

# **Memoirs**

**Of The New York Botanical Garden**

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**Volume 36**

**The Systematics of Montanoa  
(Asteraceae, Heliantheae)**

**V. A. Funk**

**Issued 26 November 1982**

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# THE SYSTEMATICS OF MONTANOA (ASTERACEAE, HELIANTHEAE)

V. A. Funk

## CONTENTS

Summary .....	1
Introduction .....	1
Taxonomic history .....	2
Synopsis of the taxonomy .....	4
Generic affinities .....	4
Morphology and taxonomic characters .....	7
Leaf morphology .....	14
Cytology .....	18
Cladistic analysis .....	21
Taxonomic treatment .....	31
Key to the species .....	32
Subgenus <i>Montanoa</i> .....	34
Subgenus <i>Acanthocarphae</i> .....	67
Doubtful and excluded species .....	123
Acknowledgments .....	124
Literature cited .....	124
Collector abbreviations .....	126
Index .....	132

## MEMOIRS of THE NEW YORK BOTANICAL GARDEN Volume 36

The New York Botanical Garden  
Bronx, New York 10458

ISSUED 26 November 1982

**Library of Congress Cataloging in Publication Data**

Funk, V. A. (Vicki A.), 1947–

The Systematics of Montanoa (Asteraceae, Heliantheae)

(Memoirs of the New York Botanical Garden; v. 36)

Based on the author's thesis (Ph.D.—Ohio

State University, 1980)

Bibliography: p.

Includes index.

1. Montanoa—Classification. 2. Botany—Latin America—  
Classification. I. Title. II. Series.  
QK1.N525. vol. 36 [QK495.C74] 581s 82-7878  
ISBN 0-89327-243-4 [583'.55] AACR2

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International Standard Book Number 0-89327-243-4

**THE SYSTEMATICS OF MONTANOA  
(ASTERACEAE, HELIANTHEAE)<sup>1</sup>**

V. A. FUNK<sup>2</sup>

SUMMARY

*Montanoa* Cerv. (Asteraceae, Heliantheae) includes woody, white-rayed composites with Latin American distributions. Species recognition has always been difficult in the genus because of variation in such features as leaf shape, size and number of involucral bracts and head size. This variation was studied on the individual, inter- and intra-populational levels. Data collected from extensive field and herbarium studies were combined with the results of greenhouse experiments to determine the usefulness of such characters for species determination. Characters with high levels of consistency were used to delimit 25 species (30 taxa) within the genus. These taxa are divided into two subgenera, *Montanoa* and *Acanthocarphae* DC. Chromosome counts for 21 of the taxa are presented and revealed three high level polyploids that are all high altitude trees. A cladistic analysis showed extensive parallel evolution in a number of the more conspicuous characters. Basing the hierarchy of *Montanoa* on the branching pattern produced from the cladistic analysis has resulted in a more natural and predictive classification. Twenty-two of the species recognized are from the over 100 previously described species. There are three new species described here, *M. standleyi*, *M. josei* and *M. imbricata*. Subgenus *Montanoa* is divided into two sections *Montanoa* and *Echinocephalae* sect. nov., with the latter having three series, *Frutescentes* ser. nov., *Amoenae* ser. nov. and *Apertae* ser. nov. Subgenus *Acanthocarphae* has five series, all described here: *Ovalifoliae*, *Quadrangulares*, *Hibiscifoliae*, *Intermediae* and *Grandiflorae*. [*Montanoa*, Asteraceae, cytology, morphological variation, cladistics]

INTRODUCTION

*Montanoa* Cerv. in Llave & Lex. is a genus of attractive, woody Asteraceae, appropriately referred to as the "Daisy Trees" because of their white rays and yellow disc florets. Most members of this genus are shrubs, but a few are truly arborescent, and when in flower they present a spectacular display. The genus is widespread in Latin America and several species are cultivated in the warmer parts of the world.

*Montanoa* is a well-defined genus occupying an isolated position within the tribe Heliantheae. Although definition of generic boundaries has never been a serious problem, the taxonomy within the genus has long plagued synantherologists. The only revision of *Montanoa* was by Robinson and Greenman in 1899. While adequate for the time, this study was based entirely on herbarium material

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and therefore could not effectively deal with the two major problems in the genus: extensive morphological variation and widespread parallel evolution. The most extensive variation occurs in the leaves, but the involucre bracts, pubescence, disc florets and achenes also vary widely.

In the present treatment the problem of morphological variation was approached from three directions. First, variation on the individual and populational levels was examined during nine months of field studies in Latin America. Second, over 6000 herbarium sheets were examined in the laboratory to determine broad patterns of variation throughout the range of the taxa. Based on these field and laboratory observations, hypotheses were generated concerning the extent and causes of the variation. Third, whenever possible, these hypotheses were tested in greenhouse studies. These data were combined with information from cytological studies and correlated with patterns of geographical distribution; the result has been an improved understanding of the taxa.

Once the morphological variation in *Montanoa* had been documented and the taxa circumscribed, an evolutionary branching pattern was constructed, using the method of Hennig (1950, 1966), to help understand the phylogeny of the genus. The resulting branching diagram (cladogram) was used to identify the characters that had probably undergone parallel evolution.

An understanding of the morphological variation and an interpretation of parallel evolution in *Montanoa* has resulted in a classification in the present treatment that is believed to be both informative and predictive. Also, the methods that have been used in studying the patterns of morphological variation in *Montanoa* may be useful to other workers in dealing with variable genera in other parts of the Asteraceae as well as in other families.

#### TAXONOMIC HISTORY

*Montanoa* was first described by Kunth in Humboldt, Bonpland and Kunth (1820) as *Eriocoma* with the single species *E. floribunda*. This name, however, was a later homonym and therefore illegitimate because Nuttall in 1818 had used the same name for a genus of the Poaceae. The first valid description of *Montanoa* was by Cervantes in La Llave and Lexarza (1825), named for Dr. Luis Montaña, a physician and naturalist from Puebla, Mexico (Blake, 1926a). One species, *M. tomentosa*, collected from the riverbanks near Mexico City, was included in the genus.

Several other generic names have been applied to *Montanoa*. Cassini (1829 [reprint 1975]) used *Eriocarpha*, perhaps because he was aware that *Eriocoma* was a later homonym but not aware of the work of Cervantes. De Candolle (1836) changed the spelling of *Montanoa* to *Montagnaea* to more closely approximate the Spanish pronunciation of Dr. Montaña's name (Koch, 1864). In his treatment he recognized eight species in two subgenera: *Eriocarphae* (distinguished by five ligules and hirsute pales) with two species; and *Acanthocarphae* (10 ligules and sparingly hirsute pales mucronate at the apex) with six species. All of the species in the second subgenus were new. De Candolle also listed in synonymy *Priestleya*, a Sessé and Mociño name for an unpublished plate of the *Flora Mexicana*. Two species were listed: *P. longifolia* (= *Montanoa grandiflora*) and *P. squarrosa* (= *M. frutescens*). A final monotypic genus, *Uhdea*, was published by Kunth (1847) as a taxon closely related to *Montanoa* but having larger flowering heads. It was named after the Prussian consul, Uhde, who sent seeds from Mexico to Paris where the plant was cultivated.

Probably the most confusing treatment for *Montanoa* was published by Koch

(1864), who based it on a manuscript sent to him by Schultz Bipontinus. *Montanoa* was divided into three subgenera (invalidly published) which differed in the size of the head: *Kleinblüthige* (seven species), *Mittelblüthige* (ten species), and *Grossblüthige* (five species). The latter subgenus contained Kunth's *Uhdea*. Fourteen new species were given very short descriptions that were primarily based on the differences in leaf morphology (one species, *M. elegans* K. Koch, was known only from the vegetative condition), and little, or no information on collectors and type localities was included.

*Montanoa* was treated briefly by Bentham and Hooker (1873) who listed 14 species from Mexico and Colombia. Hemsley (1881) listed 24 species but mentioned that he believed there were only about half that number of good taxa. Kuntze (1891) added to the confusion by incorrectly transferring all taxa back to the earlier name, *Eriocoma* H.B.K. Hoffmann (1890) used the name *Montanoa* and cited 20 species from Mexico and Colombia.

The first major revision of *Montanoa* was by Robinson and Greenman (1899). They recognized 31 species in three subgenera that were based on size of heads and number of ligules. Because of the short descriptions and unavailability of most types for the names of Schultz Bipontinus, they placed most of these under excluded or doubtful species. Robinson and Greenman recognized three subgenera more or less following the two of de Candolle (1836; *Eriocarphae* and *Acanthocarphae*) and an additional one from Schultz Bipontinus (in Koch, 1864; *Grossblüthige*). Robinson and Greenman used orthographic variants of the names of de Candolle and gave the third subgenus of Schultz Bipontinus the name *Uhdea*. They described ten new species and relied heavily on leaf morphology to differentiate the taxa.

Blake (1926a) used Robinson and Greenman's revision for his treatment of *Montanoa* in Standley's *Trees and Shrubs of Mexico* in which he listed 31 species in Mexico alone. Since the treatment of Robinson and Greenman (1899), there has been no comprehensive work on the genus, but new species have continually been published (Blake, 1917, 1924a, b, 1926b, 1930, 1937, 1950; Aristeguieta, 1964; McVaugh, 1972; Badillo, 1974, 1978; Rzedowski, 1975; H. Robinson, 1976). Over 100 names have been published for the genus.

In this treatment *Montanoa* is divided into two subgenera (*Montanoa* and *Acanthocarphae*) and subgenus *Montanoa* is divided into two sections, *Montanoa* and *Echinocephalae*. Within these three major divisions eight series are recognized. Section *Montanoa* corresponds to the subgenus *Eriocarphae* of de Candolle (1836), the subgenus *Kleinblüthige* of Schultz Bipontinus (in Koch, 1864) and the subgenus *Eriocarpha* of Robinson and Greenman (1899), and it is primarily characterized by deciduous heads, and fruiting receptacular bracts which are indurate, more or less triangular, pubescent, and parallel-veined. Section *Echinocephalae* shares with section *Montanoa* indurate, more or less triangular mature pales with parallel veins but differs in having non-deciduous heads, and glabrous or subglabrous pales that have prominent veins. The second subgenus, *Acanthocarphae*, contains some of the species of de Candolle's subgenus of the same name, as well as some of the species of the Schultz Bipontinus subgenera *Mittelblüthige* and *Grossblüthige* and the subgenus *Uhdea* of Robinson and Greenman. Subgenus *Acanthocarphae* is characterized by the fruiting pales being papery, subglabrous, obtrullate, deciduous and net veined. In general, the variation within the species is discussed but not formally recognized. There are three species, however, where the variation involves several characters and is correlated with the distribution. These three species have been divided into subspecies. The taxa recognized in *Montanoa* in this treatment are given below:

## SYNOPSIS OF THE TAXONOMY

- I. Subgenus *Montanoa*.
- A. Section *Montanoa*: 1. *M. tomentosa* Cerv. in Llave & Lex., 1a. subsp. *tomentosa*, 1b. subsp. *microcephala* (Schultz Bip. in K. Koch) V. A. Funk, 1c. subsp. *rosei* (Rose ex Robins. & Greenm.) V. A. Funk, 1d. subsp. *xanthiifolia* (Schultz Bip. in K. Koch) V. A. Funk.
- B. Section *Echinocephalae* V. A. Funk.
- a. Series *Frutescentes* V. A. Funk: 2. *M. frutescens* Mairet ex DC., 3. *M. guatemalensis* Robins. & Greenm., 4. *M. mollissima* Brongniart ex Groenland, 5. *M. andersonii* McVaugh, 6. *M. standleyi* V. A. Funk.
- b. Series *Amoenae* V. A. Funk: 7. *M. liebmannii* (Schultz Bip. in Klatt) S. F. Blake, 8. *M. echinacea* S. F. Blake.
- c. Series *Apertae* V. A. Funk: 9. *M. revealii* H. Robinson.
- II. Subgenus *Acanthocarphae* DC.
- a. Series *Ovalifoliae* V. A. Funk: 10. *M. ovalifolia* Delessert ex DC., 10a. subsp. *ovalifolia*, 10b. subsp. *australis* V. A. Funk, 11. *M. fragrans* Badillo.
- b. Series *Quadrangulares* V. A. Funk: 12. *M. angulata* Badillo, 13. *M. quadrangularis* Schultz Bip. in K. Koch, 14. *M. josei* V. A. Funk.
- c. Series *Hibiscifoliae* V. A. Funk: 15. *M. leucantha* (Lag.) S. F. Blake, 15a. subsp. *leucantha*, 15b. subsp. *arborescens* (DC.) V. A. Funk, 16. *M. karwinskii* DC., 17. *M. atriplicifolia* (Pers.) Schultz Bip. in Seemann, 18. *M. pteropoda* S. F. Blake, 19. *M. hibiscifolia* Benth. in Oerst., 20. *M. hexagona* Robins. & Greenm.
- d. Series *Intermediae* V. A. Funk: 21. *M. laskowskii* McVaugh.
- e. Series *Grandiflorae* V. A. Funk: 22. *M. grandiflora* Alamán ex DC., 23. *M. speciosa* DC., 24. *M. imbricata* V. A. Funk, 25. *M. bipinnatifida* (Kunth) K. Koch.

## GENERIC AFFINITIES

*Montanoa* is morphologically distinctive within the Heliantheae. The pales that at maturity envelop the achenes and surpass them in length (Fig. 1A), the brown-black, 4-edged, hard, smooth achenes, the woody habit, the white sterile rays and the lack of pappus separate it easily from other genera. Whereas the boundaries of the genus are easily recognized, the affinities of *Montanoa* with other genera of the Heliantheae are unclear.

*Montanoa* has been consistently placed in the Heliantheae (Lessing, 1832; de Candolle, 1836; Bentham and Hooker, 1873; Hoffman, 1890; Stuessy, 1977). Opinions of these authors as to the position of the genus within the tribe have varied. Two characters used frequently in previous studies to show relationships were the lack of pappus and the sterility of ray florets. Grouping by the absence of characters can be misleading because one does not know if the characters lost were the same event or even if the characters were present in the first place (Davis and Heywood, 1963; Platnick, 1979; Farris, 1979). The genera that historically have been suggested as being closely related to *Montanoa* are: *Sclerocarpus* and *Enhydra* (Cassini, 1829); *Aldama* and *Gymnolomia* (Lessing, 1832); *Sclerocarpus* (de Candolle, 1836); *Sclerocarpus* and *Gymnolomia* (Bentham and Hooker, 1873); *Aldama*, *Rhysolepis*, *Rojasianthe*, *Scalesia* and *Sclerocarpus* (Stuessy, 1977). Of these genera none is here considered to be particularly closely related to *Montanoa*.



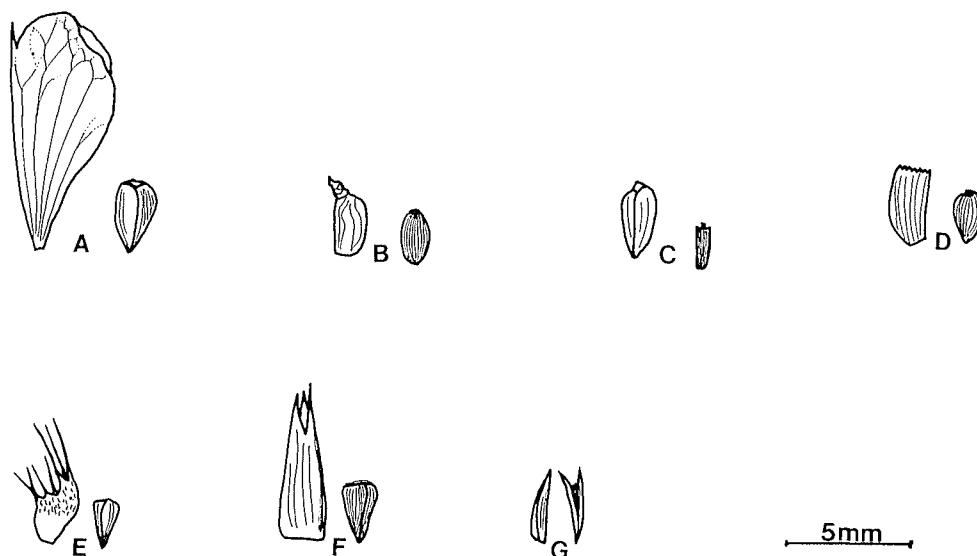


Fig. 1. Mature pales (followed by the achenes) of *Montanoa* and some possibly closely related genera: A, *Montanoa hibiscifolia*, Sa 77655 (F); B, *Sclerocarpus uniserialis*, Bush 1206 (US); C, *Enhydra sessilis*, Osten 5419 (US); D, *Rhysolepis kingii*, King & Soderstrom 4972 (US); E, *Rojasianthe superba*, Matuda 8620 (US); F, *Scalesia atractyloides*, Eliasson 1008 (adapted from Eliasson, 1974); G, *Podachaenium emins*, Smith 2864 (US).

*Sclerocarpus* Jacq. and its segregate *Aldama* Llave & Lex. are most frequently listed as relatives of *Montanoa* (Cassini, 1829; Lessing, 1832; de Candolle, 1836; Bentham and Hooker, 1873; Stuessy, 1977). This is based primarily on the common possession of receptacular bracts that completely surround the achenes. In *Sclerocarpus* and *Aldama*, however, these bracts are not much larger than the achenes and wrap tightly around them. At maturity they become indurate and appear almost fused to the achene (Fig. 1B). In *Montanoa* they are larger, usually papery, and loosely enfold the achene (Fig. 1A). *Sclerocarpus* and *Aldama* differ from *Montanoa* in many other characters (contrasted respectively): annuals vs. perennials; yellow vs. white ray florets; deeply lobed throats and recurved lobes on disc florets vs. shallow erect lobes; pappus present vs. absent; thin-walled and black vs. thick-walled and brown-black achenes; and chromosome base numbers of  $x = 12$  or  $17$  vs.  $x = 19$ . Based on these differences, *Sclerocarpus* and *Aldama* are not considered close relatives of *Montanoa*.

*Gymnolomia* has also been suggested as being closely related to *Montanoa* (Bentham and Hooker, 1873). The genus, as originally conceived, was apparently an artificial concept, based on a lack of pappus (Blake, 1918). The species of *Gymnolomia* have now been variously dispersed into *Viguiera* and *Verbesina*, and the type is now in *Aspilia* Thou. (Robinson, 1977). The genus need not be discussed further.

The genus *Enhydra* was suggested as closely related to *Montanoa* by Cassini (1829). It has been placed recently by Stuessy (1977) in the Ecliptinae near *Blainvillea* Cass., *Eclipta* L., and relatives. *Enhydra* shares with *Montanoa* an absence of pappus and a somewhat similar pale (Fig. 1C). However, the pales are laterally compressed, the heads are sessile, solitary, and in the axils of the leaves, the ray florets are pistillate, many-seriate with short ligules, and they are herbaceous

aquatics of world-wide distribution (Hoffmann, 1890; Stuessy, 1977). In all of these characters *Montanoa* contrasts sharply. Robinson (1978) has placed *Enhydra* in a subtribe by itself. *Enhydra* and *Montanoa* share no known unique characters other than the enveloping pales which is viewed here as a parallel development.

In a more recent treatment Stuessy (1977) has placed *Montanoa* in the subtribe Verbesininae in the informal "Group 1" along with *Aldama*, *Rhysolepis* S. F. Blake, *Rojasianthe* Standl. & Steyerm., *Scalesia* Arn., and *Sclerocarpus*. *Sclerocarpus* and *Aldama* have already been discussed and the other genera share with *Montanoa* only a superficial resemblance of the mature pales. In *Rhysolepis* the fruiting pales wrap around the achene but they are small and cross-wrinkled (Fig. 1D). S. F. Blake (1917, p. 38) originally described the genus as related "on the one hand to *Sclerocarpus* . . . and on the other to *Viguiera*." It shares with these genera a similar pappus, achene, chromosome number, ray color, involucre type and other characters. *Scalesia*, also listed by Stuessy (1977) as a possible relative to *Montanoa*, is a genus of white-flowered shrubs endemic to the Galápagos Islands. Whereas the pales of the members of this genus cup the achenes, they do not surround them (Fig. 1F), and so resemble those of *Montanoa* very little.

*Rojasianthe* was also suggested as a possible relative of *Montanoa* (Stuessy, 1977), but this genus has so many unusual characters that it is as difficult to place in relation to *Montanoa*. For instance, it has black anthers, purple-white rays, disc florets that have a long black and white corolla that is deeply lobed and densely pubescent, ecaudate filaments, and a pappus of 10 serrate caducous awns. The achenes are pubescent and the stems are hollow and fluid-filled. The pales (Fig. 1E) wrap around the achenes but have 10–12 awns and are pectinate, becoming indurate. Although the affinities of *Rojasianthe* cannot be accurately identified at this time, the genus seems not closely related to *Montanoa*.

There are other genera that resemble *Montanoa*. Three that seem particularly similar are: *Podachaenium* Benth. ex Oerst., *Polymnia* Cav., and *Rumfordia* DC. The similarity is, however, superficial. All three are separated from *Montanoa* by a wide variety of pappus, achene and floret characters.

Because the chromosome number of *Montanoa* ( $n = 19$ ) is unusual in the Heliantheae, it is worth looking at other genera with the same number for possible relatives. The ten genera having at least some species with a chromosome number of  $n = 19$  are (subtribal classification after Stuessy, 1977): Bahiinae, *Villanova* Lag.; Coreopsidinae, *Jaumea* Pers., *Venegasia* DC.; Ecliptinae, *Synedrella* Gaertn.; Gaillardinae, *Actinospermum* Ell., *Amblyolepis* DC., *Gaillardia* Foug.; Galinsogninae, *Calea* L.; Melampodiinae, *Espeletia* Mutis ex H. & B.; and Verbesininae, *Podachaenium* Benth. ex Oerst. These genera are spread throughout the subtribes of the Heliantheae, and despite the chromosomal similarity, they are all widely separated from *Montanoa* by a variety of achene, pappus, and pale characters and are much too different to be regarded as a close-knit group.

None of the taxa examined in this study appears to be particularly close to *Montanoa*. In its overall appearance, the genus resembles some members of both the subtribes Helianthinae and Verbesininae (sensu Stuessy), but upon close examination, it shares no important characters with either subtribe and it seems equidistant from both. Robinson (1978) has described a new monotypic subtribe, Montanoninae, perhaps due to the difficulty of placing the genus in any of the existing subtribes. Because many of the characters used for the previous subtribal classifications are not well understood it is difficult to evaluate the validity of the subtribe Montanoninae. As new characters are explored and the homologies of

old ones better understood, the subtribal classifications will most likely change. Resolution of the problem will, therefore, have to await future work in the tribe. For the time being, it seems best to utilize the subtribe Montanoninae for the placement of *Montanoa*.

#### MORPHOLOGY AND TAXONOMIC CHARACTERS

For a character to be taxonomically dependable it must be either stable or variable in predictable ways. In *Montanoa* many of the characters show a great deal of variation, and the extent of the phenotypic variation in the genotype must be examined in order to determine the usefulness of these characters. This documentation is also necessary to initiate the cladistic analysis (presented later).

*Habit.* All taxa are woody, most are shrubs, but the taxa range in size from vines (four species) to trees of 20 meters (five species). There is some intraspecific variation, e.g., *Montanoa pteropoda* and *M. atriplicifolia* are usually scrambling, or in some instances climbing, vines; sometimes in wetter areas they are branching shrubs. *Montanoa tomentosa* is even more variable. It is usually a small shrub of 1–2 m, but it is also known as a vine (FRA 2383; for explanation of abbreviations see APPENDIX A) and in Costa Rica one subspecies is sometimes found as a small tree (F 3062, FGo 3065) although a plant within a few meters along the roadside (F 3061) is a shrub. The determining factors for habit appear to be altitude and water. In general, the lower the altitude, the less water available at certain periods of the year and the more likely the plant is to be a vine. The habit differences of the small shrubs and vines should, therefore, be used with care.

*Pubescence.* Four types of pubescence are found in *Montanoa*: Type A (Fig. 2A, B) is the standard uniseriate multicellular hair that is common in the tribe Heliantheae (Robinson and Brettell, 1973). It has an acute apical cell, varies in length from 0.25 to 5.0 mm, and can be slender (Fig. 2A) or thick (Fig. 2B). The hairs are measured at their maximum length. They are found on almost all parts of the plant from the disc corollas to the stems. The amount of pubescence must be used with care, however, since it varies greatly with the environment. The length can be very helpful in some species, for instance the section *Montanoa* has much longer hairs than do the other infrageneric groups of the genus. Unless otherwise specified all pubescence is this type. Type B (Fig. 2C) is similar to type A in that it is uniseriate and multicellular, however, it has a rounded apical cell and is less than 0.5 mm long. It is, except in *M. leucantha*, restricted to the section *Montanoa* where it is found on the apices of the disc and ray corollas. Type C (Fig. 2D) hairs are unusual. They are multicellular, uniseriate, stiff, often recurved hairs with an acuminate apical cell and a multicellular base. The base can be either greatly elaborated or reduced. So far this type has been found only on the upper surface of the blades where it varies from scattered to dense and is responsible for the scabrous upper leaf surfaces. The hairs are always regularly spaced and in some taxa the base tends to be white (e.g., *M. laskowskii*, *M. bipinnatifida*). *Glands* (Fig. 2E–H) are found on all taxa. Although they appear to differ in structure, apparently they are all developmental stages of the same gland (pers. obser.). The gland is actually a biseriate multicellular hair. During the development of the hair it appears to change somewhat and when viewed from different angles it appears structurally different (Fig. 2H, G). These short-stalked capitate glandular hairs are referred to in this treatment as glands and are less than 0.5 mm long. They are found primarily on the undersurface of the leaf blades, on the anthers and on the immature pales.

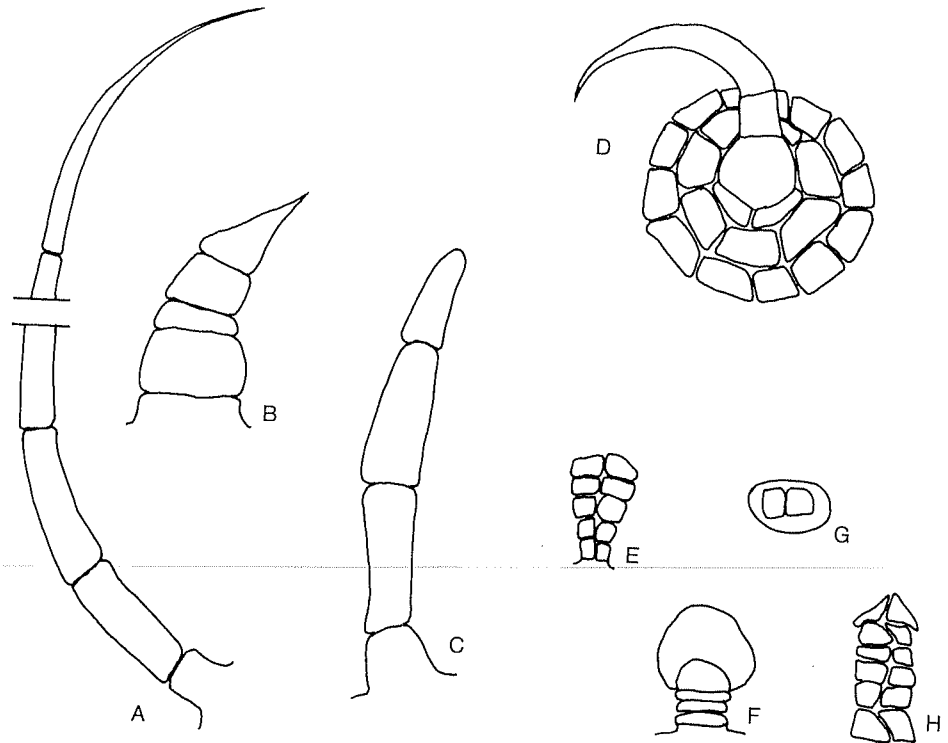


Fig. 2. Hair types in *Montanoa*. A-B, Type A; C, Type B; D, Type C; E-H, Glands.

In *Montanoa* the pubescence has been used in the past heavily for species delimitation. Observations from herbarium sheets and from field studies indicate that members of a species from different parts of its range sometimes have different amounts of pubescence. To determine whether or not such variation was clinal, a series of greenhouse experiments was run using a number of species growing in both the wet and dry greenhouses. The results are illustrated in Fig. 3A-D using one taxon, *M. tomentosa* subsp. *microcephala*. Varying the amounts of water resulted in abaxial vestiture ranging from densely glandular and pubescent to only sparsely glandular. Likewise, the adaxial surface showed not only a reduction in the number of multicellular based hairs, but also a reduction in the size of the base with increased amounts of water. This same variation was observed on most species grown in the greenhouse. The amount of pubescence cannot be used in delimiting the species unless the condition has been thoroughly studied in a variety of environments.

*Stems.* Because all species of *Montanoa* are woody, the stems are divided into two parts: the herbaceous parts which are usually green, and the woody parts which make up the remainder of the plant. The stems are usually terete but in some species (e.g., *M. bipinnatifida*, *M. quadrangularis*), the stems are quadrangular becoming terete. The woody parts are almost always glabrous and should be considered so unless otherwise specified in the description. The herbaceous parts vary from densely glandular and pubescent to subglabrous; in general, however, they are moderately glandular and pubescent. The woody parts are light brown to gray with a large number of lenticels. The herbaceous parts are usually

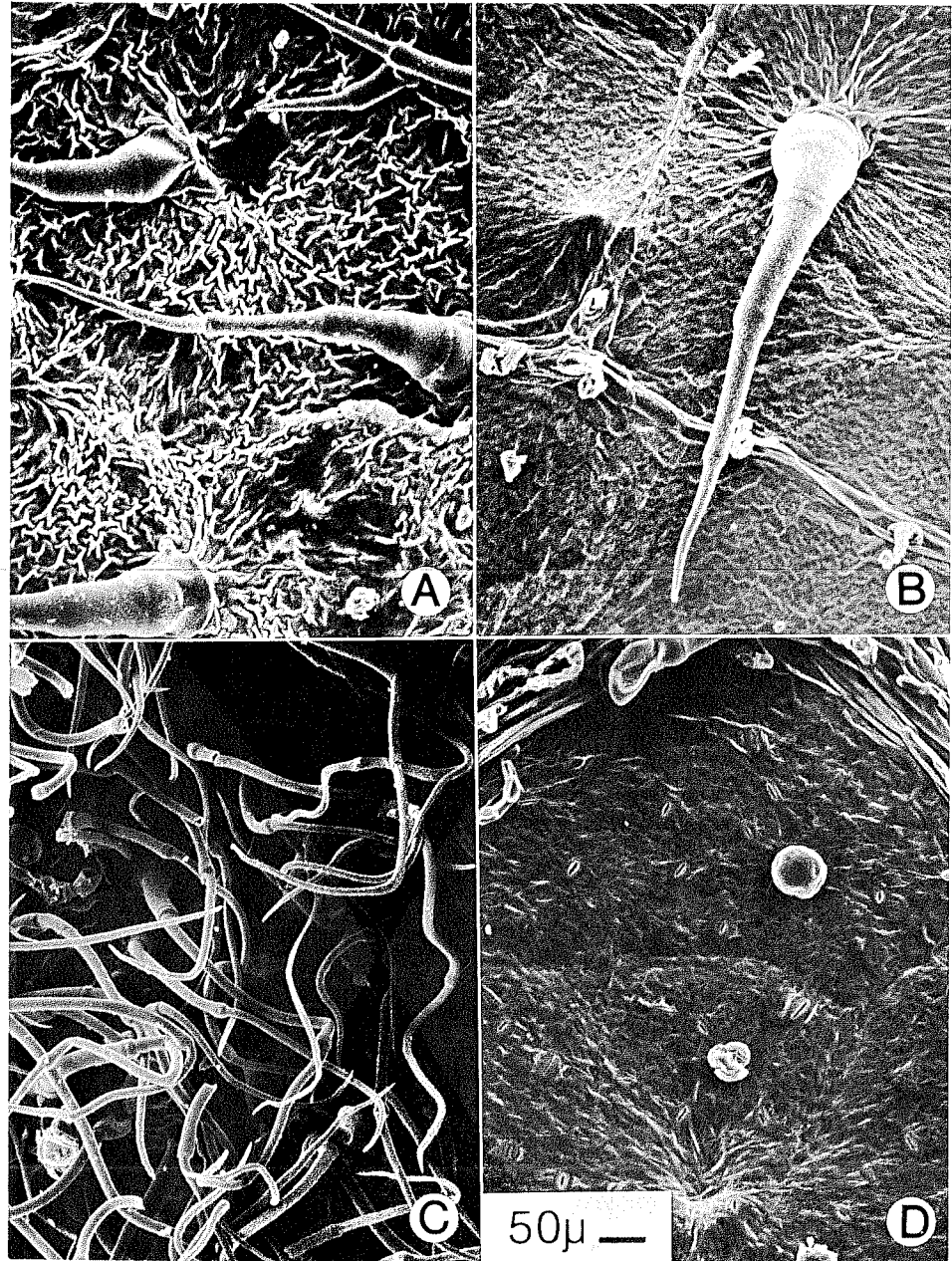


Fig. 3. Variation in vestiture of leaves in *Montanoa tomentosa* subsp. *microcephala* (F 2896, OS). A, C, adaxial and abaxial surfaces of a leaf from a plant grown in a very dry greenhouse environment; B, D, adaxial and abaxial surfaces of the same individual grown in a very wet greenhouse environment.

green but in at least one species they are consistently purple (*M. frutescens*). The internodal distance varies depending on the time of year and the amount of water available. All taxa appear to stump-sprout when cut back and many also produce sucker shoots. These shoots tend to have longer internodes, sometimes up to 45

cm. These shoots have been observed to 8 m long (pers. obser. in one wet season). Two species (*M. tomentosa* and *M. pteropoda*) are known from greenhouse studies to root at the nodes. In areas with adequate water, most stems have at least half their diameter in pith (especially the sucker shoots). In drier areas very little pith is present.

*Leaves.* All leaves have three main veins in the blades. Where these veins meet is here considered the base of the blade and the beginning of the petiole. Sometimes this main juncture is at the base of the blade (*Montanoa karwinskii*), but usually it is inside the laminar portion of the leaf. The definition of the petiole is supported by the fact that proximal to the juncture the petiole is raised above the surface. Most taxa have petioles that are less than half winged with only seven having petioles that are completely winged or nearly so (*M. grandiflora*, *M. laskowskii*, *M. liebmannii*, *M. mollissima*, *M. pteropoda*, *M. speciosa* and *M. tomentosa* subsp. *microcephala*). The winged nature of the petiole is useful in distinguishing among several closely related species, but cannot be used in the genus as a whole because it is found in all three infrageneric groups. Auricles can occur at the distal or proximal end of the petiole or anywhere in between. Usually they are small but occasionally they are as large as the lobes of the leaf that they subtend (e.g., *M. bipinnatifida*). In some species the position and size of the auricles can be used to aid in the determination of the species (e.g., *M. bipinnatifida*, *M. laskowskii*). The blades of *Montanoa* are highly variable with the most common shapes being ovate and pentagonal. The margins vary from unlobed to deeply 3–5 lobed and the pubescence from absent to dense. Usually the leaves are so variable that they are not useful in delimiting species, but in some taxa they are remarkably consistent (e.g., *M. hibiscifolia*, *M. karwinskii*). There is some correlation of blade shape and size with location on the plant and habitat of the plant and this is further discussed in the following section.

*Peduncle.* The peduncles are usually densely pubescent and glandular, but in one species (*Montanoa fragrans*) they are consistently glabrous. The length of the peduncle is usually less than 6 cm except in the 4 species that have solitary or nearly solitary heads (*M. fragrans*, *M. echinacea*, *M. laskowskii*, and *M. liebmannii*).

*Synflorescence.* All taxa have a terminal synflorescence with the heads solitary or arranged in open to tightly clustered, sparsely to densely leafy-bracteolate, compound corymbiform or paniculiform cymes. The estimation of the abundance of heads is difficult because the number often depends on the age of the branch. Most plants flower for 2–3 months, and the synflorescence continues to increase in size. The character of floral abundance in the descriptions, therefore, covers a wide range of values. The descriptions are complicated by the fact that the heads are usually clustered on three levels: they are usually in cymes which are aggregated in either panicles or "corymbs" and these in turn can be arranged into doubly compound panicles.

*Heads.* The receptacle is slightly convex and becomes more so in fruit. Usually it is as tall as it is wide, but in one species (*Montanoa frutescens*) it is strongly convex. The height vs. the diameter is given in the descriptions only when it exceeds 1:1. The number of disc florets varies from 3 to 160 and as the number decreases the heads often are more closely aggregated and the disc corollas are often longer (pers. obser.). In the descriptions the heads were measured without the rays because the length of the rays can vary in some taxa up to one cm on an individual plant.

*Phyllaries.* The involucre is uniseriate or biseriate with a few taxa having the triseriate condition. The phyllaries are ovate to lanceolate, herbaceous and

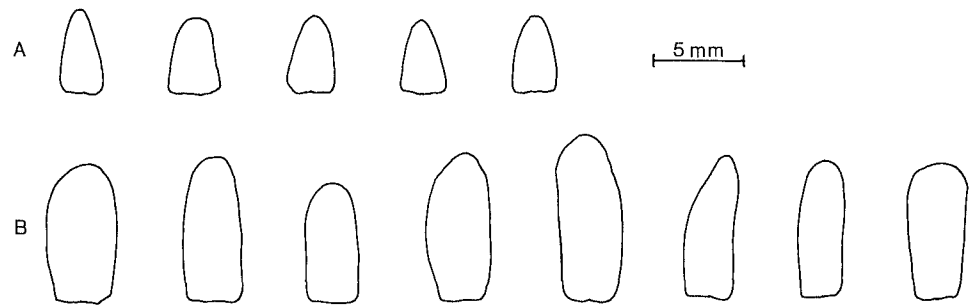


Fig. 4. Involucral bracts of *Montanoa guatemalensis*. A, F 3047; B, F 3049.

spreading, and often reflexed at late anthesis or during fruiting. The phyllary number and length are relatively uniform among the species. The phyllaries are usually pubescent and sometimes glandular. In one instance (e.g., *Montanoa imbricata*) the involucre is quite distinct, wrapping around the capitula prior to anthesis. The number and size of the phyllaries are often variable within a species, but this study has failed to show any environmental correlation. The involucral bracts in at least five species (*M. guatemalensis*, *M. mollissima*, *M. ovalifolia*, *M. speciosa* and *M. tomentosa* subsp. *tomentosa*) vary greatly in size, and those of *M. guatemalensis*, *M. ovalifolia*, and *M. speciosa* also vary in number. For instance, Fig. 4 illustrates the bracts from two individuals of *M. guatemalensis* growing next to one another. Note the difference in length and number. Other members of the population showed intermediate conditions. The random varying of this character suggests that this variation is little more than phenetic plasticity, and emphasizes that the character must be used with caution.

*Ray florets.* The rays are neutral, spreading, and white or cream in color. The ray corolla is usually obovate or elliptic, but some species have diagnostic shapes (*Montanoa tomentosa*, ovate; *M. revealii*, almost lanceolate). The apex varies from acute or rounded to one- or two-notched, but some taxa have a consistently acute (e.g., *M. standleyi*) apex. Usually the adaxial surface of the rays is glabrous or subglabrous and the abaxial surface is sparsely to densely glandular and occasionally pubescent. The apex of the corollas in section *Montanoa* bears round-tipped, multicellular, uniseriate hairs. The cells of the adaxial surface are papillose and the cells of the lower surface are "sinuate-shaped" (Baagøe, 1977).

The bracts that subtend the ray florets have been regarded by some workers as the inner involucre (Gleason, 1952; Stuessy, 1977). By others they have been categorized as the outer row of the receptacular bracts (Gleason, 1952). They are considered here to be the outer row of the receptacular bracts (pales), because of their development during fruiting. Instead of remaining herbaceous and approximating the size and shape of the phyllaries, they develop as do the pales. Often they are not quite as long as the pales subtending the disc florets, but they do surround the abortive achene and they do elongate and become either indurate or papery. This tendency to develop in the same fashion as the pales of the disc florets suggests that their affinity lies with the bracts of the receptacle rather than those of the involucre.

*Disc florets.* The disc florets are hemaphroditic, 5-lobed, and yellow to gray-green or black. The throat and tube are cylindrical in all taxa, but the size as well as the color is useful in circumscribing some of the taxa (e.g., *Montanoa laszkowskii*, *M. pteropoda*). The cells are papillose on the inner surface of the lobes

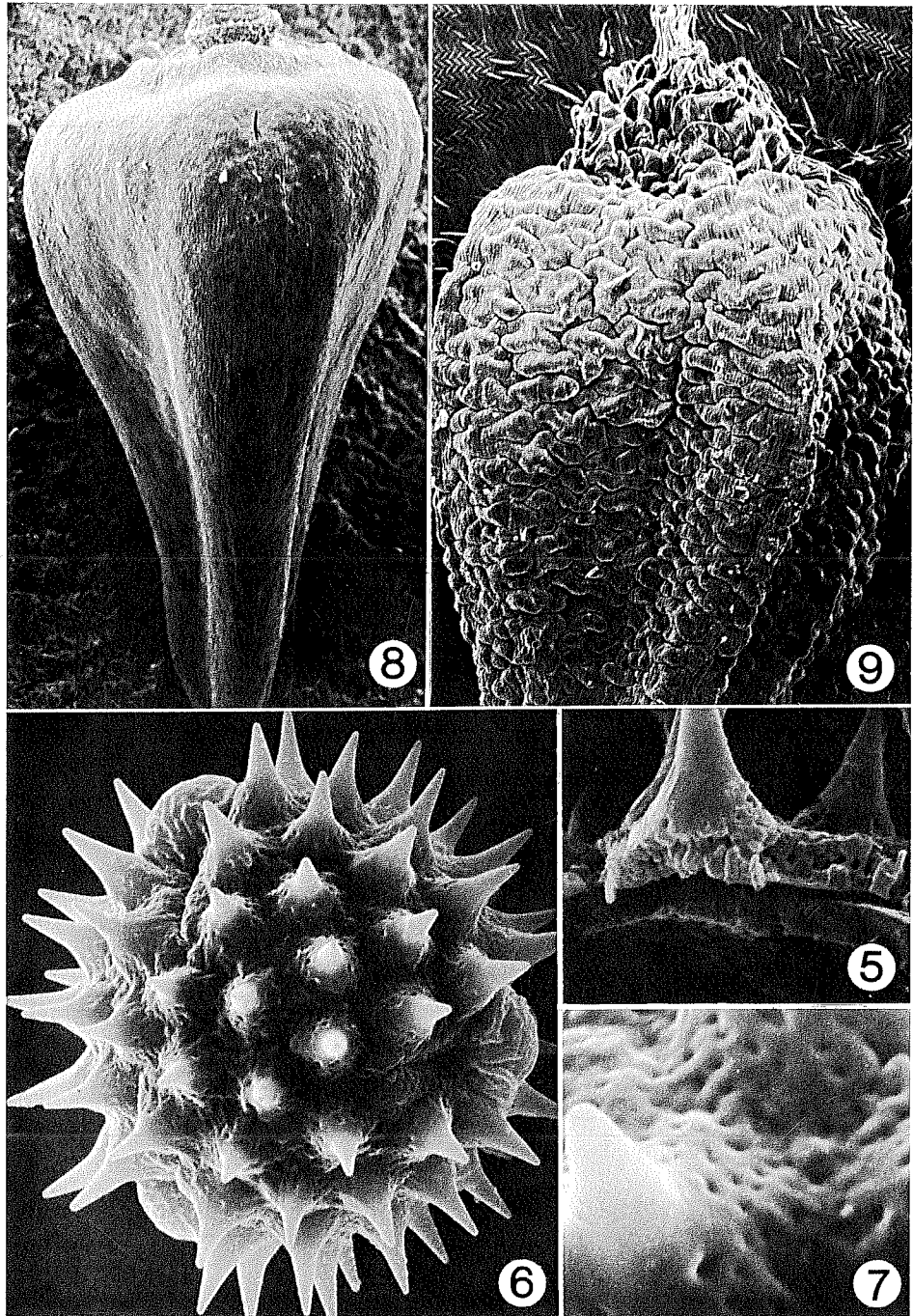
of the corolla. The surface varies from glabrous to densely glandular and pubescent. This character is somewhat useful in differentiating among closely related taxa; e.g., the members of series *Grandiflorae* tend to have nearly glabrous corollas, whereas the closely related species, *M. laskowskii*, has a densely glandular and pubescent one. The stamens are uniform in structure, the filaments are yellow, and the base of the thecae acute, but they can also demonstrate a number of useful characters. For instance, the apex can be long-acuminate to short-acute, black or yellow and glandular or glabrous. The thecae can be brown or yellow or occasionally black. The size of the stamens is also useful because in some species they are extremely long (e.g., *M. andersonii*, 8.0–9.2 mm) and in others very short (e.g., *M. atriplicifolia*, 2.25 mm). In most species the anthers are not fully exerted from the corolla but in several species they are fully exerted (e.g., *M. andersonii*, *M. speciosa*). The styles also vary, their apices being either acute or long-acuminate and yellow or black. The stigmatic surface is yellow or brown with two receptive lines, and the abaxial surface of the style branches is yellow except for *M. pteropoda* in which it is black. At the base of the style there is usually an enlarged node that develops late in anthesis after the achene has already begun to mature.

*Pollen.* An SEM survey showed that all of the species of *Montanoa* have pollen grains with a spiny exine (Figs. 5–7). This was not unexpected, inasmuch as the pollen of the Heliantheae is known to be remarkably uniform (Skvarla and Larson, 1965). In addition, pollen viability (measured by using Lactophenol Cotton Blue; Hauser and Morrison, 1964) showed almost 100% stainability for all species. There was, however, some variation in pollen size within the genus when the size of the known polyploids was compared with the size of the known diploids; the polyploid pollen was about twice the size of the diploid sister-species.

*Pales.* At anthesis the pales are relatively similar throughout the genus. They all have an ovate or elliptic base that encloses the achene. The apex is uniformly acuminate, but in some it is longer than the base (subgenus *Montanoa*), whereas in the others it is shorter (subgenus *Acanthocarphae*). They are usually moderately to densely pubescent, with members of section *Montanoa* having the latter condition. The pales are light yellow when immature and either stramineous or purple at maturity, but in between, when they are increasing rapidly in size, they are green. They are rarely longer than 5 mm at anthesis (6–8 mm in *M. echinacea* and *M. liebmanni*) but grow rapidly once the ovaries begin maturing into achenes. In one head (*M. revealii*, *FRi* 2820) the difference in length between early and late anthesis was 2 mm. Because of rapid growth the immature pales were always measured when the disc florets were at anthesis; in the descriptions they are referred to “pales at anthesis.” There are other pale distinctions such as length: *M. echinacea* and *M. liebmanni* with extremely long pales at anthesis (6–8 mm) and *M. pteropoda* and *M. atriplicifolia*, with very small ones (2.25–3.0 mm). The cell walls of the pales are sinuate. The mature pales were measured folded and the immature ones flattened out. Pales at maturity offer a number of useful characters. Not only do they help circumscribe the genus, but they are also used at the subgeneric and specific levels. The types of pale characters used include the condition, margin, apex, length, venation, pubescence, shape, and folding. Of all the structures in the genus this one has yielded the largest number of useful characters (to be discussed more fully in the Cladistic Section).

*Achenes.* All the taxa in the genus have obpyramidal, quadrangular achenes that have a vascular strand in each edge. They range in size from 2.5 mm (*Montanoa pteropoda*) to 4–5 mm (*M. echinacea*). *Montanoa hibiscifolia* and *M. hexagona* have a convoluted amorphous outer surface (Fig. 9) but all other taxa have a





Figs. 5-9. SEM photos of *Montanoa* pollen and achenes. 5-7, pollen grains of *M. leucantha* subsp. *arborescens* (FTK 2701, OS): 5, broken grain showing internal structure; 6, non-acetylated grain; 7, acetylated grain. 8, 9, mature achenes: 8, *M. leucantha* subsp. *arborescens* (FTK 2701, OS); 9, *M. hibiscifolia* (Standley & Chacon 69450, F).

smooth outer surface (Fig. 8). All taxa of *Montanoa* have a phytomelanin layer that is interrupted at regular intervals (pers. obser.). The achene is indurate, and the interruptions, which only show up after soaking, may facilitate the emergence of the radicle at germination. The achenes are brown-black and have at the apex (of all taxa except *M. hibiscifolia*) a ring-shaped structure that is presumably a gland.

#### LEAF MORPHOLOGY

The greatest difficulty in delimiting species in *Montanoa* is the extensive morphological variation within the genus. Such characters as leaf morphology, habit, amount and type of pubescence, number and shape of phyllaries, and number of disc and ray florets vary dramatically within and among the species until the limits are clouded. The most confusing feature is the variability of the leaf morphology. In the past, characters of the leaves have been used frequently in the delimitation of species. For instance, of the 14 species described by Schultz Bipontinus (in K. Koch, 1864) all were based either entirely or primarily on leaf shape. One species, *M. elegans*, was described from cultivated material that had never flowered. Robinson and Greenman (1899) described 10 species as new, all of which were based primarily on leaf shape or size. Although the use of leaf morphology may not be problematical in other genera, in *Montanoa* it has led to severe confusion in specific limits. Because of the emphasis on leaf morphology in past studies, and because initial studies indicated problems with this character, it became apparent that in order to develop a useful taxonomy of *Montanoa* the efficacy of leaf morphology would have to be evaluated. This problem was approached in three distinct ways: 1) a detailed study of herbarium material to obtain preliminary data on the limits of variation and to identify problem areas in the distribution; 2) extensive fieldwork in Latin America to determine more precisely the limits of the variation, and to develop hypotheses for the causes of the variation; and 3) greenhouse studies to test these hypotheses.

*Kinds of variation.* Studies of over 6000 herbarium sheets revealed some species in which leaf morphology was fairly consistent (e.g., *Montanoa bipinnatifida*, *M. echinacea*). However, it also revealed that a majority of the species have extensive variation. Principal among these are section *Montanoa* and the *M. leucantha-arborescens* complex.

Examination of herbarium specimens and observations made in the field showed that variation in leaf morphology of *Montanoa* is present on three levels: individual, populational, and interpopulational. These variations can be illustrated by one taxon, *M. tomentosa* subsp. *tomentosa*. Fig. 10A-C illustrates three individuals from this subspecies from various parts of the range. On a single individual the leaves vary in shape from triangular to pentagonal, entire to irregularly dentate, unlobed to deeply 3-5-lobed, and with bases that are acute or partially winged.

Variation on the intrapopulational and interpopulational levels is equally extensive. Figure 10D shows leaves collected from a population in the Distrito Federal of Mexico. Note, however, that all of the variation found on the three individuals from different populations (Fig. 10A-C) can be found in this populational sample. Finally, variation on the interpopulational level in *M. tomentosa* subsp. *tomentosa* was mapped geographically (Fig. 11). All collections of this subspecies are illustrated and the leaves were selected to illustrate the maximum variation. At first there seem to be areas of consistent leaf morphology, and these were often recognized in past treatments as distinct species. However, closer inspection reveals that this is not so. For instance, the cordate leaf shape that predominates

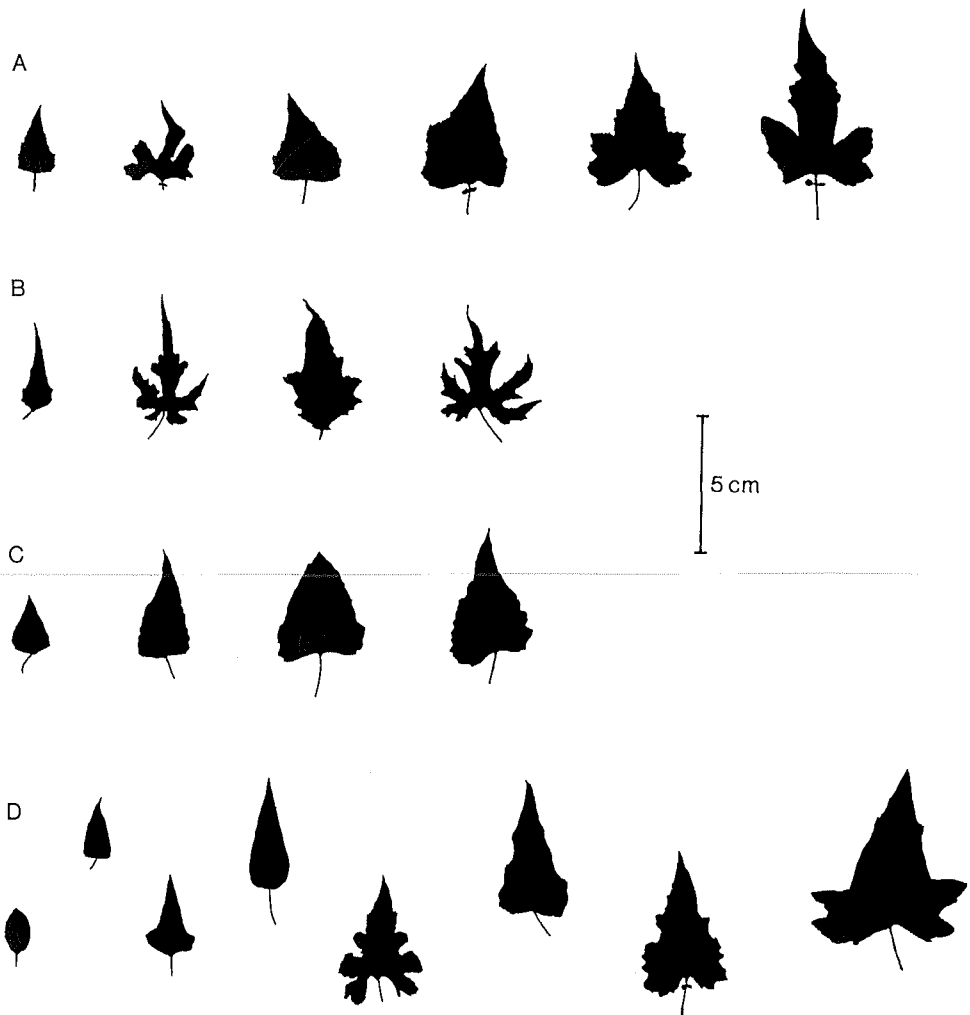


Fig. 10. Variation in leaf shape in *Montanoa tomentosa* subsp. *tomentosa* at the individual (A–C) and populational (D) levels. A, San Luis Potosí, *AL 4062* (MICH); B, Hidalgo, *FT 2820* (OS); C, Oaxaca, *FRa 2383* (OS); D, Distrito Federal, many collections in the pedregal area near the University of Mexico.

in Oaxaca can also be found in Puebla, Hidalgo and Distrito Federal. Total variation on the interpopulational level can be accounted for in the sample from one population (Fig. 10D).

*Causes of variation.* A study of such factors as location of leaves on the plant, time of year in relation to amount of water and the age of the stems upon which the leaves were collected has led to the formulation of hypotheses concerning the causes of the extensive leaf variation in *Montanoa*. These hypotheses have then been tested in greenhouse experiments. The causes of the variation in leaf morphology were found to be either developmental or environmental.

Variation due to developmental factors is illustrated by one taxon, *Montanoa tomentosa* subsp. *xanthiifolia* in Fig. 12, and is the result of age and origin of the

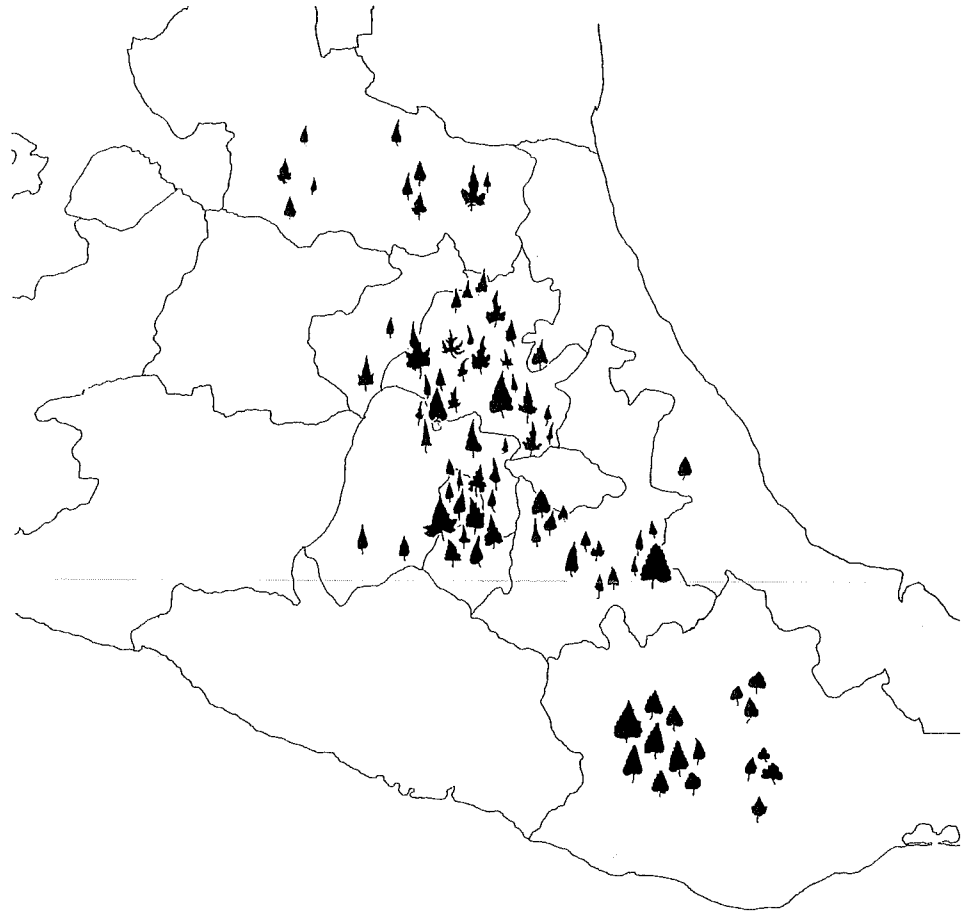


Fig. 11. Map of central Mexico showing distribution and interpopulational leaf variation in *Montanoa tomentosa* subsp. *tomentosa*.

stems bearing the leaves. For instance, leaves from portions of stems of the previous seasons (woody parts) are often quite different in shape from those produced on the new year's growth (herbaceous parts). Figure 12A illustrates a leaf taken from the herbaceous part, 12B one from the woody part, and 12C two leaves from an axillary branch. Also, leaves on shoots arising from the base of the plant (sucker shoots) are larger and often greatly dissected or deeply lobed (Fig. 12D). Finally, there is a difference in the shapes of leaves from flowering and non-flowering branches. All of the leaves in Fig. 12A–D were collected from non-flowering branches and those in 12E were collected from flowering ones. The leaves from the flowering branches are less lobed and smaller in size. All three of these observations were corroborated with collections from greenhouse-grown plants.

Variation due to environmental stress is a result of such factors as amount of water, nutrients, and wind. An example of this is seen in southern Oaxaca in the taxon *Montanoa tomentosa* subsp. *microcephala*. All individuals have winged petioles, but the shape and lobing of the leaves varies (Fig. 13). One population south-east of Oaxaca City on Hwy 190 has been collected many times by a variety of col-

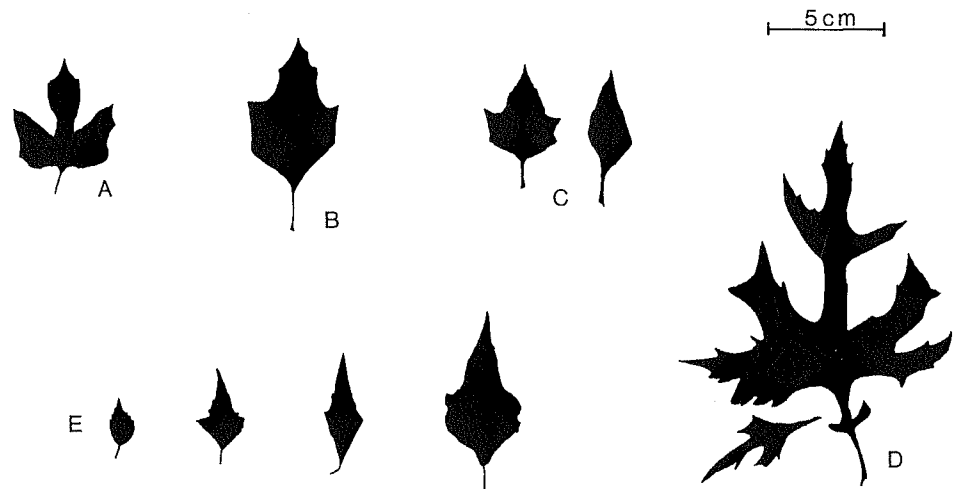


Fig. 12. Developmentally induced individual variation in the leaves of *Montanoa tomentosa* subsp. *xanthiifolia*, FT 2813 (OS). A, herbaceous section of branch; B, woody section of branch; C, axillary shoot; D, sucker shoot; E, flowering branches.

lectors (see REPRESENTATIVE SPECIMENS). The leaves of this population varied to the extent that they encompassed the range of variation for the taxon. Examination of the collection data indicated that the size of the leaves produced at drier times was smaller. To verify this, two plants from one collection of this population (F 2896) were grown in the greenhouse. One was placed in a "dry" greenhouse where the plant was not watered for one month until all of the leaves had fallen off. Watering was then resumed and leaves were collected at one month intervals until the leaves were once again the size of those produced in the "wet" greenhouse (in which plants had been watered continuously). In the "dry" greenhouse, after the leaves fell off, the plants resembled those collected from south-east of Oaxaca in December in late fruiting stages. The leaves from the same population in August–September at early anthesis, however, had larger and often more lobed leaves (corresponding to plants in the "wet" greenhouse and the "dry" greenhouse after three months of water). In both the field collections and the greenhouse collections there was a gradual change from one leaf size to the other (Fig. 14) suggesting that the changes in leaf shape and size in the field collections are a result of the amount of water the plant receives.

The same type of variation mentioned above was noticed in plants that were not fertilized regularly or became pot-bound, which suggests that a lack of nutrients could produce similar effects. Wind is another factor that can affect leaf shape and size. For instance, *Montanoa guatemalensis*, when found growing in protected areas, has large, lobed leaves on the non-flowering branches and small rhombic, unlobed leaves on the flowering ones. Plants collected in one locality in Costa Rica, however, were on the side of a steep mountain slope in a continual updraft and all of the leaves of these plants were small and resembled those of the flowering stems of other collections in the general vicinity.

*Conclusion.* Within *Montanoa*, developmentally and environmentally induced variation in the morphology of the leaves renders these characters nearly useless as delimiters for most species. Further, they rarely correlate with other features. The leaf shapes of many distantly related species are very similar (e.g., *M. hex-*



Fig. 13. Map of Oaxaca showing distribution and interpopulational leaf variation in *Montanoa tomentosa* subsp. *microcephala*.

*agona* and *M. quadrangularis*) whereas those of closely related species are very different. To facilitate verification of species identifications in this treatment, each description in the taxonomy section is accompanied by illustrations of representative leaves.

#### CYTOLOGY

Prior to this study, the cytology of *Montanoa* had been little investigated. Only eleven chromosome counts (all  $n = 19$ ) were known for five presently recognized species: *M. tomentosa* (Urbatsch, 1974; Solbrig et al., 1972; Turner and Flyr, 1966; Turner and Johnston, 1961); *M. leucantha* subsp. *arborescens* (Solbrig et al., 1972; Turner and Flyr, 1966); *M. quadrangularis* (Powell and Cuatrecasas, 1970); *M. grandiflora* (Solbrig et al., 1972); and *M. bipinnatifida* (Keil and Stuessy, 1977). Of the 30 taxa recognized here, chromosome counts are presented for 21 (Table I; specimens counted are indicated in the TAXONOMIC TREATMENT). Of the nine taxa not counted in this study, eight are restricted endemics. The ninth species, *M. quadrangularis*, was collected but not in flower. A number has, however, been published for this taxon (Powell and Cuatrecasas, 1970) so that determinations are now available for 22 taxa. A total of 105 counts is presented here.

Chromosome counts were made from bud and root tip material collected in the field and greenhouse, placed in 4:3:1 (chloroform : ethanol : acetic acid) followed by transferal to 70% ethanol and freezer stored upon returning to the laboratory. Buds were stained for 24 hours at 60°C in Snow stain (Snow, 1963) and root tips for 6 hours. They were then dissected in 45% acetic acid, mixed half and half with Hoyer's medium, and squashed thoroughly.

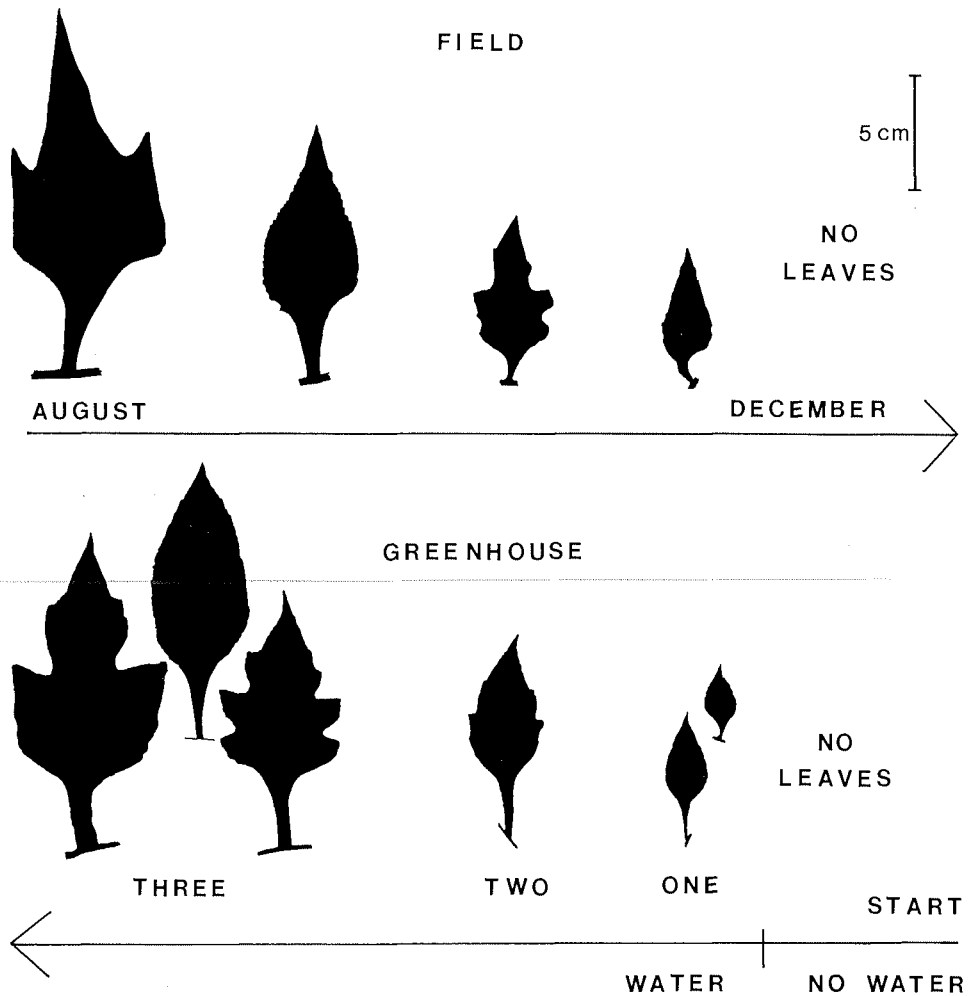


Fig. 14. Correlation of variation in *Montanoa tomentosa* subsp. *microcephala* in field collected leaves and those produced by plants grown under different moisture regimes in the greenhouse.

*Montanoa* has a base number of  $x = 19$ , which is not a common number in the Heliantheae (Stuessy, 1977). Smith (1975) has suggested that this could be a reduction from a primitive number for the tribe of  $n = 20$ . Another opinion (Stuessy, 1977) is that it could represent an increase from ancestral hybridization of  $n = 8$  and  $n = 9$  followed by aneuploid increase. There is no evidence from the cytology of *Montanoa* that could indicate a preference for either theory, although some of the counts showed several B chromosomes. This could indicate a reduction from a higher number, but even if this were so, there is no way to determine whether the higher number was the primitive number for the tribe. While numbers in the range of  $n = 17-18$  are widely distributed in the Heliantheae, the  $n = 19$  is less common, occurring in scattered comparatively unrelated groups.

The majority of taxa (18) in *Montanoa* are diploids. The meiotic and mitotic divisions are normal and all pairing at metaphase is bivalent. Based on obser-

TABLE I  
Chromosome counts of *Montanoa* made for the present study<sup>a</sup>

Taxon	Gametic C.N. <i>n</i> =	No. of counts	Collectors
Subgenus <i>Montanoa</i> Section <i>Montanoa</i>			
<i>M. tomentosa</i> subsp. <i>tomentosa</i>	19	8	
	19 ± 1B	1	SG 4264
	ca. 19	1	SG 4246
	2 <i>n</i> = 38	1	FRa 2361b
subsp. <i>microcephala</i>	19	1	
subsp. <i>rosei</i>	19	3	
subsp. <i>xanthiifolia</i>	19	10	
Subgenus <i>Montanoa</i> Section <i>Echinocephalae</i>			
<i>M. frutescens</i>	19	3	
<i>M. guatemalensis</i>	108-115	1	F 3010
	104-111	1	F 3010
	111-114	1	F 3049
	104-114 ± 8B	1	F 3053
	113-122	1	F 3048
	107-116	1	F 3056
<i>M. mollissima</i>	19	4	
<i>M. revealii</i>	56 ± 1	1	FRi 2826
	57 ± 1	1	FRi 2830
Subgenus <i>Acanthocarphae</i>			
<i>M. ovalifolia</i> subsp. <i>ovalifolia</i>	19	9	
<i>M. lencantha</i> subsp. <i>lencantha</i>	19	6	
	ca. 19	1	JH 472A
subsp. <i>arborescens</i>	19	12	
	19 ± 1B	1	FH 2264
	2 <i>n</i> = 38	1	FS
<i>M. karwinskii</i>	19	4	
<i>M. atriplicifolia</i>	19	4	
<i>M. pteropoda</i>	19	3	
<i>M. hibiscifolia</i>	19	7	
<i>M. hexagona</i>	74 ± 2	1	FL 2909
	75-80	1	FL 2920
	75 ± 1	1	FL 2920
	74 ± 2	1	SG 4339
	73-77	1	FRa 2643
	75 ± 2	1	FRa 2562
<i>M. laskowskii</i>	19	2	
<i>M. grandiflora</i>	19	1	
	19 ± 2B	1	SG 4176 (double-rayed)
<i>M. speciosa</i>	19	2	
	ca. 19	1	HF 4240 (double-rayed)
<i>M. imbricata</i>	19	2	
<i>M. bipinnatifida</i>	19	2	

<sup>a</sup> Only numbers other than *n* = 19 are listed as to collector and number, all other specimens from which counts were obtained are indicated in the respective representative specimens.





Fig. 15. Camera lucida drawing of meiotic chromosomes of *Montanoa guatemalensis*, F 3049 (OS),  $n = 111-114$ .

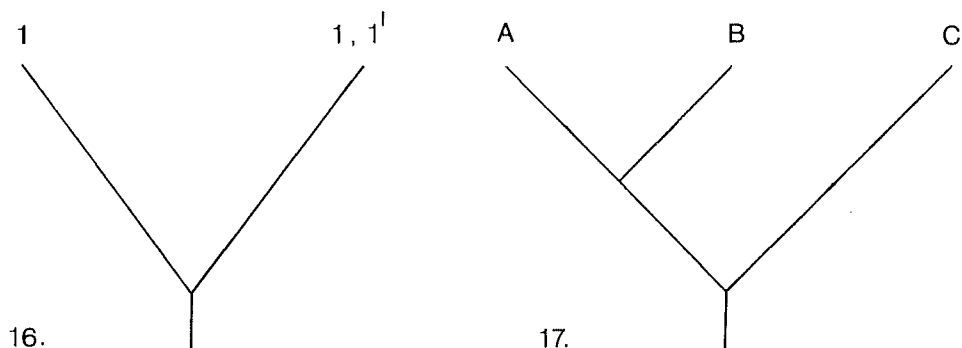
vations at meiosis and mitosis, there were no obvious differences among the taxa in chromosome shape and size. No satellites were found.

There are three known polyploids in the genus. *Montanoa revealii* from Guerrero, Mexico, is a hexaploid; *M. hexagona* from Chiapas, Mexico and northern Guatemala is an octoploid; and *M. guatemalensis* from southern Guatemala to Costa Rica is a dodecaploid (Fig. 15; Funk and Raven, 1980). Most cells of the polyploids showed normal meiosis, although there was lagging in some cells at telophase II in the dodecaploid. The chromosomes of all the polyploids are "sticky" in late metaphase. Most of the cells of the tetrads are the same size with an equal number of chromosomes, however, occasionally the division at telophase II was not equal and some of the cells of the tetrad received more chromosomes than others. A more complete discussion on the significance of the polyploids is found in the Cladistic Analysis.

#### CLADISTIC ANALYSIS

One of the objectives of this study was to develop a predictive classification for the genus. A classification that can easily accommodate new information and that can convey the maximum amount of information (predictive) can only be accomplished by basing the classification on the evolutionary patterns within the genus (natural). An estimation of the branching pattern of evolution in *Montanoa* has been developed using the technique of Hennig (1950, 1966), and this was used to develop the classification of the genus.

The technique of Hennig (1950, 1966) is here referred to as cladistics and the



Figs. 16, 17. Cladograms. 16, Taxonomic outgroup comparison; 17, Functional outgroup comparison.

resulting branching diagram as a cladogram. In this method one must assume that there is only one history of the group and that it can be detected by internested sets of synapomorphies and illustrated by a branching pattern. Synapomorphies can be generally defined as shared derived character states. The taxon used in the analysis should be monophyletic, i.e., it should contain all of the known descendants of a common ancestor. If the group is not monophyletic, then its members share no common history and a cladistic analysis is not informative. Within the group, a set of characters must be selected for use in the analysis, and these characters must be divided into discrete states or conditions. These states must be ordered into apomorphic (advanced or derived) and plesiomorphic (ancestral or primitive) states. It is important to remember that the two are relative to one another. An apomorphic state of a character is advanced only in reference to the plesiomorphic one. One can order the states in a number of ways proposed by Hennig (1966) and others (Crisci and Stuessy, 1980; de Jong, 1980; Stevens, 1980). In my opinion, the most logical way to determine the polarity of character states is by outgroup comparison and/or ontogeny (Funk, 1981). Once the states have been polarized (ordered as to primitive and advanced), the taxa are then grouped by synapomorphies.

There is little doubt that *Montanoa* represents a monophyletic group. The enveloping, greatly elongated pales and the quadrangular, obpyramidal, smooth, hard achenes are apomorphies that separate it from all other genera in the tribe Heliantheae. The selection of the characters to be used for the cladistic analysis was based on the detailed morphological study that accompanied the revision. The polarization of the characters, was, however, a problem. Ordinarily in outgroup comparison one takes a specific character, checks the states of that character in the outgroup and makes the state that both groups share plesiomorphic. The condition that is unique to a group is the apomorphic state. For instance, in Fig. 16 two genera, A and B, are sister groups, or rather, more closely related to one another than either is to any other genus. One character has states 1 and 1' in genus B and state 1 in genus A. Using outgroup comparison one assumes that it is more likely that 1 is the plesiomorphic condition and 1' is the apomorphic one. This is not the same as "common is primitive" (Crisci and Stuessy, 1980) because there could be many species in genus B with state 1' and only one with state 1, and genus A could be monotypic or have only one species with state 1 and many with an entirely different state.

The outgroup is usually of the same taxonomic rank. However, in some cases the identification of a taxon of the same level, that is, more closely related to the subject group than any other is difficult. This is the case in *Montanoa*; the genus is so isolated from the rest of the tribe that determination of its sister-group is not possible at this time (see GENERIC AFFINITIES). The next alternative is to move to the next higher taxon, in this case the subtribe, and use that as the outgroup. This is not possible in *Montanoa* because it is not certain to which subtribe *Montanoa* belongs. If one moves to the next higher taxon, the tribe, parallel and convergent evolution are extensive and most of the characters could not be polarized because both states would be present in both the groups.

An alternative to using the next higher taxon as the outgroup is to use "functional outgroups" rather than "taxonomic outgroups." This is a technique that has recently been formalized by Watrous and Wheeler (1981). It works in the following manner. If one can use some reliable criterion for dividing the genus into two or more infrageneric groups, then these can be used as the outgroups of one another. Figure 17 illustrates genus X that has been divided into three groups. Group B can now be used as the outgroup of A and vice versa. The plesiomorphic states of all the characters for these two infrageneric groups (A and B) then become the state of the outgroup to be used to polarize the characters of C.

The technique of "functional outgroup" can be applied effectively to *Montanoa*. The shape, consistency, venation, vestiture, and persistence of the mature and immature pales and the number of mature achenes per head yield 12 characters that can be polarized (the characters are listed in APPENDIX B; the states of the characters for each taxon are in APPENDIX C).

The pales of *Montanoa* are unique in the tribe Heliantheae. Although a few other genera have pales that wrap around the achenes (Fig. 1) none has the same shape or texture as those of *Montanoa*, and none is as long. The states of the first 12 characters, most of which deal with these unusual pales (APPENDIX B: I), were polarized by ontogeny, the later stages of development being considered apomorphic. The direction of evolution within each character was reinforced by using outgroup comparison with the entire tribe as the outgroup. For example, the states of character three, regarding the venation of the pales, were polarized in the following manner. Some species of *Montanoa* have parallel veins in the mature pales and others have netted. The immature pales of all species have parallel veins. As the pales near maturity some develop netted venation patterns. Ontogenetically the netted pattern is the apomorphic one. The same conclusion is reached using outgroup comparison with the whole tribe as the outgroup because netted venation is found only in *Montanoa* (pers. obser.).

Using the 12 characters listed in APPENDIX B: I, an initial subdivision of *Montanoa* into infrageneric groups is accomplished (Fig. 18). In the first major subdivision of the genus the two groups are here recognized as subgenera (*Montanoa* and *Acanthocarphae*). Subgenus *Montanoa* is further divided into two groups which are here recognized as sections (*Montanoa* and *Echinocephalae*).

Section *Montanoa* has only one wide-ranging, highly-variable species and it becomes the outgroup of section *Echinocephalae*. Characters that could not be polarized using the tribe as the outgroup, because both states were in the genus and the tribe, now can be polarized (characters 13-32; APPENDIX B: II and APPENDIX C). Using this method these character states were rather easy to polarize. The only problem (and this occurs several times in other infrageneric groups) was in determining whether all observed features represent distinct and separate characters. For instance, regarding the condition of the mature pales (characters 15 and 16), the mature pales of section *Montanoa* are stiff and moderately in-

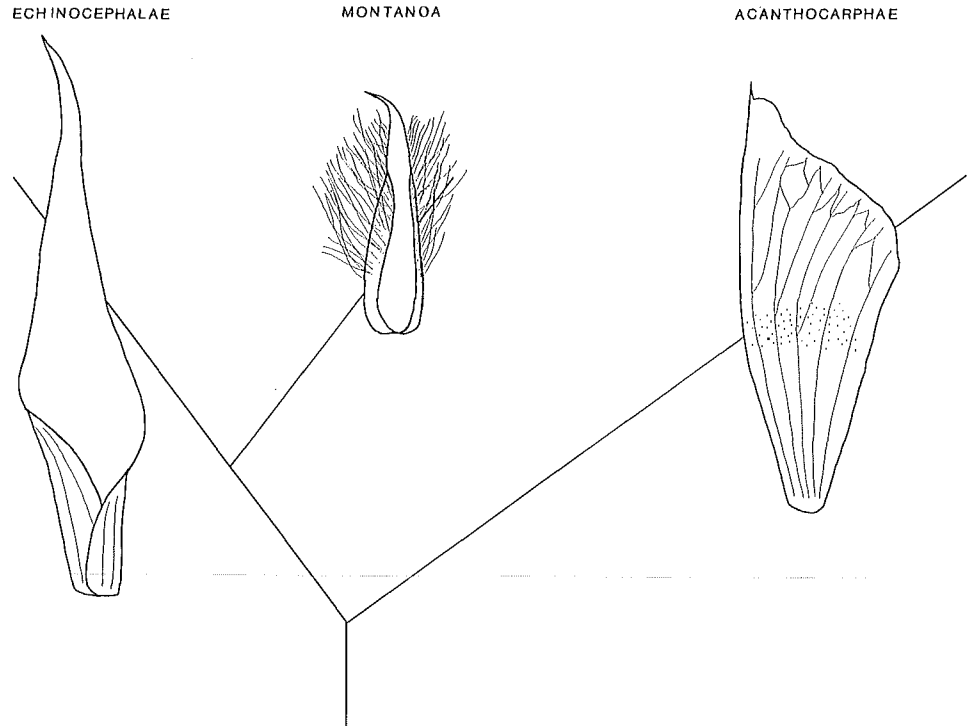


Fig. 18. Cladogram showing initial subdivision of *Montanoa*.

durate; those of section *Echinocephalae* are moderately indurate, very indurate and transparent but nevertheless somewhat indurate. The moderately indurate condition is the plesiomorphic condition, but should the other states be treated as one character or two? I have chosen to use two characters for three reasons: first, there is no reason to assume the two apomorphic conditions have any relation to one another; second, there is no evidence that they had the same plesiomorphic condition; and third, it gives a clearer picture of the data without affecting the outcome of the cladogram in any way. Using characters 1–32 on subgenus *Montanoa* results in the cladogram in Fig. 19.

In order to determine the polarity of the characters for the analysis of subgenus *Acanthocarphae*, the plesiomorphic states for the 32 characters in subgenus *Montanoa* were used as the condition of the outgroup. Characters 1–12 had already been used in the initial subdivision of the genus and characters 13, 14, 15, 16, 21, 22 and 32 were plesiomorphic in *Acanthocarphae*. Several additional characters were used in the analysis that either did not vary or could not be divided into discrete states in subgenus *Montanoa* (additional characters 33–47, APPENDIX B: III). All other characters have been used as they were in the analysis of *Echinocephalae*.

The two subgeneric cladograms of *Montanoa* can then be combined (Fig. 20) and the pattern of evolution within the genus illustrated. The diagram shows that certain lines within the subgenera reflect a great deal of parallel evolution (dots). For instance, an increase in head size has occurred more than once in the genus (characters 25 and 43). The distribution of this character indicates that it is a morphocline, and that 25 is probably an intermediate condition between the ple-

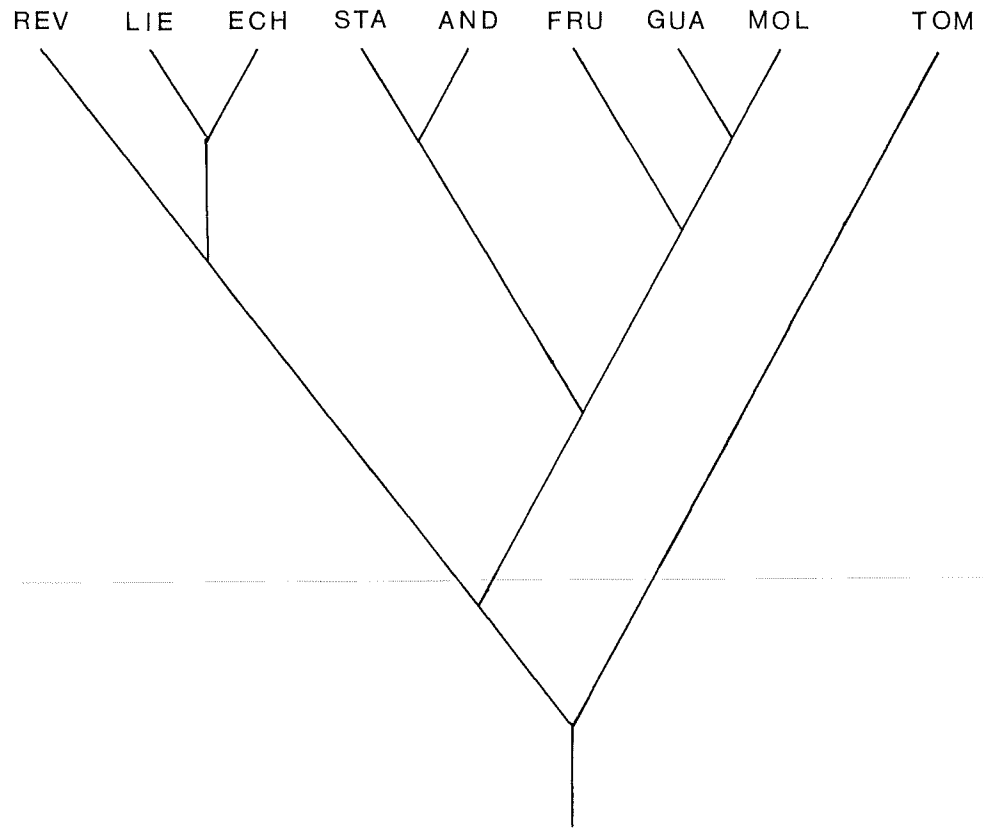


Fig. 19. Cladogram of subgenus *Montanoa*.

siomorphic condition of less than 40 disc florets and the other apomorphic condition (character 43).

The taxa from South America are defined almost entirely by parallel characters (Fig. 20) except for the autapomorphic characters (an autapomorphy is a character found only in one taxon). However, these characters give conflicting patterns and so the present explanation of parallelism is the most parsimonious one available.

Once the cladogram has been established, it is informative to examine some characters that were too variable to use in the construction of the cladogram (APPENDIX B: IV). For instance, petioles that are winged over half the length are found in all three infrageneric groups and could not be polarized using outgroup comparison. Figure 21 shows the placement of this character. It apparently has evolved independently within the genus at least five times and possibly six. In the case of the two species, *Montanoa speciosa* and *M. grandiflora*, this could be a common evolutionary event, in which case it would conflict with the number of disc florets (character 25), or it could be two independent evolutionary events. There is a third alternative. In the two unrelated species, *M. imbricata* has little leaf-like appendages along the petiole and *M. bipinnatifida* has two leaf-like appendages at the base of the petiole and is sometimes partially winged. It is possible that the plesiomorphic condition for these four taxa is a winged petiole, and the apomorphic character within this group of four species is the unwinged condition. Therefore, winged petioles have occurred five times in the genus. No other char-

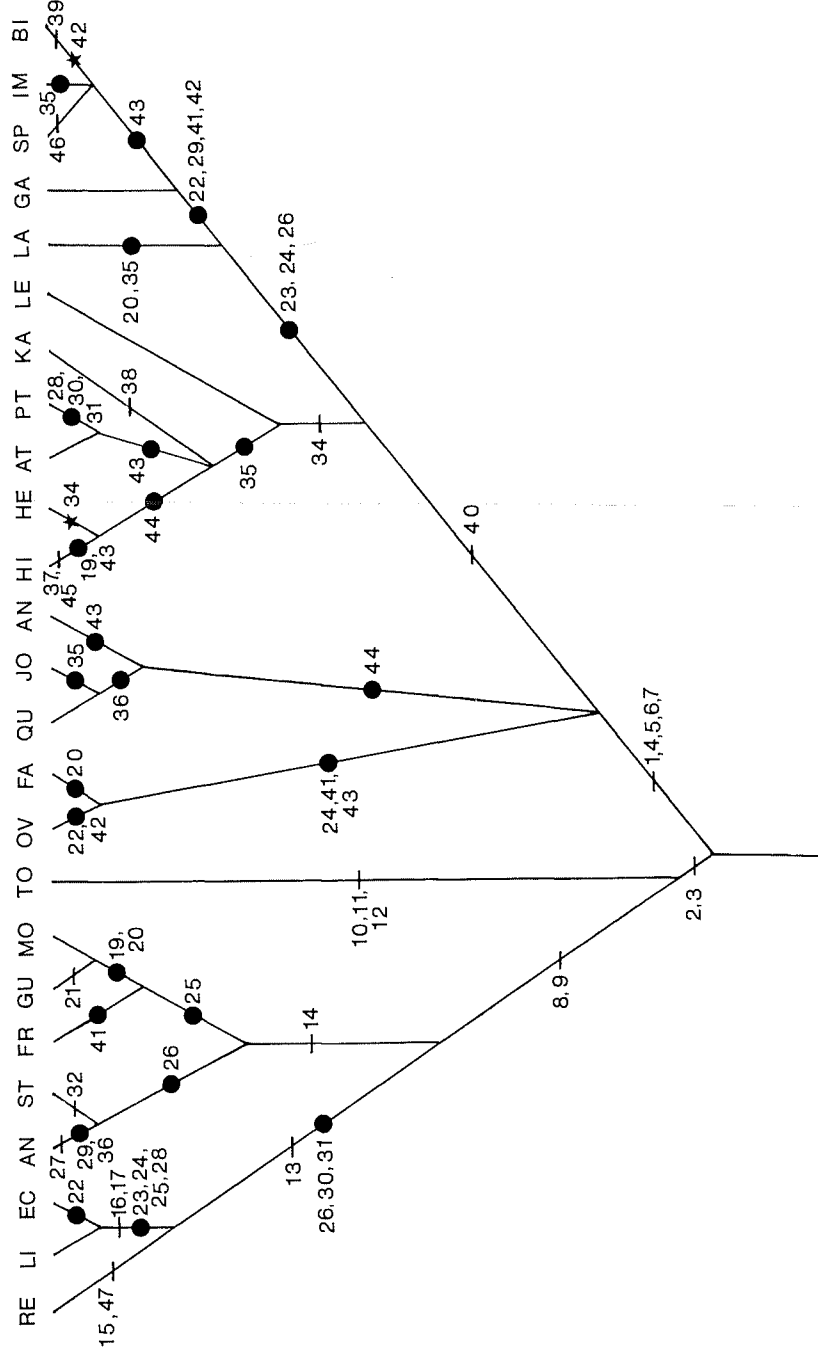


Fig. 20. Cladogram of *Montanoa* (lines indicate apomorphies, stars reversals and dots parallelisms).

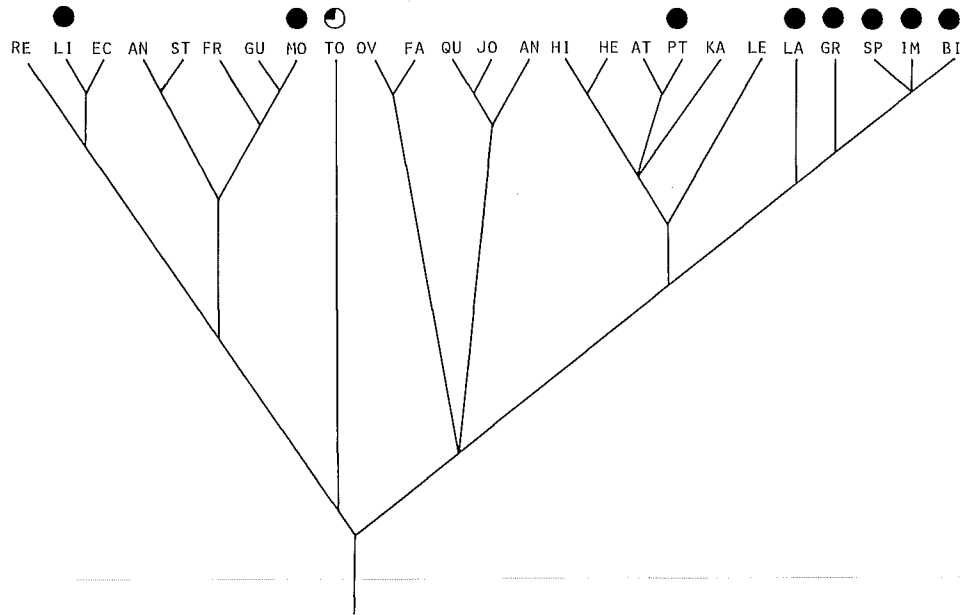


Fig. 21. Cladogram of *Montanoa* indicating the location of taxa with winged petioles.

acters will be examined here but one can look at all the characters that were not used in the analysis and in this manner use the cladogram as an aid in determining the plesiomorphic condition of many characters in the genus.

The habit of *Montanoa* species is varied even though they are all woody. Most species are shrubs, some are vine-like and others are trees. Fig. 22 shows the distribution of these characters. "Functional outgroup comparison" shows the shrub habit to be the plesiomorphic condition and the alternative habits are considered to be apomorphic and independent because there is no information to suggest that they are linked (characters 50 and 51). Apparently the tree habit has evolved four times and the vine habit three.

This type of repeated parallel evolution appears in approximately 80% of the non-autapomorphic characters examined in the genus and one cannot help but consider whether this is the best cladogram that can be constructed. I believe it is, because the characters that show parallel evolution on this cladogram do not give congruent patterns. For instance, very large numbers of disc florets are present in five parts of the tree; two times in the *Echinocephalae* (*Montanoa echinacea*, *M. frutescens*) and three times in the *Acanthocarphae* (*M. speciosa*–*M. imbricata*–*M. bipinnatifida*; *M. pteropoda*–*M. atriplicifolia*; and *M. ovalifolia*). Likewise a reduction has occurred twice, in *M. karwinskii* (*Acanthocarphae*) and *M. revealii* (*Echinocephalae*). Could this character be indicating that the evolution within the genus really traveled in these directions rather than in the ones indicated by the cladogram? Other characters that show parallel evolution do not have patterns that correspond to this one. For instance, there has been an increase in the disc floret size in both the *Acanthocarphae* and in the *Echinocephalae* as well as a decrease, but they are sometimes in different species and in some instances they give opposite patterns. For instance, *M. revealii* has large

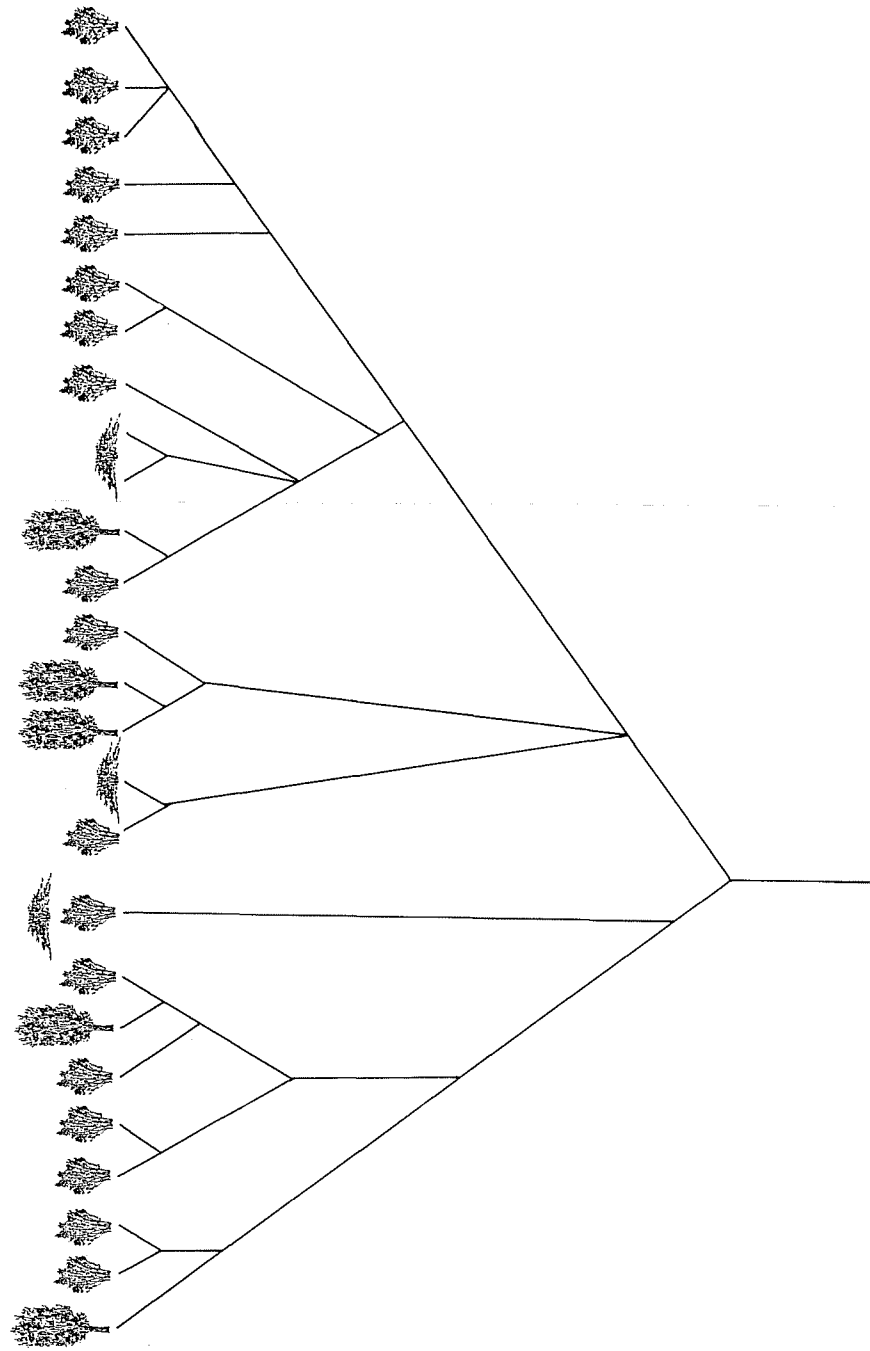


Fig. 22. Cladogram of *Montanoa* indicating the habit of each taxon (includes both subsp. of *M. leucantha*).



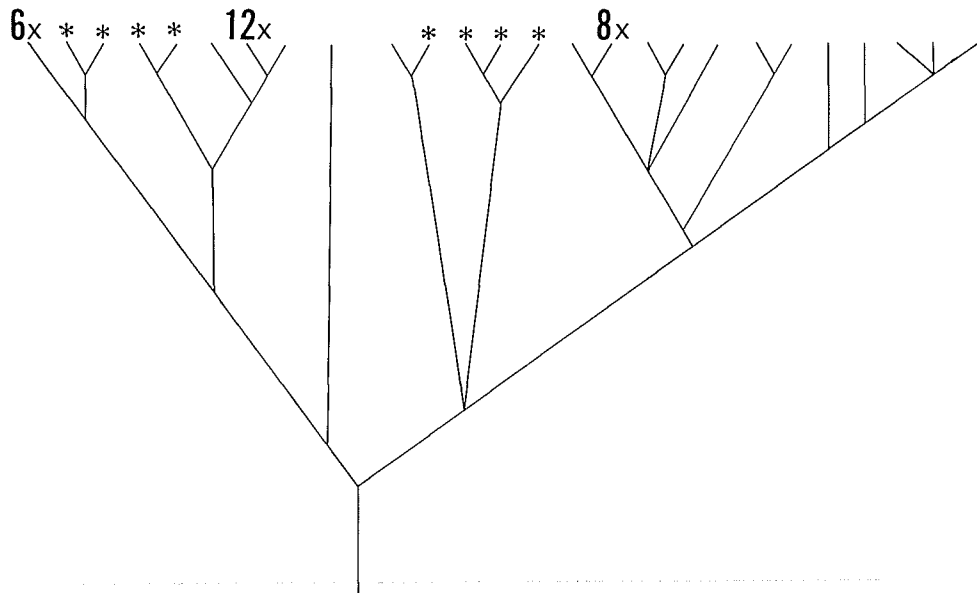


Fig. 23. Cladogram of *Montanoia* indicating the ploidy level of each taxon (unmarked taxa are known diploids; includes both subsp. of *M. leucantha*).

disc florets and *M. karwinskii* has small ones. *Montanoia grandiflora* has large disc florets but so does *M. laskowskii* which does not have a large number of disc florets. The lack of congruency in the characters showing parallel evolution supports the present cladogram (the characters showing parallel evolution can be referred to as false synapomorphies).

The results of the cytology can also be placed on the cladogram to determine their relationship with the morphological data (Fig. 23). *Montanoia hexagona* (8x) and *M. guatemalensis* (12x) each have closest relatives that are diploids, whereas no chromosome counts have been made of *M. liebmännii* or *M. echinacea*, the closest relatives of *M. revealii* (6x). All of the known polyploids are trees of cloud forests or subcloud forests. In South America there are two trees, *Montanoia quadrangularis* and *M. josei*, of which little or no information is available concerning the chromosome numbers. There have been no counts of *M. josei* and only one of *M. quadrangularis*,  $n = 19 \pm 1$  (Powell and Cuatrecasas, 1970). It is possible that at least some of the members of this species are diploids, but since the specimen counted was a 10 m tree it seems likely that all members are at the diploid level. One cannot make judgments on the ploidy level because there has only been one count, and because the ploidy level of the sister taxon, *M. josei*, is not known.

The South American taxa are the least well understood in the genus. In this study only two of the five species were observed in their natural habitat. These five taxa are similar to one another in a number of characters, but none of these character states are known synapomorphies. For instance, they all have mature pales that are 7–11 mm long, disc corollas that are less than 5 mm long, blades that tend to be ovate to rhomboid or 3-lobed and small numbers of phyllaries. These are, however, plesiomorphic states and do not help define the group as monophyletic. As it stands now, the cladogram indicates that the five species

from South America could have had one or two introductions by an ancestral taxon.

The dispersal mechanism of the three infrageneric groups corresponds well with the cladogram. The heads of section *Montanoa* are deciduous, and they usually have only one mature achene per fruiting head (Fig. 24). This head is easily blown around on the dry hard-packed soil of the xeric or semi-xeric areas where they often grow. Section *Echinocephalae* has indurate, essentially glabrous mature pales (Fig. 32) that are non-deciduous and that form smooth "chutes" for the mature achenes; when the mature head overturns it sends out a shower of achenes. The final group (subgenus *Acanthocarphae*) has mature pales that are papery, conduplicate, glabrous, and deciduous with the achenes (Fig. 44). The pales act as samaras in the wind and they float in water. This correlation of the branching pattern of the cladogram and the dispersal mechanisms indicates the usefulness of cladistics in defining and discussing features of the genus.

This discussion clearly indicates that cladistics is useful not just in attempting to understand the evolutionary relationships within *Montanoa* but also in a better understanding of confusing characters (e.g., head size, habit). It is also more informative in understanding the evolution of the polyploids of the genus and the dispersal mechanisms. Cladistics is, therefore, a method that can add much understanding to a carefully studied group of organisms.

One more task remains and that is the development of a predictive and informative classification. In order to make the most informative classification possible, the hierarchy of *Montanoa* was based on the cladogram. This is in accordance with the goals of Mayr (1969), who said that the best classifications combine the greatest amount of information content with the greatest ease of information retrieval. Basing a classification on a cladogram has two aspects (Nelson, 1973): 1) subordination (concerns how a group may be divided into subgroups of lesser but equivalent rank); and 2) sequencing (how subgroups of equivalent rank may be listed in a specific order). These subordinal groups must be monophyletic (Cracraft, 1974). The sequencing is based on the property that the taxon in question is the sister group of all those taxa listed below it at the same level of indentation. The entire cladogram can be reconstructed from the final listing of the taxa. It is, therefore, the most informative, and since the classification is a natural one it is also the most predictive method. For a more detailed explanation see Nelson (1972, 1973), Cracraft (1974) and Wiley (1979). The following list orders the taxa of *Montanoa* phylogenetically, and the levels at which the groups are recognized in this treatment are in parentheses next to the subordinal group. All listings of the species in *Montanoa* in this treatment follow this order (asterisks represent unresolved trichotomies).

## MONTANOA

Montanoa supergroup (subgenus *Montanoa*)

Montanoa group (section *Montanoa*)

1. *M. tomentosa*

Frutescens supergroup (section *Echinocephalae*)

Frutescens group (series *Frutescentes*)

Mollissima group

2. *M. frutescens*

3. *M. guatemalensis*

4. *M. mollissima*

- Andersonii group
  - 5. *M. andersonii*
  - 6. *M. standleyi*
- Liebmannii group (series *Amoenae*)
  - 7. *M. liebmannii*
  - 8. *M. echinacea*
- Revealii group (series *Apertae*)
  - 9. *M. revealii*
- Ovalifolia supergroup (subgenus *Acanthocarphae*)
  - \*Ovalifolia group (series *Ovalifoliae*)
    - 10. *M. ovalifolia*
    - 11. *M. fragrans*
  - \*Quadrangularis group (series *Quadrangulares*)
    - 12. *M. angulata*
    - 13. *M. quadrangularis*
    - 14. *M. josei*
  - \*Arborescens supergroup
    - Arborescens group (series *Hibiscifoliae*)
      - Arborescens subgroup
        - 15. *M. leucantha*
      - \*Karwinskii group
        - 16. *M. karwinskii*
      - \*Pauciflora group
        - 17. *M. atriplicifolia*
        - 18. *M. pteropoda*
      - \*Hibiscifolia group
        - 19. *M. hibiscifolia*
        - 20. *M. hexagona*
  - Laskowskii supergroup
    - Laskowskii group (series *Intermediaeae*)
      - 21. *M. laskowskii*
    - Grandiflora group (series *Grandiflorae*)
      - 22. *M. grandiflora*
      - 23. *M. speciosa*
      - 24. *M. imbricata*
      - 25. *M. bipinnatifida*

## TAXONOMIC TREATMENT

**Montanoa** Cervantes in La Llave & Lexarza, Nov. Veg. Desc. 2: 11. 1825. Type species: *Montanoa tomentosa* Cerv. in Llave & Lex.

*Eriocoma* H.B.K., Nov. Gen. & Spec. 4: 210. t. 396. 1820, nom. illegit., non *Eriocoma* Nutt., Gen. Amer. Pl. 1: 40. 1818. Type species: *Eriocoma floribunda* H.B.K.

*Eriocarpha* Cass., Dict. Sci. Nat. 59: 236. 1829, nom. superfl. Based on type of *Eriocoma* H.B.K.

*Montagnaea* DC., Prodr. 5: 564. 1836, orthogr. variant of *Montanoa* Cerv. in Llave & Lex.

*Priestleya* Sessé & Mociño ex DC., Prodr. 5: 564. 1836, nom. nud. pro syn.

*Uhdea* Kunth, Ind. Sem. Hort. Berol. 13. 1847. Type species: *Uhdea bipinnatifida* Kunth.

Small shrubs or vines to large trees. *Stems* terete to tetragonal, herbaceous parts green to purple or brown, glabrous, puberulent, or densely pubescent and glandular, woody parts brown to gray, with sticky resinous sap, usually glabrous. *Leaves* opposite, petiolate, with or without wings and/or auricles; blades highly variable, ranging from ovate to pentagonal, with 3 main veins, apex acute to long-

acuminate, margin entire to irregularly dentate, unlobed to deeply 3-5-lobed, adaxial surface sparsely to densely pubescent, hairs white or clear, multicellular, uniseriate, multicellular-based, abaxial surface glabrous to densely glandular and pubescent. *Peduncles* glabrous to densely glandular and pubescent. *Heads* erect or pendulous, solitary or in leafy-bracteate compound corymbiform or paniculiform cymes. Receptacle slightly to strongly convex. *Phyllaries* 3-16(-22), uni- to triseriate, equal or subequal, round to lanceolate with 3 anastomosing veins, green to dark green, apex acuminate to rounded, margin entire, herbaceous, ciliate or glabrous, abaxial surface glabrous to densely glandular and pubescent. *Ray florets* neutral, 0-15; corollas white or cream; ligules obovate to oblanceolate, 3.0-35.0 mm long, apex acute or blunt to 1-2 notched, adaxial surface usually glabrous or sparsely pubescent on veins, abaxial surface usually moderately glandular, sometimes pubescent on veins; tube cylindrical, glabrous to moderately pubescent. *Disc florets* 3-160; corollas 5-lobed, yellow to gray-green or black, glabrous to densely glandular and pubescent, apex acute to acuminate, throat and tube cylindrical; stamens yellow to brown or black, apex acute to acuminate, usually with abaxial surface glandular; styles yellow or yellow and black, apex acute to acuminate, usually glabrous, base enlarged, two stigmatic lines. *Pales* at anthesis wrapping around ovary, obtrullate to triangular or pentagonal, usually light yellow, sometimes with dark areas on veins and midrib, apex long-acuminate, often indurate, margin usually ciliate, entire, abaxial surface glabrous to densely glandular and pubescent, adaxial surface usually glabrous; pales at fruiting wrapping around achene and surpassing it in length, persistent or deciduous, mostly obtrullate to obdeltoid or triangular, greatly elongated, indurate to papery, venation parallel or netted, stramineous to purple, apex acute, truncate or cordate with short or long apiculate or tapering tip, at times recurved, margin glabrous to ciliate, entire, abaxial surface glabrous to densely glandular and pubescent, adaxial surface glabrous to sparsely pubescent. *Achenes* brown-black, quadrangular, narrowly obpyramidal, usually smooth but occasionally sculptured, epappose, hard, apex with a ring-shaped collar, probably a nectary. Chromosome numbers,  $n = 19$ , ca. 57, ca. 76, ca. 114 ( $x = 19$ ).

**FLOWERING (AND FRUITING) PERIOD:** Usually flowering in the fall or winter, with the species in the northern part of the range or in drier habitats flowering in September and those of the cloud forests flowering as late as January or February (fruits maturing at least one month after anthesis); one species, *Montanoa ovalifolia*, appears to flower throughout the year.

**DISTRIBUTION AND HABITAT:** Sonora, Mexico to Peru, largest number of species in southern Mexico and Guatemala; usually locally abundant; dry roadsides to cloud forests, usually in pine-oak forests; 100-3300 m, most between 1000 and 2000 m.

#### Key to the Species of *Montanoa*

1. Mature pales indurate, parallel-veined, broadest at base, apex sometimes recurved or reflexed (Figs. 311, J; 41D), persistent on receptacle; pales at anthesis with apex as long as or longer than base (Fig. 31G; 41D), usually visible prior to anthesis; Mexico and Central America. [subgenus *Montanoa*.]
2. Pales densely glandular, long-pilose, prior to anthesis not longer than florets; disc florets usually 8-9 (occasionally 3-17); ligules usually (0-)3-5(-6), 3-9 mm long. [section *Montanoa*.]
  1. *M. tomentosa*.
2. Pales glabrous to sparsely glandular and/or short pilose, prior to anthesis longer than florets; head appearing spiny; disc florets mostly 30-150 (11-20 in *M. revealii*); ligules usually 8 or more (3-5 in *M. revealii*), 9.0-35.0 mm long. [section *Echinocephalae*.]

3. Mature pales 14–22 mm long, spreading upper section much exceeding folded basal portion (usually around  $\frac{1}{4}$  folded; Fig. 41D); anthers and styles with at least apices black.
4. Disc florets 11–20; ray florets 3–5; disc florets as well as mature pales spreading outward, giving the head a stellate appearance. 9. *M. revealii*.
4. Disc florets 60–150; ray florets 10–15; disc florets as well as mature pales erect, not spreading.
5. Petiole conspicuously winged, sparsely puberulent; leaf blades often deeply lobed; mature pales 10–16 mm long. 7. *M. liebmannii*.
5. Petioles wingless, long-pilose or hispid; leaf blades cordate or ovate-triangular, unlobed; mature pales 15–22 long. 8. *M. echinacea*.
3. Mature pales 9–15 mm long with the spreading upper portion shorter than or as long as the folded basal portion (usually over  $\frac{1}{2}$  folded; Fig. 33J, K); anthers and styles with yellow apices.
6. Disc florets 25–50, corollas 4.0–5.0 mm long.
7. Anthers fully exerted from the corolla at anthesis; disc corolla, anther and stigma apices yellow but often tinged with purple; style and anthers more than 9 mm long. 5. *M. andersonii*.
7. Anthers not fully exerted from the corolla at anthesis; disc corolla, anther and stigma apices completely yellow; style and anthers less than 7 mm long. 6. *M. standleyi*.
6. Disc florets 70–150, corollas 6.0–7.0 mm long.
8. Stems purple, glabrous; mature pales 10–15 mm long; receptacle strongly convex, 3–4 mm tall, 1.5–2 mm wide; disc florets green or cream, more than 100; abaxial surface of leaves green. 2. *M. frutescens*.
8. Stems green, pubescent; mature pales 9–11 mm long; receptacle about as tall as wide; disc florets yellow, fewer than 100; abaxial surface of leaves white-pubescent.
9. Tree; petioles wingless and without auricles; apex of phyllaries rounded. 3. *M. guatemalensis*.
9. Shrub; petioles completely winged and auriculate; apex of phyllaries acute or acuminate. 4. *M. mollissima*.
1. Mature pales papery, net-veined, broadest near apex, deciduous with achenes, apex straight, never reflexed or recurved, curled in one taxon (*M. leucantha* subsp. *arborescens*; Fig. 53E); pales at anthesis with apex shorter than base, rarely visible prior to anthesis (Fig. 73F; except in some South American taxa); Mexico, Central and South America. [subgenus *Acanthocarphae*.]
10. Disc corollas 6.5–9.5 mm long, plants of Mexico and Central America.
11. Anther thecae black; disc corolla glandular and pubescent throughout; mature pales 8–12 mm long, with distinct apical sinus. 21. *M. laskowskii*.
11. Anther thecae yellow or brown; corolla glabrous or pubescent only at apex; mature pales over 15 mm long, without distinct apical sinus.
12. Petioles broadly winged to base.
13. Cymes in open usually leafless panicles, lateral branches mostly 1-headed, longer than subtending leaves; disc florets 140–160; achene pubescent at apex; phyllaries 9–16(–22). 23. *M. speciosa*.
13. Cymes clustered at tips of leafy branches, lateral branches mostly several-headed, shorter than subtending leaves; disc florets 65–95; achenes glabrous; phyllaries 7–10. 22. *M. grandiflora*.
12. Petioles with auricles but otherwise mostly without wings.
14. Phyllaries 10–12 mm long, longer than disc floret buds and overlapping (Fig. 73A); leaves medium green, shallowly lobed with small leaf-like appendages on petiole; corollas in bud moderately pubescent at apex with soft hairs; upper parts of stems terete; mature pales 15 mm long, base completely surrounding the achene. 24. *M. imbricata*.
14. Phyllaries 6.0–8.5 mm long, shorter than disc floret buds; leaves dark green, usually deeply pinnately or bipinnately lobed, bearing two auricles at base, petiole wingless; corollas in bud densely pubescent at apex with stiff interlocking hairs; upper parts of stems quadrangular; mature pales 16–22 mm long, base with achene partially exposed. 25. *M. bipinnatifida*.
10. Disc corollas 2.0–4.75 mm long; plants of Mexico, Central and South America.
15. Heads erect throughout development; mature pales straw-colored, never purple; plants of South America.

16. Ray florets 12-15; disc florets 40-75; style apex yellow.
17. Apex of pales truncate with 2 mm long, narrow, apiculate tip; scandent shrub; cymes in oppositely branched panicles on long slender branches; achenes 3.5 mm long. 11. *M. fragrans*.
17. Apex of pales gently tapering to a short, broad tip; erect shrubs; cymes in irregularly branched compound dichasia on short thick branches; achenes 2.5-3.0 mm long. 10. *M. ovalifolia*.
16. Ray florets 6-8; disc florets 90-135; style apex with black spots.
18. Pales with deep apical sinus (2 mm deep at maturity), margins irregular; achenes 3.5 mm long; upper stems purple, synflorescence a group of irregular cymes with heads tightly clustered on short peduncles; tree. 14. *M. josei*.
18. Pales without apical sinus, margins entire; achenes 1.0-2.5 mm long; upper stems green; synflorescence with cymes at ends of long slender branches of oppositely branched panicles; tree or shrub.
19. Shrub; leaves (including petiole) 7-16 cm long, blades ovate-lanceolate to rhombic, unlobed; ligules 6-10 mm long. 12. *M. angulata*.
19. Tree; leaves (including petiole) 20-90 cm long; blades ovate, often shallowly to deeply lobed; ligules 12.5-13.0 mm long. 13. *M. quadrangularis*.
15. Heads pendulous at late anthesis and in fruit; mature pales straw-colored or purple; plants of Mexico and Central America.
20. Disc florets 85-120, corollas 2-3 mm long; plants of Central America.
21. Leaf-margins usually deeply and irregularly 3-5-lobed, irregularly dentate, abaxial surface densely white-pubescent, petiole with two distal auricles; achenes sculptured, 3 mm long; erect shrubs. 19. *M. hibiscifolia*.
21. Leaf-margins unlobed to shallowly and regularly 3-lobed, entire to serrate, abaxial surface green, petiole with or without auricles, with or without broad wings; achenes smooth, 2.0-2.5 mm long; shrubs or vines.
22. Petioles sometimes auriculate but otherwise unwinged; apices of disc florets, styles and anthers yellow; ligules of ray florets 12-24 mm long; disc corollas 2 mm long. 17. *M. atriplicifolia*.
22. Petioles both auriculate and winged to base; apices of disc florets, styles and anthers with black areas; ray florets 10-12 mm long; disc corollas 2.5-3.0 mm long. 18. *M. pteropoda*.
20. Disc florets 23-60, corollas 3.5-4.75 mm long; plants of Mexico and Guatemala.
23. Three main veins of leaf branching at base of laminar portion of blade, petiole unwinged and without auricles; mature pales 7.5-10.0 mm long with deep sinus (2 mm deep at spine); disc florets 20-35. 16. *M. karwinskii*.
23. Three main veins of leaf branching above base of laminar portion of blade, petiole at least partially winged, usually auriculate; mature pales usually over 10 mm long (8-17), apex usually tapering, without sinus or with sinus less than 1 mm deep; disc florets 30-60.
24. Tree; mature pales with apex truncate or sloping, sinus present; achenes 3-4 mm long, sculptured; apex of style black; disc corollas green turning yellow. 20. *M. hexagona*.
24. Shrub; mature pales with apex tapering, sinus absent; achenes 2-3 mm long, surface smooth; apex of style yellow; disc corollas yellow. 15. *M. leucantha*.

### I. *Montanoa* subgenus *Montanoa*

Subgenus *Eriocarpha* DC., Prodr. 5: 564. 1836. Lectotype chosen: *Montanoa tomentosa* Cerv. in Llave & Lex.

Subgenus *Eriocarpha* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 509. 1899, orthogr. variant of subgen. *Eriocarpha* DC.

Shrubs or trees; ray florets 0-15, white or cream, disc florets 3-160, yellow or dark; pales at anthesis 2-8 mm long, apex equal to or longer than the body, visible at anthesis, pales at fruiting persistent, more or less triangular or pentagonal, base broad, 4.5-22.0 mm long, indurate, parallel veined, apex elongate, often recurved, base strongly incurved, encircling achene. Type species: *Montanoa tomentosa* Cerv. in Llave & Lex.

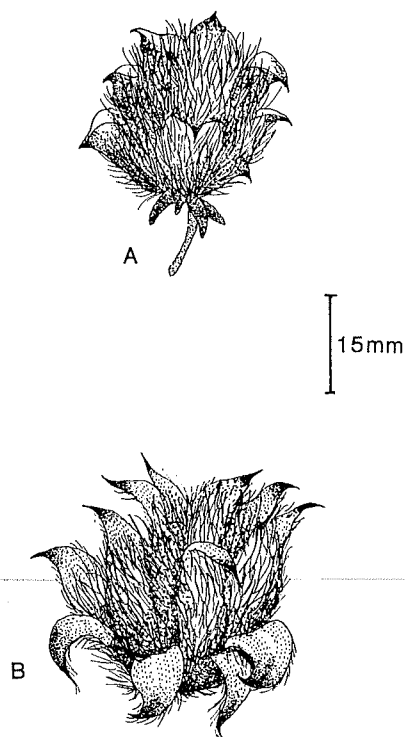


Fig. 24. Mature fruiting heads of section *Montanoa*. A, *M. tomentosa* subsp. *tomentosa* (Ramos s.n., OS); B, *M. tomentosa* subsp. *tomentosa* (Arsène 268a, US).

#### IA. *Montanoa* subgenus *Montanoa* section *Montanoa*

Much branched shrubs to 3 meters (rarely small trees); ray florets 0–6 (usually 5), white or cream; disc florets 3–17 (usually 8–9), yellow; pales at anthesis 2–4 mm long; pales at fruiting more or less pentagonal with broad base, 4.5–10.0 mm long, veins inconspicuous, abaxial surface densely glandular and pubescent; achenes 2.5–3.5 mm long; heads deciduous. Type species: *Montanoa tomentosa* Cerv. in Llave & Lex. Species 1.

The taxa of this section have a number of features in common. The fruiting head is distinct in having relatively small indurate, densely pubescent, glandular pales with stiff recurved tips (Fig. 24). There is usually only one mature achene per head, although there are up to 17 disc florets. The entire head is deciduous at maturity and is dispersed easily by wind across the hard-packed ground in the dry areas they inhabit. Figure 24 illustrates two heads. They share the following features: xeric or semi-xeric habitat as well as similar involucre, ray and disc florets, and pubescence type. Eighteen species have previously been described in this section and with all of the similarities among the species, the number of characters available to delimit these species is limited.

Of the 18 species described in this section only 13 have been recognized by the last worker (Blake, 1926a). He listed 11 species from Mexico, had previously described one from Guatemala (Blake, 1924a), and later described one more from Mexico (Blake, 1950). In Blake's key as well as his descriptions he relied heavily on characters such as leaf shape and margin. The same is true of the earlier work

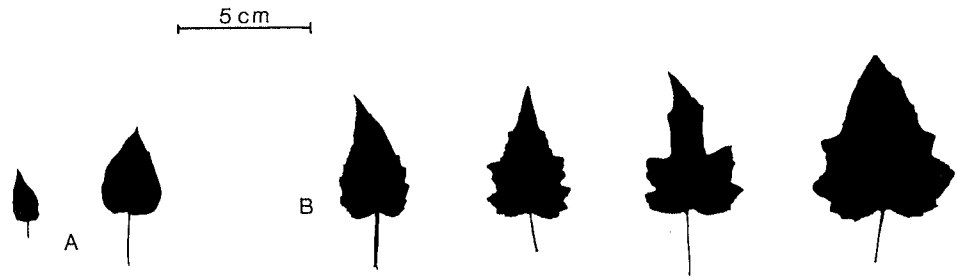


Fig. 25. Greenhouse leaf variation in *Montanoa tomentosa* subsp. *tomentosa* (FRa 2382, OS): A, leaves from the "dry" greenhouse; B, leaves from the "wet" greenhouse.

by Robinson and Greenman (1899) in which they recognized nine species. When trying to use the keys and descriptions there proved to be so many intermediates that identification was rarely certain.

An examination of flowering and fruiting characters among the 13 previously recognized species resulted in the conclusion that they were essentially identical with the maximum amount of variation occurring in individuals or within the same population. All the collections of this section were then placed together and the leaf morphology was examined to ascertain its usefulness for taxon delimitation. The 13 species were broken down into four groups. The first group consists of three previously recognized species from central Mexico. The leaf morphology was examined on the populational (intra- and inter-) and individual levels. The range of leaf morphology found is illustrated in Figs. 9 and 10 (in the LEAF MORPHOLOGY section). All the variability found in these species can be seen in the populational sample from the Distrito Federal, Mexico (Fig. 9D). The leaves have several features in common: blades longer than broad, more or less deltoid, with cordate or truncate bases and irregular dentate margins that are rarely deeply lobed. They exhibited a great deal of variation in the greenhouse experiments (Fig. 25). All of the variation found throughout the range of this group can be found on the individual and populational levels (see Figs. 10-12).

The second group includes seven species and ranges from Jalisco, Mexico to Costa Rica. The leaves of these species show a different type of variation from that found in Group I but for the same reasons. The interpopulational variation as well as the distribution is illustrated in Fig. 26 (the leaves were selected to maximize the amount of variation). There is a tendency for individuals in Central America to have 3-lobed leaves and for those in Mexico to have 5-lobed ones. Also, some individuals in San Luis Potosí have acute leaf bases whereas those in the rest of the range have partially winged petioles. The variation at the individual level is illustrated in Fig. 27A-C with three individuals from the extremes of the range. Note the individual from San Luis Potosí has both acute and partially winged bases. In addition, leaves in both the western and southern collections have both 3- and 5-lobed leaves (Fig. 27A, C). In the intrapopulational sample (Fig. 27D) the large irregularly margined leaves were collected from sucker shoots. In the greenhouse experiments the leaves from the "dry" greenhouse (Fig. 28A) were much smaller but retained the same lobed margin as those from the "wet" greenhouse (Fig. 28B). All the individuals of this group have leaves that are usually as wide as they are long, are more or less pentagonal, with partially winged petioles or with acute bases, and their margins are entire with 3-5 lobes.



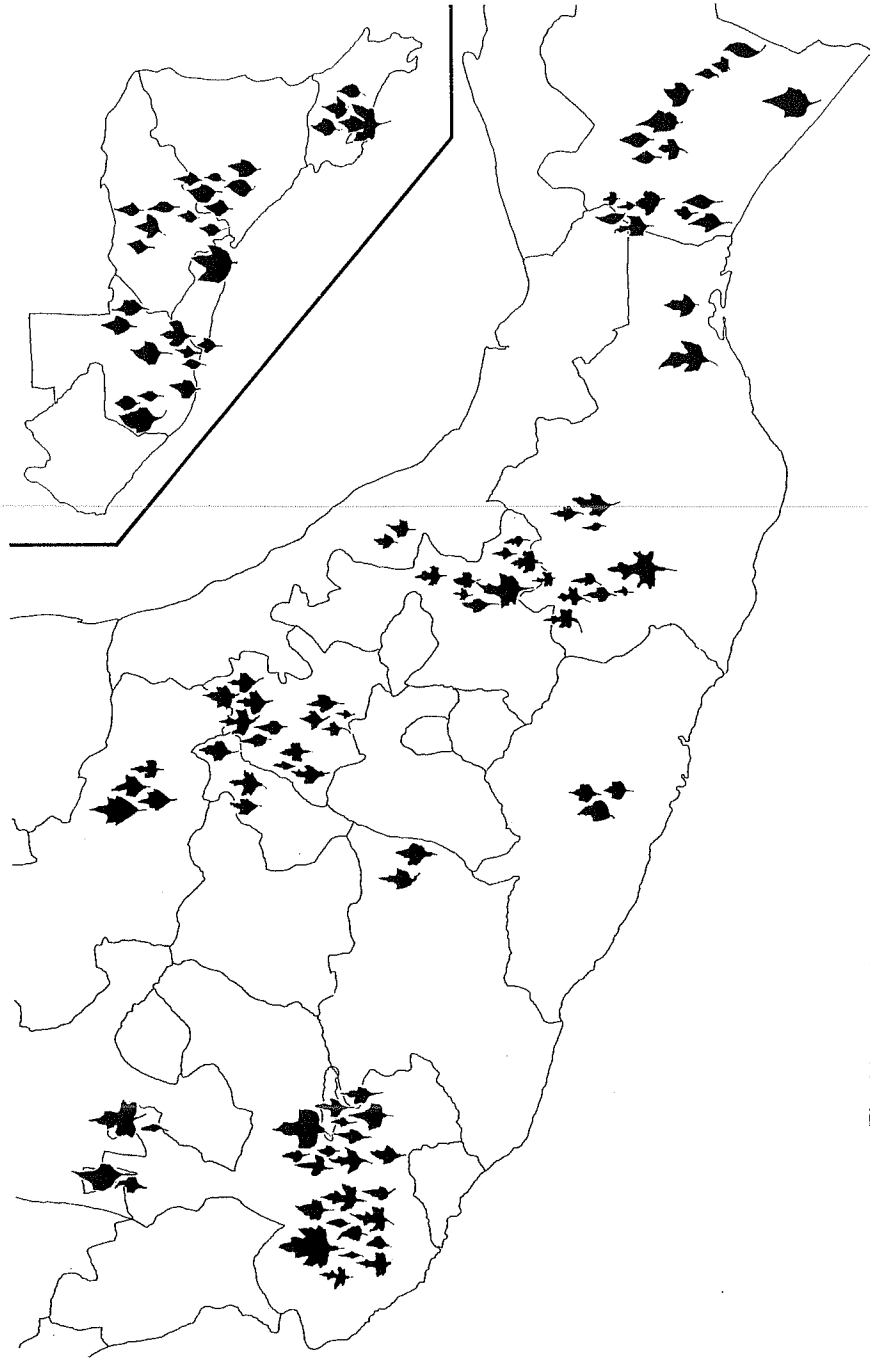


Fig. 26. Map of Mexico and Central America showing the distribution and interpopulational leaf variation of *Montanoa tomentosa* subsp. *xanthiifolia*.

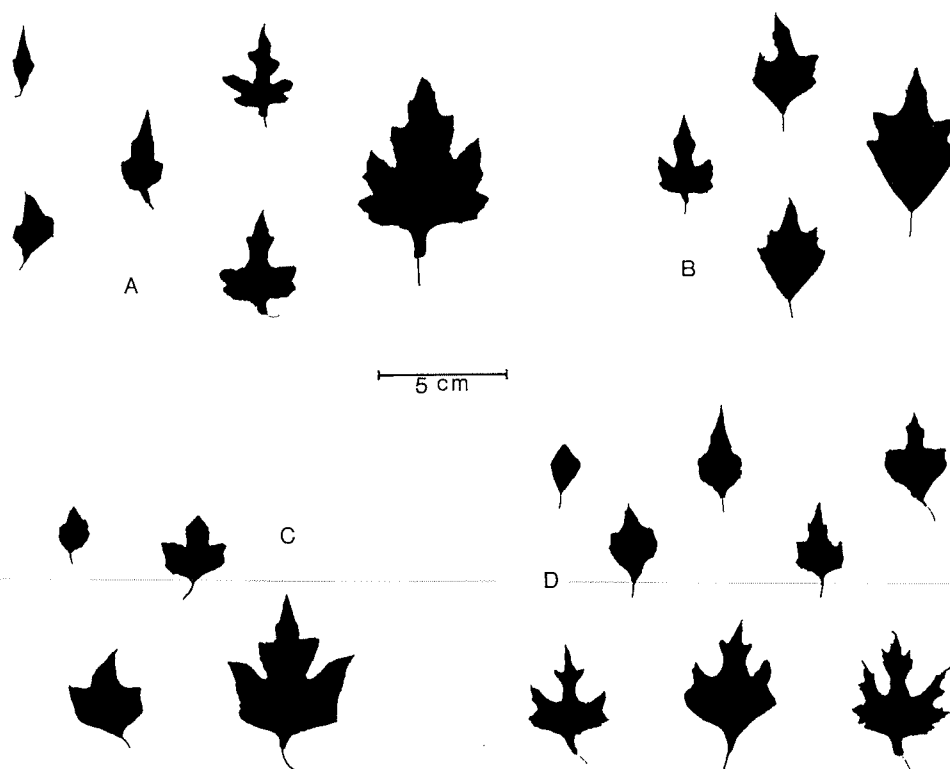


Fig. 27. Intrapopulational and individual leaf variation in *Montanoa tomentosa* subsp. *xanthiifolia*: A–C, Individual variation (Jalisco, *AL* 3872; San Luis Potosí, *FH* 2207; Costa Rica, *FGo* 3065); D, intrapopulational variation (Jalisco, Lake Chapapa).

Although the distributions of Groups 1 and 2 appear to overlap, they are separated by altitude with Group 1 growing at 1900–2800 m (usually 1900–2100), and Group 2 at 230–1800 m (usually 1000–1500). Only in two areas (Jacala, Hidalgo and Tehuacán, Puebla) are they actually found in the same area. In each of these areas there are some very unusual leaf types (e.g., *Fra* 2368, *HF* 4138, *HF* 4139, *AL* 4021) which do not fit into either category very well, indicating possible hybridization.

The third group contains only one species from Oaxaca. It is characterized by a winged petiole although there is a great deal of variation in size, shape and lobing. The variability and its causes are discussed, and distribution and leaf morphology maps are found in the LEAF MORPHOLOGY section (Figs. 13, 14).

The final group of species (Group 4) is found in northwest Mexico. Two species have been described from this area, based more on leaf size than shape. There is a large population near Alamos, Sonora (Fig. 29) that shows the full range of size for the group. The smaller-leaved individuals are not unique in the group.

It seems then that there are four, not 13, types of leaves in section *Montanoa*: 1) those of central Mexico that have cordate-truncate bases, are longer than broad, tend to have irregular margins and are deltoid and unlobed; 2) those of southern Mexico and Central America that have acute to partially winged bases, are as broad as long, tend to have regular margins and are usually pentagonal and

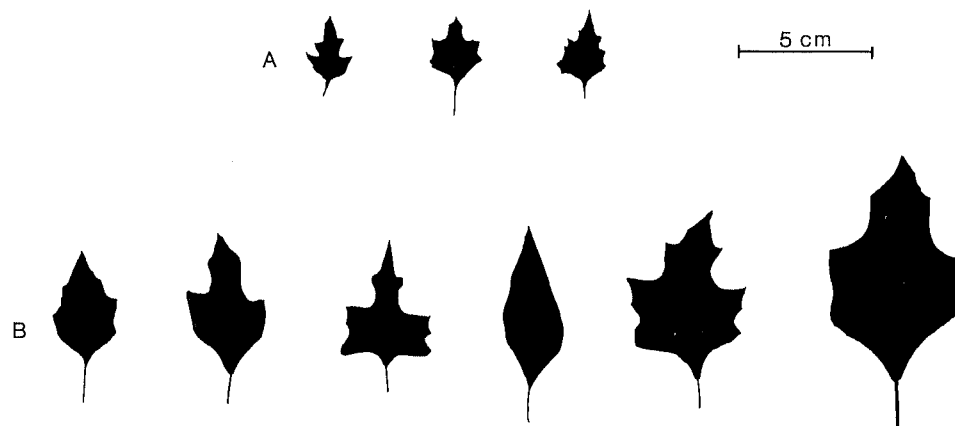


Fig. 28. Greenhouse leaf variation in *Montanoa tomentosa* subsp. *xanthiifolia* (FRa 2637): A, leaves from the "dry" greenhouse; B, leaves from the "wet" greenhouse.

3–5-lobed; 3) those of Oaxaca that have winged petioles; and 4) those of northwest Mexico that are ovate, serrate to dentate and unlobed.

Head size has been used by Robinson and Greenman (1899) and Blake (1926a) to distinguish three previously described species: *Montanoa gentryi*, *M. hemisleyana*, and *M. rekoii*. All are known only from the type collection and have only three disc florets and one or no rays. Since these plants were identical in all other respects to the members of the groups to which they have been assigned it appears that the reduction in head sizes occurs sporadically in the section. Table II gives the number of disc florets and the number of rays for the previously recognized species as well as the total and range for all collections of section *Montanoa*. The first three groups overlap completely and the fourth one to a great extent.

In order to insure that all possible characters had been examined, 58 flowering and fruiting characters were measured for 44 individuals from this section. As many type specimens as possible were used in this survey and when they could not be used (missing information), specimens that matched as closely as possible in both leaf morphology and locality were substituted. Once the data were compiled (APPENDIX D, list of characters; APPENDIX E, data matrix), the values were standardized and a PCA analysis was undertaken. The results were plotted in both two and three dimensions (Fig. 30 shows the results of the two-dimensional plot) and showed no strong groupings.

Because of the many unifying characters within this subgenus, including habit, pubescence, floret shape, flowering and fruiting receptacular bract shape and many others and because it is not felt that leaf morphology alone is sufficient to base species recognition upon in *Montanoa*, it has been decided to recognize only one species, *Montanoa tomentosa*, with four subspecies based on the patterns found in the leaf morphology.

#### 1. *Montanoa tomentosa* Cervantes in La Llave & Lexarza

Much branched shrubs 1–3 m tall. *Stems* terete, brown, herbaceous parts moderately to densely pubescent, hairs 2 mm long. *Leaves* highly variable; petioles 1.5–4.0 cm long, with or without auricles and wings, moderately to densely glandular and pubescent, hairs 2 mm long; blades often deltoid or ovate (Figs. 10, 11,

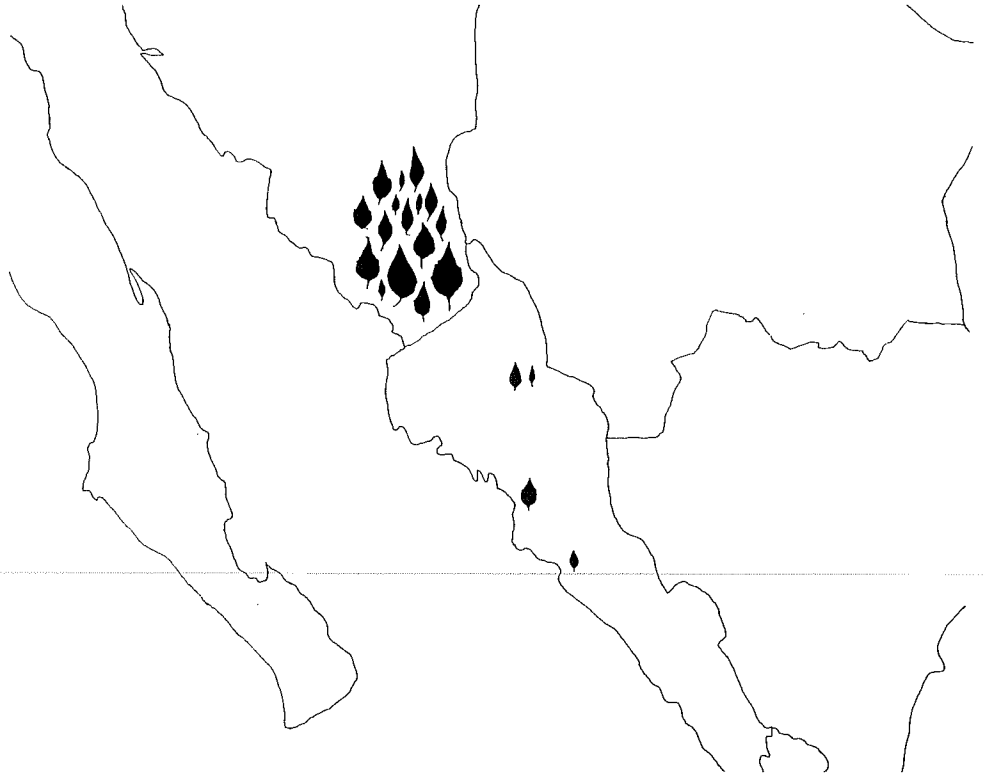


Fig. 29. Map of southern Sonora and northern Sinaloa, showing the distribution and leaf variation of *Montanoa tomentosa* subsp. *rosei*.

13, 26, 27, 29), 3–20 cm long, 1.5–15.0 cm wide, apex acute to acuminate, margin serrate to irregularly dentate, unlobed to 3–5-lobed, adaxial surface moderately to densely pubescent, hairs pustular, abaxial surface sparsely glandular to densely pubescent, hairs 2 mm long. *Peduncles* 1.0–3.5 mm long, moderately to densely glandular and pubescent, hairs 0.25–2.0 mm long. *Heads* erect, 0.3–0.8 cm diam in flower, 0.5–1.2 cm diam in fruit, extremely numerous in dense cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* (Fig. 31A, B) 4–6, uniseriate, subequal, ovate-lanceolate, 2.5–5.0 mm long, 1–2 mm wide, green to dark green, apex acute to acuminate, mucronate, margin ciliate, entire, abaxial surface sparsely to densely glandular and pubescent, hairs 0.5–1.5 mm long, adaxial surface glabrous. *Ray florets* 0–6; corollas cream to white, ligules ovate to obovate to oblanceolate, 3–5(–9.5) mm long, (1.25–)2–4(–5) mm wide, apex truncate to rounded, with or without 1–2 notches and with clusters of round tipped hairs, adaxial surface essentially glabrous, abaxial surface sparsely to moderately glandular, tube (0.5–)1.0–1.5(–2.25) mm long, 0.5 mm diam, glabrous to sparsely pubescent, hairs less than 0.5 mm long. *Disc florets* (Fig. 31C, D) (3–)8–9(–17); corollas light to deep yellow, tube 1–2 mm long, 0.5–1.0 mm diam, glabrous to sparsely pubescent, throat cylindrical, 1.0–1.25 mm long, 0.5 mm wide, sparsely pubescent, hairs less than 0.5 mm long, lobes 5, 0.5–1.0 mm long, 0.5–0.75 mm wide, apex acute, with clusters of round tipped hairs; stamens with filaments 1.2–3.5 mm long, 0.2 mm wide, anthers not fully exerted

TABLE II

Number of disc and ray florets from the type collection previously recognized species of *Montanoa* section *Montanoa* and the total variation for each group

Group	Species	No. disc florets	No. ray florets
1	<i>tomentosa</i> <sup>d</sup>	12-15	4-5
	<i>floribunda</i> <sup>d,p</sup>	15	5
	<i>pilosipalea</i> <sup>s</sup>	12	5
	collections	7-16	3-5
	range	7-16	3-5
2	<i>xanthiifolia</i> <sup>s</sup>	ca. 9	ca. 3
	<i>myriocephala</i> <sup>s</sup>	ca. 9	4
	<i>seleriana</i> <sup>s</sup>	8-10	3-4
	<i>subglabra</i>	12	4
	<i>palmeri</i> <sup>s</sup>	10-14	3-5
	<i>hemsleyana</i> <sup>s</sup>	3-4	0
	<i>rekoii</i> <sup>s</sup>	3-4	0
	collections	6-17	3-5
range	3-17	0-5	
3	<i>microcephala</i> <sup>s</sup>	11	5
	collections	8-16	4-6
	range	8-16	4-6
4	<i>rosei</i> <sup>s</sup>	4	3-4
	<i>gentryi</i> <sup>s,d</sup>	3-5	0-1
	collections	3-10	1-4
	range	3-10	0-4

<sup>s</sup> = specimen.

<sup>d</sup> = description.

<sup>p</sup> = photo.

from corolla, thecae yellow to brown, 1.25-1.5 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5-0.6 mm long, 0.5 mm wide, abaxial surface of apical appendages and thecae with or without glands; styles (Fig. 31E, F) yellow, (4.5-)-5.5(-7.5) mm long, enlarged at base, stigmatic surfaces yellow to brown, 1 mm long, apical appendages yellow, acute, 0.5-0.6 mm long, 0.5 mm wide, abaxial surface of stigmatic area sometimes glandular. *Pales* at anthesis more or less pentagonal to triangular (Fig. 31G, H), 2-6 mm long, 1-4 mm wide, light yellow to yellow with dark bands near midrib, apex long-acuminate, light or dark, indurate, margin ciliate, entire, abaxial surface moderately to densely glandular and pubescent, hairs 1-5 mm long, adaxial surface glabrous; pales at fruiting persistent, obtusulate to obtriangular (Fig. 31I, J), 4.5-10.0 mm long, 1-4 mm wide, indurate with inconspicuous parallel veins, stramineous, apex tapering, sometimes recurved and indurate, margin ciliate, entire, abaxial surface moderately to densely glandular and pubescent, hairs 0.5-4.0 mm long, adaxial surface glabrous. *Achenes* usually only one maturing per head, brown-black, 2.5-3.5 mm long, 1.0-1.5 mm diam, smooth. Chromosome number,  $n = 19$ .

#### Key to the Subspecies of *Montanoa tomentosa*

1. Petioles winged to base; Oaxaca, Mexico.
  - 1b. subsp. *microcephala*.
1. Petioles never winged to the base.
  2. Leaf blades ovate, margins never lobed; disc florets 3-9, usually 6-7; Sonora and Sinaloa, Mexico.
    - 1c. subsp. *rosei*.

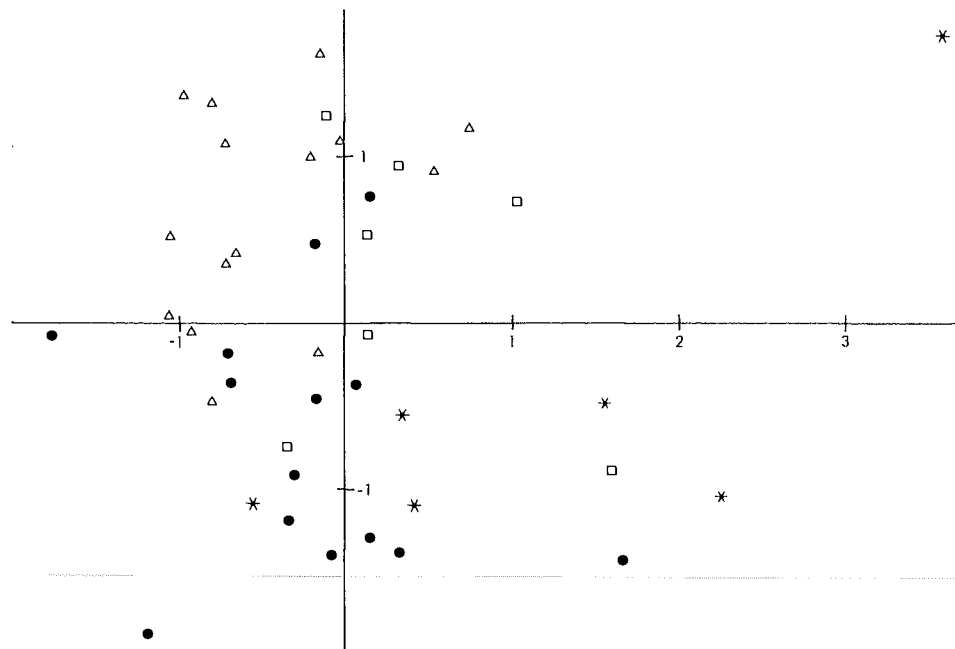


Fig. 30. PCA of *Montanoa tomentosa*: subsp. *microcephala* (squares); subsp. *rosei* (stars); subsp. *tomentosa* (dots); subsp. *xanthiifolia* (triangles).

2. Leaf blades triangular or pentagonal, usually lobed; disc florets 3–17, usually 9–12; Jalisco, Mexico to Costa Rica.
3. Leaf blades usually longer than broad, dark green, at base truncate or cordate, with margins usually irregular; central Mexico to Oaxaca; 1900–2800 m. 1a. subsp. *tomentosa*.
3. Leaf blades usually as broad as long, bright green, base with partially winged petiole or acute, with margins usually entire or 3–5-lobed; Jalisco, Mexico to Costa Rica; up to 1800 m. 1d. subsp. *xanthiifolia*.

**1a. *Montanoa tomentosa* subsp. *tomentosa*** Cervantes in La Llave & Lexarza, Nov.

Veg. Descr. 2: 11. 1825. Type: MEXICO, Distrito Federal, riverbanks near México City, date and collector unknown. The holotype has not been located. Neotype: MEXICO, Distrito Federal, immediately W of Avenue Insurgentes and S of the Universidad Nacional Autónoma de México, in the pedregal area, common on rocky flats, 3 Sep 1976, R. L. Hartman & V. A. Funk 4225 (neotype, OS!; isoneotypes, K! MA! MEXU! MO! NY! TEX! UC! US!). The most likely place for the holotype is Madrid, but the specimen was not received on loan. A search of the Madrid herbarium by T. F. Stuessy (pers. comm.) was also unsuccessful. The description is, however, quite detailed, containing information on the flowering and fruiting heads as well as on the leaves and habit; it is unlikely that Cervantes could have been describing another taxon. *Eriocoma tomentosa* (Cerv.) Kuntze, Rev. Gen. Pl. 1: 336. 1891. Figs. 10, 11, 24, 25, 31.

*Eriocoma floribunda* H.B.K., Nov. Gen. Sp. 4: 210. t. 396. 1820, nom. illegit. Type species of *Eriocoma* H.B.K., a later homonym of *Eriocoma* Nutt., Gen. Amer. Pl. 1: 40. 1818. Type: MEXICO, Distrito Federal, between the sanctuary of Guadalupe and México City, in dry places, 2200 m, Oct 1803–Jan 1804, A. von Humboldt & A. J. Bonpland 4394 (holotype).

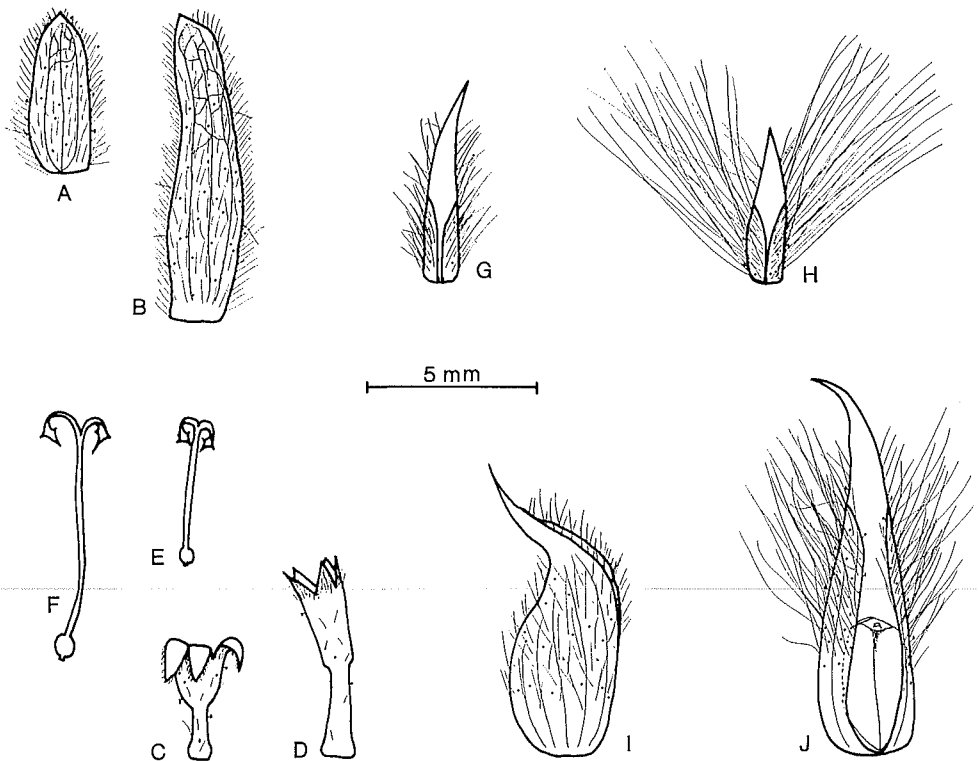


Fig. 31. Variation in flowering and fruiting characters in *Montanoa tomentosa*. Involucral bracts in subsp. *tomentosa*: A, Cruz 291 (ENCB); B, Pineada 892 (DS). Disc corolla in subsp. *rosei*: C, Palmer 394 (US); C, FCa 3006 (OS). Styles in subsp. *xanthiifolia*: E, Seler 1965 (US); F, FRa 2637 (OS). Pales subtending disc florets at anthesis: G, subsp. *microcephala*, Cronquist & Sousa 10449 (NY); H, subsp. *rosei*, Palmer 394 (US). Pales subtending mature achenes in subsp. *microcephala*: I, AL 4265 (OS); J, Cronquist & Sousa 10449 (NY).

P-HBK, photo, OS!). *Montanoa floribunda* (H.B.K.) Schultz Bip. in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864.

*Eriocoma fragrans* D. Don in Sweet, Brit. Fl. Gard. 11: 1. t. 44. 1830. Type: MEXICO, introduced by R. Barclay in 1827 (holotype not located, the illustration is taken as the holotype).

*Eriocoma heterophylla* Schrader, Ind. Sem. Hort. Gott. 1833: 3. 1833. Type: MEXICO, location unknown, s.d., D. Muhlenfordt s.n. (holotype, not located). The author stated that this species has cordate leaves and that it is taller than *Eriocoma floribunda* H.B.K., suggesting that these are the only characters by which the two species differ. Because these features are known to be variable, it is here placed in synonymy along with *E. floribunda*.

*Montagnaea tomentosa* Cerv. in Llave & Lex. var. *cordifolia* DC., Prodr. 5: 565. 1836. Type: MEXICO, near México City, 27 Jul 1827, J. L. Berlandier 574 pro parte (holotype, G-DC, photo IDC 800. 565:III.3!; isotypes, FI! W!). Both varieties described by de Candolle for *M. tomentosa* have the same Berlandier collection number (574), but they differ in date of collection. They were separated by the description of the blades, with those of *M. tomentosa* var. *ternifolia* oblong-lanceolate and those of *M. tomentosa* var. *cordifolia* cordate.

*Montagnaea tomentosa* Cerv. in Llave & Lex. var. *ternifolia* DC., Prodr. 5: 565. 1836. Type: MEXICO, México to Chapolopa, 15 Jul 1827, J. L. Berlandier 574 pro parte (holotype, G-DC, photo IDC 800. 565:III.4!; isotypes, BM! FI[2]! G! OXF! S!). *Montanoa ternifolia* (DC.) Schultz Bip., Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864. *Eriocoma ternifolia* (DC.) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa pilosipalea* S. F. Blake, Contr. U.S. Natl. Herb. 22: 612. 1924. Type: MEXICO, Puebla, Puebla, near Fort de la Guadalupe, 2170 m, 11 Nov 1906, Bro. G. Arsène 268a

(holotype, US!). This fruiting specimen is in all respects identical to other members of this taxon except for the number of mature pales per head. Another collection, also by Arsène, from the same locality had a flowering specimen typical for the species.

FLOWERING (AND FRUITING) PERIOD: August–October (September–November).

DISTRIBUTION AND HABITAT: Central Mexico (Fig. 11); xeric to semi-xeric thorn forest and deserts; roadsides, stream banks, and arroyos; 1900–2800 m, usually 1900–2100 m.

REPRESENTATIVE SPECIMENS (an asterisk indicates that a chromosome count was obtained from the collection; for explanation of abbreviations of collectors see APPENDIX A: MEXICO. DISTRITO FEDERAL: Chapultepec, Aug 1952, *Paray 990* (ENCB); Cerro del Chiquihuite, Sierra de Guadalupe, 4 Oct 1969, *Vega s.n.* (ENCB, MICH); Xochimulco, 3 Oct 1910, *Orcutt 4256* (F, MO); Cerro del Estrella, Ixtapalapa, 19 Sep 1977, *García 452* (CA, ENCB, OS); Chimalhuacan, 22 Oct 1950, *Matuda 19530* (NY); Tizapan, 21 Oct 1900, *Pringle 9054* (F, GH, MICH); San Juan Citaltepec, 15 Oct 1950, *Matuda 19512* (MEXU); Cerro Teutli, Milpa Alta, 20 Sep 1974, *Flores 85* (OS); pedregal, Dec 1977, *Ramos s.n.* (OS); S of Universidad Nacional Autónoma de México, 3 Sep 1976, *HF 4223\** (OS); pedregal 1 mi S of Universidad, 11 Oct 1965, *C 10317* (CA, DUKE, ENCB, MEXU, MICH, NY, TEX, US); Avenuc Insurgentes, pedregal S of Universidad, 3 Sep 1976, *HF 4224\** (OS); Universidad Nacional Autónoma de México, 3 Sep 1976, *HF 4225\** (OS). HIDALGO: Jacala, 20 Oct 1937, *Kenoyer 431* (F, MO); 8.8 mi S of Zimapán, 12 Nov 1978, *FT 2820* (OS); 4 km N of Orizabita, 14 Oct 1965, *Quintero 3139* (DS, ENCB, MICH, MSC); 8 km N of Tasquillo, 27 Aug 1965, *González Quintero 2959* (DS, ENCB, LL, MICH, MSC); 16 km N of Ixmiquilpan, 29 Oct 1977, *FH 2228* (OS); 7.5 mi NW of Ixmiquilpan, 27 Oct 1965, *González Quintero 3213* (DS, ENCB, MSC); 10 km SE of Tezontepec, 19 Nov 1971, *Jiménez 178* (ENCB, MICH); 2 km WNW of Epazoyucan, 1 Oct 1972, *Rzedowski 29480* (ARIZ, CA, COL, ENCB, MICH); Cerro Ventoso, btw Pachuca and Real del Monte, 29 Aug 1965, *Rzedowski 20568* (DS, ENCB, MICH, MSC, TEX); Cerro de los Pitos, Zempoala, 11 Sep 1976, *Ventura 2096* (ENCB, OS); btw Tulancingo and Santiago, 19 Oct 1946, *Moore 1604* (BH, GH, MICH, US); 17 km NW of Apan, 26 Jul 1966, *West TT-5* (MICH, WIS); 8 km SSW of Alfajayucan, 6 Sep 1965, *González Quintero 2994* (DS, ENCB, MICH, MSC); 10–12 mi ENE of Huichapán, 11 Dec 1978, *F 2955* (OS); 5 mi ENE of Huichapán, 11 Dec 1978, *F 2960* (OS); 2.5 mi NE of Huichapán, 12 Nov 1978, *FT 2823* (OS); 2 mi SW of Huichapán, 11 Dec 1978, *F 2961* (OS); 2.5 mi W of Huichapán, 7 Oct 1962, *C 9616* (GH, MICH, MSC, NY, SMU, TEX); 8 mi SW of Huichapán, 11 Dec 1978, *F 2962* (OS); near Tula, 30 Sep 1902, *Pringle 9940* (CM, CU, F, GH, K, MICH, MO, NY, SMU). MÉXICO: Las Cuevas, ca. 3 km N of San Juan Teotihuacán, 12 Sep 1965, *Cruz 291* (DS, ENCB, MICH, MSC, WIS); Tlayacampa, Tlalnepantla, 14 Sep 1969, *Pineda 892* (DS, ENCB, MICH); Molino de Flores, 24 Aug 1936, *MacDaniels 599* (BH, F); 4 km N of Huehuetoca, 16 Sep 1975, *Jacquemin 1070* (ENCB, OS); Río Hondo Canyon, 22 Aug 1890, *Pringle 3155* (A, BM, BR, CM, F, G, GH, K, M, MICH, MO, MSC, NY, S, UC, UNG); Temascaltepec, 25 Nov 1939, *Hinton 5144* (K, MO); 6 km SE of Tezcoco, 9 Sep 1977, *García 422* (CA, ENCB, OS). OAXACA: 6 mi SE of jct of hws 190 and 125, 23 Nov 1978, *F 2882A* (OS); S of Tamasulapa, Río Oro, 20 Nov 1977, *Fra 2383* (OS); S of Tamasulapa, Río Oro, 20 Nov 1977, *Fra 2382* (OS); 25 mi SE of Tlaxiaco, 25 Oct 1965, *Cronquist & Sousa 10412* (ENCB, GH, MICH, NY); Coiztlahuaca, 12 Nov 1894, *Nelson 1920* (GH, US); btw Huahuapan de León and Yanhuítlan, 18 Oct 1976, *SG 4246\** (OS); Ixtlán, 47 mi NNE of Oaxaca, 22 Nov 1977, *Fra 2411* (OS); near Ixtlán de Juárez, 26 Nov 1971, *Dieterle 4208* (CA, ENCB, MICH, OS); Monte Albán, 21 Nov 1977, *Fra 2408* (OS); just N of Monte Albán, 19 Oct 1976, *SG 4264\** (OS); 20 mi SSE of Oaxaca, 7 Nov 1966, *AL 4142* (MICH, OS). PUEBLA: Fort de Guadalupe, 6 Oct 1907, *Arsène 1177* (US); near Tepeaca, 19 Nov 1977, *Fra 2361b\** (OS); ca. 15 mi N of Tlacotepec, 19 Nov 1977, *Fra 2362a* (OS); La Candelaria, 20 Sep 1971, *Ventura 4284* (ARIZ, CA, ENCB, LL, MICH, TEX); Acatzingo, 15 Sep 1911, *Nicolas s.n.* (G); ca. 10 km S of Esperanza, 5 Jan 1970, *Anderson & Anderson 5316* (ENCB, MICH); San Antonio, Atzizintla, 17 May 1938, *Balls 4531* (A, BM, K, UC); ca. 20 mi NW of Tehuacán, 20 Aug 1976, *HF 4137\** (OS); 6 mi N of Tehuacán, 20 Aug 1976, *HF 4138\** (OS). QUERETARO: municipio de Tecozautla, 1 Nov 1968, *Puig 3497* (ENCB); 10 mi S of Zimapán, 20 Aug 1957, *Waterfall & Wallis 14115* (SMU); near Vizarron, 15 Oct 1968, *Puig 3475* (ENCB); btw San Juan del Río and Tequisquiapan, 19 Aug 1905, *Rose et al. 9622* (GH, MEXU, NY); near Cadereyta, 22 Aug 1905, *Rose et al. 9726* (GH); Cadereyta, 13 Jun 1952, *Kelly 621* (UC). SAN LUIS POTOSÍ: Ojo Caliente, 27 Aug 1954, *Rzedowski 3905* (ENCB); ca. 15 km NW of Tierra Nueva, 7 Sep 1954, *Rzedowski 4287* (ENCB); Santa María Del Río, 1904, *Palmer 155* (F, GH, MO, NY, US); 39 mi E of San Luis Potosí, 19 Oct 1966, *AL 4080* (OS); E of Villa Hidalgo, 22 Aug 1954, *Rzedowski 3771* (ENCB); 5 km S of Ciudad del Maíz, 27 Oct 1956, *Rzedowski 8303* (ENCB); Las Minas "Las Cuevas," Zaragoza, 8 Oct 1971, *Robert 1203* (CA, ENCB); near Cárdenas, 7 Oct–30 Nov 1890, *Pringle 3307* (A, BM, BR, CM, F, G, GH, M, MEXU, MICH, MO, MSC, NY, S, UC, UNG). TAMAULIPAS: btw Hcrmosa and Miquihuana, 23



Jul 1949, *Stanford et al.* 2680 (NY, SMU, TEX, UC, US); 6 km W of Miquihuana, 6 Aug 1941, *Stanford et al.* 723 (NY, SMU, TEX, UC, US). VERACRUZ: hills of Macuiltepec, Xalapa, 18 Nov 1974, *Ventura* 10683 (ENCB, OS); 4 mi SW of Ciudad Mendoza, 1 Nov 1966, *AL* 4092 (MICH, OS); E of barranca de Santiago, Huayacocotla, 23 Oct 1970, *Hernandez & Trigos* 850 (OS).

**1b. *Montanoa tomentosa* subsp. *microcephala* (Schultz Bipontinus in K. Koch)**  
V. A. Funk, comb. et stat. nov. Figs. 3, 13, 14, 31.

*Montanoa microcephala* Schultz Bip. in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864. Type: MEXICO, Oaxaca, Ejutla, Oct 1842, *F. M. Liebmann* 483 [Liebm. pl. Mex. 9052] (holotype, P!; isotypes, C[3]! K!; photos of C isotype, F! MO! NY! US!; photo of holotype, OS!; fragment of holotype, US!). *Eriocoma microcephala* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

FLOWERING (AND FRUITING) PERIOD: July–November (October–December).

DISTRIBUTION AND HABITAT: Oaxaca, Sierra Madre del Sur (Fig. 13); semi-xeric to slightly mesic; well drained roadsides and slopes; 800–1850 m.

REPRESENTATIVE SPECIMENS: MEXICO. OAXACA: near Mitla, 4 Oct 1972, *Messer* 721150 (MICH); hwy 190 16.7 mi SE of rd to Mitla, 24 Nov 1978, *F* 2896 (OS); hwy 190 just S of Agua Santa, 23 Nov 1977, *F* 2535\* (OS); 57 mi SE of Oaxaca and 20 mi NW of Nejapa, 30 Oct 1965, *Cronquist & Sousa* 10449 (CA, DUKE, ENCB, GH, MEXU, MICH, NY, TEX); hwy 190 2 mi NW of rd to Nejapa, 24 Nov 1978, *F* 2897 (OS); near Nejapa, 23 Nov 1977, *FRa* 2540 (OS); btw Oaxaca and Nejapa near El Jigolengo, 23 Nov 1977, *FRa* 2543 (OS); below Cueva Blanca, 16°55'N, 96°25'W, 16 Jul 1966, *Schoenwetter JSOX-4* (ENCB, US); 3.7 mi W of El Camaron, 20 Nov 1966, *AL* 4265 (MICH, OS); 13 mi S of Matatlán, 11 Nov 1966, *AL* 4198 (MICH, OS); hwy 175, 6.8–7.7 mi SE of Ejutla, 7 Nov 1966, *AL* 4146 (MICH, OS).

**1c. *Montanoa tomentosa* subsp. *rosei* (Rose ex Robinson & Greenman) V. A.**  
Funk, comb. et stat. nov. Figs. 29, 31.

*Montanoa rosei* Rose ex Robins. & Greenm., Proc. Amer. Acad. Arts 32: 45. 1896. Type: MEXICO, Sonora, Alamos, 26 Mar–8 Apr 1890, *E. Palmer* 394 (holotype, US[accession no. 21399]!; isotypes, A! ARIZ! CS! GH! K! LE! MEXU! NY! S! UC! US!; photo of K isotype, OS!).

*Montanoa gentryi* S. F. Blake, J. Wash. Acad. Sci. 40: 49. 1950. Type: MEXICO, Sinaloa, Capadero, Sierra Tacuichamona, 1065 m, 13 Feb 1940, *H. S. Gentry* 5614 (holotype, US!; isotypes, ARIZ! GH! MEXU! MICH! MO! NY!).

FLOWERING (AND FRUITING) PERIOD: December–March (January–April).

DISTRIBUTION AND HABITAT: Sonora and Sinaloa, Mexico (Fig. 29); deciduous thorn forests; roadsides, ditches and hillsides; 100–600 m.

REPRESENTATIVE SPECIMENS: MEXICO. SINALOA: Cerro Tecomate, W of Pericos, 29 Feb 1940, *Gentry* 5755 (ARIZ, DS, MICH, MO, NA, NY). SONORA: rd to Alamos, 25 mi E of hwy 15, 21 Dec 1978, *FCa* 3006\* (OS); just E of Los Lomas, hwy to Alamos, 21 Dec 1978, *FCa* 3005\* (OS); just E of Los Lomas, hwy to Alamos, 21 Dec 1978, *FCa* 3005A\* (OS); Agua Caliente de Zevada, 8 Jan 1976, *Shapiro* 299 (CA, MEXU); 0.7 mi S of Alamos, 18 Dec 1966, *AL* 4555 (MICH, OS); 7.5 mi W of Alamos, 30 Jan 1968, *Krizman* 11 (ARIZ); ca. 12 mi E of Alamos, 30 Jan 1968, *Soule & Patton s.n.* (ARIZ); rd to Advana, 15 Feb 1976, *Goldberg & Van Devender* (ARIZ, ENCB); near Alamos, Mar 1910, *Rose et al.* 12839 (F, GH, MO, NY, US); 2.4 mi from Alamos on rd to San Bernardo, 13 Aug 1978, *FS* 2778 (OS); 3.8 mi from Alamos on rd to San Bernardo, 13 Aug 1978, *FS* 2779 (OS); San Bernardo, Sep 1961, *Arguelles* 114 (LL, US); San Bernardo, 31 Jan 1935, *Gentry* 1248 (A, ARIZ, F, LL, MICH, MO, NA, NY, S, UC, W).

**1d. *Montanoa tomentosa* subsp. *xanthiifolia* (Schultz Bipontinus in K. Koch)**  
V. A. Funk, comb. et stat. nov. Figs. 12, 26, 27, 28, 31.

*Montanoa xanthiifolia* Schultz Bip. in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864. Type: MEXICO, Chacalapa, s.d., *F. M. Liebmann* 265

[Licb. Pl. Mex. 9057] (holotype, P!; isotypes, C[3]! K!; photos of holotype, GH! OS! US[2]!; photos of C isotype, F! MO! NY! US!; photo of K isotype, OS!; fragment of holotype, US!; fragment and drawing of C isotype, GH!). *Eriocoma xanthiifolia* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa triloba* Schultz Bip. in K. Koch, Wochenschr. Vercines Beförd. Gartenbaues König. Preuss. Staaten 7: 406. 1864. Type: MEXICO, 18 Dec 1863, *C. de Berges 123* (holotype, P!; photos of holotype, F! GH[2]! MO! OS! US!). *Eriocoma triloba* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Eriocoma hemsleyana* Hemsl. ex Kuntze, Rev. Gen. Pl. 1: 336. 1891. Type: MEXICO, Veracruz, valley of Cordoba, near la Piñuela, 14 Mar 1866, *E. Bourgeau 2057* (holotype, K!; isotypes, G! GH! L, LE! MPU! P!; photos of holotype, OS! US[2]!; fragment of holotype, US!; fragment and negative of L isotype, MSC!). *Montanoa anomala* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 509. 1899, nom. superfl. Based on type of *E. hemsleyana* Hemsl. ex Kuntze. *Montanoa hemsleyana* (Hemsl. ex Kuntze) S. F. Blake, Contr. U.S. Natl. Herb. 23: 1530. 1926. Hemsley (1881) listed this as *Montanoa* sp. with only three disc florets and apparently no rays, but he provided no epithet. Kuntze (1891) referred to Hemsley's description and gave it the name *Eriocoma hemsleyana*. Robinson and Greenman (1899) either missed Kuntze's reference or did not believe the description was adequate, so they described it as new using the same type.

*Montanoa palmeri* Fernald, Proc. Amer. Acad. Arts 33: 93. 1897. Type: MEXICO, Guerrero, hillsides near Acapulco, Nov 1894, *E. Palmer 44* (holotype, GH!; isotypes, BM! F[2]! GH! K! MA[2]! MO! NY! UC! US[2]!; photo of K isotype, OS!; negative and fragment of BM isotype, MSC!).

*Montanoa seleriana* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 510. 1899. Type: MEXICO, Chiapas, Tuxtla, 19 Feb 1896, *C. & E. Seler 1965* (holotype, GH!; photos of holotype, DS! LL! US!).

*Montanoa myriocephala* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 511. 1899. Type: MEXICO, Jalisco, at Chapala, Oct–Nov 1886, *E. Palmer 714* (holotype, GH!; isotypes, BM! G! K! LE! MO! NDG[2]! P! US[2]!; photo of K and P isotypes, OS!).

*Montanoa rekoii* S. F. Blake, Contr. U.S. Natl. Herb. 22: 610. 1924. Type: MEXICO, Oaxaca, Apango, 450 m, 11 Oct 1917, *B. P. Reko 3534* (holotype, US[accession no. 1012313]!; isotype, US!).

*Montanoa subglabra* S. F. Blake, Contr. U.S. Natl. Herb. 22: 610. 1924. Type: GUATEMALA, near Neuton, 915–1200 m, 13–15 Dec 1895, *E. W. Nelson 3536* (holotype, US!; isotype, F!).

FLOWERING (AND FRUITING) PERIOD: August–January (September–February).

DISTRIBUTION AND HABITAT: Jalisco, Mexico, to Costa Rica (Fig. 26); flowers earlier in the northern part of its range and later in the southern part; xeric to semi-xeric thorn forests and desert; sometimes a small tree as well as a shrub in wetter habitats; roadsides, stream banks and arroyos; 230–1800 m, usually 1000–1500 m.

REPRESENTATIVE SPECIMENS: COSTA RICA. GUANACASTE: btw Cañas and Tilarán, 3 Dec 1963, *Jiménez 1324* (F). PUNTARENAS: ca. 11 km S of Montverde, 10 Jan 1980, *F 3061*\* (CR, OS). SAN JOSÉ: S of Santa Anna, 11 Jan 1980, *FGo 3065* (CR, OS). EL SALVADOR. LA UNION: Sierra de Conchagua, Gulf of Fonseca, 3 Dec 1838, *Barclay 2685* (BM, US). GUATEMALA. CHIMALTENANGO: Carrarnos, 14 Dec 1938, *Johnston 1562* (F). CHIQUINULA: btw Santa Bárbara and Petapilla, Río Chiquimula, 22 Oct 1939, *Se 30266* (F). ESCUNTLA: Río Guacalate, 16 Dec 1938, *Sa 60186* (F). GUATEMALA: btw Guatemala and Rabinal, Río Motagua, 8 Dec 1938, *Sa 59300* (F). HUEHUETENANGO: btw Huehuetenango and Guatemala/Chiapas border at km 314, 15 Dec 1977, *FRK 2691*\* (OS). JUTIAPA: near Jutiapa, 24 Oct–5 Nov 1940, *Sa 75326* (F). PROGRESO: 43 km NE of Guatemala on hwy CA-9, 5 Dec 1977, *FRA 2637* (OS). QUICHÉ: 1.7 mi N of Río Blanco on rd to Ncbaj, 28 Nov 1978, *FL 2918* (OS). ZACAPA: btw Agua Blanca and Cumbre de Chiquimula, 15 Oct 1940, *Sa 74444* (F). HONDURAS. COMAYAGUA: btw Tegucigalpa and Siguatepeque at km 128, 8 Nov 1932, *Edwards 505* (F, GH, K, S, UC, US). MORAZÁN: near Tegucigalpa, 7 Dec 1949, *Sa 24873* (F, GH); SE of El Zamorano, 25 Nov 1949, *Sa 24690* (F, GH). CHOLUTECA: btw El Espino and San Marcos de Colón, 7 Nov 1968, *Molina 23225* (BM, DS, NY, S); btw Morolica and San Antonio de Flores, 20 Oct 1963, *Molina 13028* (F, LL, NY, US). MEXICO. CHIAPAS: 3 mi W of Los Amates, 14 Oct 1962, *C 9666* (GH, MEX, MICH, MSC, NY, SMU, TEX, US); Oaxaca/Chiapas state line, 24 Nov 1977, *FRA 2551b* (OS); near Cinco Cerros, 24 Nov 1977, *FRA 2553* (OS); 13 km N of Arriaga, 4 Oct 1972, *Breedlove 28295* (DS, MICH, MO); 3 km N of Ocozocoautla, 9 Jan 1972, *Breedlove & McClintock 23581* (DS, MICH, MO); rd from Acala to Venustiano Carranza, 7 Jan 1967, *Laughlin 3011* (DS, MICH); 11 mi from El Sumidero on rd to Tuxtla, 24 Jan 1970, *Anderson & Anderson 5551* (DUKE, ENCB, MICH,

MO); 5.6 mi E of Chiapa de Corzo, 20 Feb 1965, *Breedlove 9100* (DS, ENCB, F, MICH); 14 mi S of Comitán, 3 Nov 1965, *Cronquist & Sousa 10484* (ENCB, MEXU, NY); Mt. Ovando, Escuintla, 14 Nov 1945, *Matuda 16247* (MEXU, MO, US); Las Cardenas, near Escuintla, Jan 1938, *Matuda 1889* (F, GH, LL, MICH, MO, NA, NY, US); 6–8 km E of Frontera Comalapa, 29 Dec 1971, *Breedlove 23414* (DS, DUKE, LL, MICH, MO, RSA). GUERRERO: 3.5 mi N of Zumpango del Río, 16 Nov 1978, *Fri 2846* (OS); 5 km N of Zumpango del Río, 2 Dec 1966, *Rzedowski 23527* (DS, ENCB, LL, MSC, WIS); 3 mi N of Zumpango del Río, 2 Dec 1966, *AL 4331* (MICH, OS). HIDALGO: overlooking Jacala, 29 Oct 1977, *FH 2219\** (OS); just N of Jacala, 29 Oct 1977, *FH 2223* (OS); 3.3 mi N of Jacala, 12 Nov 1978, *FT 2811* (OS); within Jacala, 12 Nov 1978, *FT 2812\** (OS); near Jacala, 12 Nov 1978, *FT 2813* (OS); 2 mi SW of Jacala, 16 Nov 1959, *Graham & Johnston 4738* (TEX); rd from Zimapán to Mina Loma del Toro, 8 Aug 1948, *Moore & Wood 4387* (A, MICH); Puente de Venados, Metztlán, 25 Sep 1968, *Puig 3210* (ENCB); 8 mi N of jct of hwy 85 and 45 on descent to Río Tula, 16 Oct 1966, *AL 4021* (MICH, OS); 6 km NW of Tasquillo, 27 Oct 1965, *González Quiñtero 3202* (ENCB, MICH). JALISCO: 3.6 mi E and S of Mezquitic, 14 Sep 1966, *AL 3630* (MICH, OS); 10 km NW of Huejuquilla el Alto, 2 Nov 1963, *Feddema 2358* (DUKE, ENCB, MICH, TEX); near rd to Tapalpa from Amacueca, 3 Nov 1960, *M 20715* (BM, DS, DUKE, ENCB, LL, MICH, NY, US); 30 mi E of El Molina, 3 Nov 1977, *F 2267* (OS); 30 mi E of El Molina, 3 Nov 1977, *F 2268* (OS); 35 mi E of El Molina, 3 Nov 1977, *F 2266\** (OS); S shore of Lago de Chapala, 7 Oct 1965, *C 10288* (CA, DUKE, GH, MICH, MSC, NY, TEX); N shore of Lago de Chapala, 3 Oct 1966, *AL 3872* (MICH, OS); 32 mi W of Ciudad Guzmán, 31 Oct 1962, *C 9771* (MICH, MO, NY, TEX, US); 2 mi N of Juchitlán, 24 Sep 1966, *AL 3717* (MICH, OS); 7 mi S of Juchitlán, 24 Sep 1966, *AL 3722* (MICH); 15.4 mi N of Colotitlán, 6 Nov 1977, *F 2286* (OS); 3.7 mi N of Colotitlán, 6 Nov 1977, *F 2289* (OS); N of Autlán, 5 Oct 1960, *M 19906* (DUKE, LL, MICH, NY, TEX, US). MICHOACÁN: Zitacuaro-Jungapeo, 21 Oct 1938, *Hinton 13387* (C, F, G, K, MICH, MO, NY, S, TEX, UC, W). OAXACA: ca. 1 mi NW of Huajuapán de León, 23 Nov 1978, *F 2874\** (OS); 2.9 mi S of Miltepec, 21 Nov 1966, *AL 4281* (MICH, OS); hwy from Tehuacán to Huajuapán de León, 19 Nov 1977, *Fra 2369* (OS); N of Reforma, 20 Nov 1977, *Fra 2375* (OS); 20 km S of Huajuapán de León, 20 Nov 1977, *Fra 2372* (OS); 2 mi from Teotitlán del Camino on rd to Huautla de Jiménez, 22 Nov 1966, *AL 4283* (OS); 6 mi above Dominguito, 30 Oct 1894, *Nelson 1854* (GH, US); Nizanda, Juchitán, 15 Nov 1966, *MacDongall 61* (US); N of Jayacatlan, 4 Nov 1973, *Breedlove 35929* (CA, MICH); 6 km NE of Chilapa de Díaz, 2 Nov 1976, *Rzedowski 34492* (ENCB); 10.9 mi NE of Tapanatepec, 12 Nov 1966, *AL 4208* (MICH). QUERETARO: Jalpan, 4 Nov 1968, *Puig 3596* (ENCB); btw Vizarrón and Jalpan, 8.5 mi S of Peña Blanca, 8 Nov 1970, *Webster 16280* (DUKE, F, GH, LL, MICH); 14 mi E of Landa, 12 Dec 1960, *Critchfield & Johnston 6115* (LL, MICH, NY, TEX, UC). PUEBLA: 10.9 mi SE of Izucar de Matamoros, 22 Nov 1978, *F 2872* (OS); 22 mi NW of Huajuapán de León, 22 Nov 1978, *F 2873* (OS); 6 mi N of Tehuacán, 20 Aug 1976, *HF 4139\** (OS); 6 mi N of Tehuacán, 20 Aug 1976, *HF 4138* (OS); 1 mi SE of Tehuacán, 22 Oct 1965, *Cronquist & Sousa 10386* (CA, DUKE, ENCB, MEXU, MICH, MSC, NY, TEX, US, WIS); ca. 25 mi SW of Tehuacán, 21 Aug 1976, *HF 4147\** (OS); near Acatepec, 19 Nov 1977, *Fra 2368* (OS). SAN LUIS POTOSÍ: 5 km S of Río Pinihuan, 20 Jan 1957, *Rzedowski 8635* (ENCB); hwy 70 at jct with rd to Cárdenas, 11 Nov 1978, *FT 2808\** (OS); rd near jct of hwy 70 and rd to Cárdenas, 28 Oct 1977, *FH 2207\** (OS); 60 mi W of Ciudad Valles, 18 Oct 1966, *AL 4076* (MICH, OS). VERACRUZ: La Concepción, Jilotepec, 20 Oct 1977, *Ventura 14600* (ENCB); La Mesa, Naolinco, 17 Dec 1977, *Ventura 14722* (ENCB); Huayacocotla, 21 Oct 1970, *Hernandez & Trigos 801A* (CA, GH, MEXU). NICARAGUA. BOACO: Cacao, 14 Nov 1946, *Williams & Molina 10963* (F, GH, MICH, MO). ESTELÍ: near Guava, 5 Nov 1968, *Molina 23127* (BM, DS, DUKE, F, GH, S, SMU, UC). MATAGALPA: on hwy to Matagalpa, 29 Oct 1968, *Molina 22846* (F, NY, US).

## IB. Montanoa section *Echinocephalae* V. A. Funk, sect. nov.

Frutex vel arbor; flosculi radiorum 6–13 albi; flosculi discorum 11–100 (plerumque ultra 35), lutei vel lutei et cinereo-virides vel nigri; paleae in immaturitate 4–8 mm longae; paleae in maturitate 8–22 mm longae, triangulares, venis prominentibus, adaxialiter glabris; achaenia 3–5 mm longa; capitula persistentes. Typus: *Montanoa frutescens* Mairet ex DC. Species 2–9.

Section *Echinocephalae* has eight species in three series usually from wet, high altitude habitats and of restricted distributions. The synfrutescence is unusual in having large pales that are indurate, glabrous, and have long tapering tips. The heads are persistent and there are many achenes per head. When the achenes are mature the heads apparently bend over and the indurate recurved pales make chutes so the achenes can slide out. The spiny appearance of the synfrutescence is responsible for the section name (spiny headed). One of the smallest heads in the series (9–12 mm diam and 75–100 disc florets) and the largest (15–22 mm diam

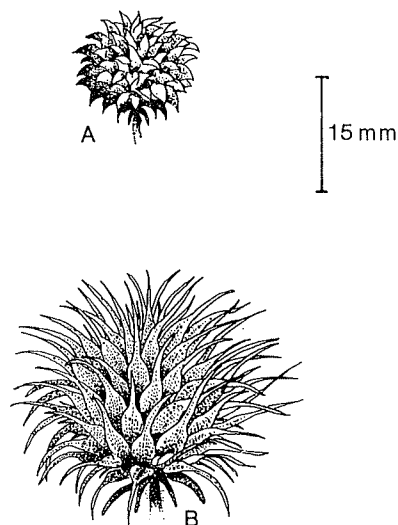


Fig. 32. Mature fruiting heads of section *Echinocephalae*. A, *Montanoa mollissima* (FRA 2380, OS); B, *M. echinacea* (Breedlove 29677, DS).

and 100–150 disc florets) are illustrated in Fig. 32. *Montanoa revealii* has rather different pales, they are somewhat indurate, and thinner and fewer in number (11–22). Figure 42 illustrates the head when the achenes are mature, note the stellate appearance.

**IBa. *Montanoa* section *Echinocephalae* series *Frutescentes* V. A. Funk, ser. nov.**

Paleae in maturitate marginibus valde incurvatis ultra dimidiis longitudinibus, apicibus recurvis. Typus: *Montanoa frutescens* Mairet ex DC. Species 2–6.

Series *Frutescentes* has five species from Mexico and Central America, all of which have very similar indurate recurved pales differing only in size and amount of curvature. The species are delimited by a variety of characters including: number and color of disc and ray florets, stem color, leaf shape and condition of the petiole.

2. *Montanoa frutescens* Mairet ex A. P. de Candolle, Prodr. 5: 565. 1836, "*Montagnoaea*." Type: MEXICO, México, mountains near México City, 22 Jul 1827, J. L. Berlandier 908 (lectotype, chosen from five syntypes, G-DC, photo of lectotype, IDC 800. 565:III.3!; isolectotypes, BM! FI[2]! G[3]! K! LE[2]! OXF! P! W!). Other syntypes listed by de Candolle were: Alamán s.n., 1831; Berlandier 1154; Mairet a7435; Mairet s.n., 1833. *Eriocoma frutescens* Alamán [ex DC., Prodr. 5: 565. 1836, nom. nud. pro syn.] ex Kuntze, Rev. Gen. Pl. 1: 336. 1891.

Figs. 33, 34.

*Priestleya squarrosa* Sessé & Mociño ex DC., Prodr. 5: 565. 1836, nom. nud. pro syn. De Candolle's treatment of this taxon as a synonym was based on the drawing from Ic. Fl. Mex. 8: 677. (Original drawing at G; photo, F! US!)

*Aldama montanoa* Schultz Bip. ex K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864, nom. nud. pro syn. Listed in a footnote as a synonym of *M. frutescens*, but never described.

Shrubs 1–5 m tall. Stems terete, herbaceous parts purple, glabrous. Leaves relatively consistent; petioles 1.5–7.5 cm long, with or without partial wings,

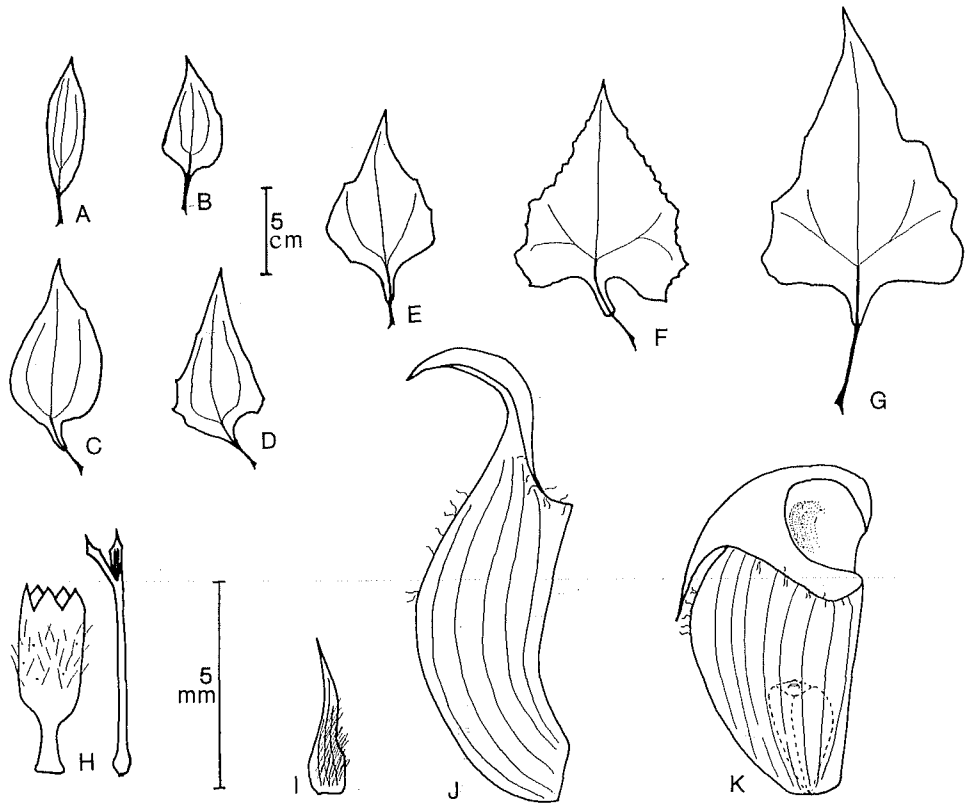


Fig. 33. *Montanoa frutescens*. A-G, variation in mature leaves: A, C, D, *C 10326* (NY); B, E-G, *AL 4315* (OS). H, disc corolla and style, *AL 4315* (OS); I, pale subtending disc floret at anthesis, *FRa 2361A* (OS); J, K, mature pales, *Ramos s.n.* (OS). A-G, H-K, same scale respectively.

sparsely pubescent with the hairs 0.5–1.0 mm long; blades ovate to trullate or triangular (Fig. 33A–G), 4.0–14.5 cm long, 2.3–12.5 cm wide, apex acute to acuminate, margin entire to dentate, unlobed, adaxial surface sparsely to moderately pubescent, hairs pustular, abaxial surface moderately glandular and sparsely pubescent on veins, hairs 1.0 mm long. *Peduncles* 1.0–6.5 cm long, densely pubescent, hairs 0.5–1.0 mm long. *Heads* erect, 1.0–1.25 cm diam in flower, 1.5–2.0 cm diam in fruit, few to many in cymose synflorescences in oppositely and alternately branched compound corymbs. Receptacle at fruiting 3–4 mm tall, 1.5–2.0 mm diam. *Phyllaries* 6, uniseriate, equal, strongly reflexed at anthesis, ovate-lanceolate, 4.5–5.5 mm long, 1.0 mm wide, green, apex acute to acuminate, some mucronate, margin ciliate, entire, abaxial surface essentially glabrous, adaxial surface sparsely glandular. *Ray florets* 8–13; corollas white, ligules oblong, 15–25 mm long, 5–8 mm wide, adaxial surface glabrous, abaxial surface sparsely glandular, tube 1.0–1.5 mm long, 0.5–0.8 mm wide, glabrous. *Disc florets* (Fig. 33H) 100–150; corollas green to cream, tube 1.0–1.25 mm long, 0.5 mm diam, essentially glabrous, throat cylindrical, 2.0–2.5 mm long, 1.5 mm diam, sparsely pubescent especially near center, hairs thick, 0.5 mm long, lobes 5, 0.75–1.0 mm long, 0.75 mm wide, apex acute, glabrous; stamens with filaments 1.5–2.0 mm long, 0.3 mm wide, anthers not fully exserted from corolla, thecae brown, 1.5–2.0 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5 mm long, 0.4

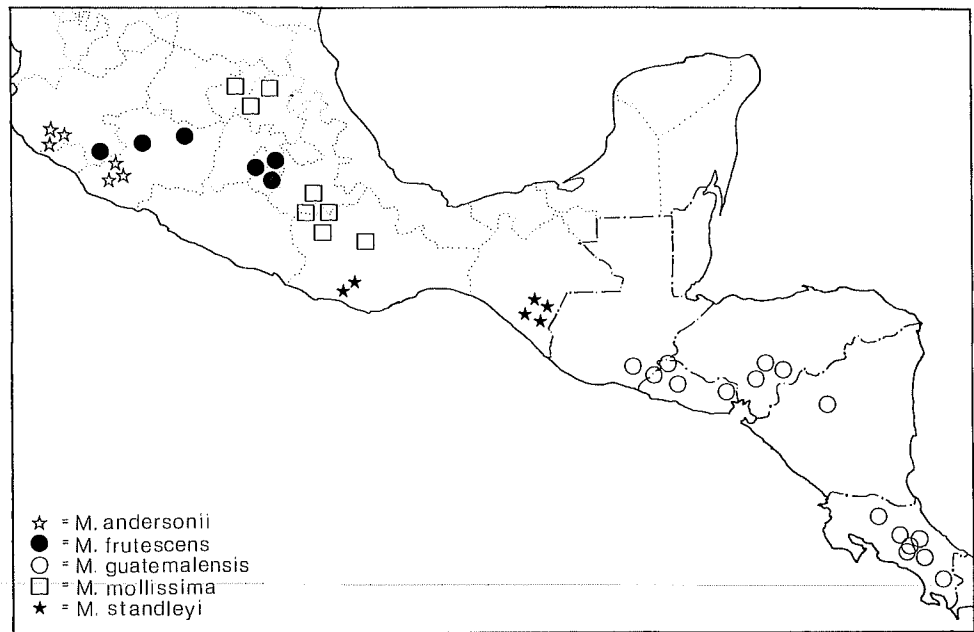


Fig. 34. Map of southern Mexico and Central America showing the distribution of *Montanoa andersonii*, *M. frutescens*, *M. guatemalensis*, *M. mollissima*, and *M. standleyi*.

mm wide, glabrous; styles yellow, 4.5–5.0 mm long, enlarged at base, stigmatic surfaces dark (Fig. 33H), 0.75 mm long, apical appendages yellow, short-acute, 0.25 mm long, 0.25 mm wide. *Pales* at anthesis triangular (Fig. 33I), 4.5–5.0 mm long, 1.0–1.5 mm wide, light yellow with dark bands near midrib, apex long-acuminate, yellow and indurate, margin ciliate and entire, abaxial surface densely pubescent except at apex, hairs 0.5–1.0 mm long, adaxial surface glabrous; *pales* at fruiting persistent, almost triangular (Fig. 33J, K), 10–15 mm long, 1.5–3.0 mm wide, indurate with prominent parallel veins, stramineous with a dark band along midrib, apex long-acuminate, often strongly recurved, margin ciliate, entire, abaxial and adaxial surfaces glabrous. *Achenes* brown-black, 3.0 mm long, 1.5 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: July–November (August–December).

DISTRIBUTION AND HABITAT: Central Mexico in the states of Distrito Federal, Jalisco, México, Michoacán and Morelos (Fig. 34); cool wet habitats usually on slopes and in at least partial shade; 2300–2800 m.

*Montanoa frutescens* is a striking species because of its strongly convex receptacle and often strongly reflexed apex of the fruiting *pales* (Fig. 33K). Also, although the leaves vary in shape, they are distinct in being ovate or triangular and unlobed with partially winged bases (Fig. 33A–G). This species is further distinguished by its purple stems. It is most closely related to *M. mollissima* and *M. guatemalensis* and can be separated from both of these species by its green to cream disc corollas, short-acute apex on the style (Fig. 33H;  $0.25 \times 0.25$  mm) and larger number of disc florets (100–150). Both *M. mollissima* and *M. guatemalensis* have yellow disc corollas and acute to acuminate apices ( $0.5 \times 0.4$  mm and  $0.5 \times 0.25$  mm), and less than 100 disc florets. In addition, *M. mollissima*

has completely winged petioles while those of *M. frutescens* are only partially winged. *Montanoa guatemalensis* is a tree with a rounded apex on the involucre bracts, and achenes that are 4 mm long; *M. frutescens* has acute-acuminate apices on the bracts, and achenes 3 mm long.

REPRESENTATIVE SPECIMENS. MEXICO. DISTRITO FEDERAL: Valle de México, 1865–1866, *Bourgeau* 592 (BR, C, G, GH, K, MOU, MSC, S, US); ea. 10 mi NE of DF/Morelos state line, 17 Nov 1978, *FRi* 2848\* (OS); on the DF/Morelos state line, Dec 1977, *Ramos s.n.* (OS); near Esclava, 22 Sep 1903, *Pringle* 11549 (C, CU, F, GH, K, MICH, SMU, TEX, US); Cerro Guarda, 13 Jul 1952, *Matuda* 26226 (MEXU, NY); Esclava, Sep 1928, *Lyonnet* 394 (BM, GH, K, MO, NY, US); near Contreras, 20 Nov 1966, *Rzedowski* 23506 (DS, ENCB, MEXU, MICH). JALISCO: Nevado de Colima, *Boutin & Brandt* 2364 (MICH). MÉXICO: 5 mi N of Cuernavaca, 12 Nov 1977, *FGe* 2317 (OS); near San Pedro Nexapa, 9 Oct 1966, *Rzedowski* 23284 (BH, DS, ENCB, F, MEXU, MICH, MSC, WIS); 3 km N of San Juan Tehuixtlan, 20 Sep 1972, *Elias* 307 (ENCB); 3 km SW of San Rafael, 30 Sep 1974, *González* 9 (ENCB); Salto de Agua, Jan 1906, *Purpus* 1536 (F, G, GH, MO, NY, US); near Ozumba, 13 Sep 1953, *Matuda* 28955 (MEXU, NY); 6.6 mi S of Amecameca, 25 Nov 1966, *AL* 4314 (*Hinton* 15517 (GH, US)). MORELOS: 3.7 mi S of Tres Cumbres, 26 Nov 1966, *AL* 4315 (MICH, OS); S of México City, 16 Nov 1977, *FGe* 2361a (OS); mountain slopes overlooking Cuernavaca from the N, 3 Oct 1965, *C* 10326 (CA, DUKE, ENCB, MICH, MSC, NY, TEX, US, WIS); just S of DF/Morelos state line, 14 Nov–1978, *FRi* 2824\* (OS); near Huitzilae, 25 Oct 1967, *Crespo* 157 (OS); 5 km SE of Tres Marias, 25 Aug 1967, *Franco s.n.* (ENCB); Sierra de Morelos, 20 Sep 1969, *Hinton* 17402 (ENCB); above Cuernavaca, 13 Oct 1900, *Pringle* 9170 (CU, F, MO); Tres Cumbres, 3 Nov 1965, *Rzedowski* 21646 (DS, ENCB, LL, MICH, MSC).

**3. *Montanoa guatemalensis* Robinson & Greenman, Proc. Amer. Acad. Arts 34: 514. 1899. Type: GUATEMALA, Santa Rosa, Volcán Junaytepeque, 1800 m, Dec 1892, *E. T. Heyde* & *E. Lux* 4216 (holotype, NY!; isotypes, F! G! M! MO! NDG!). Figs. 4, 15, 34, 35.**

Trees 4–15 m tall. *Stems* terete, brown, herbaceous parts densely pubescent with the hairs 0.5–1.0 mm long. *Leaves* variable; petioles 1.0–14.5 cm long, occasionally with auricles at distal end, densely puberulent; blades ovate to pentagonal (Fig. 35A–I), 5–19 cm long, 3–18 cm wide, apex acuminate, margin entire to irregularly serrate-dentate, unlobed to 3-lobed, adaxial surface of younger leaves moderately pubescent, hairs pustular, older leaves often glabrous, abaxial surface densely glandular and pubescent, hairs whitish, giving the surface a light color, 0.5–1.0 mm long. *Peduncles* 1.5–2.5 mm long, densely hispid, hairs 0.5–1.0 mm long. *Heads* erect, 1.0–1.5 cm diam in flower, 2.0 cm diam in fruit, several to many in dense cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* extremely variable (Fig. 4), 5–9, biserrate, subequal, reflexed in flower, ovate to ovate-lanceolate, 3–8 mm long, 2–4 mm wide, green, apex usually rounded but occasionally acute to acuminate and mucronate, margin ciliate, entire, dark, abaxial surface densely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Ray florets* 6–10; corollas white, ligules obovate, 20–26 mm long, 6–9 mm wide, apex acute to 2-notched, adaxial surface glabrous, abaxial surface sparsely glandular and pubescent, hairs less than 0.5 mm long, tube 1.0–1.5 mm long, 0.5 mm wide, essentially glabrous. *Disc florets* (Fig. 35J) 70–100; corollas yellow, tube 0.75–1.5 mm long, 0.5–0.75 mm diam, densely glandular and pubescent, hairs less than 0.5 mm long, throat cylindrical, 2.0–2.25 mm long, 1.5–2.0 mm diam, sparsely glandular and pubescent, hairs less than 0.5 mm long, lobes 5, 0.75–1.00 mm long, 0.5 mm wide, apex acute, densely glandular and pubescent, hairs less than 0.5 mm long; stamens

with filaments 2.0–2.75 mm long, 0.2 mm wide, anthers not fully exerted from corolla, thecae brown, 1.5–1.75 mm long, 0.5 mm wide, apical appendages yellow, acuminate, 0.5 mm long, 0.3 mm wide, glabrous; styles yellow, 4.5–5.25 mm long, enlarged at base, stigmatic surfaces yellow, 1.0–1.25 mm long, apical appendages yellow, long-acuminate, 0.5 mm long, 0.4 mm wide. *Pales* at anthesis ovate (Fig. 35K), 4.5–5.5 mm long, 2.0–2.5 mm wide, light yellow with dark bands on distal half and midrib, apex very long acuminate, dark, margin ciliate, entire, abaxial surface densely glandular and pubescent especially near the center, hairs 0.5–1.0 mm long, adaxial surface glabrous; *pales* at fruiting persistent, ovate to triangular (Fig. 35L), 9–11 mm long, 2.5–3.0 mm wide, indurate with prominent parallel veins, stramineous, apex narrowly tapering to a recurved, indurate tip, margin sparsely ciliate, entire, abaxial surface moderately glandular near the center and sparsely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous; *achenes* brown-black, 3.5–4.0 mm long, 2.0 mm wide, smooth. Chromosome number,  $n = ca. 114$ .

FLOWERING (AND FRUITING) PERIOD: January–February (February–March).

DISTRIBUTION AND HABITAT: Primarily in Costa Rica but scattered collections from El Salvador, Guatemala, Honduras, and Nicaragua (Fig. 34); mountain slopes just below cloud forests; 1200–2000 m, cultivated at lower elevations near San José and Cartago but does poorly (pers. obser.).

Truly a “Daisy Tree” of the most spectacular nature. Distinguished not only by its habit but also by its leaves which vary from ovate to pentagonal and unlobed to 3-lobed with an essentially unwinged petiole (Fig. 35A–I) and have a white abaxial surface. The mature *pales* are typical of this series (Fig. 35L), but the involucre bracts are distinct in having a rounded apex (although they vary in size and number; Fig. 4). *Montanoa guatemalensis* is most closely related to *M. mollissima* which is easily distinguished, being a shrub of Puebla and Oaxaca with completely winged petioles and apically acute involucre bracts.

Herbarium identifications of this taxon have been confused by the misapplication of two names. *Montanoa guatemalensis* has been frequently but incorrectly identified as *M. dumicola*. Examination of the type of the latter showed that it was synonymous with *M. atriplicifolia*. Further, the name *M. guatemalensis* has usually been misapplied to the species recognized in this treatment as *M. hexagona*, both being trees. These species, however, are easily distinguished in the fruiting condition (in flowering condition they are more difficult to separate, as was the case with the type material).

REPRESENTATIVE SPECIMENS: COSTA RICA. ALAJUELA: ca. 2 km W of Zareero on rd to San Luis, 7 Jan 1980, *F 3047\** (CR, OS); ea. 2 km W of Zareero on rd to San Luis, 7 Jan 1980, *F 3049\** (CR, OS); 10 km N of Naranjo, 7 Jan 1980, *F 3053\** (CR, OS); btw San Ramón y Palmares, 6 Jan 1964, *Jiménez 1593* (F, MO, NY, US). CARTAGO: btw Turrialba and Paraiso, 6 Feb 1965, *Godfrey 66223* (COL, CR, MO). PUNTARENAS: 5 mi S of Monte Verde, 4 Jan 1972, *Wilbur et al. 15920* (DUKE, OS); ea. 6 km S of Monte Verde, 10 Jan 1980, *F 3056\** (CR, OS); San Francisco, NE of San Miguel, 9 Jan 1978, *Croat 44380* (CR, MO). SAN JOSÉ: near San Ramon de Tres Ríos, 4 Jan 1980, *F 3010\** (CR, OS); 5–10 km SW of San José on rd to Joreo, 12 Jan 1980, *FGo 3078* (CR, OS); rd from Jorco to Acosta, 13 Jan 1980, *FPF 3087* (CR, OS); 2 km NE of Joreo, 6 Jan 1972, *Wilbur et al. 16005* (DUKE); San Gabriel, 25 Nov 1964, *Jiménez 2589* (CR, F, NY, US); near San Ramon, 7 Jan 1927, *Brenes 447* [5296] (CU, F, NY); btw San Pedro de Montes de Oca and Curridabat, 2 Feb 1924, *Sa 32860* (US); Savana of San José, Feb 1893, *Tonduz 7331* (BM, CR, F, GH, M, US); near San Sebastián, 23 Feb 1926, *Sa 49322* (US); above Escasú, 31 Jan 1924, *Sa 32551* (US). EL SALVADOR. MORAZÁN: Mt. de Caaguatique, 27 Dec 1941, *Tucker 628* (BH, F, G, K, LL, MICH, NY, UC, US). SANTA ANA: Cerro Verde, 20 Feb 1968, *Molina & Molina 21515* (NY, US); 2 km SE of Cerro Verde, 11 Jan 1972, *Wilbur et al. 16273* (DUKE); slopes of Volcán Santa Ana, 11 Jan 1972, *Wilbur et al. 16256* (DUKE); slopes of Volcán Monte Cristo, 12 Jan 1972, *Wilbur et al. 16331* (DUKE). SONSONATE:



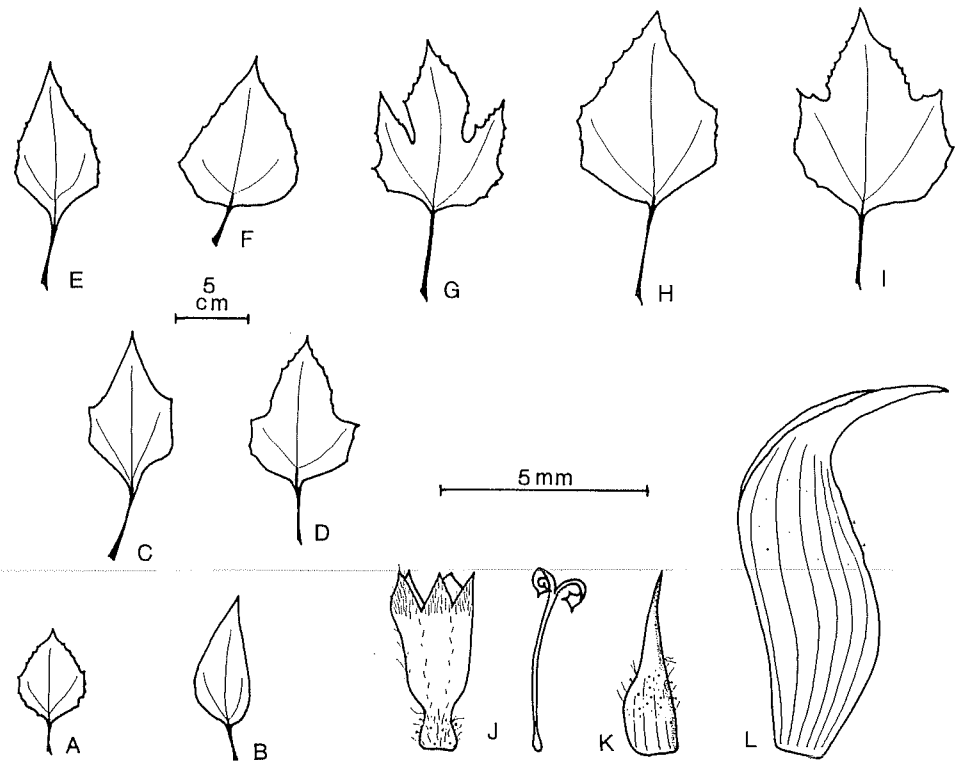


Fig. 35. *Montanoa guatemalensis*. A-I, variation in mature leaves: A, B, F-I, *F* 3087 (OS); C-E, *F* 3010 (OS). J, disc corolla and style, *F* 3010 (OS); K, pale subtending disc floret at anthesis, *Sa* 49322 (F); L, mature pale, *Sa* 49322 (F). A-I, J-L, same scale respectively.

Cerro Verde, 4 Feb 1959, *Allen* 7220 (F, LL, NY, US). GUATEMALA. GUATEMALA: in ravine near Canales, 25 Jan 1947, *Williams & Molina* 11828 (F, GH, US). HONDURAS. EL PARAÍSO: 4 km E of Yuscarán, 28 Dec 1962, *Williams & Molina* 23247 (B, BM, BR, C, DS, F, G, GH, LL, MICH, NY, UC, US, W). MORAZÁN: near El Sauce, 13 Jan 1947, *Standley & Williams* 2407 (F); rd to Cerro de Hule, 14 Jan 1968, *Molina* 21461 (F, NY, US). NICARAGUA. MATAGALPA: 5 km N of Matagalpa, 13 Jan 1963, *Williams et al.* 23730 (F, GH, NY, US).

4. *Montanoa mollissima* Brongniart ex Groenland, *Ann. Rev. Hort.* 543. 1857. Type: MEXICO, collected from Hort. Paris, 1851 from plant "grown from seeds sent from Mexico by A. B. Giesbreght in 1843," A. B. Giesbreght *s.n.* (holotype, P!; isotypes, FI! P!; photos of holotype, GH! OS! US!; fragment of holotype, GH!). *Eriocoma mollissima* (Brongniart ex Groenland) Kuntze, *Rev. Gen. Pl.* 1: 336. 1891.

Figs. 32A, 34, 36.

*Montanoa pringlei* Robins. & Greenm., *Proc. Amer. Acad. Arts* 34: 512. 1899. Type: MEXICO, Puebla, calcareous hills near Tehuacán, 28 Jul 1897, *C. G. Pringle* 7491 (holotype, GH!).

*Montanoa teluacana* Robins., *Proc. Amer. Acad. Arts* 47: 209. 1911. Type: MEXICO, Puebla, tufa bluffs near Tehuacán, 1680 m, 7 Aug 1901, *C. G. Pringle* 8585 (holotype, GH!; isotypes, BM! C! CM! CU! F! FI! G! GOET! K! LE! M! MEXU! MICH! MO! MSC! NY! P! S! UC! US! W!; photo of isotypes from K and P, OS!).

Shrubs 1-2(-4) m tall. *Stems* terete, brown, herbaceous parts puberulent. *Leaves* variable; petioles 1-6 cm long, partially or completely winged with auri-

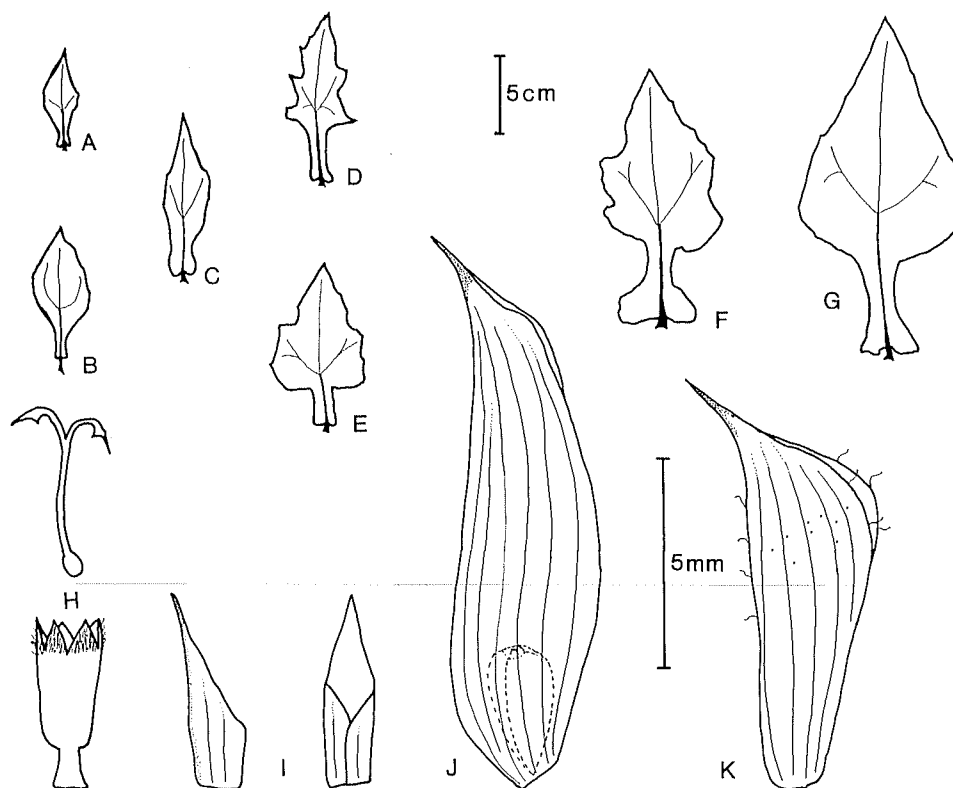


Fig. 36. *Montanoa mollissima*. A-G, variation in mature leaves: A, *Rose & Rose 11376* (NY); B, *F s.n.* (OS); C, *Cisneros 2568* (OS); D, *HF 4146* (OS); E, F, *AL 4294* (OS); G, *HF 4156* (OS). H, disc corolla and style, *HF 4146* (OS); I, two views of pale subtending disc floret at anthesis, *HF 4156* (OS); J, K, mature pales, *AL 4295* (OS). A-G, H-K, same scale respectively.

cles at base, puberulent to moderately pubescent, hairs 0.5–1.0 mm long; blades lanceolate to triangular (Fig. 36A–G), 2.5–14.5 cm long, 1–10 cm wide, apex acute to acuminate, margin entire to irregularly dentate to 3-lobed, adaxial surface densely pubescent, hairs pustular, abaxial surface densely glandular and pubescent, hairs white, less than 1.0 mm long. *Peduncles* 1.5 cm long, densely puberulent. *Heads* erect, 1.0–1.2 cm diam in flower, 2.0–2.5 cm diam in fruit, several to many in open cymose synflorescences in oppositely branched compound corymbs. *Phyllaries* 6–8, more or less uniseriate, equal, ovate-lanceolate, 4–7 mm long, 1.5–2.0 mm wide, green, apex acute to acuminate, margin ciliate, entire, abaxial surface densely pubescent, hairs 1.0 mm long, adaxial surface essentially glabrous. *Ray florets* 8–12; corollas white, ligules 15–30 mm long, 6–8 mm wide, adaxial surface essentially glabrous, abaxial surface moderately glandular and sparsely pubescent especially on the veins, hairs less than 0.5 mm long, tube 1.0–1.5 mm long, 0.5 mm wide, glabrous. *Disc florets* (Fig. 36H) 75–100; corollas yellow, tube 1.0–1.5, 0.5 mm diam, glabrous, throat cylindrical, 2.0 mm long, 1.0 mm diam, essentially glabrous, lobes 5 (rarely 4), 1.0 mm long, 0.75 mm wide, apex acute, densely glandular and pubescent, hairs thick, less than 0.5 mm long; stamens with filaments 2.0 mm long, 0.2 mm wide, anthers not fully exerted from corolla, thecae yellow to brown, 1.5–1.75 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5 mm long, 0.5 mm wide, abaxial surface of apical

appendage glandular, styles yellow, 4.5–5.5 mm long, enlarged at base, stigmatic surface yellow, 1.0 mm long, apical appendage yellow, long-acuminate, 0.5 mm long, 0.25 mm wide. *Pales* at anthesis ovate-triangular (Fig. 36I) 4–5 mm long, 1.0 mm wide, light yellow, apex long-acuminate, indurate, yellow, abaxial surface sparsely glandular and pubescent, hairs 1.0 mm long, adaxial surface glabrous, margin ciliate, entire; *pales* at fruiting persistent, almost narrowly triangular (Figs. 32A; 36J, K), 9–12 mm long, 2.5–3.0 mm wide, indurate with prominent parallel veins, stramineous, apex tapering to a slightly recurved and indurate tip, margin sparsely ciliate, entire, abaxial surface sparsely glandular and pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Achenes* brown-black, 3.0–3.5 mm long, 2.0 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: July–September (August–November).

DISTRIBUTION AND HABITAT: Mexican states of Puebla and Oaxaca, especially near Tehuacán (Fig. 34); hot dry mountainsides, tufa bluffs, open rocky slopes and thorn forests; 1600–2150 m.

A much-branched shrub that usually appears straggly because of the relatively small leaves (blades not over 14.5 cm long), that are often few and widely spaced on the branches. The species is distinct because of its habit and completely or nearly completely winged petioles. *Montanoa mollissima* is most closely related to the sub-cloud forest tree, *M. guatemalensis* with which it shares a white abaxial leaf surface, 70–100 disc florets and similar mature *pales*. But, it is easily distinguished from this species by the presence of winged petioles and the shrubby habit. Also, the mature *pales* of the two species, although similar in shape and size, differ in that those of *M. guatemalensis* are more recurved (cf. Figs. 36J, K; 35L).

Plants of this species (e.g., *Cronquist & Sousa 10394*) have been collected growing with members of *M. tomentosa* subsp. *xanthiifolia* (e.g., *Cronquist & Sousa 10395*) near Tehuacán where both taxa are common. No morphological evidence for hybridization has been found; the two species appear distinct in all collections from that area.

REPRESENTATIVE SPECIMENS. MEXICO. HIDALGO: 8 km NW of Zimapán, 17 Aug 1967, *Quintero 3797* (ENCB); 10 km NW of Zimapán, 27 Oct 1965, *Quintero 3237* (ENCB); Jacala, 19 Oct 1937, *Kenoyer 388* (F, MO); Barranca de Toliman near Zimapán, 8 Aug 1948, *Moore & Wood 4388* (BM, MICH). OAXACA: near Tamasulapa on Río de Oro, 20 Nov 1977, *Fra 2380* (OS); La Huerta, 9 Oct 1970, *Cisneros 2568* (ENCB, OS); 16 mi SE of Huajuapán de León, 22 Aug 1976, *HF 4156\** (OS); 22 mi SE of Huajuapán de León, 21 Nov 1966, *AL 4271* (OS); 5 km NE Chilapa de Díaz, 12 Aug 1967, *Rzedowski 35131* (ENCB); N of Jayacatlan on rd to Nacaltepec, 4 Nov 1973, *Breedlove 35954* (CA, MICH); 4.6 mi NE of Chazumba, 23 Nov 1966, *AL 4292* (MICH, OS). PUEBLA: Acatlán, 18 Sep 1943, *Miranda 3023* (MEXU); 34 mi SE of Tehuacán, 21 Aug 1976, *HF 4148* (OS); near Acatepec, 19–27 Aug 1963, *Gentry et al. 20289* (US); Agua Escondida, 3 Oct 1942, *Miranda 2295* (MEXU); near San Antonio Texcala, 19 Nov 1977, *Fra 2363\** (OS); btw Nacozcalco and San Antonio Canada, 13 Jul 1961, *Smith et al. 4074* (F, US); 6 mi N of Tehuacán, 1 Nov 1966, *AL 4091* (MICH, OS); near Tehuacán, 8 Sep 1906, *Rose & Rose 11376* (C, F, GH, K, MO, NY); 3 mi NW of Oaxaca/Puebla state line, hwy 190, 23 Nov 1966, *AL 4295* (MICH, OS); 8 mi SW of Tehuacán, 21 Aug 1976, *HF 4146\** (OS); San Luis Tultitlanapa, Aug 1908, *Purpus 3105* (BM, F, G, GH, MO, NY, UC); 26 mi SW of Tehuacán, 23 Oct 1965, *Cronquist & Sousa 10394* (CA, DUKE, ENCB, MICH, MSC, NY, TEX, US). QUERETARO: 3 mi E of Bernal on rd to Jalpán, 2 Sep 1965, *Johnston & Johnston 7286* (TEX). UNITED STATES. MISSOURI: cultivated at Missouri Botanical Garden, Oct 1976, *F. s.n.\** (OS).

5. *Montanoa andersonii* McVaugh, Contr. Univ. Michigan Herb. 9: 421. 1972.

Type: MEXICO, Jalisco, 30–35 mi SE of Autlán, on steep slopes near summits, in pine-oak forest, 2500 m, 2 Nov 1952, *R. McVaugh 13849* (holotype, MICH!; isotypes, BM! DUKE! LL! MEXU! NY! SMU!; photo of BM isotype, OS!). Figs. 34, 37.

Shrubs to small trees 3–7 m tall. *Stems* terete, grooved, brown, herbaceous parts moderately pubescent with reddish or brownish-white appressed hairs. *Leaves* variable; petioles 2.0–18.5 cm long, occasionally with auricles at distal end, moderately pubescent, hairs reddish, 0.5–1.0 mm long; blades ovate to pentagonal (Fig. 37A–G), 6.5–18.5 cm long, 3.0–17.5 mm wide, apex long-acuminate, margin entire to irregularly serrate, adaxial surface dark green, sparsely to moderately pubescent, hairs pustular, abaxial surface paler green, moderately glandular, hairs in axils of major veins. *Peduncles* 0.3–1.0 cm long, densely pubescent, hairs less than 1.0 mm long. *Heads* erect, less than 1.0 cm diam in flower, ca. 1.0 cm diam in fruit, few to several in dense cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* 3–6, more or less biseriate, elliptic or ovate-lanceolate, loosely reflexed, 3–5 mm long, 1.0–1.5 mm wide, green, apex obtuse or mucronate, margin ciliate, entire, abaxial surface densely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Ray florets* 7–8; corollas white, ligules elliptic to obovate, 20–35 mm long, 4–6 mm wide, apex truncate to 2-notched, adaxial surface glabrous, abaxial surface sparsely glandular and pubescent, hairs 0.5–1.0 mm long, tube 1.0 mm long, 0.5 mm wide, glabrous. *Disc florets* (Fig. 37H) 25–35; corollas yellow, tube 1.5 mm long, 0.3–0.5 mm diam, moderately glandular and pubescent, hairs 0.5–1.0 mm long, throat narrowly cylindrical, 4.0–4.5 mm long, 1.0–1.5 mm diam, sparsely glandular and pubescent especially on veins, hairs less than 0.5 mm long, lobes 5, 1.0–1.2 mm long, 0.5 mm wide, apex acute to narrowly acute, densely glandular and pubescent, hairs less than 0.5 mm long; stamens with filaments 5.0–5.5 mm long, 0.2 mm wide, anthers fully exerted from corolla (Fig. 37H), thecae brown to purple, 2.5–3.0 mm long, 0.5 mm wide, apical appendages yellow, usually with purple on tip, narrowly acute to acute, 0.5–0.7 mm long, 0.25–0.3 mm wide, glabrous; styles yellow, 10.0–11.5 mm long, enlarged at base, stigmatic surface yellow, 1.0 mm long, apical appendage yellow with purple, acuminate, 0.5 mm long, 0.25 mm wide. *Pales* at anthesis ovate-triangular (Fig. 37I), 5–6 mm long, 1.5–3.0 mm wide, light yellow sometimes with purple on distal half, apex long-acuminate, indurate, often purple, margin ciliate, entire, abaxial surface densely glandular near center and pubescent on the veins, hairs 0.5–1.0 mm long, adaxial surface glabrous; pales at fruiting and *achenes* not available. Chromosome number unknown.

FLOWERING PERIOD: September–March.

DISTRIBUTION AND HABITAT: Two restricted areas in Jalisco and Guerrero (Fig. 34); cool, wet, pine-oak forests, mountain crests and ridges; 2150–2500 m.

This shrub-tree is an attractive plant with several distinct features: long rays (20–35 mm) with an obtuse apex, anthers which are completely exerted from the corolla at anthesis, and styles and anthers that are very long (10.0–11.5 mm and 8.0–9.2 mm respectively). Also, the apices of the disc florets and anthers and styles are often red-purple.

*Montanoa andersonii* has not been collected in mature fruit. One of the specimens (*M* 13849) bears some apparently abortive fruiting heads left over from the previous year (Fig. 37J). The pales subtending the disc florets at anthesis (Fig. 37I) can be compared with others of the series (e.g., Figs. 36J, K; 38G) and the similarities indicate that *M. andersonii* belongs in this series. *Montanoa andersonii* is most closely related to *M. standleyi* and a comparison of the two species is included in the discussion of the latter.

REPRESENTATIVE SPECIMENS. MEXICO, JALISCO: 30–35 km SE of Aullán, 29 Sep 1966, *AL* 3812 (MICH); 30–35 km SE of Aullán, 29 Sep 1966, *AL* 3824 (MICH, OS); 28.5 mi from El Chante, 29 Sep

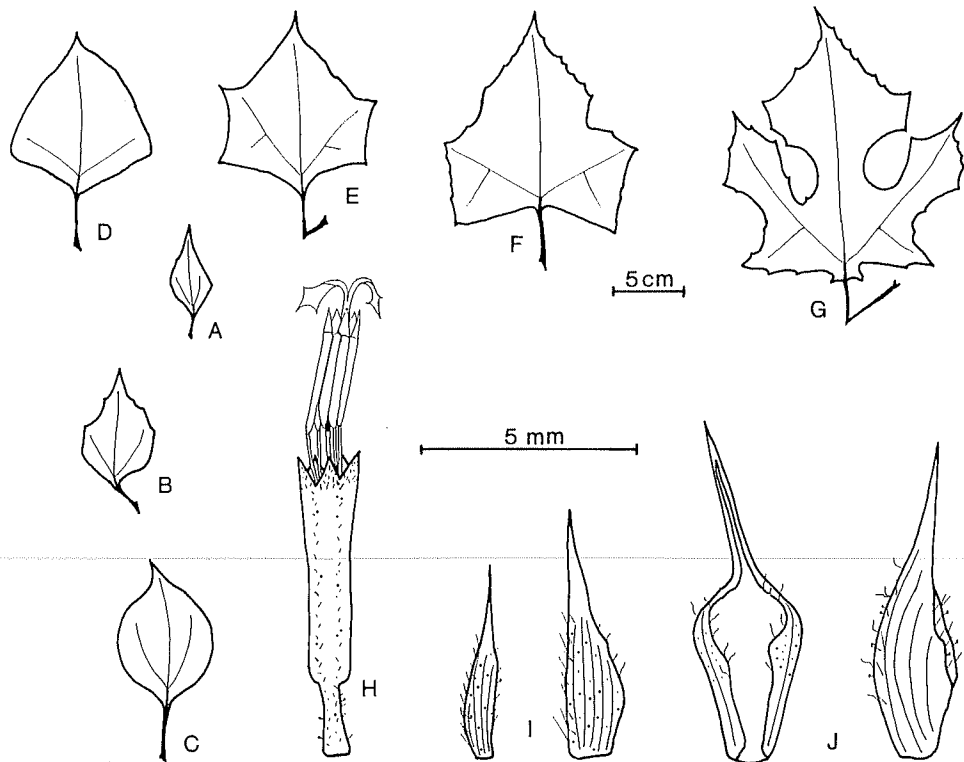


Fig. 37. *Montanoa andersonii*. A-G, variation in mature leaves: A, AL 3814 (OS); B, Hinton 12794 (MICH); F, AL 3812 (OS); C, Boutin & Brandt 2519 (ENCB); D, M 22822 (MICH); E, AL 3822 (OS); G, AL 3824 (OS). H-J, M 13849 (MICH): H, disc floret; I, pales subtending disc floret at anthesis; J, two views of more mature pale. A-G, H-J, same scale respectively.

1966, AL 3814 (MICH, OS); Sierra de Manantlán or Cerro del Muneco, 7-8 mi from crest, 29 Sep 1966, AL 3822 (MICH, OS); Sierra de Manantlán, above Aserradero, 23 Nov 1968, Boutin & Brandt 2519 (ENCB). MICHOCÁN: Coacomán, Torricillas, 19 Dec 1938, Hinton 12794 (C, F, G, GH, MICH, M, MO, NY, S, TEX, UC, US, W); ca. 25 km SW of Aserradero Dos Aguas, 6 Mar 1965, M 22822 (DS, DUKE, ENCB, MICH, NY).

6. *Montanoa standleyi* V. A. Funk, sp. nov. Type: MEXICO, Chiapas, Mt. Ovan-do, 2300 m, shrub of 4 m, 14-18 Nov 1939, E. Matuda 3939 (holotype, MEXU!; isotypes, A! F! MICH! MO! NY! TEX! US!; photo of ho-  
 lotype, OS!). Figs. 34, 38.

Frutices 4-metrales. Caules teretes brunneoli glabri. Folia vix variabilia; petioli 1.5-7.0 cm longi, puberuli; laminae ovata-lanceolatae vel pentagonae (Fig. 38A), 7-12 × 3.5-10.0 cm, apice acuminatae, marginibus serratae, pagina adaxiali pilis pustuliformibus subpubescenti, pagina abaxiali glabra. Pedunculi 1.0-3.5 cm longi, puberuli. Capitula erecta florifera 1.0 cm fructifera 1.5 cm lata, nonnulla vel multa in synflorescentia cymosa corymbis composita. Phyllaria 5, 1-seriata inter se aequalia, lanceolata, 5-6 × 1.0-1.5 mm, viridia, apice acuminata mucronata, marginibus glabra integra, pagina adaxiali sparsim pubescenti, pagina abaxiali glabra. Radii (Fig. 38B) 5-10, albi, ligula obovata 18-22 × 6-8 mm, apice acuta, pagina adaxiali glabra, pagina abaxiali glandulosa et sparsim pubescenti, tubo minimo glabro. Flosculi disci (Fig. 38C) 35-50, lutei, tubo 1.0 × 0.5 mm, subglabro, fauce cylindraceo 3.0-3.5 × 1.5 mm, glabro, lobis 5, 1.0-1.5 × 0.5 mm apice acuminatis, glabris; stamina filamentis inclusis 2.7-3.0 × 0.2 mm, antheris (Fig. 38D) semi-exsertis, thecis luteis vel brunneolis, 2.0 × 0.5 mm, connectivo apice acuminato, 1.0 × 0.4 mm, luteo, glabro; stylus (Fig. 38E) luteus, 6.25-6.75 mm longus, basi tumefactus, lineolis stigmaticis luteis vel brunneolis, 1.0 mm longis, ap-

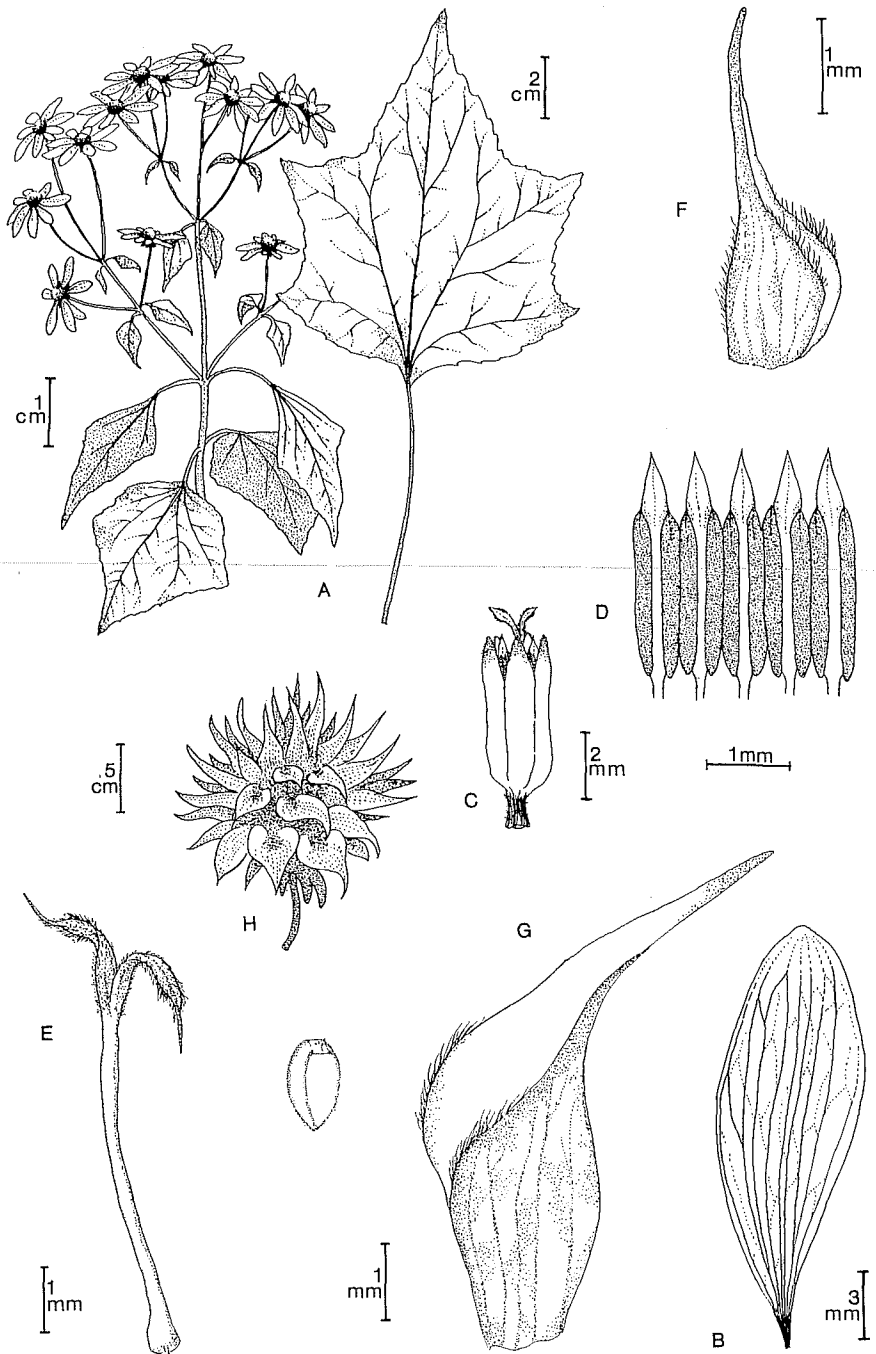


Fig. 38. *Montanoa standleyi* (Matuda 3939, MEXU): A, distal section of flowering branch and primary leaf; B, ray floret; C, disc floret; D, anthers; E, style; F, pale at anthesis; G, pale surrounding mature achene; H, fruiting head; I, mature achene. E, I, same scale.

the corollas, anthers and stigmas, 35–50 disc florets, and anthers not fully exerted from the corolla.

This species is named in honor of Paul C. Standley (1884–1963) who annotated the type specimen as a new species, naming it after the state of Chiapas, but never published a description. His extensive collecting in Mexico and Central America and numerous monographs on the plants of these areas are well known.

**SPECIMENS EXAMINED:** MEXICO. CHIAPAS: Mt. Ovando, Apr 1936, *Matuda 2235* (MICH); Mt. Pasitan, 31 Dec 1936, *Matuda 749* (MICH); along southern slopes to crest of Sierra de Soconusco, 6 Nov 1945, *Xolocotzi & Sharp 362* (MEXU). OAXACA: 48 mi N of Puerto Escondido, 8 Nov 1965, *Cronquist & Sousa 10515* (ENCB, MICH, NY); btw Puerto Escondido and Lachao, Oct 1965, *Talbot s.n.* (ENCB).

**IBb. *Montanoa* section *Echinocephalae* series *Amoenae* V. A. Funk, ser. nov.**  
(delightful to look at.)

Paleae in maturitate marginibus valde incurvatis minus quam dimidiis longitudinibus, apicibus complanatus effusus. Typus: *Montanoa liebmannii* (Schultz Bip. in Klatt) S. F. Blake. Species 7–8.

Series *Amoenae* contains two species of restricted range in Oaxaca and Chiapas, Mexico, and Huehuetenango, Guatemala. The pales of both species are similar, varying only in length. The species are delimited by a number of characters, including the number and color of disc florets and leaf shape.

**7. *Montanoa liebmannii* (Schultz Bipontinus in Klatt) S. F. Blake, Contr. Gray Herb. 52: 37. 1917. *Polymnia liebmannii* Schultz Bip. in Klatt, Leopoldina 23: 89. 1887. Type: MEXICO, Oaxaca, Cumbre de Estepa, Sep 1842, *F. M. Liebmann 385* [Liebm. Pl. Mex. 8990] (holotype, C!; isotypes, C[2]!; photo and fragment of holotype, GH!; photo of C isotype F! US!).** Figs. 39, 40.

*Montanoa macrolepis* Robins. & Greenm., Proc. Amer. Acad. Arts 32: 44. 1896. Type: MEXICO, Oaxaca, Las Sedas, in gulches of hills, 6000 ft, 29 Sep 1894, *C. G. Pringle 4932* (holotype, US!; isotypes, BM! BR! CM! ENCB! F! G[2]! GH! GOET! K! LE! M! MEXU! MO! MSC! NDG! NY! P! S! US! W!; photos of K and P isotypes, OS!).

Much branched shrubs 1–2 m tall. *Stems* terete, brown, herbaceous parts densely pubescent, hairs white, 0.5–1.0 mm long. *Leaves* relatively consistent; petioles 1.0–4.5 cm long, partially winged, sparsely to densely pubescent, hairs 1.0 mm long; blades ovate to pentagonal (Fig. 39A–E), 3–11 cm long, 2–9 cm wide, apex acute to acuminate, margin entire to irregularly serrate, usually deeply 3-lobed, adaxial surface moderately pubescent, hairs pustular, abaxial surface nearly glabrous to densely glandular and pubescent, hairs 1.0 mm long. *Peduncles* 1–13 cm long, glabrous to densely glandular and pubescent, hairs 1.5 mm long. *Heads* erect, 1.5–2.0 cm diam in flower, 2.5–3.5 in fruit, solitary to few in cymose synflorescences. *Phyllaries* 10, biseriate, equal to subequal, reflexed, ovate, 5–9 mm long, 3.5–5.0 mm wide, green, apex acute, rounded or acuminate, margin ciliate, entire, abaxial surface moderately pubescent, hairs 0.5–1.0 mm long, adaxial surface moderately pubescent on distal half, hairs 0.5 mm long. *Ray florets* ca. 10; corollas white, ligules oblong, 14–16 mm long, 4–6 mm wide, apex rounded to 2-notched, adaxial surface sparsely pubescent on the veins, abaxial surface moderately glandular, tube 1.0 mm long, 0.5 mm wide, sparsely pubescent, hairs 0.5–1.0 mm long. *Disc florets* (Fig. 39F) 60–80; corollas yellow, tube 1.0–1.5 mm long, 0.5 mm diam, glabrous, throat cylindrical, 3.5–4.0 mm long, 1.5 mm diam, sparsely pubescent, lobes 5, 1.0–1.5 mm long, 0.5–0.75 mm wide, apex acute, cells along the margin black, densely pubescent, hairs thick, 0.5–1.0 mm long; stamens with filaments 3–4 mm long, 0.2 mm wide, anthers not fully

pendiculis acuminatis, 0.75 × 0.25 mm, apice luteis. Paleae sub anthesi ovato-triangules (Fig. 38F), 3.5–4.0 × 2.0 mm, dorso carinatae, luteolae secus venas atrovirides, apice longiuscule acuminatae, fuscae, induratae, margine ciliatae integrae, utrinque glabrae; paleae fructiferae persistentes, triangulares (Fig. 38G, H), 8.0 × 1.5 mm, dorso carinatae, induratae, prominule parallele venosae, stramineae, apice longiuscule acuminatae, recurvae, margine subglabrae integrae, utrinque glabrae. Achaenia brunneo-nigra prominule 4-angulata (Fig. 38I), 2.25 × 1.25 mm, laevia. Chromosomatum numerus ignotus.

Shrubs 4 m tall. *Stems* terete, light brown, glabrous. *Leaves* scarcely variable; petioles 1.5–7.0 cm long, puberulent; blades ovate-lanceolate to pentagonal (Fig. 38A), 7–12 cm long, 3.5–10.0 cm wide, apex acuminate, margin serrate, adaxial surface sparsely pubescent, hairs pustular, abaxial surface glabrous. *Peduncles* 1.0–3.5 cm long, moderately puberulent. *Heads* erect, 1.0 cm diam in flower, 1.5 cm diam in fruit, several to many in cymose synflorescences in oppositely or alternately branched compound corymbs. *Phyllaries* 5, uniseriate, equal, lanceolate, 5–6 mm long, 1.0–1.5 mm wide, green, apex acuminate, mucronate, margin glabrous, entire, abaxial surface nearly glabrous, adaxial surface glabrous. *Ray florets* (Fig. 38B) 5–10; corollas white, ligules obovate, 18–22 mm long, 6–8 mm wide, apex acute, adaxial surface glabrous, abaxial surface sparsely glandular and pubescent, hairs less than 0.5 mm long, tube almost non-existent and glabrous. *Disc florets* (Fig. 38C) 35–50; corollas yellow, tube 1.0 mm long, 0.5 mm diam, essentially glabrous, throat cylindrical, 3.0–3.5 mm long, 1.5 mm diam, glabrous, lobes 5, 1.0–1.5 mm long, 0.5 mm wide, apex acuminate, glabrous; stamens with filaments 2.7–3.0 mm long, 0.2 mm wide, anthers (Fig. 38D) not fully exerted from corolla, thecae yellow or brown, 2.0 mm long, 0.5 mm wide, apex of connective yellow, acuminate, 1.0 mm long, 0.4 mm wide, glabrous; styles (Fig. 38E) yellow, 6.25–6.75 mm long, enlarged at base, stigmatic surfaces yellow or brown, 1.0 mm long, apical appendages acuminate, yellow, 0.75 mm long, 0.25 mm wide. *Pales* at anthesis ovate-triangular with slight keel on abaxial surface of the midrib (Fig. 38F), 3.5–4.0 mm long, 2.0 mm wide, light yellow with dark green bands on veins, apex long-acuminate, dark, indurate, margin ciliate, entire, adaxial and abaxial surfaces glabrous; pales at fruiting persistent, triangular (Fig. 38G, H) with slight keel on abaxial surface of midrib, 8 mm long, 1.5 mm wide, indurate with prominent parallel veins, stramineous, apex long-acuminate, recurved, margin essentially glabrous, entire, adaxial and abaxial surfaces glabrous. *Achenes* brown-black, prominently 4-edged (Fig. 38I), 2.25 mm long, 1.25 mm wide, smooth. Chromosome number unknown.

**FLOWERING (AND FRUITING) PERIOD:** October–November (November–January), bears fruiting heads with achenes at least until April.

**DISTRIBUTION AND HABITAT:** Mexican states of Chiapas and Oaxaca (Fig. 34); collected on isolated mountain tops in Chiapas and high on the Pacific slopes of the Sierra Madre del Sur in Oaxaca; mixed pine and deciduous sub-tropical forests and granitic areas; 2000–3000 m.

This rarely collected species is distinct in the genus because of the slightly keeled abaxial surface of the pales and the rather sharp edges of the achenes (Fig. 38I). The mature pales are similar to others in this series but are not as recurved (Fig. 38G) as those of *Montanoa frutescens*. *Montanoa standleyi* is most closely related to *M. andersonii* which does not have keeled pales and achenes. It can be distinguished further because *M. andersonii* has appressed-pubescent stems, acute apices on the corollas, anthers and stigmas, a smaller number of disc florets (25–35), and anthers fully exerted from the corolla. *Montanoa standleyi* on the other hand has glabrous stems, very acuminate apices on



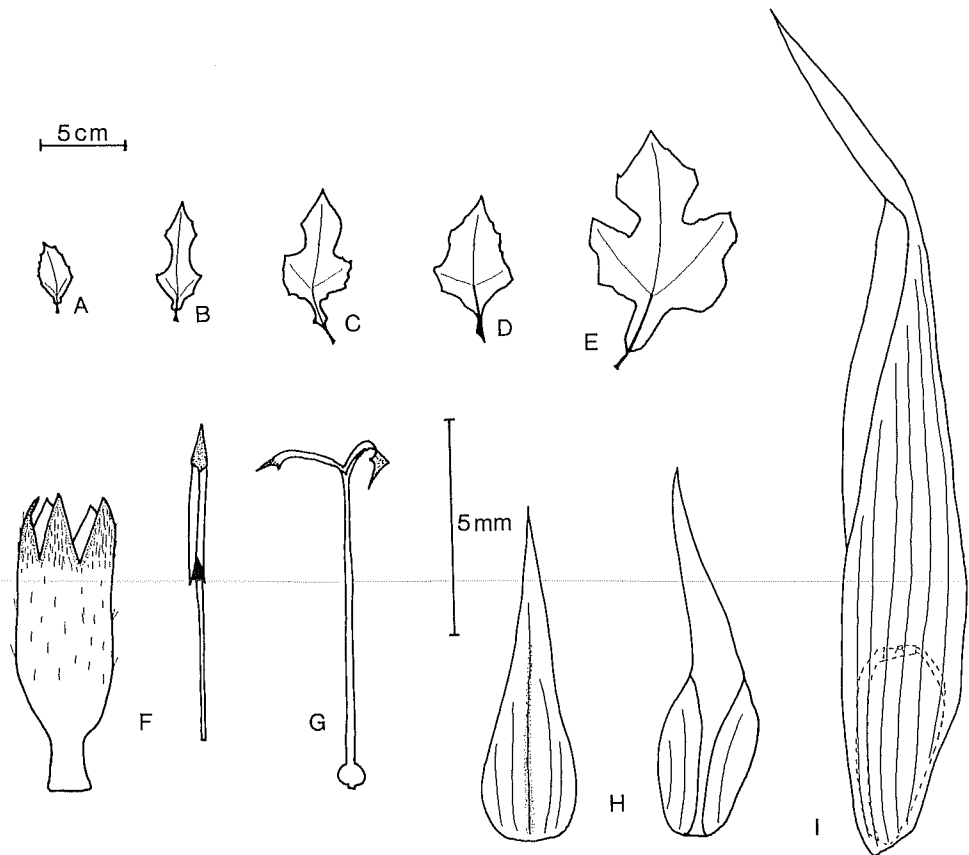


Fig. 39. *Montanoa liebmannii*. A-E, variation in mature leaves: A, Nelson 1375 (US); B-E, AL 4137 (OS). F, disc corolla and stamen, Nelson 1375 (GH); G, style, Nelson 1375 (US); H, I, two views of pale subtending disc floret at anthesis and mature pale, AL 4137 (OS). A-E, F-I, same scale respectively.

exserted from corolla, thecae black, 2.5–3.0 mm long, 0.5 mm wide, apical appendages black (Fig. 39F), acuminate to very long-acuminate, 1.0 mm long, 0.25 mm wide, abaxial surface of apical appendage glandular; styles (Fig. 39G) yellow, 5.5–6.75 mm long, enlarged at base, stigmatic surface yellow, 1.5–2.0 mm long, apical appendages black, acuminate, 0.5–0.75 mm long, 0.4–0.5 mm wide. *Pales* at anthesis narrowly triangular (Fig. 39H), 7–8 mm long, 1.5 mm wide, light yellow, apex long-acuminate, margin entire, abaxial surface sparsely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous; *pales* at fruiting persistent, narrowly triangular (Fig. 39I), 14–16 mm long, 4.0 mm wide, indurate with prominent parallel veins, stramineous, apex long-acuminate, indurate, margin glabrous, entire, abaxial and adaxial surfaces glabrous. *Achenes* brown-black, 3.5 mm long, 1.5 mm wide, smooth. Chromosome number unknown.

**FLOWERING (AND FRUITING) PERIOD:** August–September (September–November).

**DISTRIBUTION AND HABITAT:** Known only from Oaxaca, Mexico (Fig. 40); dry rocky soil along roadsides and at the edge of fields, probably pine-oak forests; 1850–3000 m.

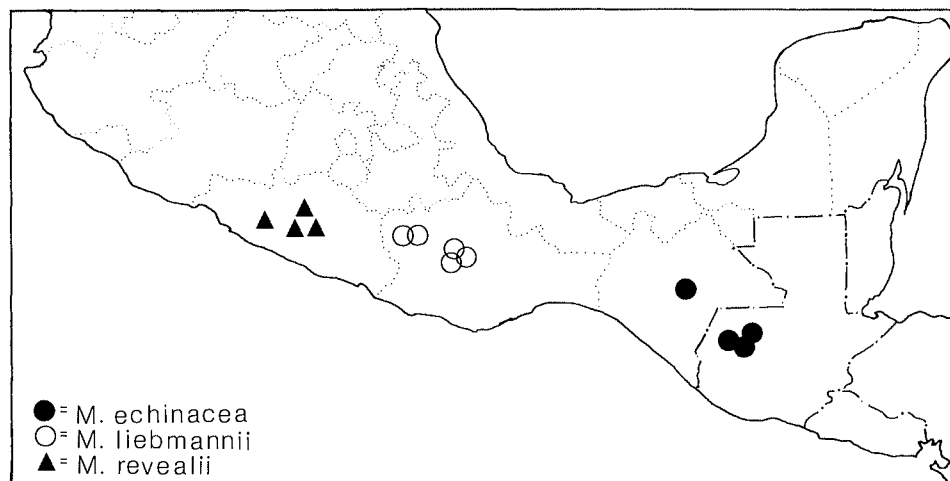


Fig. 40. Map of southern Mexico showing the distribution of *Montanoa echinacea*, *M. liebmannii*, and *M. revealii*.

This species is another of the elusive species of the Las Sedas area of Oaxaca. The leaves of *Montanoa liebmannii* are distinct, with almost completely winged petioles and blades that are usually 3-lobed (Fig. 39A–E). It is closely related to *M. echinacea*, sharing large flattened mature pales that are erect and cup around the achene only near the base (Figs. 39I; 41D). Further, the two species have black on the apices of the corolla, anthers and stigma, and the heads are solitary or in a simple dichasium. *Montanoa liebmannii* is readily separated from *M. echinacea*, however, by the leaves. Those of *M. echinacea* are cordate with 3–4 lateral veins located proximally to the juncture of the 3 main veins of the blade (Fig. 41A). Further, *M. echinacea* has longer involucre bracts (9–18 mm) and more disc florets (100–150) per head than *M. liebmannii* (involucre bracts 5–9 mm long, and 60–80 disc florets).

SPECIMENS EXAMINED: MEXICO. OAXACA: near Jaycatlan, 6 Nov 1966, AL 4137 (MICH, OS); 22 mi SE of Huajuapán de León, 21 Nov 1966, AL 4271 (MICH); near Acatepec, 19–27 Aug 1963, Gentry et al. 20289 (ENCB); 18 mi SW of Oaxaca, 10–20 Sep 1894, Nelson 1375 (GH, US).

8. *Montanoa echinacea* S. F. Blake, *Brittonia* 2: 345. 1937. Type: GUATEMALA, Huehuetenango, above Chiantla, 10,000 ft, 16 Sep 1934, A. F. Skutch 1276 (holotype, A!; isotypes, F! LL! NY! US!).

Figs. 32B, 40, 41, 42.

Shrubs 1–4 m tall. *Stems* terete, light brown, herbaceous parts glandular and pubescent, hairs 0.8 mm long. *Leaves* very consistent; petioles 1.6 cm long, densely hispid, hairs 1–2 mm long; blades ovate to cordate (Fig. 41A), 7–15 cm long, 3–12 cm wide, apex long-acuminate, base below the juncture of the 3 main veins with 3–4 lateral veins, margin sparsely serrulate to entire, adaxial surface densely pubescent, hairs pustular, abaxial surface densely glandular and pubescent, hairs 1.0 mm long. *Peduncles* 2–11 cm long, densely glandular, hispid, hairs 1.0 mm long. *Heads* erect, 2 cm diam in flower, 3 cm diam in fruit, solitary to few in open cymose synflorescences. *Phyllaries* 12, reflexing in fruit, biseriate, subequal, ovate to ovate-lanceolate, 9–18 mm long, 3–5 mm wide, dark green,

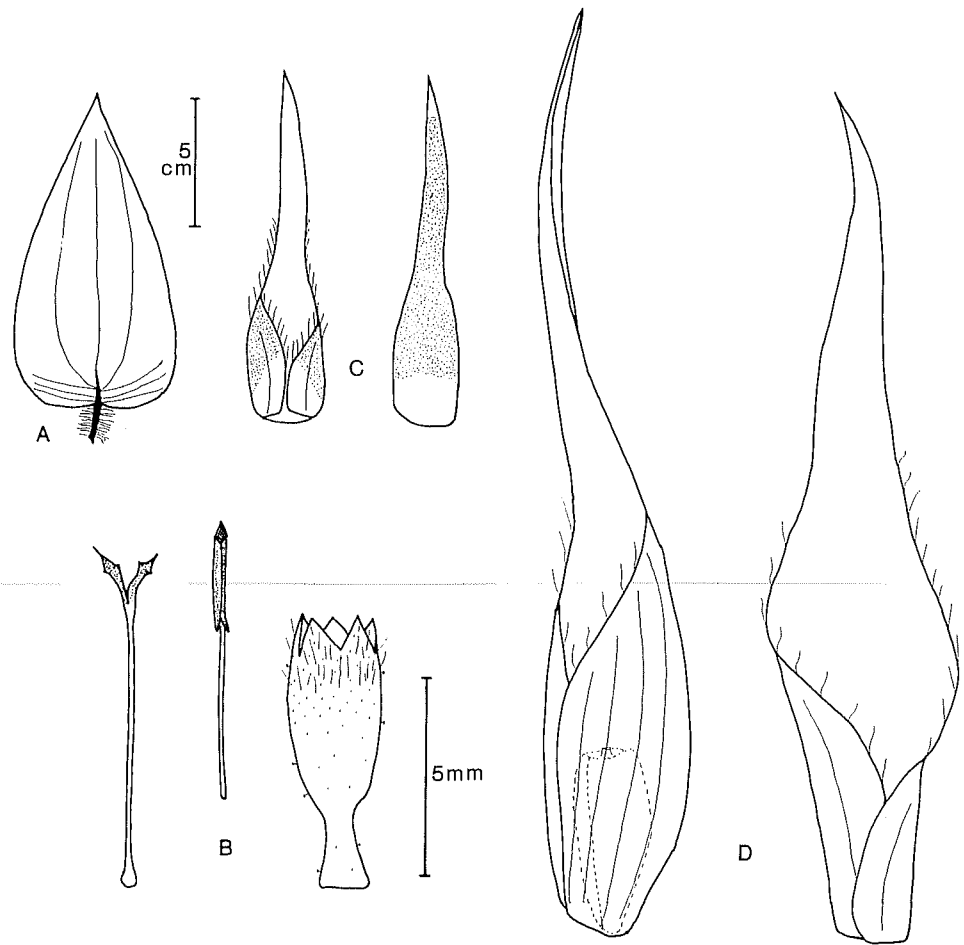


Fig. 41. *Montanoa echinacea*. A, leaf, Skutch 1276 (NY); B, disc corolla, style and stamen, Skutch 1276 (NY); C, two views of pale subtending disc floret at anthesis, Williams et al. 22012 (NY); D, mature pales, Breedlove 29677 (DS). A, B-D, same scale respectively.

apex acute with mucronate tips, margin entire, abaxial surface densely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Ray florets* 12–15 (usually 14); corollas white tinged with purple, ligules obovate, 9–16 mm long, 2.0–4.5 mm wide, apex acute to rounded or 2-notched, sometimes indurate, adaxial surface glabrous, abaxial surface moderately glandular and sparsely pubescent on veins, tube 2.0 mm long, less than 1.0 mm diam, glabrous. *Disc florets* (Fig. 41B) 100–150; corollas yellow and gray-black, tube 3.0 mm long, 0.5 mm diam, densely glandular; throat cylindrical, gray-black and yellow, 4.0 mm long, 0.75 mm diam, densely glandular and pubescent near the distal half, lobes 5, 0.75 mm long, 0.75 mm wide, shallow, apex acute, black and densely glandular and pubescent, hairs less than 0.5 mm long; stamens (Fig. 41B) with filaments yellow, 3.5 mm long, 0.2 mm wide, anthers not fully exerted from corolla, thecae black, 2–3 mm long, apical appendage black, acuminate, 0.6 mm long, 0.4 mm wide, glabrous; styles yellow, 7.5 mm long, 0.2 mm wide, enlarged at base, stigmatic surface

yellow, 1.0 mm long, apical appendages black, acuminate, 0.5 mm long, 0.3 mm wide. *Pales* at anthesis triangular (Fig. 41C), 6–8 mm long, 1.2 mm wide, yellow with a dark base, apex long-aristate, yellow, indurate, up to 5.5 mm long, margin ciliate, entire, abaxial surface densely glandular near center and moderately pubescent, hairs 2.0 mm long, adaxial surface glabrous; *pales* at fruiting persistent, more or less triangular (Figs. 32B; 41D), 15–22 mm long, 3.0–4.5 mm wide, indurate with prominent parallel veins, stramineous, apex long-acuminate, erect or slightly recurved, margin glabrous, entire, abaxial surface sparsely glandular and pubescent, hairs 1–2 mm long, adaxial surface glabrous. *Achenes* brown-black, 4.5–5.0 mm long, 1.5 mm wide, smooth. Chromosome number unknown.

FLOWERING (AND FRUITING) PERIOD: September–October (November–December).

DISTRIBUTION AND HABITAT: Collected from only two localities, one in Chiapas, Mexico and the other in Huehuetenango, Guatemala (Fig. 40); pine-oak forests, along roadsides and on steep mountain slopes; 2000–3000 m.

*Montanoa echinacea* is a striking plant with large, solitary, dark-colored heads with long spiny *pales*. Members of this species have 100–150 disc florets and mature *pales* that are 15–22 mm long (Fig. 41D), resulting in a fruiting head the size of a spiny golf ball (Fig. 32B). The leaves are equally unique with a more or less cordate shape, dark green color, blades that have 3–4 lateral veins below the junction of the 3 main veins, and with hispid petioles. *Montanoa echinacea* is most closely related to *M. liebmanni*, under which this relationship is discussed.

SPECIMENS EXAMINED: GUATEMALA, HUEHUETENANGO: btw kms 100 and 107 near Campo de Bolas on rd to El Mirador, 12 Sep 1971, *Molina & Molina 26374* (BM, ENCB, F, MICH, NY); just below Calaveras, 7 Oct 1966, *Williams et al. 22012* (BM, NY); rd to San Juan Ixcocoy, 18 Nov 1967, *Molina 21279* (ENCB, F, MO). MEXICO, CHIAPAS: 3 mi S of Aguacatenango on rd to Pinola Las Rosas, 10 Sep 1971, *Laughlin 1930* (DS, ENCB, F, MICH); 5 km S of Aguacatenango, 18 Nov 1972, *Breedlove 29677* (DS).

**IBc. *Montanoa* section *Echinocephalae* series *Apertae* V. A. Funk, ser. nov. (to uncover or reveal.)**

*Paleae* in maturitate marginibus valde incurvatis solum prope ad bases, apicibus et basibus complanatis, ad instar stellae; achenia visibilia. Typus: *Montanoa revealii* H. Robinson. Species 9.

One species from Guerrero, Mexico, distinguished by numerous features, principal among these is the stellate flowering and fruiting head (Fig. 42).

9. *Montanoa revealii* H. Robinson, *Phytologia* 33: 285. 1976 [Apr 1976]. Type: MEXICO, Guerrero, along the Milpillas-Atoyac road via Puerto del Gallo, ca. 42.5 mi SW of Hwy 95, 11.5 mi SW of Filo de Caballo and 6.3 mi SW of Carrazal del Bravo, 8500 ft, 16 Oct 1975, *J. Reveal et al. 4233* (holotype, US!; isotypes, K! MARY! MEXU! OS!; photos of holotype, GH! MO! US[2]!). Figs. 40, 42, 43.

*Montanoa gigas* Rzedowski, *Bol. Soc. Bot. México* 35: 37. 1975 [Jun 1976]. Type: MEXICO, Guerrero, 3 km SW of Omiltemi, municipio of Chilpancingo, 2200 m, 4 Dec 1966, *J. Rzedowski 23604* (holotype, ENCB!; photo of holotype, OS!).

Trees to 20 m tall. *Stems* striate, quadrangular becoming terete, brown or gray, herbaceous parts puberulent. *Leaves* variable; petioles 1.5–16.0 cm long, with or without auricles at the distal end, adaxial surface glabrous or sparsely to moderately glandular and pubescent, hairs 1.0 mm long; blades ovate to pentagonal (Fig. 43A–I), 5–25 cm long, 3.5–28.0 cm wide, apex acute to acuminate, margin

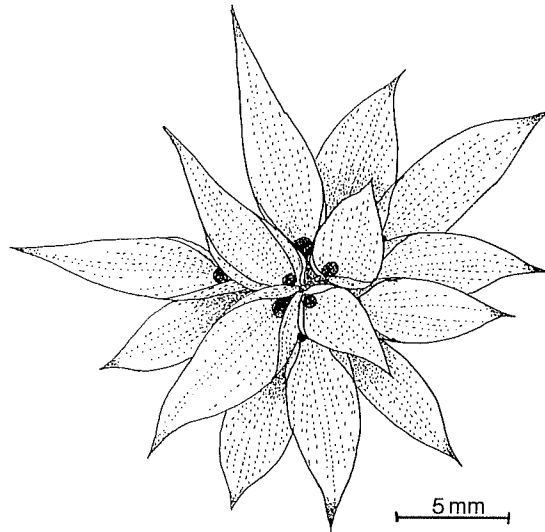


Fig. 42. Mature fruiting head of *Montanoa revealii*, Rzedowski & McVaugh 192 (ENCB).

occasionally ciliate, irregularly serrate or dentate, unlobed to deeply 3-lobed, adaxial surface essentially glabrous or sparsely pubescent, hairs pustular, much reduced, abaxial surface glabrous to densely glandular with pubescence in axils of main veins. *Peduncles* 1.0–3.5 cm long, densely glandular, hispid. *Heads* erect, 0.7–0.8 cm diam in flower, 3–4 cm diam in fruit, many to extremely numerous in dense cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* 5–6, uniseriate, equal in size, ovate or occasionally ovate-lanceolate, 2.5–6.0 mm long, 1.5–2.5 mm wide, green, apex acute to acuminate, margin ciliate, entire, abaxial surface densely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Ray florets* 3–5; corollas white, ligules oblanceolate to elliptic, 17–35 mm long, 6–8 mm wide, apex acute to 2-notched, adaxial surface glabrous, abaxial surface sparsely glandular to puberulent, tube 1.5–2.5 mm long, 0.5–0.7 mm wide, sparsely pubescent, hairs less than 0.5 mm long. *Disc florets* (Fig. 43J) 11–20, spreading; corollas pale yellow to yellow-green, tube 1.0–1.5 mm long, 0.5 mm diam, densely pubescent, hairs less than 0.5 mm long, throat cylindrical, 3.0–3.5 mm long, 1.5–1.75 mm diam, densely pubescent, hairs 0.5–1.0 mm long, lobes 5, 1.0–1.25 mm long, 0.5–0.6 mm wide, apex very narrowly acute, densely pubescent, hairs less than 0.5 mm long; stamens with filaments 3.5 mm long, 0.25 mm wide, anthers almost fully exerted from corolla, thecae becoming black (Fig. 43J) 2.25 mm long, 0.5 mm wide, apical appendages black, acuminate with rounded tip, 0.8–1.0 mm long, 0.25–0.3 mm wide, glabrous; styles (Fig. 43J) yellow, 9.0–9.75 mm long, base not enlarged, stigmatic surface yellow, 1.0–1.25 mm long, apical appendages yellow with dark tip, very long-acuminate, 1.0 mm long, 0.4 mm wide. *Pales* at anthesis more or less triangular (Fig. 43K), 4–5 mm long, 2.0 mm wide, light yellow with dark bands along midrib, apex long-acuminate, equal to length of body, indurate, light yellow with dark bands near midrib, margin entire, densely ciliate, hairs 0.5–1.0 mm long, abaxial surface densely glandular near center and sparsely to moderately pubescent on midrib, hairs 1.0 mm long, adaxial surface glabrous; pales at fruiting spreading, persistent, more or less lanceolate-triangular (Fig. 43L), 18–20 mm long, 2.5 mm wide, somewhat indurate with parallel veins, stramineous or light green, veins sometimes

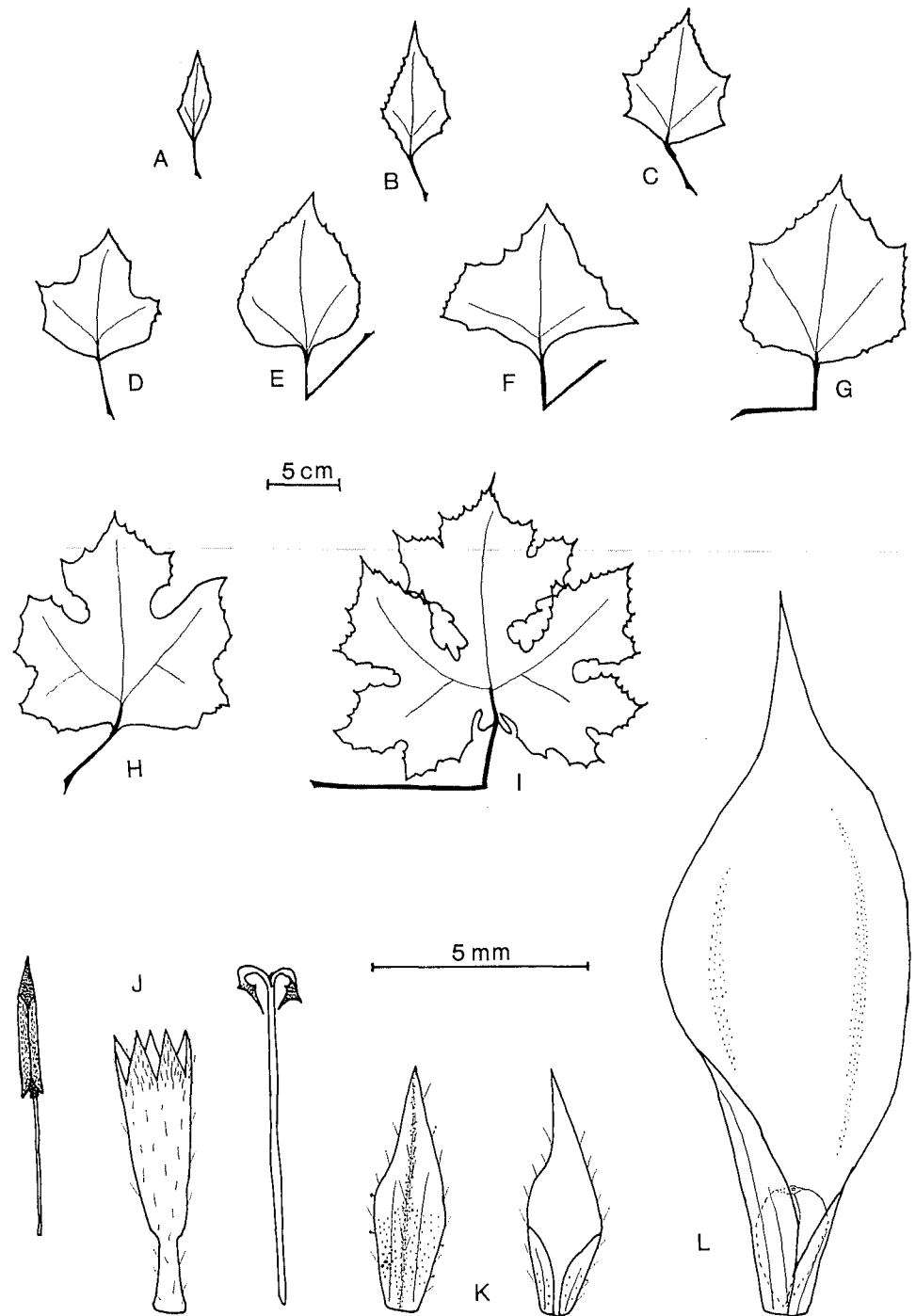


Fig. 43. *Montanoa revealii*. A-I, variation in mature leaves: A, D, E, G, AL 4365 (OS); B, Breedlove 36065 (CA); C, F, H, FRi 2826 (OS); I, AL 4380 (OS). J, disc corolla, style and stamen. FRi 2826 (OS); K, two views of pale subtending disc floret at anthesis, FRi 2830 (OS); L, mature pale, Rzedowski & McVaugh 192 (ENCB). A-I, J-L, same scale respectively.

purple, apex acuminate to caudate, extending into a tail-like appendage 2–4 mm long, margin ciliate, entire, abaxial surface moderately glandular near center, adaxial surface glabrous. *Achenes* brown, 3–4 mm long, 2.0 mm wide, smooth. Chromosome number,  $n = ca. 56$ .

FLOWERING (AND FRUITING) PERIOD: October–December (late (November–January).

DISTRIBUTION AND HABITAT: Known only from Guerrero, Mexico (Fig. 40); principal constituent of dense, wet, mesophytic, pine-oak forest; 2200–2750 m.

This tree is an amazing sight in flower and fruit. Not only does the entire tree flower almost simultaneously but the spreading nature of the disc florets and the mature pales gives the head a stellate appearance (Fig. 42). The pales are spreading and they wrap around the achene only at the base, which exposes or *reveals* the achene (and thus makes the choice of the epithet fortuitous). In addition, the mature pales are apically abaxially keeled. The flattened pales of *Montanoa revealii* and the black on the apices of the anthers and styles and on the thecae place it closer to *M. echinacea* and *M. liebmanni* than to any other taxon but it is widely separated from these two species. Among other characters, *M. echinacea* and *M. liebmanni* are shrubs with solitary or simple dichasia and the heads have over 10 ray florets and over 60 disc florets. *Montanoa revealii* is a tree with a dense compound dichasia, 3–5 rays and 11–20 disc florets.

*Montanoa revealii* is lumbered in Guerrero (pers. obser.). One fruiting collection (*Sa* 63728) from a finca was collected from Antigua, Guatemala in 1939. This is a very showy tree and was possibly cultivated in this heavily touristed area.

SPECIMENS EXAMINED: MEXICO. GUERRERO: 32–40 km W of Chilpancingo, near Omiltemi, 4 Dec 1966, *AL* 4365 (MICH, OS); 32–40 km W of Chilpancingo, 4 Dec 1966, *AL* 4369 (MICH, OS); 32–40 km W of Chilpancingo, 4 Dec 1966, *AL* 4380 (MICH, OS); 1–3 km NW of Puerto El Gallo, 11 Nov 1973, *Breedlove* 36065 (CA, MICH); 15 km W of Camotla, 2 Dec 1963, *Feddema, Dieterle & Rzedowski* 2833 (MICH); 5.1 mi SW of Filo de Caballo, 15 Nov 1978, *FRi* 2826\* (OS); 5.3 mi SW of Filo de Caballo, 15 Nov 1978, *FRi* 2830\* (OS); Galeana, Piedra Ancha-Tres Cruces, 25 Dec 1939, *Hinton* 15395 (GH, K, MICH, NY, TEX, UC, US); ca. 2 km NE of the Campamento El Gallo, Cerro Teotepec, 28 Jan 1965, *Rzedowski & McVaugh* 192 (ENCB, MICH); near Camotla, 9 Apr 1963, *Rzedowski* 16456 (ENCB, MICH); 9 km E of Camotla, 1 Dec 1963, *Rzedowski* 18018 (ARIZ, ENCB, MICH, OS); hwy btw Milpillas and Atoyac, 6 mi W of rd to Chichihualco, 14 Jan 1979, *Croat* 45667 (OS).

## II. *Montanoa* subgenus *Acanthocarphae* A. P. de Candolle, Prodr. 5: 565. 1836.

*Montanoa* subgenus *Acanthocarpha* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 512. 1899, orthogr. variant of subgenus *Acanthocarphae* DC.

*Montanoa* subgenus *Uhdea* (Kunth) Robins. & Greenm., Proc. Amer. Acad. Arts 34: 518. 1899.

Type species: *Uhdea bipinnatifida* Kunth = *Montanoa bipinnatifida* (Kunth) Schultz Bip. in K. Koch.

Shrubs or trees; ray florets 5–15 and white; disc florets 23–160, yellow or yellow and green-gray or black; pales at anthesis 2.5–4.5 mm long, inconspicuous, apex shorter than the body, pales at fruiting deciduous, obtrullate to nearly obdeltoid, 8–21 mm long, papery, net-veined, conduplicate in cross section, apex not recurved (curled in one species), abaxial surface sub-glabrous; achenes 2.0–4.5 mm long. Lectotype: *Montanoa grandiflora* Alamán ex DC. Species 10–25.

The subgenus *Acanthocarphae* has 16 species (18 taxa) divided into five series and distributed throughout the range of the genus in a variety of habitats. Some of the members of this subgenus are the most difficult to distinguish in the genus. Members of *Acanthocarphae* share deciduous pales that are conduplicate, papery and sub-glabrous. These pales are deciduous with the achenes and are easily

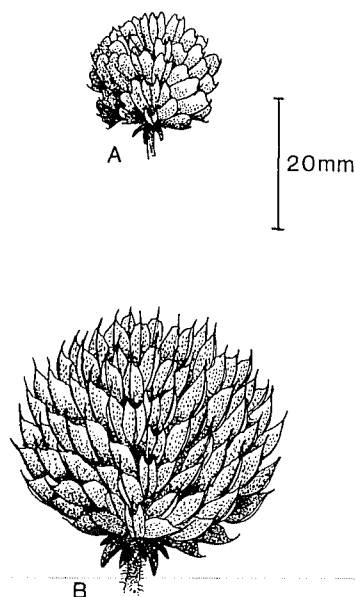


Fig. 44. Mature fruiting heads of subgenus *Acanthocarphae*. A, *Montanoa karwinskii*, F 2288 (OS); B, *M. bipinnatifida*, Mexia 1487 (NY).

dispersed by wind, in a samara manner, and by water. Figure 44 illustrates the smallest (pales 7.5 mm long; disc florets 23–34) and one of the larger (pales 16–21 mm long; disc florets 95–125) fruiting capitula in the subgenus.

#### IIa. *Montanoa* subgenus *Acanthocarphae* series *Ovalifoliae* V. A. Funk, ser. nov.

Synflorescentia capitulis numerosis vel paucis; capitula in maturitate erecta, phyllariis 4.5–12.0 mm longis; flosculi radiorum 8–15; flosculi discorum 50–135, stylis ad apices luteis, antheris inclusis; paleae in maturitate 10–11 mm longae, stramineae, ad apices sine sinibus. Typus: *Montanoa ovalifolia* Delessert ex DC. Species 10, 11.

Series *Ovalifoliae* has two South American species from the northern Andes. The two species are separated by a number of flowering and fruiting characters as well as habit and altitude. One species, *M. ovalifolia*, is divided into two subspecies based on the number of ray and disc florets.

#### 10. *Montanoa ovalifolia* Delessert ex A. P. de Candolle, Prodr. 5: 565. 1836, as "*Montagnaea*." Fig. 45.

Shrubs 1.5–5.0 m tall. *Stems* terete, brown, herbaceous parts essentially glabrous to sparsely glandular and pubescent, hairs less than 0.5 mm long. *Leaves* variable; petioles 2–17 cm long with or without partial wings and auricles, moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long; blades ovate to triangular or pentagonal (Fig. 45A–J), 4.5–23.0 cm long, 2.2–27.0 cm wide, apex acute to acuminate, margin serrate-dentate, unlobed to shallowly 3-lobed, adaxial surface moderately pubescent, hairs pustular, abaxial surface moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Peduncles* 1.0–3.5 cm long, densely glandular and pubescent, hairs 0.5–1.0 mm long. *Heads* erect, 0.9–1.2 cm diam in flower, ca. 2.0 cm diam in fruit, few to many in open cymose synflorescences in oppositely and alternately branched compound cor-



ymbs. *Phyllaries* 4–9, uni- or biseriate, when biseriate the inner row somewhat shorter, ovate-lanceolate, 4.5–12.0 mm long, 1.0–2.5 mm wide, green, apex acute to acuminate, margin ciliate, entire, abaxial surface densely glandular and pubescent, hairs 0.5–1.0 mm long, adaxial surface sometimes pubescent on distal half, hairs 0.5–1.0 mm long. *Ray florets* 8–15; corollas white, ligules ovate-lanceolate, 12–25 mm long, 4–8 mm wide, apex acute to 2-notched, adaxial surface essentially glabrous, abaxial surface sparsely glandular and pubescent especially on veins, hairs less than 0.5 mm long, tube 0.5–1.0 mm long, 0.5–1.0 mm wide, glabrous. *Disc florets* (Fig. 45K) 50–135; corollas yellow, tube 0.6–1.0 mm long, 0.5 mm diam, glabrous to moderately glandular and pubescent, hairs less than 0.5 mm long, throat cylindrical, 1–2 mm long, 1.0 mm diam, essentially glabrous to sparsely glandular and pubescent, hairs less than 0.5 mm long, lobes 5 (rarely 4), 0.5–0.75 mm long, 0.5 mm wide, apex acute, sparsely pubescent, hairs thick, less than 0.5 mm long; stamens with filaments 1.0–1.5 mm long, 0.25 mm wide, anthers not fully exerted from corolla, thecae brown, 1.0–1.25 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5–1.0 mm long, 0.25–0.5 mm wide, abaxial surface of apical appendage with or without glands; styles (Fig. 45K) yellow, 3.25–4.0 mm long, enlarged at base, stigmatic surface brown or yellow, 0.75 mm long, apical appendage yellow, short acute, 0.25 mm long, 0.25 mm wide. *Pales* at anthesis obtrullate to obdeltoid (Fig. 45L), 3.5–4.0 mm long, 2.0 mm wide, light yellow with dark bands near midrib and on distal half, apex long-acuminate, yellow, indurate, margin ciliate, glandular, entire, abaxial surface densely glandular and pubescent near center, hairs 1.0 mm long, adaxial surface glabrous; pales at fruiting (not quite mature) deciduous, obtrullate (Fig. 45M), ca. 10.0 mm long, 5.0 mm wide, papery with netted venation, stramineous with dark bands near midrib, apex acuminate, apiculate, dark, margin moderately glandular, ciliate on distal half but not apical, abaxial surface sparsely glandular and pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Achenes* (not quite mature) brown-black, 2.5–3.0 mm long, 1.5 mm wide, smooth. Chromosome number,  $n = 19$ .

*Montanoa ovalifolia* is a roadside shrub that is noteworthy for its abundant, densely clustered heads and the extreme amount of variation in a number of its characters. The leaves in particular vary considerably on the individual and populational levels. In one population in Santander, Colombia (*SF 5622 A–H*) all of the leaf shapes for the entire species were found so there does not appear to be any correlation with locality. The other variable characters, however, do appear to have clinal variation that is here recognized on the subspecific level.

*Montanoa ovalifolia* is most closely related to *M. fragrans* from Venezuela. The relationship between these two species is discussed under the latter species.

#### Key to the Subspecies of *Montanoa ovalifolia*

- |                                                                        |                                 |
|------------------------------------------------------------------------|---------------------------------|
| 1. Ray florets 10–15, 18–25 mm long; disc florets 90–135; Colombia.    | 10a. subsp. <i>ovalifolia</i> . |
| 1. Ray florets 8, 12–15 mm long; disc florets 50–75; Ecuador and Peru. | 10b. subsp. <i>australis</i> .  |

#### 10a. *Montanoa ovalifolia* Delessert ex A. P. de Candolle subsp. *ovalifolia*. Fig. 45.

*Montanoa ovalifolia* Delessert ex DC., Prodr. 5: 565. 1836, as "*Montagnaea*." Type: COLOMBIA, Cundinamarca, Santa-Fe de Bogotá, 1826, *M. B. Delessert s.n.* (holotype, G-DC, photo IDC 800. 566:1.6!; photos of holotype, F[2]! GH[2]! MO! NY! TEX! US!). *Eriocoma ovalifolia* (DC.) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa auriculata* Cuatr., Rev. Acad. Colombia Cienc. Exactas Físicas y Nat. 9: 243. 1954. Type: COLOMBIA, Norte de Santander, between La Quebrada de Pulido and Chitaga, 2300 m, 28 Nov 1941, *J. Cuatrecasas 13454* (holotype, F!; isotypes, COL[2]! F[2]! US!).

Involucral bracts (6–)7–9 and 5–12 mm long; ray florets 10–15, 18–25 mm long; disc florets 90–135.

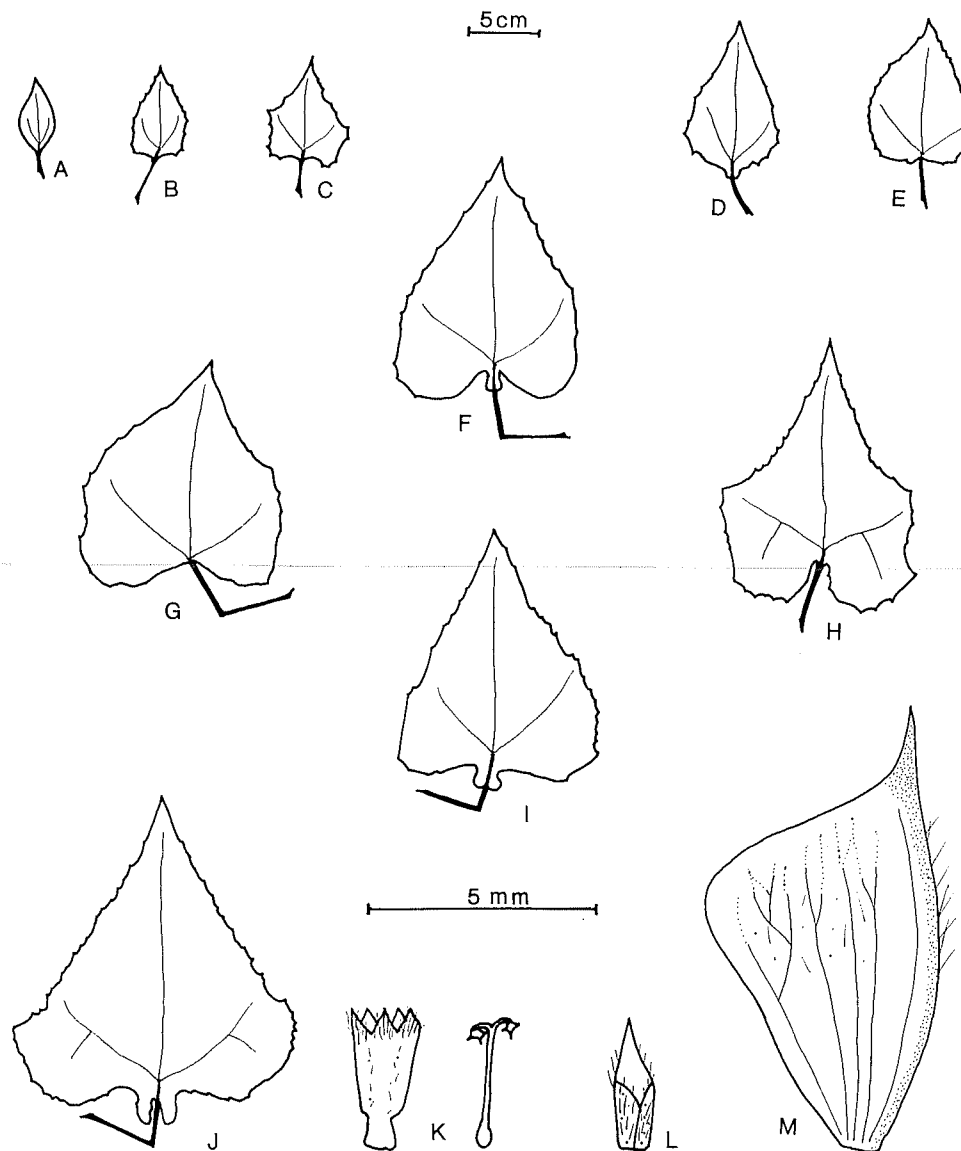


Fig. 45. *Montanoa ovalifolia*. A-J, variation in mature leaves: A, I, *SF* 5639 (OS); B, *Cuatrecasas* 56226 (F); C, *SF* 5638 (OS); D, E, *SF* 5622D (OS); F, *Killip & Smith* 18001 (US); G, *SF* 5543 (OS); H, *SF* 5547 (OS); J, *SF* 5579 (OS). K, disc corolla and style, *SF* 5639 (OS); L, M, pale subtending disc floret at anthesis and mature pale, *Harling & Anderson* 14268 (GB). A-J, K-M, same scale respectively.

FLOWERING PERIOD: May-January, primarily June-September.

DISTRIBUTION AND HABITAT: Colombian states of Boyaca, Caldas, Cundinamarca, Santander and Norte de Santander (Fig. 46); wet transitional forests and sub-paramo areas; 1900-3100 m.

REPRESENTATIVE SPECIMENS: COLOMBIA. BOYACÁ: Duitama, 11 Dec 1969, *Cuatrecasas 1693* (F, US); Gambita, 20 Oct 1972, *García-Barriga 20376* (COL); Chiquinquirá, 9 Jul 1964, *Espinal 1769* (COL); Güican, 18 Sep 1969, *Cuatrecasas & Rodriguez 27856* (US); Tunja, 30 Jun 1971, *Guarín & Villarreal 1028* (COL); Cocuy, 14 Sep 1938, *Cuatrecasas & García-Barriga 1693* (COL); Tota, 1 Sep 1951, *Yepes-Agrede 3147* (COL); Tabor, Cocuy, 1 Aug 1957, *Grubb, Curry & Fernandez-Perez 214* (COL); 29 km N of Boyacá/Cundinamarca departmental limits, 15 Jul 1979, *SF 5579\** (COL, OS); 1 km NE of Arcabuco, 16 Jul 1979, *SF 5592\** (COL, OS); 8 km S of Tunja, 20 Jul 1979, *SF 5634* (COL, OS); 16 km S of Tunja, 20 Jul 1979, *SF 5635* (COL, OS); 17 km S of Tunja, 20 Jul 1979, *SF 5637\** (COL, OS); 1 km S of Boyacá, 20 Jul 1979, *SF 5638\** (COL, OS); 5 km S of Jenesano on rd to Tibana, 20 Jul 1979, *SF 5639\** (COL, OS). CALDAS: 2 km N of Nerra, 30 km S of Aranzazu, 29 Jul 1979, *SF 5699* (COL, OS). CUNDINAMARCA: 19 km NW of jct of rd from Zipaquirá to Urbate and rd to Neusa, 14 Jul 1979, *SDF 5543\** (COL, OS); 6 km N of Zipaquirá on rd to Pacho, 14 Jul 1979, *SDF 5547\** (COL, OS); 29 km N of Boyacá/Cundinamarca departmental limits, 15 Jul 1979, *SF 5579* (COL, OS); ca. 1 km SSW of Boyacá/Cundinamarca departmental limits, 15 Jul 1979, *SF 5578\** (COL, OS); near Sesquile, 6 Jul 1947, *Haught 5931* (COL, NY, US); Bogotá Plateau, 27 Dec 1926, *Niemeyer 152* (US); Sabana de Bogotá, 20 Nov 1949, *Dugand 4350* (COL, CM); Zipaquirá, 18 Aug 1944, *Jaramillo s.n.* (COL); Simijaca, May 1930, *Perez 241* (COL); near Bogotá, Aug 1933, *García-Barriga 49* (COL); Zipaquirá, 20–24 Oct 1919, *Pennell 2620* (GH, NY); Usme, 9 Jan 1946, *Díaz 12* (US); Sabana de Bogotá, Jun 1916, *Dawe 300* (K, US). SANTANDER: near Tona, 17 Feb 1927, *Killip & Smith 19446* (GH, NY, US); btw California and Vetas, 15–22 Jan 1927, *Killip & Smith 18001* (GH, NY, US); near Vetas, 16 Jan 1927, *Killip & Smith 17885* (A, GH, NY, US). NORTE DE SANTANDER: 24 km SE of Pamplona, 4 km SE of La Legia, 18 Jul 1979, *SF 5622* (OS); Pamplona, 26 Jun 1940, *Cuatrecasas & García-Barriga 10245* (COL, F, US).

**10b. *Montanoa ovalifolia*** Delessert ex A. P. de Candolle subsp. *australis* V. A. Funk, subsp. nov. Type: ECUADOR, Loja, along the road from Loja to Zaruma, 3 May 1974, *Harling & Anderson 14268* (holotype, GB!). Figs. 45, 46.

Bractea involucrorum 4–5(–7), 5–6 mm longae; flosculi radiorum 8, 12–15 mm longi; flosculi discorum 50–75.

FLOWERING PERIOD: March–November.

DISTRIBUTION AND HABITAT: Southern Ecuador and Lambayeque, Peru (Fig. 46); hot, dry roadsides; 2200–3000 m.

All collections of this rare subspecies have been made south of the equator; hence the name *australis*. This subspecies is in most respects similar to the type subspecies, it has fewer, shorter involucral bracts (4–5, 5–6 mm long), fewer and shorter ray florets (8, 12–15 mm long), and fewer disc florets (50–75).

SPECIMENS EXAMINED: ECUADOR. AZUAY: Pasaje–Santa Isabel–Giron rd, 7 May 1974, *Harling & Anderson 14466* (GB). EL ORO: Zaruma–Pocto Velo, 1 May 1974, *Harling & Anderson 14147* (GB). LOJA: Valle a Jipiro, 2–5 km NE of Loja, 6 Mar 1947, *Espinosa 1359* (NY); Chiquiribaniba, 16 Nov 1876, *Andre 4444* (GH, K); Las Chinchas, 12 Apr 1944, *Solis 7715* (F). PERU. LAMBAYEQUE: above Olmos, May 1915, *Weberbauer 7102* (F, S, US).

**11. *Montanoa fragrans*** Badillo, Acta Bot. Venez. 9: 129. 1974. Type: VENEZUELA, Aragua, Dist. Girardot, road from Cata to Cuyagua, 400 m, 20 Nov 1971, V. M. Badillo 4766 (holotype, MY!; photo of holotype, OS!). Figs. 46, 47.

Shrubs with some scandent branches, 1–3 m tall. *Stems* terete, brown to gray, glabrous. *Leaves* relatively consistent; petioles 2–13 cm long, glabrous to sparsely pubescent, hairs 0.5–1.0 mm long; blades ovate to triangular (Fig. 47A–G), 4–24 cm long, 2.5–22.0 cm wide, apex acute to acuminate, margin serrulate, unlobed to shallowly 3-lobed, adaxial surface sparsely to moderately pubescent, hairs pustular, abaxial surface essentially glabrous to moderately glandular and pubescent. *Peduncles* 1.0–4.5 cm long, essentially glabrous to sparsely pubescent, hairs

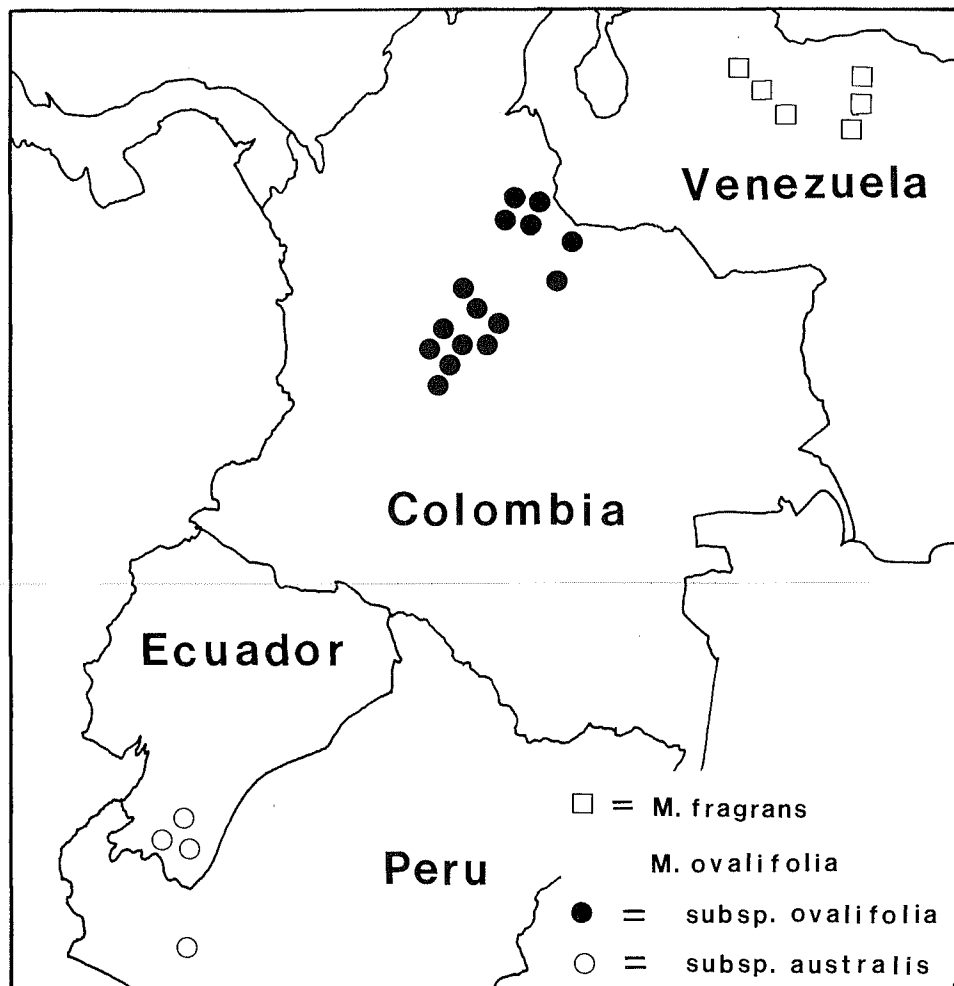


Fig. 46. Map of NW South America showing the distribution of *Montanoa fragrans*, *M. ovalifolia* subsp. *australis*, and *M. ovalifolia* subsp. *ovalifolia*.

0.5–1.0 mm long. *Heads* erect, 1.0–1.3 cm diam in flower, 2.0 cm diam in fruit, solitary to few in open cymose synflorescences. *Phyllaries* 6–9, uni- to biseriate, subequal, lanceolate to ovate-lanceolate, 5–7 mm long, 1.5–2.0 mm wide, green to light green, apex acute to acuminate, margin ciliate, entire, abaxial surface glabrous to sparsely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Ray florets* ca. 12; corollas white, ligules obovate, 10–16 cm long, 3–5 cm wide, apex acute to deeply 2-notched, adaxial surface glabrous, abaxial surface moderately glandular and sparsely pubescent, hairs concentrated on veins, less than 0.5 mm long, tube 0.5–1.0 mm long, 0.5 mm wide, glabrous to sparsely glandular and pubescent, hairs less than 0.5 mm long. *Disc florets* (Fig. 47H) 90–100; corollas yellow, tube 0.5–0.75 mm long, 0.5 mm diam, moderately glandular and pubescent, hairs 0.5–1.0 mm long, throat cylindrical, 2.25–2.75 mm long, 1.0 mm diam, nearly glabrous; lobes 5, 0.5–0.75 mm long, 0.4–0.5 mm wide, apex acute, sparsely pubescent, hairs less than 0.5 mm long; stamens with filaments 2.0–2.25

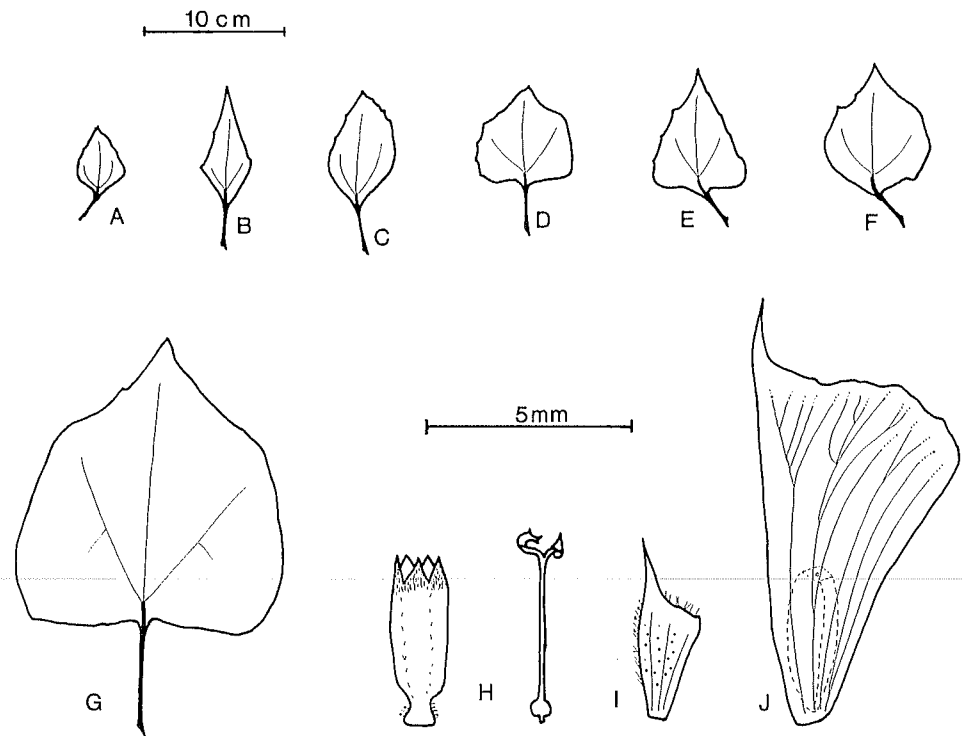


Fig. 47. *Montanoa fragrans*. A-G, variation in mature leaves: A, E, Fernandez 1496 (MY); B, D, F, Badillo 4766 (MY); C, Badillo 4831 (MY); G, Badillo 4823 (MY). H-J, Badillo 4766 (MY): H, disc corolla and style; I, pale subtending disc floret at anthesis; J, mature pale. A-G, H-J, same scale respectively.

mm long, 0.2 mm wide, anthers not fully exerted from corolla, thecae brown, 1.5 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5 mm long, 0.5 mm wide, abaxial surface of apical appendages glandular; styles (Fig. 47H) yellow, 4.5–5.5 mm long, enlarged at base, stigmatic surface yellow, 1.0 mm long, apical appendage yellow, acuminate, 0.5 mm long, 0.25 mm wide. *Pales* at anthesis obdeltoid (Fig. 47I), 3.5 mm long, 2.0 mm wide, light yellow sometimes with dark bands near midrib, apex long-acuminate, yellow, indurate, margin ciliate, glandular, entire to irregular, abaxial surface densely glandular on distal half except on apex, moderately pubescent on midrib, hairs 0.5–1.0 mm long, adaxial surface glabrous; pales at fruiting deciduous, obdeltoid (Fig. 47J), 10–11 mm long, 4–5 mm wide, papery with netted venation, stramineous, apex long-acuminate, apiculate, indurate, margin glabrous, entire, abaxial and adaxial surfaces glabrous. *Achenes* brown-black, 3.5 mm long, 1.1–1.25 mm wide, smooth. Chromosome number unknown.

FLOWERING (AND FRUITING) PERIOD: November (January).

DISTRIBUTION AND HABITAT: Restricted to the Venezuelan states of Aragua and Lara (Fig. 46); dry hillsides and along the roadsides; 300–400 m.

This sprawling shrub is distinct from other species in the genus by its habit and mature pales. The mature pales have a truncate apex with a very long apiculate apex that is evident even at anthesis (Fig. 47J). It is most closely related to

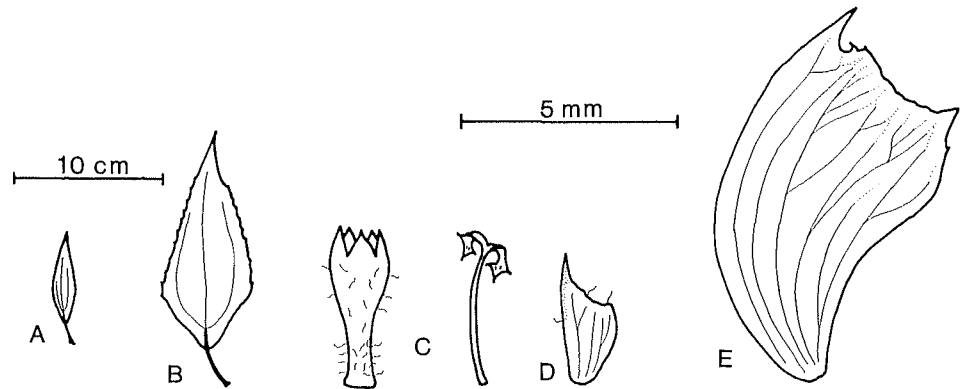


Fig. 48. *Montanoa angulata*, Badillo 7009 (MY): A, B, leaves; C, disc corolla and style; D, pale subtending disc floret at anthesis; E, mature pale. A, B, C-E, same scale respectively.

*Montanoa ovalifolia* and can be easily separated by the pales, which in *M. ovalifolia* are broad with a tapering apex. In addition, *M. fragrans* is nearly glabrous while *M. ovalifolia* is pubescent on most parts of the plant, and the leaves of the former are consistently ovate or deltoid while those of the latter vary greatly in size and shape.

REPRESENTATIVE SPECIMENS: VENEZUELA. ARAGUA: Girardot, rd from Cata to Cuyagua, 25 Jan 1972, *Badillo 4808* (MY); Girardot, rd from Cata to Cuyagua, 30 Jan 1972, *Badillo 4823* (MY); Girardot, rd from Cata to Cuyagua, 30 Jan 1972, *Badillo 4831* (MY). LARA: near Aguada Grande, 2 Nov 1972, *Fernández 1496* (MY); Duaca, 1893-1894, *Mocquerys s.n.* (COL, VEN); railroad near Yaracuy, 18 Aug 1968, *Smith V4314* (VEN).

**I**ib.** *Montanoa* subgenus *Acanthocarphae* series *Quadrangulares* V. A. Funk, ser. nov.**

Synflorescentia capitulis numerosis; capitula in maturitate erecta phyllariis 3-5 mm longis; flosculi radiorum 6-8; flosculi discorum 40-65, stylis ad apices luteis et nigris, antheris inclusis; paleae in maturitate 7-11 mm longae stramineae ad apices cum sinibus. Typus: *Montanoa quadrangularis* Schultz Bip. in K. Koch. Species 12-14.

Of the three species in series *Quadrangulares*, two are known only from the type collections and as a result the relationships among these three species are poorly understood. They are, however, easily separated by the apex of their fruiting pales, pubescence color and type of synflorescence.

**12. *Montanoa angulata*** Badillo, *Acta Bot. Venez.* **13**: 109. *t. 115*. 1978. Type: VENEZUELA, Trujillo, Distrito Balera, road between La Puerta and La Lagunita, after La Lagunita, 2350 m, 24 Oct 1975, V. M. *Badillo 7009* (holotype, MY!; photo of holotype, OS!). Figs. 48, 49.

Shrubs: *Stems* brown, glabrous. *Leaves* poorly known; petioles 2-4 cm long, partially winged at distal end, densely glandular and pubescent, hairs 0.5-1.0 mm long; blades ovate-lanceolate to trullate (Fig. 48A, B), 5-12 cm long, 1-5 cm wide, apex long-acuminate, margin serrate, adaxial surface moderately pubescent, hairs pustular, more evident on young leaves, abaxial surface moderately glandular and pubescent, hairs 0.5-1.0 mm long. *Peduncles* 1.5-3.5 cm long, densely glandular and pubescent, hairs 0.5-1.0 mm long. *Heads* erect, 0.8 cm diam in flower, ca. 1.0-1.2 cm diam in fruit, many to numerous in open cymose

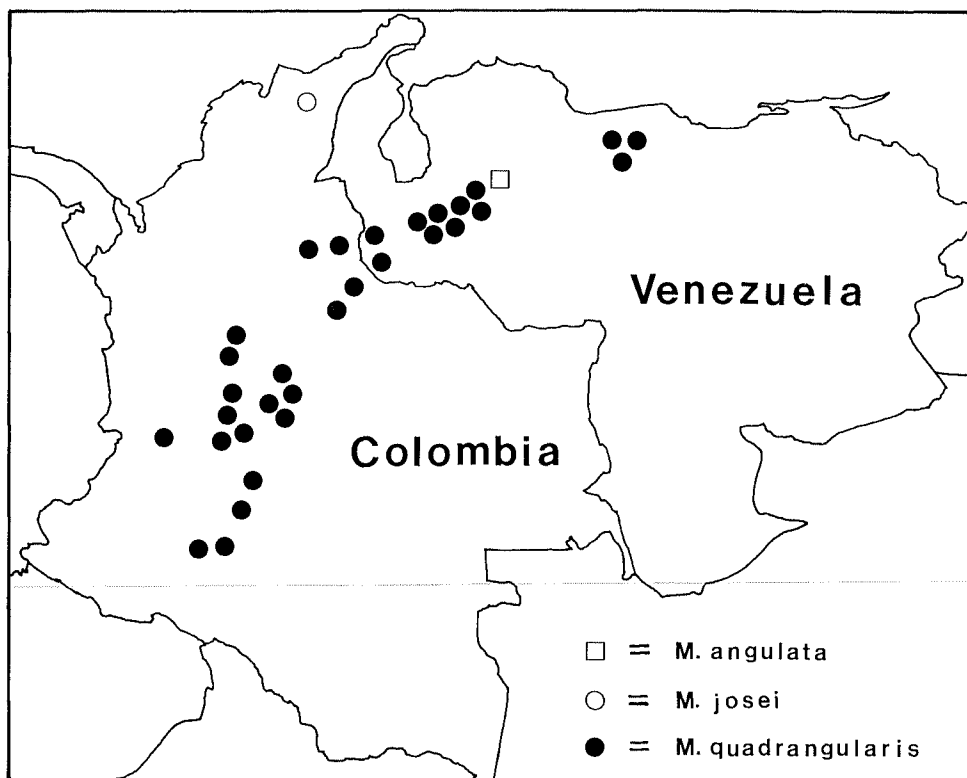


Fig. 49. Map of northern South America showing the distribution of *Montanoa angulata*, *M. josei* and *M. quadrangularis*.

synflorescences in oppositely branched compound corymbs. *Phyllaries* 5–6, uniseriate, subequal, ovate to ovate-lanceolate, 3–5 mm long, 1.0 mm wide, dark green, apex acute to acuminate, mucronate, margin ciliate, entire, abaxial surface sparsely pubescent, adaxial surface glabrous. *Ray florets* 6–7; corollas white with dark veins, ligules obovate, 6–10 mm long, 3–4 mm wide, apex acute to 2-notched with clusters of hairs, adaxial surface glabrous, abaxial surface moderately to densely glandular and pubescent, hairs less than 0.5 mm long, tube less than 0.5 mm long, almost non-existent, with a few scattered hairs. *Disc florets* (Fig. 48C) 49–53; corollas yellow, tube 0.75–1.0 mm long, 0.5 mm diam, moderately glandular and pubescent, hairs 0.5–0.75 mm long, throat cylindrical, 1.5 mm long, 1.0 mm diam, sparsely glandular and pubescent primarily on the veins, hairs less than 0.5 mm long, lobes 5, 0.5–0.7 mm long, 0.5–0.7 mm wide, apex acute and moderately glandular and pubescent, hairs less than 0.5 mm long; stamens with filaments 1.0 mm long, 0.2 mm wide, anthers not fully exerted from corolla, thecae yellow with brown, 1.0 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5 mm long, 0.4 mm wide, abaxial surface of apical appendages glabrous; styles (Fig. 48C) yellow, 4.0 mm long, slightly enlarged at base, stigmatic surfaces yellow, 0.6 mm long, apical appendages yellow with dark spots (Fig. 48D), acute, 0.4 mm long, 0.4 mm wide. *Pales* at anthesis obtrullate, 2.5 mm long, 2.0 mm wide, light yellow with dark bands on midrib and veins, apex long-acuminate, dark, indurate, margin sparsely ciliate, entire, abaxial and adaxial surfaces glabrous; pales at fruiting (not quite mature) deciduous, almost obdeltoid

(Fig. 48E), 8–9 mm long, 4–5 mm wide, papery with netted venation, stramineous with dark bands on veins, apex abruptly short apiculate, dark, indurate, margin sparsely ciliate, entire, abaxial and adaxial surfaces glabrous. *Achenes* seemingly typical but too young for certainty. Chromosome number unknown.

FLOWERING (AND FRUITING) PERIOD: October (October–November?).

DISTRIBUTION AND HABITAT: Trujillo, Venezuela (Fig. 49); habitat unknown; 2350 m.

This poorly known species is distinct in this series in having angular leaves (Fig. 48B) and it is probably most closely related to *Montanoa quadrangularis* and *M. josei*, with which it shares the same number of disc (40–60) and ray (6–8) florets and dark areas on the apical appendages of the stigmas. *Montanoa quadrangularis* and *M. josei* are, however, trees with reddish hairs, whereas *Montanoa angulata* is a nearly glabrous shrub.

**13. *Montanoa quadrangularis* Schultz Bipontinus** in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 407. 1864. Type: VENEZUELA, Caracas, Monte Galipan, 1846, *N. Funck & L. J. Schlim 131* (holotype, P!; isotypes, BM! G-BOIS! LE! MOU! P[2]! W!; photo of holotype, F! GH! MO! OS! US!). Figs. 49, 50.

*Montagnaea excelsa* Ernst, Vargasia 7: 186. 1870. Type: VENEZUELA, Caracas, Monte Galipan, 1845–1852, *J. W. K. Moritz 1386* (holotype, K; probable isotypes, BM! BR! CGE[2]! G! GH! K! P[2]! W!; fragments of holotype, GH! US!; photos of holotype, GH! US[2]!; photos of B isotype [destroyed in WWII; in litt., H. W. Lack], F! GH! MO! US!; photos of P isotype, US[2]!; fragment of P isotype, US!). *Eriocoma moritziana* Schultz Bip. in Kuntze, Rev. Gen. 1: 336. 1891, nom. nud. in syn. Although no description was ever published, the type of *Montagnaea excelsa* was annotated by Schultz Bipontinus as *M. moritziana*.

*Eriocoma lehmannii* Hieron., Bot. Jahr. Syst. 19: 54. 1895. Type: COLOMBIA, Cundinamarca, around Pacho, frequent, 1700–2200 m, Jan 1892, *F. C. Lehmann 7480* (holotype, B [destroyed in WWII; in litt., H. W. Lack] lectotype chosen, K!; isolectotype, K; photo of B specimen, MO! US!; photo of lectotype; GH! US!; fragments of isolectotype, US[2]! fragment of B, US!). *Montanoa lehmannii* (Hieron.) S. F. Blake, J. Wash. Acad. Sci. 16: 215. 1926.

*Montanoa tamayonis* Aristeguieta, Flora Venez. 10: 522. 1964. Type: VENEZUELA, Merida, near La Encrucijada, Pregonero-La Grita, 2500 m, Sep 1956, *L. Aristeguieta 2502* (holotype, VEN!; isotype, NY!; photo of holotype, OS!).

Trees to 20 m tall. *Stems* often quadrangular becoming terete and brown or gray, herbaceous parts puberulent, hairs sometimes rust colored. *Leaves* variable; petioles 1.5–48.0 cm long, sometimes quadrangular, with or without partial wings and auricles (Fig. 50A–H), essentially glabrous to densely glandular and pubescent, hairs 0.5–1.0 mm long; blades ovate to triangular or pentagonal, 4.5–42.0 cm long, 4.0–46.0 cm wide, apex acute to acuminate, margin entire to minutely serrate, larger leaves sometimes irregularly serrate, unlobed to 3-lobed, adaxial surface essentially glabrous to densely pubescent, hairs pustular, often with much reduced multicellular base; abaxial surface sparsely to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Peduncles* 1–4 cm long, moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Heads* erect, 0.9–1.0 cm diam in flower, 1.5–2.0 cm diam in fruit, extremely numerous in dense cymose synflorescences in oppositely branched compound corymbs. *Phyllaries* 5–6, uniseriate, equal, ovate-lanceolate, 4.0–4.5 mm long, 1.0–1.5 mm wide, green, apex acute, mucronate, margin ciliate, entire, abaxial surface moderately to densely pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous to sparsely pubescent near the distal end. *Ray florets* 8; corollas white, ligules obovate, 12.5–13.0 mm long, 4.0–4.5 mm wide, apex acute to 2-notched, adaxial surface glabrous, abaxial



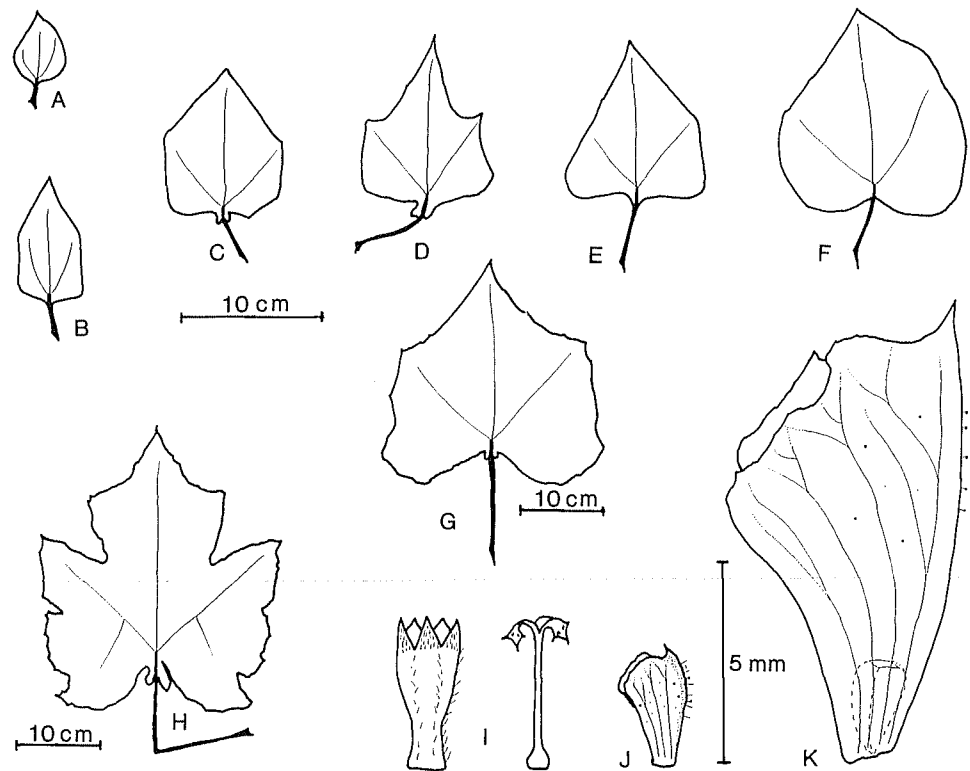


Fig. 50. *Montanoa quadrangularis*. A-H, variation in mature leaves: A, Dawe 770 (VEN); B, Daniel 137 (US); C, SF 5704 (OS); D, Oberwinkler 14252 (VEN); E, Badillo 5632 (MY); F, SF 5784 (OS); G, SF 5570 (OS); H, SF 5631 (OS). I, disc corolla and style, Uribe 5061 (COL); J, K, pale subtending disc floret at anthesis and mature pale, Killip & Smith 17026 (NY). A-F, G, H, I-K, same scale respectively.

surface moderately glandular and sparsely to moderately pubescent especially near proximal end, hairs less than 0.5 mm long, tube 0.5–1.0 mm long, 0.5 mm wide, sparsely glandular and pubescent. *Disc florets* (Fig. 50I) 40–60; corollas yellow, tube 0.5–1.25 mm long, 0.5–0.6 mm diam, sparsely to moderately glandular and pubescent, hairs 0.5–1.0 mm long, throat cylindrical, 1.25–1.5 mm long, 1.25–2.5 mm diam, sparsely to densely glandular and pubescent usually more so at distal end, hairs less than 0.5 mm long, lobes 5, 0.5–0.75 mm long, 0.4–0.5 mm wide, apex acute, sparsely glandular and densely pubescent, hairs less than 0.5 mm long; stamens with filaments 1.5–1.75 mm long, 0.2 mm wide, anthers not fully exerted from corolla, thecae yellow to brown, 1.0 mm long, 0.4 mm wide, apical appendages yellow, acute, 0.5 mm long, 0.25 mm wide, abaxial surface of apical appendage glandular; styles (Fig. 50I) yellow, 3.5–4.1 mm long, enlarged at base, stigmatic surface sometimes dark, 0.5–0.6 mm long, apical appendage acute, 0.5 mm long, 0.4–0.5 mm wide. *Pales* at anthesis ovate to obdeltoid (Fig. 50J), 2.5–3.0 mm long, 2.0–2.5 mm wide, light yellow with dark bands near midrib, apex acuminate to long-acuminate, yellow, indurate, margin ciliate, glandular, entire, abaxial surface densely glandular and moderately pubescent, hairs concentrated on distal half, 0.5–1.0 mm long, adaxial surface glabrous; pales at

fruiting deciduous, obovate (Fig. 50K), 7–11 mm long, 3–6 mm wide, papery with netted venation, stramineous, apex short apiculate, acuminate, margin glabrous, irregular, abaxial surface glabrous to sparsely glandular, adaxial surface glabrous. *Achenes* brown-black, 2.0–2.5 mm long, 1.5 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: October–January (January–April).

DISTRIBUTION AND HABITAT: Central Colombia and northern Venezuela (Fig. 49); cool, wet forests, sometimes on volcanic soil; sometimes a major constituent of the forest; 1900–2700 m.

A commanding tree species with leaves up to 90 cm long (including petiole). These large leaves are not present all the time, particularly at anthesis when the leaves are much smaller (Fig. 50A–F). The mature pales also vary in size ranging from 7–11 mm long but all maintaining the same obovate shape. *Montanoa quadrangularis* is extremely showy with very dense single or double panicles bearing hundreds of small heads per branch. No other species in the genus can match this display. The species is distinguished on herbarium sheets by the herbaceous parts of the stems which collapse when pressed although they are never known to be flat when living. *Montanoa quadrangularis* is most closely related to *M. josei*. The discussion of this relationship is included under the latter species.

The stems have a large pith that later disintegrates and results in a hollow bole. Nevertheless, reports from Colombia (Dawe 770) indicate that the wood is very durable. In addition, Dawe reported that the wood is used for beams in buildings and for billiard cues. Its reputation for strength and durability is supported by the fact that the trees are grown in Cundinamarca for use as telephone poles (pers. comm., J. Idrobo). Its usefulness is enhanced by the fact that it, like most species of the genus, stump sprouts very rapidly. *Montanoa quadrangularis* has been reported to put up shoots 8–10 m tall in a matter of weeks that are very straight and “bamboo-like” (pers. obser.). The common name of this plant in Colombia is “arbol loco” (e.g., Dawe 770; Cuatrecasas 13949; pers. obser.).

REPRESENTATIVE SPECIMENS: COLOMBIA. ANTIOQUIA: Rionegro, Aug 1937, *Daniel 1504* (COL); Rionegro, 16 Dec 1933, *Daniel 137* (US). CALDAS: 2 km N of Neira, 29 Jul 1979, *SF 5699* (COL, OS); 49 km N of Aranzazu, 29 Jul 1979, *SF 5704* (COL, OS); Pereira, s.d., *Duque 1840* (US); 14 mi N of Manizales, 3 Nov 1965, *Breteler 4470* (NY). CUNDINAMARCA: Sasaima, 6 Jan 1970, *García-Barriga 20025* (COL); 5 km from Pacho on rd to Zipaquirá, 14 Jul 1979, *SF 5570* (COL, OS); near Anolaima, Jan 1954, *Augusto & Daniel 4611* (COL); Pacho, 13 Jan 1944, *Huertás & Camargo 985* (F); Zipacón, 24 Dec 1953, *Idrobo & Hernández 1558* (COL); near Sasaima, 10–11 Jan 1946, *García-Barriga 11907* (COL, US); Pacho, Patasia, 28 Jan 1965, *Uribe 5061* (COL). HUILA: N of Palacio, 12 Jan 1944, *Little 7094* (COL, F, US); SE of Neiva, 19 Jan 1945, *Little 9093* (COL, F, US); Pitalito, Calamo, 30 Dec 1942, *Schultes & Villarreal 5135* (DS, GH, NY); below Galilea, 28 Dec 1942, *Fosberg 19640* (F, NY, US). NORTE DE SANTANDER: around Ocaña, 1846–1852, *Schlim 347* (BH, BR, G). SANTANDER: 3 km ENE of Córdoba, 19 Jul 1979, *SF 5631* (COL, OS); near California, 11–27 Jan 1927, *Killip & Smith 17026* (A, F, GH, NY, US); near Charta, 1–11 Feb 1927, *Killip & Smith 19253* (GH, NY, US). TOLIMA: El Libano, 10 Dec 1939, *García-Barriga 8442* (COL, US); canon del río Coello, 5 Mar 1969, *Cuatrecasas & Echeverry 27717* (US); 53 km E of Armenia, 5 Aug 1979, *SF 5784* (COL, OS). VALLE: El Cairo, btw Darien and Mediacanoa, 6–7 Jan 1943, *Cuatrecasas 13949* (COL, F). VENEZUELA. DISTRITO FEDERAL: Seitanias del Avila, Dec 1943, *Lasser 968* (US, VEN); El Avila, Los Venados, *Badillo 1093* (VEN); S slope of Cerro Avila, 25 Jan 1940, *Vogl 54* (F); just above Caracas, 27 Dec 1943, *Se 55012* (F, US); Caracas, Jan–Apr 1842, *Liudeu 33* (BM, G, K, OXF, P, US frag of BM). MERIDA: btw La Azulita and La Carbonera, 24 Apr 1944, *Se 56063* (F, US); near Merida, 27 Jan 1928, *Pittier 12749* (G, GH, M, NY, US, VEN); near Timotcs, 22 Jan 1928, *Pittier 12663* (LL, US, VEN); La Mucuy, 15 km ENE of Merida, 19 Dec 1963, *Breteler 3464* (COL, G, M, MO, NY, S, US, VEN); near Merida, Dto. Libertador, 20 Dec 1972, *Badillo 5632* (MY); around Merida la Axulita, 20 Dec 1972, *Badillo 5634* (MY); btw El Molino and Capuri, 23 Dec 1972, *Badillo 5850* (MY); near Las Cruces, 6 Mar 1962, *Trujillo 5215* (MY); Rio Milla, near Merida, 29 Dec 1969, *Riuero 74627* (VEN); btw Tabay and Mucuruba, 15 Dec 1968, *Oberwinkler 13907* (M, VEN); Jagi, near Ejido, 11 Feb 1939, *Alston 6988* (BM, NY, S, US); rd from Bailadores to El Dclgado, 19 Dec 1972, *Badillo 5200* (MY);



Fig. 51. *Montanoa josei* (Cuatrecasas 24768, US) distal section of flowering branch and primary leaf.

Bailadores, 20 Sep 1942, *Tamayo* 2399 (VEN); Las Chorreras, Bailadores, 19 Sep 1942, *Tamayo* 2445 (VEN); La Mucuy, Dec 1956, *Bernardi* 5966 (MY, VEN); btw Morro and Aricagua, 15 Feb 1957, *Bernardi* 6111 (VEN); Mucurubá, 2 Jan 1973, *Romero* 166 (MY). TRÁCHIA: above El Cobre, 25 Dec 1972, *Badillo* 5938 (MY); Abejales, 30 Mar 1972, *Benitez* 1255 (MY); btw Las Delicias and Paraguita, 17 Jul 1944, *Se* 57424 (F, US); Capacho, 8 Apr 1971, *Guevara* 1295 (MY); near las Porqueras, 24 Dec 1972, *Badillo* 5920 (MY); Páramo La Negra, Dto. Jauregui, 22 Oct 1972, *Badillo* 5315 (MY). TRUJILLO: Tuñame-Jajó, Aug 1958, *Aristeguieta* 3696 (NY, VEN).

**14. *Montanoa josei* V. A. Funk, sp. nov.** Type: COLOMBIA, Magdalena, Sierra Nevada de Santa Marta, SE slopes; hoyo del Río Donachui, Cancurua, fields and forests, 2400–2650 m, 10 Oct 1959, *J. Cuatrecasas* and *R. Romero Castaneda* 24768 (holotype, US!; isotypes, COL! NY!).

Figs. 49, 51, 52.

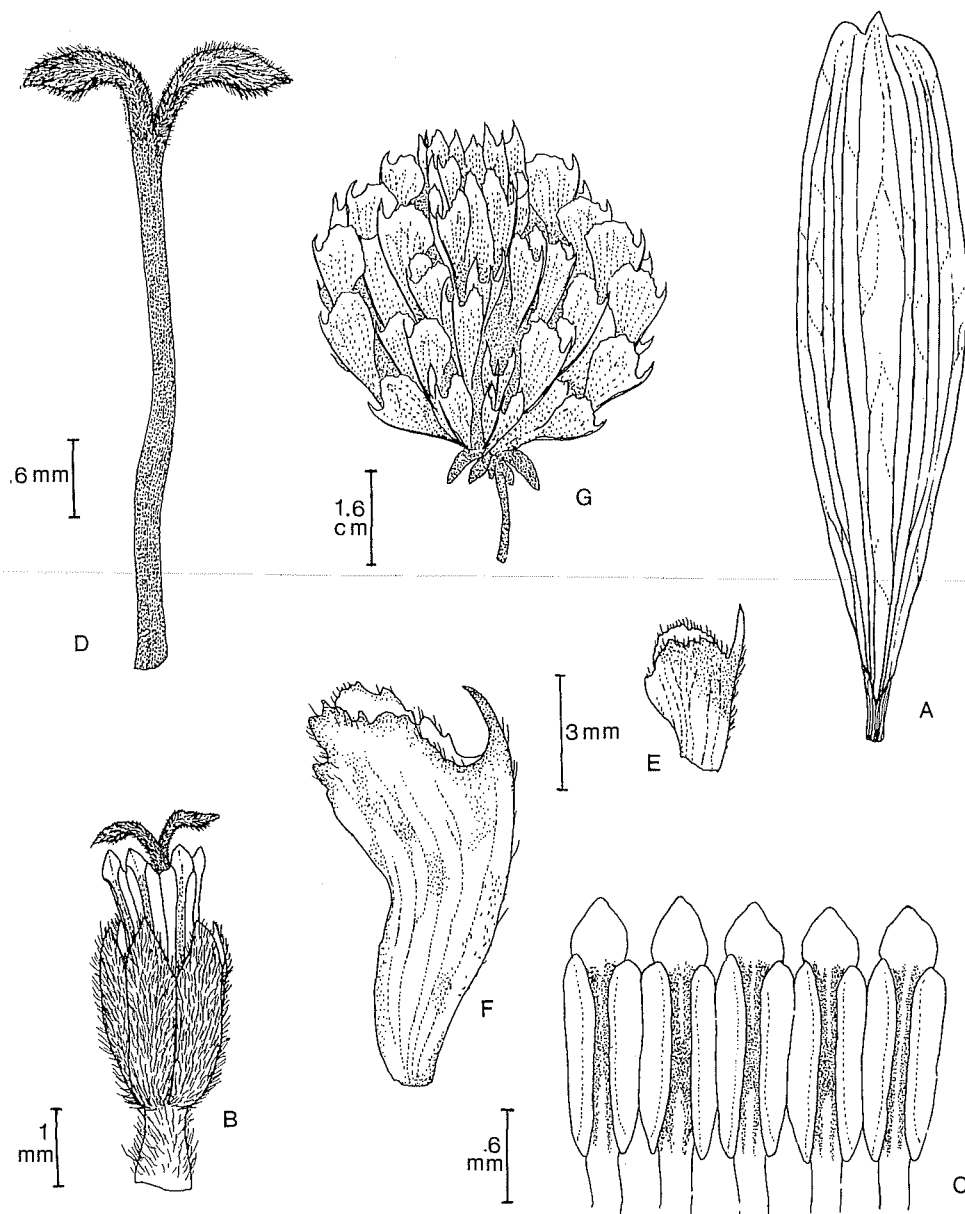


Fig. 52. *Montanoa josei* (Cuatrecasas 24768, US): A, ray floret; B, disc floret; C, anthers; D, style; E, pale subtending disc floret at anthesis; F, mature pale; G, fruiting head. A, E, F, same scale.

Arbores 8-metrales. Caules quadrangulares basin versus teretiores, glabri vel praeter nodos dense pilis 2.0 mm longis rubellis pubescentibus subpubescentibus partibus herbaceis purpureis grisescentibus. Folia variabilia; petioli 1.5–5.5 cm longi, interdum partim alata et auriculata, glabra vel praeter paginas adaxiales dense pilis 1.5 mm longis rubellis pubescentibus subpubescentibus; laminae ovatae trullatae vel 5-angulatae (Fig. 51), 6–22 × 2–18 cm, apice longa acuminatae, margine serrulatae vel serratae lobatae vel haud lobatae, pagina adaxiali modice pilis pustuliformibus pubescenti, pagina abaxiali glandulosa

et modice vel dense pilis 2.0 mm longis pubescenti. Pedunculi 1–3 cm longi, glandulosi et pilis 2.0 mm longis rubellis dense pubescentes. Capitula erecta florifera 1.0 cm fructifera 2.0 cm em lata, multa vel numerosa in synflorescentia cymosa corymbis eomposita. Phyllaria 7–8 subuniseriata, fructifera reflexa inter se aequalia, lanceolata vel ovata-lanceolata, 4–5 × 1.0–1.25 mm, viridia, apice acuta vel acuminata mucronata, marginibus ciliata integra, pagina adaxiali dense pilis 1.0 mm longis rubellis pubescenti, pagina abaxiali glabra. Rarii (Fig. 52A) 8, albi, ligula obovata, 14–19 × 3.0–3.5 mm, apice acuta vel 1–2-denticulata, pagina adaxiali glabra, pagina abaxiali glandulosa et sparsim pubescenti, tubo 1.0 × 0.5 mm, glanduloso et sparsim pubescenti. Floreuli disci (Fig. 52B) 53–62, lutei, tubo 1.0 × 0.5 mm, glanduloso et pilis 1.0 mm longis dense pubescenti, fauce cylindraceo, 1.5 × 1.5 mm seeus venas sparsim pubescenti, lobis 5, 0.5 × 0.5 mm, apice acutis sparsim glandulosis pilis minus quam 0.5 mm longis dense pubescentibus; stamina filamenta incluso 1.5 × 0.2 mm, antheris (Fig. 52C) semi-exsertis, thecis luteo-rubellis vel brunneolis, 1.0 × 0.5 mm, eonnectivo apice acuto, 0.5 × 0.5 mm, luteo, glabro; stylus (Fig. 52D) luteus, 4.25–4.75 mm longus basi tumefactus, lineolis stigmaticis luteis, 0.75 mm longis, appendiculis acutis, 0.4 × 0.4 mm, apice atromaeulatis. Paleae sub anthesi cordatae ± (Fig. 52E), 2.5–3.0 × 2.0–2.5 mm, luteolae seeus venas atrovirides, apice longis-eule acuminatae, induratae, luteae, margine ciliatae irregulares, dorso glandulosae et pilis 1–2 mm longis pubescentes, ventre glabrae; paleae fructiferae deciduae, obovatae (Fig. 52F, G), 10 × 5 mm, papyraceae reticulatim venosae, stramineae, apice spina 2 mm longa et sinu profundo oriente obsitae, margine irregulari ciliatae, abaxialiter seeus eostam sparsim glandulosa, adaxialiter glabrae. Achaenia brunnea, 3.5 × 1.25 mm laevia. Chromosomatum numerus ignotus.

Trees 8 m tall. *Stems* quadrangular becoming terete, herbaceous parts purple possibly turning gray, glabrous to sparsely pubescent except at nodes densely pubescent, hairs 2.0 mm long, reddish. *Leaves* variable; petioles 1.5–5.5 cm long, sometimes partially winged and auriculate, glabrous to sparsely pubescent except adaxial surface densely pubescent, hairs reddish, 1.5 mm long; blades ovate, trullate or pentagonal (Fig. 51), 6–22 cm long, 2–18 cm wide, apex long-acuminate, margin serrulate to serrate, sometimes deeply lobed, adaxial surface moderately pubescent, hairs pustular, abaxial surface moderately to densely glandular and pubescent, hairs 2.0 mm long. *Peduncles* 1–3 cm long, densely glandular and pubescent, hairs reddish, 1.0 mm long. *Heads* erect, 1.0 cm diam in flower, ca. 2.0 cm diam in fruit, many to numerous in cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* 7–8, more or less uniseriate, reflexing in fruit, equal, lanceolate to ovate-lanceolate, 4.0–5.0 mm long, 1.0–1.25 mm wide, green, apex acute to acuminate, mucronate, margin ciliate, entire, abaxial surface densely pubescent, hairs reddish, 1.0 mm long, adaxial surface glabrous. *Ray florets* (Fig. 52A) 8; corollas white, ligules obovate, 14–19 mm long, 3.0–3.5 mm wide, apex acute to deeply 2-notched, adaxial surface glabrous, abaxial surface sparsely glandular, tube 1.0 mm long, 0.5 mm wide, sparsely glandular, pubescent. *Disc florets* (Fig. 52B) 53–62; corollas yellow, tube 1.0 mm long, 0.5 mm diam, densely glandular and pubescent, hairs 1.0 mm long, throat cylindrical, 1.5 mm long, 1.5 mm diam, sparsely pubescent on veins, lobes 5, 0.5 mm long, 0.5 mm wide, apex acute, sparsely glandular and densely pubescent, hairs less than 0.5 mm long; stamens with filaments 1.5 mm long, 0.2 mm wide, anthers (Fig. 52C) not fully exerted from corolla, thecae yellow-red or brown, 1.0 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5 mm long, 0.5 mm wide, glabrous; styles (Fig. 52D) yellow, 4.25–4.75 mm long, enlarged at base, stigmatic surfaces yellow, 0.75 mm long, apical appendages with dark areas, acute, 0.4 mm long, 0.4 mm wide. *Pales* at anthesis almost cordate (Fig. 52E), 2.5–3.0 mm long, 2.0–2.5 mm wide, light yellow with dark bands at midrib, apex long-acuminate, yellow, indurate, margin ciliate, irregular on distal half, hairs 0.5–1.0 mm long, abaxial surface moderately glandular to pubescent, hairs 1–2 mm long, adaxial surface glabrous; pales at fruiting (not quite mature) deciduous, obdeltoid to cordate (Fig. 52F, G), 10 mm long, 5 mm wide, papyry with netted venation, stramineous, apex deep (2 mm) sinus with

apiculate tip of same length, dark, margin ciliate, irregular, abaxial surface sparsely glandular on midrib, adaxial surface glabrous. *Achenes* brown, 3.5 mm long, 1.25 mm wide, smooth. Chromosome number unknown.

FLOWERING AND EARLY FRUITING PERIOD: October.

DISTRIBUTION AND HABITAT: Known only from the Santa Marta Mountains in Colombia (Fig. 49); fields, forests, riverbeds and on mountain slopes; 2400–2650 m.

A little known tree from an area of high endemism in northern Colombia, *Montanoa josei* is easily separated from other species of the genus. A number of the more prominent features are the irregular-margined pales that have a deep (2 mm) sinus, the grayish-green leaves and involucre, reddish pubescence on the peduncles and stems, and the long, thin achenes. *Montanoa josei* is most closely related to *M. quadrangularis*, which is also a tree with red pubescence but which has entire-margined pales with no sinus, dark green leaves and involucre and regular-shaped achenes. In addition, *M. quadrangularis* has a paniced synflorescence and achenes that are 2.0–2.5 mm long while *M. josei* has a corymbiform one and achenes that are 3.5 mm long.

This species is named in honor of Dr. José Cuatrecasas (1903–present) who collected the type specimen and has added much to our knowledge of Latin American plants by his extensive collecting and numerous publications.

### **Ic. *Montanoa* subgenus *Acanthocarphae* series *Hibiscifoliae* V. A. Funk, ser. nov.**

Synflorescentia capitulis numerosis; capitula in maturitate pendula, phyllariis 2.5–5.0 mm longis; flosculi radiorum 7–10; flosculi discorum 40–120, stylis ad apices luteis vel luteis et nigris, antheris inclusis; paleae in maturitate 8–17 mm longae stramineae vel purpurascens ad apices cum sinibus (praeter *Montanoa leucantha*). Typus: *Montanoa hibiscifolia* Benth. in Oerst. Species 15–21.

Series *Hibiscifoliae* contains seven species from Central America and Mexico. It is a diverse group characterized by the abundant flowering branches and the pendulous heads with stramineous and purple mature pales. The species are distinguished by characters of the branching pattern, color of the disc florets, pales and achenes.

Within this series there is one species, *Montanoa leucantha*, that consists of nine previously described species that range from Sonora, Mexico, to Guatemala. All of these species have consistently been placed in the subgenus *Acanthocarphae* DC., because they have medium-sized heads (less than 8 cm wide including rays). They fall into the same subgenus in this treatment because they have mature pales that are conduplicate and papery with netted venation and are deciduous with the achenes. Furthermore, they have the same number of ray (8–10) and disc (30–60) florets. The synflorescences of these nine species of shrubs are many-headed and moderately densely clustered and, like others in this series, occasionally have purple pales.

The descriptions of the nine species relied heavily on leaf morphology, but also included a number of other characters as well, such as width and apex of the pales. Examination of the individuals throughout the range indicated that the species broke down into two groups using the following characters:

GROUP 1 (five species): Leaves membranaceous, blades more or less pentagonal but extremely variable in proportion, often lobed; stems of synflorescence longer and more numerous with a more open appearance; apex of mature pale curled with tapering tip; plants of lower altitudes (usually 1500–1800 m) and in wetter environment (Figs. 53, 56).

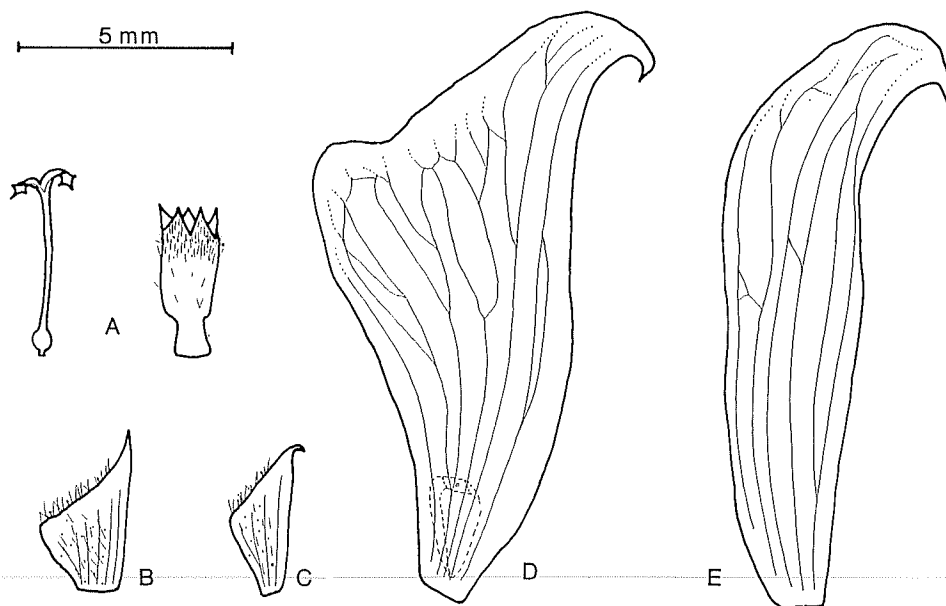


Fig. 53. *Montanoa leucantha* subsp. *arborescens*. A, disc floret and style (F 2852, OS); B, pale subtending disc floret at anthesis (Hartman 302, OS); C, pale subtending disc floret at anthesis (F 2580, OS); D, mature pale (Hartman 302, OS); E, mature pale (F 2852, OS).

GROUP 2 (four species): Leaves coriaceous, blades triangular to rhombic, relatively consistent and unlobed; heads on shorter peduncles and fewer in number with a more compact inflorescence; apex of mature pale broad, straight and flattened; plants of higher altitudes (usually 2000–2400 m) but in drier environment (Figs. 54, 55).

In certain areas of Michoacán and Jalisco these differences grade into one another and distinguishing between the two groups becomes difficult. Because of this breakdown the two groups are here recognized as subspecies of *Montanoa leucantha*: subsp. *arborescens* (Group 1) and subsp. *leucantha* (Group 2). The two subspecies were then examined to see if the leaf variation warranted varietal recognition (Figs. 54, 56).

*Montanoa leucantha* subsp. *leucantha* occurs on the north side of the Sierra Madre del Sur (Fig. 57) in habitats that have a pronounced dry season. The leaves of this subspecies range from ovate-lanceolate to triangular or rhomboid and like other taxa from similar environments they show variation because of the habitat as well as developmental variation and phenotypic plasticity (see LEAF MORPHOLOGY section). The range of variation for the entire subspecies is illustrated by leaves collected from the field and greenhouse from Zacatacas (Fig. 54A–H). No varietal categories were recognized in this subspecies.

In the greenhouse one collection (Jansen & Harriman 247A) flowered after an unusually cool and sunny spring. The heads were bagged and self-pollinated but they set no seed. Although it is difficult to draw any conclusions from this limited sample it appears likely that they are self-incompatible.

The leaf morphology in *Montanoa leucantha* subsp. *arborescens* is more variable than in subsp. *leucantha*. Subspecies *arborescens* ranges throughout the south face of the Sierra Madre del Sur and in the Sierra Madre Occidental with

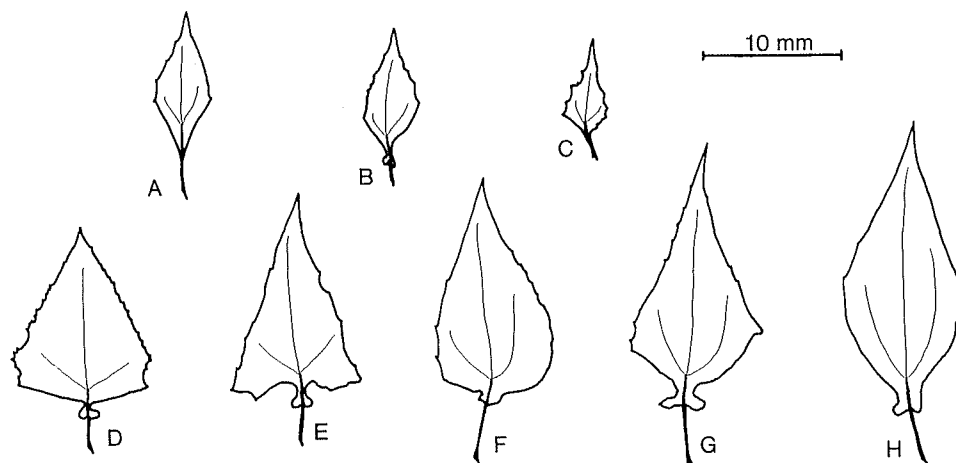


Fig. 54. *Montanoa leucantha* subsp. *leucantha* variation in mature leaves (Jansen & Harriman 247A, OS).

one isolated collection locality in Guatemala (Fig. 57). The leaves are, for the most part, pentagonal but also ovate, lanceolate and elliptic. *Montanoa leucantha* subsp. *arborescens*, like other taxa that undergo a dry period, experiences the resulting leaf variation as well as the developmental variation and phenotypic plasticity (see LEAF MORPHOLOGY section). There appears to be some geographic correlation with the leaf morphology. The leaves in Fig. 56A were taken from an individual collected in Chihuahua (Hartman *et al.* 5107) and illustrate all of the variation from the northern part of the range. In contrast, the leaves of Fig. 56B were collected from an individual from Oaxaca (FTK 2701) and illustrate the variation found in the southern members of this subspecies. Some differences are evident, the leaves of Fig. 56A are often, although not always, elongate with a pronounced apex. Those of Fig. 56B are more pronounced in their pentagonal shape with more acuminate lobes and apices and they are broader. The differences, however, are subtle and overlap.

There is some variation in the pales. The mature and immature pales of subspecies *arborescens* vary in width. Fig. 53C, E shows the narrow pale found in the central part of the range (México, Michoacán, Jalisco, and Guerrero), whereas Fig. 53B, D represents the broader pales found throughout the rest of the distribution (Chihuahua, Sinaloa, Durango, Oaxaca, and Chiapas). Because these two grade into one another and because they are not geographically distinct, they are not recognized as varieties.

Two collections of subspecies *arborescens* (Hartman *et al.* 5107 and FTK 2701) also flowered the same spring as *M. leucantha* subsp. *leucantha* but did not set seed either.

**15. *Montanoa leucantha* (Lagasca y Segura) S. F. Blake, Contr. U.S. Natl. Herb. 26: 245. 1930.**

Shrubs 1–7 m tall. *Stems* terete, brown to gray, herbaceous parts puberulent to glabrous. *Leaves* extremely variable; petioles 1.5–12.0 cm long, sometimes partially winged, with or without auricles, puberulent to densely pubescent, hairs 1.25 mm long; blades ovate-lanceolate, triangular, rhombic or pentagonal (Figs.



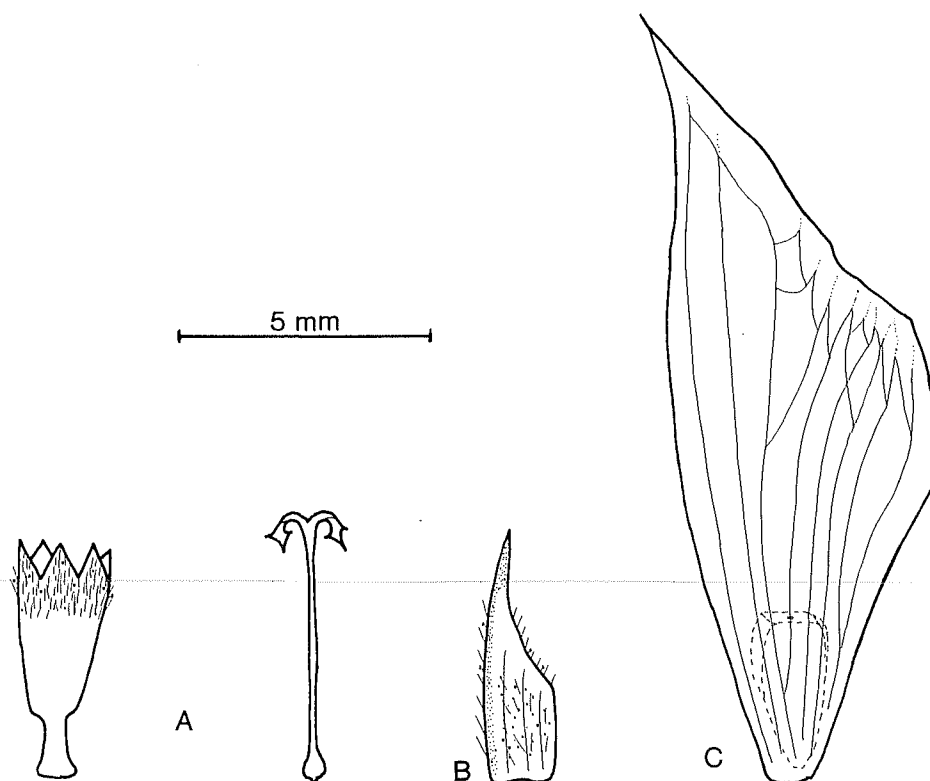


Fig. 55. *Montanoa leucantha* subsp. *leucantha*. A, disc floret and style (AL 3639, OS); B, pale subtending disc floret at anthesis (C 10273, NY); C, mature pale (F 2958, OS).

54, 56), 2.5–24.0 cm long, 2–24 cm wide, apex acute to long-acuminate, margin entire to serrate-dentate, sometimes 3–5-lobed, adaxial surface moderately pubescent, hairs pustular, sometimes with numerous small hairs covering surface, abaxial surface moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Peduncles* 1–4 cm long, sometimes tinged with purple, moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Heads* pendulous at fruiting, 0.8–1.2 cm diam in flower, 1.8–3.0 cm diam in fruit, many to extremely numerous in cymose synflorescences in oppositely branched compound corymbs with hemispherical appearance. *Phyllaries* 5–7(–9), more or less uniseriate, reflexed at anthesis, subequal, lanceolate to ovate-lanceolate, 4–6 mm long, 1–2 mm wide, brown to green or green and purple, apex acute, mucronate, margin entire, ciliate, abaxial surface densely glandular and pubescent, hairs 0.5–1.0 mm long, adaxial surface moderately glandular and pubescent on distal half, hairs 0.5–1.0 mm long. *Ray florets* usually 8; corollas white, ligules elliptic to obovate, 13–18 mm long, 5–8 mm wide, apex acute to 2-notched, with clusters of round-tipped hairs, adaxial surface glabrous to sparsely pubescent, hairs 0.5–1.0 mm long, abaxial surface sparsely to moderately glandular, tube 1.0 mm long, 0.5 mm wide, glabrous. *Disc florets* (Figs. 53A, 55A) 30–60; corollas yellow, tube 1.0–1.25 mm long, 0.5–0.75 mm diam, glabrous, throat cylindrical, 2.0–2.25 mm long, 1.0–1.75 mm diam, sparsely to densely pubescent primarily on distal half, hairs round-tipped, lobes 5, 0.5–1.0 mm long, 0.5 mm wide, apex acute, densely glandular and pubescent,

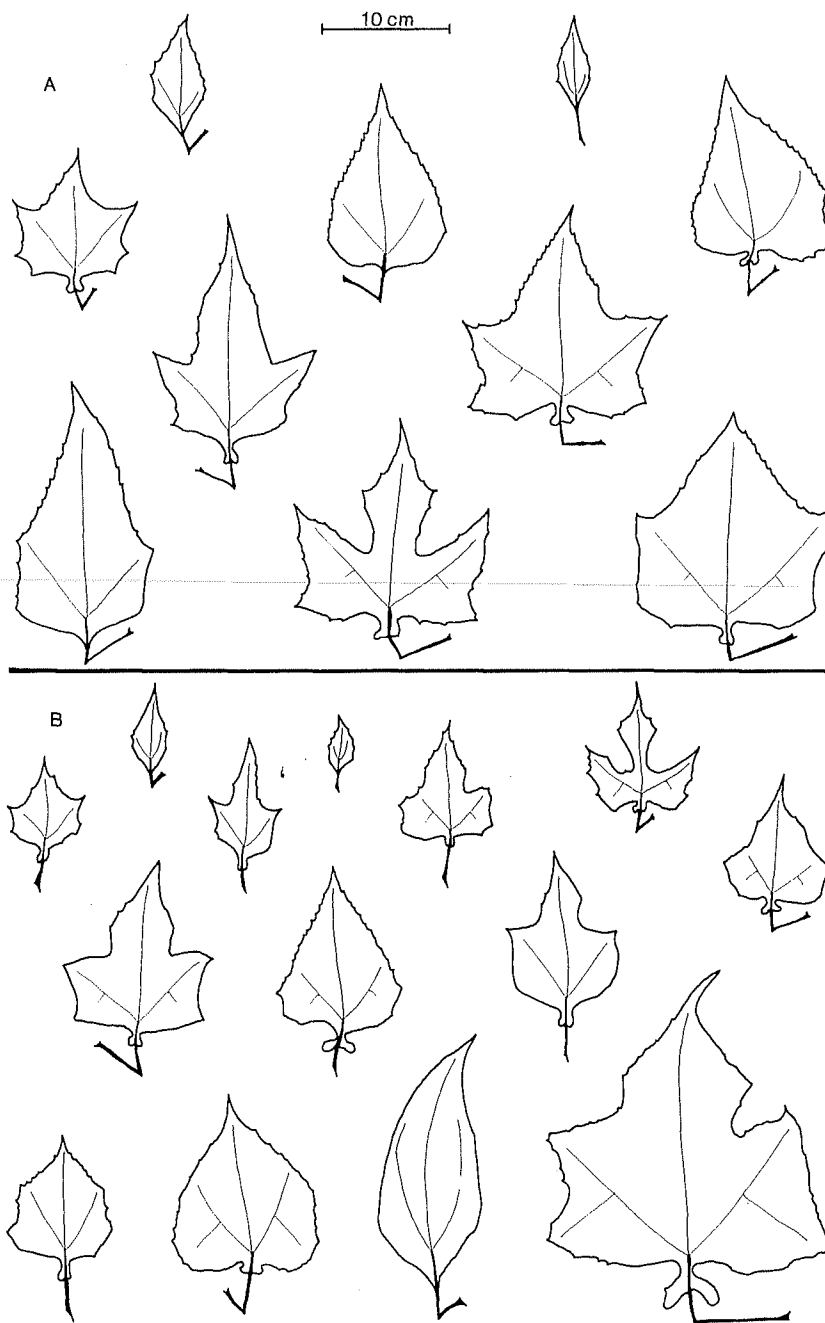


Fig. 56. *Montanoa leucantha* subsp. *arborescens* leaf variation: A, Chihuahua (Hartman et al. 5107, OS); B, Oaxaca (FTK 2701, OS).

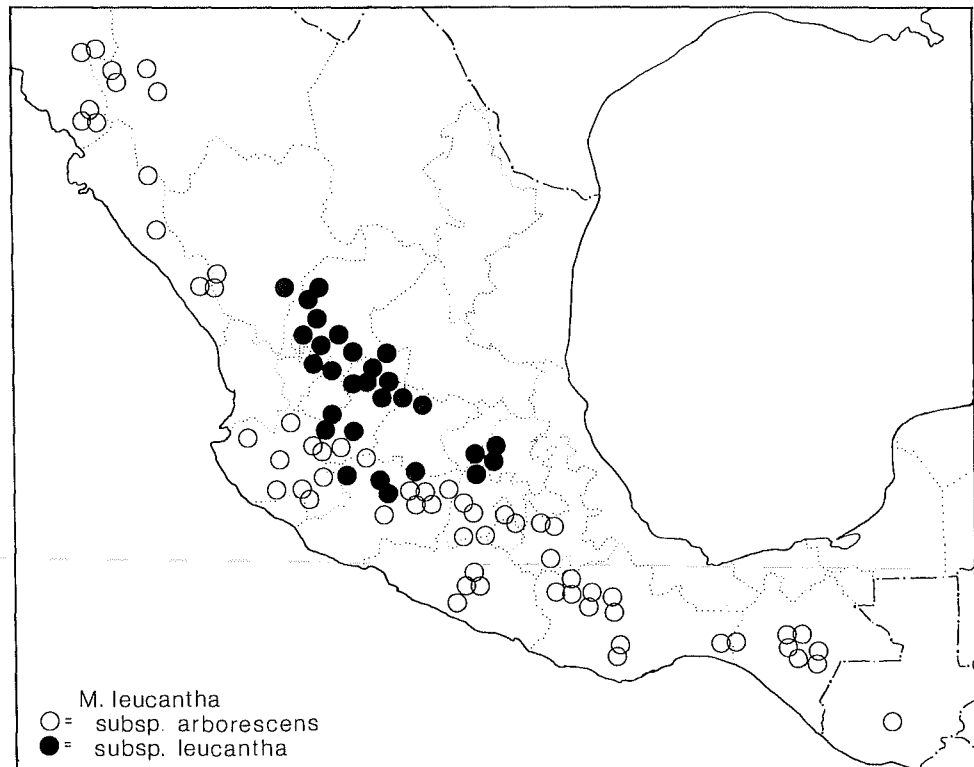


Fig. 57. Map of Mexico and Guatemala showing the distribution of *Montanoa leucantha* subsp. *arborescens*, and *M. leucantha* subsp. *leucantha*.

hairs round-tipped; stamens with filaments 1.5–3.0 mm long, less than 0.25 mm wide, anthers not fully exerted from corolla, thecae yellow to brown, 1.25–2.0 mm long, 0.5–0.75 mm wide, apical appendages yellow, acuminate, 0.5–0.75 mm long, 0.25–0.5 mm wide, abaxial surface of apical appendage glandular; styles yellow, 4.25–6.25 mm long, enlarged at base, stigmatic surface brown, 0.75–1.25 mm long, apical appendages yellow, acuminate, 0.5 mm long, 0.25 mm wide. *Pales* at anthesis obrullate to pentagonal (Figs. 53B, C; 55B) 3.5–4.5 mm long, 2–4 mm wide, light yellow with dark bands on midrib, apex long-acuminate, indurate, curling outward prior to anthesis, margin ciliate, entire to irregular, abaxial surface densely glandular and pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous; *pales* at fruiting deciduous, obrullate to obovate or almost rhombic (Figs. 53D, E; 55C), 8–17 mm long, 4–6 mm wide, papery with netted venation, stramineous or purple, apex acuminate, apiculate, curled outward, margin glabrous, entire, adaxial and abaxial surfaces glabrous to sub-glabrous. *Achenes* brown-black, 2–3 mm long, 1.25–2.0 mm wide, smooth. Chromosome number,  $n = 19$ .

#### Key to the Subspecies of *Montanoa leucantha*

1. *Pales* 13–17 mm long at maturity, apex erect; principal leaves triangular to rhombic and unlobed; disc corollas 4.25–4.75 mm long. 15a. subsp. *leucantha*.
1. *Pales* 8–15 mm long at maturity, apex curled outward; principal leaves pentagonal and often shallowly 3–5-lobed; disc corollas 3.5–4.25 mm long. 15b. subsp. *arborescens*.

**15a. *Montanoa leucantha* (Lagasca y Segura) S. F. Blake subsp. *leucantha*.**

Figs. 54, 55, 57.

*Rudbeckia leucantha* Lag., Gen. Sp. Pl. 32. 1816. Type: collected in 1806 in the Madrid garden from a plant introduced in 1804 from seeds sent by *M. Sessé* from Nova Hispania (lectotype selected from two syntypes, MA!; photo of lectotype, OS!). The two syntypes were both collected from the Madrid garden. The lectotype was collected in 1806 and the remaining syntype in 1816. Both specimens are in good condition but the earlier collection date was chosen. The plant blooms in Spain in the fall and it is possible that the latter specimen was not collected early enough to have been used for the description. *Montanoa leucantha* (Lag.) S. F. Blake, Contr. U.S. Natl. Herb. 26: 245. 1930.

*Montanoa crenata* Schultz Bip. in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864. Type: MEXICO, 1854, *C. de Berges s.n.* (holotype, P!; photo of holotype, F! GH! MO! OS! US!). *Eriocoma crenata* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa purpurascens* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 515. 1899. Type: MEXICO, Agua Calientes, Jul-Sep 1837, *C. T. Hartweg 134* (lectotype chosen from six syntypes, GH!; isolectotypes, CGE[2]! FI! G! K! LE! OXF! WI; photo of K isolectotype, OS!). The remaining five syntypes are: *Guillemín-Tarayre, Dugès 456*; *Pringle 2184 & 3985*; *Rose 3647*; and *Schumann 115*. The lectotype specimen was referred to *Montagnaea grandiflora* and attributed to Bentham (Hemsley, 1881). *Eriocoma hartwegiana* Kuntze, Rev. Gen. Pl. 1: 336. 1891, nom. nud. Based on referral of Kuntze to *Montagnaea grandiflora* Benth. non DC.

*Montanoa arsenei* S. F. Blake, Contr. U.S. Natl. Herb. 22: 611. 1924. Type: MEXICO, Michoacán, vicinity of Morelia, Rincón, 1900 m, 8 Sep 1910, *Bro. G. Arsène 5290* (holotype, US!; isotype, NY!).

FLOWERING (AND FRUITING) PERIOD: August–September (September–October).

DISTRIBUTION AND HABITAT: South central Mexico from Hidalgo to Durango and Sinaloa (Fig. 57); dry rocky areas along streams and roads, in ditches and on slopes; 1700–2800 m, usually between 2000 and 2400 m.

*Montanoa leucantha* subsp. *leucantha* is found in one locality growing sympatrically with *M. tomentosa* subsp. *tomentosa*. The area is east of Huichapán, Hidalgo, and both taxa are found along a dry creekbank (*F 2955, 2957*). Apparently *M. leucantha* subsp. *leucantha* has moved in from the west and *M. tomentosa* subsp. *tomentosa* from the south (pers. obser.). There is no morphological evidence of hybridization in the area and all chromosome counts from these taxa are normal.

REPRESENTATIVE SPECIMENS: MEXICO. AGUASCALIENTES: Cerro San Juan, 13 Aug 1976, *HF 4072\** (OS); btw Cerro Altamira and Cerro de San Juan, 4–8 Sep 1967, *M 23686* (ENCB, MICH); 5 km E of Tepezalá, 31 Oct 1967, *Rzedowski 25010* (DS, ENCB, F, MICH, TEX, US); 4 km E of San José de Gracia, 15 Oct 1973, *Rzedowski & McVaugh 719* (ENCB, MICH); near Calvillo, 28 Aug 1960, *Rzedowski 14151* (OS); above Presa Calles, 30 Aug 1939, *Shreve 9257* (ARIZ, NA, UC); 29 mi E of Aguascalientes, 15 Sep 1966, *AL 3639* (MICH, OS). GUANAJUATO: E of San Miguel Allende, 13 Aug 1947, *Keuoyer 2162* (GH); 11 km E of Villalpando marketplace, 18 Nov 1971, *Dieterle 419A* (MICH); btw Valenciana and Santa Rosa, 29 Aug 1948, *Moore & Wood 4757* (BH, MICH); ca. 10 km ESE of Guanajuato center, 12 Nov 1970, *M. 24233* (MICH); 22–23 km W of Dolores Hidalgo, 9 Nov 1970, *M 24103* (ENCB, MICH). HIDALGO: 10–12 mi ENE of Huichapán, 11 Dec 1978, *F 2958* (OS); 14 mi E of Huichapán, 7 Oct 1962, *C 9620* (GH, MEXU, MICH, MO, NY, TEX); 18 km W of Ixmiquilpan, 20 Oct 1965, *Quintero 3189* (DS, ENCB, MICH, TEX); SW of Nopala near rd to Dentho, 11 Dec 1978, *F 2963* (OS); Mt Leña, 10 Oct 1946, *Moore 1451* (BH, GH, UC, US). JALISCO: 7 mi SW of Ayutla, 2 Nov 1962, *M 22005* (MICH); 9 mi N of Huejuquilla el Alto, 12 Sep 1966, *AL 3618* (MICH, OS); above Río Verde near hwy from Yahualica to Tepatitlán, 6 Nov 1959, *McVaugh & Koelz 244* (DUKE, ENCB, MICH); 7 mi E of Zapotlaejo, 6 Oct 1962, *C 9614* (MICH, MO, MSC, NY, SMU, TEX, US); near Ixtlahuacán de Los Membrillos, 16 Nov 1971, *Dieterle 4191B* (ENCB, MICH); hwy 45 near jct with rd along N shore of Lago de Chapala, 1 Oct 1966, *AL 3856* (MICH); Paso de la Troje, 30 mi E of Aguascalientes, 16 Sep 1966, *AL 3642* (MICH); N of Guadalajara, 16 Sep 1966, *AL 3650* (MICH, OS); 23.4 mi S of Aguascalientes/Jalisco border on rd to Guanajuato, 1 Jan 1970, *Anderson & Anderson 5287* (ENCB, MICH); Paso de la Troje, SW of Ojuelos, 13 Aug 1958, *M 16873* (DUKE, ENCB, MICH, NY, US); El Puerto, 30 km S of Ojuelos, 19 Oct 1973, *Villarreal 5597* (ENCB, MICH);

7 mi W of Huejúcar, 14 Sep 1966, *AL 3634* (MICH, OS). MÉXICO: Tultenango Canyon, 7 Oct 1902, *Pringle 8676* (F, G, GH, MEXU, MO, MSC, NY, UC); 1.5 mi N of Atlacomulco, hwy 55, 15 Oct 1966, *AL 4010* (MICH, OS); 60 mi SE of Queretaro, 19 Oct 1966, *AL 4082* (MICH, OS); hwy 57 near México/Queretaro state border, 18 Nov 1976, *SG 4579* (OS); 7 mi W of Jiquilpan, 15 Dec 1966, *AL 4534* (MICH, OS); 2 mi W of Zacapu, 8 Oct 1965, *C 10302* (CA, ENCB, MICH, NY, US); 9 mi W of Morelia, 15 Dec 1966, *AL 4531* (MICH, OS); Loma Santa María, near Morelia, 1910, *Arsène 5941* (GH, MO, US); 5 mi N of Huiramba, 9 Oct 1966, *AL 3910* (MICH, OS). QUERETARO: Tequisquiapan, 25 Sep 1956, *Paray 2136* (ENCB). ZACATECAS: ca. 1 mi E of hwy 45 at Ojocaliente, 3 Aug 1976, *HF 4077*\*\* (OS); pass through Sierra Papantón, near Durango/Zacatecas border, 25–30 Sep 1948, *Gentry 8446* (CA, GH, MICH, US); Zacatecas, 13 Aug 1976, *HF 4083*\*\* (OS); hills of Zacatecas, 26 Oct 1891, *Pringle 3935* (DS, F, G, GH, MICH, MO, MSC, NY, UC, US); edge of Zacatecas, 23 Dec 1977, *Jansen & Harriman 472A*\*\* (OS, OSH); near Noria de los Molinos, Luis Moya, 15 Oct 1976, *Bustos s.n.* (OS); 7.5 mi S of Villa Nueva, 4 Oct 1965, *C 10273* (CA, ENCB, GH, MEXU, MICH, NY, US); ca. 1 mi S of Valparaíso, 11 Sep 1966, *AL 3608* (MICH); 18 mi S of Valparaíso, 4–5 Sep 1958, *M 17647* (ENCB, DUKE, MICH, NY, US); rd to Monte Escobedo, 10 mi SE of Mezquitic, 14 Sep 1966, *AL 3631* (MICH).

**15b. *Montanoa leucantha* subsp. *arborescens* (A. P. de Candolle) V. A. Funk, comb. et stat. nov. Figs. 5, 6, 7, 8, 53, 56, 57.**

*Montanoa arborescens* DC., Prodr. 5: 566. 1836, as "*Montagnaea*." Type: MEXICO, Cordillere de Guchilaque, Aug 1827, *J. L. Berlandier 1006* (lectotype chosen from four syntypes, G-DC, photo IDC 800. 565:III.4 top!; isolectotypes, FI! G! P!; photo of P isolectotype, FI! MO! US!). This syntype was selected because it has the most collection information, the largest number of specimens at various herbaria and because it was the only one specified by number in the protologue. Other syntypes are: *L. Alamán s.n.*, 1831; *L. Alamán s.n.*; and *Mairet 59*.

*Montagnaea clematidea* Walpers, Linnaea 14: 308. 1840. Type: MEXICO, locality unknown, s.d., *W. F. Karwinski s.n.* (holotype LE, not seen; isotype, KIEL!). Karwinski's original herbarium is deposited at LE (Holmgren and Keuken, 1974), but the specimen was not present in the loan from that institution. *Eriocoma clematidea* (Walpers) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa uncinata* Schultz Bip. in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864. Type: MEXICO, Cumbre de Estepa, Sep 1842, *F. M. Liebmann 484* [Liebm. Pl. Mex. 9056] (holotype, P!; isotypes, C[4]! G! K! P!; photo of holotype, OS!; photos of C isotype, FI! MO! NY! US!; tracing of C isotype, GH!). *Eriocoma uncinata* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa patens* A. Gray, Proc. Amer. Acad. Arts 21: 388. 1886. Type: MEXICO, Chihuahua, mountains above Batopilas, Aug–Nov 1885, *E. Palmer 164* (holotype, GH!; isotypes, BM! G[2]! GH! K! LE! NY[2]!; photo of K isotype, OS!).

*Polymnia nervata* M. E. Jones, Contr. W. Bot. 12: 44. 1908. Type: MEXICO, Chihuahua, Guayanopa Canyon, Sierra Madre Mts., 24 Sep 1903, 3600 ft, *M. E. Jones s.n.* [acc. #40414] (lectotype chosen from two syntypes with identical information, POM!; isolectotype, POM!).

**FLOWERING (AND FRUITING) PERIOD:** October–November (November–December), in the center of its range, but the reproductive cycle begins earlier (September) in the northern part of the range and later (late November) in the southern part of the range.

**DISTRIBUTION AND HABITAT:** Mountains of western and southern Mexico from Sonora to Chiapas and Guatemala (Fig. 57); cool wet forests on mountain slopes, in higher altitudes in fields and along forest margins and at lower altitudes along roadsides and riverbanks as well as on steep slopes; 1000–2300 m, usually between 1500–1800 m.

This subspecies is one of the few taxa in *Montanoa* found growing sympatrically with another taxon: *Montanoa leucantha* subsp. *arborescens* is found in at least one area in Oaxaca growing with *M. tomentosa* subsp. *tomentosa*. Both species are found along stream banks in the area. In this particular instance, *M. tomentosa* subsp. *tomentosa* is found along the Río Oro which parallels the road from Huahuapan de León to Oaxaca. *Montanoa leucantha* subsp. *arborescens* is found along the river that runs parallel to the road from Huahuapan de León

to Tehuacán. The two rivers merge near Tamazulapan and so do the distributions of the two taxa, which grow together (*FRa* 2383, 2382) at the junction and for a short distance downstream. No morphological evidence of hybridization was found. All chromosome counts from both taxa were normal.

REPRESENTATIVE SPECIMENS: GUATEMALA. SACATEPEQUEZ: above Dueñas, 21 Jan 1939, *Sa* 63257 (F). SOLOLÁ: 3–5 km W of Panajachel, 6–7 Dec 1963, *Williams et al.* 25317 (F, NY, US). MEXICO. CHIAPAS: 16 km NW of Rizo de Oro, 3 Nov 1971, *Breedlove & Smith* 21746 (DS, ENCB, MICH, MO); 30 mi E of Tuxtla, 26 Nov 1977, *FRa* 2571\* (OS); ca. 45 km E of Tuxtla, 16 Dec 1977, *FK* 2700 (OS); ca. 5 km E of Tuxtla, 16 Dec 1977, *FK* 2699 (OS); hwy 195 7 mi N of hwy 190, 27 Nov 1977, *FRa* 2574 (OS); jct of hwy 190 and 195, 25 Nov 1977, *FRa* 2561 (OS); 24.6 mi N of jct of hwy 190 and 195, 27 Nov 1977, *FRa* 2576 (OS); 34.2 mi N of jct of hwy 190 and 195, 27 Nov 1977, *FRa* 2580 (OS); Zinacatán, 29 Nov 1971, *Breedlove* 22913 (DS); 5 km above Soyalo, 2 Nov 1965, *Breedlove* 14053 (DS, ENCB, F, LL, MICH); 23 mi SE of San Cristóbal, 18 Nov 1966, *AL* 4248 (MICH, OS); 2–3 km SW of Aguacatecango, 16 Dec 1977, *FK* 2693 (OS); 3–4 km SW of Aguacatecango, 16 Dec 1977, *FK* 2695 (OS). CHIHUAHUA: San José de Pinal, Río Mayo, 21 Sep 1936, *Gentry* 2840 (ARIZ, F, GH, MO, S, UC); Barranca del Cobre, 30 Dec 1977, *Hartman et al.* 5107\* (OS, RM); Arroyo Hondo, 11 Sep 1935, *Gentry* 1776 (MEXU, MO, NA, UC, US); Maguarichic, 20 Sep 1939, *Knobloch* 6029 (LL, MSC, US). DURANGO: jct of hwy 40 and rd to Santa Lucía, 20 Dec 1978, *FCa* 3001 (OS); 4 mi E of jct of hwy 40 and rd to Santa Lucía, 20 Dec 1978, *FCa* 3002 (OS); 4 mi E of jct of hwy 40 and rd to Santa Lucía, 20 Dec 1978, *FCa* 3003 (OS); 1.5 mi E of La Fraguita, 20 Dec 1978, *FCa* 3004 (OS); ca. 45 km SW from La Ciudad, 21–22 Oct 1971, *Dieterle* 3828 (ENCB, MICH); 17 mi ESE of Durango, 3 Oct 1965, *C* 10261 (CA, DUKE, ENCB, GH, MEXU, MICH, MSC, NY, TEX, WIS); 7 mi E of La Palmito, 27 Sep 1973, *Reveal & Arwood* 3618 (US). GUERRERO: 5.8 mi E of Chichihualco, 15 Nov 1978, *FRi* 2838 (OS); 22 mi from hwy 95 on rd to Filo de Caballo, 13 Nov 1977, *FRa* 2325b (OS); Carrizal-Chichihualco rd, 4.2 mi SE of jct of road to Filo de Caballo, 15 Nov 1978, *FRi* 2834 (OS); Cruz de Ocote, 3 Dec 1963, *Rzedowski* 18099 (DS, ENCB, MICH, MSC, WIS); Otlatlán, 14 Nov 1939, *Hinton* 14852 (F, LL, MO, NA, NY); Pueblo Viejo, 8 Nov 1939, *Hinton* 14818 (F, GH, LL, MO, NA, US). JALISCO: 5 mi NNE of Talpa de Allende, 14 Oct 1960, *M* 20189 (DUKE, ENCB, LL, MICH, NY); rd to Tapalpa from hwy to Ciudad Guzmán, 15 Nov 1968, *Boutin & Braudt* 2142 (CA, MEXU, MICH); ca. 5 mi SW of Tepatitlán, 8 Oct 1976, *SG* 4096\* (OS); 47 mi S of Jiquilpan, 8 Nov 1977, *F* 2297 (OS); N shore of Lago de Chapala, 1 Oct 1966, *AL* 3858 (MICH, OS); btw Lagos de Moreno and San Juan de los Lagos, 7 Oct 1976, *SG* 4088\* (OS). MÉXICO: 2 km S of Temescaltepec, 30 Oct 1977, *F* 2232\* (OS); 2 km S of Temescaltepec, 30 Oct 1977, *F* 2233\* (OS); 3 km S of Temescaltepec, 30 Oct 1977, *F* 2234\* (OS); 3 km S of Temescaltepec, 30 Oct 1977, *F* 2236\* (OS); rd N from Valle de Bravo to hwy 15, 19 Nov 1978, *F* 2852 (OS); 3.2 mi N of jct of hwy 1 and hwy 5, 19 Nov 1978, *F* 2854 (OS); near Jopantla, 10 Dec 1978, *FV* 2954 (OS). MICHOACÁN: ca. 11 mi E of Coalcomán de Matamoros on rd to Dos Aguas, 17 Dec 1978, *FCa* 2981 (OS); 2 km W of Zacapu, 3 Nov 1977, *F* 2264\* (OS); ca. 15 mi E of Morelia, 15 Dec 1978, *FCa* 2966 (OS); 24 mi W of Zitacuaro, 1 Nov 1977, *FH* 2251 (OS); 4.1 mi W of Zitacuaro, 20 Nov 1978, *F* 2865\* (OS); ca. 7 mi SE of Ciudad Hidalgo, 4 Sep 1976, *HF* 4245\* (OS); just E of Zitacuaro, 1 Nov 1977, *FH* 2244 (OS). MORELOS: 1.2 mi S of México/Morelos state line on Cnautla-Amecameca rd, 25 Nov 1966, *AL* 4310 (MICH, OS); hwy 95D near km marker 74, 16 Nov 1977, *FG* 2360 (OS); 6.3 mi SW of Tepoztlán, 25 Nov 1966, *AL* 4307 (MICH, OS); 2 mi N of Cuernavaca, 27 Jan 1971, *Freeland & Spetzman* 74 (MEXU, NA). OAXACA: 27 mi NE of jct of hwy 190 and 125, 23 Nov 1978, *F* 2877 (OS); 14 mi NE of jct of hwy 190 and 125, 23 Nov 1978, *F* 2880 (OS); btw Huahuapan de León and Yanhuítlan, 18 Oct 1976, *SG* 4250\* (OS); 30.7 mi NW of Oaxaca, 23 Nov 1978, *F* 2895 (OS); 14.7 mi SE of jct of hwy 190 and 1.2 mi NW of Tamazulapan, Río Oro, 23 Nov 1978, *F* 2891 (OS); 12–14.5 mi S of Suchiztepec, 8 Nov 1966, *AL* 4177 (MICH, OS); Las Sedas, 20 Oct 1907, *Conzatti* 2079 (F, MEXU, MICH); near Ixtlán de Juárez, 4 Nov 1966, *AL* 4120 (MICH, OS); 39 km N of jct of hwy 190 and 131, 20 Nov 1977, *FRa* 2399 (OS); 6.8 mi N of Oaxaca on hwy 175, 17 Dec 1977, *FTK* 2701 (OS); Sierra de San Felipe, 9 Oct–16 Nov 1894, *Pringle* 4929 (BM, BR, CM, F, G, GH, M, NY, S, US); 2 mi N of jct of hwy 190 and rd to Jaycatlan, 6 Nov 1966, *AL* 4134 (MICH, OS). PUEBLA: ca. 3 mi E of Puebla, 20 Aug, *HF* 4135\* (OS); near San Miguel Papaxtla, Cholula, 31 Sep 1967, *Rzedowski* 24898 (ENCB); 1 km NW of San Pedro Yaucuítlan, 24 Oct 1976, *Mexica* 159 (ENCB); 20 mi N of Huajuapán de León, 24 Oct 1965, *Cronquist & Sousa* 10402 (CA, DUKE, ENCB, GH, MEXU, MICH, MSC, NY, TEX, US). SINALOA: 5 mi NW of Los Ornos, Sinaloa and Vela, 6 Nov 1969, *Breedlove & Kawahara* 17076 (MICH); Palmito, 14–15 Nov 1959, *Gentry & Arguelles* 18173 (TEX, US). SONORA: 12.5 mi W of Yecora, 12 Aug 1978, *FS* 2775\* (OS); Huchuerachi, 4 Dec 1890, *Hartman* 302 (GH, K, NY, UC, US); near La Nopalera, 4 Oct 1939, *Muller* 3613 (GH, LL, MICH, NA, UC); San Bernardo, 8 Nov 1934, *Gentry* 1146 (A, ARIZ, F, MICH, MO); Sierra de Alamos, 30 Oct 1939, *Gentry* 4788 (ARIZ, DS, F, GH, MICH, MO, NA, NY, UC, US).

16. *Montanoa karwinskii* A. P. de Candolle, Prodr. 5: 565. 1836, as "*Montagnaea karwinskii*." Type: MEXICO, s.d., *W. F. Karwinski s.n.* (holotype, G-DC, IDC 800. 565:III.7!; isotypes, M! P!; photos of holotype, F! GH! MO! US!; photo of P isotype, OS!; tracing of holotype, GH!). *Eriocoma karwinskii* (DC.) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

Figs. 44A, 58, 59.

*Montanoa gracilis* Schultz Bip. in K. Koeh, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864. Type: MEXICO, San Miguel, La Galera, Oct 1842, *F. M. Liebmann 633* [Liebman. Pl. Mex. 9050] (holotype, P!; isotypes, C[3]!; photo of holotype, OS!; photos of C isotype, F! MO! NY! US!). *Eriocoma gracilis* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa olivae* Schultz Bip. in K. Koeh, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 406. 1864. Type: MEXICO, Jalisco, near Guadalajara, Sep 1855, *L. Oliva 347* (holotype, P!; photos of holotype, F! MO[2]! OS! US[2]!; fragment, US!). *Eriocoma olivae* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa subtruncata* A. Gray in Watson, Proe. Amer. Acad. Arts 22: 424. 1887. Type: MEXICO, Jalisco, Rio Blanco on sides of barranca, Sep 1886, *E. Palmer 599* (holotype, GH!; isotypes, BM! G! K! LE! NY[2]! US!; photo of K isotype, OS!).

*Montanoa affinis* S. F. Blake, Contr. U.S. Natl. Herb. 22: 612. 1924. Type: MEXICO, Guerrero, El Oeote, near Río Petatlan btw Murga and La Botella [MeVaugh, 1951], 660 m, 12 Nov 1898, *E. Langlassé 621* (holotype, US!; isotypes, G! GH! K!).

Shrubs 1–6 m tall. *Stems* terete, slender, herbaceous parts purple turning brown, glabrous to puberulent. *Leaves* distinct; petioles 1–9 cm long, usually lightly puberulent to essentially glabrous, occasionally densely pubescent, hairs 0.5–1.0 mm long; blades ovate to pentagonal (Fig. 58A–I), 5.0–18.5 cm long, 3.5–9.0 cm wide, apex acute to acuminate, laminar section delimited by two lateral veins, margin entire to serrate-dentate, adaxial surface moderately pubescent, hairs pustular, abaxial surface sparsely to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Peduncles* 1.5–3.5 cm long, sometimes purple, moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Heads* pendulous at fruiting, 0.8–1.1 cm diam in flower, 1.7–2.0 cm diam in fruit, several to many in open cymose synflorescences in oppositely branched compound corymbs. *Phyllaries* 5, uniseriate, reflexed at fruiting, equal, ovate-lanceolate, bracts 3.0–3.25 mm long, 1.0–1.25 mm wide, green, apex acute, mucronate, margin ciliate, entire, abaxial surface moderately pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous. *Ray florets* 5–8; corollas white, ligules elliptic to obovate, 12–15 mm long, 5.0–5.5 mm wide, apex acute to 2-notched, adaxial surface sparsely pubescent, hairs 0.5–1.0 mm long, abaxial surface moderately glandular, tube 1.0 mm long, 0.5 mm wide, moderately glandular and pubescent, hairs 0.5–1.0 mm long. *Disc florets* (Fig. 58J) 23–34; corollas green turning yellow, tube 0.5–1.0 mm long, 0.75–1.0 mm diam, densely glandular and pubescent, hairs less than 0.5 mm long, throat cylindrical, 2.0–2.5 mm long, 1.25–1.5 mm diam, densely glandular and pubescent on proximal half, hairs less than 0.5 mm long, lobes 5, 1.0 mm long, 0.75–1.0 mm wide, apex acute, glabrous; stamens with filaments 2–3 mm long, 0.25 mm wide, anthers not fully exerted from corolla, thecae brown, 1.5–2.0 mm long, 0.5 mm wide, apical appendages yellow, acuminate, 0.5–0.75 mm long, 0.25–0.5 mm wide, abaxial surface of apical appendage glandular; styles yellow, 5.5–6.25 mm long, enlarged at base, stigmatic surface yellow, 1.0 mm long, apical appendages acuminate, yellow, 0.5–0.75 mm long, 0.4 mm wide. *Pales* at anthesis rhombic (Fig. 58K), 2.5 mm long, 3–4 mm wide, light yellow, apex long-acuminate, indurate, margin ciliate, entire, abaxial surface glandular in center, densely pubescent on midrib and near margins, hairs 0.5–1.0 mm long, adaxial surface sparsely glandular near margin; pales at fruiting deciduous, cordate (Figs.

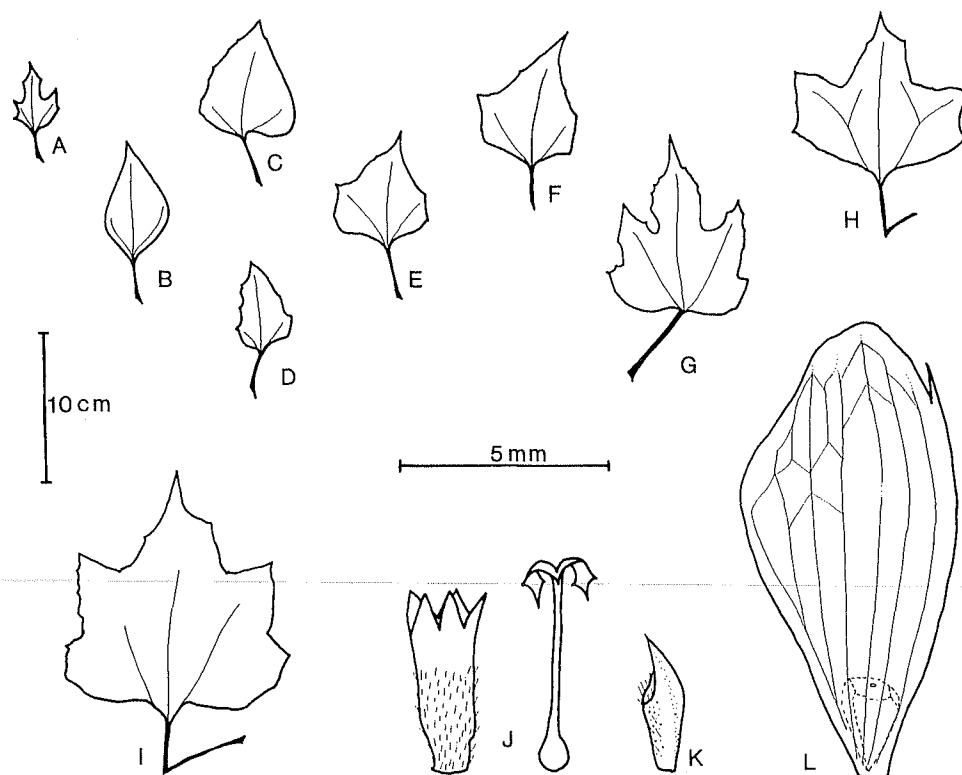


Fig. 58. *Montanoa karwinskii*. A-I, variation in mature leaves: A, D, H, AL 4341 (OS); B, I, M 20282 (MICH); C, Cronquist & Fay 10852 (NY); E, AL 4173 (OS); F, FGe 2351 (OS); G, M 19377 (MICH). J, disc corolla and style, FGe 2351 (OS); K, pale subtending disc corolla at anthesis, AL 3866 (OS); L, mature pale, FH 2288 (OS). A-I, J-L, same scale respectively.

44A, 58L), 7.5–10.0 mm long, 3.75–5.0 mm wide, papery with netted venation, stramineous or purple, apex a deep sinus and short apiculate tip, margin glabrous, entire, abaxial and adaxial surfaces glabrous. *Achenes* brown-black, 2.25–2.75 mm long, 1.5 mm wide, smooth, apex slightly enlarged. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: September–October (October–November).

DISTRIBUTION AND HABITAT: Sierra Madre del Sur from Nayarit to Oaxaca (Fig. 59); semi-deciduous forests and below the pine-oak forests, on roadsides, hillsides and occasionally along streams; 350–2000 but usually around 1000 m.

*Montanoa karwinskii* is a very graceful species having slender, ascending branches bearing relatively small, long-petioled leaves. The leaves are unique in the genus in having the base of the blade delimited by the two main lateral veins and a completely unwinged petiole (Fig. 58A–I). It is further distinguished by the mature pales, which are small (7.5–10.0 mm long) with a rounded apex and an apiculate tip that is shorter than the deep (2 mm) sinus. In addition, members of this species have small numbers of disc florets (23–34) and all the branches on the plant, including those of the synflorescence, are long and slender, giving the plants a delicate, open appearance. *Montanoa karwinskii* is rarely confused with



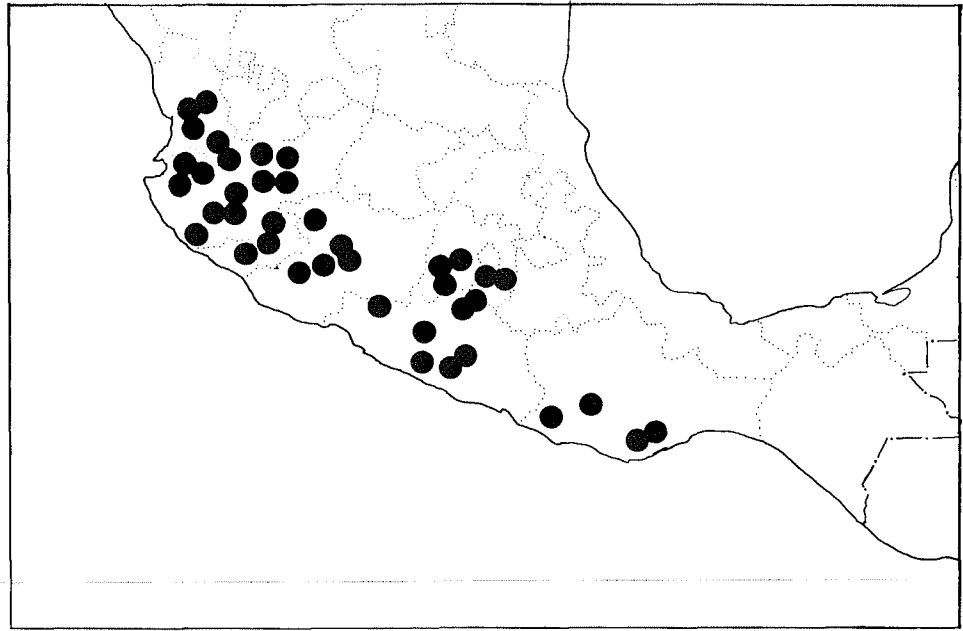


Fig. 59. Map of southern Mexico showing the distribution of *Montanoa karwinskii*.

any other species when collected in fruit; in flower, however, there is a superficial resemblance to *M. leucantha* subsp. *arborescens* and *leucantha*. It is easily distinguished from these two subspecies which have larger pales (8–17 mm long) with a tapering apex and without a sinus, 30–60 disc florets, and lack the slender branches and have leaves that are partially winged and usually auriculate.

*Montanoa karwinskii* is most closely related to *M. atriplicifolia* and *M. pteropoda* with which it shares both mature pales with a sinus, and the slender habit. It differs from these species in having fewer disc florets (23–34) that are longer (3.5–4.25 mm). In comparison *M. atriplicifolia* and *M. pteropoda* have 90–120 disc florets that are less than 3.0 mm long. Additionally, *M. atriplicifolia* and *M. pteropoda* are often vine-like whereas *M. karwinskii* is a shrub.

REPRESENTATIVE SPECIMENS: MEXICO. COLIMA: 0.8 mi NE of Cuauhtémoc, 12–13 Nov 1971, *Dieterle 4174* (CA, ENCB, MICH, US). DURANGO: La Bajada, Tamajula, Nov 1921, *Ortega 4433* (GH, US). GUERRERO: rd from El Ocotito to Coatepin, 16 Nov 1977, *FGe 2351* (OS); 6.5 mi W of Chilpancingo on rd above Amojileca, 3 Dec 1966, *AL 4341* (MICH, OS); 10–30 mi S of Sabana Grande, 15 Oct 1976, *SG 4213\** (OS); 24 km S of Chilpancingo, 8 Dec 1966, *AL 4474* (MICH, OS); 10 km N of Agua de Obispo, 9 Oct 1969, *Rzedowski 26892* (OS); Rincón de la Vía, 17 Oct 1965, *Kruse 1217* (ENCB); E slope of Cerro de la Guacamaya, Temisco, 18 Nov 1937, *Mexia 8842* (ARIZ, F, K, MO, NY, S, UC, US); Atoyac-San Juan, 13 Oct 1939, *Hinton 14618* (ARIZ, F, GH, MO, NA, NY, US); Vallecitos, 19 Nov 1937, *Hinton 11565* (GH, LL, MICH, NY, UC, US); Manchon, 7 Oct 1936, *Hinton 9662* (G, GH, MICH, NY, S, TEX, UC, US, W). JALISCO: 10.9 mi NE of Tonila, 6 Nov 1977, *F 2288* (OS); above La Cuesta, 15–16 Oct 1960, *M 20282* (DUKE, ENCB, LL, MICH, NY); 11.5 mi N of Zapopan, 8 Sep 1966, *Melchert et al. 6346* (ENCB, MICH); 8 km NE of Tonila, 13 Nov 1971, *Dieterle 4178* (CA, ENCB, MICH, OS); 4 km SE of Tequila, 6 Nov 1971, *Dieterle 4242* (ENCB, MICH, OS); 32.5 km from Melaque toward La Huerta, 8–9 Nov 1971, *Dieterle 4121* (CA, ENCB, MICH, OS); btw Cuale and Los Lobos, 14 Oct 1971, *González 497* (ASU, COL, MICH); near Los Corales, 24 Oct 1963, *Rzedowski 17440* (MICH); El Platanarillo, 6 Oct 1968, *Villarreal de Puga 2132* (ENCB); Cerro del Cuatro, S of Guadalajara, 3 Oct 1965, *Villarreal de Puga 360* (ENCB); Ixtlahuacán de los Membrillos, 12 Oct 1961, *Detling 8698* (ENCB); 21.3 mi N of jct of hwy 80 and hwy 200 to Barra de

Navidad, 6 Nov 1977, *F 2292\** (OS); 47 mi S of Jiquipán, 8 Nov 1977, *FH 2296* (OS); 2 mi NW of Tequila, 7 Sep 1976, *HF 4284* (OS); btw Pihuamo and San Pedro, 12 Oct 1976, *SG 4148\** (OS); 1.3 mi NNE of Santa Cruz, 2 Sep 1973, *SG 3069* (ASU, OS, UC); ca. 26 mi NW of Tequila, 9 Oct 1976, *SG 4107* (OS); ravines 9–10 mi N of Bahía Navidad, 10 Nov 1960, *M 20937* (BM, DUKE, ENCB, LL, MICH, NY, US); near El Molina, 2 Sep 1960, *M 18609* (DUKE, ENCB, LL, MICH); 7 mi S of Juchitlán, 24 Sep 1966, *AL 3720* (MICH, OS); 30–35 km SE of Autlán, 28 Sep 1966, *AL 3782* (MICH, OS); 1.2 mi NW of Magdalena airport, 16 Sep 1971, *Keil & Canue 9007* (ARIZ, MICH, OS); near Etzatlán, 2 Oct 1903, *Rose & Painter 7561* (GH, NY, US); barrancas near Guadalajara, 19 Sep 1893, *Pringle 4545* (ARIZ, ASU, C, DUKE, F, G, GH, LL, MICH, NY, S, TEX, UC); 35 mi S of Tamazula, 25 mi NE of Jalisco/Colima border, 15 Sep 1966, *AL 4541* (MICH). MÉXICO: Rincón, Dto. Temascaltepec, 2 Oct 1932, *Hinton 1880* (BM, DS, G, K, US); Naranjo, Dto. Temascaltepec, 4 Oct 1932, *Hinton 1977* (BM, G, GH, MEXU, MO, NY, US); Ixtapan de la Sal, 12 Oct 1952, *Matuda 27051* (NY); Barranca de Tonatico, 26 Sep 1954, *Matuda 31683* (NY); Valle de Bravo, 23 Nov 1952, *Matuda 27333* (MEXU, NY); 5.5 mi S of Tejuipilco, 12 Oct 1966, *AL 3955* (MICH); 3–4 mi N of Amatepec, 13 Oct 1966, *AL 3970* (MICH). MICHOACÁN: 4 mi S of Ario de Rosales, 8 Oct 1966, *AL 3903* (MICH, OS); 2 mi W of Jiquipán, 2 Oct 1966, *AL 3866* (MICH, OS); 9 mi S of Uruapan, 7 Oct 1966, *AL 3892* (MICH, OS); 11 mi N of La Huacana, 8 Oct 1966, *AL 3901* (MICH, OS); N facing slopes of Cerro Santa María, 8–10 km SW of Jiquipán, 5–7 Aug 1959, *Feddema 151* (MICH, OS); 15 mi S of Uruapan, 9 Nov 1977, *FH 2300* (OS); 15–16 km SE of Aseradero Dos Aguas, 25–26 Nov 1970, *M 24717* (ENCB, MICH); W facing slopes of Cerro de Carboneras, ca. 22 km S of Uruapan, 16–22 Oct 1961, *King & Soderstrom 4816* (MICH, NY, SMU, TEX, UC, US); ca. 5 mi N of Cotja, 22 mi S of Jiquipán, 5–9 Oct 1961, *King & Soderstrom 4653* (MEXU, MICH, NY, SMU, TEX, UC, US); Coalcomán, 28 Oct 1938, *Hinton 12473* (F, GH, K, LL, MICH, MO, NY, TEX, UC, US, W). MORELOS: near Cuernavaca, 1905, *Lemmon & Lemmon 108* (F, GH, MO, US); Fraccionamiento Analco, 27 Oct 1972, *Vázquez 3954* (MEXU); Tlayacapan, 23 Sep 1956, *Paray 2120* (ENCB); 3.2 mi SW of Tepoztlán, 25 Nov 1966, *AL 4308* (MICH, OS); btw Cuautla and Amecameca, 25 Nov 1966, *AL 4309* (MICH, OS); 0.7 mi NE of Morelos/Guerrero state border, 2 Dec 1966, *AL 4316* (MICH, OS); W edge of Cocoyoc, 25 Dec 1977, *Jausen & Harriman 487* (OS). NAYARIT: 60 km SE of Tepic, 11 Oct 1970, *Cronquist & Fay* (CA, DUKE, ENCB, F, MICH, MSC, NY, S, TEX, US); 2.6 mi NW of Jalisco/Nayarit state line, 19 Dec 1978, *Fca 2998* (OS); Cerro de la Cruz, near Tepec, 17 Sep 1926, *Mexia 645* (A, BM, F, GH, MICH, MO, NY, UC, US); 17–18 mi NW of Tepic, 26 Oct 1971, *Dieterle 3873* (CA, ENCB, MICH, OS); 9.5 mi W of Tepic, 25 Sep 1960, *M 19377* (DUKE, ENCB, LL, MICH); S of Las Varas, 10 Oct 1976, *SG 4127\** (OS); 2–9 mi W of Jalcoctán on rd to Miramar, 15 Nov 1959, *McVaugh & Koelz 682* (DUKE, ENCB, LL, MICH). OAXACA: 35 km NNW of Pinotepa Nacional, 29 Oct 1970, *Cronquist & Fay 10852* (CA, DUKE, ENCB, F, GH, MICH, MSC, NY, RSA, S, TEX); 12.5 mi N of Pochutla and 20.2 mi N of Puerto Angel, 10 Nov 1966, *AL 4194* (MICH, OS). SINALOA: rd from Rosario to Plamosa, 4.2 mi E of La Rastra, 7 Oct 1975, *Reveal & Harley 4030* (K, US); 42–43 km NE of Concordia, 22–23 Oct 1971, *Dieterle 3843* (CA, ENCB, MICH, OS).

**17. *Montanoa atriplicifolia* (Persoon) Schultz Bipontinus in Seeman, Bot. Voy. Herald 7–8: 304. 1856, as "*Montagnaea*." Figs. 60, 61.**

*Verbesina atriplicifolia* Pers., Syn. Pl. 2: 472. 1807. Type: Hort. Ital. (holotype, P?; non-flowering isotype, FI!). Persoon often used Jussieu's herbarium (Staffeu, 1967) which is now at Paris. No possible holotypes were found in the loan material from P and Persoon's description is cryptic. It would not be possible to place this species except that Jussieu and Desfontaines published a better description (Colla, 1824), synonymy, and a drawing, and attributed the species to Persoon. The drawing is somewhat questionable, however, as the rays are too blunt for *Montanoa*, and they have well-developed stigmas. Although there is still some doubt, the evidence is sufficient to warrant recognition of this name. *Eriocoma atriplicifolia* (Pers.) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Clerodendron phlomooides* Juss. & Desf. in Lamarck, Hort. Ital. 8: 460. 1808, nom. nud. pro syn. *Galinsoga discolor* Spreng., Nov. Prov. 19. 1819. Type: Hort. Ital., *G. B. Balbis s.n.* (holotype, P!; isotype, G-DC; photo of holotype, US!; photo of G-DC isotype, GH! US!).

*Montanoa dimicola* Klatt in Durand & Pittier, Bull. Soc. Roy. Bot. Belgique (Brussels) 31: 200. 1882. Type: COSTA RICA, San José, hedgerow on the "llanos de Alajuelita," 1100 m, 1 Dec 1889, *H. Pittier 1454* (holotype, GH! isotypes, BR[2]! G! US!).

*Montanoa pauciflora* Klatt, Leopoldina 23: 90. 1887. Type: "Middle America . . . in Herb. Klatt." (holotype not located). The most likely place for this specimen is GH. However, the types as well as the general collections of *Montanoa* have been searched to no avail. *Coriopsis trilobata* Vahl ex Klatt, Leopoldina 23: 90. 1887, nom. nud. pro syn. This is listed as the type of *M. pauciflora* Klatt in the type description. The types as well as the general collections at GH have been checked for this specimen (in litt., M. Canoso) but it has not

been located. The possibility exists that the specimen will be located at a later date; a neotype has not been selected.

*Montanoa schottii* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 518. 1899. Type: MEXICO, Yucatán, on the road between Merida and Sisal, 24 Oct 1865, A. Schott 913 (holotype, FI).

Shrubs or vines to 3 m tall or 15 m long. *Stems* terete, light brown, herbaceous parts puberulent. *Leaves* variable; petioles 1.5–11.5 cm long, usually partially winged and auriculate, densely glandular and pubescent, hairs 0.5–1.0 mm long, blades ovate to pentagonal (Fig. 60A–K), 4.5–14.5 cm long, 1.5–15.0 cm wide, apex acute to acuminate, margin entire to irregularly serrate, sometimes deeply 3-lobed, adaxial surface moderately pubescent, hairs pustular, abaxial surface densely glandular and pubescent, hairs 0.5–1.0 mm long. *Peduncles* 1.5–7.5 cm long, densely glandular and pubescent, hairs 0.5–1.0 mm long. *Heads* pendulous at fruiting, 0.6–0.8 cm diam in flower, 1.7–2.7 cm diam in fruit, few to many in open cymose synflorescences in oppositely branched compound corymbs. *Phyllaries* 5–6, uniseriate, equal, quickly becoming reflexed, ovate-lanceolate, 4–5 mm long, 1.0–1.25 mm wide, dark green, margin ciliate, entire, abaxial surface densely pubescent, hairs 0.5–1.0 mm long, adaxial surface with a few scattered hairs. *Ray florets* 8–15, corollas white, ligules lanceolate to narrowly elliptic, 12–24 mm long, 3–6 mm wide, apex acute to 2-notched, adaxial surface essentially glabrous, abaxial surface moderately to densely glandular, tube 0.5–1.0 mm long, 0.25 mm wide, essentially glabrous. *Disc florets* (Fig. 60L) 90–120; corollas yellow, tube 0.5 mm long, 0.5 mm diam, sparsely glandular and pubescent, hairs less than 0.5 mm long, throat cylindrical, 1.0 mm long, 1.0 mm diam, essentially glabrous or sparsely glandular and pubescent, hairs less than 0.5 mm long, lobes 5, 0.5 mm long, 0.5 mm wide, apex acuminate, moderately glandular and pubescent, hairs thick, less than 0.5 mm long; stamens with filaments 1.0 mm long, 0.10 mm wide, anthers not fully exerted from corolla, thecae brown, 0.75 mm long, 0.25 mm wide, apical appendages yellow, acute-acuminate, 0.5 mm long, 0.15 mm wide, abaxial surfaces of apical appendages glandular; styles (Fig. 60M) yellow, 2.5 mm long, enlarged at base, stigmatic surface brown, 0.75 mm long, apical appendages yellow, acute, 0.25 mm long, 0.25 mm wide. *Pales* at anthesis obtrullate (Fig. 60N) 2.25 mm long, 2.0 mm wide, light yellow with dark bands in center and along veins, apex long-acuminate, indurate, yellow, margin ciliate, entire, abaxial surface moderately glandular and pubescent near distal half, not on apex, hairs 1.0 mm long, on adaxial surface glabrous; pales at fruiting deciduous, more or less obdeltoid (Fig. 60M), 10–14 mm long, 3–4 mm wide, papery with netted venation, stramineous or purple, apex sinus with apiculate tip, margin sparsely pubescent, hairs less than 1.0 mm long, adaxial and abaxial surfaces glabrous. *Achenes* brown-black, 2.5 mm long, 1.5 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: November–January (December–March).

DISTRIBUTION AND HABITAT: Chiapas and the Yucatán to Costa Rica (Fig. 61); wide range of habitats from cool forests to dry roadsides; 450–2000 m, more vine-like at lower altitudes and in drier environments.

A delicate appearing plant with slender, often erect branches and heads with a large number (90–120) of extremely small (2 mm) disc florets. When *Montanoa atriplicifolia* is found as a vine it is characterized by large (1–2 cm diam) branches sprawling across other vegetation or the ground and short, slender, erect, lateral branches bearing small groups of capitula. This type of growth form is found primarily in the Yucatán Peninsula. At higher altitudes and in wetter habitats this

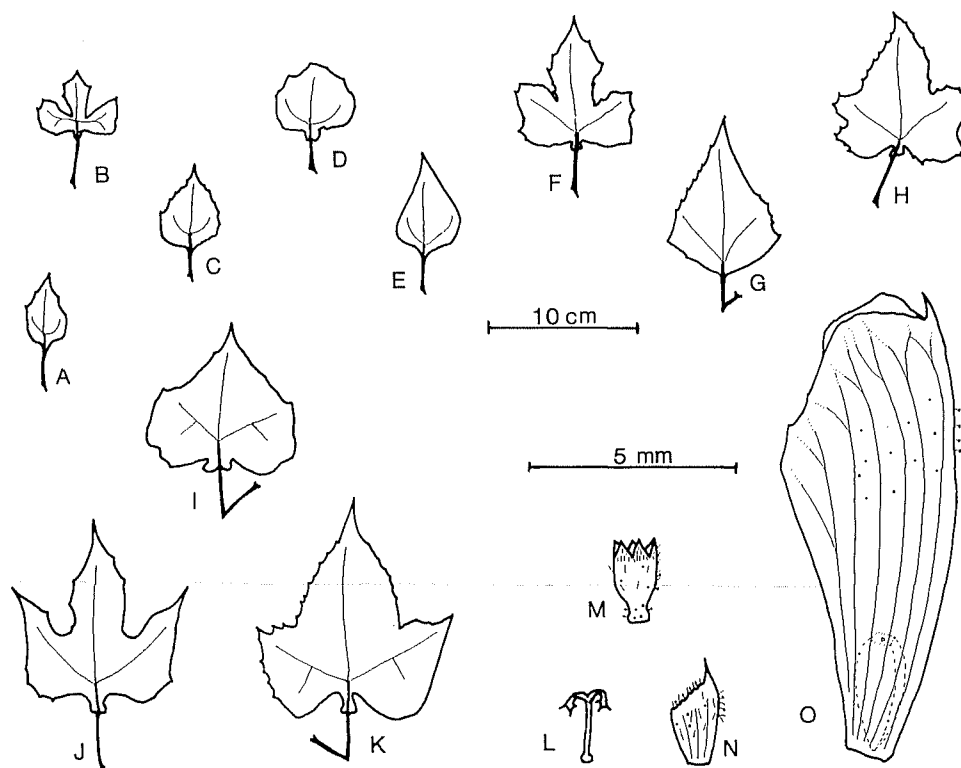


Fig. 60. *Montanoa atriplicifolia*. A-K, variation in mature leaves: A, D, K, FL 2934 (OS); B, C, E-I, FRa 2638 (OS); J, FL 2932 (OS). L, M, disc corolla and style, FL 2932 (OS); N, O, pale subtending disc floret at anthesis and mature pale, FRa 2593 (OS). A-K, L-O, same scale respectively.

species gradually changes to a shrub habit. Both growth forms have relatively small leaves that have the same range of shapes (Fig. 60A-K).

*Montanoa atriplicifolia* is most closely related to *M. pteropoda* with which it shares the occasional vine-like habit, large number of small disc florets (less than 3.0 mm long) and obtrullate pales with a moderate sinus. The two species are easily distinguished by *M. pteropoda* having a dark aspect to the heads caused by the dark gray-green-black color of the apices of the corolla, stigma and anthers, and by *M. atriplicifolia* not having all the parts of the disc florets yellow. In addition, the apices of the stigmata, anthers and petals are blunt-acute in *M. pteropoda* and the petioles are winged to the base, whereas the apices of parts of the disc florets are acuminate in *M. atriplicifolia*, and the petioles are unwinged for most of their length.

REPRESENTATIVE SPECIMENS: BELIZE. CAYO: El Cayo, 12 Feb 1931, Bartlett 11421 (F, GH, MICH, MO, NA, US); Bejuco, 15 Feb 1938, Gentle 2169 (F, K, MICH, US); 5 mi N of Blaneaneau Lodge, 12 mi S of Georgeville, 24 Jan 1974, Liesner & Dwyer 1630 (OS); 3 mi S of Grano de Oro, 2 Jun 1973, Gentry 7761 (MO, OS); Georgeville to Augustine rd at mile 8, 3 May 1969, Proctor 30268 (BM, LL); 9 mi S of the Western hwy on rd to Augustine, 28 Jan 1970, Wilbur & Weaver 11491 (DUKE); Maeal River 1 mi past Guaeamallo Bridge, rd to Millionario, Dwyer & Liesner 12355 (MO); S of San Luis and E of Camp Six, 19 Mar 1967, Dwyer et al. 377A (LL, MO); Cave Branch Section, Humming Bird hwy, 18 Feb 1956, Gentle 9029 (LL). COSTA RICA. SAN JOSÉ: San Pedro, E of San José, 25 Jan 1922, Greenman & Greenman 5315 (GH, MO); San José, 18 Jan 1916, Holway 444 (GH). EL SAL-

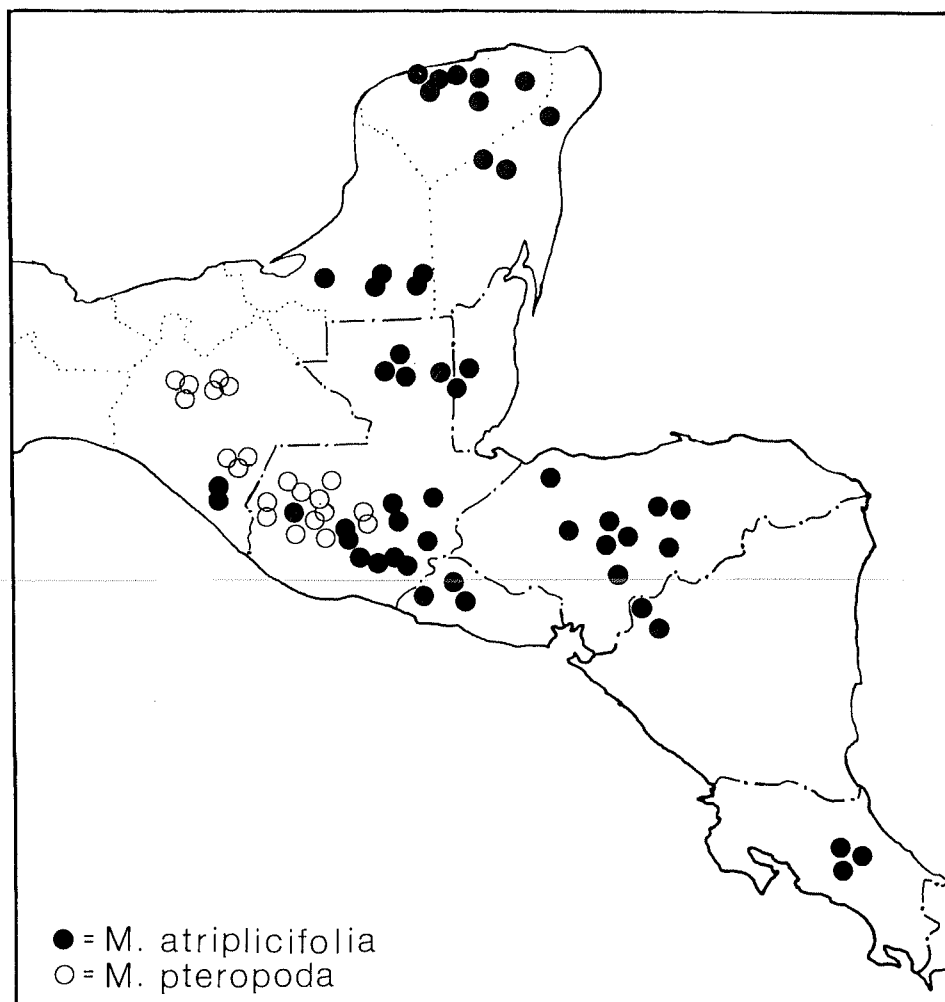


Fig. 61. Map of Chiapas, the Yucatán and Central America to Costa Rica showing the distribution of *Montanoa atriplicifolia* and *M. pteropoda*.

VADOR. AHUACHAPÁN: near Ahuachapán, 9–27 Jan 1922, *Sa 20018* (GH, NY, US); vicinity of Ahuachapán, 16–25 Jan 1947, *Standley & Padilla 2610* (F). LA LIBERTAD: stream near Colón, 21 Jan 1949, *Williams & Molina 15222* (F). SANTA ANNA: just SE of pueblo of Coatepeque along old free rd to San Salvador from Santa Anna, 30 Nov 1978, *FL 2922\** (OS); 3 km SE of Santa Anna, 18 Nov 1963, *Porter 1285* (DS, GH, MEXU). SONSONATE: Finca Chilata, 26–27 Dec 1921, *Sa 19229* (GH, NY, US). GUATEMALA. AMITITLAN: Moran, 22 Dec 1916, *Holway 625* (US). CHIMALTENANGO: above Las Calderas, 15 Dec 1938, *Sa 60086* (G); Quisaché, 5–6 Jan 1939, *Sa 62009* (F). CHIQUIMULA: btw Chiquimula and La Laguna, 27 Oct 1939, *Se 30702* (F); hills near Ipala, 23 Oct 1939, *Se 30355* (F); 2 km from village of Esquipulas, 6 Dec 1969, *Molina & Molina 25168* (F, LL). GUATEMALA: Santa Catarina Pinula, just S of Guatemala City, 7 Dec 1977, *FRa 2638* (OS); SE of Guatemala City on rd to San Salvador, 7 Dec 1977, *FRa 2645\** (OS). JALAPA: N of Jalapa on rd to Volcán Jumáy, 8 Dec 1977, *FRa 2653* (OS). JUTIAPA: near El Molina, 26 Nov 1940, *Sa 78459* (F). PETEN: Tikal National Park, Bajo del Hormiguero, ca. 12 km on old Remate rd, 28 Jan 1961, *Contreras 1887* (LL); Tikal, top of Temple IV, 5 Feb 1959, *Lundell 15366* (LL); La Libertad, 16 Mar 1935, *Aguilar 476* (LL, MICH, MO, US); El Paso, 25 Apr 1932, *Lundell 1537* (MICH, US); Sacpuy, 10 km S of Flores, 28 Jan 1971, *Ortiz 1555* (BM, F, MICH, US); Melchor de Mencos rd, btw kms 35–36, 5 Feb 1966, *Contreras 5476* (ENCB, F, MICH, US); rd btw San Andres and Santa Elena, 10 Jan 1970, *Ortiz 548*

(ENCB, F, MO, NY). PROGRESO: along railroad btw Barranquillo and Cruz, 30 Jan 1942, *Se* 43328 (F); btw Zanarate and El Chato bridge, 28 Nov 1969, *Molina & Molina* 24920 (MO, NY, US). SANTA ROSA: SE of Barberena, 7 Dec 1977, *FRa* 2646 (OS); SE of Barberena, 7 Dec 1977, *FRa* 2647 (OS); near El Molina, 20 Dec 1936, *Sa* 60472 (F); E of Cuilapa, 25 Nov 1940, *Sa* 78257 (F); near Cuilapilla, 23 Nov 1940, *Sa* 78117 (F); Casillas, Nov 1892, *Heyde & Lux* 4242 (F, G, K, M, MO, NDG, NY). SACATEPEQUEZ: ca. 19 km N of Escuintla, 23 Jan 1977, *King* 7184 (MO, US); barranco above Dueñas, 21 Jan 1939, *Sa* 63203 (F); near Tejar, 14 Dec 1938, *Sa* 59863 (F). HONDURAS. COMAYAGUA: near Comayagua, 12–13 Mar 1947, *Staudley & Chacou* 5935 (F); upstream from main vado in El Zamorano, 2 Dec 1978, *FL* 2932 (OS); near Esquila Agrícola Panamericana on rd to Güinope, 4 Dec 1978, *FL* 2939 (OS); El Quibracho, 29 Nov 1946, *Sa* 368 (F); Poza del Tacuazín, 13 Dec 1947, *Molina* 671 (BH, F, GH, MO, US); near El Zamorano, 26 Nov–9 Jan 1947, *Sa* 1495 (F); rd btw El Jicarito and El Pedregal, 13 Nov 1948, *Sa* 14478 (F); Río Yeguarac at Güinopc, Nov 1943, *Rodriguez* 1568 (F). OLANCHO: btw Catacamas and El Hatillo along Río de Catacamas, 27 Mar 1949, *Sa* 18866 (F); near Juticalpa, 5–16 Mar 1949, *Sa* 17409 (MICH); rd to San Francisco La Paz, 20 Nov 1963, *Molina* 13309 (F, LL, NY, US). EL PARAÍSO: NE of Danlí, 3 Dec 1978, *FL* 2934\* (OS); ca. 1 mi N of El Paraíso on rd to Danlí, 3 Dec 1978, *FL* 2937 (OS). SANTA BÁRBARA: San Pedro Sula, Feb 1888, *Thieme* 5324 (F, G, GH, K, M, MO, NY, US). MEXICO. CAMPECHE: Campeche/Yucatán state line on hwy 261, 11 Nov 1975, *Dwyer* 334 (CA); 17 mi E of Xpuuil, 29 Nov 1977, *FRa* 2593\* (OS); near Escorsega, 16 Jan 1966, *Matuda* 37483 (F, MEXU); km 5 on the rd from Escárcega to Candelaria, 27 Dec 1965, *Hernández et al.* ES-229 (MEXU); Tuxpeña, 22 Dec 1931, *Lundell* 1093 (ARIZ, DS, F, GH, MICH, MO, S, UC, US). CHIAPAS: Piedra de Huixtla, 20 Jan 1949, *Matuda* 18603 (F, MEXU); rd from Toliman to Niquivil near Ojo de Agua, 14 Dec 1976, *Breedlove* 42607 (DS); jct of Río Perlas and Río Jatate at San Quintín near Laguna Miramar, 15 Mar 1955, *Sohus* 1589 (MICH, US). QUINTANA ROO: Coba, 2 Mar 1976, *Moreno* 535 (MEXU); Chichankanab, s.d., *Gaumer* 1479 (F, G, GH, K, MEXU, NY). YUCATÁN: Valladolid, 2 Jul 1932, *Steere* 1688 (LL, NA, MICH); Pcto. 26–27 Jul 1932, *Steere* 2291 (MICH); Chichen Itzá, 23 Jun 1932, *Steere* 1488 (MICH, US); Calotmul, s.d., *Gaumer* 2108 (B, BM, C, F, GH, MO, NY, S); Izamal, s.d., *Gaumer* 2499 (F); Temax, s.d., *Gaumer* 2357 (BR, DS, MICH, UC, US). NICARAGUA. ESTELÍ: 3–7 km NW of Pueblo Nuevo, 24 Nov 1973, *Williams & Molina* 42393 (F). MADRIZ: mt. above Somoto, 15 Nov 1946, *Williams & Molina* 10943 (F, GH, MICH, MO).

**18. *Montanoa pteropoda*** S. F. Blake, Proc. Biol. Soc. Wash. 37: 56. 1924. Type: GUATEMALA, Huehuetenango, between San Martín and Todos Santos, 7000–8500 ft, 25 Dec 1895, *E. W. Nelson* 3616 (holotype, US!). Figs. 61, 62.

Shrubs or vines of 4 m. *Stems* terete, brown, herbaceous parts densely to moderately pubescent, hairs 1.0–1.5 mm long. *Leaves* variable; petioles 2.0–6.5 cm long, winged with or without auricles, sometimes connate-perfoliate, densely pubescent, hairs 1.0–2.0 mm long; blades ovate to triangular (Fig. 62A–G), 5–21 cm long, 2–21 cm wide, apex acute to acuminate, margin entire to irregularly dentate or serrate, adaxial surface moderately pubescent, hairs pustular, abaxial surface moderately to densely glandular and pubescent, hairs 1.0 mm long. *Peduncles* 1.5–3.0 cm long, densely glandular and pubescent, hairs 1.0 mm long. *Heads* pendulous at fruiting, 1.0 cm diam in flower, 2–3 cm diam in fruit, few to many in open cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* 5–6, uniseriate, equal, ovate-lanceolate, 4–5 mm long, 1.5–1.75 mm wide, dark green, apex acute to long-acuminate, margin ciliate and entire, abaxial surface moderately pubescent, hairs less than 1.0 mm long, adaxial surface essentially glabrous. *Ray florets* 8, corollas white, veins sometimes dark, ligules elliptic to lanceolate, 10–12 mm long, 2.5–3.5 mm wide, adaxial surface essentially glabrous, abaxial surface densely glandular, tube 0.5–0.75 mm long, 0.3 mm wide, glabrous. *Disc florets* (Fig. 62I) 90–110; corollas green to grey-black, remaining yellow at base, tube 0.5 mm long, 0.5 mm diam, moderately glandular and pubescent, hairs 0.5 mm long, throat cylindrical, 1.5 mm long, 1.5 mm diam, moderately glandular and pubescent, hairs thick, less than 1.0 mm long, lobes 5, 1.0 mm long, 0.5 mm wide, apex acute, densely glandular and pubescent, hairs thick, less than 1.0 mm long; stamens with filaments 1.0 mm

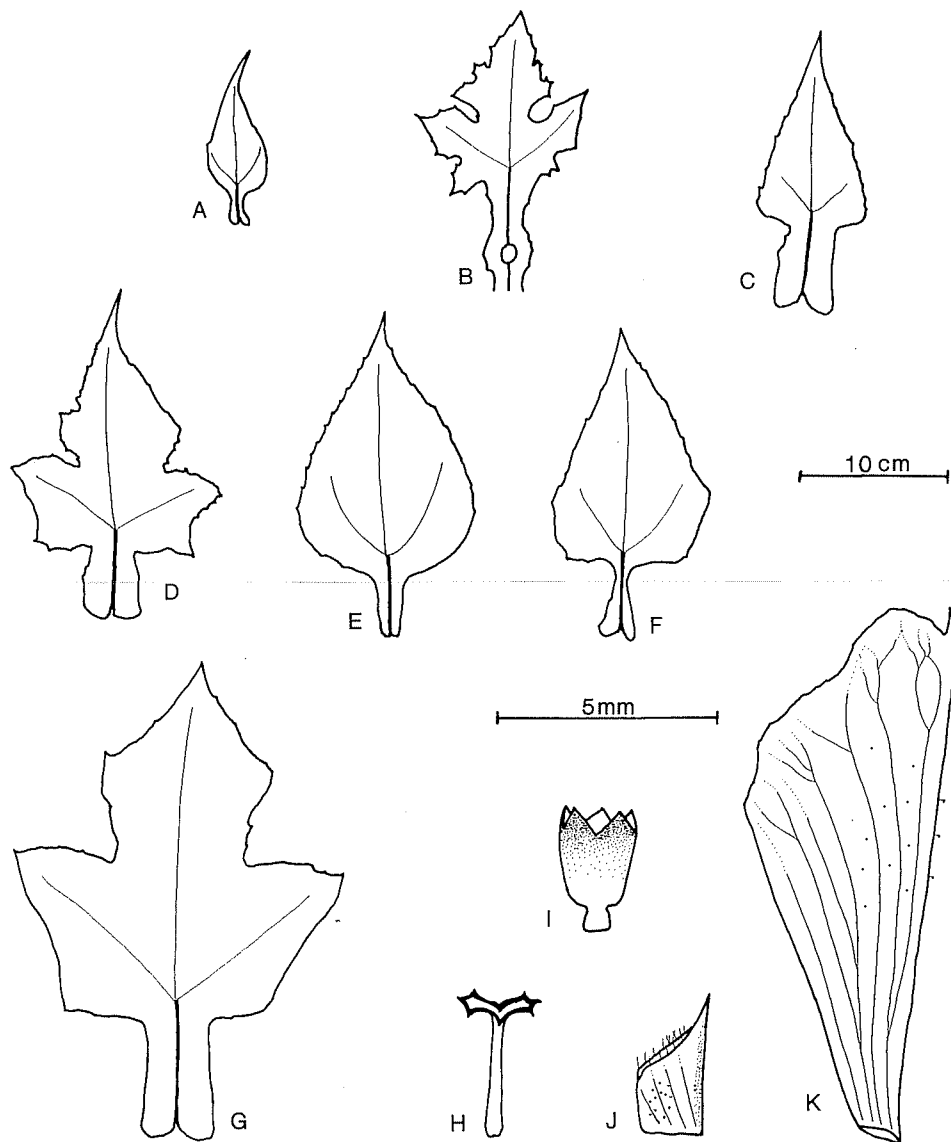


Fig. 62. *Montanoa pteropoda*. A-G, variation in mature leaves: A, C 10472 (MICH); B, E, FL 2952 (OS); C, SG 4331 (OS); D, Skutch 1746 (A); F, AL 4245 (OS); G, FL 2953 (OS). H, I, style and disc corolla, Molina & Molina 25014 (NY); J, pale subtending disc floret at anthesis, Molina & Molina 25014 (US); K, mature pale, FRa 2569 (OS). A-G, H-K, same scale respectively.

long, 0.2 mm wide, anthers not fully exerted from corolla, thecae yellow, 1.0 mm long, 0.5 mm wide, apical appendage dark green to grey-black, acute, 0.33 mm long, 0.25 mm wide, glabrous; styles (Fig. 62H) yellow and black, 3.5 mm long, not enlarged at base, stigmatic surface yellow on adaxial surface, dark green or grey-black on abaxial one, 0.75 mm long, apical appendage dark green, especially on abaxial surface, short acute with small mucronate tip, 0.25 mm long, 0.33 mm wide. Pales at anthesis pentagonal (Fig. 62J), 3.0 mm long, 2.5 mm

wide, light yellow with dark bands on midrib and base, apex long-acuminate, indurate, yellow, margin ciliate, glandular, entire, abaxial surface densely glandular and sparsely pubescent, hairs less than 0.5 mm long, adaxial surface glabrous; pales at fruiting deciduous, obtrullate (Fig. 62K), 8–14 mm long, 4–5 mm wide, papery with netted venation, stramineous or purple, apex small sinus with small spine, margin irregular, abaxial surface moderately glandular, adaxial surface glabrous. *Achenes* brown-black; 2.5 mm long, 1.5 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: October–December (November–March).

DISTRIBUTION AND HABITAT: Chiapas, Mexico and western Guatemala (Fig. 61); wet pine-oak forests and humid slopes; 1650–3800 m, usually over 2000 m.

This high altitude shrub-vine is common in the high areas of Chiapas and Guatemala and is easily recognized. The leaves are winged to the base of the petiole and at times connate-perfoliate (Fig. 62B). Also, the heads have a dark aspect because of the grey-green-black coloration on the apices of the disc corolla, anthers and stigma. The synflorescence of this species is dense and the heads sit on thick densely pubescent pedicels that contrast with the slender, delicate appearance of its closest relative, *Montanoa atriplicifolia*. A more detailed discussion of the relationship between these two species is included under the discussion of *M. atriplicifolia*.

The distribution of these two species overlaps in the area of Guatemala City, but they are separated altitudinally and have never been collected in precisely the same locality.

REPRESENTATIVE SPECIMENS: GUATEMALA. CHIMALTENANGO: rd to Patzún, 14 km NW of CA-1, 24 Jan 1977, *King 7203* (MO, US); rd to Patzún, 16 km NW of CA-1, 24 Jan 1977, *King 7206* (MO, US); Chichavac, Nov–Dec 1930, *Skutch 120* (MICH, US); above Tecpam, 9 Dec 1933, *Skutch 756* (GH, LL, US); above Las Calderas, 15 Dec 1938, *Sa 60086* (F, US); near Parramos, 14 Dec 1938, *Sa 59884* (F, NY); near Chimaltenango, 11–22 Dec 1940, *Sa 79951* (F); btw Chimaltenango and San Martín Jilotepeque, 3 Feb 1939, *Sa 64352* (F, NY); near Patzúcia, 4 Dec 1938, *Sa 58656* (MICH). GUATEMALA: btw rd and milpa below San Francisco El Alto, 31 Oct 1970, *Harmon 4558* (DS, ENCB); Antigua, 3 Dec 1963, *Molina 13465* (F, NY, US). HUEHUETENANGO: jct of three depts: Huehuetenango, Totoncapán and Quezaltenango, 8–9 Dec 1962, *Williams et al. 22728* (DS, F, US); 10 km W of Aguacatán, 28 Dec 1962, *Williams et al. 21818* (F, NY); CA-1 btw Huehuetenango and Mexico border, 15 Dec 1977, *FRK 2690* (OS); near Malacatanquito, 31 Dec 1977, *Harriman 14476* (OS, OSH); 6.6 mi N of Huehuetenango, 27 Nov 1978, *FL 2901* (OS); near Chiantla, 6 Jan 1941, *Sa 82516* (F, G); 10 km E of Huehuetenango, 2 Jan 1941, *Sa 82133* (F). QUEZALTENANGO: above Palojunuj, Volcán Santa María, 6 Mar 1939, *Sa 67532* (F); SE of San Martín Chile Verde, region of Boxantín, 16 Jan 1941, *Sa 83786* (F); near Río Samala, on rd btw Zunil and Cantel, 18 Jan 1941, *Sa 83961* (F); mountains above (N of) Olinstepeque, 29 Jan 1941, *Sa 85212* (F, NY); Canton La Esperanza, ca. 6 km from San Juan Ostuncalco, 12–23 Jan 1966, *Molina et al. 16604* (NY, US); below Zunil, 25 Jan 1941, *Sa 84806* (F); Volcán Zunil, 22 Jan 1944, *Se 34608* (F); Volcán Santa María de Jesús, E slope, 24 Oct 1975, *SG 4342\** (OS); btw Cantel and Zunil, 31 Dec 1977, *Harriman 14481* (OS, OSH); near Quezaltenango, Jan–Feb 1941, *Sa 84618* (F). QUICHÉ: Nebaj, 21 Nov 1934, *Skutch 1746* (A); btw El Tesoro and Chicuas, 1 Dec 1969, *Molina & Molina 25014* (NY, US); Pascual Abaj, Chichicastenango, 1 Nov 1965, *Molina 15295* (F, MO); btw Los Encuentros and Chichicastenango, 22–23 Dec 1972, *Williams et al. 41702* (F); mts. E of Quiché, 20 Nov–4 Dec 1940, *Grant 684* (F). SACATEPEQUEZ: Volcán de Agua above Santa María de Jesús, 11 Feb 1939, *Sa 65056* (F); above Las Calderas, 15 Dec 1938, *Sa 59990* (F); forests of Volcán Agua, 13 Nov 1967, *Molina 21067* (F, NY); near Antigua, 26 Nov 1969, *Molina & Molina 24815* (F, MO, NY). SAN MARCOS: 3.5 mi SW of Palo Gordo, 6 Dec 1978, *FL 2952* (OS); 6.2 mi SW of Palo Gordo, 6 Dec 1978, *FL 2953* (OS); 13 mi E of San Antonio Sac., 6 Dec 1978, *FL 2947\** (OS); 0.5 mi W of Palo Gordo, 6 Dec 1978, *FL 2949* (OS); 8–10 km W of San Marcos, 31 Dec 1964–1 Jan 1965, *Williams et al. 26770* (F, NY, US); above San Antonio, 22 Feb 1939, *Sa 66137* (F, GH); btw San Rafael and Palo Gordo, 10–18 Dec 1963, *Williams et al. 25624* (F); 15 km W of San Marcos, 15 Dec 1962, *Williams et al. 23049* (F, US). SOLOLA: near Nahualá, 20 Dec 1972, *Williams et al. 41434* (ENCB, MO, NY); 4 km E of Godíncz, 5 Dec 1963, *Williams et al. 25170* (F); above San Andrés Semctabaj, 15 Jan 1939, *Sa 62774* (F, GH). TONONICAPÁN: ca. 1.8 mi N of San Cristobal



Tonicapán, 24 Oct 1976, *SG 4331* (OS); near Monostenango, 21 Nov 1967, *Molina 21437* (F, NY); btw Los Encuentros and María Tecun, 21 Nov 1965, *Molina 15880* (F, NY, US). MEXICO. CHIAPAS: 10 mi W of San Cristobal, 2 Nov 1965, *C 10472* (NY); btw San Cristobal and Tuxtla, 16 Dec 1977, *FK 2697* (OS); btw Chilil and Huistan, 26 Nov 1977, *FRa 2569\** (OS); 8 km from San Cristobal on rd to Zinacatán, 25 Nov 1977, *FRa 2564* (OS); 40 mi E of Tuxtla, 26 Nov 1977, *FRa 2570* (OS); 32 mi E of Chiapa de Corzo, 17 Nov 1966, *AL 4245* (MICH, OS); below Zinacatán, 5 Dec 1966, *Laughlin 2941* (DS, F, MICH); near Niquivil, municipio Motozintla de Mendoza, 16 Dec 1976, *Breedlove 42732* (DS); rd from Zinacatán to Ixtapa, 28 Oct 1976, *Breedlove 41120* (DS); 3–4 km W of El Porvenir, 19 Sep 1976, *Breedlove 40392* (DS); 11 km NW of jct of rd to Motozintla, on rd to El Porvenir, 21 Nov 1976, *Breedlove 41641* (DS); 2 mi SW of Huistan, 17 Nov 1964, *Breedlove 7346* (DS, F, MICH); above Siltepec on rd to Huixtla, 18 Jan 1973, *Breedlove & Smith 31902* (DS).

**19. *Montanoa hibiscifolia* Bentham in Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjöbenhavn 1852(5–7): 89. 1852, as "*Montagnaea*." Type: NICARAGUA, Prov. Nueva Segovia, canyons and foothills, 1845–1848, A. S. Oersted 235 [9051] (lectotype, K; isolectotypes, C[2]!; fragment of lectotype, US!; photos of isolectotypes, MO! NY! US!). Bentham listed two collections in the protologue, the lectotype and a collection by Oersted from Costa Rica (134). *Eriocoma hibiscifolia* (Benth. in Oerst.) Kuntze, Rev. Gen. Pl. 1: 336. 1891.**

Figs. 1A, 9, 63, 64.

*Montanoa wercklei* Berger, Gard. Chron. 50: 122. 1911. Type: COSTA RICA, seeds sent by C. Werckle in 1905 and grown at La Mortola (Italy) and collected there 3 Jan 1908 by A. Berger s.n. (holotype, K; isotype, G[3]!; photos of holotype, GH! OS! US!). Morley (1980) selected a lectotype but the data are sufficient to designate the above specimen as the holotype.

*Montanoa pittieri* Robins. & Greenm., Proc. Amer. Acad. Arts 34: 517. 1899. Type: COSTA RICA, San José, hedgerows on the "llanos de Alajuelita," 1 Dec 1899, H. Pittier 1455 (holotype, GH!; isotypes, BR[2]! G!).

*Montanoa samalensis* Coulter, Bot. Gaz. (Crawfordsville) 20: 49. 1895. Type: GUATEMALA, Retalulen, Río Samala, 1700 ft, April 1892, J. D. Smith 2858 (holotype, F!; isotypes, G-BOIS! K! US!; photo of K isotype, OS!).

Shrubs 1–6 m tall. *Stems* terete, slender, light-brown to brown, essentially glabrous. *Leaves* consistent; petioles 1.0–6.5 cm long, often with prominent auricles at distal end, glabrous to sparsely pubescent, hairs short; blades ovate to pentagonal (Fig. 63A–C), 7–40 cm long, 2.5–30.0 cm wide, apex long-acuminate (rarely acute), margin nearly entire to irregularly serrate, usually deeply 3–5 lobed, adaxial surface moderately pubescent, hairs pustular, variable in length, abaxial surface moderately to densely glandular and pubescent, hairs white, 0.5 mm long, giving the surface a light green to grey color. *Peduncles* 2–6 cm long, slender, densely glandular and pubescent, hairs short. *Heads* pendulous, 1.0–1.2 cm diam in flower, 2.0–2.5 cm diam in fruit, many in open cymose synflorescences in oppositely and alternately branched compound corymbs. Receptacle convex, 5 mm tall, 3 mm diam. *Phyllaries* 5–7, more or less uniseriate, equal, reflexed in early fruit, ovate-lanceolate, 4–5 mm long, 1–2 mm wide, dark green, apex acute, mucronate, margin ciliate, entire, abaxial surface densely pubescent, hairs 0.5–1.0 mm long, on adaxial surface glabrous. *Ray florets* 7–8; corollas white, ligules elliptic to obovate, 15–17 mm long, 8–9 mm wide, adaxial surface with scattered hairs, less than 0.5 mm long, on abaxial surface moderately glandular, tube 0.5–0.75 mm long, 0.5 mm wide, with scattered hairs less than 0.5 mm long. *Disc florets* (Fig. 63D) 85–105; corollas yellow, tube 0.5 mm long, 0.5 mm diam, moderately to densely pubescent, hairs less than 0.5 mm long, throat cylindrical, 1.5 mm long, 1.0–1.25 mm diam, densely pubescent, hairs less than 0.5 mm long, lobes 5, 0.5–0.7 long, 0.5 mm wide, apex acute, densely glandular and pubescent, hairs less than 0.5 mm long; stamens with filaments 1.5 mm long, 0.25 mm wide,

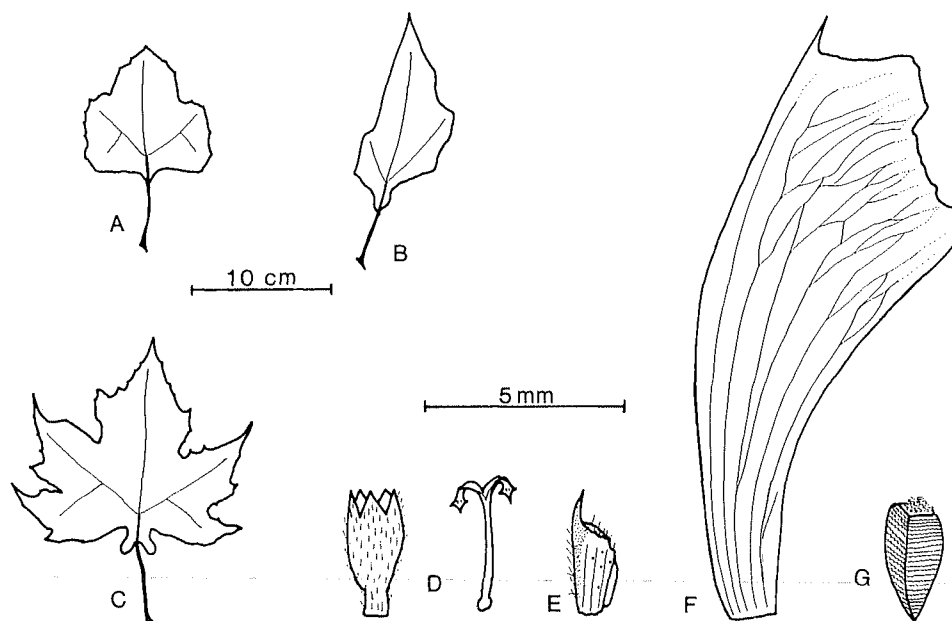


Fig. 63. *Montanoa hibiscifolia*. A-C, variation in mature leaves: A, B, FL 2940 (OS); C, Williams *et al.* 27769 (F). D, disc corolla and style, FL 2929 (OS); E, pale subtending disc floret at anthesis, FL 2940 (OS); F, mature pale, Standley & Chacon 6940 (F); G, mature achene, Standley & Chacon 6940 (F). A-C, D-G, same scale respectively.

anthers not fully exerted from corolla, thecae yellow to brown, 1.0–1.25 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5 mm long, 0.5–0.3 mm wide, abaxial surfaces of apical appendages glandular; styles (Fig. 63D) 2.5–3.0 mm long, not enlarged at base, stigmatic surfaces yellow, 0.75 mm long, apical appendages yellow with two black areas, acute, 0.3 mm long, 0.3 mm wide. *Pales* at anthesis obrullate (Fig. 63E), 3.0–3.5 mm long, 2 mm wide, light yellow, apex long-acuminate, indurate, margin ciliate, glandular, entire, abaxial surface densely glandular and pubescent, hairs less than 1.0 mm long, concentrated near the center, adaxial surface glabrous; *pales* at fruiting deciduous, more or less obrullate (Fig. 63F), 9–15 mm long, 4.5–6.0 mm wide, papery with netted venation, stramineous or purple, apex sinus with indurate spine, margin undulating, irregular, adaxial and abaxial surfaces glabrous. *Achenes* brown to red-brown with convoluted outer surface of amorphous nature (Figs. 9, 63G), 3 mm long, 1.5 mm wide with mass of gland-like structures at apex. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: November–January (December–March).

DISTRIBUTION AND HABITAT: Chiapas to Costa Rica (Fig. 64); cool pine-oak forests to banana plantations, on hillsides and along streams, lakes and roads; 350–2500 m.

*Montanoa hibiscifolia* is a widely cultivated shrub both because of its attractive heads and leaves and because it thrives in diverse environments (*pers. obser.*). This species is rarely misidentified, primarily because of its irregularly 5-lobed leaves (Fig. 63C) that are densely white tomentose on the abaxial surface. The

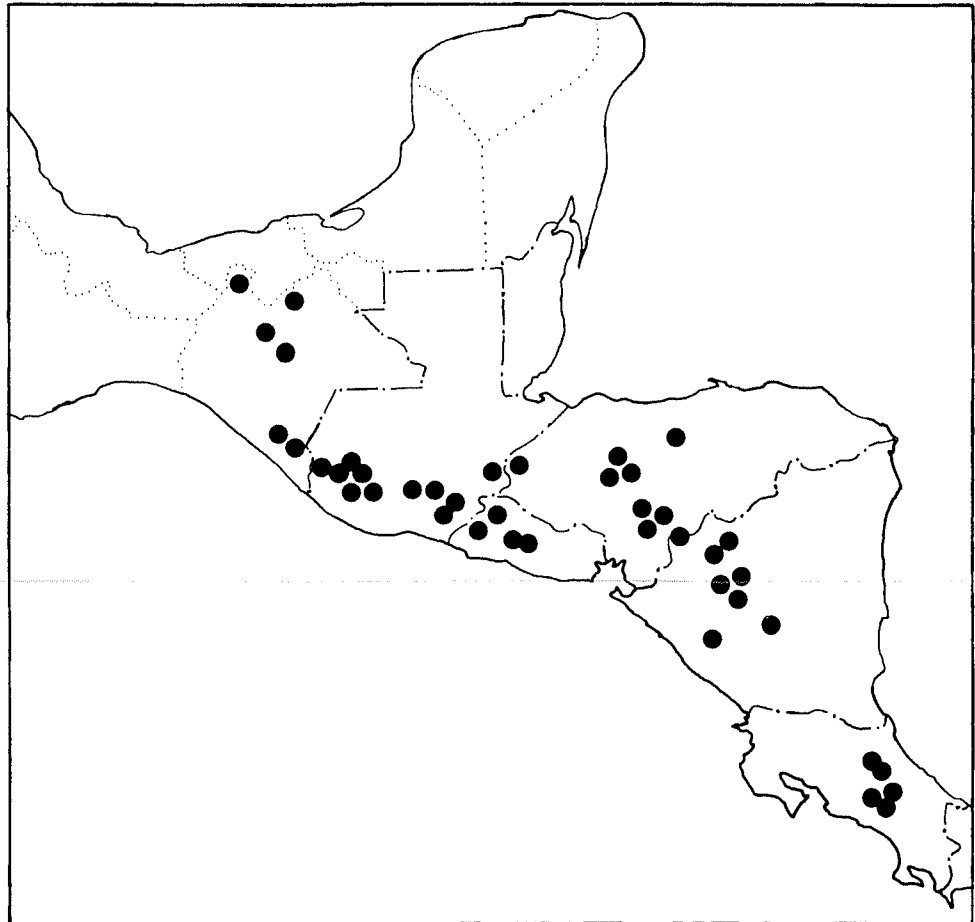


Fig. 64. Map of Chiapas and Central America to Costa Rica showing the distribution of *Montanoa hibiscifolia*.

leaves are nearly uniform on the entire plant, although occasionally near the inflorescence they are less lobed (Fig. 63B), as are the leaves produced by the axillary buds (Fig. 63A). *Montanoa hibiscifolia* was introduced onto Oahu, Hawaii and now grows as if it were native (pers. comm., N. Harriman). It is also known from herbarium specimens to be cultivated in the following places: Australia, Canary Islands, Kenya, Madagascar, Puerto Rico, South Africa, Tanzania, Trinidad and Tobago, United States (Florida and California), Zimbabwe, and throughout Central America in yards and near shrines. One collection (*White & White 113*) was reported from Panama and was included in the flora of Panama (D'Arcy, 1975) as the only species of the genus known from that country. The plant was collected in the Chiriquí area, but this area has been well-collected since then (pers. comm., W. D'Arcy) and has not been found. The label data are brief and do not indicate whether or not the plant was cultivated, which seems most likely.

*Montanoa hibiscifolia* is most closely related to *M. hexagona* and the discussion of these two species is included under the latter.

REPRESENTATIVE SPECIMENS: COSTA RICA. ALAJUELA: just N of Alajuela, rd to Volcán Poas (hwy 130), 5 Jan 1980, *FGPF 3023* (CR, OS); ca. 15 mi N of Naranjo on rd to Zarcero, 7 Jan 1980, *F 3052* (CR, OS); San Pedro de San Ramón, 12 Dec 1925, *Brenes 5217* (CR, NY, S); near San Ramón, 2 Feb 1940, *Hunnell 16792* (DUKE, GH); San Luis de Zarcero, 4 Dec 1939, *Smith 2047* (GH, NA, US). CARTAGO: San Ramón, 7 Dec 1971, *Mc Caffrey 58* (CR); 2 km NNE of San Rafael on rd to Irazú, 23 Dec 1974, *Wilbur & Luteyn 18725* (DUKE); 3 km SW of Cervantes, 5 Jan 1979, *Wussow et al. 159* (OS). HEREDIA: 1.2 km NW of Río Virilla on Costa Rica hwy 1, 28 Dec 1978, *Wussow et al. 109* (OS); rd from San Antonio to Puente de Mulas, 3 Jan 1979, *Wussow et al. 144* (OS); near Heredia, 25 Dec 1930, *Brenes 13270* (F, NY). SAN JOSÉ: S of San José on rd to Jorco, 12 Jan 1980, *FGO 3077\** (CR, OS); E of Jorco on rd to Cerro Cedral, 13 Jan 1980, *FPF 3083* (CR, OS); San Francisco de Guadalupe, Nov 1895, *Toumaz 7072* (BM, CU, F, G, GH, K, M, MO, NY); along the Río Virilla ca. 1 km S of Santa Domingo, 20 Dec 1974, *Taylor 17306* (SMU, US); Zurquí, 13 Feb 1926, *Standley & Valerio 48039* (US); near Paracito, 6 mi NE of San José, 14 Dec 1974, *Wilbur & Luteyn 18147* (DUKE, OS); near San José, 11 Jan 1938, *Orozco 93* (F); btw San José and Guadalupe, 27 Dec 1965, *Jiménez 3518* (F, MO, NY, US). EL SALVADOR. AHUACHAPAN: Lagunita de las Ninphas, above Apaneca, 5 Dec 1978, *FL 2940* (OS). LA LIBERTAD: Volcán San Salvador above Santa Tecla, 22 Jan 1949, *Williams & Molina 15253* (F). MORAZÁN: Montes de Cacagnatique, 3 Jan 1942, *Tucker 710* (BH, F, G, LL, MICH, US). SAN SALVADOR: rd to Boqueron, 9 Dec 1971, *Flores 297* (MO). SANTA ANA: near Santa Ana, 28–30 Jan 1922, *Sa 20425* (GH, NY, US). GUATEMALA. AMATITLÁN: Amatitlán, Oct 1928, *Morales 1176* (F). CHIMALTENANGO: along Río Guacalate, SE of Chimaltenango, 14–23 Dec 1940, *Sa 81056* (F). Volcán Ipala, near Amatillo, 25 Oct 1939, *Se 30469* (F). ESCUINTLA: along Río Guacalate, 28 Nov 1938, *Sa 58250* (F, GH). JALAPA: mts along rd btw Jalapa and Paraiso, 14 Nov 1940, *Sa 77223* (F). JUTIAPA: above Ovejero on rd btw Monjas and El Progreso, 19 Nov 1940, *Sa 77655* (F). QUEZALTENANGO: hwy 95 just S of Santa María de Jesús, 29 Nov 1978, *FL 2921\** (OS); Colomba, 20 Dec 1934, *Sketch 1981* (BM, F, G, LL, NY). RETALHULEU: San Felipe, 13 Jan 1917, *Holway 705* (GH, US). SACATEPEQUEZ: ca. 5 mi W of Ciudad Vieja on rd to Ycopaca, 25 Oct 1976, *SG 4358* (OS); Volcán de Agua, rd btw Santa María de Jesús and Palín, 7 Nov 1965, *Molina 15368* (F, NY). SAN MARCOS: SW of San Rafael Pie de la Cuesta, near bridge, 6 Dec 1978, *FL 2945A* (OS). SANTA ROSA: Canchón, Oct 1892, *Heyde & Lux 6155* (F, G, GH, K, MO, NDG, NY, US); SOLOLA: near Patalúl, 15 Feb 1906, *Kellerman 5559* (NA). HONDURAS. COPAN: E of ruins, 23 Nov 1969, *Molina & Molina 24782* (F, NY). CORTES: Santa Cruz de Yojoa, 9 Dec 1933, *Edwards P-726* (F, GH, MO, NY). COMAYAGUA: near Siguatepeque, 25 Mar–5 Apr 1947, *Standley & Chacón 6940* (F). MORAZÁN: ca. 5 mi W of Zamorano, 2 Dec 1978, *FL 2929* (OS); along Río de la Orilla on rd from El Zamorano to Chagüite, 5 Feb 1949, *Sa 16151* (F, GH). EL PARAÍSO: above Yuscarán, 2 Dec 1978, *FL 2928* (OS); along stream in Yuscarán, 28 Dec 1962, *Williams & Molina 23241* (B, BM, BR, C, DS, G, MEXU, MICH, S, UC, W); Güinope, Dec 1943, *Rodríguez 1670* (F). YORO: Yoro, Sep 1937, *Hagen & Hagen 1093* (F, NY). MEXICO. CHIAPAS: hwy 195, 24.6 mi N of jct with hwy 190, near San Vicente, 27 Nov 1977, *FRa 2580\** (OS); near Habenal, Tenejapa, 26 Nov 1964, *Breedlove 7662* (DS, ENCB, F, MICH); Escuintla, 26 Dec 1936, *Matuda 723* (MEXU, MICH, MO, NA, US). NICARAGUA. CHONTALES: ca. 2.8 mi N of Cuapa, 21 Jan 1978, *Pipoly 1544* (OS). JINOTEGA: Ocoteil near Santa Lastenia, 17 Jan 1965, *Williams et al. 27769* (F); 10 mi NE of Jinotega, 11 Jan 1969, *Selaya & Moore 2148* (BM, F, GH, MICH, MO, NY, SMU, US); rd to La Fundadora from Managua, region of Santa María de Ostuma, 7 Dec 1958, *Hawkes et al. 2207* (C, F, G, S). MANAGUA: near El Crucero, summit of Sierra de Managua, 14–25 May 1947, *Sa 8318* (F). NUEVA SEGOVIA: 3.7 mi S of Las Manos, 7 Jan 1978, *Jansen & Harriman 548\** (OS, OSH). MATAGALPA: Santa María de Ostuma, 8–15 Jan 1963, *Williams et al. 23419* (F, GH, NY, US, WIS). UNITED STATES. HAWAII: Oahu, Tantalus Dr. [cultivated], 18 Dec 1979, *Harriman 16248\** (OS, OSH).

20. *Montanoa hexagona* Robinson & Greenman, Proc. Amer. Acad. Arts 34: 514. 1899. Type: MEXICO, Chiapas, temperate regions in the mountains, Oct 1864–1870, A. B. Ghiesbreght 535 (holotype, GH!; isotypes, BM! K[2]! LE! MO! NY!). Figs. 65, 66.

Trees or rarely large shrubs to 20 m tall. *Stems* quadrangular becoming terete, brown to grey, herbaceous parts puberulent. *Leaves* variable; petioles 2–17 cm long, moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long; blades ovate-lanceolate to pentagonal (Figs. 65A–L), 6–26 cm long, 4–36 cm wide, apex acute, margin entire to irregularly serrate, unlobed to 3–5 lobed, adaxial surface glabrous to moderately pubescent, hairs pustular, abaxial surface moderately to densely glandular and pubescent, hairs 0.5–1.0 mm long. *Peduncles* 1–5 cm long, densely glandular and pubescent, hairs less than 1.0 mm long. *Heads*

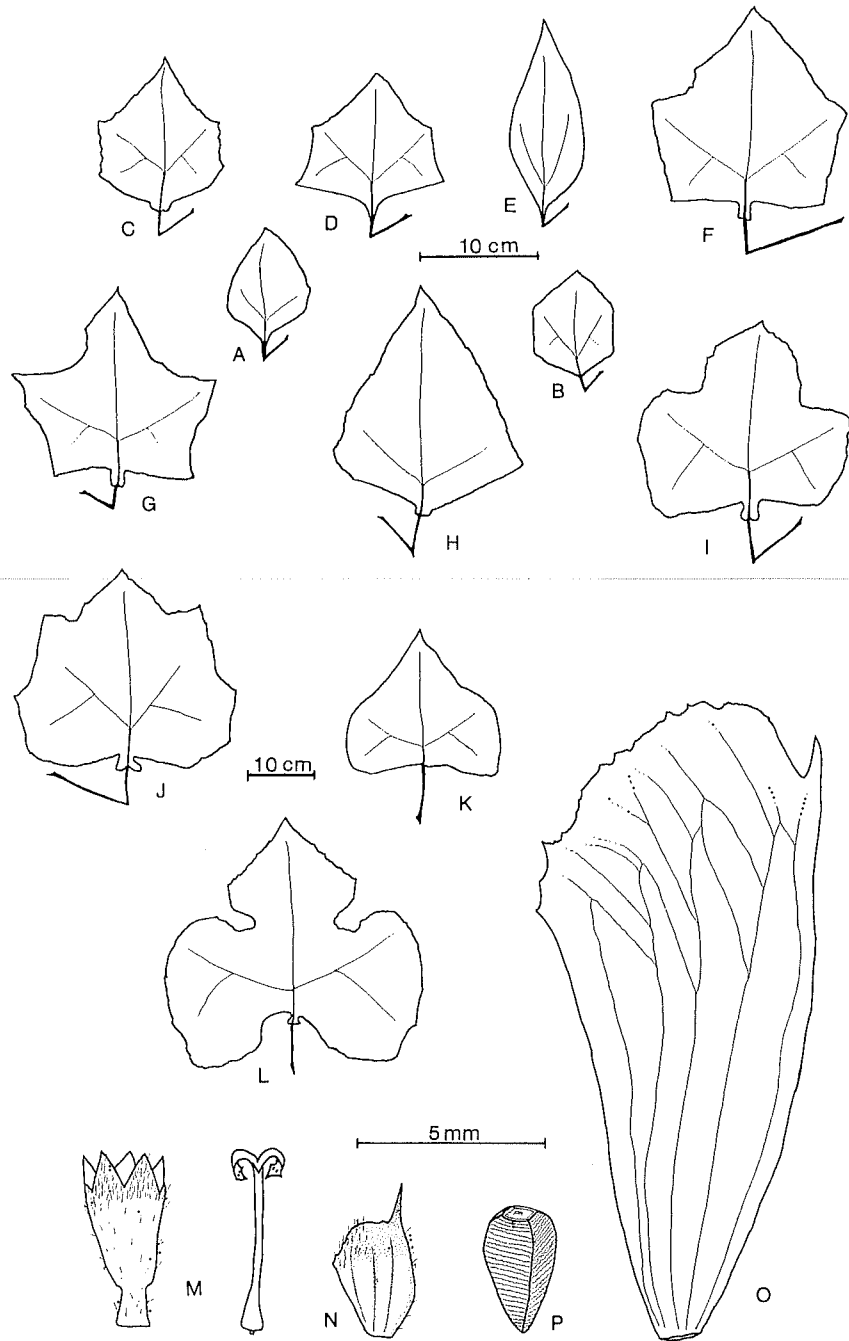


Fig. 65. *Montanoa hexagona*. A-L, variation in mature leaves: A, B, I, *FRa* 2643 (OS); C, E, H, *FL* 2944A (OS); D, F, *FL* 2951 (OS); G, *FL* 2910 (OS); J-L, *FRa* 2562. M, disc corolla and style, *FL* 2909 (OS); N, pale subtending disc floret at anthesis, *FL* 2909 (OS); O, mature pale, *Se* 34583 (F); P, mature achene, *Se* 34583 (F). A-I, J-L, M-P, same scale respectively.

pendulous, 1.2–1.4 cm diam in flower, 2.5–3.5 cm diam in fruit, several to many in cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* 5–7, more or less uniseriate, equal, ovate-lanceolate, reflexed in early fruiting, 2.5–4.5 mm long, 1.5–2.0 mm wide, dark green, apex acute, mucronate, margin ciliate, entire, abaxial surface moderately to densely pubescent, hairs 0.5–1.0 mm long, abaxial surface glabrous. *Ray florets* 8–10; corollas white, ligules elliptic-lanceolate to obovate, 13–17 mm long, 5–9 mm wide, apex rounded to 2-notched, adaxial surface essentially glabrous, abaxial surface moderately glandular, tube 1.5–2.0 mm long, 0.5–0.75 mm wide, sparsely pubescent, hairs less than 0.5 mm long. *Disc florets* (Fig. 65M) 40–60; corollas green turning yellow, tube 1.0 mm long, 0.5–0.75 mm diam, moderately to densely glandular and pubescent, hairs less than 0.5 mm long, throat cylindrical, 1.5–2.0 mm long, 1.25–1.5 mm diam, moderately to densely glandular and pubescent especially distal half, hairs less than 0.5 mm long, lobes 5, 1.0–1.5 mm long, 0.5–0.75 mm wide, apex acute, densely glandular and pubescent, hairs less than 0.5 mm long; stamens with filaments 2.0–2.5 mm long, 0.25 mm wide, anthers not fully exerted from corolla, thecae brown, 1.5 mm long, 0.4–0.5 mm wide, apical appendages yellow, 0.6–0.7 mm long, 0.4–0.5 mm wide, abaxial surfaces of apical appendage glandular; styles (Fig. 65M) yellow, 5.5–6.5 mm long, enlarged at base, stigmatic surface yellow, 0.5–0.8 mm long, apical appendages yellow with black areas on abaxial surface, long-acuminate, 0.5–0.6 mm long, 0.3–0.4 mm wide. *Pales* at anthesis obtrullate (Fig. 65N), 3.0–4.0 mm long, 2.0–3.0 mm wide, yellow, apex long acuminate, indurate, dark on distal half, margin ciliate, entire, abaxial surface moderately glandular and pubescent near center and margins, hairs 0.5–1.0 mm long, adaxial surface glabrous; pales at fruiting deciduous, more or less obdeltoid (Fig. 65O), 13–17 mm long, 5–7 mm wide, papery with netted venation, stramineous, apex sinus with apiculate tip, margin irregular, abaxial and adaxial surfaces glabrous. *Achenes* brown-red with convoluted outer surface of amorphous nature (Fig. 65P), 3–4 mm long, 2.0–2.25 mm wide. Chromosome number,  $n = ca. 76$ .

FLOWERING (AND FRUITING) PERIODS: Late October–December (late November–February).

DISTRIBUTION AND HABITAT: Chiapas, Mexico and the mountains of Guatemala (Fig. 66); cloud forests and subcloud forests at the base of cliffs, banks of streams, edge of waterfalls and on steep slopes; 2000–3000 m.

An imposing tree with heads arranged in dense dichasia and large leaves that sometimes reach 43 cm long (including petiole, Fig. 65L). *Montanoa hexagona* shares with *M. hibiscifolia* the unusual convoluted achene surface, but the two are easily separated because *M. hibiscifolia* is a shrub. In addition, *M. hexagona* has 8–10 rays, 40–60 long (3.5–4.5 mm) disc florets and large, usually pentagonal, entire and sometimes 3-lobed leaves. *Montanoa hibiscifolia* on the other hand has 7–8 rays, 85–105 small (2.5–2.7 mm) disc florets and the characteristic irregularly 5-lobed leaves (Fig. 63C).

The collections of *Montanoa hexagona* from lower elevations near Guatemala City are usually cultivated and often do not appear to grow well (e.g., *FRa* 2664).

REPRESENTATIVE SPECIMENS: GUATEMALA. ALTA VERAPAZ: rd to Tamahua, 2 mi from jct with hwy to Cobán, 10 Dec 1977, *FRK* 2669 (OS); Cobán, Dec 1906, *Türkheim* 1513 (BM, BR, C, F, FI, G, GH, M, MICH, MO, NY). GUATEMALA: 17 km from Guatemala City on CA-1 (cultivated), 7 Dec 1977, *FRa*\* (OS). JALAPA: Volcán Jumay, 8 Jan 1908, *Kellerman* 7684 (F, NY, US). QUETZALTENANGO: 0.5 mi S of Zunil, 29 Nov 1978, *FL* 2920 (OS); Volcán Santa María de Jesús, E slope, 24 Oct 1976, *SG* 4339\* (OS); Volcán Zunil, 22 Jan 1940, *Se* 34583 (F, NY, TEX); S of San Martín Chile Verde, 16 Jan 1941, *Sa* 83665 (F). QUICHÉ: Nebáj, 20 Nov 1934, *Skutch* 1744 (F, LL, NY, US);

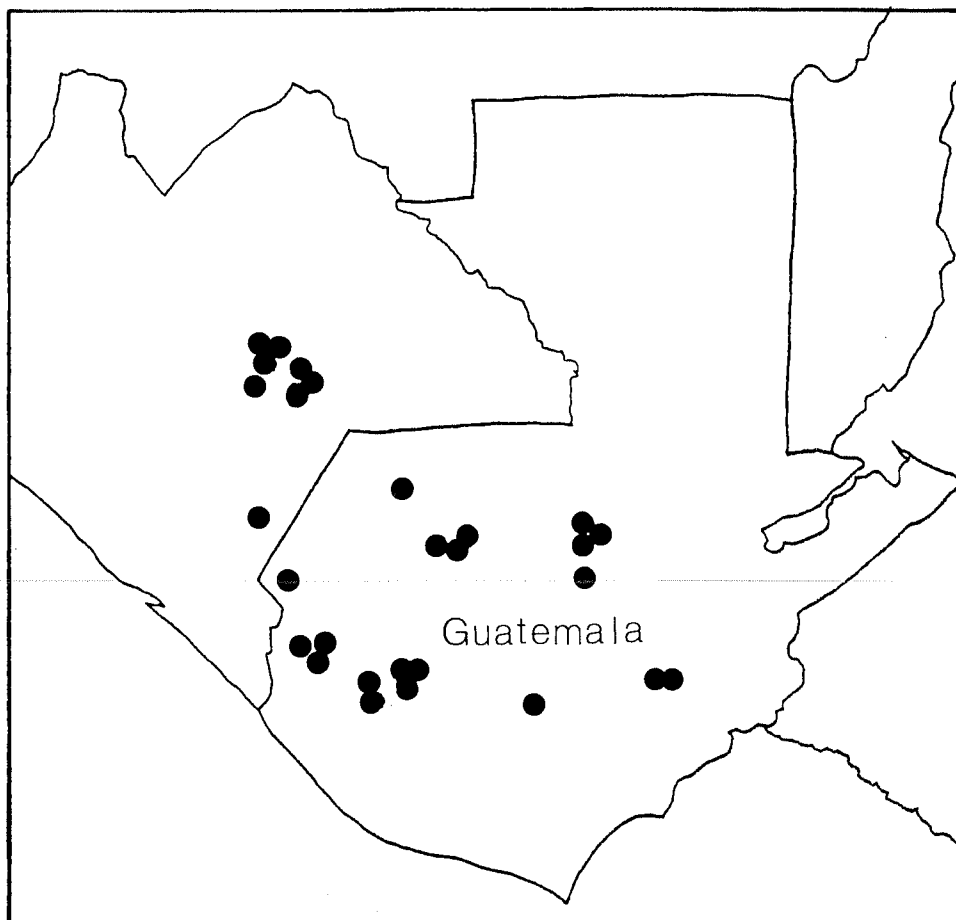


Fig. 66. Map of Chiapas and Guatemala showing the distribution of *Montanoa hexagona*.

above Ncbáj on rd to Sacapulas, 28 Nov 1978, *FL 2909\** (OS); just outside of Nebáj, 28 Nov 1978, *FL 2910* (OS); near Zuníl, 29 Nov 1978, *FL 2920\** (OS); San Mateo Ixtatán, 6 Feb 1965, *Breedlove 3685* (DS, MICH). SAN MARCOS: 3.5 mi W of Palo Gordo, 6 Dec 1978, *FL 2951* (OS); 6 mi NE of San Rafael Pie de la Cuesta, 6 Dec 1978, *FL 2944A* (OS); near Sibinal, 18 Feb 1940, *Se 35949* (F); 8–10 km W of San Marcos, Volcán Tajumulco, 31 Dec 1964, *Williams et al. 26836* (F, NY). MEXICO. CHIAPAS: rd to Chenalho, near schoolhouse of Yal'Ichin, 25 Nov 1977, *FRA 2562\** (OS); rd to Tenejapa, 18 km from San Cristóbal, 26 Nov 1977, *FRA 2565* (OF); in Colonia Ach'lum, municipio Tenejapa, 12 Dec 1966, *Ton 1761* (DS, ENCB, LL, MICH, MSC, NY); trail from Zinacatán to Ixtapa, 13 Apr 1966, *Laughlin 656* (DS, ENCB, NY, WIS); Siltepec, Jan 1937, *Matuda 1549* (MEXU, MICH, US).

#### II d. *Montanoa* subgenus *Acanthocarphae* series *Intermediae* V. A. Funk, ser. nov.

Synflorescentiae capitulis paucis vel solitariis; capitula in maturitate pendula, phyllariis 4.0–5.5 mm longis; flosculi radiorum 10–15; flosculi discorum 65–80, stylis ad apices luteis, antheris inclusis; palcac in maturitate 8–12 mm longae stramineae ad apices cum sinibus. Typus: *Montanoa laskowskii* McVaugh. Species 22.

The one species of series *Intermediae* is a restricted endemic essentially occurring in only three localities in Colima and Jalisco, Mexico. It has several features such as larger disc florets, number of rays and number of involucrel

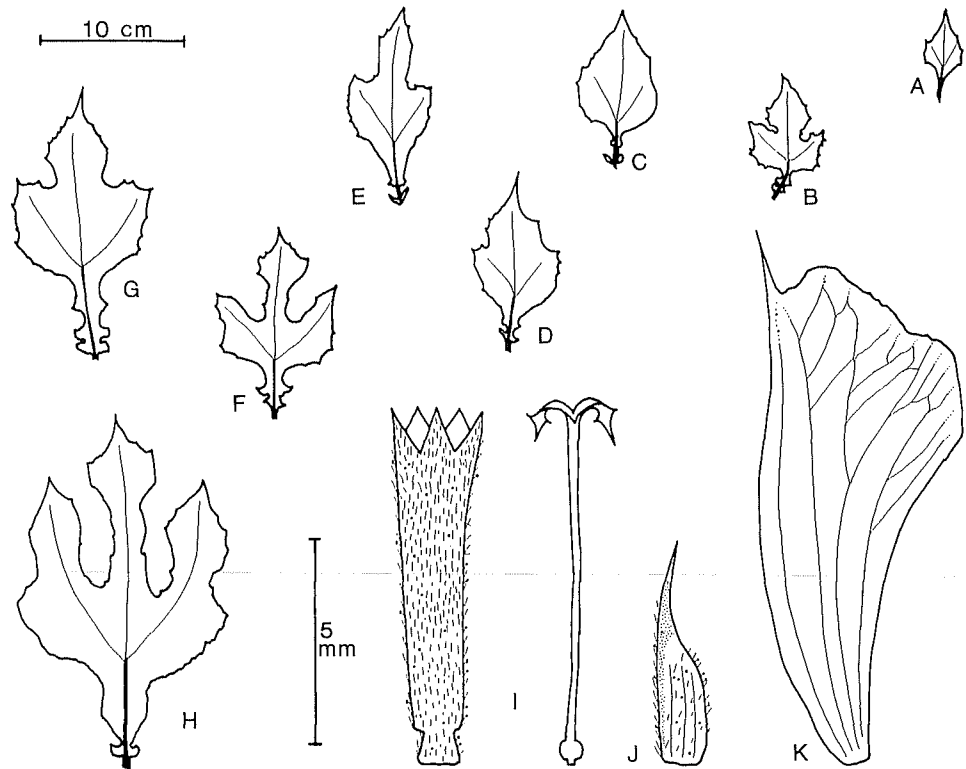


Fig. 67. *Montanoa laskowskii*. A-H, variation in mature leaves, *FCa 2899* (OS); I, disc corolla and style, *M 18053* (MICH); J, pale subtending disc floret at anthesis, *M 18053* (MICH); K, mature pale, *FCa 2899* (OS). A-H, I-K, same scale respectively.

bracts in common with series *Grandiflorae* but it also retains a number from series *Hibiscifoliae* including the number of disc florets, pubescence type and mature pale length. In many features it is intermediate between the two series, hence the name.

**21. *Montanoa laskowskii* McVaugh, Contr. Univ. Michigan Herb. 9: 423. 1972.**

Type: MEXICO, Jalisco, between La Huerta and Barra de Navidad, mountain slopes in deciduous forest within sight of the ocean, less than 570 m, 26 Sep 1966, *W. Anderson & C. Laskowski 3777* (holotype, MICH!; isotypes, MICH[2]! OS!). Figs. 67, 68.

Shrubs 2-5 m tall. *Stems* terete, light brown to grey, usually glabrous but sometimes pubescent at nodes. *Leaves* variable; petioles 1.5-7.5 cm long, adaxial surface sparsely glandular and densely pubescent, hairs less than 1.0 mm long, partially to completely winged often with auricles at base of wing and usually with two small leaf-like structures at proximal end (Fig. 67A-H); blades ovate, 5-16 cm long, 2.25-15.0 cm wide, apex long-acuminate, margin serrate to irregularly serrate-dentate, deeply 3-lobed, adaxial surface moderately pubescent, hairs pustular, base white, abaxial surface glabrous to sparsely glandular and pubescent, hairs less than 1.0 mm long. *Peduncle* 2.0-7.5 cm long, glabrous to densely pubescent, hairs less than 1.0 mm long. *Heads* pendulous, 1.5-2.25 cm



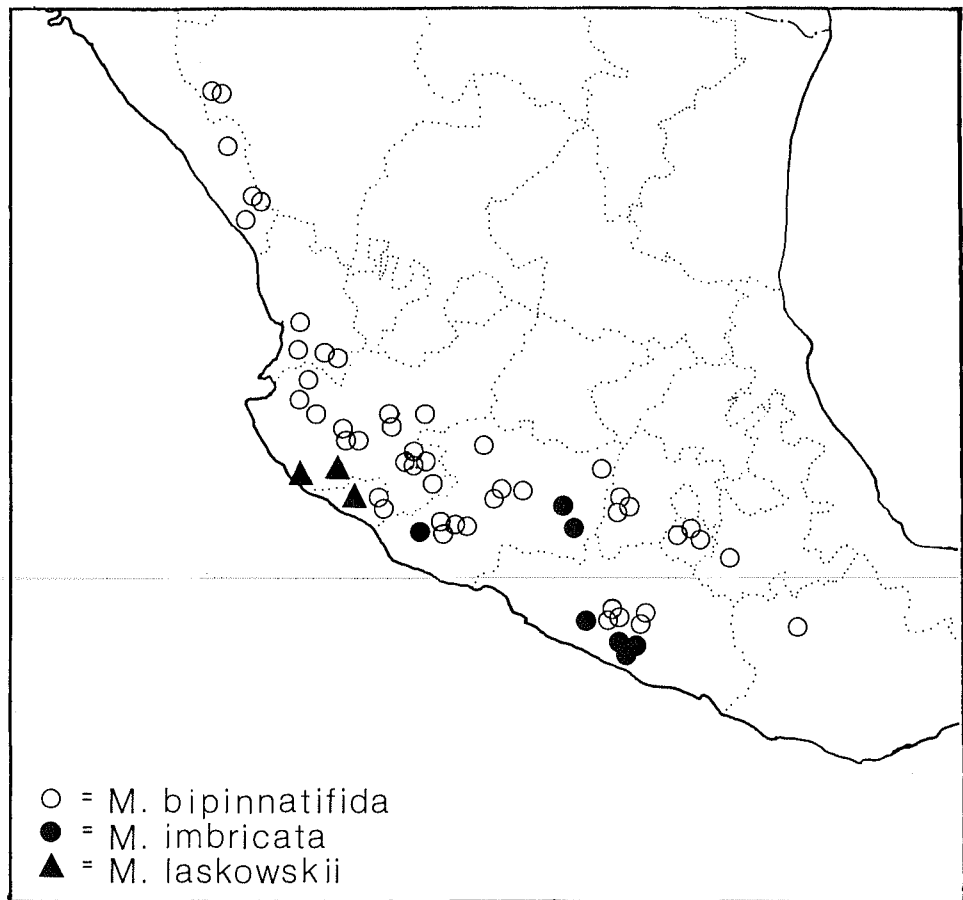


Fig. 68. Map of central and southern Mexico showing the distribution of *Montanoa bipinnatifida*, *M. imbricata*, and *M. laskowskii*.

diam in flower, 2.5–3.0 cm diam in fruit, few in open rigidly branched cymose synflorescences in oppositely and alternately branched compound corymbs. *Phyllaries* 8–10, reflexed at late anthesis, biseriate, subequal, ovate to ovate-lanceolate, 4.5–5.5 mm long, 1.5–2.0 mm wide, dark green, apex acute to acuminate with mucronate tips, margin ciliate, entire, abaxial surface pubescent near center and margins, hairs less than 1.0 mm long, adaxial surface essentially glabrous. *Ray florets* 10–15; corollas white, ligules obovate, 15.0–22.5 mm long, 5–12 mm wide, apex rounded to 1–2-notched, adaxial surface mostly glabrous with dense cluster of thick hairs, abaxial surface sparsely glandular and pubescent on veins, hairs less than 0.5 mm long, tube 1.0 mm long, 0.5 mm wide, essentially glabrous. *Disc florets* (Fig. 67I) 65–85; corollas yellow, tube 0.5–1.0 mm long, 0.5 mm diam, sparsely pubescent, hairs thick, 0.5–1.0 mm long, throat cylindrical, 5.5–6.5 mm long, 1.5–1.75 mm diam, densely glandular and pubescent, hairs thick, 0.5–1.0 mm long, lobes 5, 0.5–1.0 mm long, 0.5–0.75 mm wide, apex acute, densely glandular and pubescent, hairs thick, less than 0.5 mm long; stamens with filaments 4.0–4.5 mm long, 0.25 mm wide, anthers not fully exerted from corolla, thecae black, 2–3 mm long, 0.5 mm wide, apical appendages black, acuminate,

0.5 mm long, 0.4 mm wide, abaxial surface of apical appendages and connective glandular; styles (Fig. 67I) yellow, 8.0–11.5 mm long, enlarged at base, stigmatic surfaces yellow, 1.0–3.0 mm long, apical appendages yellow, acuminate, 0.5–1.0 mm long, 0.5 mm wide. *Pales* at anthesis almost elliptic-triangular (Fig. 67J), 3.5–4.5 mm long, 1.2 mm wide, dark near midrib and base, apex long-acuminate, indurate, light yellow, margin ciliate, entire, abaxial surface, except near apex, densely glandular and pubescent, hairs 0.5–1.0 mm long, adaxial surface glabrous; pales at fruiting, deciduous, obtrullate (Fig. 67K), 8–12 mm long, 4–5 mm wide, papery with netted venation, stramineous, at apex a deep sinus and spinose tip 2 mm long, margin entire, somewhat curled, abaxial and adaxial surfaces essentially glabrous. *Achenes* brown-black, 3.0–4.5 mm long, 1.5–2.0 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: September–October (October–December).

DISTRIBUTION AND HABITAT: Three populations in Jalisco and Colima, Mexico (Fig. 68); south facing slopes of Sierra Madre del Sur, in sight of the ocean or on dry hilltops; ca. 500 m.

This rare species has unusual leaves that can be deeply lobed (Fig. 67H) and unlobed (Fig. 67D) on the same branch. In addition, the corollas of the disc florets are covered with hairs and glands, the throat is much longer than the tube (10:1; Fig. 67I), the anthers are black, the heads are solitary or in simple cymes and the mature pales have a distinct sinus (Fig. 67K). *Montanoa laskowskii* superficially resembles *M. leucantha*, but the latter species has no sinus on the mature pales, yellow to brown anthers, a dense synflorescence, and large (Figs. 53A, 55A) tubes on the disc corolla. *Montanoa laskowskii* is not closely related to any particular species but it is more closely related to the four species of the series *Grandiflorae* than any others.

*Montanoa laskowskii* and the species of the series *Grandiflorae* share a large number of disc florets (over 65) and ray florets (over 10), large disc florets (over 6 mm) and a biseriate involucre with over 10 bracts. But, *M. laskowskii* differs by the anthers not fully exerted from the disc corollas. Further, the species of *Grandiflorae* have 15 mm long mature pales without a sinus and phyllaries over 6 mm long. *Montanoa laskowskii*, on the other hand, has pales less than 12 mm long and phyllaries less than 5.5 mm long.

SPECIMENS EXAMINED: MEXICO. COLIMA: 10.5 mi S of jct of hwy to Manzanillo and hwy to Juquillo, 18 Dec 1978, *FCa 2988\** (OS); ca. 11 mi SSW of Colima, 21 Sep 1958, *M 18053* (DUKE, ENCB, LL, MICH, NY, US). JALISCO: 10 mi N of Barra de Navidad, 16 Dec 1966, *AL 4543* (MICH, OS); between Chamela and Barra de Navidad, 11 Oct 1976, *SG 4134\** (OS).

## IIe. *Montanoa* subgenus *Acanthocarphae* series *Grandiflorae* V. A. Funk, ser. nov.

Synflorescentiae capitulis numerosis; capitula in maturitate pendula, phyllariis 6–12 mm longis; flosculi radiorum 10–13; flosculi discorum 65–160, stylis ad apices luteis, antheris exsertis; paleae in maturitate 15–21 mm longae stramineae, ad apices sine sinibus (praeter *M. imbricata*). Typus: *Montanoa grandiflora* Alamán ex DC. Species 23–26.

The four species of series *Grandiflorae* are all large headed shrubs with long rays and quadrangular to terete stems. Because three of the four species are cultivated their original ranges are difficult to decipher, but they appear to be in central Mexico. The species are similar and fruiting characters are often used to distinguish them.

22. *Montanoa grandiflora* Alamán ex A. P. de Candolle, Prodr. 5: 565. 1836, as "*Montagnaea*." Type: MEXICO, 1831, *F. Alamán s.n.* (holotype, G-DC, photo IDC 800. 565:III.6!; photos of holotype, F! GH! MO! US[2]!). *Eriocoma grandiflora* Alamán [in DC., Prodr. 5: 565. 1836, nom. nud. pro syn.] ex Kuntze, Rev. Gen. Pl. 1: 336. 1891. Figs. 69, 70.

*Priestleya longifolia* Sessé & Mociño ex DC., Prodr. 5: 565. 1836, nom. nud. pro syn. De Candolle's observation was based on the drawing from Ic. Fl. Mex. 8: 679. (Original at G; photo, F!)

Shrubs 1–4 m tall. *Stems* terete, gray to brown, herbaceous parts sparsely puberulent. *Leaves* variable; petioles 2.5–12.5 cm long, broadly winged, sometimes with auricles and occasionally connate-perfoliate, moderately to densely glandular and puberulent; blades ovate-lanceolate to pentagonal (Fig. 69A–E), 5–23 cm long, 2.5–27.0 cm wide, apex acute to acuminate, margin serrate to irregularly dentate, sometimes 3–5 lobed, adaxial surface moderately pubescent, hairs pustular, abaxial surface sparsely to moderately or occasionally densely glandular and pubescent, hairs less than 1.0 mm long. *Peduncle* 1.0–4.5 cm long, moderately to densely glandular and pubescent, hairs less than 1.0 mm long. *Heads* pendulous, 1.5–2.0 cm diam in flower, 3–4 cm diam in fruit, few to several in open cymose synflorescences in oppositely to alternately branched compound corymbs, lateral branches usually not exceeding in length subtending leaves. *Phyllaries* 7–10, uni- or biseriate, subequal, not reflexed until far into fruit, ovate-lanceolate, 7–10 mm long, 1.5–2.5 mm wide, green to brown, apex acute to acuminate, mucronate, margin ciliate, entire, abaxial surface moderately to densely pubescent, hairs less than 1.0 mm long, adaxial surface moderately pubescent on distal half, hairs less than 1.0 mm long. *Ray florets* 10–12; corollas white, ligules ovate-lanceolate, 20–30 mm long, 7–11 mm wide, apex acute to deeply 2-notched, adaxial surface sparsely glandular, tube 1.0 mm long, 0.5 mm wide, essentially glabrous. *Disc florets* (Fig. 69F) 65–95; corollas yellow, tube 1.0–1.5 mm long, 0.5–1.0 mm diam, essentially glabrous; stamens with filaments 3.5–4.0 mm long, 0.25 mm wide, anthers fully exerted from corolla, thecae yellow, 2.0–2.5 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5–0.6 mm long, 0.25–0.33 mm wide, abaxial surface of apical appendages glandular; styles (Fig. 69F) yellow, 6.5–9.75 mm long, enlarged at base, stigmatic surfaces yellow, 1.0–1.25 mm long, apical appendages yellow, acuminate, 0.5 mm long, 0.3 mm wide. *Pales* at anthesis more or less obtrullate (Figs. 69G, H), 2–3 mm long, 2.0–2.5 mm wide, light yellow, apex long-acuminate, indurate, margin ciliate, entire, abaxial surface sparsely to moderately glandular and pubescent, hairs less than 1.0 mm long, adaxial surface glabrous; pales at fruiting deciduous, obtrullate (Fig. 69I), 17–20 mm long, 5.5–6.5 mm wide, papery with netted venation, stramineous, apex apiculate, indurate, margin subentire, abaxial surface glandular near the center, margins and adaxial surface glabrous. *Achenes* brown-black, 4 mm long, 2 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: October–November (December–January).

DISTRIBUTION AND HABITAT: Sierra Madre del Sur in Michoacán, Guanajuato, and Méxicio (Fig. 70); cool pine forests on steep mountain slopes and in drier pine-oak forests along roadsides; 750–2500 m but usually over 2000 m.

This lovely plant is common along the roadsides from the Morelia area to the México state border, but scattered elsewhere. It is a plant of somewhat dry habitats with the principal leaves large and lobed halfway to the midrib or less,

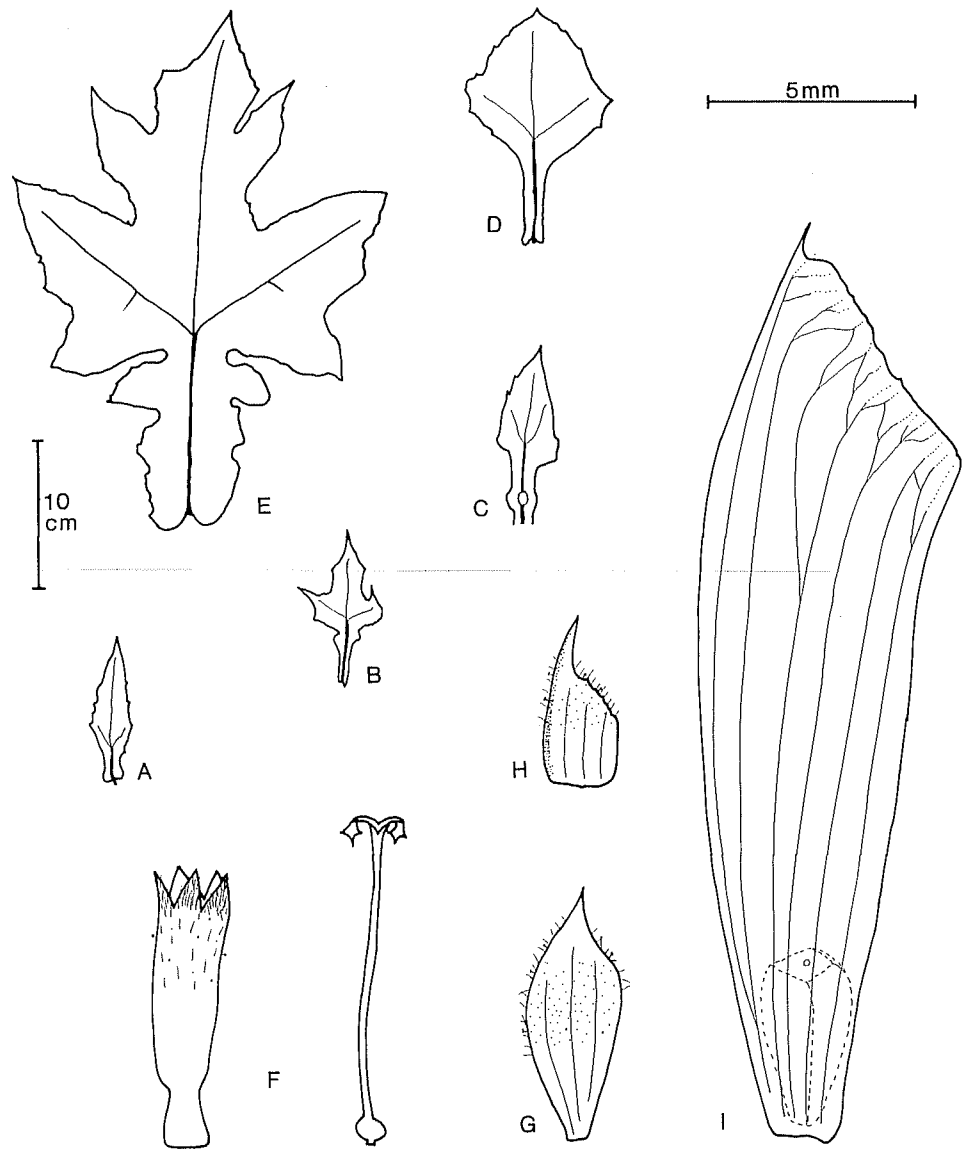


Fig. 69. *Montanoa grandiflora*. A-E, variation in mature leaves: A, AL 3914 (MICH); B, C, Flores 177 (OS); D, F 2861 (OS); E, F 2254 (OS). F, disc corolla and style, F 2861 (OS); G, H, pales subtending disc floret at anthesis, F 2861 (OS); I, mature pale, FCa 2967 (OS). A-E, F-I, same scale respectively.

and a wing to the base of the petiole (Fig. 69A-E). The synflorescence of this species has 3-5 heads on short petioles aggregated in corymbiform to paniculiform cymes and these are often arranged in a panicle. There are many such panicles per plant and the flowering display is very appealing. *Montanoa grandiflora* is most often confused with *M. speciosa*, from which it can be separated by the following characters. *Montanoa grandiflora* has 7-10 involucre bracts that reflex

early in flower and coriaceous leaves, whereas *M. speciosa* has 9–16 bracts that do not reflex until far into fruit; *M. speciosa* has light green densely puberulent principal leaves that are lobed almost all the way to the midrib; and *M. grandiflora* has 65–95 disc florets, whereas *M. speciosa* has 140–160. These two species are both found near Morelia, Michoacán, and there are several specimens that are difficult to place in either species. However, they have not been reported growing sympatrically. Both species are cultivated and their cultivated forms are discussed under *M. speciosa*.

REPRESENTATIVE SPECIMENS: MEXICO. GUANAJUATO: Puerto Jondo, 26 km ESE of Tarimoro, 14 Oct 1974, *Flores 177* (ENCB, OS); 6 km S of Acámbaro, 4 Dec 1971, *Illis & Cochrane 272* (ENCB, US, WIS). MÉXICO: 24.1 mi S of Queretaro/México border along hwy 55, 24 Dec 1977, *Jansen & Harriman 479* (OS); 26 mi S of México/Queretaro border along hwy 55, 15 Oct 1966, *AL 4011* (MICH, OS); btw Acambay and Atlocumulco, 15 Oct 1956, *Langman 4070* (ENCB, MEXU); Temascaltepec, 11 Dec 1932, *Hinton 2579* (BM, G, NY, US). MICHOACÁN: 0.2 mi W of Michoacán/México border on rd btw El Oro and Tlalpujahuá, 15 Oct 1966, *AL 4009* (MICH, OS); 19 mi W of Atlacomulco, NE of El Oro, 15 Oct 1966, *AL 4008* (MICH, OS); 69 mi E of Morelia, just E of Ciudad Hidalgo, 1 Nov 1977, *FH 2252* (OS); 60 mi E of Morelia, just W of Ciudad Hidalgo, 1 Nov 1977, *FH 2253* (OS); 49 mi E of Morelia, 14 Dec 1966, *AL 4527* (MICH, OS); 41 mi E of Morelia, 9 Oct 1966, *AL 3919* (MICH, OS); Mirador Mil Cumbres, 40.5 mi E of Morelia, 20 Nov 1978, *F 2865* (OS); 20.4–22 mi E of Morelia, 15 Dec 1966, *AL 4529* (MICH); 20 mi E of Morelia, 20 Nov 1978, *F 2861* (OS); ca. 18 mi E of Morelia, 14 Oct 1976, *SG 4176\** (OS); 1.7–2.5 mi E of Morelia, 9 Oct 1966, *AL 3914* (MICH); 10 mi E of Morelia, 1 Nov 1977, *F 2258* (OS); near Morelia, Loma Santa María, 1910, *Arsène 5775* (BM, G, GH, MO, NY); near Morelia, Carriéres Rincón, 17 Oct 1912, *Arsène 8291* (BM, F, GH, MO, NY, US); 9 mi W of Morelia, 15 Dec 1966, *AL 4530* (MICH, OS); 2 mi S of Morelia on rd to Santa María, 2 Nov 1977, *F 2254* (OS); 5 mi S of Ouiroga, 3 Nov 1977, *F 2262* (OS); N end of Lago de Patzcuaro, 15 Dec 1966, *AL 4532* (MICH, OS); 9 mi ENE of Patzcuaro, 9 Oct 1966, *AL 3909* (MICH, OS); NE edge of Patzcuaro, 16 Dec 1978, *FCa 2967* (OS); near Patzcuaro, 22 Oct–20 Nov 1890, *Pringle 3306* (BM, BR, CM, DS, F, G, GH, K, M, MEXU, MICH, MO, MSC, NDG, NY, S, UC, US); ca. 28 mi E of Uruapan, 16 Dec 1978, *FCa 2968* (OS). VERACRUZ: 12 mi N of Córdoba (cultivated), 18 Dec 1977, *FTK 2736\** (OS).

**23. *Montanoa speciosa*** A. P. de Candolle, Prodr. 5: 565. 1836, as "*Montagnaea*."

Type: MEXICO, Morelia, Cuernavaca, 20 Oct 1827, *J. L. Berlandier 1057* (holotype, G-DC, photo IDC 800. 565:III.5!; photos of holotype, MO! US!; isotype, GH! KIEL! W[2]!; probable isotypes, F! G! LE! MICH! SMU!). Figs. 70, 71.

Shrubs 1–4 m tall. *Stems* quadrangular becoming terete, brown to gray, herbaceous parts puberulent. *Leaves* relatively consistent; petioles 2–12 cm long, winged, broader in middle and near base, moderately glandular and pubescent, hairs less than 1.0 mm long; blades pentagonal (Fig. 71A–E), 8–16 cm long, 5.5–20.0 cm wide, apex long-acuminate, margin entire to serrate, very deeply lobed, adaxial surface densely to moderately pubescent, hairs pustular, abaxial surface densely glandular and pubescent, hairs less than 1.0 mm long, white, giving a light green color to surface. *Peduncles* 4–10 cm long, sparsely to moderately glandular and pubescent, hairs less than 1.0 mm long. *Heads* pendulous, 2 cm diam in flower, 3.5–3.8 cm diam in fruit, few to several in open cymose synflorescences in oppositely to alternately branched compound corymbs, the lateral branches usually exceeding subtending leaves. *Phyllaries* variable, 9–16(–22), bi- to triseriate, subequal, ovate-lanceolate to lanceolate, 7–12 mm long, 2–3 mm wide, green on abaxial surface, dark on adaxial one, apex acute to acuminate, margin ciliate, entire, abaxial surface densely glandular and pubescent, hairs less than 1.0 mm long, adaxial surface sparsely glandular and pubescent on distal third of bract, hairs less than 0.5 mm long. *Ray florets* 10–13; corollas white, ligules elliptic to lanceolate, 20–29 mm long, 5–10 mm wide, apex acute to 2-notched, adaxial surface glabrous, abaxial surface sparsely glandular and pubescent, par-

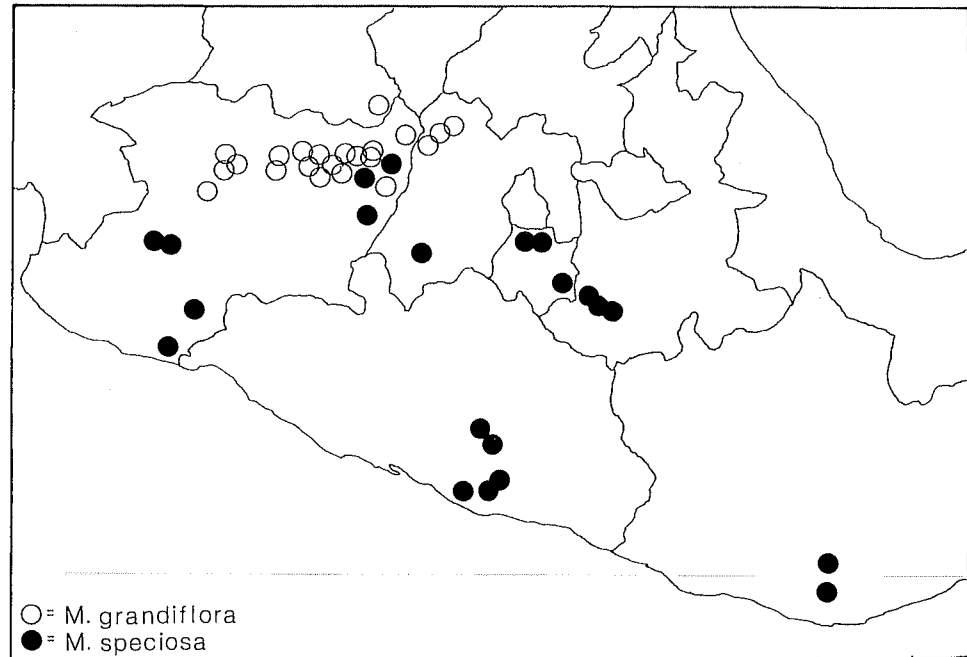


Fig. 70. Map of southern Mexico showing the distribution of *Montanoa grandiflora* and *M. speciosa*.

ticularly on veins, hairs less than 0.5 mm long, tube 1.0 mm long, 0.5 mm wide, essentially glabrous. *Disc florets* (Fig. 71F) 140–160; corollas yellow, tube 1.5 mm long, 0.5–0.75 mm diam, essentially glabrous, throat cylindrical, 4.0–5.0 mm long, 1.0–1.5 mm diam, essentially glabrous, lobes 5, 1.0 mm long, 0.5 mm wide, apex acute with clusters of hairs less than 0.5 mm long; stamens with filaments 6.0–7.0 mm long, 0.2 mm wide, anthers fully exerted from corolla, thecae yellow, 2.0–2.5 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.5–0.6 mm long, 0.4 mm wide, abaxial surface of apical appendages glandular; styles (Fig. 71F) yellow, 9.0–10.5 mm long, enlarged at base, stigmatic surfaces yellow, 1.5 mm long, apical appendages yellow, acuminate, 0.5 mm long, 0.3 mm wide. *Pales* at anthesis obtrullate (Fig. 71G), 2.5–3.0 mm long, 2.0–2.25 mm wide, light yellow with dark bands near midvein and at base of apex, apex long-acuminate, indurate, margin entire, glandular and pubescent, hairs on distal half, less than 1.0 mm long, abaxial surface moderately glandular and pubescent on distal half, hairs less than 1.0 mm long, adaxial surface glabrous; pales at fruiting (not quite mature) deciduous, obtrullate (Fig. 71H), 16–17 mm long, 5–6 mm wide, papery with netted venation, stramineous, apex tapering to apiculate, indurate tip, margin ciliate, sparsely glandular, entire, abaxial surface moderately glandular and sparsely pubescent in center, adaxial surface glabrous. *Achenes* brown-black, 3.5 mm long, 2.0 mm wide, apex with few hairs (Fig. 71I). Chromosome number,  $n = 19$ .

**FLOWERING (AND FRUITING) PERIOD:** October–November (late November–January).

**DISTRIBUTION AND HABITAT:** Sierra Madre del Sur in the states of Michoacán, México, Morelos, Oaxaca, Puebla and Guerrero (Fig. 70); mixed tropical decid-

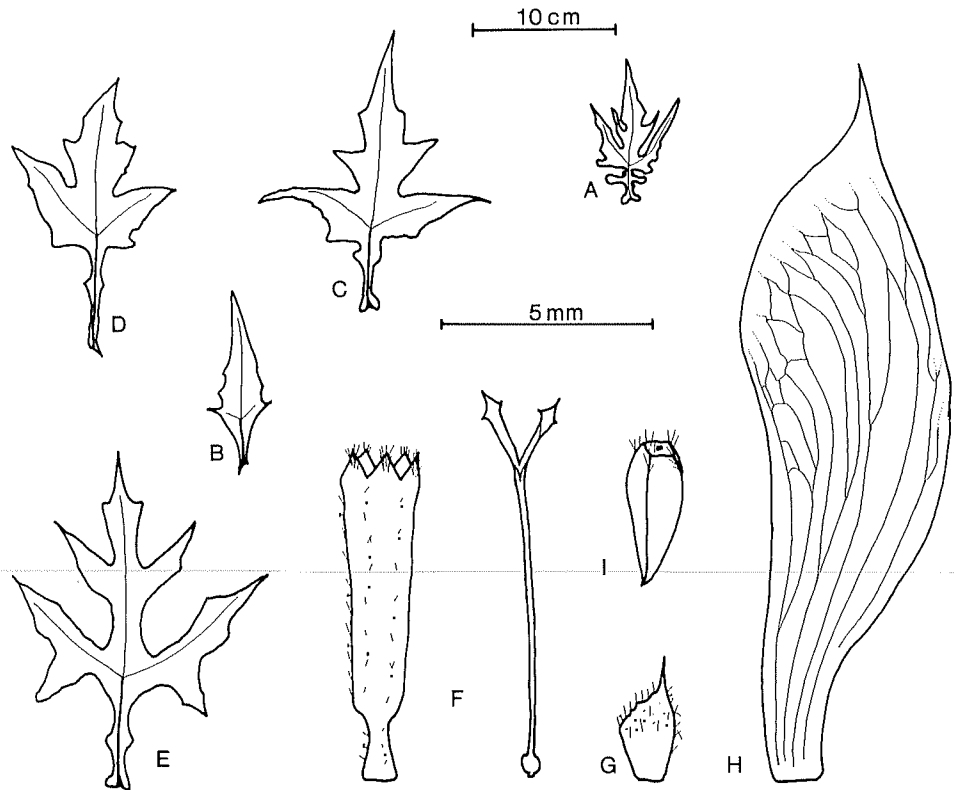


Fig. 71. *Montanoa speciosa*. A-E, variation in mature leaves: A, C, AL 4300 (OS); B, SG 4237 (OS); D, E, King & Soderstrom 4934 (US). F, disc corolla and style, C 9698 (NY); G, pale subtending disc floret at anthesis FGe 2347 (OS); H, I, mature pale and achene, AL 4504 (OS). A-E, F-I, same scale respectively.

uous forest, arid scrubby hillsides, and grassy roadsides; 140-1400 m, the lower elevations in Guerrero and Oaxaca.

*Montanoa speciosa* is an attractive shrub that is commonly cultivated in Mexico. The leaves of this species are attractive, being, in general, greatly dissected (Fig. 71A-E) and densely pubescent giving the surface a soft appearance and a light green color. Further, this species has the largest number of disc florets (140-160) in the genus. The achenes are unique, having several small hairs on the veins near the apex (Fig. 71I). The open panicles contrast with the synflorescence of the most closely related species, *M. grandiflora*, which has a tightly clustered leafy synflorescence. The two species are further compared under *M. grandiflora*.

*Montanoa speciosa* and *M. grandiflora* are both cultivated throughout southern Mexico (pers. obser.) and both have individuals that have an increased number of ray florets referred to as "double forms." These double form ray florets are most likely derived from the disc florets for many are light yellow rather than white and are somewhat irregularly lobed. There are usually at least a few regular disc florets in the center of the capitula of these plants. Since the ray florets are sterile, heads of this type have a reduced reproductive capacity. Most individuals of this type are cultivated with only a few collections reported from the wild (e.g., HF 4121, HF 4202). When the double forms occur, distinguishing between the

two species is difficult since most of the reliable characters are lost. Like the rest of the genus, these two species grow well from cuttings.

*Montanoa speciosa* has an involucre that also doubles and at times has as many as 20–22 bracts. This occurs in a number of populations of non-cultivated plants and does not appear to affect the plant. It is most often found SW of Oaxaca City.

REPRESENTATIVE SPECIMENS: MEXICO. GUERRERO: W of Chilpancingo, 21 Oct 1944, *Sharp 441418* (MEXU, NY); ca. 20 mi W of Chilpancingo, 17 Oct 1976, *SG 4237\** (OS); San Agustín, ca. 20 km N of Acapulco, 14 Nov 1977, *FGe 2345* (OS); ca. 36 km N of Acapulco, near Triente y seis, 15 Nov 1977, *FGe 2346* (OF); 21 mi NE of Acapulco, 10 Dec 1966, *AL 4501* (MICH, OS); N of Acapulco, Cuarenta y dos, 15 Nov 1977, *FGe 2347* (OS); 22 mi N of Acapulco, 4 Nov 1960, *Crutchfield & Johnston 4980* (MICH, TEX); below Tierra Colorada, 9 Oct 1949, *Moore 5272* (BM, CU, G, UC); 2 mi N of Tierra Colorada, 10 Dec 1966, *AL 4504* (MICH, OS); Atoyac, 23 Nov 1937, *Hinton 10962* (ENCB, GH, K, LL, MICH, TEX, W). MICHOACÁN: San José Pura, 20 Oct 1956, *Paray 2201* (ENCB); Rancho Viejo, Apatzingán, 14 Oct 1939, *Hinton 15332* (F, GH, LL, MO, NY, US); Tuzantla, 28 Dec 1972, *Medrano et al. 5074* (MEXU); Zitacuaro, 21 Oct 1938, *Hinton 13390* (ARIZ, ENCB, GH, LL, MICH, US, W); ca. 32 km N of Playa Azul, 25–31 Oct 1961, *King & Soderstrom 4934* (MEXU, MICH, NY, SMU, TEX, UC, US); 8 km N of Arteaga, 24 Oct 1961, *King & Soderstrom 22* (US). MORELOS: 1 km S of Jonacatepec, 17 Oct 1965, *Rzedowski 21454* (DS, DUKE, ENCB, MICH, TEX); Sierra de Tepoxtlán, 26 Nov 1902, *Pringle 9939* (CM, CU, F, GH, MICH, MO, NY, US); Sierra de Tepoxtlán, 30 Oct 1900, *Pringle 9131* (F, GH, MEXU). OAXACA: hwy 131, ca. 76 mi SW of Oaxaca (double-rayed), 28 Aug 1976, *HF 4202\** (OS); 15.5 mi SSE of Miahuatlán, 7 Nov 1966, *AL 4150* (MICH, OS); 12–14.5 mi S of Suchitlán, 8 Nov 1966, *AL 4178* (MICH, OS). PUEBLA: 5.6 mi SE of Izúcar de Matamoros, 22 Nov 1978, *F 2871* (OS); 11 mi SE of Izúcar de Matamoros, 18 Oct 1962, *C 9698* (GH, MEXU, MICH, MO, MSC, NY, SMU, TEX, US); 10–11 mi SE of jct S of Izúcar de Matamoros with rd to Chautla, 24 Nov 1966, *AL 4303* (MICH, OS); 18 km SE of Izúcar de Matamoros, 4 Nov 1976, *Rzedowski 34525* (ENCB); ca. 38 km SE of Izúcar de Matamoros, 18 Oct 1976, *SG 4240\** (OS); 20 mi SE of Izúcar de Matamoros, 24 Nov 1966, *AL 4300* (MICH, OS).

**24. *Montanoa imbricata* V. A. Funk, sp. nov.** Type: MEXICO, Guerrero, 43.6 mi S of Chilpancingo and 2.3 mi S of El Ocotito along Hwy 95 (Chilpancingo to Acapulco), ca. 1000 m, 16 Nov 1978, *V. A. Funk & M. L. Rico 2840\** (holotype, OS!; isotypes, MEXU! NY! OS[2]! TEX!). Figs. 68, 72, 73.

Frutices 4-metrales. Caules quadrangulares basin versus teretiores grisescentes, partibus herbaceis puberuli. Folia vix variabilia; petioli 2–18 cm longi, interdum partim foliolis alata (Fig. 72), glandulosa et dense pilis minus quam 1.0 mm longis pubescentes; laminae ovatae vel 5-angulatae (Fig. 72), 4–34 × 3–38 cm, apice acutae, margine serratae vel ± profunde-lobatae, pagina adaxiali glandulosa, pagina abaxiali glandulosa et sparsim vel dense pilis minus quam 1.0 mm longis pubescenti. Pedunculi 2–10 cm longi, glandulosi modice vel dense pilis minus quam 1.0 mm longis pubescentes. Capitula pendula florifera 1.75–2.25 cm fructifera 3.0–3.5 cm lata, nonnulla vel multa in synflorescentia laxa cymosa corymbis composita, ramis lateralis effuse ascendentibus. Phyllaria 8–11, 2–3-seriata, non reflexa, inter se subaequalia, ovato-lanceolata, imbricata (Fig. 73A), 10–12 × 3.0–4.5 mm, viridia, apice acuta vel acuminata mucronata, marginibus ciliata integra, pagina adaxiali dense pilis minus quam 1.0 mm longis pubescenti, pagina abaxiali glabra. Rarii (Fig. 73B) 12, albi, ligula ovata vel lanceolata, 18–27 × 8–10 mm, apice acuta vel 2-denticulata, pagina adaxiali subglabra, pagina abaxiali sparsim glandulosa, tubo 1.0 × 0.5 mm, subglandulosa. Flosculi disci (Fig. 73C) 80–100, lutei, tubo 1.5 × 0.5 mm, glabro vel subglanduloso et pilis minus quam 0.5 mm longis subpubescenti, fauce cylindraco 3.5–4.0 × 1.25–1.5 mm, glanduloso et modice pilis minus quam 0.5 mm longis pubescentia, lobis 5, 0.75–1.0 × 0.5–0.75 mm, apice acutis glandulosi ct modice pilis minus quam 0.5 mm longis pubescentia; stamina filamentis inclusis 3.5–4.0 × 2.5 mm, antheris (Fig. 73D) semi-exsertis, thecis luteis, 2.25 × 0.5 mm, connectivo apice acuto, 0.6 × 0.4 mm, luteo, adaxiali glanduloso; stylus (Fig. 73E) luteus, 8.0–8.5 mm longus, basi tumefactus, lineolis stigmaticis luteis vel brunneolis, 1.25 mm longis, appendiculis acuminatis, 0.75 × 0.4 mm, apice luteis. Palcae sub anthesi obrullatae (Fig. 73F), 2.5–3.0 × 2.5–3.0 mm, luteolae secus venas atrovirides, apice longiuscule acuminatae, induratae, margine ciliatae integrae, dorso glandulosae et distaliter et dense pilis minus quam 1.0 mm longis pubescentes, ventre glabrae; paleae fructiferae deciduae, obrullatae (Figs. 73G, H), 15 × 8 mm, papyraceae, reticulatim venosae, stramineae, apice spina minus quam 0.75 mm longa obsitae margine integrae ciliatae, abaxialiter dense glandulosa et sparsim pubescentes, adaxialiter glabrae. Achaenia brunneo-nigra, 4.5 × 1.25 mm laevia. Chromosomatum numerus  $n = 19$ .



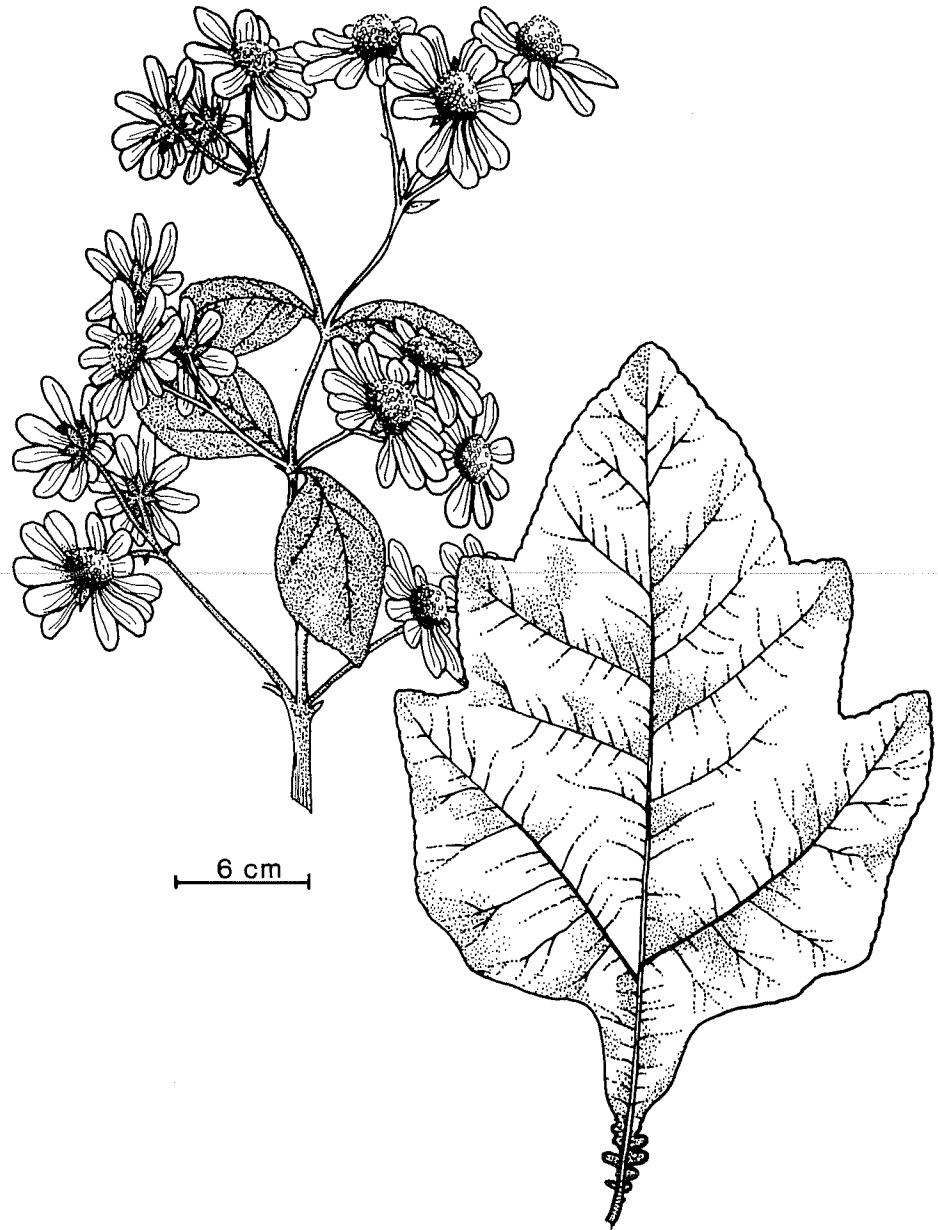


Fig. 72. *Montanoa imbricata* distal section of flowering branch and primary leaf (FRi 2840, (OS).

Shrubs 2–4 m tall. *Stems* quadrangular becoming terete, brown to gray, herbaceous parts puberulent. *Leaves* consistent; petioles 2–18 cm long, partially winged with auricles, many small leaf-like structures on petiole, moderately to densely glandular and pubescent, hairs less than 1.0 mm long; blades ovate to pentagonal (Fig. 72), 4–34 cm long, 3–38 cm wide, apex acute, margin serrate to irregularly and shallowly lobed, adaxial surface moderately glandular, abaxial surface sparsely to densely glandular and pubescent, hairs less than 1.0 mm long.

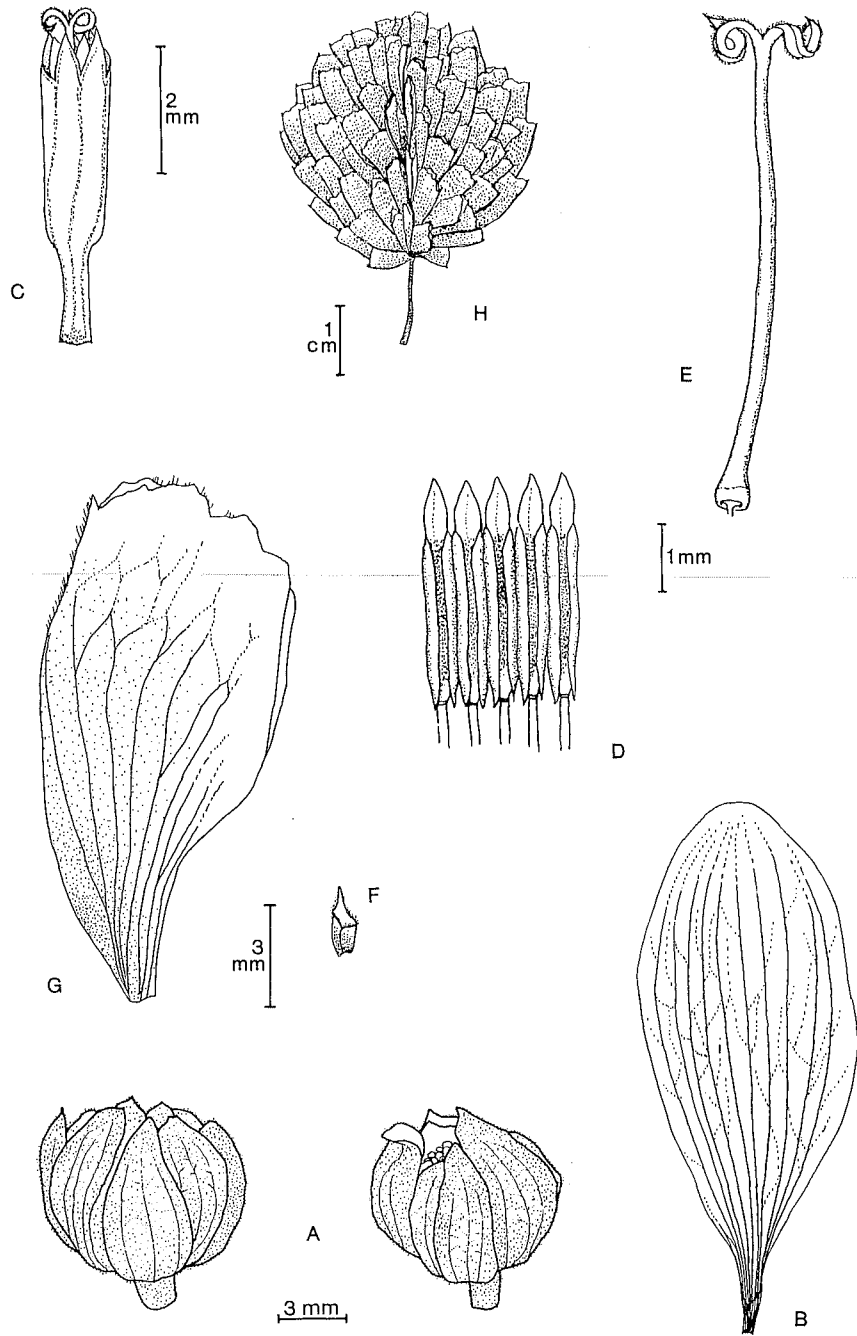


Fig. 73. *Montanoa imbricata*, FRi 2840 (OS): A, capitula prior to anthesis; B, ray floret; C, disc floret; D, anthers; E, style; F, pale subtending disc floret at anthesis; G, mature pale; H, fruiting head.

*Peduncles* 2–10 cm long, moderately to densely glandular and pubescent, hairs less than 1.0 mm long. *Heads* pendulous, 1.75–2.25 cm diam in flower, 3.0–3.5 cm diam in fruit, several to many in open cymose synflorescences in oppositely branched compound corymbs with lateral branches spreading to ascending. *Phyllaries* 8–11, bi- to triseriate, nonreflexed, subequal, ovate-lanceolate, imbricate (Fig. 73A), 10–12 mm long, 3.0–4.5 mm wide, green, apex acute to acuminate, mucronate, margin ciliate, entire, abaxial surface densely pubescent, hairs less than 1.0 mm long, adaxial surface glabrous. *Ray florets* (Fig. 73B) 12; corollas white, ligules ovate to lanceolate, 18–27 mm long, 8–10 mm wide, apex acute to 2-notched, adaxial surface nearly glabrous, abaxial surface sparsely glandular, tube 1.0 mm long, 0.5 mm wide, sparsely glandular. *Disc florets* (Fig. 73C) 80–100; corollas yellow, tube 1.5 mm long, 0.5 mm diam, glabrous to sparsely glandular and pubescent, hairs less than 0.5 mm long, throat cylindrical, 3.5–4.0 mm long, 1.25–1.5 mm diam, sparsely to moderately glandular and pubescent, hairs less than 0.5 mm long, lobes 5, 0.75–1.0 mm long, 0.5–0.75 mm wide, apex acute, moderately glandular and pubescent, hairs less than 0.5 mm long; stamens with filaments 3.5–4.0 mm long and 0.25 mm wide, anthers (Fig. 73D) fully exerted from corolla, thecae yellow, 2.25 mm long, 0.5 mm wide, apical appendages yellow, acute, 0.6 mm long, 0.4 mm wide, abaxial surface of apical appendage glandular; styles (Fig. 73E) yellow, 8.0–8.5 mm long, node enlarged at base, stigmatic surfaces yellow, 1.25 mm long, apical appendages yellow, acuminate, 0.75 mm long, 0.4 mm wide. *Pales* at anthesis obrullate (Fig. 73F), 2.5–3.0 mm long, 2.5–3.0 mm wide, light yellow with dark bands near midrib, apex long-acuminate, dark, indurate, margin ciliate, entire, abaxial surface densely glandular and pubescent on distal half, hairs less than 1.0 mm long, adaxial surface glabrous; pales at fruiting (not quite mature) deciduous, obrullate (Figs. 73G, H), 15 mm long, 8 mm wide, papery with netted venation, stramineous, apex with very small sinus and apiculate tip, margin ciliate, entire, abaxial surface densely glandular and sparsely pubescent, hairs less than 1.0 mm long, adaxial surface glabrous. *Achenes* brown-black, 4.5 mm long, 2.5 mm wide, smooth. Chromosome number,  $n = 19$ .

**FLOWERING (AND FRUITING) PERIOD:** October–November (November–December).

**DISTRIBUTION AND HABITAT:** Sierra Madre del Sur in Michoacán and Guerrero (Fig. 68); oak forests along roadsides and on steep embankments; 800–1450 m.

A handsome species with abundant capitula and involucre bracts that overlap (imbricate; hence the name) prior to anthesis (Fig. 72). The involucre bracts are long and broad (10–12 mm × 3.0–4.5 mm) and numerous (8–11) and most likely protect the head from predation while still in bud. The leaves are consistent in having a row of leaf-like appendages on the petiole and being relatively unlobed (Fig. 72). This species is most closely related to *Montanoia bipinnatifida*, with which it shares an open pyramidal synflorescence and similar characters of the flowering heads. They can easily be distinguished because of the involucre bracts in *M. bipinnatifida* are shorter, about as long as the disc florets. In addition, the apex of the disc corollas of *M. imbricata* are essentially glabrous while in *M. bipinnatifida* they are densely pubescent with stiff interlocking hairs that give the bud a “fuzzy” appearance. The mature pales of *M. bipinnatifida* are narrow at the base exposing part of the achene (Fig. 74F), whereas those of *M. imbricata* are broad, not exposing the achene (Fig. 73G). The two species overlap in distribution but have never been found together in the field.

SPECIMENS EXAMINED: MEXICO. GUERRERO: 6 mi N of Tierra Colorada 10 Dec 1966, *AL 4506* (MICH, OS); 14–14.5 mi N of Tierra Colorada, 10 Dec 1966, *AL 4509* (MICH, OS); hwy 95 near jet with rd to Acahuzotla, 14 Nov 1977, *FGe 2332* (OS); near Xaltignaguís, 14 Nov 1977, *FGe 2344* (OS); between Tierra Colorada and Chilpancingo, km 39, 15 Nov 1977, *FGe 2349* (OS); 8.9 mi N of Tierra Colorada, 16 Nov 1978, *FRi 2841\** (OS); 11.7 mi N of Tierra Colorada, 16 Nov 1978, *FRi 2842* (OS); Mina, Campo Morado-Otatlan, 13 Nov 1939, *Hinton 14832* (K, GH, MICH, NY, TEX, US); Rincon Viejo, 4 Dec 1962, *Kruse & Rzedowski 1211* (ENCB). MICHOACÁN: 15–16 km SE of Ascraadero Dos Aguas, 25–26 Nov 1970, *M 24697* (ENCB, MICH); 63.6 km from Temascal on rd to Huetamo, 13 Nov 1949, *Moore et al. 5694* (BH, BM, F, UC); 19.8 km from Temascal on rd to Huetamo, 13 Nov 1949, *Moore et al. 5711* (BH, BM, F, GH, UC).

**25. *Montanoa bipinnatifida* (Kunth) K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 408. 1864. Figs. 44B, 68, 74.**

*Uldea bipinnatifida* Kunth, Ind. Sem. Hort. Berol. 1847: 17. 1847. In this description the reference Verh. Vereins Beförd. Gartenbaues Königl. Preuss. Staaten, 1847, was cited, however a search of this journal revealed that the description was published in 1849. According to K. Koch (1864) this species was discovered by the Prussian consul Uhde at "Matmaderos" in Mexico and was brought to the Botanic Garden in Berlin 1845 from where it was widely spread, *Ulde s.n.* The holotype has not been located, neotype selected by Morley (1980) is as follows: Herb. Schultz Bip. *s.n.*, ex Hort. 25.ii.1864 (P!).

*Polymnia grandis* Kunth, Ind. Sem. Hort. Berol. 1847: 13. 1847, nom. nud pro syn. Kunth listed this name in synonymy but no description can be found. According to K. Koch (1864) this was a name under which the plant was sent to the Botanic Garden at Berlin and after it bloomed Kunth assigned it to *Montanoa*.

*Montanoa heracleifolia* Brongniart ex Groenland, Ann. Rev. Hort. 544. 1857, nom. nud. Based upon the following collection: MEXICO: seeds collected in 1843 and harvested in Hort. Bot. Paris, Dec 1845, A. B. Ghiesbreght *s.n.* (P[2]!). *Montagnaea heracleifolia* Brongniart ex Andre, Ann. Rev. Hort. 369. 1863. f. 38. Type: MEXICO, the description is probably based on the same material as that for *Montanoa heracleifolia* Brongniart ex Groenland but this is not so stated in the protologue (illustration is taken as the holotype; tracing of illustration, GH!). Morley (1980) selected a neotype but this is unnecessary because elements of the original material are available (illustration) and the neotype is therefore rejected.

*Montanoa elegans* K. Koch, Wochenschr. Vereines Beförd. Königl. Preuss. Staaten 7: 408. 1864. Type: unknown. In the protologue Koch states that there is no information on how the plant came to Europe and that it has never flowered. The description of the leaf type is sufficient for it to be assigned to this taxon. *Eriocoma elegans* (Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

*Montanoa pyramidata* Schultz Bip. in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 408. 1864. Type: MEXICO, Jalisco, Guadaluajara, 1853, D. Oliva *s.n.* (lectotype [Morley, 1980], P). Two collections are mentioned in the protologue. One is the lectotype and the other is A. Aschenborn *s.n.*, which was probably at B (destroyed in WWII; in litt., H. W. Lack). *Eriocoma pyramidata* (Schultz Bip. in K. Koch) Kuntze, Rev. Gen. Pl. 1: 336. 1891.

Shrubs 2–10 m tall. *Stems* (Fig. 74A) quadrangular becoming terete, brown to gray, herbaceous parts puberulent. *Leaves* consistent; petioles 4–20 cm long with two auricles, sometimes with thin blade margin extending down adaxial surface, usually with two small leaf-like structures at proximal end, sparsely pubescent, hairs less than 1.0 mm long; blades ovate to ovate-lanceolate (Fig. 74B, C), 12–30 cm long, 9–40 cm wide, dark green, apex acute to acuminate, margin regularly to irregularly serrate, pinnatifid to bipinnatifid adaxial surface densely pubescent, hairs pustular, turning white, abaxial surface sparsely to densely glandular and pubescent, hairs less than 1 mm long. *Peduncles* 2–7 (usually 3) mm long, sometimes purple, densely glandular and pubescent, hairs less than 1.0 mm long. *Heads* pendulous, 1.8–2.5 cm diam in flower, 3.5–4.0 cm diam in fruit, several to many in open cymose synflorescences in oppositely branched compound corymbs, lateral branches spreading to ascending. *Phyllaries* 8–9, reflexed in fruit, biseriate, subequal, ovate-lanceolate to lanceolate, 6.0–8.5 mm long, 1.0–3.0 mm wide, green, apex acute to acuminate, mucronate, margin ciliate, entire, abaxial surface densely pubescent, hairs less than 1.0 mm long, adaxial surface glabrous

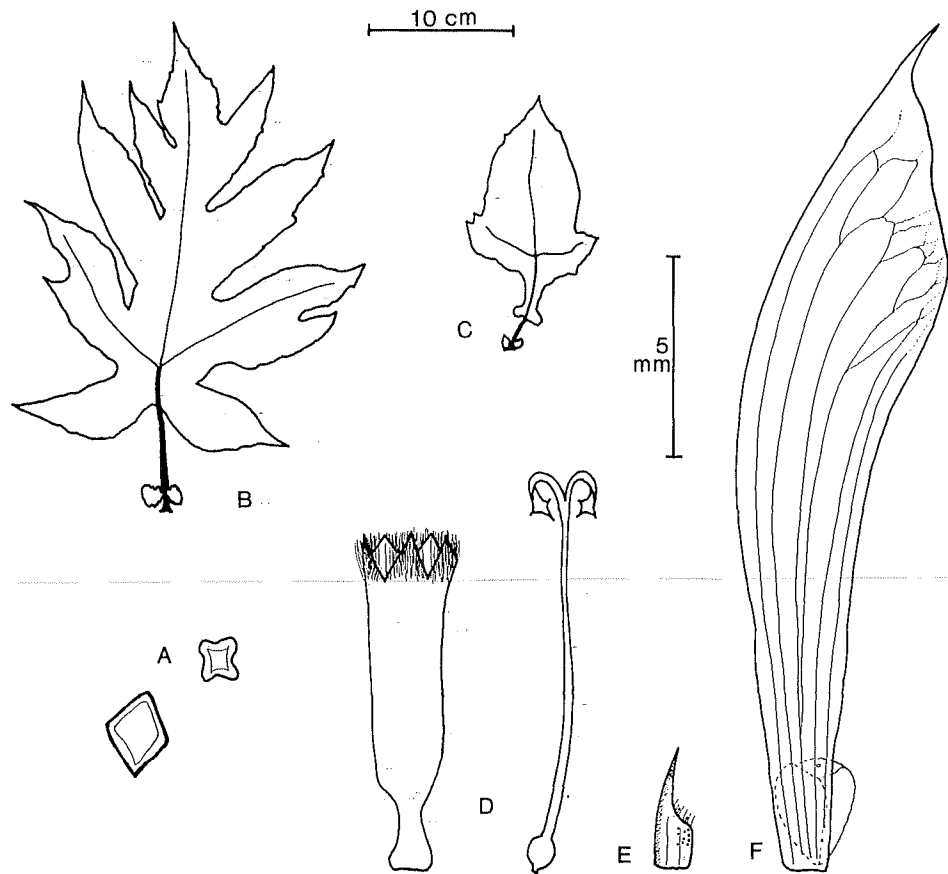


Fig. 74. *Montanoa bipinnatifida*. A, cross sections of one year old stems, *F 2870* (OS); B, C, variation in mature leaves: B, *F 2870* (OS); C, *FCa 2968* (OS). D, disc corolla and style, *FCa 2968* (OS); E, pale subtending disc floret at anthesis, *F 2870* (OS); F, mature pale, *Mexia 1487* (NY). B, C, D-F, same scale respectively.

to sparsely pubescent on distal half, hairs less than 0.5 mm long. *Ray florets* 10-12; corollas white, ligules ovate-lanceolate, 25-35 mm long, 6-11 mm wide, apex acute to two-notched with clusters of hairs less than 0.5 mm long, adaxial surface essentially glabrous, abaxial surface sparsely to moderately glandular and pubescent, hairs primarily on veins, less than 0.5 mm long, tube 1.5 mm long, 0.5 mm wide, essentially glabrous. *Disc florets* (Fig. 74D) 95-125; corollas green turning yellow, tube 1.5 mm long, 0.5-1.0 mm diam, glabrous to sparsely glandular and pubescent, hairs less than 0.5 mm long, throat cylindrical, 4-5 mm long, 1.5-2.0 mm diam, moderately to sparsely glandular and pubescent, hairs less than 0.5 mm long, lobes 5, 1.0-1.25 mm long, 0.5-0.75 mm wide, apex acute and densely pubescent, hairs less than 0.5 mm long; stamens with filaments 5.0-6.0 mm long, 0.25 mm wide, anthers fully exerted from corolla, thecae yellow, 2.5 mm long, 0.5 mm wide, apical appendages yellow, acuminate, 0.5-0.75 mm long, 0.5 mm wide, abaxial surface of apical appendages glandular; styles (Fig. 74D) 7.0-9.5 mm long, enlarged at base, stigmatic surfaces yellow, 1.5-2.0 mm long, apical appendages yellow, acuminate, 0.5-2.0 mm long. *Pales* at anthesis pentagonal (Fig. 74E), 2.0-2.5 mm long, 1.5 mm wide, light yellow, apex long-

acuminate, yellow, indurate, margin ciliate, entire, abaxial surface glandular and pubescent near center, hairs to 1.1 mm long, adaxial surface glabrous; pales at fruiting deciduous, obovate (Figs. 44B, 73E) 16–21 mm long, 4–5 mm wide, papery with netted venation, stramineous, light in color, indurate, margin entire, abaxial surface sparsely glandular near center, adaxial surface glabrous. *Achenes* brown-black, 3.5 mm long, 2.0 mm wide, smooth. Chromosome number,  $n = 19$ .

FLOWERING (AND FRUITING) PERIOD: Late November–December (December–February).

DISTRIBUTION AND HABITAT: Southern Mexico from Sinaloa to Oaxaca (Fig. 68); pine-oak forests, along streams or on hill and road sides; 450–2000 m.

This striking species has the most diagnostic leaf shape of the genus. The margins are deeply pinnatifid or bipinnatifid (Fig. 74B), the adaxial surface is dark green with white pustular hairs that appear as spots on the surface. Occasionally some of the leaves near the synflorescence are less lobed (Fig. 74C), but the lower ones on the plant are consistently lobed. The species is further distinguished by the mature pales which are the only ones in the genus that expose part of the achene because of a narrow base (Fig. 74F). The disc florets (8 mm), and the stigmata (12 mm) are the largest in the genus. The apex of the disc corolla is covered with short stiff hairs that are interlocking and perhaps serve to protect the head from predation while in bud. If so, it does not work well because this species shows more evidence of insect damage on the heads than any other species in the genus (pers. obser.). This species is most closely related to *Montanoa imbricata* and the relationship between the two is discussed under that species.

Because this plant is very showy it is often cultivated, in fact it is second only to *Montanoa hibiscifolia* in numbers cultivated. Data from herbarium sheets show that it is cultivated from the following countries: Argentina, Ceylon, Burma, Southern India, United States (Florida, California), and throughout its native range in Mexico. One collection (*F* 2272) was found in the "double rayed" form growing in a yard near Guadalajara.

REPRESENTATIVE SPECIMENS: MEXICO. COLIMA: 20–30 mi NE of Colima, 26 Dec 1958, *Thompson & Fields* 355 (MSC, TEX); rd btw Tonila and Colima, 12–13 Nov 1971, *Dieterle* 4175 (ENCB, TEX). DURANGO: Tamazula, La Bajada, Nov 1921, *Ortega* 4451 (US). GUERRERO: 4.4 mi SE of Taxco, 14 Nov 1978, *FRI* 2825 (OS); 8 km SW of Taxco, 22 Dec 1967, *Rzedowski* 25264 (DS, ENCB, MICH, MSC); 12 km N of Iguala, 2 Dec 1966, *Rzedowski* 23515 (DS, ENCB, LL, MSC); btw Iguala and Teloloapan, 16 Dec 1963, *Porter* 1364 (DS, GH, MEXU); Ashotla, s.d., *Reko* 4940 (GH, US); rd from Carrizal to Chichihualco, 5.6 mi SE of jct of rd to Filo de Caballo, 15 Nov 1978, *F* 2836 (OS); rd to Filo de Caballo, 20 mi W of jct with hwy 95, 13 Nov 1977, *FG* 2320 (OS); Acahuizotla, 14 Dec 1963, *Porter* 1324 (GH, MEXU); 14.0–14.5 mi N of Tierra Colorada, 10 Dec 1966, *AL* 4507 (MICH, OS). JALISCO: 16 mi NW of Ameca, 1 Nov 1970, *Breedlove* 18665 (MICH); 3–5 mi N of La Cuesta on rd to Talpa de Allende, 20–21 Nov 1960, *M* 21255 (DUKE, ENCB, MICH); 6–10 mi SW of Talpa de Allende, 22 Nov 1952, *M* 14344 (MICH, SMU); San Sebastian, Arroyo, 15 Jan 1927, *Mexia* 1487 (BM, DS, F, G, GH, MICH, MO, NA, NY, UC, US); Guadalajara, Jul–Oct 1886, *Palmer* 492 (BM, G, K, MEXU, MO, NDG, US); 5 mi S of Guadalajara (cultivated, double-rayed), 5 Nov 1977, *F* 2272\* (OS); 8.5 mi N of Jocotepec, 6 Nov 1977, *F* 2282\* (OS); W end of Lake Chapala, 8 Nov 1959, *McVaugh & Koelz* 367 (DUKE, ENCB, LL, MICH, NY); ca. 15 km SSE of Acatlán de Juárez, 7–8 Nov 1959, *McVaugh & Koelz* 309 (ENCB, MICH); 1.8 mi S of jct of hwy 80 and rd from Union de Tula to Ejutla, 6 Nov 1977, *F* 2290 (OS); 14.7 mi NE of Autlán, 16 Dec 1966, *AL* 4546 (MICH, OS); 12–15 mi SSE of Autlán, 22–23 Nov 1959, *McVaugh & Koelz* 966 (ENCB, MICH); 3–6 km S of La Huerta, 16–17 Mar, *M* 23052 (ENCB, MICH); 16 km N of Ciudad Guzmán, 13 Nov 1971, *Dieterle* 4181 (CA, ENCB, MICH, OS); E of Ciudad Guzmán, 18 Nov 1968, *Boutin & Brandt* 2280 (MICH); Tamazula de Gordiano, 24 Dec 1967, *Clarke et al.* 2185-1 (MICH); 8 km W of Jilotlán de los Dolores, 22 Nov 1970, *M* 24590 (DUKE, ENCB, MICH); 12.5–14.5 mi SW of Mazamitla, 15 Dec 1966, *AL* 4539 (MICH, OS); Jiquilpan-Colima hwy, 3 mi above La Garita, 2 Dec 1959, *McVaugh & Koelz* 1336

(DUKE, ENCB, LL, MICH). MÉXICO: ca. 5 mi N of Ixtapán de la Sal, 10 Dec 1974, *Stuessy & Roberts 3699* (OS, UC); near Amatepec, 29 Dec 1953, *Matuda 30047* (NY); btw Mal País and Santa Bárbara, 6 Dec 1953, *Matuda 30125* (MEXU, NY, US); Temascaltepec, 14 Nov 1932, *Hinton 2401* (BM, G, K, GH, US); Valle de Bravo, 23 Dec 1952, *Matuda 27335* (DS, MEXU, NY); Ocoteppec, Tejupilco, 10 Dec 1967, *Rzedowski 25290* (DS, ENCB, MICH, MSC). MICHOACÁN: btw Zamora & Sahuayo, km 159 hwy 15, 3 Nov 1977, *F 2265* (OS); 3 mi W of Zitacuaro, 20 Nov 1978, *F 2866* (OS); ca. 28 mi E of Pátzcuaro, 16 Dec 1978, *FCa 2968* (OS); ca. 8 mi S of Uruapan, 16 Dec 1978, *FCa 2971* (OS); Rancho Viejo, Apatzingan, 14 Oct 1939, *Hinton 15332* (NA); 16 mi N of Coalcomán on rd to Tepalcatepec, 17 Dec 1978, *FCa 2976* (OS); Sierra Naranjillo, Coalcomán, 26 Nov 1938, *Hinton 12684* (MICH, TEX, US); 15–16 km SE of Asserradero Dos Aguas, 25–26 Nov 1970, *M 24727* (DUKE, ENCB, MICH); 11.3 mi E of jct of rd from Tepalcatepec to Coalcomán and side rd to Dos Aguas, 17 Dec 1978, *FCa 2982* (OS); ca. 12 mi SW of Coalcomán on rd to Villa Victoria, 17 Dec 1978, *FCa 2985* (OS); ca. 15 mi SW of Coalcomán on rd to Villa Victoria, 17 Dec 1978, *FCa 2986* (OS). MORELOS: near Cuernavaca, 15 Nov 1865, *Bourgeau 1199* (BR, C, G, GH, K, MPU, US); 16.7 mi NW of Cuautla on rd to Cuernavaca, 24 Nov 1966, *AL 4306* (MICH, OS); ca. 5 mi SW of Morelos/México border on hwy 95, 17 Nov 1978, *FRi 2847* (OS). NAYARIT: 11.7 mi NW of Tepic, 18 Dec 1966, *AL 4551* (MICH, OS); 5–10 mi from Tepec on rd to Compostales, 27 Nov 1967, *Grashoff 181* (MSC); btw Ixtlan del Río Tetitlan, 22 Nov 1955, *Carter & Kellogg 3639* (MEXU, MICH, US); 10 mi SE of Ahuacatlán, 17–18 Nov 1959, *McVaugh & Koelz* (DUKE, ENCB, LL, MICH). OAXACA: btw Coixtlahuaca and Tamazulapam, 12 Nov 1894, *Nelson 1948* (US). PUEBLA: 5.6 mi SE of Izucar de Matamoros, 22 Nov 1978, *F 2870* (OS). SINALOA: San Ignacio, 28 Jun 1926, *Ortega 4998* (GH, K, US); Balboa, Jan 1923, *Ortega 4998* (US); Panuco, 28–30 Dec 1970, *Smith 195* (ARIZ); 3.5 mi E of Copala on rd to Durango, 7 Dec 1966, *Gentry 22279* (NA, US); 32–33 mi NW of jct of hws 15 and 40, 18 Dec 1966, *AL 4554* (MICH, OS).

## DOUBTFUL AND EXCLUDED SPECIES

- Montanoa aschenbornii* Schultz Bip. in K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 407. 1864. Type: no information, *A. Aschenborn s.n.* (holotype destroyed in WWII; in litt., H. W. Lack). All other herbaria known to house Aschenborn collections were contacted and no type specimen has been located. The type description is too brief to determine the exact placement of this species, although it is definitely a *Montanoa*. It may be a synonym of *M. frutescens*, but it would not have priority.
- Montagnaea ensifolia* Schultz Bip. in Seemann, Bot. Voyage Herald 7–8: 304. 1856. Type: MEXICO, Sierra Madre, *B. S. Seemann 2007* (holotype, P; fragment of holotype, US!) = *Viguiera ensifolia* (Schultz Bip.) S. F. Blake, Contr. Gray Herb. 54: 58. 1913.
- Montanoa orbignyana* Klatt, Abh. Naturf. Ges. Halle 15: 8. 1881. Type: [BOLIVIA?] Prov. Chiquitos, *A. d'Orbigny 763* (holotype, P!; photo of holotype, F! GH! MO! US!) = *Hyptis* sp. (Lamiaceae), fide R. Sanders (pers. comm.).
- Montanoa purpurea* Brongniart ex Groenland, Ann. Rev. Hort. 543. 1857, nom. nud.
- Montanoa serrata* Rusby, Desc. New Sp. South Amer. Pl. 151. 1920. Type: COLOMBIA, Atlantico, open ground in dry water course near the coast at Playa Brava, 1 Apr 1898–1901, *H. H. Smith 516* (holotype, NY; isotypes, BM! G! GH! S! US!; photo of holotype, US[2]!). Evidently Smith gave all the plants of this kind the same number because there are four other localities and some with other dates that are at a variety of herbaria. = *Viguiera serrata* (Rusby) H. Robinson, Phytologia 36: 210. 1977.
- Montanoa thomasii* Klatt, Abh. Naturf. Ges. Halle 15: 8. 1881. Type: MEXICO, Veracruz, Orizaba, 1866, *Thomas s.n.* (holotype, GH!) = *Viguiera cordata* (H. & A.) D'Arcy, Phytologia 30: 6. 1975.

## ACKNOWLEDGMENTS

I thank my advisor, Tod F. Stuessy as well as a number of friends and colleagues who have given of their time to supply me with conversation and encouragement, they include: Daniel R. Brooks, Joe Bruner, Jere Brunken, Daniel J. Crawford, Arthur Cronquist, James S. Farris, Robert K. Jansen, Dave Keil, John LaDuke, Guy L. Nesom, Harold Robinson, Roger W. Sanders, Edith L. Smoot, Billie L. Turner, Larry Watrous and Quentin Wheeler. In addition, plant material for this project has been sent by: Neil Harriman, Ronald L. Hartman, Rogers McVaugh and Mario Sousa. The following people have accompanied me on various collecting trips to Latin America and deserve a great deal of admiration for their tolerance and perseverance: Judy Canne, Fernando Chiang F., Santiago Díaz, M. E. Fraile, M. Teresa Géman, Luis D. Gómez, Ronald L. Hartman, Kathleen Kerr, Ken Landon, G. Blanca Pérez, Clara Ramos A., M. L. Rico, Roger W. Sanders, Tod F. Stuessy, Mathew Turner and last, but certainly not least, Billie L. Turner. Above all, I must acknowledge my family whose support has made this task much easier. My thanks go to John Nagey who drew the illustrations for the three new species.

The following herbaria have assisted in the loan of material: A, ARIZ, ASU, B, BH, BM, BR, BUF, C, CA, CGE, CM, COL, CR, CU, DS, DUKE, ENCB, F, FI, G, GH, GOTT, K, KIEL, LE, M, MA, MEXU, MICH, MO, MPU, MY, NA, ND, NDG, NY, OXF, P, POM, RSA, S, SMU, TEX, UC, US, VEN, W and WIS. A number of curators have supplied needed information, they include: H. W. Lack (B), P. Hyypio (BH), M. Canoso (GH) and E. Schofield (NY).

Aid was received from the following granting institutions: National Science Foundation (DEB 77-14812), World Health Organization, The Society of Sigma Xi and The Ohio State University Graduate School. Without these grants, the field studies necessary for this project could not have been completed.

## LITERATURE CITED

- Aristeguieta, L. 1964. Compositae. Flora de Venezuela 10: 1-941.
- Baagøe, J. 1977. Taxonomical application of ligule microcharacters in Compositae. Bot. Tidsskr. 71: 193-224.
- Badillo, V. 1974. *Montanoa fragrans*, una nueva especie de la Cordillera de la Costa. Acta Bot. Venez. 9: 129-132.
- . 1978. Tres compuestas de Venezuela. Acta Bot. Venez. 13: 109-115.
- Bentham, G. & J. D. Hooker. 1873. Genera Plantarum. 2(1): 163-533. Reeve and Co., London.
- Blake, S. F. 1917. New and noteworthy Compositae, chiefly Mexican. Contr. Gray Herb. n.s. 52: 16-59.
- . 1918. The revision of the genus *Viguiera*. Contr. U.S. Natl. Herb. 54: 1-205.
- . 1924a. New American Asteraceae. Contr. U.S. Natl. Herb. 22: 610-613.
- . 1924b. Eight new Asteraceae from Mexico, Guatemala, and Hispaniola. Proc. Biol. Soc. Wash. 37: 55-62.
- . 1926a. *Montanoa*. In: Standley, P. C., Trees and Shrubs of Mexico. Contr. U.S. Natl. Herb. 23: 1529-1536.
- . 1926b. New South American Verbesininae. J. Wash. Acad. Sci. 16: 215-217.
- . 1930. Notes on certain type specimens of American Asteraceae in European Herbaria. Contr. U.S. Natl. Herb. 26: 244-248.
- . 1937. New Asteraceae from Guatemala and Costa Rica collected by A. F. Skutch. Brittonia 2: 239-361.
- . 1950. Five new Asteraceae from Mexico and South America. J. Wash. Acad. Sci. 40: 47-50.
- Candolle, A. P. de. 1836. Prodrômus systematis naturalis regni vegetabilis. 5: 1-706. Treuttel and Wuerz, Paris.
- Cassini, H. 1829. Zaluzanie. In: Cuvier, F. (ed.). Dictionnaire des Sciences Naturelles, second edition. 59: 232-237. [Reprint 1975, Cassini on Compositae collected from the Dictionnaire des Sciences Naturelles arranged with introduction and an index by Robert M. King and Helen W. Dawson. 3: 1874-1879. Oriole Edition, New York.]



- Colla, L. A.** 1824. Hortus Ripulensis. Pp. 1-163. Turin.
- Cracraft, J.** 1974. Phylogenetic models and classification. Syst. Zool. **23**: 71-90.
- Crisci, J. V. & T. F. Stuessy.** 1980. Determining primitive character states for phylogenetic reconstruction. Syst. Bot. **5**: 112-135.
- D'Arcy, W.** 1975. Flora of Panama, Part IX. Family 184. Compositae. Ann. Missouri Bot. Gard. **62**: 835-1321.
- Davis, P. H. & V. H. Heywood.** 1963. Principles of Angiosperm Taxonomy. Pp. 1-556. Krieger Publishing Co., Huntington, NY.
- Eliasson, U.** 1974. Studies in the Galápagos plants XIV. The genus *Scalesia* Arn. Opera Bot. **36**: 1-117.
- Farris, J. S.** 1979. The information content of the phylogenetic system. Syst. Zool. **28**: 483-519.
- Funk, V. A.** 1981. Special concerns in estimating plant phylogenies. Pp. 73-86. In: Funk, V. A. and D. R. Brooks (eds.). Advances in cladistics: proceedings of the first meeting of the Willi Hennig Society. The New York Botanical Garden, Bronx.
- & **P. H. Raven.** 1980. Polyploidy in *Montanoa* Cerv. (Compositae, Heliantheae). Taxon **29**: 417-419.
- Gleason, H. A.** 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. 3 volumes. Hafner Press, NY.
- Hauser, E. J. O. & M. H. Morrison.** 1964. The cytochemical reduction of nitro blue tetrazolium as an index of pollen viability. Amer. J. Bot. **51**: 748-752.
- Hemsley, W. B.** 1881. Biologia Centrali-Americana. **2**: 1-621. R. H. Porter and Dulac and Co., London.
- Hennig, W.** 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.
- . 1966. Phylogenetic Systematics. Pp. 1-263. (Trans. by D. D. Davis and R. Zangerl). Univ. Illinois Press, Urbana.
- Hoffmann, O.** 1890. Compositae. In: Engler, A. & K. Prantl. Die natürlichen Pflanzenfamilien. **4(5)**: 210-267.
- Holmgren, P. K. & W. Keuken.** 1974. Index Herbariorum. Part I. The Herbaria of the World. Edition 6. 1-397. Utrecht, Netherlands.
- Humboldt, F. H. A. von, A. J. Bonpland & C. S. Kunth.** 1820. Nova Genera et Species. **4**: 1-274. Paris.
- Jong, R. de.** 1980. Some tools for evolutionary and phylogenetic studies. Z. Zool. Syst. Evolut. **18**: 1-23.
- Keil, D. J. & T. F. Stuessy.** 1977. Chromosome counts of Compositae from Mexico and the United States. Amer. J. Bot. **64**: 791-798.
- Koch, K.** 1864. *Montanoa*, *Uhdea*. Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten **7**: 406-408.
- Kunth, C. S.** 1847. Index Seminum in Horto Botanico Berolinensi. no. **17**.
- Kuntze, O.** 1891. Revisio Generum Plantarum. Pp. 1-1011. Wurzburg.
- Llave, P. de La & I. Lexarza.** 1825. Novorum Vegetabilium Descriptiones. Fasc. **2**: 1-13.
- Lessing, C. F.** 1832. Synopsis Generum Compositarum. Pp. 1-473. Berlin.
- McVaugh, R.** 1972. Compositarum Mexicanarum Pugillus. Contr. Univ. Michigan Herb. **9**: 361-484.
- Mayr, E.** 1969. Principles of Systematic Zoology. Pp. 1-428. McGraw-Hill Book Co., New York.
- Morley, B.** 1980. Nomenclature of and a key to some cultivated species of *Montanoa* Cervantes (Compositae). J. Adelaide Bot. Gard. **2**: 151-161.
- Nelson, G. J.** 1972. Phylogenetic relationship and classification. Syst. Zool. **21**: 227-231.
- . 1973. Classification as an expression of phylogenetic relationships. Syst. Zool. **22**: 344-359.
- Nuttall, T.** 1818. The Genera of North American Plants and a Catalogue of the Species, to the Year 1817. **2**: 1-254. Philadelphia.
- Platnick, N. S.** 1979. Philosophy and the transformation of cladistics. Syst. Zool. **28**: 537-546.
- Powell, A. M. & J. Cuatrecasas.** 1970. Chromosome numbers in Compositae: Colombian and Venezuelan species. Ann. Missouri Bot. Gard. **57**: 374-379.
- Robinson, B. L. & J. M. Greenman.** 1899. Revision of the genera *Montanoa*, *Perymenium* and *Zaluzania*. Proc. Amer. Acad. Arts **34**: 507-521.
- Robinson, H.** 1976. Three new Asteraceae from Guerrero, Mexico. Phytologia **33**: 285-292.
- . 1977. Studies in the Heliantheae (Asteraceae). VIII. Notes on genus and species limits in the genus *Viguiera*. Phytologia **36**: 201-215.
- . 1978. Studies in the Heliantheae (Asteraceae). XV. Various new species and new combinations. Phytologia **41**: 33-44.
- & **R. D. Brettell.** 1973. Tribal revisions in the Asteraceae IV. The relationships of *Neurolaena*, *Schistocarpa* and *Aletidocline*. Phytologia **25**: 439-445.
- Rzedowski, J.** 1975. Tres dicotiledoneas mexicanas de posible interes ornamental. Bol. Soc. Bot. México **35**: 37-50.

- Skvarla, J. J. & D. A. Larson. 1965. An electron microscopic study of pollen morphology in the Compositae with special reference to the Ambrosiinae. *Grana Palynol.* 6: 210-269.
- Smith, E. B. 1975. The chromosome numbers of North American *Coreopsis* with phyletic interpretations. *Bot. Gaz.* 136: 78-86.
- Snow, R. 1963. Alcoholic hydrochloric acid-carmines as a stain for chromosomes in squash preparations. *Stain Tech.* 38: 9-13.
- Solbrig, O. T., D. W. Kyhos, M. Powell & P. H. Raven. 1972. Chromosome numbers in Compositae VIII: Heliantheae. *Amer. J. Bot.* 59: 869-878.
- Staffeu, F. A. 1967. Taxonomic Literature. Pp. 1-556. Utrecht, Netherlands.
- Stevens, P. 1980. Evolutionary polarity of character states. *Ann. Rev. Ecol. Syst.* 11: 333-358.
- Stuessy, T. F. 1977. Heliantheae—systematic review. *In: Biology and Chemistry of the Compositae* (Eds. V. H. Heywood, J. B. Harborne, and B. L. Turner), pp. 621-671. Academic Press, NY.
- Turner, B. L. & D. Flyr. 1966. Chromosome numbers in the Compositae. X. North American species. *Amer. J. Bot.* 53: 24-33.
- & M. C. Johnston. 1961. Chromosome numbers in the Compositae—III. Certain Mexican species. *Brittonia* 13: 64-69.
- Urbatsch, L. E. 1974. IOPB report. *Taxon* 23: 619-624.
- Watrous, L. & Q. Wheeler. 1981. Polarization of character states. *Syst. Zool.* 30: 1-11.
- Wiley, E. O. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Syst. Zool.* 28: 308-337.

## APPENDIX A

## Collector Abbreviations

**AL** = Anderson & Laskowski; **C** = Cronquist; **F** = Funk; **FCa** = Funk & Canne; **FGe** = Funk & Géman; **FGo** = Funk & Gómez; **FH** = Funk & Hill; **FK** = Funk & Kerr; **FL** = Funk & Landon; **FPF** = Funk, Pérez & Fraileo; **FRa** = Funk & Ramos; **FRI** = Funk & Rico; **FRK** = Funk, Ramos & Kerr; **FS** = Funk & Sanders; **FT** = Funk & Turner; **FTK** = Funk, Turner & Kerr; **FV** = Funk & Vogelahn; **HFC** = Hartman, Funk & Chiang; **M** = McVaugh; **Sa** = Standley; **Se** = Steyermark; **SF** = Stuessy & Funk; **SG** = Stuessy & Gardner.

## APPENDIX B

Characters and Character States Used in the Cladistic Analysis of  
*Montanoa* (apomorphic state listed last)

I. Characters for the initial subdivision of the genus: 1. mature pales herbaceous vs. papery; 2. mature pales herbaceous vs. indurate; 3. mature pales with walls thin vs. thick; 4. mature pales parallel vs. net-veined; 5. mature pales triangular vs. obtrullate; 6. mature pales circular or conduplicate in cross section; 7. mature pales persistent vs. deciduous with the achenes; 8. mature pales with inconspicuous vs. prominent veins; 9. immature pales with apex shorter vs. longer than the base; 10. immature and mature pales essentially glabrous vs. densely pubescent and glandular; 11. mature heads with nearly as many achenes as disc florets vs. only one achene per head; 12. mature heads persistent vs. deciduous.

II. Characters for the analysis of subgenus *Montanoa*: 13. pales overlapping at least half way vs. distal end spreading; 14. pales straight vs. recurved; 15. pales indurate vs. transparent; 16. pales indurate vs. very indurate; 17. mature pales less than 10 mm long vs. over 15 mm long; 19. abaxial surface of leaves green vs. white; 20. branches of synflorescence many headed vs. solitary or nearly so; 21. phyllaries acute-acuminate vs. rounded; 22. phyllaries 5-9 vs. 9-18 mm long; 23. phyllaries uni- vs. biseriate; 24. ray florets less than vs. more than 10; 25. disc florets fewer than 50 vs. more than 60; 26. disc corollas less than 5 mm vs. more than 5 mm long; 27. disc corolla, style and anther apices yellow vs. tinged with

purple; 28. disc corolla yellow vs. yellow and black; 29. anthers partially contained within vs. exserted from the corolla; 30. anther theca yellow/brown vs. black, 31. abaxial surface of style yellow vs. black; 32. abaxial surface rounded vs. keeled.

III. Additional characters for the analysis of subgenus *Acanthocarphae*: 34. mature pales stramineous vs. stramineous and purple; 35. mature pales with vs. without a sinus; 36. stems pubescence clear vs. red; 37. leaf blades unlobed or regularly lobed vs. 5-irregularly lobed; 38. junction of the three main veins of the leaf within the laminar portion of the leaf vs. at the proximal edge; 39. leaf blades unlobed or palmately lobed vs. pinnately lobed; 40. heads erect vs. pendulous; 41. phyllaries 2.5-5.0 vs. 5-7 mm long; 42. phyllaries 5-7 vs. 7 or more mm long; 43. disc florets fewer than vs. more than 80; 44. style apex yellow vs. black spotted; 45. achene surface smooth vs. sculptured; 46. achenes glabrous vs. pubescent; 47. achenes at maturity covered vs. partially exposed.

IV. Additional characters: 49. petioles unwinged vs. winged; 50. shrub vs. tree; 51. shrub vs. vine.

## APPENDIX C

Data Matrix for the Cladistics of *Montanoa*

Taxa	Characters																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	19	20	21	22	23	
tomentosa	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	
frutescens	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
guatemalensis	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	1	0	
mollissima	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	
andersonii	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	
standleyi	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	
liebmannii	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	
echinacea	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	
revealii	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	
ovalifolia	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
badilloi	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
angulata	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
quadrangularis	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
josei	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
leucantha	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
karwinskii	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
atriplicifolia	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
pteropoda	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
hibiscifolia	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
hexagona	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
laskowskii	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	
grandiflora	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
speciosa	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
imbricata	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
bipinnatifida	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	

## APPENDIX D

Characters Used in PCA of Section *Montanoa*

1B. Involucral bract shape (acute = 0, both = 1, acuminate = 2); 1A. involucral bract length; 2. involucral bract width; 3B. involucral bract color (light = 0, brown = 1, dark brown = 2, green = 3, dark green = 4); 4. involucral bract pubescence (ciliate = 0, moderate = 1, dense = 2); 5. involucral bract glands (absent = 0, present = 1, cells filled = 2); 6. involucral bract gland types (one = 0, two = 1); 7. involucral bract maximum number; 8. involucral bract minimum number; 9A. involucral bract vein number; 10. width of flowering heads including rays; 11. width of flowering heads excluding rays; 12. width of heads in fruit; 13A. ray floret limb length; 13B. ray floret limb shape (lanceolate = 0, ovate-lanceolate = 1, spatulate = 2, ovate = 3); 14. ray floret limb width; 15. ray floret tube length; 16. ray floret limb pubescence (apex only = 0, apex and veins = 1); 17. ray floret tube pubescence (absent = 0, present = 1); 19. ray floret vein number; 21. ray floret number; 22. pollen diameter maximum; 23. pollen diameter minimum; 24. peduncle pubescence (sparse = 0, moderate = 1, dense = 2); 25. peduncle pubescence length; 26. disc floret tube length; 27. disc floret throat length; 28. disc floret lobes (straight = 0, reflexed = 1); 29. disc floret tube width;

## APPENDIX C

## Continued

Characters																									
24	25	26	27	28	29	30	31	32	34	35	36	37	38	39	40	41	42	43	44	45	46	47	49	50	51
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0
0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1
0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1
0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0
1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0
1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0
1	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0
1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0

30. disc floret color (cream = 0, yellow = 1, green = 2); 31. disc floret rounded pubescence location (apex = 0, moderate on throat = 1, dense on throat = 2); 32. disc floret acute pubescence (sparse = 0, moderate = 1); 33. disc floret throat pubescence (glabrous = 0, pubescent = 1); disc floret minimum number; 36. disc floret maximum number; 37A. theca length; 37B. filament length; 38. stamen vesture (glands absent = 0, present = 1); 39. style base (without node = 0, with = 1); 40. style length; 41. anther color (yellow = 0, brown = 1); 42. flowering pale length; 43. flowering pale width; 44. flowering pale apex (erect = 0, erect and recurved = 1, recurved = 2, reflexed and recurved = 3, reflexed = 4); 45. flowering pale pubescence (ciliate = 0, moderate = 1, dense = 2); 46. flowering pale pubescence length; 49B. flowering pale color (light = 0, dark = 1); 50. fruiting pale width; 51. fruiting pale apex (erect = 0, erect and recurved = 1, recurved = 2, recurved and reflexed = 3, reflexed = 4); 52. fruiting pale pubescence (ciliate = 0, medium = 1, dense = 2); 53. fruiting pale pubescence length; 56. achene length; 57. achene width; 58. flowers persistent at fruiting (absent = 0, present = 1); 59. number of achenes per head; 3A. involucre bract pubescence length; 9B. involucre bract vein condition (non-anastomosing = 0, anastomosing = 1); 49A. fruiting pale length.

## APPENDIX E

Data Matrix for the PCA of Section *Montanoa*

Subsp. number	Characters																											
	1B	1A	2	3B	4	5	6	7	8	9	10	11	12	13A	13B	14	15	16	17	19	21	22	23	24	25	26	27	28
1a	0	28	10	4	1	0	0	5	4	4	15	5	8	58	0	33	17	1	0	6	5	23	18	1	5	15	13	1
1a	0	30	10	4	2	1	0	5	5	3	20	5	8	70	0	30	10	0	0	5	5	21	17	2	8	20	15	0
1a	0	30	10	0	0	1	1	5	5	4	13	4	6	40	0	14	15	0	0	6	5	21	18	2	5	18	18	1
1a	0	30	12	4	0	1	1	6	4	3	13	5	10	43	0	13	15	1	0	7	5	23	18	1	5	18	20	1
1a	0	35	10	3	2	1	1	5	5	3	15	6	9	45	0	33	14	1	0	8	5	20	18	2	3	18	14	1
1a	0	35	15	3	1	1	1	5	4	3	14	8	10	30	0	20	10	0	0	7	5	23	20	2	3	18	13	1
1a	0	40	11	3	2	1	0	5	5	3	21	7	10	30	0	20	10	0	0	7	5	22	18	2	8	18	18	1
1a	0	43	10	1	1	1	1	6	5	4	16	6	10	50	0	15	10	0	0	5	5	21	18	2	8	25	15	1
1a	0	45	15	1	2	1	1	5	5	3	17	8	12	45	1	20	18	1	0	5	5	20	18	2	8	20	18	1
1a	0	35	10	1	2	1	0	5	5	7	13	5	10	38	0	28	10	1	0	7	3	25	18	2	3	20	10	1
1a	1	40	12	2	1	1	0	5	5	5	13	6	11	35	0	20	10	1	0	5	3	22	20	2	5	15	15	0
1a	1	50	15	0	2	1	1	5	5	3	25	7	7	50	0	18	18	1	0	8	5	20	18	2	5	20	20	1
1a	1	32	10	2	2	1	1	6	5	3	15	5	8	45	0	20	10	0	0	7	5	22	18	1	3	18	20	1
1a	1	28	10	2	1	1	0	5	5	7	15	7	8	43	0	20	10	0	0	7	5	23	17	1	8	15	14	0
1d	1	20	10	1	2	2	0	6	5	3	13	3	10	48	0	30	10	1	0	5	3	25	23	2	10	25	15	0
1d	2	30	15	2	1	2	1	6	5	3	14	5	8	48	3	40	10	1	0	7	3	27	24	2	5	25	15	0
1d	2	23	13	1	1	1	1	5	5	3	10	4	6	30	0	15	10	0	0	6	3	25	23	2	8	13	10	1
1d	2	25	13	2	2	2	1	5	4	5	14	5	6	45	0	20	10	0	1	7	4	25	23	2	8	15	10	1
1d	2	25	13	1	2	2	0	5	5	5	14	6	8	40	0	25	10	1	0	6	5	25	23	2	8	20	20	0
1d	2	25	14	1	2	2	0	5	5	5	14	6	7	38	0	30	10	0	0	6	5	22	18	2	10	25	10	0
1d	2	34	13	1	2	2	1	6	5	3	13	5	10	40	3	20	14	1	1	5	5	22	20	1	2	25	15	0
1d	2	40	17	1	1	2	0	6	4	2	20	6	10	80	0	25	20	2	0	10	5	18	16	2	10	35	15	0
1d	2	37	13	1	2	1	1	5	5	3	16	9	7	50	3	25	10	0	1	5	5	20	20	2	8	20	15	0
1d	2	28	13	2	2	1	1	5	4	3	10	4	8	30	2	15	13	0	1	5	5	25	22	2	5	25	15	0
1d	2	23	15	0	2	1	1	5	5	3	15	7	8	38	2	30	15	0	1	6	5	25	23	2	5	20	13	0
1d	2	40	20	1	2	2	1	6	5	7	13	7	7	30	2	15	15	0	0	5	5	25	24	2	8	25	15	0
1d	0	40	15	1	2	1	1	6	5	3	16	6	10	50	2	40	15	0	0	5	5	27	25	2	5	25	15	0
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1d	2	19	10	—	0	1	1	3	3	3	—	4	—	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—
1d	0	50	10	1	2	1	1	3	3	3	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
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1b	1	33	13	3	1	1	1	5	5	5	15	5	8	30	0	20	10	0	0	7	5	25	22	1	5	20	10	0
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APPENDIX E  
Continued

Characters																													
29	30	31	32	33	34	36	37A	37B	38	39	40	41	42	43	44	45	46	49B	50	51	52	53	56	57	58	59	3A	9B	49A
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## INDEX

Page numbers in **boldface** indicate primary page reference, page numbers with "f" indicate pages with illustrations or maps.

- Acanthocarpha (subgenus) 67  
 Acanthocarphae (subgenus) 2, 3, 4, 12, 20, 23, 24,  
 27, 30, 31, 33, **67**, f68, 82, 127  
 Actinospermum (genus) 6  
 affinis 91  
 Aldama (genus) 4-6  
 Amblyolepis (genus) 6  
 Amoenae (series) 4, 31, **60**  
 andersonii 4, 12, 31, 33, f50, **55**, 56, f57, 59  
 angulata 4, 31, 34, f74, **74**, f75, 76  
 anomala 46  
 Apertae (series) 4, 31, **64**  
 arborescens 14, 89  
 arsenei 88  
 aschenbornii 123  
 Aspilia (genus) 5  
 atractyloides f5  
 atriplicifolia 4, 7, 12, 20, 27, 31, 34, 52, 93, **94-96**,  
 f96, f97, 100  
 auriculata 69  
 Bahiinae (subtribe) 6  
 bipinnatifida 4, 7, 8, 10, 14, 18, 20, 25, 27, 31,  
 33, 67, f68, f109, **120**, f121  
 Blainvillea (genus) 5  
 Calea (genus) 6  
 clematidea 89  
 crenata 88  
 cordata 123  
 Coreopsidinae (subtribe) 6  
 discolor 94  
 dumicola 52, 94  
 echinacea 4, 10, 12, 14, 27, 29, 31, 33, f48, f62,  
 62, f63, 64, 67  
 Echinocephalae (section) 3, 4, 20, 23, 24, 27, 30,  
 32, **47**, f48  
 Eclipta (genus) 5  
 Ecliptinae (subtribe) 5, 6  
 elegans 3, 14, 120  
 emins f5  
 Enhydra (genus) 4-6, f5  
 ensifolia 123  
 Eriocarpha (genus) 2, 31  
 Eriocarpha (subgenus) 2, 3, 34  
 Eriocarphae (subgenus) 2, 3, 34  
 Eriocoma (genus) 2, 3, 31, 42  
 Espeletia (genus) 6  
 Espeletina (subtribe) 6  
 excelsa 76  
 floribunda 2, 31, 41, 42, 43  
 fragrans Badillo 4, 10, 31, 34, 69, **71**, f72, f73, 74  
 fragrans D. Don in Sweet 43  
 Frutescentes (series) 4, 30, **48**  
 frutescens 2, 4, 9, 10, 20, 27, 30, 33, 47, **48**, f49,  
 f50, 50, 51, 59, 123  
 Gaillardia (genus) 6  
 Gaillardinae (subtribe) 6  
 Galinsogninae (subtribe) 6  
 gentryi 39, 41, 45  
 gigas 64  
 gracilis 91  
 grandiflora Benth. non D.C. 88  
 grandiflora D.C. 2, 4, 10, 18, 20, 25, 29, 31, 33,  
 67, 110, **111**, f112, 112-115  
 Grandiflorae (series) 4, 12, 31, 108, **110**  
 grandis 120  
 Grossblüthige (subgenus) 3  
 guatemalensis 4, f11, 11, 17, 20, f21, 21, 29, 30,  
 33, f50, 50, **51**, 52, f53, 55  
 Gymnolomia (genus) 4, 5  
 hartwegiana 88  
 Heliantheae (tribe) 4, 23  
 hemsleyana 39, 41, 46  
 heracleifolia 120  
 heterophylla 43  
 hexagona 4, 12, 17, 20, 21, 29, 31, 34, 52, 103,  
**104**, f105, 106, f107  
 hibiscifolia 4, f5, 12, f13, 14, 20, 31, 34, 82,  
**101**, f102, 102, f103, 103, 106, 122  
 Hibiscifoliae (series) 4, 31, **82**, 108  
 Hyptis (genus) 123  
 imbricata 4, 11, 20, 25, 27, 31, 33, f109, 110,  
**116**, f117, f118, 119, 122  
 Intermediae (series) 4, 31, **107**  
 Jaumea (genus) 6  
 josei 4, 29, 31, 34, f75, 76, 78, f79, **79**, f80, 82  
 karwinskii 4, 10, 20, 27, 29, 31, 34, f68, **91**, f92,  
 92, f93, 93  
 kingii f5  
 Kleinblüthige (subgenus) 3  
 laskowskii 4, 7, 10-12, 20, 29, 31, 33, 107, f108,  
**108**, f109, 110  
 lehmannii 76  
 leucantha 4, 7, 14, f28, f29, 31, 34, 82, **84**, 88, 110  
 leucantha subsp. arborescens 4, f13, 18, 20, f83,  
 83, 84, f86, f87, 87, **89**, 93  
 leucantha subsp. leucantha 4, 20, 83, f84, 84, f85,  
 f87, 87, **88**, 93  
 liebmannii 4, 10, 12, 29, 31, 33, **60**, f61, f62, 62,  
 64, 67  
 longifolia 2, 111  
 macrolepis 60  
 Melampodiinae (subtribe) 6  
 microcephala 41, 45  
 Mittelblüthige (subgenus) 3  
 mollissima 4, 10, 11, 20, 30, 33, f48, f50, 50,  
**53**, f54, 55  
 Montagnaea (genus) 2, 31  
 Montanoa (genus) 1-8, f8, 11, 12, 14, 18-20,  
 22-24, f24, f26, f27, 27, f28, f29, 30, **31**, 39,  
 126, 128  
 Montanoa (subgenus) 3, 4, 12, 20, 23, 24, f25,  
 30, 32, **34**, 126



- Montanoa (section) 3, 4, 7, 11, 12, 20, 23, 30, 32, 35, 39, 41, 128, 130  
 montanoa 48  
 Montanoninae (subtribe) 6, 7  
 moritziana 76  
 myriocephala 41, 46  
 nervata 89  
 olivae 91  
 orbignyana 123  
 ovalifolia 4, 11, 27, 31, 32, 34, 68, 69, f70, 74  
 ovalifolia subsp. australis 4, 69, 71, f72  
 ovalifolia subsp. ovalifolia 4, 20, 69, f72  
 Ovalifoliae (series) 4, 31, 68  
 palmeri 41, 46  
 patens 89  
 pauciflora 94  
 phlomoides 94  
 pilosipalea 41, 43  
 pittieri 101  
 Podaehaenium (genus) f5, 6  
 Polymnia (genus) 6  
 Priestleya (genus) 2, 31  
 pringlei 53  
 pteropoda 4, 7, 10, 11, 12, 20, 27, 31, 34, 93, 96, f97, 98, f99  
 purpuraseens 88  
 purpurea 123  
 pyramidata 120  
 Quadrangulares (series) 4, 31, 74  
 quadrangularis 4, 8, 18, 29, 31, 34, 74, f75, 76, f77, 78, 82  
 rekoii 39, 41, 46  
 revealii 4, 11, 12, 20, 21, 27, 29, 31-33, 48, f62, 64, f65, f66, 67  
 Rhysolepis (genus) 4, f5, 6  
 Rojasianthe (genus) 4, f5, 6  
 rosei 41, 45  
 Rumfordia (genus) 6  
 samalensis 101  
 Sealesia (genus) 4, f5, 6  
 sehottii 95  
 Selerocarpus (genus) 4-6, f5  
 seleriana 41, 46  
 serrata 123  
 sessilis f5  
 speeiosa 4, 10-12, 20, 25, 27, 31, 33, 112, 113, f114, f115, 115, 116  
 squarrosa 2, 48  
 standleyi 4, 11, 31, 33, f50, 56, 57, f58, 59  
 subglabra 41, 46  
 subtruncata 91  
 superba f5  
 Synedrella (genus) 6  
 tamayonis 76  
 tehuaeana 53  
 ternifolia 43  
 thomasi 123  
 tomentosa 2, 4, 7, 10, 11, 18, 30, 32, 34, 35, f36, 39, 41, f42, f43  
 tomentosa var. eordifolia 43  
 tomentosa subsp. microcephala 4, 8, f9, 10, 16, f18, f19, 20, 41, f42, f43, 45  
 tomentosa subsp. rosei 4, 20, f40, 41, f42, f43, 45  
 tomentosa var. ternifolia 43  
 tomentosa subsp. tomentosa 4, 11, 14, f15, f16, 20, f35, f42, 42, f43, 88, 89  
 tomentosa subsp. xanthiifolia 4, 15, f17, 20, f37, f38, f39, f42, 42, f43, 45, 55  
 triloba 46  
 trilobata 94  
 Uhdea (genus) 2, 31  
 Uhdea (subgenus) 3, 67  
 uneinata 89  
 uniserialis f5  
 Venegasia (genus) 6  
 Verbesina (genus) 5  
 Verbesininae (subtribe) 6  
 Viguiera (genus) 5, 6  
 Villanova (genus) 6  
 wereklei 101  
 xanthiifolia 41, 45, 46

## Blank Page - Back

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Thanks, Vicki

Volumes 1–10, 12–18, 20–24, 26 and 27 have been published and are available. The status of other volumes and recent issues is as follows:

Vol.	Issue	Publication date	Title	Author
11	1	March, 1963	A Manual of the Leafy Hepaticae of Latin America	Margaret H. Fulford
	2	June, 1966		
	3	December, 1968		
	4	February 11, 1976		
	5	in preparation		
19	1	June 30, 1969	Cryptogamae Exsiccatae, An Annotated Bibliography of Published Exsiccatae of Algae, Lichenes Hepaticae and Musci	Geneva Sayre
	2	June 22, 1971		
	3	May 1, 1975		
	4	in preparation		
25	1	November 27, 1973	Leguminosae of the United States I. Subfamily Mimosoideae	Duane Isely
	2	November 12, 1975	Leguminosae of the United States II. Subfamily Caesalpinioideae	Duane Isely
	3	November 9, 1981	Leguminosae of the United States III. Subfamily Papilionoideae. Tribes Sophoreae, Podalyriaceae, Loteae	Duane Isely
28	1	May 3, 1976	Issue Commemorating the 70th Birthday of Dr. Josiah L. Lowe	36 authors
	2	December 7, 1977	New Combinations and New Taxa of Mosses Proposed by Nils Conrad Kindberg	William C. Steere and Howard A. Crum
	3	October 28, 1976	A Revision of the Mexican-Central American Species of <i>Cavendishia</i> (Vacciniaceae)	James L. Luteyn
	4	November 19, 1976	A Revision of the Genus <i>Declieuxia</i> (Rubiaceae)	Joseph H. Kirkbride, Jr.
29		June 14, 1978	The Botany of the Guayana Highland-Part X	Bassett Maguire and Collaborators
30		February 28, 1978	Monographic Studies in <i>Cassia</i> (Leguminosae Caesalpinioideae). III. Sections <i>Absus</i> and <i>Grimaldia</i>	H. S. Irwin and R. C. Barneby
31	1	July 21, 1978	A Revision of the New World Species of <i>Rhynchosia</i> (Leguminosae-Faboideae)	John W. Grear
	2	December 7, 1979	A Monograph of the Genus <i>Lasianthaea</i> (Asteraceae)	Kenneth M. Becker
32		May 20, 1981	The Botany of the Guayana Highland-Part XI	Bassett Maguire and Collaborators
33		August 25, 1981	Monograph of <i>Crocicreas</i> (Ascomycetes, Helotiales, Leotiaceae)	Steven E. Carpenter
34		December 22, 1981	Taxonomy of <i>Amauroderma</i> (Basidiomycetes, Polyporaceae)	João S. Furtado
35		in press	The American Cassiinae	Howard S. Irwin and Rupert C. Barneby
36		published herewith	The Systematics of <i>Montanoa</i> (Asteraceae, Heliantheae)	V. A. Funk

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