. Pl. 4:193. 1843, nom. inval.,

pro syn. = Zigadenus mexicanus (Kunth) Hemsley.

LITERATURE CITED

- BAKER, J. G. 1879. Synopsis of the Colchicaceae and aberrant tribes of the Liliaceae. J. Linn. Soc. Bot. 17: 405-413; 469-489.
- BERKELEY, E. & D. S. BERKELEY. 1963. John Clayton pioneer of American botany. Chapel Hill.
- BENTHAM, G. & J. D. HOOKER. 1883. Genera plantarum. Vol. 3. London.
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA & O. ZAKARYEVA. 1969. Chromosome numbers of flowering plants. Leningrad.
- BORROR, D. J. & D. M. DeLONG. 1971. Introduction to the study of insects. New York.
- BRITTON, N. L. & A. BROWN. 1913. Illustrated flora of the northeastern United States, Canada and British possessions. Vol. 1. New York.
- BROWN, D. M. 1941. Vegetation of Roan Mountain. Ecol. Monogr. 11: 61-97.
- CANDOLLE, A. P. de. (ed.). 1823-1873. Prodromus systematis naturalis regni vegetabilis. Vols. 1-17. Paris.
- CHAPMAN, A. W. 1860. Flora of the southern United States. New York.
- DAVIS, P. H. & V. H. HEYWOOD. 1963. Principles of angiosperm taxonomy. Princeton.
- DEAM, C. C. 1940. Flora of Indiana. Indianapolis.
- EAMES, A. J. 1961. Morphology of the angiosperms. New York.
- ELLIOT, S. 1817. A sketch of the botany of South Carolina and Georgia. Vol. 1. Charleston.
- ENDLICHER, S. L. 1836. Genera plantarum. Vienna.
- ENGLER, H. G. A. & K. A. E. PRANTL. 1887. "Veratreae." Pflanzenr. II. 5(Heft 6): 49-96.
- EWAN, J. 1974. [Introductory comments in] Flora boreali-americana by André Michaux (fascimile of 1803 edition). New York.
- FAHN, A. 1952. On the structure of floral nectaries. Bot. Gaz. 113: 464-470.
- FERNALD, M. L. (ed.). 1950. Gray's manual of botany. 8th ed. New York.
- GATES, R. R. 1918. A systematic study of the North American Melanthaceae from the genetic standpoint. J. Linn. Soc., Bot. 44: 131-172.

- GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. 1. Lancaster.
- GRAY, A. 1848. A manual of botany of northern United States. Boston.
- _____. 1858. A manual of the botany of the northern United States. Rev. edit. Chicago.
- _____. 1862a. A manual of botany of the northern United States. 3rd ed. Chicago.
- _____. 1862b. First lessons in botany. New York.
- _____. 1866. A manual of the botany of the northern United States. 4th ed. New York.
- _____. 1868. A manual of botany of the northern United States. 5th ed. New York.
- _____. 1875. Gray's school and field book of botany. New York.
- _____. 1887. Gray's lessons and manual of botany. New York.
- GRONOVIVS, J. F. 1739. Flora virginica. Leiden.
- HOLMGREN, P. K. & W. KEUKEN. 1974. Index herbariorum. Part I, The herbaria of the world. Regnum Veg. 92: 1-397.
- JACKSON, B. D. (ed.). 1895. Index kewensis plantarum phanerogarum. Vol. 1. Oxford.
- JOHNSON, R. 1969. A taxonomic and floristic study of the Liliaceae and allied families in the southeastern United States. Unpublished doctoral dissertation, West Virginia University. Morgantown.
- JUSSIEU, A. L. 1789. Genera plantarum. Paris.
- KRAUSE, K. 1930. "Liliaceae." Pflanzenr. 15a: 227-386.
- KUPCHAN, S. M., J. H. ZIMMERMAN & A. AFONSO. 1961. The alkaloids and taxonomy of Veratrum and related genera. Lloydia 24: 1-26.
- KUZENEVA, O. I. 1935. Veratrum L. Fl. U.S.S.R. 4: 10-16.
- LAWRENCE, G. H. M., A. F. G. BUCHHEIM, G. S. DANIELS & H. DOLEZAL. 1968. B-P-H Botanico-periodicum-Huntianum. Pittsburgh.
- LINNAEUS, C. 1737. Genera plantarum, ed. 1. Stockholm.
- _____. 1742. Genera plantarum, ed. 2. Stockholm.
- _____. 1753. Species plantarum. Vol. 1. Stockholm.
- _____. 1762. Species plantarum, ed. 2. Vol. 1. Stockholm.

- _____. 1764. *Amoenitates academicae*. Vol. 6. Stockholm.
- _____. 1771. *Mantissa plantarum*, Pt. 2. Stockholm.
- LOESENER, O. 1927-1928. Übersicht über die Arten der Gattung Veratrum. *Repert. Spec. Nov. Regni Veg. Beih.* 24: 61-72; 25: 1-10.
- LÖVE, A. & D. LÖVE. 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. *Univ. Colorado Stud.* 24: 1-74.
- MICHAUX, A. 1803. *Flora boreali-americana*. Vol. 1. Paris.
- MOORE, R. J. 1973. Index to plant chromosome numbers 1967-1971. *Regnum Veg.* 90: 1-539.
- NAKAI, T. 1937. Japanese species of Veratrum. *J. Jap. Bot.* 13: 631-645; 701-713.
- NUTTALL, T. 1818. *Genera of North American plants*. Vol. 1. Philadelphia.
- RADFORD, A. E., H. E. AHLES & C. R. BELL. 1964. *Manual of the vascular flora of the Carolinas*. Chapel Hill.
- RADFORD, A. E., et al. 1974. *Vascular plant systematics*. New York.
- ROBINSON, B. L. & M. L. FERNALD (eds.). 1908. *Gray's new manual of botany*. 7th ed. New York.
- RYDBERG, P. A. 1900. The Rocky Mountain species of Melanthaceae. *Bull. Torrey Bot. Club* 27: 523-538, 650.
- SAVAGE, S. 1945. *A catalogue of the Linnean herbarium*. London.
- SMALL, J. K. 1898. Studies in the botany of the southeastern United States - XV. *Bull. Torrey Bot. Club* 25: 605-621.
- _____. 1903. *Flora of the southeastern United States*. Lancaster.
- _____. 1933. *Manual of southeastern flora*. Lancaster.
- SPRENGEL, K. P. J. 1830. *Caroli Linnaei...Genera plantarum*. Vol. 1. Göttingen.
- STAFLEU, F. A. 1967. Taxonomic literature. *Regnum Veg.* 52: 1-556.
- _____ et al. (eds.). 1972. International code of botanical nomenclature. *Regnum Veg.* 82: 1-426.
- STEARNS, W. T. 1957. An introduction to the Species plantarum and cognate botanical works of Linnaeus. In: C. Linnaeus, *Species plantarum*. A facsimile of the first edition. 1753. Vol. 1, pp. v-xiv, 1-176. London.
- STEYERMARK, J. A. 1962. *Flora of Missouri*. Ames, Iowa.

- STRAUSBAUGH, P. D. & E. L. CORE. 1970. Flora of West Virginia.
Part 1. Morgantown.
- THUNBERG, C. P. 1797. "Dissertatio Botanico de Melanthio." Uppsala.
- TORREY, J. 1824. A flora of the northern and middle sections of
the United States. New York.
- WATSON, S. 1879. Contributions to American botany, I. Revision
of the North American Liliaceae. Proc. Amer. Acad. Arts 14:
213-303.
- _____ & J. COULTER (eds.). 1889. Gray's manual of botany of
the northern United States. 6th ed. New York.
- WILLDENOW, C. L. 1799. Caroli a Linné Species plantarum. Vol. 2.
Berlin.
- ZIMMERMAN, J. H. 1958. A monograph of Veratrum. Unpublished doctoral
dissertation, University of Wisconsin. Madison.

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BIBLIOGRAPHY

- Ahles, H. E. 1978. Personal communication. Univ. of Massachusetts.
- Baker, J. G. 1879. Synopsis of the Colchicaceae and aberrant tribes of the Liliaceae. J. Linn. Soc. Bot. 17: 405-413; 469-489.
- Berkeley, E. & D. S. Berkeley. 1963. John Clayton pioneer of American botany. Univ. North Carolina Press, Chapel Hill. 236 pp.
- Benth, G. & J. D. Hooker. 1883. Genera plantarum. Vol. 3. Pt. 2. London.
- Bolkhovskikh, Z., V. Grif, T. Matvejeva, & O. Zakaryeva. 1969. Chromosome numbers of flowering plants. Leningrad: Academy of Sciences of U.S.S.R. 926 pp.
- Borror, D. J. & D. M. DeLong. 1971. Introduction to the study of insects. Holt, Rinehart & Winston, New York. 812 pp.
- Braun, E. Lucy. 1950. Deciduous forests of eastern North America. The Blakiston Company, Philadelphia. 596 pp.
- Britton, N. L. & A. Brown. 1913. Illustrated flora of the northern United States, Canada and British possessions. Charles Scribners Sons, New York.
- Brown, D. M. 1941. Vegetation of Roan Mountain. Ecol. Monog. 11: 61-97.
- Candolle, A. P. De. 1823-1873. Prodrromus systematis naturalis regni vegetabilis. Paris.
- Chapman, A. W. 1860. Flora of the southern United States. New York.
- Davis, P. H. & V. H. Heywood. 1963. Principles of angiosperm taxonomy. D. Van Nostrand Company, Inc. Princeton.
- Deam, C. C. 1940. Flora of Indiana, Indianapolis.
- Demaree, Delzie. 1975. Personal communication. Hot Springs, Arkansas.
- Eames, A. J. 1961. Morphology of the angiosperms. McGraw-Hill Book Company, Inc., New York. 518 pp.
- Ebinger, J. E. 1978. Personal communication. Eastern Illinois Univ.
- Elliot, S. 1817. A sketch of the botany of South Carolina and Georgia. Vol. 1. Charleston.

- Endlicher, S. L. 1836. *Genera plantarum*. Vienna.
- Engler, H. G. A. & K. A. E. Prantl. 1887. *Die natürlichen pflanzenfamilien*. Pt. 2. Sec. 5 Berlin.
- Ewan, J. 1974. (Introductory comments to) *Flora boreali-americana* by Andre Michaux (fascimile of 1803 edition). *Classica Botanica Americana*. Vol. 3. Hafner Press, New York.
- Fahn, A. 1952. On the structure of flora nectaries. *Bot. Gaz.* 113: 464-470.
- Fernald, M. L. 1950. *Gray's manual of botany*. 8th ed. American Book Company, New York.
- Gates, R. R. 1918. A systematic study of the North American Melanthaceae from the genetic standpoint. *J. Linn. Soc., Bot.* 44: 131-172.
- Gleason, H. A. 1952. *The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada*. Lancaster Press, Lancaster.
- Gray, A. 1848. *A manual of Botany of northern United States*. James Monroe & Company, Boston.
- _____. 1858. *A manual of the Botany of the northern United States*. Rev. ed. Ivison, Phinney & Company, Chicago.
- _____. 1862. *A manual of botany of the northern United States*. 3rd ed. Ivison & Phinney, Chicago.
- _____. 1866. *A manual of the botany of the northern United States*. 4th ed. Ivison, Phinney, Blakemore & Company, New York.
- _____. 1868. *A manual of botany of the northern United States*. 5th ed. Ivison, Phinney & Blakemore, New York.
- _____. 1862. *First lessons in botany*. Ivison, Phinney & Company, New York.
- _____. 1875. *Gray's school and field book of botany*. Ivison, Blakeman, Taylor & Company, New York.
- _____. 1887. *Gray's lessons and manual of botany*. American Book Company, New York.
- Gronovius, J. F. 1739. *Flora Virginica*. Leiden.
- Hardin, James W. 1978. Personal communication.
- Holmgren, P. K. & Wil Keuken. 1974. ed. 6. *Index herbariorum*. Part 1. *The herbaria of the world*. Oosthoek. Scheltema & Holkema, Utrecht.

- Jackson, B. D. 1895. Index kewensis plantarum phanerogarum. Oxford.
- Johnson, Robert. 1969. A taxonomic and floristic study of the Liliaceae and allied families in the southeastern United States. Ph.D. Dissertation. West Virginia University.
- Jussieu, A. L. De. 1789. Genera plantarum. Paris.
- Komarov, V. L., ed. 1968. Flora of U.S.S.R. (Translated from Russian) Israel Program for Scientific Translations. Jerusalem.
- Krause, K. 1930. Englers Das pflanzenreich. Berlin.
- Kupchan, S. M. J. H. Zimmerman and A. Afonso. 1961. The alkaloids and taxonomy of Veratrum and related genera. Lloydia 24: 1-26.
- Ladd, Douglas. 1978. Personal communication. Southern Illinois Univ.
- Lawrence, G. H. M., et. al., eds. 1978. Botanico-Periodicum-Huntianum. Pittsburgh.
- Linnaeus, C. 1737. Genera plantarum, ed. 1. Stockholm.
- _____. 1742. Genera plantarum, ed. 2. Stockholm.
- _____. 1753. Species plantarum. Vol. 1. Stockholm.
- _____. 1754. Genera plantarum, ed. 5. Stockholm.
- _____. 1762. Species plantarum, ed. 2. Vol. 1. Stockholm.
- _____. 1764. Amoenitates academicae. Vol. 6. Stockholm.
- _____. 1771. Mantissa plantarum, Pt. 2. Stockholm.
- Loesener, O. 1927-1928. Übersicht über die arten der gattung Veratrum. Feddes Repert. Spec. Nov. Regni Veg. 24: 61-72; 25:1-10.
- Love, A. & D. Love. 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. Univ. Colorado Stud. 24: 1-74.
- Michaux, A. 1803. Flora boreali-americana. Vol. 1. Paris.
- Mohlenbrock, R. 1978. Personal communication. Southern Illinois Univ.
- Moore, R. J. 1973. Index to plant chromosome numbers 1967-1971. Regnum Veg. 90: 1-539.
- Nakai, T. 1937. Japanese species of Veratrum J. Jap. Bot. 13: 631-645; 701-713.

- Nuttall, T. 1818. Genera of North American plants. Vol. 1. Philadelphia.
- Radford, A. E., H. E. Ahles & C. R. Bell. 1964. Manual of the vascular flora of the Carolinas. Univ. of North Carolina Press. Chapel Hill.
- Radford, A. E., W. C. Dickison, J. R. Massey, C. R. Bell, et. al. 1974. Vascular plant systematics. Harper & Row. Publishers, New York. 891 pp.
- Radford, A. E. 1978. Personal communication. Univ. North Carolina.
- Redfearn, Paul L. Personal communication. Southwest Missouri State Univ.
- Robinson, B. L. & M. L. Fernald. 1908. Gray's new manual of botany. 7th ed. American Book Company, New York.
- Rydberg, P. A. 1900. The Rocky Mountain species of Melanthaceae. Bull. Torr. Bot. Club 27: 523-538; 650.
- Savage, S. 1945. A catalogue of the Linnaean herbarium. London. 225 pp.
- Sheviak, Charles. 1978. Personal communication. Illinois Natural Land Institute.
- Small, J. K. 1898. Studies in the botany of the southeastern United States. - XV. Bull. Torrey Bot. Club 25: 605-621.
- _____. 1903. Flora of the southeastern United States. Lancaster.
- _____. 1933. Manual of southeastern flora. Lancaster.
- Sprengel, K. P. J. 1830. Caroli Linnaei...Genera plantarum. Vol. 1. Gottingen.
- Stafleu, F. A. 1967. Taxonomic literature. Regnum Vegetabile. Vol. 52. Utrecht.
- Stafleu, F. A. et. al., eds. 1972. International code of botanical nomenclature. Utrecht.
- Stearn, W. T. 1957. An introduction to the Species plantarum and cognate botanical works of Linnaeus. In: Linnaeus, C. Species plantarum. A facsimile of the first edition. 1753. Vol. 1, pp. v -xiv, 1-176. Ray Society, London.
- Steyermark, J. A. 1962. Flora of Missouri. Iowa State University Press. Ames.

- Strausbaugh, P. D. & E. L. Core. 1970. Flora of West Virginia. West Virginia Univ. Bulletin, Morgantown.
- Thunberg, C. P. 1797. Dissertationes academicae. Upsalae habitae. Uppsala.
- Torrey, J. 1824. A flora of the northern and middle sections of the United States. New York.
- Utech, F. 1977. Personal communication.
- Watson, S. 1879. Contributions to American botany. I. Revision of the North American Liliaceae. Proc. Amer. Acad. Arts 14: 213-303.
- Watson, S. & J. Coulter. 1889. Gray's manual of botany of the northern United States. 6th ed. American Book Company, New York.
- Willdenow, C. L. 1799. Caroli A Linne species plantarum. Vol. 2. Berlin.
- Zimmerman, J. H. 1958. A monograph of Veratrum. Ph.D. Dissertation. University of Wisconsin.