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Revision of *Lagascea* (Compositae, Heliantheae)

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Approximately 40 genera within the Compositae have secondarily aggregated flowering heads called "synflorescences" (Schultz-Bipontinus, 1861; Good, 1956; Kunze, 1969; Crisci, 1974). These usually are composed of uniflowered primary heads and sometimes are surrounded by a series of secondary involucral bracts. *Lagascea* Cav. from Mexico and Central America is the only genus of the tribe Heliantheae with secondary heads of this type (Stuessy, 1976, 1977).

In addition to provoking interest due to its synflorescence, *Lagascea* is engaging because the systematic relationships of the genus have never been understood clearly. The generic relationships have been studied recently (Stuessy, 1976), but the specific and evolutionary affinities have not been investigated in detail. The only comprehensive treatment of the genus is the synopsis of Robinson (1901), which was based upon limited herbarium material and is inadequate for a thorough understanding of the genus. The present paper is the first revision of *Lagascea*, and it is based upon herbarium, field, and laboratory studies.

TAXONOMIC HISTORY

As the history of the tribal and subtribal placements of *Lagascea* has been outlined recently in another paper (Stuessy, 1976), the following comments focus on the history of generic and infrageneric

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concepts. Only the more important contributions will be emphasized.

Plants belonging to *Lagascea* were first described as *Nocca rigida* from "New Spain" by Cavanilles (1795). Eight years later, Cavanilles (1803) described another monotypic new genus, *Lagasca*, containing *L. mollis* from Cuba. Variant spellings of both genera were provided by Willdenow as *Noccaea* (1803) and *Lagascea* (1809). In 1818, Humboldt et al. added three new species to *Lagascea*, at the same time recognizing and including the earlier described *L. mollis*.

Cassini (1822) was the first to regard *Nocca* and *Lagascea* as congeners, and for several reasons he believed *Nocca* to be the more appropriate name. Despite Cassini's merger of the two genera, Lessing (1832) continued to recognize both *Nocca* (as *Noccaea*) and *Lagascea* as distinct. DeCandolle (1836) followed Cassini in treating the two genera as synonymous (under the name *Lagascea*) and, following previous generic distinctions, he recognized two sections: *Lagasca* (with *L. mollis*); and *Noccaea* (with six species, three newly described). This perspective was followed by Bentham and Hooker (1873) and Hoffmann (1890) who recognized seven to eight species.

Robinson's synopsis in 1901 was the first overview of the genus since the treatment by DeCandolle (1836). Thirteen valid species were included, with two described as new. No sections were used. In addition, the earliest name, *Nocca*, was adopted for the genus. This position was changed later by Robinson (1907) in accord with the decision to conserve *Lagascea* against *Nocca* at the third international Botanical Congress of 1905 in Vienna (a position followed by subsequent congresses; cf. Rickett and Stafleu, 1960; Stafleu et al., 1972).

Two additional new species were described by Blake in 1924, but more important during that year was the description of a new genus, *Calhounia*, by Nelson. *Calhounia* was erected to incorporate all the species of *Lagascea* except *L. mollis*, which was regarded as belonging to *Lagascea* proper. Erroneously believing *Nocca rigida* (Cavanilles, 1795) to be invalid "through some deficiency in publication" (p. 57), Nelson thought that *Nocca* was typified by *N. mollis* (Jacquin, 1809) and, hence, a superfluous generic name. On this basis, Nelson provided the new name, *Calhounia* (after the maiden name of his wife), for what properly should have been called *Nocca*. In addition, a new type species was described, *C. nelsonae*, that is clearly a synonym of the earlier described *L. decipiens* (Hemsley, 1879).

In the present treatment, a new classification of *Lagascea* recognizes eight species in three sections. *Lagascea aurea* (sp. nov.) and *L. mollis* are in section *Lagascea*; *L. decipiens* and *L. palmeri* in section *Calhounia*; and *L. angustifolia*, *L. helianthifolia*, *L. heteropappus*, and *L. rigida* in section *Nocca*.

GENERIC AND SUBTRIBAL RELATIONSHIPS

Lagascea was placed originally in the Vernonieae by Cassini (1815, 1822, 1829), and this disposition was followed by Lessing (1832) and DeCandolle (1836). Bentham and Hooker (1873) first moved the genus to the Heliantheae as a monotypic subtribe, the Lagasceinae. Vasey and Rose (1890) added to the subtribe a second genus, *Coulterella*, and this has remained the composition of the Lagasceinae to the present day.

Recent studies comparing *Coulterella* and *Lagascea* (Stuessy, 1976), however, indicate that the two genera are distantly related to each other. *Coulterella* seems closest to *Flaveria* Juss., now of the Helenieae (Hoffmann, 1890), but perhaps belonging in or near the Senecioneae (Turner and Powell, 1977). *Lagascea* seems clearly a member of the Heliantheae, but not as a monotypic subtribe. The most recent suggestion (Stuessy, 1976, 1977) is that the genus belongs to the restructured subtribe Verbesininae near *Alvordia* Brandg. and *Agiabampoa* Rose ex O. Hoffm., and this is the position adopted in the present revision. *Lagascea* has no obvious close relatives, but *Alvordia* seems similar for a number of reasons (see Stuessy, 1976, for a detailed discussion of these relationships).

MORPHOLOGY AND TAXONOMIC CRITERIA

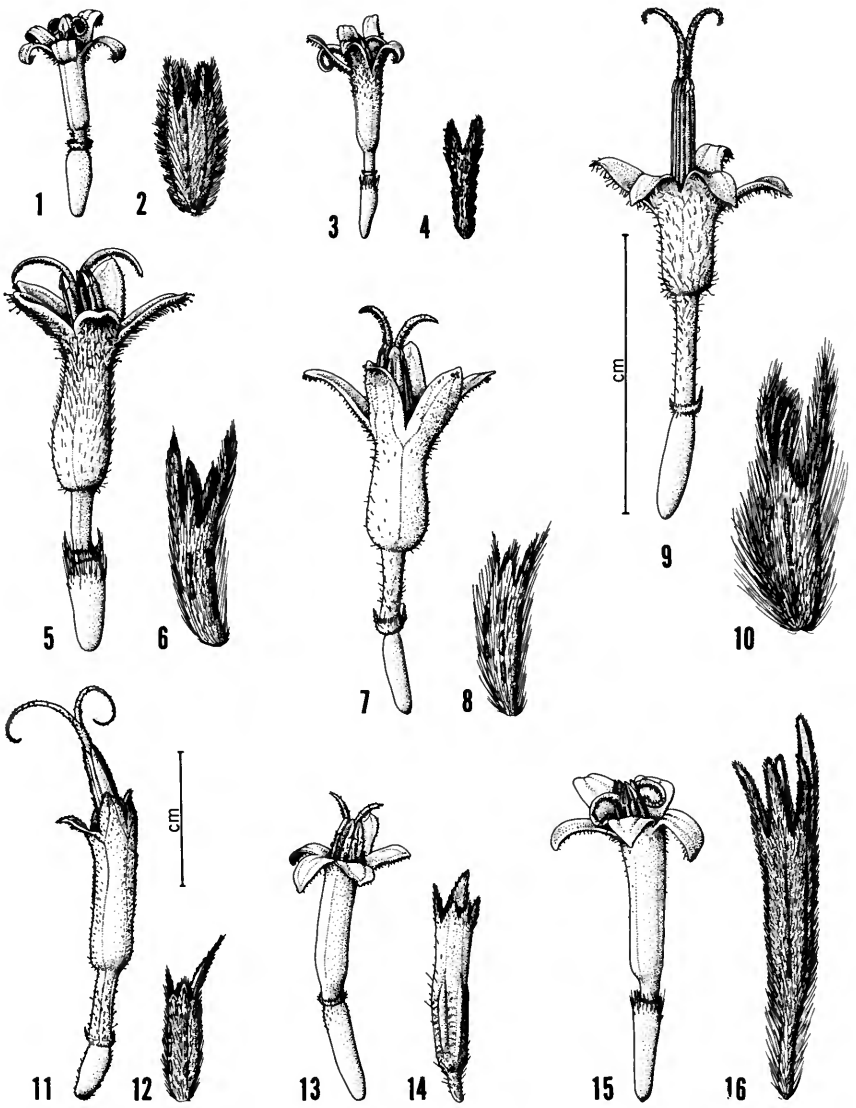
As with all revisionary studies, the resolution of the systematics of *Lagascea* has depended upon an understanding of the morphology of the genus. In this section of the paper, therefore, the structure of the synflorescence in *Lagascea* is discussed first, followed by the taxonomic value of various morphological features.

Structure of Synflorescence: Although Cavanilles (1795) believed the flowering clusters of *Lagascea* to be simple capitula, most subsequent botanists have treated them as secondary aggregations of uniflowered heads (Brown, 1818; Schultz-Bipontinus, 1861; Bentham and Hooker, 1873; Kunze, 1969). The fact that each floret of *Lagascea* is surrounded by its own set of herbaceous connate phyllaries (figs. 1-16), suggests that each represents a single small head. Addi-

tional evidence for regarding *Lagascea* to have secondary capitula comes from an aberrant collection of *L. decipiens* var. *decipiens* (*Hinton et al. 13206*). In a synflorescence of one of these specimens (GH), 54 heads containing from one to eight florets were observed in the following quantities: 1 floret per head (2 heads); 2 (31); 3(9); 4(5); 5(4); 6(1); 7(1); and 8(1). In the heads with more than three florets, scarious paleae were also usually present (up to three in the eight-flowered head). Furthermore, each small head was pedicellate and all were attached together in umbellate fashion. This condition is similar to that of other genera of the Compositae, which are few-headed and closely but not secondarily aggregated (e.g., *Flaveria* Juss. and *Alvordia* Brandg.).[1] The difficulties of attributing evolutionary significance to abnormal forms have been frequently discussed (e.g., Wagner, 1968; Eyde, 1971). In this instance, however, I believe that an ancestral condition is being illustrated in these multiflowered heads, because such a stage must have preceded reduction to the uniflowered state and the simultaneous or subsequent secondary condensation. A further contribution to understanding the structure of the synflorescences in *Lagascea* is the developmental anatomical study on *L. mollis* by Kunze (1969), in which the synflorescence is reported to be at the third order of aggregation. Eight secondary clusters of five to seven uniflowered heads each are aggregated together and surrounded by a common involucre. Whether this condition exists within other species of the genus remains to be determined.

Taxonomic Value of Morphological Features: Habit.—Three basic types of habit exist within *Lagascea*. The first is the herbaceous condition with ascending to decumbent stems found in *L. mollis* and *L. aurea*. These scrambling herbs can sometimes become woody at the base (e.g., *SR 3770*), but this is unusual. The second is the erect, coarse, herbaceous to shrubby habit of *L. angustifolia*, *L. helianthifolia*, *L. heteropappus*, and *L. rigida*. Although the gnarled base of the plant is often very woody (up to 15 cm. diam.), the erect stems apparently arise anew each year. The third type is the more woody and taller shrubby habit of *L. decipiens* and *L. palmeri*. These species often reach 3 m. in height (even unsupported). Aspects of habit,

[1]The distinction between a group of closely aggregated small heads and a secondary cluster is arbitrary, but I regard only those which are completely sessile on a common receptacle as truly secondarily aggregated. Often a secondary involucre also is present (as in *Lagascea*).



FIGS. 1-16. Capitula of species of *Lagascea* showing florets (odd numbered figures) and primary involucres (even numbered figures). **1, 2,** *L. aurea, SR 3743;* **3, 4,** *L. mollis, SR 3770;* **5, 6,** *L. heteropappus, SG 3130;* **7, 8,** *L. rigida* (var. *rigida*), *SG 3170;* **9, 10,** *L. angustifolia, Anderson & Anderson 5993* (ENCB); **11, 12,** *L. helianthifolia* (var. *helianthifolia*), *SR 3698;* **13, 14,** *L. palmeri, SR 3767;* **15, 16,** *L. decipiens* (var. *decipiens*), *SG 3012.* All vouchers on deposit at OS except as noted. All figures same scale except 11 and 12. Here and throughout this paper, *SG=Stuessy & Gardner, SR=Stuessy & Roberts.*

therefore, do vary within the genus and are correlated with sectional limits.

Leaves.—Leaf shape and vesture are very important as diagnostic features within *Lagascea*, particularly within section *Nocca*. The four species of this section, in fact, are difficult to discriminate on floral features alone (except for the obviously larger florets of *L. helianthifolia* and the usually longer corolla tubes of *L. angustifolia*). The types of leaf bases (petiolate or sessile) and vesture (strigose, sericeous, or tomentose) are the important diagnostic characters within this group of taxa. Within section *Lagascea* and section *Calhounia* the leaves vary only slightly in vesture between pairs of species.

Synflorescence.—The general shape of the entire synflorescence is globose in *L. decipiens* and *L. palmeri* (section *Calhounia*) and campanulate in the other taxa of *Lagascea* (sections *Lagascea* and *Nocca*).

Phyllaries.—The shape, size, and vesture of the secondary phyllaries vary tremendously within *Lagascea*. In *L. decipiens* these bracts are large and appear essentially the same as small leaves elsewhere on the plant. In *L. mollis* and *L. aurea*, on the other hand, the secondary involucre is small and compact and looks essentially like a primary involucre typical of asteraceous genera. The vesture on these secondary phyllaries varies from subglabrous (*L. palmeri*) to pilose (*L. decipiens*) and often to stipitate-glandular (known in all species except *L. palmeri*). In regard to the primary phyllaries, the number of fused bracts is usually five except for occasional larger numbers (6-11) in *L. decipiens* and the common variations of four or five in *L. mollis* and six (-7) in *L. aurea*. Although the pubescence of the primary involucre is diagnostic in some cases at the specific (*L. palmeri*) or varietal levels (*L. decipiens* var. *glandulosa*, *L. rigida* var. *mocinniana*), the most diagnostic features, especially for sectional delimitation, are the number and configuration of resinous "glands" on each phyllary (see even numbered figs. 2-16). In the species of section *Calhounia*, only one long gland usually is present on each phyllary. In section *Nocca*, a single row of two or more glands is present. And finally in section *Lagascea*, a single row of many small glands (*L. aurea*) or three rows of small glands (*L. mollis*) are present.

Florets.—Corolla color is the most obvious variation among the florets of the genus. White, red (including pink), and yellow corollas

occur. These are quite useful at different levels within *Lagascea*, for example, at the sectional level (section *Nocca* with white and red corollas and section *Calhounia* with yellow corollas) or at the specific level (*L. mollis*, white; *L. aurea*, yellow). Within *L. helianthifolia*, however, both white and red corolla forms occur (even in the same population) that are not accorded formal status. One specimen with white corollas also has been found (*Rzedowski 23534*) in *L. rigida* var. *mocinniana*, which usually has pink to red corollas. The variations of pappus in the genus also follow sectional lines. It is rudimentary in section *Calhounia* (figs. 13, 15), of small awns in section *Nocca* (figs. 5, 7, 9, 11), and a collar of fused short awns in section *Lagascea* (figs. 1, 3). Other variations in floret structure occur among species within each section. In section *Nocca* few qualitative differences in floral features exist. In the two other sections, however, diagnostic differences occur in achenial vesture (glabrous to pilose), size of pappus, and color of anthers (e.g., black to dark-brown in *L. mollis* and tan to yellow in *L. aurea*). The styles are uniform throughout the genus.

CYTOLOGY

In addition to morphological data being obtained from the species of *Lagascea*, cytological information also was gathered. In particular, emphasis was placed on chromosome number, as this type of data is often very helpful in constructing classifications as well as inferring evolutionary relationships (Stuessy, 1971). All populations of *Lagascea* encountered were studied using conventional techniques of killing, fixing, and acetocarmine squashing as outlined in Stuessy (1970).

Ten of the 11 taxa of *Lagascea* have been examined chromosomally from 60 plants in 45 populations. All are $n=17$ (table 1), with one exception. A variant count of $2n=36$ has been reported by Chopde (1965) for *L. mollis*, without citation of vouchers or graphic documentation, but this is regarded as atypical for the species. *L. angustifolia* is the only species still unexamined. Seven taxa had been counted previously, but counts for the remaining three taxa are first reports.

The uniformity of chromosome numbers within *Lagascea* helps indicate the closeness of relationship of all taxa within the genus. The data are not useful, however, for suggesting infrageneric classification. They do indicate that speciation within *Lagascea* has occurred

TABLE 1. Chromosome counts for taxa of *Lagascea*.

Taxon	Chromosome number (*n*)	Reference or voucher
L. aurea Stuessy	17	*SR 3743C & D.**
L. decipiens Hemsl.		
var. *decipiens*	17	Turner and Flyr, 1966 (*Flyr 94*); Pinkava et al., 1972; Stuessy, 1976; *SG 3012A; SR 3782B, 3786, 3787.*
var. *glandulosa* (Fernald) Stuessy	17	Turner and Flyr, 1966 [as *L. decipiens*]; *SG 3030A, 3039.*
L. helianthifolia H.B.K.		
var. *helianthifolia*	17	Solbrig et al., 1972; Stuessy, 1976; *SR 3698A & C, 3701B, 3702C, 3719B, 3734A & B.*
var. *levior* Robins.	17	*SR 3757A, 3780A.*
L. heteropappus Hemsl.	17	Stuessy, 1976; *SG 3095, 3130A & B, 3131C.*
L. mollis Cav.	17	Prameshwar, 1960; Turner et al., 1961; Torres and Liogier, 1970; Strother, 1976; Stuessy, 1976; *SG 3180 & A & B, 3183A & B, 3184A & B; SR 3645, SR 3654A, 3764, 3770, 3774.*
	18	Chopde, 1965 ($2n=36$).
L. palmeri (Robins.) Robins.	17	Stuessy, 1976; *SR 3767B & C, 3778.*
L. rigida (Cav.) Stuessy		
var. *mocinniana* (DC.) Stuessy	17	Stuessy, 1976; *SG 3156*
var. *rigida*	17	*SG 3135C & E, 3161 & A & B, 3170A; SR 3688.*

*Full information on these vouchers is indicated in the representative specimen citations; all on deposit at OS.

solely at the diploid level and probably via the common mode of allopatric divergence (to be discussed in more detail later).

DISTRIBUTIONAL SUMMARY

The taxa of *Lagascea* are principally Mexican and are most abundant and occur in the greatest diversity along the Sierra Madre Occidental. The full and apparently native range of the genus stretches from southern Arizona (*L. decipiens* var. *decipiens*) south to Nicaragua (*L. helianthifolia* var. *helianthifolia* and *L. mollis*). One species, *L. mollis*, has also been introduced to the West Indies, South America, and isolated localities in Africa, India, Java, Sri Lanka, and Thailand. Two of the taxa are known from the United

States: *L. decipiens* var. *decipiens*, from Pima Co., Arizona; and *L. mollis*, from Franklin Co., Florida.

In general, the habitat and elevational preferences of the taxa of *Lagascea* follow sectional lines. *Lagascea mollis* and *L. aurea* (section *Lagascea*) are most prevalent in disturbed moist lowland areas in savannas or tropical deciduous forests. *Lagascea angustifolia, L. helianthifolia, L. heteropappus*, and *L. rigida* (section *Nocca*) are commonly found in pine and oak forests above 800 m. The last group, containing *L. decipiens* and *L. palmeri* (section *Calhounia*), is most common in dry areas of tropical deciduous and thorn forests at low elevations (50-500 m.).

EVOLUTION

The determination of evolutionary relationships within *Lagascea* must be based on an analysis of morphological, cytological, and distributional data followed by appropriate inferences. Having cytogenetic information from all taxa would have facilitated the understanding of evolutionary trends, but the perennial shrubby habit of many of the species of *Lagascea* made this approach impracticable. Two types of evolutionary considerations are of interest: 1) the phylogeny of the genus; and 2) the evolutionary mechanisms that have been operative.

Phylogeny.—Before evolutionary trends within *Lagascea* can be established, the primitive conditions of selected characters must be ascertained. These are: 1) habit shrubby; 2) leaves petiolate; 3) synflorescence solitary; 4) secondary involucre very leaf-like and loosely compacted; 5) primary involucre of phyllaries with a single long resinous gland; 6) heads bi- or multiflowered with pales; and 7) corollas yellow and anthers yellow-brown. The rationale for according these character states primitive status is discussed below.

Four assumptions have been made that allow assignment of primitive status to character states in *Lagascea*: 1) those most common within the genus;[1] 2) those present in the related genus *Alvor-*

[1]This assumption, obviously, will not always be true, but it can be suggestive of primitive status for a character state when unusual specializations are present in only a few taxa of a genus (e.g., sessile leaves in only *L. helianthifolia* suggest the petiolate condition as primitive) and when some or all of the other assumptions are not applicable. It is used here as a helpful criterion but by no means as an absolute one. The treatment of yellow corollas as being primitive, in fact, goes contrary to this assumption, because most species of *Lagascea* have white to pink corollas. The other three assumptions, however, suggest primitive status for the yellow florets.

dia; 3) those representing the beginning stage of a hypothetical sequence of secondary head development that has evolved repeatedly throughout the family; and 4) those representing generalized conditions within the Compositae. Some of the primitive assignments result from an application of only one criterion; others result from several.

Character states that seem to show primitiveness by their commonness in the genus are the shrubby habit and petiolate leaves. All species of *Lagascea* are shrubby except for *L. mollis* and *L. aurea*, which are principally herbaceous. A thick woody stem was found at the base of one collection (*SR 3770*), which may indicate a woody ancestry. Likewise, petiolate leaves are found exclusively in all taxa except in *L. helianthifolia* (and principally in var. *helianthifolia*), which has sessile leaves and subauriculate leaf bases (collections are found occasionally, however, that are petiolate; e.g., *Nelson 2121*).

Several character states are also regarded as primitive in *Lagascea* because of their occurrence in the related genus *Alvordia*. Such features are the shrubby habit and petiolate leaves, yellow corollas, yellow-brown anthers, and primary phyllaries with a single resinous gland on the midrib. The phyllaries of *Alvordia*, however, are not fused laterally (Carter, 1964) as are those of *Lagascea*.

Another independent criterion for primitiveness relates to the hypothetical sequence in the evolutionary development of secondary and third-level heads in the Compositae. This sequence, as outlined by Kunze (1969), is viewed as having four recognizable stages: 1) solitary heads; 2) closely aggregated small heads; 3) secondarily aggregated heads (often uniflowered); and 4) third-order heads. From a theoretical perspective, this is the simplest and most logical evolutionary transition that can be envisioned. Within *Lagascea*, different degrees of aggregation of secondary heads exist. In *L. decipiens* and *L. palmeri* (section *Calhounia*), the secondary heads are usually solitary; in section *Nocca* they are in cymose or racemose clusters; in *L. mollis* and *L. aurea* (section *Lagascea*) they are solitary, but are apparently at the third level of condensation (at least in *L. mollis*; Kunze, 1969). Within the context of the evolutionary scheme presented, the solitary secondary heads are regarded as most primitive. Using similar reasoning, secondary involucres that have very leaf-like secondary phyllaries are primitive, whereas those which are shorter, narrower, more glandular, or otherwise modified from typical leaves are advanced. An additional consideration in this scheme is the number of florets per head. In the transi-

tion from aggregated small heads to the secondary condition, usually a change from few-flowered to the uniflowered state has occurred. Taxa still showing the multiflowered state, if only residually, would be regarded as primitive. The only species in *Lagascea* that are known ever to possess bi- to multiflowered heads are in section *Calhounia*. One collection (*Hinton et al. 13206*) of *L. decipiens* has up to eight florets and three pales per head.

Finally, generalized evolutionary considerations within the entire family, and to a lesser degree within the angiosperms, can be used to suggest primitiveness in a few features. The most common and probably the most primitive pigments within the Compositae are the carotenoids (Cronquist, 1955), which impart a yellow color to floral parts (principally corollas). That carotenoids are primitive is most certainly also the case in the Heliantheae (Stuessy, 1977). These compounds are also regarded as primitive pigments throughout the flowering plants (J. B. Harborne, pers. comm.). In *Lagascea*, therefore, the yellow pigments are regarded as primitive and the red and white pigments derived. In addition, hummingbird pollination within *L. helianthifolia* (pers. observations) is believed to be an advanced condition within *Lagascea*. Within the flowering plants, hummingbird pollination certainly is regarded as an advanced pollination system (Grant and Grant, 1968; Proctor and Yeo, 1973).

By application of these assumptions and determination of primitive character states, *Lagascea decipiens* becomes the most primitive species of the genus. This taxon possesses a shrubby habit and petiolate leaves, which are common features within the genus. It most nearly resembles *Alvordia* in all aspects. It has the most primitive features of the evolutionary sequence of head condensation, and it possesses yellow corollas, which are common within the entire family.

From this ancestral condition, trends of evolution in selected characters can be determined. The characters of most interest are those used for sectional classification (fig. 17): habit, aggregation of synflorescences, number and size of resinous glands of the primary phyllaries, and corolla and anther pigmentation. A trend exists in *Lagascea* from completely woody shrubs to those woody only at the base, and finally to herbs. The resinous glands show an increase in number on the midribs and finally cover all three veins in one of the evolutionary lines. These structures may serve a protective function against chewing insects, because they cover only that portion of the

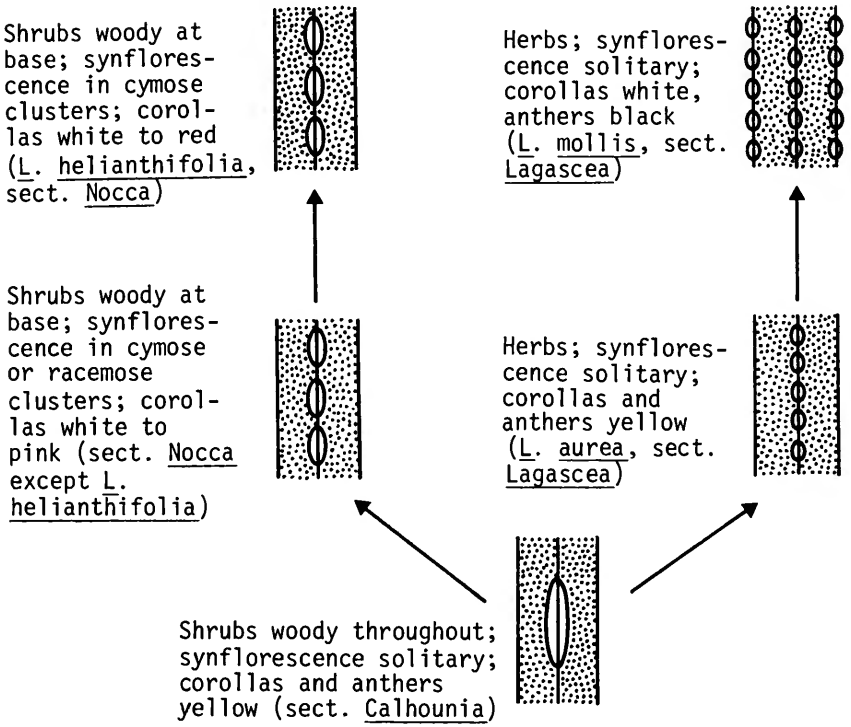


FIG. 17. Trends of evolution in selected characters of *Lagascea*. Diagrams represent the size, number, and distribution of resinous glands on the midribs and lateral veins of a single primary phyllary.

involucre below which the ovary lies. The corolla and anther pigments follow a trend from yellow (carotenoid) to white pigments (flavonoids, J. B. Harborne, pers. comm.) independently derived in two evolutionary lines, and finally to red pigments (probably cyanidin-3-glucoside, Harborne, pers. comm.). Last, a generalized evolution of pollination systems has gone from principally butterfly and bee pollination to hummingbird vectors in *L. helianthifolia*.

Taking all factors into account, one can speculate on the phylogeny of the entire genus and present branching relationships in phylogram form (fig. 18). Section *Calhounia* is viewed as possessing the most primitive features of the genus, with section *Lagascea* and section *Nocca* being derived, but in independent lines. Because of its weedy nature, section *Lagascea* is believed to have appeared more recently and, therefore, it is shown as having diverged from section *Calhounia* later than did section *Nocca*.

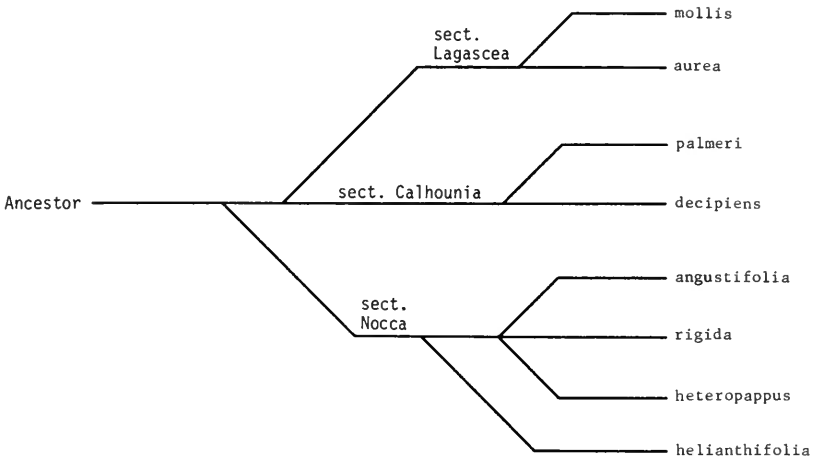


FIG. 18. Phylogram of the species of *Lagascea*.

Evolutionary Mechanisms.—Without extensive cytogenetic data, only limited information is available on the mechanisms of evolution that have occurred in *Lagascea*. That the genus is small and the species very distinctive, however, recommends some comments on: 1) past modes of speciation within *Lagascea*; and 2) present isolating mechanisms.

It seems clear that the most common mode of evolution within *Lagascea* has been allopatric speciation at the diploid level. This is suggested by the absence of polyploidy (all known species $n=17$) plus geographical distributions of species pairs or groups that reflect this mode of origin. The geographically restricted taxon, *L. palmeri*, is known only at the southern end of the range of *L. decipiens* (fig. 23), but at lower elevations. Likewise, *L. aurea* occurs in only one valley in Michoacán and adjacent Jalisco and is separated by only a small distance from the more common *L. mollis* in Colima and neighboring states (fig. 19). In this case, however, the more geographically restricted *L. aurea* seems a relic population resembling closely (except in primary phyllary number) the ancestral type that gave rise to both species rather than a derivative of the more widespread *L. mollis*. *L. mollis*, however, seems to have originated on the west coast of Mexico and from there to have been introduced to eastern Mexico in historical times (probably post-conquest) near Veracruz and finally to many ports of the world. In section *Nocca*, an ancestral widely distributed species may have been broken into three populational systems now recognized as *L. angustifolia*, *L.*

heteropappus, and *L. rigida* (fig. 22). The only species of this section (or for that matter within any section) that has passed the test of sympatry (Mayr, 1942; Levin, 1971) is *L. helianthifolia*. The distribution of this taxon overlaps those of all other taxa of section *Nocca*, and the only known hybrids within the genus occur between *L. helianthifolia* and these three closely related species (fig. 21).

The isolating mechanisms that are operative within *Lagascea* are of three types. The first, spatial isolation, has already been alluded to in the previous discussion. Obviously, this type of isolation prevails between the species pairs of section *Lagascea*, section *Calhounia*, and all species of section *Nocca* except *L. helianthifolia*. The latter species illustrates a second type, temporal isolation, by flowering later than its relatives. An overlap in flowering time leads usually to hybridization. The third and last type, genetic isolation (or perhaps structural chromosomal in some cases), has developed between *L. helianthifolia* and the other species of section *Nocca*. Hybrids between these taxa have a markedly reduced pollen viability and show meiotic irregularities (see discussion under the former species). More effective genetic isolation apparently occurs between species of different sections, for although sympatry does occur and flowering times are synchronous (such as with *L. palmeri* and *L. mollis*), no hybrids have ever been found.

TAXONOMIC TREATMENT

LAGASCEA Cav. nom. cons.

Lagasca Cav. An. Cien. Nat. 6:331. 1803. *Lagascea* [implicated as being attributed to Cav. by] Willd. Enum. Hort. Berol. 941. 1809. *Orthogr. var., nom. cons.* [cf. Intern. Code Botan. Nomen. #9101, p. 371; Stafleu et al., 1972]. Type species: *Lagascea mollis* Cav.

Nocca Cav. Icon. 3:12. *t. 224.* 1795. *Nom. rejic.* Type species: *Nocca rigida* Cav. [=*Lagascea rigida* (Cav.) Stuessy]. *Noccaea* [attributed to Cav. by] Willd. Spec. Pl. ed. 5. 3:2393. 1803. *non* Moench. 1802. *Orthogr. var.*

Calhounia A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:55. 1924. Type species: *Calhounia nelsonae* A. Nelson [=*Lagascea decipiens* Hemsl.].

Annual herbs to shrubby perennials. Stems terete, gray, yellow-green or purple, glabrous to pilose and often stipitate-glandular. Leaves opposite, petiolate to sessile; blades ovate to oblanceolate, at apex acute to acuminate, at base obtuse to subauriculate, at the margin obscurely to strongly serrate, subglabrous to strigose above, subglabrous to sericeous below. Flowering cluster a synflorescence of 8-55 uniflowered (rarely bi- to multiflowered) capitula aggregated secondarily (perhaps at the third level of condensation in *L. mollis*) into terminal, subglabrous to cam-

panulate, solitary, cymose or racemose clusters. Peduncles subglabrous to pilose and often stipitate-glandular. Receptacle convex. Secondary phyllaries 4-6, separate, herbaceous, lanceolate to obovate, abaxially subglabrous to pilose and sometimes stipitate-glandular. Primary phyllaries 4-6 (-11), connate laterally into an involucral tube, abaxially subglabrous to densely pilose, each with 1-3 rows of 1-8 elliptic resinous glands, at apex acute to acuminate and sometimes stipitate-glandular. Florets hermaphroditic, corollas yellow, white, pink, or red, narrowly funnelform, with lobes 5; anthers yellow, tan, brown, black, pink, or red; style bifid, with branches tapered at apex, hairy on abaxial surface, with stigmatic ridges shortly papillate; achenes brown to black, narrowly cylindrical to obovoid, minutely grooved, at base tapered. Chromosome number, $n=17$.

KEY TO TAXA

a. Herbs [section *Lagascea*]. (b)
  b. Peduncles stipitate-glandular; primary involucre of 4 or 5 phyllaries, with 2-3 rows of small glands per phyllary; pappus a short, erose crown of fused scales up to 0.5 mm. diam.; corolla and pollen white (sometimes purplish); anthers dark brown to purple or black..... 1. *L. mollis*
  b. Peduncles strigose; primary involucre of 6 (-7) phyllaries, with one row of small glands per phyllary; pappus an erose crown of fused scales 1 mm. diam.; corollas and pollen yellow; anthers yellow to light brown..... 2. *L. aurea*
a. Shrubs or very coarse herbs 1-2 m. tall, woody at the base [sections *Nocca* and *Calhounia*]. (c)
  c. Corollas and anthers white to purple; synflorescence campanulate in cymose or racemose clusters [section *Nocca*]. (d)
    d. Leaves densely sericeous below..... 5. *L. heteropappus*
    d. Leaves subglabrous, strigose, or tomentose below. (e)
      e. Leaves lanceolate to oblanceolate, at the apex obtuse. 6. *L. angustifolia*
      e. Leaves ovate to narrowly ovate, at the apex acute to acuminate. (f)
        f. Leaves appearing varnished above, always petiolate; secondary involucral bracts lanceolate-linear, much darker and narrower than the associated upper leaves. (g)
          g. Secondary involucral bracts and peduncles strigose; stalks of cymose or racemose floral clusters 1-7 cm.; leaves narrowly ovate, subglabrous to strigose below.... 4a. *L. rigida* var. *rigida*
          g. Secondary involucral bracts and peduncles stipitate-glandular; stalks of cymose or racemose floral clusters 4-18 cm.; leaves narrowly ovate to ovate, usually pilose below..... 4b. *L. rigida* var. *mocinniana*
        f. Leaves not appearing varnished above, leathery, sessile or petiolate; secondary involucral bracts ovate to narrowly ovate, smaller than but resembling the associated upper leaves. (h)
          h. Leaves sessile, at base subauriculate, with undersurface subglabrous to tomentose; synflorescences (2.5-)3-4 cm. diam., often solitary or few together..... 3a. *L. helianthifolia* var. *helianthifolia*

h. Leaves shortly petiolate, at base obtuse to attenuate, with undersurface strongly reticulate and copiously tomentose-hirsutulous; synflorescences 1.5-3.5 cm. diam., numerous and densely aggregated..... 3b. *L. helianthifolia* var. *levior*

c. Corollas yellow with anthers yellow to tan; synflorescence globose to hemispheric, solitary [section *Calhounia*]. (i)

i. Primary involucre with lobes 1 mm. long and one-fifth or less its length, sub-glabrous becoming pilose near base; achenes subglabrous..... 8. *L. palmeri*

i. Primary involucre with lobes 2 mm. long and one-fourth its length, strigose or pilose to stipitate-glandular; achenes pilose and/or stipitate-glandular toward apex. (j)

j. Peduncles and lobes of primary involucre strigose to pilose; leaves densely strigose with hairs 0.7 mm. long..... 7a. *L. decipiens* var. *decipiens*.

j. Peduncles and lobes of primary involucre conspicuously stipitate-glandular; leaves moderately strigose with hairs 0.3 mm. long..... 7b. *L. decipiens* var. *glandulosa*

I. LAGASCEA section LAGASCEA

Lagascea Cav. An. Cienc. Nat. 6:331. 1803. Type species: *Lagascea mollis* Cav.

Herbs; synflorescence campanulate, solitary; primary phyllaries with 1-3 rows of 5-8 small, elliptical, resinous glands; corollas white or yellow; anthers yellow, tan, brown, or black. Species 1 and 2.

1. **Lagascea mollis** Cav. An. Cienc. Nat. 6:332. *t. 44.* 1803. TYPE: CUBA, seeds sent from Havana and grown in Roy. Bot. Gard. Madrid, flowering June-Sept. 1803, *M. Espinosa & J. N. Peralta s.n.* (Lectotype, MA!; probable isolectotype, F!; photograph of lectotype, OS!). Figures 3, 4.

Noccaea mollis (Cav.) Jacq. Frag. 58. *t. 85.* 1806.

Lagascea campestris Gardn. Hook. Lond. J. Bot. 5:238. 1846. TYPE: BRAZIL: Ceará, "arid campas near Villa do Ico" ["banks of the Río Jaguaribe below Icó" (from label)], Aug. 1838, *G. Gardner 1741* (Holotype, K!).

Lagascea kunthiana Gardn. Hook. Lond. J. Bot. 5:238. 1846. TYPE: BRAZIL: Piauí, "dry Campos, near Boa Esperanca," Feb 1839, *G. Gardner 2220* (Holotype, K!; isotypes, GH! NY! US!).

Lagascea parvifolia Klatt, Ann. Naturh. Hofmus. Wien 9:360. 1894. TYPE: VENEZUELA, 1835-1866, *J. W. K. Moritz s.n.* (Holotype, GH!).

Annual herb to 1 m. tall (rarely persisting as a perennial, e.g., *SR 3770*). Stems to 5 (-15) mm. diam., yellow-green to purple, subglabrous below to hirtellous and stipitate-glandular above with hairs 0.1-0.3 mm. long. Leaves with petioles 5-27 mm. long and 0.1-0.9 mm. diam., at margin hirtellous and sometimes ciliate with hairs 0.3-2 mm. long; blades narrowly ovate to ovate, 4.2-7.2 cm. long, 2.3-4 cm. wide, at apex acute-acuminate, at base obtuse to slightly attenuate, at the margin subentire to serrate, on both surfaces strigose with hairs 0.3-0.5 mm. long. Synflorescence with 8-25 uniflowered capitula, solitary, terminal, campanulate, 0.8-1.3 cm. tall, 0.9-3 cm. diam. Peduncles 3.5-5.2 (-14) cm. long, 0.3-1.5 mm. diam., retrorsely strigose and stipitate-glandular with hairs 0.3-0.5 mm. long. Receptacle 2 mm. diam., 1.2 mm. tall, hirtellous with hairs 0.3 mm. long. Secondary phyllaries 5, lanceolate to obovate, 5-15 mm. long, 1-6 mm. wide, on both surfaces strigose and stipitate-glandular with hairs 0.3 mm. long, at the margin ciliate with hairs to 1 mm. long. Primary involucre 4-5 mm. long, 1 mm. diam., of 4-5 phyllaries each with 2-3 rows of 5-8 small elliptic resinous glands 0.3 mm. long, abaxially densely pilose with hairs 0.3 mm. long; lobes 1-1.7 mm. long, 0.8 mm. wide at base, at apex acuminate, abaxially stipitate-glandular, adaxially glabrous except hirtellous toward apex. Florets with corollas white to pink-purple, with throat 3 mm. long and 0.6 mm. diam., with lobes narrowly ovate and 1-2 mm. long, with tube 0.6 mm. long and 0.3 mm. diam.; anthers dark brown to black, 1.3-2.8 mm. long; style 3.5-6.5 mm. long; achenes obovoid, 3 mm. long, 1.2 mm. diam., pubescent near apex; pappus an erose pubescent crown 0.5 mm. diam., 0.1-0.2 mm. long. Chromosome number, $n=17$.

Distribution.—Disturbed sites such as roadsides, old fields, and waste areas primarily in tropical deciduous forests and lowland savannas, near Appalachicola, Franklin Co., Florida (recent introduction on ballast dumps) and in Colima, Jalisco, Michoacán, Veracruz, and the Yucatan Peninsula, Central and South America, West Indies, and isolated localities in Africa, India, Java, Sri Lanka, and Thailand (figs. 19, 20); 0-1,200 (-2,700) m.

Flowering Dates.—Throughout the year.

Lagascea mollis is the most widespread species of the genus, having been introduced to many parts of the world, such as Africa, India, and Java, as well as to the West Indies and South America. Such a cosmopolitan distribution is understandable in light of the weedy nature of the species. On both coasts of Mexico, *L. mollis* grows in large patches along roadsides and cultivated fields. It is easy to imagine fruits being transported by boat from Manzanillo or Veracruz to numerous ocean ports.

Representative specimens.—AFRICA. KENYA: Kikemu, 21 April 1927, *Linder 2641* (GH). ARGENTINA. FORMOSA: 1 July 1919, *Jorgensen 2732* (GH, MO, US). JUJUY: between Palo Blanco and Pauja Blanca, 18 May 1962, *Cabrera et al. 14603* (GH). SALTA: Coronel Moldes, 12 Feb. 1943, *Bartlett 19648* (GH, MICH, US).

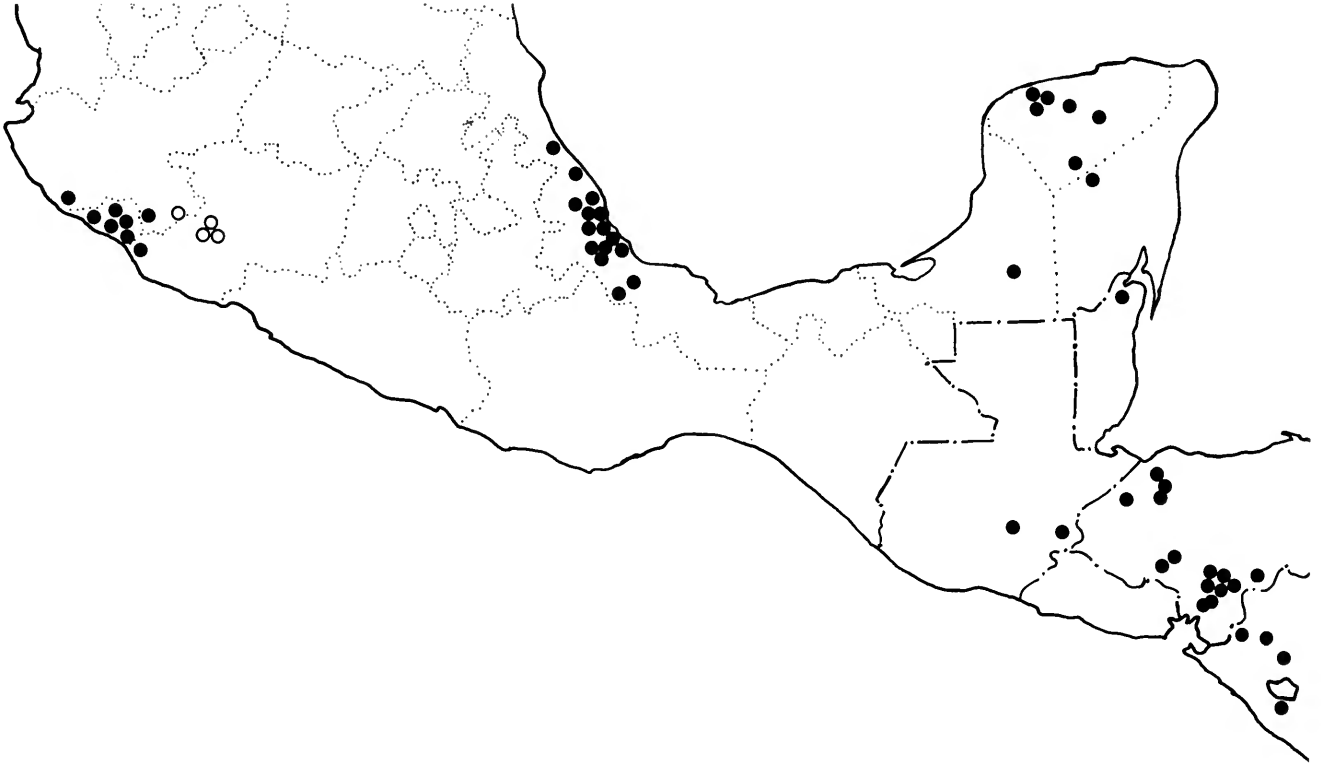


FIG. 19. Map of southern Mexico and adjacent Central America showing distribution of *Lagascea aurea* (open circles) and *L. mollis* (closed circles).

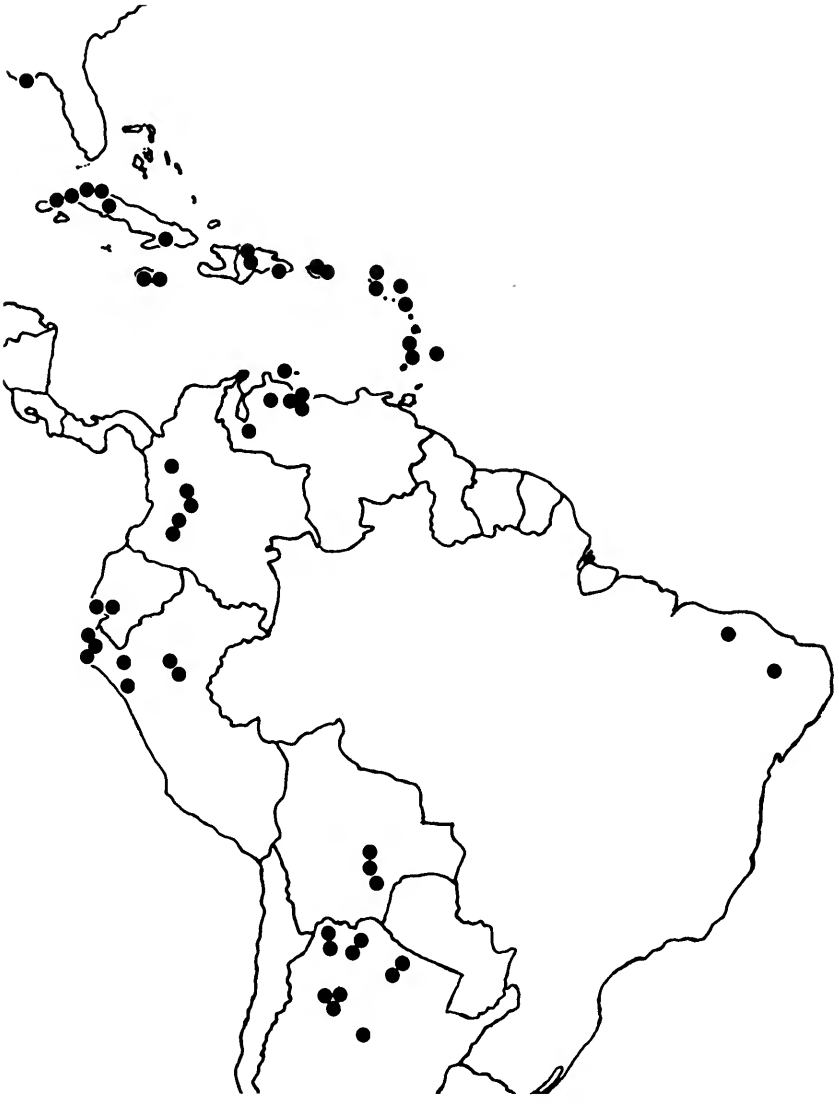


FIG. 20. Map of Florida, West Indies, and northern South America showing distribution of *Lagascea mollis*. For additional introduced localities of *L. mollis* in countries not on this or the previous map, refer to the representative specimens.

SANTIAGO DEL ESTERO: near Pellegrini, Cerro del Remate, March 1928, *Venturi 5965* (GH, US). TUCUMÁN: W of La Canada, 13 May 1900, *Lillo 2527* (A). BELIZE. COROZAL: Corozal-Orange Walk Rd, July 1933, *Gentle 4924* (NY, UC). BOLIVIA. SANTA CRUZ: Cercado, Urubo, 31 May 1925, *Steinbach 7133* (GH, MO, NY, UC). BRITISH ANTILLES. ANTIGUA: Gunthorpes, 8 Sept. 1937, *Box 1042* (GH, MO, US). GRENADINES: Carriacou, 7-25 March 1950, *Howard 10830* (A, NY). ST KITTS-NEVIS-ANGUILLA: St. Christopher, 8 Sept.-5 Oct. 1901, *Britton & Cowell 146* (NY). ST VINCENT: near Kingston, May-June 1890, *Smith & Smith 898* (NY). COLOMBIA. ANTIOQUÍA: 4 km. from Palmitas, 5 March 1949, *Araque & Comea 469* (US). CUNDINAMARCA: Narino, July 1930, *Arbelaez 441* (US). HUILA: on Río Ambica, near Río Cabrera, 15 Dec. 1942, *Fosberg 19352* (US). CUBA. CIENFUEGOS: Limones, Soledad, 25 July 1927, *Jack 6110* (US). LA HABANA: Regla, 18 Jan. 1905, *Curtiss 604* (F, GH, MO, NY, US). LAS VILLAS: Cieneguita, 28 June 1895, *Combs 251* (F, GH, MO, NY). MATANZAS: near Matanzas, valley of the San Juan, 14 March 1903, *Britton & Shafer 226* (GH, NY). ORIENTE: between El Caney and Santiago de Cuba, Nov. 1951, *Alain 1996* (NY). PINAR DEL RÍO: near Pinar del Río, 5-12 Sept. 1910, *Britton & Gager 7263* (F, NY, US). DOMINICAN REPUBLIC. LA ALTAGRACIA: near Higuey, between Yuma and Boca de Yuma, 22 Aug. 1968, *Liogier 12260A* (NY). LA VEGA: Constanza, 31 May 1969, *Liogier 15509* (NY, US). SANTIAGO: near Santiago, Hoya del Caimito, 22 Nov. 1971, *Jiménez 5955B* (NY). ECUADOR. GUAYAS: between Guayaquil and Salinas, 21-24 June 1923, *Hitchcock 20022* (GH, NY, US). MANABI: Bahía de Caraquez, June 1903, *Lehmann 754* (GH, NY). FRENCH ANTILLES. GUADELOUPE: Basse-Terre, Des Saintes Islands, 1892-1893, *Duss 2508* (F, NY, US). GUATEMALA. CHIQUIMULA: above El Rincón, 17 Oct. 1940, *Standley 74643* (F, US). JUTIAPA: between Jutiapa and La Calera, 2 Nov. 1940, *Standley 76048* (F). PROGRESO: 2 miles NE of Progreso, 14 Nov. 1943, *White 5114* (LL, MICH). HONDURAS. ATLANTIDA: Villa Franca, 24 Jan. 1928, *Standley 54950* (F, US). CHOLUTECA: near Pespire, 18-27 Oct. 1950, *Standley 27005* (F). COMARCA DEL CABO: near Comayagua, 12-23 March 1947, *Standley & Chacón 5654* (F). CORTÉS: near La Lima, 11-20 April 1947, *Standley & Chacón 7120* (F). EL PARAÍSO: near Danlí, 11-23 Feb. 1949, *Standley 16674* (F). FRANCISCO MORAZÁN: between Suyapa and Tegucigalpa, 11 Dec. 1948, *Molina 1835* (F).

LA PAZ: near La Paz, 6 Dec. 1949, *Standley 24981* (F). MORELOS: vicinity of El Zamorano, 17 Feb.-8 March 1947, *Standley 4979* (UC). SANTA BARBARA: Los Dragos, SW of Quimistán, 16-17 April 1947, *Standley & Lindelie 7321* (F). YORO: Naranjo Chino, 30 Dec. 1927, *Standley 53906* (GH, US). INDIA. BANDALORE: Mt St Joseph, 15 Aug. 1964, *Saldanha 8860* (US). BOMBAY: Mumbra, 27 Aug. 1966, *Gupta 101* (MO). HASSAN DISTRICT: Mysore, 21 Sept. 1971, *Gandhi 2102* (US). RAJASTRAN: Ramapura, 19 Dec. 1963, *Verma 1794* (MO). JAMAICA. CLARENDON: Clarendon Park, 24 Sept. 1908, *Britton 3789* (NY). MANCHESTER: Mandeville, 21 Sept. 1908, *Harris & Britton 10598* (F, NY). ST CATHERINE: Mt Rosser, along Mt Diablo rd., 29 June 1955, *Howard & Proctor 14175* (A). ST ELIZABETH: Comfort, 6 July 1955, *Howard & Proctor 14488* (A). ST THOMAS: Holland Bay, 1-13 March 1909, *Britton 4066* (F, NY). SURREY: St Andrew, Mona Heights, 11 Nov. 1959, *Adams 5442* (DUKE). JAVA. Bot Gard Bogor, 1886-1887, *Warburg 1796* (GH, NY). MEXICO. CAMPECHE: Tuxpena, 21 Dec. 1931, *Lundell 1105* (F, US). COLIMA: 15 km. E of Tecomán, 14 March 1965, *McVaugh 22977* (DS, DUKE, ENCB, LL, MICH); 11.1 miles S of Colima, 17 Dec. 1974, *SR 3764* (OS), 0.6 miles W of Armería, 17 Dec. 1974, *3770* (OS). JALISCO: 2.6 miles WNW of Col-Jal state line on rt. 110, 18 Dec. 1974, *SR 3774* (OS). MICHOACÁN: 5 km. S of Coahuayana, 25 Nov. 1963, *Feddema 2733* (CAS, DUKE, ENCB, MICH, TEX). VERACRUZ: ca. 30 miles NW of Veracruz, S of Paso de Ovejas, 23 July 1971, *Strother 1095* (OS, UC); 6.1 miles E of La Tinaja, 14 Sept. 1973, *SG 3180* (MEXU, OS), 14.6 miles NW of Macambo, 14 Sept. 1973, *3183* (OS), 4.8 miles NW of Puente Nacional, 14 Sept. 1973, *3184* (OS); 3.4 miles W of Tecolutla, 6 Dec. 1974, *SR 3645* (OS), 25 miles S of Gutiérrez Zamora, 6 Dec. 1974, *3648* (OS), 18 miles S of Palma Sola, 6 Dec. 1974, *3654* (OS); Dos Ríos, Cerro Gordo, 15 Oct. 1970, *Ventura 2619* (DS, ENCB, F, MICH, NY, TEX). YUCATÁN: Peto, 26-27 July 1932, *Steere 2191* (MICH, US). NETHERLANDS ANTILLES. CURAÇAO: Mt Pleasant, 20-27 March 1913, *Britton & Shafer 3122* (NY, US). NICARAGUA. ESTELÍ: San Juan Limay, 6 Nov. 1968, *Molina 23181* (DS, F, MO, NY). MANAGUA: Managua, 19 June 1927, *Chaves 270* (F, US). MATAGALPA: 5 km. N of Dario, 12 May 1970, *Harmon & Fuentes 5031* (ENCB). PERU. AMAZONAS: Chachapoyas, Balsas, Río Maranón, 7 Aug. 1958, *Ferreyra 13328* (US). CAJAMARCA: Colasay, 2 Nov. 1961, *Woytkowski 7060* (GH). LA LIBERTAD: Trujillo, 7 Aug. 1948, *Lopez 162* (US).

PIURA: Cerro Prieto, 31 March 1929, *Haught 231A* (GH, NY, US). PUERTO RICO. BAYAMON: Aibonito, 14 Nov. 1937, *Otero 286* (MICH, MO). GUANICA: 3 March 1935, *Sargent 31* (LL). JUANA DÍAZ: 3 Oct. 1943, *Sargent 3187* (US). MAYAGUEZ: Yaneo to Guayanilla, 4 July 1901, *Underwood & Griggs 594* (NY, US). PONCE: 2 miles W of Ponce, 6 Dec. 1902, *Heller 6221* (F, GH, MO, NY, US). RÍO PIEDRAS: Santa Rita, Guanica, 30 Aug. 1915, *Smyth 3018* (US). SRI LANKA. Kandy District, on banks of Mahaweli River, 27 April 1969, *Grierson 1160* (US). THAILAND. Muak Lek, 19 Feb. 1962, *Larsen 9680* (A). TRINIDAD. San Fernando, 9 May 1932, *Broadway 7946* (MO, NY). UNITED STATES. FLORIDA: Apalachicola, date unknown, *Chapman 22* (MO); locality unknown, 1842-1849, *Rugel 105* (MO, US). VENEZUELA. ARAGUA: Maracay, Dec. 1927, *Pittier 144* (MO). DISTRITO FEDERAL: Caracas, 6 Dec. 1938, *Alston 5358* (GH, US). LARA: near Barquisimeto, 29 June 1913, *Pittier 6397* (US). MÉRIDA: above Río Chama, rd. to Chiguara, 31 Aug. 1966, *Steyermark & Rabe 97009* (NY, US). VIRGIN ISLANDS. ST THOMAS: Bergs Estate, 9 Jan. 1888, *Eggers 3420* (F, NY).

2. **Lagascea aurea** Stuessy, sp. nov.

TYPUS: MEXICO: MICHOACÁN, 4-5 km. WNW of Apatzingán, along rd. to Buena Vista Tomatlán, ca. 300 m., 10 Sept. 1972, *J. V. A. Dieterle 4359* (Holotype, MICH!; isotypes, DUKE! ENCB!). Figures 1, 2.

Herbae annuae usque ad 1 m. altae. Caules ad 4.5 mm. diametro, luteovirides vel purpurei, retrorse strigosi pilis 0.1-0.3 (-1.5) mm. longis. Folia petiolis 5-30 mm. longis et 0.5-0.8 mm. diametro, margine ciliatis pilis 1-1.5 mm. longis; laminae anguste ovatae vel ovatae, 1-6.5 cm. longae, 0.7-4.3 cm. latae, apice acuto-acuminatae, basi obtusae vel parum attenuatae, margine subintegrae vel serratae, strigosae pilis 0.3-1.5 mm. longis. Synflorescentia capitulis 8-15 omnibus unifloris, solitaria, terminalia, campanulata, 0.8-1.1 cm. alta, 0.8-1.5 cm. diametro. Pedunculi 0.5-4.2 cm. longi, 0.3-0.8 mm. diametro, retrorse strigosi pilis 0.5 mm. longis. Receptaculum 1.3 mm. diametro, 1 mm. altum, pubescens pilis 0.3 mm. longis. Phyllaria secundaria 5, ovata vel obovata, 3-17 mm. longa, 1.5-9 mm. lata, strigosa pilis 0.5 mm. longis, margine ciliatis pilis 1.5 mm. longis. Involucrum primarium 4-4.8 mm. longum, 1-1.2 mm. diametro, 6(-7) phyllariis plerumque 5-7 parvis ellipticis resinosis glandibus 0.2-0.4 mm. longis in una serie in costis, abaxialiter pilosum (praesertim in costis pilis 0.3 mm. longis); lobi 1-2 mm. longi, 0.3 mm. lati probe basin, apice acuminati, abaxialiter stipitato-glandulosi, adaxialiter hirsutuli. Flosculi corollis aureis, fauce 2.6-3 mm. longa et 0.7 mm. diametro, lobis anguste ovatis et 1.8-2 mm. longis, tubo 0.7 mm. longo et 0.3 mm. diametro; antherae aureae vel hepaticae, 3 mm. longae; stylus 7 mm. longus; achenia anguste obovoidea, 2.8 mm. longa, 1.1 mm. diametro, glabra sed apice leviter pubescentia; pappus ex corona erosa pubescenti 1 mm. diametro, 0.3 mm. longa. Chromosomatum numerus, $n=17$.

Distribution.—Tropical deciduous and thorn forests in the valley surrounding Apatzingán, Michoacán, and extending westward into adjacent Jalisco (fig. 19); 250-300 m.

Flowering Dates.—September through January.

Lagascea aurea is very similar to *L. mollis*. This resemblance initially suggested ranking it as only a *forma* or *varietas*. Subsequent study, however, recommends status as a distinct species because of several conspicuous differences, including some which are qualitative (those of *L. aurea* listed first): yellow *vs.* white corollas; light brown *vs.* dark brown to black anthers; primary involucres of 6(-7) phyllaries *vs.* 4-5; and one row of involucral glands per phyllary *vs.* three. These differences are approximately of the same magnitude as those used to distinguish *L. palmeri* from *L. decipiens*. In addition, the usual pattern of intergrading characters between varieties in the zone of contact, as in *L. decipiens*, *L. helianthifolia*, and *L. rigida* is not present here. These considerations, plus the ease of morphological recognition of *L. aurea*, are the reasons for specific rank.

Specimens Examined.—MEXICO. JALISCO: between Sierra de Los Corales (Tecalitlán) to Tepalcatepec, 26 Oct. 1963, *Feddema 2241* (CAS, DUKE, ENCB, MICH, TEX). MICHOACÁN: 11-13 km. WSW of Apatzingán, 5-9 Sept. 1972, *Dieterle 4274* (ENCB, MICH); Apatzingán, 5 Jan. 1939, *Hinton et al. 12830* (ARIZ, ENCB, GH, LL, MICH, TEX, US); 2.2 miles W of Apatzingán, 15 Dec. 1974, *SR 3743* (OS).

II. LAGASCEA section NOCCA (Cav.) DC.

Nocca Cav. Icon. 3:12. 1795. *Lagascea* section *Noccaea* (Cav.) DC. Prodr. 5:92. 1836. Type species: *Nocca rigida* Cav. [=*Lagascea rigida* (Cav.) Stuessy].

Shrubs, or coarse herbs to 2 m. tall, woody at the base; synflorescence campanulate, in cymose or racemose clusters; primary phyllaries each with 2-3 small, elliptical, resinous glands at the midrib; corollas and anthers white to purple. Species 3-6.

3. **Lagascea helianthifolia** H. B. K. Nov. Gen. et Sp. 4:19. folio. 1818.

Erect shrub to 3 m. tall, with branches arising anew each season from a woody base. Stems solitary or several, erect, lignescent, to 2 cm. diam., brown to yellow-brown, pilose and often stipitate-glandular with hairs 4 mm. long. Leaves sessile or shortly petiolate; blades narrowly ovate to ovate, 14-33 cm. long, 4-12.5 cm. wide, at apex acute to acuminate, at base obtuse (sometimes attenuate) to subauriculate, at the margin obscurely serrate to dentate, with the upper surface glabrous to strigose

with hairs to 0.7 mm. long, with the lower surface subglabrous to conspicuously tomentose-hirsutulous with hairs 0.1-0.7 mm. long. Synflorescence with 19-32 uniflowered capitula, campanulate, terminal, 1.5-3 cm. tall, 1.5-4 cm. diam., closely associated in cymose groups of 3 and subtended by a pair of leaves (sometimes several to many of these units are borne on the same and/or on adjacent axes). Peduncles 2-10 mm. long, 1-2 mm. diam., pilose and usually stipitate-glandular with hairs 2 mm. long. Receptacle subglabrous, 3-4 mm. diam., 1.5-2 mm. tall. Secondary phyllaries 5-6, lanceolate to narrowly obovate, 21-27 mm. long, (2-) 6-10 mm. wide, abaxially pubescent and sometimes stipitate-glandular with hairs 0.3 mm. long, adaxially strigose with hairs 0.3 mm. long, at margin ciliate with hairs 1-2 mm. long. Primary involucre (4-) 7-9 mm. long, 1-1.5 mm. diam., of 5(-6) phyllaries most with (1-) 2-3 elliptic resinous glands 1-2 mm. long on the midribs, abaxially pilose with hairs 3-5 mm. long; lobes (0.5-) 2.6-3.8 mm. long (with one lobe usually longer than the rest) and 0.5-0.9 mm. wide at base, at apex acuminate, adaxially pubescent. Florets with corollas white to deep red above, at base of throat sometimes black, pubescent with hairs 0.1 mm. long, narrowly funnelform, with throat (3.2-) 6-9 mm. long and 1.5 mm. diam., with lobes narrowly triangular and (1.5-) 2-3 mm. long, with tube (2-) 3-4 mm. long and 0.7 mm. diam.; anthers brown to deep red, (3.2-) 5-6 mm. long; style 12-23 mm. long; achenes narrowly ellipsoid to obovoid, 4-5 mm. long, 1.2 mm. diam., glabrous; pappus 1 mm. diam., of short pubescent awns 0.5 mm. long. Chromosome number, $n=17$.

Lagascea helianthifolia is the most morphologically variable species in the genus. This variability, primarily in leaf shape and pubescence, head size, and corolla color, has resulted in proliferation of many names within the taxon. Within this morphological variation, two distinct populational systems are recognized in the present study at the varietal level (var. *helianthifolia* and var. *levior*), and these are the most striking and consistent morphological and geographical patterns that can be satisfactorily defined. Numerous forms might be recognized (such as the petiolate or corolla color variants in var. *helianthifolia*), as has been recommended as a general practice by Valentine (1975), but these are simply mentioned and discussed here rather than given formal status.

Although hybridization is not rampant among species of *Lagascea*, the phenomenon is known to occur between *L. helianthifolia* and all other species of section *Nocca*: *L. angustifolia*, *L. heteropappus*, and *L. rigida*. That hybridization might occasionally be occurring among these taxa was initially suggested by morphological intermediacy of certain collections. Field studies, however, revealed an introgressing hybrid population between *L. helianthifolia* and *L. heteropappus* in which not only unusual segregation of morphological features prevailed, but also meiotic chromosomal irregularities and low pollen viabilities (table 2). It was this detailed examination of a known hybrid population that has allowed more

TABLE 2. Pollen viabilities and meiotic configurations of plants of hybrid population, *Lagascea helianthifolia* × *L. heteropappus* (Michoacán, 9.7 miles S of Uruapan, *SR 3748*).

Taxon and plant number[a]	Number of stained pollen[b]	Number of unstained pollen	% stained pollen	Meiotic configuration[c]
L. heteropappus				
3784-3	368	25	94	—
3748-5	297	68	81	—
3748-8	267	51	84	17 II
3748-9	321	21	94	—
3748-28	306	35	90	17 II & 1 or 2 frags.
Hybrids				
3748	297	220	57	—
3748-2	189	109	63	15 II & 1 IV & frag.
3748-6	69	300	19	—
3748-7	240	152	61	—
3748-10	216	225	49	—
3748-26	138	148	48	17 II & 4 frags.
L. helianthifolia				
3748-30	328	47	87	—

[a]A complete set of vouchers of these plants is on deposit at OS.
[b]Using acetocarmine stain.
[c]Cytological techniques are the same as those outlined previously in this paper.

confident identification of hybrid types in other situations. The other hybrid collections are (pollen viabilities as percent of at least 300 grains in acetocarmine are given after the herbarium acronyms): with *L. angustifolia* (Jalisco, 3 miles S of Mazamitla, *McVaugh & Koelz 446*, DUKE, 48 per cent; Nayarit, Tepic, *Palmer 1879*, F, 50 per cent); and with *L. rigida* var. *mocinniana* (Morelos, 6.5 miles E of Jiutepec, *SR 3688A*, OS, 66 per cent; Guerrero, 2 miles S of Cacahuamilpa, *Webster & Breckon 16173b*, MICH, 70 per cent). *Lagascea helianthifolia* has also been collected in the latter two populations *SR 3687A*, OS; *Webster & Breckon 16173a*, MICH).

Ordinarily, the principal flowering time of *L. helianthifolia* is later (Nov.-March) than that of *L. rigida* and *L. heteropappus* (both Sept.-Dec.) which effects a high degree of temporal isolation. Field observations of hybrid population *SR 3748* indicated that plants of *L. heteropappus* were just finishing flowering while those of *L. helianthifolia* were just beginning.

3a. **Lagascea helianthifolia** H.B.K. var. **helianthifolia**. Figures 11, 12.

Lagascea helianthifolia H.B.K. Nov. Gen. et Sp. 4:19. folio. 1818. TYPE: MEXICO: Guerrero, near Acapulco, April 1803, *A. von Humboldt & A. Bonpland s.n.* (Holotype, P!; photograph of holotype, IDC 6209. 90: III. 6!).

Lagascea suaveolens H.B.K. Nov. Gen. et Sp. 4:20. folio. 1818. TYPE: MEXICO: Guerrero, "crescit in declivitate occidentali montium Mexicanorum inter fluvium Papagallo et Venta Colorada," 540-1,200 m., April 1803, *A. von Humboldt & A. Bonpland 3899* (Holotype, P!; photograph of holotype, IDC 6209, 90: III. 7!).

Noccaea helianthifolia (H.B.K.) Cass. Dict. Sci. Nat. 25:104. 1822.

Noccaea suaveolens (H.B.K.) Cass. Dict. Sci. Nat. 25:105. 1822.

Nocca latifolia Cerv. in LaLlav. & Lex. Nov. Veg. 1:31. 1824. TYPE: "Habitat in horto Mexicano, floret toto anno," date of collection and collector unknown (Holotype, MA?, not located). The description which, among others features, mentions white florets and subconnate leaves, indicates probable synonymy with *L. helianthifolia* var. *helianthifolia*.

Lagascea latifolia (Cerv. in LaLlav. & Lex.) DC. Prodr. 5:92. 1836.

Nocca macrophylla Zucc. ex DC. Prodr. 5:92. 1836. *pro syn.*

Lagascea macrophylla (Zucc. ex DC.) Steud. Nom. 2:4. ed. 2. 1841.

Lagascea tomentosa Robins. & Greenm. Proc. Amer. Acad. Arts 32:43. 1896. TYPE: MEXICO: Guerrero, between Ayusina and Petatlán, 5,000-7,000 ft., 14 Dec. 1894, *E. W. Nelson 2121* (Holotype, GH!, isotype, US!).

Nocca helianthifolia (H.B.K.) Cass. var. *suaveolens* (H.B.K.) Robins. Proc. Amer. Acad. Arts 36:468. 1901.

Nocca tomentosa (Robins. & Greenm.) Robins. Proc. Amer. Acad. Arts 36:470. 1901.

Lagascea helianthifolia H.B.K. var. *adenocaulis* Robins. Proc. Amer. Acad. Arts 43:38. 1907. TYPE: MEXICO: Michoacán, Uruapan, 24 Jan. 1907, *C. G. Pringle 13907* (Holotype, GH; isotypes, CAS! F! MICH! MO! MSC! SMU! TEX! UC! US!).

Lagascea helianthifolia H.B.K. var. *suaveolens* (H.B.K.) Robins. Proc. Amer. Acad. Arts 43:38. 1907.

Calhounia helianthifolia (H.B.K.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:58. 1924.

Calhounia suaveolens (H.B.K.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924.

Calhounia tomentosa (Robins. & Greenm.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924.

Nocca pteropoda Blake, Contrib. U.S. Nat. Herb. 22:597. 1924. TYPE: MEXICO: Oaxaca, district of Cuicatlán, Cuyamecala, 14 April 1919, *C. Conzatti & I.C. Gómez 3470* (Holotype, US!, isotype, MEXU!).

Lagascea pteropoda (Blake) Standley, Field Mus. Publ. Bot. 8:398. 1931.

Leaves sessile, at base subauriculate to auriculate, with the lower surface subglabrous to tomentose. Synflorescence 2.5-3 cm. tall, (2.5-) 3-4 cm. diam., often solitary or loosely aggregated.

Distribution.—Tropical deciduous and pine and oak forests throughout central and southern Mexico, south to Nicaragua in Central America (fig. 21); 650-2,600 m.

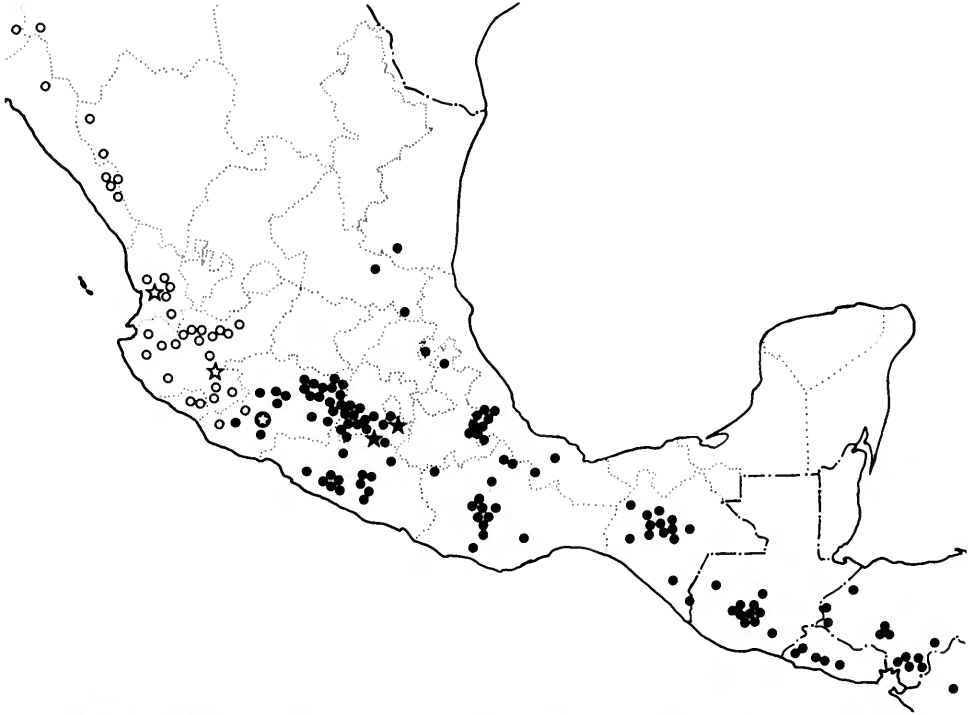


FIG. 21. Map of Mexico and adjacent Central America showing distribution of *Lagascea helianthifolia* var. *levior* (open circles) and *L. helianthifolia* var. *helianthifolia* (closed circles). Also mapped are hybrids of *L. helianthifolia* with *L. angustifolia* (open stars), with *L. heteropappus* (encircled star), and with *L. rigida* var. *mocinniana* (closed stars).

Principal Flowering Dates.—November through March.

Considerable morphological diversity prevails within var. *helianthifolia*. A number of taxa have been recognized by other workers within this variety (such as *L. pteropoda* and *L. tomentosa*), but in my opinion, these are not deserving of formal rank. Two trends of character variation do exist, however, that should be noted (only single specimens are cited in each case as examples): 1) hispid and eglandular stems and peduncles and excessively tomentose undersurfaces of leaves from material of Central America (*Standley 59124*), Chiapas (*Breedlove 9011*), and Veracruz (*Purpus 12013*); and 2) copiously stipitate-glandular peduncles and secondary phyllaries in plants of México (*Dodds & Simpson 46*) and Morelos (*SR 3692*), with these same features occurring also but less commonly in collections from Oaxaca (*Conzatti 4543*).

In addition to these trends, another morphological variation, originally called *L. tomentosa*, occurs in var. *helianthifolia* in west-central Guerrero. Here the collections (*Hinton et al. 11672; Langlassé 782; Mexia 8971, 9030;* and *Nelson 2121*) have shortly petiolate leaves that are very tomentose (approaching the type of vesture sometimes found in plants from Veracruz). This petiolate condition grades into the more typical subauriculate leaf base as seen in the duplicate collections of *Mexia 8971*.

Several noteworthy individual collections also occur; undersurface of leaves subglabrous (*Hinton et al. 11057*); long and narrow secondary phyllaries with short florets (*Nevling & Gómez-Pompa 658*); and very long leaves (33 cm.; *SR 3711*).

Populations of var. *helianthifolia* exist that approach var. *levior* (e.g., *Moore, Hernandez & Porras 5626; Pringle 13907* [type of var. *adenocaulis*]; *SR 3702, 3734*). These have a more reticulate undersurface of the leaves than typical, and the populations are restricted to the northern edge of the taxon's range in Michoacán.

Both red and white corolla forms are known within var. *helianthifolia*. The white form predominates throughout the species in both varieties, but in northeastern Michoacán, southwestern México, and central Guerrero, red forms occur within var. *helianthifolia* (e.g., *Mexia 8971, SG 3103; SR 3710, 3734*). That these corolla color variants should not be accorded formal status is supported by their morphological similarity in all other respects and by their occurrence together in some populations (e.g., *SR 3702, 3711, 3719*).

Representative Specimens.—EL SALVADOR. AHUACHAPAN: near Ahuachapan, 9-27 Jan. 1922, *Standley 20296* (GH, NY, US). SAN SALVADOR: near San Salvador, 20 Dec. 1921-4 Jan. 1922, *Standley 19116* (GH, MO, US). SAN VICENTE: near Vicente, 2-11 March 1922, *Standley 21653* (GH, US). GUATEMALA. ALTA VERAPAZ: San Joaquin, Dec. 1907, *Von Tuerckheim 2049* (F, MO, NY, US). CHIMALTENANGO: Finca La Alameda, near Chimaltenango, 7 Dec. 1938, *Standley 59124* (F, GH). ESCUINTLA: Texcuaco, Oct. 1928, *Morales 1077* (F). GUATEMALA: Cd Guatemala, 2 Feb. 1905, *Kellerman 4737* (OS, US). HUEHUETENANGO: ca. 15 km. E of Huehuetenango, 2 Jan. 1941, *Standley 81916* (F). JALAPA: between Jalapa and Paraíso, 14 Nov. 1940, *Standley 77277* (F). JUTIAPA: near Jutiapa, 24 Oct.-5 Nov. 1940, *Standley 75282* (F). QUICHÉ: near Río Blanco, 6 Dec. 1962, *Williams, Molina & Williams 22454* (F). SACATEPEQUEZ: SE of Barberena, 21 Nov. 1940, *Standley 77775* (F). SOLOLÁ: N shore of Lake Atitlán, NW of Panajachel, 4 Jan. 1965, *Williams et al. 27297* (F, NY). ZACAPA: near Gualán, Jan. 1907, *Pittier 1783* (NY, US). HONDURAS. CHOLUTECA: San Marcos, 16 Nov. 1946, *Williams & Molina 10888* (F). COMARCO DEL CABO: El Achote, near Siguatepeque, 18 Feb. 1928, *Standley 56096* (US). COPÁN: 3 km. NW of Copán, 29 Dec. 1973, *Williams, Williams & Molina 42954* (US). EL PARAÍSO: near Danlí, 11-23 Feb. 1949, *Standley 16921* (F). FRANCISCO MORAZÁN: Río Yeguare, 5 Dec. 1948, *Williams & Molina 14804* (F, MO, US). OCOTEPEQUE: between El Moral & Sinuapa, 10 March 1969, *Molina 24197* (F, NY, US). SANTA BÁRBARA: Los Dragos, 16-17 April 1947, *Standley & Lindelie 7412* (F). MÉXICO. CHIAPAS: Ixtapa, 3 miles SE jct. rt. 190 & rd. to Bochil, 16 Feb. 1965, *Breedlove 9011* (DS, ENCB, F, MICH); El Zapotal, along trail from Zinacantán to San Lucas, 15 Dec. 1966, *Laughlin 2973* (DS, ENCB, MICH, US); Montecristo, Jan. 1938, *Matuda 1961* (F, LL, MEXU, MICH, MO, NY, US). GUERRERO: Galeana, Plan de Carrizo, 15 Dec. 1937, *Hinton et al. 11057* (ARIZ, ENCB, LL, US), Montes de Oca, San Antonio Buenos Aires, 14 Dec. 1937, *11672* (GH, LL, MICH, NY, UC, US); Sierra Madre, 23 Jan. 1899, *Langlaseé 782* (MICH); Achotla, 12 Nov. 1937, *Mexia 8809* (CAS, F, MO, NY, UC, US), Mina, Petlacala, 16 Dec. 1937, *8971* (CAS, F, LL, MO, NY, UC), Mina, Petlacala, below mine Sta Elena, 24 Dec. 1937, *9030* (F, MO, NY, UC); 7.2 miles S of Chilpancingo, 11 Sept. 1973, *SG 3146* (OS), 7.1 miles S of Palo Blanco, 11 Sept. 1973, *3153* (OS), 4.4 miles E of Chilpancingo, 12 Sept. 1973, *3157* (OS), 7.2 miles NNE

of beginning of toll rd. from Iguala to Cuernavaca, 12 Sept. 1973, *3158* (OS). MÉXICO: Valle de Bravo, Rancho San Lorenzo, 28 Jan. 1943, *Dodds & Simpson 46* (MICH, MSC); Temascaltepec, Volcán, 3 Nov. 1932, *Hinton 2485* (F, MO, NY); 8 km. W of Ixtapan de la Sal, 15 Jan. 1966, *Rzedowski 21828* (DS, DUKE, ENCB, MEXU, MICH, MSC, TEX); 7.3 miles S of Zitácuaro, then 13 miles SE toward Ixtapan del Oro, 7 Sept. 1973, *SG 3121* (OS); 0.2 miles S of Tonatico, 10 Dec. 1974, *SR 3698* (OS), 2.2 miles N of Villa Guerrero, 10 Dec. 1974, *3701* (OS), 11.1 miles SE of Zitácuaro, 12 Dec. 1974, *3711* (OS), 6.5 miles S of Zitácuaro, then 20 miles SE on rd. to Ixtapan del Oro, 12 Dec. 1974, *3719* (OS). MICHOACÁN: near Morelia, Rincón, 8 Sept. 1910, *Arsène 5289* (GH, MO, NY, US); ca. 18 miles E of Morelia, 9-18 Nov. 1961, *King & Soderstrom 5019* (MICH, NY, SMU, TEX, UC, US); 8-10 miles NW of Ciudad Hidalgo, 22 Mar. 1949, *McVaugh 10004* (MEXU, MICH, NY, US); ca. 5 km. below Tacambaro on rd. to Chipio, 10 Nov. 1949, *Moore, Hernández & Porras 5626* (UC); Uruapan, 27 Nov. 1907, *Pringle 10411* (ARIZ, ASU, CAS, DUKE, F, LL, MICH, MSC, SMU, UC, US); 16.7 miles E of Morelia, 6 Sept. 1973, *SG 3103* (OS), 37.4 miles E of Morelia, 6 Sept. 1973, *3115* (OS), 7.9 miles S of Zitácuaro, 7 Sept. 1973, *3116* (OS); 7.8 miles S of Zitácuaro, 12 Dec. 1974, *SR 3702* (OS), 8.9 miles SSE of Zitácuaro, 12 Dec. 1974, *3710* (OS), 41.7 miles W of Ciudad Hidalgo, 13 Dec. 1974, *3734* (OS). MORELOS: 6 km. SE of Cuajomulco, 17 Oct. 1965, *Rzedowski 21467* (DS, ENCB, MEXU, MICH); 8.3 miles E of Cuernavaca, 13 Sept. 1973, *SG 3159* (OS); ca. 6 miles E of Jiutepec, 9 Dec. 1974, *SR 3692* (OS). OAXACA: 15-18 km. WSW of Cd Oaxaca, 20-25 Jan. 1937, *Camp 2510* (MICH, NY, UC); Tuquila, Plan de Minas, 28 Dec. 1921, *Conzatti 4543* (US); Tuxtepec, near Chiltepec, July 1940-Feb. 1941, *Martínez 537* (LL, MEXU, UC, US); Sierra de San Felipe, 19 Nov. 1894, *Smith 381* (MICH, MO, NY, UC, US). PUEBLA: 6 miles S of Villa Juárez, 23 Feb. 1961, *McGregor 16424* (MSC, NY). SAN LUIS POTOSÍ: km. 253 hwy. San Luis Potosí-Antiguo Morelos, 28 Oct. 1956, *Rzedowski 8384* (ENCB, TEX). TAMAULIPAS: near Santa Bárbara, Nov. 1830, *Berlandier 2173* [=*753*] (MO). VERACRUZ: Maltrata, May 1937, *Matuda 1287* (MEXU, MICH, US); near La Victoria, 11 April 1969, *Nevling & Gómez-Pompa 658* (CAS, MEXU, MICH); Zacuapan, Aug. 1929, *Purpus 12013* (DS, F, MICH, MO, NY, UC); El Paso Triste, 4 km. SE of Orizaba, 15 Dec. 1966, *Rosas 122* (DS, MEXU, MICH, MO); 4.2 miles E of Puebla-Veracruz boundary on rte. 150-D, 14 Sept. 1973, *SG 3175* (OS);

Totutla, El Encinal, 10 Dec. 1970, *Ventura 2966* (DS, ENCB, MICH, NY). NICARAGUA. JINOTEGA: near Jinotega, 19 June-9 July 1947, *Standley 9876* (F).

3b. **Lagascea helianthifolia** H.B.K. var. **levior** Robins. Proc. Amer. Acad. Arts 43: 38. 1907.

Nocca helianthifolia (H.B.K.) Cass. var. *levior* Robins. Proc. Amer. Acad. Arts 36:468. 1901. TYPE: MEXICO: Colima, 9 Jan.-6 Feb. 1891, *E. Palmer 1148* (Lectotype chosen, US!; isolectotype, NY!).

Leaves shortly petiolate or sometimes sessile, at base usually obtuse to attenuate, with the lower surface strongly reticulate and copiously tomentose-hirsutulous. Synflorescences 1.5-3 cm. tall, 1.5-3.5 cm. diam., usually numerous and densely aggregated.

Distribution.—Hillsides and steep slopes in tropical deciduous and pine and oak forests, primarily in Jalisco, Colima, and Nayarit with extensions southward into western Michoacán and northward into Sinaloa, Sonora, Durango, and Chihuahua (fig. 21); 450-2,000 m.

Principal Flowering Dates.—November through March.

The morphological limits of var. *levior* encompass not only the very distinct populations in Jalisco, Nayarit, and Colima, but also those with slightly modified features extending northward into Sinaloa, Sonora, Chihuahua, and Durango. Populations in this region have longer and narrower leaves with obtuse (rarely subauriculate) bases and slightly less reticulate undersurfaces (e.g., Sinaloa, *Breedlove 19276*; Sonora, *Gentry 1426*; Durango, *Gentry 5299*; Chihuahua, *Gentry 8068*).

Representative Specimens.—MEXICO. CHIHUAHUA: Arroyo Hondo, Sierra Charuco, 16-30 April 1948, *Gentry 8068* (MICH, US). COLIMA: Alzada, 4 Nov. 1910, *Orcutt 4660* (DS, F, MO). DURANGO: Sierra Tres Picos, 20 Dec. 1939, *Gentry 5299* (ARIZ, DS, MO, NY); Chacala, 5 March 1899, *Goldman 347* (NY, US); Sianori, 1942, *González 5284* (ENCB, US). JALISCO: Agua Fría, Tamazula, 20 Nov. 1972, *Díaz 3646* (MICH); Barranca of Río Santiago, Dec. 1899, *Diguet s.n.* (MICH, NY); Ixtlahuacán del Río, Los Pitayitos, 12 Jan. 1971, *González 8* (DS, ENCB, MICH); km. 742 on rt. 15 from Guadalajara to Tepic, 28 Nov. 1967, *Grashoff 182* (MSC); 10-12 km. N of La Cuesta, 30 March 1965, *McVaugh 23339* (ENCB, MICH); between Jocotepec & San Juan Cosala, 8 Nov. 1959, *McVaugh & Koelz 373* (DUKE, ENCB, LL, MICH); San Sebastian,

Segundo Arroyo, 22 Jan. 1927, *Mexia 1554* (CAS, DS, F, MICH, MO, NY, UC, US), trail to Tranquillas, 19 Feb. 1927, *1709* (US); Baños de Oblatos, near Guadalajara, 16 Jan. 1968, *Moran 14709* (MICH); on rd. from Altenguilla to Jacala, 5 March 1897, *Nelson 4013* (US); Río Blanco, June-Oct. 1886, *Palmer 664* (MICH, NY, US); near Guadalajara, 14 Nov. 1889, *Pringle 2763* (F, MEXU, MO, MSC, UC); 3 km. W of Arenal, 8 March 1975, *Stuessy & Díaz 3793* (OS), 1 km. W of Tequila, 8 March 1975, *3796* (OS), 1 km. SE of Santa Cruz del Astrillero, 8 March 1975, *3799* (OS); ca. 5 miles SW of Tamazula, 16 Dec. 1974, *3757* (OS); 20.1 miles N of La Huerta, 18 Dec. 1974, *SR 3780* (OS); 8.6 miles N of jct. rt. 80 on rd. to Yahualica, 20 Dec. 1974, *3788* (OS). MICHOACÁN: Coalcomán, 27 Nov. 1938, *Hinton et al. 12689* (LL, MICH, NY, UC, US); NW of Aguililla, ca. 6-7 km. S of Aserradero Dos Aguas, 3 March 1965, *McVaugh 22709* (DS, ENCB, MICH). NAYARIT: on hwy 15 between Tepic & jct. of San Blas rd., 24 Dec. 1957, *Alava & Cook 1592* (UC); Cerro de Sanganguey, E of Tepic, 13 Jan. 1966, *Breedlove & Gregory 14214* (CAS, ENCB, MICH); 4 miles on rd. Tepic to Santa Cruz, 17 Dec. 1970, *Cummins 70-311* (ARIZ); Mirador del Águila, ca. 14 miles N of Tepic, 21 Aug. 1959, *Feddema 809* (MICH); 14-17 miles W of Tepic, 24 June 1951, *Gentry & Gilly 10680* (LL, MEXU, MICH); Tepic, 10 Feb. 1927, *Jones 23409* (CAS, MO, NY, POM, UC); Zopelote, Tepic, Feb. 1895, *Lamb 564* (DS); 10 miles SE of Ahuacatlán, on rd. to Barranca del Oro, 7 July 1957, *McVaugh 15182* (MICH), 6-12 km. NE of Miramar, rd. to Jalcocotán, 11 April 1965, *23556* (DS, ENCB, MICH); ca. 5.5 miles SW of Jalisco, 14 Nov. 1959, *McVaugh & Koelz 679* (DUKE, ENCB, MICH). SINALOA: Rosario, 7.6 miles W of El Palmita, 31 Jan. 1962, *Breedlove 1690* (DUKE, MICH), Sierra Surutato, rd. above La Joya in upper Cañon de Tarahuma, 9 May 1971, *19276* (MO, RSA); Sierra Tacuichamona, Capadero, 10 Feb. 1940, *Gentry 5540* (ARIZ, MO, NY); Balboa, Jan. 1923, *González 5056* (US); San Ignacio, Tinamartila, 20 Feb. 1919, *Montes & Salazar 786* (US). SONORA: Río Mayo, Tepopa, 10 March 1935, *Gentry 1426* (ARIZ, F, MEXU, MO, UC).

4. **Lagascea rigida** (Cav.) Stuessy, comb. nov.

Nocca rigida Cav. Ic. 3:12. *t. 224.* 1795.

Erect shrub to 2 m. tall. Stems several from the base, branching, woody, to 18 mm. diam., brown to purple, glabrous below to antrorsely strigillose above with hairs less than 0.1 mm. long. Leaves with petioles 3-7 mm. long and 1.5-2.5 mm. diam.; blades narrowly ovate to ovate, 4.3-10 (-12.7) cm. long, 1.5-6.7 cm. wide, at apex acute, at base obtuse to slightly attenuate, at the margin subentire to obscure-

ly serrate, with both surfaces varnished and sparingly strigillose with hairs less than 0.1 mm. long (in var. *mocinniana* sometines tomentose with hairs to 1 mm. long). Synflorescence with 9-21 uniflowered capitula, campanulate, terminal, 1.5-2.4 cm. tall, 1.2-3 cm. diam., in racemose (sometimes cymose) clusters of 3-15, subtended by leaf-like bracts, on stalks 1-18 cm. long. Peduncles 3-35 mm. long, 1-2 mm. diam., antrorsely strigose or stipitate-glandular with hairs to 0.7 mm. long. Receptacle subglabrous, 2.5 mm. diam., 0.5 mm. tall. Secondary phyllaries 5-7, lanceolate, 10-23 mm. long, 2.5-6 mm. wide, with both surfaces strigose and sometimes stipitate-glandular with hairs 0.3 mm. long, at margin ciliate with hairs 1 mm. long. Primary involucre 5-8.5 mm. long, 1-1.8 mm. diam., of 5 phyllaries each with 2-3 elliptic resinous glands 0.7-1.3 mm. long on the midribs of most bracts, abaxially pilose especially near base with hairs to 2 mm. long; lobes 1.2-3.5 mm. long (with one lobe sometimes twice as long as the rest), 0.3-1 mm. wide at base, at apex acuminate, adaxially pubescent. Florets with corollas white to pink-purple above, at base of throat often black, pubescent with hairs 0.1 mm. long, with throat 4-5 mm. long and 1.3-1.6 mm. diam., with lobes narrowly triangular and 1.6-3.2 mm. long, with tube 2.8-3.7 mm. long and 0.3-0.4 mm. diam., anthers brown (rarely gray) to pink-purple, 5 mm. long; style 16 mm. long; achenes narrowly ellipsoid to obovoid, 4 mm. long, 1.2 mm. diam., glabrous except pilose at apex with hairs 0.5 mm. long; pappus of short awns, 0.5-3 mm. long (2 awns usually twice as long as the rest). Chromosome number, $n=17$.

Lagascea rigida is very closely related to *L. heteropappus*. The two species are readily distinguishable by the subglabrous undersurface of the leaves of the former and sericeous vesture of the latter. Both species have varnished upper surfaces of the leaves, although this is much more obvious in *L. rigida*. In floral features, the two are nearly identical, except that the corollas of *L. heteropappus* tend to be slightly more pubescent.

A comment regarding the typification of *L. rigida*, the oldest name in the genus, is in order. During the course of this study, a request for a loan of the type of this name was made to Madrid, where Cavanilles' original herbarium is deposited. Although a thorough search for the specimen was completed, it could not be found (C. Sáenz de Rivas, *in litt.*). In the absence of type material, therefore, the plate (*t. 224*) from the protologue was taken as the holotype. The diagnostic features of this drawing, especially the subauriculate leaf bases and conspicuously toothed leaf margins, suggested that the taxon was what previously had been called *L. helianthifolia*. Consequently, at the close of the study in the summer of 1976, all specimens on loan were annotated to reflect this nomenclatural judgment. The sheets were returned to their respective institutions, and the manuscript was sent off for publication. In the winter of 1977, an opportunity arose to travel to European herbaria for study of type materials relating to other projects, and Madrid was includ-

ed in the itinerary. While there in July of 1977, I looked for the type of *L. rigida*. Although no specimen with that name is in the historical collection of Cavanilles, another sheet was found, filed under an unpublished herbarium name, that matches clearly (allowing for some artistic liberties) the plant depicted in the protologue. In addition, the notation "*t. 224*" appears on the sheet. The specimen biologically, however, is not *L. helianthifolia*, but rather what has been commonly known as *L. rubra*. Through the kindness of Dr. J. W. VanStone, Scientific Editor of *Fieldiana*, the manuscript was retrieved before being set in type, and the necessary changes in nomenclature effected. The annotated specimens, however, still bear names based upon the previous nomenclatural interpretation, which is now known to be incorrect.

4a. **Lagascea rigida** (Cav.) Stuessy var. **rigida**. Figures 7, 8.

Nocca rigida Cav. Ic. 3:12. *t. 224.* 1795. TYPE: "Nova-Hispania," exact locality unknown, "floruit ultimo Decembri 1793," collector unknown (Holotype, MA!; photograph of holotype, OS!).

Lagascea rubra H.B.K. Nov. Gen. et Sp. 4:19. *t. 311.* folio. 1818. TYPE: MEXICO: "Crescit in temperatis Regni Mexicani" [probably near Mexico City, cf. Sprague, 1924], 4,200 ft., July 1803, *A. von Humboldt & A. Bonpland 4402* (Holotype, P!; photograph of holotype, IDC 6209. 90:III. 5!; isotype, P!).

Noccaea rubra (H.B.K.) Cass. Dict. Sci. Nat. 25:104. 1822.

Calhounia rubra (H.B.K.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924.

Leaves narrowly ovate to ovate; blades 4.3-10 (-12.7) cm. long, 1.5-4.5 cm. wide, with undersurface sparingly strigose. Cymose or racemose clusters of synflorescences on stalks 1-7 cm. long. Peduncles 3-24 mm. long, antrorsely strigose with hairs to 0.7 mm. long. Secondary phyllaries stigose.

Distribution.—Hillsides (often near cultivated fields or in lava flows) in pine and oak forests in Distrito Federal, northern Guerrero, México, northern Morelos, Puebla, and Tlaxcala (fig. 22); 880-2,600 m.

Principal Flowering Dates.—September through December.

Lagascea rigida var. *rigida* is quite variable morphologically, and several interesting variant collections should be noted. Gray an-

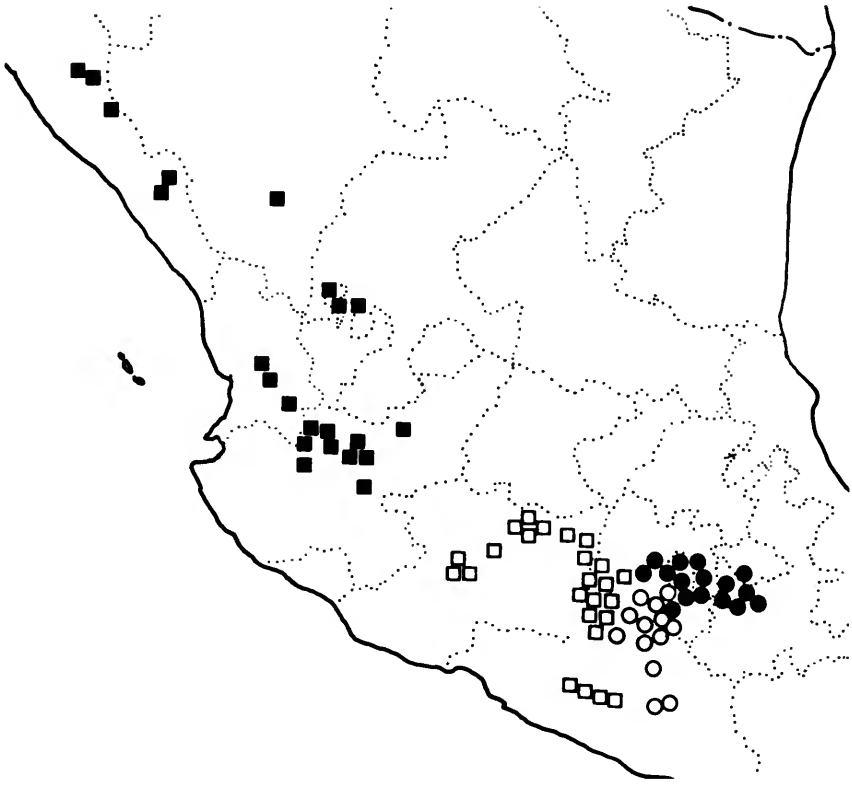


FIG. 22. Map of central Mexico showing distribution of *Lagascea angustifolia* (closed squares), *L. heteropappus* (open squares), *L. rigida* var. *mocinniana* (open circles), and *L. rigida* var. *rigida* (closed circles).

thers occur in *Rzedowski 30836* and purple ones are known in *Rzedowski 29314.* Unusually long and narrow leaves (12.7 × 3 cm.) occur in *Miranda 896* and very broad leaves (9 × 4.5 cm.) are found in *Lyonnet 379.*

A stipitate-glandular condition, which is usually only found in var. *mocinniana* occurs in two collections of var. *rigida*: *Arsène & Nicolas 376*; and *Nicolas s.n.* In the former, both eglandular and copiously glandular branches are mounted together on the same sheet. Three collections from Cerro Tepoxuchil in Puebla (*Arsène s.n., 468, 1004*) are also stipitate-glandular, and they show an intergradation of characters from few glands and very condensed clusters of synflorescences (*468*) to numerous glands and more open clusters of synflorescences (*s.n.*). Because of the isolation of this

population (and the two glandular collections mentioned above also from Puebla) from var. *mocinniana* which is characteristically glandular, it seems likely that an independent trend toward glandular pubescence has developed within var. *rigida* in this region.

Representative Specimens.—MEXICO: DISTRITO FEDERAL: Pedregal, Nov. 1929, *Lyonnet 379* (GH, MO, NY, US). Cerro Santa Catarina, near Los Reyes, Sept. 1953, *Paray 271* (ENCB); above Valley of Mexico, 8 Nov. 1900, *Pringle 9098* (CAS, F, GH, MICH, MO, NY, US); Pedregal de San Angel, near Tlalpan, 6 Sept. 1972, *Rzedowski 29314* (CAS, ENCB, MICH, US), near Santa Marta Astahuacán, 8 July 1973, *30836* (ENCB); 1 mile S of Ciudad Universitaria, 10 Sept. 1973, *SG 3135* (OS). MÉXICO: Mixcoac, 10 Sept. 1865-1866, *Bourgeau 1235* (F, GH, MSC); Temascaltepec, Anonas, 14 Nov. 1932, *Hinton 2589* (MEXU, MO, US); Río Hondo, 5 Sept. 1891, *Pringle 3896* (F, GH, MEXU, MICH, MO, MSC, NY, UC, US); 2 km. S. of Ocotepec, Tejupilco, 10 Dec. 1967, *Rzedowski 25276* (ENCB), Cerro del Pino, Ixtapaluca, 29 Oct. 1972, *29668* (ENCB). MORELOS: Cuernavaca, Iturbide, 15 Nov. 1865, *Bourgeau 1205* (GH, MSC); 20 km. NE of Cuautla, 3 Aug. 1950, *Boyd 73* (SMU); 9 miles NNE of Cuautla, 14 Oct. 1965, *Cronquist 10332* (CAS, DUKE, ENCB, GH, MEXU, MICH, NY, TEX, US); Sierra de Ocuila, toward Mexicapa, 16-18 Dec. 1938, *Lyonnet 2929* (US); Tepoztlán, 15 Dec. 1940, *Miranda 896* (MEXU); 1.6 miles S. of Nepantla, 13 Sept. 1973, *SG 3170* (OS), 3.7 miles N of Yautepec, 13 Sept. 1973, *3161* (OS). PUEBLA: Cerro Tepoxuchil, near Puebla, 14 Nov. 1908, *Arsène s.n.* (CAS, MO), 11 Oct. 1906, *468* (US), 11 July 1907, *1004* (US); Rancho Posada, near Puebla, 10 Oct. 1909, *Arsène & Nicolas 376* (MO, US); Nealticán, near Atlixco, 13 Oct. 1968, *Ern 387* (ENCB); San Francisco, 10 Oct. 1909, *Nicolas s.n.* (NY, US); E of Cerro Tecajete, near San Miguel Papaxtla, 31 Sept. 1967, *Rzedowski 24895* (DS, ENCB, MICH, MSC). TLAXCALA: Tlaxcala, 15 Nov. 1906, *Arsène 3* (US).

4b. **Lagascea rigida** (Cav.) Stuessy var. **mocinniana** (DC.) Stuessy, comb. et stat. nov.

Lagascea mocinniana DC. Prodr. 5:92. 1836. TYPE: MEXICO: the copy of the unpublished plate (#571) of Sessé & Mociño at G is taken as the holotype (photograph of holotype, F!; tracing of holotype, GH! US!).

Noccaea mociniana (DC.) O. Ktze, Rev. Gen. Pl. 1:354. 1891.

Nocca pringlei Robins. Proc. Amer. Acad. Arts. 36:469. 1901.

TYPE: MEXICO: Guerrero, "on limestone ledges above Iguala," 10 Oct. 1900, *C. G. Pringle 8400* (Holotype, GH!; isotypes, F! MEXU! MICH! MO! MSC! NY! POM! UC! US! [3]!).

Lagascea pringlei (Robins.) Robins. Proc. Amer. Acad. Arts 43:38. 1907.

Calhounia mocinniana (DC.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924.

Calhounia pringlei (Robins.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924.

Calhounia robinsonii A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924. TYPE: MEXICO: exact locality unknown, 1791, *T. Haenke 826* (Holotype, G-DC; photograph of holotype, IDC 800. 786: II. 1!; isotype, F!). Nelson based this new species on a description and type specimen given by Robinson (1901) under the invalid name "*Nocca* n. sp.?"

Nocca media Blake, Contrib. U.S. Nat. Herb. 22:596. 1924. TYPE: MEXICO: Guerrero, between Tixila and Chilpancingo, 1,830-2,135 m., 16 Dec. 1894, *E. W. Nelson 2178* (Holotype, US!).

Nocca robinsonii (A. Nelson) Blake in Standley, Contrib. U.S. Nat. Herb. 23:1516. 1926.

Lagascea media (Blake) Standley, Field Mus. Publ. Bot. 8:398. 1931.

Leaves usually ovate; blades 5.6-10.3 cm. long, 3.2-6.7 cm. wide, with undersurface sparingly strigose or sometimes tomentose (in Guerrero) with hairs to 1 mm. long. Cymose or racemose clusters of synflorescences on stalks 4-18 cm. long. Peduncles 4-35 mm. long, stipitate-glandular. Secondary phyllaries strigose and stipitate-glandular.

Distribution.—Hillsides in tropical deciduous, thorn, and pine-oak forests in Guerrero and adjacent Morelos and México (fig. 22); 1,000-2,330 m.

Principal Flowering Dates.—September through December.

The morphological distinctions of stipitate-glandular phyllaries and peduncles, more ovate leaves with increased pubescence on the undersurface, and open clusters of synflorescences that characterize *Lagascea mocinniana* (DeCandolle, 1836) or *L. pringlei* (Robinson, 1901), are here regarded as warranting not more than varietal

status. In all other features, this taxon falls easily within *L. rigida*. *Lagascea media*, described later by Blake (1924), represents a minor variant of this same variety. As might be expected between varieties of the same species, some populations of var. *mocinniana* approach var. *rigida* (e.g., *Anderson & Laskowski 4311; Moore 5555;* and *Rzedowski 25233*). A white-flowered form of *L. rigida* var. *mocinniana* has been collected (*Rzedowski 23534*), which parallels the dimorphic floral color also occurring in *L. helianthifolia* var. *helianthifolia* (white and red).

Representative Specimens.—MEXICO. GUERRERO: Taxco, 23 Dec. 1936, *Abbott 178* (ENCB, GH); 9 miles N of Iguala, 7 Feb. 1970, *Anderson 5654* (MICH); trail from Taxco to Casahuates, 6 Nov. 1949, *Moore 5555* (GH, UC, US); 15 miles W of Teloloapan, 17 Dec. 1963, *Porter 1362* (GH); 12 miles E of Chilpancingo, 2 Dec. 1966, *Rzedowski 23534* (ENCB, MSC), 7 km. NW of Taxco, 21 Nov. 1967, *25233* (ENCB, MICH, MSC), 6 km. S of Zacacoyuca, 3 Nov. 1972, *29826* (ENCB); 4.3 miles E of Chilpancingo, 12 Sept. 1973, *SG 3155* (OS), 3.2 miles W of Tixtla, 12 Sept. 1973, *3156* (OS). MEXICO: Coatepec Harinas, Rancho Santo Tobias, 19 Nov. 1943, *Gilly 105* (MICH, MSC, NY); Ixtapan de la Sal, 12 Oct. 1958, *Paray 2746* (ENCB, MEXU, MICH); 5.4 miles N from Mex-Gue state line on rt. 55, 10 Dec. 1974, *SR 3694* (OS), 6.3 miles S of Villa Guerrero on rt. 55, 10 Dec. 1974, *3700* (OS). MORELOS: Cuautla-Amecameca rd., 1.2 miles S of Mex-Mor border, 25 Nov. 1966, *Anderson & Laskowski 4311* (GH); barranca W of Cuernavaca, 6 Nov. 1967, *Crespo 208* (ENCB); Xochitepec, Dec. 1932, *Lyonnet 784* (US).

5. **Lagascea heteropappus** Hemsl. Diagn. Pl. Nov. 33. 1879. TYPE: MEXICO: "sine loco speciali," date unknown, *W. Parkinson s.n.* (Holotype, K!). Figures 5, 6.

   Noccaea heteropappus (Hemsl.) O. Ktze. Rev. Gen. Pl. 1:354. 1891.

   Calhounia heteropappus (Hemsl.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:58. 1924.

Erect shrub to 2 m. tall. Stems several from the base, branching, woody, to 12 mm. diam., brown, sericeous on uppermost branches with hairs to 1 mm. long. Leaves with petioles 3-11 mm. long and 1-2 mm. diam.; blades narrowly ovate to ovate, 3.7-9.8 cm. long, 2-3.2 cm. wide, at apex acute, at base obtuse to attenuate, at the margin subentire to obscurely serrate, with the upper surface strigose and varnished with hairs 0.2 mm. long, with the lower surface densely sericeous with hairs 1 mm. long. Synflorescence with 8-15 uniflowered capitula, campanulate, terminal,

1.5-2 cm. tall, 1-2.5 cm. diam., closely associated in cymose groups of 3 and subtended by a pair of leaves (sometimes 3 of these cymose units are borne near the branch apex resulting in as many as 9 synflorescences close together). Peduncles 2-8 mm. long, 1.5-2 mm. diam., sericeous with hairs 1 mm. long. Receptacle subglabrous, 2.3 mm. diam., 1.2 mm. tall. Secondary phyllaries 4-6, lanceolate, 8-12 mm. long, 2.5-5 mm. wide, abaxially pilose with hairs 1 mm. long, adaxially glabrous except near apex, at margin ciliate with hairs 1.8 mm. long. Primary involucre 6.5-8.2 mm. long, 1.2-1.7 mm. diam., of 5 (-6) phyllaries most with 2-3 elliptic resinous glands 0.4-1.3 mm. long on the midribs, abaxially pilose especially near base with hairs 2-3 mm. long; lobes 1-3 mm. long (with one lobe sometimes twice as long as the rest), 0.3-0.8 mm. wide at base, at apex acuminate, adaxially pubescent. Florets with corollas white to pink-purple above, at base of throat often black, pubescent with hairs 0.1 mm. long, with throat 4-5 mm. long and 1.5 mm. diam., with lobes narrowly triangular and 2-3 mm. long, with tube 2.8 mm. long and 0.8 mm. diam.; anthers brown to pink-purple, 4-5 mm. long; style 15 mm. long; achenes narrowly ellipsoid to obovoid, 3-3.5 mm. long, 1-1.5 mm. diam., glabrous except pilose at apex with hairs 1 mm. long; pappus of pilose, short awns, 0.5-1.5 mm. long (2 awns usually longer than the rest). Chromosome number, $n=17$.

Distribution.—Hillsides in pine and oak forests in Michoacán and adjacent México (fig. 22); 750-2,700 m.

Principal Flowering Dates.—September through December.

Lagascea heteropappus is a very close relative of *L. rigida*. These taxa are allopatric and are usually easily distinguishable by the sericeous undersurface of the leaves in the former, and the strigose to tomentose vesture in the latter. Another important difference is the tighter aggregation of synflorescences in *L. heteropappus* in contrast to the more open clusters in *L. rigida*.

Within *Lagascea heteropappus* are several collections that intergrade toward *L. rigida*, and these occur in two general regions. The first is in the zone of contact of the two species in the state of México, and the following collections may be cited as examples: *Hinton 2589*; *Hinton et al. 8656*; *Matuda et al. 29848, 29861, 30089, 32024*; *Medrano et al. 5054*; and *Paray 2224*. The second is in the mountains of central Guerrero, where *L. rigida* is not known. Collections from this area are: *Hinton 9876*; *Hinton et al. 11063, 11106, 14918*; and *Mexia 9029*. The lesser degree of pubescence on both sides of the leaves in the specimens from both areas suggests possible hybridization and/or introgression with *L. rigida*. This particularly would seem plausible in the state of México, where the two species grow close together. All of the collections from that area, however, have pollen viabilities of 94-99 per cent (300 grains sampled in lactophenol cotton blue) which would be more suggestive of

parental rather than hybrid types. The collections from Guerrero likewise have high pollen stainabilities with only *Hinton et al. 14918* having slightly lowered viability (72 per cent). More study on these populations, including additional field work, is obviously needed to understand more clearly the biological basis for the observed morphological intermediacy.

Representative Specimens.—MEXICO. GUERRERO: Mina, Río Frío, 21 Nov. 1936, *Hinton 9876* (F, GH, LL, MICH, NY, UC, US); Galeana, 16 Dec. 1937, *Hinton et al. 11063* (US), Galeana, Teotepec, 24 Dec. 1937, *11106* (ENCB, GH, LL, US), Mina, Chilacayote to Carrizal, 29 Nov. 1939, *14918* (LL, MO, US); Petlacala, below mine Santa Elena, 24 Dec. 1937, *Mexia 9029* (F, LL, NY, UC, US). MÉXICO: Peña Blanca, 4.5 km. SSW of Valle de Bravo, 16 Dec. 1965, *González 3339* (ENCB); Telpintla, 17 Nov. 1932, *Hinton 2421* (GH, MO, NY, US), Anonas, 14 Nov. 1932, *2589* (GH, NY); Temascaltepec, Cajones, 17 Nov. 1935, *Hinton et al. 8656* (ARIZ, GH, LL US); Otzoloapán, Valle de Bravo, 5 Sept. 1954, *Matuda 31448* (US); La Junta, Santo Tomás, 12 Oct. 1953, *Matuda et al. 29410* (NY US), near Amatepec, 27 Dec. 1953, *29848* (NY, US), near Amatepec, 27 Dec. 1953, *29861* (MEXU), between Sultepec and Amatepec, 31 Dec. 1953, *30089* (NY, US), Cerro de Pinal, Otzoloapán, 18-22 Oct. 1954, *31793* (MEXU, NY), Cañada de Nanchititla, 4-12 Dec. 1954, *32024* (ENCB, NY); 5 km. SW of Nanchititla, Tejupilco, 27 Dec. 1972, *Medrano et al. 5054* (MEXU); Temascaltepec, 1 Nov. 1956, *Paray 2224* (ENCB); 3 km. S of Colorines, Valle de Bravo, 29 Dec. 1966, *Rzedowski 23740* (ENCB, MICH, MSC); 7.3 miles S of Zitácuaro, then 19.4 miles SE toward Ixtapan del Oro, 7 Sept. 1973, *SG 3127* (OS), ca. 7.3 miles SSE of Ixtapan del Oro, 8 Sept. 1973, *3131* (OS). MICHOACÁN: near Morelia, Campanaris, Dec. 1910, *Arsène 5360* (A, GH, MO, NY, US), near Morelia, Loma Sta Maria, 11 Sept. 1910, *5527* (GH, MO); 13 miles S of Uruapan, 28 Oct. 1962, *Cronquist 9750* (MEXU, MICH, NY); Zitácuaro-Guanoro, 18 Nov. 1938, *Hinton et al. 13461* (ARIZ, ENCB, GH, LL, MICH); 8-10 miles NW of Ciudad Hidalgo, 22 March 1949, *McVaugh 10005* (DUKE, ENCB, GH, MEXU, NY, TEX, US); 8 km. SE of Uruapan, 14 Nov. 1949, *Moore, Hernández & Porras 5274* (GH, UC); near Morelia, 22 Oct. 1893, *Pringle 4541* (F, GH, MICH, MO, MSC, NY UC, US), near Coru Station, 26 Jan. 1907, *10365* (F, GH, MEXU, MO, MSC, NY, UC, US); 2 km. SE of San Miguel del Monte, Morelia, 18 Nov. 1967, *Rzedowski 25192* (DS, ENCB, MICH, MSC), Presa Cupatit-

zio, 13 km. S of Uruapan, 28 Nov. 1968, *26599* (ENCB); 5 miles S of Uruapan, 5 Sept. 1973, *SG 3095* (OS), 8.9 miles SSE of Zitácuaro, 12 Dec. 1974, *3709* (OS); Uruapan, 21 Jan. 1926, *Woronow 2791* (US).

6. **Lagascea angustifolia** DC. Prodr. 5:92. 1836 TYPE: MEXICO: Guanajuato, "Leon a l'ouest de Guanajuato" [from label], 1829, *W. Mendez s.n.* (Holotype, G-DC; photograph of holotype, IDC 800. 786:III. 3! possible isotype, G-DC; photograph of possible isotype, F! IDC 800. 786:II. 8! US!). Figures 9, 10.

   Noccaea angustifolia (DC.) O. Ktze. Rev. Gen. Pl. 1:354. 1891.

   Calhounia angustifolia (DC.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:58. 1924.

Erect shrub to 1.5 m. tall. Stems several from the base, branching, woody, to 14 mm. diam., brown, antrorsely strigose and sometimes stipitate-glandular on uppermost branches with hairs 1.5 mm. long. Leaves with petioles 2-17 mm. long (in some instances almost sessile) and 1-2 mm. diam.; blades oblanceolate to narrowly ovate, 3.8-8.8 cm. long, 1-3.2 cm. wide, at apex acute, at base attenuate, at the margin subentire to obscurely serrate, with the upper surface strigose with hairs 1 mm. long, with the lower surface reticulate and strigose to tomentose with hairs 1 mm. long. Synflorescence with 8-18 uniflowered capitula, campanulate, terminal, 1.7-2.5 cm. tall, 1.7-2.3 cm. diam., closely associated in cymose (rarely racemose) groups of 3 and directly subtended by a pair of leaves (sometimes 3 of these cymose units are borne near the branch apex resulting in as many as 9 synflorescences close together). Peduncles 2-35 (-42) mm. long, 1 mm. diam., pilose and stipitate-glandular with hairs 2 mm. long. Receptacle pilose, 1.5 mm. diam., 0.4 mm. tall. Secondary phyllaries 4-6, narrowly ovate to lanceolate, 10-22 mm. long, 2-5 mm. wide, abaxially strigose and stipitate-glandular on upper two-thirds with hairs 0.5 mm. long, adaxially subglabrous toward base with apex strigose, at margin ciliate with hairs 1.5 mm. long. Primary involucre 7.5-9.7 mm. long, 1 mm. diam., of 4-5 phyllaries most with (1-) 2 elliptic resinous glands 1-2 mm. long on the midribs, abaxially densely pilose with hairs 1.5-5 mm. long (longest near base); lobes 2-3.5 mm. long, 0.3-0.5 mm. wide at base, at apex acuminate, adaxially pilose with hairs 1.5 mm. long. Florets with corollas white to purplish brown, at base of throat sometimes black, pubescent with hairs less than 0.1 mm. long, with throat 4 mm. long and 2.5 mm. diam., with lobes narrowly triangular and 2-3.8 mm. long, with tube 3-6 mm. long and 0.3 mm. diam.; anthers brown, 4-5 mm. long; style bifid, 11-21 mm. long; achenes narrowly ellipsoid to obovoid, 4-5 mm. long, 1.3 mm. diam., glabrous except pilose at apex; pappus a short pilose crown 0.8 mm. diam. with 2 short awns 0.3-1.2 mm. long. Chromosome number unknown.

Distribution.—Rocky and generally arid slopes in oak and pine forests primarily in the states of Jalisco and Nayarit, with extensions northward into Zacatecas, Durango, and Sinaloa (fig. 22); 300-1,850 m.

Principal Flowering Dates.—November through March.

Among all taxa of *Lagascea*, *L. angustifolia* is distinguished by its oblanceolate leaves. In floral features, the species is very similar to *L. rigida* and *L. heteropappus*, both of which are distributed further south. *Lagascea angustifolia* is the only species of the genus that has not yet been counted chromosomally.

Representative Specimens.—MEXICO. DURANGO: near Durango, April-Nov. 1896, *Palmer 853* (F, GH, MEXU, MO, NY, UC, US). JALISCO: 2-6 km. SW of San Sebastián, 3 March 1970, *Anderson & Anderson 5993* (DUKE, ENCB, MICH); 5 miles W of Arenal, 24 March 1957, *DeLeon 1610* (MICH); Guadalajara, La Barranca, 19 Nov. 1930, *Jones 27781* (POM); Tequila, 9 Dec. 1940, *Langman 3152* (MEXU); 15-18 miles W of Ameca, 29 April 1951, *McVaugh 12157* (MEXU, MICH); 5 miles N of Río Verde, 6 Nov. 1959, *McVaugh & Koelz 262* (DUKE, ENCB, LL, MICH, US); Río Blanco, June-Oct. 1886, *Palmer 643* (GH, MEXU, MO, NY, US); Barranca near Guadalajara, 12 Nov. 1888, *Pringle 1784* (F, GH, MEXU, MO, NY, UC, US); hills near Guadalajara, Nov. 1889, *Pringle 2737* (F, MSC, UC); slopes of Guadalajara, 4 Dec. 1902, *Pringle 9933* (F, GH, MO, NY, US); rd. between Huejuquilla & Mesquitec, 25 Aug. 1897, *Rose 2566* (US); 11 km. N of Río Verde on Tepatitlán-Yahualica rd., 9 March 1975, *Stuessy 3800* (OS); Magdalena, 15 May 1931, *Viereck 1322* (US); San Juan Cosalá, Tecuán, 12 Jan. 1966, *Villarreal 446* (ENCB). NAYARIT: along hwy. 15 between Tepic & San Blas rd., 24 Dec. 1957, *Alava & Cook 1561* (MICH, UC); La Barranca, 21 Feb. 1927, *Jones 23351* (MO, POM, UC); Ixtlán, 18 Feb. 1927, *Jones 23410* (CAS, MO, NY, POM, UC). SINALOA: Cerro Colorado, Cofradía, 5 Nov. 1904. *Brandegee s.n.* (UC); Mesa Malqueson, Cerro Colorado, 8 Dec. 1939, *Gentry 5159* (ARIZ, GH, MEXU, MICH, MO, NY); Capadero, Sierra Tacuichamona, 12 Feb. 1940, *Gentry 5589* (ARIZ, GH, MO, NY); Cienegita, SE of Badiraguato, 23 March 1940, *Gentry 5938* (ARIZ, GH, MICH, NY, UC); Balboa, Jan. 1923, *González 5053* (US); San Ignacio, El Roblar, 24 Jan. 1919, *Narvárez & Salazar 720* (US). ZACATECAS: San Antonio, ca. 19 km. SE of Huejuquilla el Alto (Jalisco), 3 Nov. 1963, *Feddema 2401* (CAS, DUKE, ENCB, MICH, MO, TEX); 1 km. N of San Francisco de Valparaiso, 3 Nov. 1963, *Rzedowski 17633* (ENCB, MICH).

III. LAGASCEA section CALHOUNIA (A. Nelson) Stuessy, comb. et stat. nov.

Calhounia A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:55. 1924. Type species:

Calhounia nelsonae A. Nelson [=*Lagascea decipiens* Hemsl.].

Shrubs to 3 m. tall, woody; synflorescence globose to hemispheric, solitary; primary phyllaries each with a single, long, resinous gland at the midrib; corollas yellow with anthers yellow to tan. Species 7 and 8.

7. **Lagascea decipiens** Hemsl. Diagn. Pl. Nov. 33. 1879.

Arching or scrambling shrub to 3 m. tall. Stems several from the base, woody, to 12 mm. diam., gray-brown and glabrous when old, light green and hirtellous with hairs 0.1 mm. long when young (on uppermost branches sometimes also stipitate-glandular). Leaves with petioles 5-13 mm. long and 0.6-0.8 mm. diam.; blades ovate to narrowly ovate, 2.3-8 cm. long, 1.8-5.5 cm. wide, at apex acuminate, at base obtuse to slightly attenuate, at the margin obscurely to moderately serrate, with both surfaces strigillose (more conspicuously so on veins of undersurface) with hairs 0.1 mm. long. Synflorescence with 13-51 uniflowered (sometimes bi- or multi-flowered; see table 3 and fig. 24) capitula, solitary (infrequently 2-3), terminal, hemispheric to globose, 1.3-4.5 cm. tall, 2.5-5.5 cm. diam. Peduncles 0.5-5.5 cm. long, 0.5-0.9 mm. diam., hirtellous and sometimes also stipitate-glandular with hairs 0.1 mm. long. Receptacle 1-2 mm. diam., 1 mm. tall. Secondary phyllaries 3-7, lanceolate (rarely narrowly ovate), 5-20 mm. long, 1-5 mm. wide, on both surfaces strigose with hairs 0.1-1 mm. long, at margin ciliate and sometimes stipitate-glandular. Primary involucre 7-15 mm. long, 0.9-1.5 mm. diam., of 5 (-11) phyllaries most with a resinous gland to 3 mm. long on the midrib, abaxially strigose to pilose with hairs to 1 mm. long and sometimes also stipitate-glandular; lobes 1-4 mm. long, 0.2-0.7 mm. wide at base, at apex acuminate, adaxially antrorsely strigose with hairs less than 0.1 mm. long. Florets with corollas yellow, glabrous, with throat 3.5-4.5 mm. long and 1.2-1.5 mm. diam., with lobes ovate to elliptic and 1-2 mm. long, with tube 1 mm. long and 0.5 mm. diam.; anthers yellow to tan, 3 mm. long; style 8 mm. long; achenes narrowly cylindrical, 3 mm. long, 0.8 mm. diam., subglabrous except pilose near apex with hairs 0.2 mm. long; pappus a small erose, pubescent crown 0.1 mm. long. Chromosome number, $n=17$.

Lagascea decipiens is a common taxon of the western foothills of the Sierra Madre Occidental. It is also a morphologically variable taxon, with the most conspicuous variations involving the vesture and length of lobes of the primary involucre plus number of florets per head. Glandular *vs.* strigose vesture of the primary involucre is so dramatic that a variety, var. *glandulosa*, can be distinguished principally by these features. Sometimes the strigose pubescence is very long (1 mm.) and dense (e.g., *Abrams 13316*); in other cases it is short (0.2 mm.) and sparse (e.g., *Wiggins 7519*). The length of the lobes of the primary involucre varies from very short (1 mm.; as in *Gentry 14392*) to quite long and narrow (to 4 mm.; many collections, e.g., *Rinehart 7047, SR 3782,* and *Hinton et al. 14827;* this latter collection is additionally unusual in having black anthers instead of the typical brown). The long and narrow-lobed variants are centered in and around Jalisco, but they are not sufficiently distinct to merit

formal varietal recognition. The number of heads in each involucre varies from one (most common) to eight (very rare), but neither of these forms is accorded formal taxonomic rank (see discussion under var. *decipiens*).

7a. **Lagascea decipiens** Hemsl. var. **decipiens.** Figures 15, 16.

Lagascea decipiens Hemsl. Diagn. Pl. Nov. 33. 1879. TYPE: MEXICO: Sierra Madre, "NW of Mexico" [from label], *B. C. Seemann 2056* (Holotype, K!; isotype, GH!; photograph and fragment of holotype, US!; photograph of holotype, F! GH! MICH! US!).

Lagascea biflora Hemsl. Diagn. Pl. Nov. 33. 1879. TYPE: MEXICO: "sine loco speciali," date unknown, *W. Parkinson s.n.* (Holotype, K!; photograph and fragment of holotype, US!; photograph of holotype, GH! US!).

Lagascea liebmanii Sch.-Bip. in Klatt, Leopoldina 20:91. 1884. TYPE: MEXICO: Oaxaca, Pochutla, Oct. 1842, *F. M. Liebmann 250* (Holotype, C; photograph and fragment of holotype, US!; fragment and slightly inaccurate sketch of holotype, GH!; photograph of holotype, DS! US!).

Noccaea biflora (Hemsl.) O. Ktze. Rev. Gen. Pl. 1:354. 1891.

Noccaea decipiens (Hemsl.) O. Ktze. Rev. Gen. Pl. 1:354. 1891.

Nocca liebmannii (Sch.-Bip. in Klatt) Robins. Proc. Amer. Acad. Arts 36:470. 1901.

Calhounia biflora (Hemsl.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:58. 1924.

Calhounia decipiens (Hemsl.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:58. 1924.

Calhounia liebmannii (Sch.-Bip.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924.

Calhounia nelsonae A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:55. 1924. TYPE: ARIZONA: Pima Co., SE slopes of Baboquivari Mts., 24 Feb. 1923, *H. C. & E. E. Hanson 1023* (Holotype, RM!; isotypes, MO! MSC! US!).

Stems on uppermost branches hirtellous with hairs 0.1 mm. long. Leaves with blades 2.3-7.2 cm. long, 3.5-5.5 cm. wide, densely strigose with hairs 0.7 mm. long. Synflorescences 1.3-2.4 cm. tall, 2-4 cm. diam. Peduncles 0.5-4 cm. long, hirtellous.

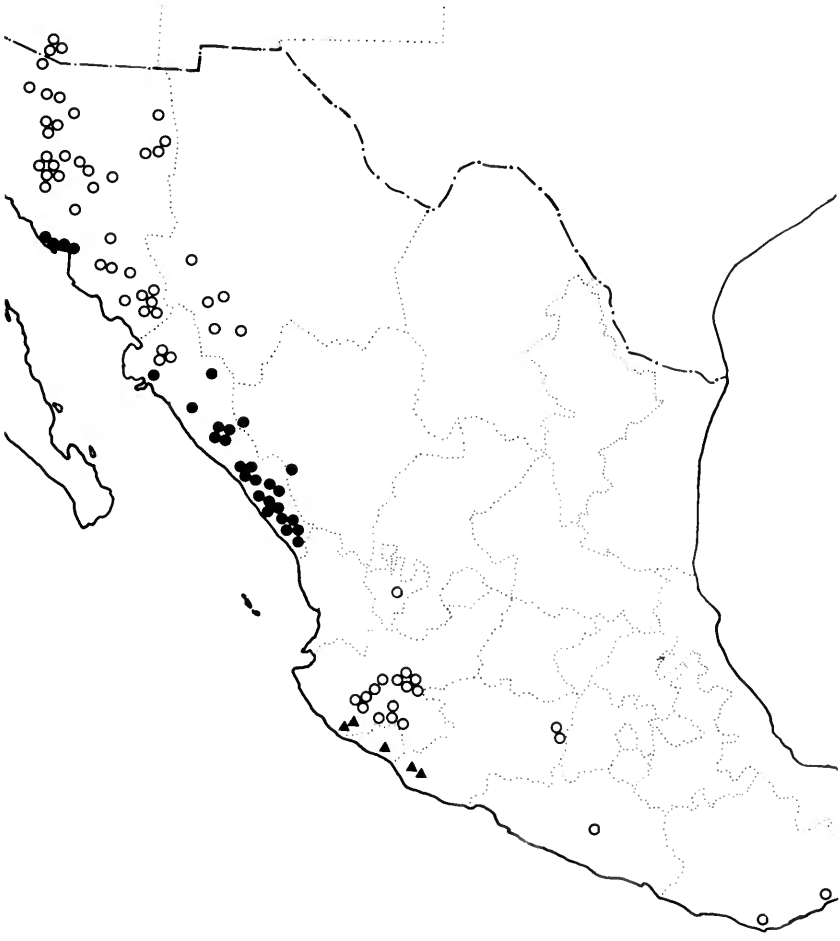


FIG. 23. Map of Mexico showing distribution of *Lagascea decipiens* var. *decipiens* (open circles), *L. decipiens* var. *glandulosa* (closed circles), and *L. palmeri* (triangles).

Secondary phyllaries ciliate at the margin. Primary involucre strigose to pilose, 5 (-11) lobed, with lobes 1-4 mm. long and 0.2-0.5 mm. wide at base.

Distribution.—Usually on dry, low, granitic slopes in tropical deciduous and thorn forests and oak-grassland along the western coast of Mexico from Sonora south to Oaxaca (fig. 23); also known from Mt. Baboquivari in Pima Co., Arizona; 50-2,000 m.

Principal Flowering Dates.—Known flowering in every month, but most abundantly from August through May; strongly dependent upon local rainfall.

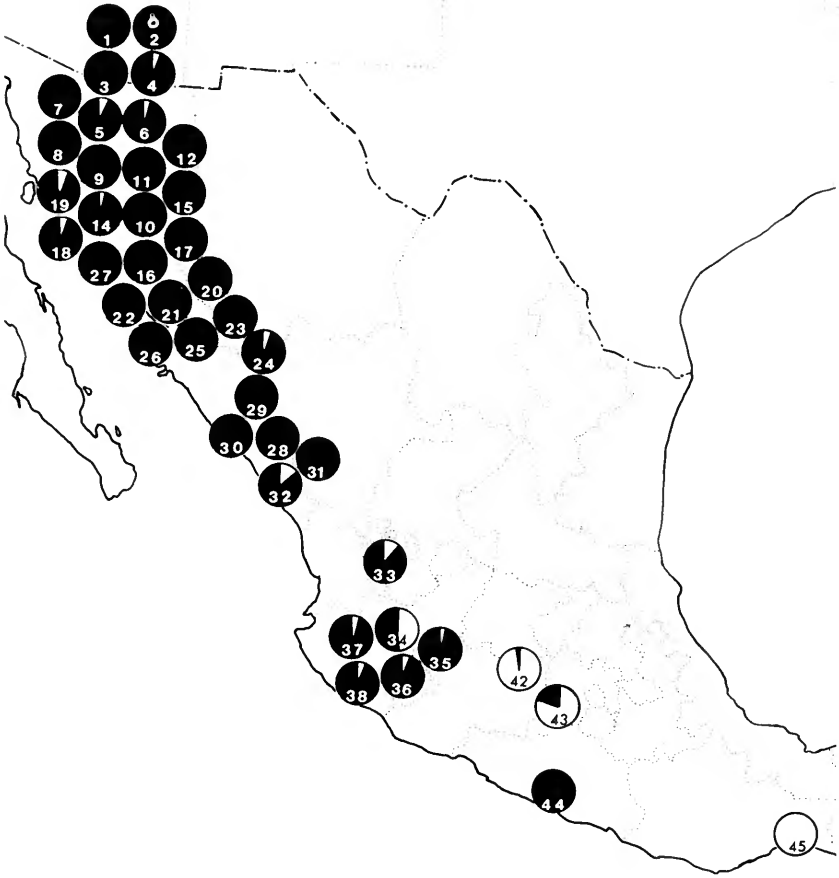


FIG. 24. Occurrence of uni- and biflowered heads within *Lagascea decipiens*. Circles represent individual collections and 100 per cent of the sample of heads analyzed; the shaded portion indicates the percentage of uni-flowered heads, and the light portion the percentage of bi-flowered heads. Refer to Table 3 for voucher data and numbers of heads sampled.

Lagascea biflora was described as new by Hemsley (1879) at the same time that he also described *L. decipiens*. From the original description, the type material, and the plates that appeared two years later in the Biologia Centrali-Americana (Hemsley, 1881), the two species differed only in the number of florets per head: *L. decipiens* with one, and *L. biflora* with "nearly always two" (Hemsley, 1879, p. 33). Robinson (1901), following these morphological differences, also recognized two distinct species. Because no additional diagnostic features were found in the present investigation, it

TABLE 3. Analysis of uni- and biflowered heads in *Lagascea decipiens*.

Collection	Map population number (cf. fig. 24)	Number of 1-flowered heads	Number of 2-flowered heads	% 1-flowered heads	% 2-flowered heads
SG 3002 (OS)	1	85	0	100	0
Harrison & Kearney 8546 (F)	2	44	0	100	0
Gilman 228 (NY)	3	39	0	100	0
Kearney & Peebles 14974 (GH)	4	45	3	94	6
Hartman 249 (GH)	5	17	1	94	6
McGill & Pinkava 6562 (ASU)	6	57	1	98	2
White 3097 (GH)	7	96	0	100	0
White 3797 (GH)	8	75	0	100	0
White 3624 (GH)	9	46	0	100	0
Mueller 3688 (GH)	10	33	0	100	0
Drouet, Richards & Lockhart 3727 (F)	11	8	0	100	0
Wiggins 7247 (GH)	12	60	0	100	0
SG 3012 (OS)	14	99	2	98	2
Drouet, Richards & Lockhart 3608 (F)	15	21	0	100	0
Wiggins & Rollins 321 (GH)	16	29	0	100	0
Wiggins & Rollins 406 (GH)	17	46	0	100	0
Hastings & Turner 69-69 (ENCB)	18	44	2	96	4
Ferris 8740 (US)	19	28	2	93	7
Hewitt 19 (GH)	20	38	0	100	0
Abrams 13316 (NY)	21	18	0	100	0
Drouet & Richards 3965 (F)	22	55	0	100	0
Goldman 201 (GH)	23	47	0	100	0
Palmer 145 (GH)	24	24	1	96	4
Rose, Standley & Russell 13217 (US)	25	32	0	100	0
Jones 23238 (NY)	26	20	0	100	0

Collection	Map population number (cf. fig. 24)	Number of 1-flowered heads	Number of 2-flowered heads	% 1-flowered heads	% 2-flowered heads
Gentry 11466 (LL)	27	28	0	100	0
Breedlove 19119 (RSA)	28	38	0	100	0
González 4435 (US)	29	51	0	100	0
Chan & Folkner s.n. (MEXU)	30	25	0	100	0
Paray 3271 (ENCB)	31	13	0	100	0
SG 3039 (OS)	32	15	2	88	12
Rose 2856 (NY)	33	32	4	89	11
SR 3786 (OS)	34	54	46	54	46
SR 3787 (OS)	35	101	3	97	3
Holway 5122 (GH)	36	80	4	95	5
SG 3084 (OS)	37	24	1	96	4
Cronquist 9770 (NY)	38	44	2	96	4
Paray 1753 (ENCB)	42	1	36	3	97
Hinton et al. 13206 (GH)	43	36	149[a]	19	81[a]
Hinton et al. 14827 (F)	44	21	0	100	0
Deam s.n. (GH)	45	0	20	0	100

[a]Included in these totals are multi- (3-8) flowered heads (24; 13%).

seemed possible that the biflowered condition represented simply a developmental variant within a species that is also variable in other features.

To document more clearly the existence of the biflowered condition within *L. decipiens* (including var. *glandulosa*), 41 collections were analyzed for numbers of florets per involucre (table 3). These data were then plotted geographically (fig. 24). It is evident that the biflowered condition occurs sporadically and at a low percentage throughout the entire range of the species, but is more common in the southern part. Occasionally, due to developmental phenomena, the biflowered condition predominates, sometimes obviously as a result of fusion of adjacent involucres (10 lobes observed instead of the usual five). As additional evidence for developmental anomaly, the highly biflowered collection *SR 3786* (map population #34) was from a plant that also had other irregular features: 3-lobed stigmas; fasciated stems; and unusually short internodes (resulting in clustered leaves).

Lagascea liebmannii was first described by Schultz-Bipontinus (in Klatt, 1884). Robinson (1901) also recognized this species as distinct, and he related it most closely to *L. palmeri*. An examination of the type material from Oaxaca reveals that *L. liebmannii* is clearly synonymous with *L. decipiens* var. *decipiens*. The type specimen has short lobes of the primary involucre, but this feature is known in other widely scattered collections of the species (e.g., *Rose 2856* from Jalisco; and *White 3097* from Sonora). The holotype of *L. liebmannii* also contains some biflowered heads, but as pointed out in the previous paragraph (see also fig. 24), this is not uncommon within *L. decipiens*.

Representative Specimens.—MEXICO. CHIHUAHUA: near Batopilas, 3-5 Oct. 1898, *Goldman 201* (GH, NY, US); Barranca del Cobre, 17 Feb. 1945, *Hewitt 19* (GH); La Bufa, SE of Creel, 13 Sept. 1957, *Knobloch 431* (MEXU, MSC, SMU); SW part of state, Aug.-Nov. 1885, *Palmer 145* (GH, MEXU, MICH, NY, US). GUERRERO: Bravos, Pueblo Viejo, 9 Nov. 1939, *Hinton et al. 14827* (ENCB, F, GH, LL, MO, TEX, US). JALISCO: 7 miles SW of Autlán, 28 Dec. 1957, *Alava & Cook 1670* (MICH, UC); Tuxacacuesco, 13 Nov. 1943, *Anderson s.n.* (MO); 8.2 miles W of Chapala, 13 Aug. 1968, *Anderson & Anderson 5167* (ENCB, MICH); 31 miles W of Ciudad Guzman, 31 Oct. 1962, *Cronquist 9770* (MICH, MO, MSC, NY, TEX, US); 13 miles S of Acatlán, 29 Oct. 1971, *Cummins*

71-318H (ARIZ); San Juan Cosalá, 23 Sept. 1961, *Detling 8661* (ENCB, MICH); Sayula, 7 Oct. 1903, *Holway 5122* (GH); 6-8 miles SW of Autlán, 9 April 1951, *McVaugh 11925* (MICH, US), 5 km. E of Tuxcueca, 29 June 1957, *15100* (MEXU, MICH); ca. 15 km. SSW of Acatlán de Juárez, 7-8 Nov. 1959, *McVaugh & Koelz 320* (DUKE, ENCB, MICH); 110 miles S of Guadalajara, 29 March 1965, *Rinehart 7047* (MICH); Bolaños, 10-19 Sept. 1897, *Rose 2856* (MEXU, MO, NY, US); 30 km. NE of Autlán, 2 Oct. 1960, *Rzedowski 14645* (ENCB, MICH), Barranca de Chavanda, 2 km. S. of Atenquique, 6 Feb. 1966, *21939* (DS, ENCB, MICH, MSC); 4.3 miles SSE of Autlán, 3 Sept. 1973, *SG 3084* (OS); 11 miles NNE of Autlán, 19 Dec. 1974, *SR 3782* (OS), 16.2 miles NNE of Autlán, 19 Dec. 1974, *3783* (OS), 13.1 miles S of Acatlán,19 Dec.1974, *3786* (OS), 1.2 miles W of Ajijic, 20 Dec. 1974, *3787* (OS); San Juan Cosalá, 10 Oct. 1963, *Villarreal s.n.* (ENCB), vicinity of San Juan Cosalá, 30 June 1963, *10* (MICH), above Ajijic, N of Lake Chapala, 13 Feb. 1966, *105* (ENCB). MICHOACÁN: near Lago Chapala SE on hwy. 15 toward Jiquilpan, 21 July 1971, *Gibson & Gibson 2262* (ARIZ); Zitácuaro-San José Purua, 6 Sept. 1938, *Hinton et al. 13206* (ARIZ, ENCB, GH, LL, MICH, TEX, US); San José Purua, 26 Nov. 1955, *Paray 1753* (ENCB). OAXACA: Salina Cruz, 20 Dec. 1898, *Deam s.n.* (GH). SINALOA: San Blas, 1 Feb. 1927, *Jones 23238* (CAS, GH, LL, MO, NY, POM, TEX, UC); San Blas, 22 March 1910, *Rose, Standley & Russell 13217* (GH, NY, US). SONORA: Sierra Lopez Rancho, 13 April 1932, *Abrams 13316* (DS, F, NY); W of Álamos, 12 Dec. 1939, *Drouet & Richards 3965* (F); 20 miles NE of Ures, 16 Nov. 1939, *Drouet, Richards & Lockhart 3608* (DS, F), 21 miles NE of Ures, 22 Nov. 1939, *3727* (F); near Navojoa, 18 Jan. 1931, *Erlanson & Souviron 28* (US); 60 miles N of Hermosillo, 26 Jan. 1964, *Flyr 94* (TEX); 20 miles N of Hermosillo, 24 Sept. 1933, *Gentry 238* (DS, MICH, US), Canyon Sapopa, Río Mayo, 20 Oct. 1934, *1092* (F, MO), San Bernardo, Río Mayo, 2 Feb. 1935, *1258* (A, ARIZ, MEXU, MICH, NY, UC, US), Cañon Estrella, Dist Álamos, 1 Oct. 1933, *417M* (DS, MICH), Álamos, Quiricoba, 12 Nov. 1933, *755M* (DS, MICH, SMU, US), Cañon Estrella, Dist Alamos, 1 Oct. 1933, *359M* (DS, MICH, US); Ures, 15 April 1957, *Gold 740* (MEXU); La Tinaja, 18 Nov. 1890, *Hartman 249* (GH); 15 miles SW of Colonia Aribabi, 6 Oct. 1965, *Hastings & Turner 65-75* (ARIZ, DS), 0.5 miles SE of Rancho Las Peñitas, 4 Oct. 1969, *69-109* (ARIZ, DS, ENCB), 14.4 miles E of Hornos, 10 Oct. 1969, *69-140* (ARIZ, ENCB); 5.9 miles S of jct with rd. to Benjamin Hill on rt. 15, 6 Sept. 1971, *Keil & Canne*

8599 (OS); Alamo Grande Mt., Magdalena, 26 May 1925, *Kennedy 7023* (CAS, UC); 3 miles S of Mesquite, 16 March 1926, *Long 70* (GH, US); ca. 16 miles S of Cucurpe, 30 March 1970, *McGill & Pinkava 6562* (ASU); between Caborca & Santa Ana near Altar, 19 Feb. 1959, *Miranda 8929* (MEXU); Río Bonito about La Nopalera, 7 Oct. 1939, *Muller 3688* (GH, LL, MICH, UC); Álamos, 26 March-8 April 1890, *Palmer 401* (GH, NY, US); 2 miles NE of airport, NW of Hermosillo, 18 Sept. 1971, *Pinkava, Brown, McGill & McLeod 938* (ASU); ca. 5 miles below Minas Nuevas, 12 March 1910, *Rose, Standley & Russell 12684* (US), Sierra de Álamos, 14 March 1910, *12835* (NY, US); few miles NW of Ures, March 1946, *Sauer 5* (UC); near Sasabe, 16 March 1926, *Shreve 5821* (US), 25 miles NW of Hermosillo, 13 April 1932, *5979* (ARIZ, F), Estación Moreno, 25 Feb. 1933, *6093* (ARIZ, MICH); ca. 13 miles NE of Ures, 17 April 1962, *Straw 2112* (DUKE, RSA); 14.7 miles S jct. rt. 15 & rd. to Carbó, 22 Aug. 1973, *SG 3012* (OS); 3 miles S of Mazocahui, 1 April 1959, *Turner 59-64* (ARIZ, CAS, DS); Cañon del Carricito, 30 July 1940, *White 3097* (GH, MICH), Cañon del Agua Amarga, 30-31 Aug. 1940, *3624* (ARIZ, GH, LL, MEXU, MICH), Horconcitos, Arroyo del Salto, 6 Sept. 1940, *3797* (GH, MICH); 2 miles E of Moreno, 25 Feb. 2033, *Wiggins 6292* (DS, MICH, US), 17 miles NE of Cajeme on rd. to Tesopaco, 3 March 1933, *6392* (DS, MICH, POM, UC, US), 12 miles N of Carbó, 16 Sept. 1934, *7247* (DS, F, GH, MICH, UC, US), 17 miles N of Hermosillo, 2 Oct. 1934, *7519* (A, DS, MICH, US); 5 miles NE of Colorado, 6 Sept. 1941, *Wiggins & Rollins 321* (ARIZ, DS, GH, MICH, MO, NY, UC, US), 4 miles N of Matape, 8 Sept. 1941, *406* (ARIZ, DS, GH, MICH, NY, UC, US). UNITED STATES. ARIZONA: PIMA CO: Baboquivari Canyon, 5 April 1928, *Gilman 74* (ARIZ, GH, NY, US), Baboquivari Canyon, 28 Sept. 1931, *228* (ARIZ, DS, F, MO, NY); Baboquivari Mts. 1 Sept. 1940, *Kearney & Peebles 14974* (ARIZ, GH); 11.7 miles E of Topawa, Baboquivari Peak, 21 Aug. 1973, *SG 3002* (OS).

7b. **Lagascea decipiens** Hemsl. var. **glandulosa** (Fernald) Stuessy, comb. et stat. nov.

Lagascea glandulosa Fernald, Bot. Gaz. (Crawfordsville) 20:534. 1895. TYPE: MEXICO: Sinaloa, Rosario, Hacienda Chele, 16-20 Jan. 1895, *F. H. Lamb 483* (Lectotype chosen GH!; isolectotypes, DS! MO! MSC! NY! US!).

Nocca glandulosa (Fernald) Robins. Proc. Amer. Acad. Arts. 36:470. 1901.

Calhounia glandulosa (Fernald) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:58. 1924.

Stems on uppermost branches often stipitate-glandular. Leaves with blades 5-8 cm. long, 1.8-4.7 cm. wide, moderately strigose with hairs 0.3 mm. long. Synflorescences 1.5-4.5 cm. tall, 2.5-5.5 cm. diam. Peduncles 2.2-5.5 cm. long, hirtellous and stipitate-glandular. Secondary phyllaries ciliate and stipitate-glandular at the margin. Primary involucre stipitate-glandular, 5 (-6) lobed, with lobes 1-3 mm. long and 0.3-0.7 mm. wide at base.

Distribution.—Tropical deciduous and thorn forests on western coast of Mexico primarily in Sinaloa, but isolated populations also occur in Sonora (near Guaymas) and Durango (fig. 23); 10-600 m.

Principal Flowering Dates.—August through April.

Variety *glandulosa* was described as a distinct species by Fernald (1895). The extremely glandular variants are, indeed, very distinct morphologically and worthy of formal recognition. However, the degree of glandularity and the size of the stipitate glands varies to such an extent that varietal rather than specific status seems more appropriate. Most of the collections of this taxon are from Sinaloa, except for a series of disjunct populations near Guaymas, Sonora (fig. 23). The existence of shipping routes between Guaymas and Mazatlán, Sinaloa, where var. *glandulosa* is very common, suggests the possibility of recent introduction northward to the Guaymas area.

Representative Specimens.—MEXICO. DURANGO: La Bajada, Tamazula, Nov. 1921, *González 4435* (US); mts. above Tayoltita, 5 Nov. 1961, *Paray 3271* (ENCB). SINALOA: 13 km. E of Villa Union, 11-12 March 1970, *Anderson & Anderson 6171* (DUKE, ENCB, MICH); 31 miles S of Mazatlán, 18 Jan. 1964, *Barr & Mason 2319* (ARIZ, DS); Culiacán, 22 Sept. 1904, *Brandegee s.n.* (GH, POM, UC, US); 4.2 miles E of hwy. 15 on hwy. 40, 22 Nov. 1969, *Breckon, Hildreth & Randall 978* (MICH); ca. 68 miles S of Culiacán on hwy. 15, 28 Jan. 1962, *Breedlove 1553* (DUKE, MICH, SMU), NE of Imala above Cofradía, 22 Oct. 1973, *35603* (MEXU), Sierra Surutato, along rd. from Mocorito to Surutate, 3 March 1971, *19119* (RSA); Culiacán, 21 April 1960, *Chan & Folkner s.n.* (ARIZ, MEXU); ca. 100 km. N of Mazatlán, 29 Dec. 1968, *Clarke, Bennet, Essig & Freeman 681229-3* (MICH); ca. 15 miles S of Río Presidio, 19 Dec. 1967, *Clarke, Essig & Bringle 1494-2* (MICH); 5 miles E of jct. rt. 15 on rt. 40, 2 Dec. 1963, *Cummins 63-658* (MICH); 60 miles S of Culiacán, 29 Jan. 1964, *Flyr 120* (TEX), 73 miles S of Los Mochis, 28

Jan. 1964, *108A* (TEX); between Culiacán & Las Flechas, 21 Feb. 1899, *Goldman 312* (NY, US); San Juan, 1921, *González 4133* (US), El Roble, Dec. 1926, *6544* (CAS, DS, US), El Norote, 1925, *5885* (US); La Noria, 7 Oct. 1925, *Mexia 136* (CAS, UC); Pueblo de Las Trancas, San Ignacio, 29 Oct. 1918, *Montes & Salazar 20* (US); 62 miles N of Mazatlán, 20 Nov. 1962, *Moran 9978* (DS, US); Lodiego, 9-15 Oct. 1891, *Palmer 1627* (F, GH, NY, US), Imala, 25 Sept.-8 Oct. 1891, *1717* (ARIZ, F, GH, MICH, NY, UC, US); Rosario, 24 July 1897, *Rose s.n.* (US); 1.2 miles E of La Lima, 25 Aug. 1973, *SG 3030* (MEXU, OS), 17.6 miles W of Imala, 25 Aug. 1973, *3034* (OS), 4.3 miles NW of jct. rt. 15 on dirt rd. to La Noria, 26 Aug. 1973, *3039* (OS). SONORA: ca. 10 miles N of Guaymas, 27 Jan. 1962, *Breedlove 1466* (DS, DUKE); Bahía San Carlos, 8 Feb. 1940, *Dawson 1064* (F, MICH, US); ca. 8 miles N of Guaymas, 19 March 1934, *Ferris 8740* (DS, LL, US); Bahía Topolobampo in Sierra Navachiste, 5 Jan. 1952, *Gentry 11466* (LL); 8.2 miles W of San Carlos Bay Turnoff, N of Guaymas, 15 Aug. 1969, *Hastings & Turner 69-69* (ARIZ, DS, ENCB); Guaymas, 3 Oct. 1887, *Palmer 256* (GH, NY, UC, US).

8. **Lagascea palmeri** (Robins.) Robins. Proc. Amer. Acad. Arts. 43:38. 1907. Figures 13, 14.

   Nocca palmeri Robins. Proc. Amer. Acad. Arts 36:471. 1901. TYPE: MEXICO: Colima, 27-28 Feb. 1891, *E. Palmer 1320* (Holotype, GH!; isotypes, MO! NY! UC! US!).

   Calhounia palmeri (Robins.) A. Nelson, Univ. Wyom. Publ. Sci., Bot. 1:59. 1924.

Arching or scrambling shrub to 3 m. tall. Stems several from the base, woody, to 10 m. long when vine-like, to 15 mm. diam., gray-brown when old, yellow-green when young, glabrous. Leaves with petioles 7-15 mm. long and to 1 mm. diam.; blades narrowly ovate, 5-8 cm. long, 1.7-3.5 cm. wide, at apex acuminate, at base attenuate to obtuse, at the margin obscurely to moderately serrate, with both surfaces glabrous or subglabrous. Synflorescence with 13-55 uniflowered (only rarely biflowered) capitula, terminal, hemispherical to subglobose, 1.5-2.2 cm. tall, 2-3 cm. diam. Peduncles 2.5-5.5 cm. long, 0.6-0.9 mm. diam., glabrous. Receptacle 2 mm. diam., 1.4 mm. tall. Secondary phyllaries 5-9, lanceolate to ovate, of very different lengths, 3-42 mm. long, 1-18 mm. wide, on both surfaces subglabrous. Primary involucre 5-9 mm. long, 1-2 mm. diam., of 5 (-9) phyllaries most with a resinous gland to 3 mm. long on the midrib, abaxially subglabrous, becoming pilose near base with hairs to 1 mm. long; lobes 0.2-3 mm. long, 0.3-0.8 mm. wide at base, at apex acute, adaxially antrorsely strigillose with hairs less than 0.1 mm. long. Florets with corollas yellow, glabrous, with throat 4.5-5.5 mm. long and 1-1.3 mm. diam., with lobes narrowly triangular to obovate and 1-2 mm. long, with tube 0.7 mm. long and 0.6 mm. diam.; anthers 5, yellow to tan, 3 mm. long; style 5 mm. long; achenes narrowly cylindrical, 3 mm. long, 0.5 mm. diam., subglabrous except pilose on upper one-third with hairs

0.3 mm. long; pappus a small erose hairy crown 0.2 mm. long. Chromosome number, $n=17$.

Distribution.—Hills in tropical deciduous forests in Colima and adjacent Jalisco and Michoacán (fig. 23); 150-520 m.

Principal Flowering Dates.—November and December.

Lagascea palmeri is a very close relative of *L. decipiens*. In general, the former can be distinguished most easily by its subglabrous primary involucres with very short lobes (ca. 1 mm. long). In contrast to the wide distribution of *L. decipiens*, *L. palmeri* is restricted to Colima, Jalisco, and Michoacán.

As in *Lagascea decipiens,* a tendency also exists in *L. palmeri* for the occasional production of biflowered heads. Three collections have been analyzed with the following results: *SR 3767,* 100 uniflowered heads (99 per cent), 1 biflowered head (1 per cent); *SR 3775,* 109 (98 per cent), 2 (2 per cent); *SR 3778,* 220 (96 per cent), 9 (4 per cent).

Specimens Examined.—MEXICO. COLIMA: rd. from Poco del Río to Colima, Nov. 1906, *Emrick 219* (F); locality uncertain, 8 Dec. 1959, *Koelz 34196* (MICH); 11 miles SSW of Colima, 25 Nov. 1959, *McVaugh & Koelz 1048* (DUKE, ENCB, LL, MICH); 11.1 miles S of Colima, 17 Dec. 1974, *SR 3767* (OS). JALISCO: 13.6 miles S of La Huerta, 18 Dec. 1974, *SR 3775* (OS), 12.3 miles S of La Huerta, 18 Dec. 1974, *3778* (OS). MICHOACÁN: 20 km. SE of Coahuayana, 23 Nov. 1963, *Feddema 2687* (CAS, DUKE, ENCB, MICH, MO, TEX); Coalcomán, Huizontla, 16 Nov. 1938, *Hinton et al. 12586* (ARIZ, GH, LL, TEX, US), Coalcomán, 25 March 1941, *15844* (LL, US).

DOUBTFUL SPECIES

Lagascea spinosissima [attributed to Cav. by] C. Wehmer, Die Pflanzenstoffe. 761. 1911. *nomen nudum.* The original reference to this name is cited by Wehmer (1911) as Dymock and Warden (1892). This latter article, however, deals with alkaloids in *Noaea* (*Noëa*) *spinosissima* Moq. of the Chenopodiaceae. A clerical error may have occurred in preparation of the manuscript for Wehmer's (1911) compilation, such that the generic name became *Nocca.* Before Wehmer's final manuscript went to press, this could have been changed to *Lagascea* in accordance with its nomenclatural conservation against *Nocca* in 1905.

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