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A REVISION OF NORTH AMERICAN AND CARIBBEAN *MELANTHERA* (COMPOSITAE)

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The genus *Melanthera* Rohr *sensu stricto* comprises a small group of helianthoid composites restricted to the Western Hemisphere. The center of distribution is Caribbean, with representatives present in Mexico, Central America, South America, and the southeastern United States. The various species occupy beaches, pine flatwoods, and moist or dry forests from sea level to fairly high mainland elevations. *Melanthera aspera* exhibits weedy tendencies. This ecological and corresponding morphological variability, coupled with the wide distribution of some species in habitats favorable for collecting, has led to a proliferation of synonyms in the genus. Natural hybrids also have contributed to the confusion.

Although Schulz (1911) published the only comprehensive revision of North American *Melanthera*, his ineffective reconciliation of biological and nomenclatural problems has caused most subsequent workers to rely on regional manuals for identification. Standley (1938) cogently expressed the difficulties encountered in dealing with *Melanthera* but, I believe, offered a much too conservative solution in recognizing only one species.

In the present treatment of *Melanthera*, I recognize five species and two varieties, and provide a morphological and nomenclatural basis for more intensive studies of all taxa

in the genus. During the course of this investigation, my personal collections and approximately 2200 herbarium specimens from 27 herbaria have been examined. (A complete list of specimens studied is available from the author upon request.) An important aspect of this revision has been the observation of living plants of *Melanthera* both in the field and in the greenhouse. Specimens of all taxa were either transplanted from the field or germinated from seed and grown in the Vanderbilt University greenhouses. Observation for approximately two years was most helpful in discovering and evaluating taxonomic characters at all stages of development.

HISTORICAL ACCOUNT

Elements of the genus *Melanthera* were first described by Dillenius (1732) in his *Hortus Elthamensis* in which he mentioned that the description was based on live plants grown from seed shipped from Carolina. Linnaeus (1753) cites Dillenius' polynomial under the name *Bidens nivea*. The second of Dillenius' two excellent plates (*t.* 47), each representing leaf variations, best serves as the lectotype for *Melanthera nivea* (L.) Small. Patrick Browne (1756) described another species of *Melanthera* based on Jamaican material and placed it in his genus *Amellus*, giving it a polynomial epithet. Linnaeus subsequently acquired Browne's herbarium, and his treatment of Browne's genera *Amellus* and *Santolina* has resulted in confusion for students of *Melanthera*. Robert Brown (1817) correctly elucidated this problem, but a few points should be noted here.

Linnaeus apparently concluded that the Browne specimen, now housed in the Linnaean herbarium as *Bidens nivea*, was equal to *B. nivea* of *Species Plantarum* (1753), for he cited it in *Amoen. Acad.* 5: 381 (1759) as part of the Jamaican flora. However, each of these elements represents a distinct species of *Melanthera*. *Bidens nivea* of the *Species Plantarum* (1753) is *M. nivea*, a species restricted to the mainland, and *B. nivea* of the *Amoen. Acad.* (1759) is *M. aspera* Jacq. As a partial result of the Linnaean con-

fusion, the Browne specimen identified as *Bidens nivea* eventually came to represent the name, while the Dillenean plate was ignored. Michaux (1803) redescribed the true *B. nivea* as *Melananthera hastata*, the epithet commonly used today.

The genus *Amellus* P. Bn. (1756) would be the valid name for *Melanthera* except that Linnaeus selected it for a distinct assemblage of species (*Syst. Nat.*, 1759, p. 1225 and 1377), and this latter usage has been conserved (Lanjouw *et. al.*, 1966). *Melanthera* was described by Rohr (1792) who used specimens from Martinique. Although Rohr did not include a specific epithet or cite specimens, his clear description, plus the fact that only one species of *Melanthera* grows on Martinique, soundly establishes *M. aspera* as the type species. Rohr's editor, Vahl, included a citation to *Bidens nivea* in Swartz (1791), which is *Melanthera aspera*.

Strother (1970) established that specimens in Copenhagen likely represent material Rohr used in describing *Melanthera*. I examined photographs and drawings of these specimens and find them to represent material of *M. aspera* var. *glabriuscula*. I compared Rohr's specimens to the Dillenean plates typifying *M. nivea* and to Jacquin's description and plant of *M. aspera* and find them closer to the Jacquin work. I agree with Strother that *M. nivea* should not be the type species of *Melanthera*. Thus, I find it strange that he would select *M. panduriformis* H. Cass., which he correctly observes to be a taxonomic synonym of *M. nivea* based on a trivial leaf-form variant, to typify the genus.

Adanson (1763) described the genus *Ucacou* based on material now distributed in *Melanthera* Rohr (1792) and *Synedrella* Gaertn. (1791). J. E. Dandy of the British Museum (1969, and personal correspondence, 1968) has found that *Synedrella* best typifies *Ucacou* and has proposed conservation of the former.

Browne's *Amellus* species was described by Jacquin (1788) as *Calea aspera*, and in 1803 Michaux described

the genus *Melananthera* with the epithets *hastata* and *deltoidea*, which are synonyms for *nivea* and *aspera* respectively. Cassini (1823) contributed a thorough morphological discussion but added three superfluous epithets. In 1850 A. Richard described *M. angustifolia*. Later, J. K. Small (1903, 1905) described the Florida endemics *M. parvifolia* and *M. ligulata*.

In my opinion, Schulz (1911), in his revision of North American and Caribbean *Melanthera*, failed to understand the morphological variability within the genus and added many superfluous names to the literature. Other early twentieth century works which treated *Melanthera* were usually floristic studies of a limited Caribbean area (e.g. Britton & Wilson, 1925) or reports of botanical expeditions (e.g. Blake, 1922, 1924, 1932, and J. K. Small, 1905, 1909). While the type specimens of some of the species described in these works appear distinct, they are actually local variants or hybrids. In this treatment I have attempted to present a comprehensive view of the genus (*sensu* Rohr) whereby the 47 specific or varietal epithets are properly disposed and the taxa clearly delimited.

INTERGENERIC RELATIONSHIPS

Most synantherologists have placed *Melanthera* in the tribe Heliantheae and the subtribe Verbesininae. Obviously *Melanthera* is morphologically similar to *Verbesina*. A difficult problem is the satisfactory delimitation of these genera. As originally defined by Rohr, *Melanthera* is said to have corollas "composita uniformis, tubulosa"; *M. aspera*, on which this description was based, is indeed discoid. In the strictest sense, then, *Melanthera* is easily distinguished from similar genera by its discoid capitulum of white florets. However, the description of *Melanthera* was broadened by later workers, e.g. Bentham & Hooker (1873), to include radiate representatives, and this concept was accepted by Wild (1965) in his treatment of the exclusively radiate African *Melanthera*. If this broadened circumscription is recognized, *Melanthera* intergrades with

Echinocephalum and *Perymenium* and is often confused with *Aspilia*, *Bainvillea*, *Eleutheranthera*, *Wedelia*, *Wulffia*, and occasionally with *Calea* and *Bidens* of the subtribe Coreopsidinae.

Possibly one or more of the genera noted should be combined with *Melanthera*. I have examined material of *Echinocephalum latifolium* Gardn. and find it nearly identical with *M. nivea* except for the pale yellow rays of the former (cf. Blake, 1930). Since consideration of these generic limits is beyond the scope of the present work, I have eliminated South America, and hence *Echinocephalum*, from consideration. Therefore, I have chosen to treat only those entities which justifiably could be included in the original description. While there is some overlap in distribution of these taxa, western hemisphere *Melanthera* is centered in the Caribbean, while *Echinocephalum* and *Perymenium* are distributed principally in South America. Until further study reveals the natural relationships of these genera, *Melanthera* can be distinguished from the others, albeit somewhat artificially, by its discoid capitulum. Distinguishing morphological features of *Melanthera* are presented in Table I.

CYTOLOGY

Chromosome counts of $n=15$ for two species of *Melanthera* have been reported by Turner *et al.* (1961), Powell & Turner (1963), and Turner & Flyr (1966). Upon examining the vouchers of these plants, I find the specimen cited by Turner & Flyr (1966) is indeed *M. aspera* var. *glabriuscula*, but those cited by Turner *et al.* (1961) and Powell & Turner (1963) are misidentified and represent *M. nivea*. I have studied meiotic material of all North American species of *Melanthera* using squash techniques and have determined a haploid number of $n=15$ for all of the species covered in this treatment (Table II).

ECOLOGY AND HYBRIDIZATION

Field and herbarium studies indicate that in the United

TABLE I
DISTINGUISHING MORPHOLOGICAL TRAITS OF MELANTHERA ROHR

<i>Trait</i>	<i>M. nivea</i>	<i>M. aspera</i> <i>var. aspera</i>	<i>M. aspera</i> <i>var.</i> <i>glabriuscula</i>	<i>M. angustifolia</i>	<i>M. parvifolia</i>	<i>M. ligulata</i>
Rootstocks	swollen-hemispheric, partly exposed	swollen	elongate-diffuse	slightly swollen	swollen-hemispheric, partly exposed	slightly swollen
Stems	erect, maroon-mottled, to 3 m	diffusely branched, to 1.5 m	diffusely branched, to 1.5 m	erect, several from rootstock, to 9 dm	decumbent-erect, often diffusely branched, to 6 dm	decumbent, many side branches, node swollen, to 9 dm
Indumentum	slightly hirsute	trichomes erect hirsute-strigose	trichomes appressed-ascending	glabrescent	trichomes erect, hirsute-strigose	glabrescent
Leaves	ovate-deltoid base often hastate; dark green; serrate	ovate; sub-coreaceous; crenulate; asperous	deltoid-ovate membranaceous crenate	lance-linear	like small <i>M. nivea</i> lvs., to cm, triplinerved	variable, lance-ovoid; base may be hastate, triplinerved
Capitulum no. & peduncle length	numerous on peduncles 4-12 cm	numerous on peduncles 2-14 cm	numerous on peduncles 2-17 cm	one per stem on peduncles 9-20 cm	few per stem on peduncles 2.5-10 cm	one per stem, peduncles 6-14 cm
Phyllaries	lanceolate; green tipped recurved; greatly exceed disc	lance-ovate green tipped slightly exceed disc	ovate, equal disc	ovate, equal disc	lanceolate; green tipped recurved; greatly exceed disc	lanceolate; green tipped recurved; greatly exceed disc

TABLE 1 continued

Apical aristae of pales	1.4 + mm, recurved	0.5-1.5 mm, straight	up to 0.5 mm	0.5 mm	1-1.5 mm, straight- recurved	1 mm, straight- recurved
	spreading	spreading	tubular	spreading	spreading	spreading
Corolla limb						
Achene apex	truncate- concave	concave- truncate	truncate or often convex- tufted	truncate- concave	concave- truncate	truncate- concave

TABLE II
CHROMOSOME VOUCHERS IN *MELANTHERA*

<i>Taxon</i>	<i>Locality and Collection</i>	<i>Repository</i>
<i>M. nivea</i>	FLORIDA. WAKULLA CO.: Newport, woods near road. <i>Parks</i> 135.	VDB
	LOUISIANA. TENSAS PAR.: moist woods near Newellton. <i>Parks</i> 337.	VDB
	MEXICO. VERA CRUZ: Cordoba, roadside, <i>King</i> 2361. cit. Turner et. al., 1961.	TEX
	Huatusco, roadside, <i>Powell</i> 642. cit. Powell and Turner, 1963.	TEX
<i>M. aspera</i> var. <i>aspera</i>	FLORIDA. COLLIER CO.: Naples, back of beach, sand, roadside. <i>Parks</i> 124.	VDB
	SARASOTA CO.: Longboat Key, oolitic spoil bank. <i>Parks</i> 125.	VDB
<i>M. aspera</i> var. <i>glabriuscula</i>	FLORIDA. MONROE CO.: Long Key, dry beach. <i>Parks</i> 98. Islamorada, <i>Anderson</i> 3226. cit. Turner and Flyr, 1966.	VDB TEX
<i>M. angustifolia</i>	FLORIDA. COLLIER CO.: Monroe Sta., moist glade, on oolite. <i>Parks</i> 298.	VDB
<i>M. parvifolia</i>	FLORIDA. MONROE CO.: Big Pine Key, dry pine flat- woods on oolite. <i>Parks</i> 289.	VDB
<i>M. ligulata</i>	FLORIDA. PALM BEACH CO.: Loxahatchee, dry, sunny palmetto-pine flatwoods. <i>Parks</i> 89.	VDB

States the various taxa of *Melanthera* are usually distinct morphologically and ecologically. *Melanthera nivea* inhabits fairly moist forests and borders in the lower Coastal Plain southward to central Florida. *Melanthera ligulata* frequents the low hammocks of south-central Florida but may exhibit weedy tendencies. *Melanthera parvifolia* is restricted to oolitic "pine islands" of southern Florida and to Big Pine Key. *Melanthera angustifolia* is relatively rare, but is usually found in moist, open glades in southern Florida. *Melanthera aspera* var. *aspera* is often weedy, preferring dry, rocky places such as roadsides and calcareous spoil banks fairly near the ocean in southern Florida, while *M. aspera* var. *glabriuscula* is a strand species growing high on beaches in extreme southern Florida and throughout the Caribbean.

In Mexico and Central America, *Melanthera nivea* is usually found in the habitat already noted at altitudes above 150 m. When found at lower altitudes it may intergrade into *M. aspera* var. *aspera*, possibly due to occasional hybridization and introgression. Such occurrences may explain Guatemalan collections by *Skinner* 1867 (NY) and *Brenckle* 47-242 (WIS), each of which contains plants best placed in either *M. nivea* or *M. aspera*. Hybridization between *M. nivea* and *M. angustifolia* can be seen in *Blake* 7601 and 7601A (US), which were collected along a Guatemalan railroad bank; *M. linearis* is typified by the latter number (Blake, 1922).

A field study in southern Florida revealed a situation that seems representative of those found throughout the genus. In southern Florida, hammocks, or high spots of coquina rock run southwest from Miami into the everglades where they gradually disappear (Young, 1953). Sometimes called pine islands, these hammocks are dominated by *Pinus elliottii* and are distinct ecologically. Examination of herbarium records, including appropriate type collections of J. K. Small, indicated that a morphological gradient exists between *Melanthera parvifolia* and *M. angustifolia* along these pine islands. Plants found on oolitic

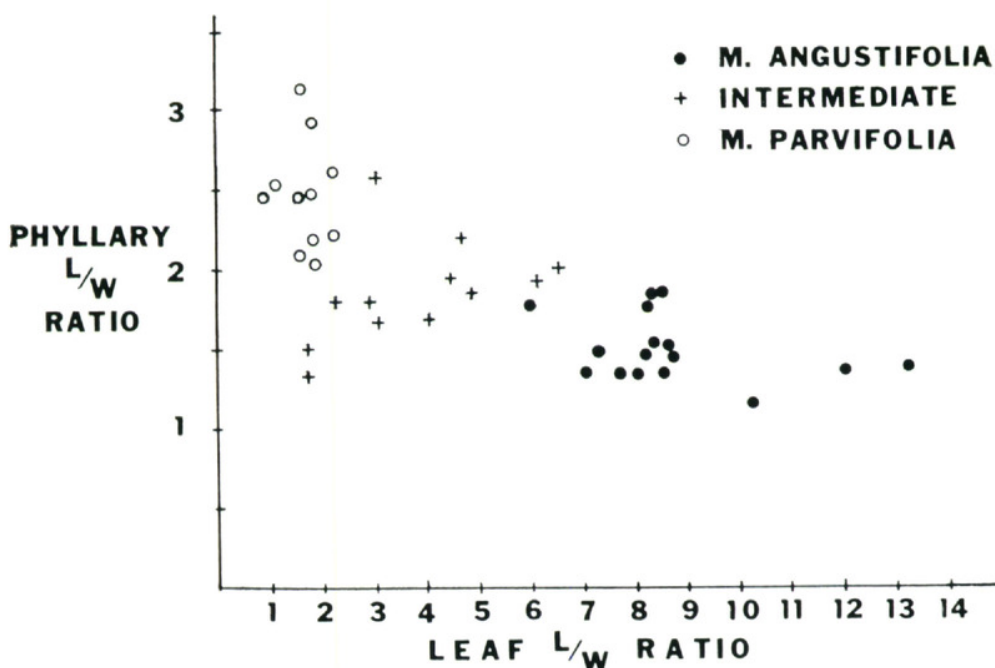


Fig. 1. Three populations of *Melanthera* from southern Florida analyzed to show interpopulational relationships of phyllary and leaf length-width ratios.

rock near Miami are much like *M. parvifolia*, while those on the lower everglades keys resemble strongly *M. angustifolia*. Morphological intermediates were collected at geographically intermediate localities.

In order that the above-described variation be understood more fully, population samples were collected and analyzed. The data obtained were analyzed (Fig. 1) in the manner of Anderson (1949). The population sample of *Melanthera parvifolia* (Parks 289), taken from Big Pine Key, formed a closely knit group with an average leaf L/W ratio of 1.5 and an average phyllary L/W ratio of 2.5. The population sample of *M. angustifolia* (Parks 298), collected near Monroe Station, Collier Co., Fla., formed a group with an average leaf L/W ratio of 8.0 and an average phyllary L/W ratio of 1.5. The other population plotted on the graph was collected on a pine island in Everglades National Park (Parks 280). It exhibits more variability in the traits considered, being intermediate morphologically

between *M. parvifolia* and *M. angustifolia*. Representative specimens of these populations were grown in the Vanderbilt University greenhouses under uniform conditions for about a year where they maintained their morphological distinctiveness.

This study seems to indicate that some gene exchange is occurring between *Melanthera parvifolia* and *M. angustifolia* in the area studied. This knowledge is valuable in helping to delimit properly these taxa, to annotate unusual herbarium specimens, and to determine synonymies more accurately. For example, *M. radiata* Small is quite likely an introgressant between *M. parvifolia* and *M. angustifolia*. The type collection is from oolitic rock near Miami and is similar to the Everglades Park collection noted above. As such material most closely resembles *M. parvifolia*, it is treated here as a synonym of that taxon.

During the two year period when living *Melantherae* were grown in the greenhouse, numerous reciprocal crosses were conducted to see if the taxa recognized would hybridize and to note the morphology of any hybrids recovered. Quantitative data were not taken, but vigorous F_1 offspring were recovered from all interspecific crosses and many of these were grown to flower. As the potential for interbreeding exists among all species, ecological differences appear to be most important in maintaining the identity of *Melanthera* taxa in nature. While my limited biosystematic studies have been most helpful in interpreting anomalous plants seen in both the field and herbarium, they indicate that more extensive work might be profitable in further elucidating evolutionary relationships in the genus.

PHYLOGENETIC SPECULATIONS

The origin, phylogeny, and evolution of the Compositae are lucidly discussed by J. Small (1917-1919) and Cronquist (1955). Cronquist would choose a helianthoid genus, e.g. *Wyethia*, to represent the fundamental composite group. Upland South America is the present center of dis-

tribution for the Heliantheae and the Senecioneae and contains many primitive composites.

Echinocephalum certainly would be considered a primitive genus of composites. Its geographic range includes the uplands of South America. It has opposite leaves, an herbaceous perennial habit, and a ligulate, paleaceous capitulum, all of which are accepted by many authors as primitive characters in the Compositae. *Melanthera* differs from *Echinocephalum* in that it lacks ray florets and, as a discoid capitulum is considered an advanced trait, I regard *Melanthera* to have been derived from *Echinocephalum*.

Present distributional data suggest that *Melanthera nivea* is the ancestral species of the genus. It resembles strongly *Echinocephalum latifolium* and is partially sympatric with it. Though the range of *M. nivea* is extensive, it is restricted to the mainland and, in the south, to higher elevations. Ecologically, this species prefers the stable habitat of forests and borders.

Melanthera nivea probably migrated northward from South America, the postulated area of its origin, during Eocene time and came to be continuously distributed throughout the southern United States and Mexico. As increasing aridity sporadically occurred during Oligocene and Miocene time, *M. nivea* would have failed to survive in northern Mexico and southern Texas; this failure would account for its present disjunct distribution. *Melanthera nivea* may have migrated southward into the newly formed areas of Florida during the colder climate of the Pleistocene period. Differentiation to form *M. parvifolia* and *M. ligulata* may have occurred during this and more recent time. Other plant migrations which occurred during Tertiary time are believed to have taken place in a similar manner (Chaney, 1947).

Perhaps *Melanthera nivea* migrated to the sea along the Orinoco or other local rivers, and in the process, differentiated into *M. aspera* which then was dispersed by water throughout the Caribbean. The pattern of Caribbean currents (Cruxent & Rouse, 1969) and the observation of

Millspaugh (1907) that *M. aspera* var. *glabriuscula* may readily inhabit newly formed strands or islets both support this hypothesis. The varieties of *M. aspera* may represent ecotypes developed in accordance with factors noted by Carlquist (1965). More recent differentiation, possibly from *M. aspera*, may have given rise to *M. angustifolia*. This could have occurred in one or several regions but most likely took place in southeastern Mexico or Yucatan.

SYSTEMATIC TREATMENT

Melanthera Rohr, Skriv. Nat. Selskabet (Copenhagen) 2: 213. 1792. Type species: *M. aspera* (Jacq.) Small.

Ucacou Adanson, Familles des Plantes 2: 131. 1763. (ex parte, non *Synedrella* propos. nom. cons.).

Lipotriche R. Br., Trans. Linn. Soc. (London) 12: 118. 1817.

Melananthera Michx., Flora Bor. Amer. 2: 106. 1803.

Suffrutescent perennials, 0.2-2.2 m tall, arising from a hemispheric or elongate, caudex-like rootstock. Stems one or several, quadrangular to sulcate, erect or sprawling, glabrescent to hispid-hirsute, green, sometimes with maroon mottling, rarely maroon. Leaves opposite, petiolate, triple-nerved, broadly ovate or deltoid to narrowly lanceolate-linear, glabrescent to hispid-hirsute; base attenuate, cuneate to nearly truncate, hastate or with basal lobes ascending in some species; apex mostly acute; margin crenate to serrate, sometimes irregularly so. Capitula terminal, solitary or arranged in very loose cymes, borne on rather elongate, sulcate, generally pubescent peduncles. Involucre 0.6-1.5+ cm broad, of two subequal, often loosely imbricate series, grading somewhat into pales. Phyllaries ovate to lanceolate, equal to or much longer than florets at first anthesis, apices more or less herbaceous, pallid basally with or without green nerves. Pales oblanceolate, strongly keeled and membranaceous basally where they clasp florets; apex thicker, aristate or caudate with cauda 0.4-1.5+ mm long, straight or recurved, sometimes pubescent api-

cally and marginally. Florets 25-100 per capitulum, all discoid, regular, hermaphroditic; corolla white; tube 4-7 mm long, constricted and pale yellow toward a nectariferous base; limb 0.5-1 mm long, spreading or rarely ascending, papillate adaxially, strigillose or glabrous abaxially. Anther sacs black, 1.5-2 mm long; apical appendages white, sagittate, 0.5 mm long; basal appendages absent, style branches white, 1.2-2.5 mm long, narrowing to a lanceolate, papillate or hairy tip, this partly or completely recurved upon senescence; pappus of 2 to 5+ delicately barbed, caducous awns. Achene indurate, obpyramidal, compressed-quadrangular (triangular in outer florets), 2-3 mm long, 1-2.5 mm wide; apex usually truncate or slightly concave due to marginal cusps of crown, usually convex in *M. aspera* var. *glabriuscula*, sparsely to moderately pubescent; surface usually brown with fine striations, warts and/or gold to silver mottling may be present.

Key to the Species

- a. Aristae of pales greater than 1 mm, usually recurved when long; phyllaries narrowly lanceolate, the upper $\frac{1}{2}$ to $\frac{3}{4}$ green, often recurved; leaf shape various but base often hastate. b.
- b. Largest leaves 4 cm or less long; plants averaging 0.3 m in height. Southern Florida oolitic "pine islands" and Big Pine Key. 5. *M. parvifolia*.
- b. Largest leaves greater than 4 cm long; plants averaging 0.8-1 m in height. c.
- c. Peduncles and leaves hispid and pale aristae 1-1.4 mm long; phyllaries and pales lanceolate, moderately longer than disc, never recurved; leaves moderately coarse. Greater Antilles and tropical mainland, often weedy. 2. *M. aspera* var. *aspera*.
- c. Peduncles and leaves strigose to glabrescent or if these hispid, the caudae of the pales 1.4 mm long; phyllaries and pales narrowly lanceolate, noticeably longer than disc, the longest often

- recurved; leaves moderately membranaceous (occasionally rugose in *M. nivea*). *d.*
- d.* Plants erect, up to 2.2 m tall with several stems arising from large, woody root; leaves ovate, very rarely lanceolate, rich, dark green, often rugose, base commonly hastate, vestiture moderate, strigose; larger capitula up to 2 cm across the involucre. Central Florida, the coastal plain from S. Carolina to Louisiana; Mexico, and Central America.
 1. *M. nivea.*
- d.* Plants decumbent to weakly erect, bushlike, with one main stem freely branched at the often jointed nodes; leaves ovate to lanceolate (quite variable), rarely rugose, trichomes sparse; larger capitula up to 1.5 cm across the involucre. South-central Florida at the approximate latitude of Lake Okeechobee.
 6. *M. ligulata.*
- a.* Aristae of pales usually 1 mm or less (may be slightly longer in *M. aspera* var. *aspera*), commonly less than 0.5 mm, never recurved; phyllaries ovate to broadly lanceolate, the upper $\frac{1}{4}$ to $\frac{1}{2}$ green never recurved; leaves various, rarely hastate. *e.*
- e.* Leaves lanceolate-ob lanceolate-elliptical, older stems glabrescent, weakly erect, av. 0.5 m in height; capitula small, av. 1 cm in diameter, mostly solitary; phyllaries ovate. Southern Florida, through Cuba to Yucatan and the tropical mainland.
 4. *M. angustifolia.*
- e.* Leaves ovate, deltoid or weakly hastate; pubescence various; sprawling or bushy plants av. 1 m in height; capitula various. *f.*
- f.* Trichomes of peduncle appressed-ascending and moderately sparse; cauda of pale 0.5 mm long; phyllaries ovate; capitulum 1.3 cm wide or less across the involucre; achenes usually 2.5 mm long or less, the apex often convex-hairy, or

- truncate. Beaches of the Caribbean.
 3. *M. aspera* var. *glabriuscula*.
- f. Trichomes of peduncle spreading (hispid) and relatively abundant; cauda of pale 1 mm long; phyllaries broadly lanceolate; capitulum 1.3 cm or more across the involucre; achenes usually 2.5 mm or more in length, the apex truncate to concave, sparsely pubescent. Greater Antilles and tropical mainland, often weedy.
 2. *M. aspera* var. *aspera*.
1. **Melanthera nivea** (L.) Small, Flora SE. United States 1251, 1340. 1903. Fig. 2.
Bidens nivea L., Sp. Pl. 2: 833. 1753. Lectotype: Dillenius, J. 1732 Hort. Elth. tab. 47 (!)
Athanasia hastata Walt., Flora Caroliniana 201. 1788.
 Type: ?
Melanthera hastata Michx., Flora Bor. Amer. 107. 1803. Type: Carolina-Virginia, Michaux (photo. GH!)
Melanthera hastata Michx. vars. *lobata* and *pandurata* Pursh, Flora Amer. 2: 519. 1814. based on Dillenius, l.c.
Melanthera panduriformis H. Cass. in Levrault, F. G. (ed.). Dict. Sci. Nat. 29: 483. 1823. based on Dillenius, l.c.
Melanthera trilobata H. Cass., l.c. based on Dillenius, l.c.
Melanthera oxylepis DC., Prodr. 5: 545. 1836. Type: ex. herb. Haenke (photo & fragment US!)
Elephantopus cuneifolius Fourn., Bull. Soc. Bot. France 30: 186. 1883. Type: not ascertained. (photo. US!)
Melanthera carpenteri Small, Flora SE. United States 1251, 1340. 1903. Type: Louisiana: W. Feliciana Par., pine thickets, *Carpenter s.n.* (NY! isotype NO!)
Melanthera lobata Small, l.c. Type: Florida; Lake Co., Eustis, lake edge, *Nash* 1141 (NY! isotypes GH! MICH! MO! UC! US!)
Melanthera oxycarpa Blake, Contr. U.S. Ntl. Herb. 22:

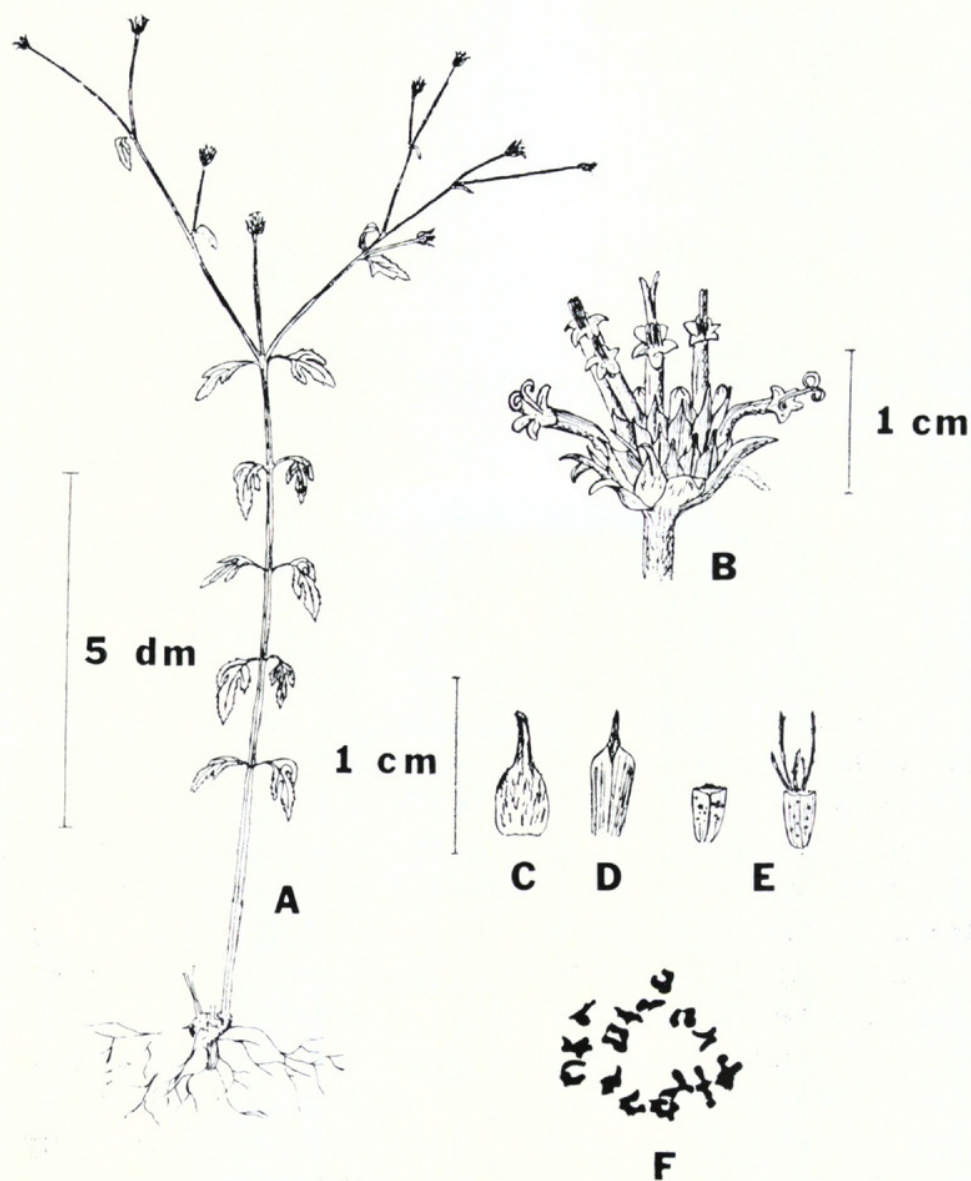


Fig. 2. *Melanthera nivea* (L.) Small. A. habit sketch, B. capitulum, C. phyllary, D. pale, E. achenes. F. meiotic chromosomes, metaphase one, $\times 1000$.

628. 1924. Type: Mexico; Vera Cruz: Zacuapan, fields, *Purpus* 2437 (US! isotypes F! MO! UC!)

Melanthera hastata (Walt.) L. C. Rich. spp. *lobata* (Pursh) Borhidi. Botanikai Kozlemenyei 58: 177. 1971. based on Pursh, *l.c.*

Coarse, perennial, caespitose herb, 0.8-2.2 m tall arising from a woody, noticeably swollen, hemispheric, caudex-like rootstock. Stems erect, quadrangular to sulcate, green, often with maroon mottling in the hollows, branched apically, puberulent to pubescent at the nodes. Leaves mostly ovate, 8-12 cm long, 3-8 cm wide, triple-nerved, membranaceous, sometimes rugose, rich, dark green, strigose to hispidulous; base broadly acute to hastate, the lobes divergent or ascending, the petioles averaging 4.5 cm; apex acute to acuminate; margin serrate. Capitulum borne on a hispidulous, sulcate peduncle 4-12 cm long; involucre in two loosely imbricate series 1.5-2 cm broad; phyllaries lanceolate, green for $\frac{1}{2}$ or more of the length apically, white with green nerves basally, strigillose, noticeably longer than florets at first anthesis; pales 5-7 mm long, 2.5 mm wide, strongly keeled, translucent and nerved basally, thicker, often red-tipped, fimbriate to pubescent apically; apical aristae 1.4+ mm long, often recurved; corolla tube 5 mm at anthesis, 6 mm at style exertion, limb 1-1.5 mm, spreading, color snow-white, pale yellow at constricted nectariferous base; anther sacs 2 mm long; style branches long, white, often completely recurved upon senescence; pappus of 2 to several caducous awns; achene obpyramidal, 2-3 mm long, 1.5-2 mm wide; apex truncate to slightly concave, corolla base sessile; surface finely striated, often verrucose; color golden brown to dark brown.

Moist forests and borders from Lake Okeechobee, Florida, north into the Coastal Plain from South Carolina to Louisiana; then at somewhat higher elevations (usually greater than 150 meters) in Mexico and Central America (Fig. 3). Schwegman (1968) reports *Melanthera nivea*

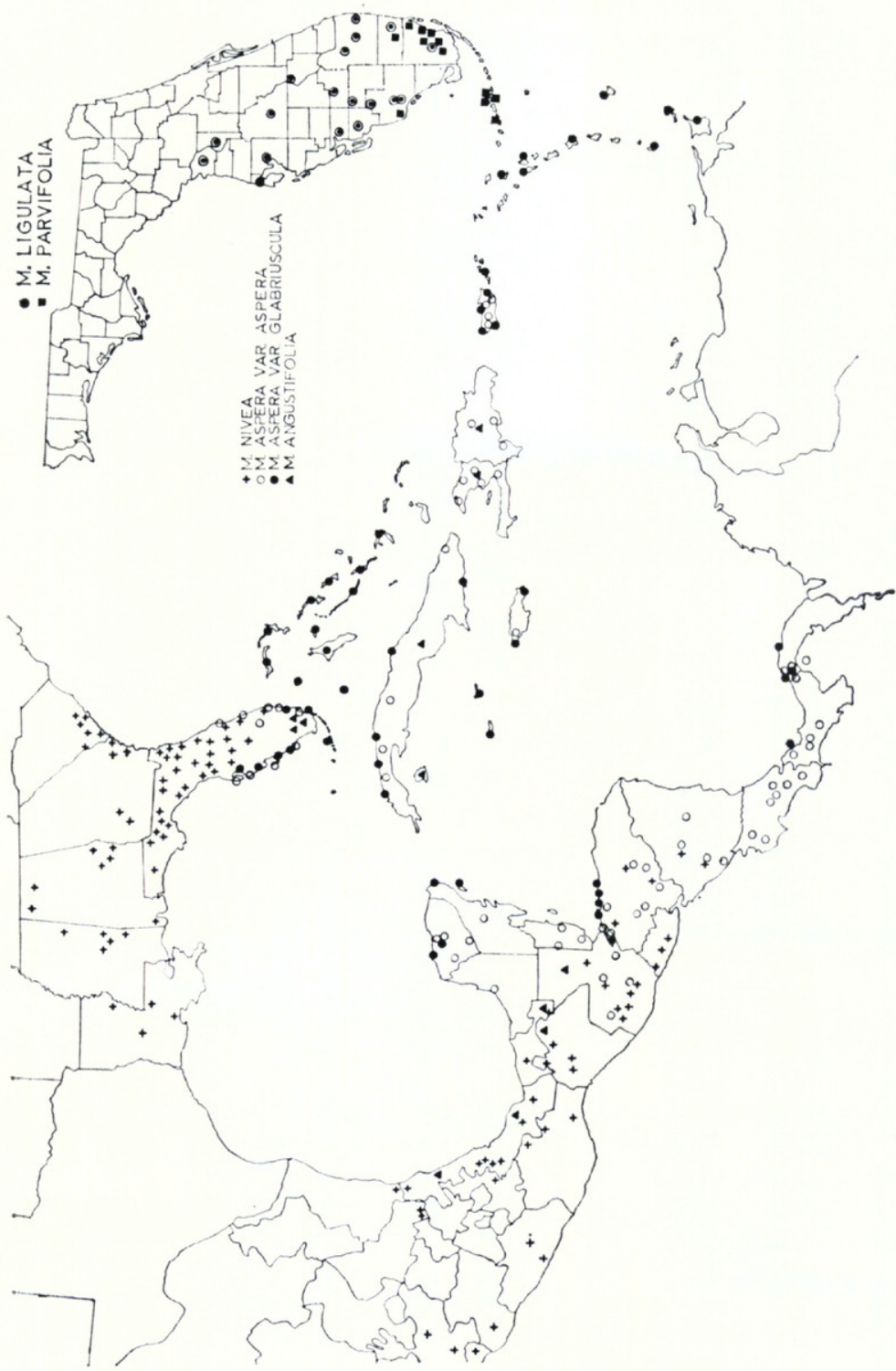


Fig. 3. Distribution of *Melanthera* Rohr

from Massac and Pulaski Counties, Illinois. Athey (personal correspondence, 1972) says that he has collected it in McCracken, Ballard, and Livingston Counties, Kentucky. The sheets, nos. 403, 779, and 1160 respectively, are on deposit at Memphis State University. These would establish Kentucky state records for Mr. Athey. I have not yet seen these collections. Dr. Kral assures me that Athey 403, VDB is *M. nivea*. These are significant northern range extensions and establish this taxon in the Mississippi embayment. Flowers in summer and fall.

The unambiguous Dillenean treatment was overlooked by many later workers (c.f. Historical Account) and the epithet *nivea* was usually applied to plants properly called *Melanthera aspera*. Perhaps as a result of this confusion, Dillenius' species was renamed *Athanasia hastata* by Walter (1788) and *Melananthera hastata* by Michaux (1803). I concur with Coulter's opinion (1891) that *M. oxylepis* DC. merely represents a leaf variant common in Mexico.

In southeastern Mexico and adjacent Guatemala, *Melanthera nivea* may intergrade with *M. aspera* var. *aspera* but in the United States it is distinct in morphology and in geographic range, being best recognized in the field by its habit and on herbarium sheets by its large, dark green, often rugose leaves, lanceolate phyllaries and long-caudate pales.

REPRESENTATIVE SPECIMENS EXAMINED. EL SALVADOR: **Morazan:** stream bed in coffee grove, Montes de Cacaquatique, *Tucker* 723 (F, MICH, NY, UC, US). GUATEMALA: **Alta Verapaz:** 2 mi E of Coban, open sun, fields, *King* 3320 (DS, MICH, NY, TEX, UC, US); near Amatitlan, brushy bank, alt. 1170 m, *Standley* 61374 (F). **Izabal:** 25 km SSW Puerto Barrios, weedy openings along river in rain forest, *Raven & Gregors* 615 (F, MICH). **Soloa:** Santa Barbara, *Shannon* 589 (US). HONDURAS: **Cortes:** E of San Pedro Sula, Bosque Iluvioso de Montana La Zona, alt. 190 m, *Molina* 3437 (F). **El Paraiso:** Yuscaran, moist thicket, alt. 930 m, *Standley* 25777 (F). MEXICO: **Chiapas:** 4 mi NE Bochil, slope with *Pinus* & *Liquidambar*, alt. 4500 ft, *Breedlove* 8838 (MICH); between Tumbala & El Salto, alt. 1500-4500 ft, *Nelson* 3389 (US). **Guerro:** 2 mi S Coahuayutla, pine-oak forest, alt. 3600 ft, *Rowell* 3086 (SMU). **Jalisco:** hillsides S of Zapotlan, *Goldsmith* 107 (DS, MO, NY, UC, US). **Michoa-**

can: Aquila, coconut grove, *Hinton* 15848 (PH, TEX, US). **Oaxaca:** 4 km NE Tehuantepec, grazed area in thorny legumes, alt. 50 m, *King* 425 (MICH). **San Luis Potosi:** 7-8 mi NE Xilitla, mountains, roadside weed, *King* 4344 (F, MICH, NY, TEX, UC, US). **Tabasco:** Tenosique, second growth, *Matuda* 3450 (F, MICH, NY, UC). **Tamaulipas:** Tampico, alt. 15m, *Palmer* 174 (F, MO, NY, US). **Vera Cruz:** Jalapa, alt. 4000 ft, *Pringle* 8194 (F, MICH, MO, NY, PH, UC, US); Orizaba, open woods, *Purpus* 1161 (F, MO, UC). **NICARAGUA:** **Matagalpa:** Santa Maria de Ostuma, Cordillera Central, alt. 12-1500 m, *Heller* 35, 39 (F). **UNITED STATES:** **Alabama:** BARBOUR CO., Spring Hill, common in swamp, *Bush* 169 (MO, NY). COLBERT CO., Muscle Shoals, *Buckley* Aug. 1826? (PH). MORGAN CO., Decatur, *Shimek* s.n. (F). MOBILE CO., Mobile, *Mohr* Aug. 1893 (MO). **Florida:** BREVARD CO., rich hammocks, Cape Canaveral, *Burgess* 684 (F, NY). DUVAL CO., Jacksonville, shore of St. John's river, *Curtiss* 1414 (F, GA, GH, MICH, MISSA, MO, NY, PH, SMU, UC). HERNANDO CO., 1 mi N of Brooksville, moist roadside shade, *Parks* 314 (F, FSU, GA, NY, PAC, SMU, US, VDB, WIS). HIGHLANDS CO., Parker Is., 5 mi S of Lake Istokpoga, among saw palmetto, edge of hammocks, *Brass* 15690 (GH, US). MARION CO., Orange Lake, in open shade around sink hole, *Parks* 224 (EVG, F, FSU, GH, NY, PAC, SMU, US, VDB, WIS). PALM BEACH CO., loc. not spec., *Hitchcock* 1026 (F). POLK CO., 7 mi E of Haines City, pineland burned & cleared 2 yrs ago, *Conard* 20 Aug. 63 (FLAS). SUMTER CO., in swamp, 0.5 mi E of wahoo ch., 5 mi W of Bushnell, *Beckner* 1582 (DUKE, FLAS). SUWANNEE CO., wooded stream bank, Ichetucknee Springs, *Will* 17 Sept. 60 (FLAS). WAKULLA CO., W side of Newport, rt. 98, roadside ditch, wooded border, *Parks* 135 (EVG, F, FSU, GH, PAC, MICH, MO, NY, SMU, US, VDB, WIS). WALTON CO., sandy, wooded ravine, rt. 81, Red Bay Springs, *Hood* 2982 (FLAS). **Georgia:** CHATHAM CO., sandy hammock, Ft. Pulaski Mon., *Eyles* 4634 (DUKE). LEE CO., rich woods along Mill Creek, *Harper* 1074 (GH, MO, NY, US). MCINTOSH CO., open live oak woods. Sapelo Is., *Duncan* 20511 (DUKE, FLAS, GH, LAF, MICH, NCU, SMU, TEX, US, USF, WIS). **Louisiana:** IBERIA PAR., disturbed, sandy soil along pipeline clearing, Weeks Is., *Thieret* 9721 (FSU, LAF, NCU, SMU, VDB). RAPIDES PAR., Alexandria, *Hale* s.n. (GH). TENSAS PAR., 8.5 mi W of Newellton, along gravel rd. from Sikes grocery, mature sweet gum-hickory bottom, *Parks* 337 (DS, DUKE, EVG, F, FLAS, FSU, GA, GH, LAF, MICH, MO, NCSC, NCU, NY, PAC, PH, SMU, TEX, UC, US, VDB, WIS). **Mississippi:** LOWNDES CO., bottom land woods, Bylers Lake, *Ray* 6683 (NCU, USF). NEWTON CO., wooded bluffs, chunky, *Bailey* 129 (MISSA). **South Carolina:** ALLENDALE CO., cypress swamp, Pipe Creek, *Bell* 18466 (NCU). BERKELEY CO., roadside ditch, 1.1 mi S. of Monck's Corner, *Bradley* 3530 (FSU, NCU, NY, VDB). CHARLESTON CO., border of live oak woods, Edisto Is. Rd., *Godfrey* 50475 (NCSC).

2. **Melanthera aspera** (Jacq.) Small, Bull. Torrey Bot. Club 36: 164. 1909.

Suffrutescent perennial, 0.5-1.5 m tall, sprawling to subscandent arising from a woody, swollen, elongate or knobby root. Stem sulcate or rounded near base, 0.5-1.5 cm in diameter, green may be maroon tinged, glabrescent to hispid particularly at nodes. Leaves ovate to deltoid, 6-12 cm long, 4-8 cm wide, membranaceous, rarely rugose, may be triple-nerved, light green and drying dark green; indument below sparse, appressed-ascending to hispid with noticeable accumulation or webbing in vein axils, erect-ascending above; base broadly acute to truncate, becoming short attenuate; petiole 1.5-4.5 cm long; apex acute to acuminate; margin crenulate-crenate to serrulate. Capitulum borne on a slender to sturdy sulcate peduncle 2-14 cm long, which has sparse appressed-ascending or abundant erect hairs; involucre in two imbricated series, 1.2-1.5 cm in diameter; phyllaries broadly ovate and 3-5 mm long, 3-4 mm wide or lanceolate and 5-7 mm long, 2-3 mm wide, tips green and equalling or surpassing the disc at anthesis by 1 mm; pales oblanceolate, 4-6 mm long, 1.5-2 mm wide, strongly keeled, translucent and nerved basally, thicker, pale green and puberulent apically, apical arista or cauda 0.5-1.4 mm long, never recurved; corolla tube 5-7 mm long, basally constricted for 1-1.5 mm, strigillose; corolla limb spreading or ascending 0.8-1.5 mm long, papillate adaxially; anther sacs 2 mm long; style branches about 2.5 mm long, partly or completely recurved when senescent; pappus of two to several caducous awns; achenes obpyramidal 2-3 mm long, 1-2 mm wide, apex truncate to concave and glabrescent or convex and tan pubescent, corolla base stipitate; surface finely striated; color shiny to dull tan.

Much of the confusion in *Melanthera* centers on this widespread, often weedy and variable taxon; problems of typification and of synonymy are discussed in the historical treatment. Because criteria for delimitation of some *Melanthera* species are not always reliable, conservative workers have tended to recognize few species; in one case a sin-

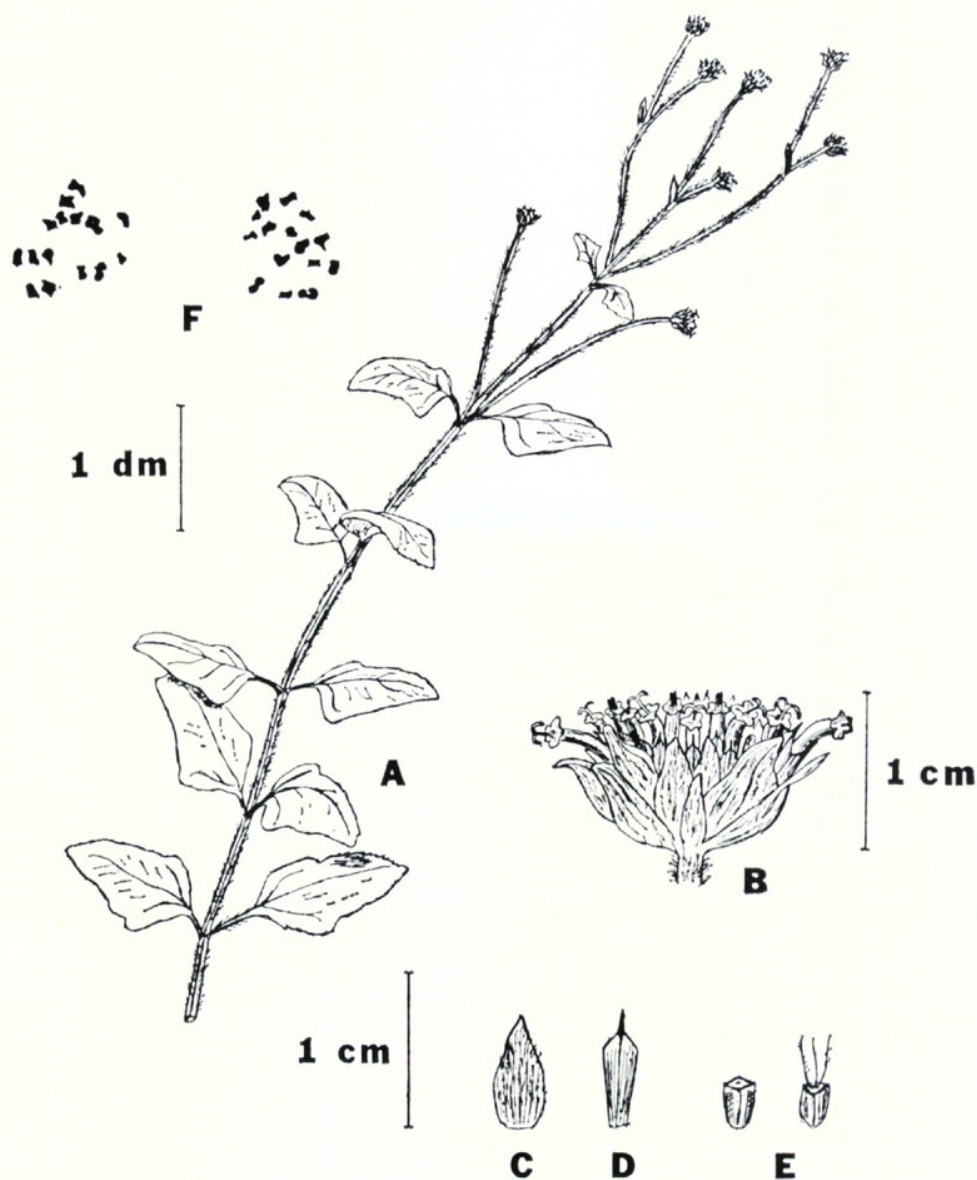


Fig. 4. *Melanthera aspera* Jacq. var. *aspera*. A. flowering branch, B. capitulum, C. phyllary, D. pale, E. achenes, F. meiotic chromosomes, late anaphase one, $\times 1000$.

gle taxon (Standley, 1938). I believe that the two varieties of *M. aspera* treated here are reasonably distinct morphologically and ecologically and that ignoring this variability would obscure the true character of this species. While intermediates do occur, close consideration of morphology and habitat will usually enable one to determine a specimen with confidence.

- 2a. **Melanthera aspera** (Jacq.) Small var. **aspera**. Fig. 4.
Calea aspera Jacq., Collectanea 2: 290. 1788. Type:
Jacquin (BM, photo. US!) Plate in Icon. Plantarum
 Rariorum 3: 13, t. 583. 1789.
Melananthera deltoidea Michx., Flora Bor. Amer. 107.
 1803. Type: based on O. Swartz, Obs. Bot. 296. 1791.
Melananthera Linnaei H.B.K., Nov. Gen. & Sp. 4: 199.
 1820. Type: ?
Melanthera corymbosa Spreng., Neue Entdeckungen 2:
 135. 1821. Type: ?
Melanthera urticifolia H. Cass., in Levrault, F. G.
 (ed.), Dict. Sci. Nat. 29: 484. 1823. based on Dil-
 lenius, *op. cit.*
Amellus asper O. Kuntze vars. *normalis* et *canescens*
 O. Kuntze, Rev. Gen. Pl. 305. 1891. Types: ?
Melanthera buchii Urban, Symb. Antillanae 3: 411.
 1903. Type: Haiti: ad Bilbaro, 700 m, *Buch* 364 n.v.
Melanthera amethystina O. E. Schulz, in Urban, Symb.
 Antillanae 7: 127. 1911. Type: not designated,
 Lectotype: Santo Domingo, *Turckheim* 3199b (NY!,
 c.f. *M. molliuscula*)
Melanthera canescens (O. Kuntze) O. E. Schulz, *l.c.*
 based on *Amellus asper* O. Kuntze var. *canescens*
 O. Kuntze, *l.c.* numerous cited specimens examined
Melanthera hastata var. *cubensis* O. E. Schulz, *l.c.*
 Type: not designated, Lectotype: Cuba: prope Ha-
 bana, *Wright* 3608 (NY! dup. US!)
Melanthera molliuscula O. E. Schulz, *l.c.* Type: not
 designated, Lectotype: Santo Domingo, *Turckheim*
 3199 (NY!, cf. *M. amethystina*)

Melanthera montana O. E. Schulz, *l.c.* Type: Porto Rico: San Juan, near Bayamon in montane woods, *Sintenis* 1145, ex parte, n.v.

Melanthera hastata (Walt.) L. C. Rich. spp. *cubensis* (O. E. Schulz) Borhidi, *Botanikai Kozlemenyek* 58: 177. 1971. based on Schulz, *l.c.*

Melanthera aspera var. *aspera* is distinguished by its coarseness and by the presence of short, often stiff, erect trichomes on stems and leaves. Its leaves are usually subcoriaceous and ovate with broadly acute bases and crenulate margins. In flower it is distinguished by broadly lanceolate phyllaries, pales with apical caudae 0.5-1.4 mm in length, corolla with a spreading limb, and by achenes with truncate to concave, sparingly pubescent apices.

Variety *aspera* grows on dry old beaches, rocky banks, and weedy fields from near sea level to 100-150 m altitude in the Greater Antilles, Florida, Mexico, and Central America (Fig. 3). Flowering in the summer and fall.

REPRESENTATIVE SPECIMENS EXAMINED. BRITISH HONDURAS: Stann Creek railway, 50 ft alt., small shrub, *Schipp* 282 (F, MICH, MO, NY, UC, US). COSTA RICA: prov. unknown, in brush, roadside, 17 km E of Turrialba, *Cronquist* 8833 (MICH, TEX, UC, USF). GUANACASTE: Rio Liberia, NE of Liberia, alt. 100 m, *Dodge* 6243 (F, MO). CUBA: **Habana:** Santiago de las Vegas, *Baker* 4983 (F, UC, US). **Oriente:** Baracoa, *Pollard* 8 (F, MO, UC, US). DOMINICAN REPUBLIC: **Barahona:** Barahona, *Fuertes* 40B (F, MO, UC). **La Vega:** loc. unknown, *Ekman* 14122 (F, US). SANTO DOMINGO: vicinity of Ciudad Trujillo, alt. 0-25 m, *Allard* 13120, 13133, 14014, 14463 (US). EL SALVADOR: **La Union:** openings, roadside, sea level, *Beetle* 26267 (SMU, US). **Sonsonate:** Armenia, *Standley* 23443a (US). GUATEMALA: **Alta Verapaz:** damp limestone thickets, 43 km NE of Coban, *Standley* 70118 (F). **Huehuetenango:** swampy places, below Miramar, alt. 300 m, *Steyermark* 51504 (F). **Izabal:** Puerto Barrios, sea level, *Standley* 24916 (US). **Santa Rosa:** wet forested quebrada, E of Taxisco, alt. 225 m, *Standley* 79007 (F). HAITI: dept. unknown: Cap Haitien, *Leonard* 5308 (US); **Port au Prince,** Morne l'Hospital, alt. 350 m, *Holdridge* 1037 (F, MICH, US). HONDURAS: **Atlantida:** stream bank thicket, foothills of Ceiba, *Yuncker* 8266 (MICH, MO, NY). **Comayagua:** moist thickets, Siguatepeque, alt. 1050 m, *Standley* 6717 (F). **Olancho:** mimosa thickets, 400 m alt., Juticalpa, *Standley* 17762 (F). JAMAICA: parish unknown, Lititz

Savanna, alt. 300-900 ft, *Harris* 11739 (F, MO, US). MEXICO: **Jalisco**: cultivated areas W of airport, sea level, *Feddema* 2547 (MICH). **Oaxaca**: near Totontepec, alt. 3700-5500 ft, *Nelson* 819 (US). **Vera Cruz**: near Cordoba, *Greenman* 152 (F). **Yucatan**: Izamal, *Gaumer* 404 (DS, F, MICH, MO, NY, PH, UC, US). NICARAGUA: dept. unknown: dry bushy slope, sierras de Managua, alt. 400 m, *Grant* 950 (F, MICH). **Matagalpa**: Santa Maria de Ostuma, alt. 1200-1500 m, *Heller* 68 (F). PANAMA: Bocas del Toro: Almirante, roadside, *Blum* 1319 (FSU, MO). **Canal Zone**: Ft. Clayton, old Las Cruces Trail, *Standley* 29008 (US). **San Blas**: Irandi airport, *Duke* 6516 (MO). **San Jose Is.**: *I. Johnston* 1100 (US). PUERTO RICO: **Arecibo**: roadside herb, Florida, *Wagner* 94 (DUKE, MO). **Mayaguez**: sandy soil near Mayaguez, alt. 350 m, *Holm* 170 (MO). TRINIDAD: St. Ann's Cascade, *Broadway* 5147 (F, MO). UNITED STATES: **Florida**: BREVARD CO., Hammock, Merritt's Island, *Small* 9437 (GH, MICH). COLLIER CO., roadside by the gulf, Naples, *Parks* 124 (DS, DUKE, EVG, F, FLAS, FSU, GA, GH, MICH, MO, NCU, MCSC, NY, PAC, PH, SMU, UC, US, VDB, WIS). DADE CO., hammocks on sand dunes, Lemon City, *Small* 5821 (DUKE, FLAS, MO, NCU, NY, US). LEE CO., waste places, Sanibel Is., *Cooley* 2515 (FLAS, GH, NY, US, USF). MANATEE CO., Palmetto, *Nash* 2433 (F, GH, MICH, NCU, MO, NY, US). MARTIN CO., one pt., open sand on new levee, Port Mayaca, *Parks* 83 (VDB). PINELLAS CO., sandy soil, Maximo Pt., *Thorne* 15430 (GH).

2b. **Melanthera aspera** (Jacq.) Small var. **glabriuscula** (O. Kuntze) Parks, comb. nov. Fig. 5.

Amellus asper O. Kuntze var. *glabriusculus* O. Kuntze, Rev. Gen. Pl. 305, 306. 1891. Lectotype: Panama: Colon, O. Kuntze (NY!)

Melanthera brevifolia O. E. Schulz, in Urban, Symb. Antillanae 7: 123. 1911. Type: not designated, Lectotype: Florida: Monroe Co., Elliot's Key in arenosis maritimis, *Curtiss* 1415 (US! dup. F! MISSA! NY! PH!)

Melanthera crenata O. E. Schulz, l.c. Type: not designated, Lectotype: Bahamas, New Providence, J. & A. Northrop 58 (NY!)

Melanthera calcicola Britton, Sci. Survey Puerto Rico and the Virgin Islands 6(1): 309. 1925. Type: Puerto Rico, Britton 6784 (NY!)

Melanthera confusa Britton, l.c. Type: Virgin Is.: Tortola, *Fishlock* 440 (NY!)

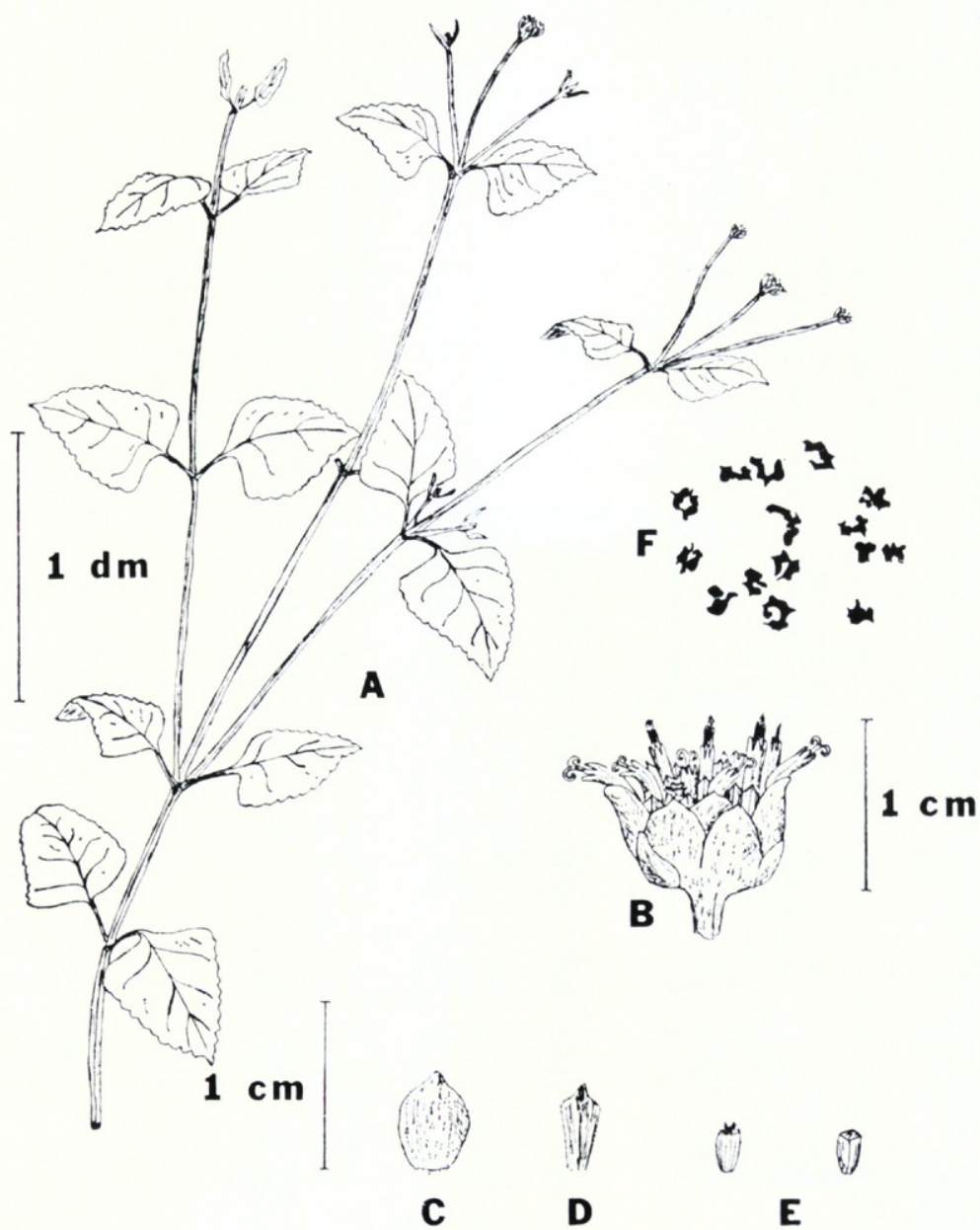


Fig. 5. *Melanthera aspera* Jacq. var. *glabriuscula* (Ktze.) Parks.
 A. flowering branch, B. capitulum, C. phyllary, D. pale, E. achenes,
 F. meiotic chromosomes, metaphase one, $\times 1000$.

This variety is glabrescent with appressed-ascending hairs on stems and leaves. The leaves are ovate to deltoid, membranaceous, light green, and with crenate margins. The capitulum is 1.2 cm or less in diameter; the phyllaries are broadly ovate, subequal and only slightly exceed the disc at first anthesis; the apical caudae of the pales is 0.5 mm or less in length; the corolla limb is usually ascending; the style branches usually recurve upon themselves when senescent; the achenes are smaller than in the typical variety being 2.0-2.5 mm long, apex usually convex and tan-pubescent.

Kuntze (1891) cited no specimens with his descriptions, but his itinerary fits well the location and time noted on the specimen I have designated as lectotype. Possibly, duplicates of this specimen were deposited at Berlin and Kew.

This variety grows high on beaches throughout the Caribbean and on the mainland of southern Florida, Mexico, and Central America (Fig. 3).

REPRESENTATIVE SPECIMENS EXAMINED. BAHAMAS: mangrove bay, Andros, *Brace* 4886 (F); Long Is., beach near dock, Clarence Town, *Hackett* 136 (DUKE, MICH, UC); **South Bimini**, cleared land near dock, *Hackett* 87 (DUKE, LAF, MICH, UC, US, USF). CUBA: **Camaguey**, near Pueblo Romano, Cayo Romano, *Shafer* 2453 (F, US). **Habana**: high on sandy beach, Playa Baracoa, *Sauer* 1770 (WIS). HONDURAS: **Atlantida**: near beach, Salado, *Yuncker* 8329 (F, MICH, MO). JAMAICA: **Portland**: Long Bay, *Adams* 7586 (DUKE). **Westmoreland**: scrub woodland near lighthouse, West Pt., *Webster* 6067 (MICH). LESSER ANTILLES: **Antigua**, seashore, *Box* 1157 (F, MICH, MO, US); **Barbados**: Christchurch Parish, in dunes, *Sauer* 2185 (F); **Grand Caymen**, Georgetown, *Armour* 1395 (F); **Grenada**, wayside, *levera, ign.* 1268 (US); **Guadeloupe**, *Griesbach* Dec. 1857 (MO); **Martinique**, alt. 40 m, *Stehle* 5125 (US); **Virgin Is.**, St. Thomas, *Delanses* 1845 (F). MEXICO: **Quintana Roo**: Cozumel Is., *Gaumer* Aug. 1886 (US). **Yucatan**: Izamal, *Gaumer* 15543 (WIS). PANAMA: **Bocas del Toro**: Bocas del Toro, *Carleton* 154 (US). **Canal Zone**: Ft. Sherman, bathing beach, *Tyson* 2263 (FSU, MO). PUERTO RICO: **Aguadilla**: roadside, Lares, *Liogier* 9956 (DUKE, FPDB, US). **Culebra Is.**: Southshores, *Armour* 627 (F). **Humacao**: coastal bank, Playa de Fajordo, *Britton* 1592 (F, US). TRINIDAD: upper beach, Manzanilla Bay, *Sauer* 2249 (F). UNITED STATES:

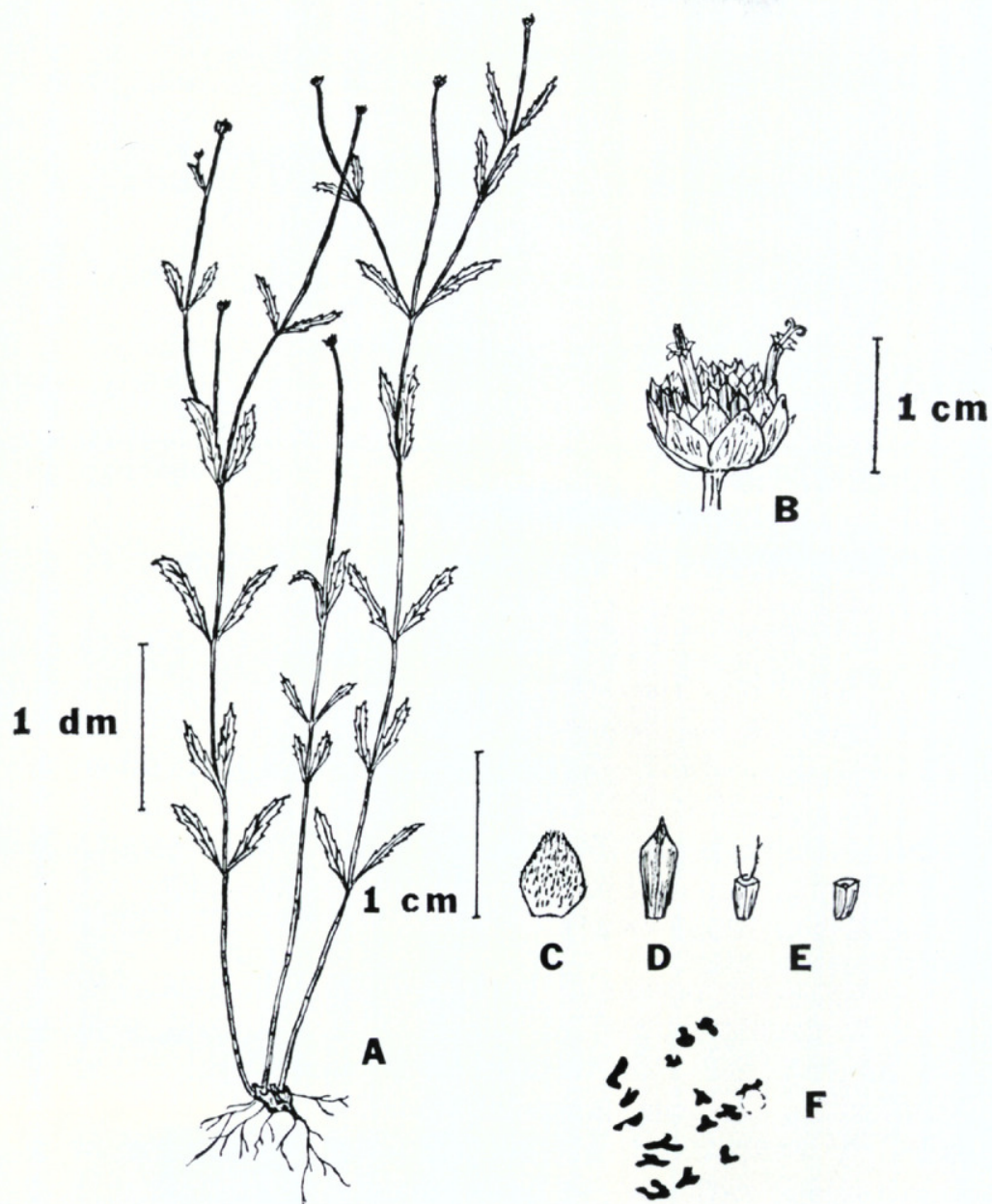


Fig. 6 *Melanthera angustifolia* A. Rich. A. habit sketch, B. capitulum, C. phyllary, D. pale, E. achenes, F. meiotic chromosomes, diakinesis, $\times 1000$.

Florida: BROWARD CO., Sandy soil, Lauderdale beach, *Moldenke* 262 (DUKE, MO, NY). Collier Co., sand island, Everglades City, *Parrott* 189 (DUKE). DADE CO., coral rock, Totten Key, *Cooley* 9343 (USF). LEE CO., weedy on shell mound, Bird Is., *Brass* 18092 (US). MONROE CO., beach, Bradley Key, off East Cape, *Parks* 274 (EVG, F, US, VDB); Long Key, common high on ocean beach, *Parks* 283 (GA, MICH, NCSC, NCU, PAC, VDB); Marquesas Key, *Lansing* 2116 (F, NY).

3. ***Melanthera angustifolia*** A. Rich., *in* Sagra, R., Hist. Isla Cuba 11: 54. 1850. Fig. 6. Lectotype: Cuba: Isla de los Pinos: *La Sagra* (P)

Melanthera lanceolata Benth. ex Oerst., Kjoeb., Vidensk. Meddel. 88. 1852. Type: Coll. & date not ascertained (BM, photo & fragment US!)

Melanthera microphylla Steetz, Bot. Voy. Herald 156. 1854. Type: Panama, *Seemann* 254 (photo US!)

Melanthera linearis Blake, Contr. U.S. Ntl. Herb. 24: 30. 1922. Type: Guatemala: Izabal: Cristina, R.R. ditch, *Blake* 7601 (US!)

Melanthera purpurascens Blake, Contr. U.S. Ntl. Herb. 22: 629. 1924. Type: Mexico: Chiapas: tableland about Ocuilapa, *Nelson* 2995 (US!)

Melanthera angustifolia A. Rich. var. *subhastata* O. E. Schulz, Report Sp. Nov. 26: 109. 1929. Type: Cuba: *Ekman* 12359 (NY!)

Weakly erect perennial herb, 3-9 dm tall, arising from a woody usually buried rootstock. Stems several, slender, 3-9 dm tall, 2-3 mm in diameter, quadrangular, mostly red-maroon. Leaves lanceolate-oblong-linear, rarely narrowly ovate-elliptical, 3-8 cm long, 0.5-1.5 cm wide, length-width ratio av. 8; base cuneate to attenuate; apex acute; margin irregularly serrate-serrulate; pubescence sparse, appressed-ascending. Capitulum solitary, terminal borne on a slender, sulcate, glabrescent, usually long (9-20 cm) peduncle; involucre of one to two subequal series, 0.6-1.2 cm in diameter; phyllaries ovate, 4-5 mm long, 2-3 mm wide, length-width ratio av. 1.5, the apical 1/4-1/3 green, pubescence appressed-ascending; pales oblanceolate, 4-5 mm long, 1 mm wide, aristae 0.5 mm long. Neither

floret nor fruit is distinctive. They resemble those of *Melanthera ligulata* but fewer of each are present in the *M. angustifolia* capitulum.

Melanthera angustifolia seems to frequent low, moist to swampy, lightly shaded areas but is apparently found in drier situations in parts of its range. Distributed from southern Florida, through western Cuba and the Isle of Pines into Yucatan, southeastern Mexico, and Central America (Fig. 3), it is sparsely collected throughout its range and is nowhere a common plant. It flowers from mid to late summer.

Achille Richard did not designate a type specimen for this taxon. However, Dr. Alicia Lourteig of the Museum of Natural History, Paris (P), has informed me (personal correspondence) that a specimen exists there labeled in the author's hand as noted above. In light of the supporting evidence, it seems reasonable to designate this sheet as the lectotype of the distinctive *Melanthera angustifolia*. (For additional discussion see Jennings, 1917.)

Melanthera angustifolia is usually considered one of the most distinct species in the genus. Unfortunately, this assumption is based solely on the unstable character of leaf shape. Occasional specimens of *M. nivea* exhibit lanceolate leaves, as do *M. parvifolia* and *M. ligulata*. While the type specimens of *M. lanceolata* and *M. purpurascens* are somewhat extreme in leaf characters, other traits indicate that they are best considered synonyms of *M. angustifolia*.

REPRESENTATIVE SPECIMENS EXAMINED. CUBA: Camaguey: Airoyo, Britton 13133 (US). Isle of Pines: savannahs, road to San Francisco de las Piedros, Killip 45440 (US). DOMINICAN REPUBLIC: Puerto Plata: coastal swamp, Cabarete, Ekman 14537 (F, US). SANTO DOMINGO: in savannas, Ekman 13323 (F). GUATEMALA: Alta Verapaz: slopes near coves, SW of Lanquin, Steyermark 44027 (F, US). Izabal: dry pine slopes, Izabal, alt. 65-600 m, Steyermark 38559 (F). Peten: La Libertad, Aguilar 4 (MICH, MO, NY, US). HAITI: prov. unknown, Pearice, Ramielle, Ekman H6244 (US). MEXICO: Tabasco: Tenosique, in savanna, Matuda 3502 (F, MICH, MO, NY, UC). Vera Cruz: meadow in oak forest, SE of Catemaco, Dressler 122 (F, MICH, MO, NY, UC, US); E of Tuxpan,

toward La Playa, *Strother* 541 (SMU, TEX). PANAMA: Panama: Los Sabanas, open slope near sea level, *Standley* 40777 (US). UNITED STATES: Florida: BROWARD CO., rocky, calcareous land, Ft. Lauderdale, *Curtiss* 5846 (DS, F, FLAS, GA, GH, MO, NCU, NY, PAC, SMU, UC, US). COLLIER CO., pine-palmetto flatwood on lime rock, Monroe Sta., *Parks* 298 (EVG, F, FSU, MICH, NY, PAC, SMU, US, VDB, WIS); Tamiami Trail near Naples, *Horner* 22 Dec. 55 (WIS). DADE CO., everglades, Camp Longview, *Small* 1790 (NY); burned pine flatwoods on limestone, 3 mi N of Rock Reef Pass, *Godfrey* 63420 (FLAS, FSU); 3 mi W of Everglades Ntl. Park entrance, open glades, *R. Smith* 643 (NCU); wet, marly prairie, Grossman Hammock, *Webster* 10261 (DUKE); rocky pineland, Long Pine Key, *Scull* 18 Mar. 40 (FLAS). MONROE CO., Pinecrest rd., Cypress ponds, pinelands, ditches, *Lakela* 29894 (USF). PALM BEACH CO., sandy peat in pine flatwoods, NW of Loxahatchee, *Kral* 5642 (FSU, SMU, VDB).

4. *Melanthera parvifolia* Small, Flora SE. United States 1251, 1370. 1903. Fig. 7. Type: Florida: (Monroe Co.), Big Pine Key, *Blodgett*, s.n. (NY! isotype GH!)
Melanthera radiata Small, Bull. Torrey Bot. Club 36: 163. 1909. Type: Florida: Dade Co., Camp Longview, *Small & Wilson* 1575 (NY!)
Melanthera hastata var. *parvifolia* (Small) O. E. Schulz, in Urban, Symb. Antillanae 7: 126. 1911. based on Small *l.c.*

Suffrutescent perennial, 3-6 dm tall, sprawling to weakly erect with numerous, sparingly branched stems arising from large hemispheric, caudex-like, woody rootstock. Stems slender, obscurely 4 angled, green with a dark red tinge, rarely red; indument strigose to hirsute. Leaves ovate, 1.5-4 cm long, 1-1.5 cm wide, moderately coriaceous, rich, dark green; base broadly acute to obtuse, hastate or ascending basal lobes common, petiole very short; apex acute; margin coarsely serrate, sometimes undulate, basal teeth may be large, salient or ascending; indument strigose to hispid. Capitulum solitary, terminal, borne on a slender, sulcate, hispid to strigose peduncle which is 2.5-10 cm long; involucre in two loosely imbricate series, 1-1.4 cm in diameter; phyllaries lanceolate, 5-7 mm long, 1.5-3 mm wide, length-width ratio av. 2.5, tip often recurved, notice-

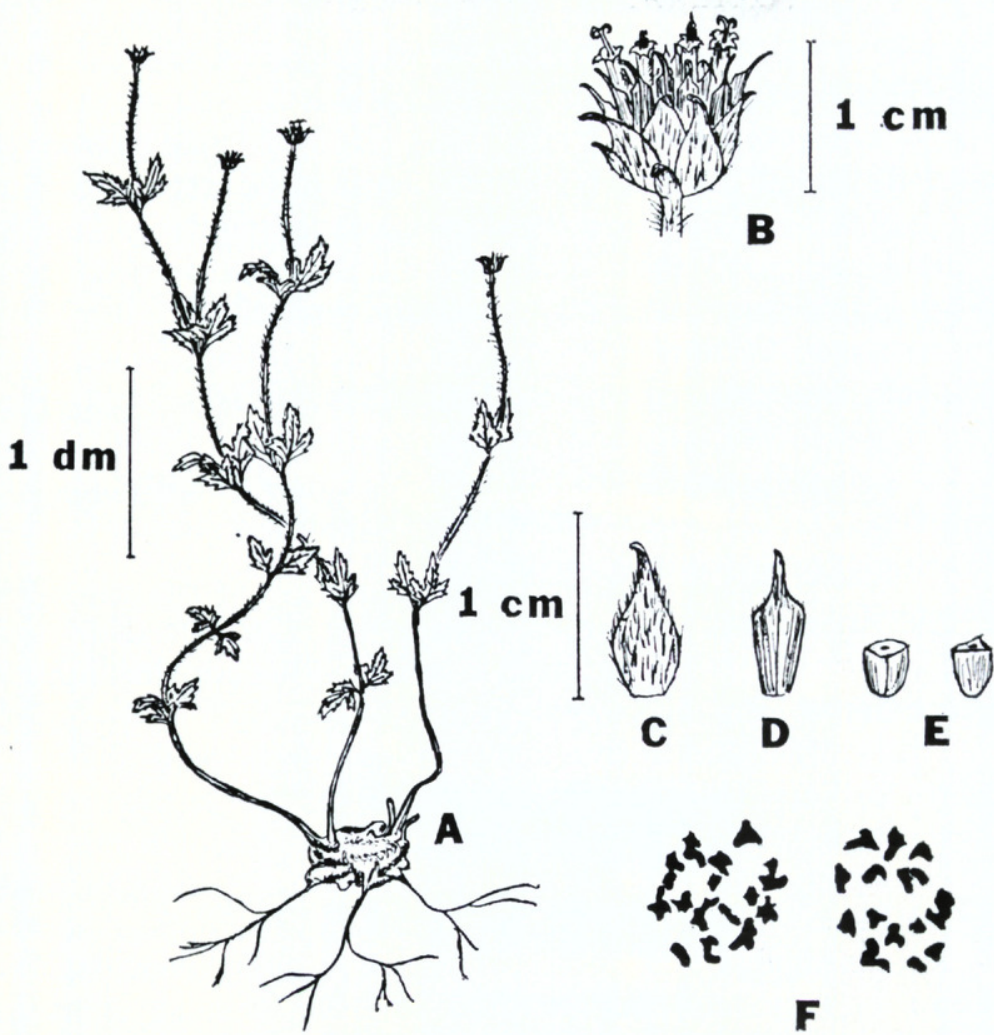


Fig. 7. *Melanthera parvifolia* Small. A. habit sketch, B. capitulum, C. phyllary, D. pale, E. achenes, F. meiotic chromosomes, late anaphase one, $\times 1000$.

ably longer than florets at first anthesis, green for $\frac{3}{4}$ length apically, pallid basally, pubescence of short, erect-ascending trichomes, abundant marginally and abaxially; pales oblanceolate 6-7 mm long, 2 mm wide, strongly keeled, apical aristae 1-1.5 mm long, often recurved, numerous hairs present on the upper, abaxial surface. Corolla tube 4 mm long, some hairs present; corolla limb 0.5 mm long, spreading, papillate adaxially, strigillose abaxially; anther sacs 1.5 mm long; style branches 1.2 mm long, apex slightly sagittate, drawn out into an unusually long, slender, pubescent tip. Achene obpyramidal, 2.5-3 mm long, 1.5-2 mm wide; apex truncate, margin may be cuspidate or crowned, apical hairs sparse; surface finely striated, lustrous, dark brown.

Old coral reefs or porous oolitic rock, Big Pine Key and the everglades keys, southern Florida. Flowers throughout the summer. Fig. 3.

This rather diminutive, endemic species is quite distinct. It is perhaps most easily recognized by its sprawling or bushlike habit and its large, knobby root. The achenes and capitula of this species are, proportionally, fairly large while the number of florets per capitulum is small. Anomalous plants, likely a result of introgression from *Melanthera angustifolia*, may exhibit slightly smaller capitula with broadly lanceolate phyllaries. Plants growing on Big Pine Key are a bit different morphologically, having spreading rather than flat margins.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES: **Florida:** BROWARD CO., near new River Canal, S of Lake Okeechobee, *Small* 4441 (DUKE, FLAS, GH, NCU, NY). COLLIER CO., dry sandy pineland, E Naples, *Moldenke* 24160 (WIS). DADE CO., pinelands, Addison's Hammock, *Small* 6639 (NY); cut pineland over limestone, Bauer Hammock, *Webster* 10115 (DUKE); hammocks, Black Pt. Creek, *Small* 5970 (MO, NCSC, NY); dry, sandy soil, Buena Vista, *Moldenke* 309 (DUKE, MO, NY); 8 mi W of Everglades Ntl. Park inf. center, pinewoods, *Parks* 112 (EVG, F, FSU, GH, MO, NY, PAC, SMU, US, VDB, WIS); thin soil over old coral reef, Florida City, *Kral* 12044 (VDB); pine-palmetto woods, Grossman Rd, *Parks* 291 (EVG, PAC, US, VDB); pinelands over limestone, Homestead, *Brass* 21149

(GH), *Godfrey* 65609 (LAF, NCU, USF); vacant lot behind Tradewinds Motel, *Parks* 109 (DUKE, EVG, F, FSU, GH, MO, NY, PAC, SMU, US, VDB, WIS); pinelands, Inlikita, 8 mi N of Homestead, *Parks* 113 (EVG, F, FSU, NY, PAC, SMU, US, VDB); rocky land, Miami, *Curtiss* 5851 (DS, F, FLAS, GA, GH, MO, NCU, NY, PAC, SMU, UC, US); NW 54th St. & 27th Ave. Miami, *C. & J. Javish* 535 (DS, MO); pinelands, Murden Hammock, *Small* 6439 (NY), 6450 (MO, NY); Nixon-Lewis Hammock, *Small* 7351 (DUKE, NCU, NY). MONROE CO., open hammock, Big Pine Key, *Brown* 128 (NY, PH); pine-palmetto woods, Big Pine Key, *Killip* 40217 (DS, GA, US); pine-palmetto woods, end of Rt. 940, Big Pine Key, *Parks* 289 (EVG, SMU, US, VDB); hammocks, Boca Chica Key, *Small* 3918 (NY); Key West, *Chapman s.n.* (NY); Long Key *Frost* 8 Feb. 1931 (PAC); Old Rhode's Key, *Small* 6 Nov. 1901 (NY).

5. *Melanthera ligulata* Small, Bull. New York Bot. Gard. 3: 439. 1905. Fig. 8. Type: Florida: Broward Co., pinelands below Ft. Lauderdale, 1904, *Small & Wilson* 1775. (NY!)

Suffrutescent, often luxurious perennial, 3-9 dm tall, arising from a slightly swollen root. Main axis decumbent, freely branched at the jointed nodes, sulcate to obscurely quadrangular, usually reddened or red-mottled on upper surfaces, glabrescent. Leaf shape highly variable, ovate-elliptical-lanceolate forms often on the same plant, 4-12 cm long, 1-4 cm wide, noticeably triple-nerved, commonly light green, glabrescent; base acute-cuneate, obtuse or hastate, commonly basal lobes strongly ascending; apex acute, margin serrate, lanceolate leaves saliently and irregularly toothed. Capitulum mostly solitary, terminal, borne on a sulcate, glabrescent peduncle 6-14 cm long; involucre in two loosely imbricate series 1.2-1.4 cm in diameter; phyllaries lanceolate, 5-7 mm long, 2 mm wide, dark green for 2/3-3/4 length apically, pallid basally with obscure nerves, pubescence short, appressed-ascending, phyllaries often noticeably longer than florets at first anthesis and recurved; pales oblanceolate, 6-7 mm long, 2 mm wide, apical aristae about 1 mm long, may be recurved. Corolla tube 4.5 mm long; limb spreading, 1 mm long, papillate adaxially. Anther sacs 2 mm long; style branches 1.5 mm long, may completely recurve when senescent. Achene not dis-

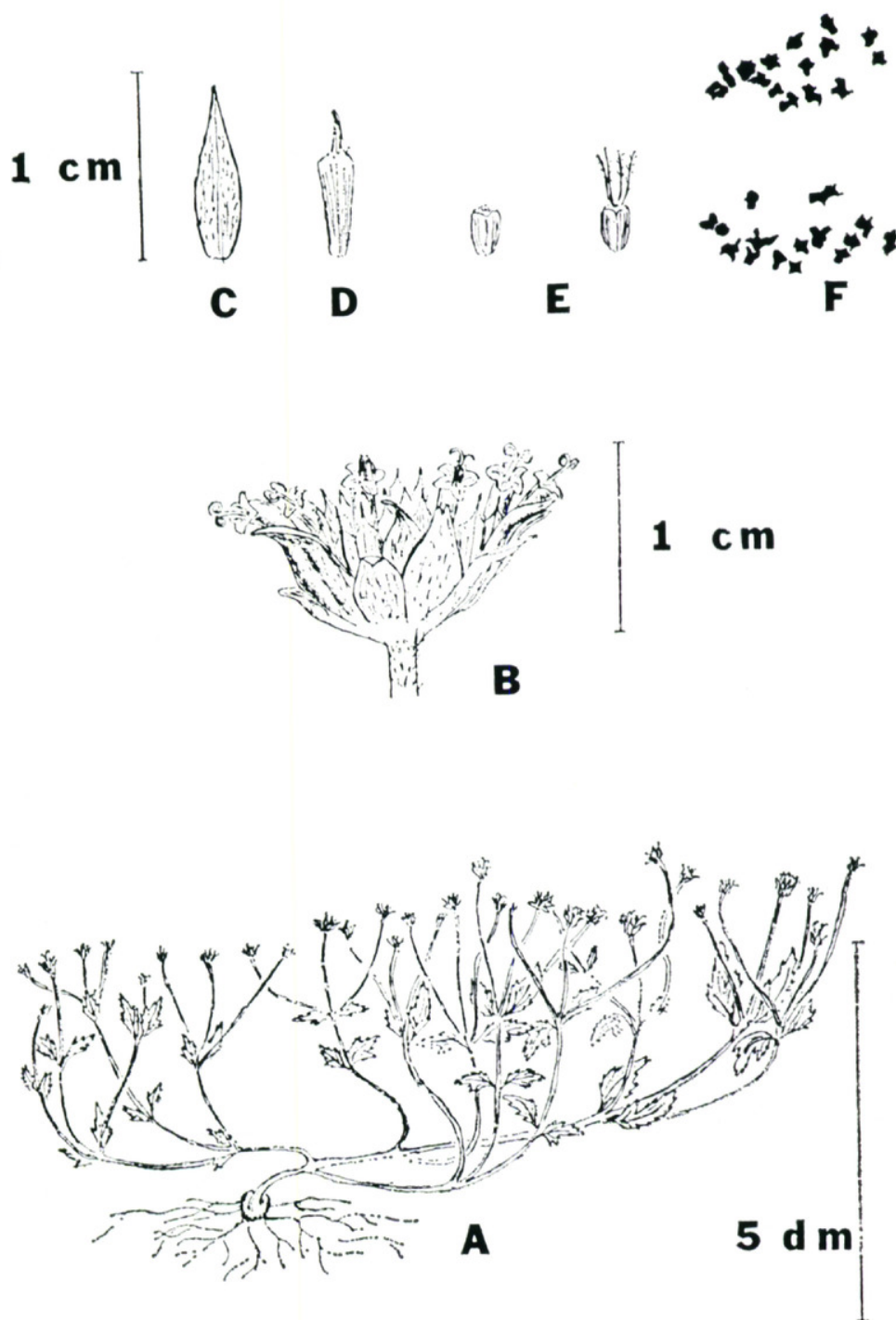


Fig. 8. *Melanthera ligulata* Small. A. habit sketch, B. capitulum, C. phyllary, D. pale, E. achenes, F. meiotic chromosomes, late anaphase one $\times 1000$.

tinctive, obpyramidal, 2.5 mm long, 1.5 mm wide; apex truncate to slightly concave, with short, tan to white hairs at maturity; color dull tan.

Pine-palmetto flatwoods, usually in sun, from central to southern Florida. Flowers in early summer. Fig. 3.

This species of *Melanthera* is sparingly represented in herbaria and most of the specimens available have not been properly identified. It has not been well understood partly because it is restricted, largely to inaccessible areas such as the region south of Lake Okeechobee, and partly because the original circumscription is too narrow. As a result of my field observations in southern Florida, it became evident that certain anomalous plants seen were probably *M. ligulata*. I have included the considerable variability expressed by the leaves in the description.

Melanthera ligulata is easily recognized in the field by its decumbent stem which is profusely branched from the slightly swollen nodes. On herbarium specimens, one must note the stem characters, a generally glabrous vesture, and the capitulum which is similar to, but a bit smaller than that of *M. nivea*.

SPECIMENS EXAMINED. UNITED STATES: **Florida:** county unknown, South Florida, *Chapman* 63 (US). BROWARD CO., roadside, Ft. Lauderdale, *Crevasse* 23 July 1940 (FLAS); low pineland, Hammondville, *Brown* 16 March 1928 (FLAS). CHARLOTTE CO., Cabbage Hammock, *Frye* 181 (FLAS); pasture, *Parrott* 90 (DUKE). CITRUS CO., moist soil on limestone, 8 mi SW of Inverness, *Kral* 7891 (FLAS, GH, VDB). COLLIER CO., roadside spoil heap, 5.5 mi N of Rt. 41 on Rt. 79, *Parks* 308 A&B (EVG, F, FSU, GA, MICH, NCSC, NCU, NY, PH, SMU, US, VDB); roadsides in glades, *Brass* 15408 (US); East Henson Marsh, Big Cypress, *Brass* 15960 (US); bank sloping to swamp, intersection Rts. 29 & 82, Immokalee, *Lakela* 27442 (SMU, USF), *Parks* 310 (DS, DUKE, EVG, F, FSU, GH, MO, NY, PAC, SMU, UC, US, VDB, WIS); between Miles City & Immokalee *Seymour* 5177 (FLAS); ranchlands with cypress heads, Collier-Hendry Co. line, Rt. 846, *Lakela* 28959 (USF); railroad gravel, 10 mi N of Jerome, *Godfrey* 61003 (FSU); wet glade, W of Miles City, *Lakela* 29344 (USF); roadside, Tamiami Trail, *Atwater* M237 (EVG, FLAS). DADE CO., pinelands near Camp Longview, *Small* 13 May 1904 (GH, US) (Sheet at US later labeled as no. 1575, type of *Melanthera radiata* is *M. ligulata*), *Small* 1807 (NY); Miami,

Garber 1 May 1877 (FLAS, NY, PAC); everglades, Miami, *Small* 1764 (NY); Tamiami Trail, *W. M. R.* 15 Feb. 1935 (NY). GLADES CO., roadsides on prairie, Palmdale, *Brass* 15449 (GH, US). HENDRY CO., weedy in burned live oak hammock, Ft. Denaud, *Brass* 20623 (US); roadside, 4 mi W of Labelle, *Henderson* 63-1608 (FSU, TEX). HILLSBOROUGH CO., border, wet woods, Tampa, *Britton* 39 (NY). LEE CO., near swamp, Alva, *Francis* 152 (US); flatwood ponds, Ft. Myers, *Hitchcock* 157 (F, GH, MO, NY, US); pineland, 8 mi SE of Ft. Myers, *J. Standley* 452 (F, GH, MO, US); dooryard, near Ft. Myers, *Standley* 19024 (US); prairies near Okaloacoochee slough, *Small* 8305 (NY). OSCEOLA CO., swamp, *Fredholm* 6100 (NY); pineland, Kissimmee, *Singeltary* 167 (DUKE, NCSC). PALM BEACH CO., sandy soil, 2 mi N of Canal Pt., *Moldenke* 252 (NY); Lake Worth, *Beardslee* Dec. 1928 (UC), *O'Neill* 831 (US); dry, sandy, pine-palmetto flatwoods, Loxahatchee, *Parks* 89 (DS, DUKE, EVG, F, FLAS, FSU, GA, GH, MICH, MO, NCSC, NCU, NY, PAC, PH, SMU, UC, US, VDB, WIS), *Parks* 90 (SMU, VDB), 91 (VDB), 92 (EVG, PAC, SMU), 93 (FSU, US), 237 (DS, DUKE, F, GA, MO, NCSC, NY, PAC, PH, SMU, US, VDB, WIS). PINELLAS CO., sandy soil, rare, St. Petersburg, *Mrs. C. Deam* 2888 (US), 2898 (US). POLK CO., moist, open woods, Kissengens Spring, *Correll* 6295 (DUKE, NCSC), *McFarlin* 3033 (MICH). SUMTER CO., Esperawell, *Smith* 18 March 1879 (US).

DOUBTFUL OR EXCLUDED SPECIES

Melanthera fruticosa Brandgee, Univ. California Publ. Bot. 10: 421. 1924. = *Philactis Liebmanii* (Klatt) Blake, Contr. Gray Herb. n.s. 52: 35. 1917. Type: Mexico: Chiapas: near Tuxtla along rocky road, *Purpus* 9117 (US!, isotypes MO! NY! US!) Having examined the type collection, I concur with the treatment of Torres (1969).

Melanthera hastifolia Blake, Contr. U.S. Ntl. Herb. 24: 29. 1922. Type: Guatemala: Izabal: near Cristina in ditch along railway, *Blake* 7601A (US!, isotype US!). Only one collection other than the type collection was available for examination, *Lundell* 4928 at MICH, US, NY. These were determined by Blake, but are not like the type material and seem to represent *M. aspera*. I believe the type collection of *M. hastifolia* probably represents elements of a hybrid swarm, with the putative parents being *M. angustifolia* and *M. nivea*.

Melanthera parviceps Blake, Jour. Washington Acad.

Sci. 22: 384. 1932. Type: British Honduras: El Cayo District: in ravine, Little Mountain Pine Ridge, *Bartlett* 11882 (US!, isotypes F! UC!) I have seen only four herbarium specimens of this taxon, all from the same locality and three from the type collection. *Melanthera parviceps*, on the basis of these few specimens, appears rather distinctive. Although similar to *M. aspera* var. *glabriuscula* in capitulum characters, the heads of *M. parviceps* are more numerous, smaller, and bear fewer florets. Also the peduncles and phyllaries are strongly hispid to hirsute. Vegetatively the plant seems to resemble *M. nivea*, with the leaves being mostly narrowly ovate with divergent hastate lobes. Until more collections become available, I prefer to place this as a dubious species, rather than to recognize it, or reduce it to *M. aspera* var. *glabriuscula*.

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