1981

A Systematic Study of the Mexican, Central American, and Jamaican Species of the Genus Calea.

James Richard Wussow

Louisiana State University and Agricultural & Mechanical College

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A SYSTEMATIC STUDY OF THE MEXICAN, CENTRAL AMERICAN, AND JAMAICAN SPECIES OF THE GENUS CALEA

The Louisiana State University and Agricultural and Mechanical Col. Ph.D. 1981

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A Systematic Study of the Mexican, Central American, and Jamaican Species of the Genus *Calea*

A Dissertation

Submitted to the Graduate School of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

The Department of Botany

James Richard Wussow
B.A., University of Texas, 1976
M.S., Louisiana State University, 1978
August, 1981
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ABSTRACT

_Calea_, a large genus in the Asteraceae, tribe Heliantheae, consists of mostly shrubs that occur throughout the Neotropics. Robinson and Greenman's treatment of the Mexican and Central American species has remained the definitive study of _Calea_ for this area since 1896. Recent studies, including the present one, have greatly modified their earlier treatment. From among the more than 75 names attributed to _Calea_ in Mexico, Central America, and Jamaica, the present study recognizes 18 taxa representing 8 species and 10 varieties. The species recognized in this treatment include _C. crassifolia, C. fluviatilis, C. longipedicellata, C. jamaicensis, C. prunifolia, C. ternifolia, C. trichomata_, and _C. urticifolia_. One variety, _C. urticifolia var. yucatanensis_ is described as new. _Calea megacephala_ is excluded from _Calea_ with the recommendation that it be accommodated in the monotypic genus _Tonalanthus_ Brandegee.
INTRODUCTION

_Calea_ is a large genus in the Asteraceae, consisting of mostly shrubs that occur throughout the Neotropics. The greatest centers of diversity are Mexico, Central America, northern South America, and Brazil. The only inclusive treatments for the genus are those by De Candolle (1836), Bentham and Hooker (1873), and Hoffmann (1894); no modern, comprehensive investigation has been attempted.

Concerning the Mexican, Central American, and Jamaican species of _Calea_, most early studies consisted of isolated reports of new taxa or combinations, or had a narrow geographic perspective. Consequently, the interrelationships among taxa have been poorly understood, and the nomenclature is highly superfluous. The paper by Robinson and Greenman (1896), which was based on limited material, had been the only comprehensive treatment for the Mexican and Central American caleas. Only recently have additional studies of enlarged scope have been carried out (Longpre, 1970; Fay, 1975; Robinson, 1978; Wussow and Urbatsch, 1979; Fernandez and Urbatsch, 1981), and these have greatly modified their earlier treatment.

The present study of the Mexican, Central American, and Jamaican species represents the first segment of a program to revise the entire genus. A combination of data from herbarium specimens, fixed material, greenhouse grown plants, and field observations was employed in formulating the present treatment.

From among the more than 75 names attributed to _Calea_ in Mexico, Central America, and Jamaica, the present study recognizes 18 taxa.
representing eight species and ten varieties. One species is endemic to Jamaica, two are restricted to Central America, four are found in Mexico and Central America, and one occurs in Central America and South America. One variety Calea urticifolia var. yucatanensis is described as new.
The genus Calea was established by Linnaeus (1763) in the second edition of his Species Plantarum to accommodate three species, C. jamaicensis, C. oppositifolia, and C. amellus that he had originally included in the genus Santolina (Linnaeus, 1760). Two of the three original Linnean species were transferred to other genera by Brown (1818), leaving only C. jamaicensis in Calea.

The only inclusive study of the Mexican and Central American species of Calea was the cursory treatment by Robinson and Greenman in 1896. Since then a considerable amount of collections and information have been accumulated. In addition to the isolated publications of new taxa, various new combinations, and taxonomic transfers, Canne (1975) treated the Panamanian species for the Flora of Panama, while Nash (1976) similarly investigated the Guatemalan species.

Recent studies by H. Robinson (1978), Fernandez and Urbatsch (1981), and Wussow and Urbatsch (1979) have greatly redefined Calea by reinstating the genera Alloispermum and Tetrachyron. In the present study, eight species and eighteen taxa are recognized from an excess of 75 names that have been attributed to the Mexican, Central American, and Jamaican species of Calea.

The following list is a chronological summary of the taxonomic history for the Mexican, Central American, and Jamaican species of Calea:
1763: Linnaeus established the genus Calea based on the 3 species, C. jamaicensis, C. oppositifolia \(\text{[=}\text{Isocarpha oppositifolia (L.) Br. }]\), and C. amellus \(\text{[=}\text{Salmea scandens DC. var. amellus (L.) Ktz. }]\), that he had originally placed in Santolina (Linnaeus, 1760).

1788: Jacquin described Calea aspera \(\text{[=}\text{Melanthera aspera (Jacq.) Rich. ex Spreng. }]\) based on material from Jamaica.

1788: Swartz described Calea lobata \(\text{[=}\text{Nuerolaena lobata (Sw.) Br. }]\) based on material from Jamaica.

1794: Moench published the superfluous name Calea trifida based on C. jamaicensis (L.) L.

1806: Swartz described Calea cordifolia \(\text{[=}\text{Calea jamaicensis (L.) L.}]\) The description agrees perfectly with that of C. jamaicensis, although in the same article he gives a slightly different account of C. jamaicensis.

1818: Robert Brown suggested the generic name Caleacte based on Solidago urticifolia of Miller from near Vera Cruz. \(\text{[=}\text{Calea urticifolia (Mill) DC.}]\). The genus differed from Calea solely in the possession of ray flowers.

Robert Brown also proposed the genus Isocarpha to accommodate C. oppositifolia and placed C. amellus in synonymy with Salmea scandens.

1820: Humboldt, Bonpland, and Kunth described as new C. prunifolia and C. ternifolia, both reportedly from Colombia. (It was discovered during this study that C. ternifolia was undoubtedly based on a Mexican collection — see discussion in taxonomic
section). They also described: *Calea peduncularis* HBK
\[ = *Alloispermum scabrum* (Lag.) H. Rob. var. *scabrum* ]
from Mexico,

1828: Cassini proposed the genus *Calebrachys* to include *Calea peduncularis* \[ = *Alloispermum scabrum* (Lag.) H. Robinson var. *scabrum* ].

1830: Lessing published *C. cacosmioides* \[ = *C. urticifolia* (Mill.) DC. var. *urticifolia* ] from Mexico,

1834: Schlechtendal described as a new species *C. zacatechichi* \[ = *C. ternifolia* HBK var. *zacatechichi* (Schlect.) Wussow and Urbatsch ] based on material from near Jalapa, Vera Cruz, Mexico.

1836: De Candolle published the new species *C. verbenaefolia* \[ = *Lasianthaea ceanothifolia* (Willd.) K. Becker var. *ceanothifolia* ] from Mexico. In addition they made the new combination *C. brachiata* (Spreng,) and described as new *C. elegans* \[ = *Otezia acuminata* La Llave ] based on an Alaman collection from Mexico, and *C. axillaris* \[ = *C. urticifolia* (Mill.) DC. var. *urticifolia* ] from Mexico.

1847: Schauer described the monotypic genus *Aschenbornia* based on *Aschenbornia heteropoda* \[ = *C. ternifolia* HBK. var. *ternifolia* ],

1873: Bentham and Hooker reduced the genera, *Allocarpus*, *Calydermos*, *Calebrachys* and *Tetrachyron* to infrageneric rank with *Calea*. 
1880: Asa Gray proposed the subgenus Tephrocalea to include

*C. discolor* [*= Tetrachyron discolor* (A. Gray) Wussow
and Urbatsch J] and *C. tomentosa* [*= Tetrachyron grayi*
(Klatt) Wussow and Urbatsch J. Both are based on specimens
collected by Coulter from Mexico. He also described

*C. albida* [*= C. ternifolia* HBK var. *calyculata* (Robins.)
Wussow and Urbatsch J] based on material from near San
Luis, Mexico.

1881: Hemsley proposed several new combinations:

*Calea integrifolia* (DC.) Hemsley [*= Alloispermum
integrifolium* (DC.) H. Robins. J; *Calea manicata* (Schlect.)
B. and H. ex Hemsley [*= Tetrachyron manicatum* Schlechtendal J];
*Calea rugosa* [*= Calea ternifolia* HBK. var. *ternifolia* J];
*Calea sabaziodes* [*= Sabazia sarmentosa* Less var. *sarmentosa* J];
*Calea salmaefolia* (DC.) Hemsley [*= C. ternifolia* HBK. var.
calyculata* (Rob.) Wussow and Urbatsch J]; and *Calea scabrifolia*
(Hook. and Arn.) Hems. [*= Alloispermum scabrifolium* (Hook.
and Arn.) H. Robinson J.

1884: Klatt proposed the name *C. grayii* for the illegitimate name

*C. tomentosa* Gray [*= Tetrachyron grayi* (Klatt) Wussow and
Urbatsch J.

1887: A. Gray described *Calea palmeri* [*= Alloispermum palmeri*
(Gray in Watson) Fernandez and Urbatsch J] from Mexico, and
reduced *Calydermos longifolius* (Lag.) Gray to varietal status,
*Calea peduncularis* var. *longifolia.*
Klatt described C. liebmannii [= C. ternifolia HBK. var. ternifolia] from Gualulu, Mexico. He also designated the plant as belonging to section (subgenus) Calydermos. He also proposed as new Calea orizabaensis [= Tetrachyron orizabaensis Sch. Bip. ex Klatt] from Orizaba, Mexico.

1888: J. Donnell Smith described C. trichomata based on material from near Coban, Guatemala.


1893: Seaton described as new C. multiradiata [= Sabazia multiradiata (Seaton) Longpre] based on material from Mt. Orizaba, Mexico.

1895: Coulter described C. integrifolia var. dentata [= Alloispermum scabrifolium (Sch. Bip.) H, Robins.] from Mexico.

1896: Robinson and Greenman produced the only comprehensive treatment of the Mexican and Central American species of Calea prior to the present study. In their treatment several new taxa were proposed: Calea megacephala [= Tonalanthus aurantiacus Brandegee] from Mexico; C. thysanolepis [= Alloispermum scabrum var. thysanolepe] from Mexico; C. peduncularis HBK. var. livida [= Alloispermum scabrum var. lividum] and C. peduncularis var. epapposa [= Alloispermum scabrum var. scabrum] from Mexico; C. hypoleuca [= C. ternifolia HBK. var. calyculata (Robins.,) Wussow and Urbatsch] from Mexico; C. nelsonii [= C. ternifolia HBK. var. nelsonii (R. and G,) Wussow and Urbatsch] based on
a Nelson collection from Tonala, Chiapas, Mexico; Calea zacatechichi Schlect. var. macrophylla [= C. ternifolia HBK. var. ternifolia] from Guatemala; and C. longipedicellata based on a Nelson collection from Choapam, Oaxaca, Mexico. They also reduced C. rugosa to varietal status under C. zacatechichi [= C. ternifolia HBK. var. ternifolia] and made the new combination Calea axillaris DC. var. urticifolia [= C. urticifolia (Mill.) DC.].


1899: Calea pittieri [= Calea prunifolia HBK. var. prunifolia] was described by Robinson and Greenman based on material from Costa Rica.

1901: Robinson proposed the new species C. pringlei [= Calea ternifolia HBK. var. ternifolia] from Guerrero, Mexico, and the new variety C. zacatechichi var. calyculata [= C. ternifolia HBK. var. calyculata (Rob.) Wussow and Urbatsch] based on material from near Monterrey, Mexico.

1905: Millspaugh published the superfluous name C. urticifolia.

1907: Greenman proposed the new variety Calea pringlei var. rubida [= Calea ternifolia var. zacatechichi] based on material from near Chavarillo, Vera Cruz, Mexico.

1908: Brandegee described as new C. rupestris = Tetrachyron orizabaensis Sch. Bip. ex Klatt var. orizabaensis based on material from Puebla, Mexico.
1909: Robinson made the new combination *Calea scabra* (Lag.) and reduced *C. peduncularis* to varietial status under *C. scabra*, making the new combination *C. scabra* var. *peduncularis* [= *Alloispermum scabrum* var. *scabrum*]. He also placed *C. peduncularis* var. *eppaposa* in the synonymy of *C. scabra* var. *scabra* and recognized as varieties of *C. scabra* var. *longifolia* [= *Alloispermum scabrum* var. *scabrum*] and *C. scabra* var. *livida* [= *Alloispermum scabrum* var. *lividum*]. In addition the species *C. peckii* [= *C. trichomata* D. Smith var. *peckii* (Rob.) Wussow and Urbatsch] was described by Robinson based on a Peck collection from British Honduras.

1912: Greenman proposed *C. brandegei* *Tetrachyron brandegei* (Greenman) Wussow and Urbatsch from Puebla, Mexico.

1917: Blake described *Calea insignis* [= *Otezia raucophila* (Donn. Sm) Fay] from Guatemala.

1924: *Calea purpusii* [= *Alloispermum scabrum* var. *scabrum*] was described as new by Brandegee based on material from Chiapas, Mexico. Blake published several new species: *C. leptocephala* [= *C. ternifolia* HBK. var. *ternifolia*] based on material from Tonameca, Oaxaca, Mexico; *Calea sororia* [= *Calea ternifolia* HBK. var. *ternifolia*] based on a Nelson collection from Huehuetenango, Guatemala; and *C. tejadae* [= *C. ternifolia* HBK. var. *ternifolia*] based on a collection by Tejada from Guatemala. Blake also transferred *Altamirania pachyphylla* to *Calea*, section *Tetrachyron* [= *Verbesina pachyphylla* (Sch. Bip. ex Klatt) Wussow and Urbatsch].
1926: Blake included Calea in Standley's Trees and Shrubs of Mexico, based largely on Robinson and Greenman's 1896 treatment.

1929: Moore proposed the new variety C. jamaicensis (L.) L. var. parvifolia [= C. jamaicensis (L.) L.] from Jamaica.

1930: After comparison of the types, Blake placed his C. leptocephala in synonymy with C. liebmannii Schultz Bip. ex Klatt.

1932: Blake described the new species C. fluviatilis based on a Bartlett collection found on stones in the Rio Pravacion of Belize.

1934: Blake described Calea skutchii [= Podachaenium skutchii (Blake) H. Robins.] based on a Skutch collection from Guatemala.

1938: Standley published C. dichomata [= C. ternifolia HBK. var. ternifolia ] based on material from Maderal de San Mateo, Costa Rica. This collection still represents the only report of this species from Costa Rica.

1940: Calea standleyi [= Verbesina pachyphylla ] was described by Steyermark based on material from Guatemala.

1947: Standley and Steyermark published C. savannarum [= Spilanthes uliginosa Sw. ] based on material from Guatemala. They also described Calea crassifolia from Cerro Chinaja, Guatemala. This species is still only known from the type collection.

1950: Standley and Williams described the new species C. acuminata [= C. ternifolia HBK. var. ternifolia ] as well as a new variety of it, var. xanthactis [= C. ternifolia X urticifolia ]. They also proposed the new varieties C. zacatechichi var. laevigata [= C. ternifolia HBK. var. ternifolia ] and C.
zacatechichi var. xanthia [ = C. ternifolia X urticifolia ].
All the taxa were based on material from Honduras.

1954: Cuatrecasas described C. chocoensis [ = C. prunifolia HBK. var. chocoensis (Cuatr.) Wussow and Urbatsch ] based on material from Colombia.

1972: McVaugh described C. colimensis [ = Alloispermum colimense (McVaugh) H. Robinson ] from Colima, Mexico. He also described C. scabra var. palustris [ = Alloispermum scabrum var. scabrum ]. He also published the new variety C. scabra var. palustris [ = Alloispermum scabrum var. scabrum ] based on material from Nayarit, Mexico.

Adams recognized Calea jamaicensis in his study entitled: Flowering Plants of Jamaica.

1975: Canne provided a treatment of Calea for Panama.

Nash transferred Calea standleyi to Verbesina making the new combination V. standleyi [ = Verbesina pachyphylla (Sch. Bip. ex Klatt) Wussow and Urbatsch ].

Urbatsch and Turner transferred C. palmeri Gray in Watson to Sabazia [ = Alloispermum palmeri ].


1978: H. Robinson proposed the transfer of Calea from the subtribe Galinsoginae to the Neurolaeninae. H. Robinson also proposed the resurrection of the genus Alloispermum from the synonymy of Calea and made several new combinations: A. scabrifolium (HBK.); A. colimensis (McVaugh); A. scabrum (Lag.); A. liebmannii (Sch. Bip. ex Klatt) and A. integrifolium (DC.). In addition
he transferred *C. skutchii* to the genus *Podachaenium*.

Wussow and Urbatsch transferred *C. pachyphylla* to the genus *Verbesina* making the new combination *Verbesina pachyphylla*. They placed *C. standleyi* in the synonymy of the latter. In addition, they placed *C. guatemalensis* and *C. rupestris* in synonymy with *C. orizabaensis* and described the new variety, *C. orizabaensis* var. *websteri*.

1979: Wussow and Urbatsch resurrected the genus *Tetrachyron* from the synonymy of *Calea* and included in it *Calea*, subgenera *Tetrachyron* (in part) and *Tephrocalea*. 


MATERIALS AND METHODS

This study was based primarily on approximately 5000 herbarium specimens borrowed from several major herbaria: A, ENCB, F, GH, K, LL, MEXU, MICH, MO, MSC, TEX, UC, US, and XAL, as well as personal collections from Jamaica, Mexico, Guatemala, and Costa Rica. Representative herbarium specimens from collecting trips were prepared and are contained in the LSU herbarium; duplicates are to be distributed. When possible, root stocks collected in the field were brought back and grown in the greenhouse to help interpret developmental variation, to observe the effects of growing the plants under common conditions, to establish a living collection as a source of materials for study, and to carry out interspecific hybridizations.

In addition, plant material was fixed in the field in FAA (formalin-acetic-alcohol, 1:1:18) for use in morphological analyses. Both fixed materials and samples from dried herbarium specimens were observed with scanning electron microscopy. Fixed materials were rinsed in distilled water, then dehydrated using acidified 2,2 dimethoxypropane, DMP (Muller and Jacks, 1975), followed by three changes of absolute acetone. Specimens were critical point dried with CO₂ in a Denton DCP-1 critical point drier, mounted on glass slides with either Walsco Tubekoat or doublestick tape, coated with Au-Pd in a Technics Hummer I sputter coater or with Au in an Edwards 150A sputter coater, and observed in a Hitachi S-500 scanning electron microscope. Samples from herbarium material were processed in the same manner but were first rehydrated for about 24 hrs. in a 10% aq. solution of Aerosol OT.
For the investigation of chromosome numbers, buds were fixed in the field for at least 24 hrs. in modified Carnoy's solution (chloroform-ethanol-acetic acid, 4:3:1), transferred to 70% aq. ethanol and kept under refrigeration until staining. Snow's staining procedure (Radford, et al., 1974) was utilized.

When available, pollen samples were collected from unopened anthers on herbarium specimens and were acetolized following the procedure of Erdtman (1960). Samples were mounted in stained glycerine jelly and observed by light microscopy. Acetolized pollen was also air dried to a glass slide, coated, and observed by scanning electron microscopy.

Bulk collections of leaves and heads for chemical analysis were made for most taxa. Investigation of the chemistry of these collections is currently under way by Dr. N. H. Fischer and students in the Department of Chemistry at LSU.
RESULTS AND DISCUSSION

MORPHOLOGY: The Mexican, Central American, and Jamaican species of Calea are shrubs varying from compact and erect, to lax and arching or even scandent. Field and greenhouse observations suggest that habitat strongly influences habit; plants with dense erect forms tend to occur in open habitats, and more lax to arching ones are found in shaded areas. Young plants or new shoots from older plants that have been cut or grazed often will exhibit quite vigorous and spindly growth with abnormally large, less pubescent leaves, having more coarsely serrate margins.

Caleas normally have simple and opposite leaves, but occasionally plants will have stems with three or four leaves per node. Leaf margins are generally serrate or crenate, but shallowly lobed and entire forms also occur. Leaf surfaces vary from glabrous to densely tomentose (Figs. 1 and 2); there may even be considerable variation within a single individual. The three basic types of leaf trichomes are shown in Figs.1, 3-6. The long, straight, uniseriate hairs and curled, uniseriate hairs (which have several bulbous basal cells and one long attenuate apical cell) are normally found on the lower surface (Figs. 1, 4, 5, 6), whereas short uniseriate (only 2 or 3 cells) hairs are found on the upper surface (Fig. 3). In C. trichomata and C. prunifolia, more pubescent forms occur in dry, high elevation areas, whereas more glabrous forms occur in coastal or more mesic, low elevation areas, suggesting that habitat strongly
influences pubescence. The same general trend was observed within these species for leaf size, with small ones in high, dry areas, and large ones in lower, more mesic areas.

Except for \textit{C. ternifolia} var. \textit{nelsonii}, all taxa normally have resinous dotted lower leaf surfaces (Figs. 1, 2, 7). Studies in other genera (Langenheim et. al., 1978) have shown that secondary chemical constituents are largely concentrated in similar resinous globular trichomes. Chemical investigations by Dr. N. H. Fischer and students, have shown most species of \textit{Calea} to contain large amounts of sesquiterpene lactones, which may be localized in the resin dots.

Leaf texture is also quite variable. It ranges from smooth, chartaceous, to coriaceous and lustrous, or rugose and scabrous.

Capitula occur in umbellate, cymose or corymbose clusters, or in one species (\textit{C. longipedicellata}) may be solitary. Peduncles may be virtually lacking to 7 cm long, and occur either terminally on branches or in axillary positions. Within \textit{C. ternifolia} peduncle length appears to be quite variable. Sessile heads and those with elongated peduncles may occur even on the same plant, making taxonomic separation based on this character impossible.

The shape of the involucre varies from cylindric to campanulate or hemispheric. Phyllaries are imbricate, 2-6 seriate, and graduate. Often the outermost phyllaries are herbaceous or herbaceous-tipped, but otherwise are scarious, occasionally with membranous and/or ciliate margins. Phyllary shape ranges from orbiculate to broadly ovate, to lanceolate or elliptic. The nature of the outermost
phyllaries has considerable taxonomic value, especially in delimiting taxa within *C. prunifolia* and *C. ternifolia*.

All taxa have conduplicate, scarious palea, either with trifid, aristate apices, or obtuse, laciniate ones. Receptacles are also fairly uniformly conical, although one species (*C. longipedicellata*) may have more flattened, dome-shaped ones.

Ray flowers, when present, are pistillate and fertile. Ligules range from bright yellow to yellow-orange, to white or cream colored, and are normally shallowly 2-4 lobed. Ligule length ranges from barely 2 mm to 12 mm. All species have five-lobed disk corollas, with lobes ranging in length from 1-3 mm. Color variation is the same as that for the ray flowers. Most species have glabrous corolla tubes, while those of *C. ternifolia* are resin dotted (Fig. 17). Style branches, and pollen grains of all species investigated are similar in form and size (Figs. 15, 16, 18).

Ray and disk achenes of all species are similar in being black and obconic to cylindric, and somewhat prismatic (Figs. 9 and 10). Some differences in trichome and pappus features were noted. *C. longipedicellata* has essentially glabrous achenes while those of *C. jamaicensis* are antrorsely hirsute and resin dotted. The remaining species have achenes that are slightly to densely antrorsely hirsute, with bifid trichomes (Figs. 11 and 14) often dispersed in vertical rows. Pappus scales are of two basic types (Figs. 12 and 13); *C. ternifolia* has broad, generally blunt tipped scales with laciniate margins that are at most one half the length of the achene (Fig. 12), while the other species have narrow, attenuate
scales that equal or exceed the achene in length (Fig. 13).

**KARYOLOGY:** Chromosome numbers have been reported for four of the eight species presently under consideration (Table 1). From the present study, all taxa investigated have been found to be uniformly n = 19 (Fig. 8). Most of the previous reports in the literature have been approximations or are for taxa no longer included in *Calea*. In addition, inaccurate secondary reporting of numbers in some papers has led to some confusion as to the actual numbers.

**GREENHOUSE STUDIES:** Root stocks were collected and packed in moist sphagnum in the field, and transplanted to pots in the greenhouse. Potting medium consisted of loam, peat moss, and sand in approximately equal proportions. Table II lists the taxa grown along with their sources.

Experiences with greenhouse cultures suggest that the species of *Calea* will not tolerate wide temperature extremes. Plants were kept in the greenhouse during the winter months to prevent cold injury. The few plants that were left unprotected during winter did not survive, giving evidence of their cold susceptibility. As the summer approached, accompanied by heat and humidity, the pots were moved to a shaded spot outside because conditions in the greenhouse could not be controlled. Plants that were left in the uncontrolled greenhouse were soon attacked by various fungal diseases.

Several plants grown from root stocks flowered in the greenhouse, but only after two years growth. Flowering usually continued for approximately one to two months. One plant (*C. ternifolia* var.
(zacatechichi) was isolated in an insect-free environment while flowering to determine if it was self-compatible. Normal appearing achenes were harvested from this plant approximately six weeks later. These achenes were planted in both small pots with soil and in sterile culture tubes containing non-nutrient agar. In both cases, the achenes proved viable. The seedlings were transplanted to pots with soil and resulted in mature flowering plants in approximately two years.

**NATURAL HYBRIDIZATION:** Natural hybridization is apparently a rare phenomenon among the species of *Calea* observed. To have the potential for hybridization, the species must first of all be growing together and flowering at the same time. Except for *C. urticifolia* and *C. ternifolia*, and to a lesser degree *C. urticifolia* and *C. prunifolia*, this first condition is rarely met. From the present study, only about two or three cases of suspected hybridization between *C. urticifolia* and *C. ternifolia* were detected, even though these two species were observed growing and flowering together in numerous instances. Factors that may be limiting hybridization are self-compatibility, and perhaps, various internal reproductive isolating mechanisms.

Hybridization between *C. urticifolia* and *C. prunifolia* was not detected, despite apparent opportunities for it. At best, the reproductive biology of the taxa under investigation is poorly understood and should be a topic for continued study.
DISTRIBUTION AND ECOLOGY: The two species of Calea having the
greatest geographic range are C. urticifolia and C. ternifolia.
Both occur from northern Mexico well into Central America, are
largely sympatric, and even grow intermixed in some localities.
In contrast, C. crassifolia has the most restricted range, being
known only from the type locality. However this species may not be
different from C. trichomata once its variability is better known.
Calea fluviatilis is a markedly distinct species, and is restricted
to the Mountain Pine Ridge area of Belize. The only species that
occurs in Central America and South America is C. prunifolia, whereas
C. trichomata and C. longipedicellata range from southern Mexico
into Central America. Calea jamaicensis is restricted to Jamaica,
where it is known from numerous localities.

The northeastern most limit for Calea is the foothills of the
Sierra Madre Oriental near Monterey, Nuevo Leon, Mexico. Preference
for moderately xeric, mountainous habitats and intolerance of freezing
appear to limit its northeastern distribution. A similar situation
seems to limit its distribution in northwestern Mexico.

Although the range of some species is quite large, the distri­
bution is not at all continuous, rather plants are at most locally
abundant in restricted habitats. Most taxa are restricted to poor,
thin, rocky soils in moderately xeric mountainous areas. Within
these areas, plants often grow on steep exposed slopes, in pastures,
sparsely forested areas, along roadsides, or other disturbed habitats.
Three taxa, C. longipedicellata, C. trichomata var. peckii, and
C. prunifolia var. chocoensis, occur in coastal areas and wet lowland
thickets.

**TAXONOMIC CRITERIA:** Specific and varietal categories have been treated as consistently as possible with regard to the data available in each situation. Species are recognized on the basis of morphological discontinuities in several features. Varieties are regarded as morpho-geographical subdivisions of a species (Kapadia, 1964) that presumably reflect genetic differences.
SYSTEMATIC RELATIONSHIPS

Previously, the relationships between the Mexican and Central American taxa, and those of South America have been largely ignored. The present study is the first to try and assess these relationships. Because the proposed relationships are based on currently scanty data for the South American taxa, modification may become necessary as these taxa become more completely known.

_Calea jamaicensis, C. trichomata, C. crassifolia, and C. berteriana_ form a closely allied group of species that occur in Chiapas, Mexico, Jamaica, Central America, and northern South America. All species are similar in habit and overall appearance, but can be readily distinguished by a few key morphological features, as discussed in conjunction with each species in the taxonomic treatment.

_Calea longipedicellata_ and _C. fluviatilis_ are not closely related to the other Mexican, Central American or Jamaican species, but do have affinities for South American ones. _Calea longipedicellata_ is most similar to the Colombian and Venezuelan _C. cardonae_, but differs in having larger heads on longer peduncles, and essentially entire leaf margins. The foliar characters of _C. fluviatilis_ are unique among the species studied. This species appears to have affinities for the South American species _C. saxatilis, C. angustifolia, and C. hypericifolia_. The exact nature of these relationships is discussed in the taxonomic treatment of _C. fluviatilis_.

_Calea ternifolia_ is quite distinct from any other North or South
American *Calea* by virtue of its short broad pappus scales and inconspicuous ray flowers. However, according to Fischer (unpublished), *C. urticifolia* and *C. ternifolia* are nearly identical in their sesquiterpene lactone complements, which along with their largely sympatric distributions and suspected hybridization, lends support to the close relationship of these two species. Although chemical data are incomplete, *C. prunifolia* appears to be closely related to *C. urticifolia* and *C. ternifolia* on the basis of inflorescence type and other floral and foliar characters.

Although each species is morphologically distinct, the Mexican, Central American, and Jamaican caleas form a close-knit group. Based on the present study, one species, *C. megacephala*, known from the vicinity of Tonala, Chiapas, Mexico, is not closely related to any of the Mexican or Central American taxa. Its perennial herbaceous habit with a reduced stem and rosette of basal leaves, large solitary heads with numerous bright orange ligules, non-graduate, thin, green outer phyllaries, and absence of sesquiterpene lactones are anomalous for this group. Its relationship to superficially similar large-headed Brazilian taxa (which are at present poorly known) is doubtful. Therefore, it is proposed that the monotypic genus, *Tonalanthus* Brandegee, be recognized to accommodate *C. megacephala*.

Concerning the subtribal placement of *Calea*, the genus traditionally had been placed in the subtribe Galinsoginae (De Candolle, 1894; Stuessy, 1977). This subtribal placement was no doubt largely supported by numerous species previously included in *Calea* that do have strong affinities for the Galinsoginae. Recent studies, primarily based on
morphological and karyological data, have shown these elements to be anomalous in *Calea* and have been transferred to the genera *Alloispermum*, *Sabazia* and *Oteiza* (Longpre, 1970; Fay 1975; Robinson, 1978; Fernandez and Urbatsch, 1981), all of which are considered members of the Galinsoginae. *Calea* differs from the aforementioned in chromosome number, ray corolla form, disk corolla pubescence, leaf trichomes, and secondary chemical constituents. Primarily on the strength of these data, Robinson, et. al. (1978) transferred *Calea* to the subtribe Neurolaeninae. Additional chemical evidence (Fischer, personal comm.; Bohlman, et.al., 1981) continue to support this subtribal placement. The presence of numerous identical or similar heliangolide lactones in *Calea* (sensu strictu) and other Neurolaeninae suggest that this subtribe is closely allied with the subtribe Helianthinae (Bohlman, et. al., 1981; Fischer, personal comm.).
TAXONOMIC TREATMENT


**TYPE:** *C. jamaicensis* (L.) L.


*L. peruvianum* HBK.

**Mocinna** Lagasca, *Gen. Sp. Pl.* Nov. 31. 1816. **TYPE:**

*M. serrata* Lag.


**Lemmatus** DC., *Prodr.* 5: 669. 1836. **TYPE:** *L. rotundifolium* (Less) DC.

**Meyeria** DC., *Prodr.* 5:670. 1836. **TYPE:** not designated.


Shrubs, stems erect to scendent, glabrous to densely tomentose, leaves opposite, simple, blades linear to broadly ovate, margins entire, serrate, crenate, or shallowly lobed, usually 3 or 5 nerved, upper and lower surfaces entirely glabrous to densely pubescent, often resin dotted, petiolate or sessile; capitulescences solitary, corymbose, cymose or umbellate, peduncles axillary or terminal, lacking to ca. 7 cm long; involucres cylindric, campanulate, or hemispheric, phyllaries imbricate, 2-several seriate, graduate, lanceolate to orbiculate, scarious throughout, or outermost herbaceous throughout, or merely herbaceous tipped; capitula radiate or discoid, variable in size; receptacle conic to flattened; palea scarious, flattened to strongly conduplicate, apices aristate to truncate and lacinate; ray flowers, 0 to several, fertile, ligules, white, (cream) yellow, or yellow-orange, 2-4 (5) lobed, style branches (ray and disk) ca. 1-1.5 mm long, apices acute to obtuse; disk flowers fertile, yellow, white, (cream) or yellow-orange, 5 lobed, lobes 1-3 mm long, limb cylindrical to campanulate, tube often flaring at the base, sometimes glandular dotted, anthers exerted, yellow, apical appendage present, bases rounded; achenes (ray and disk similar) cylindric to somewhat prismatic, usually 1.5-3.5 mm long, black, glabrous to densely hirsute, carpopodium present or wanting, pappus of ca. 8-25 stramineous, broad, blunt to narrowly lanceolate scales; chromosome number $n = 19$. TYPE SPECIES: 
Calea jamaicensis (L.) L.
KEY TO THE MEXICAN, CENTRAL AMERICAN, AND JAMAICAN SPECIES OF CALEA

A. Heads radiate  ..........  B.

B. Rays conspicuous, exceeding the disk in length; ray and disk corollas bright yellow; pappus scales narrowly lanceolate, 2.0 mm or larger

C. Pappus of ca. 20 narrowly lanceolate scales, approximately equal length or longer than the achene; plants common

C. urticifolia

B. Rays inconspicuous, not exceeding the disk; ray and disk corollas white or cream-colored; pappus scales oblong to broadly lanceolate usually with obtuse apices, pappus less than 2 mm long  .......... 2 C. ternifolia

B. Rays conspicuous, exceeding the disk in length; ray and disk corollas bright yellow; pappus scales narrowly lanceolate, 2.0 mm or larger

C. Pappus of ca. 20 narrowly lanceolate scales, approximately equal length or longer than the achene; plants common

C. urticifolia

C. Pappus of ca. 20 narrowly lanceolate scales, approximately equal length or longer than the achene; plants common

C. urticifolia

C. Pappus of ca. 20 narrowly lanceolate scales, approximately equal length or longer than the achene; plants common

C. urticifolia

C. Pappus of ca. 10-15 broadly lanceolate scales with acute to obtuse apices, pappus approximately 1/2 the length of the achene or shorter; rare hybrids

C. ternifolia X urticifolia

B. Rays inconspicuous, not exceeding the disk; ray and disk corollas white or cream-colored; pappus scales oblong to broadly lanceolate usually with obtuse apices, pappus less than 2 mm long  .......... 2 C. ternifolia

A. Heads discoid

D. Corollas cream-colored or white (some heads lacking rays or with rays inconspicuous)  .......... 2 C. ternifolia

D. Corollas bright yellow to yellow-orange  ..........  E

E. Heads large (ca. 50 flowered), solitary or in clusters of 2-4 heads on long peduncles, 3-7 cm long  .......... 4 C. longipedicellata
E. Heads smaller (ca. 8-25 flowered) in umbellate or corymbose clusters; peduncles generally less than 3 cm in length ...... F

F. Leaves linear-lanceolate (known only from the Mountain Pine Ridge area in Belize)

...... 5 C. fluviatilis

F. Leaves ovate to elliptic ...... G

G. Corolla lobes 1.2 - 1.7 mm long ...... H

H. Capitulescence of mostly terminal, loosely corymbose to umbellate clusters of 3-12 heads, leaves usually ovate-lanceolate, achenes hirsute and resin dotted, (endemic to Jamaica)

...... 6 C. jamaicensis

H. Capitulescence of terminal of axillary clusters of 7-30 heads, leaves ovate to elliptic, achenes hirsute, not resin dotted, (Nicaragua South into northern South America)

...... 7 C. prunifolia

G. Corolla lobes 1.9-2.7 mm long ...... I

I. Heads subsessile or on short peduncles to ca. 3 mm long (known only from type near Chinaja, Guat.)

...... 8 C. crassifolia

I. Heads on peduncles 3-15 mm long (widely distributed in southern Mexico to Honduras)

...... 9 C. trichomata
1. *Calea urticifolia* (Miller) DC., Prodr. 5:674. 1836.

Shrubs 1.0 - 3.5 m tall; stems moderately to densely branched, erect, terete, striate, lower portions glabrous to slightly tomentose, upper portions moderate to densely pubescent (especially new growth); leaves opposite, simple, blades widely ovate (elliptic) to narrowly lance-ovate, 3-14 cm long, 1.5 - 8 cm wide, apices acute to attenuate, bases acute to obtuse (sometimes rounded), margins serrate to crenate (rarely entire), upper surface rugose and scabrous (rarely smooth chartaceous), dark green, prominently triplinerved, lower surface typically paler green, resin dotted, thinly to densely hirsute, normally denser along the veins, petioles 0.2 - 1.5 cm long, hirsute; capitulescence of axillary or terminal umbellate clusters of heads, peduncles 0.3 - 3 cm long, tomentose to glabrous; involucres campanulate to cylindric, 3-15 mm wide, 4-9 mm tall, phyllaries imbricate, 4-5 seriate, generally the 2 lowermost lanceolate to lance-oblong, 3-7 mm long, 1.0 - 2.5 mm wide, usually herbaceous throughout, densely hirsute and resin dotted, intermediate phyllaries usually grading from ovate to oblong to obovate, 3-8(9) mm long, 2.0 - 3.5 (6) mm wide, scarious to membranous, apex usually membranous and sometimes purple, innermost phyllaries usually lanceolate to lance-ovate, 5-8 (10) mm long, ca. 2 mm wide, membranous, yellowish, apices acute; capitula radiate, usually 20-35 (52) flowered; receptacle conic, ca. 1.0 - 1.5 (2.2) mm tall, ca. 1 mm wide; palea scarious, often yellowish, 5 - 6.5 (7.5) mm long, 1.2 - 2.5 mm wide, lanceolate, conduplicate, often trifid with 2 shorter lateral lobes
and one central attenuate lobe; ray flowers 3-8, pistillate, fertile, ligules yellow (occasionally white or cream-colored), shallowly 2-3 (4) lobed, sometimes sparsely gland dotted, 3-7 (10) mm long, 1.5 - 3.0 (4) mm wide, throat ca. 2-3 mm long, flaring slightly at the base, style branches ca. 1 mm long, apices, acute to obtuse; disk flowers 15-30 (42), fertile, corolla yellow, 4-6 mm long, lobes 5, acute, 1.0 - 1.6 mm long, sometimes gland dotted, tube 2-3 mm long, flaring about 1 mm below the lobes and slightly at the base, anthers yellow, exerted, apical appendage acute, bases rounded, style branches same as on ray flowers; achenes (ray and disk similar) cylindric to somewhat prismatic, 1.5 - 3.0 mm long, black, sparsely to densely antrorsely hirsute, light colored carpopodium present, pappus of 12-23 narrowly lanceolate, stramineous bristles arising from an annulus, ca. 3 - 4.5 mm long, sometimes purple at the base; chromosome number $n = 19$.

*Calea urticifolia* is a weedy, morphologically variable, shrubby species that ranges from Sinaloa, Mexico to central Panama. It is locally abundant in pastures, thickets, pine-oak forests, and along roadsides. Flowering normally occurs from September to June.

Concerning leaf shape, there is a general trend for longer narrower leaves in western Mexico and other dry areas, to broader, more ovate leaves in Central America. Although leaf shape has been used to distinguish varieties in *C. urticifolia* (i.e. var. *axillaris*), it was found to be too variable a character to be useful taxonomically. Likewise, leaf pubescence is not a good taxonomic character; it varies from glabrous to densely hirsute, with
thinly hirsute being the normal condition. Field observations suggest that shaded plants typically have thinner, more glabrous leaf blades, long internodes and weak stems, whereas more typical forms have rugous, hirsute leaves on more compact, erect plants. Typically, the ligules are colored bright yellow, but white or cream-colored forms sporadically occur, even within a head with normal yellow ones.

Heads normally have 18 to 30 flowers, but much larger forms (up to 52 flowers per head) do occur. Those from the Yucatan have consistently large heads on long peduncles and are treated here as a distinct variety. Others from Honduras (namely Harmon and Fuentes 5247; Ochoa 43; Pittier 1827, 1830; Thieme 5333; Villeda 143; and Williams et. al. 42908) also have very large-heads (up to 52 flowered). Although these extremely large headed individuals appear to be quite different, they are not given taxonomic recognition because of the numerous individuals from the same geographic area that grade into the typical form. This atypical Honduran material may be introgressed with genes from _Calea_ trichomata as evidenced in their more densely pubescent leaves, fewer larger heads, and strongly purple phyllaries.

Among the Mexican and Central American species of _Calea_, _C. urticifolia_ is readily recognized by its umbellate capitulescences, radiate heads, generally bright yellow ligules, linear lanceolate pappus scales, and generally pubescent stems.

_Calea urticifolia_ appears to be closely related to the Ecuadorian _C. kingii_ which is widely disjunct and has relatively fewer, larger heads per capitulescence, and more densely hirsute leaves.
KEY TO THE VARIETIES OF C. URTICIFOLIA

Heads of 40-52 flowers, on long peduncles 20-35 mm long, restricted to Yucatan and Quintana Roo, Mexico

... var. yucatanensis

Heads usually of 20-30 flowers, (or if larger not on long peduncles) on peduncles 3-20 mm long; Sinaloa, Mexico to Panama (not found in Yucatan and Quintana Roo)

... var. urticifolia

l.a. Calea urticifolia (Miller) DC. var. urticifolia, Prodr. 5: 674. 1836.


**Calea axillaris** DC., Prodr. 5:673. 1836. **TYPE:** In Amer. callid., without date, **Neé s.n.** (LECTOTYPE: G, here chosen; PHOTOS: F! GH!); In Mexico, 1791, **Haenke s. n.** (SYNTYPE: PR?; fragment: F!). **Calea urticifolia** (Mill.) DC. var. **axillaris** (DC) Blake, Contr. Gray Herb. 52:57. 1917.

**Calea pellucidinerva** Klatt, Bull. Soc. Bot. Belg. 31:207. 1892. **TYPE:** COSTA RICA. Environs de Boruca, 450 m., Feb 1891, (Pittier) **Tonduz 3726** (LECTOTYPE: US!, here chosen). Klatt in his protologue cited **Pittier 3707** and 3726. However the latter number was chosen as the lectotype because 3707 could not be located for study, and both specimens are from the same area in Costa Rica.

**Calea sartorii** Schultz Bipontinus, in sched. (fragments at US!).

This variety is common and widely distributed, ranging from Sinaloa, Mexico to central Panama (Fig. 19). Several common names are reported for it; in Nayarit it is known as "prodigiosa" or "tacote", in San Luis Potosi as "Xalacatl" or "chilchaca", in Oaxaca and Chiapas as "hierba de la rabia", "chichiquizo", and "hojo amarga", in Chiapas as "quinina", in Guatemala as "Mosca amarilla", and in Costa Rica as "jaral" or "jalacate" (in part from Standley, 1926). Reportedly, in some areas a decoction of the leaves is drunk as an intoxicant and as a treatment for various stomach troubles (Hinton, in sched.).
C. ADDITIONAL SPECIMENS EXAMINED: BELIZE. EL CAYO DISTRICT: river bluffs, El Cayo, 15 Feb 1931, Bartlett 11521 (LL, MICH, US); Pine Ridge, Duck Run, 17 Feb 1931, Bartlett 11557 (MICH, US); El Cayo, 23 Mar 1931, Bartlett 12084 (F, GH, LL, MICH, MO, US); Macal (Macaw) River, Guacamallo Bridge, 29 Jan 1974, Dwyer and Liesner 12286 (LL, MO); at base of hill, Vaca, 3 Mar 1938, Gentle 2284 (F, GH, MICH, MO, TEX, US); road south to Augustine and San Luis to Camp Six, 19 Mar 1967, Dwyer et. al. 335 (MO); Vaca Falls, Feb 1926, Record s.n. (US); STANN CREEK DISTRICT: Thicket, Sittee River, 7 Apr 1907, Peck 847 (GH, K, NY); Secondary forest, All Pines, 1 May 1931, Schipp 757 (F, GH, K, MICH, MO, NY, UC). COSTA RICA. ALAJUELA: Alajuela, elev. 900 m., Sept 1887, Alfaro 5822B (US); San Mateo, elev. 600 m., Jan 1892, Bioley 7023 (US); Colinas a San Pedro de San Ramón, elev. 1050 m., 4 Dec 1925, Brenes 600 (F), 19 Nov 1926, Brenes 251 (F), 19 Jan 1933, Brenes 16940 (F); caminos entre la carretera Alajuela - Grecia, 10 Dec 1933, Brenes 17504 (F); colinas de San Pedro de San Ramón, 5 Dec 1940, Brenes 23153 (NY); Oriollos de Río Poas, 26 Nov 1932, Brenes s.n. (LIL, NY); San Ramón, 1936, Brenes s.n. (NY); between Alajuela and Volcán Poas, 30 Jan 1922, Greenman and Greenman 5400 (MO); en desague seco entre Naranjo y San Juanillo de Naranjo, camino a San Carlos, elev. 1200 m., 30 Mar 1963, Jimenez 557 (F, NY); entre Esparta y San Ramón, elev. 1000 m., 6 Jan 1964, Molina 13561 (F); near Artezalea and Methodist Rural Center, about 8 km N.E. of Villa Quesada, elev. 550 m., 16 Feb 1966, Molina et. al. 17161 (F, MICH, US); El Silencio de Lácer, elev. 1350 m., 11 Jan 1939, Smith 1437 (F, NY); San Luis, elev. 1500 m., 18 Dec 1939, Smith P2127 (GH); roadside banks and border of stream about 1.9 km north of Cinco
Esquinas, elev. 1900 m., 2 Jan 1972, Wilbur et al. 15732 (F, MICH, MO, US); weedy roadside about 11 km north of San Ramón, 16 Jan 1968, Wilbur and Stone 9711 (F, GH, MICH, MO, US); along Costa Rica 3, 11.9 km southeast of San Ramón, 30 Dec 1978, Wussow and Pruski 124 (LSU, TEX); 9.7 km, southwest of San Ramón on Pan American Highway (Costa Rica 1), 2 Jan 1979, Wussow and Pruski 142 (LSU, TEX). CARTAGO: Las Concavas, near Cartago, elev. 1140-1260 m., 17 Dec 1927, Cooper 47 (F); Cartago, elev. 4250 ft., Nov 1887 J. Cooper 5822 (133) (F, US); thickets bordering coffee plantation, vicinity of Cartago, 16 Feb 1965, Godfrey 66493 (MO); Aguacaliente, 10 Feb 1922, Greenman and Greenman 5541 (GH, MO); entre Río Navarro y Río Sombrero, 3 km al Sur de El Muñeco, elev. 1275 m., 26 Jan 1964, Jimenez 1637 (F, NY); vicinity of Santiago, elev. 1050 m., 20 Apr 1906, Maxon 1121 (NY); Cartago, elev. 1400 m., 10 Jan 1925, Rojas 37 (US); camino viejo de Cartago a San Rafael, 5 Mar 1944, Saenz 26 (F); Navarro, elev. 3500 ft., Mar 1894, D. Smith 4857 (F, GH); vicinity of Cartago, elev. 1425 m., Feb 1924, Standley 33360 (US); el Muñeco, on the Río Navarro, elev. 1400-1500 m., 6-7 Mar 1926, Standley and Torres 50930 (US); Cartago, 23 Jun 1923, Stevens 98 (US); Aguacaliente, elev. 4500 ft., 22 Feb 1925, Stork 1012 (F, MICH, UC, US); Cartago, 1931, Torres 249 (F); weedy pasture about 13 miles northeast of Paraiso, 31 Jan 1971, Wilbur and Teeri 13755 (ENCB, F, GH, LL, MICH, MO, MSC, NY, TEX, US); pasture at Las Concavas, elev. 1400 m., 14 Mar 1948, Williams and Molina 13947 (F); just east of Paraiso along Costa Rica 10, elev. 1400 m., 4 Jan 1979, Wussow and Pruski 149 (LSU, TEX) GUANACASTE: Potreros near farmhouse at Hacienda Santa Maria and source of Río Liberia, elev. 680-780 m., 21-24 Jan 1930, Dodge and
Thomas 6301 (MO, US); entre Esparta y San Ramón, elev. 975 m., Jan 1964, Jimenez 1583 (F); Nicoya, Jan 1900, Tonduz 13608 (GH, K, MICH, NY, US); pastured grasslands and woody thickets on the northwestern approach to Volcán Orosí about 15 km southeast of La Cruz, 17 Jan 1968, Wilbur and Stone 9713 (F, MICH, MO); savanna about 5 km south of La Cruz, elev. 200 m., 12 Feb 1963, Williams and Williams 24507 (F, NY, US); savanna and scrub forest area, 5-15 km south of La Cruz, elev. 150 m., 1 Jan 1964, Williams et. al. 26429 (F, NY, US); escarpment of the savanna down to Río Guajiniquil on Bahía de St. Elena, elev. 50-200 m., 5 Jan 1964, Williams et. al. 26738 (F, NY, US). HEREDIA: both banks of Río Virilla, below bridge on highway to Heredia, elev. 1000-1100 m., 1 Dec 1937 - 1 Jan 1938, elev. 1200 m., Allen 589 (F, MO); Heredia, 17 Dec 1915, Holway 265 (GH); weedy roadside banks 2 km southeast of Cinco Esquinas towards Heredia, elev. 1500 m., 2 Jan 1972, Wilbur et. al. 15766 (MO); at bridge over river Virilla on Costa Rica 1 to Heredia, 28 Dec 1978, Wussow and Pruski 106 (LSU, TEX); 1.2 km northwest of Río Virilla along road bank of Costa Rica 1 to Heredia, 28 Dec 1978, Wussow and Pruski 111 (LSU). PUNTARENAS: Occasional along river, vicinity of Palmar Norte de Osa, 18 Jan 1951, Allen 5780 (F); Río Volcán, 48 kms SE of San Isidro El General, elev. 300 m., 1 Mar 1966, Molina et. al. 18172 (F, NY); savannas de Buenes Aires, elev. 250 m., Feb 1891, Pittier 3695 (GH). SAN JOSE: Asseri, 2 Feb 1941, Echenerria 262 (F); foothills south of San Jose, 28 Jan 1922, Greenman and Greenman 5341 (GH, MO); Asseri, elev. 5000 ft., 23 Jan 1940, Hunnewell 16779 (GH); vicinity of La Verbena, elev. 1200 m., 29 Jan 1924, Stanley 32207 (US); vicinity of Escasu, elev. 1200 m., 29 Jan 1924, Standley 32359 (US);
vicinity of San Sebastián, elev. 1150 m., 1 Feb 1924, Standley 32735 (US); vicinity of San José, elev. 1150 m., Feb 1924, Standley 33253 (US); vicinity of San José, elev. 1130 m., 4 Dec 1925 - 10 Feb 1926, Standley 41196 (US), 47357 (US); vicinity of San Sebastián, south of San José, elev. 1160 m., 23 Feb 1926, Standley 49308 (US); along the Río Virillo about 1 km south of Santa Domingo, elev. 1100 m., 20 Dec 1974, Taylor 17329 (LSU, NY, US); steep roadside bank over the Río Lajas, about 6.4 km east of Santa Domingo, elev. 1260 m., 22 Dec 1974, Taylor 17434 (NY, US), San José, 23 Nov 1884, Tonduz 1430 (US), elev. 1135 m., Nov 1893, Tonduz 1557 (US); Río Poas, Aserrí, elev. 1200 m., 15 Jan 1935, Valerio 1114 (F); roadside banks of Interamerican Hwy (Costa Rica 2), 7.6 km S of intersection of I.A. Hwy and main Hwy. (Costa Rica 10) into Cartago, elev. 1450 m., 29 Dec 1978, Wussow and Pruski 113 (LSU). PROVINCE UNKNOWN: elev. 3500 ft., Oct 1872, Endres 20 (K); borders del Río Segundo, elev. 1150 m., 4 Dec 1940, Jonteri 405 (F); Villa Colón, Orozco 143 (F); Jan 1891, Pittier 3219 (US); Costa Rica, Serre s.n. (K); Costa Rica, elev. 1100 m., 4 Jan 1935, Solís 4 (F); Guadalupe de Zarcero, elev. 4500 ft., 9 Dec 1937, Smith A664 (F); bordes de Río María Aguilar, 13 Nov 1892, Tonduz 1540 (F, GH, K, US); Costa Rica, Apr 1910, Worthen s.n. (MO). GUATEMALA. ALTA VERAPAZ: along road to Sacapulas, ca. 15 km generally W of San Cristobal Verapaz, elev. 4150 ft., 31 Jan 1977, King 7345 (MO, NY, US); near Túcuru, elev. 450 m., 5 Apr 1939, Standley 70699 (F, MICH), 70713 (F); near Pancachche, elev. 360 m., 5 Apr 1939, Standley 70810 (F, MICH); along Río Polochic, near Pancacche, elev. 900 m., 10 Apr 1941, Standley 91852 (F); vicinity
of caves, southwest of Lanquin, elev. 600-1000 m., 21 Feb 1942, Steyermark 44032 (F). AMATITLAN: between Amatitlan and Palio, 26 Mar 1922, Greenman and Greenman 5890 (MO); Amatitlan, elev. 1102 m., Oct 1928, Morales 1159 (F); Río Amatitlan, elev. 3900 ft., Feb 1890 Smith 2337 (F, GH, US). CHIQUIMULA: thickets along Esquipulas creek, 2 km from Esquipulas village, elev. 1000 m., 6 Dec 1969, Molina and Molina 25175 (F, MO, NY, US). ESCUINTLA: San Luis, north of Escuintla, elev. ca. 450 m., 16 Dec 1938, Standley 60131 (F, MICH, NY). GUATEMALA: 6.8 km NE of Amatitlan (measured from Puente El Mico) on CA-9, 16 Sept 1972, Keil 9430 (F, OS); near Amatitlan, elev. 1170 m., 29 Dec 1936, Standley 61427 (F, NY); vicinity of Lago de Amatitlan, elev. 1255 m., 15 Mar 1941, Standley 89461 (F). PETEN: La Libertad and vicinity, 4 Feb 1935, Aguilar 460 (K, LL, MICH, MO, NY, US); Lake Peten Itza, San Miguel, in savanna, 1 km. west, 1 Feb 1968, Contreras 7503 (LL, US); Poptun, pine savanna, 28 Jan 1950, Lamb 59 (F); La Libertad, 28 Mar 1933, Lundell 2109 (GH, MICH); Kantetul, 2 May 1933, Lundell 3174 (MICH, US); 2 km de San Miguel, 22 Jan 1969, Ortiz 138 (F, MICH, US); en bosque bajo, alrededor la cueva en aldea Santa Elena, 20 Jan 1970, Ortiz 577 (ENCB, F, MO, NY); Santa Elena, en orrilando Camino Remate, km 12, lado norte del camino, 11 Feb 1972, Ortiz 2268 (F, MICH). SANTA ROSA: Jumaytepeque, elev. 6000 ft., Aug 1892, Heyde and Lux 3790 (F, GH, US); in thicket, vicinity of Chiquimulilla, elev. ca. 325 m., 29 Nov-8 Dec 1940, Standley 79204 (F). ZACAPA: Gualan, 19 Jan 1905, Deam 196 (GH, MICH, NY); Gualan, elev. 122 m., 30 Dec 1905, Kellerman 5334 (F, MICH, TEX, UC, US); along the road to Gualan, ca. 7 km generally SW of Gualan, elev. 700 ft., 2 Feb 1977, King 7366 (MO, NY, US);

CHOLUTECA: vicinity of San Marcos de Colón, elev. 960 - 1150 m., 12-22 Jan 1949, Standley 15693 (F). COMAYAGUA: Coyocutena, San Luis, elev. 4000 ft., 24 May 1932, Edwards P-282 (F); Pito Solo, Lake Yojoa, elev. 2000 ft., 8 Aug 1932, Edwards P-409 (A, UC); in pine forest, El Achote, near Siguatepeque, elev. 1500 m., 18 Feb 1928, Standley 56171 (F, US); vicinity of Siguatepeque, elev. 1080 to 1400 m., 14-27 Feb 1928, Standley 56358 (F, US), 56373 (F, K, US); vicinity of Comayagua, elev. 600 m., 12-23 Mar 1947, Standley and Chacon 5361 (F), 5549 (F). COPAN: 11 km. north of Santa Rosa de Copán, 14 Dec 1970, Harmon and Fuentes 5247 (ENCB, MO, NY); thickets La Vegona, Copán River 2 km east of Copán Ruins, elev. 500 m., 23 Nov 1969, Molina and Molina 24768 (F, NY, US); Llano de la Puerto, near Copán, elev. 900 m., 7 Jan 1907, Pittier 1827 (US); Hacienda grande, near Copán, elev. 900 m., 8 Jan 1907, Pittier 1830 (US); cutover montane forest area near Tierra Blanca, about 30 km northeast of Santa Rita de Copán, elev. 1200 m., 28 Dec 1973, Williams et. al. 42908 (F, MICH). CORTES: San Pedro Sula, 1887, Thieme 5333 (F). EL PARAISO: bosque de nubes de Montana Apauhis Sobre Danli, elev. 1600 m., 24 Feb 1952, Molina 5121 (F); Pinares de Montaña Agua Fria, elev. 1300 m., 14 Mar 1956, Molina 7393 (F); s.o. del Mineral de Agua Fria, elev. 1600 m., 15 Mar 1957, Molina 7663 (F); bosque humedo y mixto Montaña Agua Fria, elev. 1400 m., 14 Mar 1963, Molina 11354 (F, NY); bosque mixto cerca de San Lucas, elev. 1500 m., 20 Oct 1963, Molina 13069 (LL, NY, US); Yuscaran, 30 Apr - 2 May 1977, Ochoa 43 (MO);
near Yuscaran, elev. 960 m., 11 Dec 1962, Standley et al. 1193 (F);
Yuscaran, alrededores de la ciudad, 14 May 1977, Villeda 143 (MO);
Yamaranguila, elev. 1800 m., 7 Apr 1956, Molina 6340 (F, US);
vicinity of La Esperanza and Intibuca, elev. 1500-1600 m., 31 Jan –
12 Feb 1950, Standley 24495 (F, US). LA PAZ: Pinares del Huis, km
110 sobre carretera Marcala, elev. 1600 m., 11 Apr 1956, Molina 6490
(F); common along river bank, Marcala River, vicinity of Marcala
town, elev. 1215 m., 20 Mar 1969, Molina and Molina 24280 (F, NY,
US); vicinity of La Paz, elev. 750 m., 6 Dec 1949, Standley 24989
(F). MORAZAN: cerro La Tigra, near Tegucigalpa, elev. 1800 m., 18
Mar 1973, Clewell 3811 (NY); roadside in cloud forest (la Tigra) ca.
10 km N of Tegucigalpa, 16 Feb 1972, Clewell and Hernandez 3050 (MO);
area del Valle del Zamorano, Rio Yeguare, elev. 950 m., 24 Apr 1948,
Molina 780 (F); entre Las Flores y San Juan del Rancho, elev. 1500
m., 9 Nov 148, Molina 1486 (F); margenes de la Quebrada de las Burras
entre Suyapa y Tegucigalpa, elev. 1050 m., 11 Dec 1948, Molina 1834
(F); pendientes enguamiladas del Rio Capa Rosa, 1 km de Zamorano,
elev. 900 m., 19 Nov 1949, Molina 2646 (F, MO); bosque de nubes de
Montaña Miscoco, elev. 1600 m., 20 Mar 1956, Molina 6130 (F); Montaña
Kepaterique, elev. 1400 m., 31 Mar 1957, Molina 7832 (F); common in
barley and corn field in Monte Redondo drainago of Yeguare River,
Dept. of Agronomy, El Zamorano, elev. 800 m., 9 Dec 1971, Molina
27165 (F, US); forest on mountain La Tigra, southwest of San
Juancito, elev. 1800-2100 m., 2 Feb 1966, Molina et. al. 16979 (F, NY, US); Tegucigalpa, 10 May 1977, Rubio 127 (MO); vicinity of El Zamorano, elev. 780-900 m., 26 Nov 1946-9 Jan 1947, Standley 152 (F); 3875 (F); 4056 (F); along Río Yeguare, east of El Zamorano, elev. 750 m., Sept-Dec 1948, Standley 14623 (F); along and near Río Agua Amarilla, above El Zamorano, elev. 1000-2000 m., Oct-Nov 1948, Standley 14672 (F); Ojojona, rocky pine forest, elev. 1335-1450 m., 28 Nov 1949, Standley 24723 (F); puente Colorado north of Tegucigalpa, elev. 900-1000 m., 7 Dec 1949, Standley 24893 (F); new wood road above Río Agua Amarilla, elev. 1100 m., 10 Jan 1951, Standley 28252 (F, MO); wet thicket in pineoak forest, lower slopes of Cerro de Uyuca, elev. 1530-1600 m., 22 Feb 1947, Standley and Molina 4279 (F), 4294 (F); ca. 18 mi S of Tegucigalpa on Rte. 1, 29 Oct 1976, Stuessy and Gardner 4426 (OS); Río de la Orilla, elev. 800 m., 20 Oct 1943, Valerio 1330 (F, LIL); Uyuca, elev. 1238 m., Nov 1943, Valerio 1640 (F, LIL); Jicarito, elev. 800 m., 27 Oct 1945, Valerio 3547 (F, US); pine forest about 5 km north of Sabana Grande, elev. 1100 m., 23 Dec 1947, Williams 13596 (F, GH); edge of forest in mountain above San Juancito, elev. 1800 m., 20 Feb 1948, Williams and Molina 13714 (F); slopes of Mt. Uyuca, elev. 1700 m., 21 Feb 1949, Williams et. al. 15583 (F). OLANCHO: bosques de pinos, Pisijire, cerca de 30 kms NE de Culmi, elev. 500-700 m., 12-17 Mar 1972, Nelson and Clewell 608 (MO); forest along Río Juticalpa, near Juticalpa, elev. 380-480 m., 5-16 Mar 1949, Standley 17635 (F); trail between Catacamas and La Presa, elev. 500-600 m., 20-25 Mar 1949, Standley 18328 (F). SANTA BÁRBARA: Llano del Conejo, 1 km de
Santa Bárbara, elev. 300 m., 11 Dec 1950, Molina 3663 (F); matorrales húmedos a orillas del Río Siscapa, elev. 300m., 12 Dec 1950, Molina 3749 (F, GH). YORO: Yoro, dense river forest, elev. 2800 ft., 15 Jan 1934, Edwards 735 (F, GH, MO, NY, US).

MEXICO. CHIAPAS: barria of San Antonio, paraje of Mahben Chauk, Munc. de Tenejapa, elev. 4500 ft., 28 Nov 1964, Breedlove 7735 (ENCB, F, MICH); slope of creekbank near junction of Mex 190 and road to Bochil, elev. 3500 ft., 11 Feb 1965, Breedlove 8809 (ENCB, F, MICH); steep walled canyon with tropical deciduous forest, above El Chorreadero, Munc. de Chiapa de Corzo, elev. 500 m., 24 Jan 1973, Breedlove 32291 (LL, MO, NY); steep-walled ravine and sandstone bluffs 3 km north of Ocozocoautla along road to Mal Paso, elev. 900 m., 9 Jan 1972, Breedlove and McClintock 23577 (LL, MO); Teopisco, 30 Dec 1906, Collins and Doyle 126 (US); Hwy 195, 4.5 mi. north of jct. with Hwy 190, 27 Nov 1977, Funk and Raymos 2572 (OS, LSU); stream on Rte. 35 toward Arriaga, off Rte. 190, just south of village of Tierra and Libertad, elev. 770 m., 28 Dec 1977, Harriman 14425 (OS); trail from Zinacantan Center to Ixtapa below Paraje Vobits at Burrero, elev. 4000 ft., 20 Apr 1966, Laughlin 720 (ENCB, LL, MICH); Berriozabal, Las Vistas, 18 Dec 1949, Miranda 5850 (MEXU); slope along Mex Hwy 190 at Zinacantan paraje of Muktajok, elev. 3500 ft., 12 Dec 1967, Ton 3372 (ENCB, F, LL, MICH); slope with Quercus near Rancho Mumuntik near Ocosingo, elev. 4200 ft., 10 Jan 1968, Ton 3461 (ENCB, F, MICH, NY); steep heavily wooded slope near Rancho Viejo of the Finca Prusia, Munc. of Angel Albino Corzo, elev. 2400 ft., 23 Jan 1968, Ton 3629 (ENCB, F, MICH); 32.7 miles WSW of Tuxtla Gutierrez
along Hwy 190, roadside, elev. 3100 ft., 9 Jan 1977, Urbatsch and Pridgeon 2891, 2982 (both LSU); along Hwy 190, 32.1 miles W of San Cristobal de las Casas, elev. 4200 ft., 9 Jan 1977, Urbatsch and Pridgeon 2896 (LSU); 18.2 mi. S of jct. of Hwy 190 and road to Arriaga, in pasture among scattered pines, 30 Jul 1978, Urbatsch and J. and B. Wussow 3342 (LSU). COLIMA: Colima 9 Jan to 6 Feb 1891, Palmer 1215 (GH, NY, US). DURANGO: Steep side canyons of the Rio Tamazula between La Bajada and La Junta, elev. 1300 m., 20 Mar 1972, Breedlove 24481 (MICH, MO); near Chacala, 23 Feb 1899, Goldman 328 (GH, US); 20 miles west of Laguna del Progreso, 120 miles west of Durango, 1 Apr 1948, Hurd 68 (MICH); Sianori, elev. 800 m., Feb 1924, Ortega 5264 (GH, MEXU, US). GUERRERO: Chilpancingo, 15 Nov 1966, Clark s.n. (F); dirt road from El Ocotito to Coatepin, 16 Nov 1977, Funk and Geman 2352 (LSU); district of Mina, Zapo, elev. 840 m., 18 Nov 1936, Hinton 9843 (GH, K, LL, MICH, NY, US); district of Mina, Los Barrales, elev. 1200 m., 27 Nov 1939, Hinton 14911 (F, GH, MO, NY, US); Rincon de la Via, elev. 700 m., 30 Oct 1960, Kruse 43 (ENCB); El Ocote, elev. 300 m., 10 Nov. 1898, Langlasse 614 (MICH, P); Achotla, elev. 1000 m., Feb 1927, Reko 5076 (US); ca. 34 miles S of Chilpancingo, ca. 17° 15' N 99° 30' W, elev. 2900 - 3300 ft., 6 Nov 1970, Webster and Breckon 16236 (F, GH, MICH). HIDALGO: Mabodo, 5 km al N de San Bartolo Tutotepec, elev. 1100 m., 19 Nov 1972, Gimate 767 (ENCB), 773 (ENCB, OS). JALISCO: 9-12 km by road from Puerto Vallarata, elev. 2-30 m., 7 Mar 1970, Anderson and Anderson 6007 (ENCB, MICH), 6026 (ENCB, MICH); in canyon E of Ciudad Guzmán, elev. 6100 ft., 18 Nov 1968, Boutin and Brandt 2244 (MICH); along road between Union de Tula and Ejutla, ca. 2 miles south of junction
with Hwy 80, elev. 3600 ft., 27 Nov 1969, Breckon et. al. 1043 (GH, LL, MICH); along small stream, 16 miles northwest of Ameca along road to Mascota, elev. 4300 ft., 1 Nov 1970, Breedlove 18670 (MICH); 10-14 km southwest of Tequila on Volcán de Tequila, elev. 2100-2400 m., 8 Nov 1974, Breedlove 39317 (MICH); in small ravine in oak zone about 17 road miles northeast of Tamazula, elev. 4900 ft., 29 Oct 1962, Cronquist 9761 (MICH, NY, TEX); Ixtlahuacan de los Membrillos, elev. 1738 m., 28 Oct 1961, Detling 8758 (MICH); along the main highway from Guadalajara to Autlan and Barra de Navidad, 9-10 km SW of Quililla, elev. ca. 1500 m., 8-9 Nov 1971, Dieterle 4096 (ENCB, LL, MICH, MO); Cerro de Omeca, Dec 1899, Diguet s.n. (MICH, NY, US); Huejotitan, Dec 1912, Diguet s.n. (P); cerro de Amatitan, elev. 1700 m., 30 Nov 1975, Estrada 8592 (ENCB, MICH); Rancho Viejo, about 10 km east-northeast of Huejiquilla el Alto, elev. 1900 m., 31 Oct 1963, Feddema 2306 (ENCB, MICH, TEX); 15.4 miles north of Colotitlan along Hwy 80, 6 Nov 1977, Funk 2285 (LSU, OS); 47 miles south of Jiquilpan on Hwy 110, 8 Nov 1977, Funk and Hill 2298 (LSU, OS); hills above Etzatlan, 11 Jan 1940, Gentry 5355 (NY); entre cumbre Tejamanil y Cuale, municipio de Talpa, elev. 1500 m., 4 Mar 1971, Gonzalez 96 (ENCB, MICH, TEX); entre Milpillas y la Ermita, municipio de San Sebastián, elev. 1200 m., 15 Feb 1971, Gonzalez y Palafox 65 (ENCB, MICH); oak woods at km 773-774 on Mexico 15 from Guadalajara to Tepic, 27 Nov 1967, Grashoff 173A (MSC); Orendain, 27 Nov 1930, Jones 27778 (GH, LL, MO, UC); Puente Grande, cerca al Guadalajara, 19 Nov 1940, Langman 3092 (MEXU); km 49 between Chapala - Guadalajara, 27 Nov 1940, Langman 3116 (MEXU); cerro Tepopote, la Primavera, 22 km al W de Guadalajara, elev. 1600-1700 m., 4 Sept 1967, Luna 392 (ENCB);
Agua Fria, km 35 Brecha a manuel M. Dieguez, Tamazula, elev. 2000 m., 20 Nov 1972, Luna 3627 (MICH, OS); near the road ascending to Tapala from Amacueca, elev. 1500-1800 m., 3 Nov 1960, McVaugh 20718 (ENCB, MICH); in the baranca above (south of) Rio Verde, near the highway from Yahualica to Tepatitlán, elev. 1500-2000 m., 6 Nov 1959, McVaugh and Koelz 242 (MICH); ca. 15 km south-southeast of Acatlan de Juarez, elev. 1600 m., McVaugh and Koelz 336 (ENCB, MICH); Sierra del Halo, near a lumber road leaving the Colima highway 7 miles south-southwest of Tecalitlán and extending southeasterly to San Isidro, 7-9 miles from the highway, elev. 1700-1800 m., 1 Dec 1959, McVaugh and Koelz 1254 (ENCB, MICH); open valley, San Sebastián, elev. 1500 m., 19 Jan 1927, Mexia 1524 (F, GH, MICH, MO, NY, UC, US); Rio Blanco Jun−Oct 1886, Palmer 675 (MO, NY, US); rocky slopes of the barranca near Guadalajara, 10 Nov 1888, Pringle 1788 (F, GH, MO, MSC, NY, UC, US); hills near Guadalajara, 29 Oct 1889, Pringle 2729 (F, MEXU), hills near Guadalajara, elev. 5000 ft., 4 Dec 1902, Pringle 9878 (F, MO, NY, US), 17 Oct 1903, Pringle 11501 (F, MICH, MO, LIL, US); Canoas-Tuxpan, Feb 1904, Purpus 510 (MO, US); Rancho Viejo, municipio de Huejúquilla, elev. 1900 m., 31 Oct 1963, Rzedowski 17580 (ENCB, MEXU, MICH); between La Huerta and Autlán, 4 Feb 1963, Templeton 9486 (ENCB, NY); Jardín Botánico L. Oliva, elev. 1550 m., Nov 1965, Villarreal 3 (ENCB); on steep slopes 6.5 mi. by road SW of Mazamilta, elev. 6100 ft., 1 Nov 1970, Webster and Breckon 16137 (GH, MICH); along Hwy 15 to Tepic, 12.1 miles west of jct. with bypass around Guadalajara and Hwy 15 to Tepic, 23 Oct 1980, Wussow and Landry 337 (LSU). MEXICO: herb market in Toluca, 12 Dec 1969, Halbing s.n. (MEXU); Rincón, district of Temascaltepec, 22 Jan 1932, Hinton 188
Ixtapan, district of Temascaltepec, elev. 1000 m., 15 Dec 1932, Hinton 2948 (K, MO, NY, US); Temascaltepec, 29 Dec 1932, Hinton 3038 (K, NY, US); Malpias, San Nivolas, 2.5 km al suroeste de Valle de Bravo, elev. 1300 m., 4 Jan 1953, Matuda et. al. 27388 (MEXU, NY); Tejupilco, 28 Dec 1952, Matuda et. al. 27482 (MEXU, NY); Amatepec y cercanías, elev. 1800 m., 27 Dec 1953, Matuda et. al. 29869 (MEXU, US); C de la Corona Zacualpan, elev. 2000-2500 m., 1 Feb 1954, Matuda et. al. 30272 (MEXU); 3 km al S de Colorines, municipio de Valle de Bravo, elev. 1700 m., 29 Dec 1966, Rzedowski 23739 (ENCB, MICH, MSC); Ocotepec, municipio de Tejupilco, elev. 1650 m., 10 Dec 1967, Rzedowski 25285 (ENCB, LL, MICH, MSC); Feb 1886, Urbina s.n. (MEXU).

MICHOACAN: Ostula, Nov 1906, Emrick 47 (F); Coalcoman, elev. 1000 m., 3 Feb 1939, Hinton et. al. 12932 (LL, MICH, MO, NY, US), 4 Mar 1939, Hinton et. al. 13595 (GH, NY, US). MORELOS: Tizapotla, 3 Nov 1967, Vazquez 1923 (MEXU); montañas N de Cuernavaca, elev. 2000 m., 5 Nov 1972, Vazquez 3979 (MEXU). NAYARIT: Tepic, Coulter 330 (K); 11 km by road east of Las Varas toward Compostela, elev. ca. 200 m., 28-29 Oct 1971, Dieterle 3938 (ENCB, LL, MICH); 1 km north of El Cuatante, about 40 km (airline) north-northeast of Puerto Vallarta, elev. 100 m., 17 Nov 1963, Feddema 2607 (ENCB, LL, MICH, NY); wooded grassland near Pochotitlan, elev. ca. 3000 ft., 12 Nov 1961, Gentry et. al. 19520 (LL, US); Tepic, 9 Feb 1927, Jones 23404 (GH, LL); open brushy palm savannah, 12 miles northeast of San Blas, elev. 60-100 m., 21 Apr 1951, McVaugh 12073 (MICH, US); steep hills, 6-12 km northeast of Miramár, road to Jalcocotan, elev. 250-350 m., 11 Apr 1965, McVaugh 23541 (ENCB, MICH); 2-9 miles west of Jalcocotan, on road to Miramár, elev. 200-700 m., 5 Nov 1959, McVaugh and Koelz 689.
arroyo del Navarrete, elev. 30 m., 1923, Ortega 18 (US); Tepic, Jan - Feb 1892, Palmer s.n. (F, MICH, US);
cerro de la Cruz, cerca de Tepic, 30 Mar 1958, Paray 2679 (ENCB); 1 km al N de El Cuatante, municipio de Valle de Banderas, elev. 100 m., 17 Nov 1963, Rzedowski 17841 (ENCB, MEXU, MICH, TEX); 3 km al oeste de Mazatan, elev. 800 m., 20 Nov 1963, Rzedowski 17904 (MICH);
Ixtlan, elev. ca. 700 m., Viereck 1142 (US). OAXACA: Tuchitan, Palmenwald zwischen Rancho Jobinna und Chicapa, 30 Jan 1896, Caec. et Seler 1981 (GH, K, MO, NY); steep hillsides ca. 15 km southwest of Sta. Maria Zacatepec, Municipio de Putla, elev. 550 m., 5 Feb 1965, McVaugh 22226 (ENCB, LL, MICH, NY); Rio Cascabel, 15 Mar 1934, Mell 2222 (NY); Chivela, 7 Mar 1934, Mell 2274 (NY); trail to Rio Yaveo, elev. 445 m., 25 Mar 1938, Mexia 9211 (F, GH, LL, MO, NY, UC); Chivela, 16 Apr 1910, Orcutt 3276 (F, GH, MO, US). PUEBLA: Mesa de San Diego, 2 May 1952, Cantu 628 (EXU); Agua Fria, antes de Poza Rica, 26 May 1961, Gomez-Pamph 461 (XAL); 3 miles east of Maria Andrea, elev. 600 ft., 24 Feb 1961, McGregor 16465 (MICH). SAN LUIS POTOSI: Tamazunchale, 28 Nov 1937, Kenoyer 737 (F, MO); near the waterfall at El Salto, 20 Feb 1961, King 3894 (MICH, TEX, US); en route from San Luis Potosí to Tampico, Dec 1878 to Feb 1879, Palmer 1111 (F, GH, MO, NY, US); municipio de Tamasopo, elev. 1070 m., 6 Nov 1968, Puig 3649 (ENCB); Cienga Juan Jilote, municipio de Tamasopo, elev. 350 m., 10 Jan 1969, Puig 3664 (ENCB); 5 km al SE de Tamasopo, elev. 700 m., 16 Jan 1956, Rzedowski 6902 (ENCB); San Isidro, ca. 4 km al ESE de Tamazunchale, elev. ca. 100 m., 25 Feb 1959, Rzedowski 9810 (ENCB); ca. 20 miles W of Rayón on Rte. 86, 6 Oct 1976, Stuessy and Gardner 4055 (OS); along Hwy 80, 14.6 miles
east of Cd. Maiz, dense pine-oak forest, 15 Oct 1980, Wussow and Landry 314 and 315 (both LSU); along small paved road to Canoaas, 2.2 miles north of jct. with Hwy 70 (Cd. Valles to Rioverde Hwy.), 16 Oct 1980, Wussow and Landry 321 (LSU). SINALOA: Capadero, Sierra Tacuichamona, elev. 2500 ft., 10 Feb 1940, Gentry 5531 (GH, MICH, MO, NY, UC); 8 miles north of Badiraguato, 2 Mar 1940, Gentry 5791 (MICH, MO, NY); San Ignacio, Río de los Humays, May 1921, Ortega 432 (K).

TAMAULIPAS: 4.7 miles west of jct. of Hwy 80 and 85 on Hwy 80, elev. 1100 ft., 31 Dec 1970, Dunn et. al. 17593 (ENCB); vicinity of Tampico, elev. ca. 15 m., 1-31 Jan 1910, Palmer 14 (F, MO, NY, US); common along roadsides near Río Sabinas, ca. 6-8 km. northwest of El Encino, 2 Apr 1980, Pruski 1696 (LSU); near Gomez Farias, 24 Nov 1968, Richardson 928 (LSU); ca. 5 miles northwest of Encino, along riverslopes and adjacent hillsides of the Río Sabinas near the Nacemento, 10 Apr 1979, Wussow and Landry 190 (LSU). VERA CRUZ: Banderilla, municipio de Banderilla, elev. 1500 m., 12 Oct 1973, Acosta and Dorantes 543 (ENCB); La Mancha, elev. 10 m., 25 Nov 1975, Acosta and Dorantes A-606 (XAL); alrededores de la Laguna de la Mancha, elev. 20 m., 28 Nov 1975, Acosta and Dorantes A-654 (XAL); Banderilla, elev. 5500 ft., 17 Sept 1938, Balls 5490 (K, UC, US); lado sur de Santa Rosa ca. 20 km al sur de Catemaco, elev. 450 m., 18 Jan 1972, Beaman 5479 (F); Orizaba, 186?, Bilimett s.n. (P); Orizaba, no date, Botteri 481 (F); Valle de Cordova, 10 Jan 1865-66, Bourgeau 1675 (GH, MICH, P); Región de Orizaba, 24 Oct 1886, Bourgeau 3241 (P); Jalapa, 13 Dec 1902, Caec. et Seler 3598 (GH); Ejido Palmases Cuata, elev. 6 m., 23 Dec 1966, Calderon 1237 (F, MICH, MO, US); Playa Azul, Catemaco, elev. 300 m., 21 Dec 1968, Calderón 1816 (A,
ENCb, F, MEXu, MICH, MO); Calzada 681 (XAL); 2 km de Catemaco, carreira a Sontecomopan, no date, Calzada 884 (F, MO, XAL); El Salto de Eypantla, 6 km de Sihuapan, San Andrés Tuxtla, 19 Jan 1973, Calzada 964 (XAL); en el Jardín Botánico Fco. J. Clavijero a 3 km W de Xalapa antigua carreira Xalapa-Coatepec, elev. 1450 m., 22 Feb 1977, Calzada 3043 (XAL); en la colinas de Banderilla, elev. 1500 m., 20 Mar 1978, Calzada and Jimenez 4282 (XAL); Rancho Guadalupe Jardín Botánico a 3 km de Jalapa, carreira vieja a Coatepec, elev. 1300 m., 13 Oct 1978, Castillo et al. CC-100 (XAL); Laguna Encantada 7 km al NE de San Andrés Tuxtla, 26 Jan 1973, Cedillo and Calzada 82 (F, XAL); 4 km al oeste de Ozuluama, 6 Dec 1970, Chiang 196 (MICH); Huatusco, elev. 1200 m., Dec 1898, Conzatti 860 (GH); 3.8 km de Tuzamapansobre la carreira a Totutla, Coatepec, 10 Nov 1975, Corrál 18 (F, XAL); San Andrés Tuxtla, 14 Apr 1960, Dioscoreas 9216 (MEXu); Consolapan, municipio de Coatepec, elev. 1200 m., 23 Oct 1971, Dorantes 425 (ENCb, F, GH); 1 km al E de el Castillo, elev. 900 m., 8 Feb 1972, Dorantes 492 (F, MEXu); Potrero de Orilla W de La Laguna Salada o de Boca Andrea, elev. 60 m., 26 Jun 1972, Dorantes et al. 1022 (F); 3 km al N de Lencero, carreira Jalapa-Vera Cruz, elev. 1100 M., 15 Oct 1972, Dorantes and Acosta 1685 (ENCb, XAL); El Castillo, elev. 1100 m., 10 Dec 1972, Dorantes et al. 1879 (XAL); Alrededores de Laguna Verde, Alto Lucero, elev. 100 m., 18 Nov 1975, Dorantes et al. 5206 (F, XAL), 5213 (F, XAL); Hotel Playa Azúl, Catemaco, elev. 340 m., 29 Dec 1968, Gomez-Pampa 4014 (XAL); 10 miles southeast of Jalapa on road to Vera Cruz, elev. ca. 3500 ft., 19 Nov 1959, Graham and Johnston 4797 (MICH, TEX); La Laguna near Vera Cruz, 23 Jan 1906, Greenman 46 (F); along the shore north of Vera Cruz, 24
Jan 1906, Greenman 122 (F, NY); La Purga, 25 Jan 1906, Greenman 280 (F, GH); El Miradór, camino a Yecuatla, elev. 490 m., 28 Apr 1976, Hernandez et. al. C-218 (XAL); Alvarado, elev. 0 m., 7 Mar 1971, Hernandez and Trigos 1110 (F, MEXU, MICH); Jalapa, elev. 4300 ft., 22 Sept 1906, Johnson s.n. (NY); Vera Cruz, 21 Dec 1925-6, Juzepczuk 1118 (US); Fortín, Feb 1883, Kerber 310 (MICH, US); along Rte. 150, about 9 miles west of Córdoba, 26 Jan 1960, King 2363 (MICH, TEX, US); along Rte. 150, about 5 miles east of Cuitlahuac, 27 Jan 1960, King 2385 (MICH, TEX, US); Misantla, Mar 1841, Liebm. 373 (US); km 7 carretera Catemaco-Coyame, elev. 260 m., 14 Apr 1960, Leija et. al. 2779 (MEXU); Vera Cruz, ca. 1838-9, Linden 1184 ICH); Potrero el Ojite, de la congregación Palma Sola., elev. 20 m., 4 Dec 1969, Lot 622 (MEXU); Potrero Guautian Hacia el Plan de las Hayas en el Rancho La Mesa, elev. 15-50 m., 5 Dec 1969, Lot 656 (F, MEXU); transecto Punta Limón a Cerro Monte de Oro, elev. 40-60 m., 20 Jun 1972, Lot et. al. 1936 (MEXU); on hill about a mile from Jalapa, elev. ca. 4600 ft., 30 Aug 1935, MacDaniels 385 (F), 386 (F); Jalapa, 6 Sept 1936, MacDaniels 940 (F); ejido El Jovo, carretera Martínez de la Torre, Tlapacoyan, elev. 160 m., 25 Feb 1976, Marquez 534 (F, XAL); Orizaba, Martíass 1104 (F); frequent with Calea zacatechich, Orizaba, no date, Mohr 251 (US); Jul 1857, Mohr 30 (NY); Hda. Miradór, elev. 3600-4000 ft., Feb 1894, Nelson 68 (US), 81 (US), 20 Feb 1894, 124 (US); near Motzorongo, elev. 800-1000 ft., 22 Feb 1894, Nelson 138 (US); Vera Cruz, Neuling and Gomez-Pampa 654 (XAL); Jalapa, 10 Feb 1910, Orcutt 2815 (F, K, MO); Vera Cruz, 10 Feb 1910, Orcutt 2900 (F, MO); 4 km al sureste de Coacoatzintla, carretera Banderilla-Naolinco, elev. 1300 m., 30 Dec 1975, Ortega et. al. D-55 (XAL); 1 km antes del
Rio El Espinal, Naolinco, elev. 950 m., 28 Oct 1976, Ortega 592 (XAL); Jalapa, Nov 1947, Paray 613 (ENCB); cerca de la playa, El Viejo, cerca de la playa, El Viejo, cerca de Villa Rica, 28 Dec 1958, Paray 2893 (ENCB); near Jalapa, elev. 4000 ft., 30 Mar 1899, Pringle 7818 (GH); near Jalapa, elev. 4000 ft., 1 Dec 1903, Pringle 11823 (F, LIL, MICH, MO, MSC, US); Tuxpan, Feb 1904, Purpus 510 (UC); Zacuapan, Dec 1906, Purpus 2182 (F, MO, NY, UC, US); Corral de Piedras, Zacuapan, Jan 1912, Purpus 5736 (F, MO, NY, UC, US); Vera Cruz, Purpus 8640 (UC); Zacuapan, Mar 1929 Purpus 13083 (F); 1932, Purpus 14312 (F), Mar 1931, Purpus 15019 (A, F, MICH, UC, US); alredores del Puente en la camino LaLaja-Pinoltepec 21 Nov 1975, Ramas 335 (MEXU); Cuapichapa, km 2 al sur del Puente de Sn. Miguel, elev. 300 m., 7 Jan 1968, Rosas 937 (XAL); Paso de Macho, elev. 550 m., 19 Mar 1968, Rosas 1136 (F, MICH); near Jalapa, 15 Aug 1901, Rose and Hay 6128 (US); Ocotal Chico, region of Los Tuxtlas, elev. 1900 ft., 23 Mar 1965, Ross 108 (US); barranca de Chavastla near Huatusco, Feb 1932, Rozynski 790 (F); Hacienda El Palmar, .5 km northwest of Campo Experimental de Hule, 4 Mar 1944, Santos 2846 (LL, MICH); Mexico, Mirador, 1867, Sartorius s.n. (P); Orizaba, 1896, Schaffner s.n. (GH, NY); 2 miles below La Perla north of Orizaba, 2 Mar 1966, Smith and Tejeda 4420 (US); ca. 6 miles above Orizaba on the Zongolica road, 17 Mar 1966, Smith and Tejeda 4455 (US); Jalapa, elev. 4000-4500 ft., 6 Jan. 1894, Smith 1713 (MICH, UC); Orizaba, 17 Feb 1892, Smith 132 (MO), 11 Jan 1892, Smith 266 (MO); Salto de Eyipantla, cerca de San Andrés Tuxtla, 22 Jan 1965, Sousa 2060 (F, MEXU); sur de la Laguna Encantada, cerca de La Laguna Catemaco, 24 Jan 1965, Sousa 2117 (MEXU); north side of Lago Catemaco, about 1 km
W of village of Coyame in grazed pasture near forest, 12 Jan 1972, Spellenberg 2746 (NY); 10 miles east of Jalapa, 28 Dec 1940, Stahler s.n. (UC); 0.9 miles N jct. road to Ozuluma on Rte. 180 (ca. 38 jct. road to Ozuluma on Rte. 180 (ca. 38 miles S of Villa Cuauhtemoc), 5 Dec 1974, Stuessy and Roberts 3639 (F, LSU, OS, XAL); along a small creek about 6 miles N of temporal VeraCruz, 25 Dec 1970, J. and C. Taylor 7279 (MO); ca. 14 miles SE of Jalapa along Hwy. 140, elev. 2900 ft., 6 Jan 1977, Urbatsch and Pridgeon 2880 (LSU); 7 miles N of Miradores along Hwy. 140 via local trail, elev. 900 m., 25 Jul 1978, Urbatsch and J. and B. Wussow 3321 (LSU); 8.5 miles E of jct. of Hwy. 140 and road to Misantla, along road to Misantla, elev. 1500 m., 25 Jul 1978, Urbatsch and J. and B. Wussow 3322, 3324 (both LSU); Jalapa, Jan 1885, Urbina s.n. (MEXU); Banderilla, municipio de Banderilla, elev. 1500 m., 3 Mar 1970, Ventura 632 (ENCB, F, LL, MICH, MSC); 23 Mar 1970, Ventura 750 (ENCB, MICH, MSC); Esquilón, municipio de Jilotepec, elev. 1230 m., 7 Oct 1971, Ventura 4378 (ENCB, MICH, TEX); El Cucero, municipio de Puente Nacional, elev. 50 m., 13 Jan 1973, Ventura 7715 (ENCB, OS); La Mesa de Chiveros, municipio de Xalapa, elev. 1350 m., 16 Jul 1974, Ventura 10344 (ENCB); El Encanto, municipio de Tlapacoyan, elev. 300 m., 17 Nov 1975, Ventura 12084 (ENCB, OS); Casa Blanca, municipio de Xalapa, elev. 1250 m., 28 Oct 1976, Ventura 13475 (ENCB); Apazapan municipio de Apazapan, elev. 300 m., 29 Jan 1979, Ventura 15714 (ENCB); no date, Wawra 447 (NY); Rio Seco near Cordoba, 1931, Woronow 3035 (US); 3.6 miles north of jct. of Hwy. 140 and road to Misantla, along road to Misantla, 27 Oct 1980, Wussow and Landry 349 (LSU); Miradores, 15 km SE of Jalapa along main Hwy. to Vera Cruz, 28 Oct 1980, Wussow and
Landry 351 (LSU); carretera a plan de Las Hayas, a 1 km del entronque con la carretera a Nautla, elev. 90 m., 24 Jun 1972, Yanes 669 (MEXU); Coapexan, municipio de Xalapa, elev. 1470 m., 8 Jan 1976, Young 29 (XAL); carretera al Lencero, Emiliano Zapata, 28 Jul 1976, Zola 573 (F, NY, XAL), 7 Oct 1976, Zola 855 (MEXU, XAL). ZACATECAS: road from Zacatecas to Guadalajara via Jalpa, 6 miles south of Villanueva, elev. 2060 m., 30 Dec 1969, Anderson and Anderson 5246 (MICH), 5248 (ENCB, MICH); 3-4 miles south of Villanueva, elev. 6300 ft., 29 Nov 1959, Gentry 18269 (LL, US). STATE UNKNOWN: Mexico, 1856, Botteri s.n. (P); Dec 1839, Ehrenberg 1186 (GH); Wartenberg, near Tantoyuca, prov. Huasteca, 1858, Ervendberg 96 (K); Progresso, May 1933, Flores s.n. (F); 1848-9, Gregg 1002 (MO), 1042 (MO): 1845-48, Oersted 10,952 (US); San Blas, elev. 30 m., no date, Ortega 18 (ENCB, MEXU); 1787-1795-1804, Sesse, et. al. 2859, 2974, 3024, 3444 (all F); Valle de Mexico, 187?, Schaffner s.n. (P).

NICARAGUA. BOACO: Rte. 9, 1 km west of Boaco, 30 Dec 1968, Hamblett et. al. 1455 (GH); hillside pasture, Campoupa, 16 Jan 1970, Seymour 3503 (F, MO); hillside pasture, Boaco, 24 Jan 1970, Seymour 3875 (F, MO). CARAZO: shady clay bank, Rte. 2, Santa Teresa, 27 Dec 1968, Atwood 1284 (NY, UC). CHONTALES: Jun 1868, Tate 179 (289)(K). (CABO) GRACIAS A DIOS: in sabana on east side of airstrip, vicinity of Waspam, elev. 50-100 ft., 9 Mar 1961, Bunting and Licht 492 (F). COMARCA DEL CABO: pine woods, Thaeler Memorial Hospital, Bilwaskarma, elev. 0-100 m., 13 Mar 1971, Nelson 4643 (GH, LL, UC). ESTELI: thickets along Estanzuela creek, 8 km west of Esteli, elev. 1000 m., 4 Nov 1968, Molina 23093 (F, MO, NY, US); cutover hills, 3-7 km northwest of Pueblo Nuevo, elev. 600-700 m., 24 Nov 1973, Williams...
and Molina 42409 (F, MICH, US). GRANADA: slopes of Mt. Mombacho, near Granada, elev. 460 m., Grant 768 (MICH); Island Ometepe, Lake Nicaragua, Jan 1893, Smith s.n. (GH). JINOTEGA: open grassy field, Jinotega, elev. 1300 m., 18 Dec 1940 – 9 Feb 1941, Grant 7291 (F); pine woods, San Rafael del Norte, elev. 1200-1350 m., 25-26 Mar 1917, Miller and Griscom 77 (US); ravines of Cordillera Central de Nicaragua, 2-4 km south of Jinotepa, elev. 1200 m., 10 Jan 1963, Williams et. al. 23575 (F), 23576 (F). MANAGUA: along rte. 2 ca. 20 miles east of Managua, 24 Feb 1976, Croat 32189 (MO); Sierra de Managua, elev. 600-900 m., 1930-1940, Garnier 2, 27, 28 (all F); open fields, Managua, elev. 40 m., 18 Dec 1940 – 9 Feb 1941, Grant 7340 (F); vicinity of Casa Colorada near El Crucero, summit of Sierra de Managua, elev. 800-900 m., 14-25 May 1947, Standley 8146 (F). MASAYA: Masaya, 27 Jan 1903, Baker 2199 (GH, K, MICH, MO, MSC, UC, US). MATAGALPA: hillside above Santa Maria de Ostumo, elev. ca. 1500 m., 22 Dec 1975, D'Arcy 10481 (LL, MO); 5 km north of Sta. Maria de Ostuma, elev. 1500 m., 15 Jan 1963, Williams et. al. 23927 (F, NY); Matagalpa, 23 Dec 1968, Zelaya 978 (F, GH, MICH, MO, NY, UC). NUEVA SEGOVIA: hillside, Jalapa, 29 Jun 1972, Seymour 5533 (GH). ZELAYA: region of Toumarin, Rio Grande, area de la Bahia de Bluefields, elev. 0-30 m., 25 Mar 1949, Molina 2437 (F). DEPT. UNKNOWN: U.S. North Pacific Exploring Expedition, 1853-56, Wright s.n. (GH, MO, US). PANAMA. CANAL ZONE: forest along banks of Quebrada La Palma and Canon of Rio Charges, elev. 70-80 m., 9 Jan 1935, Dodge and Allen 17335 (GH, MO, NY); in Government forest along Las Cruces Trail, elev. 75 mi, 25 Feb 1935, Hunter and Allen 708 (MO); around El Paraíso, elev. 30-100 m., Jan 1911, Pittier 2578 (F, GH, NY, US);
Balboa, Nov 1923 - Jan 1924, Standley 29254 (US), 29280 (US), 32144 (US); along moist limestone cliff, drowned forest along R. charges between junction with Rio Pequeni and with Rio Indio, elev. 66 m., 5 Dec 1934, Steyermark and Allen 16780 (MO). CHIRIQUI: El Huacal, 26 Dec 1971, Atencio 21 (F, MO); vicinity of Boquete, from quete to 3 miles N, elev. 3300-4200 ft., 12-13 Dec 1966, Lewis et. al. 573 (MO, UC, US); Frances Arriba School, ca. 14 miles N of David, elev. 1200 ft., 14 Dec 1966, Lewis et. al. 650 (K, MO, UC, US). COLCE: vicinity of El Valle, elev. 800-1000 m., 22 Dec 1936, Allen 77 (MO); ridge south of El Valle, 23 Dec 1972, Gentry 6809 (MO); El Valle de Anton, elev. 1000-2000 ft., 2-3 Dec. 1967, Lewis et. al. 2600 (MO, UC); Potrero, 5 Nov 1972, Puga 20 (F, MO). HERRERA: 4 mi. south of Los Pozos, 17 Jan 1966, Tyson 2680 (O); 10 mi. south of Ocu, 21 Jan 1966, Tyson et. al. 2807 (MO). PANAMA: Nuevo Emperador, 15 Jan 1972, Atencio 33 (ENCB); dry sabanas, Aquarubia, 20 Jan 1918, Killip 3356 (US); Nuevo Emperador, a 300 m. de la entrada, 14 Jan 1972, Osorio 43 (F, MO); coastal thicket, Bella Vista, 28 Nov 1923, Standley 25344 (US); thicket between Matias Hernandez and Juan Diaz, 21 Jan 1924, Standley 31967 (US). PROVINCE UNKNOWN: Cuming 1116 (K); 1790, Haenke 2346 (F); Halsted 1850 (NY).

lb. Calea urticifolia (Mill.) DC. var. yucatanensis Wussow and Urbatsch, var. nov. TYPE: MEXICO. YUCATAN: Valladolid, 16 Jan 1938, R. L. Crockett 79 (HOLOTYPE: MICH!, Fig. 26).

Differs from the typical variety in having terminal capitulescences with large heads (40-52 flowered) on long peduncles (20-35 mm).
This variety differs from the typical one in its large heads (40-52 flowered) on long peduncles (20-35 mm). The capitulescences are terminal on the branches and not axillary as is common in var. urticifolia. This variety is restricted to the states of Yucatan and adjacent Quintana Roo, Mexico where the typical variety has never been reported (Fig 19). (There are a few large-headed specimens from Honduras but these lack the long peduncles consistently found in the Yucatan material). According to Gaumer (23588, in sched.) var. yucatanensis is called "Xicin", a Mayan word which signifies ear or hearing.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. QUINTANA ROO: Chichankanab, Gaumer 2096 (A, F, MICH, MO, UC, US); Lake Chichankanab, Apr 1917, Gaumer 23649 (F, US). YUCATAN: 17 Mar 1903, Caec. et Seler 3960 (F, GH); Izamal, Gaumer s.n. (F, K); San Anselmo, Gaumer 23209 (F, MO, NY, US); south Kancabdzonot, Mar 1917, Gaumer 23588 (F, US); 1917-1923, Gaumer 24159 (F, GH, MO); Izamal, 22 Feb 1906, Greenman 456 (F).


(originally considered a Colombian species, see discussion following species description).

Shrubs 0.5-3 m tall; stems erect to lax and spreading, glabrous to pilose-tomentose; leaves opposite, simple, blades broadly ovate to lance-ovate or elliptic, 0.5-12 cm long, 0.5-7 cm wide, apices obtuse to acuminate, bases rounded or obtuse to acute, margins coarsely crenate to serrate (rarely subentire), upper surface scabrous to glabrous, usually dark green, triplinerved, lower surface matted
tomentose to essentially glabrous, usually resin dotted, petioles lacking to 1 cm, glabrous to densely pubescent and resin dotted; capitulescence of axillary or terminal cymose or corymbose clusters of heads, secondary peduncles lacking to ca. 3 cm long, primary peduncles ca. 1-10 mm long, tomentose to sparsely pubescent; involucres cylindric, 4-6 mm tall, 2-4 mm wide, phyllaries imbricate, 4-6 seriate, the outermost broadly ovate or elliptic to suborbicular, 1-6 mm long, 0.5-3.5 mm wide, herbaceous or scarious throughout or herbaceous tipped, densely hirsute to essentially glabrous, usually resin dotted, intermediate phyllaries grading from ovate, elliptic or obovate to oblong or narrowly elliptic, 2.5-6 mm long, 1-3 mm wide, scarious, apices rounded to acute, margins and apex often ciliate and membranous, sometimes purplish; capitula obscurely radiate, 5-15 flowered; receptacle conic, ca. 0.5-1 mm long and wide; palea oblong, scarious, slightly yellowish, ca. 5-6 mm long, 2-3 mm wide, conduplicate, apices blunt and laciniate; ray flowers inconspicuous but 1-3 normally present, pistillate, fertile, ligules white or cream colored, shallowly to deeply 2-3 (4) lobed, ligule usually ca. 2 mm long (not exceeding the disk florets in length), throat 2-3 mm long, often resin dotted, style branches ca. 1 mm long, apices acute to obtuse; disk flowers normally 4-12, fertile, corolla white to cream colored, ca. 3.5-4.5 mm long, lobes 5, acute, 1.0-1.6 mm long, tube 2-3 mm long, usually gland dotted, flaring abruptly ca. 0.5 mm below the lobes and again slightly at the base, anthers exerted, yellow, apical appendage acute, bases rounded, style branches same as on ray flowers; achenes (ray and disk similar) cylindric to somewhat
prismatic, 2-3.5 mm long, black, shining, glabrous to densely antrorsely hirsute, light colored carpopodium present, pappus of 8-12 broadly lanceolate to oblong, stramineous scales, 1-1.5 (2) mm long, margins laciniate, apices rounded to acute, sometimes purplish at the base or throughout; chromosome number \( n = 19 \).

The name *Calea ternifolia* has remained virtually unused since it was proposed by Humboldt, Bonpland and Kunth (1820), reportedly based on a collection from Colombia. In the original description, the locality was given as "crescit cum praecedente" (growing with the preceding), which refers to *C. prunifolia*, the first of four species of Calea described in their publication. Although the published description of *C. prunifolia* gives Colombia as the type locality, the type specimen has both "Honda Magdalene" (Colombia) and "Mexico" written on the label, and the specimen of *C. ternifolia* gives just "Honda".

Blake (1930), while visiting several European herbaria, discovered that another Humboldt collection, *C. sessiliflora*, reportedly collected in Mexico, was actually the same as his newly described *C. brevipes* from Colombia. Blake goes on to say, "This region (Colombia) was visited by Humboldt and Bonpland and the specimen in the Willdenow herbarium was undoubtedly collected there by them...". *Calea sessiflora* does not occur in Mexico or Central America and *C. prunifolia* is known only from Venezuela, Colombia and Central America.

Obviously, there has been considerable confusion regarding the exact location of some of the Humboldt and Bonpland collections.
After examining photographs of the type material of *C. ternifolia*, there is no doubt that it agrees perfectly with the type material of *C. pringlei*, a species described by Robinson in 1901, based on material from mountains near Iguala, Guerrero, Mexico. Current studies by Pruski and Urbatsch (in prep.) confirm that neither *C. ternifolia* nor any species closely resembling it is known from Colombia. Further evidence that Humbold and Bonpland visited the region in Mexico where *C. pringlei* grows is that they described *C. peduncularis* (in the same publication with *C. ternifolia*) which has a similar distribution.

Clearly the original locality data for *C. ternifolia* is in error. Since the name *C. ternifolia* has priority over the other names of this complex, it must be used, and the latter names are appropriately placed in synonymy.

*Calea ternifolia* is a morphologically variable, wide ranging species, occurring from northeastern Mexico to northern Costa Rica (Fig. 20). It grows mainly along roadsides, and in pastures and open forests, having virtually the same distribution and habitat preferences as *C. urticifolia*. Within this species, there is an extreme amount of variability in leaf shape, size and pubescence as well as other morphological features. Many specific and varietal names have been ascribed to the extreme forms in this complex. However, an analysis of the variation shows that they are connected by numerous intermediates, thereby obliterating suspected specific limits. The present study recognizes four varieties within this species. Features that are diagnostic are texture of the involucral bracts along with leaf size, pubescence, and shape.
In the vicinity of Jalapa, Orizaba, and Vera Cruz, the plants consistently have small leaves with densely pubescent lower surfaces, and scarious phyllaries with reddish, membranous, crisped margins. Although some intergrading forms do occur near Lago Catemaco, these small, pubescent leaved forms have geographic integrity, and are treated here as a distinct variety (var. zacatechichi).

A second variety (var. calyculata) has somewhat more variable leaf shape and pubescence but is readily recognized by its large, foliaceous outermost phyllaries. This variety has a disjunct distribution. The plants from Oaxaca are fairly uniform and essentially like those from near San Luis. The others tend to show more variability in leaf pubescence and shape with those from Tamaulipas and Nuevo Leon having more acuminate leaf apices and less pubescent leaf surfaces.

The most restricted variety (var. nelsonii) grows near Tonola and Arriaga, Chiapas, Mexico. Its leaves, stems, and corollas are totally glabrous and without resinous globules.

In contrast, var. ternifolia is widely distributed geographically and as might be expected, is highly variable. Its leaves range from relatively small to quite large (ca. 3-12 cm long, 2-7 cm wide), while their shapes vary from broadly ovate to narrowly elliptic, with apices that are obtuse to acuminate. Leaf texture ranges from rugose to smooth, with blades that are essentially glabrous to densely pubescent below. In habit, plants range from dense, erect shrubs to large, lax, weak stemmed ones. Although the extremes of this variety appear to be quite distinct, the numerous intermediates make taxonomic recognition of them impractical. Based
on field observations, much of the variation appears to be habitat related, with erect plants having broad pubescent leaves occurring in sunny open habitats, and more lax, narrow, glabrous-leaved forms occurring in wooded and shaded areas.

Among the Mexican, Central American, and Jamaican species of *Calea*, *C. ternifolia* is easily recognized by the combination of its radiate heads with cream-colored corollas, inconspicuous ligules that normally do not exceed the disk florets in length, and achenes with short, broad pappus scales.

Since considerable confusion has existed in the application of names to these taxa, it seems appropriate to discuss common names and uses here, rather than try to assign them to specific varieties. Previously the name commonly used for this taxon was *C. zacatechichi*, an epithet which in itself is interesting. Supposedly (Standley, 1926) the name comes from the Nahuatl, "zaca chichic" meaning "bitter-grass." The plant reportedly is used as a remedy for various stomach afflictions, cholera, and malaria. It is known under the common name of "xicin", "zacatechichi", "jacachicio", "zaratillo blanco", "amargosa", "vera blanca", "canilla de zanate", "oreja de conejo", "juralillo", "zacate amargo", "simonillo", "falso simonillo", and "bejuco chismuyo" (in part from Standley, 1926, and Nash, 1975). An interesting account of hallucinogenic uses of the plant by the Chontal Indians of the state of Oaxaca comes from MacDougall (1968); "a 'pinch' of the crumbled dried leaves is infused in hot water, and a cup of the resulting tea is sipped slowly; then the partaker lies down in a quiet, secluded spot and smokes a cigarette made of the dried leaves. Sufficiency of dose taken is
said to be indicated by a sense of repose, when the person 'hears his own heart and pulse beats.' A feeling of well being is said to continue for one or more days, with no disagreeable after-effects."

He goes on to say that to the Chontal herb doctors, the plant is "pela kano" (leaf of God) used "for the clarification of the senses."

KEY TO THE VARIETIES OF C. TERNIFOLIA

A. Outermost phyllaries conspicuous, 2/3 as long to equalling the length of the involucre, broadly ovate to lance-ovate, herbaceous throughout (known from the states of Nuevo León, San Luis Potosí, Tamaulipas, Querétaro and Oaxaca, Mexico)

...... 2.b. var. calyculata

A. Outermost phyllaries small, inconspicuous, not more than 1/2 length of the involucre, orbicular to lanceolate, membranous throughout or herbaceous-tipped

......B

B. Leaves and corollas totally glabrous, not resin dotted (known only around Arriaga and Tonola)

...... 2.c. var. nelsonii

Leaves and/or corollas resin-dotted, otherwise essentially glabrous to densely pubescent

.........C
C. Leaves consistently small, mostly 0.5 to 3 cm long, 0.5-2 cm wide, ovate, apices obtuse, rugose, dark green and scabrous above, light green and densely matted tomentose below, phyllaries often with reddish, crisped, membranous margins (known from around Jalapa and Orizaba, Veracruz).

...... 2.d. var. zacatechichi

C. Leaves small to quite large, ca. 3-12 cm long, 2-7 cm wide ovate to elliptic, apices obtuse to acuminate, surfaces rugose to smooth, glabrous to densely pubescent below, (western and southern Mexico, Belize, Guatemala, Honduras, Nicaragua and northern Costa Rica).

...... 2.a. var. ternifolia

2a. _Calea ternifolia_ HBK var. _ternifolia_, Nov. Gen. et Sp. 4 : 294. 1820. TYPE: MEXICO. (COLOMBIA) Humboldt and Bonpland herb. no. 38070 (HOLOTYPE: P ; PHOTOS: F!, GH!, Fig. 27).


This variety is the most broadly circumscribed of the species in containing a considerable amount of leaf variation. It has a broad geographic distribution occurring in western and south central Mexico, the Yucatan, Belize, Guatemala, Honduras, and northern Costa Rica (Fig. 20). Flowering generally occurs during the dry season from late August to early February.

C. ternifolia var. ternifolia can be distinguished from the other varieties of the species by its generally large, ovate to elliptic leaves (3-12 cm long, 2-7 cm wide) and scarious phyllaries (the outermost sometimes herbaceous-tipped).
along road to San Cristobal, elev. 1350 m., 16 Apr 1941, Standley 92848 (F); savanna north of Concepcion, 3-5 miles southeast of Finca Yalpemeh, near Alta Verapaz-Peten boundary line, elev. 100-110 m., 23 Mar 1942, Steyermark 45255 (F, LL); Coban, elev. 1350 m., Jan 1907, Turckheim 1365 (F, LL, MICH, Mo, US); canyon Rio Chixoy, open slopes of Sierra de Chama, about 10-15 km west of San Cristobal, elev. 1200-1600 m., 2-4 Feb 1969, Williams et. al. 40564 (F, NY).

BAJA VERAPAZ: arid slopes above Rio Matagua, 12 km SW of Granados, 2 Sept 1970, Harmon and Dwyer 4205 (ENCB, F, MICH, MO, NY, US); along road between Salama and Robinal, 4 Sept 1970, Harmon and Dwyer 4357 (MO); Sierra de Las Minas, elev. 3500 ft., 1 Jan 1908, Kellerman 8035 (F, US); along the road to San Jeronimo, ca. 15 km generally S of Purulha, elev. ca. 5050 ft., 23 Jun 1976, King 7069 (US); Niño Perdido, west of km 148 of road, 6 Dec 1976, Lundell and Contreras 266 (US), 20466A (US); dry rocky hills north of Santa Rosa, 30 Mar 1939, Standley 69690 (F); Sierra de Las Minas, about 15 km north of Salama, near Pantin, elev. 1600-1800 m., 5 Jan 1973, Williams et. al. 42173 (F, MICH). CHIMALTENANGO: along road from Chilmantenango to San Martin Jilotepeque, elev. 1500-1900 m., 25 Nov 1938, Standley 57879 (F, NY). CHIQUIMULA: 3 km south of Quezaltepeque on CA-10, 4 Aug 1970, Harmon and Dwyer 3672 (MO, NY); thickets in pine-oak woodland, 3 km S of Quezaltepeque on CA-10, 12 Aug 1970, Harmon and Dwyer 3698 (MO); thickets along Esquipulas creek, 2 km from Esquipulas village, elev. thickets along Esquipulas creek, 2 km from Esquipulas village, elev. 1000 m., 6 Dec 1969, Molina and Molina 25180 (F, MO, NY, US); in pine forest of Quebrada
Resimiento, 4 km N of Esquipulas, elev. 1100 m., 27 Sept 1971, Molina and Molina 26795 (ENCB, F, MICH); divide on the railway above El Rincon, elev. 870 m., 17 Oct 1940, Standley 74667 (F), 74729 (F); rocky banks, 3 miles SE of Quezaltepeque, elev. 1200-1500 m., 6 Nov 1969, Steyermark 31255 (F); El Cedral de Guolan, elev. 500 m., Jan 1907, Pittier 1785 (F, US). ESCUINTLA: Guanagazapa, elev. 2000 ft., 1894, Heyde et Lux 6159 (F); Texcuaco, elev. 100 m., Oct, Morales 1082 (F); Puerto de San Jose, elev. 5 m., Nov, Morales 1317 (F).

GUATEMALA: 20 km NW of Guatemala City, elev. 5100 ft., 24 Oct 1965, Andrews 158 (NY); weedy vacant lots in Guatemala City, elev. 1500 m., 20 Oct 1970, Harmon 4462 (ENCB); Guatemala City, 1 Jan 1915, Holway 7 (GH); 89 (GH); Antigua, elev. 5000-5500 ft., 28 Dec 1916, Holway 3 (US); along Hwy 17 about 2 miles directly E of Salawa, elev. 4600 ft., 4 Jan 1973, Luteyn and Almeda 3486 (MO); carretera FDR a la Antigua, 20 km al Este de Ciudad Guatemala, elev. 2000 m., 3 Dec 1963, Molina 13489 (F, NY); carretera FDR km 20 NO de Ciudad Guatemala, elev. 1500 m., 24 Oct 1965, Molina 15247 (F, NY); moist thickets and mixed forest in deep ravines, vicinity of San Andrecillo, elev. 1700 m., 26 Sept 1972, Molina and Molina 27573 (F, US); Oct 1928, Morales 1111 (F), 1144 (F); near Fiscal, elev. 1080-1140 m., 12 Dec 1938, Standley 59615 (F); on hills along road between Guatemala and San Raimundo, elev. 1650-1950 m., 18 Jan 1939, Standley 62950 (F, MO); near Fiscal, elev. 1100 m., 18 Dec 1940, Standley 80440 (F). HUEHUETENANGO: Huehuetenango, elev. 6400 ft., 3 Sept 1934, Skutch 1117 (A, LL); elev. 6300 ft., 10 Nov 1934, Skutch 1625 (A, F, LL); northwest of Malacatancito, at km 8 of the highway from Huehuetenango, elev. 1950 m., 4 Jan 1941, Standley.
82222 (F); rocky hills N of Chiantla, elev. 2000-2250 m., 6 Jan 1941, Standley 82542 (F); pine-oak forest and ravines about 6 km south of Huehuetenango, elev. 1900 m., 30 Nov 1962, Williams et. al. 22036 (F, NY, US); pine forest area, 10-20 km west of Huehuetenango, elev. 2000 m., 3 Dec 1963, Williams et. al. 22254 (F, NY); in mountains near El Reposo, about 8 km from Mexican frontier, elev. 900-1000 m., 14-18 Dec 1972, Williams et. al. 41102 (F, MICH), 41389 (F, MICH), 41260 (F). IZABAL: trail from Los Amates to Izabal, 31 May 1919, Blake 7752 (US); Sierra del Mico, between Los Amates and Izabal, elev. 750 ft., 23 Feb 1907, Kellerman 7455 (US), 15 Feb 1908, Kellerman 7561 (F, NY, US); along road to Gualan, ca. 21 km generally NE of Gualan, elev. 650 ft., 2 Feb 1977, King 7369 (MO, NY, US); prairie margin, between Milla 49.5 and Cristina, elev. 65-70 m., 30 Mar 1940, Steyermark 38446 (F). JALAPA: km 88 on National Hwy 19 between Sonare and Jalapa, 10 Dec 1967, Grashoff 270 (MSC); vicinity of Jalapa, elev. 1360 m., 7-8 Nov 1940, Standley 76489 (F); between Jalapa and La Laguna, north of Jalapa, elev. 1400 m., 11 Nov 1940, Standley 76960 (F). JUTIAPA: low mountains west of Jutiapa, elev. 900 m., 21 Dec 1938, Standley 60570 (F); vicinity of Jutiapa, elev. 850 m., 24 Oct-5 Nov 1940, Standley 74972 (F, LL), 74997 (F). PETEN: La Libertad and Vicinity, 14 Dec 1934, Aguilar 224 (MICH, MO, NY); Dolores, in pineland on old Machaquillla Rd., 15 May 1961, Contreras 2299 (LL, US); Poptun, in pineland, km 97 of road, 24 Oct 1961, Contreras 3097 (LL, US); Poptun, in pineland, km 97 of road, 28 Mar 1967, Contreras 6846 (LL, US); La Libertad savanna, km 48 of Sayaxche Road, 23 Nov 1967, Contreras 7249 (LL); Quexil, Turicentro, in high forest bordering lake, 6 Feb 1970, Contreras 9613 (LL);
La Cuinbre, km 122-3 of Cadenas Road, in high forest, 10 Feb 1971, Contreras 10466 (LL, US); La Libertad, 4 Apr 1933, Lundell 2488 (MICH, US); sabana el Jaucute, 12 km camino la Libertad, aldea Santa Elena, 21 Jan 1920, Ortiz 583 (UC); Santa Elena, en orillando, el camino para Paxcaman, a km 11, lado sur, 27 Nov 1970, Ortiz 1429 (ENCB, F, MO, NY). QUEZALTENANGO: bushy thicket, Palmar, elev. 3700 ft., 13 Oct 1934, Skutch 1437 (F, LL, NY, US); Santa Maria de Jesús, elev. 1530 m., 1 Mar 1939, Standley 66808 (F); along road between Finca Pirineos and Patzulin, elev. 1200-1400 m., 9 Feb 1941, Standley 87102 (F); along Río Saurola, near Santa Maria de Jesús, elev. 1500-1650 m., 25 Jan 1941, Standley 84794 (F). SACATEPEQUEZ: colonias nublosas de San Mateo del Milpar, 10 km de Antigua, elev. 2500 m., 6 Feb 1949, Molina 15508 (F); near Antigua, elev. 1500-1600 m., Nov 1938-Feb 1939, Standley 58615 (F, NY); Cuesta de Las Canas, above Antigua, elev. 1950 m., 6 Dec 1938, Standley 58902 (F, NY). SAN MARCOS: 3 km SW of San Rafael Pie de Cuesta, elev. 2750 ft., 10 Nov 1970, Harmon and Fuentes 4737 (MO). SANTA ROSA: Guanagaz, elev. 2000 ft., Sept 1894, Heyde et Lux 6159 (US); along road southeast of Barberena, elev. 1100-1180 m., 21 Nov 1940, Standley 77769 (F). SOLOLA: above San Andres Semetabaj, 15 Jan 1939, Standley 62752 (F); ravine about 4 km east of Godinez, elev. 2100 m., Dec 5 1963, Williams et. al. 25154 (F, NY, US); mountain slopes above Lake Atitlan, 3-5 km west of Panajachel, elev. 2100 m., 6-7 Dec 1963, Williams et. al. 25321 (F). ZACAPA: Sierra de las Minas, along trail above Río Hondo, elev. 1000 m., 11 Oct 1939, Steyermark 29564 (F), 29632 (F), 29670 (F); along Rillito del Volcán de Monos, elev. 1150-2100 m., 10 Jan 1942, Steyermark
42353a (F); Sierra de Las Minas, 5-10 km north of Río Hondo, elev. 30500 m., 31 Dec 1972, Williams et al. 41849 (F, US). DEPT. UNKNOWN: Bernoulli 187 (K, NY); Heyde 435 (US); Rauno 540 (US); Rauno 761 (F); Salvin s.n. (K, NY); Skinner s.n. (K); Tejade 283 (US); Tonduz 812 (NY, US). HONDURAS. CHOLUTECA: vicinity of San Marcos de Colón, elev. 960 1150 m., 12 - 22 Jan 1949, Standley 15691 (US), 15849 (F). COMAYAGUA: Siguatepeque, 15 Nov 1972, Clewell 3516 (O, NY), 2 Nov 1973, Clewell 1043 (MO); vicinity of Comayagua, elev. 600 m., 12 - 23 Mar 1947, Standley and Chacon 5374 (F); vicinity of Siguatepeque, elev. 1050 m., 25 Mar - 5 Apr 1947, Standley and Chacon 6474 (F), 14 - 27 Feb 1928, Standley 55883 (A, F, US), 55936 (A, F, US); mountains above Agua Salada, elev. 1200 m., 29 Sept - 5 Oct 1951, Williams and Williams 18343 (F). COPAN: pine woods 2 km N of Santa Rosa de Copan, 9 Sept 1973, Hazlett 792 (MO); colinas y pinares 5 km SE de Santa Rosa de Copan, elev 1200 m., 29 Mar 1963, Molina 11709 (F, NY); wet thickets between Copan Ruins and Sta. Rita, elev. 665 m., 20 Nov 1969, Molina and Molina 24685 (F, NY); forest along Yaragua Creek, 1 mile W of Copan Ruins, elev. 500m., 29 Aug 1975, Molina and Molina 30869 (MO). COOTES: pine hills and pastures Cienga Tract near Agua Azul, 9 Feb 1952, Allen 6434 (F); montaña La Cumbre, caserio Las Pinatas, elev. 600 m., 21 Mar 1962, Molina 10537 (F); Agua Azul, on shores of Lake Yojoa, elev. 600 m., 9 - 12 Apr 1951, Morton 7675 (US), 14 Apr 1951, Williams and Molina 17936 (F). EL PARAISO: llano de Lizapa, elev. 1050 m., 1 Nov 1950, Molina 3362 (F),3368 (F,US); cerca de San Lucas, elev. 1500 m., 20 Oct 1963, Molina 13077 (F, NY); Las Mesas region near Yuscaran, Aug 1960, Pfeifer 1532 (US); 3 - 4 miles
down the road to Tuscaran after turn off from Rte 4, elev. 700 m.,
24 Sept 1975, Simpson 7093 (US): Las Casitas, elev. 550 m., 4 Dec
1446 Standley 542 (); along small stream by road 5 km east of Ojo
de Agua, elev. 7 m., 27 Feb 1947, Standley 4702 (F); between Las
Mesas and Yuscaran, elev. 600 m., 23 Nov 1948, Standley 14943 (F),
14978 (F), 15029 (F); vicinity of Danli, elev. 700 – 800 m., 11 Feb
1949, Standley 16439 (F); near Moroceli, elev. 650 m., 31 Dec 1950,
Standley 28037 (F, GH); in quebrada along Río Choluteca, elev. 600
m., 18 Oct 1951, Standley 28938 (F), Swallen 10874 (F, US); woods
along the road from Zamorano to Yuscaran, 3 Jul 1962, Webster et. al.
11926 (F, MICH); in pine forest about 8 km W of Ojo de Agua, elev.
900 m., 19 Oct 1946, Williams and Molina 10673 (F, LL, M?, UC, US);
Galeras, elev. 800 m., 20 Oct 1946, Williams and Molina 10692 (F);
Yeguare River, 16 Jul 1948, Glassman 1915 (F, GH, NY); aguas arriba
del Río de la Orilla, faldas del Cerro Majicaran, elev. 950 m., 10
elev. 780 – 900 m., 26 Nov 1946 – 9 Jan 1947, Standley 221 (F);
region of Ell Valle Encantado, elev. 1300 – 1500 m., 8 Dec 1946,
Standley et. al. 981 (F); El Zamorano, Standley 12875 (F, GH, US);
near Santa Clara, elev. 850 m., 19 Oct 1948, Standley 13193 (F),
13200 (F), 13211 (F); 13222 (F); along road from El Zamorano toward
San Antonio de Oriente, elev. 825 – 950 m., Sept - Nov 1948,
Standley 13664 (F), 14617 (F); trail between Hoya Grande and 1st
Encantado, elev. 1400 – 1500 m., 2 Dec 1948, Standley 15234 (F);
along Río Yeguare, elev. 750 m., Sept – Dec 1948, Standley 15436 (F,
GH, US): Finca Lizapa, elev. 850 m., 19 Dec 1948, Standley 15618 (F);
Ojojona, elev. 1400 m., 28 Nov 1949, Standley 24755 (F); Puente
Colorado north of Tegucigalpa, elev. 900 - 1000 m., 7 Dec 1949, Standley 24914, 24929 (both F); summit of hills just above San Antonio, elev. 1200 m., 20 - 21 Oct 1951, Swallen 10944 (F, US); along Santa Clara Creek, 9 Oct 1946, Williams and Molina 10546 (F, LIL, MICH, MO, UC), 10547 (F, LIL, MICH, MO, UC). OCOTEPQUE: El Moral on Cordillera Meredon, elev. 1600 m., 27 Aug 1968, Molina 22262 (F, NY, US); Nueva Ocotepeque, elev. ca. 800 m., 9 - 19 Dec 1950, Standley 27964 (F); along Río Yoroconte, few miles E of Ocotopeque on main Hwy between El Moral and Sinuapa, elev. 1300 m., 27 Oct 1976, Stuessy and Gardner 4399 (ENCB, LSU, OS). OLANCHO: Montaña Uval, carretera a San Francisco La Páz, elev. 550 m., 20 Nov 1963, Molina 13330 (F, NY); vicinity of Juticalpa, elev. 380 - 480 m., 5 - 16 Mar 1949, Standley 17961 (F); trail from Catacanas to Loma Pelona, north of Catacamas, elev. 500 - 900 m., 19 Mar 1949, Standley 18230 (F). SANTA BARBARA: 1 km de Santa Barbara, elev. 300 m., 11 Dec 1950, Molina 3708 (F), 3767 (F, US); Los Dragos on Río Chamelecon southwest of Quimistan, elev. 265 - 360 m., 16 - 17 Apr 1947, Standley and Lindelie 7451 (F), 7505 (F); San Pedro Sula, Dec 1888, Thieme 5300 (F, GH, K, NY, US). MEXICO. CHIAPAS: on steep slopes, barrio Shmutut, paraje of Mahben Chauk, munc. of Tenejapa, elev. 4000 ft., 25 Nov 1964, Breedlove 7580 (ENCB, F, MICH); on slope of creek in Shaki "UK'um, Breedlove 7592 (ENCB, F MICH); along road to Pinola, 2 km SW of Aguacatenago, munc. of Carranza, elev. 5600 ft., 18 Dec 1964, Breedlove 7941 (ENCB, F, MICH); rainforest near San Quintin along the Río Jatate, elev. 1200 ft., munc. of Las Margaritas, 23 Feb
1965, Breedlove 9124 (ENCB MICH); gradual heavily wooded slope 17 Km north of Tuxtla Gutierrez along road to El Sumidero, elv. 4000 ft., 27 Oct 1965, Breedlove 13907 (ENCB, MICH, NY); 1 Km. N of Ocozocoautla de Espinosa, elev. 830 m., 25 Sept 1971, Breedlove 19791 (MICH, MO); 6-7 Km north if Berrizabal near Pozo Turipache and Finca El Suspiro, elev. 900 m., 10 Oct 1971, Breedlove 20348 (MO); steep walled canyon above El Chorreadero, munc. of Chiapa de Corzo, elev. 800 m., 11 Aug 1972, Breedlove 26807 (MICH, MO, NY, TEX); steep walled canyon at the head of the Río de la Venta at the Chorreadero near Derna, munc. of Ocozocoautla de Espinoza, elev. 800-1000 m., 24 Aug 1972, Breedlove 27396 (MICH, MO, NY); Tropical rain forest on the west side of Laguna Mirimar east of San Quintin, munc. of Las Margaritas, elev. 350 m., 11 Feb 1973, Breedlove 33328 (LL, MO, NY), bluffs above Presa La Angostura, 45 Km from Tuxtla, munc. of Acala, elev. 700 M., 9 Sept 1974, Breedlove 37397 (LL); 3-5 Km above Jaltenango along road to Finca Prusia, munc. of Angel Albino Corzo, elev. 900 M., 11 Oct 1974, Breedlove 38547 (LL); steep canyon at the head of the Río Venta at the Chorreador near Derma, elev. 800-1000 m., 1 Sept 1976, Breedlove 39812 (MO); 5 Km south west of MEX 190 at Belem, elev. 2300 m., 16 Oct 1976, Breedlove 40825 (MO); 6-10 Km NNE of Soledad along logging road from Las Margaritas to Campo Alegre, elev. 1600 m., 24 Oct 1976, Breedlove 40958 (MO, TEX); dry slope at west edge of Teopisca, elev. 2050 m., 30 Oct 1976, Breedlove 41137 (MO); banks of the Río Blanco between Pugiltie and Venustiano Carranza, elev. 650 m., 30 Oct 1976, Breedlove 41175 (MICH, MO); grassy savannas 6 Km northeast of La Trinitaria, elev. 1550 m., 2 Nov
1976, Breedlove 41196 (MO); dry limestone ridge at Mirador for
Chicoasen Dam along road from Tuxtla Gutierrez to the Chicoasen Dam
along road from Tuxtla Gutierrez, elev. 850 m., 17 Nov 1976,
Breedlove 41521 (ENCB, MICH, TEX); small dirt road 5 Km
west-southwest of Teopisca, elev. 1750 m., 27 Nov 1976, Breedlove
41812 (LL); grassy flats east of La Trinitaria on road to Monte
Bello, elev. 1600 m., 28 Nov 1976, Breedlove 41888 (LL, MO); along
small dirt road to Boquerón and Ejido Mujica, west of MEX 190 at
point 18 Km SW of La Trinitaria, elev. 900 m., 5 Dec 1976,
Breedlove 42156 (LL, MO); 8 Dec 1976, Breedlove 42312 (MO, TEX);
vacant field near ranch house on south edge of Teopisca, elev. 5900
ft., 13 Oct 1965, Breedlove and Raven 13069 (ENCB, F, LL, MICH, NY);
along MEX 190, 3 miles south of La Trinitaria, elev. 5100 ft., 14 Oct
1965, Breedlove and Raven 13167 (ENCB, F, MICH, NY); 2 miles south of
Tuxtla Gutierrez along road to Villa Flores, elev. 2800 ft., 16 Oct
1965, Breedlove and Raven 13312 (MICH, NY); wooded slope near crest
of ridge, 2 miles south of Tuxtla Gutierrez along road to Villa
Flores, elev. 2800 ft., 16 Oct 1965, Breedlove and Raven 13326 (F,
MICH, NY); wooded slope 5 Km north of Tuxtla Gutierrez along road to
El Sumidero, elev. 2200 ft., 18 Oct 1965, Breedlove and Raven 13542
(ENCB, F, LL, MICH, NY, US); steep heavily wooded slope 19 Km north of
Ocozocoautla along road to Mal Paso, elev. 4300 ft. 19 Oct 1965,
Breedlove and Raven 13648 (ENCB, F, LL, MICH, NY, US); SE of Cerro
Baul on the border with the state of Oaxaca, 16 Km northwest of Rizo
de Oro along a logging road to Colonia Figaroa, elev. 1600 m., 3 Nov
1971 Breedlove and Smith 21781 (MO, TEX); 6-8 Km N of Ocacsingo along
road to Bachajon, elev. 900 m., 9 Nov 1971, Breedlove and Smith 22187
(ENCB, MICH, MO, NY); steep walled canyon above El Chorredor, munc. de Chiapa de Corzo, elev. 800 m., 15 Oct 1971, Breedlove and Thorne 20428 (ENCB, MICH, MO); near the microwave station of La Mina, 12 km south of MEX 190 near Rizo de Oro, elev. 1000 m., 16 Oct. 1971, Breedlove and Thorne 20569 (ENBC, MICH, MO, NY); along the Comitan River at its sumidero, Lagos de Montebello, 42 Km NE of La Trinitaria, elev. 1300 m., 23 Oct 1971, Breedlove and Thorne 21177 (ENCB, MICH, MO, NY, ); bushy places along the road, Pan Amer. Hwy, 4 miles E of Ocozocoautla, elev. ca. 3300 ft., 14 Oct 1962, Cronquist 9673 (GH, MICH, MO, NY, TEX, US); in calcereous mountains 20 miles south of Comitan, elev. ca. 3700 ft., 3 Nov 1965, Cronquist and Sousa (ENCB, GH, MICH, NY, US); edge of roadside woods, along Hwy 190 at Km 144, north of Comitan, 12 Jan 1978, Harriman and Jansen 14681 (OS); wooded slope along Río Grijalua 10 km south of MEX 190 along the road to Acala at Nandaburri, elev. 1600 ft., 24 Aug 1966, Laughlin 1707 (ENCB, MICH); shrubby slope in the Zinocautan paraje of Muk'tahok', monc. of Ixtapa, elev. 3200 ft., 26 Sept 1966, Laughlin 2096 (ENCB, MICH); from near Yajalon, 21 Nov 1895, Nelson 3402 (GH, US); south of the center of Amateango del Valle, elev. 6100 ft., 11 Nov 1966, Ton 1474 (F, MICH, NY); shrubby slope at the Colonia Choro, munc. of Chemalho, elev. 4300 ft., 15 Nov 1966, Ton 1544 (ENCB, F, MICH, MSC, NY); slope in the paraje of Mohbenchouk, munc of Tenejapa, elev. 4000 ft., 28 Nov 1966, Ton 1803 (ENBC, F, MICH, MSC, NY, US); El Chorreadero, 5.6 miles SE of Chiapa de Corzo along MEX 190, elev. 2400 ft., 20 Sept 1967, Ton 2958 (ENCB, LL, NY); south edge of Teopisca along MEX 190, pasture just below bridge, N side of Hwy elev. 6600 ft., 10 Jan 1977, Urbatsch and Pridgeon 2898 (LSU); road
to El Porvenir microwave station, along Hwy 190 between Teopisca and Comitan, elev. 6600 ft., 10 Jan 1977, Urbatsch and Pridgeon 3002 (LSU); 0.9 miles SE of Teopisco town square along Hwy 190, pasture of N side of road just before the creek, elev. 1660 m., 29 Jul 1978, Urbatsch and J. and B. Wussow 3333 (LSU); 31.8 miles SE of Teopisco town square at El Porvenir microwave station along Hwy 19, elev. 1750 m., 29 Jul 1978, Urbatsch and J. and B. Wussow 3334 (LSU); 14.2 miles W of Tuxtla Gutierrez (Hotel Bonampak) along MEX 190 (6.1 miles NE of Ocozocautla, elev. 980 m., 30 Jul 1978, Urbatsch and J. and B. Wussow 3336 (LSU); on limestone hills 3 miles NW of Comitan, elev. 5700 ft., 10 Aug 1962, Webster et. al. 12920 (MICH, MO).

COLIMA: Alzada, 4 Nov 1910, Orcutt 4661 (F, GH, MO). GUERRERO: Acuitlapan, 11 Sept 1937, Abbott 398 (GH); at the pass, 8 road miles south of Chilpancingo, elev. 4200 ft., 20 Oct 1962, Cronquist 9709 (MICH, NY); 5 miles N of Ocotito on the Chilpancingo-Acapulco Hwy, near both Agua del Obispo and Achuizotla, 4 Nov 1960, Crutchfield and Johnston 5984 (LL, MICH, TEX, UC, US); along the main road about 10 miles N of Taxco, 6 Sept 1959, Degener 26295 (K, NY, US); Taxco, 16 Sept 1937, Lyonnet 1724 (US); Galeana, elev. 560 m., 20 Oct 1937, Hinton et. al. 10831 (GH, K, LL, MICH, NY, UC, US); Rincon Viejo, elev. 750 m., 8 Oct 1960, Kruse 44 (ENCB); Choapan, elev. 1900 m., 15 Nov 1941, Matuda 25997 (MEXU, NY); Acapulco and vicinity, Oct 1894–Mar 1895, Palmer 52 (A, F, GH, MO, NY, UC, US); 18 km al N de Buenvista de Cuellar, sobre la carretera a Amacuzac, elev. 1050 m., 3 Nov 1972, Rzedowski 29865 (ENCB, LL, MICH); few miles W of Chilpancingo on dirt road toward Omiltemi, 16 Oct 1976, Stuessy and Gardner 4221 (OS); Acapulco, 1868, Thiebaux s.n. (F); along Hwy 55,
4.8 miles NW of jct with Hwy 95 to Taxco, 25 Oct 1980, Wassow and Landry 344 (LSU). JALISCO: oak-grass savanna region ca. 16 road miles N of Guadalajara, on the road to San Cristobal de la Barranca, elev. 5100 ft., 8 Nov 1962, Cronquist 9820 (H, MICH, MO, MSC, NY, US); ca. 4 km southeast of Tequila, elev. ca. 1250 m., 14 Sept 1974, Cronquist and Becker 11192 (LL, MICH, NY, US); km 6, carretera Guadalajara-Saltillo, elev. 1600 m., Luna 6214 (XAL); Mata de Buie, Sierra de los Corales, munc. de Tactalitlan, elev. 1300 m., 25 Oct 1963, Feddema 2223 (ENCB, MICH, TEX); 1.2 miles NW of Magdalena airport on MEX 15, 16 Sept 1971, Keil and Canne 9008 (OS); mountains 3 miles above (south of) La Huerta, road to Barra de Navidad, elev. 500-550 m., 3 Oct 1960, McVaugh 19816 (ENCB, LL, MICH, NY); steep rounded hills, 4.5 miles S of El Rincón (12-13 miles S of La Huerta), elev. 350 m., 13-14 Nov 1960, McVaugh 21054 (ENCB, MICH); miles N of Zapopan, road to San Cristobal de la Barranca, elev. 1600 m., 9 Nov 1962, McVaugh 22117 (ENCB, LL, MICH, NY); ca. 11-12 km west of Jilotlan de los Dolores, elev. 1300 m., 21 Nov 1970, McVaugh 24585 (MICH); Sierra del Halo, 7 miles SSE of Tactalitlan, elev. 1700-1800 m., 1 Dec 1959, McVaugh and Koeltz 1291 (ENCB, LL, NY); Guadalajara, Jul-Oct 1886, Palmer 352 (GH, MO, NY, US); near Guadalajara, Oct 1889, Pringle 2475 (F, GH, MEXU, MO, MSC, NY, UC, US), Oct 1903, Pringle 11503 (F, LL, MO, US); carretera Guadalajara-Saltillo, 5 km al E de Guadalajara, elev. 1600 m., 8 Oct 1967, Puga 1288 (MICH); El Platanarcillo, cerca de Tequila, 6 Oct 1968, Puga 2134 (ENCB); 1 km a W de El Rincon, elev. 550 m., 13 Nov 1960, Rzedowski 14959 (ENCB, MEXU, MICH); ca. 16 Mata de Bule, Sierra de los Corales, munc. de Tactalitlan, 22 Oct 1963, Rzedowski 17330 (ENCB, MEXU, MICH, MSC,
TEX); ca. 4 miles N of north edge of Guadalajara on Hwy 54 to Zacatecas, 22 Oct 1980, Wussow and Landry 336 (LSU); along Hwy 15 to Tepic, 11.9 miles W of jct with bypass around Guadalajara and Hwy 15 to Tepic, 23 Oct 1980, Wussow and Landry 338 (LSU). MEXICO:
thickets along the Esteli River 5 km from Esteli town, elev. 900 m.,
3 Nov 1968, Molina 23025 (F, MO, NY, US); cutover hills, El Portillo,
20 km N of Esteli, elev. 800 m., 23 Nov 1973, Williams and
Molina 42342 (F, MICH, NY, US). JINOTEGA: 2 km south of Jinotega,
elev. 1200 m., 10 Jan 1963, Williams et. al. 23575 (NY); along Tuma
Lake, north of Jinotega, elev. 1000m., 13 Jan 1965, Williams et. al.
27447 (F, NY, US). NUEAVA SEGOVIA: Rte 15, Dipilto, elev. 1000 - 1500
m., 2 Nov 1973, Neill and Seymour 6366 (NY, UC).

2b. Calea ternifolia HBK var. calyculata (Robinson) Wussow and
Urbatsch, comb. nov.

Calea zacatechichi Schlecht. var. calyculata Robinson, Proc.
Amer. Acad. Arts 36 : 488. 1901. TYPE: MEXICO. Nuevo
León: in the Sierra Madre near Monterey, 16 Jul 1888, C.G.
Pringle 2224 (HOLOTYPE: GH!, Fig. 28).

Calydermos salmaefolius DC., Prodr. 5 : 670. 1836. TYPE:
MEXICO. Tamaulipas: between Tula and Tampico,
Berlandier 2135 (=718) (LECTOTYPE: P! here chosen;
ISOTYPES: GH!, K!, MO!, NY!, P!); in Mexico, Haenke s.n.
(SYNTYPES: P!). Calea salmaefolia (DC.) Hemsley, Biol.

TYPE: MEXICO. San Luis Potosí: on gravelly soil near San
Luis, 1878, C.C. Parry and E. Palmer 448 (HOLOTYPE: GH!;
ISOTYPES: F!, K!, MO!, NY!).

This variety is disjunct from the others occurring in the Sierra Madre Oriental in Nuevo Leon, Tamaulipas, San Luis Potosí, and Queretaro, and the mountains near Oaxaca (Fig. 20). Although leaf shape and pubescence are somewhat variable, this variety is readily recognized by its large foliaceous outermost phyllaries, often equalling the length of the involucre. Flowering occurs from August through January.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. NUEVO LEON: near Monterey, 12 Oct 1895, Caec. et Seler 1080 (GH, MO); rocky canyon near quarry, 20 mi W of Linares on Hwy 6, 9 Aug 1972, Dunn et. al. 20161 (ENCB); 2 miles SE of Allende toward Montemorelos, elev. 2500 ft., 11 Nov 1959, Graham and Johnston 4638 (MICH, TEX); Monterey, Obispado, elev. 1700 ft., 3 Nov 1946, Lucas 111 (F); Dulce Nombres, Nuevo Leon, and just east of border into Tamaulipas, elev. 2000 m., 8 Aug 1948, Meyer and Rogers 2886 (MO, US); Galeana Canyon, 6 miles below Iturbide, elev. 3650 ft., 30 aug 1940, Shreve and Tinkham 9786 (GH); near Montemorelos, along N.L. Hwy 6 (gravelled) to Rayones, 3.5 miles west of jct. with MEX 85, elev. 500 m., 14 Oct 1980, Wussow and Landry 277 (LSU); along main hwy to Iturbide, 14.2 miles west of General Hospital on west edge of Linares, elev. 600 m., 14 Oct 1980, Wussow
and Landry 278 (LSU). OAXACA: Valley of Etna, Sept 1895, Alvarez 766 (GH); on road to Tehuantepec, ca. 38 miles by road east and south. Totolapan, elev. 1080 m., 14 Jan 1970, Anderson and Anderson 5455 (MICH); alluras de Oaxaca, elev. 1600 m., 7 Oct 1907, Conzatti 2081 (F, MEXU); Cerro del Fortin, elev. 1600 m., 25 Sept 1919, Conzatti 3648 (MEXU); Xochinilco, elev. 1600 m., 8 Oct 1932, Conzatti 4783 (LL); 4.5 miles N of intersection of Hwys 190 and 175, just E of Oaxaca along Hwy 175 to Tuxtepec, elev. 1710 m., 16 Aug 1975, C. and J. Davidse 9702 (LL, MO); 6-8 miles NE of Cd. Oaxaca along road to Ixtlan, elev. 5000-6000 ft., 28 Aug - 1 Sept 1952, Gentry 12071 (LL, MICH); Natividad Road northeast of Oaxaca, elev. 7000 ft., 28 Jul 1947 Kenoyer 1596 (GH); Chivela, Jan 1927, Mell s.n. (ENCB, MEXU, MICH); vicinity of Mitla, valley of Río Grande de Mitla, elev. 1600-1700 m., 21 Aug 1972. Messer 72/110 (MICH); camino Cuicatlan-Reyes Papalo, 15 Sept 1948, Miranda 4640 (MEXU); dry hills of Valley of Oaxaca, elev. 5100 - 5900 ft., 8 Sept 1894, Nelson 1217 (GH), 1192 (GH); El Trapiche, municipio de Zimatlan, elev. 1600 m., 29 Oct 1965, Rzedowski 21260 (ENCB, LL, MICH, MSC); 4 km al N de San Juan del Estado, elev. 1900 m., 26 Aug 1974, Rzedowski 32192 (ENCB); Monte Alban, near Oaxaca, elev. 5500-6000 ft., Sept 1894, Smith 393 (MICH, MO, UC, US); Las Sedas, elev. 6000 ft., 8 Sept 1894, Smith 393a (NY, UC). QUERÉTARO: Loma del Cierro, 20 Aug 1905, Altamirano 1628 (US); 7.8 mi SW of the San Luis Potosí-Querétaro state line, 17 Nov 1976, Smith et al. 855 (LL). SAN LUIS POTOSÍ: one mile south of the Tamaulipas line on the Antiguo Morelo-Valles Hwy, elev. 900 ft., 16 Nov 1959, Graham and Johnston 4729 (MICH, TEX); 4 miles E of Cd. del
Maiz, 2 Sept 1948, Kenoyer and Crum 3800 (A, MICH); hills near Cardenas, 7 Oct 1890, Pringle 3474 (A, LIL); limestone hills, Las Canoas, 30 Oct 1891, Pringle 3936 (F, GH, MEXU, MO, MSC, NY, UC, US); Minas de San Rafael, Nov 1910, Purpus 4813 (MO, UC); Sierra de San Miguelito, frente a Jesús Ma, elev. 2200 m., 24 Oct 1971, Robert and Gomez 1002 (ENCB); Sierra de San Miguelito, canon arriba de Terrero, elev. 2100 m., 8 Oct 1954, Rzedowski 4360 (ENCB, MEXU, MICH); Sierra de San Miguelito, Canon del Muerto, al SW de la Ciudad de San Luis Potosí, elev. 2150 m., 18 Sept 1954, Rzedowski 4636 (ENCB, F, TEX); Aguaje de Garcias, 10 km al W de Guadalcazar, elev. 1600 m., 20 Sept 1954, Rzedowski 4701 (ENCB); Pozo de Acuna, 15 km al E de Guadalcazar, elev. 1450 m., 26 Sept 1955, Rzedowski 6780 (ENCB, MSC); km 233, carretera San Luis Potosí-Antiguo relos, elev. 1350 m., 28 Oct 1965, Rzedowski 8387 (ENCB); 1 km al S de Ciudad Valles, elev. 100 m., 2 May 1959, Rzedowski 10388 (ENCB, MEXU); alrededores de la Salitrera, elev. 1900–2100 m., 2 Aug 1959, Rzedowski 11360 (ENCB, MSC); Sept 1879, Schaffner 269 (=701) (F, GH, P, MEXU, MICH, NY, US); ca. 20 miles W of Rayon on Rte 86, 6 Oct 1976, Stuessy and Gardner 4056 (ENCB, OS); Aug 1851, Virlet 232 (P); 0.9 miles south of Tamps.-SLP state line on Hwy 85, elev. 350 m., 16 Oct 1980, Wussow and Landry 319 (LSU); along small paved road to Canoas, 2.2 miles N of jct. with Hwy 70 (Cd. Valles – Río Verde Hwy), 16 Oct 1980, Wussow and Landry 320 (LSU). TAMAULIPAS: Cerro del Chino, vicinity of San Miguel, 30 Jul 1930, Bartlett 10727 (MICH, US); lerro Zamora, vicinity of El Milargo, 21 Aug 1930, Bartlett 11035 (F, GH, MICH, US); Mesa de Llera, 28 Nov 1946, Davis s.n. (TEX); Sierra de Tamaulipas, above Juan Tomas, east of Las Yacas, 13 Oct 1957,
Dressler 2387 (GH); near Juamave, 7 km al N de Magdelano Aguilar, elev. 1800 m., 18 Sept 1976, Gonzalez - Medrano et. al. 9766 (MEXU, MICH); Paso Real de Guerrero, munc. Juamave, elev. 1600 m., 22 Sept 1976, Gonzales - Medrano 9930 (MEXU); 2 miles east of Ejido de San Larazo, 11 Oct 1959, Graham and Johnston 4301 (MICH, TEX); at km 647 on top of Mesa de Llera, elev. ca. 2000 ft., 21 Oct 1959, Graham and Johnston 4405A (MICH, Tex); 4 miles from Aldama on road north to San Rafaél, elev. 950 ft., 10 Dec 1959, Johnston 4942 (MICH, TEX); Tampico Rd., 25 Nov 1937, Kenoyer 745 (MO); 11 miles W of Victoria, 28 Aug 1948, Kenoyer and Crum 3374 (A); Manuel, elev. 240 m., 29 Nov 1968, Puig 3724 (ENCB); Bustamante, elev. 900 m., 1 Sept 1975, Robert and Passini 85-6099 (MICH); Juamave, Viereck 807 (US); San Lucas, Viereck 915 (US); turn-out along Hwy, 6.9 miles N of Río Chihuuk, along Hwy 101 to Victoria, elev. 1300 m., 15 Oct 1980, Wussow and Landry 279 (LSU).

2.c. **Calea ternifolia** HBK var. *nelsonii* (Robinson and Greenman)

Wussow and Urbatsch, stat. nov.

**Calea nelsonii** Robinson and Greenman, Proc. Amer. Acad. Arts 32 :25. 1896. TYPE: MEXICO. Chiapas: on ridge back of Tonola, elev. 1200 - 2500 ft., 10 Aug 1895, E.W. Nelson 2887 (HOLOTYPE: GH!, Fig. 29; ISOTYPES: K!, UC!).

This restricted variety occurs near Tonola and Arriaga, Chiapas, Mexico (Fig. 20). It is distinguished by its totally glabrous leaves, stems, and corollas, even lacking resin globules, otherwise found throughout the species. Flowering reportedly occurs from June through September.
ADDITIONAL SPECIMENS EXAMINED: MEXICO. CHIAPAS: small forested stream and adjacent savanna, 2 km SE of Arriaga, elev. 100 m., 27 Aug 1974, Breedlove 36865 (LL, MO); ca. 21 miles NE of the Tehuantepec - Tapachula intersection at Tapantepec, elev. 570 m., 12 Aug 1975, G. and J. Davidse 9577 (LL, MO); fields along Rte 190, about 10 miles east of the Oaxaca - Chiapas border, 23 Jun 1960, King 2982 (MICH, NY, TEX, UC, US); Jalisco, Sept 1923, Purpus 9105 (F, GH, MO, NY, UC).

2d. Calea ternifolia HBK var. zacatechichi (Schlecht.) Wussow and Urbatsch, comb. nov.

Calea zacatechichi Schlechtendal, Linneea 19 : 589. 1934.

TYPE: MEXICO. Vera Cruz: Hacienda de la Laguna, near Jalapa, Schiede 234 (HOLOTYPE: HAL! ; ISOTYPE: P!, Fig. 30; PHOTOS: GH!, LSU!).


This variety grows in the vicinity of Jalapa, Orizaba, and Vera Cruz (Fig. 20), and is distinguished by its small (0.5- 3 cm long, 0.5-2 cm wide), ovate, rugose leaves which are dark green and scabrous above, and light green and usually densely matted tomentose
below. In addition it has scarious phyllaries that often have reddish, crisped, membranous margins. Flowering occurs from August through January.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. VERA CRUZ: Tiradores, munc. de Emiliano Zapata, elev. 1000 m., 15 Apr 1973, Acosta and Dorantes 1932 (ENCB); Carretera al Lencero, 28 Jul 1976, Baez Z588 (XAL); camino al sumidero, munc. de Xalapa, elev. 1210 m., 22 Sept 1976, Baez Z744 (XAL); Chilteyac, munc. de Xalapa, elev. 970 m., 24 Sept 1976, Baez Z787 (XAL); five miles SE of Xalapa, 3 Aug 1947, Barkley et. al. 2565 (F, MEXU); Orizaba, Botteri 481 (F, GH), 488 (GH, US); Valle de Cordova, 12 Dec 1865, Bourgeau 1559 (P); Orizaba, Jan 1866 Bourgeau 3095 (GH, P); Catemaco, a 200 m., del Hotel Playa Azul, 6 Nov 1973, Calzada 1045 (XAL); rancho paso largo de la congregación de Rancho Gavilan, munc. del Paso del Macho, elev. 350 m., 21 Jan 1977, Calzada 3017 (XAL); disturbed sites along the roadside, 12 miles SE of Xalapa, elev. 2800 ft., 20 Oct 1965, Cronquist and Sousa 10369 (ENCB, MICH, MSC, NY, TEX, US); pasture along Hwy 140, E of Xalapa, between kms 344 and 345, elev. 3500 ft., 25 Jul 1965, DeJong 1611 (MSC); 3 km al N de Lencero, carretera Xalapa - Vera Cruz, elev. 1100 m., 15 Oct 1972, Dorantes and Acosta 1684 and 1864 (ENCB, XAL); cerca de la Laguna el Farallón, elev. 10 m., 22 Oct 1975 Dorantes et. al. 5003 (XAL); Alreedores de Laguna Verde, munc. Alto Lucero, elev. 0 - 100 m., 11 Nov 1975, Dorantes et. al. 5177 (XAL); 3 km de El Randal rumbo a Vega de Alatorre, elev. 0 - 20 m., 3 Feb 1965, Gomez-Pampa and Riba 75 (MEXU); province de la Vera Cruz, 1867, Gouin 22 (P); 10 miles SE of Xalapa on road to Vera Cruz, elev. 3500 ft., 19 Nov 1959, Graham and Johnston 4798 (MICH, TEX); cerca de Los
Mangos, 17 Jan 1972, Hernandez 1353 (F, GH, MEXU, MO, XAL); Chavarillo, elev. 2900 m., 21 Sept 1906, Johnson s.n. (US); La Luz pr. Cordoba, 13 Oct 1882, Kerber 101 (GH, MICH, US); Mirador, Aug 1841, Liebm. 410 (GH, US); Vera Cruz, 1838, Linden 1186 (MICH, P); a km 17 de Playa Vicente rumbo al encinar, elev. 60 m., 19 Dec 1970, Lot 1152 (F, GH, MEXU); near Jalapa, elev. 4600 ft., 30 Aug 1935, MacDaniel 346 (F); on hill about one mile from Xalapa, elev. 4600 ft., 30 Aug 1935, Mac Daniel 388 (F); camino de San Andres Tenejapa a Tequilo, 15 Sept 1940, Miranda 753 (MEXU); Hatusco, no date, Mohr 256 (US); Orizaba, Sept 1855, Muller 2211 (K, NY); Chinameca, Dec, Peniche 39 (F, US); Zacuapan, Mar 1930, Purpus 14175 (F, UC), 1932, Purpus 14176 (A); Ocota Chico, elev. 1900 ft., 29 Oct 1962, Ross 37 (US); near Mata Obscura, 1932, Rozynski 593 (F, MICH, NY); Mirador, Oct, Sartorius s.n. (GH); carretera Jalapa-Veracruz, desv. a 16 km. al Sede Jalapa, elev. 900 m., 20 Sept 1975, Sousa 4858 (MEXU); 7 miles N.of Miradores, alg Hwy 140 via local trail, elev. 900 m., 25 Jul 1978, Urbatsch and J.and B. Wussow 3319 (LSU); Cerro Gordo, munc. de Dos Ríos, elev. 552 m., 13 Oct 1971, Ventura 4442 (ENCB, MICH, TEX); El Hato, munc. de Puente, elev. 400 m., Ventura 6056 (ENCB, MICH, OS); Miradores, elev. 850 m., 3 Aug 1975, Ventura 8528 (ENBC, MICH, MO, OS); Encinal, munc. de Totutla, elv. 700 m., 20 Sept 1973, Ventura 9003 (ENCB); Cerro Gordo, elev. 600 m., 11 Oct 1973, Ventura 9108 (ENCB, MEXU, OS); Blanca Espuma, elev.800m., 27 Nov 1973, Ventura 9331 (ENCB, OS); Banos, munc. de Apazapan, elev. 400 m., 24 Sept 1974, Ventura 10577 (ENCB); Almolonga, munc. de Naolinco, elv. 500 m., 13 Aug 1975 Ventura 11792 (ENCB, MEXU, OS); San Antonio
munc. de Zalapa, elev. 650 m., 10 Aug 1976, Ventura 13167 (ENCB, OS); La Mesa, munc. de Naolinco, elev. 950 m., 17 Nov 1977, Ventura 14725 (ENCB); Orizaba, Oct 1874, Saunders 400 (K); Miradores, 15 km SE of Xalapa along main Hwy to Vera Cruz, elev. 950 m., 28 Oct 1980, Wussow and Landry 350 (LSU).

3. Calea ternifolia HBK X urticifolia (Mill.) DC.

Calea acuminata Standley and Williams var. xanthactis
Stand. and Wms., Ceiba 1:93. 1950. TYPE: HONDURAS.
Morazan: area de pino-roble, entre El Jicarito y Quebrada La Pita, valle del Río Yeguare, elev. 900 m., 13 Nov 1948, A. Molina 1563 (HOLOTYPE: PANAMA; ISOTYPE: F!).


Although C. ternifolia and C. urticifolia are largely sympatric and often were observed growing side by side, no hybrids were detected in the field during this study. However, examination of herbarium specimens suggests that hybrids are formed, but apparently are quite rare.

The morphological form of the putative hybrids is variable no doubt depending on the exact parentage. Generally the hybrids can be
detected by their intermediate pappus length and shape, and yellow corollas and ligules, which are also intermediate between the two species. Attempted controlled greenhouse crosses have resulted in fully formed achenes which are being planted to test their viability and to produce authentic hybrids. In publishing C. acuminata var. xanthactis, Standley and Williams (1950) suggested that it might be a hybrid between C. acuminata and C. urticifolia but apparently they felt substantial proof for this was lacking.

MORAZAN: Aguas arriba del Río de la Orilla, faldas del Cerro Majicaran, elev. 950 m., 10 Nov 1948, Molina 1518 (F); entire Jicarito y Que brada de La Pita, Valle del Río Yeguare, elev. 900 m., 13 Nov 1948, Molina 1562 (F), 1563 (F, MO); Zamorano, 1 Nov 1943, elev. 800 m., Ríndiguez 1432 (F, LIL); Río de La Orilla, SE of El Zamorano, base of Cerro Majicaran, elev. 750-800 m., Nov 1948, Standley 14385 (F); road between El Jicarito and El Pedregal, elev. 800-950 m., 13 Nov 1948, Standley 14516 (F, GH, US), 14517 (F); along Río Yeguare, east of El Zamorano, elev. 750 m., Sept-Dec 1948, Standley 14574 (F); San Juan del Rancho, north of Cerro de Uyuca, elev. 1500 m., Nov-Dec 1948, Standley 15054 (F), 15074 (F); Río de La Orilla, southeast of El Zamorano, base of Cerro Majicaran, elev. 750-800 m., Nov 1948, Standley 15199 (F); slopes of Cerro de Uyuca, along trail between Hoya Grande and Valle Encantado, elev. 1400-1500 m., 2 Dec 1948, Standley 15235 (F); moist thicket, Santa Clara, elev.

Weak shrubs 0.5-2.5 m tall, arising from a woody base; stems erect, glabrous to slightly pubescent; leaves opposite, simple, blades elliptic to ovate elliptic, 3-9 cm long, 1.5-5 cm wide, apices and bases acute to obtuse, margins remotely denticulate to entire and slightly revolute, texture thin and fleshy to coriaceous, upper surface glabrous or nearly so, sometimes lustrous, triplinerved, lower surface same as above except paler green, petioles 1-2 mm or lacking, slightly pubescent; capitulescence of 1 to 4 terminal heads on long peduncles, 3-7 cm long, puberulent; involucres hemispheric, 8-10 mm tall, 10-15 mm wide, phyllaries imbricate, 3 seriate, the outermost often very large and leaf-like, ovate to elliptic, 8-10 mm long, 4-6 mm wide, herbaceous throughout, apices acute to obtuse to rounded, inner phyllaries oblong to obovate, 6-8 mm long, 3-5 mm wide, scarious throughout or at least at the apex, apices obtuse to rounded; capitula discoid, usually 40 to 50 flowered; receptacle conic to dome shaped, ca. 3 mm long and wide; palea lanceolate to oblong, trifid with 2 shorter lateral lobes and one central attenuate
lobe, scarious and slightly yellowish; corollas yellow-orange, 5.5-7.5 mm long, glabrous, lobes 5, acute, 0.7-1.1 mm long, tube 2.5-4 mm long, flaring about 2 mm below the lobes and again slightly at the base, anthers yellow, apices acute, bases obtuse to rounded, style branches ca. 1 mm long, apices acute to obtuse; achenes cylindric, slightly striate, ca. 2-2.5 mm long, black, glabrous, carpopodium present, pappus of ca. 20 narrowly lanceolate, stramineous scales, 5-6.5 mm long.

*Calea longipedicellata* is a small to moderate shrub (often described as a "shrubby herb") that occurs in wet savannas in southern Mexico, Belize, Guatemala, and Honduras (Fig. 21). It occurs from near sea level to about 1000 meters and flowers from May to February. According to Molina (in sched.) in Honduras its common name is "Chiltota".

Among the Mexican and Central American species of *Calea*, *C. longipedicellata* is easily recognized by its large, terminal, discoid heads on long peduncles, and its glabrous, coriaceous foliage. It appears to be most closely related to the Venezuelan *C. cardonae* which differs in having smaller heads on shorter peduncles, and more densely serrate leaves.

ADDITIONAL SPECIMENS EXAMINED: BELIZE. BELIZE DISTRICT: Pine Ridge, Cornhouse Creek, Manatee River, 31 Jan 1931, Bartlett 11309 (GH, MICH, US); Gracie Rock, Sibun River, 28 May 1935, Gentle 1657 (GH, MICH, MO, NY, US); wet areas, Baker's Pine Ridge, Jul 1933, Gentle 4704 (NY); mile 21, Northern Highway, 6-7 Jun 1974, Dwyer 12708 (MO); Baker's Pine Ridge, 30 Jun 1933, Lundell 3790 (LL,
MICH, US), 3 Jul 1933, Lundell 4704 (TEX, UC); pine ridge, 3 miles west of Boomtown, 23 Aug 1936, O'Neill 8359 (LL); low open ground near Manatee Lagoon, 2 Aug 1905, Peck 94 (GH,K); Dr. McCleary Property, 1.5 mi NE of Hattieville, 0.2-0.5 mi N of Hector Creek Rd., area inundated for long periods, 17 Aug 1971, Sorensen 7091 (F, MO, US); ca. 1/4-1/2 mile north of Western Hwy. at Mile 15, elev. ca. 5 m., 2-4 Jul 1970, Spellman 1510 (MO); South of Western Hwy, ca. mile 15, 27 Jul 1971, Wunderlin et. al. 368 (MO). EL CAYO DISTRICT: Mountain Pine Ridge, 25 Feb 1931, Bartlett 11744 (F, GH, LL, MICH, US); Baldy Beacon, Summit and below Summit, elev. 2500-3000 ft., 13 Jul 1973, Dwyer 11683 (MO); Augustine, Mountain Pine Ridge, Habet's Road, elev. 1800 ft., 26 Aug 1959, Hunt 30 (US); in sandy pine uplands, San Augustine, Mountain Pine Ridge, Jul-Aug 1936, Lundell 6765 (GH, MICH, NY, TEX); sabanas rocosas de Baldy Beacon, elev. 1000 m., 25 Mar 1954, Molina 165 (F); along road to Baldy Beacon, 8 mi from junction with Chiquibul Rd in a zone of pine and oak scrub, 20 Aug 1971, Sorensen 7132 (F, MO); upper 200 m of Baldy Beacon, elev. ca. 1000 m. 10 Jul 1970, Spellman 1638 (MO); ravine near Blancaneaux Lodge, Mountain Pine Ridge, 13 Aug 1970, Wiley 249 (MO). STANN CREEK DISTRICT: in pine ridge, Commerce Bight Pine Ridge, 6 Aug 1954 Gentle 8292 (LL); vicinity of Cabbage Haul Fire Lookout, elev. 300-400 m. 17 Nov 1976, Proctor 36575 (US); All Pines, elev. 5 ft., 21 Jul 1930, Schipp 558 (A, F, GH, K, MICH, MO, NY, UC). TOLEDO DISTRICT: wet forest, Río Temash, elev. 0-50 ft., 5-6 Aug 1975, Dwyer 12910 (MO); in pine ridge, Monkey River, 30 Aug 1941, Gentle 3622 (MICH); edge of hammock in pine ridge, Monkey River near Jenkins Creek, 28 Sept 1942, Gentle 4202 (GH, LL, MICH); in edge of wooded

**TYPE:** BELIZE. EL CAYO DISTRICT: On stones in Rio Privacion, Mountain Pine Ridge, 26 Feb 1931, Bartlett 11790 (HOLOTYPE: US; ISOTYPE: MICH!, Fig. 32).

Shrubs 0.2 to 1 m tall; stems densely branched, erect to scandent, slender, glabrous to minutely hispidulous; leaves opposite, simple, blades linear-lanceolate, 2.0-5.5 cm long, 0.2-0.5 cm wide, apices and bases attenuate, margins remotely serrulate and slightly revolute, coriaceous upper surface with scattered resin dots, green and lustrous, triplinerved with prominent central vein and obscure laterals, lower surface typically paler green with scattered resin dots, otherwise glabrous or with only occasional small hairs, petioles lacking or at most ca. 1.5 mm long; capitulescence of mostly terminal, loosely umbellate clusters of 3 to 8 heads, peduncles 5 to 20 mm long, slender, hispidulous and glandular dotted; involucres cylindric, 6-7 mm tall, 4-5 mm wide, phyllaries imbricate, 3-4 seriate, the outermost triangular to lanceolate, 4-7.5 mm long, 0.5-1.5 mm wide, at least upper half herbaceous with scattered resin dots, inner phyllaries grading from rounded to ovate, 3-5 mm long, 1.5-2.5 mm wide, scarious, yellowish, apex often purplish; capitula discoid, usually 20 to 25 flowered; receptacle conic, ca. 1.5 mm tall, ca. 1 mm wide; palea lanceolate, trifid with 2 shorter lateral lobes and one central attenuate lobe, conduplicate, scarious, yellowish; corollas yellow, ca. 5 mm long, glabrous, lobes 5, acute, 1.2-1.6 mm long, tube 1.5-1.2 mm, flaring about 1.5 mm below the lobes, anthers yellow, exerted, apical appendage acute, bases
rounded, style branches ca. 1 mm long, apices acute to obtuse; achenes cylindric to somewhat prismatic and striate, ca. 2 mm long, blackish, slightly to moderately antrorsely hirsute, carpopodium present or wanting, pappus of ca. 20 narrowly, lanceolate, stramineous scales, 4-5 mm long.

*Calea fluviatilis* is a small, rare shrub reported only from the Mountain Pine Ridge Area, El Cayo District, Belize (Fig. 21). It occurs in rocky areas and apparently flowers from May thru February.

In foliar characters, *C. fluviatilis* is unique among the Mexican and Central American caleas. Its closest allies appear to be the Columbian species *C. saxatilis*, and two Brazilian species, *C. angustifolia* and *C. hypericifolia*. *Calea saxatilis* has wider leaves and solitary radiate heads on long peduncles, and *C. angustifolia* has longer leaves and solitary heads while *C. hypericifolia* has shorter, broader leaves with minute pappus squamellae.


*Calea cordifolia* Swartz, *Flora Indae Occidentalis* 3: 1326. 1806. TYPE: Jamaica (HOLOTYPE: BM?).


Shrubs 1 - 3 m tall; stems erect to lax and arching, striate, hispidulous to hirsute; leaves opposite, simple, blades ovate to ovate-lanceolate, 2 - 6 cm long, 0.8 - 3 cm wide, apices acute to attenuate, bases acute to obtuse or rounded, margins entire to remotely serrate, often rugose, upper surface scabrous, triplinerved, lower surface slightly to moderately scattered hirsute with hairs often concentrated along veins, punctate-resin dotted, usually slightly paler green than above, veins prominent, petioles 2 - 5 mm, hispidulous to hirsute, often resin dotted; capitulescence of mostly terminal, loosely corymbose to umbellate clusters of 3 - 12 heads, peduncles 3 - 20 mm long, hispidulous to hirsute, resin-dotted; involucres cylindric to hemispheric, 5 - 7 mm tall, 3 - 4.5 mm wide,
phyllaries imbricate, 3 - 4 seriate, the outermost usually triangular to ovate lanceolate, 1 - 4.5 (7) mm long, 1 - 2.5 (4) mm wide upper half herbaceous or herbaceous throughout, hirsute and resin dotted, margins often ciliate, inner phyllaries grading from broadly ovate to ovate-oblong, 4 - 7 mm long, 1.0 - 3.5 mm wide, scarious, yellowish, apices rounded to acute, occasionally purplish; capitula discoid, ca. 20-flowered; receptacle conic, 1 - 1.5 mm long, 0.5 - 1 mm wide; palea ovate-lanceolate, laciniate to trifid with two short lateral lobes and one central attenuate lobe, conduplicate, scarious, yellowish; corollas yellow, glabrous, 4 - 5.5 mm long, lobes 5, acute, 1.2 - 1.8 mm long, tube 1.4 - 1.8 mm, gradually flaring, anthers yellow, exerted, apical appendage acute, bases rounded, style branches ca. 1 mm long, apices acute to obtuse; achenes cylindric ca. 2 - 3 mm long, usually slightly antrosely hirsute and resin-dotted, small light-colored carpopodium present, pappus of 18 - 25 narrowly lanceolate, stramineous scales, 3 - 5 mm long.

_Calea jamaicensis_ is endemic to Jamaica where it is locally common on exposed limestone and shale banks, and rocky pastures. Flowering appears to occur year round but most heavily from June through December. A variant from St. Andrew Parish with smaller, blunt leaves has been described as var. _parviflora_ by Moore (1929). Because small and large leaves may occur on a single plant, this variant is hardly worthy of taxonomic recognition. Another variant, found near Ritchies and Mandeville in Clarendon and Manchester parishes respectively, (Proctor 16207 and Proctor, Morley and Whitefoord 956)
has somewhat larger, more coriaceous, less attenuate leaves, and
larger, more leaf-like outer phyllaries than the typical form. The
leaves are also widely spaced which implies that these may represent
etiolated shade forms. Although some of the heads have quite large,
abnormal outer phyllaries, this is not a consistent feature. Based
on the present data, this variant does not seem to warrant taxonomic
recognition.

_Calea jamaicensis_ is most closely related to the _C. trichomata -
_C. berteriana_ group from which it differs by virtue of its shorter
lobed corollas, resin-dotted achenes, and hirsute leaves with
attenuate apices.

**ADDITIONAL SPECIMENS EXAMINED:** JAMAICA. CLARENDON: Somerset Woods,
5 miles northwest of Mandeville, elev. 2300 ft., 29 - 30 Dec 1956,
Proctor 16027 (US); Mason River Savanna, 2 - 3 miles NW of Kellits
P.O., elev. ca. 2300 ft., 20 Nov 1958, Proctor 18384 (A, NY); Mahoe
Hill, west of Colonels Ridge, elev. 1500 - 1700 ft., 22 Nov 1970,
Proctor 31530 (ENCB, F, LL, MO); Quaco Rock, near Ritchies, 4 Jan
1974, Proctor, Morley and Whitefoord 956 (MO). HANOVER: dry
hillside, Green Island and vicinity, 13 - 15 Mar 1908, Britton and
Hollick 2126 (NY). MANCHESTER: Alligator Pond to Lititz, elev. 300
ft., 5 Nov 1961, Adams 9861 (MO); rocky hillsides near Lincoln, 3 - 7
Sept 1908, Britton 3137 (NY); Lititz savanna, elev. 300 - 900 ft., 7
Jul 1914, Harris 11763 (F, MO, NY, US); Gully Head, 1 mile NW of
Warwick, elev. ca. 1750 ft., 8 Nov 1962, Proctor 22884 (NY) ST. ANN:
ST. ANDREW: Kingston, 1850, Alexander s.n. (GH, NY); Mt. Charles
district, below Mavis Bank, elev. ca. 1800 ft., 3 Jun 1954, Proctor 8756 (A, LL, NY); in thicket near Bellevue, elev. 3000 - 4000 ft., 17 Nov 1957, Yuncker 17463 (F, MICH). ST. CATHERINE: Planters Hall, elev. ca. 1000 ft., 12 Nov 1971, Proctor 32700 (F). ST. THOMAS: Albion, elev. 200 ft., 10 Nov 133, Harris 11653 (F, CH, MO, NY, US); Sheldon district, below Penlyne Castle, elev. 3000 ft., 22 Nov 1953, Proctor 8205 (A, NY); lower southeast slopes of Union Hill, along road to Serge Island marble quarry, elev. 700 - 1000 ft., 11 Apr 1964, Proctor 24785 (LL, MICH); Four Mile Woods, 0.8 miles northeast of Grants Pen (14 mi. east of Kingston) along St. Thomas road (JAM-A4), 4 Dec 1979, Urbatsch et. al. 3401 (LSU) WESTMORELAND: 1/2 mile south of Mt. Moreland School, elev. 500 ft., 19 Nov 1955, Proctor 11181 (A, LIL). PARISH UNKNOWN: Cane River Valley, 18 Dec 1907, Harris 10057 (F, NY, US), 10064 (F, NY, US); Hitchcock s.n. (F, MO); McLadyen s.n. (K); Orcutt s.n. (LL, UC, US); summit of Bull Head, 18 Sept 1906, Underwood 3371 (NY); Wilson, s.n. (K).


Shrubs 1 - 5 m tall; stems erect to arching, striate, puberulent to tomentose; leaves opposite, simple, blades ovate to elliptic, 2 - 9 cm long, 1.5 - 6 cm wide, apices acute to obtuse (rounded), bases obtuse to rounded, margins serrate to subentire, often slightly revolute, rugose to smooth, upper surface green, glabrous to slightly pubescent along veins and raised areas, 3 - 5 nerved, lower surface usually paler green, resin-dotted and otherwise glabrous to moderately pubescent (usually along veins), petioles 4 - 15 mm long,
moderately to densely tomentose; capitulescence of terminal or
axillary umbellate clusters of 7 to 30 heads, peduncles 5 - 30 mm
long, hirsute to tomentose, resin dotted; involucres cylindric to
hemispheric, 5 - 8 mm tall, 4 - 6 mm wide, phyllaries imbricate, 3 -
4 (5) seriate, the outermost oblong-lanceolate to broadly ovate
(rotund), 1 - 7 mm long, 1 - 4 (6) mm wide, usually herbaceous
throughout, hirtellous to tomentose, resin-dotted, inner phyllaries
grading from broadly ovate to elliptic or obovate, 3.5 - 7 mm long,
1.5 4 mm wide, yellow, membranous to scarious, apices acute to
rounded, sometimes scarious and ciliate; capitula discoid, 8 - 23
flowered; receptacle conic, 1 - 2 mm tall, 0.5 - 1.2 mm wide, palea
lanceolate to elliptic, trifid with 2 shorter lateral lobes and one
central attenuate lobe, 4.5 - 7 mm long, 1 - 2 mm wide, conduplicate,
scarious, yellowish; corollas yellow, ca. 4 - 6 mm long, essentially
glabrous, lobes 5, acute, 1.2 - 1.6 mm long, tube 1 - 2.5 mm long,
flaring ca. 1 - 1.5 mm below the lobes and slightly at the base,
anthers yellow, exserted, apical appendage narrowly ovate and acute,
bases obtuse-rounded, style branches ca. 1 - 1.4 mm long, apices
acute to obtuse; achenes cylindric to slightly prismatic, ca. 2 - 3
mm long, black, slightly to moderately antrorsely hirsute,
carpopodium present or wanting, pappus of 19 - 25 narrowly
lanceolate, stramineous scales arising from an annulus, 4 - 6 mm
long.

_Calea prunifolia_ is a dense to spreading, morphologically
variable shrub that occurs in thickets, roadsides, and coastal bluffs
from Costa Rica to Venezuela, Colombia, Ecuador and northern Peru
(Fig. 22). Flowering occurs from June to February.
Calea prunifolia traditionally has been considered a South American species that extends into Panama, whereas C. pittieri was thought to occur in Costa Rica and western Panama. Comparison of the types and other materials of these species indicates that they differ in no significant way. Since the name C. prunifolia has priority, C. pittieri is placed in synonymy with it.

Furthermore, as a result of the present investigation, C. chocoensis was observed to be extremely similar to C. prunifolia and is treated here as a variety of it. As seen in Fig. 23, C. prunifolia var. prunifolia has narrower outermost phyllaries, shorter leaves, and more pubescent lower leaf surfaces. These varieties have distinctive geographical distributions (Fig. 22) and ecological preferences except for an area just west of the Canal Zone where they overlap and intergrade morphologically.

Calea prunifolia var. prunifolia grows in xeric, high elevation areas of Costa Rica, Panama, Venezuela, and Colombia, whereas var. chocoensis generally occurs in coastal and low elevation areas of the Caribbean coastal plain of Nicaragua, Costa Rica, through Panama into the Pacific coast of Colombia, Ecuador, and northern Peru (Fig. 22).

**KEY TO THE VARIETIES OF C. PRUNIFOLIA**

Outermost herbaceous phyllaries 0.5 - 1.0 (1.2) mm wide, leaves mostly 2 - 5 cm long, lower surface resin dotted, slightly to moderately pubescent, Pacific watershed of central and western Costa Rica and Panama to the Canal Zone (also Colombia and Venezuela)

... var. prunifolia
Outermost herbaceous phyllaries 1.2 - 3.1 mm wide, leaves mostly 4.5 - 8.5 cm long, lower surface resin-dotted, glabrous to slightly pubescent, Caribbean coastal plain from southern Nicaragua and Costa Rica, through Panama (into Pacific coastal regions of Colombia, Ecuador and northern Peru)

... var. chocoensis

4:294. tab. 406. 1820. TYPE: COLOMBIA. MAGDALENA: banks of Rio Magdalena, near Honda, elev. 140 hex., no date, Humboldt and Bonpland s.n. (HOLOTYPE: P; ISOTYPES: P!, F!, Fig. 34, F!; PHOTOS: F!, MICH!, NY!).


This variety is an erect to arching shrub that occurs in rocky hillsides, roadsides and savannas in Costa Rica, Panama (west of Canal Zone), as well as Colombia and Venezuela (Fig. 22). Flowering occurs from October through February. Based on our current collections, chromosome number is n = 19.
Although intermediate forms occur in areas just west of the Canal Zone, var. *prunifolia* can be distinguished by the combination of its narrow outermost herbaceous phyllaries (0.5 - 1 mm), and small (2.5 cm long), generally rugose leaves with slightly to moderately pubescent lower surfaces.


COLCE: vicinity of El Valle, elev. 600 - 1000 m., 8 Dec 1938, Allen 1181 (F, MO, US); dry hills south of El Valle de Anton, elev. 600 - 800 m., 13 Nov 1941, Allen 2813 (GH, MO, US); vicinity of Rio Teta and Inter Amer. Hwy, 8 Dec 1965, Blum and Tyson 1875 (MO); savannas near El Valle, 4 Aug 1963, Duke and Mussell 6609 (LL, MO); Margarita, near chicken farm, 18 Jan 1968, Dwyer 8291 (MO); thicket along Pan Amer. Hwy, 2 miles E of Río Hondo, 11 Dec 1971, Gentry 2909 (MO); ridge south of El Valle, elev. 600 m., 23 Dec 1972, Gentry 6801 (MO); Aguadulce, open or locally wooded savanna, vicinity of airport, 29 Dec 1970, MacDaniel and Cooke 14761 (MO); Aguadulce, in savannas, 3 - 6 Dec 1911, Pittier 4907 (NY, US); between Aguadulce and the Chico River, elev. ca. 20 m., 7 - 9 Dec 1911, Pittier 5103 (US); Angostura de Penonme, 16 Dec 1972, Puga 38 (MO); Río Hato Military Reservation along Inter Amer. Hwy, 8 Dec 1965, Tyson and Blum 2554 (MO). COLON: lumber road about 8 km NE of Santa Rita along ridge, elev. ca. 650 ft., 12 Jan 1970, Wilbur and Weaver 10834 (F, GH, LL, MICH, MO, NY). HERRERA: vicinity of Chitre, elev. ca. 20 m., 26 Nov
1938, Allen 1109 (F, GH, MO, US); vicinity of Ocu, elev. 100 m., 22 Jan 1947, Allen 4054 (GH, MO); road between Los Minas and Pese, elev. 900 - 1200 ft., 25 Dec 1966, Burch et. al. 1320 (GH, MO, NY, UC, US); vicinity of Ocu, 2 m NW, 16 Feb 1963, Stern et. al. 1697 (MICH, MO, US); 10 mi S of Ocu, 21 Jan 1966, Tyson et. al. 2859, 2860 (Both MO). PANAMA: vicinity of Bejuco, 18 Oct 1938, Allen 979 (F, GH, MO); La Ermita San Carlos, 9 Dec 1972, Bernal 39 (ENCB, MO); Cerro Campana, 12 Nov 1975, D'Arcy 9594 (MO, NY, OS); ca. 10 km SW of San Carlos along Inter- Amer. Hwy, elev. 120 m., 18 Nov 1975, Davidse and D'Arcy 10125 (LL, MO); near beach at Nueva Gorgona, 8 Oct 1961, Duke 4492 (GH, MO, US); La Campana, Cerro Campana, 17 Aug 1960, Ebinger 916 (F, MO); Cerro Campana, 10 Dec 1967, Lewis et. al. 3031 (MO, UC); road to San Carlos, 18 Nov 1945, Harvey 5151, 5156 (both F); thickets and weedy roadside on the road to El Valle de Anton on the outer rim of the crater about 18 km of Pan Amer. Hwy, 31 Dec 1971, Wilbur et. al. 15586 (MICH). VERAGUAS: La Yeguada, a orilla de Rio San Juan, 15 Dec 1973, Correa et. al. 1980 (MO); just below San Jose, 5 Dec 1975, D'Arcy 10253 (MO); savanna 13 km W of Santiago, elev. 0 - 500 m., 15 Mar 1977, D'Arcy 10666 (MO); thicket near road 15.5 miles S of Santa Fe, 11 Dec 1971, Gentry 2928 (MO); roadside just S of Santa Fe, elev. ca. 450 m., 17 Nov 1973, Nee 8021 (LL, MO); near tower on top of Cerro San Cristobal, elev. 500 m., 25 Feb 1974, Nee 10140 (LL, MO); vicinity of La Mesa, 27 Dec 1968, Tyson 6052 (MO); dry savanna about 5 miles northwest of Santiago, 17 Jan 1971, Wilbur and Teeri 13341 (F, GH, LL, MICH, MO, NY).


This variety occurs in the Caribbean coastal plain and low elevation areas from southern Nicaragua to the Canal Zone, where it continues eastward and southward, growing along the Pacific coast of Colombia, Ecuador and northern Peru (Fig. 22). Flowering occurs from June to January. In Panama the common name is "escobilla" (Celestine, in sched.).

Although intergrading forms occur near the Canal Zone, this variety can be distinguished from the typical one on the basis of its broader outermost phyllaries (1.2 - 3.1 mm), and generally larger leaves (4.5 - 8.5 cm long) which are essentially glabrous.

ADDITIONAL SPECIMENS EXAMINED: COSTA RICA. LIMON: 100 m behind beach, near Limón, 3 - 7 Sept 1971, Burger and Burger 8459 (F, MO); Limon, 1910, Debeaux s.n. (P); Limón, Dec 1935, Quiros 478 (F); shrub at roadside near beach, just north of town, Puerto Limón, 12 Sept 1963, Porter 1127 (GH); in thicket, on edge of headland above sea, just E of Portete, ca. 3 mi NW of Limón, 17 Aug 1961, Rossbach 3785 (GH); Playas del Parismina, 9 Oct 1951, Shank and Molina 4345 (F, GH, US); Puerto Limón, 11 Aug 1923, Stevens 893 (US). NICARAGUA.
CHONTALES: bosques pantanosos de San Miguelito, drenaje del Lago Granada, elev. 30 m., 13 Nov 1951, Shank and Molina 4570 (F, GH, US); Chontales, Jun 1868, Tate 175 (K). ZELEYA: moist hillside, Panta Masaya, Bluefields, 14 Dec 1968, Narvaez 681 (MO); vicinity of Bluefields, elev. ca. 0 m., 21 Apr - 23 May 1949, Standley 19987 (F).


area on point just outside fort, 1 Sept 1965, Blum and Dwyer 381 (MO); vicinity of Río Piedras along road to Puerto Bello, 16 Jul 1966, Blum et. al. 2539 (MO); Portobello, 13 Jul 1964, Dwyer 4399 (GH, MO); beach and adjacent area, mouth of Río Piedras, 11 Dec 1967, Lewis et. al. 3178 O, UC). CAMARCA DE SAN BLAS: through cultivation in mainland in front of Ustupo, 9 Nov 1975, D'Arcy 9478 (MO); Isla Soskatupu, 6 Aug 1966, Duke 8514 (MO, OS); near Mandinga on the mainland, 7 Oct 1966, Duke 8888 (US); Soskatupu, 14 Feb 1967, Duke 10193 (MO); river mouth, Ailigandi, Aug 1965, Dwyer 6806 (MO, TEX); Soskatupu, elev. 0 - 150 ft., 15 Aug 1967, Elias 1665 (GH, MO, US); Isla Pino, near Mulatupo, elev. 0 - 200 ft., 16 Aug 1967, Elias 1713 (GH, MO); mainland opposite Playón Chico, elev. 0 - 200 m., 4 Oct 1972, Gentry 6340 (Oj; west end of Suskatupu Island, 15 Aug 1967, Kirkbride 203 (NY). PANAMA: shrubby or forested ravines, Cerro Campana, west of the Canal Zone, 1 Sept 1940, Bartlett and Lasser 16923 (GH, MICH, MO, US); 3 – 4 miles N beyond Goofy Lake in Cerro Azul, 7 Nov 1967, Correa and Dressler 440 (MO); beyond Goofy Lake along dirt road to Cerro Jefe, 4 Jan 1968, Correa and Dressler 578 (MO, US); along road between Panama and Chepo, 29 Nov 1934, Dodge et. al. 16645 (MO); Panama Viejo, 25 Sept 1962, Duke 5726 (MO); forest bordering grasslands on Cerro Campana, elev. 2400 - 2700 ft., 9 Sept bordering grasslands on Cerro Campana, elev. 2400 - 2700 ft., 9 Sept 1966, Duke 8682 (O, US); Isla del Rey, 28 Jan 1967, Duke 9530 (MO, OS); San Jose Island, along road between Bodega Bay and Río Mata Puerco, 18 – 19 Jul 1967, Duke 12512 (MO); Isla de la Bayonetta, Perlas Archipel, 22 Aug 1961, Dwyer 1734 (MO); Cerro Azul, 31 Dec 1962, Dwyer 1963 GY); Goofy Lake toward Cerro Jefe, 26 Nov
1966, Dwyer 7066 (GH, MO, UC, US); open thicket, coastal bluffs, Punta del Cabo, San Jose Island, 29 Jun 1945, Erlanson 394 (GH, NY, US); Goofy Lake, 1 – 2 mi beyond in dir. Cerro Jefe, elev. 2000 ft., 1 Jan 1972, Gentry and Dwyer 3395 (F, MO); west slope Cerro Campana, 9 Nov 1965, Tyson et. al. 2368 (US); San José Island, 18 Aug 1945, Harlow 19 (GH); camino de Los Sabanas, 25 Oct 1921, Heriberto 198 (GH, NY, US); Bald Hill, San José Island, 6 Oct 1944, Johnston 29 (GH, MO); hill west of Camp, San Jose Island, 5 Jan 1946, Johnston 1038 (GH); Sabanas NE of Panama City, Dec 1932, Paul 198 (MICH, US), 1934-5, Paul 555 (LL, MICH, MO, US); Sabana de Juan Corso, near Chepo, elev. 60 – 80 m., Oct 1911, Pittier 4538 (GH, US), 4674 (GH, US); carretera de Nuevo Emperador, Aug 1969, Rodriguez 18 (MO); moist thicket, Las Sabanas, 4 Dec 1923, Standley 25921 (US); along the Corozal Road, near Panama City, 13 Dec 1923, Standley 26807 (US); vicinity of Juan Franco Race Track, 21 Dec 1923, Standley 27744 (H, US); Tobago Island, Dec 1923, Standley 27994 (US); Rio Tapia, 7 Dec 1923 – 11 Jan 1924, Standley 28170 (US); Cerro Azul, elev. 2000 ft., 3 Nov 1965, Tyson 2071 (MO); on edge of mangrove swamp, Playa Grande, San José Island, 18 Dec 1968, Tyson and Loftin 5086 (MO); Cerro Azul, elev. 2000 ft., 22 Nov 1970, Tyson 6327 (MO). VERAGUAS: 7 km NW of road to Santa Fe, 5 Dec 1975, D'Arcy 10284 (MO); beach, cliffs and adjacent swamp, mouth of Rio Concepcion, 4 Dec 1967, Lewis et. al. 2842 (MO, UC). PROVINCE UNKNOWN: 1851, Duchassaing s.n. (P); Duke 6185 (MO); 1859 – 1862, Hayes 21 (GH); Manzallio Island, Oct 1859, Hayes 689 (NY).

1947. TYPE: GUATEMALA. ALTA VERAPAZ: Along knife ridge of limestone ridge, Cerro Chinaja, between Finca Yalpemech and Chinaja, above source of Rio San Diego, alt. 150 - 700 m., April 1 - 2 1942, J. A. Steyermark 45627 (HOLOTYPE: F!, Fig. 36; ISOTYPE: GH!).

Shrub 1.5 - 2.5 m tall; stems thick, terete, densely hispidulous with short, spreading brown hairs; leaves opposite, sessile or short, thick petiolate, coriaceous or subcoriaceous, rigid, blades ovate to broadly deltoid-ovate or rounded-ovate, 5 - 7 cm long, 3.5 - 6 cm wide, apices obtuse to subrotund, bases shallowly cordate to rounded, upper surface green, scabrous, lower surface somewhat paler, with short, spreading, rough hairs, margins coarsely crenate-serrate with mucronate teeth, triplinerved from the base, veins prominent and conspicuous beneath, laxly reticulate; capitula few, sessile, (to sub-sessile), ca. 8 mm tall, occurring at the tips of branches densely aggregated; phyllaries imbricate, 3 seriate, outermost herbaceous, green, oblong to lance-oblong, acute to subacute, mostly about equaling the inner ones, usually spreading, densely hispiduous, ciliate, inner phyllaries stramineous, oblong, obtuse to subacute, ciliate, glabrous or nearly so; corollas 4 - 4.5 mm long, yellow, glabrous, tube flaring abruptly at the throat; achenes narrow, angular, 2.6 mm long, sparsely pubescent; pappus of about 20, attenuate scales, ca. 4 mm long.
Calea crassifolia is known only from the type material. It is mainly the large coriaceous leaves and subsessile heads that distinguish this species from C. trichomata, which is represented by only a few collections from this area of Guatemala. Calea crassifolia may merely represent an extreme growth form of C. trichomata, however this cannot be determined with certainty until additional sampling is done in this remote area.


Shrubs 0.5 - 3.5 m tall; stems erect to arching or scandent, often densely secondarily branched with branches at right angles to main stem, striate, puberulent to pilose-tomentose; leaves opposite, simple, blades triangular-ovate to ovate or lance-ovate, 2 - 7 cm long, 1.5 - 5.5 cm wide, apices obtuse to acute (attenuate), bases subcordate to rounded or obtuse, margins usually remotely serrate to crenate or subentire, thick and somewhat coriaceous, upper surface glabrous to scabrous or short pilose, green and sometimes lustrous, triplinerved, lower surface glabrous and resin dotted to densely cano-tomentose and resin dotted, petioles 2 - 7 mm long, puberulent to cano-tomentose; capitulescence corymbose or umbellate of 3 to 10 heads in the upper leaf axils, penduncles ca. 3 - 15 mm long, puberulent to canescent; involucres cylindric to hemispheric, ca. 5 - 7 mm long, 3 - 4.5 mm wide, phyllaries imbricate, 3 - 4 seriate, outermost ovate to lanceolate, ca. 2 - 5 mm long, 0.5 to 1.5 mm wide, herbaceous throughout or at least the upper half, puberulent to densely tomentose, resin dotted, apices acute to obtuse, inner
phyllaries ovate to lanceolate, 3 - 6 mm long, 2 - 3 mm wide, striate, yellowish and often purplish, membranous, apices obtuse to acute, usually scarious; capitula discoid, ca. 10 - 20 flowered; receptacle conic, ca. 1 mm long and wide; palea lanceolate to elliptic, trifid with 2 shorter lateral lobes and one central attenuate lobe, 4.5 - 6 mm long, 1 - 1.5 mm wide, conduplicate, scarious, slightly yellowish; corollas yellow, ca. 5 - 6 mm long, glabrous, lobes 5, narrow, attenuate, 1.9 - 2.7 mm long, tube ca. 3 mm long, narrow, flaring abruptly just slightly below the lobes, anthers exerted, yellow, apical appendage acute to attenuate, bases obtuse-rounded, style branches ca. 1 mm long, apices acute to obtuse; achenes cylindric to somewhat prismatic, ca. 2 - 3 mm long, black, slightly to moderately antrosely hirsute, carpopodium present pappus of ca. 20 - 25 narrowly lanceolate, stramineous scales, often arising from an annulus, 5 - 6.5 mm long.

_Calea trichomata_ is an erect to arching or scandent shrub (the habit is often described as "vine-like" or a "woody-vine") that occurs in wet thickets, savannas, and pine forests from southern Mexico to northwestern Costa Rica (Fig. 24). Flowering apparently occurs year round but probably most abundantly from May to January.

_Calea trichomata_ is easily distinguished from the other Mexican, Central American, and Jamaican caleas by the combination of its shrubby to viney habit, discoid heads containing yellow corollas with long, erect narrow lobes (1.9 - 2.7 mm long), and its triangular-ovate, remotely serrulate leaves.

This species is very closely related to the Colombian-Venezuelan _C. berteriana_ which differs in having generally more heads per
capitulescence, oblanceolate palea with laciniate apices (not trifid), and lower leaf surfaces with more prominent veins. 

_Calea trichomata_ has strong affinities to _C. jamaicensis_ which is similar in habit and overall appearance but differs in having smaller corollas with shorter lobes, resin-dotted achenes, narrower leaves with attenuate apices, and less densely pubescent lower leaf surfaces.

**KEY TO THE VARIETIES OF _C. TRICHOMATA_**

Lower leaf surface glabrous and resin-dotted, usually in wet swampy areas at or near sea level

... var. _peckii_

Lower leaf surface moderately pubescent to densely cano-tomentose and resin-dotted, usually in savannas or pine forest from near sea level to 2000 m. elevation

... var. _trichomata_


This variety grows in drier areas at higher elevations than var. _peckii_. It is easily distinguished on the basis of its densely cano-tomentose lower leaf surfaces. Two areas were detected where
the varieties intergrade; on the temples of the Tikal ruins in Guatemala, and near the midway point of the Belize-Cayo Highway in Belize. Perhaps the habitat strongly influences the degree of pubescence, with intermediate plants found in intermediate habitats. Based on field observations, flowering plants are heavily visited by bees. The flowers are nectariferous, and both flowers and foliage impart a sweet saffron-like odor.

Turner et al., 1962, reports a chromosome number of \( n = 18 \) for this variety. Our materials from the same area were found to be \( n = 19 \).

ADDITIONAL SPECIMENS EXAMINED: BELIZE. BELIZE DISTRICT: Manatee
Pine Ridge, Jan 1900, Camm. & Campbell 35 (K); in wooded island,
Colonel English Pine Ridge, Belize Cayo Road, 15 Nov 1957,
Gentle 9430 (LL, US); pineland in the vicinity of Privacion Creek,
Mountain Pine Ridge, ca. 12 miles south of Cayo, elev. ca. 600 m.,
Apr 1972, Burch s.n. (MO); along road at Río Ma Cal between San Luis
and Cuevas, elev. 1050 ft., 28 May 1973, Croat 23509 (MO); Pine
Ridge, Río Frio Cave area, 28 Dec 10, Dieckman 302 (MO); Blancaneaux
Lodge, Mountain Pine Ridge, 11 miles north of Augustine, 11 Jul 1973,
Dwyer 11593 (LL, MO); 2 - 5 miles north of Blancaneaux Lodge,
Mountain Pine Ridge, 12 Jul 1973, Dwyer 11616 (LL, MO); Mai Lookout
Station and down trail, 18 Mar 1967, Dwyer et al. 225 (A, MO);
Cabbage Hall near fire tower, elev. 1500 ft., 21 Mar 19, Dwyer
et. al. 457 (MO); clearing, 38 miles section, Belize-Cayo Road, 4 Oct
1957, Gentle 9370 (LL, US); tall bunch - grass pine savanna, elev.
1800 ft., 26 Aug 1959, Hunt 29 (LL, US); Mountain Pine Ridge, San
Augustine, Jul - Aug 1936, Lundell 6820 (GH, LL, MICH, TEX, US); in marginal forest on cliff, Vaquero, Mountain Pine Ridge, Jul - Aug 1936, Lundell 6890 (LL, MICH, NY, TEX, US); Mahogany Creek, ca. 4 miles south of Augustine, elev. ca. 530 m., 31 Aug 1970, McDaniel 14402 (MO); open pine savanna at about mile 33 along Western Hwy, 18 Aug 1971, Sorensen 7102 (MO, US); 30 miles SW of Belize City, 13 Jun 1977, Turner 0 - 78 (LL); near bridge over Roaring Creek Town, 27 Jul 1971, Wunderlin et. al. 360 (LL, MO). ORANGE WALK DISTRICT: mile 58 of Northern Hwy, ca. 4 miles south of Tower Hill, 23 Jun 1973, Gentry 8495 (LL, MO). DISTRICT UNKNOWN: Camp 32, British Honduras - Guatemala survey, elev. 2700 ft. 2 Mar 1934, Schipp S - 734 (GH). GUATEMALA. ALTA VERAPAZ: Coban, elev. 4000 ft., 28 Aug 1920, Johnson 633 (US); near Coban, elev. 1260 - 1440 m., 26 Mar - 15 Apr 1939, Standley 69179 (F); brushy hillside, along Rio Carcha, between Coban San Pedro Carcha, elev. 1360 m., 26 - 27 Mar 11, Standley 89952 (F); vicinity of caves, southwest of Lanquin, elev. 600 - 1000 21 Feb 1942, Steyermark 44044 (F); vicinity of Cubilguitz, 1 1/2 - 2 miles south of Cubilguitz, elev. 300 - 350 m., 1 Mar 1942, Steyermark 44443 (F, LL); Coban, elev. 1400 m., Feb 1903, Turckheim 8413 (GH, US); Coban, elev. 1350 m., 6 Jun 1906, Turckheim 11688 (F, GH, LIL, MICH, MO, NY, US); cut-over forest area along Rio Coban near San Pedro Carcha, 15° 29' N, 90° 17' W, elev. 1400 m., 27 Jan 1969, Williams et. al. 40197 (F, MICH); pastures, mixed and secondary forest on hills along Rio Chio about 2 - 4 km SW of Coban, elev. 1300 - 1400 m., 8 Feb 1969, Williams et. al. 40726 (F, MICH, US); cut-over mixed forest and pastures, along Río Coban 4 km east of Coban, 21 Jan 1974, elev. 1300 m., Williams et. al.
43632 (F, NY). GUATEMALA: along Hwy. 9 to Puerto Barrios, 12 miles NE of Guatemala City, elev. 1100 m., 23 Jul 1977, Croat 41917 (MO).

HUEHUETENANGO: Uaxac-kenal, elev. 1300 - 1400 m., 13 Jul 1896, Caec. et Seler 2789 (GH, NY, US); swampy places, Cienaga de Lagartero, below Miramar, elev. 300 m., 29 Aug 1942, Steyermark 51496 (F, NY).

IZABAL: along RR tracks, Morales, 22 May 1919, Blake 7563 (GH, US); RR embankment, Cristina, 23 May 1919, Blake 7654 (GH); trail from Los Amates to Izabal, 31 May 1919, Blake 7789 (US); Puerto Mendez, on Rio Dulce road, 9 km, 10 Jun 1970, Contreras 10000 (LL, US); hills above Eximbal mining area west of El Estor, elev. 100 m., 4 Sept 1970, Harmon and Dwyer 4335 (MO); Finca Murcielago, ca. 10 miles E of El Estor on Lake Izabal, elev. ca. 50 ft., 14 Sept 1961, Popenoe 56 (F); vicinity of Quirigua, elev. 75 - 225 m., 15 - 31 May 1922, Standley 23886 (GH, MO, NY, US), 24518 (GH, NY, US); near Quirigua, elev. 72 - 150 m., 26 - 27 Apr 1939, Standley 72283 (F); between Milla 49.5 and Cristina, elev. 65 - 70 m., 30 Mar 1940, Steyermark 38372 (F); between Milla 49.5 and ridge 6 miles from Izabal, Montaña del Mico, elev. 65 - 600 m., 1 Apr 1940, Steyermark 38531 (F); on top of Temple VI, Tikal, Tikal National Park, 9 Oct 1959, Contreras 247 (LL, US); on top of Temple I, Tikal, Tikal National Park, 14 Dec 1959, Contreras 438 (LL, US); on top of Temple IV, Tikal, Tikal onal Park, 27 Jun 1960, Contreras 1179 (US), 30 Jul 1960, Contreras 1378 US); on top of Temple VI, Tikal, Tikal National Park, 17 Aug 1960, Contreras 1417 (LL, US); Dolores, on hill in pineland west of road, km 79, 15 Jul 1961, Contreras 2612 (LL, US); Santo Toribio, bordering the road, 24 Aug 1961, Contreras 2764.
(LL, US); La Cumbre, W of km 139 of Cadenas Road, 22 Sept 1966, Contreras 6197 (LL, US); Lake Peten, 4 May 1933, Lundell 3158 (MICH, US); Temple V, Tikal, 16 Jul 1959, Lundell 16482 (LL, US); sabanas y pinares de un, elev. 500 m., 11 Nov 1965, Molina 15601 (F). HONDURAS.

COPAN: Boca de Caballo, Tutiapa area 15 km W of Cofradilla, Chamelecon River Valley, 29 Jul - Aug 1951, Howard et. al. 576 (A).


CHIAPAS: along trial from Hebenal to Tsahal Kesh in the paraje of Mahben Chauk, municipio of Tenejapa, elev. 3300 ft., 13 Jul 1964, Breedlove 6397 (ENCB, F, MICH); along Mex 190, 3 miles south of La Trinitaria, municipio of la Trinitaria, elev. 5100 ft., 15 Aug 1965, Breedlove 11769 (F, MICH), 10 Jul 1966, Breedlove 14479 (ENCB, MICH); in the Selva Negra 10 km above Rayón Mezcalapa along road to Jitotol, municipio of Rayon, elev. 1700 m., 13 Jul 1972, Breedlove 26117 (MICH, MO, NY); 3 - 5 km N of Palenque along road to Catazaja and Villa Hermosa, elev. 250 m., 28 Jul 1972, Breedlove 26660 (MO); 3 north of Ocozocoautla along road to Mal Paso, municipio of Ocozocoautla de Espinosa, elev. 900 m., 1 Sept 1976, Breedlove 39869 (MO, TEX); Santa Domingo, 15 miles southeast of Simojovel, 13 Jul 1958, Chemsak 2 (UC); limestone area, near Laguna Ocotal Grande, ca. 25 - 30 km southeast of Monte (Cerro) Libano, (which is ca. 45 km E of Ocosingo), 20 Jul - 20 Aug 1954, Dressler 1705 (F, GH, MICH, NY, UC, US); mountains along Route 190, about 23 miles southeast of Comitan, 25 Jun 1960, King 3043 (MICH, TEX); savanna, Palenque, 9 -


*Calea peckii* Robinson, Proc. Amer. Acad. Arts 44:624. 1909. TYPE: BRITISH HONDURAS. Thicket near Manatee Lagoon, 16 Jul. 1905, M. E. Peck 64 *(HOLOTYPE: GH!, Fig. 38)*.

This variety occurs in wet savannas and thickets in southern Mexico, Peten, Belize, Honduras, Nicaragua, and northwestern Costa Rica *(Fig. 24)*. It differs from the typical variety in having virtually glabrous upper and lower leaf surfaces.

*Calea peckii* here is treated as a variety of *C. trichomata* because the two differ morphologically only in leaf pubescence and
are geographically separated (Fig. 24). According to Lundell (in sched.), in Yucatan, Mexico, the common name is "Kintak".

vicinity of Canas, about 11 miles S of Liberia, 13 Jun 1970,
Daubenmire 811 (F); dry woodland, 5 km SE of Liberia on the Canas
Road, 1966, Harris 77 (F); east park entrance Santa Rosa National
Park, 20 Sept 1975, Janzen 10119 (MO); 3.5 km E of Bagaces, 20 Jul
1977, Liesner 3423 (MO); savanna, La Pacifica, 4 km NW of Canas, 13
Aug 1972, Opler 1531 (F); Comelco, 5 km NW of Bagaces, elev. 150 m.,
28 Jun 1973, Opler 1815 (MO, UC); west of the Inter-American Hwy. at
junction with dirt road to coast, about 5 km south of La Cruz, elev.
260 m., 10 Jun 1967, Weston 5022 (F, MO, NY). GUATEMALA. PETEN: Dos
Lagunas, in bajo bordering airfield, 15 Jun 1969, Contreras 8725 (LL,
US); orillando aereopuerto, lado Sur en Acagual, Tikal, Parque
Nacional, 5 Aug 1969, Ortiz 212 (MICH, US); en orillando el camino
para El Remate, a km 52, lado oeste del camino, en Parque Nacional de
Tikal, 11 Nov 1971, Ortiz 2033 (ENCB, F, MO, NY). HONDURAS. ISLAS
DE LA BAHIA: along beaches Roatan, Island of Roatan, 16 Aug 1970,
Harmon and Dwyer 3982 (LL, MO); sandy bank at sea shore of Roatan
Island, 19 Apr 1967, Molina 20636 (ENCB, F, NY, US); on moist bank
along road to Sandy Bay, north of Coxenhole, Roatan Island, elev. 40
m., 24 Apr 1967, Molina 20799 (F, NY, US); Cerro Coxen Hole, Coxen
Hole, Roatan Island, 29 Nov 1970, Nelson and Hernandez 113 (MO);
camino sobre Flowers Bay, Roatan Island, 30 Nov 1970, Nelson and
Hernandez 203 (MO). MEXICO. CAMPECHE: 4 miles N of Escarcega
along MEX 261, 22 Jul 1971, Vaughan et. al. 229 (MO); 30 miles N of
Palenque along Mex f86, 22 Jul 1971, Vaughan et. al. 246 (MO).
CHIAPAS: steep walled ravine and sandstone bluffs along road to Mal
Paso, elev. 900 m., 25 Jun 1972, Breedlove 25675 (MICH, MO, TEX); 6 -
8 km north of Berriozabal along road to Pozo Turipache and Finca
DOUBTFUL SPECIES

Calea brachiata DC., Prodr. 5: 673. 1836. Based on Mocinna brachiata Lagasca, Gen. Sp. Platarum p. 31. 1816. Reportedly a Panamanian species, although no type or other specimen is referred to. No authentic specimen could be located and the description is too brief and general to allow any specific placement.
EXCLUDED TAXA


**Calea rupestris** Brandegee, Zoe 5: 258. 1908. = **Tetrachyron orizabaensis** Sch. Bip. ex Klatt var. orizabaensis, Leopoldina 23: 145. 1887.


   = Alloispermum scabrum (Lag.) Robinson var. scabrum, Phytologica
   38: 412. 1978.

Calea scabra (Lag.) B.L. Rob. var. longifolia (A. Gray) B.L. Rob.

Calea scabra (Lag.) B. L. Rob. var. peduncularis (HBK.) B.L. Rob.,

Calea scabra (Lag.) B. L. Rob. var. livida (Rob & Greenm.) B.L.
   Rob., Proc. Amer. Acad Arts 44: 625. 1909 =
   Alloispermum scabrum var. lividum (Rob. & Greenm.) Fernandez
   & Urbatsch, ined.

   var. scabrum, Phytologia 38: 412. 1978.

Calea scabrifolia (Hook. & Arnot) Benth. & Hook., Gen Pl. 2: 391.
   1873. = Alloispermum scabrifolium (Hook & Arnot) H. Robins.,

   Podachaenium skutchii (Blake) H. Robinson, Phytologia 38(5):
   1978.

Calea standleyi Steyermark in Standley & Steyermark, Field Mus.
   (Schultz Bip. ex Klatt) Wussow & Urbatsch, Brittonia 30(4):
   479. 1978.
1895. = *Alloispermum scabrifolium* (Hook & Arnot) H. Robins.,

1896. = *Alloispermum scabrum* var. **thysanolepe** (Rob. & Greenm.)
Fernandez and Urbatsch, ined.

*Tetrachyron grayi* (Klatt) Wussow And Urbatsch, Syst. Bot. 4
315. 1979.

Calea **verbenaefolia** DC., Prodr. 5: 673. 1836. = *Lasianthaea ceano-
thifolia* (Willd.) K. Becker. var. **ceanothifolia**, Mem. N.Y.
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**PLATE LEGENDS**

Fig. 1  **Calea ternifolia var. zacatechichi.** Lower leaf surface showing uniseriate hairs and globular resinous trichomes. Scanning electron microscope (SEM) photograph. X 100.

Fig. 2  **Calea ternifolia var. calyculata.** Lower leaf surface showing globular resinous trichomes, 3 filamentous hairs, and stomata. SEM photograph. X 200.

Fig. 3  **Calea urticifolia.** Upper leaf surface showing short, uniseriate hairs. SEM photograph. X 100.

Fig. 4  **Calea trichomata var. trichomata.** Lower leaf surface showing globular resinous trichome, curled bulbous celled hair and long, straight uniseriate hair. SEM photograph. X 600.

Fig. 5  **Calea trichomata var. trichomata.** Lower leaf surface showing curled, uniseriate hair with several bulbous basal cells and one long attenuate, apical cell. SEM photograph. X 1000.

Fig. 6  **Calea prunifolia var. prunifolia.** Similar hair as in Fig. 5 but straight which shows component cells. SEM photograph. X 1000.

Fig. 7  **Calea prunifolia var. prunifolia.** Globular resinous trichome on lower leaf surface. SEM photograph. X 1000.

Fig. 8  **Calea ternifolia var. ternifolia.** Pollen mother cell during meiosis showing 19 pair of chromosomes (arrow indicates two pair clumped together). Light microscope photograph.
Fig. 9  *Calea ternifolia* var. *ternifolia*. Achene with short, broad, blunt-tipped pappus scales. SEM photograph. X 26.

Fig. 10  *Calea urticifolia*. Achene with numerous, long, narrowly lanceolate pappus scales. SEM photograph. X 20.

Fig. 11  *Calea trichomata* var. *trichomata*. Achene surface showing biseriate, bifid trichomes. SEM photograph. X 175.

Fig. 12  *Calea ternifolia* var. *ternifolia*. Close-up of pappus showing broad oblong to oblanceolate scales. SEM photograph. X 65.

Fig. 13  *Calea urticifolia*. Close-up of pappus showing numerous long, narrowly lanceolate scales. SEM photograph. X 20.

Fig. 14  *Calea trichomata* var. *trichomata*. Close-up of biseriate, bifid, achene trichome. SEM photograph. X 500.
Fig. 15  **Calea ternifolia var. ternifolia.** Style branches. SEM photograph. X 90.

Fig. 16  **Calea ternifolia var. ternifolia.** One arm of style branches enlarged showing collecting hairs. SEM photograph. X 200.

Fig. 17  **Calea ternifolia var. zacatechichi.** Disk corolla showing deep lobing and glandular dotted surface. SEM photograph. X 35.

Fig. 18  **Calea prunifolia var. prunifolia.** Pollen grain. SEM photograph. X 3000.
Fig. 19  Documented distribution of Calea urticifolia (Mill.) DC.
Calea urticifolia var. urticifolia

Calea urticifolia var. yucatanensis
Fig. 20  Documented distribution of *Calea ternifolia* HBK.
- *Calea ternifolia var. ternifolia*
- *Calea ternifolia var. calyculata*
- ◀*Calea ternifolia var. nelsonii*
- ◇*Calea ternifolia var. zacatechichi*
Fig. 21 Documented distribution of *Calea fluviatilis* Blake and *Calea longipedicellata* Robinson and Greenman.
- Calea longipedicellata
- Calea fluviatilis
Fig. 22  Documented distribution of *Calea prunifolia* HBK.
• Calea prunifolia var. prunifolia
• Calea prunifolia var. chocoensis
Fig. 23 Scatter diagram plotting average leaf length, lowermost phyllary width, and leaf pubescence for *C. prunifolia* HBK.
The diagram illustrates the relationship between the average leaf blade length (cm) on the x-axis and the width of the lowermost herbaceous phyllaries (mm) on the y-axis. The data points are categorized into two types:

- **Pubescent leaves** (open circles)
- **Glabrous leaves** (closed circles)

The distribution of points indicates a trend where the width of the lowermost herbaceous phyllaries increases with the average leaf blade length.
Fig. 24  Documented distribution of *Calea crassifolia* Standley and Steyermark, and *Calea trichomata* Don. Smith.
Calea crassifolia
Calea trichomata var. trichomata
Calea trichomata var. peckii
Fig. 25 Representative specimen of *Calea urticifolia* (Mill.) DC. var. *urticifolia*, Wussow and Landry 349 (LSU), (only small photograph of type available for study).
PELATHEA

LOUISIANA STATE UNIVERSITY HERBARIUM (LSU)

FAMILY: ASTERACEAE

Cola denticulata (Vell.) DC.

STATE: VERA CRUZ: 1.6 miles north of Jct. of Hwy 146 (cross to Mexico City) and road to Matamoros along road to Matamoros; oak forest. Common.

COLL. F.M. Wayman & Currie 2369
27 OCTOBER 1991

Acted by T.N. Grant 1994-75-40203

PLANTS OF MEXICO

LOUISIANA STATE UNIVERSITY HERBARIUM (LSU)
Fig. 26  HOLOTYPE of Calea urticifolia (Mill.) DC. var. yucatanensis Wussow and Urbatsch., R. L. Crockett 79 (Mich).
Fig. 27  HOLOTYPE of Calea ternifolia HBK. var. ternifolia., Herb. HBK. no. 38070 (P).
Fig. 28  HOLOTYPE of Calea ternifolia HBK. var. calyculata (Robinson) Wussow and Urbatsch., G. G. Pringle 2224 (GH).
C. O. PRINGLE.
PLANTÆ MEXICANÆ.
1888.

STATE OF NUEVO LEÓN

Elaeostigma subulatum

Sierra Madre. Near Mier.
15 July.
Fig. 29  HOLOTYPE of Calea ternifolia HBK. var. nelsonii (Robinson and Greenman) Wussow and Urbatsch., E.N. Nelson 2887 (GH).
Fig. 30  ISOTYPE of *Calea ternifolia* HBK var. *zacatechichi* (Schlecht.) Wussow and Urbatsch., *Schiede* 234 (P).
Fig. 31  Representative specimen (type only a fragment) of *Calea longipedicellata* Robinson and Greenman., *Bartlett 11744* (US).
Fig. 32 ISOTYPE of Calea fluviatilis Blake., Bartlett 11790 (MICH).
Fig. 33 Representative specimen (only photo of type available) of *Calea jamaicensis* (L.) L., G.R. Proctor 11181 (A).
Name: Calycanthus floridus L.
Locality: 6 miles south of Mt. Nireland School.
Altitude: c. 500 ft.
Date: November 26, 1956
Habitat: Scrubby roadside bank, yellow limestone substrate.
Notes: Small shrub; heads yellow.
Collector: George R. Proctor No. 11101
Fig. 34  ISOTYPE of *Calea prunifolia* HBK. var. *prunifolia* Humboldt and Bonpland (P).
Fig. 35  HOLOTYPE of Calea prunifolia HBK. var. chocoensis (Cuatr.) Wussow and Urbatsch., O. Haught 5455 (US).
Calce choocensis Cuat.

holotypus

det. Camus VII-53

54956 - Jan. 21, 1912 - Nagal, lal. del Choco.

Slender climber, hanging over some cliffs.

Leaves yellow, leathery.

UNITED STATES NATIONAL MUSEUM
Fig. 36  HOLOTYPE of *Calea crassifolia* Standley and Steyermark.,
J. A. Steyermark 45627 (F).
PLANTS OF GUATEMALA

Clearea grandifolia

Shrub 5-6 ft, tall; leaves stiff, subcoriaceous, dark green above, pale green beneath with raised nerves, Fusion both sides; outer bracts spreading, pale green; flowers dull yellow; innermost bracts appressed with purple tips, along Knife-edge of limestone ridges.

Dept. Alta Verapaz: Cerro Chiquito, between Playa Valiente and Chiquito, lower reaches of the San Jorge, at 100-150 m.

JULIAN A. STEWART

[Herbarium label]
Fig. 37  HOLOTYPE of Calea trichomata D. Smith var. trichomata, H. von Turckheim 1353 (US).
Fig. 38  HOLOTYPE of *Calea trichomata* D. Smith var. *peckii* (Robins.) Wussow and Urbatsch., M. E. Peck 64 (GH).
Table I. Chromosome Reports for Mexican, Central American and Jamaican Species of *Calea*

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*References giving collectors and numbers indicate results from the present study.*
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<td>Vera Cruz, east of Jalapa</td>
<td>Wussow and Landry 351</td>
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*More precise locality data given in specimens examined.

**Voucher specimens deposited in LSU Herbarium.
VITA

James Richard Wussow was born in Dallas, Texas on March 22, 1954, the son of Norman Richard Wussow and Aileen Voges Wussow. After graduating from Thomas Jefferson High School, Dallas, Texas in 1972, he entered the University of Texas at Austin. He received the degree of Bachelor of Arts from the University of Texas in May 1976. In August, 1976, he entered the Graduate School of Louisiana State University. On December 26, 1976 he married Rebeca Rousso. He received the degree of Master of Science from Louisiana State University in December 1978. On January 18, 1980 he was blessed with a daughter, Shereen Louise. He is currently a candidate for the Doctor of Philosophy degree in Botany.

Permanent Address: 2308 Blue Cypress
Richardson, Texas 75081
EXAMINATION AND THESIS REPORT

Candidate: James Richard Wussow

Major Field: Botany

Title of Thesis: A systematic study of the Mexican, Central American, and Jamaican species of the genus Calea

Approved:

[Signatures]

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination:

July 20, 1981