A MONOGRAPH OF THE GENUS *LASTHENIA* DC. (ASTERACEAE)

by

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Introduction

The present revision is based on research undertaken while a graduate student at The City University of New York and The New York Botanical Garden.

Herbarium citations follow Index Herbariorum (Holmgren & Keuken, 1974).

All measurements of involucral and floral parts given in the systematic treatment are based on material reconstituted by boiling.

New names and combinations appearing in this paper are intended solely to indicate the author's plans for future publication. They are not meant to be and should not be construed to constitute effective publication of those names and combinations.

Acknowledgments

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History of the Genus

The genus *Lasianthaea* as here treated is a natural group of eleven species of New World Asteraceae. It has gone unrecognized as a distinct taxon at the generic level since its establishment by DeCandolle in 1836 (Prodr. 5:607), with the single species *Lasianthaea helianthoides* DC.

Three other taxa belonging to *Lasianthaea* were also treated by DeCandolle in 1836 when he established the genus *Lipochaeta* (Prodr. 5: 610). He divided *Lipochaeta* into the "Species Americanae" (three Mexican and one "carribean" species) and the "Species Sandwicenses" (five Hawaiian species). A fifth taxon belonging to *Lasianthaea* was placed in *Calea* L.

Since that time, these taxa and their congeners have been treated in floras (Gray, 1852; Blake, 1926), worldwide treatments (Bentham & Hooker, 1873; Hoffmann, 1894), and in a monograph (Jones, 1905), as members of the genus *Zexmenia* LaLlave & Lexarza, which was established in 1824 with the single species *Zexmenia serrata* LaLlave & Lexarza. The name *Zexmenia* went unused until Gray restored it and expanded the concept of the genus (Gray, 1852). At the same time, Gray restricted *Lipochaeta* to DeCandolle's Hawaiian species.

Included in Gray's concept of the genus *Zexmenia* were two distinct sets of species - a 'wedelioid' group (including *Zexmenia serrata* and three other species) and a 'lasianthoid' group (including *Zexmenia helianthoides* (DC.) A. Gray = *Lasianthaea helianthoides* DC. and five other species). Gray's concept of the genus was clarified in 1886, when he gave a description and specifically stated that the genus was to contain *Lasianthaea* DC. and the American species of *Lipochaeta* DC.

Bentham & Hooker (1873) recognized about twenty-five species in the genus Zexmenia and divided it into three sections: Lipochaeta, Lasianthaea, and Wedelioides. The section Lipochaeta of the genus Zexmenia, as defined by Bentham& Hooker, should not be confused with the Hawaiian genus Lipochaeta DC. (accepted as distinct from Zexmenia by Bentham & Hooker and by all later authors since Gray's treatment in 1852).

In 1894, Hoffmann took a broader view of Zexmenia than most authors. He divided the genus into two sections: Euzexmenia and Otopappus. Included in Hoffmann's section Euzexmenia were both the 'wedelioid' and 'lasianthoid' species of Zexmenia (the entire genus Zexmenia in the sense of Gray and of Bentham & Hooker). Also falling within Hoffmann's concept of the genus Zexmenia were the species comprising the genus Otopappus Bentham (1873). Otopappus has been recognized as a distinct genus by later authors - a view here adopted.

W. W. Jones (1905), in his revision of Zexmenia, recognized two sections: "Euzexmenia" (containing the sections Lipochaeta and Lasianthaea of Bentham & Hooker) and "Auchenocarpa" (basically the section Wedelioides of Bentham & Hooker). Jones placed Zexmenia serrata LaLlave & Lexarza (type species of Zexmenia) in the section "Euzexmenia", although he did not see any type material. Blake (1930) later recognized that the species known as Zexmenia scandens Hemsley (1881) is a taxonomic synonym of Zexmenia serrata LaLlave & Lexarza. Zexmenia scandens was known to Jones and was placed by him in the section "Auchenocarpa". Zexmenia serrata LaLlave & Lexarza clearly belongs among the 'wedelioid' species. Indeed, so close are Zexmenia serrata and its relatives to Wedelia Jacq. and its allies that the 'wedelioid' Zexmenias have been treated as Wedelias in recent works by McVaugh (Flora Novo-Galiciana, ined.) and Rzedowski

(Clave para generos de la tribu Heliantheae, ined.).

An attempt was made to conserve the name Zexmenia as used in the sense of Gray (1852) for application to the species of the genus Lasianthaea in the event that Zexmenia serrata LaLlave & Lexarza be placed in Wedelia (Becker, 1972). The proposal was rejected by the Committee for Spermatophyta of the International Association for Plant Taxonomy (Stafleu & Voss, 1975), and thus the name Lasianthaea DC. is taken up for the species here treated.

Systematic Position of Lasianthaea

Lasianthaea DC. is a member of the tribe Heliantheae, subtribe Verbesininae of the family Asteraceae. Within the subtribe, Lasianthaea is distinguished by its combination of fertile rays, opposite leaves (or in some taxa occasionally alternate in the inflorescence), and achenes with stout awns (2 or very rarely 3 in the disc, 3 or very rarely 4 in the rays) which are not separated from the body of the achene by a constriction or "neck", usually several membranous pappus squamellae (occasionally reduced to a ciliate fringe or none), and a ventral edge which is typically drawn out to a thin margin often adnate to the ventral awn (Figure 1).

Members of Lasianthaea have most often been confused with Verbesina L. on the one hand and with the Wedelia complex on the other. Lasianthaea as defined above is distinct from the above genera. Table 1 gives characters separating Lasianthaea from genera which are close to it morphologically or have been confused with it, and Figure 1 shows achenial structure in the various genera.

	Lasianthaea	*Wedelia*, *Zexmenia*, *Lipochaeta*	*Verbesina*	*Otopappus* (incl. *Notoptera*)
Achenes (disc)	Body flattened, not mottled	Body plump, often mottled (Fig. 1)	Body flattened, not mottled	Body flattened, not mottled
	Ventral edge narrowed out to a thin margin	Winged (2) or non-winged	Winged	Unwinged
	Awns 2 (very rarely 3), stout	Awns 1, 2 or none, fragile	Awns 2, stout or fragile	Awn 1, stout
	Pappus squamellae usually present	Pappus squamellae present	Pappus squamellae none	Pappus squamellae present or none
	No neck separating body from awns and pappus	Neck separating body from awns and pappus	No neck present	No neck present
Ray floret color	Yellow, orange-red, or red-violet (always present)	Yellow or purple	Yellow, orange-red, white, or rays none	Yellow
Leaves	Opposite (or occasionally alternate in inflorescence)	Opposite or alternate	Opposite or alternate	Opposite
	Not lobed	Sometimes lobed	Often lobed	Not lobed
	Leaf bases not decurrent onto stem	Leaf bases not decurrent	Leaf bases often decurrent onto stem	Leaf bases not decurrent

Table 1. Comparison of *Lasianthaea* with related genera or genera often confused with it.

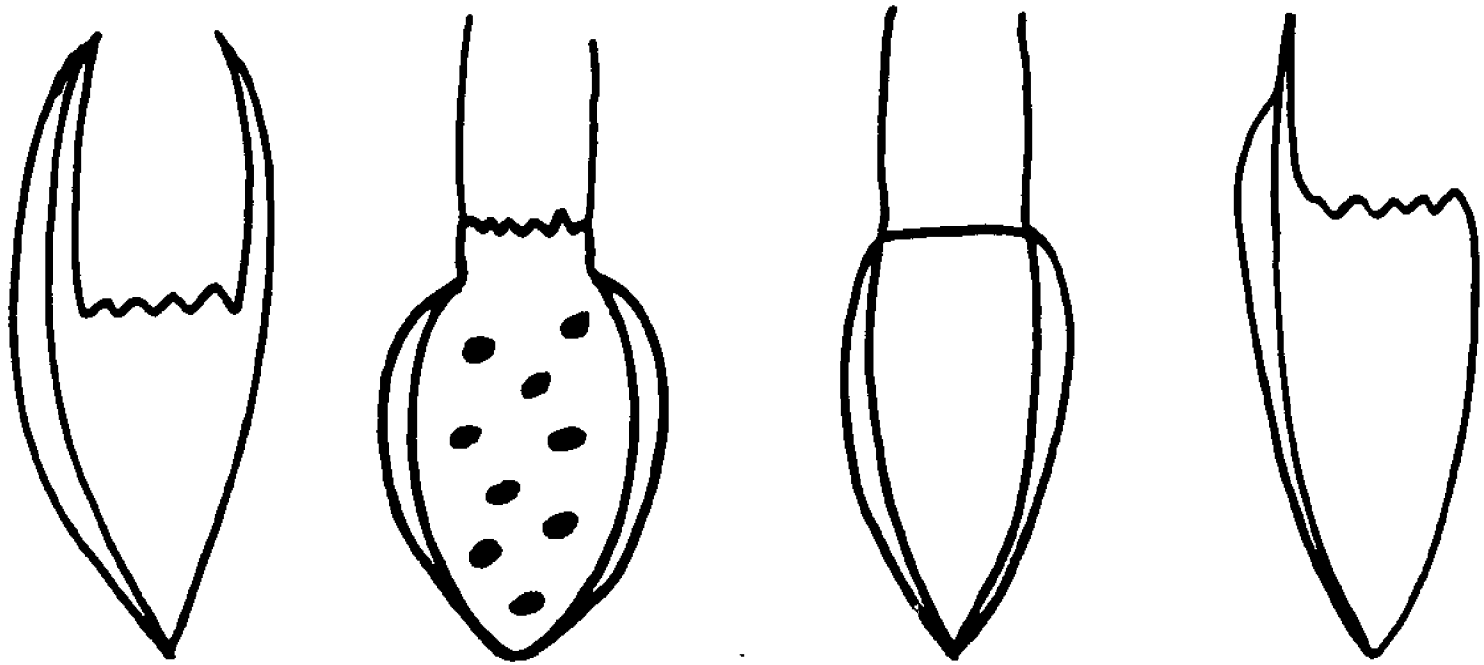

Figure 1. Typical disc achenes in Lasianthaea and some other genera.

Flavonoid Studies

Chemosystematic investigation of the flavonoid compounds present in the various species of *Lasianthaea* has involved: 1) a preliminary survey of leaf flavonoid patterns in the genus, and 2) an attempt to correlate flavonoid pattern data with morphological data in a study of apparent hybridization between *L. helianthoides* and *L. crocea*.

Leaf material was pre-extracted in chloroform. Whenever possible, and for each collection sampled, leaves at all stages of growth from very young to mature and full-sized were selected. Leaf, ray, and disc floret material was extracted in methanol. Descending two-dimensional chromatograms were run on Whatman 3MM paper using TBA in the first direction and 15% HOAc in the second, according to the methods given in Mabry, Markham & Thomas (1970).

Results of the general survey of leaf flavonoid patterns are presented in Table 2, while results of the *L. helianthoides* - *crocea* study are presented and discussed in the Systematic Treatment (page 61).

Cytology

Chromosome counts: Flower buds were obtained in the field or from plants grown in the Research Greenhouse of The New York Botanical Garden, fixed and preserved in Newcomer's Solution (Newcomer, 1953), and squashed in aceto-carmine or in lactic-acetic orcein (Cooperrider & Morrison, 1967) (if in the latter, buds were first transferred to a fixative composed of methanol:chloroform:propionic acid 5:3:2). Data from personal counts and from the literature are presented in Table 3. All vouchers cited in Table 3 have been seen by the author.

Pollen Stainability Studies: Mature polleniferous anthers from un-

Taxon	Designated spots																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
L. fruticosa var. fruticosa	x	x	x	x	x	x	x			x	x	x	x	x				x				
L. fruticosa var. michoacana	x	x	x	x	x	x	x			x	x	x	x	x	x							
L. fruticosa var. fasciculata	x	x		x	x	x	x	x		x			x	x	x			x				
L. fruticosa var. alamosana	x	x		x	x	x	x															
L. fruticosa var. aggregata			x	x	x	x				x					x							
L. macrocephala											x	x							x			
L. helianthoides var. helianthoides		x			x					x			x					x	x	x	x	x
L. helianthoides var. nayaritense	x	x	x		x	x	x	x	x				x		x	x		x				
L. crocea		x			x	x			x				x		x			x	x			x
L. squarrosa	x				x																	
L. ceanothifolia var. ceanothifolia	x	x	x	x	x	x	x			x	x	x	x	x	x	x						
L. ceanothifolia var. gracilis	x	x		x	x	x	x					x		x		x						
L. seemannii	x	x		x	x	x	x			x		x		x			x	x				
L. zinnioides	x	x		x	x	x	x	x	x	x												
L. palmeri	x	x	x	x	x	x	x															
L. podocephala	x	x	x	x	x	x	x						x									
L. aurea				x	x																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22

Table 2. Designated spots from paper chromatograms of leaves of Lasianthaea species. Data for each species are cumulative for several collections.

Taxon	Voucher	Reference	n=
L. aurea	King 3663	Turner, Powell & King, 1962	10
L. ceanothifolia var. ceanothifolia	Becker & Cronquist 45	* new report	10
L. ceanothifolia var. ceanothifolia	Becker & Cronquist 47	*	10
L. ceanothifolia var. gracilis	Becker & Cronquist 4	*	10
L. crocea	Becker & Olsen 54	*	10
L. fruticosa var. fruticosa	Becker & Cronquist 40	*	11
L. fruticosa var. fruticosa	Breedlove 13806	Solbrig et al., 1972	11
L. fruticosa var. fruticosa	Breedlove & Raven 13701	Solbrig et al., 1972	11
L. fruticosa var. fruticosa	King 3347	Turner, Powell & King, 1962	11
L. fruticosa var. fruticosa	King 5262	Turner & King, 1964	11 or 12
L. fruticosa var. fruticosa	King 5282	Turner & King, 1964	11
L. fruticosa var. fruticosa	King 5353	Turner & King, 1964	ca. 11
L. fruticosa var. fruticosa	King 6843	Turner & King, 1964	ca. 8
L. fruticosa var. fruticosa	Porter & Montalvo 1237	Solbrig et al., 1972	11

Table 3. Reported chromosome counts in Lasianthaea.

Taxon	Voucher	Reference	n=
L. fruticosa var. fasciculata	Turner & Powell 1097	Turner & Flyr, 1966	11
L. fruticosa var. michoacana	Becker & Cronquist 20	*	11
L. helianthoides var. helianthoides	Becker & Olsen 57	*	10
L. macrocephala	Becker & Olsen 60	*	10
L. macrocephala	Breedlove 1622	Solbrig et al., 1972	10
L. palmeri	Becker & Cronquist 25	*	ca. 20
L. palmeri	King 3624	DeJong & Longpre, 1963	ca. 17
L. podocephala	Becker & Cronquist 1	*	ca. 40
L. ?zinnioides	Becker & Cronquist 5	*	ca. 20

Table 3. Reported chromosome counts in Lasianthaea, continued.

opened disc florets were macerated in lacto-phenol and cotton blue for 24 to 36 hours and observed. Pollen grains which were dark blue after that period were counted as stained, light blue or colorless grains were counted as non-stained. Percent stainability was based on counts of 200 grains. Results from specific cases are presented in the Systematic Treatment under the discussions of *H.* *fruticosa*, *H.* *helianthoides*, *H.* *macrocephala*, and *H.* *crocea*.

Discussion

General

The genus Lasianthaea as recognized in this treatment consists of eleven species. Three of these are divided into a total of twelve varieties (L. fruticosa with six, L. ceanothifolia with four, and L. helianthoides with two).

The species of Lasianthaea do not exhibit patterns of character variation and distribution which would suggest autogamy or apomixis. Indeed, they appear to be sexually reproducing and strongly outcrossing. The pattern of variation in the genus is such that it has been found useful to recognize only one infraspecific category (varietas). Varieties, when recognized in this treatment, to a large extent represent members of geographical replacement series within a species. Usually, where varietal boundaries converge, a relatively small number of populations will exhibit morphologies more or less intermediate between the varieties. "Forms", differing from the norm of a species in one or a few sharply marked characters, and which do not exhibit coherent geographic distributions, are found in many of the species of Lasianthaea. It has not been found taxonomically useful to recognize these "forms", although several are discussed.

Habit

Of the eleven species of Lasianthaea recognized in this treatment, seven are typically shrubs. The half-shrubby habit exhibited by several of the typically shrubby species (eg., L. macrocephala, L. seemannii, L. helianthoides, L. ceanothifolia (rarely)) may be an adaptation to local conditions, such as intense grazing, resulting from strong selection

pressure, but this remains to be determined. This "habital indeterminacy" is found fairly often among Mexican Asteraceae.

The other four species are typically perennial herbs (sometimes woody in age below), with perennating structures very close to or at ground level, and which produce fleshy - tuberous rootstocks below ground (the shrubs do not).

Distribution

The genus Lasianthaea ranges from Arizona to Panama (also, there is one record from northern Venezuela), however, all but two taxa are apparently restricted to Mexico. The genus as it occurs in Mexico is found mainly in the west and south (Sierra Madre Occidental, Transverse Volcanic Belt, Sierra Madre del Sur). The Sierra Madre Oriental is relatively poor in Lasianthaea species (only two, and these not restricted to it). The above comments hold equally well for both the shrubs and perennial herbs. Only one taxon crosses the Isthmus of Tehuantepec into the Central American floristic region. These facts of present-day distribution and relative diversity of Lasianthaea in various regions suggest that the genus may have originated in western or southern Mexico.

Species of Lasianthaea vary from widely distributed ones such as L. fruticosa (Central America through Mexico to near the United States border) and L. ceanothifolia (northern Sierra Madre Occidental to Chiapas), to much more local species such as L. squarrosa (northern Guerrero and adjacent Morelos), L. seemannii (southern Sierra Madre Occidental and northern Nayarit), and L. sinnioides (distribution similar to L. seemannii). The most wide-ranging species are divisible into the largest number of varieties. Among the species with intermediate-sized distributions, L. macrocephala, L. palmeri, and L. aurea tend to exhibit considerable intra-

specific variation, while *L. crocea*, *L. podocephala*, and *L. helianthoides* tend to be relatively less variable in this respect (the two varieties of *L. helianthoides* are relatively homogenous within their respective ranges).

Taxa with disjunct distributions include *L. fruticosa* var. *fasciculata* (Sierra Madre Oriental and also in western Mexico) and *L. helianthoides* (with two disjunct varieties). In the former case, little or no morphological divergence between eastern and western populations is in evidence. In contrast, the divergence between the two population systems in *L. helianthoides* is marked enough so that two varieties are recognized in this treatment, corresponding to the two disjunct population systems.

Habitats

Most taxa in *Lasianthaea* appear to be adapted to a wide array of habitats within their respective ranges. In general, species of *Lasianthaea* are not found in deserts or in lowland moist tropical forest (an exception to the latter being *L. fruticosa* var. *fruticosa*). Leaving out the above two habitat types, species of *Lasianthaea* can be found in most habitats available in Mexico and Central America, except for several specialized types such as the aquatic habitat and high-montane grassland.

Two extremes in habitat preference may be mentioned, both of them occurring in varieties of *L. fruticosa*. *L. fruticosa* var. *fruticosa*, found throughout Central America and southern Mexico, occurs in a wide array of habitats ranging from high-montane fir forest to moist lowland tropical forest. In contrast, *L. fruticosa* var. *fasciculata* appears to be rather "fastidious" within its range, generally being found in high-moist montane sites, "selecting" these from among the several habitat-types which, *a priori*, would seem to be available to it. Competition may be excluding

it from successful colonization of other habitats.

Taxa of Lasianthaea tend to exhibit an indifference towards, if not a "preference" for, disturbance (again, this is typical of many groups of Mexican Asteraceae). Thus, in the Sierra Madre Occidental, some taxa which, until the advent of major human and human-related distrurbance, were probably adapted to pine, oak, or mixed forest have been able to survive in, or possibly expand into, areas which have been considerably degraded by, for example, grazing (e.g., L. seemannii, L. zinnioides).

Divergence and Unusual Forms

Well-defined, distinctive morphological variants within a taxon in Lasianthaea often appear near the edges of the range of that taxon. The gradual process of divergence which has presumably given rise to varieties and species in the past is thus apparently still operative. Examples of morphologically distinctive variants near the edges of the range of taxa include Sinaloan populations of L. fruticosa var. fasciculata, San Luis Potosi populations of L. aurea, coastal Oaxacan L. crocea, etc.

Unusual forms variant from the norm in one or two marked characteristics and which can be found throughout the range of a taxon are also known (the "forms" discussed above). Examples include glabrous plants of L. palmeri (ordinarily pubescent) found scattered within its range in Jalisco, monocephalic plants of L. fruticosa var. fruticosa scattered throughout Central America and southern Mexico, etc.

Usefulness of Characters

Characters which, a posteriori, have been found most use-

ful in delimiting taxa in Lasianthaea include the following:

1) habit (at the level of "species-group" in the split between the shrubs and the perennial herbs);

2) head size, correlated with the number of disc florets (at the level of "species-group" in the distinction between the "large-headed assemblage" and the other shrubs; also at the intraspecific level in L. fruticosa);

3) involucral graduation (at the specific level within the shrubs);

4) length of achenial awns relative to involucre in ripe heads (at the infraspecific level in L. ceanothifolia and L. fruticosa);

5) peduncle length (at the specific level in both the shrubs and perrennial herbs; at the infraspecific level in L. fruticosa);

6) ray color (at the specific level in both the shrubs and perrennial herbs).

Other characters found particularly useful in certain cases include: nature of outer phyllaries (distinctive in L. squarrosa, L. crocea), nature of pales (distinctive in L. aurea), anther thecae color (distinctive in L. crocea, etc.), nature of achenes (L. podocephala, L. aurea, L. fruticosa var. alamosana).

Environmentally relatively labile characters such as pubescence and leaf shape, size, degree of serration, and texture tend to be less useful in delimiting taxa in Lasianthaea. Thus, there is usually considerable variation in amount of pubescence, and often of degree of appression/spreading of hairs within any particular taxon. Sometimes, this is apparently related to altitudinally influenced factors (for instance, in L. fruticosa var. fruticosa, plants from higher elevations tend to be more pubescent than plants from lower elevations). However, in some cases

nature of pubescence is of use in delimiting taxa (in combination with other characters). This is the case, for example, in distinguishing between *E. ceanothifolia* var. *ceanothifolia* (hairs spreading) and *E. ceanothifolia* var. *verbenifolia* (hairs appressed) in Jalisco where they are sometimes closely sympatric.

Leaf texture is variable within most taxa, but general statements using leaf texture as a criterion for distinguishing between taxa are sometimes warranted (for example, *E. crocea* (thin-leaved) vs. *E. helianthoides* (thick-leaved), *E. podocephala* (thin) vs. *E. palmeri* (firm)).

Leaf shape is sometimes very labile, as for example in *E. aurea* (almost linear to broadly lance-ovate). In general, species are characterized by leaf shapes which vary within closer limits. General tendencies, such as towards breadth in *E. helianthoides*, oblong shape in *E. macrocephala*, etc., are sometimes of use, especially when cases of apparent hybridization are being analyzed. In some cases, such as in *E. seemannii*, leaf shape and texture are distinctive and characteristic.

Flavonoid Studies

Definite statements regarding the taxonomic significance of flavonoid data await further studies of intrapopulational, developmental, seasonal, and edaphically influenced variation, as well as the systematic identification of compounds. The following tentative statements are ventured at this time: 1) leaf flavonoid pattern appears to be of most value at the level of species-group in Lasianthaea; 2) the perennial herbs as a group tend to lack many of the compounds found in the shrubs; 3) among the shrubs, the "large-headed assemblage" appears to lack a spot, tentatively identified as ellagic acid, which is found in most

of the other shrubs; 4) it appears that some species may possess unique marker compounds, such as L. seemannii (spot number 17).

The results of the L. crocea - helianthoides hybridization flavonoid study are discussed below under "Hybridization" and in the Systematic Treatment in the discussion of L. crocea.

Chromosome Numbers

Chromosome numbers are known for all species of Lasianthaea except L. seemannii and L. zinnioides (that is, all species except the two mentioned have been counted at least once). Species with n=10, n=11, and polyploids are known. All the shrubs counted exhibit n=10 except for L. fruticosa with n=11. Among the perennial herbs, L. aurea is diploid with n=[illegible], and the others are polyploids apparently based on n=10 or n=11.

At the present time, it appears that the basic, ancestral number, x, for Lasianthaea may well be 11, with consequent aneuploid reduction to 10 and also polyploidy at the n=10 or n=11 level. The possibility that x=[illegible] is not discounted here, however.

The morphological distinctiveness of Lasianthaea from other genera is supported by the cytological information available. Thus, in Lasianthaea, x=10 or 11, n=[illegible], ca. 20, ca. 40; in Verbesina, x=17, n=16, 17, 18, 34; in Otopappus, n=15; in Wedelia- Zexmenia- Lipochaeta and allies, x=14 or 15, n=11?, 14, 15, 28 (Solbrig, 1972). Aneuploid series and polyploidy appear to be involved in the cytological evolution of these genera. Much remains to be learned of the cytological situation in Lasianthaea and related genera.

Isolation Mechanisms

Chromosomal, phenological, and ethological isolation mechanisms appear to be operative in Lasianthaea. Thus, L. fruticosa, with n=11, is effectively isolated from the n=10 shrubs, and among geographically sympatric shrubby Lasianthaeas in the Sierra Madre Occidental, phenological isolation appears to effectively isolate L. seemannii (a late bloomer) from the other species with which it might hybridize.

Differences in ray color, presumably influencing behavior of at least some potential pollinators, between sympatric species of Lasianthaea is an isolation mechanism which is apparently operative under certain circumstances. Thus, L. helianthoides var. helianthoides and L. crocea are commonly sympatric both geographically and phenologically in the Balsas Depression of south-central Mexico. Both are n=10 shrubby species. Ray color in helianthoides is orange-yellow, while in crocea it is orange-red. Evidence is presented elsewhere in this paper that the two species apparently hybridize in nature. However, they maintain their specific distinctness to the extent that the vast majority of plants can be assigned to either one or the other species. It is hypothesized that, in this case, ethological factors tend to keep the genetic balance shifted, on the whole, towards intraspecific rather than interspecific breeding.

Hybridization

There is no convincing evidence that the two basic species-groups in Lasianthaea, the shrubs and the perennial herbs, hybridize with each other. Also, the perennial herbs appear to be isolated among themselves. Among the shrubs, however, the situation appears to be much different. Although several isolating mechanisms appear to be in action (as discus-

sed above), exchange of genetic information among the shrubs is apparently common. Except for the relatively effectively isolated *L. fruticosa* and *L. seemannii*, it appears that the shrubs typically tend, when sympatric, to produce some hybrids. Those plants which are apparently products of hybridization between species of *Lasianthaea* tend to be morphologically intermediate between the putative parents. Also, they usually exhibit much reduced pollen stainability (and therefore presumably much reduced pollen fertility). The stainability is almost always reduced at least 25%, and is commonly reduced 50% or more from that of the putative parents. Specific cases are discussed in the Systematic Treatment under *L. fruticosa*, *L. macrocephala*, *L. helianthoides*, *L. crocea*, and *L. ceanothifolia*.

It appears that information on flavonoid patterns (and possibly on the production of "hybrid" compounds) in cases of apparent hybridization in *Lasianthaea* may be strongly corroborative of morphological and cytological evidence of hybridization and subsequent introgression. Data and interpretation of one case (involving *L. crocea* and *L. helianthoides*) are presented in the Systematic Treatment under the discussion of *L. crocea* (p. 6_).

Phylogeny

The elucidation of a phylogeny within *Lasianthaea* requires more information on cytological, chemical, anatomical, etc. trends within and without the genus. However, a few general statements, to a large extent speculative, may be made at this time. For purposes of this discussion, the following "guiding principles" are being followed:

a) the polyploid condition is derived from the diploid condition;

b) in the Asteraceae, inflorescence reduction is a strong and wide-

spread trend;

c) within the Asteraceae, tribe Heliantheae, the presence of anthocyanins in ray florets is in most cases a derived condition;

d) within the Asteraceae, tribe Heliantheae, the herbaceous condition is in general derived from the shrubby condition.

Briefly, then, it is interesting to note that when one presumably derived condition is found within a species-group in Asclepiadeae, other presumably derived characteristics are likely to exist in that group as well. Thus, the perennial herbs exhibit inflorescence reduction (all four species), anthocyanic ray pigments (one species), and polyploidy (three of the four species). Among the shrubs, the large-headed assemblages exhibits inflorescence reduction (all three species), anthocyanic ray pigments (two species), and a strong tendency towards habitat intermediacy (two species).

In contrast, both A. cyanothifolia and A. fruticosa exhibit a more "primitive" array of characteristics. Both are yellow-rayed, diploid as far as is known, bear many-headed inflorescences, and are almost always normally shrubby.

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Lasianthaea DC. Prodr. 5:607. 1836.
Telesia Raf., Fl. Tellur. pt. 2:41, 1836.

Trees, shrubs, or half-shrubs, sometimes woody near base only, or tuberous-rooted perennial herbs from a woody caudex, 0.1-7 m high. Leaves usually all opposite, occasionally becoming alternate in inflorescence; petiole flattened; blade unlobed, margin coarsely serrate to denticulate-mucronulate, usually triplinerved, occasionally trinerved or subpenninerved. Inflorescence of 3-12- or more-headed cymose umbelliform clusters, or reduced to a solitary head, axillary and/or terminal. Heads radiate, rays fertile. Involucre turbinate to hemispherical, in 2-several series, these subequal to strongly graduated. Outer phyllaries usually indurate-membranous below, often herbaceous above, margin usually ciliate, inner phyllaries membranous, sometimes herbaceous above. Rays 4-30, commonly 8-21, yellow, orange-yellow, orange-red, or purple-red, lamina elliptic to oblong, tube short. Disc florets 8-200, yellow, orange-yellow, or purple-red, tube cylindro-campanulate, throat narrowly campanulate to campanulate, glabrous, lobes 5, deltoid-ovate, papillose within, glabrous or sparsely hispidulous dorsally, mature corollas often exserted several mm from ripe heads. Anther thecae light brown to blackish, appendages triangular-ovate, pale yellow to colorless, base short-auriculate. Style branches filiform-subulate, appendages hispidulous dorsally. Pales membranous, conduplicate, acute to obtuse. Disc achenes compressed, biconvex, body cuneate to broadly cuneate, with 2 (rarely 3) stout awns at apex, these directly confluent with achenial margins, adaxial margin narrowed to a thin sharp edge, pappus of several free or connate membranous squamellae usually adnate

to base of awns, sometimes reduced to a ciliate fringe. Ray achenes similar to disc but shorter and broader, compressed or thickened, triquetrous (rarely 4-angled), usually broadly cuneate, 3 (rarely 4) awned or toothed, adaxial awn or tooth longest. Receptacle low-convex to flat.

Key to the Species of *Lasianthaea*

1. Phyllaries graduate, usually strongly so (occasionally weakly graduate and then heads less than 6 mm wide as pressed)
    2. Rays yellow to orange-red; shrubs or half-shrubs
        3. Involucre usually less than 1 cm high and wide as pressed, heads generally in umbelliform clusters of 3-12

            6. *L. ceanothifolia*

        3. Involucre usually more than 1 cm high and wide as pressed, heads variously arranged
            4. Leaves coriaceous-hardened, elliptic; peduncles 1 cm long or less; heads in umbelliform clusters of 3-6

                7. *L. seemannii*

            4. Leaves thin to firm in texture (but not coriaceous-hardened), lanceolate, ovate, or oblong; peduncles often more than 1 cm long; heads usually solitary or ternate
                5. Peduncles usually more than 4 cm long; leaves lance-oblong to ovate-oblong, acuminate, not rugose

                    2. *L. macrocephala*

                5. Peduncles usually less than 4 cm long; leaves

mostly ovate to suborbicular, acute to obtuse, often rugose

6. Outer phyllaries plane, erect, often herbaceous above but not foliaceous 3. L. helianthoides

6. Outer phyllaries weakly conduplicate, recurved, and foliaceous at apex 5. L. squarrosa

2. Rays red-violet (unique in the genus); perennial herbs 8. L. zinnioides

1. Phyllaries usually subequal, or the outer longer than the inner (if weakly graduate then the heads greater than 6 mm wide as pressed)

7. Perennial herbs from a woody caudex

8. Pales with a dark line on midrib, conspicuously exserted from ripe heads; peduncles usually less than 6 cm long 11. L. aurea

8. Pales not lined along midrib, not exserted from ripe heads; peduncles usually more than 6 cm long

9. Leaves rounded to subcordate at base, thin-textured; outer phyllaries usually spreading-hispid 10. L. podocephala

9. Leaves truncate to usually cuneate at base, narrowed onto petiole, firm-textured; outer phyllaries usually with appressed pubescence, occasionally glabrous except for the ciliate margins 9. L. palmeri

7. Shrubs or trees

10. Rays orange-red above (rarely yellow); heads solitary or ternate, peduncles usually more than 7 cm long 4. L. crocea

10. Rays yellow; heads usually in umbelliform clusters of 3-12, peduncles usually less than 7 cm long 1. L. fruticosa

1. Lasianthaea fruticosa (L.) K. Becker, comb. nov. Bidens fruticosa L., Sp. Pl. 833, 1753 (based on Bidens foliis ovatis serratis petiolatis, caule fruticoso. Hort. Cliff. 399, 1737), not Zexmenia fruticosa Rose, Contr. U.S. Nat. Herb. 1:103, 1891. Verbesina frutícosa L., Sp. Pl. ed. 2:1271, 1763. Narvalina fruticosa (L.) Urb., Symb. Ant. 5:265, 1907. TYPE: Cultivated in Hort. Cliff. (HOLOTYPE: BM; Photo: NY).

Shrubs or rarely half-shrubs woody near base only, (0.3-) 0.5-6 (-7) m high; young branches glabrous to villous. Leaves with petiole 0.5-7 mm long, glabrous to tomentose; blade thin to firm, ovate to narrowly lance-ovate, (1.5-) 3-22 cm long, (0.4-) 1-22 cm wide, acute to long-acuminate, rounded to cuneate at base, nearly glabrous to scabrous and hispid above, nearly glabrous to tomentose below, margin denticulate-mucronulate to coarsely serrate, triplinerved, rarely subpenninerved. Inflorescence 3-15-headed, terminal and from upper leaf axils, and solitary from upper leaf axils. Peduncles 0.2-14 cm long, stout to slender, glabrate, hispid, or villous; heads 1.5-3.5 cm wide across extended rays. Involucre campanulate to hemispherical, 0.5-1.4 cm high, 0.4-1.9 cm wide, phyllaries usually subequal, occasionally graduated in 2-3 series. Outer phyllaries membranous-indurate below, herbaceous above, ovate, lanceolate, or oblong in outline, 3.5-16 mm long, 1-8 mm wide, acute to obtuse, glabrous to hirsute dorsally, middle phyllaries often 3-lobed at apex, inner phyllaries ovate to oblong in outline, 5-10 mm long, 1-5 mm long, acute to rounded. Rays 4-13, yellow, lamina 5.5-20 mm long, 2.4-7.0 mm wide, tube 1.0-4.0 mm long. Disc florets 9-ca. 100, yellow, 4.5-8 mm long, throat campanulate, 4-7.5 mm long, 0.9-1.8 mm wide, lobes 0.5-1.0 mm long. Anther thecae brown to blackish, 1.5-3.1 mm long, appendage (0.3-) 0.5-0.9 mm long. Style branches 1.5-3.0 mm long, appendage 0.3-1.0

mm long. Disc achenes cuneate, 2-awned, body 3-6 mm high, 0.9-2.1 mm wide, glabrate, puberulent, or hispidulous, occasionally glandular, awns 1.5-5.5 mm long, pappus squamellae connate and ca. 0.2 mm long, with individual squamellae to 0.8 mm long, or reduced to a ciliate fringe. Ray achenes 3-awned, body 1.5-5 mm long, 1.0-2.3 mm wide, awns 0.5-4 (-4.5) mm long, pappus squamellae 0-1.3 (-2.3) mm long. Receptacle convex or low-convex.

Key to varieties of L. fruticosa

1. Involucres 4-6 mm wide as pressed, usually turbinate or cylindro-campanulate, disc florets few (9-19), peduncles less than 2 cm long; Oaxaca 1f. L. fruticosa var. aggregata

1. Involucres usually wider, campanulate to hemispherical, disc florets relatively many (usually over 13), if narrower than 6 mm then on peduncles over 2 cm long

2. Involucres usually 5-8 mm wide as pressed, usually less than 7 mm high, hemispherical to campanulate, peduncles slender, heads usually in clusters of 6-15; Sierra Madre Oriental and also Jalisco, Nayarit, and southern Sinaloa 1c. L. fruticosa var. fasciculata

2. Involucres usually more than 7 mm high and wide as pressed, disc relatively many-flowered

3. Awns conspicuously exserted (to 3 mm) from ripe heads, divergent; heads solitary or ternate; peduncles slender; leaves thin-textured; Sonora 1e. L. fruticosa var. alamosana

3. Awns exserted to 5 mm or not exserted from ripe heads, not divergent; terminal inflorescences usually 3-12-headed; peduncles

stout to slender; leaf texture various

4. Peduncles usually stout, terminal inflorescences 1-or 3-(-5)-headed, outer phyllaries usually with thickened green tips, leaves often rugose, usually firm-textured; State of Mexico to Jalisco 1b. L. fruticosa var. michoacana

4. Peduncles usually slender, terminal inflorescences 3-12-headed, leaf texture various

5. Involucre weakly graduate (outermost phyllaries shorter than middle and inner), stem pubescence hispid to hirsute, often spreading; outer phyllaries usually narrowed at middle; Chihuahua, Sonora 1d. L. fruticosa var. occidentalis

5. Involucre not graduate (outer phyllaries equal to or exceed middle and inner series), if weakly graduate then pubescence of stems and leaves sparsely hispidulous or strigillose; Veracruz, southern Oaxaca, and south 1a. L. fruticosa var. fruticosa

1a. Lasianthaea fruticosa (L.) K. Becker var. fruticosa.

Bidens frutescens Mill., Gardn. Dict. ed. 8, no. 4, 1768. Zexmenia frutescens (Mill.) Blake, Contr. Gray Herb. 52:50, 1917. Z. frutescens var. genuina Blake, Contr. Gray Herb. 52:51, 1917. TYPE: Specimen in Herb. Sloane 316.75 from Chelsea Garden, 1737, raised from seed sent from Carthagena (Costa Rica)(HOLOTYPE: BM; Photos: GH,MICH,NY,US(2)).

Lipochaeta monocephala DC. Prodr. 5:610, 1836. TYPE: Cultivated, Hort. Par. (HOLOTYPE: G; Photos: GH,US(2); Drawing: GH).

Zexmenia costaricensis Benth. in Oersted, Videnak. Meddel. 1852:95, 1853. Zexmenia nicaraguensis "Benth." ex C. Muell. in Walp. Ann. Bot. 5:226, 1858 (sphalm.). TYPE: COSTA RICA: "In monte Aguacate",

Nov 1846, Oersted 8516 (HOLOTYPE: K(herb. Benth.); Fragment: GH; Fragment and Photo: US(2); Photos: GH,US; ISOTYPE : C; Tracing: GH; W).

Zexmenia villosa Polak., Linnaea 41:579, 1877. Zexmenia costariensis Benth. var. villosa (Polak.) Blake, Journ. Bot. 53:14, 1915. Zexmenia frutescens (Mill.) Blake var. villosa (Polak.) Blake, Cont. Gr. Herb. 52:51, 1917. TYPE: COSTA RICA: SAN JOSÉ: San José, ad margines hortorum, Nov, Polakowsky 466 (HOLOTYPE: W; Photos: F,US; ISOTYPE: BM; Photos: GH,US).

Zexmenia elegans Sch. Bip. ex W. W. Jones, Proc. Amer. Acad. 41:157, 1905. TYPE: MEXICO: VERACRUZ: Mirador, Nov 1841, Liebmann 378 (HOLOTYPE: GH; Photo: US; ISOTYPES: C(2); Photos: (of one sheet at C) F, MICH,NY (of both sheets at C) US; G,K,NY,P).

Zexmenia elegans Sch. Bip. var. kellermannii Greenm. Field Col. Mus. Bot. Ser. 2:348, 1912. TYPE: GUATEMALA: IZABAL: Los Amates, 15 Feb 1908, Kellerman 7612 (HOLOTYPE: F; ISOTYPES: NY,US).

Zexmenia purpusii Brandeg., Univ. Calif. Pub. Bot. 6:75, 1914. TYPE: MEXICO: CHIAPAS: Cerro del Boqueron, Sept 1913, Purpus 6660 (HOLOTYPE: UC; Photos: ENCB,MEXU).

Zexmenia macropoda Blake, Contr. U. S. Nat. Herb. 22:634, 1924. TYPE: GUATEMALA: Solola, 25 Jan 1915, Holway 109 (HOLOTYPE: GH; Photo: ENCB).

Shrubs or small trees, soft-wooded and usually slender-stemmed, sometimes straggling or climbing, or occasionally half-shrubs, (0.3-) 1.5-6 (-7) m high; young branches varying from nearly glabrous to

densely villous. Leaves with petioles (0.5-) 1-4 (-4.5) cm long; blades thin to firm, lance-ovate to ovate, varying to lanceolate and broadly ovate, (3-) 5-16 (-22) cm long, 1.5-9 (-12) cm wide, sparsely strigillose to pilose below, triplinerved or occasionally subpenninerved. Inflorescence (1-) 3-9-headed. Peduncles 0.5-9 (-14) cm long, slender to stout; heads 2-3.5 cm wide across extended rays. Involucre usually campanulate to broadly campanulate, varying to narrowly campanulate and hemispherical, 0.5-1.3 cm high, (0.5-) 0.7-1.9 cm wide, phyllaries in 2-3 equal or slightly graduated series. Outer phyllaries usually reticulate and often slightly ampliated above, ovate-oblong to lance-ovate in outline, 5-16 mm long, 1-8 mm wide, middle phyllaries usually conspicuously nerved, inner phyllaries 5-9 mm long, 1-4.5 mm wide. Rays (5-) 8-13, lamina 7.5-15 (-20) mm long, 2.5-7 mm wide. Disc florets 35-100, 5-8 mm long. Disc achenes with body 3.5-5 mm long, 0.9-1.5 mm wide, awns (2-) 3-5 mm long, not exserted or exserted up to 5 mm from ripe heads. Ray achenes with body 3.0-4.2 mm long, 1.0-1.5 mm wide. Chromosome number, from meiotic material, n=11. Wet or dry thickets, roadsides, slopes, wood edges, often in secondary communities; in lowland perennial and subperennial, tropical deciduous, pine-oak, and cloud forest. Oaxaca and Veracruz to Panama, rarely in northern Venezuela, at altitudes from 0-1800 m. Blooming year round.

Selected Specimens:

BELIZE: El Cayo, 12 Feb 1931, Bartlett 11424 (GH,LL,MICH ,US). El Cayo District, Augustine, Mountain Pine Ridge, 16°34'N, 88°54'W, alt. 1500 ft, 27 Oct 1959, Hunt 180 (BM,US). Hope Creek, alt. 50 ft, 10 Dec 1931, Schipp 857 (AA,F,GH,K,MICH,MO,NY,UC). COSTA RICA: ALAJUELA: La Balsa de San Ramon, alt. 1075 m, 17 Oct 1925, Brenes 4535 (F,NY). Be-

tween San Josecito & La Garita, alt. 800m, 18 Aug 1963, Jimenez M. 1077 (F,LL). Between Los Chiles & Venecia, alt. 200 m, 20 Feb 1966, Molina et al. 17560 (F,S). Turrialba, alt. 600m, 5 Nov 1961, Cuatrecasas 26517 (F,GH,RSA,US(2)). NW slope of Cerro Carpintera above La Union de Tres Rios, alt. 1320-1500 m, 25 Oct 1929, Dodge & Thomas 4831 (GH). Around Turrialba, alt. 200 m, 6 May 1891, Pittier 4138 (BR,G,GH,US). Around Carpintera, alt. 1700 m, 2 Aug 1891, Pittier 4359 (BR(2),G,GH, US). San Rafael de Cartago, alt. 1500 m, 28 Aug 1892, Pittier 7111 (BR(2), GH). Las Vueltas, Tucurrique, alt. 635 m, Dec 1898, Tonduz 12911 (G,LL,M MICH,P,US). Mts along Rio Pejibaye, near Atirro, alt. 650 m, 5 May 1956, Williams 19591 (F). Nicoya, Tonduz 13617 (G,GH,LL,MICH,P ,W). HEREDIA: El Muelle, bord du Sarapiqui, Feb 1893, Biolley 7428 (BM,BR(2), GH,P,US). Along Rio Virilla, ca. 10 km S of Heredia, alt. 1000 m, 25 Mar 1949, Williams 16058 (F). LIMÓN: Port Limón, at sea level, 1 May 1903, Cook & Doyle 437 (US). Guapiles, alt. 300 m, 14 Apr 1941, Leon 582 (F). La Emilia, Llanuras de Santa Clara, alt. 250 m, Apr 1896, J. D. Smith 6618 (G,M,US). PUNTARENAS: Boruca, Nov 1891, Pittier 4522 (BM,BR,G,GH(2), M,US). Rio Ceibo, at Buenos Aires, Jan 1892, Pittier 4912 (BR(2),G,GH,M) SAN JOSÉ: Vicinity of El General, alt. 880 m, Dec 1935, Skutch 2219 (GH, LL,MO,NY,S,US). Vicinity of San José, alt. ca. 1150 m, Feb 1924, Standley 34801 (US). Rio Tiliri near San José, 3 Dec 1890, Tonduz 3134 (BR,G,GH,US). EL SALVADOR: AHUACHAPÁN: Vicinity of Ahuachapán, alt. 800-1000 m, 9-27 Jan 1922, Standley 20292 (GH,NY,US). LA LIBERTAD: Los Chorros, 31 Oct 1963,Porter 1227 (GH,MEXU). LA UNIÓN: Vicinity of La Unión, alt. 150 m or less, 13-21 Feb 1922, Standley 20681 (GH,MO,NY,US). SAN SALVADOR: Along rd from San Martín to Laguna de Ilopango, 1 Apr 1922, Standley 22521 (GH,NY,US). SAN VICENTE: Vicinity of San Vicente, alt. 400-500 m, 7-14 Feb 1947, Standley & Padilla B. 3670 (F,GH). SANTA ANA:

Hacienda San Miguel near Metapan, chiefly between Rio San Miguel and summit of Cerro El Pinal, alt. 600-1380 m, 22 Feb 1946, Carlson 793 (F,UC). GUATEMALA: ALTA VERAPAZ: Valley along National rt 7W, ca. 11 mi W of San Cristobal Verapaz, 13 July 1960, King 3347 (DS,MICH,NY,TEX,UC, US). CHIMALTENENGO: Along rd from Chimaltenango to San Martín Jilotepeque, alt. 1500-1900 m, 25 Nov 1938, Standley 57974 (GH,LL,NY). CHIQUIMULA: Divide on the railway above El Rincón, alt. 870 m, 17 Oct 1940, Standley 74657 (F,GH). ESCUINTLA: Aguilar 1734 (F). GUATEMALA: Near Amatitlán, alt. ca. 1170 m, 29 Dec 1938, Standley 61265 (F,US). Near Guatemala, alt. 1400 m, July 1921, Tondus 610 (GH,NY,US). HUEHUETENANGO: Near El Reposo, ca. 8 km from Mexican frontier, alt. 900-1000 m, 14-18 Dec 1972, Williams et al. 41239 (F,NY). IZABAL: Los Amates, alt. 160 ft, 6 Feb 1905, Deam 323 (GH,MICH,NY,US). JALAPA: Vicinity of Jalapa, alt. ca. 1360 m, 7-18 Nov 1940 , Standley 76753 (F). JUTIAPA: Vicinity Jutiapa, alt. ca. 850 m, 24 Oct-5 Nov 1940, Standley 74986 (F). PETÉN: La Libertad & vicinity, 25 Nov 1934, Aguilar H. 426 (GH,LL(2), MICH,MO,NY). Km 48 on Remate Rd, Parque Nacional de Tikal, 2 Sept 1969, Tún Ortíz 325 (F,NY). QUEZALTENANGO: Colomba, alt. 2800 ft, 21 Dec 1934, Skutch 1992 (AA,LL,NY,US). QUICHE: Finca Chaila, alt. 1100 ft, 29 Nov 1934, Skutch 1784 (AA,BM,F,LL,NY,US). RETALHULEU: Vicinity of Retalhuleu, alt. 240 m, 17 Feb-1 Mar 1941, Standley 88617 (F,MO). SACATEPÉQUEZ: Slopes of Volcán de Agua, S of Santa María de Jesús, alt. 1800-2100 m, 10 Dec 1938, Standley 59343 (F,NY). SANTA ROSA: Cuajiniquilapa, alt. 800 m, Sept 1892, Heyde & Lux 3786 (BR,G,GH,M,US). Cerro Gordo, alt. 3500 ft, Dec 1892, Heyde & Lux 4196 (F,G,GH,NY,US). Region of La Sepultura, W of Chiquimulilla, alt. 220 m, 5 Dec 1940, Standley 79399 (F,S). ZACAPA: Along Rio Lima, Sierra de las Minas, between Rio Hondo & summit of mountain at Finca Alejandria, alt. 1500-1700 m, 11 Oct 1939, Steyer-

mark 29619 (F). HONDURAS: CHOLUTECA: Near Bella Vista, alt. 1200 m, 17 Nov 1946, Williams & Molina 10874 (F,GH,MEXU,US). COMAYAGUA: Near Siguatepeque, alt. 1850 m, 7 Mar 1936, Yuncker et al. 5601 (F,G,GH,MICH,NY,S, US). COPÁN: Between Hacienda Grande and Ostuman on way to Guatemala border, alt. 700 m, 22 Nov 1969, Molina & Molina 24744 (F,NY,US). CORTES: Santa Cruz de Yojoa, alt. 2000 ft, 28 Oct 1933, Edwards P-707 (F,GH,MO, NY,US). EL PARAÍSO: Rio Teupasenti near Teupasenti, alt. 600 m, 26-27 Apr 1963, Molina 11904 (F,NY,US). INTIBUCA: Yamaranguila, alt. 1800 m, 6 Apr 1956, Molina 6275a (F,GH,US). LEMPIRA: Pinares de la Presa de Gracias, alt. 1300 m, 15 Apr 1956, Molina 6554 (F). MORAZÁN: Along Rio Yeguare, near Villa Nueva, alt. 850 m, 13 June 1947, Molina 82 (F,GH, MEXU,MO,UC,US). Along Santa Clara Creek, Zamorano Valley, alt. 850 m, 9 Oct 1946, Williams & Molina 10548 (AA,F,LL,MICH,MO,UC). Above Jicarito, alt. 1000 m, 18 Oct 1949, Williams & Molina 16965 (F,GH,MO). OCOTEPEQUE: El Moral on Cordillera Merendón, alt. 1600 m, 27 Aug 1968, Molina 22266 (DS,F,G,NY,US). OLANCHO: Near Rio Juticalpa, 6 km from Juticalpa, alt. 430 m, 18 Nov 1963, Molina 13231 (F, LL,NY). SANTA BÁRBARA: Tiquitapa near Quimistan, 29 July-10 Aug 1951, Howard et al. 562 (B,GH,NY). TEGUCIGALPA: Mont. de la Flor. alt. 3200 ft, Dec 1937, Hagen & Hagen 1155 (F,US). MEXICO: CAMPECHE: Campo Experimental Forestal "El Tormento", km 5 on Escárcega-Candelaria rd, 22 Dec 1965, Chavelas P. et al. ES-1072 (MEXU). CHIAPAS: 34 km S of Pichucalco & 7 km S of Solosuchiapa, alt. 200 m, 6 Oct 1974, Becker & Cronquist 39 (NY). 11 km SW of Cintalpa, alt. 600 m, 7 Oct 1974, Becker & Cronquist 40 (NY). 12 mi E of La Trinitaria along rd to Lagos de Monte Bello, mun. La Trinitaria, alt. 4800 ft, 6 Nov 1965, Breedlove 14127 (DS,ENCB,F, LL,MICH,NY). Near Microwave station La Mina, 12 km S of Mex 190 near Riso de Oro, mun. Cintalpa, alt. 1000 m,

Oct. 16, 1971, Breedlove & Thorne 20546 (DS). 18-20 km N of Ocozocoautla along rd to Mal Paso, mun. Ocozocoautla de Espinosa, alt. 800 m, 4 Nov 1971, Breedlove & Smith 21899 (DS,NY). SW of Solosuchiapa, alt. 285 m, July 1965, Chavelas et al. 742 (ENCB,MEXU(2)). Pan-Am hwy 14 km W of Ocozocoautla, alt. ca. 2200 ft, 16 Oct 1962, Cronquist 9679 (GH,MEXU,MICH,MO,NY,TEX,US). 14 mi NE of Arriaga, alt. 2500 ft, 31 Oct 1965, Cronquist & Sousa 10458 (DS,ENCB,F,GH,MEXU,MICH,MSC,NY,TEX,US) El Sumidero, overlooking canyon of Rio Mescalapa, 14 rd-mi N of Tuxtla Gutierrez, alt. ca. 4500 ft, 5 Nov 1965, Cronquist & Sousa 10494 (DS, ENCB,GH,MEXU,MICH,MSC,NY,TEX,US). Mt. Ovando, near Escuintla, alt. 800 m, 1-16 July 1940, Matuda 4200 (F,GH(2),LL,MEXU(2),MICH,NY,US). Finca La Esperanza, near San Juan El Bosque, SE of Simojobel, 27 Nov 1949, Miranda 5787 (MEXU). Cerro del Boqueron, Sept 1913, Purpus 6661 (BM,F, GH(photo:ENCB),MO,NY); Purpus 6677 (UC). Tih Ha', paraje of Mahbenchauk, mun. Tenejapa, alt. 3200 ft, Jan-Mar 1964, Shilom Ton 1392 (DS,ENCB,MICH, MSC,NY). OAXACA: Along Mex. 190, 9 mi SE of Tapanatepec, alt. 1100 ft, 20 Oct 1965, Breedlove & Raven 13701 (DS,ENCB,LL,MICH,NY). Presa M. Aleman, mun. Tuxtepec, 25 Oct 1964, Gonsáles Quintero 1853 (ENCB(2)). Chiltepec and vicinity, alt. ca. 20 m, July 1940-Feb 1941, Martínez-Calderón 286 (GH,LL,MEXU,UC,US); Martínez-Calderón 435 GH,LL,MEXU,UC,US). Yaveo, trail to Rio Yaveo to north, alt. 460 m, 17 Mar 1938, Mexia 9169 (B,F,GH,LL,NY,UC,US). Rio Tonto, Temazcal, 2 Dec 1954, Paray 1451 (ENCB). VERACRUZ: Orisaba, Botteri 800 (F, in part). Orisaba, Jan 1855, Botteri 1096 (BM,G,K(herb. Hook.),P). Fortin, alt. 2800ft, 30 July 1935, Fisher 35294 (F,MO,NY,US). La Isla, near Cordoba, alt. 940 m, 25 Sept 1882, Kerber 59 (BM,C,G(3),K,M,P(3),US,W). Mirador, Jan 1843, Liebmann 377 (C,M,P,US). Mun. Gabino Barreda, alt. 15 m, 24 Jan 1968, Martínez-Calderón 1614 (AA,CAS,ENCB,F,MEXU(2),MICH,MO,US). Cerro del Borrigo,

near Orizaba, alt. 5000 ft, 21 Jan 1895, Pringle 5911 (GH,MEXU(2)). Vaxin, at foot of Volcan San Martin, 30 Jan 1965, Sousa 2230 (MEXU). Mata Obscura, mun. Tututla, alt. 900 m, 9 Dec 1970, Ventura A. 2957 (DS,ENCB,F,MICH,NY). Rio Seco near Cordoba, 31 Jan 1926, Woronow 3032 (US). YUCATAN: 8 mi SW of Izamal, Nov 1895, Gaumer 960 (BR,DS,F, GH(2),MICH,NY,PH,S,US); Gaumer 962 (C,CAS,F,GH,S,W). Chichankanab, Gaumer 2344 (F,GH). Calotmul, Gaumer 2350 (B,F,POM). Xnocac, Dec 1916, Gaumer et al. 23499 (BM,C,F,G,GH,MO,NY,S,US). Chichen Itza, 10 June 1932, Steere 1095 (GH,LL,MICH(2),US). Peto, 26-27 July 1932, Steere 2229 (MICH). NICARAGUA: CARAZO: Vicinity of Jinotepe, alt. ca. 600 m, 20 May 1947, Standley 8570 (F). ESTELI: Along Estelí River 5 km from Esteli, alt. 900 m, 3 Nov 1968, Molina R. 23026 (F,MO,NY,US). JINOTEGA: Vicinity of Jinotega, alt. 1030-1300 m, 19 June-9 July 1947, Standley 10056 (F). MANAGUA: Sierra de Managua, alt. 600-900 m, ca. 1930-40, Garnier 17 (F). Sierra de Managua, Sept 1938, Garnier A.1356 (AA,F). MATAGALPA: Finca Santa Maria de Ostuma, Cordillera Central de Nicaragua, alt. 1400 m, 18 Jan 1965, Williams et al. 27981 (F). ZELAYA: El Recreo, 22 Nov 1948, Long 225 (F). Zona del Tio Samuel, Rio Grande, alt. 0.15 m, 22 Apr 1949, Molina R. 2310 (F). PANAMA: CHIRIQUI: Vicinity of San Felix, alt. 0-120 m, Jan 1912, Pittier 5455 (GH,NY,US). COCLÉ: Between Las Margaritas and El Valle, 15 July, 8 Aug 1938, Woodson et al. 1748 (AA,NY,US). PANAMA: La Campana: Cerro Campana, alt. 2400-2700 ft, 9 July 1960, Ehinger 372 (MEXU,NY,US). VERAGUAS: W of Sona, alt. ca. 500 m, 24 Nov 1938, Allen 1038 (MICH(2),US). VENEZUELA: CARABOBO: Carabobo, alt. 500 m, 22 Dec 1938, Alston 5608 (BM,F,GH,NY,P,S,US).

1b. Lasianthaea fruticosa (L.) K. Becker var. michoacana (Blake) K. Becker, comb. nov. Zexmenia michoacana Blake, Contr. U. S. Nat. Herb.

22:631, 1924. TYPE: MEXICO: MICHOACAN: Loma Santa Maria, alt. 1950 m, 28 Aug 1910, Arsène 5829 (HOLOTYPE: US; ISOTYPES: AA,B,F,G,MO).

Shrubs, often single-stemmed and with leaves aggregated towards branch-tips, 0.5–4 m high; young branches finely strigillose, strigose, or occasionally hirsute. Leaves with petioles (1–) 2–15 mm long; blades usually firm and rugose, sometimes chartaceous, lance-ovate to ovate, or occasionally lanceolate, 3–14 cm long, 1.3–6 cm wide, usually hispidulous, sometimes densely appressed-hispid below, especially along veins, triplinerved or rarely subpenninerved. Inflorescence 1- or 3- (–5)-headed, terminal. Peduncles 0.5–1.5 (–3.5) cm long; heads (1.5–) 2–3 cm wide across extended rays. Involucre hemispherical to broadly campanulate, 0.6–1.1 (–1.4) cm high, 0.5–1.6 cm wide, phyllaries usually subequal, rarely weakly graduated in 2–3 series. Outer phyllaries firm, ovate, ovate-oblong, or lanceolate, apex sometimes thickened, 3.5–8 mm long, 1.5–5 mm wide, inner phyllaries 6–10 mm long, 1.5–4 mm wide. Rays 8–13, lamina 7–9.5 mm long, 3–5 mm wide. Disc florets 17–30 (–50), 5.5–8 mm long. Disc achenes with body 2.5–4.7 mm long, 1.2–2.1 mm wide, awns 1.5–5.5 mm long, usually not exserted from ripe heads. Ray achenes with body 2.5–4.0 mm long, 1.3–2.3 mm wide. Chromosome number, from meiotic material, n=11. Roadcuts, talus slopes, and gulley banks, often eroded; in oak, pine and pine-oak forest. Mostly in the Transverse Volanic Belt of south-central Mexico, at altitudes from 1000–2500 m. Blooming mostly August to October, through to January.

Selected specimens:

MEXICO: GUERRERO: Pilas, Mina, alt. 1600 m, 28 Sept 1937, Hinton et al. 10742 (ENCB,GH,K(2),PH,TEX(2),US,W). JALISCO: 8.5 mi from summit of Volcán Tequila on rd from Tequila, alt. 1720 m, 11 Aug 1968, Anderson

& Anderson 5151 (ENCB,MICH). 1 km S of Puerto Los Mazos & 17 km SW Autlan, alt. 1250 m, 16 Sept 1974, Becker & Cronquist 20 (NY). NE of Tonila, alt. 1900-1950 m, 17 Sept 1974, Becker & Cronquist 23 (NY). Arroyo de las Cruces, mun. Talpa, alt. 1650 m, 26 Aug 1971, González Tamayo 290 (ENCB, MICH). South- & west-facing slopes, 11-12 mi SW of Autlan, about 2 mi below the pass, alt. ca. 1000 m, 21 Nov 1959, McVaugh & Koelz 872 (ENCB, MICH). Above Amacueca, rd to Tapalpa, alt. 2100-2500 m, 2 Nov 1960, McVaugh 20608 (ENCB,LL,MICH). Barrance of Guadalajara, alt. 4500 ft, 19 Oct 1903, Pringle 11617 (F,GH,K,MICH,US). Volcán Tequila, along rd to microwave station, ca. 20°47'N, 103°50'W, alt. 5800 ft, 25 Oct 1970, Webster & Breckon 15962(MICH). STATE OF MEXICO:5 km S Temascaltepec, hwy 130, 18°57'N, 100°05'W, alt. 1900 m, 4 Sept 1965, Roe et al. 1793 (ENCB, MICH,UC). MICHOACAN: 7.5 km SW of Jacona, alt. 1800 m, 20 Sept 1974, Becker & Cronquist 26 (NY). NE outskirts of Patzcuaro, alt. 2000 m, 20 Sept 1974, Becker & Cronquist 27 (NY). Lower N-facing slopes of Cerro Santa Maria, 8-10 km SW of Jiquilpan & 5 km NE of Quitupan, Jalisco, alt. ca. 2000 m, 5-7 Aug 1959, Feddema 64 (CAS,ENCB,MICH,TEX). NW foothills of Cerro Tancitaro, 13-14 km S of Periban de Ramos, alt. 1650-1700 m, 29 Nov 1970, McVaugh 24788 (LL,MICH,NY). Patzcuaro, 2 Nov 1895, Seler 1200 (GH(2),K,MEXU,NY). MORELOS: Valle del Tepeite, 16 Oct 1937, Lyonnet & Elcoro 1772 (US). Sierra de Ocuila, alt. 1900 m, 18 Sept 1941, Lyonnet 3334 (US).

1c. Lasianthaea fruticosa (L.) K. Becker var. fasciculata (DC.) K. Becker, comb. nov. Lipochaeta fasciculata DC., Prodr. 5:610, 1836. Zexmenia fasciculata (DC.) Sch. Bip., in Seem. Bot. Voy. Herald 306, 1856, not Z. fasciculata Coult.(= Perymenium grande Hemsl.). TYPE: MEXICO: TAMAULIPAS (presumably): Sacahuales de Tula a Sa Barbara,

Nov 1830, Berlandier 2134 (=717)(HOLOTYPE: G; Photo: US; ISOTYPES: BM,G,GH,K(herb. Hook.)(2),MO,P(2)).

Shrubs or small trees with slender, spreading branches, 1.5-6 m high; young branches glabrate, hispidulous, or hirsute. Leaves with petioles 0.5-1.5 (-2) cm long; blades usually thin, usually narrowly lance-ovate, varying to lanceolate and narrowly ovate, (4-) 5.5-13 (-16.5) cm long, 1.5-5 (-6.2) cm wide, acute and often long-acuminate, cuneate at base, hispid and hispidulous below, especially along veins, sometimes sparsely so, triplinerved. Inflorescence (3-) 6-15 -headed. Peduncles (0-) 1.5-5.5 cm long (terminal head often sessile), slender; heads 1.5-2 cm wide across extended rays. Involucre broadly campanulate to hemispherical, 0.5-0.7 (-0.9) cm high, (0.4-) 0.5-0.7 (-0.8) cm wide, phyllaries usually subequal, occasionally weakly graduated in 2-3 series. Outer phyllaries often spreading above, deltoid-ovate to oblong, 3.5-7 (-9) mm long, 2-3.5 mm wide, nerves conspicuous, inner phyllaries 5-6 (-7) mm long, 1-5 mm wide wide. Rays (4-) 8-11, lamina 5.5-6.5 (-9) mm long, 2.4-4.5 mm wide. Disc florets 13-34, 5.0-6.4 (-7.3) mm long. Disc achenes with body 2.5-3.7 mm long, 1.1-1.5 mm wide, awns 2-3.5 (-4) mm long, usually exserted (1-) 2-3 (-4) mm from ripe heads. Ray achenes with body (2.0-) 2.4-3.5 mm long, 1.1-1.7 mm wide. Chromosome number, from meiotic material, n=11. Woods, clearings, and ravines; in oak, pine, and cloud forest. Mostly in the southern Sierra Madre Occidental and in the Sierra Madre Oriental of Mexico, at altitudes from 700-2200 m. Blooming May - December.

Selected specimens:

MEXICO: DURANGO: Ca. 90 km SW of El Salto, alt. ca. 2050 m, 7 Oct 1970, Cronquist & Fay 10788 (NY). HIDALGO: Mex. hwy 85, 23 mi by rd SW of

San Luis Potosi - Hidalgo border, alt. 1540 m, 7 July 1968, Anderson & Anderson 4663 (ENCB,MICH,NY). 9 mi NE of Jacala, alt. 4500 ft, 6 Sept 1975, Becker & Olsen 52 (NY). Ca. 16 km NE of Jacala, alt. 1600 m, 22 Oct 1974, Cronquist 11270 (NY). Xochicoatlan, mun. Molango, 13 Sept 1964, González Quintero 1562 (DS,ENCB,MICH,MSC). East slope of divide, just above Palo Semita, 25 mi NE of Jacala, alt. ca. 4800 ft, 6-16 Oct 1962, Weber & Charette 11923 (CAS,GH,MICH,UC). JALISCO: 7 km SE of Tequila, alt. 1700 m, 14 Sept 1974, Becker & Cronquist 13 (NY). Ca. 50 km SE of Guadalajara & 18 km W of Ocotlan, alt. 1600 m, 19 Sept 1974, Becker & Cronquist 24 (NY). Mountains above Etzatlan, 2 Oct 1903, Pringle 11560 (distributed as Perymenium pringlei Rob. & Greenm.)(C,CAS,F,GH,K,LL,MICH, MO,MSC,US). About 10 rd-mi E of Jalcocotán, on rd to Tepic, alt. 1050-1100 m, 4 Oct 1952, McVaugh 13336 (MEXU,MICH,US). PUEBLA: Near Necaxa, ca. 95 km WSW of Poza Rica, alt. 1200 m, 19 Oct 1974, Cronquist 11256 (NY). Near Huauchinango, Mt. Tepexinala, alt. 1300 m, 2 Sept 1932, Fröderström & Hultén 739 (S). QUERETARO: 11 mi W of Ahuacatlan, San Luis Potosi, alt. 1900 m, 5 Sept 1975, Becker & Olsen 51 (NY). 23.5 mi SW of Xilitla, rd from Jalpan, ca. 21°15'N, 99°10'W, alt. ca. 4500 ft, 9 Nov 1970, Webster & Breckon 16347 (MICH). SAN LUIS POTOSI: 55 mi W of Ciudad Valles, alt. 4000 ft, 4 Sept 1975, Becker & Olsen 50 (NY). En route from San Luis Potosi to Tampico, Dec 1878 to Feb 1879, Palmer 1100 (BM,GH,K, NY,PH,US). Barranca of Las Canoas, 23 June 1891, Pringle 3753 BM,BR,CAS, F,G,GH,K,LL,M,MEXU(2),MICH,MO,MSC,NY(2),P,PH(2),S,UC(2)). 39 km (by rd) NE of Ciudad del Maiz on Mex 80 at km 223, 22°30'N, 99°25'W, alt. ca. 1200 m, 1 Oct 1965, Roe & Roe 2302 (ENCB,MICH,UC). S of San Nicolas de los Montes, mun. Tamasopo, alt. 800 m, 29 May 1959, Rzedowski 10695 (ENCB,MSC). 5 km W of Ahuacatlan, mun. Xilitla, alt. 1450 m, 16 Sept 1970, Rzedowski 27724 (ENCB). SINALOA: Sierra Surutato, below Buenas Juntas, 5

mi NW of Los Ornos along rd to Mocorito, mun. Sinaloa y Vela, alt. 5800 ft, 30 Sept 1970, Breedlove & Thorne 18223 (CAS,MICH,RSA). Quebrado de Mansana, Sierra Surutato, alt. 4000-5000 ft, 10-14 Sept 1941, Gentry 6464 (CAS,GH,MICH,MO,NY,PH). Santa Lucia, mun. Concordia, alt. 1000 m, Sept 1922, Ortega 755 (MEXU).

1d. Lasianthaea fruticosa (L.) K. Becker var. occidentalis K. Becker, var. nov. TYPE: MEXICO: CHIHUAHUA: Near Seven Star Mine, alt. 8000 ft. 29 Aug 1899, Townsend & Barber 364 (HOLOTYPE: GH; ISOTYPES: F, G(2),K,MEXU,MICH,MO,NY,P(2),POM,UC,US).

Small shrubs 0.5-2 m high; young branches usually spreading-hispidulous to hirsute. Leaves with petioles 2-12 mm long; blades usually firm, lance-ovate to ovate, or occasionally lanceolate, 4-12 cm long, 1-5.5 (-6) cm wide, hispid and hispidulous below, especially along veins, venation conspicuous below, triplinerved. Inflorescence 3-13 -headed. Peduncles (0.2-) 0.8-5.0 cm long, slender; heads 1.5-2.5 cm wide across extended rays. Involucre broadly campanulate, 0.6-1.0 cm high, 0.6-1.1 cm wide, phyllaries usually subequal, occasionally graduated in 2-3 series. Outer phyllaries conspicuously reticulate-veined and sometimes spreading above, ovate-oblong or lance-oblong in outline, usually narrowed near middle, 5-7 mm long, 2-3 mm wide, inner phyllaries 6-7.5 mm long, 1.5-3 mm wide. Rays 7 or 8, lamina 7.5-9.5 mm long, 4.5-5 mm wide. Disc florets 17-30, 6-7.5 mm long. Disc achenes with body 3.0-3.7 mm long, 0.9-1.8 mm wide, awns 2.5-4 mm long, usually not exserted or exserted to 1 mm from ripe heads. Ray achenes with body 1.5-3.3 mm long,

1.8–2.0 mm wide. Hills and canyons in pine-oak forest. Northern Sierra Madre Occidental in Mexico, at altitudes from 1100–2000 m. Blooming August to October (–December).

Specimens examined:

MEXICO: CHIHUAHUA: Sierra Charuco, Arroyo Hondo, 12 Sept 1935, Gentry 1797 (in part) (AA). Guasaremos, Rio Mayo, 26 Aug 1936, Gentry 2469 (F,GH,K,MEXU,MO,S,UC,US(2)). Guayanopa Canyon, alt. 3600 ft, 24 Sept 1903, M. E. Jones s.n. (POM(2)). Maguarichic, SW of San Juancito, ca. 27°52'N, 108°W, alt. 1660 m, 7 Aug 1954, Knobloch 1131 (MICH,MSC); Knobloch 1265 (MICH,MSC). Rio Aros, 23 July 1937, LeSueur 1479 (F,TEX). SINALOA: Cerro de la Prieta, Choix, alt. 1100 m, Dec 1922, Ortega 665 (MEXU). SONORA: Sierra des Papas, near Chihuahua border, 21 October 1933, Gentry 621 (DS,MICH). El Rio Bonito about La Nopalera, mun. Nacore Chico, 6 Oct 1939, Muller 3686 (GH). Puerto de Huepari, NW of Aribabi, alt. 4550 ft, 7 Sept 1939, White 2781 (GH,MICH).

1e. Lasianthaea fruticosa (L.) K. Becker var. alamosana K. Becker, nom. nov. Zexmenia fruticosa Rose, Contr. U. S. Nat. Herb. 1:103, 1891. TYPE: MEXICO: SONORA: Common along streams and on mountain side about Alamos, 16–30 Sept 1890, Palmer 645 (HOLOTYPE: US; ISOTYPES: BR,C,CAS,F,G,GH(photo: ENCB),K,MEXU,NY,S, UC(2),US(2)).

Shrubs with long, slender, often brittle branches, 1–2 m high; young branches strigose to glabrate. Leaves with petioles 2–4 mm long; blades thin, usually lance-ovate, varying to lanceolate and ovate, 3–10 cm long, (0.8–) 1–4 (–4.5) cm wide, hispid and hispidulous below, triplinerved. Inflorescence 1- or 3-headed. Peduncles 1.5–3.5 cm long,

slender; heads 1.5 cm wide across extended rays. Involucre broadly campanulate to hemispherical, 0.6-0.8 cm high, 0.7-1.2 cm wide, phyllaries equal or weakly graduated in 2-3 series. Outer phyllaries lance-oblong in outline, 4.5-5.5 mm long, 2-4.5 mm wide, inner phyllaries 5-6.5 mm long, 2-3 mm wide. Rays 8, lamina 7.5-12 mm long, 4-5.5 mm wide. Disc florets 17-20, 4.5-6 mm long. Disc achenes with body 3-5 mm long, 0.7-1.3 mm wide, often brown-gland-dotted, awns 3.5-5.5 mm long, usually exserted 2-3 mm from ripe heads, divergent. Ray achenes with body 2.5-4 mm long, 1.1-1.7 mm wide. Wooded mountainsides and canyons in tropical deciduous and thorn forest. Mostly near Alamos, Sonora, and adjacent areas in the Sierra Madre Occidental in Mexico, at altitudes from 500-700 m. Blooming August to October.

Specimens examined:

MEXICO: SONORA: 4 km E of Alamos, alt. 500 m, 8 Sept 1974, Becker & Cronquist 3 (NY). W of Alamos, 12 Dec 1939, Drouet & Richards 3962 (DS,F). Canyon Sapopa, Rio Mayo, 28 Aug 1935, Gentry 1639 (F,GH,K, MEXU,MO,NY,TEX,UC,US). Along Arroyo Cuchujaqui at ford on dirt rd from Alamos to Guirocoba, 8 Sept 1971, Keil & Canne 8678 (OS). 23 mi S of Divisadero, alt. 2000 ft, 26 Sept 1934, Wiggins 7484 (DS,TEX,US).

1f. Lasianthaea fruticosa (L.) K. Becker var. aggregata (Blake) K. Becker, comb. nov. Zexmenia aggregata Blake, Contr. U. S. Nat. Herb. 22:634, 1924. TYPE: MEXICO: OAXACA: Santa Catarina, 14 July 1910, Rusby 86 (HOLOTYPE: US; ISOTYPE: NY).

Shrubs, slender stemmed, 0.5-1.5 (-2) m high, leaves aggregated towards branch tips; young branches loosely hirsute. Leaves with petioles (2-) 3-7 mm long; blades thin, ovate to lance-ovate, (1.2-) 3-7 cm

long, (0.4-) 1.5-3.5 cm wide, softly and densely pilose below, triplinerved. Inflorescence (1-) 3-9 -headed. Peduncles (0.1-) 0.2-0.8 cm long, slender; heads to 1.5 cm wide across extended rays. Involucre cylindro-campanulate to occasionally campanulate, (0.6-) 0.7-0.8 (-1.1) cm high, (0.3-) 0.4-0.6 (-0.8) cm wide, phyllaries equal or slightly graduated. Outer phyllaries lanceolate to narrowly lance-ovate, 6-8 (-11) mm long, 1.5-1.7 (-3.5) mm wide, sometimes spreading above, inner phyllaries 6.5-8 mm long, 1.7-3.7 (-4.0) mm wide. Rays on well-developed heads 5, lamina 5-8 mm long, 5-6 mm wide. Disc florets 9-13 (-19), 5.9-6.8 mm long. Disc achenes with body 4.7-5 (-6) mm long, 0.9-1.2 mm wide, awns 4.7-5.5 mm long, exserted several mm from ripe heads. Ray achenes 4.0-4.5 mm long, 1.0-1.5 mm wide. Arid slopes in thorn scrub. Northwestern Oaxaca, at ca. 1900 m altitude. Blooming July to October.

Specimens examined:

MEXICO: OAXACA: 2 km SE Tutla, alt. 1900 m, 3 Oct 1974, Becker & Cronquist 37 (NY). On PanAm hwy 2 km SW (sic) of Tutla on rd to Tamalazupan, 20 Aug 1960, Iltis et al. 1334 (MEXU,MICH,TEX,US; complete sets of wood samples are deposited in the U. S. Forest Products Laboratory Madison, Wisc. (MADw),USw,MEXU (these not seen)).

Lasianthaea fruticosa is a wide-ranging species which has become differentiated into a number of more or less distinctive geographic varieties. Six varieties are recognized here, ranging from northern Mexico to Central America. All are united by their yellow rays, shrubby habit, and a general tendency to non-graduated or weakly graduated involucres. L. fruticosa appears to have a distinctive chromosome number (n=11, as

opposed to n=10 in the other shrubby Lasianthaeas), and, as discussed below, is rather isolated from the rest of the shrubs with respect to hybridization.

Lasianthaea fruticosa var. fruticosa is a basically Central American variety which reaches southeastern Mexico. It occurs throughout its range in a wide variety of habitats and altitudinal situations. It is variable in pubescence of stems, leaves, and phyllaries, in head size, and in peduncle length. Degree of pubescence seems to be related to altitude. Plants from lower elevations (down to sea level) are less pubescent, often almost glabrous, while plants from higher elevations (to pine and cloud forest) tend to be more pubescent, often densely so. Length of outer phyllaries is also variable, being usually equal or subequal to the inner, but varying to decidedly longer or shorter.

Several of the variants and extreme forms of L. fruticosa var. fruticosa have been given taxonomic recognition at the specific level in the past. Zexmenia monocephala represents an extreme in inflorescence reduction, occasionally seen throughout the range of the variety, especially in heads produced from upper leaf axils, where only one head, rather than 3-12, is produced. Zexmenia macropoda, with long, stout peduncles and large heads represents another extreme. Cronquist & Sousa 10458 exhibits variation in head size within one collection, ranging from that found in the type of Z. macropoda (Holway 109) down to heads one-third that size. Zexmenia villosa represents a particularly densely pubescent form well within the normal range of variation for the variety. Zexmenia elegans represents a relatively glabrous, narrow-leaved form with slightly imbricate involucres commonly found in southeastern Mexico but also occasionally in Central American populations. Collections which

are of particular interest with regard to intermediacy with varieties michoacana and fasciculata are cited below.

Lasianthaea fruticosa var. michoacana is a central Mexican variety common in the Transverse Volcanic Belt, characterized by its stout peduncles, outer phyllaries often with thickened green tips, usually rugose leaves, and its stout, several-stemmed shrubby habit. It exhibits a general variability which compares well with that of variety fruticosa but contrasts with the other Mexican varieties, discussed below, which are relatively less variable. This variability is exhibited in head size, quite variable, for example, in the type collection (Holway 3632; compare also McVaugh 24788 in this regard), peduncle length, leaf size, and leaf texture (the Lyonnnet collections, from the eastern edge of the range in Morelos, are interesting in this respect). Collections which are of particular interest with regard to intermediacy with varieties fruticosa and fasciculata are cited below.

Lasianthaea fruticosa var. fasciculata shows an interesting range disjunction, occurring at the southern end of the Sierra Madre Occidental - western end of the Transverse Volcanic Belt and also in the Sierra Madre Oriental (where it is common and is the sole shrubby Lasianthaea). It is characterized by its relatively small heads in ample inflorescences, the conspicuous venation of its outer and middle phyllaries, and in its treelike habit. Tending to prefer high-moist montane habitats, it exhibits a variability in pubescence density which tends to be related to altitude as in variety fruticosa. Plants from Sierra Surutato in central Sinaloa (near the northwestern limit of its range) have particularly large heads and leaves. Collections which are of interest with regard to intermediacy with varieties fruticosa and michoacana are cited

below.

Lasianthaea fruticosa var. occidentalis is restricted in range to the northern Sierra Madre Occidental. It is known from relatively few collections, perhaps reflecting the fact that the area is poorly collected. It is typically a small shrub with long internodes, conspicuously veined leaves, and outer phyllaries which are more or less ampliated above, green, and conspicuously reticulate-veiny. This variety has a relatively strong tendency towards graduation of phyllaries. Variety occidentalis comes closest, both geographically and morphologically, to varieties fasciculata and alamosana.

Lasianthaea fruticosa var. alamosana is restricted to a relatively small area of the northwestern Sierra Madre Occidental. It is characterized by its long-exserted awns, the small number of heads per inflorescence, its non-graduated involucre, its thin leaves, and its often glandular disc achenes, a series of characteristics and tendencies which separate it from var. occidentalis. Further collections from montane Sonora and Chihuahua would be of considerable interest.

Lasianthaea fruticosa var. aggregata is morphologically the most distinct and geographically the most isolated variety of L. fruticosa, as far as known occurring only in northwestern Oaxaca. It is characterized by its relatively narrow heads and low number of disc florets, and by its short peduncles. It comes closest morphologically to Puebian populations of var. fasciculata.

Lasianthaea fruticosa, as mentioned above, is relatively isolated from other members of the genus, and does not tend to hybridize with them (as the other shrubby species strongly tend to do when sympatric). The most convincing evidence that L. fruticosa does, on rare occasion,

hybridize with other members of the genus comes from Mt. Orizaba, where L. fruticosa var. fruticosa and L. ceanothifolia var. ceanothifolia are sympatric. While the two species maintain their distinctive morphological natures, plants are occasionally found which are intermediate between the two species in head size, involucral imbrication, and leaf size, shape, and pubescence, and show extremely poor pollen stainability (less than 10% vs. 95% for L. fruticosa var. fruticosa and L. ceanothifolia var. ceanothifolia at that locality (e.g. Botteri 800, sheet at F, material labeled "IV" and "V"). Further stulies at that location would be of considerable interest.

Selected intermediates between L. fruticosa var. fruticosa and var. michoacana. The following two collections, from within the range of var. fruticosa, exhibit inflorescence characters typical of var. michoacana: Miranda 5787 (Chiapas), Yuncker et al. 5601 (Honduras).

Selected intermediates between var. fruticosa and var. fasciculata: Breedlove & Thorne 20546 (Chiapas), Gonzalez-Quintero 1853, Martinez-Gonzales 286, Mexia 9169, Paray 1451 (Oaxaca), Fisher 35294, Kerber 59, Sousa 2230, Woronow 3032 (Veracruz).

Selected intermediates between var. michoacana and var. fasciculata: Anderson & Anderson 5151, Becker & Cronquist 13, Gonzalez T. 290, Webster & Breckon 15962 (Jalisco).

2. Lasianthaea macrocephala (Hook. & Arn.) K. Becker, comb. nov. Lipochaeta macrocephala Hook. & Arn., Bot. Beech. Voy. 436, 1841. Zexmenia macrocephala (Hook. & Arn.) Hemsl., Biol. Cent.-Am. Bot. 2:173, 1881. TYPE: MEXICO: GUERRERO: Acapulco, Sinclair s.n. (HOLOTYPE: K

(herb. Hook.); Photos: GH,MICH,US).

Zexmenia greggii A. Gray, Pl. Wright. 1:113, 1852. TYPE: MEXICO: "Between the city of Mexico and Mazatlan", 1848-49, Gregg 1003 (HOLOTYPE: GH; Photo: ENCB).

Zexmenia ghiesbreghtii A. Gray, Pl. Wright. 1:113, 1852. TYPE: MEXICO: Oct-Nov 1844, Ghiesbreght 385 (HOLOTYPE: GH; Photo: ENCB; ISOTYPES: P(2)).

Zinnia barrancae M. E. Jones, Contr. W. Bot. 18:78, 1933. TYPE: MEXICO: JALISCO: La Barranca, Guadalajara, 17 Nov 1930, M. E. Jones 27698 (HOLOTYPE: POM; Photo: UB; ISOTYPES: DS,MO,UC).

Zexmenia mexiae Blake, J. Wash. Acad. Sci. 18:27, 1928. TYPE: MEXICO: NAYARIT: Tuxpan, Palapar Redondo, alt. 20 m, 5 Nov 1926, Mexia 1049 (HOLOTYPE: US(USNH# 1317609); ISOTYPES: AA,BM,CAS,DS,F,G,GH,MICH,MO, NY,UC,US).

Zexmenia helianthoides (DC.) A. Gray var. jaliscana McVaugh, [illegible]. TYPE: MEXICO: JALISCO: In oak woodlands below the pass, 16-20 km SW of Autlan, alt. 1000-1500 m, 1 Nov 1962, Cronquist 9778 (HOLOTYPE: MICH; ISOTYPES: GH,MEXU NY,TEX,US).

Large, slenderly branched, often scrambling shrubs, or occasionally half-shrubs woody near base only, 1-4 m high; young branches densely to sparsely hispid to strigose. Leaves all opposite; petiole 0.2-1 cm long, densely strigose; blade usually firm, occasionally thin-textured, occasionally rugulose, lance-ovate to oblong, or occasionally narrowly

lance-elliptic, 4–20 cm long, 1–10 cm wide, usually acuminate, occasionally blunt at apex, subcordate or cordate, occasionally cuneate-rounded at base, scabrous and hispid above, softly pilose to rough and sparsely strigose below, margin denticulate-mucronulate to coarsely serrate, often slightly revolute, triplinerved. Inflorescence 1–3 -headed, terminal and from uppermost leaf axils, heads also occasionally produced in axils of small peduncular bracts. Peduncles (3–) 4–22 cm long, stout and usually fistulose, strigose, especially above; heads 3–4.5 (–7) cm wide across extended rays. Involucre hemispherical to broadly campanulate, (1–) 1.5–2.5 cm high, (1–) 1.5–3.5 (–4) cm wide, phyllaries graduated in 3–4 series. Outer phyllaries indurate below, more or less herbaceous above, deltoid-ovate, ovate-oblong, to orbicular, (5–) 7–16 mm long, 5–10 mm wide, blunt-mucronulate to acuminate, often erose, densely white-strigose and puberulent to appressed-hispid dorsally, middle phyllaries usually conspicuously nerved, sometimes 3-lobed at apex, inner phyllaries oblong or ovate to occasionally linear, 10–23 mm long, 3–9 (–11) mm wide, obtuse, greenish, ampliated and often spreading at apex. Rays 8–30, bright orange, orange-red, or orange-yellow, lamina 6.5–16 (–20) mm long, 3–5 mm wide, tube 3–5.5 (–6) mm long. Disc florets 80–170 or more, orange, 8–13.5 mm long, throat cylindric, 7.5–12 mm long, 0.8–1.5 mm wide, lobes 0.7–1.4 mm long. Anther thecae brown or yellow-brown, 2.5–4.5 mm long, appendage 0.6–1.2 mm long. Style branches 2.8–4.8 mm long, appendage 0.5–0.9 mm long. Pales 6–10.5 mm long, 0.6–1.1 mm wide as folded. Disc achenes cuneate, 2-awned, body 5–6.5 (–7) mm long, 1–1.7 (–2) mm wide, glabrate, or occasionally sparsely puberulent above, awns (2–) 3–6 mm long, pappus squamellae 0.3–2.3 mm long, free or connate and adnate to awns, or none. Ray achenes 3-awned, body 5–7 mm long, 1.3–2 mm wide, awns 1–5 mm long.

Receptacle flat. Chromosome number, from meiotic material, $n = 10$. Roadside thickets, openings, steep slopes, often in secondary communities; tropical deciduous (occasionally subdeciduous), oak, or occasionally pine forest, or in oak-palm savannah. Throughout southwestern and central Mexico in the southern Sierra Madre Occidental, Transverse Volcanic Belt, and Sierra Madre del Sur, from near sea level to 1800 m. Blooming year round.

Selected specimens:

MEXICO: COLIMA: Alzada, 4 Nov 1910, Orcutt 4679 (DS,F). 9 Jan - 6 Feb 1891, Palmer 1241 (BM,G,GH,K,MO,NY,UC,US). DURANGO: Paso de Sihuacori, alt. 1450 ft, 1 Dec 1970, Soule 2259 (MO). GUERRERO: Rd between Juchitango & Ometepec, alt. 300-1000 ft, 10 Feb 1895, Nelson 2312 (GH, US). Acapulco, Oct 1894 - Mar 1895, Palmer 491 (F,GH,MO(2),NY,UC,US). JALISCO: SE shore of Bahia de las Banderas, 9-12 km by road from Puerto Vallarta, alt. 2-30 m, 7 Mar 1970, Anderson & Anderson 6008 (ENCB,MICH, SD). 4 km SE of Tequila, alt. 1250 m, 14 Sept 1974, Becker & Cronquist 11 (NY). 1 km NE of Acatlan, alt. 1400 m, 15 Sept 1974, Becker & Cronquist 15 (NY). 11 mi N of Guadalajara, alt. 4500 ft, 11 Sept 1975, Becker & Olsen 60 (NY). Ca. 6 mi SW of Pihuamo and ca. 7 mi from border of Colima, alt. ca. 2200 ft, 29 Oct 1962, Cronquist 9763 (GH,MEXU,MICH,NY,TEX). Valley of Rio las Juntas, 10-13 km SE of El Tuito, alt. 250-330 m, 14-16 Dec 1970, McVaugh 25411 (ENCB,LL,MICH,MO,NY,PH ,US). Barranca near Guadalajara, 18 Nov 1889, Pringle 2742 (F,MEXU,MO,MSC,UC). Barranca of Guadalajara, alt. 5000 ft, 4 Dec 1902, Pringle 9999 (F,GH,K,MICH,MO,NY, US). Barranca of Guadalajara, alt. 5000 ft, Pringle 11618 (C,CAS,F,GH,MICH, MO,US). Barranca W of Atenquique, alt. 1000 m, 6 Feb 1966, Rzedowski 21894 (ENCB,MICH). MICHOACAN: Salitre, Coalcoman, alt. 1140 m, 12 Sept 1938, Hinton et al. 12172 (G,GH,LL,MICH,MO,NY,P ,UC,US). Coalcoman, Coal-

coman, alt. 1000 m, 2 Nov 1939, Hinton 12854 (F,GH,LL,MO,NY(2),US). W-facing slopes of Sierra Madre del Sur, ca. 32 km N of Playa Azul, alt. 1200-1500 ft, 25-31 Oct 1961, King & Soderstrom 4950 (LL,MEXU,MICH,NY UC,US). NAYARIT: 11 km by road E of Las Varas toward Compostela, alt. ca. 200 m, 28-29 Oct 1971, Dieterle 3946 (ENCB,LL,MICH). NE of Santa María del Oro, alt ca. 1000 m, 18-20 Aug 1959, Feddema 696 (CAS,ENCB, MICH,TEX). Along rt 15, ca. 2 mi N of Tepic, 11 Aug 1960, King 3689 (DS,MEXU,MICH,NY,TEX,UC,US). 5 mi N of Compostela, alt. 900 m, 13-14 Nov 1959, McVaugh & Koelz 641 (MICH). Road from Calixcillo to Compostela, alt. 1000 m, 13 Sept 1926, Mexia 587 (AA,CAS,DS,F,G,GH,MICH,MO, NY,UC,US). 25 km by rd S of Tepic, alt. ca. 3000 ft, Webster & Breckon 15762 (F,GH,MEXU,MICH,TEX). SINALOA: Capadero, Sierra Tacuichamona, alt. 3000 ft, 12 Feb 1940, Gentry 5566 (DS,MICH,NY,UC). 9 mi from La Noria, alt. 850 ft, 15 Oct 1925, Mexia 357 (C,CAS,UC). Picachos, mun. Rosario, Cerro de Azafran, 2 Nov 1917, Ortega 7135 (CAS,F,MEXU,US).

Lasianthaea macrocephala is closest to L. helianthoides and L. crocea (the three together may be informally termed the "large-headed assemblage"), and amply distinct from both. It is found in a wide range of habitats, and is abundant over much of Nayarit and Jalisco. From L. helianthoides, L. macrocephala is distinct in its long peduncles, its narrower, usually oblong leaves which are firm but not thick as in L. helianthoides, in ray color (in the field: orange or red-orange in macrocephala, orange-yellow in helianthoides), and in other characters. The two species are almost completely allopatric. From L. crocea (basically restricted to the Balsas Depression), macrocephala is distinguished by its graduated phyllaries, the outer much the shortest, by leaf and stem pubescence, and in ray color (upon drying: yellow in macrocephala, usually

orange-red or purple in crocea).

The type of L. macrocephala (Sinclair s.n.) is from coastal Guerrero (near Acapulco), and resembles other southern Pacific-coastal collections in its small leaves (ca. 5 cm long), dense pubescence of stems and leaf undersides, and its relatively short peduncles (3-5 cm long vs. 8 or more cm long as is more commonly the case in L. macrocephala). These populations gradually merge, morphologically, with inland populations through Michoacan and Colima.

Zinnia barrancae M. E. Jones (sic!) represents the typically robust, large-headed L. macrocephala found in the area around Guadalajara, Jalisco.

In the Tepic-Compostela area of Nayarit, plants of L. macrocephala are commonly found which are distinctive in habit, growing as half-shrubs or perennial herbs, rather than as ordinary shrubs. These plants also have shorter peduncles (4-5 cm vs. 9 cm), smaller heads (usually less than 1.5 cm wide), and more strongly oblong leaves than most L. macrocephala found in Nayarit and Jalisco. These plants are often found in the proximity of ordinary L. macrocephala. Intensive grazing pressure may be responsible, at least in part, for this peculiar form. A plant of this kind (Ghiesbreght 385, mounted on the same sheet as the type of Zexmenia ghiesbreghtii A. Gray, Ghiesbreght 385 (GH)), was designated as var. β of Z. ghiesbreghtii by Gray.

Zexmenia helianthoides var. jaliscana McVaugh is intermediate morphologically between L. macrocephala and L. helianthoides. These plants, from the area south of Autlan, Jalisco, are found near the edge of the ranges of both species. They usually exhibit leaf shape and texture similar to L. macrocephala, with heads and peduncle length resembling L. helianthoides. Much reduced pollen stainability is typically exhibited by

these plants (50-70% vs. 95%+ for putative parents), and they may well represent products of hybridization. Relevant collections include the following: JALISCO: Cronquist 9778 (the type of Zexmenia helianthoides (DC.) A. Gray var. jaliscana McVaugh), ca. 10 mi SW Autlan; Gentry 18318, 6-9 mi W Autlan; McVaugh 10197, ca. 2 mi N of La Resolana, ca. 20 mi SW of Autlan; McVaugh 11953, 18-rd mi SW of Autlan.

Several collections from coastal Nayarit and Jalisco exhibit morphological intermediacy between L. macrocephala and L. ceanothifolia var. verbenifolia, which are sympatric in those areas (Mexia 1049, the type of Zexmenia mexiae Blake; Gonzales T. 514; Paray 3414). These plants exhibit much reduced pollen stainability (37-77% vs. 95% for putative parents), and may well represent products of hybridization.

3. Lasianthaea helianthoides DC., Prodr. 5:608, 1836. Zexmenia helianthoides (DC.) A. Gray, Pl. Wright. 1:113, 1852 (not Z. helianthoides (HBK.) Benth. & Hook. = Wedelia helianthoides HBK.). TYPE: MEXICO: Between Saltepec and Cuito, Karwinski s.n. (HOLOTYPE: M; Photos: MICH, NY, US).

   Tithonia ovata Hook., Bot. Mag. t. 3901, 1841. Zexmenia ovata (Hook.) Benth. & Hook. f., Gen. 2:373, 1873. TYPE: MEXICO: cultivated in Hort. Kew (HOLOTYPE: K(herb. Hook.); Photo: GH).

Shrubs or more commonly half-shrubs woody near base only, 0.3-4 m high; young branches sordid-hirsute to viscid-pubescent. Leaves all opposite; petiole (2-) 3-15 mm long, hispid to occasionally viscid-pubescent; blade thick, firm, often rugose, usually ovate to lance-ovate, varying to lanceolate and suborbicular, (3-) 4-9.5 (-12) cm long, 2-6 (-9) cm wide, obtuse to acute or occasionally short-acuminate, cuneate

to cordate at base, scabrous to viscid above, pilose to hirsute below, margin denticulate-mucronulate to serrate, occasionally slightly revolute, triplinerved or occasionally trinerved. Inflorescence (1-) 3-5 -headed, terminal and from upper leaf axils. Peduncles 0.1-4 cm long, stout, white- or sordid-hirsute; heads 2-4 cm wide across extended rays. Involucre campanulate to hemispherical, 1.0-1.6 cm high, 0.6-2.5 cm wide, phyllaries graduated in 3-6 series. Outer phyllaries firm, membranous-indurate below, more or less herbaceous above, broadly ovate to ovate in outline, 5-10 mm long, 2-8 mm wide, acute to usually obtuse, white-hirsute and puberulent dorsally, middle phyllaries often 3-lobed, inner phyllaries ovate-oblong to elliptic, 7-20 mm long, 1.5-5.6 mm wide, obtuse, often ampliated at apex. Rays 8-13 (-21), orange-yellow or yellow, lamina 3-20 mm long, 4-9 mm wide, tube 4-6.5 mm long. Disc florets 10-100 (-125), orange or yellow, 8-15 mm long, throat narrowly campanulate to campanulate, 4.5-13 mm long, 1.5-4.5 mm wide, lobes 0.9-1.9 mm long. Anther thecae dark brown or brown, 2.5-4.0 mm long, appendage 0.6-1.5 mm long. Style branches 2.1-4.5 mm long, appendage 0.5-1.5 mm long. Pales 0.7-1.5 mm long, 0.5-1.8 mm wide as folded. Disc achenes cuneate, 2-awned, body 3-6.5 mm long, 1-4 mm wide, glabrate to puberulent, awns 4-7.5 mm long, pappus squamellae 1-2.7 mm long, usually connate. Ray achenes 3-awned, body 3.5-6 mm long, 2-4 mm wide, awns 1.5-5 mm long, pappus squamellae 1-3.2 mm long. Receptacle flat to low convex.

Key to varieties of *L. helianthoides*

1. Involucre usually more than 1 cm wide as pressed, squamellae of disc achenes 1-2.5 mm long, Balsas Depression 3a. *L. helianthoides* var. *helianthoides*

1. Involucre 6-13 mm wide as pressed, but usually less than 1 cm wide, squamellae of disc achenes 1.5-2.7 mm long, Nayarit 3b. *L. helianthoides* var. *nayaritense*

3a. Basianthaea helianthoides DC. var. helianthoides.

Plants with sordid-hirsute pubescence. Leaf blades cordate to rounded, or occasionally cuneate at base, scabrous and hispid above. Peduncles (0.1-) 1-3 (-4) cm long; heads 2-4 cm wide across extended rays. Involucre graduated in usually 3 series. Outer phyllaries 5-9 (-10) mm long, margin often long-ciliate towards apex. Rays usually orange-yellow, varying to yellow, lamina (3-) 5-20 mm long. Disc florets 25-75 (-100 or more), 9-15 mm long, lobes (1-) 1.4-1.9 mm long. Disc achenes 1.5-2.2 (-4.0) mm wide, awns 4-7 mm long, pappus squamellae 1-2.5 mm long. Ray achenes with body 2-4 mm wide. Chromosome number, from meiotic material, n=10. Tropical deciduous, oak, or occasionally open pine forest. Throughout the Balsas Depression of southern Mexico, at altitudes from 300-1750 m. Blooming mostly August to November, but sporadically throughout the rest of the year.

Selected specimens:

MEXICO: COLIMA: Alzada, 4 Nov 1910, Orcutt 4667 (DS,F,US). GUERRERO: Hills overlooking Iguala from the NE, just under microwave station Tuxpan, alt. 1600-1650 m, 23 Sept 1974, Becker & Cronquist 25 (NY). Vacas, Mina, alt. 900 m, 16 Aug 1936, Hinton 9275 (ENCB,GH,LL,US). Vallecitos, Montes de Oca, 30 Aug 1937, Hinton 11340 (GH,LL,PH,US,W). At km 339-40 on hwy to Acapulco between Acahuizotla & Agua del Obispo, alt. ca. 3000 ft, 30 Sept 1949, Moore 5113 (GH,MEXU,MICH,UC). 6 km SE of Chichihualco, alt. 1350 m, 7 July 1966, Rzedowski 22718 (ENCB,MICH). STATE OF MEXICO: Rincón del Carmen, Temascaltepec, alt. 1340 m, 6 Sept 1932, Hinton 1627 (G,GH,MEXU,MO,NY,US). 8 km SW of Luvianos, on road to Nanchititla, alt. 1500 m, 2 Sept 1965, Rzedowski 20745 (DS,ENCB,MEXU,MICH). MICHOACAN: Tiamaro, Zitacuaro, alt. 1600 m, 30 Sept 1938, Hinton et al. 13288 (ENCB,GH,

LL,MICH,PH,US). Acahuato, Apatzingan, alt. 3200 ft, 17 Aug 1941, Leavenworth & Hoogstraal 1669 (F,GH,MICH,MO,NY). El Cerro Piedra Parada, alt. 1000 m, 2 Oct 1970, Rzedowski 2505 (DS,ENCB,F,MICH,MO, SD). MORELOS: 50 km W of Iguala, alt. 1700 m, 22 Sept 1974, Becker & Cronquist 29 (NY). 1 mi N of Guerrero border on Mex 95 Toll, alt. 4000 ft, 9 Sept 1975, Becker & Olsen 57 (NY). 9 mi NNE of Cuautla, alt. ca. 5400 ft, 14 Oct 1965, Cronquist 10337 (MEXU,NY). Cuernavaca, alt. 1700 m, 26 Jan 1932, Fröderström & Hultén 436 (S). Cañon de Lobos, 26 Oct 1941, Miranda 1623 (MEXU). Near Cuernavaca, alt. 5000 ft, 27 Oct 1895, Pringle 6225 (BM,BR,F,G,GH,K,LL,M,MEXU(2),MICH,MO,MSC,NY,P(3),PH,S,UC, US,W,WU). OAXACA: Sept 1842, Ghiesbreght 257 (P(3)). PUEBLA: Sierra de Chalchi, July 1945, Miranda 3582 (MEXU).

3b. Lasianthaea helianthoides DC. var. nayaritense K. Becker, var. nov. TYPE: MEXICO: NAYARIT: 12 mi SE of Acaponeta, alt. ca. 150 ft, 3 Oct 1962, Cronquist 9594 (HOLOTYPE: NY; ISOTYPES: GH,MEXU,MICH,MO,TEX,US).

Plants viscid-pubescent. Leaf blades cuneate to truncate at base, viscid-scabrous above. Peduncles 0.5-1.8 cm long;heads to ca. 2.5 cm wide across extended rays. Involucre graduated in (3-) 4-6 series. Outer phyllaries 5-6 mm long, margin ciliate towards apex. Rays yellow, lamina 8-11 mm long. Disc florets 10-ca. 32, 8-9 mm long, lobes 9-11 mm long. Disc achenes 1-1.5 mm wide, awns 6.5-7.5 mm long, pappus squamellae 1.5-2.7 mm long. Ray achenes with body 2.0-2.5 mm wide. Grazed pastures and roadsides in oak-palm savannah region. Northern Nayarit at altitudes from 50-1000 m. Blooming August to November.

Specimens examined:

MEXICO:NAYARIT: 3 mi NE of Puga, alt. ca. 1000 m, 22 Aug 1959, Feddema 900 (MICH). Near Pocotitlán, 16 Jan 1971, Freeland & Spetsman 9 (MEXU).

N of Tepic, 14 Nov 1953, Templeton 7793a (NY).

Lasianthaea helianthoides, the type species of the genus, is most closely related to L. macrocephala and L. crocea. As recognized here, L. helianthoides consists of two varieties, var. helianthoides, common in the Balsas Depression of southern Mexico, and the relatively small-headed var. nayaritense, apparently restricted to northern Nayarit. Both varieties are relatively constant morphologically within their respective ranges. The hiatus in range in Jalisco is of interest.

L. helianthoides and L. crocea are often found growing together throughout the Balsas Depression. The major isolating mechanism between them apparently is pollinator differentiation (rays orange-yellow in helianthoides, orange-red to purplish in crocea). This mechanism apparently breaks down often enough so that they hybridize fairly freely (evidence is presented in the discussion of L. crocea below).

L. helianthoides var. helianthoides and L. ceanothifolia var. ceanothifolia apparently hybridize on occasion. Paray 1605, from Tepoztlan, Morelos, where both species occur, is intermediate between the two in size and number of heads, and in leaf shape, texture, and pubescence. Paray 1705, from the same area, is also intermediate but shows a somewhat different assortment of characters. The hybrid nature of these collections is supported by pollen stainability data (Paray 1605: 69%; Paray 1705: 72%; putative parents: 96+%).

For discussion of the relationship of L. helianthoides with L. squarrosa, see under the latter.

4. Lasianthaea crocea (A. Gray) K. Becker, comb. nov. Zexmenia crocea A. Gray, Pl. Wright. 1:114, 1852. TYPE: MEXICO: Nov 1844, Ghiesbreght 387 (HOLOTYPE: P; ISOTYPE: GH; Photo: ENCB).

Zexmenia stenantha Hemsl., Biol. Cent.-Am. Bot. 2:174, 1881. TYPE: MEXICO: MORELOS: Cuernavaca (Iturbide), 15 Nov 1865, Bourgeau 1204 (HOLOTYPE: K; Photos: GH,US; ISOTYPES: BR,F,G(2),GH,P(3),S,US).

Weak, often lax and scrambling soft-woody shrubs, 1-4.5 m high; young branches densely short-hispid to pilose, often viscid. Leaves all opposite; petioles 0.5-2 cm long, hispid and hirsute; blade usually thin, occasionally firm, occasionally rugose, lance-ovate to oblong, or occasionally ovate, (2.5-) 5-14 cm long, (1.5-) 2-8 cm wide, usually acuminate, occasionally obtuse, usually rounded, occasionally cuneate or cordate at base, densely short-hispid with appressed hairs and occasionally scabrous above, densely short pilose to subcanescent, often softly, below, margin serrulate to occasionally coarsely serrate, triplinerved. Inflorescence 1-3 -headed, terminal and sometimes also axillary. Peduncles (2.5-) 8-16 (-22) cm long, stout, usually fistulose above, densely hirsute, especially above; heads 3-4 cm wide across extended rays. Involucre broadly campanulate to hemispherical, (0.9-) 1-3 cm high, 1-2 cm wide, in 2-3 series, outer phyllaries much differentiated from inner. Outer phyllaries usually much longer than inner, indurate-membranous below, herbaceous and usually foliaceous, expanded and reticulate-veiny above, lance-elliptic to lance-ovate or oblong in outline, (6-) 7-30 mm long, (2-) 3-10 mm wide, acuminate to occasionally blunt-tipped, venation usually conspicuous, appressed-hispid to white-sericeous dorsally, inner phyllaries sharply distinct, membranous, elliptic to ovate-oblong, (6-) 6.5-8.5 (-11) mm long, (1.0-) 1.4-5 mm wide, acute to obtuse, often purple-tinged above. Rays (6-) 8-21, deep orange, orange-red or dark red above, orange below, lamina 9.5-17 mm long, (2-) 3.4-6.5 mm wide, tube 2.5-4 mm long. Disc florets 60-90 (-150), orange, 7.5-11 mm long, throat

cylindro-campanulate, 7-10 mm long, (0.5-) 0.8-1.2 mm wide, lobes 0.6-1.2 mm long. Anther thecae yellow-brown or light brown, 2.4-3.5 mm long, appendage 0.5-1 mm long. Style branches (2.5-) 3.2-4.5 mm long, appendage 0.5-1 mm long. Pales 6.5-9.5 mm long, 0.6-1.2 mm wide as folded, often purple-tinged. Disc achenes narrowly cuneate, 2-awned, body 4.5-6 mm long, 0.8-1.4 mm wide, glabrate to strigose and puberulent above, awns 1.5-5.5 mm long, exserted 1-2 mm from ripe heads, often purple-tinged, pappus squamellae 0.5-0.6 mm long, free, often reduced to a ciliate fringe. Ray achenes 3-awned, body 4-4.5 mm long, 0.8-1.3 mm wide, puberulent above, awns 0.5-2 (-3) mm long. Receptacle slightly convex or flat. Chromosome number, from meiotic material, n=10. Wooded slopes, roadsides; tropical deciduous, oak, or open pine forest. Balsas Depression of southern Mexico, at altitudes from 600-2200 m. Blooming May to December.

Selected specimens:

MEXICO: GUERERRO: 50 km W of Iguala, alt. 1700 m, 22 Sept 1974, Becker & Cronquist 30 (NY). 43 km W of Iguala, alt. 1400 m, 22 Sept 1974, Becker & Cronquist 32 (NY). Hills overlooking Iguala from the NE, just under microwave station Tuxpán, alt. 1650 m, 23 Sept 1974, Becker & Cronquist 33 (NY). Just N of Chilpancingo, alt. 5000 ft, 9 Sept 1975, Becker & Olsen58 (NY). About 7 mi W of Chilpancingo, alt. ca. 4700 ft, 21 Oct 1962, Cronquist 9717 (GH,MEXU,MICH,MO,MSC,NY,TEX,US). Guayameo, Mina, alt. 680 m, 11 Sept 1936, Hinton 9387 (GH,K,MICH,NY,US). Manchon, Mina, 25 Sept 1936, Hinton 9577 (ENCB,GH,LL,W). Calavera, Mina, alt. 800 m, 11 Nov 1936, Hinton 9828 (GH,LL). Rio Frio, Mina, 22 Sept 1937, Hinton 10703 (C,G,GH,M,MO,NY,S,US,W). Campo Morado, Mina, alt. 1300 m, 13 Nov 1939, Hinton 14835 (F,GH,LL,MICH,MO,NY,US). Achotla, Adama, alt. 720 m, 15 Nov

1937, Mexia 8825, (B,CAS,F,G,GH,LL,MO,NY,S,UC,US). 2 km N of Taxco, on road to Amacuzac, alt. 1750 m, 21 Oct 1965, Rzedowski 21499 (ENCB, MICH,MSC). JALISCO: 8 km W of Jilotlán de los Dolores, alt. 1100-1200 m, 22 Nov 1970, McVaugh 24612 (ENCB,LL,MICH,NY). STATE OF MEXICO: Limones, Temascaltepec, alt. 910 m, 12 Sept 1932, Hinton 1779 (G,LL,MO,US). Tejupilco, Temascaltepec, alt. 1340 m, 30 Sept 1932, Hinton 1936 (BM,DS, MO,NY,S,US). Timbres, Temascaltepec, alt. 1660 m, 15 Oct 1932, Hinton 2136 (BM,G,MO,NY,S,US). Ixtapan, Temascaltepec, alt. 1000 m, 20 Oct 1932, Hinton 2251 (G,MEXU,MO,NY,US). Ixtapan, Temascaltepec, 24 Sept 1935, Hinton 8486 (ENCB,GH,LL(2),MICH,PH). Ocotepec, mun. Tejupilco, alt. 1650 m, 10 Dec 1967, Rzedowski 25302 (DS,ENCB,LL,MICH,MSC). MICHOACAN: 3.8 km S of Tzitzio, alt. 1450 m, 26 Sept 1974, Becker & Cronquist 26 (NY). 24 mi S of Ario de Rosales, alt. 2600 ft, 26 Oct 1962, Cronquist 9737 (GH,MEXU,MICH,MSC,NY,TEX,US). W-facing slopes of Cerro de Carboneras above the Rio Cupatitzio, ca. 22 km S of Uruapan, alt. 3300-3700 ft, 16-22 Oct 1961, King & Soderstrom 4858 (MEXU,MICH,NY,TEX,UC,US). 3 km S of Paricuaro, on road to Tuzantla, alt. 1200 m, 21 Nov 1970, Rzedowski 26606 (ENCB). MORELOS: Ca. 5 mi E of Tezoyuca, alt. 1300 m, 9 Sept 1975, Becker & Olsen 54 (NY). 5 mi W of Tezoyuca, alt. 1300 m, 9 Sept 1975, Becker & Olsen 55 (NY). 1 mi N of Guerrero border on Mex 95 Toll, alt. 1300 m, 9 Sept 1975, Becker & Olsen 56 (NY). 9 mi NNE of Cuautla, alt. ca. 5400 ft, 14 Oct 1965, Cronquist 10336 (MEXU,NY). Amador Salazar, Cañada de Lobos, mun. Jiutepec, alt. 1500 m, Díaz M. 203 (DS,ENCB,MICH). Near Cuernavaca, alt. 5000 ft, 6 Nov 1895, Pringle 6187 (BM,BR,CAS(2),F,G(2), GH,K,LL,M,MO(2),MEXU(2),MSC,NY,P(3),PH,S,UC,US,W,WU). Near Yautepec, alt. 4500 ft, 22 Oct 1902, Pringle 8701 (BM,C,CAS,F,G(2),GH,K,LL(2),M,MEXU(2), MICH(2),MO,MSC,NY,P(3),PH,RSA,S,UC,US,W). OAXACA: Huatulco, Oct 1842,

Liebmann 577 (C(2),P,US;Drawing:GH). Near Huajuapam, alt. 5600-6500 ft, 16 Nov 1894, Nelson 1978 (GH,US). PUEBLA: Matamoros, 9 Oct 1942, Miranda 2444 (MEXU).

Lasianthaea crocea is allied to the two other members of the large-headed assemblage, L. helianthoides (sharing its range in the Balsas Depression), and L. macrocephala (with which it is allopatric). It is common throughout the Balsas Depression of southern Mexico, to which it is almost totally restricted, and where it occurs in a wide range of habitats. Typical L. crocea is distinct from both L. helianthoides and L. macrocephala in its involucre, which has the outer phyllaries foliaceous and longer than the inner, and in its ray color, dark-purple or orange-red on drying (vs. yellow on drying in the others). Vegetative and other characters also serve to distinguish crocea from its close relatives. L. crocea apparently does not exhibit the habital variation shown in several other Lasianthaea species; it consistently grows as a shrub. L. crocea is especially variable in length and width of outer phyllaries.

Liebmann 577, from an isolated station in coastal Oaxaca, is unusual in its short outer phyllaries (subequal to inner), and rays which are yellow upon drying. It resembles certain collections from inland stations in this ray color feature. Whether the rays are indeed yellow in the field remains to be determined.

L. crocea appears to hybridise with L. ceanothifolia and L. helianthoides. There is strong evidence of the former in collections made near Cuernavaca, Morelos, where both L. crocea and L. ceanothifolia var. ceanothifolia occur and where plants intermediate between the two in ray color, head size, head number, and vegatative characters are found (such

as Pringle 7073). A marked reduction in pollen stainability is exhibited by the intermediates (45-50% vs. 95% for the putative parents). Both putative parental species appear to maintain their distinctness at this locality.

L. crocea and *L. helianthoides* var. *helianthoides* apparently hybridize freely throughout the Balsas Depression. The two species are ordinarily distinct in nature of involucre (discussed above), leaf shape (lance-ovate in *crocea*, usually ovate in *helianthoides*), leaf texture (typically thin in *crocea*, thick in *helianthoides*), and peduncle length (usually more than 5 cm. long in *crocea*, less than 5 cm. long in *helianthoides*), etc. Plants are rather frequently found which are intermediate between the two in all the abovementioned characters as well as in ray color. Pollen stainability in these plants is typically much reduced (GUERRERO: Becker & Cronquist 30 - 20%; Hinton 9387 - 22%; Hinton 10703 - 39%; STATE OF MEXICO: Matuda 31483 - 37%; MICHOACAN: King & Soderstrom 4886 - 35%; MORELOS: Pringle 6225 - 50%; putative parents: 95-98%).

Ray florets of putative hybrids exhibit the anthocyanic *crocea* pigment (tentatively identified as cyanidin) to varying degrees, and this suggested a study of the flavonoid compounds in putative hybrids and parents. Flavonoid patterns of leaf, ray floret, and disc floret material were prepared as discussed above ("Flavonoid Studies"). Leaf and ray floret patterns were of considerable interest and the data are summarized in Table 4 (p. 62). The study showed that: 1) distinctive marker compounds for *L. crocea* and *L. helianthoides* appear to exist, and 2) putative hybrids usually exhibit more or less additive patterns, usually exhibiting markers for both *L. crocea* and *L. helianthoides*. In apparent introgressants, compounds indicative of hybrid geneaology are typically

Taxon	Collection	Designated Spots: Leaves 2	5	6	9	10	13	15	18	19	20	21	22	Ray Florets R1	R2	R3	R4	R5	R6	R7	R8
L. crocea	King & Soderstrom 4853	x		x			x	x	x	x			x	x	x	x	x				x
	Pringle 6187	x		x	x		x	x	x	x			x		x		x				x
	Becker & Cronquist 32	x		x	x		x	x	x	x			x		x		x				x
	Becker & Cronquist 28	x		x	x		x	x	x				x		x		x				x
	Becker & Cronquist 33	x		x			x	x	x	x			x		x		x				x
	Hinton 9577	x	x	x	x		x	x							x		x				x
	Hinton 9828	x		x	x		x	x	x	x					x		x				x
	Hinton 10703	x		x	x		x	x	x	x					x		x				
	Hinton 14835	x	x	x	x		x	x	x	x			x		x		x				x
"*L. crocea* x *helianthoides* var. *helianthoides*"	Becker & Cronquist 31a	x	x	x			x	x	x	x	x		x		x		x				x
	Becker & Cronquist 31b	x	x	x	x		x	x	x	x	x		x		x		x				x
	Becker & Cronquist 31c	x	x	x	x		x	x	x	x	x		x		x		x	x			x
	Hinton 10703	x		x	x		x	x	x	x	x				x	x	x	x		x	x
	Hinton 9387	x			x		x	x	x		x		x	x	x	x	x	x		x	x
	King & Soderstrom 4886	x	x	x			x	x	x		x		x	x	x	x	x	x		x	x
	Pringle 6225	x	x				x	x	x	x	x		x		x	x	x	x		x	x
L. helianthoides var. *helianthoides*	Pringle 6225	x	x			x	x	x	x		x	x	x			x	x	x	x	x	x
	Hinton 9275	x	x				x	x	x	x	x	x	x			x	x	x		x	
	Leavenworth & Hoogstraal 1669	x	x				x	x	x	x	x	x	x			x	x	x		x	x
	Becker & Cronquist 35	x	x			x	x	x	x		x	x	x			x	x	x	x	x	x
	Becker & Cronquist 39	x	x				x	x	x	x	x	x	x			x	x	x	x	x	x

Table 4. Designated spots from paper chromatograms of leaves and ray florets of *Lasianthaea crocea*, *L. helianthoides* var. *helianthoides*, and putative hybrids between them.

present.

5. Lasianthaea squarrosa (Greenm. in W. W. Jones) K. Becker, comb. nov. Zexmenia squarrosa Greenm. in W. W. Jones, Proc. Amer. Acad. 41:151, 1905. TYPE: MEXICO: GUERRERO: Limestone mountains above Iguala, alt. 4000 ft, 3 Oct 1900, Pringle 3411 (HOLOTYPE: GH; Photo: FNCB; ISOTYPES: BM,C,F,G,K,M,MEXU(2),MICH,MO,MSC,NY,P(2),PH,POM,S,TEX,UC, US(2),W).

Slender, rather brittle-stemmed shrubs, 0.5-2 m high; young branches strigose. Leaves all opposite; petioles (3-) 10-15 (-22) mm long, strigose, margins hispid; blade thin, broadly ovate to ovate or lanceolate, (2-) 3.5-9.5 cm long, (1.5-) 2-6.5 cm wide, acuminate, truncate or rounded to cuneate at base, scabrous and hispid above, soft and densely pilose to sericeous below, especially along veins, margin shallowly to coarsely serrate, triplinerved. Inflorescence (1-) 3-8 -headed, terminal. Peduncles (0.5-) 1.0-3.5 cm long, stout, sericeous with dense, appressed hairs; heads to 3.2 cm wide across extended rays. Involucre campanulate to usually broadly campanulate or hemispherical, 1.0-1.5 cm high, 0.6-1.6 cm wide, graduated in 3-4 series. Outer phyllaries indurated below, reticulate-veiny, foliaceous and squarrose above, narrowed at middle, 6-8 mm long, 2.5-3.5 mm wide, the indurated base to 5.5 mm wide, with appressed, slender hairs below, and with coarser hairs at middle, inner phyllaries membranous below, herbaceous at apex, ovate-oblong, 11-12 (-15) mm long, 5.0-6.5 mm wide, apex rounded, mucronulate. Rays on well-developed heads 7-10, lemon-yellow, lamina 7-13 mm long, 3.8-5.0 mm wide, tube (3.4-) 3.8-4.5 mm long. Disc florets 14-30, yellow, 8-9 mm long, throat narrowly campanulate to campanulate, 5-6 mm long, 1.5-2.0 mm wide, lobes 1.0-1.4 mm long. Anther thecae brown to blackish, (2.8-) 3.0-3.5 mm

long, appendage 0.8-1.0 mm long. Style branches 2.5-3.2 mm long, appendage 0.9-1.0 mm long. Pales 7.5-9 mm long, 0.9-1.2 mm wide as folded. Disc achenes cuneate, 2-awned, body 4.5-5.0 mm long, 1.0-1.8 mm wide, sparsely puberulent, awns 4-6 mm long, exserted 2-3 mm from ripe heads, pappus squamellae 0.4-1.8 mm long, weakly to strongly connate. Ray achenes with body 5.5-6.0 mm long, 1-2 mm wide. Receptacle low-convex. Limestone hills in northern Guerrero and Morelos at altitudes from 1300-1650 m. Blooming mostly August to September.

Specimens examined:

MEXICO: GUERRERO: Hills overlooking Iguala from the NE, alt. 1650 m, 23 Sept 1974, Becker & Cronquist 34 (NY). Iguala, 12 Aug 1905, Rose et al. 7411 (GH,NY,US). MORELOS: 12.5 mi SW of Cuautla, alt. 4200 ft, 9 Sept 1975, Becker & Olsen 53 (NY).

Lasianthaea squarrosa, apparently restricted to northern Guerrero and adjacent Morelos, shows relationships on the one hand with L. helianthoides var. helianthoides, and on the other with L. ceanothifolia var. gracilis. L. squarrosa, as the name implies, possesses usually squarrose outer phyllaries, the tips of which are usually also foliaceous. Near Iguala, Guerrero, where most collections have been made, L. squarrosa is distinct from L. helianthoides var. helianthoides in phyllary characters, its thin leaves (not thick as in L. helianthoides), its distinctly shrubby habit (not half-shrubby), in its mostly spreading (not appressed) pubescence, and in altitudinal location (L. squarrosa mostly above 1600-1650 m, L. helianthoides mostly below 1600 m). A plant intermediate in phyllary characters, leaf texture, and pubescence, found where the altitudinal ranges of the two species overlap, may reflect

introgression (Becker & Cronquist 36). Large-headed plants of L. ceanothifolia var. gracilis with pubescent outer phyllaries (western Michoacan, Hinton 15157) somewhat resemble L. squarrosa. Neither taxon is known to occur in eastern Michoacan or western Guerrero.

L. squarrosa sometimes exhibits a large amount of variation in number of heads per cluster (usually 1-3, but occasionally 8, and then heads relatively small). The significance of this is not known.

6. Lasianthaea ceanothifolia (Willd.) K. Becker, comb. nov. Verbesina ceanothifolia Willd., Sp. Pl. 3:2225, 1804. Zexmenia ceanothifolia (Willd.) Sch. Bip., in Seem. Bot. Voy. Herald 305, 1856. TYPE: MEXICO: GUERRERO: Acapulco, Humboldt s. n. (HOLOTYPE: B(herb. Willd. No. 16390); Fragment: P).

Shrubs, usually several-stemmed, or rarely half-shrubs woody near base only, 0.5-3 (-6) m high; young branches hispid or strigose to glabrate. Leaves all opposite; petioles 1-20 mm long, its margin usually hispid; blade firm to thin, occasionally rugose, lanceolate to ovate, 2-18 cm long, 1-7.5 cm wide, acute to long-acuminate, cuneate, rounded, or cordate at base, scabrous and hispid to hirsute above, hispid, hirsute, or pilose below, margin crenate-serrate, serrate, to closely serrate, triplinerved or occasionally subpenninerved. Inflorescence 3-12 -headed, terminal and axillary, and solitary from upper leaf axils. Peduncles 1-5 cm long, usually slender, variously pubescent; heads 0.5-3.5 cm wide across extended rays. Involucre campanulate or turbinate, 0.5-1.1 cm high, 0.2-1.0 cm wide, phyllaries in (2-) 3-6 series, usually clearly graduate. Outer phyllaries membranous-indurate below, herbaceous above, ovate, oblong or rhomboid in outline, 2-8 mm long, 1-5 mm wide, acute to obtuse, variously pubescent, inner phyllaries membranous, occasionally herbaceous

above, oblong-ovate to linear, 4.8-10.0 mm long, 1-6 mm wide, acute or obtuse. Rays 7-13, orange-yellow to bright yellow, lamina 4-10 mm long, 2-4.5 mm wide, tube 1.5-2.7 mm long. Disc florets 8-35, yellow, 5-8 mm long, throat narrowly campanulate to campanulate, 4.5-6 mm long, 0.8-1.5 mm wide, lobes 0.5-1.0 mm long. Anther thecae brown to blackish, 1.8-3.0 mm long, appendage 0.4-1.0 mm long. Style branches 1.5-3 mm long, appendage 0.5-1.0 mm long. Pales 6-8 mm long, 0.4-1.1 mm wide as folded. Disc achenes cuneate, 2-awned, body 2.5-5 mm long, 0.7-1.2 mm wide, glabrate, puberulent, or hispidulous, awns 1.5-6 mm long, pappus squamellae 0.2-1.1 mm long, free or connate. Ray achenes 3-awned, body 1.5-4.5 mm long, 0.7-1.4 mm wide, glabrate, awn (adaxial) 0.5-3.5 mm long, pappus squamellae 0.2-0.4 mm long. Receptacle low-convex.

Key to varieties of L. ceanothifolia

1. Awns of disc achenes usually less than 2 mm long, not exserted from ripe heads, if slightly longer then heads less than 5 mm wide as pressed; leaves thin-textured; Sierra Madre Occidental

   6c. L. ceanothifolia var. gradata

1. Awns of disc achenes more than 2 mm long, often exserted from ripe heads; leaves firm- to thin-textured

   2. Middle and often outer phyllaries strongly and conspicuously many-nerved below, green and membranous above, usually glabrous excepting ciliate margins; stems sparsely strigose, soon glabrate; leaves thin-textured and usually sparsely strigose

      6d. L. ceanothifolia var. gracilis

   2. Middle phyllaries relatively weakly and less conspicuously differentiated into parallel-nerved base and green-membranous apex,

this differentiation often obscured by the strigose and puberulent pubescence ; stems pilose, hirsute, or strigose; leaves usually firm-textured

3. Awns usually exserted (to 4.5 mm) from ripe heads, if not exserted then pubescence of stems and leaves spreading; leaves lance-ovate to usually ovate

6a. L. ceanothifolia var. ceanothifolia

3. Awns usually not exserted (occasionally to 2 mm) from ripe heads; pubescence of stems and leaves usually strongly appressed; leaves usually oblong

6b. L. ceanothifolia var. verbenifolia

6a. Lasianthaea ceanothifolia (Willd.) K. Becker var. ceanothifolia.

Lipochaeta umbellata DC., Prodr. 5:610, 1836. TYPE: MEXICO: MORELOS: Near Cuernavaca, Berlandier 1065 (HOLOTYPE: G; Photo: US; ISOTYPES: GH,P,W).

Zexmenia ceanothifolia var. conferta A. Gray in J.W. Jones, PAA 41:155, 1905. Lipochaeta umbellata DC. var. conferta DC., Prodr. 5:610, 1836. TYPE: MEXICO: MORELOS: Cuernavaca, Berlandier 1053 (HOLOTYPE: G; Photo: US; ISOTYPES: BM,G(2),NY,P(3),W).

Shrubs, usually many-stemmed and often spreading, or rarely half-shrubs woody near base only, 0.5-3 (-6) m high; young branches sparsely to densely hispid with often spreading hairs. Leaves with petioles (1-)3-10 (-15) mm long, its margin hispid with spreading hairs; blades usually firm and often rugose, or sometimes thin, ovate to lance-ovate, or occasionally lanceolate, (2-) 4-13 (-15) cm long, (1.0-) 1.5-5 cm wide, acute to acuminate, cuneate or cordate at base, scabrous and hispid to hirsute above, sparsely to densely hispid, especially along veins,

to soft-pilose, below, margin crenate-serrate, shallowly serrate, to serrate, often irregularly so. Peduncles (1-) 1.5-2.5 (-3.5) cm long, densely hispid to strigose. Involucre campanulate, varying to cylindro-campanulate and broadly campanulate, 5-8 (-10) mm high, 3-8 (-9) mm wide, graduated in 3-5 series. Outer phyllaries occasionally reticulate-veiny above, ovate, often broadly so, or rhomboid in outline, 2.5-4 mm long, 1.8-4 mm wide, white-strigose and often puberulent, or occasionally glabrate dorsally, inner phyllaries 4.8-7 mm long. Rays 8-13, lamina (4-) 4.5-7.5 mm long. Disc florets 10-35, 5-6.5 mm long. Disc achenes with body 3.5-5 mm long, 1-1.2 mm wide, awns 4-5 (-5.5) mm long, not exserted or exserted to 4.5 mm from ripe heads. Chromosome number, from meiotic material, n=10. Roadsides, hillsides, open scrubland, less commonly in woods or along riverbanks, in tropical deciduous, oak, oak-pine, or occasionally in pine or Juniperus forest. Central and eastern Transverse Volcanic Belt, and in the Sierra Madre del Sur of south-central and southern Mexico, occasionally as far east as Chiapas, at altitudes from 750-1900 m. Blooming June-January and sporadically throughout the rest of the year.

Selected specimens:

MEXICO: AGUASCALIENTES: 10 mi E of Calvillo, alt. 6000 ft, 3 Sept 1975, Becker & Olsen 47 (NY). 13 mi S of Aguascalientes, 6200 ft, 3 Sept 1975, Becker & Olsen 48 (NY). Road to Calvillo, 21 mi W of Aguascalientes, alt. 2100 m, 3 Nov 1959, McVaugh & Koelz 156 (MICH). CHIAPAS: Siltepec, Jan 1937, Matuda 1559 (MEXU,MICH,MO,US). GUANAJUATO: 4 mi E of Silao, alt. 5800 ft, 4 Sept 1975, Becker & Olsen 49 (NY). Near Guanajuato, 5 Aug 1947, Kenoyer 1703 (GH). Leon, 29 Sept 1906, Rose 11517 (US). GUERRERO: Ca. 1.5 km (by road) below Microondas Station El Fresno and 49 km S of

Chilpancingo, alt. ca. 900 m, 12 Oct 1974, Cronquist 11230 (NY). San Antonio, Montes de Oca, 19 Oct 1937, Hinton 11506 (ENCB,GH,LL,US,W). JALISCO: 5 mi S of Guadalajara, alt. 5000 ft, 12 Aug 1947, Barkley et al. 7533 (TEX). 1 km NE of Acatlan, alt. 1400 m, 15 Sept 1974, Becker & Cronquist 16 (NY). 4.8 km W of San Luis Soyatlan, alt. 1500 m, 15 Sept 1974, Becker & Cronquist 17 (NY). Near Tonila, alt. 1200 m, 17 Sept 1974, Becker & Cronquist 22 (NY). Ca. 5 mi N of Tecalitlan, alt. 5000 ft, 10 Sept 1974, Becker & Olsen 59 (NY). 16 mi N of Guadalajara, alt. 4500 ft, 11 Sept 1974, Becker & Olsen 61 (NY). Along roadside near S shore of Lake Chapala, 48 mi S of Guadalajara, alt. 5100 ft, 7 Oct 1965, Cronquist 10291 (ENCB,MEXU,MICH,NY). Rio Verde, near Yahualica, alt. 1372 m, 22 July 1961, Detling 8464 (MICH). Los Camachos, N of Guadalajara, 26 July 1967, Díaz Luna 230 (MICH). 6 mi E of Atotonilco el Alto, alt. 1880 m, 23 Aug 1958, McVaugh 17244 (ENCB, MICH,NY,US). Near Guadalajara, 27 Sept 1889, Pringle 2301, in part (G,GH,LL,M,MEXU(2),MICH,MO,NY(2),P,PH,S,UC(2),US,W). San Juan Cosalá, alt. 1560 m, 8 Aug 1966, Puga 667 (ENCB). 3 km E of Mezquitic, alt. 1700 m, 4 Nov 1963, Rzedowski 17648 (ENCB,MICH). 9 mi S of Autlán toward La Resolana, alt. 4000 ft, 8 Aug 1949, Wilbur & Wilbur 2195 (DS,LL,MICH,US(2)). STATE OF MEXICO: Ocotepec, Temascaltepec, alt. ca. 1500 m, 12 Dec 1932, Hinton 2880 (DS,G,MO,NY,US). Platanal, Temascaltepec, 23 Oct 1935, Hinton 8523 (GH,MICH,US). Ixtapan de la Sal, 13 Oct 1958, Paray 2773 (ENCB,MEXU). MICHOACAN: Ca. 11 mi NW of Zitacuaro, alt. 6000 ft, 24 Oct 1962, Cronquist 9722 (GH,MEXU,MICH,MO,NY, TEX,US). Ca. 6 km SE of Ciudad Hidalgo, alt. ca. 1900 m, 6 July 1974, Cronquist 11149 (NY). Saltre, dist. Coalcoman, alt. 1140 m, 9 Sept 1938, Hinton et al. 12158 (GH,K,LL,MICH(2),NY,P,UC,US). Coalcoman, alt. 1000 m,

23 Oct 1938, Hinton et al. 12445 (G,GH,LL,MICH(2),NY,P,S,UC,US,W). MORELOS: Barranca near Cuernavaca, 15 Nov 1865, Bourgeau 1219 (BR, C,F(2),G,GH,K,P(4),S,US). 9 mi NNE of Cuautla, alt. ca. 5400 ft, 14 Oct 1965, Cronquist 10331 (CAS,ENCB,GH,MEXU,MICH,MSC,NY,TEX,US). S slopes overlooking Cuernavaca, ca. 10 km N of town along toll road, alt. ca. 1900 m, 23 Oct 1970, Cronquist & Fay 10032 (NY). Cuernavaca, alt. 5000 ft, 7 Oct 1900, Pringle 9163 (GH,LL,MEXU,NY,US). Hills near Cuernavaca, alt. 5000 ft, 12 Nov 1902, Pringle 9998 (F,GH,K, MO,NY,US). Barranca of Cuernavaca, alt. 5000 ft, 18 June 1904, Pringle 13072 (C,CAS,F,GH(2),K,MEXU,MICH,US(2)). OAXACA: Hills near Oaxaca, Sierra de San Felipe, alt. 6000 ft, 10 Sept 1894, Pringle 5783 (F,GH,LL, MO,US). VERACRUZ: Orizaba, Botteri 800 (F(in part),GH). Valley of Cordoba, along rt 150 ca. 8 mi E of Puebla border, 5 June 1960, King 2654 (DS,MICH,NY,RSA,TEX,UC,US). Santa Ana, May 1905, Purpus 1162 (F, MO,UC). ZACATECAS: 3 mi E of Jalpa, alt. 6000 ft, 3 Sept 1975, Becker & Olsen 45 (NY). 16 mi E of Jalpa near Aguascalientes border, alt. 7000 ft, 3 Sept 1975, Becker & Olsen 46 (NY). 34 mi E of Jalpa, alt. 5000 ft, 11 Sept 1975, Becker & Olsen 62 (NY). Rd to Huejuquilla el Alto, Jalisco, 1 mi W of the rd-jct 18 mi S of Valparaiso on rd to Mezquitic, Jalisco, ca. 22°38' N, 103°48' W, alt. 2100 m, 4-5 Sept 1958, McVaugh 17677 (ENCB, MICH,US). 20 km S of Jalpa, on rd to Juchipila, alt. 1500 m, 16 Sept 1972, Rzedowski 29366 (CAS,ENCB,MICH).

6b. Lasianthaea ceanothifolia (Willd.) K. Becker var. verbenifolia (DC.) K. Becker, comb. nov. Calea verbenaefolia DC., Prodr. 5:673, 1836. Zexmenia verbenaefolia (DC.) Blake, Contr. U. S. Nat. Herb. 26:255. TYPE: MEXICO: Née s. n. (HOLOTYPE: G; Photos: NY,US(2)).

Zexmenia cordifolia Blake, Contr. U. S. Nat. Herb. 22:633, 1924. TYPE: MEXICO:NAYARIT: Near Acaponeta, 30 July 1897, Rose 3277 (HOLOTYPE: US).

Zexmenia microcephala Hemsl., Biol. Cent.-Am. Bot. 2:173, 1881. TYPE:MEXICO:NAYARIT: Between San Blas and Tepic, Sinclair 20 (HOLOTYPE: K(herb. Hook.); Fragment and photo: US; Fragment: GH; Photos GH,US).

Shrubs, usually compact and with stiff branches, 1-4 m high; young branches strigose, sometimes sparingly so, to crisp-puberulent. Leaves with petiole rigid, 0.5-2 cm long, its margins hispid; blade firm, rigid, usually not rugose, oblong to lance-ovate, sometimes narrowly so, (2-) 3-14 cm long, (1-) 2-7 cm wide, short-acute to obtuse, cuneate to rounded at base, more or less scabrous and hispid with short, appressed hairs above, short-hispid with appressed hairs below, especially along veins, margin regularly and usually closely serrate, triplinerved or occasionally subpenninerved, tertiary venation conspicuous on larger leaves. Peduncles 2-4 cm long, strigose to crisped-puberulent. Involucre turbinate to broadly campanulate, (0.5-) 0.7-0.8 (-1.0) cm high, (0.3-) 0.5-0.7 (-0.9) cm wide, phyllaries graduated in 3-4 series. Outer phyllaries mostly oblong in outline, 3-5 mm long, 1.5-3 mm wide, strigose, often glabrate dorsally, inner phyllaries 6-7 mm long. Rays 8-13, lamina 6.5-9 mm long. Disc florets 12-24, 6.0-6.7 mm long. Disc achenes with body 4-5 mm long, 0.8-1.2 mm wide, awns 2-3.8 mm long, not exserted from heads. Roadsides, riverbanks, stream valleys, woodlands, cultivated land; oak zone. Mostly at the western end of the Transverse Volcanic Belt in west-central Mexico, at altitudes from near sea level to 1800 m. Blooming September to January and sporadically throughout the rest of the year.

Selected specimens:

MEXICO: JALISCO: La Crucieta, mun. Talpa, alt. 1500 m, 16 Oct 1971, González T. 508 (CAS,ENCB,MICH,NY). Ca. 6-10 mi SW of Talpa de Allende, alt. 1400-1800 m, 22 Nov 1952, McVaugh 14337 (MICH,NY). Near Guadalajara, 27 Sept 1889, Pringle 2301, in part (MSC,P,RSA,WU). NAYARIT: Puga road 1 mi from Tepic, 5 Nov 1925, Ferris 5771 (DS,GH, MEXU,US). Acaponeta, Feb 1895, Lamb 519 (DS,G,GH,K,MICH,MO,MSC,NY,US). 9 mi Nof Compostela, alt. 1000-1200 m, 12 Nov 1959, McVaugh & Koelz 535 (ENCB,MICH). Ixtlan del Rio, alt. 1100 m, 28 Sept 1926, Mexia 832 (BM,CAS,F,G,GH(2),MO,NY,UC,US). Tuxpan, Palapar Redondo, alt. 20 m, 5 Nov 1926, Mexia 1050 (CAS,DS,F,GH(2),MICH,MO,NY,UC,US). Mezcaltitan, alt. 0-5 m, Jan 1926, Ortega 6107 (DS,GH,MEXU(2),PH,US). MICHOACAN: Coalcoman, alt. 1000 m, 27 Dec 1938, Hinton et al. 12823 (F,GH,LL,MO,NY (2),US). SINALOA: San Cayetano, alt. 900 m, 16 Nov 1968, Palacios s.n. (ENCB). between Escuinapa & Acaponeta, Nayarit, 13 Nov 1953, Templeton 7182 (NY).

6c. Lasianthaea ceanothifolia (Willd.) K. Becker var. gradata (Blake) K. Becker, comb. nov. Zexmenia gradata Blake, Contr. U. S. Nat. Herb. 22:632, 1924. TYPE: MEXICO: SINALOA: Lodiego, 9-15 (?25) Oct 1891, Palmer 1578 (HOLOTYPE: US (USNH # 305446); ISOTYPES: C,F,GH, MICH(2),NY,S,US; Photo of portion of isotype at US: NY).

Shrubs, usually laxly spreading and with long,slender branches; young branches strigose to pale appressed-hirsute, occasionally densely so. Leaves with petiole 1-1.5 (-2) mm long, its margins hispid, otherwise strigose; blade usually thin, lance-ovate to occasionally ovate, 4-13 (-18) cm long, 1.5-4.5 (-7.5) cm wide, acute and often long-acumin-

ate, cuneate at base, scabrous and hispid above, hispid to densely soft-pilose and often subsericeous below, margin crenate-serrate or shallowly serrate, less commonly serrate. Peduncles to 3.5 cm long, strigose. Involucre campanulate to narrowly campanulate, or occasionally turbinate, 0.5-0.8 cm high, 0.2-0.5 (-0.6) cm wide, phyllaries graduated in 3-4 series. Outer phyllaries acute to obtuse at the often spreading apex, usually white-strigose dorsally, inner phyllaries 5-5.5 mm long. Rays 7-9, lamina 4.5-6 mm long. Disc florets 10-21, 6-6.8 mm long. Disc achenes with body 2.5-3.5 mm long, 0.7-1.2 mm wide, awns 1.5-2.5 mm long, usually not exserted (occasionally exserted to 1 mm) from ripe heads. Slopes and ravines in tropical deciduous, oak, and oak-palm forest areas. Central and southern Sierra Madre Occidental in western Mexico, at altitudes from 250-1300 m. Blooming September to December.

Selected specimens:

MEXICO: CHIHUAHUA: Arroyo Hondo, Sierra Charuco, 12 Sept 1935, Gentry 1797 (F,AA,K,MEXU,MO,UC,US). Hacienda San Miguel, alt. 2400 ft, Aug 1885, Palmer 155 (GH,K,MEXU,NY(2),PH,US). DURANGO: Sierra Tres Picos, alt. 3500 ft, 21 Dec 1939, Gentry 5324 (DS,GH,MO,NY). SINALOA: Cerro Colorado, Cofradia, 3 Nov 1904, Brandegee s.n. (GH,RM,UC) 7 mi NE of El Quintero along road from Mocorito to Surutato, alt. 3800 ft, 29 Sept 1970, Breedlove & Thorne 18062 (CAS,MICH,RSA). 4 mi SW of Santa Lucia & ca. 50 mi E of Mazatlán, alt. 4000 ft, 2 Oct 1962, Cronquist 9590 (GH,MEXU, MICH,MO,MSC,NY,TEX,US). N of La Noria, alt. 800 ft, 12 Oct 1925, Mexia 277 (C,CAS,UC,US). SONORA: Cañon Estrella, dist. Alamos, 1 Oct 1933, Gentry 331 (DS,MICH). Cañon Saucito, dist. Alamos, 29 Oct 1933, Gentry 684 (DS,MICH).

6d. Lasianthaea ceanothifolia (Willd.) K. Becker var. gracilis (W. W. Jones) K. Becker, comb. nov. Zexmenia gracilis W. W. Jones, Proc. Amer. Acad. 41:154, 1905. TYPE: MEXICO: COLIMA: Colima, Aug 1897, Palmer 163, coll of 1897 (HOLOTYPE: US; ISOTYPES: C,MICH,S).

Zexmenia rotundata Blake, Contr. U. S. Nat. Herb. 22:632, 1924. TYPE: MEXICO: DURANGO: Huasemote, 14 Aug 1897, Rose 3478 (HOLOTYPE: US).

Shrubs, slender-stemmed and loosely branching, 1-3 m high; young branches sparsely strigose. Leaves with petiole 0.5-1 (-1.5) cm long, its margins usually hispid, otherwise strigose; blades thin, usually lance-ovate, varying to lancolate and ovate, occasionally somewhat falcate, 5-13 cm long, 2-5 cm wide, acute and acuminate, cuneate at base, scabrous with sparse, appressed hairs above, hirsute below, especially along veins, margins often ciliate, serrate, triplinerved. Peduncles to 5 cm long, usually slender, strigose, often white-pilosulous when young. Involucre cylindro-campanulate to broadly campanulate, 0.6-1.1 cm high, 0.3-1.0 cm wide, phyllaries graduated in 4-6 series. Outer phyllaries ovate to broadly ovate in outline, 2-4 (-8) mm long, 2-5 mm wide, white-strigose, strigillose, or glabrate dorsally, becoming conspicuously parallel-nerved inwards, inner phyllaries often 3-lobed at apex, 0.6-1.0 cm long. Rays typically 8, lamina 6-10 mm long. Disc florets 8-30, 6.5-8 mm long. Disc achenes with body 4-4.5 mm long, 1-1.2 mm wide, awns 3-6 mm long, exserted 1-3 (-4) mm from ripe heads. Roadcuts, mountainsides, stream valleys in moist tropical forest and tropical deciduous forest. Southern Sierra Madre Occidental and western Transverse Volcanic Belt in west-central and southwestern Mexico, also in low-lying coastal areas, at altitudes from 70-1250 m. Blooming August to October.

Selected specimens:

MEXICO: COLIMA: 3.5 km S of La Huerta, alt. 450 m, 16 Sept 1974, Becker & Cronquist 21 (NY). 4.7 mi N of Los Asmoles on rt 110, alt. 375 m, 4 Sept 1973, Stuessey & Gardner 3086 (OS,NY). JALISCO: 23 km E of Ixtlan del Rio, Nayarit, alt. 900 m, 14 Sept 1974, Becker & Cronquist 2 (NY). 4 km SE of Tequila, alt. 1250 m, 14 Sept 1974, Becker & Cronquist 10 (NY). MICHOACAN: Aguililla, Apatzingan, alt. 1000 m, 12 Sept 1939, Hinton et al. 15157 (ENCB,F,GH,LL(2),MO,NY,US,W). NAYARIT: Near Tepic, alt. 450 m, 12 Sept 1974, Becker & Cronquist 6 (NY). 2.4 km W of Mexpan, alt. 1000 m, 13 Sept 1974, Becker & Cronquist 8 (NY). 3.5 mi NW of Ahuacatlan, S of base of Volcán Ceboruco & ca. 1 km N of hwy, alt. ca. 1100 m, 13 Aug 1959, Feddema 402 (CAS,ENCB,MICH,TEX). NE of Santa Maria del Oro, alt. ca. 1000 m, 18-20 Aug 1959, Feddema 697 (CAS, ENCB,MICH,TEX). 2 mi NE of Santa Maria del Oro, in the basin of La Laguna, alt. 1000 m, 15-16 Sept 1960, McVaugh 19039 (ENCB,LL, MICH). Rincon de Mateo, near Ixtlan, alt. 1100 m, 25 Sept 1926, Mexia 763 (BM,CAS,DS,F,G, GH(2),MICH,MO,NY,UC,US). SINALOA: Along Mex 40, 16 km E of Concordia, alt. 200 m, 10 Sept 1974, Becker & Cronquist 4 (NY). Just S of Matatan & ca. 15 km NE of Rosario, alt. under 100 m, 10 Oct 1970, Cronquist & Fay 10791 (NY). Picachos, mun. Rosario, Sept-Oct 1932, Ortega 7161 (CAS,F,GH, K,MEXU,US).

Lasianthaea ceanothifolia, as here recognized, consists of four varieties which are well-marked morphologically and geographically. Most of the small-headed shrubby Lasianthaeas with graduated involucres belong to this species, which, in its several varieties, is common and widespread in Mexico, especially in the center and west.

L. ceanothifolia var. ceanothifolia is common in the Transverse Vol-

canic Belt and surrounding regions in the Sierra Madre del Sur and the soutern end of the Central Plateau. It tends to prefer open, relatively dry, often disturbed habitats. It is characterized by its usually coarse pubescence, its stout branches, its firm, often ovate leaves, and by its often long-exserted achenial awns. It is the most widespread variety of L. ceanothifolia and is variable over its range in head size, leaf size and pubescence, and awn exertion. Thus, plants from the Guadalajara area tend to have broad heads, spreading pubescence, and mostly non-exerted awns, plants from Guerrero tend to have narrow heads, sparse pubescence, and long-exserted awns, etc. Involucres are usually strongly graduated, but occasionally plants with weakly graduated involucres, and which are otherwise normal for the variety, are found (e.g., McVaugh 17244 from Jalisco). Rarely, the habital indeterminacy seen so clearly in L. macrocephala is exhibited; thus, plants are on occasion found growing as subshrubs woody, if at all, near the base only (e.g., McVaugh & Koelz 156 from Aguascalientes, Becker & Olsen 52 from Jalisco).

L. ceanothifolia var. verbenifolia replaces var. ceanothifolia in southwestern Jalisco, Nayarit, and extreme southwestern Sinaloa, where it is locally common; it is also found in extreme western Michoacan. It tends to prefer moister areas than does var. ceanothifolia. It is characterized by its usually fine-appressed pubescence, its mostly oblong, often subpenninerved leaves, and by its usually non-exserted awns. It is closest to var. ceanothifolia, and overlaps it in distribution in the areas near Guadalajara, Jalisco, and Coalcoman, Michoacan. Variety verbenifolia, relative to var. ceanothifolia, is a morphologically homogenous taxon. The concept of L. ceanothifolia var. verbenifolia adopted here is not equivalent to Zexmenia ceanothifolia var. conferta (DC.) A.

Gray (Lipochaeta ceanothifolia β conferta DC.), the type of which was from Morelos (and considered here to represent var. ceanothifolia). Much of the material here considered to represent var. verbenifolia has been termed "var. conferta"; the type of Calea verbenifolia DC., a specimen of Née at Geneva (!), represents var. verbenifolia as here understood. Zexmenia cordifolia Blake, based on depauperate material collected in Nayarit, is ordinary var. verbenifolia well past flowering and fruiting.

L. ceanothifolia var. gradata replaces the other varieties of L. ceanothifolia along the Pacific slope of the southern and central Sierra Madre Occidental. It is characterized by its thin leaves, soft pubescence, slender branches, and short-awned disc achenes. It is a constant and distinct taxon from Sinaloa northwards. Near San Blas, in coastal Nayarit, plants which resemble both var. gradata and var. verbenifolia occur; these have been called Zexmenia microcephala Hemsl. Plants from that area usually have purple-tinged involucres, thick leaves with white-pubescent undersides, and non-exserted awns, and are rather distinctive.

L. ceanothifolia var. gracilis is the most distinctive variety of L. ceanothifolia. It occurs mostly on the Pacific slope in southern Sinaloa and Nayarit, and tends to prefer moist wooded habitats. It is characterized by its strongly and conspicuously nerved middle and outer phyllaries, which are usually green and often glabrous, its slender branches, and its generally sparse pubescence. There appears to be a phenological differentiation between var. gracilis and var. verbenifolia in Nayarit, the former tending to bloom earlier (August-September), the latter later (October-December). Plants of this variety from western Michoacan (e.g., Hinton 15157) tend to have larger heads (ca. 1 cm wide) than plants

from farther east.

Interactions involving apparent hybridization between L. ceanothifolia and L. helianthoides, L. macrocephala, L. crocea, and L. fruticosa are discussed under those species.

7. Lasianthaea seemannii (A. Gray) K. Becker, comb. nov. Zexmenia seemannii A. Gray. Pl. Wright. 1:114, 1852. TYPE: MEXICO: Cerro de Pinal, Dec 1848, Seemann 1476 (HOLOTYPE: K(herb. Hook.); ISOTYPES: GH(2),K(herb. Benth.),NY,UC(frag.)).

Slender, often several-stemmed shrubs 1-2 m high; young branches strigose. Leaves all opposite; petiole 0.5-1 (-2) cm long, its margins usually hispid, otherwise strigose; blade coriaceous, lustrous, narrowly elliptic, elliptic -oblong, or lance-elliptic, occasionally somewhat falcate, (2-) 5-12 cm long, (0.5-) 1-3 (-4) cm wide, acute or rounded-mucronulate, cuneate at base, scabrous with appressed hairs above, strigose below, margin thickened and often slightly revolute, shallowly serrate, conspicuously triplinerved. Inflorescence (1-) 3 (-6) -headed, terminal and from upper axils. Peduncles (0.1-) 0.2-1.5 (-2.1) cm long, stout, white-strigose; heads to ca. 2 cm wide across extended rays. Involucre cylindro-campanulate to campanulate or broadly campanulate, 1.0-1.6 cm high, 0.5-1.0 cm wide, phyllaries graduated in 4-5 series. Phyllaries generally lustrous, often tinged red-violet towards apex; outer phyllaries indurated, parallel-nerved below, reticulate-veiny, and more or less herbaceous above, rounded and obtuse, or 2-several-lobed, ovate-oblong to broadly ovate in outline, 3.5-4 mm long, 2-3 mm wide, strigillose dorsally above, inner phyllaries membranous below, somewhat herbaceous at apex, elliptic- to ovate-oblong in outline, 11-16 mm

long, 3-6 mm wide, apex rounded, ampliated, and often spreading. Rays 5-8, yellow, lamina 6-10 mm long, 3.5-5 mm wide, tube 4-5 mm long. Disc florets 8-20, yellow, 7.5-8mm long, throat narrowly campanulate to campanulate, 5-6 mm long, 1.4-2 mm wide, lobes 0.7-1.0 mm long. Anther thecae dark brown, 2.5-3.5 mm long, appendage 0.7-1.0 mm long. Style branches (3.2-)4-5.5 mm long, appendage 1.0-1.2 mm long. Pales sometimes tinged red-violet towards apex, 7-10 mm long, (0.5-) 0.7-1.2 mm wide as folded. Disc achenes cuneate, 2-awned, body 4-5 mm long, 1.4-2 mm wide, lustrous and glabrous, awns (1-) 3-6 mm long, not or only slightly (to ca. 1 mm) exserted from ripe heads, pappus squamellae (0-) to 1.5 mm long, usually strongly connate; awns and squamellae often tinged red-violet. Ray achenes 3-awned, body 4-5 mm long, 1.5-2.5 mm wide, awns 2-3.2 mm long, otherwise as in disc. Receptacle flat to low-convex. Usually open slopes in grassland, oak, or occasionally pine-oak forest. Southern Sierra Madre Occidental and western end of Transverse Volcanic Belt in western Mexico, at altitudes from 300-2400 m. Blooming October to March.

Selected specimens:

MEXICO: DURANGO: La Bajada, alt. 300-600 m, Nov 1921, Ortega 4448 (GH,US). NAYARIT: Near Pochotitlan, alt. ca. 3000 ft, 12 Nov 1961, Gentry, Barclay, and Arguelles 19519 (LL,US). Tepic, 5 Jan to 6 Feb 1892, Palmer 1857 (GH,NY,US). 25 km by road S of Tepic, along road between Tepic and Compostela, alt. ca. 3000 ft, 18 Oct 1970, Webster & Breckon 15730 (F,GH,MEXU,MICH). SINALOA: E facing slope of the Bufa de Surutato, along road to Surutato, 3 mi SE of Los Ornos, alt. 7200 ft, 4 Nov 1969, Breedlove & Kawahara 16962 (CAS,MICH). Sierra de Choix, 50 mi NE of Choix,

15 Oct 1898, Goldman 249 (GH,NY,US). SONORA: Canon Estrella, dist. Alamos, 1 Oct 1933, Gentry 398 (DS,MICH); Gentry 451 (MICH). Sierra de Alamos, 14 Mar 1910, Rose et al. 12801 (NY,US).

Lasianthaea seemannii is isolated and distinct from other members of the genus morphologically and phenologically. It is found, rather sparsely, along the length of the Sierra Madre Occidental, and in Nayarit. L. seemannii is distinctive in its coriaceous, lustrous, strongly triplinerved, typically oblong leaves, and in its highly graduated (4-5 seriate) involucre with lustrous outer and middle phyllaries. Its late (November-December) date of blooming is displaced from that of the other shrubby, yellow-rayed Lasianthaeas found on the Pacific slope of the Sierra Madre Occidental and in northern Nayarit.

L. seemannii exhibits the habital variability shown in several other typically shrubby Lasianthaeas. It is usually a shrub, but, especially in grazed grasslands near the southern end of its range in Nayarit, it grows as a several-stemmed half-shrub.

8. Lasianthaea zinnioides (Hemsl.) K. Becker, comb. nov. Zexmenia zinnioides Hemsl., Biol. Cent.-Am. Bot. 2:175, 1881. TYPE: MEXICO: Cerro de Pinal, Dec 1848, Seemann 1464 (HOLOTYPE: K(herb. Hook.); Fragment: GH; Photos: F,GH,MICH,US; ISOTYPE: K(herb. Benth.)).

Perennials from a woody caudex producing several fleshy-tuberous rootstocks underground, sometimes woody near base, to 1 m high; young branches strigose to hirsute. Leaves all opposite, about 5 pairs per stem; petiole 1-2 (-5) mm long, hirsute; blade firm, lance-elliptic, lance-ovate to narrowly ovate, or occasionally lance-oblong, 3.0-7.5 (-12.5) cm long, 1.2-3.0 (-4.2) cm wide, acute, acuminate or occasion-

ally obtuse, rounded to cuneate at base, hirsute and scabrous above, hirsutulous below, margin usually shallowly serrate, occasionally serrate or denticulate-mucronulate, triplinerved. Inflorescence 1-3 (-9) -headed, terminal and from upper axils. Peduncles 0.2-3.5 cm long, stout, whitish-strigose or hirsute; heads to 4 cm wide across extended rays. Involucre broadly campanulate to usually hemispherical, 1.0-1.2 cm high, 1.0-2.0 cm wide, phyllaries in 3-4 series, not strongly graduated. Phyllaries often tinged red-violet; outer phyllaries indurated below, green and herbaceous above, narrowly ovate, ovate, or lance-deltoid, 7-8 mm long, 3-4 mm wide, to 6 mm wide at base, acute, puberulent and white-hirsute dorsally, inner phyllaries membranous-indurate below, membranous, slightly herbaceous, reticulate-veiny, and often dark-purple-tinged above, ovate-oblong to elliptic-oblong, 10-12 mm long, 5-7 mm wide, rounded to obtuse and mucronulate. Rays typically 8, dark-red or red-violet, lamina 16-18 mm long, 5-7 mm wide, tube 3-4.5 mm long. Disc florets to ca. 35, red-violet, 7.5-9 mm long, throat narrowly campanulate, 3.3-3.7 mm long, 1.0-1.6 mm wide, lobes 1.0-1.2 mm long. Anther thecae brown, 2.4-2.9 mm long, appendage 0.7-0.8 mm long. Style branches 2.5-3 mm long, appendage 0.7-1.0 mm long. Pales usually tinged red-violet, 7-10 mm long, 0.6-1.0 mm wide as folded. Achenial awns often tinged red-violet; disc achenes cuneate to broadly cuneate, body 3.0-4.1 mm long, 1.2-1.8 mm wide, hispidulous or glabrate, awns 1-4 mm long, not exserted from ripe heads, pappus squamellae 0.1-0.6 mm long, or sometimes reduced to a ciliate fringe, not strongly connate. Ray achenes 3-awned or -toothed, body 3-3.5 mm long, 1.8-2.1 mm wide, awn (adaxial) to 2.8 mm long, pappus squamellae connate. Receptacle convex or low-convex. Shaded slopes, grazed areas, in oak or pine-oak forest or palm savannah. Southern Sierra

Madre Occidental and western end of Transverse Volcanic Belt in western Mexico, at altitudes from 50-1550 m. blooming (March-) August to November.

Selected specimens:

MEXICO: DURANGO: without locality, 16 Aug 1897, Rose 2322 (GH,US). NAYARIT: 12 mi SE of Acaponeta, alt. ca. 150 ft, 3 Oct 1962, Cronquist 9592 (NY). Valley of the Rio Jesús María near village of Jesús María, alt. 600-700 m, Sept 1960, Feddema 1399 (FNCB,MICH). SINALOA: 5 km W of Santa Lucia, alt. 1100-1200 m, 11 Sept 1974, Becker & Cronquist 5 (NY). Cerro del Cuerbo, Concordia, alt. 516 m, Sept 1919, Dehesa 1070 (US). El Batel, Sierra Madre, alt. 4000 ft, 18 Nov 1925, Mexia 482 (CAS,UC). Mazatlan, May 1921, Ortega 1070B (F,K). Pichacos, Rosario, Oct 1932, Ortega 7152 (CAS,F). Santa Lucia, E of Panuco, alt. 900-1200 m, 28 Aug 1935, Pennell 20029 (PH,US).

Lasianthaea zinnioides is a very distinctive herbaceous perennial species, unique in the genus in its red-violet rays. It exhibits an extreme in a tendency towards anthocyanic, red-violet tipped pales and phyllaries shown throughout the genus. It is a species of the southern end of the Pacific slope of the Sierra Madre Occidental and of northern Nayarit, and is comparable in geographical range and morphological distinctness with L. seemannii. L. zinnioides is very uniform morphologically throughout its range. It has a stronger tendency towards distal branching than do the other herbaceous perennial Lasianthaea species.

9. Lasianthaea palmeri (Greenm. in W. W. Jones) K. Becker, comb. nov. Zexmenia palmeri Greenm. in W. W. Jones, Proc. Amer. Acad. 41:149, 1905. TYPE: MEXICO: JALISCO: In ravines, Rio Blanco, June 1886,

Palmer 50 (HOLOTYPE: GH; Photo: NCB; ISOTYPES: G,K,NY(2),P,PH,US (2)).

Zexmenia xylopoda W. W. Jones, Proc. Amer. Acad. 41:150, 1905. TYPE: MEXICO: JALISCO: Rio Blanco, Oct 1886, Palmer 757 (HOLOTYPE: GH; Photo: NCB; ISOTYPES: G,K,MEXU,MO,NY(2),P,PH,US(2),WU).

Zexmenia media Blake, Contr. U. S. Nat. Herb. 22:630, 1924. TYPE: MEXICO: JALISCO: Near Huejuquilla, 25 Aug 1897, Rose 2549 (HOLOTYPE: US; ISOTYPE: GH).

Perennials from a woody caudex usually producing several fleshy-tuberous rootstocks underground, sometimes stoloniferous, usually not branching above, 0.25–0.6 (0.75) m high; stems often purple-tinged, appressed-hispid to strigose, below often hirsute, or occasionally glabrate. Leaves opposite or sometimes alternate in inflorescence, 4–5 (–7) pairs per stem; petiole 2–7 mm long, hirsute; blade usually firm, oldest leaves orbicular to broadly ovate, ca. 2 X 2 cm, main cauline leaves lance-elliptic to ovate, 3.5–10.5 (–12.5) cm long, (1.0–) 1.3–4.5 (–5.0) cm wide, acute to short acuminate, cuneate to truncate at base, scabrous and hispid above, appressed to spreading hispid and hispidulous, occasionally sparsely so, below, margin with lower ca. $\frac{1}{4}$ entire, the remainder coarsely to shallowly serrate to serrulate, triplinerved or occasionally subpenninerved. Inflorescence 1 -or 3- headed, terminal, occasionally subtended by 1-2 small, alternate bracts to ca. 2 cm long, 0.5 cm wide, sometimes alternately branched. Peduncles (1–5.5–) 6–20 cm long, stout, whitish-strigose to hispid, especially above, or nearly glabrate; heads 3–5 cm wide across extended rays. Involucre usually broadly campanulate to hemispherical, or occasionally campanulate,

0.9-2.0 cm high, 0.9-2.0 cm wide, phyllaries in ca. 3 series, subequal or outer slightly longer than inner. Outer phyllaries membranous-indurate below, herbaceous above, lance-oblong or ovate-to lance-deltoid, 8-20 mm long, (2-) 3-7 mm wide, acute, white-strigose and puberulent, or sometimes glabrous except for ciliate margin, middle phyllaries membranous, conspicuously veined, 3-lobed, often violet-tinged near apex, inner phyllaries membranous, ovate-oblong to linear, 8-11 mm long, 2-3.5 (-4) mm wide, acute to rounded, usually violet-tinged above. Rays 8-15, yellow, or orange-yellow, lamina 12-17 (-20) mm long, 4-7 mm wide, tube 3-4.5 (-5) mm long. Disc florets 38-65, yellow, (7.0-) 7.3-10.5 mm long, throat narrowly campanulate, 6.3-9.5 mm long, 1.7-2.6 mm wide, lobes 1.0-1.7 mm long. Anther thecae brown or blackish, 2.5-3.5 mm long, appendage 1.0-1.3 mm long. Style branches 2.5-3.6 mm long, appendage 0.7-1.1 mm long. Pales 7.5-10 mm long, 0.9-1.3 mm wide as folded. Disc achenes cuneate, 2-awned, body 3.8-5.5 mm long, 1.3-2.0 mm wide, glabrous or sparsely puberulent above, awns 2-4 mm long, tips occasionally purple-tinged, pappus squamellae usually reduced to a ciliate fringe to 0.7 mm long, or none. Ray achenes 3-awned or -toothed, body 3.5-6 mm long, 1.5-3 mm wide, awns 1-3 mm long, pappus squamellae to 0.5 mm long or usually none. Receptacle low-convex. Roadsides, slopes, pasture-land in oak, pine-oak, pine, and grassland regions. Mostly at the western end of the Transverse Volcanic Belt, at altitudes from 800-2500 m. Blooming July to November.

Selected specimens:

MEXICO: AGUASCALIENTES: Road to Calvillo, 21 mi W of Aguascalientes, alt. 2100 m, 3 Nov 1959, McVaugh & Koelz 150 (MNCB,MICH). DURANGO: Canyon of the Rio Jaral, about 50 mi W of Durango and 15 mi NW of Los

Coyotes railroad station, alt. 7100 ft, 1 Oct 1962, Cronquist 7575 (MICH,NY). JALISCO: 1.7 rd-mi above (S of) Puente Guadalupe, alt. 1180 m, 9 Aug 1968, Anderson & Anderson 5103 (ENCB,MICH). 7 km SE of Tequila, alt. 1550 m, 14 Sept 1974, Becker & Cronquist 12 (NY). Hillside above Guadalajara, alt. 1700 m, 15 Sept 1974, Becker & Cronquist 14 (NY). 50 km SE of Guadalajara, alt. 1700 m, 19 Sept 1974, Becker & Cronquist 25 (NY). Lomas del Valle, alt. 1560 m, 25 July 1967, Díaz L. 210 (MICH). 4 mi NNE of Talpa de Allende, alt. 1450-1500 m, 12-13 Oct 1960, McVaugh 20101 (ENCB,LL,MICH,NY). Hills near Guadalajara, alt. 5000 ft, 12 Aug 1902, Pringle 11001 (K,F,GH,MICH,MO,NY,US). Los Yerbanis, 8 km NW of El Platanar, mun. San Martin de Bolanos, alt. 2000 m, 1 Sept 1968, Rzedowski 26139 (DS,ENCB,F,MEXU,MICH,NY). La Primavera, Venta del Astillero, 27 July 1963, Villareal P. 76 (ENCB). Cerro del Tepopote, Sierra de la Venta, 30 km W of Guadalajara, alt. 1700 m, 3 Sept 1967, Villareal P. 1317 (ENCB,MICH). 13 mi SSW of Autlan toward La Resolana, alt. ca. 4000 ft, 15 Aug 1949, Wilbur 2366 (DS,LL,MICH,US). MICHOACAN: Field along rt 15, ca. 33 mi W of Morelia, 5 Aug 1960, King 3630 (MICH, NY,TEX,UC,US). 12 mi N of Zacapu, alt. 2000 m, 14 Aug 1961, Longpre 128 (MSC). NAYARIT: 10 mi SE of Ahuacatlan, alt. 1100-1300 m, 11-12 Aug 1959, Feddema 309 (ENCB,MICH). NE of Santa María del Oro, alt. ca. 1000 m, 18-20 Aug 1959, Feddema 617 (CAS,ENCB,MICH,TEX). Km 870, 22 mi SE of Tepic, alt. 1150 m, 26 Aug 1957, McVaugh 16383 (G,MEXU,MICH,NY,US). 40 km SE of Tepic, alt. 1300 m, 4 Sept 1960, Rzedowski 14319 (ENCB). SINALOA: Mala Noche, Concordia, alt. 1600 m, Sept 1919, Dehesa 1530 (US). Santa Lucia, Concordia, alt. 1000 m, Sept 1919, Dehesa 1625 (US).

Widespread in west-central Mexico, especially Jalisco, Lasianthaea palmeri shows similarities to L. podocephala, and to a lesser ex-

tent, L. aurea (the other yellow-rayed perennial herbaceous Lasianthaeas) but is distinct from both. From L. aurea, L. palmeri is easily distinguished by its non-exserted pales, by its consistently 2-awned (not 3-awned) disc achenes, and by features of pubescence and aspect. From L. podocephala, a close relative of L. palmeri in northern Mexico and Arizona, palmeri is distinguished by leaf texture (firm in palmeri, thin in podocephala), head shape (broadly campanulate in palmeri, hemispherical in podocephala), and in shape of outer phyllaries (usually acute in palmeri, obtuse in podocephala). Further collections from the relatively poorly collected areas of the Sierra Madre Occidental in norther Durango, northern Sinaloa, and southern Chihuahua, where there is apparently an hiatus between the ranges of L. palmeri and L. podocephala, would be of considerable interest.

Included in our concept of L. palmeri are two variants which have been given taxonomic recognition at the specific level in the past. Plants of L. palmeri with small heads, short peduncles, and small leaves have been collected in Jalisco, and appear to be a dwarfed form. it has been collected in northern (Rose 2549, the type of Zexmenia media Blake) and central (Becker & Cronquist 12) Jalisco. A glabrate form of L. palmeri, with ciliate outer and middle phyllaries and leaf margins, has been called Zexmenia xylopoda W. W. Jones. It is ordinarily found growing with typically pubescent L. palmeri at the few localities in the Guadalajara region where it is known to occur. Aside from the type (Palmer 757, some plants of which collection represent L. palmeri with typical pubescence), the following collections may be cited as representing this glabrate form of L. palmeri: Becker & Cronquist 14, Villareal de P. 76, 1317.

10. Lasianthaea podocephala (A. Gray) K. Becker, comb. nov. Verbesina podocephala A. Gray, Pl. Wright. 2:92, 1853. Zexmenia podocephala (A. Gray) A. Gray, Syn. Fl. 1:286, 1884. TYPE: MEXICO: SONORA: Mountain valleys between the San Pedro and the Sonoita, and in a ravine at Santa Cruz, Sept 1851, Wright 1232 bis (HOLOTYPE: GH; ISOTYPES: BM,K(herb. Benth.),K(herb. Hook.),GH(2),P).

Perennials from a woody caudex producing several fascicles of fleshy-tuberous rootstocks below ground, occasionally branching above, 0.15-0.6 m high; stems below often densely hirsute, above often appressed-hispid. Leaves opposite or occasionally alternate in inflorescence, 4-5 pairs per stem; petiole (0.5-) 1-2 (-3) mm long, hispid; blade usually thin, oldest leaves often suborbicular, ca. 3.5 X 3.5 cm to 2 X 2 cm, most leaves ovate to lance-ovate, 0.3-1 cm long, 0.2-0.5 cm wide, acute or occasionally acuminate, rounded to subcordate at base, scabrous and hispid above, spreading-hispid, especially along veins, below, coarsely, shallowly, or crenate-serrate, triplinerved. Inflorescence 1- or 3-headed, terminal, occasionally subtended by 1-2 alternate peduncular bracts ca. 1 (-2) cm long, 0.5 -1.0 cm wide. Peduncles 6-35 cm long, stout, appressed-hispid to white-strigose, or occasionally canescent; heads 2.5-3.5 cm wide across extended rays. Involucre hemispherical, 0.7-1.4 cm high, 1.1-2.5 cm wide, phyllaries in 2-3 series, subequal. Outer phyllaries usually more or less indurate-membranous below, herbaceous and reticulate-veiny above, lance-ovate, ovate-oblong, or orbicular, 6-12 mm long, 2-8 mm wide, acute or usually obtuse, spreading and usually densely white-hispid, occasionally canescent, dorsally, middle phyllaries conspicuously nerved, often violet-tinged above, inner phyllaries membranous, oblong, 5.0-8.5 mm long, 1.4-4 mm wide, acute to rounded. Rays

11-14, yellow or orange-yellow, lamina 7.5-13 mm long, 3-6 mm wide, tube 2.5-3.5 mm long. Disc florets 36-113, yellow, 5.0-7.0 mm long, throat campanulate, 4.2-6 mm long, 1.0-2.0 mm wide, lobes 0.9-1.1 mm long. Anther thecae brown, 2.0-2.7 mm long, appendage 0.4-0.6 mm long. Style branches 1.9-3.5 mm long, appendage 0.6-1.0 mm long. Pales 6-9 mm long, 0.6-1.1 mm wide as folded, apex often violet-tinged. Disc achenes broadly cuneate, 2-awned, body (2.5-) 2.8-5.0 mm long, 1.2-2.0 mm wide, glabrate or puberulent above, awns 1.5-5.8 mm long, occasionally red-violet tipped, margins sometimes almost winglike, pappus squamellae reduced to a ciliate fringe or none. Ray achenes 3-awned, body 2.5-4.5 mm long, 1.3-2.4 mm wide, glabrate, awn (adaxial) 1.0-3.7 mm long, otherwise as in disc. Receptacle low-convex. Roadsides, hillsides, wood edges, in oak, oak-juniper, oak-pine and grassland regions. Extreme southeastern Arizona and northern Sierra Madre Occidental in northwestern Mexico, at altitudes from 1000-2300 (-3000) m. Blooming June to October.

Selected specimens:

MEXICO: CHIHUAHUA: 16 mi W of Santa Buenaventura, alt. 7500 ft, 31 Aug 1975, Becker & Olsen 43 (NY). 67 mi W of La Junta on Mex 16 (Km 50), alt. 7800 ft, 31 Aug 1975, Becker & Olsen 44 (NY). Guasaremos, Rio Mayo, 26 Aug 1936, Gentry 2468 (F,GH,K,MEXU,MO,S,UC,US). Majalca, 18-20 Aug 1935, LeSueur 155 (CAS,DS,F,GH,K,MO,PH,TEX(2),UC). Rocky hills near Chihuahua, 29 Aug, 29 Sept 1885, Pringle 349 (BM,BR,F,G,GH,K,LL,MICH(2), NY(2),P(4),PH(3),RSA(2),US(3),W,WU). Sierra Madres near Colonia Garcia, alt. 7500 ft, 4 Aug 1899, Townsend & Barber 219 (F,G,GH,K,MICH,NY,PH,RSA, UC,US). Carretas, near Sonora border, mun. Janos, alt. 4800 ft, 26-28 Aug 1939, White 2600 (GH,MEXU,MICH). SONORA: Curohui, Rio Mayo watershed, alt. 400-1000 m, 25 Aug 1959, Arguelles 149 (GH,LL,US). Alamos, 25

Mar to 8 Apr 1870, Palmer 362 (GH,US). Yecora, 3 Aug 1970, Pennington no. 111 of 1970 (TEX). Cañon de Huepari, N of Aribabi, alt. 4300 ft, 2-3 Sept 1939, White 2630 (GH,MICH). Cañon de las Estacas, 30 July 1940, White 3072a (MICH), White 3089 (MICH). Cañon de Bavispe, 11-14 Aug 1940, White 3258 (GH,MEXU,MICH). El Rancho del Noble, N. of El Tigre, alt. 6000 ft, 2-13 Sept 1941, White 4333 (GH,LL(2),MICH,PH). UNITED STATES: ARIZONA: Huachuca Mts., Coronado National Monument, Montezuma Canyon, alt. 1870 m, 6 Sept 1974, Becker & Cronquist 1 (NY). Patagonia Mts., 20 km E of Nogales, alt. 1700 m, 6 Sept 1974, Becker & Cronquist 2 (NY). Cochise Co., Ft. Huachuca, Huachuca Canyon, alt. 8000 ft. 30 Aug 1975, Becker & Olsen 42 (NY). Santa Cruz Co., Nogales to Ruby, 25 Aug 1940, Kearney & Peebles 14860 (LL,US). Huachuca Mts., Aug 1882, Lemmon 374 (F,G,P,UC,US(2)). Santa Cruz Co., 4 mi SW of Patagonia, 26 Aug 1971, Pinkava et al. 806 (ENCB). Cochise Co., 2.3 mi E of Turkey Creek, crossing Chiricahua Mts., 27 Aug 1971, Pinkava et al. 874 (ENCB). Pima Co., Florida Canyon, Santa Rita Mts., alt. 5000 ft, 18 Aug 1933, Shreve 6330 (F).

Lasianthaea podocephala, a yellow-rayed herbaceous perennial common on both slopes of the northern Sierra Madre Occidental, is most closely related to the central Mexican L. palmeri. Aside from range, L. podocephala is distinguished from L. palmeri by a number of morphological characters, as discussed under L. palmeri. L. podocephala is more uniform morphologically than is its southern relative. The disc achenes of L. podocephala are of interest in that both margins are sometimes drawn out into thin, somewhat winglike, edges.

11. Lasianthaea aurea (D. Don) K. Becker, comb. nov. Wedelia ? aurea

D. Don, Bot. Mag. t. 3384, 1835. Telesia aurea Raf., Fl. Tellur. pt. 2:41, 1836. Verbesina aurea (D. Don) DC., Prodr. 5:613, 1836. Zexmenia aurea (D. Don) B. & H., Gen. Pl. 2:371, 1873. TYPE: MEXICO: Hort. Barcl. (HOLOTYPE: K(herb. Hook.); Fragment and photo: US; Photos: GH,US; Tracing of Bot. Mag. plate # 3384: GH; ISOTYPES: K (herb. Benth.)).

Verbesina tuberosa Klatt, Ann. Naturh. Hofmus. Wien 9:361, 1894. TYPE: MEXICO: Schmitz 248 (HOLOTYPE: W; ISOTYPE: GH).

Perennials from a woody caudex usually producing several small fleshy-tuberous rootstocks underground, occasionally stoloniferous, usually unbranched above, 0.10-0.60 m high; young stems white-strigose and sometimes also sparsely hispid, or hispid to villous-canescent. Leaves opposite or rarely ternate, often becoming alternate above, usually 3-5 pairs per stem; petiole (0-) 1-2 (-3.5) mm long, white-strigose to hirsute; blade firm, oldest leaves often very small, orbicular and obtuse, main cauline leaves lance-ovate, or narrowly lanceolate, varying to linear-oblong and elliptic, (1.0-) 2.0-7 (-7.5) cm long, 0.3-3 cm wide, acute to obtuse, cuneate to rounded or subcordate at base, scabrous and hispid above, appressed white-hirsute, especially along veins, below, margin denticulate-mucronulate, shallowly serrate, serrate, or occasionally coarsely serrate, triplinerved, usually with an additional pair of strong secondary veins several mm above base. Inflorescence (1 - 2- 3-5 -headed, terminal, often subtended by 1-2 small, alternate peduncular bracts. Peduncles 0.7-16 cm long, slender to stout, white-strigose or hirsute; heads 2-3 (-3.5) cm wide across extended rays. Involucre hemispherical to occasionally broadly campanulate, 0.5-0.9 cm

high, (0.6–) 0.8–1.4 (–1.8) cm wide, phyllaries in 2–3 series, subequal. Outer phyllaries indurate below, herbaceous, occasionally spreading, and usually rigid above, ovate, suborbicular, elliptic, or occasionally lanceolate, (4.5–) 5–7 mm long, (2–) 3–6 mm wide, obtuse and mucronate to occasionally short-acute, often with red-violet tips, white-strigose to white-hispid dorsally, inner phyllaries membranous, ovate-oblong to lance-ovate, 5–7.3 mm long, (1.5–) 1.9–3 mm wide, acute and usually violet-tinged above. Rays 6–11 (–15), yellow or orange-yellow, lamina 0.8–1.7 mm long, (3–) 4–7 mm wide, tube 2.0–2.6 mm long. Disc florets 25–40 (–ca. 100), orange-yellow, 5.9–8.0 mm long, throat campanulate to narrowly campanulate, 5–7 mm long, 1.5–2.1 mm wide, lobes (0.7–) 0.9–1.5 mm long. Anther thecae brown or dark brown, 1.9–2.6 mm long, appendage 0.6–1.0 mm long. Style branches 1.7–2.7 mm long, appendage 0.5–1.0 mm long. Pales 5–7 mm long, 0.7–1.2 mm wide as folded, exserted 1–5 mm from heads. Disc achenes broadly cuneate, 2- or 3- awned, body 2.5–3.5 mm long, 1.2–2.0 mm wide, usually brown-gland-dotted, hispidulous or glabrate, awns 2–4.5 mm long (adaxial longest), adaxial margin usually with winglike edge to 0.5 mm wide, pappus squamellae none. Ray achenes triquetrous or rarely 4-angled, 3- or rarely 4-awned, body (2.3–) 2.6–3.5 mm long, 1.3–2.0 mm wide, hispidulous to glabrate, awns 0.5–2.5 mm long, pappus squamellae none. Receptacle convex. Meadows, hillsides, in oak, pine-oak forest and grassland regions. Central Transverse Volcanic Belt and in Sierra Madre Oriental in Mexico, at altitudes from 1800–2800 m. Blooming July to November.

Selected specimens:

MEXICO: FEDERAL DISTRICT: 3 km SW of Santa Fé, alt. 2650 m, 6 Oct 1968, Rzedowski 26330a (IS,MNCB,LL,MICH,ISC,RSA). GUANAJUATO: Ca. 8 km

m. of Santa Rosa, alt. ca. 2400 m, 10 Nov 1970, McVaugh 24146 (MNCB, MICH). HIDALGO: Zena Station, alt. 8000 ft, 26 Aug 1905, Pringle 13582 (C,CAS,GH,LL,MICH,S,US). JALISCO: Las Vidrieras, El Platanar, San Martín de Bolanos, alt. 2450 m, 7 Sept 1966, Díaz L. 910 (MICH). 2 km E of Tapalpa, ca. 19°57' N, 103°45' W, alt. ca. 2000 m, 5,6,7 Aug 1960, Iltis et al. 804 (TEXU,MICH,TEX,UC). Along Hex 5, ca. 17 mi NW of Tequila, 6 Aug 1960, King 3603 (DS,TEXU,MICH,NY,TEX,UC,US). Near Km 58, road from Zapotlanejo, ca. 7 mi NW of Tototlan, alt. ca. 1800 m, 24 Aug 1958, McVaugh 17260 (MNCB,MICH,NY,US). Base of Cerro Viejo, near Cuyutlan, alt. 1900 m, 14 Aug 1970, Rzedowski 27475 (DS,MNCB,MICH). STATE OF MEXICO: Along Hex 15, ca. 4 mi W of Toluca, 3 Aug 1960, King 3586A (MICH,NY). San Geronimo, Villa del Carbon, alt. 2500 m, 30 Aug 1957, Matuda 27243 (TEXU,NY). Sierra de Alcaparrosa, near Tepotzotlan, 16 Aug 1959, Paray 2735 (MNCB,MEXU). Flor de Maria, alt. 8000 ft, 4 Sept 1890, Pringle 3239 (BR,C,CAS,DS,F,G,GH,K,LL,M,MEXU,MICH,MO,NSC,NY, P(2),PH,RSA,S,UC,US,W,WU). Cerro de la Cruz, 5 km NW of Tepotzotlan, alt. 2400 m, 23 July 1974, Rzedowski 31976 (MNCB). MICHOACAN: N of Loma del Zapote, near Morelia, alt. 1900 m, 4 Aug 1910, Arsène 5574 (B,BM,F, G,GH,MO,NY,P,US). 6 km WSW of Jacona, ca. 19°54' N, 102°22' W, alt. ca. 2000 m, 29 July 1960, Iltis et al. 529 (TEXU,MICH,TEX). SAN LUIS POTOSI: 1891, d'Aoust 392 (P), 403 (P(2)), 408 (P), 494 (P), s.n. (P(3)).

One of the yellow-rayed perennial herbs, Lasianthaea aurea is most common in central Mexico. It is an isolated member of the genus, and is distinctive in its pales, which are exserted from the heads before and during anthesis. L. aurea shows much variability in leaf shape, pubescence, head size, and shape of outer phyllaries. Plants from San Luis Potosi, near the NE limit of its range, are notable for their small leaves (1-2 cm long) with coarsely serrate margins, and their spreading pubescence.

Excluded Species

Lasianthaea nowickeana D'Arcy. Phytologia 30:6, 1976. TYPE: PANAMA: along headwaters of the Rio Cuasi, Duke et al. 3632 (HOLOTYPE: MO !). This species is known only from the type, which posesses achenes (mature ?, that are not Lasianthoid in character. Although unwinged, the achenes examined do not exhibit the characteristic ventral edge nor the stout awns of Lasianthaea. Furthermore, some achenes posess only one awn, a condition not observed in Lasianthaea. Until the taxon is better known, a position in or near Wedelia Jacq. is suggested.

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Numerical List of Taxa

1. *L. fruticosa*

1a. *L. fruticosa* var. *fruticosa*

1b. *L. fruticosa* var. *michoacana*

1c. *L. fruticosa* var. *fasciculata*

1d. *L. fruticosa* var. *occidentalis*

1e. *L. fruticosa* var. *alamosana*

1f. *L. fruticosa* var. *aggregata*

2. *L. macrocephala*

3. *L. helianthoides*

3a. *L. helianthoides* var. *helianthoides*

3b. *L. helianthoides* var. *nayaritense*

4. *L. crocea*

5. *L. squarrosa*

6. *L. ceanothifolia*

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6c. *L. ceanothifolia* var. *gradata*

6d. *L. ceanothifolia* var. *gracilis*

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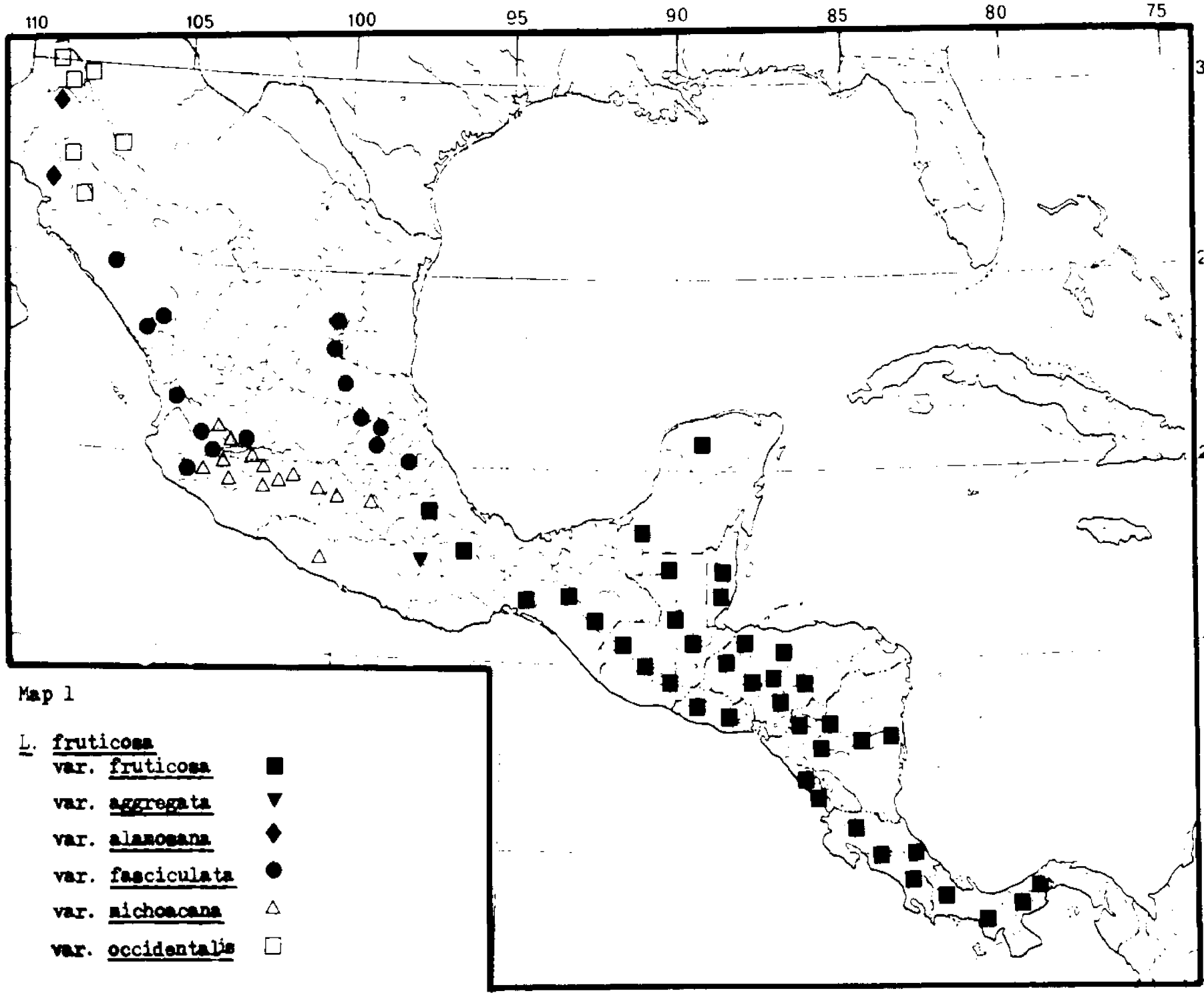


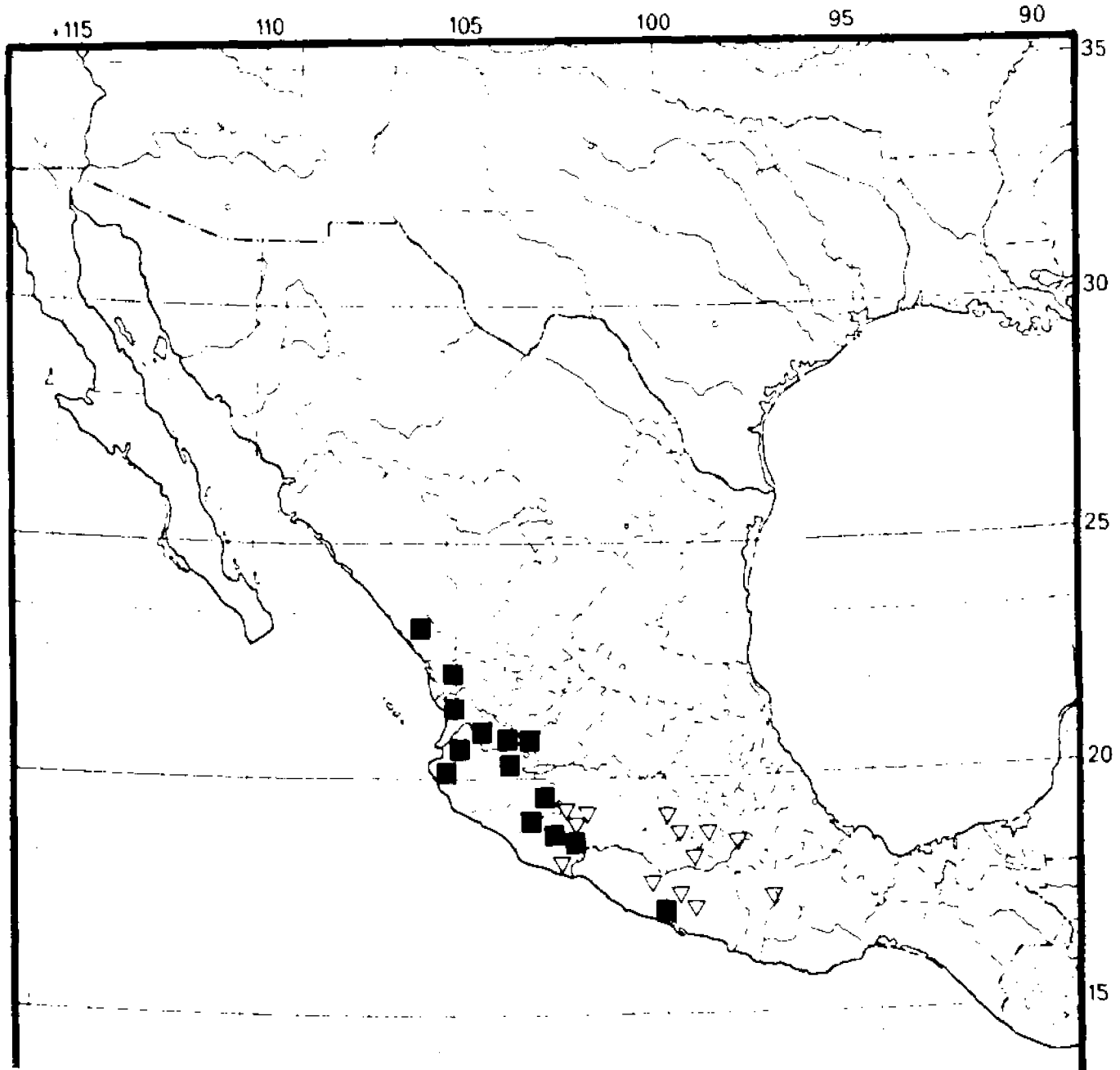
Map 1

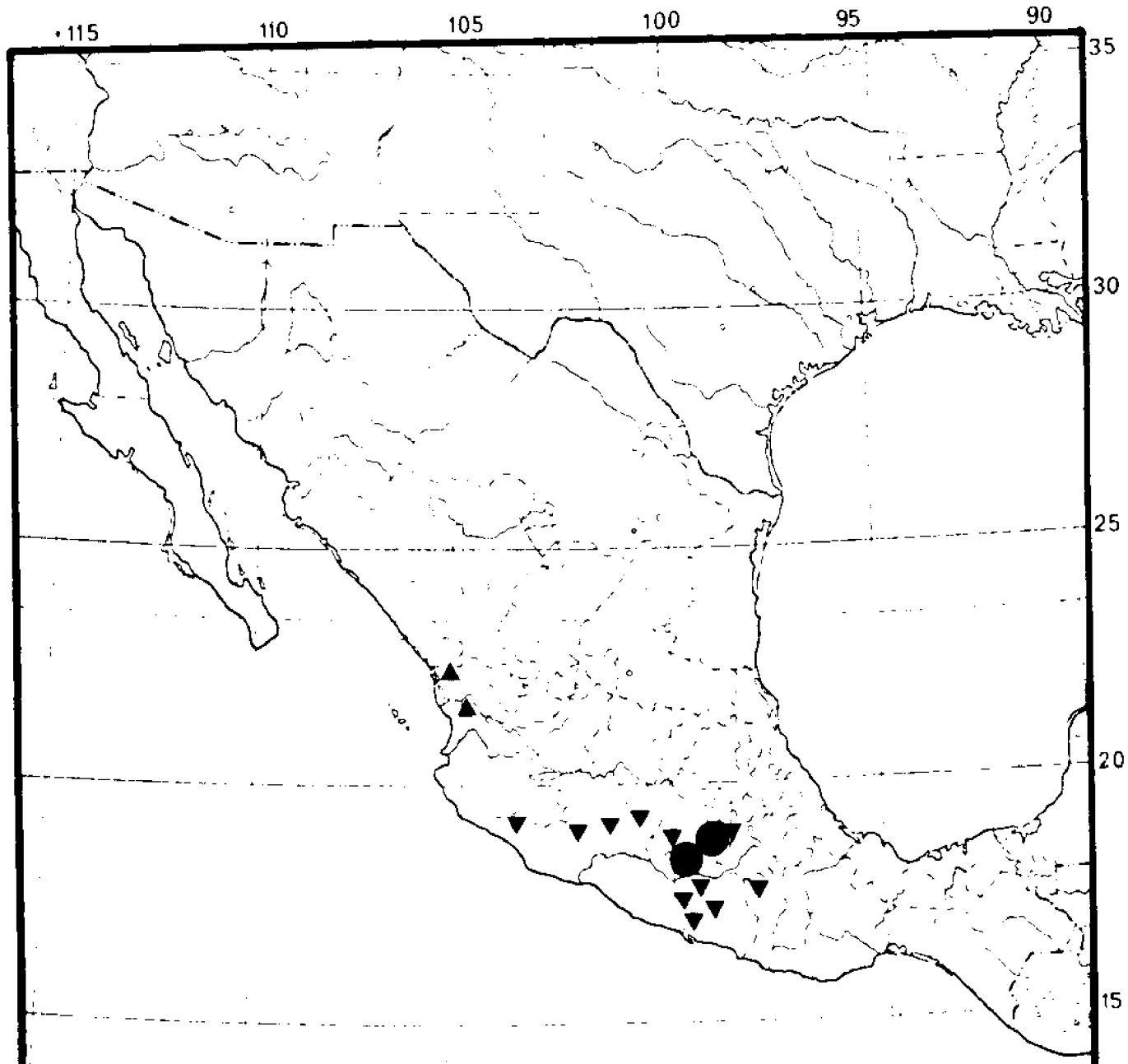
L. fruticosa
- var. fruticosa ■
- var. aggregata ▼
- var. alamosana ◆
- var. fasciculata ●
- var. michoacana △
- var. occidentalis □

Map 2

L. crocea ▽

L. macrocephala ■





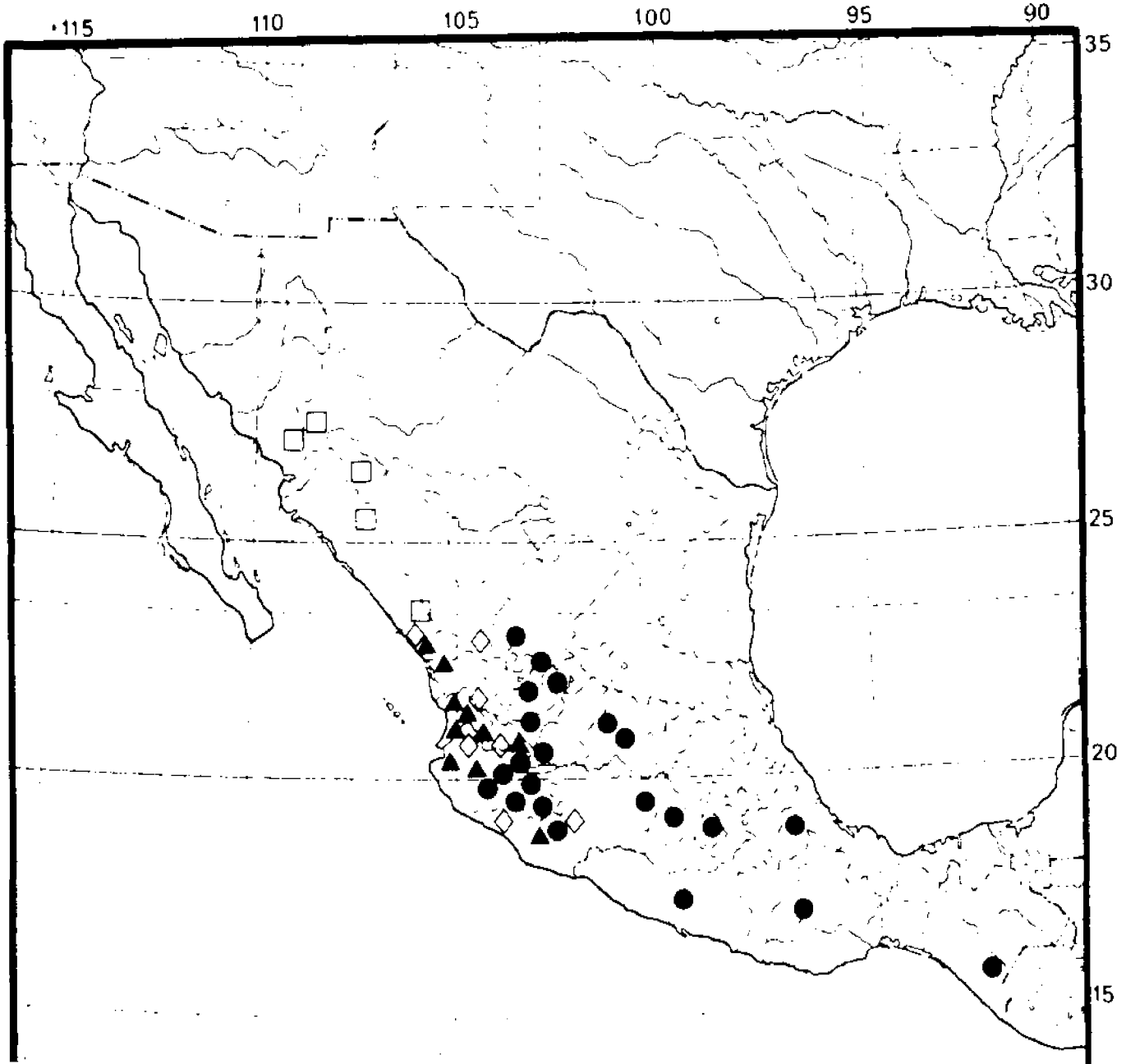
Map 3

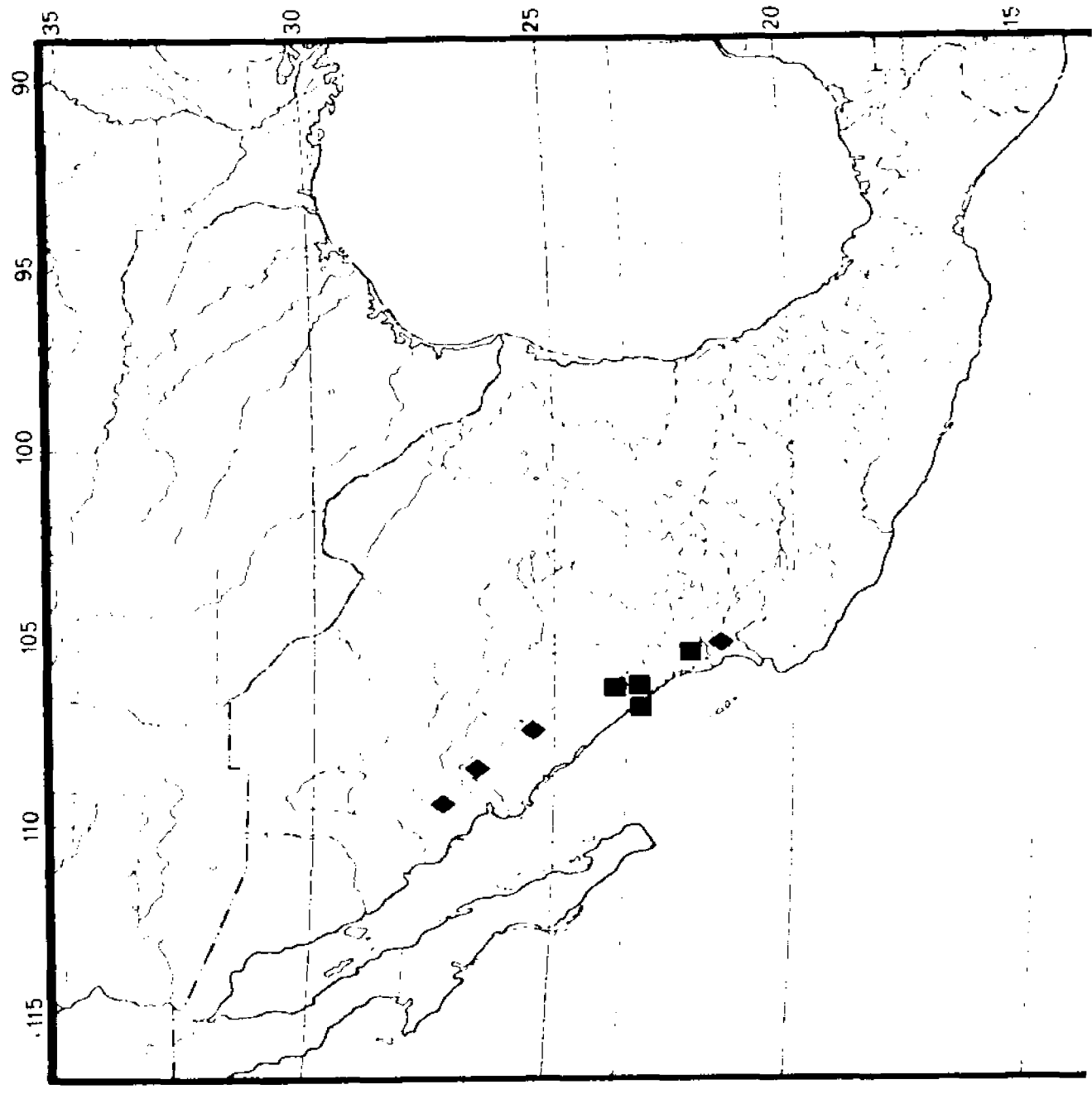
L. helianthoides
var. helianthoides ▼
var. nayaritense ▲

L. squarrosa ●

Map 4

L. ceanothifolia
- var. ceanothifolia ●
- var. gracilis ◇
- var. gradata □
- var. verbenifolia ▲





Map 5

L. **seemannii** ◆

L. **zinnioides** ■

Map 6

L. aurea ●

L. palmeri △

L. podocephala ▲