

## MONOGRAPH OF *EUPHORBIA* SECT. *TITHYMALOPSIS* (*EUPHORBIACEAE*)

K. PARK\*

*Euphorbia* sect. *Tithymalopsis* (*Euphorbiaceae*) comprises seven species of herbaceous perennials restricted to the south-eastern USA. The species of sect. *Tithymalopsis* are united and distinguished from other sections in *Euphorbia* by having a thick and cylindrical root system, a glabrous cyathium, five glands with petaloid appendages, one to three stems arising from the root, absence of vestigial sepals in pistillate flowers, rounded leaf apices, and pitted or smooth seeds without a caruncle. Cladistic analyses indicate that sect. *Tithymalopsis* consists of two subgroups: (1) *E. corollata*, *E. discoidalis*, *E. pubentissima* and *E. polyphylla*; and (2) *E. curtisii*, *E. gracilior* and *E. mercurialina*. Comparative data from vegetative morphology, pollen morphology, seed morphology, cytology, crossability, reproductive biology, habitat and distribution are presented. Keys and descriptions to the species are provided.

*Keywords.* *Euphorbia*, sect. *Tithymalopsis*.

### INTRODUCTION

The genus *Euphorbia* L. (c.1500 spp.), the largest genus in the family *Euphorbiaceae*, has been divided into several genera, subgenera and sections by various authors (Rafinesque, 1840; Boissier, 1862; Small, 1903; Millspaugh, 1913; Wheeler, 1939; Webster, 1967, 1994). However, it is usually divided into five subgenera on the basis of characters of the caruncles, stipules, stems and petaloid appendages. Subgenus *Euphorbia* (c.250 spp.), the most isolated group among the five subgenera, is endemic in Africa and India, and is characterized by succulent stems and spiny stipules (Carter, 1994). About 500 species make up subg. *Esula* Pers., which is a native, mainly Eurasian group recognized by exstipulate leaves, bibracteate cyathia, glands without petaloid appendages and carunculate seeds (Webster, 1967). The New World endemic groups, subg. *Agaloma* (Raf.) House, subg. *Poinsettia* (Graham) House and the majority of subg. *Chamaesyce* Raf., comprise over 400 species, and are distributed primarily in xeric habitats of western Mexico and the south-western USA. They are distinguished from Old World subgenera primarily by glands with petaloid appendages, stipulate leaves and ecarunculate seeds. Based on cladistic analyses of morphological data of New World *Euphorbiinae*, Park (1995) proposed that subg. *Chamaesyce* and subg. *Poinsettia* were monophyletic, and evolved independently from a paraphyletic subg. *Agaloma*. Because subg. *Agaloma* has about 150 species and has not been studied in its entirety, 10 sections of subg. *Agaloma* have been poorly delimited based on Boissier's sectional classification in 1862 (Buck & Huft,

\* Department of Biology, Kyung-Nam University, 449 Wolyoung-dong, Masan 631-701, Korea.

1977; Huft, 1984). Unfortunately, the majority of Boissier's sections appear to be paraphyletic or polyphyletic groups in the cladistic analyses (Park, 1995).

*Euphorbia* subgen. *Agaloma* sect. *Tithymalopsis* Boiss. comprises seven species of herbaceous perennials, and is endemic to the south-eastern states of the USA. The centre of diversity is in Georgia, where five of the seven species occur. The species of sect. *Tithymalopsis* are placed as the sister to a clade consisting of *E. strictior* and *E. wrightii* (Park, 1995), and are distinguished from them by having a thick and cylindrical root system, a glabrous cyathium, absence of vestigial sepals in pistillate flowers, and rounded leaf apices. Isozyme-based trees suggest that sect. *Tithymalopsis* is a group genetically distinct from *E. strictior* and *E. wrightii* (Park, 1995). The presence of a fixed unique allele in sect. *Tithymalopsis* supported hypotheses of monophyly for the section based on morphological data.

Circumscription of sect. *Tithymalopsis* and its relationship to other sections within subg. *Agaloma* have presented major problems. Several species of subg. *Agaloma* sect. *Alectoroctonum* (Schltdl.) Baill., sect. *Cyttarospermum* Boiss. and sect. *Zygophyllidium* Boiss. from Mexico and the south-western USA have been placed in the section because of the uncertain limits of Boissier's (1862) sect. *Tithymalopsis*. Although early workers, such as Rafinesque (1836) and Small (1913), defined the group as containing only species distributed in the south-eastern states of the USA, the sectional concept of *Tithymalopsis* has been expanded by recent workers to include species in the south-western USA and Mexico (Wheeler, 1939; McVaugh, 1961; Webster, 1967; Huft, 1979). However, cladistic analyses of the New World subtribe *Euphorbiinae* (Park, 1995) did not support the monophyly of Huft's (1979) sect. *Tithymalopsis*. Within sect. *Tithymalopsis* sensu Huft, a group of *E. macropus*, *E. macropodoides* + *E. ixtlana* was closely related with the group possessing tuberculate seeds such as *Poinsettia* and major sections of herbaceous *Agaloma* (Park, 1995). *Euphorbia innocua* and *E. ipecacuanhae* formed sister groups of subg. *Chamaesyce*.

Most species of sect. *Tithymalopsis* proposed in this study are easily recognized by a unique combination of morphological characters. However, because of extreme polymorphism and a lack of population-level studies, *E. corollata*, *E. pubentissima* and related species have been treated variously as species or varieties of *E. corollata* (Webster, 1967). Many incorrect names have been used by writers of floras of the south-eastern states of the USA. Although Huft (1979) made a significant contribution to the resolution of species boundaries within the *E. corollata* complex, sectional and species limits, species relationships and nomenclatural stability still remained as unresolved problems in sect. *Tithymalopsis*.

Each species of sect. *Tithymalopsis* is distinguished by a unique combination of morphological characters and occupies distinctive habitats and ranges. *Euphorbia corollata* L., the most widely distributed species in sect. *Tithymalopsis*, is characterized by several long (71–122cm) aerial stems with many nodes (27–115) and has the largest spatulate, white appendages (2.5–4.4mm long) among species in sect. *Tithymalopsis*. It extends west to Texas, north to Wisconsin and Massachusetts, and is parapatric with *E. pubentissima* Michx. throughout the Appalachian plateau. It

usually occurs in open, dry habitats such as roadsides, prairies and open hillsides. Occasionally it also grows on streamsides.

*Euphorbia curtisii* Engelm. is easily distinguished from other species by its unisexual cyathium, and pistillate flowers with short, erect pedicels. It is distributed on the Atlantic and Gulf Coastal Plains from North Carolina to the Florida Panhandle, where it is restricted to recently burned areas on sandy soils in oak or pine forests.

A linear leaf with revolute margins, and densely pubescent stems characterize *E. discoidalis* Cham. It is endemic to the Gulf Coastal Plains from southern Mississippi and the Florida Panhandle to Georgia with disjunct populations in south-eastern Texas. It grows in sandy soils in pine or oak forests.

*Euphorbia gracilior* Cronquist is defined by two unique characters: a dark purple cyathium, and glands with purple, vestigial appendages. It is sympatric with *E. curtisii* in the south-eastern Atlantic and Gulf Coastal Plains from North Carolina to the Florida Panhandle.

*Euphorbia mercurialina* Michx. has membranous and wide leaves with ciliate margins, a deeply folded gland, and is restricted to moist soils in hardwood forests of eastern Tennessee, adjacent Alabama, Georgia and Kentucky.

*Euphorbia polyphylla* Engelm. ex Holz. is endemic to southern Florida, and is characterized by purple glands with deeply crenate, white appendages, and succulent, involute and imbricate leaves. It is restricted to open or burned areas on sandy soils in pine and oak forests.

The most morphologically variable species in sect. *Tithymalopsis* is *E. pubentissima*. Its natural range is the south-eastern slope of the Appalachian plateau from North Carolina to Louisiana, where it occurs in open mesic habitats such as forest edges and streamsides. Individuals of *E. pubentissima* are highly variable in size of bracts, leaves and petaloid appendages depending on their age, microhabitat and the growing season. However, they are characterized by a single aerial stem with petiolate, exstipulate leaves, a seasonal dimorphism of bract and petaloid appendage sizes, and white, orbicular appendages (0.96–2.2mm long).

## TAXONOMIC HISTORY

The first named species in sect. *Tithymalopsis* was *E. corollata* which was described by Linnaeus (1753) in *Species Plantarum*. The name *Tithymalopsis* Klotzsch & Garcke was first proposed as a genus segregated from *Euphorbia* based on large, obovate, white petaloid appendages (Klotzsch, 1859). *Tithymalopsis* was later reduced to a sectional name in *Euphorbia* by Boissier (1862), who divided *Euphorbia* into 26 sections in de Candolle's *Prodromus*. Boissier recognized eight New World species in sect. *Tithymalopsis* Boiss. It was one of the New World endemic sections among Boissier's eleven sections with petaloid appendages. Small (1903) accepted *Tithymalopsis* as a genus in his *Flora of the Southeastern United States*, and later designated *E. corollata* L. as lectotype of the genus (Small, 1913).

*Tithymalopsis* as a generic name is illegitimate because the genus *Agaloma* Raf. was described already by Rafinesque (1836). Rafinesque (1836, 1840) clearly described the genus *Agaloma* based on *E. corollata* L., and proposed eight species and several varieties in the south-eastern USA. Unfortunately Klotzsch (1859), Boissier (1862), Small (1903) and Norton (1916) were not aware of Rafinesque's (1836, 1840) valid publications in *Flora Telluriana* and *Autikon Botanikon*. Nieuwland (1912) noted that Klotzsch and Garcke's *Tithymalopsis* was preceded by the name *Agaloma* Raf. However, the name of sect. *Tithymalopsis* Boiss. (Boissier, 1862) is unaffected by *Agaloma* Raf. (Rafinesque, 1836) according to ICBN Art. 11.2.

House (1924) presented another subgeneric classification within *Euphorbia*. He treated *Tithymalopsis* as a synonym of subg. *Agaloma*, and placed *E. corollata* and *E. ipecacuanhae* L. in subg. *Agaloma* (Raf.) House. Confusion of subgeneric boundaries was compounded when Wheeler (1939, 1943) expanded subg. *Agaloma* to include all of Boissier's (1862) sections and genera with appendiculate species, which included sect. *Tithymalopsis*. The recognition of sect. *Tithymalopsis* in *Euphorbia* subg. *Agaloma* has been widely accepted by most recent authors (Webster, 1967; Johnston, 1975; Huft, 1979, 1984).

In his revision of *Euphorbiaceae* in the south-eastern USA, Webster (1967) divided sect. *Tithymalopsis* into three subsections: subsect. *Corollatae* (10 spp.), subsect. *Innocuae* (1 sp.) and subsect. *Ipecacuanhae* (4 spp.). Subsect. *Corollatae* mostly corresponded to Boissier's sect. *Tithymalopsis*. However, Webster suggested that several species in Texas and Mexico, such as *E. maysillesii*, *E. sphaerorhiza* and *E. wrightii*, needed placement in a new subsection. Although Huft (1979) followed Webster's sectional delimitation, his infrasectional system was different. He subsumed Webster's subsect. *Corollatae* into a broader subsect. *Ipecacuanhae*, and recognized two additional subsections: *Scoparia* (2 spp.) and *Sphaerorhizae* (5 spp.).

The number of species included in sect. *Tithymalopsis* has varied greatly in taxonomic treatments. Boissier (1862) included six species which were not included in the treatments of Rafinesque (1836, 1840) and Klotzsch (1859). Boissier recognized *E. mercurialina* and *E. pubentissima* which had been described by Michaux in *Flora boreali-americana*. *Euphorbia pubentissima* Michx. was later identified as the same species as *E. corollata* or its varieties in the south-eastern flora of the USA. Boissier also transferred *E. wrightii* from genus *Alectoroctonum* (Schltdl.) Boiss. to this section.

*Euphorbia polyphylla* originally appeared without a description in Engelmann (1887) for Patterson's checklist; later, Holzinger (1892) described *E. polyphylla* as a new species using the name proposed by Engelmann. Holzinger mentioned that Chapman, on a visit to the National Herbarium in May 1892, had considered *E. polyphylla* Engelm. conspecific with his *E. discoidalis* (Holzinger, 1892). Later, Chapman (1892) independently published the description of *E. polyphylla* Engelm. in the second supplement to the *Flora of the Southern United States*. Unfortunately, the precise date of Chapman's publication is uncertain. Only the preface of Chapman's second edition was dated, as 10 August 1892 (Huft, 1979).

Small (1898) described four new species: *T. apocynifolia* Small, *T. olivacea* Small, *T. eriogonoides* Small and *T. zinniiflora* Small in the genus *Tithymalopsis*, and proposed 14 species of *Tithymalopsis* in his *Flora of the Southeastern United States* (Small, 1903). He newly included *T. exserta*, *T. ipecacuanhae* and *T. gracilis* in *Tithymalopsis*, but did not recognize *T. pubentissima* which had been proposed as a member of sect. *Tithymalopsis* by Boissier (1862). Millspaugh (1898) treated most of Small's (1898) species as varieties of *E. corollata* L., and newly described var. *molle* and var. *glauca*.

Cronquist (1949) proposed *E. gracilior* as a new species, because the *E. gracilis* Elliott name was a later homonym of *E. gracilis* Besser, and the type specimen of Elliott's species could not be located.

Wheeler (1939) proposed two new species: *E. innocua* and *E. hintonii* from southern Texas and Mexico. They were accepted in this section by the presence of pitted seeds and petaloid appendages (Webster, 1967; Huft, 1979).

In the recent monographic studies of sect. *Tithymalopsis*, Huft (1979) recognized 16 species which include most of the species previously described under sect. *Tithymalopsis*. Compared with previous concepts of *Tithymalopsis* (Rafinesque, 1840; Boissier, 1862; Small, 1903), Huft's sectional concept of *Tithymalopsis* was expanded to include not only species in the *E. corollata* complex, but also related species from the south-eastern USA, and problematic species from Texas and Mexico with uncertain sectional affinities.

## MATERIAL AND METHODS

### *Vegetative and floral morphology*

Measurements and descriptions are based on herbarium specimens and collections made by the author. Vegetative measurements were taken from dried specimens; floral measurements were taken from materials fixed in the field in 70% ethanol. More than 10 measurements per population were obtained for each quantitative character.

### *Pollen morphology*

Pollen grains of seven species of sect. *Tithymalopsis* and 10 related species that include all the species of the section included by Huft (1979) were examined by light microscopy (LM) and scanning electron microscopy (SEM). Pollen was obtained from dried specimens collected by the author, and from herbarium specimens for Mexican species. Pollen was prepared for examination using the acetolysis method (Erdtman, 1960). For LM studies, pollen grains were mounted in glycerin jelly, and sealed with paraffin. For SEM studies, acetolysed pollen grains were affixed to aluminium stubs with double-sided cellophane tape, and air-dried from 95% ethanol. Specimens were sputter-coated with a gold-palladium mixture, and observed with an ETEC Autoscan SEM at the Noble Electron Microscopy Laboratory at the

University of Oklahoma. Measurements of polar axis diameter (PA), equatorial diameter (ED), colpus length (CL) and exine thickness (ET) were carried out with light microscopy (c.  $\times 500$ ). Terminology used for morphological characters follows Erdtman (1966), Walker & Doyle (1975) and Saxena (1993).

#### *Seed morphology*

Seeds of seven species of sect. *Tithymalopsis* and 10 related species were examined by LM and SEM. Mature seeds were collected in the field, or obtained from herbarium specimens. Preparation for SEM followed the same methods as for pollen grains.

Production of a mucilaginous layer was tested using the method of Jordan & Hayden (1992), and observed under a microscope. Seeds were placed in a moist Petri dish, and observed after 5 min for the presence of bright projections (mucilage).

#### *Crossability and pollination*

Plants for crossing studies were grown from field-collected root stocks and maintained in the greenhouse of the University of Oklahoma. Artificial hybridizations were conducted by transferring pollen grains with forceps to receptive stigmas in emasculated flowers. Usually the pistillate flower emerges first above the involucre with closed style tips; young anthers can be removed successfully before stigmas mature. Hand-pollinated flowers were bagged using paper tubes for a month before seeds were collected (Ehrenfeld, 1976). Five hundred separate cross-pollinations by pairwise combinations of populations among seven species were conducted. Hand pollinations were limited in *E. gracilior*, because of its thin, fragile and long peduncles. Numbers of mature fruit set were measured for each treatment (Table 1). Observations and collections of insect visitors and pollinators were made in seven populations of five species during the flowering season.

#### *Chromosome studies*

Somatic chromosomes were observed from the root tips of plants propagated in pots in the greenhouses. Mitotic chromosome squashes were prepared by the oxyquinoline-acetic-orcein method (Radford et al., 1974).

#### *Outgroup taxa for cladistic analysis*

The sections *Zygophyllidium* (Webster, 1967) and *Alectoroctonum* (Huft, 1979) have been proposed as closely related taxa to sect. *Tithymalopsis*. However, phylogenetic analyses of New World *Euphorbiinae* (Park, 1995) portrayed the group consisting of *E. wrightii* and *E. strictior* as the close relative (sister species) to sect. *Tithymalopsis*. These species were placed in Huft's subsect. *Scoparia* which was defined by a

scoparius habit and is allopatric to sect. *Tithymalopsis* with a distribution in New Mexico, western Texas and northern Mexico. They share with sect. *Tithymalopsis* a herbaceous perennial habit, pitted seeds and a 3–5-rayed umbel.

#### *Characters and their states for phylogenetic analysis*

Seven ingroup and two outgroup species were scored for 20 characters, which consisted of 17 qualitative and three quantitative morphological characters (Tables 2, 3). The states of three quantitative characters – leaf shape, node number and peduncle length – were clearly separated, and there was no overlapping variation. The requirement for sharp gaps between quantitative character states has been treated as a methodological requirement of cladistic analysis (Stevens, 1991). *Euphorbia wrightii* and *E. strictior* have a broom-like habit with many clumped stems, while the species of sect. *Tithymalopsis* have a simple form with 1–3 stems (character 1). Leaf shape (character 2) states were divided into two states: linear (0) and oblong/ovate (1). There was no overlapping variation between two quantitative character states. Entire leaves (character 3) are common in ingroup and outgroup species, while revolute or involute leaves are present only in *E. discoidalis* and *E. polyphylla*. The leaves (character 6) appearing only from branching nodes is commonly seen in *E. curtisii*, *E. gracilior*, *E. mercurialina* and two sister taxa. On the other hand, leaves are developed all around the stem without lateral branches in other species. Minute and glanduliform stipules (character 7) are present on the base of the petioles in four species of sect. *Tithymalopsis*, while absence of the stipules is found in *E. corollata*, *E. discoidalis* and *E. pubentissima*. The presence of scale-like leaves (character 8) on the aerial stems characterizes a group of species restricted to open sandy areas and moist soils in hardwood forests. However, some species have scale-like leaves at the bases of stems only in the early growing season. The floral rays of sect. *Tithymalopsis* species branch dichasially several times, and they are subtended by an equal number of bracts. *Euphorbia corollata* complex species plus *E. polyphylla* are recognized by having white tips to the bracts (character 9), while the remaining species do not have white spots at the tips of the bracts. Although the size of bracts (character 16) decreases gradually towards the apex in most species, those of *E. mercurialina*, *E. gracilior* and *E. curtisii* are the same size throughout the rays. The shape of the terminal dichasium (character 15) is commonly asymmetric in sect. *Tithymalopsis* as a result of unequal growth of individual branches. However, the absence of asymmetric dichasia is a unique character of *E. mercurialina*, *E. gracilior* and *E. curtisii*.

#### *Cladistic analysis*

A maximum parsimony analysis (Swofford, 1991) was performed on PAUP version 3.0s with ingroup and outgroup taxa simultaneously, and rooted the resulting trees at the internode between ingroup and outgroup. The species of the sister group of

sect. *Tithymalopsis*, *E. strictior* and *E. wrightii*, were chosen as outgroups based on the cladistic study of New World *Euphorbiinae* (Park, 1995). The search for shortest trees was carried out using the exhaustive option with the ACCTRAN (accelerated transformation) optimization. Strict consensus trees were calculated. One of the most parsimonious trees was used for mapping the character states on the cladogram. In order to evaluate the relative stability of clades, decay indices (Donoghue et al., 1992) were calculated from the consensus trees of each step of a few steps longer than the most parsimonious trees.

## RESULTS AND DISCUSSION

### *Vegetative and floral morphology*

*Habit, stems, roots.* Species of sect. *Tithymalopsis* are herbaceous perennials and have one or few branches. Branches are limited to the base (*E. polyphylla*) or top (*E. corollata*) of the stem. Stems are erect, ascending, or occasionally spreading (*E. polyphylla*). A single aerial stem or several main aerial stems arise from a root. Young shoots and the base of stems are often dark purple or pale red.

All species have long, thick (1.5–10mm) and cylindrical taproots with thick bark and several lateral buds. Shoot growth from the lateral buds seems to be activated after fire or drought.

*Leaves.* Leaves are: alternate, imbricate (*E. polyphylla*) or imbricate only in the early growing season (*E. corollata*); petiolate or, occasionally, sessile (*E. corollata*); and ascending (*E. corollata*, *E. polyphylla*) or reflexed (*E. pubentissima*, *E. curtisii*). Blade texture varies from membranous (*E. mercurialina*) to leathery (*E. corollata*) or semi-succulent (*E. polyphylla*). The adaxial surface is glabrous or has unicellular trichomes (*E. curtisii*). The abaxial surface is glabrous or has unicellular hairs on the veins. The margins are entire, ciliate (*E. mercurialina*, *E. curtisii*), or revolute (*E. discoidalis*) to involute (*E. polyphylla*); dark purple leaf margins are present in *E. curtisii* and *E. gracilior*. One of the characters uniting species in sect. *Tithymalopsis* is rounded leaf apices. Most of the Texan and Mexican species that were previously included in sect. *Tithymalopsis* sensu Huft (1979) have acuminate leaves. Previous authors (Boissier, 1862; Small, 1903; Webster, 1967) identified the absence of stipules as a diagnostic character in sect. *Tithymalopsis*, but stipule presence and type are variable within the section. For example, *Euphorbia curtisii*, *E. gracilior*, *E. mercurialina* and *E. polyphylla* have glandular stipules. Reduction in leaf size occurs gradually towards the stem apex (*E. corollata*, *E. discoidalis*, *E. polyphylla*). Basal leaves vary from scale-like to fully expanded; they are occasionally broader than stem leaves (*E. polyphylla*).

*Inflorescence branching, cyathium.* The main stem is terminated by a cyathium and a 3–5-rayed umbel; rays are subtended by an equal number of bracts. Floral rays branch dichasially 2–3 times (*E. curtisii*, *E. gracilior*, *E. mercurialina*) or 3–8 times (*E. corollata*, *E. discoidalis*, *E. polyphylla*, *E. pubentissima*). Cyathia are solitary at



a branching node. The peduncle of the first or second cyathium is longer than those of terminal cyathia. Each branching node is subtended by opposite bracts, which decrease in size gradually towards the apex. Dichasial branches and cyathia are often absent apically; then the nodes only are subtended by bracts (*E. corollata*, *E. discoidalis*, *E. polyphylla*, *E. pubentissima*).

The cyathium consists of a central, naked, pistillate flower, surrounded by five male monochasia, and enclosed by five connate bracts (involucre). Five glands and lobes alternate at the tips of the involucre. The cyathium is commonly bisexual, but is unisexual in *E. curtisii*. The involucre is usually campanulate or hemispherical in shape, and glabrous or sparsely pubescent near the upper margin. The colour of the involucre is usually green or, occasionally, dark purple (*E. gracilior*). The glands are shallowly or deeply (*E. mercurialina*) depressed at the centre, and longitudinally elongated. The glands are commonly green or dark purple (*E. gracilior*, *E. polyphylla*) and subtended by petaloid appendages. Appendages are usually white or pink to dark purple, and entire to crenate. They are conspicuous or vestigial (*E. gracilior*).

Staminate flowers are numerous, yellow-green or purple, and subtended by membranous, pubescent bracteoles. The pistillate flower is naked, and is surrounded by five groups of staminate flowers. Pedicels are usually recurved and exerted out of the cyathium, but *E. curtisii* has a short, erect pedicel, and the capsule is not exerted after maturation.

#### *Pollen morphology*

Palynological studies have proven to be a useful tool in clarifying taxonomic boundaries of higher taxa, and their relationships and classification within *Euphorbiaceae* (Punt, 1962, 1987; Köhler, 1965; Webster, 1975, 1994; Levin & Simpson, 1994; Nowicke, 1994; Simpson & Levin, 1994). However, only a few studies have been conducted in *Euphorbia* (Lynch & Webster, 1975; Park & Lee, 1988; El-Ghazaly, 1989; Lin & Hsieh, 1991; Lin et al., 1991). Previous studies showed that the pollen of *Euphorbia* s.l. is tricolporate with a conspicuous margo, and a conspicuously stratified tectum, columella and footlayer. Within subfamily *Euphorbioideae*, *Euphorbia* s.l. is closely related to *Stillingia* (Lynch & Webster, 1975) by having marginated colpi. Pollen grains of Old World species in subg. *Esula* are characterized by foveolate, perforate or fossulate surface patterns (Park & Lee, 1988; Lin & Hsieh, 1991). Among the New World subgenera of *Euphorbia* s.l., species in subg. *Chamaesyce* are characterized by a foveolate sculpturing pattern, prolate or subprolate shape, and long, acute colpi (Park & Lee, 1988; El-Ghazaly, 1989; Lin et al., 1991). Pollen grains of subg. *Poinsettia* have a reticulate exine structure and thin margo (Lin & Hsieh, 1991).

Pollen of sect. *Tithymalopsis* is oblate spheroidal to prolate spheroidal (P/E = 0.96–1.09), circular in polar view, and small to medium in size (18.0–31.5µm). *Euphorbia gracilior* has the smallest grains, whereas *E. corollata* has the largest pollen in the section. The aperture type is tricolporate. Colpi are sunken, have a psilate

margo, are well marked from mesocolpia, are broadest at the equator, and taper towards the poles. Only *E. polyphylla* has rounded colpi. *Euphorbia curtisii* has a sunken margo with conspicuous margins (Fig. 1), whereas *E. gracilior* is characterized by narrow and sunken margos. All species have colpus surfaces covered with granular processes; pores are generally lalongate. Sculpturing patterns are foveolate in *E. corollata* and *E. mercurialina*, reticulate in *E. discoidalis* and *E. gracilior*, or microreticulate in *E. curtisii*, *E. polyphylla* and *E. pubentissima* (Fig. 1). Within the *E. corollata* complex (*E. corollata*, *E. discoidalis* and *E. pubentissima*), three morphotypes were distinguished easily by sculpturing pattern: *E. discoidalis* is reticulate, *E. pubentissima* is microreticulate with slightly sunken lumina, and *E. corollata* is foveolate and is larger than *E. pubentissima*.

Species in sect. *Tithymalopsis* do not have distinctive pollen grains compared with those species of subg. *Agaloma* from Texas and Mexico. Except for their thin margo, *E. strictior* and *E. wrightii* have pollen within the range of variation of species in sect. *Tithymalopsis*. *Euphorbia maysillesii* and *E. sphaerorrhiza*, endemic to western Mexico and included in Huft's (1979) expanded sect. *Tithymalopsis*, are distinguished from other species by having foveolate and larger-sized pollen grains. *Euphorbia innocua* and *E. hintonii* are the only species possessing subprolate ( $P/E = 1.20; 1.27$ ) pollen grains in this study. The polar views of *E. hintonii* and *E. marcropodoides* are semiangular instead of circular as in other species.

*Key to the pollen of species within sect. Tithymalopsis*

- |  |                        |
|--|------------------------|
| 1a. Pollen grains with reticulate exine structure _____                | 2                      |
| 1b. Pollen grains with foveolate or microreticulate structure _____    | 3                      |
| 2a. Equatorial diameter 22.5–24.8µm _____                              | <b>E. discoidalis</b>  |
| 2b. Equatorial diameter 20.3–21.8µm _____                              | <b>E. gracilior</b>    |
| 3a. Pollen foveolate _____   | 4                      |
| 3b. Pollen microreticulate _____                                       | 5                      |
| 4a. Pollen grains small (<24µm in polar axis) _____                    | <b>E. mercurialina</b> |
| 4b. Pollen grains large (>28µm in polar axis) _____                    | <b>E. corollata</b>    |
| 5a. Colpus end rounded _____   | <b>E. polyphylla</b>   |
| 5b. Colpus end acute _____   | 6                      |
| 6a. Colpus margo slightly sunken, foveola margin slightly sunken _____ | <b>E. pubentissima</b> |
| 6b. Colpus margo conspicuously sunken, foveola margin smooth _____     | <b>E. curtisii</b>     |

*Seed morphology*

Seed characters of *Euphorbia* have been used to recognize species (Krochmal, 1952; Richardson, 1968) and subgeneric or sectional boundaries (Webster, 1967; Ehler,

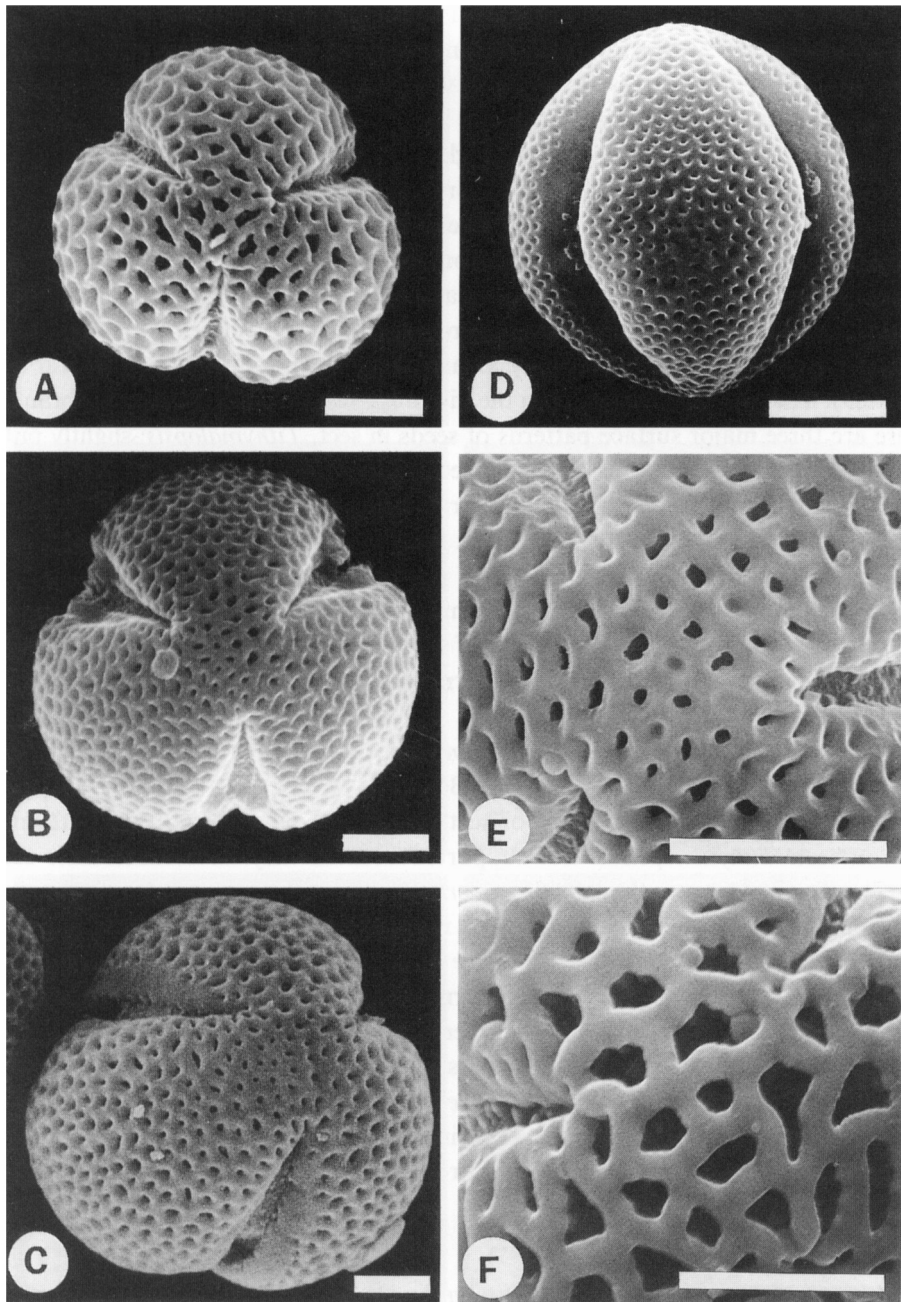


FIG. 1. SEM micrographs of *Euphorbia* sect. *Tithymalopsis* and related species pollen. Scale bar: 5 $\mu$ m. A, polar view of *E. gracillior*; B, polar view of *E. curtisii*; C, polar view of *E. corollata*; D, equatorial view of *E. innocua*; E, microreticulate sculpturing pattern of *E. pubentissima*; F, reticulate sculpturing pattern of *E. discoidalis*.

1976), and to examine the adaptive significance of seed modifications (Carlquist, 1966; Jordan et al., 1985; Jordan & Hayden, 1992). Seed characters such as caruncle, mucilage, shape and sculpturing pattern were also used to elucidate phylogenetic relationships (Park, 1995).

Seeds of sect. *Tithymalopsis* are ovate, globose, white or brown, and ecarunculate. The smallest seeds in the section (1.8–2.4mm long) are produced by *E. discoidalis*, *E. gracilior* and *E. pubentissima*; the largest seeds (2.5–3.3mm long) are produced by *E. corollata*. The side of the hilum is abruptly depressed or, occasionally, broadly depressed (*E. mercurialina*), and narrowly acute at the top. The other end is flattened with a nipple-like structure. Testal cells are generally round with several concentric circles, but they are more compactly arranged around the hilum and ventral lines (Fig. 2D). The shape of testal cells in the hilum is various, and they are membranous. There are three major surface patterns of seeds in sect. *Tithymalopsis*: slightly pitted with an irregular distribution over the seed surface in *E. corollata*, *E. pubentissima* and *E. gracilior*; pitted with a regular distribution in *E. mercurialina*; and smooth in *E. curtisii*, *E. discoidalis* and *E. polyphylla*. Seed of *E. discoidalis* has variable surface patterns even within populations.

Pitted seeds appear to be primitive within the section, because they occur in out-group taxa and among basal members of sect. *Tithymalopsis*. This hypothesis proposes that the smooth sculpturing patterns of *E. polyphylla* and *E. curtisii* result from a secondary loss of pits.

*Euphorbia ixtlana*, *E. macropus* and *E. macropodoides* have been included in sect. *Tithymalopsis* by Huft (1979), whereas Boissier (1862) and Arthur (1912) placed them in either sect. *Zygophyllidium* or sect. *Anisophyllum*. The inclusion of them by Huft in sect. *Tithymalopsis* is not supported because they have tuberculate seeds (Fig. 2). *Euphorbia macropus* and *E. macropodoides* are most similar to the species of sect. *Zygophyllidium* in seed and other morphological characters.

*Euphorbia innocua* and *E. ipecacuanhae* have been treated variously as members of subg. *Agaloma* (Wheeler, 1939), intermediate taxa between subg. *Chamaesyce* and subg. *Agaloma* (Norton, 1900; Webster, 1967) or members of sect. *Tithymalopsis* (Huft, 1979). The mucilaginous seed coats of these species are distinctive within the study group. Additionally, *E. ipecacuanhae* has a uniquely angular seed shape. These species demonstrate affinities with species in subg. *Chamaesyce*, because angular and mucilaginous seeds are common in that group (Krochmal, 1952; Richardson, 1968; Jordan & Hayden, 1992).

#### *Crossability and pollination*

Few studies of reproductive biology in *Euphorbia* have been reported. Several species of subg. *Esula* and subg. *Agaloma* are dependent on a variety of insects for pollination, whereas self-pollination was reported in the several weedy species of subg. *Chamaesyce* (Krombein, 1961; Ehrenfeld, 1976; Huft, 1979). Within sect. *Tithymalopsis*, *E. corollata* was reported previously as a completely outcrossing

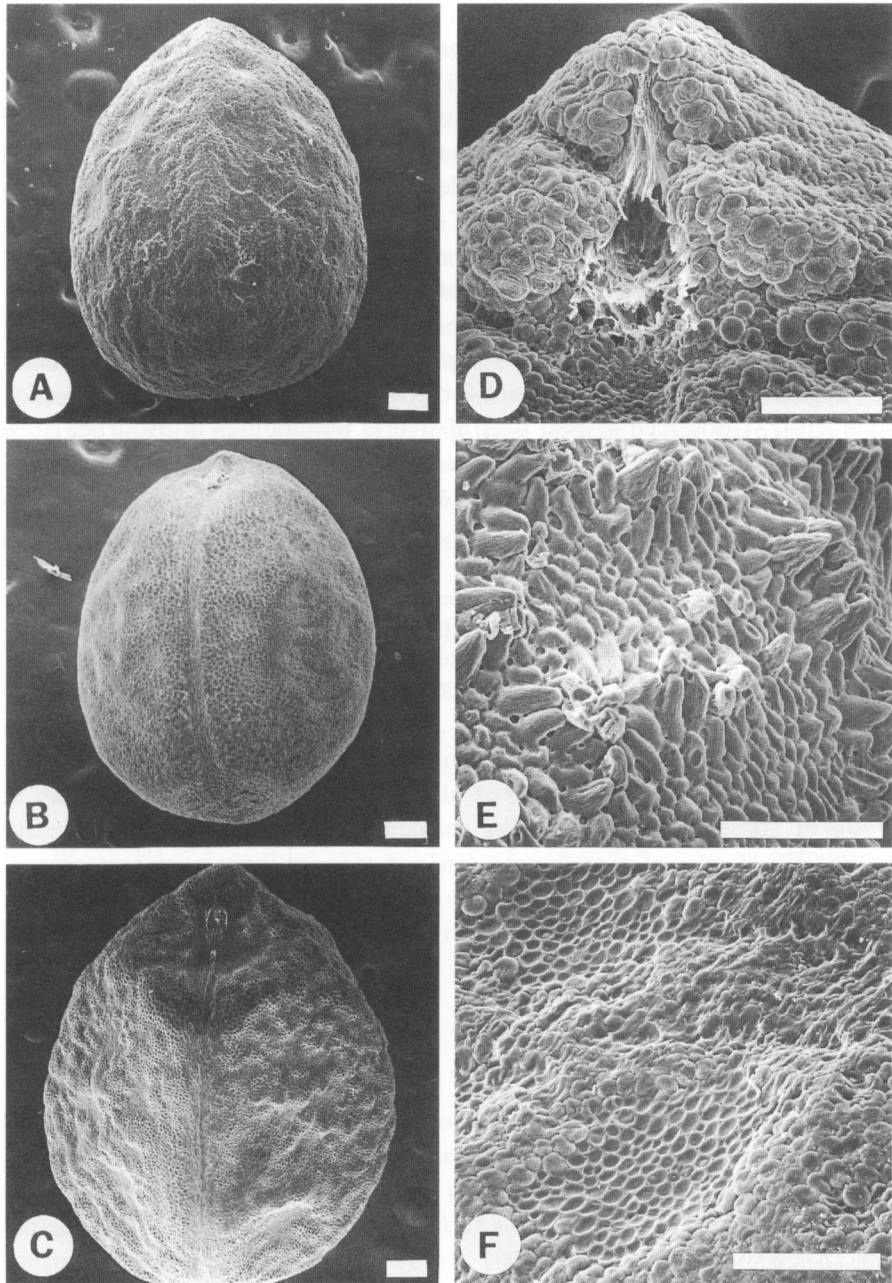


FIG. 2. SEM micrographs of *Euphorbia* sect. *Tithymalopsis* and related species seeds. Scale bar: 200 $\mu$ m. A, whole seed of *E. gracilior*; B, *E. pubentissima*; C, *E. macropus*; D, hilum portions of *E. polyphylla*; E, seed coat of *E. ixtlana*; F, pit portions of *E. gracilior*.

species based on bagging experiments (Huft, 1979). Diverse insects, such as wasps, bees, beetles and flies, were observed as common visitors to *E. corollata* (Huft, 1979).

Self-pollination results showed that *E. mercurialina* and *E. corollata* were self-incompatible. All species in this section showed high crossing compatibilities. However, *E. curtisii* had the lowest levels of interspecific fruit set when crossed with *E. discoidalis* and *E. mercurialina* (Table 1). Species of the *E. corollata* complex generally exhibited the highest levels of crossability. Although *E. discoidalis* and *E. polyphylla* are closely related and have been treated as conspecific by Chapman (Holzinger, 1892), they have low levels of fruit set when crossed.

The generally high levels of interspecific compatibility suggest that post-pollination reproductive barriers are poorly developed among species in sect. *Tithymalopsis*. There appears to be a high potential for gene flow if pollination can be effected. Consequently, I observed several sites of hybrid populations in disturbed areas of sympatry among *E. corollata*, *E. discoidalis*, *E. mercurialina* and *E. pubentissima*.

TABLE 1. Summary of interspecific crossability within and between species of *Euphorbia* sect. *Tithymalopsis*.

Species	No. of flowers pollinated	No. of capsules set	Proportion (%)
<b>Within species</b>			
<i>E. corollata</i>	22	8	36
<i>E. curtisii</i>	1	1	100
<i>E. discoidalis</i>	2	0	0
<i>E. gracilior</i>	0		
<i>E. mercurialina</i>	2	1	50
<i>E. polyphylla</i>	2	1	50
<i>E. pubentissima</i>	46	16	35
<b>Between species</b>			
<i>E. corollata</i> × <i>E. curtisii</i>	17	1	6
<i>E. corollata</i> × <i>E. discoidalis</i>	24	6	25
<i>E. corollata</i> × <i>E. mercurialina</i>	7	1	14
<i>E. corollata</i> × <i>E. polyphylla</i>	37	15	41
<i>E. corollata</i> × <i>E. pubentissima</i>	77	29	38
<i>E. curtisii</i> × <i>E. discoidalis</i>	9	0	0
<i>E. curtisii</i> × <i>E. mercurialina</i>	2	0	0
<i>E. curtisii</i> × <i>E. polyphylla</i>	6	4	67
<i>E. curtisii</i> × <i>E. pubentissima</i>	7	2	29
<i>E. discoidalis</i> × <i>E. mercurialina</i>	5	1	20
<i>E. discoidalis</i> × <i>E. polyphylla</i>	16	1	6
<i>E. discoidalis</i> × <i>E. pubentissima</i>	39	20	51
<i>E. gracilior</i> × <i>E. pubentissima</i>	4	1	25
<i>E. mercurialina</i> × <i>E. polyphylla</i>	6	3	50
<i>E. mercurialina</i> × <i>E. pubentissima</i>	16	8	50
<i>E. polyphylla</i> × <i>E. pubentissima</i>	5	1	20

Ecological, geographical and seasonal (phenological) barriers seem to be the primary and most effective mechanisms for reproductive isolation among species.

In the genus *Euphorbia*, the structure of the cyathium consists of nectar-producing glands and petaloid appendages that have been considered an adaptation to insect pollination (Cronquist, 1968). A list of insect visitors to *Euphorbia* species has been given by Krombein (1961) and Ehrenfeld (1976). Within sect. *Tithymalopsis*, Huft (1979) reported small wasps, beetles, bees and flies as visitors to *E. corollata*.

Observations indicate that *E. corollata* and *E. pubentissima* were visited frequently by flies and wasps. Small beetles were the most frequent visitors in *E. curtisii*, although other small insects such as ants also visited inflorescences and collected nectar. It is uncertain whether ants are effective pollinators or just nectar collectors. Black fruit flies were the only visitors to *E. polyphylla* and appeared to collect nectar from glands and the sticky liquid secreting from stigmas. They were large enough to contact anthers and stigmas and may be effective pollinators. The small, spreading habit and dark purple glands of *E. polyphylla* seem to be the important factors for a unique relationship with the fruit flies.

#### *Chromosome studies*

Chromosome numbers of 10 species have been reported previously for subg. *Agaloma* (Perry, 1943; Hans, 1973; Urbatsch et al., 1975; Keil, 1976). With the exception of *E. marginata* Pursh ( $n=28$ ), all species were  $n=14$ . *Euphorbia corollata* ( $2n=28, 30$ ) is the only species reported cytologically in sect. *Tithymalopsis*. *Euphorbia wrightii*, the sister group of the section, was reported as  $n=14$  (Urbatsch et al., 1975).

Chromosome counts indicate that *Euphorbia corollata* is  $2n=26, 28, 30$ , with  $2n=28$  being the most common number. *Euphorbia polyphylla* is uniformly  $2n=28$ . Most of the taxa in this section have very small chromosomes, which are difficult to count successfully.

#### *Phylogenetic relationships*

Although Huft (1979) conducted a phylogenetic analysis of the section (Wagner-groundplan divergence), recent cladistic analyses (Park, 1995) do not support the monophyly of Huft's sect. *Tithymalopsis*. Consensus trees portrayed several groups constituting sect. *Tithymalopsis* sensu Huft as a sister group to subg. *Chamaesyce* or member of the tuberculate seed taxa (Park, 1995). *Euphorbia macropus*, *E. macro-podoides* and *E. ixtlana*, previous members of sect. *Tithymalopsis*, are not closely related with a group of sect. *Tithymalopsis*, but with the group possessing tuberculate seeds such as subg. *Poinsettia* and major sections of the herbaceous *Agaloma*. *Euphorbia ipecacuanhae* and *E. innocua* of sect. *Tithymalopsis* sensu Huft possess the mucilaginous seed coat and polypodial prostrate branches which are homologous characters among species of subg. *Chamaesyce*. Previous analysis (Park, 1995)





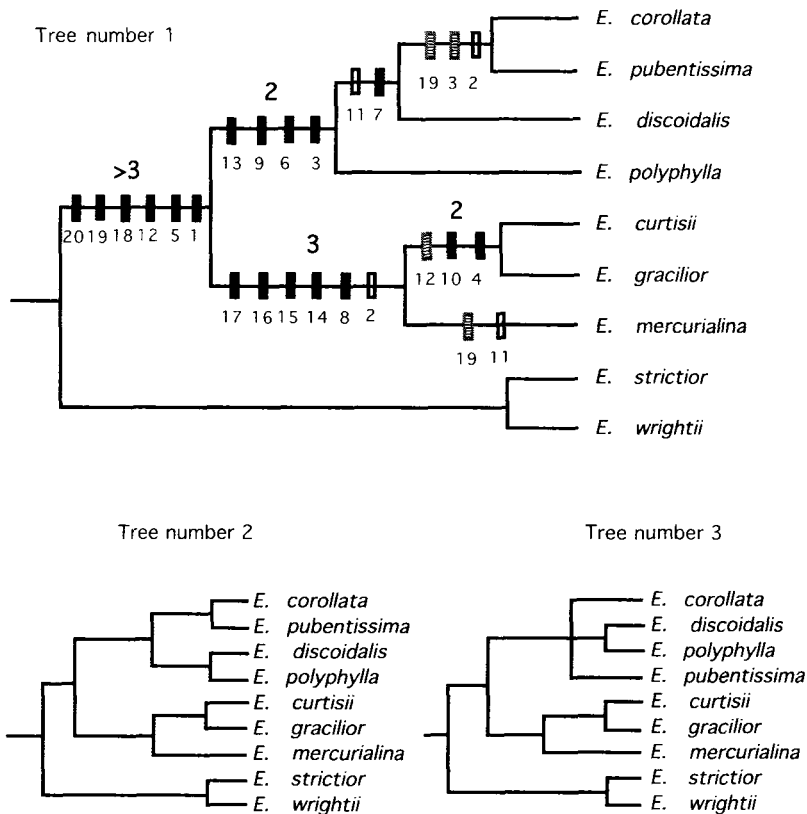


FIG. 3. Cladograms of *Euphorbia* sect. *Tithymalopsis* with *E. strictior* and *E. wrightii* as outgroups. Three most parsimonious trees, and the distribution of character states. Character numbers as in Table 2. Solid box, synapomorphy; open box, parallel change; shaded box, reversal. The numbers on the upper nodes are decay indices.

for collapsing the monophyletic structure (Fig. 3). The monophyly of ingroup taxa was supported strongly by four characters. The three most parsimonious trees indicate two major lineages: (1) the *E. corollata* complex (*E. corollata*, *E. discoidalis*, *E. pubentissima*) plus *E. polyphylla* clade; and (2) the *E. curtisii* + *E. gracilior* + *E. mercurialina* clade.

The monophyly of the second clade is strongly supported by five homologous characters: scale leaves on the base of the stem, presence of terminal branches, a symmetrical inflorescence, fully formed bracts and long peduncles. The sister-group relationship between *E. curtisii* and *E. gracilior* was depicted in all the trees.

The monophyly of the *E. corollata* complex + *E. polyphylla* clade is supported by a leaf only on the branching points (character 6), white bractal tips (character 9), and the presence of many nodes (character 13). The *E. corollata* complex may not be monophyletic, since *E. discoidalis* and *E. polyphylla* formed a clade in the second tree by the revolute or involute margin of the leaves (character 3). A similar

interpretation was obtained using maximum-likelihood and parsimony methods of allozyme data (Park, 1995). The monophyly of *E. curtisii*, *E. gracilior* and *E. mercurialina* is in complete agreement with trees generated from isozymes (Park, 1995). However, Huft (1979) placed *E. curtisii* as a sister species of *E. corollata* and *E. pubentissima*.

## TAXONOMY

**Euphorbia** L. sect. **Tithymalopsis** Boiss. in A. DC., Prodr. 15: 9 (1862). *Tithymalopsis* Klotzsch & Garcke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 249 (1859), nom. illeg. (Art. 52.1). *Euphorbia* subsect. *Tithymalopsis* (Boiss.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 106 (1890). Lectotype, designated by Small (1913): *Euphorbia corollata* L.

Syn.: *Agaloma* Raf., Fl. Tellur. 4: 116 (1836). *Euphorbia* subg. *Agaloma* (Raf.) House in New York State Mus. Bull. 254: 471 (1924). Type: *Agaloma corollata* (L.) Raf. (= *Euphorbia corollata* L.), designated by Rafinesque, Autik. Bot. 95 (1840).

Perennial herbs, erect, ascending or rarely spreading. *Stems* green or red, reddish on the base of the stem, glabrous or sparsely pubescent; underground stems present; main stem solitary or a few, simple or branched. *Roots* cylindrical, thick or slender, root buds on the surface. *Leaves* alternate, imbricating or not, petiolate or sessile, ascending or reflexed, glabrous or sparsely hairy on abaxial surface; blades linear to ovate, leathery or membranous; margins entire or ciliate, revolute or involute, green or purple; apex rounded; stipules minute, glandular or obsolete. *Main stem* terminated by a cyathium, a 2–6-rayed umbel, and subtended bracts. *Floral rays* branching several times as a dichasium; dichasial branches present or absent at terminus; each dichasial node subtended by opposite bracts; white tips present or absent at the apices of bracts. *Cyathia* solitary at each node; involucre campanulate or hemispherical, green or purple, glabrous or sparsely hairy at upper surface. *Glands* present at the top of an involucre, five, green or dark purple, slightly or deeply depressed at the centre, subtended by petaloid appendages; appendage white or pink to dark purple, ascending or reflexed, entire or erose margined, semicircular to spatulate or vestigial. *Staminate flowers* numerous, purple or yellow-green, monandrous, subtended by bracteoles. *Pistillate flowers* central, surrounded by five groups of staminate flowers; pedicel exerted beyond the involucre or very short, recurved or erect; capsule globose, green or purple, three lobed, glabrous; styles three, united at base; stigma pale green or red to pink, bifid. *Seeds* globose, white or brown, ecarunculate, pitted or smooth; hilum depressed; apex acute, with a nipple-like structure at the opposite end.

The section *Tithymalopsis* is characterized by its thick and cylindrical root system, 1–3 stems, rounded leaf apices, 2–6 umbel dichasia, glabrous cyathia, five glands with petaloid appendages, absence of vestigial sepals in pistillate flowers, and pitted or smooth seeds without a caruncle.

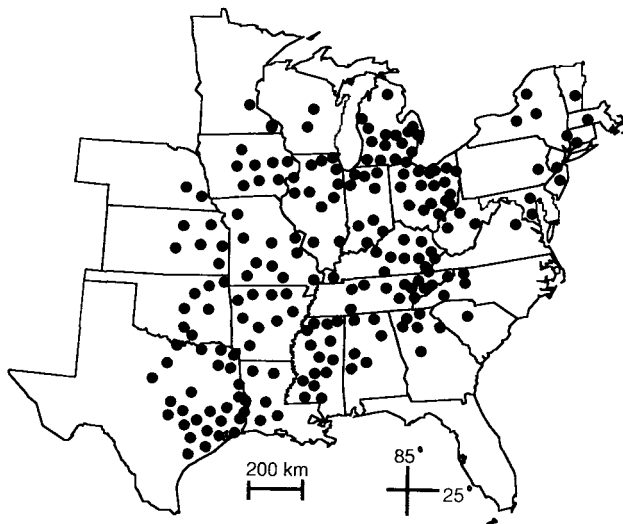


FIG. 4. Distribution of collections of *E. corollata*.

Although the name of genus *Tithymalopsis* Klotzsch & Garcke (1859) is preceded by genus *Agaloma* Raf. (1836), sect. *Tithymalopsis* Boiss. (1862) has priority at the rank of section (ICBN Art. 11.2). The name of this section must be attributed to Boissier alone (Art. 58.3).

*Key to the species of Euphorbia sect. Tithymalopsis*

- 1a. Main stems simple or branched only at base; leaves expanded and profusely arranged; dichasium with several branches missing at terminus; inflorescence bracts with white tips at apex \_\_\_\_\_ 2
- 1b. Main stem usually branched at nodes, leaves scale-like and sparsely arranged; dichasium branched throughout; inflorescence bracts without white tips at apex \_\_\_\_\_ 5
- 2a. Leaves broad (length/width < 5.5); blade slightly revolute or entire; glands green \_\_\_\_\_ 3
- 2b. Leaves linear (length/width > 8); blade conspicuously revolute or involute; glands green or dark purple \_\_\_\_\_ 4
- 3a. Plants 70–122cm tall; aerial stems multiple, 2–5mm diam.; leaves ascending, leathery, sessile; primary bracts smaller than stem leaves; appendages oblong or spatulate, 2.5–4.4mm long \_\_\_\_\_ **1. *E. corollata***
- 3b. Plants 35–65cm tall; aerial stems single, 1–2.2mm diam.; leaves usually reflexed, thin, petiolate or subpetiolate; primary bracts similar to stem leaves in size; appendages orbicular or oval, 1–2.2mm long \_\_\_\_\_ **8. *E. pubentissima***

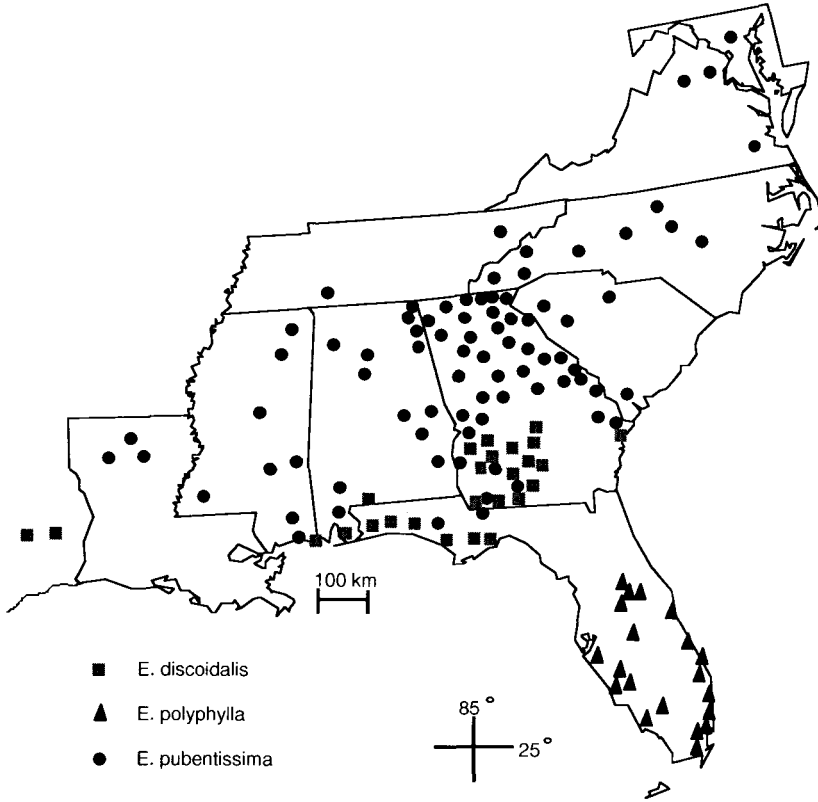


FIG. 5. Distribution of collections of *E. discoidalis*, *E. polyphylla* and *E. pubentissima*.

4a. Main stem not branching at base, erect or ascending, usually densely pubescent, dark grey or green; leaves not succulent, revolute, petiolate; stipules obsolete; glands green or rarely purple; appendages entire — **3. *E. discoidalis***

4b. Main stem branching at base, ascending or spreading, glabrous, green or greenish purple; leaves succulent, involute, sessile or short petiole; stipules present and glandular; glands purple; appendages deeply crenate \_\_\_\_\_  
**7. *E. polyphylla***

5a. Stem green; leaves green, membranous, 3.7–8.0cm long, 1.9–4.5cm wide, margin ciliate; glands green, deeply folded; appendages crenate, white; stigma green; seeds clearly pitted \_\_\_\_\_ **6. *E. mercurialina***

5b. Stem dark purple or greenish purple; leaves greenish purple, 1–5cm long, 0.2–1.0cm wide, margins purple, entire or ciliate; glands purple or green, not folded; appendages entire, purple or white; stigma purple or pink; seeds shallowly pitted or smooth \_\_\_\_\_ **6**

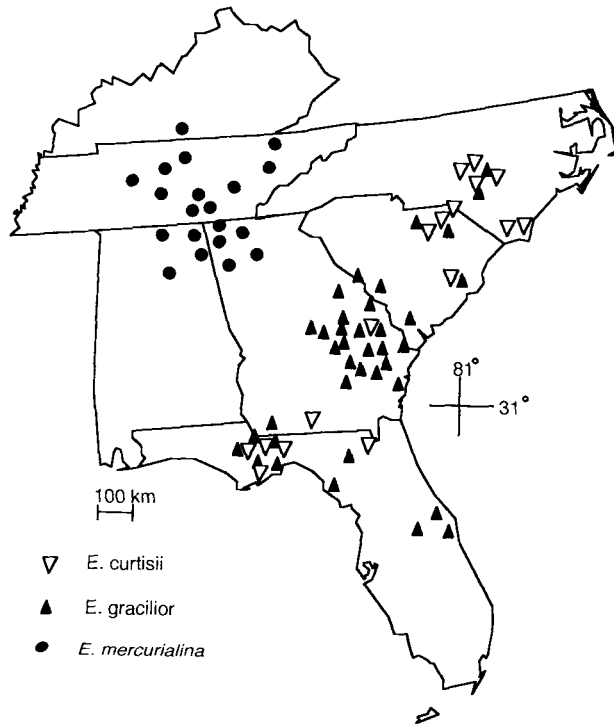


FIG. 6. Distribution of collections of *E. curtisii*, *E. gracilior* and *E. mercurialina*.

6a. Cyathia unisexual; leaves elliptic, pubescent on upper surface, margins ciliate; involucre green; capsule erect; glands green, appendages semicircular, white or pink; stigma pink; seeds smooth \_\_\_\_\_ 2. *E. curtisii*

6b. Cyathia bisexual; leaves polymorphic, glabrous, margins glabrous; involucre purple or green; capsule recurved; glands dark purple; appendages rudimentary or semicircular, purple or white; stigma purple; seeds pitted \_\_\_\_ 7

7a. Involucre purple; appendages rudimentary, purple \_\_\_\_\_ 4. *E. gracilior*

7b. Involucre green; appendages semicircular, white \_\_\_\_\_ 5. *E. exserta*

**1. *Euphorbia corollata* L.**, Sp. Pl. 459 (1753). *Galarhoeus corollatus* (L.) Haworth, Syn. Pl. Succ. 146–147 (1812). *Agaloma corollata* Raf., Autik. Bot. 95 (1840). *Tithymalopsis corollata* (L.) Kl. & Garcke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 249 (1859). *Tithymalopsis corollata* (L.) Small, Fl. SE U.S. 717–718 (1903). Type: USA, North Carolina, without date, *Kalm* (holo. 630.56 LINN, photocopy; iso. fragment F).

Syn.: *Euphorbia corollata* var. *hirsuta* Macnab in Edinburgh New Philos. J. 19: 63 (1835). Type: Canada, Ontario, banks of the St Clair River, viii 1824, *Macnab* s.n. (holo. PH).

*Euphorbia corollata* var. *grandiflora* Boiss. in A. DC., Prodr. 15: 67 (1862).  
Type: Pennsylvania, collector unknown.

*Euphorbia olivacea* Small in Bull. Torrey Bot. Club 25: 613 (1898).  
*Tithymalopsis olivacea* (Small) Small, Fl. SE U.S. 717 (1903). *Agaloma olivacea*  
(Small) Nieuwland in Amer. Midl. Nat. 2: 300 (1912). Type: USA, Mississippi,  
Biloxi, 15 vii 1894, Tracy 2883 (lecto. designated here, NY; iso. F).

*Euphorbia corollata* var. *joorii* Norton in Ann. Rep. Missouri Bot. Gard. 9:  
155 (1898). *Tithymalopsis joorii* (Norton) Small, Fl. SE U.S. 717 (1903). *Agaloma*  
*joorii* (Norton) Nieuwland in Amer. Midl. Nat. 2: 300 (1912). Type: USA, Texas,  
Milano, Joor s.n. (holo. MO, iso. fragment F).

*Euphorbia corollata* var. *viridiflora* Farwell in Amer. Midl. Nat. 8: 273 (1923).  
Type: USA, Michigan, Oxford, Farwell 6675 (lecto., designated by McVaugh et al.  
(1975), BLH; isolecto. MICH).

Perennial herb, erect, bright green, glabrous or slightly pubescent, 70–122cm tall; main stems a few, simple or sometimes branched near the top of the main stem, 45–104cm tall, 2–5mm diam.; nodes 25–115, internodes 0.3–2.0cm long. *Roots* cylindrical, c.1cm diam., root buds on the surface. *Leaves* alternate, sessile or rarely short-petiolate, ascending, imbricating at early stage of growth, size gradually reduced towards the top of main stems, glabrous or pubescent on the adaxial surface; blades oblong to oblanceolate, 2.1–6.5cm long, 0.4–1.8cm wide, leathery; margins entire, slightly revolute, green; leaf apex rounded or retuse; leaf base cuneate; stipules obsolete. *Main stem* terminated by a cyathium, a 2–6-rayed umbel, and subtended bracts. *Floral rays* branching 3–8 times as a dichasium, or sometimes trichasial at the first node; dichasial branches absent 2–3 times at terminal nodes; each dichasial node sustained by highly reduced, opposite bracts; primary bracts 2 or 3 (in case of trichasium), ascending, 3.8–9.5mm long, 1.3–3.0mm wide; terminal bracts 1.7–3.7mm long, 0.75–2.0mm wide; white tips present at the apices of bracts. *Cyathia* solitary at nodes; peduncles 2.5–5.8mm long, 0.5–1.1mm wide; involucre campanulate, green, glabrous or sparsely hairy at upper surface, 1.2–2.0mm high, 1.5–2.8mm wide. *Glands* five, green, transversely oblong, slightly depressed at the centre, 0.85–1.24mm long, 0.25–0.72mm wide, subtended by petaloid appendages; appendages white, flat or reflexed, entire or slightly erose margined, oblong, spatulate or rectangular, 2.5–4.4mm long, 1.8–3.4mm wide. *Staminate flowers* and bracteoles numerous; anthers yellow or green, 0.30–0.56mm long, 0.25–0.48mm wide; filaments 0.45–0.96mm long, 0.18–0.36mm thick. *Pistillate flowers* central, surrounded by five groups of staminate flowers; pedicel 3.5–9.2mm long, 0.83–2.0mm wide, exerted beyond the involucre; capsule globose, green, three lobed, glabrous, 2.0–3.2mm long, 4.7–5.7mm diam.; styles three, united at base, 0.8–1.4mm long; stigma pale green, bifid. *Seeds* globose, white-green or brown, ecarunculate, 2.6–3.2mm long, 1.9–2.5mm diam., shallowly pitted; hilum depressed; apex acute, with a nipple-like structure at the opposite end.

*Phenology.* Flowering and fruiting from June to September.

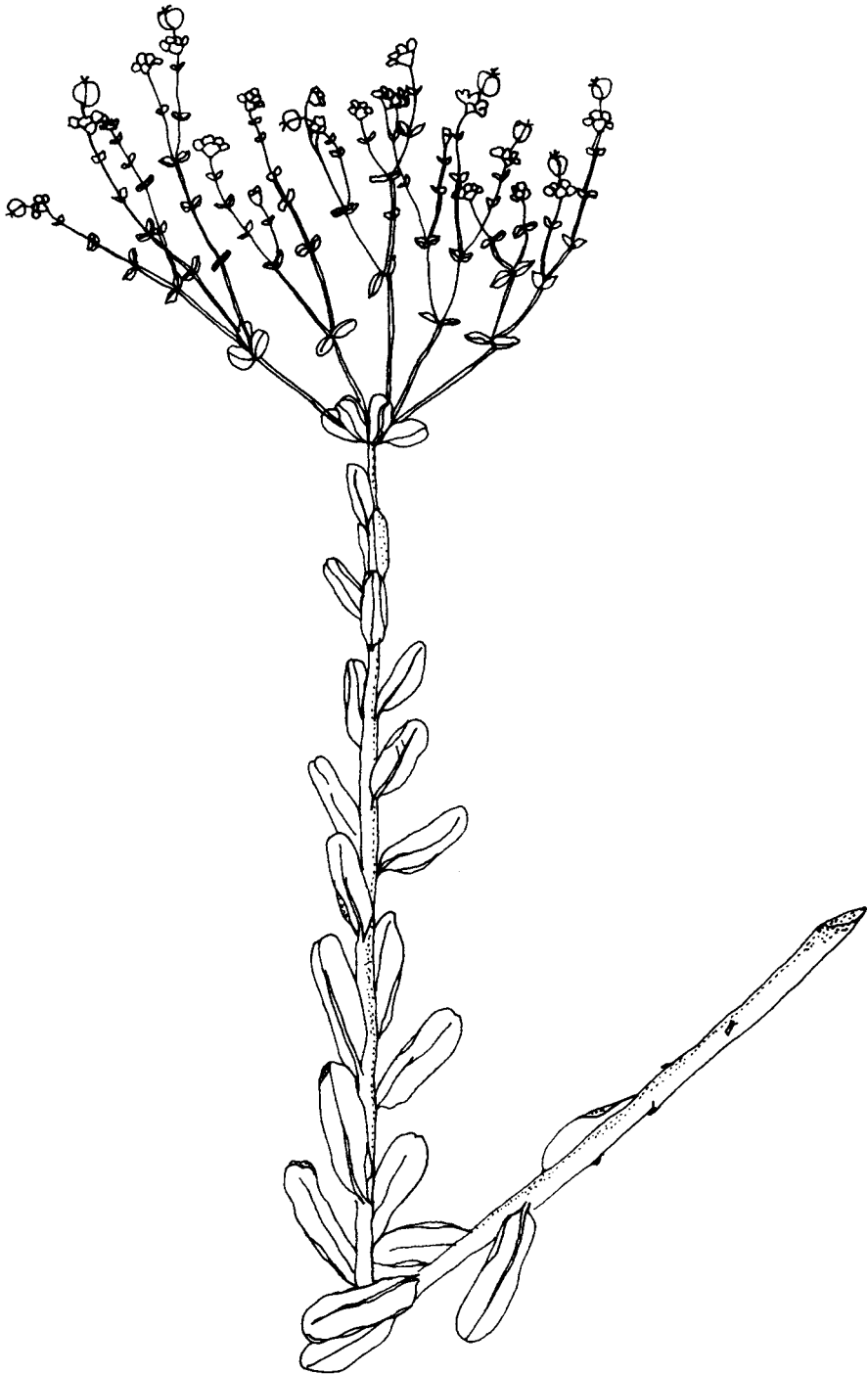


FIG. 7. *Euphorbia corollata*: habit,  $\times 0.4$ .

*Euphorbia corollata* is the most robust and widely distributed species in sect. *Tithymalopsis*. Geographically it overlaps with *E. pubentissima* along the Appalachian Plateau. This species is the most closely related to *E. pubentissima*, which has usually been included in *E. corollata* in south-eastern USA floras. However, *E. corollata* is well distinguished from *E. pubentissima* by the lack of overlap in several characters: plant height, leaves ascending and leathery, number of nodes, primary bracts smaller than stem leaves, length of appendages, and length of seeds. *Euphorbia corollata* has no seasonal dimorphism. During the early stage of growth this species has highly imbricated leaves while *E. pubentissima* has loosely arranged leaves. Also, in the case of *E. corollata*, several shoots arise together from a root, but there are only one or two stems in *E. pubentissima*.

Leaf shape and size, pubescence and number of nodes are variable within a population in *E. corollata*. The type specimens of *E. corollata* var. *hirsuta* Macnab and var. *viridiflora* Farwell seem to be individuals possessing pubescent stems and leaves. The collections from mesic habitats in Tennessee and Mississippi have more loosely arranged and longer leaves than those from open sunny habitats in Kansas and Oklahoma. Several individuals from south-eastern Texas possess linear leaves and thin stems, and approach *E. discoidalis*, although are distinguishable from *E. discoidalis* in possessing glabrous stems and petioles, entire margin of the leaves and larger appendages. However, it is hard to say whether this morphological convergence originated from environmental influences or from hybridization between *E. corollata* and *E. discoidalis*.

The type specimens of *E. corollata* var. *joorii* Norton represent individuals having highly branched main stems. This pattern of stem branching is common when the main stems are removed or from individuals collected late in the growing season. Although the type of *E. corollata* var. *grandiflora* Boiss. was not examined, it is best placed in here on the basis of the original description (Boissier, 1862), and illustration (Millspaugh, 1898). Boissier described *E. corollata* var. *grandiflora* from Pennsylvania, within the distributional range of *E. corollata*, and the sessile, lanceolate, glabrous and green leaves of var. *grandiflora* are typical characters of *E. corollata*.

**2. *Euphorbia curtisii*** Engelm. ex Chapm., Fl. Southern U.S. 401 (1860). *Tithymalopsis curtisii* (Engelm.) Small, Fl. SE U.S. 716 (1903). *Agaloma curtisii* (Engelm.) Nieuwland in Amer. Midl. Nat. 2: 300 (1912). Type: USA, North Carolina, no date, *Curtis* s.n. (holo. MO).

Syn.: *Euphorbia curtisii* var. *longipes* Boiss. in A. DC., Prodr. 15: 67 (1862). Type: USA, South Carolina, no date, *Michaux* s.n. (holo. P, n.v.; iso. fragment G; iso. P, n.v.).

*Euphorbia eriogonoides* Small in Bull. Torrey Bot. Club 25: 614 (1898). *Tithymalopsis eriogonoides* (Small) Small, Fl. SE U.S. 716 (1903). *Agaloma eriogon-*



*oides* (Small) Nieuwland in Amer. Midl. Nat. 2: 299 (1912). Type: USA, Georgia, Darien Junction, 25–27 vi 1895, *Small* s.n. (holo. NY, iso. F).

Perennial herb, erect or ascending, green or purple on the base of stem, glabrous, 23.5–41cm height; main stems 1–5, usually branched at every node, 20–34cm long, 0.11–0.16cm thick, nodes 3–11, internodes 1.30–5.50cm long. *Roots* cylindrical, 0.15–0.40cm diam., root buds on the surface. *Leaves* alternate, petiolate, 1.0–4.2mm long, 0.16–0.75mm thick, reflexed, glabrous or rarely pubescent above, pubescent on the adaxial surface; lower leaves reduced, reddish, scale-like; blades lanceolate or elliptic, 2.5–5.1cm long, 0.2–1.0cm wide; margins entire or ciliate, purple, leaf apex rounded; leaf base cuneate; stipules glandular. *Main stem* terminated by a cyathium, a 3–5-rayed umbel, and subtended bracts. *Floral rays* branching two or three times as a dichasium; dichasial branches fully formed at terminal nodes; each dichasial node with subtended, reflexed, opposite bracts; primary bracts 1.2–4.0cm long, 0.15–0.40cm wide; terminal bracts 0.4–1.4cm long, 0.2–3.2mm wide, lacking white tips at the apex. *Cyathia* unisexual, solitary at each node; peduncles slender, 0.8–2.0cm long, 0.16–0.33mm thick; involucre campanulate, green, glabrous or sparsely hairy at upper surface, 0.88–1.7mm high, 0.95–2.08mm diam. *Glands* present at the top of an involucre, five, green, transversely oblong, flat or slightly depressed at the centre, 0.8–1.0mm long, 0.3–0.5mm wide; subtended by petaloid appendages; appendages white or pink, ascending, reflexed, entire margined, semicircular, 0.52–0.92mm long, 1–1.6mm wide. *Staminate flowers* and bracteoles numerous; anthers red, 0.26–0.40mm long, 0.20–0.44mm wide; filaments 0.36–0.64mm long, 0.12–0.24mm thick. *Pistillate flowers* central, surrounded by five groups of staminate flowers; pedicels 1.3–2.1mm long, 1–1.7mm wide, barely exerted beyond the involucre; capsule erect, globose, green, three lobed, glabrous or slightly pubescent; 2.5–3.2mm high, 4.3–5.1mm diam.; styles three, united at base, 0.6–1.1mm long; stigmas pink, bifid. *Seeds* globose, grey or brown, ecarunculate, 2.3–2.7mm long, 1.7–2.1mm diam., smooth; hilum depressed; apex acute, with a nipple-like structure at the opposite end.

*Phenology.* Flowering and fruiting from March to July.

This species is easily recognized among species in sect. *Tithymalopsis* by the unisexual cyathium, and short, erect pedicels of the pistillate flowers. *Euphorbia curtisii* is sympatric with *E. gracilior* in some areas of the Atlantic and Gulf Coastal Plains, and they are closely related species. They share stems with dark purple bases, leaves with purple margins, and long peduncles. However, *E. curtisii* differs from *E. gracilior* by having fully formed involucreal appendages and reflexed leaves with ciliate margins. *Euphorbia curtisii* is sometimes confused with *E. discoidalis* in the Florida Panhandle where the two species overlap. However, *E. curtisii* can be distinguished from *E. discoidalis* by the presence of unisexual cyathia. Occasionally, *E. discoidalis* in this region is found with more hemispherical cyathia and loosely arranged leaves compared with specimens from outside the region. These unusual populations may

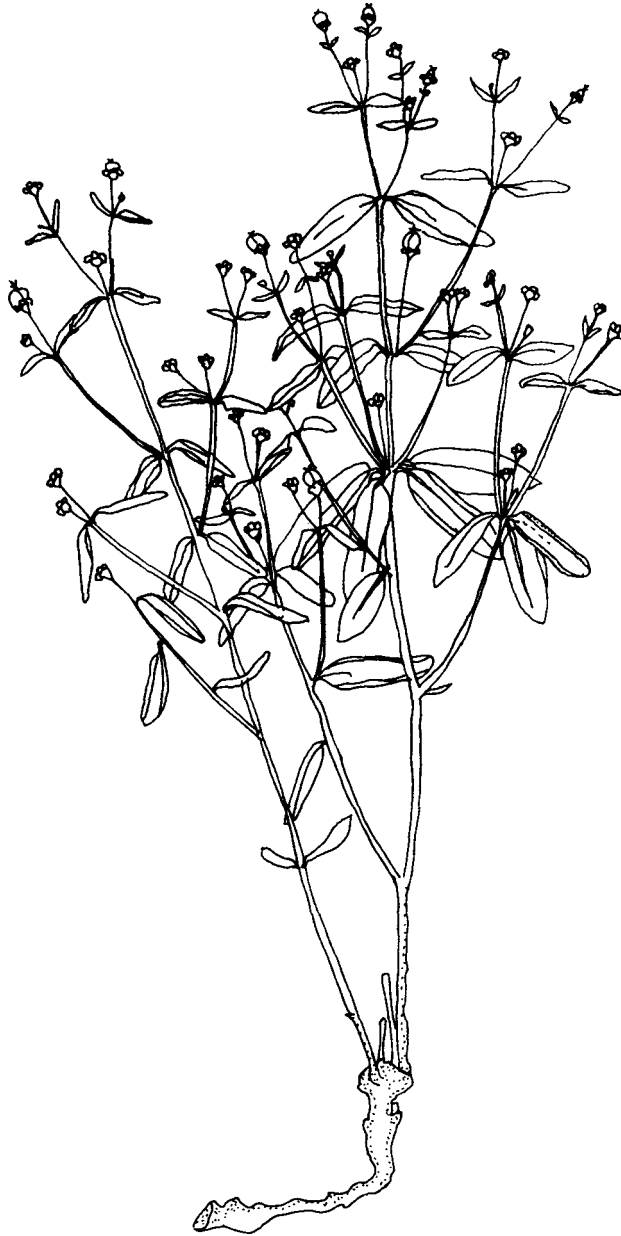


FIG. 8. *Euphorbia curtisii*: habit,  $\times 0.4$ .

have originated from hybridization with *E. curtisii*, because they were usually found in disturbed areas on clay soils.

*Euphorbia curtisii* is restricted to natural sandy habitats, recently burned areas, and open, sunny areas in oak or pine forests. Individuals of each sex grow intermixed;

however, the ratios of male and female plants among populations are significantly different (Park, unpublished data).

The type of *E. eriogonoides* Small was collected in the sands in eastern Georgia, and has highly branched inflorescence rays. This is a typical specimen collected late in the season. Besides, it has reflexed leaves, white or pink petaloid appendages and small cyathia that are all characteristic of *E. curtisii*.

**3. *Euphorbia discoidalis*** Chapm., Fl. Southern U.S. 401 (1860). *Tithymalopsis discoidalis* (Chapm.) Small, Fl. SE U.S. 717 (1903). *Agaloma discoidalis* (Chapm.) Nieuwland in Amer. Midl. Nat. 2: 300 (1912). Type: USA, Florida, dry sandy pine barrens near the coast, West Florida, no date, Chapman s.n. (holo. NY). Syn.: *Euphorbia corollata* var. *angustifolia* Elliott, Sketch Bot. S. Carolina 2: 659 (1824). *Agaloma corollata* var. *angustifolia* Raf., Autik. Bot. 95 (1840). *Tithymalopsis angustifolia* Kl. & Garcke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 249 (1859). Type: USA, South Carolina, St Thomas, near Charleston, no date, Caradeux (holo., location unknown).

Perennial herb, erect or ascending, dark grey or green, densely pubescent or rarely glabrous, 45–71cm high; main stems arising one or two, unbranched, 17–49cm tall, 1–2mm diam.; nodes 14–54, internode 0.3–2.2cm long. *Roots* cylindrical, 2–6mm diam. *Leaves* alternate, petiolate, green or red, 0.5–2.5mm long, 0.2–1.0mm thick, densely hairy on the petioles, ascending or rarely reflex, loosely arranged at early stage of growth, glabrous above, hairy on the veins; blades linear, 1.9–7.2cm long, 0.1–0.5cm wide, green adaxially, white abaxially, entire, conspicuously revolute; apex rounded; base cuneate; stipule obsolete. *Main stem* terminated by a cyathium, a usually 3 (2–5)-rayed umbel, and subtended bracts. *Floral rays* branching 3–8 times as a compound dichasium; dichasial branches absent several times at terminal nodes; primary internode very long; each dichasial node sustained by opposite bracts; bracts opposite, smaller than vegetative leaves; primary bracts 0.3–3.0cm long, 0.6–2.0mm wide; terminal bracts 1.1–2.0mm long, 0.2–0.8mm wide; white tips present at the apices of bracts. *Cyathia* bisexual, solitary at nodes; peduncles green, glabrous, 1.6–5.9mm long, 0.25–0.6mm wide; involucre campanulate or hemispherical, green, pubescent at upper surface, 0.9–1.5mm high, 1.25–1.9mm diam. *Glands* five, green or red, transversely oblong, slightly depressed at the centre, 0.5–1.1mm long, 0.2–0.52mm wide, sustained by petaloid appendages; appendages five, white, entire or slightly erose margined, semicircular or orbicular, 1.4–2.4mm long, 1.2–2.0mm wide. *Staminate flowers* and bracteoles numerous; anthers yellow or red, 0.2–0.4mm long, 0.2–0.4mm wide; filaments 0.5–1.0mm long, 0.12–0.24mm thick; *pistillate flowers* central, surrounded by five groups of staminate flowers; pedicels 3.3–5.0mm long, 0.6–1.4mm thick; exerted beyond the involucre; capsules globose, green, three lobed, glabrous or slightly pubescent, 1.8–3.0mm high, 2.5–4.8mm diam.; styles three, united at base, 0.6–1.1mm long; stigmas pink or pale green, bifid. *Seeds* globose, white or brown, ecarunculate,

2.2–2.5mm long, 1.6–2.0mm diam., slightly pitted or smooth; hilum depressed; apex acute, with a nipple-like structure at the opposite end.

*Phenology.* Flowering and fruiting from May to September.

This species is recognized by the unique combination of revolute, linear leaves, a 3-rayed umbel, densely pubescent stems, and long primary internodes in dichasial branches. A few individuals collected in the Florida Panhandle have glabrous stems.

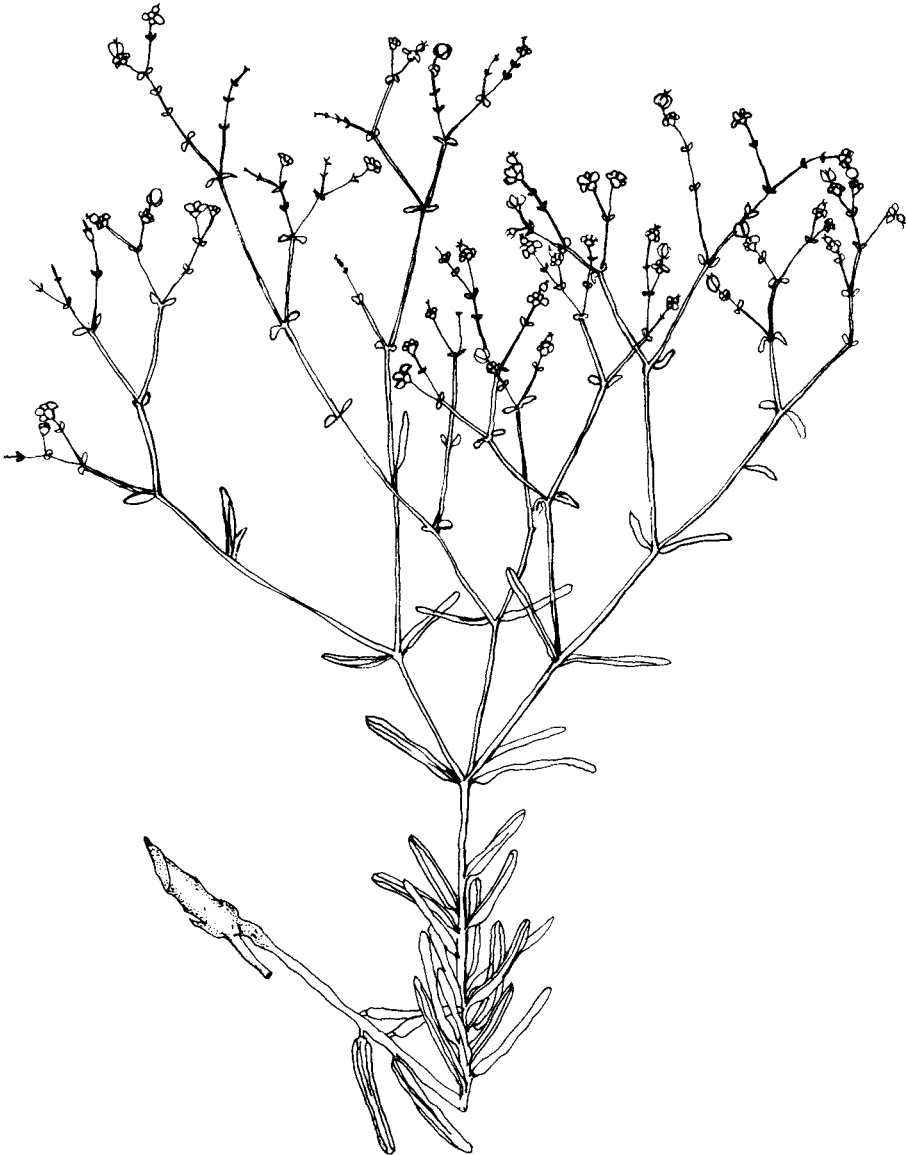


FIG. 9. *Euphorbia discoidalis*: habit,  $\times 0.5$ .

Although Chapman (loc. cit.) and Small (1903) described this species as having deep red glands, specimens collected from Georgia have green glands, whereas individuals from Mississippi and Florida have red, green or a mixture of red and green glands. *Euphorbia discoidalis* is also polymorphic in seed and pollen sculpturing patterns. The polymorphism of gland colour, pollen and seed-surface patterns suggests a hybrid origin of this species between *E. polyphylla* and *E. pubentissima*. *Euphorbia discoidalis* has intermediate characters between these two species in number of nodes and size of leaves. The hybrid origin of this species is also suggested by the intermediate geographical position between *E. polyphylla* and *E. pubentissima*. *Euphorbia discoidalis* shares several characters with *E. polyphylla*: linear leaves, a 3-rayed umbel, bracts smaller than vegetative leaves, and red glands. *Euphorbia discoidalis* is also similar to *E. pubentissima* in the petiolate leaves, pubescent petioles, reflexed leaves, and size and shape of the involucre. However, *E. discoidalis* is distinguished from *E. pubentissima* by having a small number of cyathia in terminal clusters, and linear leaves with revolute margins. *Euphorbia discoidalis* is sometimes confused with *E. curtisii* in the Florida Panhandle where the two species overlap. However, *E. curtisii* can be distinguished from *E. discoidalis* by the presence of unisexual cyathia. Occasionally, *E. discoidalis* in this region is found with more hemispherical cyathia and loosely arranged leaves compared with specimens from outside the region. These unusual populations may have originated from hybridization with *E. curtisii*, because they were usually found in disturbed areas on clay soils.

*Euphorbia corollata* var. *angustifolia* was described by Elliott (loc. cit.) based on linear leaves, a 3-rayed umbel, long primary nodes, and small scattered inflorescences. These characters are well within the range of variation of *E. discoidalis*.

**4. *Euphorbia gracilior*** Cronquist in *Castanea* 14: 102 (1949). Type: USA, Georgia, Tattnall Co., 3 mi NW of Reidsville, 16 vi 1948, *Cronquist* 5334 (holo. US; iso. GA, GH, MO, MICH, NY, PH, SMU n.v.).

Syn.: *Euphorbia gracilis* Elliott, *Sketch Bot. S. Carolina* 2: 657 (1824) (non *E. gracilis* Besser, *Cat. Hort. Cremenecei* 56 (1816)). *Tithymalopsis gracilis* (Elliott) Small, *Fl. SE U.S.* 716 (1903). *Agaloma gracilis* (Elliott) Nieuwland in *Amer. Midl. Nat.* 2: 299 (1912). Type: USA, Georgia, Ogeechee Ferry (type: unknown).

Perennial herb, erect or ascending, dark purple on the base, green on upper part, whole plants dark purple at the early stages of growth, glabrous, 21–33cm tall; main stems arising 1–6, sometimes tufted, branched or not, 8.3–24cm long, 0.7–1.3mm diam., nodes 0–5, internodes 2.2–8.5cm long; underground stems white. *Roots* cylindrical, 1.5–5.0mm diameter. *Leaves* alternate, sessile or subpetiolate, green or purple, glabrous, 0.3–2.5mm long; ascending; lower leaves reduced, scale-like, light purple; blades highly polymorphic in shape, linear, elliptic, oblanceolate, usually orbicular in young plants, 1.0–4.1cm long, 0.3–1.0cm wide, entire, green, purple margined; apex rounded, retuse or acute; base cuneate; stipules glandular, triangular, purple.

*Main stems* terminated by a cyathium, a 2 or 3-rayed umbel, and subtended bracts. *Floral rays* branching 2–4 times as a compound dichasium; dichasial branches present at terminus; each dichasial node subtended by opposite bracts; umbellate bracts smaller than upper bracts; bracts linear or elliptic; primary bracts 1.0–2.9cm long, 0.1–0.4cm wide; terminal bracts 0.5–2.3cm long, 0.1–0.3cm wide; white tips absent at the apices of bracts. *Cyathia* bisexual, solitary at node; peduncle purple, glabrous, slender, 0.1–1.8cm long, 0.2–0.7mm thick; involucre campanulate, dark purple, glabrous, 1.0–1.9mm high, 1.5–2.5mm diameter. *Glands* present at the top of an involucre, five, dark purple, transversely oblong, slightly depressed at the centre, 1.1–2.0mm long, 0.4–0.9mm wide, sustained by petaloid appendages; appendages dark purple, ascending, entire, narrow rim under the microscope, 0.06–0.2mm long, 1.3–2.1mm wide. *Staminate flowers* numerous, purple; anthers 0.26–0.44mm long, 0.18–0.44mm wide; filaments 0.48–0.80mm long, 0.06–0.08mm thick. *Pistillate flowers* central, surrounded by five groups of staminate flowers, purple; pedicels 3.2–8.3mm long, 0.5–1.5mm thick, exerted beyond the involucre, recurved; capsules three lobed, glabrous, purple or dark green at maturity, 1.8–2.5mm high, 3.6–4.4 diam.; styles three, united at base, 0.44–0.80mm long; stigmas thick, purple, bifid. *Seeds* globose, white, ecarunculate, 1.8–2.4mm long, 0.15–0.17mm diam., shallowly pitted; hilum depressed; apex acute.

*Phenology.* Flowering and fruiting from May to April.

This species is recognized by the following: the dark purple involucre, glands and capsules; leaf dimorphism; few nodes on the main stems; and glands with inconspicuous purple rim-like appendages. It is restricted to open, natural sandy habitats, burned areas, and sandy pinelands. Leaf shape and the number of main stems and inflorescences are highly variable depending on the age of the plants. Younger individuals have wide or rounded leaves, usually a single stem, fewer flowers, and no terminal umbel and bracts, whereas older plants have scale-like stem leaves, many stems, longer and linear bracts, and well-developed 3-rayed umbels with many flowers.

Cronquist (1949) proposed *E. gracilior* as a new species (not as a *nomen novum*), because *E. gracilis* Elliott was a later homonym of *E. gracilis* Besser, and the type specimen of Elliott's species could not be located. However, Huft (1979) treated *E. gracilis* Elliott and *E. gracilior* Cronquist as synonyms of *E. exserta* (Small) Coker. *Euphorbia exserta* appeared in Small's *Manual of the Southeastern Flora* as *Tithymalopsis exserta* along with *T. gracilis*. Small (1903) described *E. exserta* as a different species from *E. gracilis*, because of differences in involucre colour and appendages. The type of *E. exserta* is distinct from the types of *E. gracilior* in the green colour of the glands and involucre, white, conspicuous petaloid appendages, and larger leaves (see below).

**5. *Euphorbia exserta*** (Small) Coker, Pl. Life Hartsville 88 (1912). *Tithymalopsis exserta* Small, Fl. SE U.S. 717 (1903). *Agaloma exserta* (Small) Nieuwland in Amer.

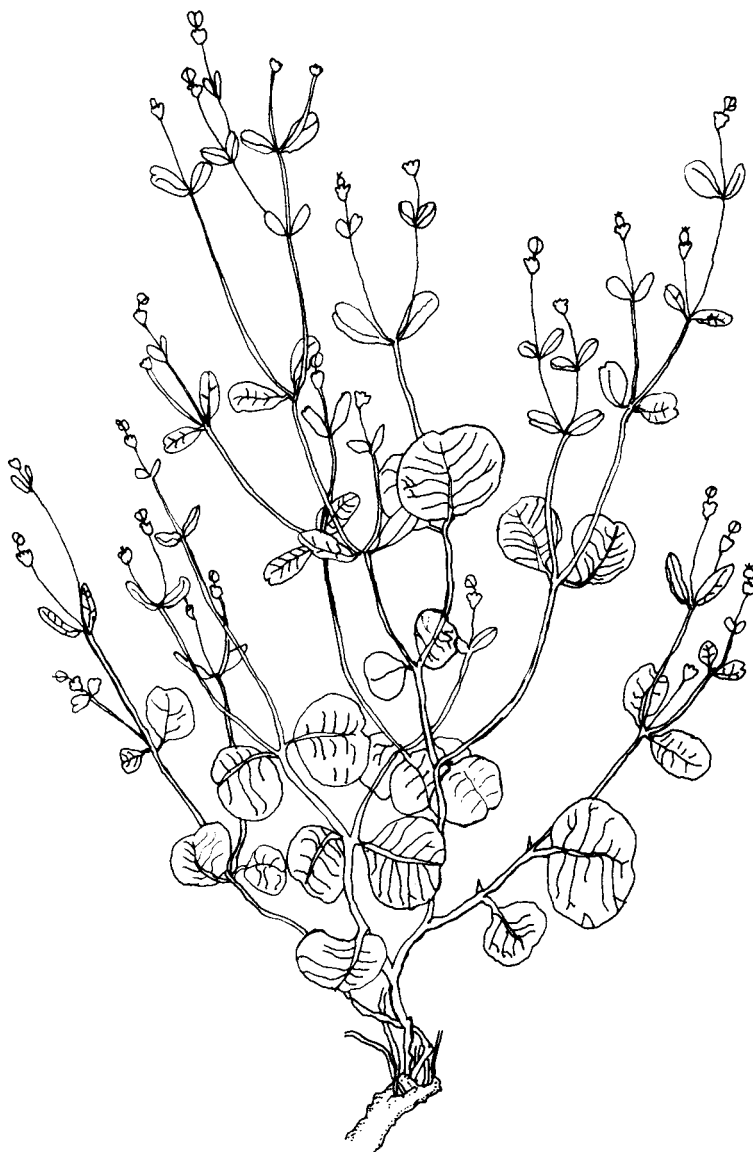


FIG. 10. *Euphorbia gracilior*: habit,  $\times 0.4$ .

Midl. Nat. 2: 300 (1912). Type: USA, Florida, no date, *Chapman* s.n. (holo. NY).

This species is distinguished from *E. gracilior* by its white, conspicuous appendages, green glands and involucre, and lack of scale-like leaves. However, it is similar in overall appearance to *E. gracilior* except for the above characters. It has not been recollected, and seems to be an extinct species or a hybrid between *E. gracilior* and either *E. pubentissima* or *E. curtisii*.

**6. *Euphorbia mercurialina*** Michx., Fl. Bor.-Amer. 2: 212 (1803). *Tithymalopsis mercurialina* (Michx.) Small, Fl. SE U.S. 716 (1903). *Agaloma mercurialina* (Michx.) Nieuwland in Amer. Midl. Nat. 2: 299 (1912). Type: USA, Tennessee, Knoxville, no date, *Michaux* s.n. (holo. P, n.v.).

Syn.: *Agaloma ciliata* Raf., Autik. Bot. 94 (1840). Type: not designated, no original material located.

Perennial herb, erect, green or red on the base, glabrous, 22.5–33.0cm high; main stems one or a few, simple or branched 1–2 times, 12–26cm high, 1–2mm diam.; nodes 0–4, internodes 2.3–12cm. *Roots* cylindrical, slender, 3–7mm diameter. *Leaves* alternate, petiolate; petioles green or dark green, 1.7–5.8mm long, 0.42–1.33mm thick, pubescent; lower leaves reduced, scale-like, pale purple; blades elliptic, oval, oblong-ovate, 3.7–8.0cm long, 1.9–4.5cm wide, membranous, green at top, white-green below, glabrous; margins ciliate; apex rounded or acute; base cuneate or rounded; stipules glanduliform. *Main stems* terminated by a cyathium, a 2–3-rayed umbel, and subtended bracts. *Floral rays* branching 1–4 times as a compound dichasium; dichasial branches present at terminus; each dichasial node subtended by opposite bracts, bracts usually larger than vegetative leaves; primary bracts 2.8–7.0cm long, 1.0–3.5cm wide; terminal bracts 1.3–5.4cm long, 0.3–2.5cm wide; white tips absent at the apices of bracts. *Cyathia* bisexual, solitary at nodes; peduncles green, glabrous, slender, 0.9–2.2cm long, 0.3–0.6mm thick; involucre hemispherical, campanulate, green, glabrous, 1.3–2.2mm high, 1.6–3.3mm diameter. *Glands* present at the top of an involucre, five, green, transversely oblong, deeply folded, 1.2–5.4mm long, 0.4–1.2mm wide, subtended by petaloid appendages; appendages white, ascending, reflexed, undulate or entire margined, narrow, 0.3–0.9mm long, 1.3–2.4mm wide. *Staminate flowers* numerous, yellow; anthers 0.3–0.5mm long, 0.2–0.4mm wide; filaments 0.5–0.8mm long, c.0.2mm thick. *Pistillate flowers* central surrounded by five groups of staminate flowers, green, glabrous; pedicels 0.57–1.53cm long, 0.7–1.3mm thick, exerted beyond the involucre, recurved; capsules three lobed, glabrous, green, 2.3–3.3mm high, 4.4–5.0mm diam.; styles three, united at base, 0.72–1.48mm long; stigmas thick, pale green, bifid. *Seeds* globose, dark brown, ecarunculate, 2.5–2.8mm long, 1.9–2.2mm diam., regularly pitted; hilum depressed; apex acute, with a nipple-like structure at the opposite end.

*Phenology.* Flowering and fruiting from April to May.

*Euphorbia mercurialina* is characterized by its large (3.7–8.0cm long, 1.9–4.5cm wide), membranous leaves with ciliate margins, glands deeply folded, appendages ascending and crenate, and seeds clearly pitted. It has a limited distribution and is less variable than any other species in sect. *Tithymalopsis*. This species is apparently most closely related to *E. gracilior* and *E. curtisii* in their scale-like, sparsely arranged leaves, no missing dichasial branches, and bracts with green tips. *Euphorbia mercurialina* has been confused with some populations of *E. pubentissima* from the northern borders of Alabama and Georgia under the name *E. corollata* var. *glauca*



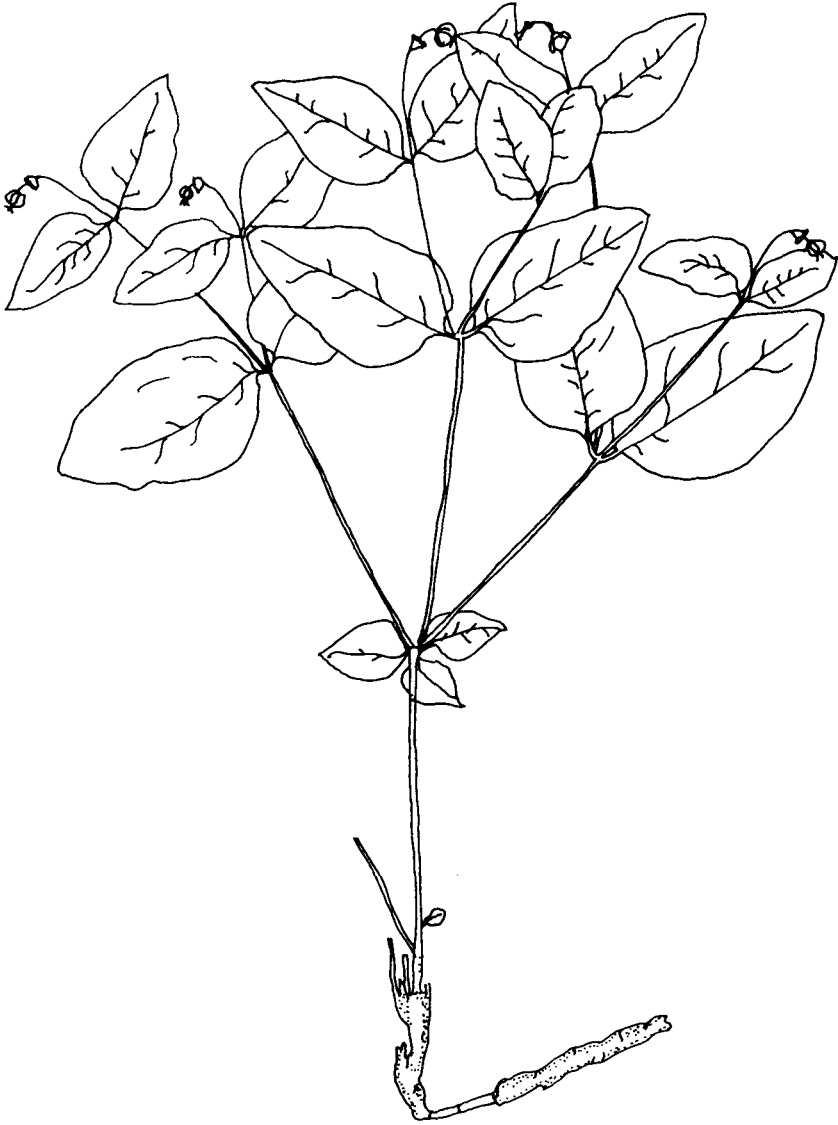


FIG. 11. *Euphorbia mercurialina*: habit,  $\times 0.5$ .

Millsp., which also have scale-like leaves and large bracts. However, *E. mercurialina* can be distinguished from 'var. *glauca*' by its ciliate leaves, deeply folded glands, and small, crenate appendages. *Euphorbia mercurialina* is the only species in sect. *Tithymalopsis* adapted to wet habitats.

Although no original material of *Agaloma ciliata* Raf. can be located, Rafinesque's protologue description (ovate or elliptic leaves with ciliate margins, small, white petaloid appendages, and a 2-4 dichasial umbel) is clearly enough to place it as

*E. mercurialina*. Also, its stated distribution of 'Alabama to Kentucky' is within the geographical range of *E. mercurialina*.

**7. *Euphorbia polyphylla*** Engelm. ex Holz. in Contr. U.S. Nat. Herb. 1: 215, 216 (1892). *Tithymalopsis polyphylla* (Engelm.) Small, Fl. SE U.S. 716 (1903). *Agaloma polyphylla* (Engelm.) Nieuwland in Amer. Midl. Nat. 2: 299 (1912). Type: USA, Florida, Indian River, 1879, *Curtiss* 2498 (holo. US; iso. GA, NY, F, PENN n.v., PH, SMU n.v.).

Syn.: *Euphorbia polyphylla* Engelm. ex Chapm., Fl. Southern U.S., ed. 2, suppl. 2: 694 (1892). Type: USA, Florida, Indian River, 1879, *Curtiss* 2498 (lecto. designated here, NY; iso. GA, F, PENN n.v., PH, SMU n.v., US).

Perennial herb, ascending or spreading, green, reddish, green-purple, purple at the base, glabrous, 14–36cm high; main stems branching only at the base or tufted at the top of the underground stem, 11.5–27.0cm high, 0.8–1.3mm diam.; nodes 22–61, internodes 1.5–7.0mm long. *Roots* cylindrical, slender, 2.5–7.5mm diameter. *Leaves* alternate, sessile or subpetiolate, petioles glabrous, green or purple, 0.2–0.4mm long, imbricate, ascending, glabrous; blades succulent, linear or linear-spathulate, basal ones usually broader, lanceolate, 0.53–1.83cm long, 0.5–2.0mm wide, green; margins entire, involute; apex rounded; base cuneate; stipules minute, glandular. *Main stems* terminated by a cyathium, a 3-rayed umbel, and subtended bracts. *Floral rays* branching 2–6 times as a compound dichasium; dichasial branches absent 3–4 times at terminus; each dichasial node subtended by opposite bracts; primary bracts broader, smaller than vegetative leaves, 2.2–5.7mm long, 0.3–1.2mm wide; terminal bracts 1.3–3.9mm long, 0.57–0.91mm wide; white tips present at the apices of bracts. *Cyathia* bisexual, solitary at nodes; peduncle green, glabrous, 1.9–8.3mm long, 0.27–0.75mm thick; involucre campanulate, green or pale purple, glabrous or pubescent only at upper surface, inner surface densely pubescent with white, 0.8–1.5mm high, 1.2–1.9mm diameter. *Glands* present at the top of an involucre, five, dark purple, transversely elliptic, slightly depressed at the centre, 1.1–1.4mm long, 0.48–0.84mm wide, subtended by petaloid appendages; appendages white or pinkish, orbicular, ascending, deeply crenate margined, 0.6–1.2mm long, 1.7–2.3mm wide. Involucral lobe fimbriate, densely pubescent with white. *Staminate flowers* numerous; anther dark purple, 0.32–0.44mm long, 0.20–0.44mm wide; filaments 0.46–0.72mm long, 0.20–0.24mm thick. *Pistillate flowers* central, surrounded by five groups of staminate flowers, glabrous, green; pedicels 5.3–7.0mm long, 1.3–1.7mm thick, exserted beyond the involucre, recurved; capsules globose, three lobed, glabrous, green with purple lines, 2.3–2.8mm high, 4.3–5.1mm diam.; styles three, united at base, 0.6–1.0mm long; stigmas thick, pink, bifid. *Seeds* globose, white, ecarunculate, 2.4–3.0mm long, 1.8–2.2mm diam., smooth; hilum depressed; apex acute.

*Phenology*. Flowering and fruiting from May to November.

*Euphorbia polyphylla* is endemic to southern Florida, and is restricted to open sandy areas and sandy pinelands. It is distinguished by its semisucculent, ascending,



FIG. 12. *Euphorbia polyphylla*: habit,  $\times 0.8$ .

imbricate leaves with involute margins, purple glands with divided appendages, few basal stem branches, and ascending or spreading habit. It is closely related to *E. discoidalis*, sharing a 3-rayed umbel, linear, revolute leaves with short internodes, long primary internodes in dichasial branches, and simple main stems. The significant red pigmentation occurs in the forms of late in the growing season, while the young plants still have a green colour in their stems and leaves. Clonal reproduction also seems to be dominant in this species, because groups of individuals are connected by the same root system.

Engelmann (1887) listed the name *E. polyphylla* without a description. Later,

Holzinger (1892) and Chapman (?1892) published *E. polyphylla* as a new species using Engelmann's name. Because the correct date of Chapman's publication is uncertain, the author citation adopted here is *E. polyphylla* Engelmann ex Holzinger.

**8. *Euphorbia pubentissima*** Michx., Fl. Bor.-Amer. 2: 212 (1803). Type: USA, Carolina, no date, *Michaux* s.n. (holo. P).

Syn.: *Euphorbia paniculata* Elliott, Sketch Bot. S. Carolina 2: 660 (1824). *Euphorbia corollata* var. *paniculata* (Elliott) Boiss. in A. DC., Prodr. 15: 67 (1862). *Tithymalopsis paniculata* (Elliott) Small, Fl. SE U.S. 718 (1903). *Agaloma paniculata* (Elliott) Nieuwland in Amer. Midl. Nat. 2: 300 (1912). Type: South Carolina, Columbia, no date, *Herbemont* s.n. (holo. photo NY, iso. MO).

*Euphorbia corollata* var. *subpetiolata* Boiss. in A. DC., Prodr. 15: 67 (1862). Type: USA, South Carolina, no date, *Rügel* s.n. (lecto. designated here, G).

*Euphorbia pubentissima* var. *glabrata* Boiss. in A. DC., Prodr. 15: 67 (1862). Type: USA, North Carolina, Gosborough, v 1841, *Rügel* s.n. (holo. G).

*Euphorbia corollata* var. *glauca* Millsp. in Bot. Gaz. 26: 267–268 (1898). Type: USA, Alabama, 1880, *Vasey* s.n. (holo. F).

*Euphorbia corollata* var. *molle* Millsp. in Bot. Gaz. 26: 267 (1898). Type: USA, Alabama, Auburn, 1897, *Earle & Baker* 13 (holo. F).

*Euphorbia apocynifolia* Small in Bull. Torrey Bot. Club 25: 467–468 (1898). *Euphorbia corollata* var. *apocynifolia* (Small) Millsp. in Bot. Gaz. 26: 268 (1898). *Tithymalopsis apocynifolia* (Small) Small, Fl. SE U.S. 717 (1903). *Agaloma apocynifolia* (Small) Nieuwland in Amer. Midl. Nat. 2: 300 (1912). Type: USA, Florida, Gadsden Co., Quincy, 4 ix 1895, *Nash* 2567 (holo. NY; iso. F, GH, NY, OS, US).

*Euphorbia zinniiflora* Small in Bull. Torrey Bot. Club 25: 615 (1898). *Tithymalopsis zinniiflora* (Small) Small, Fl. SE U.S. 717 (1903). *Agaloma zinniiflora* (Small) Nieuwland in Amer. Midl. Nat. 2: 300 (1912). Type: USA, Georgia, Yellow River Valley, spring 1895, *Small* s.n. (holo. NY, fragment F).

Perennial herb, erect, green or reddish, sparsely pubescent or glabrous, 34–65cm tall; main stems arising one or rarely a few, simple or rarely branched near the top, 23–40cm high, 1.0–2.2mm diam.; nodes c.18(6–41), internodes 0.6–3.2cm long. *Roots* thick, cylindrical, 3–5mm diameter. *Leaves* alternate, loosely arranged at the early stage of growth, subpetiolate or petiolate; petioles 1–4.7mm long, 0.25–0.83mm thick, densely hairy or sometimes glabrous, green or red; usually reflexed; one or two scale-like leaves at base; blades elliptic, lanceolate, oblanceolate, obovate, c.3.8(1.6–6.1)cm long, 0.5–2.2cm wide, entire, white-green on abaxial surface, pubescent on veins and margins or rarely glabrous; apex rounded; base cuneate or rounded; stipule obsolete. *Main stems* terminated by a cyathium, a 2–5-rayed umbel, and subtended bracts. *Floral rays* branching 3–8 times as a compound dichasium; dichasial branches absent at terminus; each dichasial node subtended by opposite bracts; nodes condensing in late summer forms; bracts reflexed; primary bracts at the first node similar in size to stem leaves, 1.0–4.5cm long, 0.35–1.0cm wide; terminal

bracts 1.7–5.7mm long, 0.83–2.3mm wide; white tips present at the apices of bracts. *Cyathia* bisexual, solitary at node; peduncles green, 1.7–3.2mm long, 0.3–0.7mm thick; involucre campanulate or hemispherical, green, glabrous or pubescent at upper surface, 1.25–1.70mm high, 1.3–1.9mm wide, late summer forms greatly reduced in size. *Glands* present at the top of an involucre, five, green, transversely oblong, slightly depressed at the centre, 0.48–0.84mm long, 0.12–0.44mm wide, subtended by petaloid appendages; petaloid appendages white, flat or reflexed, orbicular or oval, entire or slightly erose margined, 0.96–2.2mm long, 0.96–2.4mm wide. *Staminate flowers* and bracteoles numerous; anthers yellow or pale green, 0.22–0.33mm long, 0.16–0.36mm wide; filaments 0.32–0.88mm long, 0.16–0.22mm thick. *Pistillate flowers* central, surrounded by five groups of staminate flowers, green; pedicels 3.2–5.3mm long, 0.5–1.0mm thick, exerted beyond the involucre, recurved; capsules three lobed, green, glabrous or slightly pubescent, 2.0–2.4mm long, c.3.3–4.8mm diam.; styles three, united at base, 0.6–1.1mm long; stigmas thick, pale green, bifid. *Seeds* globose, white or brown, ecarunculate, 1.8–2.3mm long, 1.4–1.8mm diam., shallowly pitted; hilum depressed; apex acute, with a small nipple-like structure at the opposite end.

*Phenology.* Flowering and fruiting from April to September.

*Euphorbia pubentissima* is the most morphologically variable species in sect. *Tithymalopsis*. It occurs on the eastern side of the Appalachian Plateau from Maryland to Louisiana. This species is closely related to *E. corollata*, but they are distinguished from each other by several characters (see discussion of *E. corollata*).

This species is highly polymorphic depending on the growing season. Individuals of early summer have large bracts and inflorescences with long peduncles, whereas those of the late summer or fall have highly reduced bracts and inflorescences, and have several missing dichasial branches at the terminal nodes. Herbarium, field and greenhouse observations indicate that *E. corollata* var. *molle*, *E. corollata* var. *glauca* and *E. zinniiflora* correspond to the early summer forms of *E. pubentissima*. The type of *E. corollata* var. *glauca*, which was collected in Alabama, has reduced stems, no leaves on the main stem, and broad bracts; it closely approaches *E. mercurialina*.

The individuals of *E. pubentissima*, even within a population, are highly variable depending on their age, microhabitat and the growing season. Usually, individuals growing in less open, mesic areas have pubescent petioles, leaves and stems, long petioles and thin, broad leaves, whereas those from open sites have more robust stems, thick, glabrous leaves and short petioles. However, the sizes and shapes of leaves are very variable within a population.

The type specimen of *E. apocynifolia* was collected at Quincy, Florida in September. It is similar to typical late summer forms of *E. pubentissima*: smaller bracts and petaloid appendages, several missing dichasial branches, and short peduncles. The presence of a 2–3-rayed umbel, red or green glands, obtuse, slightly revolute leaves and rounded appendages is not typical for *E. pubentissima*. The

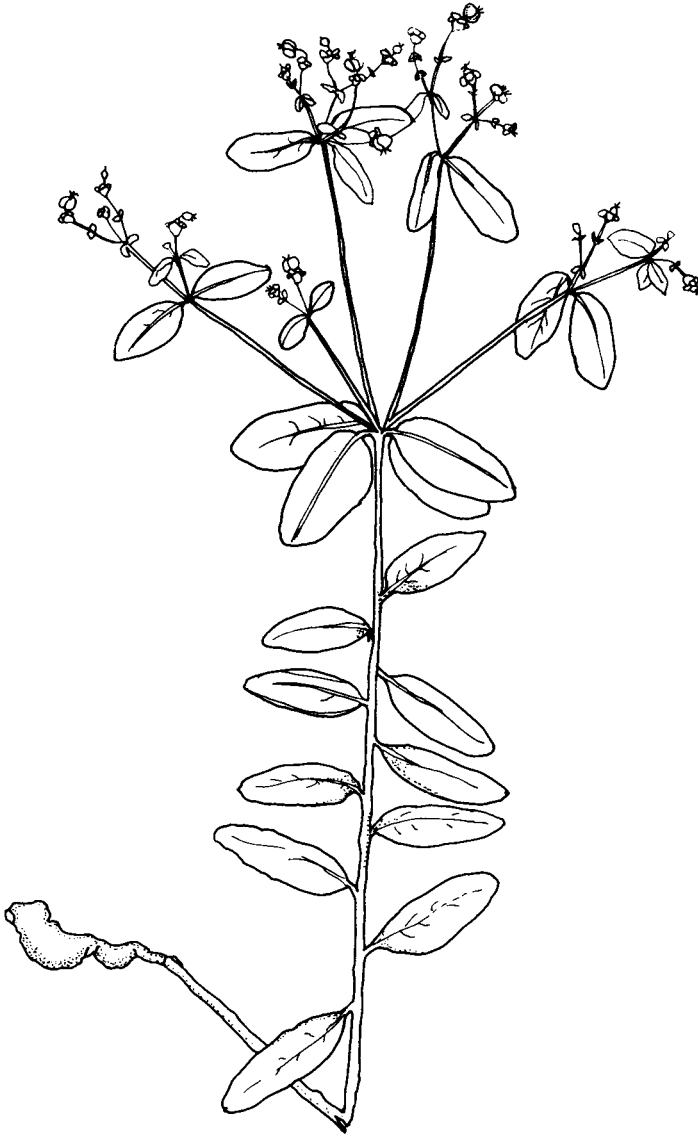


FIG. 13. *Euphorbia pubentissima*: habit,  $\times 0.4$ .

presence of these characters of *E. apocynifolia* suggests possible hybridization among *E. pubentissima*, *E. discoidalis* and *E. gracilior*.

## EXCLUDED NAMES

Because of unclear descriptions or unlocated type material, the following names of Rafinesque's (1840) *Agaloma* species are excluded.

- Agaloma ciliata* var. *monanthes* Raf.  
*Agaloma corollata* var. *cuneifolia*, *nudiflora*, *pauciflora*, *uniflora*  
*Agaloma retusa* Raf.  
*Agaloma polyscandia* Raf.  
*Agaloma linearis* Raf.  
*Agaloma tenuifolia* Raf.

## ACKNOWLEDGEMENTS

This paper represents a portion of a PhD dissertation submitted to the Department of Botany & Microbiology at the University of Oklahoma. I thank Drs W. Elisens, G. Schnell, J. Estes, G. Uno and S. Russell and two anonymous reviewers for reviewing this paper and providing helpful comments. I am grateful to the curators of F, G, GA, GH, LINN, MICH, MO, NY, OKL, OS, PH, TEX and US for loaning material and/or providing a place to study.

## REFERENCES

- ARTHUR, J. C. (1912). New combinations. *Torreyia* 24: 52.  
BOISSIER, P. E. (1862). Euphorbiaceae, subordo Euphorbieae. In: DE CANDOLLE, A. (ed.) *Prodromus Systematis Naturalis Regni Vegetalis* 15(2): 3–188. Paris: Masson and Son.  
BUCK, W. R. & HUFT, M. J. (1977). Two new species of *Euphorbia* subgenus *Agaloma* from Mexico. *J. Arnold Arbor.* 58: 343–348.  
CARLQUIST, S. (1966). The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. *Brittonia* 18: 310–335.  
CARTER, S. (1994). A preliminary classification of *Euphorbia* subgenus *Euphorbia*. *Ann. Missouri Bot. Gard.* 81: 368–379.  
CHAPMAN, A. W. (1892). *Flora of the Southern United States*. Ed. 2. New York.  
CRONQUIST, A. (1949). Noteworthy plants of Georgia. *Castanea* 14: 101–108.  
CRONQUIST, A. (1968). *The Evolution and Classification of Flowering Plants*. Boston: Houghton-Mifflin Co.  
DONOGHUE, M. J., OLMSTEAD, J. F., SMITH, J. F. & PALMER, J. D. (1992). Phylogenetic relationships of Dipsacales based on rbcL sequences. *Ann. Missouri Bot. Gard.* 79: 333–345.  
EHLER, N. (1976). Mikromorphologie der Samenoberflächen der Gattung *Euphorbia*. *Plant Syst. Evol.* 126: 189–207.  
EHRENFELD, J. (1976). Reproductive biology of three species of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). *Amer. J. Bot.* 63: 406–413.  
EL-GHAZALY, G. (1989). Pollen and orbicule morphology of some *Euphorbia* species. *Grana* 28: 243–259.  
ENGELMANN, G. (1887). *The botanical works of the Late George Engelmann*, collected

- for Henry Shaw, Esq., (eds) Trelease, W. & Gray, A., pp. 433–449. Cambridge: John Wilson and Son, University Press.
- ERDTMAN, G. (1960). The acetolysis method. *Svensk. Bot. Tidskr.* 54: 561–564.
- ERDTMAN, G. (1966). *Pollen Morphology and Plant Taxonomy. Angiosperms*. New York: Hafner Publishing Co.
- HANS, A. S. (1973). Chromosomal conspectus of the Euphorbiaceae. *Taxon* 22: 591–636.
- HOLZINGER, J. M. (1892). List of Plants collected by C. S. Sheldon and M. A. Carleton in Indian Territory in 1891. *Contr. U.S. Nat. Herb.* 1: 189–217.
- HOUSE, H. D. (1924). Annotated list of the ferns and flowering plants of New York state. *New York States Museum Bulletin* 254: 5–759.
- HUFT, M. J. (1979). *A monograph of Euphorbia section Tithymalopsis*. PhD dissertation, University of Michigan, Ann Arbor.
- HUFT, M. J. (1984). A review of *Euphorbia* (Euphorbiaceae) in Baja California. *Ann. Missouri Bot. Gard.* 71: 1021–1027.
- JOHNSTON, M. C. (1975). Studies of the *Euphorbia* species of the Chihuahuan desert region and adjacent area. *Wrightia* 5: 120–143.
- JORDAN, L. S., JORDAN, J. L. & JORDAN, C. M. (1985). Changes induced by water on *Euphorbia supina* seed coat structures. *Amer. J. Bot.* 72: 1530–1536.
- JORDAN, M. S. & HAYDEN, W. J. (1992). A survey of mucilaginous testa in *Chamaesyce*. *Collectanea Botanica* 21: 79–89.
- KEIL, D. J. (1976). Chromosome numbers for *Euphorbia* (Euphorbiaceae) from western North America. *Madroño* 23: 405–408.
- KLOTZSCH, F. (1859). Hr. Klotsch lass über Linné's natürliche Pflanzenklasse Tricoccae des Berliner Herbarium's im Allgemeinen und die natürliche Ordnung Euphorbiaceae insbesondere. *Monatsber. Königl. Preuss. Akad. Wiss. Berlin* 1859: 236–254.
- KÖHLER, E. (1965). Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonome. *Grana Palynol.* 6: 26–120.
- KROCHMAL, A. (1952). Seeds of weedy *Euphorbia* species and their identification. *Weeds* 1: 243–255.
- KROMBEIN, K. V. (1961). Some insect visitors of mat euphorbia in southeastern Arizona (Hymenoptera, Diptera). *Entomol. News* 72: 80–83.
- LEVIN, G. A. & SIMPSON, M. G. (1994). Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). *Ann. Missouri Bot. Gard.* 81: 203–238.
- LIN, S., CHAW, S. & HSIEH, C. (1991). A taxonomic study of the genus *Chamaesyce* S. F. Gray (Euphorbiaceae) in Taiwan. *Bot. Bull. Acad. Sin.* 32: 215–251.
- LIN, S. & HSIEH, C. (1991). A taxonomic study of the genus *Euphorbia* L. (Euphorbiaceae) in Taiwan. *Taiwania* 36: 57–79.
- LINNAEUS, C. (1753). *Species Plantarum*. Stockholm.
- LYNCH, S. P. & WEBSTER, G. L. (1975). A new technique of preparing pollen for scanning electron microscopy. *Grana* 15: 127–136.
- McVAUGH, R. (1961). Euphorbiaceae novae-galiciana. *Brittonia* 13: 145–205.
- MILLSPAUGH, C. F. (1898). Notes and new species of the genus *Euphorbia*. *Bot. Gaz.* 26: 265–270.
- MILLSPAUGH, C. F. (1913). The genera *Pedilanthus* and *Cubanthus*, and other American Euphorbiaceae. *Field Mus. Nat. Hist., Bot.* 2: 353–373.
- NIEUWLAND, J. A. (1912). *Tithymalopsis* and *Dichrophyllum*, synonyms. *Amer. Midl. Nat.* 2: 298–300.



- NORTON, J. B. S. (1900). A revision of the North American species of *Euphorbia* of the section *Tithymalus* occurring north of Mexico. *Missouri Bot. Gard. Annual Rep.* 11: 85–114.
- NORTON, J. B. S. (1916). Variation in *Tithymalopsis*. *Mem. New York Bot. Gard.* 6: 455–459.
- NOWICKE, J. W. (1994). A palynological study of Crotonoideae. *Ann. Missouri Bot. Gard.* 81: 245–269.
- PARK, K. (1995). *Systematic studies of Euphorbia section Tithymalopsis (Euphorbiaceae)*. PhD dissertation, University of Oklahoma, Norman.
- PARK, K. & LEE, S. (1988). A palynotaxonomic study of the Korean Euphorbiaceae. *Korean J. Pl. Taxon.* 18: 69–94.
- PERRY, B. A. (1943). Chromosome number and phylogenetic relationships in the Euphorbiaceae. *Amer. J. Bot.* 30: 527–543.
- PUNT, W. (1962). Pollen morphology of the Euphorbiaceae with special reference to taxonomy. *Wentia* 7: 1–116.
- PUNT, W. (1987). A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. *Bot. J. Linn. Soc.* 94: 127–142.
- RADFORD, A. E., DICKISON, W. C., MASSEY, J. R. & BELL, C. R. (1974). *Vascular Plant Systematics*. New York: Harper & Row.
- RAFINESQUE, C. S. (1836). *Flora Telluriana* (Parts IV et Ult.), printed by H. Probasco, pp. 116–117. Philadelphia.
- RAFINESQUE, C. S. (1840). *Autikon Botanikon*, printed by author, pp. 94–96. Philadelphia.
- RICHARDSON, J. W. (1968). The genus *Euphorbia* of the High Plains and Prairie Plains of Kansas, Nebraska, South and North Dakota. *University of Kansas Science Bulletin* 48: 45–112.
- SAXENA, M. R. (1993). *Palynology*. New Delhi: Oxford & IBH Publishing Co.
- SIMPSON, M. G. & LEVIN, G. A. (1994). Pollen ultrastructure of the biovulate Euphorbiaceae. *Int. J. Pl. Sci.* 155: 313–431.
- SMALL, J. K. (1898). Studies in the Botany of the Southeastern United States. *Bull. Torrey Bot. Club* 25: 465–615.
- SMALL, J. K. (1903). *Flora of the Southeastern United States*. New York.
- SMALL, J. K. (1913). *Flora of the Southeastern United States*. Ed. 2. New York.
- STEVENS, P. F. (1991). Character states, morphological variation, and phylogenetic analysis: A review. *Syst. Bot.* 16: 553–583.
- SWOFFORD, D. L. (1991). *PAUP. Phylogenetic Analysis Using Parsimony, version 3.0s*. Illinois Natural History Survey, Champaign, Illinois.
- URBATSCH, L. E., BACON, J. D., HARTMAN, R. L., JOHNSTON, M. C., WATSON, T. J. & WEBSTER, G. L. (1975). Chromosome numbers for North American Euphorbiaceae. *Amer. J. Bot.* 62: 494–500.
- WALKER, J. W. & DOYLE, J. A. (1975). The base of angiosperm phylogeny: palynology. *Ann. Missouri Bot. Gard.* 62: 664–723.
- WEBSTER, G. L. (1967). The genera of Euphorbiaceae in the southeastern United States. *J. Arnold Arbor.* 48: 303–430.
- WEBSTER, G. L. (1975). Conspectus of a new classification of the Euphorbiaceae. *Taxon* 24: 593–601.
- WEBSTER, G. L. (1994). Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Ann. Missouri Bot. Gard.* 81: 33–144.
- WHEELER, L. C. (1939). A miscellany of New World Euphorbiaceae II. *Contr. Gray Herb.* 127: 48–78.

WHEELER, L. C. (1943). The genera of living Euphorbieae. *Amer. Midl. Nat.* 30: 456–503.

*Received 23 July 1996; accepted with revision 29 April 1997*

## APPENDIX

Representative specimens of *Euphorbia* sect. *Tithymalopsis* examined in the preparation of this monograph.

**Euphorbia corollata.** ALABAMA. Greene Co., 1 mi W of Mt Hebron on Hwy 39, *Naugle* 310 (GA). Hale Co., Newbern, *Kral* 36869 (GA). Lauderdale Co., 3 mi N of Florence, *Isely* 4344 (GA). Madison Co., Huntsville, *Pollard & Maxon* 371, 373 (GA). Marshall Co., N of Guntersville, *Kral* 45964 (GA). Sumter Co., 3 mi SW of York, *Jones* 767 (GA). ARKANSAS. Baxter Co., Lake View, *Demaree* 28921 (MICH, TEX). Carroll Co., Eureka Springs, *Stratton* 3834 (GA). Craighead Co., Jonesboro, *Demaree* 26547 (TEX). Logan Co., Mt Mg., *Pyle* 155 (TEX). Marion Co., Bull Shoal Dam Reservoir, *Demaree* 30105 (MICH). Poinsette Co., Harrisburg, *Demaree* 27462 (TEX). Sevier Co., Rley 157 (TEX). Washington Co., Greenland Township, *Tharp* 147 (TEX). GEORGIA. Bartow Co., on top of Signal Mt., *Duncan* 8533 (GA). Elberton Co., E of Elberton, *Coile et al.* 1123 (GA). Gilmer Co., Flat Top Mt., *Duncan* 2814 (GA). Murray Co., Carters, *Kral* 50911 (GA). Upson Co., Flint River, *Jones* 21074 (GA). Walker Co., Lookout Mt., *Jones* 24271 (GA); 3 mi S of Villanow, *Hunt* 25 (GA). ILLINOIS. Cook Co., Spears Woods, *Lask* 163 (MICH). DuPage Co., Elmhurst, 1966, *Keil* 540 (OS). Iroquois Co., 1971, *Keil* 7596 (OS). Jackson Co., Pomona, *Jensen* 7 (TEX). Jo Davies Co., Hanover, *Gates* 2607 (MICH). Kane Co., 5 mi W of Aurora, *Erlanson* 1527 (MICH). Lake Co., Beach, *Gates* 2852 (MICH). Lawrence Co., 1 mi E of Sumner, 3 viii 1946, *Sivert* s.n. (TEX). McDonough Co., Bethel Twp., *Warnock* 311 (TEX). Peoria Co., Pleasant Valley, *Chase* 8972 (MICH). Tazewell Co., Meyers Lake, *Chase* 13536 (TEX). INDIANA. Cass Co., 1.3 mi N of Royal Center, *Friesner* 9735 (GA). Clay Co., Ashboro, *Friesner* 21750 (MICH, TEX). Clark Co., *Umbach* 4562 (MICH). Elkhart Co., Elkhart, *Keuffman* 224 (MICH). Jefferson Co., Hanover, *Miouller* 4910, 4908 (NY). Lawrence Co., *Wynn* 95 (TEX). Lake Co., Miller's Lake, *Bartlett & Richards* 1151 (MICH). Laporte Co., 1 mi W of Michigan City, *Deam* 7077 (MICH). Potter Co., Keiser, 1 vii 1923, *Lyon* s.n. (MICH). St Joseph Co., Walkerton, 12 viii 1925, *Lyon* s.n. (MICH). IOWA. Adams Co., Washington Twp., *Isely* 5669 (GA). Benton Co., 6 mi N of Belle Plaine, *Rohrbaugh* 85 (TEX). Cedar Co., 1938, *W.A.W.* 1193 (OS). Dubuque Co., Prix Hollow, *Worrock* 20511 (TEX). Guthrie Co., 3 mi SW of Coon Rapids, *Fay* 4025 (TEX). Palo Alto Co., 2 mi E of Ruthven, *Hayden* 6022 (GA, MICH). Polk Co., 1934, *Sehaffwer* 3335 (OS). Story Co., Washington Twp., *Morrill* 75 (TEX). KANSAS. Doniphan Co., 2 mi E of Troy, *Horr* 4283 (TEX). Harvey Co., 7 mi E of Newton, *McGregor* 33679 (GA). Linn Co., LaCygne, *Gates* 20465 (GA). Pottawatomie Co., Belvue, *Demaree* 29732 (TEX); 3.5 mi N of Lyndon, *Horr* E34 (TEX). Riley Co., Manhattan, 18 viii 1889, *Varney* s.n. (MICH). KENTUCKY. Boyd Co., Shop Creek, *Runyon* 1262 (TEX). Clark Co., 3 mi S of Indian Fields, *Wharton* 5118 (MICH). Estill Co., 0.8 mi SE of Harg, *Wharton* 3143 (MICH). Harlan Co., Poor Fork Post Office, 1893, *Kearney* 146 (OS). Hickman Co., Hwy 1283 to Bayou de Chien Creek, *Grubbs* 397 (GA). Lincoln Co., S of Crab Orchard, 5 viii 1938, *Wharton* s.n. (MICH). Madison Co., Kentucky River, Boonsborough, *Houghton* 811-b (MICH). Montgomery Co., 1.25 mi SE of Jeffersonville, *Wharton* 2781 (MICH). Nelson Co., 2.5 mi NE of Boston, *Wharton* 5590 (MICH). Powell Co., SW of West Bend, *Wharton* 1175 (MICH). Whitley Co., Corbin, *McFarland & James* 41 (GA). LOUISIANA. Acadia Co., Rayne-Crowley Road, *Crockett*

8392 (TEX). Caddo Co., Springridge, 22 vii 1941, *Penn* s.n. (TEX). Jeff Davis Co., E of Estherwood, *Rose-Innes & Warnock* 709 (TEX). Lincoln Co., Hilly, 9 iv 1952, *Barrett* s.n. (TEX). Vernon Co., 2 mi W of Leander, *Webster & Wilbur* 3232 (GA, MICH, NY). MARYLAND. Howard Co., Patuxent River, *Hill* 10779 (GA). Prince Georges Co., 1.3 mi N of Defense Hwy, *Walker & Fosberg* 2857 (GA). MASSACHUSETTS. Bristol Co., N of Easton, 2 ix 1916, *Schweinfurth* s.n. (TEX). MICHIGAN. Allegan Co., Swan Creek Wildlife Experiment Station, *Haugen* 190 (MICH). Barry Co., *Haugen* 299 (MICH). Berrien Co., Donald C. Cook nuclear power plant site, 13 viii 1974, *Evans* s.n. (MICH). Branch Co., 2 mi SW of Girard, *Voss* 7477 (MICH). Cass Co., Bear Lake, *Rapp* 667 (MICH). Clinton Co., Coloma, *Cooley* 163 (MICH). Emmet Co., Pellston, *Ehlers* 1017 (MICH). Ingham Co., Meridian Twp., *Parmelee* 608 (TEX). Lenawee Co., W of Rawin Center Hwy, *Smith* 843 (MICH). Livingston Co., Tamarack Swamp, 24 vi 1951, *Bartlett* s.n. (MICH). Montcalm Co., 2.5 mi NW of Howard City, *Voss* 7215 (MICH). Mowroe Co., 1965, *Stuckey* 2596 (OS). St Clair Co., 18 vii 1912, *Dodge* s.n. (MICH). Muskegon Co., Whitehall, *Voss* 2857 (MICH). Newaygo Co., 4 mi SE of White Cloud, *Voss* 2829 (MICH). Oakland Co., Rochester, 23 vii 1909, *Farwell* s.n. (MICH). Oceana Co., 5.5 mi SW of Hesperia, *Voss* 7183 (MICH). Washtenaw Co., 1963, *Stuckey* 2019 (OS); Ann Arbor, *Elconson* 850 (MICH). Wayne Co., Detroit, 4 vii 1870, *Foote* s.n. (MICH). MINNESOTA. Huston Co., Huston, *Bartlett & Grayson* 1419 (MICH). Ramsey Co., Bald Eagle, *SFB* 1211 (TEX). Mouth of Snake River of the St Croix, 30 vii 1832, *Houghton* s.n. (MICH). MISSISSIPPI. Alcorn Co., 11.5 mi S of Corinth, *Pullen* 64482 (GA). Attala Co., Newport, *Temple* 5304 (GA). Benton Co., 1.5 mi E of Marshall–Benton county line, *Pullen* 6412279 (GA). Calhoun Co., 4.5 mi S of Lafayette–Calhoun county line, *Pullen* 64875 (GA, MICH). Carroll Co., 8 mi SE of Greenwood, *Temple* 3400 (GA). Clark Co., N of Clark, *Temple* 9115 (GA). Copiah Co., 7.3 mi S of Hazlehurst, *Temple* 3807 (GA). Grenada Co., 3.2 mi S of Yalobusha–Grenada county line, *Temple* 3235 (GA). Kemper Co., E of Scooba, *Jones* 14977 (GA). Lamar Co., 3 mi W of Hattiesburg, *Jones* 1909 (GA); Black Creek, *Jones* 3427 (GA). Lawrence Co., 3 mi W of Monticello, *Webster & Wilbur* 3299 (MICH). Leake Co., 1.7 mi S of Edinburg, *Temple* 9410 (GA). Lincoln Co., 1 mi SE of Auburn, *Jones* 13612 (GA). Lowndes Co., 5.3 mi SW of Columbus, *Temple* 5926 (GA). Marshall Co., W of Wall Doxey Lake, *Temple* 2883 (GA). Newton Co., 2.1 mi E of Lake, *Bryson* 5932 (GA). Panola Co., SE edge of Sardis Reservation, *Temple* 2820 (GA). Pike Co., Bogue Chitto River, *Temple* 9878 (GA). Rankin Co., Robinhood Lake area, *Temple* 9785 (GA). Simpson Co., 3 mi W of Pinola, *Temple* 10317 (GA); 0.7 mi S of Simpson–Hinds county line, *Temple* 9034 (GA). Smith Co., Marathon Lake, *Jones* 2398 (GA). MISSOURI. Calloway Co., Tucker Prairie, *Dunn* 12979 (GA). Clinton Co., N of Turney, *Steyermark* 84670 (GA). Greene Co., 10 mi SW of Springfield, *Redfearn* 3704 (GA). Howell Co., Mt. View, *Rohrbaugh* 285 (TEX). Jefferson Co., 8 mi S of Hillsboro, *Poston et al.* 584 (GA). Phelps Co., Meremac River, *Spellman* S-316 (GA). Sharp Co., 2 mi W of Ash Flat, 11 vi 1958, *Dunn* s.n. (GA). St Louis Co., W of Compton, *Muehlenbach* 2425 (GA). Stoddard Co., Crowley Ridge, *Steyermark* 76739 (GA). NEBRASKA. Lancaster Co., Lincoln, no date (TEX). Nemaha Co., Auburn, 3 ix 1927, *Hansen* s.n. (MICH). NEW JERSEY. Monmouth Co., Freehold, 1859, *Willis* s.n. (MICH). Gloucester Co., Swedesboro, 27 vii 1922, *Brown* s.n. (MICH). Rocky Hill, *Kelsey* 189 (MICH). NEW YORK. Allany Co., Loufonville, *House* 21979 (TEX). Seneca Co., E of Newtons Pond, *Eames et al.* 12390 (MICH). Tompkins Co., Ithaca, *J.M.R.* s.n. (GA); Junius, 24 vii 1926, *Miller* s.n. (GA). NORTH CAROLINA. Ashe Co., Bluff Mt., *Redford* 44215 (TEX). Catawba Co., 15 mi W of Mooresville, *McNeely* 260 (TEX). McDowell Co., at jct. of Rts 226 and 221, *Perdue & Blum* 4182 (TEX). OHIO. Adams Co., Chaparral Rd, 1989, *McCormac* 1336 (OS). Athens Co., *Horn* 223936 (OS). Belmont Co., 1910, *Laughli* 15543 (OS). Buyahoga Co., Cleveland, 1897, *Stair* 5532 (OS). Columbiana Co., Washington Twp., 1964, *Cusick* 76917 (OS). Coshocton Co., 1931, *Selby*

133E (OS). Erie Co., Ceylon, 1969, *Jones* 113227 (OS). Fairfield Co., *Gorbin* 15567 (OS). Gallia Co., *Kellerman* 15560 (OS). Geauga Co., Burton, *Werner* 45220 (OS). Greene Co., John Bryan State Park, *Aree* 11543 (OS). Harrison Co., 1898, *Kellerman* 905 (OS). Hocking Co., Conkle's Hollow State Park, *Noblick* 554 (OS). Huron Co., Norwalk, *Jones* 80601 (OS). Jackson Co., Liberty Twp., *Stucky* 3305 (OS). Logan Co., 1991, *McCormac* 4262 (OS). Lorain Co., 1870, *Penfield* 366285 (OS); 1973, *Jones* 217996 (OS). Madison Co., *King* 132366 (OS). Marion Co., 1971, *Roberts* 1629 (OS). Medina Co., 1896, *Leonard* 366280 (OS). Sandusky Co., *Wright* 366295 (OS). Stark Co., *Amann* 747 (OS). Summit Co., *Jones* 220814 (OS). Van Wert Co., Dixon, *Cusick* 21 (OS). Washington Co., *Laughlin* 806 (OS). Wood Co., Weston, *Easterly* 871 (OS). OKLAHOMA. Cleveland Co., 2.5 mi E of Norman, *Massey et al.* 1460 (TEX). Murray Co., Platt National Park, *Merrill* 993 (TEX). Osage Co., Walker Ranch, *Webster* 4268 (TEX). Ottawa Co., between Miami and Quapaw, *Goodman* 5545 (TEX). Payne Co., 9 mi NW of Stillwater, *Dell* 213 (GA). Seminole Co., 20 mi S of Seminole, *Cross* 25 (TEX). PENNSYLVANIA. Lehigh Co., 1.5 mi N of West Bethlehem, *Schaeffer* 20293 (TEX). TENNESSEE. Anderson Co., Melton Hill Reservoir, *Ellis* 28869 (GA). Blount Co., Walland, *Wehmeyer* 248 (GA). Cheatham Co., Kingston Springs, *Svenson* 10509 (TEX). Cocke Co., *Kearney* 883 (OS). Coffee Co., N of Manchester, *Svenson* 6972 (TEX). Grundy Co., Cumberland Plateau, near Tracy City, 1975, *Dalton* s.n. (OS). Hardin Co., 5.5 mi E of Savannah, *Kral* 46700 (GA). Johnson City, *J.M.R.* s.n. (GA). Knox Co., *Kearney* s.n. (GA). Montgomery Co., base of King & Queen's Bluff, *Shanks* 2749 (GA). Morgan Co., Lilly Bridge, *Schmalzer* 375 (GA). Sequatchie Co., Cagle, *Svenson* 9676 (TEX). TEXAS. Angelina Co., 20 mi NW of Jasper, *Correll & Johnston* 19648 (TEX). Bastrop Co., Bastrop State Park, *Cohn & Barkley* 13786 (TEX). Bowie Co., 2 mi W of Nash, *Correll & Correll* 22521 (TEX). Brazoria Co., along road between Bastrop Bayou and Hoskins Mound, *Fleetwood* 9566 (TEX). Brazos Co., College Station, 5 v 1946, *Parks* s.n. (TEX). Cass Co., Bivins, 29 ix 1942, *Ozette* s.n. (TEX); 0.2 mi E of McLeod, *Correll* 30088 (TEX). Colorado Co., Eagle Lake, x 1930, *Biology Class* s.n. (TEX). Dallas Co., 0.5 mi S of crossing of White Rock Creek, *Cory* 54560 (GA, TEX). Dregg Co., *York* 147 (TEX). Fannin Co., 1 mi W of Windom, 15 vi 1939, *Reese* s.n. (TEX). Galveston Co., Bacliff, *Waller* 2832 (TEX). Grayson Co., 3 mi W of Bell, *Gentry* 511392 (TEX). Hardin Co., 6 mi SW of Kountze, *Tharp et al.* 54920 (TEX). Harris Co., Seabrook, *Boon* 106 (TEX). Hay Co., entrance to Hidden Valley Ranch, *Johnson* 424 (TEX). Houston Co., 4 mi E of Radcliff, *Gould & Leinweber* 6503 (TEX). Jackson Co., 9 mi W of Edna, *Turner & Tharp* 53431 (TEX). Jasper Co., S of Jasper, *Lundell* 11820 (TEX). Jefferson Co., Beaumont, *Tharp* 147 (TEX). Lamar Co., W of Paris, 28 viii 1939, *Reese* s.n. (TEX). Milam Co., outside Rockdale, *Rose-Innes & Moon* 929 (TEX). Montgomery Co., 9 mi E of Conroe, *Correll & Johnston* 19604 (TEX). Newton Co., 3 mi SE of Burkeville, *Correll* 38173 (TEX). Orange Co., 19 ix 1918, *Young* s.n. (TEX). Panola Co., 10 mi SE of Carthage, *Correll et al.* 22213 (TEX). Shelby Co., 7 mi S of Center, *Correll* 16171 (TEX). Tarrant Co., *Killian* 6838 (TEX). Travis Co., Manor, *Tharp* s.n. (TEX). Tyler Co., Clear Fork Creek, *Correll & Correll* 33460 (TEX). Victoria Co., 30 viii 1941, *Tharp* s.n. (TEX). Washington Co., *Brockett* 147 (TEX). Wharton Co., Pierce, *Tracy* 7433 (TEX). Wood Co., E of Mineola, *Lundell & Lundell* 9409 (TEX). VIRGINIA. Fairfax Co., Great Falls, *Blake* 5214 (TEX). Clarendon, *Blake* 10645 (TEX). WEST VIRGINIA. Cabell Co., Logan road, *Gilbert & Gilbert* 881 (GA). Upshur Co., 4 mi E of Buckhannon, *Rossbach* 8755 (GA). Wirt Co., 5 mi E of Elizabeth, *Wilson* 6015 (GA). VERMONT. Chittenden Co., Burlington, *Blake* 2293 (TEX). WISCONSIN. Dane Co., Madison, 20 viii 1928, *Miller* s.n. (GA). Winnebago Co., *Kellerman* s.n. (OS).

**Euphorbia curtisii.** FLORIDA. Baker Co., *Curtiss* 2477 (GA, MICH). Leon Co., Apalachicola National Forest, *Godfrey* 83714 (GA). Liberty Co., 10 mi N of Wilma, *Correll* 51610 (NY). Wakulla Co., Apalachicola National Forest, *Garland* 233 (GA); between Bloxham and

Sopchoppy, *Godfrey* 68483 (GA). Ocklocknee River, *Small et al.* 12860 (GA). GEORGIA. Candler Co., 0.4 mi W of Upper Lott's Creek Primitive Baptist Church, *Coile* 2702 (GA). Lanier Co., Unity Bay, *Faircloth* 3539 (GA). NORTH CAROLINA. Brunswick Co., 4 mi NW of Supply, *Mellichamp* 2459 (MICH). Harnett Co., 0.5 mi S of Pineview, *Carter* 3329 (GA). Lee Co., 2 mi S of Lemon Springs, *Redford* 44967 (GA, MICH). New Hanover Co., Wilmington, *Bartram & Long* 1057 (MICH). Richmond Co., between Hamlet and Rockingham, *Cappel & Godfrey* 174 (GA). SOUTH CAROLINA. Berkeley Co., Mount Holly, *Ahles* 26565 (GA). Chesterfield Co., Sugarloaf Mt., *Almeda et al.* 1840 (GA). Kershaw Co., 1.5 mi NE of Bethune, *Redford* 23505 (MICH).

***Euphorbia discoidalis***. ALABAMA. Escambia Co., Escambia National Experimental Forest, *Orzell & Edwinn* 11778 (TEX). Spring hill, ix 1880, *Langlois* s.n. (NY). FLORIDA. Bay Co., 15 x 1921, *Haven* s.n. (MICH). Calhoun Co., 3.4 mi W of FL 73 N in Clarksville, *Orzell & Bridges* 11851 (TEX). Okaloosa Co., 5 mi N of Niceville, *Hansen* 3680 (TEX); Eglin Air Force Reservation, *Ward* 5974 (NY). Santa Rosa Co., near Navarre, *Burch* 475 (GA). Wakulla Co., Apalachicola, *Chapman* s.n. (NY); W of Apalachicola, *Chapman* 3843 (NY). Walton Co., dry sandy soil, *Curtiss* 2470 (GA, MICH, NY); pine wood, summer 1885, *Curtiss* s.n. (NY). GEORGIA. Atkinson Co., near Pearson, *Curtiss* 6823 (GA, NY). Baker Co., Ichauway Plantation, *Thorne* 4094 (MICH). Ben Hill Co., 1.5 mi S of Bowen Mill, *Faircloth* 1429 (GA). Chatham Co., NW of Old Ogeechee Canal, *Duncan* 20879 (GA). Coffee Co., near Douglas, *Harper* 1458 (NY). Colquitt Co., 1.8 mi N of Berlin, *Faircloth* 3287 (GA); Lee Courthouse, *Faircloth* 3311 (GA). Dougherty Co., near Albany, *McKellar* 15 (GA). Grady Co., 6.5 mi S of Whigham, *Faircloth* 518 (GA). Irwin Co., intersect. Irwin & Ben Hill counties at US 129, *Pullen* 525 (GA); Alapaha River, *Faircloth* 5455 (GA). Lanier Co., 2.6 mi SE of Lakeland, *Faircloth* 2600 (GA). Lee Co., Leesburg, *Curtiss* 2689 (NY). Randolph Co., 3.4 mi W of Cuthbert, 8 v 1981, *Martin* s.n. (GA). Sumter Co., 16 mi SW of Americus, *Wilbur* 3232 (GA). Telfair Co., 10 mi S of McRae, *Wilbur* 3336 (GA). Thomas Co., Little Ochlocknee River, *Faircloth* 2783 (GA); N of Thomasville, 1 ix 1982, *Al Tate* s.n. (GA); Thomasville, viii 1903, *Taylor* s.n. (TEX). Turner Co., 0.3 mi N of Deep Creek alongside Ga 112, *Faircloth* 4386 (GA). Worth Co., Abram's Creek, *Faircloth* 3834 (GA); N of Sylvester, *Kral* 51578 (GA). MISSISSIPPI. Jackson Co., Ocean Spring, 1898, *Tracy* 4718 (MICH, OS); 3 viii 1889, *Earle* s.n. (NY). Handsboro, *Hood* 437 (GA). TEXAS. Polk Co., Big Thicket National Preserve, *Wyatt* 1173 (GA); 4 mi NE of Camden, *Tharp et al.* 34720 (TEX); 13 mi W of Corrigan, *Gould* 6929 (TEX). Walker Co., Huntsville, *Warnock* 4585 (TEX); Huntsville State Park, *Henderson* 631019 (TEX).

***Euphorbia gracilior***. FLORIDA. Calhoun Co., Bristol, *Small et al.* 11264 (NY). Dixie Co., Hogback, *Small et al.* 11324 (NY). Franklin Co., 5.5 mi SE of Panacea, *Anderson* 8266 (NY). Gadsden Co., Quincy, *Sargent* 6152 (GA); sandhills between Quincy and Wetumka, *Small et al.* 11400 (NY); sandhills SW of Quincy, *Small et al.* 11215 (NY). Lake Co., Eustis, *Nash* 1151 (MICH, NY). Leon Co., 6 mi SE of Tallahassee, *Godfrey* 62740 (TEX); Silver Lake, *Henderson* 631080 (TEX); near Tallahassee, *Berg* s.n. (NY). Liberty Co., between Hosford and Bristol, *Godfrey et al.* 53388 (NY). Orange Co., Forest City, 11 vii 1894, *Lewton* s.n. (NY). Suwannee Co., Oak Ridge near the Suwannee, v 1928, *Small* s.n. (GA, MICH). Volusia Co., Seville, *Curtiss* 6605 (GA, NY). Wakulla Co., between Bloxham and Sopchoppy, *Godfrey* 68483 (GA); Shadeville, *Ripley & Barneby* 10133 (NY). Aspalaga, *Curtiss* 2489 (MICH, NY). GEORGIA. Bulloch Co., summer 1901, *Harper* 826 (NY). Chatham Co., v 1957, *Dulany* s.n. (GA). Coffee Co., 6 mi E of Relee, *Blake* 1316 (GA). Decatur Co., Faceville, *Thorne & Davidson* 16720 (GA, NY). Dodge Co., open pine woods SW of Eastman, *Duncan* 5025 (GA). Emanuel Co., 7 mi W of Swainsboro, *McVaugh* 8629 (TEX). Effingham Co., N of Little Ebenezer Branch, *Hardin & Duncan* 18075 (GA). Emanuel Co., 5 mi N of Swainsboro, *Duncan*

3178 (GA). Glascock Co., E of Gibson–Glascock county line, *Duncan* 3356 (GA). Jeff Davis Co., Hazlehurst, *Wilbur* 3183 (GA). Jenkins Co., 2 mi W of Millen, *Wilbur* 3261 (GA). Laurens Co., Oconee River, *Harper* 1351 (NY). Long Co., 5 mi N of Beard's Bluff, *Bozeman* 2535 (GA). McDuffie Co., Fall Line Sand-hills, *Bartlett* 1093 (MICH). McIntosh Co., 1.3 mi N of Ft Barrington–Cox Rd, *Bozeman* 461 (GA). Pulaski Co., Hawkinsville, *Harper & Humphrey* 16877 (GA). Richmond Co., 10 mi NE of Wrens, *Pyron & McVaugh* 1706 (GA). Screven Co., 5 mi NE of Newington, *Cronquist* 5035 (NY). Tattnall Co., 3 mi W of Reidsville, *Cronquist* 4933 (GA, MICH); *Wilbur* 3102 (MICH); 4 mi SE of Reidsville, *McGhee* 28 (GA). Telfair Co., 3 mi NW of Lumber City, *Wilbur* 3174 (GA). Toombs Co., 10 mi S of Lyons, *Blake* 11653 (TEX). Wayne Co., *Kearney* 1893 (OS); Jesup, *Curtiss* 2489 (GA). Wheeler Co., W of Oconee, *Duncan* 4714 (GA). NORTH CAROLINA. Cumberland Co., Fort Bragg Military Reservation, 1973, *Keil* 9611 (OS). Harnett Co., 1.5 mi E of Pineview, *Godfrey* 52284 (NY). SOUTH CAROLINA. Berkeley Co., 3 mi NE of Summerville on Rt. 17A, *Wilbur* 3544 (GA). Darlington Co., Hartsville to Kilgores Pond, 24 viii 1909, *Coker* s.n. (NY). Hampton Co., 4.2 mi NW of Furman on US Rt. 601, *Ahles & Bell* 12479 (GA). Kershaw Co., Camden, 8 v 1857, *Gibbes* s.n. (NY).

***Euphorbia mercurialina***. ALABAMA. Blount Co., limestone slope near Blackburn Fork of Warrior River in Murphree's Valley, *Harper* 4250 (GA). De Kalb Co., E of Ft Payne, *Kral* 30357 (GA); 2 mi from Ft Payne towards De Soto State Park, *Wood* 8671 (GA). Madison Co., Monte Sano, *Sargent* 7415 (GA). GEORGIA. Catoosa Co., Ringgold, *Faircloth* 922 (GA). Cherokee Co., below Lake Arrowhead dam, *Foote & Jones* 24896 (GA). Dade Co., E of Trenton, *Cronquist* 5134 (GA); near Rising Fawn, *Curtiss* 6800 (GA). Floyd Co., 3.5 mi SW of centre of Rome, *Jones* 24054 (GA). Murray Co., Cohutta Wildlife Management Area, *Coile* 3602 (GA). Walker Co., 5 mi NW of Lafayette, *Pyron & McVaugh* 2720 (GA); Pigeon Mt. Wildlife Management Area, *Jones* 23782 (GA). KENTUCKY. Clinton Co., Cumberland River, *Jordal* 3445 (MICH). TENNESSEE. Cannon Co., near top of Short Mt., *Orzell & Bridges* 9430 (GA, TEX). Claiborne Co., along Powell River above bridge near Harrogate, *Sharp & Grear* 26844 (GA, TEX); near Tazewell, viii 1889, *Talcott* s.n. (MICH). Davidson Co., Nashville, *Demaree* 52034 (OS). Franklin Co., between Sherwood and Sewanee, roadside slope, *Sharp & Adams* 10696 (GA). Grundy Co., 2.2 mi from Monteagle towards Mountain View, *Wood & Wilson* 8876 (GA). Knox Co., 1893, *Kearney* s.n. (OS); vi 1896, *Ruth* s.n. (MICH). Marion Co., 9 mi N of Trenton, *McVaugh* 8990 (GA, MICH, TEX). Overton Co., Wilder, *Kral* 174261 (OS). Putnam Co., Monterrey, *Sharp* 1707 (GA). Rhea Co., valley of Richland Creek above Dayton, Shanks, *Sharp & Clebsch* 4309 (GA).

***Euphorbia polyphylla***. FLORIDA. Broward Co., Deerfield, *Degener* 5129 (NY); Ft Lauderdale, *Correll & McVaugh* 6110 (NY); Auto camp, Ft Lauderdale, *Welch* 1522 (NY). Collier Co., Naples, *Lakela* 30894 (GA); 4 mi SE of Naples, ix 1936, *Blanchard* s.n. (MICH); *Degener* 4941 (NY); Golden Gates residential development, *Herndon* 1259 (NY). Dade Co., 3 mi SW of Perinne, *Wilbur & Webster* 2566 (MICH); Ft Lauderdale, *Eaton* 794 (TEX); Miami, *Eaton* 880 (TEX); Cutler, *Small et al.* 6737 (MICH, NY); open pine woods near the Univ. Miami at Coral Gables, *Wilbur & Webster* 2577 (GA, MICH, NY); Miami, Montgomery Foundation, *Watson* 716 (NY); Perrine, *Finnell* 468 (NY); Ross Hammock, *Small et al.* 6604 (NY); pinelands between Miami and Kendall, *Small & Carter* 2507 (NY); Royal Palm Hammock, *Small et al.* 6655 (NY); W of Old Cutler Road, just S of Cutler Hammock, *Correll* 40076 (NY, TEX); Cutler, *Correll & Popenoe* 50075 (NY); Lemon City, *Harper* 82 (NY). Highlands Co., north-west corner of Highlands Hammock State Park, 5 viii 1948, *Garrett* s.n. (GA). Indian River Co., dry, sandy soil, Indian River, *Curtiss* 2498 (GA); Eau Gallie, *Curtiss* 5733 (NY); Biscayne Bay, *Palmer* 501 (NY). Lake Co., Eustis, *Rhoades* 12686 (NY). Lee Co., Pinelands, *Small & Wilson* 1561 (NY); vicinity of Fort Myers,

*Standley* 178 (NY). Lemon City, *Eaton* 967 (TEX). Manatee Co., Palma Sola, vi 1890, *Simpson* s.n. (NY). Okeechobee Co., Okeechobee, *Fredholm* 5871 (NY). Orange Co., Forest City, 26 vi 1894, *Lewton* s.n. (NY); Winter Park, 14 vii 1894, *Lewton* s.n. (MICH). Palm Beach Co., 0.2 mi S of Boca Raton Rd, *Brooks* 274 (GA). Polk Co., West Frostproof, *Lakela* 24584 (TEX); Eagle Lake, *McFarlin* 6385 (MICH). Seminole Co., 2 mi E of Oviedo, *Ray et al.* 10711 (NY, TEX).

***Euphorbia pubentissima***. ALABAMA. Baldwin Co., 2.7 mi S of Tensaw, *Kral* 44393 (GA). Bibb Co., 19 ix 1937, *Laessle* s.n. (GA). Cherokee Co., gravel outcrop, 6 mi S Centre along Ala 9, *Kral* 31890 (GA). Coosa Co., Ala 22, 2.9 mi E jct. Ala 9, *Kral* 36628 (GA). DeKalb Co., Canyon Mouth Park, *Kral* 53032 (GA). Etowah Co., Gadsden, 1897, *Vasey* s.n. (NY). Henry Co., 5.4 mi SE of Abbeville, *Kral* 48984 (GA). Lee Co., Auburn, 1898, *Earle & Baker* 88578 (OS). Macon Co., 11 mi from Auburn, *Williams* 167 (GA). Marion Co., North Fork Creek, *Kral* 26289 (GA). Tuscaloosa Co., Oakman, *Kral* 44430 (GA). FLORIDA. Gadsden Co., Quincy, *Nash* 2567 (MICH, OS). River Junction, *Curtiss* 5979 (GA). Washington Co., Crystal Lake, *Orzell & Bridges* 11890 (TEX). GEORGIA. Baldwin Co., Milledgeville, *Moldenke & Moldenke* 26973 (TEX). Bartow Co., 4.5 mi SE of Adairsville, *Philip & Greear* 66194, 63101 (GA). Bulloch Co., 7 mi E of Statesboro, *Varnedoe* 163 (GA). Butts Co., SE of Jackson, *Howel* 442 (GA). Chatham Co., Rose Dhu Island, *Duncan* 21542 (GA). Cherokee Co., Canton, *Duncan* 8790 (GA). Clarke Co., Oconee River, *Cronquist* 4168 (GA). Clay Co., Chattahoochee River bluff, Fort Gaines, *Thorne* 4327 (GA). Cobb Co., Camp Burt Adams, *Duncan* 3888, 3907 (GA). Dade Co., Sand Mt., *Duncan* 5437 (GA); 4 mi S of the Tennessee line, *Duncan* 5397 (GA). Dawson Co., Amicalola Falls, *Duncan* 5310 (GA). Decatur Co., N of Chattahoochee, *Thorne & Davidson* 16395 (GA). Dooley Co., 4 mi W of Lilly, *Duncan* 5066, 5068 (GA). Dougherty Co., 1 mi S of Albany, *Thorne* 5126 (GA). Elbert Co., Goss, *Duncan* 4799 (GA). Fannin Co., N slope of Springer Mt., *Duncan* 5497 (GA). Floyd Co., Rome, *Curtiss* 6792 (GA). Forsyth Co., Mt Suwanee, *Duncan* 5242 (GA). Fulton Co., Atlanta, Rainwater, E 8085 (GA). Gilmer Co., Diamond, *Duncan* 5321 (GA). Gwinnett Co., Cardinal Lake, *Jones* 1601 (GA). Habersham Co., Tullulah Mt., *Duncan* 5213 (GA). Hall Co., 3 mi SW of Flowery Branch, *Adams & Duncan* 19473 (GA, MICH). Haralson Co., NE of Bremen, *Coile* 4570 (GA). Hart Co., Richard B. Russell Dam and Lake Area, *Credle* 572A (GA). Harris Co., FRD State Park, *Jones* 21235 (GA). Jenkins Co., Magnolia Springs, *Duncan* 5610 (GA). Jones Co., near Gray, *Cypert* 5 (GA). Lincoln Co., 13 mi E of Washington, *Pyron & McVaugh* 101 (GA). Lumpkin Co., Dahlonga, *Duncan* 5475 (GA). Madison Co., along Hwy in Colbert, *Duncan* 4763 (GA). McDuffie Co., area of the Fall Line Sand-hills, *Bartlett* 954 (MICH). Meriwether Co., Hanceville, *McKellar* 60 (GA). Monroe Co., Hill Fall State Park, *Howel* 348 (GA). Morgan Co., Hard Labor Creek State Park, *Hill* 433 (GA). Murray Co., Talking Rock Creek, *Kral* 50798 (GA). Muscogee Co., Fort Benning Military Reservation, *Stutts* 492, 635 (GA). Oconee Co., Watkinsville, *Duncan* 1403 (GA). Oglethorpe Co., Buffalo Creek, *Fitzgerald* 388 (GA). Paulding Co., SW of Dallas, *Duncan* 8627 (GA). Pickens Co., Eagle Mt. Woods Road, *Jones et al.* 25081 (GA). Putnam Co., Little River, *Duncan* 4898 (GA). Rabun Co., 1 mi N of Clayton, 5 viii 1930, *McKay* s.n. (GA). Spalding Co., Pomona, *Quaintance* 102 (GA). Stephens Co., base of Currahee Mt., *Duncan* 2900 (GA). Taliaferro Co., Crawfordville, *Shackleette* 6883 (MICH). Talbot Co., N slope of Oak Mt., *Duncan* 5132 (GA). Towns Co., Mt Brasstown, *Duncan* 5515 (GA); S side of Hightower Bald, *Duncan* 6895 (GA). Union Co., along Ga Hwy 60, Woody Gap, 20 v 1964, *Foote* s.n. (GA). Walker Co., 3.1 mi W of GA 201 at Villanow, *Garland* 560 (GA). Walton Co., Apalachee River bridge, *Moldenke & Moldenke* 29284 (TEX). Warren Co., 9 mi E of Warrenton, *Wilbur* 3006 (GA). White Co., Yonah Mt., *Duncan* 5192 (GA). Whitfield Co., 4 mi NW of Dalton, *Cronquist* 5066 (GA). Wilkes Co., Anthony Shoals, *Duncan* 1629 (GA). Worth Co., Flint River, *Faircloth* 3917 (GA). LOUISIANA. De Soto Co., 4.5 mi E of Benson, *Allen* 7740 (GA). Jackson Co.,

4 mi N of Quitman, *Lohman* 81 (GA). Lincoln Co., 5 mi W of Vienna, *Ortman* 196 (GA). MARYLAND. Baltimore Co., SE of Prettyboy Reservoir, *Winder & Lombardo* 3740 (GA). MISSISSIPPI. Carroll Co., 10.3 mi S of Winona, *Temple* 2645 (GA). Itawamba Co., 6.1 mi S of Fulton, *Temple* 5228 (GA). Jackson Co., *Demaree* 31262 (TEX). Smith Co., Shongelo Recreation Area, *Jones* 13812 (TEX). Tishomingo Co., Woodall Mt., *Temple* 3191 (GA). Wayne Co., Chichasawhay River, *Jones* 9703 (GA). Wilkinson Co., Clark Creek, *Pruski* 1007 (GA). NORTH CAROLINA. Cherokee Co., Snowbird Mt., *Wilbur* 4649 (GA). Durham Co., Bragtown, 13 viii 1932, *Blomquist* s.n. (MICH). Guilford Co., Greensboro, *WVB* 3099 (TEX). Haywood Co., Lake Junaluska, *Price* 370 (GA). Henderson Co., 3 mi W of Tuxedo, vii 1954, *Adams* s.n. (GA). Lincoln Co., SW of Cat Square, *Bell* 15345 (GA). Orange Co., 3 mi S of Hillsborough, *Radford* 44772 (GA). Wake Co., Raleigh, *Godfrey* 3563 (TEX). SOUTH CAROLINA. Abbeville Co., E of Rocky River, *Credle* 3054 (GA). Anderson Co., Brown's Park, *Davis* 839 (TEX). Lancaster Co., 2 mi S of Taxahaw, *Bozeman et al.* 8825 (TEX). Hardeville, 21 vi 1940, *Brown* s.n. (TEX). TENNESSEE. Hardin Co., N of Pickwick Dam, *Kral* 46682 (GA). Morgan Co., Daddys Creek, *Schmalzer* 373 (GA). VIRGINIA. Fauquier Co., S of Thorofare Gap, *Allard* 11861 (TEX); Mt Marshall, 15 vi 1929, *Janson* s.n. (MICH). James City Co., Matoaka Park, *Fernald* 367 (MICH); Warrenton, *Blake* 11349 (TEX); N of South Hill, *WVB* 2898 (TEX).