A NEW DISJUNCT VARIETY OF *CROTON ALABAMENSIS* (EUPHORBIACEAE) FROM TEXAS

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ABSTRACT

Croton alabamensis, formerly known only from Alabama in Bibb and Tuscaloosa counties, with one report from Coffee County, Tennessee, has been found in Texas in Coryell and Travis counties. The Texas plants are here described as *C. alabamensis* var. *texensis.* As in Alabama the plants occur in dense local populations generally as understory shrubs beneath hardwood dominated forest and typically grow in shallow soils over limestone. The possibility that a long distance dispersal event was responsible for the present distribution is discussed.

RESUMEN

Croton alabamensis, anteriormente conocido solo de los condados Bibb y Tuscaloosa, Alabama, con un reporte del Condado Coffee, Tennessee, ha sido encontrado en los condados de Coryell y Travis en Texas. Las plantas de Texas se describen aquí como *C. alabamensis* var. *texensis.* Como en Alabama, las plantas ocurren en poblaciones locales densas generalmente como arbustos del sotobosque debajo de bosque predominantemente caducifolio y tipicamente crecen en suelos poco profundos sobre un substrato de piedra caliza. Se discute la posibilidad de un evento de dispersion a larga distancia como responsable de la presente distribución exhibida por este taxón.

KEY WORDS: *Croton,* Euphorbiaceae, Texas

INTRODUCTION

Croton alabamensis E.A. Smith ex Chapman was first discovered in Texas in April 1989 by Carol Beardmore and Rex Wahl at Fort Hood Military Reservation, Coryell County. Chuck Sexton independently discovered a population on Post Oak Ridge in northwest Travis County in June 1989 and brought a specimen to me which I matched at TEX with *Croton alabamensis.* Later, a second Travis County population was found by Pat McNeil 4.4 mi south-southwest of the first. After visiting the three Texas populations and the type locality in Alabama, I have determined the Texas plants to be sufficiently distinct to merit varietal status.

TAXONOMIC TREATMENT

A key to the varieties is provided below with a full description for *Croton alabamensis* var. *texensis.*

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Croton alabamensis E.A. Smith ex Chapman, Fl. South. U.S., 2nd ed. 1883.—
LECTOTYPE: To be selected (Wurdack in prep.). There were no specimens cited in Chapman's protologue. The original material of *Croton alabamensis* was collected by Eugene A. Smith in July 1877 (Wurdack in prep.) near Pratt's Ferry, Bibb County, Alabama not far from the eastern bank of the Little Cahaba River (Mohr 1889).

KEY TO VARIETIES OF *CROTON ALABAMENSIS*

1. Scale-covered surfaces silver, covered by scales of a mixture of pigmentation types; scales mostly unpigmented or light amber and lacking dark centers, scattered scales dark blackish-brown; flowers per inflorescence 9 – 18, fruits per infructescence 0 – 11 ..... *C. alabamensis* var. *alabamensis*
1. Scale-covered surfaces copper-colored, covered by scales of a mixture of pigmentation types; scales unpigmented or with dark reddish-brown centers (basal cells) and reddish-amber rays; flowers per inflorescence 6 – 14, fruits per infructescence 0 – 6 ..... *C. alabamensis* var. *texensis*

Croton alabamensis E.A. Smith ex Chapman var. **alabamensis**

Distribution. Alabama and Tennessee. In Alabama known only from Bibb County, Cahaba River valley (seven populations) and from Tuscaloosa County, Warrior River valley (three populations). There is one collection from Tennessee: Coffee County, Tullahoma, 10 Aug 1899, *T.G. Harbison 725* (NCU, not seen) (Farmer & Thomas 1969). The plants occur on shallow-soiled valley slopes in dense thickets covering up to 15 acres (McDaniel 1981). Populations along the Cahaba River occur on Ordovician limestone; those along the Warrior River are found on Pennsylvanian shale and sandstone. They begin flowering in late February with peak flowering in mid-March. Flower buds form during May and June which will not open until the following year. Fruits have matured and dehisced by early June (Farmer 1962).

Croton alabamensis E.A. Smith ex Chapman var. **texensis** Ginzbarg, var. nov. (Fig. 1).

Croton alabamensis E.A. Smith ex Chapman var. *alabamensis* similis sed differt paginis squamis obtectis cupreis vs. argenteis, squamis plerumque centris atroporphyreis et radiis rubro – succineis vel squamis absque pigmento vs. plerumque absque pigmento vel leviter succineis, floribus 6 – 14 per inflorescentiam vs. 9 – 18, fructibus 0 – 6 per infructescentiam vs. 0 – 11.

Monoecious shrub to 2 m or more tall, much-branched from the base, lower branches sometimes rooting; stems with thin gray bark giving a slightly sweet odor when scratched, leafy only near their tips, new growth angular, with projecting leaf bases; axillary branches normally only 1 – 4 cm long but those just below old inflorescences elongating to form irregular bi(tri)furcations. Indument a mixture of pigmented and unpigmented scales, *the pigmented scales with dark reddish-brown centers and reddish-amber rays, giving a copper-colored appearance to new stems, petioles, lower leaf surface, inflorescence, outer surface of sepals and petals, ovary and capsule, and outer surface of style branches.* Leaves alternate, exstipulate; petioles

FIG. 1. A. Inflorescence with an opened pistillate flower and staminate flowers in bud, scale bar 2 cm *(Ginzbarg 898).* B. Inflorescence with one pistillate flower at base and staminate flowers above, scale bar 2 cm *(Ginzbarg 898).* C. Fruit, scale bar 1 cm *(Ginzbarg 900).* D. Habit *(Ginzbarg 898).*

0.6 – 1.9 mm long, canaliculate; blades ovate or elliptic, 3.8 – 9.0 cm long, 1.5 – 4.0 cm wide, entire; apex acute, rounded or emarginate; base obtuse to slightly cordate, glandless; upper surface dark green with scattered scales, midvein canaliculate; lower surface with prominent midvein and lower lateral veins. *Inflorescence a terminal* 6 – 14 *flowered raceme,* 1.9 – 3.3 cm long with pistillate flowers near the base and staminate flowers above; early flowering racemes with 0 – 1 pistillate flower and 5 – 12 staminate flowers; later flowering racemes with 2 – 6 pistillate flowers and 4 – 10 staminate flowers. Staminate flowers broadly cup-shaped, 5.0 – 8.1 mm in diameter, on pedicels 2.2 – 4.0 mm long, subtended by bracts 1.1 – 3.0 mm long; calyx lobes 5, spreading, triangular, cymbiform at apex, 1.1 – 2.9 mm long, 1.5 – 3.0 mm wide; petals 5, oblong-ovate, cymbiform at apex, stellate ciliate, 2.0 – 3.1 mm long, 1.1 – 2.1 mm wide; stamens (11-)14 – 18(-21), with filaments 2.8 – 5.2 mm long, densely stellate-lanate at base, and anthers 0.6 – 1.2 mm long, composed of convergent anther sacs; disc of 5 pairs of orange glands opposite the sepals, the two glands of each pair lying on either side of the stamens of the outer whorl, narrowing, converging and fusing just outside the filament bases, receptacle glabrous but obscured by the filament base hairs. Pistillate flowers on pedicels 2.2 – 7.4 mm long, subtended by spatulate, apically rounded bracts 1.6 – 6.0 mm long; sepals closely enveloping ovary, ascending, cymbiform at apex, 2.0 – 4.5 mm long, 2.0 – 3.1 mm wide; petals ovate from a narrow base, cymbiform at apex, stellate ciliate, 2.0 – 3.0 mm long, 1.1 – 1.9 mm wide; disc of 5 orange semilunar glands opposite the sepals, 1.0 – 2.1 mm tangentially, 0.4 – 0.7 mm radially; ovary superior, depressed spheroidal, 1.6 – 2.5 mm tall, 2.0 – 3.0 mm wide; styles 3, recurved, connate at base for 0.2 – 0.7 mm, 2.0 – 5.0 mm long, furrowed and yellow (turning reddish brown with age) adaxially, once (twice) divided, first division (0.1-)0.5 – 2.0 mm from apex, second division 0.0 – 1.0 mm from apex. Capsules light brown, on pedicels 7.0 – 10.6 mm long, depressed spheroidal, weakly 3 – (-4) lobed apically, columella 6.8 – 9.5 mm long; seed elliptic tangentially, mucronate apically, back rounded, adaxial faces converging at a wide angle, 6.7 – 7.9 mm long, 5.2 – 6.0 mm wide, chestnut brown with white blotches and streaks, caruncle yellow, 1.2 – 2.4 mm long, 1.9 – 2.6 mm wide, above a prominent white keel at the point of attachment. Flowering Feb – Mar. Fruiting May. Fruits have dehisced by early June.

Distribution. Texas, eastern edge of the Edwards Plateau. Known only from Travis and Coryell counties.

Ecology. The plants form dense local thickets as understory shrubs in mesic canyon hardwood forests or in full sun. Flower buds form in May and overwinter, blooming the following spring. Canyon slopes are generally characterized by shallow, moderately alkaline, gravelly or stony clay or clay – loam overlying Cretaceous limestone. Soils are well drained, permeability moderate and available water capacity low (McCaleb 1985, Werchan et al. 1974).

TYPE: TEXAS. Travis Co.: Gainer Ranch, 6 mi W of Liberty Hill on RR 1869, then 6.4 mi S to gate, then 2 mi SE (5 air mi SW of Liberty Hill), NE facing drainage and adjacent plateau, 365 m, 30° 36' 24" N 97° 58' 33" W, 3 Mar 1990, *Ginzbarg 898* (HOLOTYPE: TEX; ISOTYPES: BRIT/SMU, F, GA, IBE, MO, NY, UNA, US, VDB).

Additional specimens examined: TEXAS. **Coryell Co.:** Fort Hood Military Reservation, creek bottom, 30 Apr 1989, *Beardmore & Wahl* 056 (TAMU); Fort Hood Military Reservation, 0.6 air mi SSE Cold Springs, S side of Owl Cr., N flank of Owl Cr. Mts., NW slope adjacent to drainage, 31° 14' 02"N 97° 35' 46"W, 25 Oct 1989, *Cornelius s.n.* (TEX). **Travis Co.:** Gainer Ranch, 6 mi W of Liberty Hill on RR 1869, then 6.4 mi S to gate, then 2 mi SE (5 air mi SW of Liberty Hill.), NE facing drainage and adjacent plateau, 365 m, 30° 36' 24"N 97° 58' 33"W; 15 Jun 1989, *Enquist 495* (SMU, TAES, TEX); 13 Jun 1989, *Ginzbarg 895* (IBE, TEX, UNA); 12 Aug 1989, *Ginzbarg 896* (TEX); 12 Aug 1989, *Ginzbarg 897* (IBE, TEX, UNA); 8 May 1990, *Ginzbarg 900* (BRIT/SMU, GA, IBE, MO, TEX, UNA, US, VDB); 6 Jun 1989, *Sexton s.n.* (TEX); adjacent to Penn Ranch (a.k.a. Sunset Ranch), W side of Post Oak Ridge, NW facing canyon, ca. 0.6 mi N, 0.3 mi W of Hanging Rock Spring, 305 – 365 m, 30° 32' 45"N 97° 59' 47"W, 15 May 1991, *Carr 11153* (TEX); 7 Mar 1990, *Ginzbarg 899* (IBE, MO, NY, TEX, UNA, US, VDB).

Population site descriptions. In Travis County, the plants occur mostly in deciduous forest in mesic limestone canyons and on slopes. Some plants are also found on adjacent drier slopes with Ashe Juniper woodlands and Glen Rose outcrop grassland flora. Populations occur on Cretaceous limestone. Most plants are found in canyons and slopes on upper Glen Rose Formation. Those plants found on adjacent plateau rimrock are on Walnut Formation, Bee Cave Member (marl) and Edwards Formation.

The Gainer Ranch population has about 500 – 1000 plants. Most plants are in canyon forest under *Quercus buckleyi* and *Fraxinus texensis* but at the head of the canyon they are also found in full sun on the adjacent plateau. The population ends abruptly part way down the canyon with the disappearance of limestone rock outcrops. *Croton alabamensis* is the dominant shrub at the site. The dominant shrub in a nearby canyon where *Croton alabamensis* was not found is *Garrya lindheimeri.* Canyon soils are rocky and contain considerable humus. They are mapped as Tarrant soils and Rock outcrop, steep (TdF) (Werchan et al. 1974).

The Penn Ranch main population has several thousand individuals most common on nearly level terraces, but also extending upslope. Canyon forest canopy is dominated by hardwoods, mostly *Quercus buckleyi* and some *Ulmus americana;* adjacent drier areas are dominated by *Juniperus ashei.* Shrub layer in hardwood areas is dominated by *Croton alabamensis, Ilex vomitoria,* and *Garrya lindheimeri.* Ground cover is sparse under yaupon and *Croton alabamensis* thickets consisting mainly of scattered *Carex planostachys.* Diversity is greater on more open slopes. Other associated species are listed in Table 1. Soils are clay loam or loam, with considerable duff cover. They are comparatively deep even on slopes, and generally lack stones and gravel although some large flags are present on surface. Soils are mapped as Brackett soils and Rock outcrop, steep (BoF) (Werchan et al. 1974), but the soils within the canyon are of an unmapped series. A smaller population of about 100 plants was seen near the top of a north to west-

facing slope in next drainage to the south (about 0.2 air miles north, 0.35 air miles west of Hanging Rock Spring. *Croton alabamensis* at this site does not occur on terraces but grows under a band of deciduous trees (possibly on a seep zone) on an upper slope otherwise dominated by *Juniperus ashei.* Scattered individuals were also seen in old clearings in "cedar brakes" on dry shallow Brackett soils. (Observations of the Penn Ranch population follow from Carr 1991.)

In Coryell County, The Fort Hood main population probably has several thousand plants. It was not possible during my visit to traverse the full extent of the population. A second population (not seen) is located in another canyon about 1.1 miles east at 31° 14' 02"N 97° 36' 39"W. Associated species are listed in Table 1. Populations occur on Cretaceous limestone. Most plants are found in canyons and slopes on Walnut clay and Comanche Peak limestone. Any plants found on adjacent plateau rimrock would be on undifferentiated Washita (or Edwards) limestone. Soils are mapped as Real – Rock outcrop complex (ReF) (McCaleb 1985).

TABLE 1. Plants associated with *Croton alabamensis* var *texensis.* Species observed primarily in Texas Oak Series mesic limestone canyon forest community (Diamond 1992) are indicated by TO; species observed primarily in Ashe Juniper-Oak Series woodland/grassland on adjacent drier slopes are indicated by AJO; a few herbaceous species seen mostly in creekbeds are indicated by CB; species not primarily restricted to one community are indicated by X. Species lists for the Penn Ranch site were contributed by Bill Carr; those for Gainer Ranch and Ft. Hood sites were contributed by Jackie Poole.

WOODY PLANTS	Gainer	Penn	Ft. Hood
Baccharis neglecta	TO		
Berberis trifoliolata		AJO	
Bumelia lanuginosa	TO	X	TO
Celtis laevigata	TO		
Cercis canadensis	TO	TO	TO
Cornus drummondii		TO	
Croton alabamensis	TO	TO	TO
Diospyros texana	TO	AJO	
Eupatorium havanense	TO	TO	
Eupatorium sp.	TO		
Eysenhardtia texana		AJO	
Forestiera pubescens	TO	X	
Fraxinus texensis	TO	TO	TO
Garrya lindheimeri		TO	
Ilex decidua	TO	TO	TO
Ilex vomitoria		TO	TO
Juglans microcarpa		TO	
Juniperus ashei	TO	X	TO
Mimosa borealis		AJO	
Morus microphylla		TO	
Nolina lindheimeriana		AJO	
Opuntia lindheimeri		TO	
Parthenocissus quinquefolia		X	
Platanus occidentalis		TO	
Prunus mexicana		TO	

WOODY PLANTS	Gainer	Penn	Ft. Hood
Prunus serotina		TO	
Ptelea trifoliata	TO	TO	
Quercus buckleyi	TO	TO	TO
Quercus fusiformis			TO
Quercus muhlenbergii		TO	
Quercus sinuata var breviloba	X	X	TO
Rhamnus caroliniana		TO	TO
Rhus aromatica		X	
Rhus toxicodendron	TO	X	TO
Rhus virens		AJO	TO
Rubus trivialis	TO	X	
Sapindus saponaria		TO	
Smilax bona-nox	TO	X	
Ulmus americana		TO	
Ulmus crassifolia	TO	TO	TO
Ungnadia speciosa		TO	
Viburnum rufidulum	TO	TO	
Vitis berlandieri	TO		
Vitis sp.		X	TO
Yucca rupicola	AJO		
GRASSES/SEDGES			
Bothriochloa barbinervis	TO		
Bouteloua pectinata		AJO	
Carex edwardsiana		TO	
Carex microdonta		CB	
Carex planostachys		X	TO
Dichanthelium lindheimeri		CB	
Dichanthelium pedicellatum	X		
Dichanthelium sp.		TO	
Eleocharis acutisquamata		AJO	
Eleocharis montevidensis		CB	
Erioneuron pilosum		AJO	
Muhlenbergia lindheimeri		CB	
Muhlenbergia reverchonii		AJO	
Panicum virgatum		CB	
Schizachyrium scoparium		AJO	
FORBES			
Agalinis edwardsiana		AJO	
Anemone edwardsiana		TO	
Anemone heterophylla			TO
Aristolochia serpentaria		TO	
Argythamnia simulans		X	
Asclepias oenotheroides		AJO	
Brickellia cylindracea		X	
Clematis texensis		TO	
Commelinantia anomala		TO	
Daucosma laciniatum		X	
Desmodium psilophyllum		TO	
Desmodium sp.			TO
Euphorbia angusta		AJO	
Euphorbia fendleri		AJO	

(TABLE 1 continued)

WOODY PLANTS	Gainer	Penn	Ft. Hood
Galium aparine	TO	X	
Galium circaezans			TO
Galium texense?	TO		
Hedeoma acinoides		X	
Hedeoma drummondii		AJO	
Hedyotis nigricans		AJO	
Krameria lanceolata		AJO	
Lactuca serriola	TO		
Lespedeza texana		X	
Linum rupestre		AJO	
Lithospermum incisum		AJO	
Lonicera albiflora	TO		TO
Matelea reticulata	TO	X	
Melampodium leucanthum		AJO	
Onosmodium helleri		TO	
Oxalis dillenii		X	
Parietaria obtusa		X	
Parietaria pensylvanica	TO		
Passiflora lutea		X	
Passiflora sp.	TO		
Physalis viscosa		X	
Pinaropappus roseus		X	
Polygala lindheimeri		X	
Psoralea latestipulata		AJO	
Psoralea tenuiflora		AJO	
Ruellia humilis		X	
Salvia engelmannii		AJO	
Salvia roemeriana		TO	TO
Scutellaria drummondii		X	
Senecio obovatus		TO	
Senecio obovatus?			TO
Silphium albiflorum		AJO	
Sisyrinchium ensigerum		AJO	
Solidago nemoralis		AJO	
Stillingia texana		AJO	
Thelesperma simplicifolium		AJO	
Tragia ramosa		X	
Triodanis coloradoensis		X	
Verbesina lindheimeri		X	
Verbesina virginica	TO	X	
Vicia sp.	TO		TO
Zexmania hispida		X	
Zigadenus nuttallii	TO		
FERNS			
Adiantum capillus-veneris		TO	
Asplenium resiliens		TO	
Cheilanthes alabamensis		X	
Pellaea atropurpurea		X	

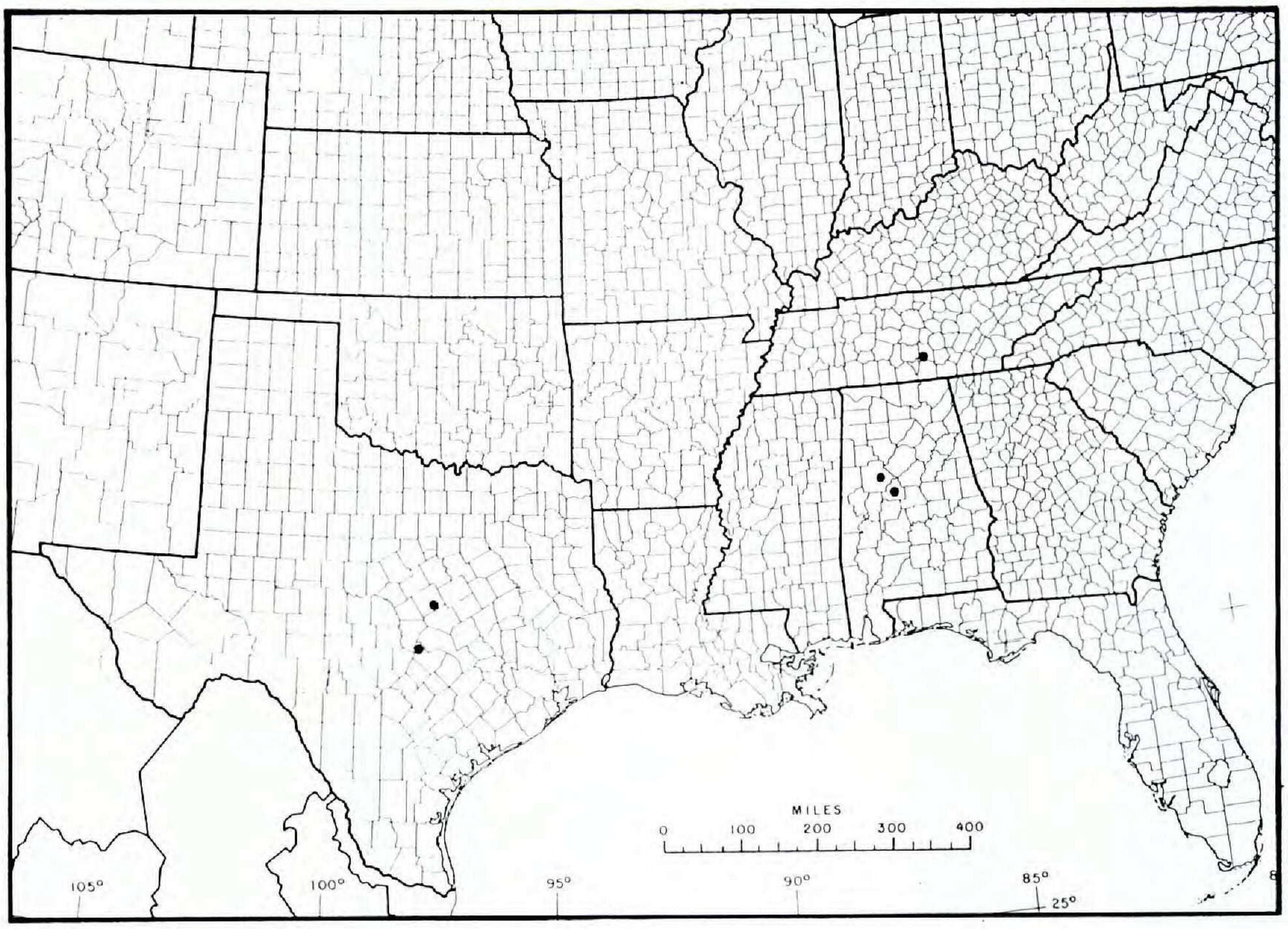

FIG. 2. Distribution of *Croton alabamensis*.

BIOGEOGRAPHY

The Texas populations of *Croton alabamensis* are separated from the Alabama populations by nearly a thousand kilometers (Fig. 2), a remarkable disjunction considering that so few populations are known. One possible explanation is that the range of *Croton alabamensis* was once much more extensive and the present distribution is relictual. During the Wisconsin Glaciation a temperate forest belt extended along the Gulf Coast (possibly broken by a southern extension of boreal forest along the lower Mississippi Alluvial Valley). Within this belt deciduous forest species would have found refuge in fire protected mesic habitats such as river bluffs. Glacial retreat was accompanied by a shift in patterns of atmospheric circulation. Influenced by the dry Pacific airmass, prairie first appeared in Texas about 12,000 yr B. P. (Delcourt & Delcourt 1987). *Croton alabamensis* is thin-barked and probably not fire tolerant (Kral 1983). It is doubtful that it could have survived frequent prairie fires. Relictual populations of *Croton alabamensis* could have survived in mesic ravines of the Edwards plateau.

The hypothesis of a relictual distribution, proposed by Mohr (1901), is supported by the fact that other species show similar distributions. Climatic change could cause species with similar habitat requirements to retreat to the same areas. *Andrachne phyllanthoides* and *Cotinus obovatus* exhibit a disjunction similar to that of *Croton alabamensis* between the Edwards Plateau in Texas and the

Appalachian Plateau in Alabama but are also known from the Ozark Plateau of Arkansas and adjacent Missouri and Oklahoma (distributions provided by Steve Orzell and Edwin Bridges). Although the similarities of the distributions of these species suggest a relictual distribution, it is equally plausible that the species occur in the same areas because these have colonized present day "islands" of suitable habitat.

The present distribution of *C. alabamensis* is more easily explained as the result of a relatively recent introduction by long distance dispersal. The local distribution of *Croton alabamensis* is characterized by exceedingly rare but very dense populations which appear to be thriving. The species is not present in many apparently suitable sites near the known populations. A relict species with a long history in the area would have had time to invade these sites unless it had come close to extinction and is now making a comeback. The density of the colonies suggests that the usual mode of seed dispersal is probably the explosive dehiscence of the capsules without significant secondary dispersal. Some vegetative propagation by root-layering of the lower branches also occurs. Although Farmer (1962) reports that root layering was never observed in the Alabama populations, I did observe it at the type locality in Alabama and at the Gainer Ranch population in Texas. Rare secondary dispersal of seeds could have led to the establishment of new colonies. Croton seeds are eaten by Mourning and White-winged doves and quail (Johnston, 1959). Seeds passing through the gut intact could found new colonies locally. It is not inconceivable that Passenger pigeons, once the most abundant bird in North America, could have carried seeds eaten in Alabama to Texas during their fall migration. Although central Texas was on the western periphery of their normal winter range (Bent 1932), in some years large flocks made forays here, stopping to roost where they found suitable habitat. Passenger pigeons were reported from both Travis and Coryell counties (Oberholser 1974). The minor morphological differences between the Texas and Alabama plants could have arisen by founder effect followed by mutation and genetic drift over a relatively short divergence time.

TAXONOMIC RELATIONSHIPS

Croton alabamensis belongs to sect. *Eluteria* Grisebach (sect. *Andrichnia* Baillon). This section is characterized by the presence of petals in pistillate flowers, a condition which may be primitive within the genus. All other crotons have pistillate flowers with petals rudimentary or lacking. As treated by Mueller (1866) the section consists of 25 species, 17 with lepidote and 8 with stellate pubescence. The stellate species are from Madagascar, Mauritius, and west Africa. Seven of the lepidote species are from Africa, Madagascar, and India and possess petiolar glands. The remaining 10 lepidote species are neotropical and lack petiolar glands. *Croton alabamensis* is the only member of this section found in the U.S. although Croizat (1945) has suggested that *Croton argyranthemus* which lacks

petals in the pistillate flowers may be related to this group. Of the lepidote species within sect. *Eluteria* there are only two other species with styles divided only once (Mueller 1866). These are *Croton joufra* Roxburgh from India, which has petiolar glands, and *Croton claussenianus* Baillon from the state of Minas Gerais, Brazil. Croizat (1945) treated the species of sect. *Eluteria* native to the region from Alabama to Panama with emphasis on seed and capsule characters. His key places *Croton alabamensis* closest to the Mexican species *C. pseudochina* Schldl. & Cham. and *C. reflexifolius* Kunth. Further study is needed to shed light on the intriguing biogeography and affinities of *Croton alabamensis.*

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