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THE SYSTEMATICS OF SIMSIA (COMPOSITAE: HELIANTHEAE)

Spooner, David Michael, Ph.D.

The Ohio State University, 1987

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THE SYSTEMATICS OF SIMSIA (COMPOSITAE: HELIANTHEAE)

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the
Degree of Doctor of Philosophy in the Graduate
School of The Ohio State University

By

David Michael Spooner, B.A., M.S.

* * * * *

1987

Dissertation Committee:

Dr. Daniel J. Crawford

Dr. Gary Floyd

Dr. Tod F. Stuessy

Dr. Thomas N. Taylor

Approved By:

A handwritten signature in black ink, appearing to read 'D. M. Spooner', is written over a horizontal line.

Advisor

Department of Botany

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David Michael Spooner
1987

Dedicated to

My family

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VITA

November 1, 1949.....Born - Downy, California

1971.....B.S., Miami University, Oxford, Ohio

1971-1974.....U.S. Army Medical Field Service
School,
Ft. Sam Houston, Texas, Honor
Graduate;
Honorable Discharge, Army, 1974

1972-1973..... University of Maryland, College Park,
Maryland, 1972-1973

1974-1976.....M.S., Ohio University, Athens, Ohio

1977.....Instructor, Ohio University
Continuing Education

1978-1980.....Field Botanist, Ohio Department
of Natural Resources, Division of
Natural Areas and Preserves

1982-1987.....Graduate Teaching Associate and
Graduate Research Associate, Botany
Department, The Ohio State University,
Columbus

PUBLICATIONS

Journal Articles

Spooner, D. M. 1982. Wetlands in Teays-age valleys in extreme southeastern Ohio: Formation and flora. 89-99. IN: B. McDonald, ed. Proceedings of symposium on wetlands of the unglaciated Appalachian region, Morgantown, West Virginia, May 26-28, 1982.

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Major Field: Plant Systematics

Studies in Plant Systematics. Professor Tod F. Stuessy

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INTRODUCTION

Simsia is a genus of herbs and shrubs widely distributed throughout the Americas from the southwestern United States to the center of Argentina (Fig. 1). Some of the species (e.g., S. amplexicaulis, S. lagascaeformis) are widespread roadside and agricultural weeds and are familiar plants to collectors of Mexican Compositae. Others, however (e.g., S. holwayi, S. steyermarkii), are narrowly restricted endemics and seldom encountered. The species share a 2-4 seriate involucre, linear sterile ray ovaries (except for one eradiate species, S. eurylepis), a convex involucre with conduplicate, medium-textured persistent pales, fertile disc florets with a well-defined glandular-puberulent tube and abruptly expanded throat, and laterally flattened ovate or obovate disc achenes with or without awns (rarely with intermediate squamellae).

The genus was last monographed by Blake (1913) who resurrected it from synonymy of Encelia and recognized 22 species and three varieties. A recent useful and insightful synopsis of Mexican and Central American species by Robinson and Brettell (1972) treated 24 species from these areas including seven new ones, and estimated 35 species total for the genus. However, this synopsis was based on limited material (only US), did not include field investigations, failed to treat species from Jamaica and South America, and did not resolve evolutionary patterns within or outside the genus.

Despite previous work on Simsia, basic taxonomic problems have remained. In some difficult species varying annotations by reputable workers frequently have been encountered; comments on specimens regarding uncertain identifications are also common. Problems with certain species have been indicated by Nash (1976), and Jansen & Stuessy (1980). The genus is taxonomically difficult by any standard, and a contributing factor is the polymorphic nature of many species. This has led to a confusing array of synonyms and taxa of uncertain circumscription. Of perhaps greater significance is the tendency of certain species to hybridize, a pattern indicated from initial herbarium investigations and later confirmed in field and greenhouse studies.

The present study of Simsia provides a taxonomic monograph based on considerably more data than available to previous workers. Over 3600 herbarium specimens have been examined from numerous institutions. In addition, Viguiera and related genera have been examined at ENCB, GH, MEXU, MO, OS, and US for a study of generic relationships. Four field trips have been conducted over a period of seven months from 1982-1985 throughout Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Colombia, and Ecuador, resulting in field observations and collections of all but one endemic variety from Jamaica. The field investigations were especially useful for observations on intra- and interpopulational variability, habitat tolerances, natural hybridization, and the collection of pertinent morphological observations difficult to obtain from herbarium collections, such as plant height, branching patterns, corolla color,

and leaf odor. Cytological collections provided material for 93 chromosome counts of all taxa except *S. foetida* var. *jamaicensis*. Numerical phenetic and cladistic studies have been utilized to help resolve taxonomic limits and develop hypotheses on evolutionary patterns in the genus. Sixteen species and five additional varieties have been grown in the greenhouse; of these, 11 species and five varieties were utilized in an artificial crossing program. These crossing studies provided data on compatibility systems, genomic compatibility among various species, stability of morphological features, and insights into the nature of taxonomic problems and evolutionary processes operative in *Simsia*.

Based on these data, *Simsia* is here treated as comprising 18 species and six varieties. Two species, *S. santarosensis* and *S. villasenori*, are newly described. The species are all diploid ($n = 17$). Three species are self-compatible; all others are self-incompatible. Hybridization is believed to have been operative on different levels in the genus, from sporadic hybrids where species co-occur, to introgression, and even diploid hybrid speciation.

An outline of the classification of the genus is given below (acronyms in brackets for taxa are those used throughout the text.

Synopsis of Classification of *Simsia* Persoon

I. Section *Fruticulosae* D. M. Spooner

IA. Series *Fruticulosae* D. M. Spooner

1. *S. ghiesbreghtii* (A. Gray) S. F. Blake [GHIE]

2. S. santarosensis D. M. Spooner [SANT]
3. S. fruticulosa (Sprengel) S. F. Blake [FRUT]
4. S. molinae H. Robinson & R. D. Brettell [MOLI]
5. S. holwayi S. F. Blake [HOLW]
6. S. steyermarkii H. Robinson & R. D. Brettell [STEY]
- 7a. S. annectens S. F. Blake var. annectens [ANNE]
- 7b. S. annectens var. grayi (Schultz-Bipontinus
ex S.F. Blake) D. M. Spooner [GRAY]
8. S. tenuis (Fernald) S. F. Blake [TENU]
9. S. villasenori D. M. Spooner [VILL]
10. S. setosa S. F. Blake [SETO]
- 11a. S. sanguinea A. Gray var. sanguinea [SANG]
- 11b. S. sanguinea var. triloba (S. F. Blake) D. M. Spooner
[TRIL]

IB. Series Calvae D. M. Spooner

12. S. calva (A. Gray & Engelmann) ex A. Gray) A. Gray [CALV]

II. Section Simsia

IIA. Series Lagascaeformis D. M. Spooner

13. S. lagascaeformis DeCandolle [LAGA]
14. S. eurylepis S. F. Blake [EURY]

IIB. Series Simsia

15. S. chaseae (Millspaugh) S. F. Blake [CHAS]
16. S. dombeyana DeCandolle [DOMB]
17. S. amplexicaulis (Cavanilles) Persoon [AMPL]
- 18a. S. foetida (Cavanilles) S. F. Blake var. foetida [FOET]

- 18b. *S. foetida* var. *jamaicensis* (S. F. Blake) D. M. Spooner
[JAMA]
- 18c. *S. foetida* var. *megacephala* (Schultz-Bipontinus ex
S. F. Blake) D. M. Spooner [MEGA]
- 18d. *S. foetida* var. *guatemalensis* (H. Robinson & R. D.
Brettell) D. M. Spooner [GUAT]
- 18e. *S. foetida* var. *grandiflora* (Bentham in Oersted)
D. M. Spooner [GRAN]
- 18f. *S. foetida* var. *panamensis* (H. Robinson & R. D.
Brettell) D. M. Spooner [PANA]

HABITAT AND DISTRIBUTION

The 25 taxa of Simsia occur sporadically throughout Latin America (Fig. 1). Twenty-two occur from southern Arizona, New Mexico, and Texas, south through Mexico to Panama. One variety occurs in Jamaica, and two species occur in the Andean regions of Venezuela, Colombia, Ecuador, Peru, and Bolivia to south-central Argentina, with disjunct populations in east-central Brazil. The genus exhibits the greatest diversity of species from central Mexico to Guatemala, where 19 of the 25 taxa occur. Some of the taxa are rather narrowly distributed (e.g., S. foetida var. jamaicensis, S. tenuis, S. villasenorii), but others (e.g., S. amplexicaulis, S. lagascaeformis) are wide-ranging weeds.

There is great variation in habitat differences and tolerances. Many taxa occur in relatively dry tropical deciduous forests (e.g., S. foetida), but others occur in more upland pine-oak to cloud forests (e.g., S. amplexicaulis, S. ghiesbreghtii), and S. eurylepis occurs along the humid Gulf coastal lowlands. There is also much variation in habitat and elevational tolerances (Fig. 2). Some taxa are restricted to a relatively narrow range of elevation and habitat (e.g., S. chaseae, S. eurylepis), but others occur over a broad range of habitats and elevations (e.g., S. calva which occurs from lowland deserts to upland pine forests from 30-2400 m, and S. fruticulosa which occurs from sea-level in areas of frequent salt spray to upland

Fig. 1. Distribution of Simsia.

Fig. 1

Fig.2. Known elevational ranges of taxa of Simsia.

ELEVATION IN METERS

Fig. 2

cloud forests at 2600 m).

Although some taxa sometimes co-occur and occasionally hybridize, sympatric species usually are kept apart by habitat differences. For example, two widespread and weedy taxa, *S. amplexicaulis* and *S. foetida* var. *foetida* are sympatric over a broad area. They rarely co-occur, however, due to elevational and habitat differences (see discussion under *S. foetida* var. *foetida*).

TAXONOMIC HISTORY

The taxonomic history of Simsia begins with the descriptions of Coreopsis foetida Cavanilles (1791) and C. amplexicaulis Cavanilles (1802). Both of these species were described from garden-grown plants from seed from the Sesse and Mocino expeditions. Persoon (1807) described the genus Simsia, including the above two species and S. heterophylla Persoon [= Iostephane heterophylla (Cavanilles) Benthams ex Hemsley]. Kunth (1818) and Sprengel (1826) lumped Simsia into Ximenesia (= Verbesina). Cassini (1829) resurrected Simsia, greatly improved the characterization of the genus, accepted Persoon's three species, and added three more.

Simsia also was accepted as a genus by later workers, and new taxa were described by DeCandolle (1836), Gray (1850, 1853), Benthams (1853), and Triana (1858). Gray (1873), however, later reduced Simsia to a section of Encelia, a decision followed by the influential work of Hemsley (1881). Subsequently, new taxa were described in Encelia (Gray, 1887; Rose, 1895; Fernald, 1897; Kuntze, 1898; Hieronymous, 1901; Greerman, 1903; Millspaugh, 1904.). A modern interpretation of Encelia and related genera (or genera at least superficially similar to Encelia) awaited the insightful work of Blake (1913), who resurrected Simsia and described eight new taxa. Simsia has been accepted since that time, with later additions provided by Blake (1917, 1918a, 1924, 1928), Loesener (1923), and Cuatrecasas (1954).

Robinson and Brettell's synopsis of Mexican and Central American species (1972) described seven new species and resulted in the last publication of new taxa in the genus.

GENERIC RELATIONSHIPS

Simsia is relatively homogeneous and rarely is confused with other genera. The most diagnostic and readily observable characters are the herbaceous 2-4 seriate imbricate involucre, the linear ray ovaries, and the laterally flattened disc achenes almost always lacking squamellae.

Gray (1873) treated Simsia as a section of Encelia and it was so treated until Blake (1913) brought it out of synonymy. It shares with Encelia many of the above features, but Encelia differs by its alternate leaves, pales deciduous with the villous, white-margined achenes, and with most taxa based on $x = 18$. Encelia is now recognized to be part of an assemblage of species that includes Enceliopsis, Flourensia, Geraea, and perhaps Phoebanthus (Robinson, 1981; Dillon, 1984; Clark & Sanders, 1986; Sanders & Clark, 1987). In addition to the above features, Encelia and Enceliopsis share similar benzofuran chemistry (Mitsakos & Proksch, 1985), and Encelia and Geraea sometimes hybridize naturally (Kyhos, 1967).

More recent hypotheses of relationships to Simsia have suggested Viguiera in a general way (Robinson & Brettell, 1972), Helianthus (Robinson, 1979), and more specifically Viguiera ser. Grammatoglossae (Spooner, 1984). Simsia, Helianthus, and much of Viguiera share most of the morphological and cytological features that help to characterize Simsia. In addition, these three genera (along with the

related genus Tithonia) are united by the presence of anthochlors, unknown in the rest of the Heliantheae except for the Coreopsidinae (Crawford & Stuessy, 1981). The differences among Simsia, Helianthus and Viguiera are few. The most diagnostic characters are in the disc achenes. Those of Simsia are very laterally flattened, thickened only in the central area, with semi-persistent awns present or absent, only rarely with squamellae. The achenes of Helianthus and Viguiera, however, although laterally compressed, are plump and biconvex throughout. Viguiera usually has persistent awns and squamellae, and Helianthus has readily deciduous awns, sometimes with squamellae. Additional differences among these taxa are less diagnostic, but they also help provide delimitation. Simsia has long (3-10.2 mm) linear ray achenes, whereas those of Helianthus and much of Viguiera are shorter or on the low end of this range and often more obovate. The style branches of Simsia are long (2-4 mm), thin, and grade to an attenuate apex with a poorly defined appendage formed by some papillae at the end. Those of Helianthus and much of Viguiera, however, are generally shorter and more deltoid, and Viguiera often has a well-defined appendage. In addition to these features, many specimens of Simsia possess characteristic nodal discs (see section Morphology and Taxonomic Criteria) unknown in Helianthus and Viguiera.

Previous (Spooner, 1984) and present investigations suggest that Simsia is most closely related to Viguiera ser. Grammatoglossae. Blake (1918b) characterized this series by its herbaceous, lanceolate to oblong phyllaries, in contrast to the more indurate phyllaries of other taxa. He included 11 species of herbs and shrubs distributed

from Texas to Guatemala. In addition to the herbaceous phyllaries resembling Simsia, most species within this series have similar elongate style branches (although with a tendency for a more well-defined appendage), and linear ray ovaries similar to Simsia. All have biconvex achenes, however, and none have the nodal discs so characteristic of many species of Simsia. Recent investigations suggest that Viguiera potosina is misplaced in V. series Dentatae, as it has floral flavonoids (Rieseberg & Schilling, 1985), chromosome numbers ($n = 17$; Schilling & Schilling, 1986), and herbaceous phyllaries more similar to V. series Grammatoglossae (pers. comm., E. Schilling) and Simsia. In addition, present investigations suggest that V. parkinsonii, V. pringlei, and V. seemanii have indurate phyllaries and an overall appearance quite different from other members of V. ser. Grammatoglossae and are best excluded from this section. Another species in V. series Grammatoglossae, V. mimia, is a little-known taxon, collected once in Guatemala in 1875, and is represented only by a single type sheet. It bears a superficial resemblance to S. foetida var. grandiflora, but has heads, rays and achenes of Tithonia.

For these reasons, Simsia is considered most closely related to a redefined V. series Grammatoglossae, including V. potosina. All species within this redefined section Grammatoglossae share with Simsia a chromosome level of $2n = 34$: V. cordifolia (Heiser & Smith, 1955; Keil & Stuessy, 1977; this study, see Table 2), V. grammatoglossa (Turner, Powell & King, 1962), V. ovata (Sundberg, Cowan & Turner, 1986), and V. potosina (Schilling & Schilling, 1986).

As is illustrated above, the differences between Simsia and Viguiera series Grammatoglossae are few and often intergrading. Other genera are similarly distinguished from Viguiera by only a few characters, and the problem of intergrading generic differences extends beyond the Simsia-Viguiera relationship. Viguiera stands as a possible focal point for the evolution of many other genera (Fig 3, Table 1). Blake (1918b) recognized 143 species, but more recent additions have been made by McVaugh (1972), Robinson (1977, 1980), Saenz (1979), Turner (1978, 1985) Panero & Schilling (V. series Maculatae, in press), In addition, Reiseberg & Schilling (1985) and Schilling & Schilling (1986) have redefined V. series Dentatae, Schilling is currently working on the rest of V. section Calanticaria, and the genus has now been estimated to contain ca. 170 species (Schilling & Schilling, 1986). Although the segregate genera are readily recognized by a suite of characters, these sometimes overlap with Viguiera or other taxa. The genera, therefore, although defined by many (albeit overlapping) features, can be most easily distinguished by the following: Simsia, by its laterally flattened disc achenes; Tithonia, by its fistulose peduncles; Zaluzania, by its fertile ray florets; and Helianthus, by its relatively deciduous pappus. Intermediates sometimes obscure these distinctions, however (e.g., S. ghiesbreghtii with some populations with biconvex thickened achenes).

If the hypothesized relationships of these genera to Viguiera are accurate, this is an example of the "core genus" concept so common in the Compositae, viz., a large, often poorly circumscribed paraphyletic

Fig. 3. Relationships of segregate genera to the core genus Viguiera (see Table 1). The different levels of concentric circles of Viguiera represent subgenera, sections, and series, respectively, and the size of each section is proportional to the number of species (sensu Blake, 1918b). The segregate genera are positioned near that portion of Viguiera to which they are allied, except Iostephane, Scalesia, Syncretocarpus, and Rhysolepis, which are of uncertain affinity to any particular portion of Viguiera.

Fig. 3.

Table 1. Relationships of other genera to Viguiera.

Taxon	Chromosome numbers (n) ^a	Relationship to <u>Viguiera</u>	Authority
<u>Haplocalymma</u>	—	sect. <u>Diplostichus</u>	Blake, 1918; Robinson, 1977, 1981; McVaugh, 1984 ^b
<u>Helianthopsis</u>	9,17	sect. <u>Aureae</u>	Blake, 1918; Heiser, 1957; Robinson, 1979, 1981
<u>Helianthus</u>	17,34,51	ser. <u>Dentatae</u> , ser. <u>Grammatoglossae</u>	Blake, 1918; Heiser et al., 1969 ^c
<u>Helioneris</u>	8,9,16	sect. <u>Helioneris</u>	Yates & Heiser, 1979; ^d Robinson, 1981
<u>Hymenostephium</u>	17,21,40+2	sect. <u>Diplostichus</u>	D'Arcy, 1975; Robinson, 1977; Turner, 1978a; McVaugh, 1984 ^b
<u>Iostephane</u>	17	<u>Viguiera</u>	Strother, 1983a; McVaugh, 1984

Table 1, Continued.

Taxon	Chromosome number (n)	Relationship to <u>Viguiera</u>	Authority
<u>Pappobolus</u>	17	sect. <u>Aureae</u>	Blake, 1916; Cuatrecasas, 1965 ^e
<u>Rhysolepis</u>	17	<u>Viguiera</u>	Blake, 1917 ^f
<u>Scalesia</u>	34	<u>Viguiera</u>	Eliasson, 1974
<u>Simsia</u>	17	ser. <u>Grammatoglossae</u>	Spooner, 1984
<u>Stuessya</u>	17	sect. <u>Leighia</u>	Turner & Davies, 1980; McVaugh, 1984 ^g
<u>Syncretocarpus</u>	—	<u>Viguiera</u>	Blake, 1916, 1918b
<u>Titbonia</u>	17	subg. <u>Amphilepis</u> ; sect. <u>Calanticaria</u>	Blake, 1918b; LaDuke, 1982
<u>Zaluzania</u>	18	ser. <u>Grammatoglossae</u>	Olsen, 1979
		ser. <u>Pinnatilobatae</u>	Turner, 1985 ^h

a. numbers mostly from Stuessy, 1977; Robinson et al., 1981.

Table 1, Continued.

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- b. These authors consider this taxon a Viguiera, but Stuessy (1977) accepts the genus.
- c. Phoebanthus also possibly is related (Stuessy, 1972; Heiser et al., 1969), but Robinson (1981) places it in the Encelia assemblage.
- d. Resurrected from Viguiera by Yates & Heiser, 1979.
- e. Cuatrecasas (1965) believes Pappobolus woodsonianus similar to South American Helianthus (= Helianthopsis sensu Robinson, 1979).
- f. Blake (1917) relates Rhysalepis to both Syncretocarpus and Viguiera.
- g. McVaugh (1984) concluded that all the generic characters defining Stuessya fit into V. sect. Leighia except the urceolate involucre. This feature also occurs in Simsia and is correlated there with self-compatibility.
- h. The relationship of Zaluzania to Viguiera is problematical. The base number of Zaluzania ($n = 18$) is different from the Grammatoglossae and Pinnatolobatae ($n = 17$). The pistillate ray florets of Zaluzania suggest it may be misplaced here, and Stuessy (1977) and Robinson (1981) place Zaluzania in subtribes other than the Helianthinae. On morphological grounds I agree with Turner (1985) that Zaluzania is more similar to Viguiera series Pinnalobatae than series Grammatoglossae.

genus with well-defined holophyletic segregates (terminology following Ashlock, 1971). Core genera are present in many tribes, such as the Astereae, Eupatorieae, Senecioneae, and Vernonieae (Cronquist, 1985). The core genus concept has been criticized as being evolutionarily unsound, and attempts have been made to define generic boundaries more precisely in the Eupatorieae and Senecioneae (Robinson & King, 1985). My experience in Simsia, Viguiera, and related genera has resulted in viewpoints more similar to that expressed by Barkley (1985a, b) with relation to Senecio and its segregates. He demonstrated blurring of generic boundaries in the Senecioneae, possibly the result of a long evolutionary history, introgression, and hybridization. The result is a series of well-defined peripheral offshoots connected by transitional taxa to a poorly defined "core". Such a paraphyletic genus, obviously, would be criticized by workers with rigid cladistic views (e.g., Wiley, 1981; Funk, 1985). My experience in Simsia and Viguiera indicates that extensive homoplasy is present in this group, which appears to be common elsewhere in the Compositae (Cronquist, 1987). Paraphyletic taxa are, and probably always will be, a practical necessity; Simsia and Viguiera certainly are useful taxonomic groups.

CYTOLOGY

All taxa of Simsia are monobasic ($x = 17$) and homoploid ($2n = 34$, Table 2). Prior to this study, 56 chromosome counts were documented for 14 of the 25 taxa and one natural hybrid of Simsia; this study provides an additional 93 counts for 24 of the taxa and two natural hybrids (Table 2). The new counts are for: S. annectens var. annectens, S. chaseae, S. foetida var. panamensis, S. holwayi, S. molinae, S. sanguinea var. triloba, S. santarosensis, S. setosa, S. tenuis, S. villasenori, and the natural hybrids S. amplexicaulis X S. lagascaeformis and S. foetida var. foetida X S. lagascaeformis. Only S. foetida var. jamaicensis remains to be counted. It is evident that Simsia has evolved entirely at the diploid or diploidized level, and therefore modes of speciation must have involved factors other than changes in ploidy level.

That Simsia and close relatives in Viguiera series Grammatoglossae (also $n = 17$; see Generic Relationships) are of ancient polyploid origin is suggested by several lines of evidence. The rest of Viguiera and its segregate genera are also largely based on $n = 17$ or 18 (Robinson, 1981). Heiser & Smith (1955) have suggested that Helianthus ($n = 17$) arose by allopolyploid origin based on hypothetical progenitors of $n = 8$ and 9, numbers today known in Helioneris. Jackson & Murray (1983) have demonstrated that premeiotic treatment of microsporocytes of Helianthus annuus and H. laciniatus produces multivalents at meiosis, lending support to a polyploid

Table 2. Chromosome counts in Simsia and Viguiera, (all $2n = 17II$). See representative specimens for vouchers for new counts (asterisks).

Taxon	References and Vouchers
<u>S. amplexicaulis</u>	Turner, Ellison, & King, 1961; Powell & Turner, 1963 (3 populations, as <u>S. foetida</u> , 1 as <u>S. lagascaeformis</u> , 1 as <u>S. cf. megacephala</u> , 1 as <u>S. triloba</u>); Powell & Powell, 1978; Jansen & Stuessy, 1980 (7); 12*
X <u>S. foetida</u>	Jansen & Stuessy, 1980 (as <u>S. foetida</u>).
X <u>S. lagascaeformis</u> 1*	
<u>S. annectens</u>	
var. <u>annectens</u>	2*
var. <u>grayi</u>	Keil & Stuessy, 1975 (as <u>S. grayi</u>); Strother, 1983b (as <u>S. grayi</u>); 3*
<u>S. calva</u>	Turner & Ellison, 1960 (as <u>Encelia calva</u>); Solbrig et al., 1972 (2); Strother, 1972; Watson, 1973; Urbatsch, 1974; Keil & Pinkava, 1976; Keil & Stuessy, 1977; Powell & Powell, 1978; Urbatsch 928; ^a 1*
<u>S. chaseae</u>	6*
<u>S. dombeyana</u>	Coleman, 1970; Robinson et al., 1981; 3*

Table 2. Continued.

Taxon	References and Vouchers
<u>S. eurylepis</u>	Keil & Stuessy, 1975; Keil & Stuessy, 1977; Jansen & Stuessy, 1980; 5*
<u>S. foetida</u>	
var. <u>foetida</u>	Keil & Stuessy, 1977; Jansen & Stuessy, 1980 (2); 5*
X <u>S.</u>	
<u>lagascaeformis</u>	2*
var. <u>grandiflora</u>	Heiser, 1958 (as <u>S. grandiflora</u>); Jansen & Stuessy, 1980 (as <u>S. grandiflora</u>); 2*
var. <u>guatemalensis</u>	Solbrig et al, 1972 (as <u>S. foetida</u>); Jansen & Stuessy, 1980 (1 as <u>S. cf. guatemalensis</u> , 2 as <u>S. amplexicaulis</u>); Strother, 1983 (2 as <u>S. grandiflora</u>); 4*
var. <u>megacephala</u>	Turner & Flyr, 1966 (as <u>S. amplexicaulis</u>); 1*
var. <u>panamensis</u>	3*
<u>S. fruticulosa</u>	Powell & King, 1969 (2 as <u>S. pubescens</u>); 7*
<u>S. ghiesbreghtii</u>	Jansen & Stuessy, 1980; 5*
<u>S. holwayi</u>	2*

Table 2. Continued.

Taxon	References and Vouchers
<u>S. lagascaeformis</u>	Heiser, 1958 (as <u>S. polycephala</u>); Turner, Ellison & King, 1961 (as <u>S. exaristata</u>); Jansen & Stuessy, 1980 (3); <u>Keil, Luckow & Luckow 13342</u> , <u>Keil & Luckow 15331</u> ; ^b 10*
<u>S. molinae</u>	4*
<u>S. sanguinea</u>	
var. <u>triloba</u>	2*
var. <u>sanguinea</u>	Powell & Powell, 1978; Jansen & Stuessy, 1980; Sundberg, Cowan & Turner, 1986; 8*
<u>S. santarosensis</u>	1*
<u>S. setosa</u>	1*
<u>S. steyermarkii</u>	Robinson et al., 1981 (as <u>S. holwayi</u>); 1*
<u>S. tenuis</u>	1*
<u>S. villasenori</u>	2*
<u>V. cordifolia</u>	USA: New Mexico: Hidalgo Co., Rt. 81, S end of Hidalgo Co., <u>Spooner & Schilling 2404</u> .

a. Unpublished counts supplied by Lowell E. Urbatsch, b. David J. Keil.

origin for Helianthus. It is likely that Simsia evolved at the same polyploid level from its ancestors within Viguiera.

ARTIFICIAL HYBRIDIZATIONS

Sporadic hybridization is known to occur naturally in Simsia between S. amplexicaulis, S. foetida, and S. lagascaeformis, and introgression possibly is responsible for many of the intermediates within the varieties of S. foetida. Morphologically intermediate taxa also occur within Simsia which possibly could have arisen by hybridization (e.g., S. annectens var. annectens, S. chaseae, S. setosa). Crossing studies were conducted to test some of these ideas and to gain insights on the biological significance of hybridization within the genus. Another goal was to discover the compatibility systems of various taxa as an aid to more clearly determining their evolutionary relationships.

Materials and Methods. Forty-eight parental individuals representing 29 populations of 11 species, five additional varieties, and one additional population of naturally occurring S. foetida X S. lagascaeformis were utilized in the crossing program in The Ohio State University greenhouses (Table 3). In addition, S. dombeyana, S. foetida var. panamensis, S. fruticulosa, and S. santarosensis were grown and tested for self-compatibility but not used in the crossing program. The only taxa of Simsia not grown and observed in the greenhouse were S. foetida var. jamaicensis, S. ghiesbreghtii, and S. molinae.

Table 3. Percentages of successful crosses (crossing attempts that produced 1-many seed per head) and pollen stainabilities of intra- and intertaxon progeny in Simsia. The female parent is listed first in each cross; the number in parentheses indicates data for the reciprocal cross. The white and red-rayed variants of S. sanguinea var. sanguinea are listed separately. Vouchers of the parents and hybrids are deposited at OS. Populations used for crosses are: Simsia amplexicaulis (Spooner 2780 2794), S. annectens var. annectens (Spooner 2845), S. annectens var. grayii (Spooner & Villasenor 2562, 2566, Spooner 2788), S. calva (Stuessy 712), S. chaseae (Spooner 2804, 2811, 2881), S. eurylepis (Spooner 2841, 2882), S. foetida var. foetida (Spooner & Dorado 2637), S. foetida var. grandiflora (Spooner & Dorado 2699), S. foetida var. guatemalensis (Spooner & Dorado 2688 2693, Spooner 2769), S. foetida var. megacephala (Spooner & Dorado 2667), S. lagascaeformis (Spooner & Burgos 2603, Spooner & Dorado 2656), S. lagascaeformis X S. foetida var. foetida (Spooner & Dorado 2635, 2644), S. sanguinea var. sanguinea (white-rayed variant, Spooner & Dorado 2657; red-rayed variant, Spooner & Dorado 2681), S. sanguinea var. triloba (Spooner & Dorado 2649), S. setosa (Spooner & Villasenor 2528), S. tenuis (Spooner & Villasenor 2550), S. villasenori (Spooner 2789, 2816).

Table 3, Continued.

Hybrid combination	Number of	Number of	Percent	Number of	<u>Pollen stainability</u>	
	crossing attempts	successful crosses	successful crosses	fertile F ₁ 's	Mean	Range
<u>Intrataxon crosses</u>						
AMPL X AMPL	8	5	63	0		
GRAY X GRAY	8	1	13	1	44	
GUAT X GUAT	6	2	33	2	99	99-99
LAGA X LAGA	3	0	0	0		
(LAGA X FOET) X (LAGA X FOET)	5	3	60		0	
SANG (red) X SANG (white)	9(5)	2(1)	21	0		
SETO X SETO	1	0	0	0		
VILL X VILL	13	8	62	12	68	49-98

Table 3. Continued.

Hybrid combination	Number of	Number of	Percent	Number of	<u>Pollen stainability</u>	
	crossing attempts	successful crosses	successful crosses	fertile F ₁ 's	Mean	Range
<u>Intervarietal crosses</u>						
ANNE X GRAY	1	1	100	2	92	84-98
GRAN X GUAT	2(2)	2(0)	50	8	75	11-99
GRAN X MEGA	4(2)	4(0)	67	6	75	45-92
GUAT X MEGA	4(1)	1(0)	20	3	61	51-57
SANG (white) X TRIL	9(7)	0(2)	13	7	68	57-78
SANG (red) X TRIL	11(14)	3(9)	48	27	79	55-93
<u>Interspecific crosses</u>						
AMPL X ANNE	4(2)	1(0)	17	0		
AMPL X EURY	1	0	0	0		

Table 3. Continued.

Hybrid combination	Number of crossing attempts	Number of successful crosses	Percent successful crosses	Number of fertile F ₁ 's	<u>Pollen stainability</u>	
					Mean	Range
AMPL X FOET	8(10)	3(4)	39	0		
AMPL X LAGA	2(7)	2(0)	22	3	67	44-99
AMPL X (LAGA X FOET)	1(4)	1(0)	20	2	99	99-99
AMPL X SANG	6(7)	2(0)	15	0		
AMPL X TENU	1(1)	1(0)	50	0		
AMPL X VILL	2(2)	0(1)	25	0		
ANNE X EURY	2	1	50	0		
ANNE X LAGA	1	1	100	0		
ANNE X SETO	4	2	50	0		
CALV X FOET	5(2)	3(2)	71	0		

Table 3. Continued.

Hybrid combination	Number of crossing attempts	Number of successful crosses	Percent successful crosses	Number of fertile F ₁ 's	<u>Pollen stainability</u>	
					Mean	Range
CALV X SETO	1	1	100	0		
FOET X ANNE	1	1	100	0		
FOET X CHAS	7	3	43	0		
FOET X EURY	29	12	41	35	39	4-67
FOET X LAGA	9(4)	0	0	0		
FOET X (LAGA X FOET)	7(8)	7(1)	53	9	75	42-99
FOET X SETO	1(6)	1(2)	43	1	12	
FOET X TENU	1(2)	1(1)	67	1	49	
FOET X VILL	4(2)	3(1)	67	0		
LAGA X EURY	5	0	0	0		

Table 3. Continued.

Hybrid combination	Number of crossing attempts	Number of successful crosses	Percent successful crosses	Number of fertile F ₁ 's	<u>Pollen stainability</u>	
					Mean	Range
LAGA X (LAGA X FOET)	6(23)	1(6)	24	7	95	80-99
LAGA X SANG	1(2)	0(1)	33	1	30	
LAGA X SETO	1	0	0	0		
LAGA X VILL	1(2)	1(0)	33	0		
(LAGA X FOET) X EURY	1	1	100	3	62	58-67
(LAGA X FOET) X VILL	1(1)	0(1)	50	0		
SANG X ANNE	2	0	0	0		
SANG X FOET	3	1	33	1	21	
SANG X VILL	2(2)	0(1)	25	0		
SETO X CHAS	2	2	100	3	1	0-2

Table 3. Continued.

Hybrid combination	Number of crossing attempts	Number of successful crosses	Percent successful crosses	Number of fertile F ₁ 's	<u>Pollen stainability</u>	
					Mean	Range
TENU X ANNE	1	0	0	0		
TENU X EURY	2	0	0	0		
TENU X LAGA	2	1	50	0		
TENU X (LAGA X FOET)	1	0	0	0		
TENU X VILL	1(2)	1(0)	33	0		
VILL X ANNE	4	3	75	6	48	36-58
VILL X CALV	1	1	100	4	34	25-41
VILL X CHAS	2	1	50	3	6	4-7
VILL X EURY	1	0	0	0		
VILL X SETO	2	1	50	0		

All parental achenes were dried with the specimens in a herbarium press under convective heat. The hybrid achenes also were dried in this manner; initial attempts to germinate mature but undried achenes resulted in lower germination success. Heads were bagged before anthesis and removed only for cross-pollinations which involved gently rubbing the heads of the maternal parent with the detached head of the paternal parent. Five to 20 heads per species were kept enclosed and never crossed, and at least three of these heads were pollinated with pollen from a different head of the same plant to test for self-incompatibility. As a further test of self-incompatibility, *S. calva*, *S. foetida* var. *foetida*, *S. foetida* var. *megacephala*, *S. lagascaeformis*, and *S. setosa*, previously indicated by the bagging experiments to be self-incompatible, were isolated in cages screened to exclude pollinators and crossed numerous times with intraplant pollinations without bagging the heads. Only one crossing attempt was made per head due to the fragile nature of some pedicels. Emasculation was not necessary because all species used as maternal parents had low rates of selfing and the hybrids were distinguishable by their intermediate morphological nature.

Pollen fertility was estimated by staining pollen in 2% lactophenol in cotton blue. Pollen was collected from at least two anthers each from at least two different heads of a plant and mixed together on the same slide with two drops of stain. Observations were made after 24 hr. This procedure was repeated a second time at least one week apart, and the higher of these two numbers was used for the pollen stainability data. Only fully-formed darkly-stained grains

were scored as stained.

The pollen stainabilities of the F_1 hybrids in this, as in other studies, showed much variation in some taxa (e.g., *S. foetida* var. *grandiflora* X *S. foetida* var. *guatemalensis*), and different degrees of staining with cotton blue sometimes made the interpretation of grains as stained or unstained difficult. This variability has been documented in other groups of plants (Jones, 1976; Nybom, 1985) and may be due to environmental variables. Cotton blue and other non-vital stains commonly have been used to assess pollen viability (Radford et al., 1974). Other techniques have been tried to obtain more direct estimates of pollen viability such as vital staining (Nybom, 1985; Chandler, Jan, & Beard, 1986), pollen germination in sucrose media (Nybom, 1985), or germination of grains on receptive styles (Hashemi, West & Waines, 1986), but these more time-consuming and expensive methods often give similar results to the simpler non-vital staining procedures (Hauser & Morrison, 1964; Nybom, 1985). Despite the occasional problems in the interpretation of grains as stained or unstained, the overall results in this study reveal much about the genetic differences of taxa at different hierarchical levels of *Simsia*.

Results and Discussion. The unmanipulated and intraplant pollinated heads set full heads of achenes over 80% of the time for *S. chaseae*, *S. dombeyana*, and *S. eurylepis*, indicating their self-compatible nature. All other tested species were essentially self-incompatible, but in one or two instances each, one to three fruits occasionally were formed on the bagged unmanipulated or

intraplant crossed heads of *S. foetida* var. *grandiflora*, *S. lagascaeformis*, and *S. sanguinea* var. *triloba*, indicating low levels of self-compatibility or possible pollen contamination from other plants.

The parental taxa were crossed 343 times; 125 of these crosses produced fruits in six intrataxon, six intervarietal, and 33 interspecific combinations (Table 3). Fruits were set in 80% of the attempted hybrid combinations. As only one crossing attempt was made per head to avoid damaging them, and as the actual number of receptive styles was difficult to assess at any one cross, a measure of seed set per se was not possible. An alternative measure of crossing success was the percentage of crosses that set 1-many seed per head (Fig. 4). This assessment does not indicate any statistically significant differences between sections.

Flowering F_1 's were produced from seed in two intrataxon, six intervarietal, and eight interspecific combinations, as well as four combinations involving naturally-occurring *S. foetida* var. *foetida* X *S. lagascaeformis* (Table 3). Hybrids were intermediate in most floral and vegetative features, but dominance was noted in the glandular and spicy-smelling leaves of all crosses involving *S. foetida*. Some of these hybrids resulted from the crosses of quite morphologically distinct parents (e.g., *S. chaseae* crossed with *S. setosa* or *S. villasenorii*, or *S. foetida* crossed with *S. sanguinea*).

The pollen stainability data support the taxonomic system here presented at the intraspecific, interspecific, and sectional levels (Fig. 5). The parental taxa have the highest levels with 88-100%.

Fig. 4. Percent of successful crosses among taxa of Simsia.

Figure 4.

Fig. 5. Average percent pollen stainability for intrataxon and interspecific taxa of Simsia.

Figure 5.

The intraspecific crosses were reduced to 68-92%, and the interspecific crosses 1-67%. In addition, unlike the percentage of successful crosses, the pollen stainability data support sectional boundaries. The intrasectional vs. intersectional ranked values, analyzed by the Wilcoxon two-sample test (Sokal & Rohlf, 1981) support the sectional boundaries at the .005 level.

Meiosis was examined for most intervarietal and interspecific hybrids (Table 4). Due to the frequent occurrence of "sticky" chromosomes, it often was difficult to distinguish true from apparent multivalents, but univalents were evident at metaphase I, and laggards and also bridges and fragments were evident at late anaphase I or telophase I. Using these measures, meiosis was normal for all of the hybrids except four combinations that exhibited various degrees of irregularity (Table 4). These abnormalities likely resulted from reciprocal translocations and paracentric inversions. Of interest is that three of these four crosses involve S. eurylepis and S. chaseae, two of the three self-compatible species in the genus (the other self-compatible species, S. dombeyana, was not intercrossed in this program). The results suggest that these self-compatible species are also inbreeders, not subjected to selection for chromosomal uniformity present in the outbreeders. The meiotic irregularities seen in the cross of S. foetida X S. setosa is anomalous here, as both species are self-incompatible.

A concentrated focus of this study involved reciprocal crosses between the red and white ligule color forms of Simsia sanguinea var. sanguinea (both with white disc florets) and S. sanguinea var. triloba

Table 4. Summary of chromosome associations in artificial interspecific F₁ hybrids at Metaphase I, and at Anaphase I or Telophase I.^a

Cross	Number of		Number of		Percent
	cells	Univalents at M I	cells	Laggards at A I or T I	
	examined	mean (range; SD)	examined	mean (range; SD)	bridges ^b
VILL X CHAS ^c	39	0.4 (0-4; 0.9)	140	1.3 (0-5; 1.6)	40
FOET X CHAS	79	1.0 (0-6; 1.3)	128	0.4 (0-3; 0.7)	10
FOET X SETO	26	1.7 (0-6; 1.7)	997	0.7 (0-5; 1.0)	16
FOET X EURY ^d	59	0.2 (1-2; 0.5)	626	0.6 (0-2; 0.3)	1

a. All other intervarietal and interspecific hybrids, including crosses with naturally occurring S. foetida X S. lagascaeformis, exhibited normal pairing and disjunction at meiosis. One individual from each cross was examined, except as noted below.

b. Percent of cells at A I or T I that exhibited bridges and fragments.

c. Pooled data from two hybrid individuals, d. from five hybrid individuals.

(with yellow ligules and disc florets) to see if the varieties were capable of crossing and to see how the flower colors sorted out in reciprocal crosses. Other than corolla color, these varieties are indistinguishable, but var. triloba completely replaces the typical variety in its range in S Puebla and NW Oaxaca. Fruit was produced in 17 successful reciprocal crosses, and these produced 34 flowering F_1 individuals. The disc and ligule colors of these hybrids varied from the extreme parental conditions to various combinations of colors restricted to each type of corolla, i.e., the disc corollas were white, yellow, or intermediate, but not pink. Sometimes the ligules were streaked with both pink and yellow. Although these crosses were not carried to the F_2 generation, the results suggest that different genes may be responsible for ray floret color. In addition, the intervarietal pollen stainability data fall within the range of other varieties in Simsia.

Another focus of this study was the possible diploid hybrid speciation of Simsia chaseae, with S. eurylepis and S. foetida var. foetida or var. guatemalensis as likely parents. I originally developed this hypothesis from examination of herbarium sheets, but the many intermediate features are even more striking in the living condition. All three species are lowland annuals, but only S. chaseae and S. eurylepis are found on the Gulf coastal lowlands. Simsia chaseae and S. foetida both are glandular with spicy smelling odors and radiate heads, and they frequently have been confused in herbarium material. Simsia chaseae and S. eurylepis share the common occurrence of lobed leaves, self-compatibility, and the associated urceolate

involucres. Simsia chaseae generally is intermediate in phyllary gradation between the two species.

Many other species of flowering plants have been hypothesized to have arisen by diploid interspecific hybridization (Raven, 1976; Grant, 1981). Most of these hypotheses have been based solely on morphological data, but some have been tested by artificial hybridization between putative parents (Table 5). An important question for all these scenarios is how natural hybrids formed in this manner maintain their integrity in the face of backcrossing to the parent(s). As is summarized in Table 5, various mechanisms have been proposed such as natural selection and isolation in a new environment, floral isolation, the independent development of sterility factors, and recombinational speciation. Despite these many examples, further study of this type of speciation is warranted.

To test the hypothesis of the origin of S. chaseae via diploid hybrid speciation, crosses were made between plants from two populations each of S. eurylepis (always serving as the pollen donor) and S. foetida var. guatemalensis. Thirty-three F_1 hybrids were produced. They were all glandular with the spicy odors of S. foetida and S. chaseae but lacked the self-compatibility of this latter species. There was much variability in other characters, however, including such features as phyllary reflexion, ratio of inner/outer phyllaries, phyllary pubescence, and the presence or absence of ray florets. Some of the F_1 hybrids were completely rayless as the S. eurylepis parent, others had a full complement of rays as in S. foetida, and still others had both rayed and rayless individuals on

Table 5. Summary of diploid hybrid speciation in flowering plants, with proposed isolating mechanisms for the newly-derived species: 1. natural selection in a new environment; 2. recombinational speciation; 3. independent development of sterility factors; 4. floral isolation.

Taxon	Reference	Isolating Mechanism	Tested by Crosses
<u>Achillea roseo-alba</u>	Ehrendorfer, 1959	1,2	X
<u>Clarkia bootae</u>	Lewis and Lewis, 1955	1	X
<u>Delphinium gypsophilum</u>	Lewis and Epling, 1959	1,2	X
<u>Elymus glaucus</u>	Snyder, 1950, 1951; Stebbins, 1957	3,3	X
<u>Galium dumosum</u>	Ehrendorfer, 1958	1	
<u>Gilia achilleaefolia</u>	Grant, 1954	2	
<u>Gilia capitata</u> ssp.	Grant, 1950	1	X
<u>Gilia ochroleuca</u> ssp.	Grant and Grant, 1960	1	X
vivida, <u>G. cana</u>			
<u>Iris</u> ("Abbeville Red")	Randolph, Nelson and Plaisted, 1967	1	
<u>Lasthenia burkei</u>	Ornduff, 1969, 1976	1,2	X
<u>Lasthenia ferrisiae</u>	Ornduff, 1966	1	X
<u>Ophrys murbeckii</u>	Stebbins and Ferlan, 1956	4	

Table 5. Continued.

Taxon	Reference	Isolating Mechanism	Tested by Crosses
<u>Penstemon spectabilis</u> , <u>P. clevelandii</u>	Straw, 1955	4	
<u>Phlox divaricata</u> ssp. <u>laphamii</u>	Levin, 1967	1	X
<u>Phlox maculata</u> ssp. <u>pyramidalis</u>	Levin, 1963, 1966a; Badley and Levin, 1969	1	X
<u>Phlox pilosa</u> ssp. <u>deamei</u> , <u>P. amoena</u> ssp. <u>lighthipei</u>	Levin and Smith, 1966	1	X
<u>Potentilla glandulosa</u> ssp. <u>hanseni</u>	Clausen, Keck and Heisey, 1940; Clausen and Heisey, 1958	1	X
<u>Purshia glandulosa</u>	Stutz and Thomas, 1964	1	
<u>Stephanomeria diagensis</u>	Gottlieb, 1971, 1972; Galez and Gottlieb, 1982	2	X
<u>Zea mays</u> (corn belt dent)	Anderson and Brown, 1952	1	X

the same plant, with some heads having only 1-4 ray florets.

The data were analyzed by PCA (Fig. 6), utilizing the 33 F_1 hybrids, and selected individuals of S. chaseae, S. eurylepis, and S. foetida var. foetida and var. guatemalensis (marked with a double asterisk in the representative specimens). Twenty-six quantitative morphological characters were utilized (Table 6, not using characters 5, 6). The first two components accounted for 45% of the total variation (the third component raised the total to 57% but did not change the overall pattern and is not presented). The analysis (Fig. 6) indicated a bimodal distribution of characters, with some hybrids more similar to one or the other parent. Some of the hybrids, however, were almost morphologically indistinguishable from naturally-occurring S. chaseae.

Two, and possibly three factors currently serve to isolate effectively S. chaseae from others within the genus: natural selection in a new environment, chromosomal sterility barriers (factors 1 & 3 of Table 5), and possibly inbreeding. Although there is slight sympatry of S. chaseae and S. eurylepis in Veracruz, most populations of S. chaseae are isolated on the Yucatan Peninsula, where it may currently be exploiting new environments. The possible inbreeding and apparently rearranged complement of chromosomes of S. chaseae (see Table 4), also would serve to inhibit hybridization in the wild.

Evidence in favor of the diploid hybrid speciation hypothesis of S. chaseae includes the intermediate morphological nature of this species to its putative parents and also the reconstruction of F_1 hybrids, some of which are almost indistinguishable morphologically

Table 6. Characters and states used in numerical phenetics of the *Simsia foetida* and *S. fruticulosa* complexes, *S. chaseae* hybridization, and the *S. chaseae*-*S. dombeyana* study.

Characters and states

Leaves. 1. Blade length (mm). 2. Width (mm). 3. Petiole length (cm). 4. Interpetiolar stipule height (mm). 5a.^dGlandular pubescence: subsessile (0), stipitate (1). 5b. Subsessile glands: absent (0), present (1). 6a. Abaxial non-glandular pubescence: strigose, hispid or hirsute (0), pilose (1). 6b. thinly pilose, hairs 0.5-to 0.8 mm long (0), intermediately sericeous, 0.8-1.3 mm long (1), densely sericeous, hairs 1.3-2 mm long (2).

Peduncles and Heads. 7. Longest peduncle length (cm). 8. Head diameter (mm). 9. Height (mm).

Phyllaries. 10. Number. 11. Outer series length (mm). 12. Width (mm). 13. Inner series width (mm). 14. Ratio inner/outer series lengths.

Ray florets. 15. Number. 16. Corolla length (mm). 17. Width (mm). 18. Achene length (mm).

Disc florets. 19. Number. 20. Corolla length (mm). 21. Tube length (mm). 22. Lobe length (mm). 23. Anther length (mm). 24. Achene length (mm). 25. Width (mm). 26. Longest awn length (mm).

Table 6, Continued.

Characters and states

Pales. 27. outermost pale length (mm). 28. width (mm).

a. Characters 5a and 6a were used in the S. foetida complex, 5b and 6b in the S. fruticulosa complex, and neither were used in the other two studies.

Figure 6. First two principal component axes of OTU's of natural populations of Simsia chaseae (triangles), S. eurylepis (squares), S. foetida var. foetida and var. guatemalensis (dots), and artificial F_1 hybrids of S. eurylepis X S. foetida var. guatemalensis (stars).

Figure 6.

from some individuals of S. chaseae. Evidence against this hypothesis is the absence of self-compatibility in any of the P_1 hybrids, and the current lack of sympatry of the two putative parents. The hypothesis depends upon the previous co-occurrence of the parents and the attainment of self-compatibility of the hybrids, either by further backcrossing to self-compatible S. eurylepis or continued inbreeding and the possible segregation for this character. An alternative to the diploid hybrid speciation hypothesis presented here might be derivation of S. chaseae from one or the other parent, or it itself might have given rise to the other two taxa (e.g., 1, EURY $\rightarrow$ CHAS $\rightarrow$ FOET; 2, FOET $\rightarrow$ CHAS $\rightarrow$ EURY; 3, EURY $\leftarrow$ CHAS $\rightarrow$ FOET). Hypotheses 1 and 3, however, suggest that a self-compatible species gave rise to a self-incompatible one, the reverse of the usual situation in plants where inbreeders usually are derived from outbreeders (Grant, 1981; Brauner & Gottlieb, 1987). In addition, the apparently rearranged chromosomes of S. chaseae and S. eurylepis in relation to most of the rest of Simsia suggest these species are derived. Hypothesis 2 does not fit the cladistic data, even when S. chaseae is included in the cladistic analysis. In addition, distributional data supports the hypothesis of diploid hybrid speciation. If S. chaseae evolved from only one of the above two species, the more similar S. foetida would be a likely progenitor, but the shared and intermediate features of S. chaseae with S. eurylepis on the relatively restricted areas along the Gulf Coastal lowlands suggests prior hybridization with this species. Simsia chaseae also shows morphological similarity to S. dombeyana of South America (see Numerical Taxonomy) which might suggest another

origin for S. chaseae. S. dombeyana occurs on the periphery of the distribution of entire genus rather than the reverse, which suggests a recent derivation of the species.

Conclusions. The foregoing hybridization data indicate much genetic and chromosomal homology for the species of Simsia. The data suggest that flowering F_1 hybrids can be produced in many combinations within the genus. Lowered genetic affinity is, however, correlated with different levels in the taxonomic hierarchy. The artificial F_1 hybrids are intermediate in many features, and the taxonomic difficulty of some naturally-occurring taxa (e.g., S. amplexicaulis intergrading with S. foetida var. foetida, and the intergradation of some of the varieties of S. foetida) may be due to natural hybridization and/or introgression. The hypothesis of diploid hybrid origin of S. chaseae suggests that other intermediate taxa may also have arisen by this method (e.g., S. annectens var. annectens, S. setosa), but these hypotheses are more conjectural and have not yet been tested by crosses. The taxonomic intergradation and intermediacy of some taxa, and the genetic and chromosomal similarity found throughout the genus suggests a recent origin of many of the species. The largely allopatric distributions and ecological partitioning of most of them suggest initial geographic isolation and only partial and possibly slow divergence after this separation.

NUMERICAL TAXONOMY

To help define concepts of taxa in Simsia and especially to help clarify taxonomic situations in the wide-ranging and taxonomically difficult S. foetida and S. fruticulosa complexes, numerical taxonomic studies have been undertaken. Numerical phenetic analyses have been used to good effect in numerous plant groups for the last 25 years (Sneath & Sokal, 1973; Duncan & Baum, 1981).

Simsia foetida complex. The Simsia foetida complex is a taxonomically difficult group of morphologically similar and intergrading taxa which traditionally have been difficult to identify and classify. Nine separate basionyms exist for the group, and conflicting annotations by reputable workers frequently are encountered. Difficulties in identifications of at least a portion of this complex previously have been noted elsewhere (Nash, 1976; Jansen & Stuessy, 1980).

As recognized here, the S. foetida complex is a natural group of related taxa. All occur in hot lowland habitats, most frequently in areas of tropical deciduous forests, from sea level to ca. 1700 m, (occasionally up to 2150 m), distributed from Jalisco, Mexico to central Panama, with disjunct populations in Jamaica, Venezuela, and Bolivia. The group is well-defined and easily distinguished by a number of shared features. All are annuals or short-lived facultative

perennials. The stems, leaves, and phyllaries are densely covered with subsessile to stipitate biseriate glands that impart a viscid feel and range of lemony and strong spicy odors to living plants. The phyllaries are linear, subequal, sometimes with caudate tips, and often with sinuate margins. All have yellow anthers.

Taxonomically significant variation is mainly of a quantitative nature, and intergradation of taxa is common. Previous workers, however, have treated this quantitative variation in a more qualitative or in more discrete quantitative ways. Compounding these taxonomic problems are considerable polymorphic traits, often within single populations. Despite considerable intergradation, geographically correlated modes of variation are present. Preliminary studies suggested that six taxa could be recognized within this group. Principal components analysis (PCA) was used to gain an overall estimate of these patterns of variation, and stepwise discriminant analysis was then used to test the significance of the groups.

Materials and Methods. One hundred and ten individuals (OTU's) were measured for 26 quantitative and 2 qualitative morphological characters (Table 6, utilizing characters 5a and 6a), including those features previously shown to be taxonomically useful. The populations were selected to represent the range of morphological variation and geographical distribution of the group. In some cases, more than one plant from a population was measured to assess intrapopulational variability. The measured populations are marked with a double asterisk in the list of representative specimens in the taxonomic section. Measurements of head parts were made from FAA-preserved

collections or from herbarium material revived in aerosol. Heads were chosen from selected collections in a random manner; width and diameter were from the widest point of a structure. Leaf and nodal disc are of the largest of these structures from a main plant axis.

The data were analyzed by PCA available in the NT-SYS package (Rohlf et al., 1985), and a stepwise discriminant analysis, available in the BMDP computer package (Dixon et al., 1985). For PCA, the data matrices were standardized using the STAND subroutine of NT-SYS, resulting in a mean of zero and a standard deviation near unity. The PCA was then performed using the subroutine FACTOR. Computations were conducted by an IBM-4341 computer.

For stepwise discriminant analysis, only the 26 quantitative characters were used (i.e., excluding 5 & 6). Normality of the character distributions were tested by a t-test for skewness and kurtosis being significantly different from 0 (for $p < 0.05$), using the PD2 program in BMDP. Non-normal distributions were normalized by the TRANSFORM functions of BMDP and these new characters were substituted in the data set. Six distributions could not be normalized and were discarded. A stepwise discriminant analysis was then performed on this reduced and partially transformed data set using the P7M program of BMDP.

Results and Discussion. The results of the PCA are presented in Fig. 7. Factors 1 and 2 account for 43.9% of the total variation. A third factor raised the total to 54.9% but did not change the overall pattern and is not presented. Intrapopulation samples, some of which represented size extremes in vegetative or floral features, all

Figure 7. First two principal component axes of OTU's of Simsia foetida var. foetida (open circles), var. grandiflora (stars), var. guatemalensis (squares), var. jamaicensis (asterisks), var. megacephala (triangles), and var. panamensis (closed circles).

Figure 7.

fall within their respective groups. This analysis indicates a pattern of variation supportive of six taxa, but with considerable overlap. Despite this overlap, however, the distinctness of these taxa is significant at the 0.001 or 0.005 level by a multiple analysis of variance generated by the stepwise discriminant analysis (Table 7). The distinctness of these groups also is supported by the high percentage of "correct" classifications generated by the analysis (87-100% for all groups except for Simsia foetida var. grandiflora with 81%, the misplaced taxa placed in the varieties megacephala and guatemalensis). Of the 21 characters utilized in this analysis, seven accounted for most of the variation: phyllary number, nodal disc length, achene length, awn length, ray corolla width, disc corolla tube length, and disc corolla length.

Using the F-values to approximate similarities and differences, it is apparent that the greatest taxonomic overlap occurs in geographically contiguous or nearby taxa. The greatest discrimination problems in a practical sense and in these more formal numerical analyses involve distinguishing the varieties foetida-megacephala-guatemalensis and guatemalensis-grandiflora. These problems are further compounded due to the common occurrence of polymorphic character states within natural populations. For example, head size and associated head parts, and nodal structures form major discriminators in these taxa, but these can vary considerably, especially in the varieties megacephala, guatemalensis, and grandiflora.

Table 7. F-matrix for a stepwise discriminant analysis of the varieties of Simsia foetida. All values are significant at p less than 0.001 (f = 12), or 0.005 (f = 7.29); degrees of freedom = 7, 79.

	<u>guatemalensis</u>	<u>foetida</u>	<u>jamaicensis</u>	<u>megacephala</u>	<u>panamensis</u>
<u>foetida</u>	11.29				
<u>jamaicensis</u>	25.27	23.99			
<u>megacephala</u>	22.22	30.91	30.44		
<u>panamensis</u>	17.28	40.08	39.06	36.64	
<u>grandiflora</u>	19.98	38.78	40.86	27.76	12.76

The existence of the overlap of these populations brings into question the recognition of any taxa within this complex. One alternative would be to recognize one highly polymorphic species without varieties. Such an approach, however, would obscure real differences and would reduce the predictive value of the classification. The varieties foetida, jamaicensis, and panamensis, while variable in many characters, possess many constant features within their respective ranges, and present few problems of interpretation. It is of interest that these taxa are all distributed marginally within this complex. The varieties megacephala, guatemalensis, and grandiflora, however, are more variable with considerable geographical overlap and are more difficult to distinguish. Nevertheless, they do represent genetically controlled variation (see Artificial Hybridizations) that is geographically correlated.

Simsia fruticulosa complex. Simsia fruticulosa is a highly variable, shrubby species usually with nodal discs (although sometimes deciduous or not present on all nodes or plants in a population), with unequal phyllaries, light orange-yellow ligules, and leaves pilose to densely sericeous below. This last character helps to distinguish it from other close relatives. It is widespread in northern South America, from eastern Venezuela to northern Ecuador, and occurs in a wide range of habitats from sea level in areas of frequent salt spray, to cool, moist upland cloud forests, in highly disturbed areas along roadsides, to more undisturbed sites.

Simsia fruticulosa exhibits much morphological variation, and as in S. foetida, this variation is of a quantitative nature. Seven species have been described in this complex based on differences of stem shape, leaf size, shape, and pubescence, stipule morphology, head size, shape and pubescence, and achene pubescence. Some taxa apparently were published without reference to previous literature, but others have been accepted by reputable workers (Blake, 1918b; Cuatrecasas, 1954). While some differences are clearly seen, preliminary investigations failed to reveal geographical or ecological correlations. The initial hypothesis to be tested, therefore, was that of one highly polymorphic species.

Materials and Methods. A PCA analysis was conducted of 47 OTU's (marked with a double asterisk in representative specimens), representing the morphological variation and geographical distribution of the group. These studies were greatly aided by field work throughout much of the range in Nicaragua, Costa Rica, Colombia, and Ecuador, resulting in 23 additional collections throughout the range of its habitat, including five of the seven type localities. The methods were the same as in the S. foetida complex above, but with characters 5b and 6b substituted for 5a and 6a.

Results and Discussion. The first three factors of the PCA (not presented) accounted for 50.0% of the total variation. This analysis indicated a high degree of variability in the OTU's much greater than that found in S. foetida. No pattern emerged that had any correlation with habitat or geography. This is confirmed by personal field investigations, in which a wide range of morphologies in plant heights

and head sizes and shapes occur throughout many areas. Some collections are quite distinctive, such as Spooner & Guevara 2933, 2935, 2936 with narrower and less unequal phyllaries, or Spooner & Guevara 2923, 2973, King & Guevara 5817, Haught 6374, Brettler 4545 with larger heads and associated head parts, but these and other minor variants are found scattered throughout the range of the species with intermediates elsewhere. These results indicate that all of the populations should be recognized as one highly polymorphic species.

Simsia chaseae and S. dombeyana. Simsia chaseae is remarkably similar to S. dombeyana. Both are annuals with glandular leaves with unwinged petioles and no discs, both have light lemon-yellow ligules, and both are self-compatible with urceolate heads. It often is difficult to distinguish these species, as the differences are minor. Experience with greenhouse-grown S. dombeyana indicates that this species lacks the strong lemony or spicy odors characteristic of S. chaseae and S. foetida. Simsia chaseae grows in the northern hemisphere and flowers Jun-Nov, whereas S. dombeyana occurs in the southern hemisphere and flowers Dec-May. The main character that previously has distinguished these two species has been phyllary gradation. Simsia chaseae originally was described with unequal phyllaries, and Blake (1913) used this character to separate the species from S. dombeyana which has subequal phyllaries. While all species of S. dombeyana appear to possess subequal phyllaries, so do some specimens of S. chaseae (e.g., Purpus 11121, Spooner 2859, 2881), and many intermediates occur.

Figs. 8 and 9. First three principal component axes of OTU's of Simsia
chaseae (stars), and S. dombeyana (dots).

Figures 8, 9.

These similarities and overlapping characters, and personal initial difficulty in distinguishing the species, led to a PCA to see if two taxa should be recognized, and to conduct stepwise discriminant analysis to discover which characters might best discriminate them.

Materials and Methods. The methods are the same used in the *Simsia foetida* complex, but characters 5 and 6 were not utilized in this study. Twenty-one OTU's from 12 populations of *S. chaseae* and 23 OTU's of 19 populations of *S. dombeyana* (marked with a double asterisk in representative specimens), representing the morphological and geographical range of the species, were utilized.

Results and Discussion. The results of the PCA are summarized in Figs. 8 and 9. The first two components accounted for 47.0% of the total variation; the third component raised the total to 59.9%. These results indicate a pattern of partially defined but overlapping taxa. The stepwise discriminant analysis statistically supports the recognition of these groups at the .001 level utilizing the character of phyllary gradation alone, but this one character is insufficient to consistently discriminate both taxa. Utilizing an additional suite of characters, however, serves to adequately separate the taxa 100% of the time, but all of these characters overlap across taxa and could not be used alone. These characters, arranged in a decreasing order of discriminant utility (see Table 6) are: 14, 16, 26, 13, 22, 12, 16. The similarity of the taxa could be used to support varietal recognition, but the consistent separation using other characters, and their distinct ranges of both more strongly suggest specific status.

The similarity of S. chaseae and S. dombeyana suggests they are closely related. The evidence presented earlier on the diploid hybrid origin of S. chaseae suggests an hypothesis of long distance dispersal of S. chaseae from Mexico to South America that later diverged to S. dombeyana. Except for the disjunct populations of S. foetida var. panamensis in Venezuela and Bolivia, the only other species of Simsia in South America is the relatively unrelated S. fruticulosa, which is an unlikely progenitor of S. chaseae.

PHYLOGENETIC ANALYSIS.

A phylogenetic analysis of Simsia was undertaken to gain information on cladistic relationships of the taxa and to provide insights for a classification of the genus. Cladistic approaches have been advanced in recent years which have made the elucidation of phylogenetic patterns more explicit (e.g., Hennig, 1966; Wagner, 1980). The main advantage of these methods is that the data, assumptions of character state polarity, and choice of algorithms are more clearly presented and therefore open to inspection and criticism. Three principal steps are involved in cladistic analysis: selection of characters and their division into discrete states, polarization of these character states, and the construction of cladograms.

Materials and Methods. The interpretation of phylogenetic relationships in Simsia has been based primarily on morphological features. Twenty-six characters (Tables 8,9) were used to analyze taxa of Simsia and Viguiera series Grammatoglossae (see Generic Relationships). Twenty-three of these possessed variable states in Simsia, and three others (18, 20, 24) were invariant in Simsia but were used to help resolve relationships in the outgroup. A major problem in dividing these characters into discrete states, however, is the polymorphic nature of most of the characters. For example, anther thecae color (character 21) commonly varies from black to brown to yellow in some taxa (e.g., S. fruticulosa, S. tenuis), or squamellae

Table 8. Characters and their states (with numerical assignments) in the phylogenetic reconstruction of Simsia.

Characters and states

Habit and Roots. 1. Two or more stems arising from the apex of the root (0), only one stem arising from the apex of the root (1). 2. Roots a narrow caudex or taproot (0), swollen and fusiform (1). 3. Plants rooting only at the base (0), occasionally rooting at the nodes at the base of decumbent stems (1). 4. Perennial (0), annual (1). Leaves. 5. Petioles and nodes without stipules or discs (0), petioles winged, no discs (1), leaves perfoliate (2), discs present (3). 6. Base of petioles and nodes strigose or pubescent (0), sericeous with long tufts of hairs (1). 7. Leaves unlobed (0), lobed (1). 8. Leaves firm and stiff (0), herbaceous (1). 9. Leaves without strong spicy or foetid odor (0), with such odor (1). 10. Leaf glands present (0), absent (1). 11. Leaves sericeous below (0), hispid, strigose, or hirsute below (1). Peduncles and Heads. 12. Inflorescence scapose (0), usually branched (1). 13. Heads radiate (0), discoid (1). Phyllaries. 14. Outer series less than 2/3 length of inner (0), more than 2/3 length of inner (1). 15. Phyllary margin entire (0), sinuate (1). 16. Phyllaries yellow to black (0), purple (1). Ray florets. 17. Ligules light lemon-yellow (0), orange-yellow (1), pink to purple (2). 18. Ray achenes narrowly obovate (0), linear (1).

Table 8. Continued.

Characters and states.

Disc florets. 19. Less than 90 (0), more than 90 (1).

20. Style branches deltoid at apex (0), filiform at apex (1). 21.

Anther thecae brown to black (0), yellow (1). 22. Apical purple band on

anther thecae absent (0), present (1). 23. Anther appendage color

stramineous (0), stramineous and black on margins or black throughout

(1). 24. Disc achene fusiform (0), very laterally flattened (1). 25.

Squamellae present (0), absent (1). Compatibility system. 26. Plants

self-compatible (0), self-incompatible (1).

Table 9. Data matrix for phylogenetic reconstruction of Simsia. Order of taxa is that used in taxonomic treatment. Names of taxa of Viguiera begin with V followed by the first three letters of the specific epithets (except VILL= S. villasenori; see pg. acronyms of taxa of Simsia). An asterisk indicates that a character does not exist, or the state is unknown in a particular taxon (for further discussion refer to Materials and Methods and Morphology and Taxonomic Criteria).

Taxa	Characters																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26		
VBOM	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	*	
VGRA	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	*	
VCOR	0	0	0	0	0	0	0	0	0	0	1	0	0	*	0	0	1	1	0	1	0	0	0	0	0	0	*	
VOVA	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	*	
VPUR	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	*	
VPOT	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	*	
VSES	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	*	
VROM	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	*	
VMIM	*	*	*	*	0	0	0	1	*	1	1	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	*
GHIE	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	
SANT	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	
FRUT	0	0	0	0	3	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	

Table 9. Continued.

Taxa	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
MOLI	0	0	0	0	3	0	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0
HOLW	0	0	0	0	3	0	1	1	0	1	1	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0
STEY	0	0	0	0	3	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
GRAY	0	0	0	0	2	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
ANNE	0	0	0	0	2	0	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0
TENU	1	0	0	0	3	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0
VILL	0	0	0	0	3	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
SETO	1	0	0	0	3	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
SANG	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	2	1	0	0	1	0	1	1	1	0
TRIL	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0
CALV	1	1	0	0	3	0	1	1	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	1	1	0
LAGA	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	1	0
EURY	0	0	0	1	3	1	1	1	0	0	1	0	1	0	0	1	*	1	0	0	1	0	0	1	1	1
CHAS	0	0	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1
DOMB	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1
AMPL	0	0	1	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0	1	1	0
FOET	0	0	0	1	0	0	0	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0
JAMA	0	0	0	1	0	0	0	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0

Table 9. Continued.

Taxa	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
MEGA	0	0	0	1	1	0	0	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0
GUAT	0	0	0	1	1	0	0	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0
GRAN	0	0	0	1	1	0	0	1	1	1	1	0	0	1	1	0	1	1	1	0	1	0	0	1	1	0
PANA	0	0	0	1	1	0	0	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	1	0

(character 15) are sometimes absent in some populations of S. villasenori. This problem of polymorphic character states is common in flowering plants, and character state coding in these situations has been handled in different ways. Cantino (1982) converted such qualitative polymorphic characters into meristic ones reflecting the proportion of different character states under consideration. Jansen (1985) coded the most common character state or discarded those that showed much variability. Cantino's method is dependent on the choice or availability of material and may not reflect the character state differences throughout the range of the species. If characters with moderate to high variability in Simsia were discarded, 3, 4, 5, 6, 7, 10, 11, 14, 16, 19, 21, 22, 23, 24, 25, and possibly 15 and 17 would disappear. The approach here has been to code the most common state because it more completely reflects the genetic nature of each taxon.

Many criteria have been advanced to polarize character states (e.g., Crisci & Stuessy, 1980; Stevens, 1980; Watrous & Wheeler, 1981; Madison et al., 1984; Donoghue & Cantino, 1984). In my opinion, the most philosophically sound technique is outgroup comparison, but the outgroup in this case (Viguiera ser. Grammatoglossae, see Generic Relationships) has few invariant characters useful for comparison (Spooner, 1986).

Due to these problems in determining polarity, a network of relationships of both Simsia and the outgroup has been constructed followed by rooting at the Viguiera node. Similar problems with character state polarity in the related genus Helianthus led Schilling and Heiser (1981) to analyze the phylogenetic structure of Helianthus

by an unrooted network.

All data of Simsia and Viguiera data were analyzed by PAUP version 2.2 (Swofford, 1984) for cladogram construction. This program was chosen because it incorporates maximum parsimony and allows multiple character state reversals which apparently are common in Simsia. It also accepts initially unpolarized character states. The program was run using UNORDERED ALL, MULPARS, SWAP=GLOBAL, ROOT=OUTGROUP, which did not order the character states, searched for multiple equally parsimonious trees, and rooted the Simsia ingroup by the outgroup taxa of Viguiera. In addition, the program was run both with and without S. chaseae and S. dombeyana due to the hypotheses of diploid hybrid speciation of the former and the derivation of S. dombeyana by long distance dispersal and subsequent differentiation of S. chaseae.

Results and Discussion. The PAUP analysis supports a monophyletic nature of Simsia and its outgroup relatives in Viguiera. One-hundred "equally parsimonious" 67-character-change trees, 50 changes within Simsia and 17 within Viguiera were generated. Thirty of these 50 changes represent parallelisms, and 8 were reversals, yielding 72% homoplasy. Unresolved trichotomies also occur. Due to these trichotomies, however, some of these trees were redundant (Swofford, 1984; Platnik, 1987), but a randomly chosen and intuitively appealing example is presented in Fig. 10. A strict consensus cladogram of all equally-parsiminious trees was generated to search for the shared information (Fig. 11), and this analysis increases the polychotomous nature of the cladogram.

FIG. 10. Cladogram of taxa of Simsia and related species of Viguiera formed by rooting a randomly chosen example of the 100 "equally parsimonious" 67-step networks. Simsia chaseae and S. dombeyana were added after the analysis. For description of characters see Table 8. Double bars and asterisks indicate parallelisms and reversals, respectively.

Figure 10.

FIG. 11. Strict consensus cladogram of Simsia and related species of Viguiera combining 100 equally parsimonious 67-step trees.

Figure 11.

These results suggest that Simsia can be naturally partitioned into two sections: a primitive section Fruticulosae characterized by a perennial habit, nodal discs, gradate phyllaries, and dark anthers, and a derived section Simsia characterized by an annual habit and yellow anthers (nodal discs present or absent and phyllaries equal to subequal). Due to the strikingly distinctive appearance of S. calva with its thickened roots, habit highly branched from the base, and monocephalous peduncles (autapomorphies), this species is positioned in a monotypic section Calvae. Simsia section Simsia is composed of two distinct series: Lagascaeformes with long-pilose nodes and gradate, purple phyllaries, and series Simsia with glabrous or strigose nodes and subequal yellow to black phyllaries. Simsia chaseae and S. dombeyana possibly evolved by reticulate evolution from species from both ser. Lagascaeformes and series Simsia, but they are placed within series Simsia due to their greater overall resemblance to other taxa in this series (see Numerical Taxonomy).

The large numbers of reversals and parallelisms (homoplasy) revealed in this phylogenetic analysis may be real and reflect mosaic evolution (sensu Stebbins, 1974) in an evolutionarily active genus. Alternatively, or additionally, this homoplasy may be due to widespread reticulate evolution or introgression which would confound efforts at phylogenetic reconstruction (Wagner, 1983; Funk, 1985). Detailed hybridization and numerical evidence supports this hypothesis for S. chaseae (see Artificial Hybridizations) and more conjectural evidence from intermediate morphological patterns suggests this may also be the case with S. annectens var. annectens, and S. setosa.

MORPHOLOGY AND TAXONOMIC CRITERIA

The following discussion is intended to clarify some of the qualitative morphological characters utilized in taxonomic decisions, indicate limits of variation in these characters, and aid use of keys and morphological descriptions. By necessity, qualifiers such as "often" or "sometimes" are used throughout to refer to the presence of character states within particular taxa.

Duration and Habit. Simsia is comprised of annuals and perennials, and this character helps to define S. section Fruticulosa (woody) from section Simsia (herbaceous). S. amplexicaulis is always annual, but other annuals (e.g., S. foetida, S. lagascaeformis) occasionally are persistent from a woody base, especially in wetter sites (see discussion under S. lagascaeformis). Other species are always perennial. The perennials are suffruticose with two or more stems arising from the apex of a woody caudex (S. calva, S. sanguinea, S. setosa, S. tenuis), or shrubby and form persistent aerial woody stems (e.g., S. annectens, S. fruticulosa). All species usually have erect or ascending branches. Simsia amplexicaulis, S. lagascaeformis, and S. sanguinea, however, are occasionally decumbent below. Plant heights vary from a maximum of about 1.5 m tall (e.g., S. calva, S. tenuis) to ca. four meters tall, including both annuals (e.g., S. foetida var. grandiflora) and perennials (e.g., S. fruticulosa, S. steyermarkii).

Roots. Simsia calva is the only species of Simsia with a fusiform-thickened woody root, and this is one of its unique features that places it in series Calvae. All other species have narrower taproots or a woody caudex. The suffruticose perennials often have more than one stem arising from the apex of the woody caudex. Simsia amplexicaulis and S. lagascaeformis often root at the lower nodes when their stems are decumbent.

Leaves. There are many taxonomically significant characters in the petioles and blades. All species have three main veins arising from the base, and this is considered the junction of the petiole and blade. Some species (e.g., S. chaseae, S. dombeyana), have entirely naked petioles and nodes. Others (e.g., S. amplexicaulis, S. foetida var. megacephala) commonly have petioles partly to entirely winged to the base, often with amplexicaulate bases, but also have individuals or some nodes with naked petioles. Others (e.g., S. setosa, S. villasenori) commonly have nodal discs that are variously developed, from minute up to 3 cm or more high and wide, attached to both petiole and node or reduced to internodal structures. Simsia annectens commonly has perfoliate leaves, but some individuals also are known with petioles only partly winged and with nodal discs. Simsia section Fruticulosa is characterized by discs or perfoliate leaves. The extensive variability of all of these conditions occasionally can make identifications difficult, and in some instances it may be necessary to examine more complete specimens or more than one plant from a population to use effectively the keys.

The Compositae generally are regarded as lacking stipules (Hutchinson, 1973; Cronquist, 1981). The term stipule commonly refers to an appendage, or pair of appendages, or sometimes a sheath, attached to the petiole or free and attached to the nodes (Fahn, 1972; Howard, 1979). These types of structures occur within Simsia, elsewhere in the Helianthinae, (e.g. Axiniphyllum, Turner 1978; Tithonia, LaDuke 1982); in other subtribes of the Heliantheae (e.g., Milleria, Stuessy, 1975; Sigesbeckia, D'Arcy, 1975), and in the tribe Liabeae (Nordenstam, 1977; Robinson, 1983, where they are referred to as "pseudo-stipulate petioles" and "stipule-like wings or nodal discs", respectively). These structures in Simsia and in these other taxa may or may not be homologous with stipules of other dicotyledons. They are referred to as stipules or nodal discs here for simplicity of description.

The blade outline of most species is ovate to deltate, with acute to acuminate apices and cordate to truncate to attenuate bases. Simsia santarosensis, however, has elliptic to ovate leaves, and S. sanguinea has some populations with linear leaves. Some species have leaves that never are lobed (e.g., S. santarosensis, S. villasenori), other species have leaves usually unlobed but rarely lobed (e.g., S. foetida, S. lagascaeformis), and others have leaves usually lobed and occasionally unlobed (e.g., S. amplexicaulis, S. fruticulosa). Frequently this latter group has lobed and unlobed leaves present on the same individual.

Leaf size can vary greatly within populations and even on single individuals. The more proximally positioned leaves on the main axis

of the plant are often larger than those more distal and on lateral branches. Leaves from plants grown in poor sites or from branches produced later in the growing season also are often smaller.

Leaf texture is taxonomically useful to distinguish Simsia santarosensis and S. villasenori which have markedly firmer leaves than the more herbaceous leaves of other species. Although evident in the field, this character is often difficult to discern on herbarium sheets.

Leaf odor also is taxonomically useful. Simsia chaseae, S. foetida, and S. setosa are characterized by a range of spicy or lemony odors that are lacking in all other species.

Vesture. Vesture is extremely variable in many species, but can be taxonomically useful in some cases. There are six basic hair types in Simsia: unicellular, uniseriate multicellular (Fig. 12, 13), uniseriate with a complex multicellular base (Fig. 12), biseriate (Zwillingshaare, Hess, 1938), uniseriate glandular (Fig. 14), and biseriate glandular (Fig. 15). These hairs are distributed in a scabrous, hirsute, hispid, strigose, pubescent, puberulent, pilose, or sericeous fashion, depending on their length, texture, and posture (terminology following Harrington & Durrell, 1957). The unicellular hairs taper to the apex except for one puberulent type that is blunt (Fig. 15). This type of trichome is universally present in all taxa on leaves, stems, and peduncles. The biseriate hairs are confined to the surfaces of the achenes. They all have straight tips and are invariant in the genus.

FIGS. 12-17. Pubescence types and style branches in *Simsia* and *Viguiera*. 12. *S. dombeyana* (Spooner 2907), adaxial leaf lamina with glandular-puberulent scabrous pubescence, with a larger uniseriate multicellular hair with a multicellular base. 13. *S. chaseae* (Spooner 2804), pedicel just below a head showing glandular-puberulent and strigose pubescence. 14. *Simsia dombeyana* (Spooner 2907), sessile uniseriate gland. 15. *Simsia foetida* var. *foetida* (Spooner & Brandenburg 2300), stipitate biseriate glands and smaller curved blunt-tipped uniseriate hairs. 16. *V. cordifolia* (Spooner & Brandenburg 2314), short style branches with deltoid tips. 17. *S. dombeyana* (Spooner 2907), apex of filiform style branch.

Figs. 12-17.

Glandular pubescence is common in the genus. The uniseriate glands are sessile and most commonly found on the lamina of the leaves of members of *S. series Fruticulosa*, but biseriate glands sometimes are found on the lamina of taxa in this section as well. The biseriate glands are sessile to stipitate, and most commonly found on the lamina of the leaves of *S. series Simsia* (usually not found on the leaves of *S. amplexicaulis*), often on veins of members of *S. series Fruticulosa*, and on the peduncles of all species (except *S. eurylepis*). Stipitate biseriate glands are present in some taxa (e.g., *S. foetida* vars. *foetida*, *guatemalensis*, *megacephala*), and they help to distinguish them from vars. *grandiflora*, *jamaicensis*, and *panamensis*, but there is much intergradation, especially in var. *guatemalensis*. Glandular pubescence of some type generally is present on the leaves of all taxa except *S. calva* and *S. santarosensis*, and generally but not universally lacking on the leaves of *S. amplexicaulis* and *S. lagascaeformis*. Uniseriate and sessile biseriate glands often appear as sessile resin droplets under binocular optics and often are difficult to distinguish from each other and sometimes from the stipitate glands. Due to the mixed distribution and gradation of these types, no designation of gland types are made in the descriptions except in the varieties of *S. foetida* where it is more diagnostic.

Capitulescence. All species have corymbiformly or paniculately branched capitulescences arising from many nodes at the apex of terminal and lateral branches, except *S. calva* and occasionally *S. foetida*, which has many monocephalous peduncles. In some species, the

peduncle length and associated aggregated nature of the capitulescence is taxonomically useful, as in *S. steyermarkii* with its tightly aggregated capitulescence, or *S. fruticulosa* which is tightly to moderately aggregated. Some other taxa, as *S. annectens*, usually, but not always have a tightly aggregated capitulescence. Many other species, however, as *S. eurylepis* and *S. villasenori*, are variable in this feature. The capitulescences usually have moderately divaricately branched peduncles, but some individuals of *S. annectens* commonly have peduncles that are widely divaricately branched. This feature is highly variable within this species, however, and of limited taxonomic utility.

Involucre. The involucre is composed of 11-66 imbricate phyllaries in two-four series. The number of series varies, however, and it often is related to the size of the head with larger heads often having four series. As a result of this variation, this character is not taxonomically useful within the genus. There are two interpretations over the identity of the bracts that subtend the ray florets. Stuessy (1977) regards them as part of the involucre. Funk (1982) regards them as pales in *Montanoa* due to their similar development with other pales during fruiting. These bracts in *Simsia*, however, are flat and herbaceous and develop similar to the other involucreal bracts and are here regarded as part of the involucre. The reflexion of the phyllaries varies in different taxa from appressed (e.g., *S. eurylepis*) to reflexed (e.g., *S. annectens* var. *annectens*), but there is much intrataxon variation elsewhere. For example, *S. calva* has some individuals with the phyllaries greatly reflexed

(Spooner & Schilling 2385) and others with the phyllaries more appressed (Spooner & Schilling, 2391).

Four aspects of the involucre which have much taxonomic utility are phyllary gradation (relative lengths of the different series), margin, type of apex, and color. Simsia section Fruticulosa and series Lagascaeformis are characterized by middle and outer series of phyllaries progressively shorter than the inner series (gradate). Simsia series Simsia have the middle and outer series subequal in length. Simsia amplexicaulis and S. sanguinea have phyllaries of intermediate gradation, but the former tends toward subequal phyllaries and the latter toward more gradate ones. The phyllaries of most species are almost always entire but S. foetida, (and rarely S. calva and S. annectens var. annectens) have sinuate margins. Phyllary color ranges from yellow to green and black to purple, with mottling (as green speckled with black) or gradations of color present on the same phyllary. Purple is apparently a derived color, only found in certain species, and it has been utilized in the cladistic analysis. The apex of the phyllaries of most taxa is acute to acuminate, but S. foetida, S. amplexicaulis, and S. annectens var. annectens commonly have caudate apices.

Pales. All species possess conduplicate, persistent to tardily deciduous pales of medium texture, which are wide at the base and taper to an acute or acuminate apex (e.g., S. villasenorii). Simsia lagascaeformis, however, has some populations which are subtruncate at the apex, and S. foetida tends to have linear-acuminate apices. The vestiture is generally antrorsely pubescent, but S. foetida tends to be

more strigose. Color varies from totally stramineous to variously flecked with black or purple, especially apically, and some taxa have pales which are totally purple. The pales often are narrower to the inside of the head and sometimes are reduced to linear bracts. All of the above features are so variable, however, as to possess limited taxonomic value. One pale character found to have more stability is the slightly longer pales of *S. foetida* var. *megacephala*, (often slightly exerted beyond the disc florets) which helps distinguish this variety from others of *S. foetida*.

Heads. *Simsia eurylepis* is discoid, whereas all other species are radiate. Reports of the occasional presence of discoid heads elsewhere [e.g., *S. chaseae*, Millspaugh, 1904; *S. dombeyana*, (Blake, 1913 as *S. hirsuta*), Burkhardt, 1974, Cabrera, 1978; *S. lagascaeformis*, (Blake, 1913 as *S. exaristata*)] are likely errors due to the occasional short ligules included or little exerted beyond the inner phyllaries, or to their readily deciduous nature. Although some populations possibly could produce ray ovaries but no ligules (as in *Acnella iodiscaeae*, Jansen, 1985), no discoid populations were observed in the field of any species other than *S. eurylepis*.

Head size and associated head part number are taxonomically useful in the varieties of *S. foetida* with vars. *grandiflora* and *panamensis* being distinguished from other varieties of the species by large numbers of disc florets (66-172 and 41-151 respectively). Also, *S. tenuis* is partly distinguished from related species by its small heads and 12-14 disc florets. All head diameters in the descriptions include the extended rays.

Head shape during flowering and early fruiting varies from campanulate to ovoid-campanulate to urceolate. The more campanulate shape often is found on the larger heads and is not considered to be fundamentally different. For example, the large campanulate heads of *S. foetida* var. *grandiflora* and var. *panamensis* grade into the more ovoid-campanulate heads of var. *foetida*. The three self-compatible species (*S. chaseae*, *S. dombeyana*, and *S. eurylepis*), however, tend to have urceolate heads. The difference between ovoid-campanulate and urceolate is often difficult to distinguish, however, especially on flattened herbarium specimens.

Ray corollas. Ligule color is taxonomically useful, and ranges from pale yellow or light lemon yellow (e.g., *S. foetida* var. *foetida*, *S. villasenori*) to light orange-yellow (e.g., *S. fruticulos*, *S. molinae*), to darker orange-yellow (e.g., *S. amplexicaulis*, *S. lagascaeformis*), to pink to deep purple or rarely white (*S. sanguinea* var. *sanguinea*). While there are intermediate colors between the two yellow categories, the pale or lemon-yellow taxa are relatively uniform (except in *S. grandiflora* and *S. panamensis* with some populations pale lemon yellow, and others orange-yellow). The intermediate yellow colors appear closer to orange-yellow and are so coded in the cladistic analysis. One caution, however, is that while ligule colors are clearly differentiated in the field, they are sometimes harder to evaluate on herbarium sheets.

Disc Corollas and Anthers. Taxonomically useful characters are found in the length of the tube of the disc corolla, the color of the anther thecae, the color of the terminal anther appendage, and the

length and shape of the style branches. The relatively longer tubes of *S. foetida* var. *jamaicensis* help to distinguish this variety from the others within *S. foetida*, but this length difference has limited utility elsewhere. Anther thecae vary in color from yellow to brown to black. *Simsia ghiesbreghtii* always has black thecae. Many other species are polymorphic for this character, however, with anthers that are predominately black or brown but occasionally yellow (e.g., *S. fruticulosa*, *S. setosa*). *Simsia chaseae* has thecae that are predominately yellow but occasionally brown or black. *Simsia amplexicaulis*, *S. lagascaeformis*, and rarely *S. sanguinea* have thecae which are yellow below but purple (often drying bronze) on the upper 1/3-1/2. *Simsia sanguinea* usually has black or black-rimmed terminal anther appendages with the black color sometimes extending to the apex of the thecae. All other species have terminal anther appendages stramineous (or green turning stramineous). The long (2-4 mm) and thin style branches with an attenuate apex provide useful generic characters that help to distinguish *Simsia* (Fig. 16) from much of *Viguiera* (Fig. 17) but ally it to some members of *V. ser.* *Grammatoglossae* (see Generic Relationships).

Achenes. The achenes of all species are very similar and provide major characters that define the genus. All species have unwinged achenes which are extremely laterally flattened. Some populations of *S. ghiesbreghtii* have unwinged but laterally thickened biconvex achenes reminiscent of some species of *Viguiera*, (e.g., *V. ovata*). Achenes of *Simsia* achenes are very similar in outline, varying from broadly ovate to suborbicular but much intrataxon variation of these

shapes precludes their use taxonomically. The apex of the achene varies from subtruncate and slightly concave to notched apically with well-developed apical shoulders, but this trait also varies within taxa and is not taxonomically useful.

Achene size varies from the relatively small achenes of *S. ghiesbreghtii* (2.6-3.5 mm long, 1.2-1.9 mm diam) to the relatively large achenes of *S. foetida* var. *jamaicensis*, var. *megacephala* and *S. dombeyana* (combined absolute values: 4.2-7.5 mm long, 2.5-4.1 mm diam). Much similarity and overlap of these sizes precludes taxonomic utility except in the cases of *S. foetida* var. *panamensis*, *S. ghiesbreghtii*, and *S. steyermarkii* where their relatively small achenes help to distinguish them from related taxa.

Pappus. Most achenes are awned and pubescent, with two ascending awns often flared basally, attached on either side of the achene. These awns are easily detached and often tardily deciduous. Many species, however, are known to have some individuals with calvous and glabrous achenes, and all known specimens of *S. tenuis* are of this type. These two achene types (awned and pubescent, calvous and glabrous) are perhaps genetically linked, but in some cases calvous and pubescent and awned and glabrous achenes are encountered. Asa Gray and S. F. Blake placed much taxonomic weight on these achenial characters. Gray (1846) originally described the genus *Barrattia* partly based on its calvous achenes, but later (Gray, 1850) realized the tenuous nature of this trait and combined *Barrattia* and *Simsia*. Awned vs. glabrous achenes also have been used to distinguish species (*S. calva* vs. *S. subaristata*, Gray, 1849; *S. ghiesbreghtii* vs. *S.*

sericea, Gray, 1883, Blake, 1913, Robinson and Brettell, 1972; S. exaristata vs. S. lagascaeformis, Gray, 1853, Blake, 1913), and varieties (within S. amplexicaulis, Blake, 1913, 1917; S. calva, Blake, 1913; S. exaristata, Blake, 1917). Unnamed variability of this character previously has been known to occur in S. setosa and S. sanguinea, (Blake, 1917). Recent investigations document intrapopulational variability of this character in the following populations: S. amplexicaulis, Spooner & Villasenor 2557; S. annectens var. annectens, Spooner 2845; S. calva, Spooner & Schilling 2385; S. chaseae, Spooner 2803; S. dombeyana, Jorgensen 1286; S. eurylepis, Spooner & Brandenburg 2209; S. lagascaeformis, Spooner & Burgos 2602; S. sanguinea, Spooner & Burgos 2604, Spooner & Villasenor 2505, 2567; S. setosa, Spooner & Villasenor 2528; and S. steyermarkii, Spooner & Dorado 2748. The S. dombeyana specimen mentioned above has awns minute to fully formed on different achenes of the same head. In addition, I obtained both awned and non-awned progeny from awned achenes of one individual of S. eurylepis, Spooner & Brandenburg 2209. These facts clearly indicate that vestiture and presence/absence of awns on the disc achenes are not taxonomically useful at any level within the genus.

Squamellae (scales, usually short and lacerate, attached to the apex of the achene between the awns) are rarely found on the achenes of only some species of Simsia. Formerly, their absence within the genus had been used in part to distinguish it from Viguiera which generally, but not universally, possesses them. Simsia ghiesbrihtii regularly has 4-12 squamellae on the apex of the achene and S.

villasenori often has four. All other species commonly lack them, but four squamellae have been located in the following taxa: S. dombeyana, Haught 249; S. foetida var. foetida, Hinton 5538; S. sanguinea var. sanguinea, Spooner & Villasenor 2570. They are not present on all achenes of these collections, however. They appear similar to squamellae of many species of Viguiera and probably are homologous structures.

CONCEPTS OF SPECIES AND VARIETIES

There is little agreement over the definition of a species in flowering plants (Sokal & Crovello, 1970; Cronquist, 1978; Loevtrup, 1987), and the nature of species in different plant groups clearly varies (Raven, 1976, 1986). Simsia presents many problems in the definition of species due to intermediates and extensive variability of characters.

The species concept adopted here is based primarily on morphology, with additional insights provided by crossing data. Species are here considered "the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist, 1978), although occasional intermediates sometimes provide ambiguous taxonomic situations.

Subspecies and varieties frequently are used interchangeably when only one infraspecific category is used (Kapadia, 1964). I regard varieties as distinct but often intergrading sets of populations with a geographic component. These are used rather than subspecies in Simsia due to historical precedence. The numerous variations in many features in Simsia could formally be recognized as formae, but I agree with Burt (1970) and Jansen (1985) that such formal recognition only serves to impose unnecessary complexity on a taxonomic system. These variations are best discussed but left unnamed.

TAXONOMY

Two notations in this section require an explanation. In the citation of representative specimens, the collections (including types) that serve as cytological vouchers are indicated by an asterisk, and those that were analyzed in the numerical study are indicated by a double asterisk. Brackets are used in the synonymy to identify information concerning the location, date, and collector of types that was obtained from sources other than the protologue or labels accompanying specimens. The source of this information is listed in the synonymy or in the species discussion.

Simsia Persoon, Syn. pl. 2: 478. 1807, non Simsia R. Brown, Trans.

Linn. Soc. London 10: 152. 1810.—LECTOTYPE (S. F. Blake, 1913): Simsia amplexicaulis (Cavanilles) Persoon.

Armania Bertero ex DeCandolle, Prodr. 5: 576. 1836.—TYPE: Armania fruticulosa (Sprengel) Bertero ex DC. = Simsia fruticulosa (Sprengel) S. F. Blake.

Barrattia A. Gray & Engelmann ex A. Gray, Proc. Amer. Acad. Arts 1: 48. Dec 1846 or Jan 1847 (fide Stafleu and Cowan, 1976).—TYPE: Barrattia calva A. Gray & Engelmann ex A. Gray = Simsia calva (A. Gray & Engelm. ex A. Gray) A. Gray.

Encelia sect. Simsia (Persoon) A. Gray, Proc. Amer. Acad. Arts 19: 8. 1883.

Erect or ascending taprooted annual or perennial herbs or shrubs (decumbent and rooting at the nodes in some populations of *S. amplexicaulis* and *S. lagascaeformis*, with roots fusiform-thickened in *S. calva*). Stems 0.1-4 m tall, sparingly to freely branched from the nodes, terete to slightly ridged, yellow to green to purple, 0.1-30 cm diameter at base, glabrous to puberulent to scabrous or hispid, glandular or eglandular. Leaves opposite below (rarely whorled), decussate, alternate above, those on successive orders of branching or on the upper parts of the stem often reduced in size and becoming bract-like in the capitulescence; petioles naked to winged throughout (perfoliate on some nodes of *S. annectens*), often with stipules of adjacent leaves forming nodal "discs" which are fused to the stem and bases of adjacent petioles or reduced to interpetiolar structures, minute-5.5 cm high and wide, sometimes deciduous; petioles absent-14 cm long, 0.5-2 mm diameter, vestiture usually as on the blades (often long-pilose at base on *S. eurylepis* and *S. lagascaeformis*); blades 3-nerved from the base, cordate to linear, unlobed to deeply 3-5 lobed (pinnatifid in some populations of *S. sanguinea*), thin and herbaceous to thick and stiff, 1-21 cm long, 1-18 cm wide, at base attenuate, margins crenulate to coarsely dentate or rarely entire, glabrous to scabrous to sericeous, glandular or eglandular. Capitulescence of solitary heads or a tightly to loosely-branched corymb or panicle, the peduncles sometimes widely divaricately-branched; peduncles subsessile-30 cm long, 0.5-2 mm diameter, usually glandular-puberulent, often scabrous to strigose or hispid. Heads

heterogamous, radiate (eradiate in *S. eurylepis*), 9-40 mm across extended rays, 9-19 mm tall; involucre campanulate to ovoid-campanulate to urceolate, 6-18 mm tall, 5-22 mm diameter, base truncate or indented at the attachment to the peduncle. Receptacle low-convex. Phyllaries 2-4-seriate, imbricate, unequal with the middle and outer series progressively shorter than the inner or all series subequal, 11-66, tightly appressed to broadly reflexed, acute to acuminate to caudate at the tips, green to yellow, purple, or blackish, scabrous to hispid to sericeous, glandular or eglandular, ciliate at the margins, the outer series ovate to linear, entire or with a single sinuate constriction at the margin in *S. foetida*, rarely in *S. calva* or *S. annectens* var. *annectens*, 2-20 mm long, 0.7-3.5 mm wide; inner series lance-ovate to linear, entire to sinuate, 6-20 mm long, 1-3.8 mm wide. Ray florets in a single series, neutral, 5-45, ligules light lemon-yellow to orange-yellow (various hues of purple to pink or rarely white in *S. sanguinea*), entire to 2-3 lobed at apex, 2.5-19.5 mm long, 1.3-7.5 mm wide; tubes 0.5-3.5 mm long, 0.2-1 mm diameter, glandular-puberulent; ovaries linear, slightly tapering from the base to the apex, trigonous, 3-10.5 mm long, 0.3-1.1 mm wide at apex, with or without awns. Disc florets 12-172; perfect; corollas 4.2-9 mm long, 0.7-2.2 mm diameter at apex, concolorous with the rays (orange-yellow in eradiate *S. eurylepis*, white in *S. sanguinea* var. *sanguinea*), usually turning purple apically; tubular below, the tubes glandular-puberulent, 0.5-2.5 mm long, 0.3-0.8 mm diameter; abruptly expanded above to a subcylindric throat which is ventricose and sparingly glandular-puberulent at the base, slightly flared and

glabrous apically; terminating in 5 triangular lobes, 0.5-1.5 mm long, 0.4-1.2 mm wide, sparingly to densely pubescent, sometimes glandular on the outer surface, papillose on the inner surface; stamens 5, anthers yellow to brown to black but sometimes darkened only apically (usually yellow below and bronze or purple above in S. amplexicaulis and S. lagascaeformis, rarely so in S. sanguinea), 1.8-4.5 mm long, glabrous or more commonly antrorsely pubescent along the connectives, terminal appendages stramineous (black or black-rimmed in S. sanguinea); achenes light brown to black or mottled, laterally flattened (thickened and biconvex in some populations of S. ghiesbreghtii), transversely obovate to elliptic in outline with minute to conspicuous apical shoulders extending beyond the attachment of the corolla, 2.6-7.5 mm long, 1.2-4.1 mm diameter, glabrous or hirsute with double hairs; pappus absent or of two ascending awns often flared basally, 1-7.4 mm long, rarely with 4-12 shorter intermediate squamellae. Pales radially conduplicate and enclosing the achenes, of medium texture, stramineous to purple or black, often mottled in color only at the apex, sometimes colored throughout, 5-14 mm long, 1.2-3.8 mm wide, glabrous or pubescent along the margins and midrib, especially apically. Chromosome number $n = 17$.

KEY TO THE SPECIES AND VARIETIES OF SIMSIA

The morphological similarity and intergradation among taxa of Simsia sometimes makes specific delimitations complex and attempts at identifications difficult. Frequently, taxa can be recognized only by a combination of characters, including some overlapping ones (e.g., S. chaseae vs. S. dombeyana, or the varieties of S. foetida). Some characters are useful only in parts of the genus (e.g., peduncle length in S. fruticulosa and S. steyermarkii; achene size in S. steyermarkii and S. foetida var. panamensis), with limited taxonomic value elsewhere. Also, some features may not be evident on herbarium specimens (e.g., plant height, habit, ligule color), but they are obtainable from field and greenhouse observations. Despite these problems, it is believed that the following key most of the time does allow taxa of the genus to be identified successfully.

1. Plants profusely branched at base, generally with two or more stems arising from the apex of a fusiform-thickened root; heads borne on monocephalous peduncles arising from many nodes; rays yellow, often brown or purple-lined below..12. S. calva.
1. Plants branched or unbranched at base, one or more stems arising from an herbaceous and fibrous root or a woody taproot or narrow woody caudex, but not fusiform-thickened; heads borne in a branched capitulescence, or if peduncles monocephalous, rays yellow above and below.

2. Plants commonly with two or more stems arising from a narrow woody caudex; petioles usually winged, sometimes unwinged, but lacking nodal discs; rays pink to deep purple, rarely white or lemon-yellow.
3. Rays pink to deep purple..11a. *S. sanguinea* var. *sanguinea*.
3. Rays light lemon-yellow..11b. *S. sanguinea* var. *triloba*.
2. Plants with one or more stems arising from a taproot or from fibrous roots, or with two or more stems arising from a narrow woody caudex, if from a caudex, petioles with nodal discs; rays light lemon-yellow to orange-yellow.
4. Phyllaries subequal in length, the outermost usually $3/4$ or more the length of the inner.
5. Plants perennial, leaves commonly with winged petioles and perfoliate, but some petioles winged only partly to base and with nodal discs..7a. *S. annectens* var. *annectens*.
5. Plants annual, but sometimes persistent and woody at base; leaves not perfoliate, but some petioles winged or with nodal discs.
6. Leaves usually eglandular; rays orange-yellow; anther thecae usually yellow below, commonly purple or bronze or more rarely yellow above..17. *S. amplexicaulis*.
6. Leaves glandular; rays light lemon-yellow; anther thecae yellow or black, never purple above.
7. Phyllaries acute to acuminate at the tips, margins entire; heads urceolate.

8. Outer phyllaries 1.6-3.1 mm wide; inner phyllaries 1.2-2.9 mm wide; S. America..16. S. dombeyana.
8. Outer phyllaries 1.1-2 mm wide; inner phyllaries 1.2-2.2 mm wide; Gulf coast of Mexico..15. S. chaseae.
7. Phyllaries often with linear or caudate tips, margins often sinuate; heads ovoid-campanulate.
9. Leaves pilose to subsericeous on both sides with intermixed glandular-puberulent hairs; achenes 3.1-5.1 mm long; Panama and S America..18f. S. foetida var. panamensis.
9. Leaves glandular-puberulent and hispid on both sides; achenes 4-7.4 mm long; Mexico to Costa Rica or Jamaica.
10. Petioles narrow throughout, not winged, nodal discs absent.
11. Leaves with stalked glands; tubes of disc florets 0.6-1.8 mm long; Mexico..18a. S. foetida var. foetida.
11. Leaves with sessile glands; tubes of disc florets 1.7-1.9 mm long; Jamaica..18b. S. foetida var. jamaicensis.
10. Petioles winged at least at some nodes, sometimes only at the base, or with nodal discs present, but these sometimes minute.

12. Leaves densely glandular with stalked glands; upper leaves frequently winged throughout with wings often 1 cm wide or more, or lower nodes with nodal discs to 3 cm high and wide; pales frequently equalling to slightly longer than the disc florets, 9.2-14 mm high; E Oaxaca..18c. S. foetida var. megacephala.

12. Leaves densely to moderately glandular with stalked or sessile glands; upper leaves naked or winged, if winged with wings generally less than 0.5 cm wide, with the nodal discs of lower nodes, if present, generally less than 1 cm high and wide; pales usually shorter than disc florets, 7-11.7 mm long; Chiapas to Costa Rica.

13. Heads 9-13 mm diameter; phyllaries 17-26; ligules light lemon-yellow; disc florets 31-70; Chiapas to El Salvador..18d. S. foetida var. guatemalensis.

13. Heads 10-22 mm diameter; phyllaries 21-66; ligules light lemon-yellow or more commonly orange-yellow; disc florets 66-172; Guatemala to Costa Rica..18e. S. foetida var. grandiflora.

4. Phyllaries unequal in length, the middle and outer progressively shorter, the outer 2/3 or less the length of the inner.
14. Heads eradiate..14. S. eurylepis.
14. Heads radiate.
15. Anthers yellow, usually purple or bronze at the apex; nodes often long-pilose, phyllaries usually purple..13. S. lagascaeformis.
15. Anthers yellow to brown to black without a purple or bronze apex; nodes glabrous to scabrous or puberulent or pubescent but not long-pilose, phyllaries purple to green or green-black.
16. Nodal discs absent; heads urceolate; Gulf coastal lowlands of Mexico..15. S. chaseae.
16. Nodal discs present or heads campanulate to ovoid-campanulate.
17. Plants 0.3-1.5 m tall; leaves sessile or with petioles 1 cm long, without nodal discs, with blades stiff and unlobed; Costa Rica..2. S. santarosensis.
17. Plants 0.3-4 m tall; leaves distinctly petiolate with petioles 0.5-11 cm long, nodal discs present (although absent on some nodes), with blades stiff to herbaceous, lobed or unlobed.
18. Leaves stiff and thick, unlobed; Oaxaca and Chiapas..9. S. villasenori.

18. Leaves herbaceous, lobed to unlobed.

19. Leaves perfoliate or petioles completely to mostly tapering to nodal discs..7b. S. annectens var. grayi.

19. Leaves with petioles naked or winged only partly to base, not perfoliate.

20. Leaves sericeous below.

21. Achenes laterally flattened to biconvex, 2.6-3.5 mm long, 1.2-1.9 mm diam, often with awns and squamellae, sometimes epappose; Chiapas and Guatemala..1. S. ghiesbreghtii.

21. Achenes laterally flattened, 4-6.4 mm long, 1.7-3.6 mm diam, awned but never with squamellae; S America..3. S. fruticulosa.

20. Leaves puberulent, pilose or hirsute below.

22. Disc florets 12-14; annuals or suffrutescent perennials; 0.5-1.5 m tall..8. S. tenuis.

22. Disc florets 15-34; suffrutescent perennials or shrubs; 1.5-4 m tall.

23. Phyllaries usually purple,
sometimes green; ray corollas 5-7
mm long; anthers yellow..5. S. holwayi.
23. Phyllaries green to green-black;
ray corollas 5.5-20 mm long;
anthers yellow to brown or black.
24. Heads tightly aggregated at
the ends of short peduncles
(sessile to 2 cm long),
achenes 3.2-4.2 mm long,
1.8-2.5 mm diam; Guatemala..6.
S. steyermarkii
24. Heads in more open
capitulescences with peduncles
to 7 cm long; achenes 4.2-6.5
mm long, 2.5-4 diam.
25. Suffrutescent perennials
to 1.5 m tall; stems
strongly hispid; ray florets
light lemon-yellow; NW
Mexico..10. S. setosa.
25. Shrubs to 4 m tall; stems
puberulent to weakly hispid;
ray florets light
orange-yellow; Central
America..4. S. molinae.

I. Simsia section Fruticulosae D. M. Spooner, sect. nov.—TYPE: Simsia ghiesbreghtii (A. Gray) S. F. Blake

Plantae lignosae; stipulis pleuremque connatis (non S. sanguinea, et S. santarosensis), phyllariis inaequalibus (non S. annectens var. annectens), antheris pleuremque brunneis vel nigris (non S. calva, S. holwayi, et S. sanguinea).

Plants woody, usually with nodal discs (except in S. sanguinea, S. santarosensis); phyllaries gradate (except in S. annectens var. annectens); anthers usually brown to black (except in S. calva, S. holwayi, S. sanguinea).

IA. Simsia series Fruticulosae D. M. Spooner, ser. nov.

Plantae caudicibus angustis, pedunculis ramosis, floribus discorum minus 85.

Plants with narrow roots; heads in branched capitulescences, disc flowers less than 85 per head.

1. Simsia ghiesbreghtii (A. Gray) S. F. Blake, Proc. Amer. Acad. Arts 49: 392. 1913. Encelia ghiesbreghtii A. Gray, Proc. Amer. Acad. Arts 8: 658. 1873.—TYPE: MEXICO. Chiapas: mountain forest near Chiapas, 1864–1870, Ghiesbreght 658 (holotype: GH!).

Verbesina argentea Bertoloni, Novi Comment. Acad. Sci. Inst.

Bononiensis 4: 435. 1840, non Verbesina argentea Gaudichaud,

Voy. Uranie 11: 463. 1829.-TYPE: GUATEMALA. Sacatepéquez:

"Vulcano d'acqua" [= Volcán de Agua], 1837, Vallasquez [=

Valasquez, fide Blake, 1926] s. n. (holotype: BOLO, not seen,

photo: OSI).

Simsia sericea (Hemsley) S. F. Blake, Proc. Amer. Acad. Arts 49:

393: 1913. Encelia sericea Hemsley, Biol. cent.-amer., Bot. 2:

185. 1881.-TYPE: GUATEMALA. Montagua Valley, 1861, Salvin &

Godman 133 (holotype: K1; photo & fragment: US1; photo: OSI).

Suffrutescent perennials to shrubs. Stems erect, 1-2 m tall, green to purple to brown; 0.3-2 cm diameter, puberulent to pilose. Leaves with petioles 1-3 cm long, 1-2 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0-1.5 cm long and wide; blades ovate to deltate, herbaceous, unlobed, 4-15 cm long, 1.5-8 cm wide, at base cordate to truncate to cuneate, at apex acute to acuminate, with margins subentire to crenate or dentate, both sides eglandular, upper surface puberulent or hispid to pubescent, lower surface sericeous. Capitulescence corymbiform, loosely-branched; peduncles 1-6 cm long, 1 mm diameter, puberulent, sometimes intermixed short-pubescent and glandular. Heads radiate, 10-15 mm tall, 20-40 mm diameter; involucre campanulate, 8-13 mm tall, 7-11 mm diameter. Phyllaries 2-3 seriate, generally unequal, sometimes subequal, 15-20,

usually appressed except slightly reflexed apically or less commonly greatly reflexed, dark green to green-black, puberulent to pilose, rarely glandular; outer phyllaries lance-ovate, 3.6-7.7 mm long, 1-2 mm wide; inner phyllaries lanceolate, 6.7-12 mm long, 1.5-2.5 mm wide. Ray florets 7-11, ligules light orange-yellow, 8-15 mm long, 3-6.6 mm wide; tubes 1-1.7 mm long, 0.3-0.6 mm diameter; ovaries 3-4.5 mm long, 0.4-1 mm diameter. Disc florets 31-50; corollas 4.9-6.7 mm long, 0.9-1.5 mm diameter; tubes 0.7-1.6 mm long, 0.3-0.8 mm diameter; lobes 0.7-1.4 mm long, 0.5-0.8 mm wide; anthers black, 3-4.2 mm long, with terminal appendages stramineous; achenes flattened to plump and biconvex, 2.6-3.5 mm long, 1.2-1.9 mm diameter, awns absent or 1-2.7 mm tall, squamellae absent or numbering 4-12, 0.4-0.7 mm tall. Pales stramineous, green-black apically, acute to aristate at the tips, 5.5-8.8 mm tall, 1.5-2.3 mm wide, strigose to antrorsely short-pubescent and sometimes glandular apically.

Phenology. Flowering October-April.

Distribution. (Fig. 18). In openings, on steep wet mountain slopes and very occasionally in dry roadside thickets; 1600-2500m; in the northern highlands of Chiapas and along the volcanic belt in Guatemala.

SPECIMENS EXAMINED: [Note: All collections listed with simply "Volcán de Agua" for the locality, including the type of Verbesina argentea, are listed under the department of Sacatepéquez, but this volcano also occurs in the departments of Escuintla and Guatemala]. MEXICO. CHIAPAS: near Navenchauk, Breedlove 9507 (DS, MICH.), 48485

Fig. 18. Distribution in southern Mexico and Central America of Simsia ghiesbreghtii, S. holwayi, S. molinae, S. santarosensis, and S. steyermarkii.

Figure 18.

(CAS, OS), Spooner 2781* (COL, MEXU, OS, TENN, WIS). GUATEMALA. BAJA VERAPAZ: near Pantín on rd to Salamá, Spooner & Linder 2753* (MEXU, OS, TEX), Williams, Molina, & Williams 42168 (BM, DUKE, F), Williams, Molina, Williams & Molina 43367 (F, MICH). EL PROGRESO: between Calera and middle slopes of quebradas of Volcán Siglo, Steyermark 43018 (F, GH). EL QUICHÉ: 10 mi NE of Sacapulas, Williams, Molina & Williams 41210 (F, NY). GUATEMALA: San Rafael, collector unknown 63 (GH). QUEZALTENANGO: E slope of Volcán Santa María de Jesús, just S of Quezaltenango, Spooner & Dorado 2675* (MEXU, OS, OSH, RSA, US, WIS), Stuessy & Gardner 4345 (ASU, ENCB, OS). SAN MARCOS: between San Marcos & Castalia, Spooner & Dorado 2674* (MEXU, OS, P, RSA, US, WIS), Williams, Molina, & Williams 26142 (F, GH, NY, US). SACATEPÉQUEZ: Antigua, Kellerman 4982 (OS, US); Volcán de Agua, Feb 1905, Kellerman (US), Maxon & Hay 3751 (US), Molina 21030 (F, NY), Molina & Molina 24895 (BM, F, S), 24913 (C, DUKE, P, NY, US), Standley 59379 CAS, F, MICH, U), 65054 (F); Finca El Hato, NE of Antigua, Standley 61158 (F, US), 61199 (F, U); 10 km from San Mateo del Milpar, Molina 15512 (F, GH, US). SOLOLA: 8 mi E of Panajachel, Spooner & Dorado 2683* (LE, MEXU, OS). 5 km E of Panajachel above Lake Atitlán, Williams, Molina, & Williams 25231 (F).

The exact localities of the types of Simsia ghiesbreghtii and Simsia sericea are unknown. Hemsley (1887), in his brief account of the travels of the collectors of these types, fails to resolve these issues. The Monagas valley, the type locality of Simsia sericea, traverses the departments of Baja Verapaz, El Progreso, Zacapa, and

Izabal. Hemsley (1887) comments that most of the collections of Salvin and Godman came from Volcán de Fuego, a possible locality for this species, but this volcano is in the departments of Escuintla, Sacatepéquez, and Sololá. Likely localities for the type of *S. sericea* are in the departments of El Progreso or Zacapa in the Sierra de las Minas that borders the Monagas valley to the north.

Simsia ghiesbreghtii exhibits great variation in achene morphology, but this is not taxonomically useful. As in many other species of *Simsia*, there is intra- and interspecific variation for presence or absence of indument and pappus, a feature that is insignificant taxonomically throughout the genus (see Taxonomic Criteria). When a pappus is present, it is of two awns or of two awns and 4-12 intermediate squamellae. *Simsia ghiesbreghtii* has been distinguished from *S. sericea* by the calvous, glabrous achenes of the former. An achenal feature of greater taxonomic significance in *S. ghiesbreghtii* is achene shape. Some populations (e.g., Kellerman 4982, Molina & Molina 24913), have typical *Simsia* achenes that are laterally flattened. Others (e.g., Standley 59379, Steyermark 43018, Williams et al. 43367) have laterally-thickened achenes with no shoulder, similar to some *Viguiera* species (e.g., *V. ovata*). Other populations exhibit intermediate morphologies. The presence of typical flattened *Simsia*-like achenes in some populations of *S. ghiesbreghtii*, plus the presence of nodal discs, unknown in *Viguiera* and common in *Simsia*, substantiates the placement of this species in *Simsia* rather than *Viguiera*. This species is here viewed as transitional linking these two genera. In addition to the difference

in shape difference, these are also the smallest achenes in the genus.

Also variable in S. ghiesbreghtii are the relative lengths and pubescence of the phyllaries, from almost subequal and subsericeous (e.g., Breedlove 48485, Kellerman s.n. [Feb 1905]) to unequal and puberulent to pubescent (e.g., Maxon & Hay 3751, Standley 59379). As this trait exhibits no geographic integrity, and as most collections are intermediate, these features are treated here as taxonomically insignificant.

Simsia ghiesbreghtii is superficially similar to S. fruticulosa, due especially to the sericeous leaves of both species. They are readily separated by the achenes, however, with those of S. fruticulosa 4-6.6 mm long and never plump and biconvex. S. fruticulosa is often a much larger plant growing to 4 m tall. They also have allopatric ranges).

2. Simsia santarosensis D. M. Spooner, sp. nov.-TYPE: COSTA RICA.

Guanacaste: along unpaved rd, 0.5 mi N of El Gallo, N of Liberia, scrubby tropical deciduous forest, in whitish sandy volcanic soil, 29 Dec 1985, Spooner 2900* (holotype: OS!; isotypes; CRI! FI! MEXU! MICH! OS (greenhouse grown specimen from seed)! OSH! TENN! UCI! US! WIS!).

Plantae lignosae, 0.3-1.5 m altae, foliis sessilibus vel petiolatis ad 1 cm longis, estipulatis, laminis ellipticis vel ovatis, rigidis, non lobatis, 1-5 cm longis, 1-2 cm latis, basibus cuneatis,

apicibus acutatis vel acuminatis, involuocratis gradatis.

Low growing shrubs. Stems erect, 0.3-1.5 m tall, brown to purple, 0.3-1 cm diameter at the base, weakly strigose and canescent, becoming glabrous with age. Leaves subsessile or with petioles to 1 cm long, 1 mm diameter, often cuneate to the base, estipulate; blades elliptic to ovoid, stiff, unlobed, 1-5 cm long, 1-2 cm wide, at base cuneate, at apex acute to acuminate, with margins subentire-crenate, with both sides scabrous, usually eglandular, but occasionally with scattered glands. Capitulescence corymbiform, loosely branched, peduncles 1-14 cm long, 1 mm diameter, puberulent, sometimes scabrous and glandular. Heads radiate, 13-15 mm tall, 20-25 mm diameter; involucre campanulate, 11-13 mm tall, 5-10 mm diameter. Phyllaries 3-seriate, unequal, 19-29, appressed or slightly reflexed apically, acute to acuminate at the tips, green to green-black, turning brown, canescent, sometimes scabrous; outer phyllaries ovate to lance-ovate, 3-6 mm long, 1.5-2.5 mm wide; inner phyllaries lanceolate, linear, or oblanceolate, 8.5-11.5 mm long, 1.4-2.5 mm wide. Ray florets 8-13, ligules light orange-yellow, 10.5-11.5 mm long, 3.2-3.8 mm wide; tubes 1-1.4 mm long, 0.4-0.6 mm diameter; ovaries 5.6-7.5 mm long, 0.4-0.7 mm diameter. Disc florets 17-25; corollas 6-6.6 mm long, 1-1.5 mm diameter; tubes 0.7-1 mm long, 0.5-0.8 mm diameter; lobes 0.9-1.3 mm long, 0.5-0.8 mm wide; anthers yellow to black, 3.3-4 mm long, with terminal appendages stramineous; achenes 4.2-6.7 mm long, 2-2.7 mm diameter, awns 3.8-4.6 mm long. Pales stramineous, acute to acuminate at tips, 9-10.8 mm tall, 1.6-2.2 mm wide, antrorsely pubescent apically. Fig. 19.

Fig. 19. Simsia santarosensis (Spooner 2900). A, stem with mature inflorescence; B, head; C, pale; D, disc floret with nearly mature achene; E, ray floret.

Figure 19.

Phenology. Flowering December–February.

Distribution. (Fig. 18). Growing in sandy volcanically derived soils; 0–400 m; in the Pacific lowlands in Guanacaste Province, Costa Rica.

SPECIMENS EXAMINED: COSTA RICA. Guanacaste: near Cañas, 11 mi S of Liberia, Daubermire 493 (F); above Playa Naranjo, Santa Rosa National Park, Leisner, Lockwood, & Vega 2661 (MO); 4 km N of Liberia, Opler 574 (F).

This very distinctive species is easily recognized by its small, firm, elliptic to ovate estipulate leaves. Only S. villasenor has leaves as firm but this latter species has nodal discs, larger leaves with longer petioles, and light lemon-ligules.

The species is named after Santa Rosa National Park, one of the many fascinating National Parks in Costa Rica.

3. Simsia fruticulosa (Sprengel) S. F. Blake, J. Bot. 53: 200. 1915.

Hopkirkia fruticulosa Sprengel, Syst. veg. 3: 444. 1826.

Armania fruticulosa (Sprengel) Bertero ex DeCandolle, Prod. 5:

576. 1836. Salmea fruticulosa (Sprengel) Steudel, Nomencl.

bot. 2: 775. 1841. Encelia fruticulosa (Sprengel) Hieronymus,

Bot. Jahrb. Syst. 19: 54. 1894.—TYPE: COLOMBIA. Magdalena:

Santa Marta, [1820–1821 fide Urban, 1902], Bertero s.n.

(holotype: P!, photos: GH! OS!; isotypes: B, destroyed,

fragment, GHI, photos: GHI NYI; G-DC, photo: IDC. 800. 946.

II. 4!).

Simsia pastoensis Triana, Ann. Sci. Nat. Bot. ser. 4, vol. 9: 40.

1858.-TYPE: COLOMBIA. [Nariño, fide Dugand, 1944; Pasto in protologue]: near Ortega, 1200 m, [1500 m on label],

1851-1857, Triana 1362 (lectotype, here chosen: PI, photo: GHI OSI, photo and fragment: USI).

Simsia pubescens Triana, Ann. Sci. Nat. Bot. ser. 4, vol. 9: 40.

1858.-TYPE: COLOMBIA. Cundinamarca: between Tena and El

Colegio, 1400 m, 1851-1857, Triana 1361 (holotype: PI, photo and fragment: USI, photo: GHI OSI, fragment: FI; isotype: BM!

B, destroyed, photos of BM isotype: GHI USI, tracing and

fragment of BM isotype: GHI, photos of B isotype: GHI TEX!).

Encelia sodiroi Hieronymus in Engl. Bot. Jahrb. Syst. 29: 43.

1901. Simsia sodiroi (Hieronymus) S. F. Blake, Proc. Amer.

Acad. Arts 49: 383. 1913.-TYPE: ECUADOR. Pichincha: dry rocky areas of the Rio Guallabamba, 18 Aug 1885, Sodiro 34/2

(holotype: B, destroyed, fragment: USI; isotype: QI).

Simsia grisea S. F. Blake, Contr. Gray Herb. 53: 53. 1918.-TYPE:

VENEZUELA. Sucre: Guanta, 1 Jul 1917, Curran & Haman 1226

(holotype: GHI; isotype: USI).

Encelia deltoidea Rusby, Desc. S. Amer. pl. 154. 1920.-TYPE:

COLOMBIA. Magdalena: Playa Brava, seashore, on dry rocks and occasionally in sand, Nov 1898, Smith 594 (holotype: NY!; isotypes: G! GH! SI).

Simsia caucana Cuatrecasas, Revista Acad. Colomb. Ci. Exact. 9:

244. 1954.-TYPE: COLOMBIA. Cauca: between Popayán and Puracé, bridge over Anambio River, 2500 m, 10 Dec 1939, Pérez & Cuatrecasas 5874 (holotype: US!; isotype, OOL! FI).

Shrubs. Stems erect, 0.5-4 m tall, green, to yellow, brown, or purple, 1-3 cm in diameter, canescent to pubescent, hirsute, or subsericeous, sometimes glandular. Leaves with petioles 0.6-5 cm long, 0.5-2 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0-1.5 cm long and wide; blades ovate to deltate, herbaceous, unlobed to deeply 3-5 lobed, 3-14.5 cm long, 1-13 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenate to dentate, with both sides pilose to densely sericeous, indument usually denser below, eglandular or with intermixed short-stalked glands. Capitulescence corymbiform, moderately clustered, peduncles minute-4.5 cm long, 0.5-2 mm diameter, hirsute and intermixed glandular-puberulent and pubescent. Heads radiate, 10-16 mm tall, 20-45 mm diameter; involucre campanulate, 7-14 mm tall, 7-13 mm diameter. Phyllaries 3-seriate, unequal, 16-35, appressed to slightly reflexed apically, acute to acuminate at the tips, light green to greenish-black, scabrous to sericeous, rarely

glandular; outer phyllaries ovate to lance-ovate, 3.2-6 mm long, 1.4-2.8 mm wide; inner phyllaries lance-linear to lance-obovate, 7.8-14.4 mm long, 1.6-3.8 mm wide. Ray florets 8-19, the ligules light orange-yellow, 5.5-14.5 mm long, 1.3-6 mm wide; tubes 1.1-2.3 mm long, 0.4-0.6 mm diameter, ovaries 4.5-8.5 mm long, 0.4-0.5 mm diameter. Disc florets 13-59; corollas 5.5-9 mm long, 1-1.5 mm diameter; tubes 0.8-2.3 mm long, 0.5-0.8 mm diameter; lobes 0.6-1.5 mm long, 0.5-0.8 mm wide; anthers yellow to black, 2.9-4.5 mm long, with terminal appendages stramineous; achenes 4-6.6 mm long, 1.7-3 mm diameter, awns 0.8-5 cm long, rarely absent. Pales stramineous to purplish or speckled greenish-black, acute to acuminate at the tips, 7.1-10.6 mm tall, 1.2-3 mm wide, antrorsely pubescent apically.

Phenology. Flowering throughout the year.

Distribution. (Fig. 20). This species exhibits the greatest range of habitat variation in the genus, growing in areas of salt spray on beaches in Colombia, in dry river valleys, and in cool, moist upland cloud forests. It grows in highly disturbed sites such as roadsides and old fields, and in relatively undisturbed sites; 0-2600 m; throughout the Andes in northern South America from eastern Venezuela to northern Ecuador.

REPRESENTATIVE SPECIMENS: VENEZUELA. MÉRIDA: near La Carbonera, Aristeguieta 2476** (F, NY, US); outskirts of Chiguara, Badillo 5181** (MY); outskirts of Estánquez, Badillo 6420** (MY), 7167** (MY); Chama Valley between Ejido & Las Gonzales, Breteler 4545** (MO, NY, US); vicinity of Cristóbal Colón, Broadway 463** (GH, NY, US); Lagunillas,

Fig. 20. Distribution of Simsia dombeyana, S. fruticulosa, and the South American populations of S. foetida var. panamensis.

Figure 20.

Jahn 682** (US); D. Cpo. Elias, Quintero 614** (MY), Quintero,
Ricardi & Carroz 215** (MER); between Ejido & Lagunillas, Oberwinkler
14120** (GZU, M); Breckenio Hacienda, Reed 596** (US); MONAGAS: Via
 Guanaguana, Cumara 2146** (MY); Cerro Guácharo cave, near Guácharo,
Steyermark 62345** (F, GH, MO, NY, US). SUCRE: between Cumanocoa &
 Cocollar, Steyermark 62424** (F, R, NY, US). COLOMBIA. BOYACA: Soatá,
Quatrecasas & Barriga 1019** (COL, F); Boavita, Quatrecasas & Barriga
1933** (COL, F, US). CAUCA: Boquerón del Dagua, Lehmann 4710 (R);
 bridge over Rio Anambio on W side of Puracé, Spooner & Guevara 2933**
 (COL, OS); 2 km W of bridge over Rio Anambio on W side of Puracé,
Spooner & Guevara 2935** (COL, OS, WIS). CUNDINAMARCA: Hacienda El
 Cucharo between Tocaima & Pubenza, Killip, Dugand & Jaramillo 38378**
 (COL, F, US); 10 km SE of Chipaque, King & Guevara 5817** (COL, SMU,
 US); 46 km NW of Bogotá, Olsen & Escobar 600** (LL, WIS); between La
 Mesa & Apulo, Spooner & Guevara 2921** (B, COL, OS). HUILA: 11 km NW
 of Gigante, Davidsee, Gentry & Llanos 5802 (COL, MO), Spooner &
Guevara 2924** (COL, OS, UC); 8 km S of Hobo, Spooner & Guevara 2923*
** (COL, OS, UC, US, WIS); 13 km from Nieva-Gigante Rd on rd to
 Tesalía, Spooner & Guevara 2925** (COL, OS, UC); 12 km W of Paicol,
Spooner & Guevara 2927 ** (BM, COL, OS). MAGDELENA: Playa Brava,
Burbidge 75/369 (NY); Playa Santa María, Reichel-Dolmatoff 26 Dec 1948
 (COL, US); beach at Santa Marta, Spooner 2975* ** (COL, OS, P, UC, US,
 WIS). NARINO: 80 km N of Pasto on rd to Popayán, Spooner & Guevara
2937* ** (COL, OS, P); 62 km N of Pasto on rd to Popayán, 15 km N of
 Juanambú River crossing, Spooner & Guevara 3938 ** (COL, OS, OSH); 1
 km N of N edge of Pasto on Rd to Popayán, Spooner & Guevara 2941* **

(COL, OS, WIS); by Rio Guaitara bridge on Pasto-Tulcan Rd, 1 km N of turnoff to Tuquerres, Spooner & Guevara 2944** (COL, OS, W); 6 km W of Pan-American Hwy on rd to Tuquerres, Spooner & Guevara 2945** (COL, OS). SANTANDER: 14 km S of Zapatoca toward La Fuente, Gentry & Forero 15458 A** (COL, MO); Rio Surata valley between El Jaboncillo & Surata, Killip & Smith 16454** (F, GH, US). TOLIMA: Chicoral, Haught 6374** (COL, NY, UC); 16 km W of Ibagué on rd to Cajamarca, Spooner & Guevara 2972* ** (COL, OS); 26 km E of Ibagué on rd to Gualanday, Spooner & Guevara 2973** (COL, OS). VALLE: Rio Dagua, Lehmann 2964** (BM, G, GH, K, US); Yumbo, Pennell 5855 (GH, NY, PH, US); Spooner & Guevara 2952** (COL, GH, OS); 7 km NW of Cali on rd to Dagua, Spooner & Guevara 2953** (COL, OS); 1 km SE of S end of Dagua on rd to Cali, Spooner & Guevara 2956** (COL, OS); Rio Dagua, 4 km W of Loboguerrero, Spooner & Guevara 2957* ** (COL, OS, TEX). ECUADOR. IMBABURA: 12 km N of Ibarra on Rd to Tulcan, Olsen & Escobar 496 (LL, NY, WIS), 497 (LL, WIS), Spooner 2909** (BM, LE, MEXU, OS, QCA, WIS); S end of Ibarra, Spooner 2916* ** (GH, MO, OS, OSH, QCA, WIS). PICHINCHA: Quito-Otavallo Rd. near Guayallabamba town, Spooner 2918** (OS, TENN, QCA, UC, US, WIS).

Triana's citation for S. pastoensis is "crescit prope Ortega, 1200 m, in prov. Pasto". Triana's types are at COL, P, and other institutions (Stafleu & Cowan, 1986). No specimens with these exact data have been located there or elsewhere. The best matches are two specimens from P: Nouvelle-Grenade, Prov. Pasto, Ortega, 1500 m, 1851-1857, Triana 1362, and Jun 1853, Triana 2553. The former is chosen as the lectotype. The exact locality of these collections is

confusing, as Ortega is in the Province of Tolima. Dugand (1944), however, indicates that Triana's collections from "Prov. of Pasto" were made on the eastern side of the Andes in the Prov. of Narino.

The type of Encelia deltoidea, Smith 594, was collected in Nov, 1898. Many other collections labeled Smith 594 were made at the type locality, but collected on 26 Oct 1898, or the printed label has 1898-1901 and no other date added. These specimens are at CM, F, G, LL, MICH, MO, NY, U, US (5), and are here regarded simply as topotypes.

4. Simsia molinae H. Robinson & R. D. Brettell, *Phytologia* 24: 375.

1972.-TYPE: NICARAGUA. Estelí: common along Estelí River, vicinity of Guava, 20 km [N] of Estelí, 5 Nov 1968, Molina 23122 (holotype: US!; isotypes: CAS! FI G! MO! NY!).

Shrubs. Stems erect, 1-3.5 m tall, green to yellow or purple, 1-3 cm diameter, puberulent to pubescent, weakly hispid. Leaves with petioles 1-4 cm long, 1 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0-2 cm long and wide; blades ovate to deltate, herbaceous, unlobed to deeply 3-lobed, 3.5-11 cm long, 2.5-14 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenate-dentate, both sides glandular-puberulent to short pilose, sometimes with intermixed hispid hairs. Capitulescence corymbiform, loosely branched, peduncles subsessile-6 cm long, 0.5-1.5 mm diameter, glandular-puberulent with

intermixed short pubescent hairs. Heads radiate, 13-17 mm tall, 20-45 mm diameter; involucre campanulate, 10-13 mm tall, 8-15 mm diameter. Phyllaries 3-seriate, unequal, 18-37, appressed except slightly reflexed apically, acute to acuminate at the tips, yellow-green to brown, glandular-puberulent and short-pubescent; outer phyllaries ovate to ovate-lanceolate, 3-8.3 mm long, 1-2.9 mm wide; inner phyllaries lanceolate, 9.5-14 mm long, 1-1.9 mm wide. Ray florets 8-24, ligules light orange-yellow, 10-19.5 mm long, 3-6.5 mm wide; tubes 1-2 mm long, 0.5-0.6 mm diameter; ovaries 4.2-8 mm long, 0.5-0.7 mm diameter. Disc florets 29-85; corollas 6-8 mm long, 1-1.5 mm diameter; tubes 1-1.8 mm long, 0.4-0.7 mm diameter; lobes 1-1.5 mm long, 0.5-0.8 mm wide; anthers yellow to black, 3.9-4.5 mm long, with terminal appendages stramineous; achenes 4.2-6.1 mm long, 2.5-3.5 mm diameter, awns 3.5-5.5 mm long. Pales stramineous, sometimes flecked purple or green-black at the apex, acute or acuminate at the tips, 8-11.1 mm tall, 2-3 mm wide, antrorsely pubescent apically.

Phenology. Flowering October-November.

Distribution. (Fig. 18). Moist thickets, roadsides, and along streams; 0-950 m; Honduras to northern Costa Rica.

SPECIMENS EXAMINED: HONDURAS. MORAZÁN: base of Cerro Majicarán, SE of El Zamorano, Molina 1413 (F, GH, MO), Standley 14009 (F, GH, US). NICARAGUA. ESTELÍ: 5 km from Esteli, Molina 23020 (BM, CAS, S), 23027 (F, GH, U); Pan-American Hwy, 10.9 mi N of bridge over Estelí River on N side of Estelí, Spooner & Dorado 2701* (F, LE, MEXU, OS, OSH, TENN, TEX UC, US, WIS); 20 km N of Estelí, Williams & Molina

42327 (MICH, US). MANAGUA: Sierra de Managua, Garnier 1930-1940 (F); along Hwy 8, 2.4 mi SW of Hwy 2, Spooner & Dorado 2704* (OS), Stevens 5171 (MO, OS); both sides of Pan-American Hwy, 2.7 mi SE of jct with Rt 8 to Masachapa, Spooner & Dorado 2714* (CR, F, MEXU, MO, OS, CCI, P, TEX, UC, US, WIS). COSTA RICA. GUANACASTE: Playas del Coco, Ciccio 45 (CR), Spooner 2901* (CR, OS).

Simsia molinae is similar in many ways to S. fruticulosa, sharing similar habit, nodal structures, leaf shapes, phyllaries, flower color, and variability of anther colors. Simsia molinae differs mainly in its reduced leaf pubescence and the more open capitulescence. Although one might prefer to treat this taxon as a variety of S. fruticulosa, its relative ease of recognition and allopatric range more strongly suggest specific status.

5. Simsia holwayi S. F. Blake, Contr. Gray Herb. 52: 46. 1917.-TYPE:
GUATEMALA. Guatemala: Agua Caliente, on Barrios-Guatemala City
Railway, 4 Feb 1917, Holway 854 (holotype: GH!; isotype: US!).

Suffruticose perennials to shrubs. Stems erect, 0.5-4 m tall, green to purple to brown, 0.3-1 cm diameter, hirsute and pubescent and intermixed glandular-puberulent. Leaves with petioles 1-4 cm long, 0.5-1 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0-1 cm long and wide; blades ovate to deltate, herbaceous, unlobed to 3-lobed one-half way to midrib, 3-8 cm long,

2-6 cm wide, at base cordate to truncate to cuneate, at apex acute or acuminate, with margins crenate to dentate, with both sides glandular, above short-hispid and pilose, below longer pilose. Capitulescence corymbiform, loosely branched; peduncles subsessile-8 cm long, 0.5-1 mm diameter, glandular-puberulent and short hirsute. Heads radiate, 10-13 mm tall, 10-15 mm diameter; involucre campanulate to ovoid, 9-11 mm tall, 6-7 mm diameter. Phyllaries 3-seriate, unequal, 18-27, appressed, acute to acuminate at the tips, usually purple and green, puberulent, sometimes glandular and pubescent; outer phyllaries ovate, 3-4.5 mm long, 1.5-2.2 mm wide; inner phyllaries lanceolate to linear, 7.2-9.5 mm long, 1.2-1.8 mm wide. Ray florets 8-9, ligules light orange-yellow, 5-7 mm long, 2.5-2.9 mm wide; tubes 0.8-1 mm long, 0.3 mm diameter; ovaries 6-7.5 mm long, 0.5 mm diameter. Disc florets 20-31; corollas 5.7-6.7 mm long, 1-1.6 mm diameter; tubes 0.9-1.2 mm long, 0.4-0.7 mm diameter; lobes 0.7-1.1 mm long, 0.6-0.8 mm wide; anthers yellow, 3.5-3.8 mm long, with terminal appendages stramineous; achenes 4.7-5.6 mm long, 2.3-3 mm diameter, awns 3.6-4.2 mm long. Pales stramineous, purple or green-black apically, acute to acuminate at the tips, 8-9.2 mm tall, 1.7-2.8 mm diameter, antrorsely pubescent apically.

Phenology. Flowering October-February.

Distribution. (Fig. 18). In dry tropical deciduous forests; 600-900 m; along the Monagas Valley and adjacent slopes in Guatemala.

SPECIMENS EXAMINED: GUATEMALA. EL PROGRESO: on rd to Coban from Guatemala-Puerto Barrios Rd, 7.5 mi S of Baja Verapaz-El Progreso

border, Spooner & Dorado 2746* ** (BM, COL, MEXU, NY, OS, TEX, UC, WIS); Guatemala-Puerto Barrios Rd, 2.4 mi SW of rd to Sanarate, Spooner & Linder 2750 (MEXU, OS); Guatemala-Puerto Barrios Rd, 0.9 mi NE of rd to Sanarate, Spooner & Linder 2759 (MEXU, OS); GUATEMALA: on railroad cut, 0.2 mi NE of railroad station at Agua Caliente, Spooner & Dorado 2692* ** (MEXU, OS, OSH, P, TENN, UC, US, WIS)

A Holway 854 specimen with similar appearance and identical label data except "10 Feb 1917" is deposited at US. This date is regarded as a typographical error, however, it the specimen here considered an isotype.

All populations of this species are found along the dry Monagas River Valley and adjacent slopes in Guatemala, where they are scattered but frequent and easy to locate. Its purple phyllaries and campanulate-ovoid heads with slightly constricted apices give it a superficial resemblance to S. lagascaeformis, which is an annual plant without nodal discs.

6. Simsia steyermarkii H. Robinson & R. D. Brettell, Phytologia 24:

375. 1972.-TYPE: GUATEMALA. Zacapa: Sierra de las Minas, trail between Santa Rosalía de Mármol and Vegas, 19 Jan 1942, Steyermark 42931 (holotype: US!; isotype FI!).

Shrubs. Stems erect, 1-4 m tall, green to purple or brown, 0.5-3 cm diameter, puberulent and mildly scabrous. Leaves with petioles 1-7

mm long, 1 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0-2 cm long and wide; blades ovate to deltate, herbaceous, unlobed, 3-15 cm long, 2-9 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins subentire to crenate, short-hispid and puberulent above, sometimes glandular, glandular-puberulent below. Capitulescence corymbiform, usually tightly clustered; peduncles subsessile-2 cm long, 1 mm diameter, glandular-puberulent and hispid. Heads radiate, 11-13 mm tall, 13-17 mm diameter; involucre campanulate, 10-12 mm tall, 6-11 mm diameter. Phyllaries 3-seriate, unequal, 18-21, appressed except slightly reflexed apically, acute to acuminate at the tips, green to green-black to brown, scabrous, sometimes puberulent and glandular; outer phyllaries ovate to lance ovate, 2-5.9 mm long, 0.7-2 mm wide; inner phyllaries lanceolate, 7.5-9.7 mm long, 1.3-1.7 mm wide. Ray florets 8, ligules light lemon-yellow, 8-10 mm long, 3.5-4.5 mm wide; tubes 1.2-1.6 mm long, 0.3-0.5 mm diameter; ovaries 4.3-6.3 mm long, 0.4-0.6 mm diameter. Disc florets 14-34; corollas 5.8-7.2 mm long, 1.2-1.5 mm diameter; tubes 0.8-1 mm long, 0.5-0.7 mm diameter; lobes 0.7-1.2 mm long, 0.6-1.1 mm wide; anthers yellow to black, 3.5-4.2 mm long, with terminal appendages stramineous; achenes 3.2-4.2 mm long, 1.8-2.5 mm diameter, awns absent or 1.9-2.7 mm long. Pales stramineous, sometimes speckled green-black apically, acute to acuminate at the tips, 7.8-9.5 mm tall, 2.2-2.7 mm wide; antrorsely pubescent apically.

Phenology. Flowering November-January.

Distribution. (Fig. 18). In pine or pine-oak forests; 1300-1500 m; in Guatemala, in the Sierra de las Minas and adjacent uplands to the west.

SPECIMENS EXAMINED: GUATEMALA. ALTA VERAPAZ: rd to Sacapulas, 5 km WNW of San Cristóbal Verapaz, King 7337 (field specimens: MO, NY; greenhouse specimens from seed: B, CAS, G, M, NY, U, US, WIS). BAJA VERAPAZ: 4.8 mi from San Miguel Chicaj town square on rd to Cubulco, Spooner & Dorado 2748* (BM, GH, MEXU, MICH, OS, OSH, TENN, TEX, UC, US).

Simsia steyermarkii is similar to other members of S. ser. Fruticulosa (e.g., S. holwayi, S. molinae), but it is most easily distinguished by its aggregated capitulescences, small achenes, and light lemon-yellow ligules. All specimens examined, including greenhouse-grown specimens from seed of Spooner & Dorado 2748 had aggregated inflorescences except greenhouse-grown specimens from King 7337, but this specimen has all other features of this species. Although my searches in the Sierra de las Minas failed to locate this species at the type locality, other collections in nearby uplands are similar to the type.

7. Simsia annectens S. F. Blake, Contr. Gray Herb 52: 43.

1917.-TYPE: MEXICO. México: Zuatepec, Almoloya de las

Alguisiras, in bushes along edge of road, 23 Dec 1904, C. & E. Seler 4472 (holotype: GH!, photo: MEXU!; isotypes: ENCB! GH!).

Simsia hintonii H. Robinson & R. D. Brettell, Phytologia 24:

368. 1972.-TYPE: MEXICO. Guerrero: Mina, Puerto Rico, 1800 m, by forest stream, 10 Dec 1939, Hinton et al. 14976 (holotype: US!; isotypes: GH! K! LL! MICH! UC!).

Simsia subsetosa H. Robinson & R. D. Brettell, Phytologia 24:

376. 1972.-TYPE: MEXICO. México: Temascaltepec, Rincón del Carmen, 1340 m, woods, 23 Nov 1932, Hinton 2693 (holotype: US!; isotypes: BM! DS! G! MICH! NY!).

Suffruticose perennials or shrubs. Stems erect, 1.5-4 m tall, green to brown or purple, 1-3 cm diameter, usually with harsh hispid hairs, sometimes merely hirsute or pubescent, sometimes glandular. Leaves with petioles 1-14 cm long, 1-2 mm diameter, often winged throughout with wings to 1.5 cm wide, or partly winged by the decurrent blade, or without wings, at base perfoliate or with stipules of opposite leaves fused to form nodal discs 0-5.5 cm long and wide; blades ovate to deltate, herbaceous, unlobed to deeply 3 (rarely 5) lobed, 3-25 cm long, 2-30 cm wide, at base cordate to truncate or cuneate, at apex acute or acuminate, with margins crenate to dentate, with both sides usually scabrous and hirsute above and below, especially above, sometimes glandular-puberulent,

especially below. Capitulescence corymbiform, of tightly clustered heads or more lax, peduncles 0.5-7 cm long, 1-2 mm diameter, sometimes wide divaricately-branched, usually hirsute, sometimes intermixed glandular-puberulent and pubescent. Heads radiate, 11-18 mm tall, 15-30 mm diameter; involucre campanulate, 9-12 mm tall, 6-15 mm diameter. Phyllaries 2-3 seriate, unequal to subequal, 14-29, appressed to greatly reflexed, acute to long attenuate at apex, green to yellow-green, dark blackish-green or rarely tinged with purple, very short puberulent and scabrous to long hispid, sometimes glandular; outer phyllaries broad ovate to lanceolate, 3.7-11 mm long, 1.4-2.8 mm wide; inner phyllaries lanceolate to linear-obovate, rarely sinuate, 7.5-15 mm long, 1.5-2.5 mm wide. Ray florets 8-14, ligules light lemon-yellow, 6.5-14 mm long, 2-7 mm wide; tubes 0.8-2.2 mm long, 0.3-0.7 mm diameter; ovaries 3.7-8.2 mm long, 0.5-1 mm diameter. Disc florets 21-67; corollas 5.5-7.1 mm long, 1-1.7 mm diameter; tubes 0.7-2.1 mm long, 0.4-0.8 mm diameter; lobes 0.6-1.2 mm long, 0.5-1 mm wide; anthers yellow to black, 3.2-4.4 mm long, with terminal appendages stramineous; achenes 3.5-7 mm long, 1.7-3.6 mm diameter; awns absent or 1.9-3.6 mm tall. Pales stramineous, acute to acuminate at the tips, 7.2-10 mm tall, 1.7-3.3 mm wide, subglabrous or antrorsely pubescent apically.

Blake (1917) cited B and GH for the type of *S. annectens*. Two sheets of this collection are at GH, and his note on one of these indicates it is the holotype.

Simsia annectens exhibits much variation in pubescence of all parts, leaf shape, inflorescence branching patterns, head size, and phyllary gradation. All of these features previously have been used taxonomically to distinguish the species here subsumed within S. annectens. Stem pubescence varies from hirsute to harshly hispid to a degree that they can even penetrate skin. Leaf pubescence varies from eglandular to glandular, hispid to puberulent. As in all species of Simsia with lobed leaves, entire leaves also are known, sometimes even on the same plant. The petioles vary in size and alation, from completely unwinged to winged throughout with a width up to 1.5 cm and forming perfoliate leaves. Perfoliate leaves are not always present on every plant within a population. The capitulescence is often a tight cluster of many heads, with the peduncles widely divergent. Although quite distinctive in some populations (e.g., Hinton 12285, Mexia 1832), this is far from a constant feature and not useful taxonomically. Phyllaries vary from gradate, appressed, and scabrous, to subequal, reflexed, and long-setose. Head size is likewise variable and not taxonomically diagnostic in this species.

The conspecific nature of all populations here grouped under S. annectens was only realized after intra- and interpopulational studies from throughout the range of the species. Two distinct but intergrading varieties are here recognized: var. annectens, with densely setose and greatly reflexed phyllaries, and var. grayi with short-puberulent, sometimes scabrous phyllaries which are appressed or slightly reflexed apically. Occasional intermediates connect

these extremes (e.g., Hinton 2693, Matuda 26954, Spooner & Villasenor 2566). Hinton 2693 is the type of S. subsetosa Robinson and Brettell.

variation in phyllary gradation and pubescence is present to a much lesser degree in other species (e.g., S. fruticulosa and S. ghiesbreghtii), but it is quite pronounced in S. annectens to a degree where var. annectens and var. grayi were not previously realized to be conspecific. Their conspecific nature is here recognized by the shared presence of perfoliate leaves, dark anthers, and other features, as well as their intermediate populations.

The origin of these varietal differences in S. annectens is unclear. While possibly representing differentiation in separate areas or habitats, the origin by hybridization with S. foetida must be considered. Many collections of S. annectens var. annectens have a yellowish coloration of all parts similar to S. foetida (the characteristic foetid odor of this species is lacking, however), and some populations, e.g., Spooner 2845, have some sinuate phyllaries characteristic of S. foetida. Although seeds were produced from a cross between S. foetida and S. annectens var. grayi (Table 3), these did not germinate, and this hypothesis, therefore, remains untested.

7a. Simsia annectens var. annectens.

Plants 1.5-4 m tall. Phyllaries usually greatly reflexed, long hispid, attenuate apically; outer phyllaries lance-ovate, 4.8-11 mm long, 1.4-2.5 mm wide; inner phyllaries lanceolate, 7-15 mm long, 1.6-2.5 mm wide.

Phenology. Flowering September-March.

Distribution. (Fig. 21). In open pine-oak forests, mountain slopes, and along streamsides; 1000-2400 m; along the transverse volcanic belt in Jalisco, Michoacan, and Mexico, and the Sierra Madre del Sur in Michoacan and Guerrero.

SPECIMENS EXAMINED: MEXICO. GUERRERO: 36 km NE of Pueblo el Gallo along rd to Filo del Caballo, Breedlove 36152 (CAS, MICH, MO), Spooner 2845* (MEXU, MICH, OS, TENN, TEX, UC, US, WIS); Chichihualco. Cruz de Ocote, 25 km WSW of Chamotla, Feddema 2866 (MICH), Rzedowski 18109 (ARIZ, ENCB, MICH); Mina. Manchón, Hinton 11271 (GH, K, LL, MICH, NY, UC, US, W); Montes de Oca. Vallecitos, Hinton 11651 (GH, K, LL, MICH, NY, UC, US); Mina. Campo Morado-Otatlán, Hinton 14843 (GH, K, LL, MICH, NY, UC, US); rd to Chilpancingo, 16 km E of Aserradero Agua Fria, Rzedowski & McVaugh 272 (ENCB, MICH); 3-5 mi W of Rt 95 on rd to Chilpancingo, Stuessy & Gardner 4225 (ASU, ENCB, MO, OS, WIS). JALISCO: Huejotitán, Oct 1912, Diguet (MICH, F); Hacienda del Ottotal, Arroyo del Ottotal, W of San Sebastian, Mexia 1832 (BM, CAS, DS, F, G, GH, MICH, MO, NY, UC). MEXICO: Temascaltepec. Temascaltepec, Hinton 2801 (BM, G, K), Matuda

Fig. 21. Distribution in Mexico of S. annectens var. annectens, S. annectens var. grayi, S. tenuis, and S. villasenorii.

Figure 21.

30468 (ENCB); Temascaltepec. Ixtapan, Hinton 2935 (BM, G, MEXU, MO); Tejupilco. Ocoatepec, Rzedowski 25298 (ENCB). MICHOACÁN: Coalcomán. Pto. Zarzamora, Hinton 12714 (K, LL, MICH, NY, S, UC); Coalcomán. Coalcomán, Hinton 12885 (ARIZ, CHAPA, ENCB, GH, LL, MO, NY, PH, US, W); along rt 15, 16.7 mi E of E limits of Morelia between Río El Salto & village of Polvilla, Stuessy & Gardner 3108 (ASU, F, MEXU, MICH, NY, OS, UC).

Intermediates with *S. annectens* var. *grayi*: MEXICO: rd between Valle de Bravo & Colorines, Matuda 26954 (MEXU, NY), Spooner & Villaseñor 2566* (GH, LE, MEXU, OS, TEX, UC, US, WIS), Villaseñor & Spooner 766 (MEXU, OS).

Robinson & Brettell (1972) placed much taxonomic weight on the widely divergent branching pattern of the capitulescence of *Simsia annectens*, but this is far from constant and of limited taxonomic utility. A focus on this feature possibly misled them from recognizing the conspecific nature of their *S. subsetosa* Robinson & Brettell. The type of *S. subsetosa* differs from many other populations of *S. annectens* by its reduced pubescence, but similar reduced pubescence is present in other populations of both varieties (e.g., var. *annectens*: Hinton 1285; var. *grayi*: Breedlove & Strother 4740, Spooner 2788).

Simsia hintonii Robinson & Brettell was distinguished from *S. annectens* by the reduced alation of the petioles, more hirsute phyllaries, puberulous rather than densely scabrous leaf pubescence, and less glandular stems. All of these differences are minor, however, and well within the range of variation present in *S.*

annectens var. annectens.

7b. Simsia annectens var. grayi (Schultz-Bipontinus ex S. F. Blake)

D. M. Spooner, comb. et stat. nov. - Simsia grayi

Schultz-Bipontinus ex S. F. Blake, J. Wash. Acad. Sci. 18:

26. 1928.- TYPE: MEXICO. Oaxaca: Prov of Oaxaca, Liebmann

561 (holotype: Pl, photo & fragment: US!, photo OS!;

isotypes C [2]1, photo & fragment: US!, tracing: GH!).

Plants 1.5-3 m tall. Phyllaries appressed to only slightly reflexed apically, acute to acuminate at the tips, short puberulent to scabrous; outer phyllaries ovate to lance-ovate, 3.7-6 mm long, 1.6-2.8 mm wide; inner phyllaries lanceolate, linear to linear-obovate, 7.5-9.1 mm long, 1.5-2.4 mm wide.

Phenology. Flowering September-November.

Distribution. (Fig. 21). In openings in pine-oak forests, often in shallow soil of volcanic and limestone rocks; 850-1930 m; in the transverse volcanic belt in Mexico, in the Sierra Madre del Sur of Guerrero, and along the northern highlands of Chiapas and Oaxaca.

SPECIMENS EXAMINED: MEXICO. CHIAPAS: N of Tuxtla Gutiérrez at mirador for Chicoasan Dam, Breedlove & Strother 47040 (CAS), Spooner 2788* (LE, MEXU, MICH, OS, OSH, TENN, TEX, UC, US, WIS). GUERRERO: Zihuatenejo-Cd. Altamirano rd, 81 km N of the coast hwy, 3 km N of highest pass on hwy, Barrie Ramamoorthy, & Martinez 650 (TEX). MICHOACÁN: 7 mi SE of Cd Hidalgo, Cronquist 10314 (CAS, DUKE, ENCB,

F, GH, MEXU, MICH, NY, TEX, US); 2 mi E of Tuxpan, Crutchfield & Johnston 5902 D (TEX); Zitácuaro-San José Purua, Hinton 13260 (B, ENCB, F, G, LL, MICH, NY, S, UC, W); along dirt rd to Rincón de la Dolores, 4 km SW of Cd Hidalgo, Iltis, Doebley, & Lasseigne 710 (OS, WIS); Rt 15, 1.8 mi S of Tuxpan town square, Keil & Canne 9081 (NY, OS), Spooner & Brandenburg 2279* (CHAPA, MEXU, NY, OS); Rt 15, 14 mi W of Cd Hidalgo, Melchert, Sorensen, & Crawford 6428 (ENCB, MICH, TEX); rd to Jungapeó, 1 mi S of rd to Zitácuaro, Panero & Schilling 443 (TENN); along Hwy 15, 0.2 mi W of rd to Maravatio, Spooner & Villasenor 2562* (COL, MEXU, MICH, LE, OS, OSH, UC, US, WIS), Villasenor & Spooner 762 (MEXU, OS); along Hwy 15, 2.5 mi E of jct of rd to Maravatio, Spooner & Villasenor 2563 (B, GH, MEXU, MO, NY, OS, TEX, UC, US, WIS); 3 mi E of Tuxpan, Spooner & Villasenor 2564 (MEXU, OS, US); OAXACA: Oaxaca, Buchinger 497 (P); Tepinapa, Liebmann 560 (P, US).

The original spelling of the basionym was Simsia grayii. The terminal y of Gray functions as a vowel, however, and following recommendation 73C.1 of the ICBN this spelling is treated as an orthographic error to be changed to grayi.

My initial impression at the beginning of this study was that the Guerrero and Michoacan populations in the north were taxonomically distinct from the more southern Oaxaca and Chiapas populations. The only complete population samples showing populational variability and the full development of the perfoliate leaves are the recent collections from Chiapas. These southern populations have a tendency for less strigose stems, more densely

glandular leaves, and less widely divergent branches of the inflorescence. Further study indicated considerable intergradation of these features in the north, however, and these differences only of degree seem best left unnamed.

8. Simsia tenuis (Fernald) S. F. Blake, Proc. Amer. Acad. Arts 49:

380. 1913. Encelia tenuis Fernald, Proc. Amer. Acad. Arts 33:

94. 1897.-TYPE: MEXICO. Guerrero: Acapulco and vicinity, Nov 1896 (fide McVaugh, 1956), Palmer 96 (holotype: GHI isotypes: F [2]! K! MO [2]! NY! UCI US!).

Annuals or suffruticose perennials. Stems erect, 0.5-1.5 m tall, green to yellow or purple, 1-11 mm diameter, subglabrous to weakly hirsute and pubescent and intermixed glandular-puberulent. Leaves with petioles 0.5-8 cm long, 0.5-1 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0-1.2 mm long and wide; blades ovate to deltate, herbaceous, usually unlobed, rarely 3-lobed, 2.5-13 cm long, 1.5-10 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenulate, with both sides hirsute and intermixed glandular-puberulent. Capitulescence corymbiform, loosely-branched; peduncles 0.5-10 cm long, 0.5-1 mm diameter, hirsute and intermixed glandular-puberulent and pubescent. Heads radiate, 9-14 mm tall, 15-30 mm diameter; involucre campanulate, 6-11 mm tall, 5-7 mm diameter. Phyllaries 3-seriate, unequal, 12-25, appressed except slightly reflexed apically, acute to acuminate at the

tips, light green to purple, scabrous and glandular, sometimes hirsute; outer phyllaries ovate to lance-ovate, 3.5-6 mm long, 1.5-2 mm wide; inner phyllaries lanceolate, 6-11 mm long, 1-2 mm wide. Ray florets 5-10, ligules light orange-yellow, 5.5-15 mm long, 1.5-7 mm wide; tubes 1-2 mm long, 0.5 mm diameter; ovaries 4-7.5 mm long, 0.4-0.5 mm diameter. Disc florets 12-14; corollas 7 mm long, 1 mm diameter; tubes 0.7-2 mm long, 0.5 mm diameter; lobes 0.7-1.2 mm long, 0.5-0.8 mm wide; anthers yellow to black, 3.2-3.5 mm long, with terminal appendages stramineous; achenes 3.2-6.1 mm long, 2-3.8 mm diameter, pappus absent. Pales stramineous, acute to acuminate at the tips, 5-8 mm tall, 1.5-2 mm wide, antrorsely pubescent apically.

Phenology. Flowering August-December.

Distribution. (Fig. 21). In tropical deciduous forests; 300-600 m; Sierra Madre Occidental near Acapulco, and in the lowlands of the Rio Balsas Basin in Michoacan.

SPECIMENS EXAMINED: MEXICO. GUERRERO: Acapulco, Sierra, Paray 2336 (ENCB). MICHOACÁN: 11-13 km WSW of Apatzingán on rd to Dos Aguas, Dieterle 4351 (ENCB, MICH, TEX); 5 km SW of Tepalcatepec on rd to Coalcomán, Spooner & Villaseñor 2550* (B, CAS, CHAPA, COL, ENCB, F, FI, G, GA, GH, GUADA, K, LE, LL, MA, MEXU, MICH, NY, OS, OSH, P, SRSC, TENN, TEX, UC, US, VEN, WIS, XAL); Villaseñor, Martínez, & Torres 292 (MEXU), Villaseñor & Spooner 742 (MEXU, OS).

This delicate species is distinctive with its small heads and thin leaves. The two Guerrero populations differ from those from Michoacan by possessing black vs. yellow anthers and smaller tubes of

the disc florets, but these features commonly vary in related species. The plants are otherwise similar and are considered conspecific. Many of the individuals of Spooner & Villaseñor 2550 were annuals, but a few possessed suffuticose bases typical of perennials in Simsia sect. Fruticulosae.

9. Simsia villaseñori D. M. Spooner, sp. nov.—TYPE: MEXICO. Chiapas:

Municipio of Cintalapa, crest of the Sierra with Pinus and Quercus and riparian situations with seasonal evergreen forest near the microwave station of La Mina, 12 km S of Mexican Hwy 190 near Rizo de Oro, 1000 m, 16 Oct 1971, Breedlove & Thorne 20576 (holotype DS!; isotypes: ENCB! LL! MEXU! MICH! MO! NY!).

Plantae lignosae, 0.5–2 m altae, foliis petiolatis, 0.5–6 cm longis, stipulis connatis, laminis ovatis vel deltatis, rigidis, non lobatis, 3–10 cm longis, 2–7 cm latis, basim cordatis vel truncatis vel cuneatis, apicibus acutatis, involucris gradatis.

Shrubs. Stems erect, 0.5–2 m tall, green to purple, 0.3–3 cm diameter, puberulent and scabrous. Leaves with petioles 0.5–6 cm long, 1–2 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0–2 cm long and wide; blades ovate to deltate, stiff, unlobed, 3–10 cm long, 2–7 cm wide; at base cordate to truncate or cuneate, at apex acute, with margins crenate–dentate, both sides puberulent and scabrous, sometimes glandular. Capitulescence corymbiform, tightly to more loosely branched; peduncles subsessile–7

cm long, 1 mm diameter, glandular-puberulent and scabrous. Heads radiate, 15-18 mm tall, 25-30 mm diameter; involucre campanulate, 14-15 mm tall, 8-11 mm diameter. Phyllaries 3-seriate, unequal, 19-28 appressed, acute to aristate at the tips, green to purple or brown, scabrous, sometimes glandular; outer phyllaries ovate, 3.2-5.5 mm long, 1.2-2.3 mm wide; inner phyllaries linear-lanceolate, linear to linear-obovate, 10-13 mm long, 1.5-2.1 mm wide. Ray florets 11-16, ligules light lemon-yellow, 7.4-14 mm long, 2.5-4.5 mm wide; tubes 1.7-3.5 mm long, 0.3-0.5 mm diameter; ovaries 7.4-10.2 mm long, 0.5-1 mm diameter. Disc florets 21-39; corollas 6.5-6.7 mm long, 1.5-2.1 mm diameter; tubes 0.7-1.1 mm long, 0.6-0.9 mm diameter; lobes 1.1-1.3 mm long, 0.8-1.2 mm wide; anthers yellow to black, 3.5-4.1 mm long, with terminal appendages stramineous; achenes 5.5-7.3 mm long, 2.5-3.5 mm diameter, awns 4.5-6.5 mm tall, squamellae absent or 0.5-1 mm tall. Pales stramineous, purple apically, acute to acuminate at the tips, 10-13.4 mm tall, 2-2.6 mm wide, antrorsely pubescent apically. (Fig. 22).

Flowering. September-November.

Distribution. (Fig. 21). In areas of tropical deciduous forest and oak-pine woods, including recently burned oak-pine woods; 800-1000 m; in Oaxaca, Sierra Madre del Sur and in Chiapas, Sierra Madre de Chiapas.

SPECIMENS EXAMINED: MEXICO. CHIAPAS: 10 km NW of Rizo de Oro along logging rd to Colonia Figaroa, Breedlove 44455 (DS); near microwave station of La Mina, Breedlove 52914 (CAS), 56333 (CAS),

Fig. 22. Simsia villasenori (Spooner 2789). A, ray floret; B, stem with mature inflorescence; C, head; D, mature achene; E, pale; F, disc floret with immature achene.

Figure 22.

Breedlove & Almeda 60160 (CAS), Spooner 2789* (BM, MEXU, MO OS); OAXACA: Pan-American Hwy, 93 mi NW of Tehuantepec & 59 mi SE of Oaxaca, Cronquist 9687 (GH, MEXU, MICH, NY, TEX); 57 mi SE of Oaxaca, Hartman & Funk 4169 (OS, US); Pan-American Hwy, 0.8 mi NW of jct of rd to San Carlos Yautepec in town of El Camarón, Spooner 2816* (MEXU, OS).

This species is named in honor of Jose Luis Villaseñor Rios, an authority on the Compositae of Mexico. He generously gave me one month of his time in the field, led me to many interesting localities of Simsia, and taught me much about Mexican Compositae.

Simsia villaseñori is a very distinctive species. All parts of the plant are firm and stiff, including the leaves. Most species of Simsia have more herbaceous leaves; only S. santarosensis has leaves which are just as firm. These differences are most evident under wilting conditions in the greenhouse.

The Chiapas populations have a tendency for tight clusters of axillary inflorescences, but this is not constant. The Oaxaca populations grow in dry, tropical deciduous forest, the Chiapas populations in oak-pine woodlands. Spooner 2789 from Chiapas came from a burned woodland, and many young plants were growing from the persistent rootstocks. Both the Oaxaca and Chiapas populations have some individuals with squamellae, which are commonly present in many species of Viguiera, indicative of their relatively primitive nature within Simsia.

10. Simsia setosa S. F. Blake, Proc. Amer. Acad. Arts 49: 379.

1913.-TYPE. MEXICO. Sonora: Alamos, 16-30 Sep 1890, Palmer 741
(lectotype, here designated: GH!; isotypes: CAS! K! MEXU! NY!
UC! US [2]!).

Suffrutescent perennials. Stems erect, 1-1.5 m tall, green to yellow, brown, or purple, 0.3-1 cm diameter, glandular-puberulent, hispid and hirsute. Leaves with petioles 1-7.5 cm long, 1 mm in diameter, at base with stipules of opposite leaves fused to form nodal discs 0-2 cm long and wide; blades ovate to deltate, herbaceous, unlobed to deeply 3-5 lobed, 3-9 cm long, 2-7 cm wide, at base cordate, truncate, or cuneate, at apex acute to acuminate, with margins crenate to dentate, both sides densely glandular-puberulent, hispid and hirsute. Capitulescence corymbiform, loosely branched; peduncles 1-7 cm long, 1 mm diameter, glandular-puberulent and hirsute. Heads radiate, 13-18 mm tall, 15-25 mm diameter; involucre campanulate, 12-15 mm tall, 9-15 mm diameter. Phyllaries 3-seriate, unequal, 14-28, appressed except slightly reflexed apically, light green to brown-yellow, rarely lightly tinged with purple, glandular-puberulent and hispid; outer phyllaries ovate to lance-ovate, 4-7 mm long, 1.5-2.2 mm wide; inner phyllaries lance-ovate, 11.5-13 mm long, 1.7-2.4 mm wide. Ray florets 8-13; ligules light lemon-yellow, 7.5-9.5 mm long, 2.5-3 mm wide; tubes 1-1.2 mm long, 0.5 mm diameter; ovaries 7-10 mm long, 0.5-0.6 mm diameter. Disc florets 18-40, corollas 6.6-8.5 mm long, 1-1.2 mm

diameter; tubes 0.9-1.2 mm long, 0.5-0.7 mm diameter; lobes 0.8-1.2 mm long, 0.7-0.9 mm wide; anthers yellow to black, 3.7-4.2 mm long, with terminal appendages stramineous; achenes 5.2-6.5 mm long, 2.6-4 mm diameter, awns absent or 2.5-3.5 mm long. Pales stramineous, sometimes speckled greenish-black apically, acute to acuminate at the tips, 8.7-11 mm tall, 2-2.8 mm diameter, antrorsely pubescent apically.

Phenology. Flowering July-November.

Distribution. (Fig. 23). In lowland tropical deciduous forests to higher elevation pine-oak forests, including recently burned-over pine woodlands; 400-1600 m; in the Sierra Madre Occidental in southern Sonora and adjacent Chihuahua, and in Nayarit.

SPECIMENS EXAMINED: MEXICO. CHIHUAHUA: Guasaremos, Rio Mayo, Gentry 2464 (ARIZ, DES, F, GH, K, MO, S, UC); Rancho Beverly, Sierra Charuco, Langille 118 (DES), 173 (DES). NAYARIT: along footpath from Jesús María to La Mesa, Colunga & Zizumbo 21 (MEXU); Spooner & Villaseñor 2528* (BM, COL, GH, LE, MEXU, MO, NY, OS, OSH, P, TENN, TEX, UC, US, WIS). SONORA: Sierra de Las Papas, Sonora-Chihuahua boundary, Gentry 654 (MICH); Arroyo Cuchuhaqui, Dist Álamos, Gentry 822M (MICH); Cañón Sapopa, Río Mayo, Gentry 1036 (DES, F, GH, MO, S); Cañón Estrella, Dist Álamos, Gentry 3430 (CAS, MICH); Cañón de Bavispe, White 3120 (GH, MICH); Puerto de los Aserraderos, Rancho de Cruz Díaz, White 3292 (MEXU, MICH); Cañón de la Palomita, N of El Tigre, White 4155 (GH, LL, MICH).

Fig. 23. Distribution in northern Mexico and adjacent United States of Simsia calva and S. setosa.

Figure 23.

Simsia setosa is recognized by its densely glandular and hispid nature with lobed leaves and unwinged petioles. This is the only species in S. section Fruticulosae with a conspicuous yellowish appearance and foetid-smelling leaves similar to that found in S. foetida. This odor was not apparent in in the field, but it was evident greenhouse-grown specimens from Spooner & Villasenor 2528. All other features, however, including its perennial nature, nodal discs, unequal phyllaries, and dark anthers ally it to section Fruticulosae. This combination suggests the possibility of prior introgression of S. foetida into S. setosa or its possible progenitor.

11. Simsia sanguinea A. Gray, Smithsonian Contr. Knowl. 3 (Pl. wright 1): 107. 1852. Encelia sanguinea (A. Gray) Hemsley, Biol. Cent.-amer., Bot. 2: 185. 1881.-TYPE: MEXICO. [without specific locality, but probably Chiapas], mountains, temperate region, s.d., Ghiesbreght 305 (lectotype, chosen by Blake, 1913: GH!).

Simsia erythranthema Schultz-Bipontinus ex A. Gray, pro. syn., Proc. Amer. Acad. Arts 19: 9. 1883.

Helianthus hastatus Sessé & Mocino, Pl. nov. Hisp. 147.

1890.-TYPE: MEXICO. Guerrero: "Chilapae" [=Chilapa] Sep [1789 fide McVaugh, 1977], Sessé, Mocino, Castillo, & Maldonado 2947 (holotype: MA, not seen; isotype: FI!).

Simsia sanguinea var. palmeri (A. Gray in Watson) S. F. Blake,
 Proc. Amer. Acad. Arts 49: 395. 1913. Encelia sanguinea var.
palmeri A. Gray in Watson, Proc. Amer. Acad. Arts 22: 427.
 1887.-TYPE: MEXICO. Jalisco: Río Blanco, Sep 1896, Palmer 602
 (holotype: GH!; isotypes: BM! G! K! LE! MEXU! MO! NY [2]!
 US!).

Simsia sanguinea subsp. albida S. F. Blake, Contr. U. S. Natl.
 Herb. 22: 630. 1924. Simsia sanguinea forma albida Loesener,
 Vehr. Bot. Vereins Prov. Brandenburg 65: 120. 1923, nom.
nud.-TYPE: GUATEMALA. Huehuetenango: among stones on lightly
 wooded limestone hills, Uaxac Canal, Quen Santo, 1300 m, 21
 Jul 1896, C. & E. Seler 3098 (holotype: GH! isotype: MO!).

Aspilia grosseserrata M. E. Jones, Contr. W. Bot. 18: 84.
 1933.-TYPE: MEXICO. Jalisco: La Barranca, Guadalajara, 17 Nov
 1930 [16 or 23 Nov on some sheets], Jones 27778 (holotype
 POM!; isotypes: CAS! MO! NY! UC!).

Cosmos hintonii Sherff, Brittonia 16: 72. 1964.-TYPE: MEXICO.
 Guerrero: Mina, Jiotes, grassy hill, 500 m, 11 Sep 1937,
Hinton et al. 10647 (holotype: MICH!; isotypes: G! GH! K! LL!
 UC! US!, photo: FI!).

Suffruticose perennials. Stems erect (rarely decumbent), 0.3-1.5
 m tall, green to brown or purple, 2-10 mm diameter, or occasionally

flowering at 1 mm diameter, usually harshly hispid and intermixed glandular-puberulent. Leaves extremely variable, petioles subsessile to 6 cm long, 1-2 mm diameter, winged throughout with wings to 3 cm wide, or only partly winged by the decurrent blade, or unwinged, often with stipular lobes at the base, these often dilated and cordate-clasping but not fused with those of adjacent leaves; blades ovate to linear ovate to linear, herbaceous, usually narrowly to deeply 3-lobed from the base, sometimes many lobed throughout into linear-pinnatifid segments, or sometimes completely unlobed, 1.5-16 cm long, 0.5-18 cm wide, at base cuneate and leading into the often winged petiole, at apex acute to long acuminate, with margins subentire to more commonly dentate, with both sides usually scabrous and with intermixed rough whitish hispid hairs, these often confined to the veins, sometimes merely puberulent below and scabrous above, glands present or absent, if present usually denser below. Capitulescence corymbiform, loosely branched; often occupying the upper one-half of the plant; peduncles 1 to more commonly 3-12 cm long, 0.5-1 mm diameter, hirsute and glandular, sometimes puberulent. Heads radiate, 9-16 mm tall, 15-25 mm diameter; involucre campanulate, 8-14 mm tall, 6-10 mm diameter. Phyllaries 2-3 seriate, unequal to nearly subequal, 15-25, appressed to reflexed, acute to long acuminate at the tips, usually green to greenish-black, rarely tinged with purple, strigose and hirsute, sometimes intermixed glandular puberulent; outer phyllaries lance ovate, 3.8-11 mm long, 1-2.2 mm wide; inner phyllaries lanceolate to linear, 6.2-13 mm long, 1.2-2.5 mm wide. Ray florets 6-15, ligules light pink to deep purple, (light

lemon-yellow in var. triloba), rarely white, 7.3-13.5 mm long, 3.7-5.5 mm wide; tubes 1.2-2.3 mm long, 0.4-0.6 mm diameter, ovaries 4-6.7 mm long, 0.5-1 mm diameter. Disc florets 17-44, white (light lemon-yellow in var. triloba); corollas 5.5-7.5 mm long, 1-1.5 mm diameter; tubes 0.7-1.6 mm long, 0.5-0.8 mm diameter; lobes 0.7-1.5 mm long, 0.5-0.9 mm wide, anthers yellow, rarely purplish on the upper 1/4 to 1/2, sometimes black immediately below the apical appendages, 3.2-4.5 mm long, with terminal appendages nearly black throughout or just below the margins; achenes 3.2-6.5 mm long, 1.9-3.7 mm diameter, awns absent or 2.3-4.3 mm long. Pales stramineous, acute to acuminate at the tips, 6.6-10.5 mm tall, 1.2-2.5 mm wide, antrorsely pubescent apically.

11a. Simsia sanguinea var. sanguinea.

Ligules light pink to deep purple, rarely white, disc florets white.

Phenology. Flowering August-February.

Distribution. (Fig. 24). Open meadows and in shallow rocky soil in rocky areas or on cliffs, and along roadsides, in areas of tropical deciduous forests to oak-pine forests; 450-2480 m; with a somewhat disjunct distribution, from the extensive barranca system about Guadalajara, Jalisco, into western Michoacán, throughout SW México, Morelos, Guerrero, and Oaxaca to central Veracruz and from Chiapas to El Salvador.

Fig. 24. Distribution in Mexico and Central America of Simsia
sanguinea var. sanguinea and S. sanguinea var. triloba.

Figure 24.

REPRESENTATIVE SPECIMENS: MEXICO. CHIAPAS: 3 km S of Comitán near old airport, Breedlove & Davidsee 54889 (CAS, MICH, TEX); 4 km above Motozintla on new rd to El Porvenir, Breedlove & Strother 46316 (DS); 36 mi W of Villa Flores, Cronquist & Sousa 10461 (DS, DUKE, ENCB, GH, MEXU, MICH, MSC, NY, TEX, US); Hacienda Monserrate, Purpus 9122 (GH, MO, NY); along Rt 190, 4.6 mi S of rd directly into centro of La Trinitaria, Spooner 2772 (MEXU, OS, UC). GUERRERO: Cutzamala, Hinton 6706 (F, GH, K, NY); Placeres-Cigarillo, Hinton 9818 (K, US); Rt. 95, just S of Chilpancingo de los Bravos, Spooner & Burgos 2604 (COL, MICH, OS, TENN, UC, US, WIS); near dam, along rd from Chilpancingo de los Bravos to Ayotzinapa, Spooner & Burgos 2607* (MEXU, OS, TEX, UC, US). JALISCO: La Barranca near Guadalajara, Pringle 1738 (BM, F, G, GH, M, MASS, LE, NY, S, TEX, UC, US, W), 4044 (M, MEXU), 11513 (CAS, F, GH, L, MEXU, MO, MSC, SMU, US); near bridge crossing of toll road over Río Grande de Santiago, SE of Guadalajara, Spooner & Villaseñor 2495* (GH, LE, MEXU, MICH, NY, OS, TEX, UC, WIS), Villaseñor & Spooner 684 (MEXU, OS); Rt 41, 4 mi N of city limits of Guadalajara, Spooner & Villaseñor 2505 (COL, CHAPA, F, GH, MEXU, MICH, NY, OS, OSH, P, TEX, UC, US WIS); 8 mi SE of Tizapán el Alto near border with Michoacán, Spooner & Villaseñor 2537* (BM, MICH, OS, OSH, P, UC, US, WIS), Villaseñor & Spooner 723 (CAS, MEXU). MÉXICO: just NE of Temascaltepec along Rt 140, Anderson & Laskowski 3937 (DUKE, ENCB, F, MICH), Spooner & Villaseñor 2572* (MEXU, MO, OS, P, TEX, US, WIS); Temascaltepec, Hinton 6706 (K); El Duranzo, 4 mi SE of dam of Lake by Valle de Bravo on rd to Colorines, Spooner & Villaseñor 2567* (G, MEXU, MICH, OS, US, WIS), Villaseñor & Spooner 767 (CAS, MEXU); 1 mi NE of rd from

intersection of Valle de Bravo Rd & rd to Zacazonapan, Spooner & Villaseñor 2570 (MEXU, MO, NY, OS). MICHOACÁN: Tiquicheo, Hinton 13320 (ARIZ, ENCB, GH, K, LL, MICH, MO, TEX, US, W); Salto de Enandio, Hinton 13487 (ARIZ, LL, MICH, US); 12 km N of Huetamo, rd to Zitácuaro, Núñez 6660 (TEX). MORELOS: Xochicalco, C. & E. Seler 5398 (GH); Jojutla, Miranda 1572 (MEXU). OAXACA: 24 km NE of Sola de Vega along rd to Oaxaca, Breedlove 12254 (CAS, ENCB, MICH, NY, US); Xochimilco, Conzatti 3655 (MEXU); Cerro San Felipe, Conzatti 4045 (MEXU), Stuessy & Gardner 4271 (ASU, ENCB, OS); 54 mi SE of Oaxaca at Portillo San Dionisio, C. & G. Davidsee 9610 (MO); 7 mi N of Oaxaca, Kenoyer 1643 (GH); Las Sedas, Pringle 5756 (GH); 3 km SEE of Ocotlán, Solano & Vara 115 (CHAPA); along rt 190, 0.1 mi S of turnoff to Etla, Spooner & Villaseñor 2658b (GH, OS, TEX, UC, US); Rt 195, 9 mi SE of Matatlán, 0.9 mi SE of intersection of rd to Ocotepc, Spooner 2819 (OS); 9 mi N of Pachutla, Turner 80A-25 (CAS, TEX). VERA CRUZ: Mirador, Consaquitla, Liebmann 492 (C, F, G, GH, L, LE, S, US), Sartorius 1146 (GH, P); Totutla. Encinal, Ventura 4121 (ASU, CAS, ENCB, MICH, TEX). GUATEMALA. BAJA VERAPAZ: above San Miguel Chicaj, Molina & Molina 27799 (ENCB, F, MICH, UC). CHIMALTENANGO: Almeda, Johnston 362 (F). ESCUINTLA: Dept Escuintla, Aguilar 1748 (F). GUATEMALA: large arroyo S of Guatemala on rd to Amatitlán, Standley 62834 (F, GH). HUEHUETENANGO: along Rt CA-1, 2.3 mi SE of border with México at La Mesilla, Spooner 2767 (F, MEXU, OS, US); Rt CA-1, ca. 35 mi WNW of Huehuetenango, Stuessy & Gardner 4316 (ASU, COL, ENCB, MO, OS, TEX, WIS). JALAPA: Montaña Durazno, 2 mi E of San Pedro Pinula, Steyermark 32982 (F, US). JUTIAPA: vicinity of Jutiapa, Standley 75023

(F). SACATEPÉQUEZ: 6 mi N of Antigua, 0.1 mi N of intersection of rd to San Andrés Itzapa, Spooner & Dorado 2684b* (BM, F, LE, MEXU, OS, OSH, UC, WIS); 1.6 mi E of El Tejar on rd to Guatemala Spooner 2761* (MEXU, OS). SOLOLA: 3 mi NW of Panajachel, Spooner & Dorado 2681* (BM, F, LE, MEXU, MICH, OS, OSH, UC, US, WIS). EL SALVADOR. SANTA ANA: Chalchuapa, Caldero 1922 (US).

The type locality of Simsia sanguinea var. sanguinea is unknown. Ghiesbreght traveled throughout many parts of Mexico, but did collect extensively in Chiapas (Hemsley, 1887). In addition, Ghiesbreght 568, the type of Simsia ghiesbreghtii, was definitely collected in Chiapas. The closeness of the collection numbers further suggests that Ghiesbreght 305 was also collected in Chiapas.

The protologue of Aspilid grosseserrata lists 17 Nov 1930 for the date of the type collection, but Jones' specimens bearing identical data differ by the dates: 16 Nov, POM; 17 Nov, MO, UC; and 23 Nov, CAS, NY. According to Lenz (1986), Jones' field notes indicate he actually collected the type on 15 November. Lenz also documents, however, that Jones visited La Barranca on all of the dates listed above. Whether these sheets represent separate collections or one collection later confused by labelling errors is unclear. They all appear similar and apparently represent the same collection, however, and are here all regarded as type material.

Simsia sanguinea var. sanguinea exhibits the greatest range of morphological diversity within the genus, and could with some justification be treated with up to three or four intergrading

varieties. The "typical" form of the plant is upright, 1-1.5 m tall, with harshly pubescent leaves, deeply to narrowly three-lobed from the base. On grassy meadows adjacent to and on rock ledges within the extensive barranca system about Guadalajara (all plants listed from Jalisco) occur populations distinguished by leaves and heads on the large end of the size range for the species. Within this area, there is relatively little variability of the plants, but similar forms are found elsewhere throughout the range of the species (e.g., Oaxaca: Breedlove & Strother 46316, Conzatti & González 899. Guatemala: Spooner 2767).

In the Sierra Madre of northwestern Guerrero [Hinton 9818, Hinton et al., 10647, (the type of Cosmos hintonii Sherff)], immediately adjacent Mexico (Hinton 6706) and Michoacan (Hinton 13320, Núñez 660), from 450-500 m, are populations distinguished by relatively thin, linear-pinnatifid leaves. While somewhat morphologically distinct and geographically isolated, most of these collections are from areas of difficult access and little is known about populational variability or intergradation of these features. While possibly deserving taxonomic recognition at the varietal level, they are not so treated here at this time due to the current lack of information.

Commonly occurring throughout much of southern Oaxaca (Conzatti 3655, 4045; C. & G. Davidsee 9610; Kenoyer 1643; Pringle 9756; Solano & Vara 115; Spooner 2819; Stuessy & Gardner 4271) from 1500-1800 m is a usually low-growing form, 0.5 m or less tall, sometimes with decumbent stems, and with small, narrow, sometimes linear leaves with

a conspicuous harsh whitish pubescence above and below. The extensive sympatric intergradation with the typical populations, however, suggests that these are best regarded as only extreme variants worthy of mention but not formal recognition.

- 11b. Simsia sanguinea var. triloba (S. F. Blake) D. M. Spooner, comb. et stat. nov. Simsia triloba S. F. Blake, Proc. Amer. Acad. Arts 49: 393. 1913.--TYPE: MEXICO. Jalisco: rocky soil, Cerro de Paxtle, vicinity of San Luis Tultitlanapa, near Oaxaca, Sep 1908, Purpus 3022 (holotype: GH!; isotypes: BM! FI MO! NY! UC! US!).

Ligules and disc florets light lemon-yellow, rarely white.

Phenology. August–September.

Distribution. (Fig. 24). Exposed dry rocky hillsides and roadsides; 1650–2050 m; S Puebla and immediately adjacent NW Oaxaca.

SPECIMENS EXAMINED: MEXICO. OAXACA: 12 km S of Huajuapán de León on Pan-American Hwy, Iltis, Koeppen, & Iltis 1189 (TEX, WIS); 3.3 mi SE of jct with Rt 125 to Tehuacan, Keil & Luckow 15491 (OB, OS), Spooner & Dorado 2641a* (MEXU, OS, UC, US, WIS); 16–17 mi S of jct of Hwys 125 & 190, Lane & Olsen 2098 (TEX), Webster 16984 (MICH); 14.4 mi SE of jct with Rt 125 to Tehuacan, Spooner & Dorado 2649b* (MEXU, OS, TEX, UC, WIS). PUEBLA: km 17, on Tehuacan–Huajuapán de León Rd, 23.5 mi N of Hwy 190, Bartholomew, Landrum, Li, Ying, & Dorado 3043 (CAS);

km 84-5 on Tehuacan-Huajuapán de León Rd, Panero & Schilling 651 (TENN); Caltepec. El Tecomite, El Gavilán, NW of San Simón, Tenorio & Romero 7558 (TEX).

Simsia sanguinea var. triloba differs from var. sanguinea only by flower color differences. Ligule color variation from yellow to red is known elsewhere in the Heliantheae (e.g., Viguiera parkinsonii f. parkinsonii with brown-purple ligules and f. flaviflora with yellow ones, Blake, 1917), but S. sanguinea var. triloba is here recognized at the varietal level because of the complete replacement of var. sanguinea in S Puebla and adjacent N Oaxaca. There is much vegetative diversity within var. triloba similar to that found in var. sanguinea. For example, Spooner & Dorado 2649b is a more typical upright broad-leaved plant, but Iltis, Koeppen & Iltis 1189, Spooner & Dorado 2641a are prostrate linear-leaved plants similar to those in var. sanguinea.

Plants with white ligules occasionally are found intermixed in populations of both var. sanguinea (e.g., MEXICO. Guerrero: Spooner & Burgos 2607) and var. triloba (e.g., MEXICO. Puebla: Bartholomew, Landrum, Li, Ying, & Dorado 3045), and some populations are composed of totally white-liguled plants (e.g., MEXICO. Chiapas: Breedlove & Davidsee 54889, Purpus 9122. GUATEMALA. Huehuetenango: C. & E. Seler 3098, this the type of S. sanguinea subsp. albida. Solola: Spooner & Dorado 2681). The white corollas often dry a very pale yellow, but are generally distinguishable from the naturally light lemon-yellow corollas of var. triloba, and all populations of this species maintain

their colors under cultivation (see Artificial Hybridizations).

- IB. Simsia series Calvae D. M. Spooner, ser. nov. -TYPE: Simsia calva
(A. Gray & Engelmann ex A. Gray) A. Gray.

Plantae caudicibus crassis, pedunculis monocephalis, floribus
discorum saepe plus 90.

Plants arising from a fusiform-thickened caudex; heads on
monocephalous peduncles, often with more than 90 disc flowers per
head.

12. Simsia calva (A. Gray & Engelmann ex A. Gray) A. Gray, Boston J.
Nat. Hist. 6 (Pl. lindheim. 2): 228. 1850. Barrattia calva A.
Gray & Engelmann ex A. Gray, Proc. Amer. Acad. Arts 1: 48.
(Dec 1846 or Jan 1847 fide Stafleu & Cowan, 1976). Encelia
calva (A. Gray & Engelmann ex A. Gray) A. Gray, Proc. Amer.
Acad. Arts 8: 658. 1873.-TYPE: USA. Texas: rocky soil, in open
woods between the headwaters of the Guadalupe & Pedernales
Rivers, Oct 1845, Lindheimer 432 (holotype: GH!; isotype:
MO!).

Simsia subaristata A. Gray, Mem. Amer. Acad. Arts 1 (Pl. fendl.):
84. 1849. Encelia subaristata (A. Gray) A. Gray ex Hemsley,
Biol. cent.-amer., Bot. 2: 185. 1881. Simsia calva var.

subaristata (A. Gray) S. F. Blake, Proc. Amer. Acad. Arts 49: 379. 1913.--TYPE: MEXICO. Nuevo León: Bishop's Hill near Monterrey, 6 Feb 1847, Gregg 47 (holotype: GH!; isotypes: MO! NY!).

Suffruticose perennials. Stems ascending to erect, 0.3-1.5 m tall, freely profusely branched from the very base with many stems arising from the apex of a fusiform-tuberous root up to 11 cm long, 3.5 cm diameter, stems green to purple, 0.2-1 cm diameter, scabrous, often hirsute and glandular-puberulent. Leaves with petioles 0.2-3 cm long, 0.5-1 mm diameter, at base with stipules of opposite leaves fused to form nodal discs 0-1.5 mm long and wide; blades dentate to ovate, herbaceous, unlobed to deeply 3-lobed, 2-8 cm long, 1.5-6 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenate-dentate, rarely subentire, with both sides eglandular, scabrous and hirsute. Capitulescence of monocephalous heads on peduncles 3-30 cm long, arising from many nodes, 1-2 mm diameter, hirsute, sometimes scabrous and glandular-puberulent. Heads radiate, 11-16 mm tall, 20-40 mm diameter; involucre campanulate, 10-12 mm tall, 7-16 mm diameter. Phyllaries 3-seriate, unequal to subequal, 21-43, appressed to moderately to greatly reflexed, acute to attenuate at the tips, green to yellow-green or green-black, rarely sinuate, scabrous and hirsute, sometimes glandular; outer phyllaries lance-ovate to lanceolate, 4.5-12.3 mm long, 1.5-3 mm wide; inner phyllaries lanceolate to linear or oblanceolate, 6.4-13 mm long, 1-2.5 mm wide. Ray florets 9-21,

ligules light orange-yellow above, often lined or sometimes totally brown or purple below, 7.2-15 mm long, 2.5-4.5 mm wide; tubes 1-2.1 mm long, 0.3-0.6 mm diameter; ovaries 3-5 mm long, 0.5-1.1 mm diameter. Disc florets 26-154, often more than 90; corollas 5.5-7 mm long, 1-1.5 mm diameter; tubes 0.5-1.2 mm long, 0.4-0.8 mm diameter; lobes 0.8-1.3 mm long, 0.6-0.9 mm wide; anthers yellow, very rarely black, 3.1-4.3 mm long, with terminal appendages stramineous; achenes 3.5-5.7 mm long, 1.8-3.1 mm diameter; pappus commonly absent or with awns minute-4 mm long. Pales stramineous, sometimes purple apically, acute to acuminate at the tips, 6.7-10 mm tall, 1.5-2.5 mm wide, scabrous apically.

Phenology. Flowering throughout the year.

Distribution. (Fig. 23). In sand to heavy clay soils, or in rock crevices, often in limestone, on open prairies or thickets or oak savannas, or in rocks along streams, often along roadsides, to upland pine or pine-oak forests; 30-2400 m; widespread throughout southcentral and southeastern Texas from the south Texas plains to the trans-Pecos mountains, SE New Mexico, and in Mexico mostly in the lower to upper slopes of the Sierra Madre Oriental to the northern part of the altiplano.

REPRESENTATIVE SPECIMENS: U.S.A. NEW MEXICO: Lincoln Co., Devil's River, El Capitan Mtns, Earle & Earle Jul 22, 1900 (NY). TEXAS: Atascosa Co., Pleasanton, Palmer 9790 (DS, MO, S, US). Baylor Co., Seymour, Clark 4695 (G). Bexar Co., rocky hills of the upper Guadalupe

River, Lindheimer 433 (BM, OGE, G, GH, GOET, K, LE, MICH, MO, NY, OKF, SMU, UC, US, W); Comanche Spring, New Braunfels, etc, Lindheimer 900 (ARIZ, BM, C, F, G, GH, LE, M, MEXU, MO, NY, SMU, TEX, US, W). Blanco Co., 4.7 mi. N of Blanco on US 281, Flyx 472 (DUKE, SMU). Brewster Co., W slopes of Baldy Peak, Glass Mountains, Warnock W 264 (ARIZ, DS, GH, LE, MO, NY, PH, S, SRSC, TEX, UC); Sul Ross Campus, Paul 1 (SRSC). Brown Co., Brownwood, Palmer 26793 (MO). Burnet Co., 3.1 mi. N of Burnet, Cory 15736 (GH). Callahan Co., Rt. 80, 2 mi. W. of Baird, Spooner & Schilling 2385 (BM, OOL, ENCB, LE, MEXU, MICH, MO, OS, P, WIS). Cameron Co., 2 mi NE of Combes, Shinners 17747 (SMU, TEX). Coke Co., 5 mi N of Sanco, Shinners 8405 (SMU). Coleman Co., Santa Anna Mtns, Pruitt 233 (TEX). Concho Co., 5.6 mi. E of Eden on US 87, Stuessy & Meacham 3511 (NY, OS). Coryell Co., N of Killeen, Wolff 3273 (SMU, US). Crockett Co., 8 mi. W of Ozona on US 290, Urbatsch 965 (LL). Culberson Co., Hurd's Draw, Janszen 61 (TEX). Dimmit Co., 3 mi S of San Diego on Hwy 1329, Mahler 5277 (SMU, WIS). Duval Co., 4 mi. SE of Bruni, Alvarez, Guajardo, Salizar & McCart 7611 (DUKE, LL, TEX). Edwards Co., 30 mi. NW of Rocksprings at substation 14, Cory 51726 (DS, MICH, NY, SMU, US). Frio Co., 6 mi. N of Pearsall, Shinners 7430 (SMU, TEX, UC). Gillespie Co., Spring Creek, Jerry 863 (F). Glasscock Co., 10 mi W of Garden City, Turner 4953 (TEX). Goliad Co., 0.5 mi W of Goliad, Cory 55138 (SMU, US). Hamilton Co., 0.3 mi. SW of Indian Gap, Cory 53791 (SMU). Hays Co., San Marcos, Palmer 12119 (G, GH, MO, NY, TEX). Hidalgo Co., 3 mi. S of Weslaco, Tidwell 111 (TEX). Howard Co., Big Spring State Park, Correll 16682 (SMU). Jeff Davis Co., Jeff Davis Mountains, Rt 118, 1 mi NW of rd into park, 4.8 mi from St Rt

17, Spooner & Schilling 2391 (BM, CHAPA, F, MEXU, MO, NY, OS, US, WIS). Jim Hogg Co., ca. 36 mi S of Hebbbronville on Rt 1017 near Starr Co line, Strother 860 (NMC, UC). Jones Co., W shore of Fort Phantom Lake, 9 mi N of Abilene, Henderson 63-699 (SMU). Karnes Co., 7 mi. NW of Karnes City, Turner 4583 (TEX). Kendall Co., 0.8 mi SW of Bergheim on Hwy 46, Shinners 32924 (SMU). Kerr Co., Kerrville, Heller 1860 (G, NY, UC, US). Kimble Co., Junction, Cory 49084 (CAS). Kinney Co., 4 mi. NE of Brackettville, Strother 268 (DS, ENCB, SMU, TEX). Kleberg Co., Kingsville, Benke 5456 (F, G, GH). Lampasas Co., Mountain View School, Tharp Jun 12, 1941 (TEX). Live Oak Co., 8 mi S of George West on Rt 281, Flyx 350 (NY). Mason Co., Mason-Eden, Whitehouse Aug 31, 1929 (TEX). Maverick Co., 12 mi E of Eagle Pass, Bray May 20, 1898 (TEX). McCulloch Co., 1 mi S of Brady on rd to Mason, Gould 5691 (SMU, TEX). McMullen Co., W of Three Rivers on Henderson Ranch, Whitehouse 11027 (SMU). Medina Co., 3 mi W of Castroville, Spooner & Brandenburg 2177* (OS). Menard Co., 4.2 mi S of Menard on US 83, Raven and Gregory 19266 (DS, TEX). Mills Co., 3.2 mi SE of Goldthwaite, Shinners 16830 (SMU). Mitchell Co., NE 1/4, Sect 17. S.P.R.R. Block 18, Pohl 4627 (S, SMU). Nolan Co., Sweetwater, Palmer 14539 (MO). Pecos Co., Tunis Creek at East Escondito Springs, Tharp 43-903 (MO, NY, PH, TEX, UC). Presidio Co., Vieja Pass, Vieja Mtns, Warnock 8887 (MICH, SRSC). Real Co., Barksdale, Connell 6506 (LL, TEX). Reeves Co., along canal at Balmorhea, Fletcher 600 (SRSC). Runnels Co., 10 mi NW of Ballinger, Shinners 31753 (TENN, SMU). San Patricio Co., Lake Corpus Cristi State Park near Mathis, Traverse 1788 (F, GH, LL, SMU, TEX). San Saba Co., Chappel, Barnette 275 (SMU). Schleicher Co., Rt. 277, 8.5 mi N of

Eldorado, Raven & Gregory 19248 (DS). Scurry Co., 5 mi. N of Fluvanna, Correll & Johnson 17198 (LL). Shackelford Co., 15 mi W of Albany, Whitehouse 16717 (MICH, SMU). Starr Co., 6 mi N of Rio Grande City, Clover 1672 (LL, MICH). Sterling Co., 1.5 mi NE of Sterling City, Correll 31722 (LL). Sutton Co., 7.3 mi N of Sonora, Cory 50555 (MICH, SMU). Taylor Co., 13 mi S of Merkel of Hwy 126, Mahler 3007 (SMU). Terrell Co., Rt 90, 6.7 mi E of Sanderson, Raven & Gregory 19203 (DS). Tom Green Co., 9 mi. N of San Angelo on Hwy 277 Watson 540 (ASU, TEX). Travis Co., Austin, Hall 339 (G, GH, MO, NY, US). Upton Co., 4.1 mi N of Rankin, Shinners 31920 (SMU). Uvalde Co., 21 mi N of Uvalde, Shinners 7315 (DS, SMU, WIS). Val Verde Co., View point, Amistad Recreation Area along Rt 90, ca. 3 mi E of dam, Urbatsch 928 (LL). Webb Co., Laredo, Magnon & Rodriguez 31 (ENCB, TEX). Willacy Co., S of Raymondville, Gentry 710 (ARIZ, SMU). Zapata Co., 4 mi E of Zapata, Ariaza 55 (SMU, TEX). Zavala Co., 15 mi N of Crystal City, Shinners 7376 (SMU). MEXICO. CHIHUAHUA: Chihuahua, Paray 2565 (ENCB). COAHUILA: La Cuesta del Plumo on the Múzquiz-Boquillas Hwy, Chiang, Wendt & Johnston 9211 (TEX); 1.1 mi N of rd to Laguna Churince along Cuatro Cienegas Hwy, Lehto, Keil & Pinkava 5233 (ARIZ, ENCB, LL, NY); Saltillo, Palmer 615 (MASS, GH, US); 0.5 mi N of Toro Viejo on Rt 57, Reeves & Pinkava 13016 (ASU, OS); 14 mi N of Sabinas on Hwy 57, Spooner & Brandenburg 2181 (CHAPA, OS); 4 mi N of Nueva Rosita on rd to Melchor, Stuessy 909 (ENCB, NY, TEX); Rancho Santa Teresa, S of Castaños, Wynd & Muller 177 (ARIZ, GH, K, NY, S, TEX, US). NUEVO LEON: Mamulique Pass, 70 km N of Monterrey, Cronquist 11299 (MEXU, MICH, NY), Spooner & Triplehorn 1058 (CHAPA, LE, NY, OS, OSH, P, RSA, WIS);

2 km S of Puerto Calvertas, 46 km N of Dr. Arroyo, Elyr 1558 (TEX); Sierra Madre above Monterrey, Pringle 8739 (BM, C, CM, ENCB, F, G, GH, GOET, LE, LL, M, MEXU, MO, MSC, NY, S, UC, US, W); 18 mi W of Linares, Roberts & Keil 10456 (F, NY, OS); Linares-Iturbide Rd., 13 mi W of Rt. 85, Spooner 2482 (ENCB, F, LE, MEXU, MICH, MO, OS, TENN, TEX, UC, US, WIS). TAMAULIPAS: 11 mi N of Jiménez, Johnston 4892 B (TEX); 17 mi E of Victoria, Johnston 5785 (MEXU, MICH, TEX); 4 mi S of Jaumave, Stanford. Taylor & Lauber 2287 (DS, GH, MICH, MO, NY, SMU, TEX, UC, US); 12 mi S of Laredo, Urbatsch 2407 (OS).

The variability of awns and pubescence on the achenes of Simsia calva led Asa Gray at various times (1846, 1849, 1850, 1873) to position this species under two species and three genera. As in most other species of this genus, however, these features often vary within single populations and are here not afforded formal taxonomic significance. Simsia calva is easily identified by its tuberous root, profuse basal branching, and monocephalous peduncles, and it is not generally confused with any other species.

II. Simsia section Simsia.

Plants annual, but occasionally persisting and woody at base. Nodal discs present or absent. Phyllaries unequal to subequal. Anthers yellow (rarely black in some populations of Simsia dombeyana).

IIA. Simsia series Lagascaeformes D. M. Spooner, sect. nov.-TYPE:

Simsia lagascaeformis DeCandolle

Plantae petiolis et nodis basi plerumque longis pilosis;
phyllariis subaequalibus, purpureis.

Plants with base of petioles and nodes usually long-pilose.
Phyllaries subequal, purple.

13. Simsia lagascaeformis DeCandolle, Prodr. 5: 577. 1836.-Encelia
lagascaeformis (DeCandolle) A. Gray ex Hemsley, Biol.
cent.-amer., Bot. 2: 184. 1881.-TYPE: MEXICO. specific
locality unknown, 1883, Mairet s.n. (holotype: G-DC, IDC 800.
946. II. 81, photos: GH! MICH! MO!).

Simsia lagascaeformis var. glabrior A. Gray, Smithsonian Contr.
Knowl. 3, Art. 5 (Pl. wright. 1): 107. 1852.-S. exaristata
var. perplexa S. F. Blake, Contr. Gray Herb. 52: 45. 1917.,
nomen superfl.-TYPE: U.S.A. Texas: [El Paso Co.], valleys in
the mountains E of El Paso, 12-17 Sep 1849 Wright 331 p.p.
(holotype: K, not seen, tracing and fragment: GH!).

Simsia exaristata A. Gray, Smithsonian Contr. Knowl. 5, Art. 6
(Pl. wright. 2): 87. 1853.-Encelia exaristata (A. Gray) A.
Gray ex Hemsley, Biol. cent.-amer., Bot. 2: 183. 1881.-Simsia
exaristata var. epapposa S. F. Blake, Contr. Gray Herb. 52:
45. 1917, nomen superfl.-TYPE: MEXICO. Sonora: valley of a
tributary of the San Pedro, Sep 1851, Wright 1224 (lectotype,

chosen by Blake, 1913: GHI).

Encelia purpurea Rose, Contr. U. S. Natl. Herb. 1: 336. 1895.

TYPE-MEXICO. Colima: Colima, in a creek bottom, 9 Jan-6 Feb 1891, Palmer 1105 (lectotype, here chosen: US-208967!; isotypes: BM! GH! K! LL! NY! US!).

Encelia pilosa Greenman, Proc. Amer. Acad. Arts 39: 111. 1903.

TYPE-MEXICO. Oaxaca: specific locality unknown, 17 Oct 1899, Holway 3747 (lectotype, chosen by McVaugh, 1984: GHI).

Annuals, but occasionally persisting and woody at base. Stems erect, sometimes decumbent and rooting at the nodes, 0.2-4 m tall, green to yellow, brown, or purple, 2-10 mm diameter, but occasionally persisting and up to 8 cm diameter, glandular-puberulent, sometimes intermixed pilose or strigose. Leaves with petioles 1-7 cm long, often long-pilose at base, 1-2 mm diameter, without wings, or vary rarely petioles amplified at the base; blades ovate to deltate, herbaceous, usually unlobed, rarely narrowly to deeply 3-lobed, 2-21 cm long, 1-16 cm wide, at base cordate to truncate or cuneate, at apex acute or acuminate, with margins crenate to dentate, indument variable, often with both sides scabrous and thinly hirsute, or sometimes puberulent to pilose, usually eglandular but sometimes with stipitate glands. Capitulescence corymbiform, tightly to loosely branched; peduncles 0.5-10 cm long, 1-1.5 mm diameter, glandular-puberulent and hirsute, sometimes eglandular. Heads radiate, 10-14 mm tall, 13-25 mm diameter; involucre campanulate, 8-12 mm tall, 5-10 mm diameter. Phyllaries 2-3 seriate, unequal, 13-19, appressed or slightly reflexed apically,

acute to acuminate at the tips, light green to yellow with purple margins or totally purple, usually glandular-puberulent and pilose, sometimes eglandular; outer phyllaries ovate to lance-ovate, 2.2-6.7 mm long, 1.5-2.5 mm wide; inner phyllaries lanceolate, 4.6-9.5 mm long, 1.5-2.7 mm wide. Ray florets 5-10, ligules orange-yellow, 5.1-12 mm long, 2.3-5.3 mm wide; tubes 1-1.7 mm long, 0.4-0.5 mm diameter, ovaries 3.3-6 mm long, 0.3-0.8 mm diameter. Disc florets 13-27; corollas 5.8-6.7 mm long, 0.8-1.2 mm diameter; lobes 0.8-1.2 mm long, 0.5-0.8 mm wide; anthers yellow below, usually purple apically, 3.2-4 mm long, with terminal appendages stramineous; achenes 4.2-6 mm long, 2-3.5 mm diameter; pappus 2.5-4.6 mm long or more rarely absent. Pales stramineous and purple apically or purple throughout, often nearly truncate apically with an apical mucro, to acute to acuminate at the tips, 5.5-9.4 mm long, 1.4-2.5 mm wide, antrorsely pubescent apically.

Phenology. Flowering specimens can be found throughout the year, but most flower from September-December.

Distribution. (Fig. 25). Mostly in areas of deserts or tropical deciduous forests, along roadsides, open fields, and along borders of agricultural fields; 140-2200 m; S Arizona, S New Mexico, SW Texas, S to central Oaxaca, then in Guatemala.

REPRESENTATIVE SPECIMENS. U.S.A. ARIZONA. Cochise Co., Tombstone, Peebles, Harrison & Kearney 3377 (ARIZ, LL), Mason A-227 (CHAPA). NEW MEXICO: Hidalgo Co., 4 mi SE of jct of NM Rt 81 along dirt rd in Hachita Valley, Keil, Luckow & Luckow 13442 (OB). TEXAS: W. Texas, valley of Rio Grande, below Donada, Parry, Bigelow, Wright, & Schott

Fig. 25. Distribution in Mexico and adjacent United States of Simsia
chaseae, S. eurylepis, and S. lagascaeformis.

Figure 25.

561 (NY, US). Brewster Co., Alpine, Steiger 938 (NY). MEXICO.

CHIHUAHUA: valley near Chihuahua, Pringle 321 (BM, DS, G, GH, K, MASS, MICH, NY); 5.1 mi N of jct of Rt 45 & 49, on rd to city of Chihuahua, Spooner & Brandenburg 2336* (CHAPA, OS, UC, WIS); Hwy 16, 17 mi NE of town square of Aldama, Spooner & Schilling 2456 (BM, COL, G, GH, LE, MEXU, MICH, NY, OS, OSH, TEX, UC, US, WIS); Rt 49, 9 mi S of S limits of Cd. Camargo, Spooner & Schilling 2458* (MEXU, OS, UC, WIS).

COAHUILA. 32 mi NE of San Pedro, on Hwy 30, Henrickson 6009a (LL); Llano de Guaje, on rd from Santa Elena mines NE to Tanque La India, Johnson & Mueller 791 (MEXU, MICH, GH, LL). COLIMA: Colima, Palmer 1105 (BM, K, GH, LL, NY, US). DURANGO: Rt 49, 1 mi NW of Peronal, Spooner & Schilling 2461 (LE, MEXU, OS, TEX, WIS). GUANAJUATO: Municipio Yuriria, Ejido Parangarico, Garcia 2-723 (CAS). GUERRERO: Coyuca, Hinton 5549 (G, GH, K, MO, NY); 15 mi N of Zumpango del Río on Rt 95, 8.4 mi S of Río Mezcala, Keil & Luckow 15331 (OB, OS); Chilpancingo de los Bravos-Chichihualco Rd, 6 mi W of Rt 95, Spooner & Burgos 2603* (BM, LE, MICH, OS, OSH); Rt 95, on S side of Chilpancingo de los Bravos, Spooner & Burgos 2606* (F, MEXU, MO, NY, OS, TENN, TEX, UC, W); 10-30 mi S of Sabana Grande on Rt 95 on rd to Chilpancingo, Stuessy & Gardner 4211 (ASU, ENCB, MO, OS, WIS). HIDALGO: Jacala, Kenoyer 594 (MO). JALISCO: Rt 80, 6 mi SW of San Juan de los Lagos, Spooner & Villaseñor 2489* (C, GUADA, LE, MEXU, MICH, NY, OS, TENN, TEX, RSA, UC, US). MEXICO: Pungarancha, Hinton 8578 (GH, LL, MICH). MICHOACÁN: San Gregorio, Villarreal 196 (ENCB). MORELOS: S side of Cuernavaca on free rd to Acapulco, Spooner & Burgos 2600* (MEXU, OS, TEX, US, WIS); S of Cuautla, 1.7 mi N of rd to Emiliano Zapata, Spooner

2836b (MEXU, OS, US); 10-20 mi S of Cuernavaca on toll rd 95-D, Stuessy & Gardner 4239 (ASU, ENCB, MO, OS, WIS). OAXACA: Rt 190, 14 mi S of Nochixtlán, King 2518 (DS, MICH, US); jct of Rts 131 & 190 in Cd Oaxaca, Spooner & Triplehorn 2098* (CHAPA, OS, TEX, US, WIS); Rt 190, 7.1 mi S of rd to Chicachua, S of Ascunción Nochixtlán Spooner & Dorado 2656* (MEXU, OS, US, WIS); along dirt rd from Jayacatlán to La Unión, 8 mi N of Jayacatlán, Spooner 2831 (MEXU, OS); 1 mi N of Monte Albán Park on rd to Cd. Oaxaca, Stuessy & Gardner 4262 (OS, TEX, WIS). PUEBLA: 20 mi N of Huahuapan de León, Cronquist & Sousa 10403 (ENCB, MEXU, MICH, NY); Cuautla-Matamoros Rd, 9 mi E of Tepexco, Spooner & Dorado 2627* (MEXU, OS, WIS); 4 mi N of Tehuitzingo, Spooner & Dorado 2636* (OS, OSH, UC, US). SAN LUIS POTOSÍ: Río Verde, Calvert 123 a (TEX); El Quelital, Rzedowski 6828 (ENCB, MEXU, MICH, WIS). VERACRUZ: Orizaba, Botteri 804 (GH), Bourgeau 3320 (G, K), Müller 143 (NY), 240 (NY, US), 597 (NY). SONORA: Sonora, Thurber 953 (GH, UC). GUATEMALA. CHIMALTENANGO: Almeda, Johnston 987 (F). GUATEMALA. Antigua, Heiser R5 (IND); caldera, Volcán de Pacaya, Tondus 508 (MO); SACATEPÉQUEZ: near Antigua, Standley 58037 (F, NY), 60374 (CAS, F, U).

Putative hybrid with *S. amplexicaulis*: JALISCO: Rt. 80, 6 mi SW of San Juan de Los Lagos, Spooner & Villaseñor 2491* (MEXU, OS).

The nomenclatural history of *Simsia lagascaeformis* is convoluted and confusing, due in large part to the great taxonomic weight that A. Gray and S. F. Blake placed on the pubescence and presence/absence of awns of the disc achenes. This species, as in many others in *Simsia*, have different individuals polymorphic for this trait within single

populations (see Morphology and Taxonomic Criteria). Simsia lagascaeformis was originally described with glabrous achenes. Gray (1852) described Simsia lagascaeformis var. glabrior based on the sericeous achenes of Wright 331, unaware of the variation of this trait on different sheets of this number. Gray (1853) later discovered this variation and described S. exaristata, based on Wright 331 p.p. (that part of the collection with glabrous, calvous achenes), and Wright 1224 (which unknown to him also varies by this trait). Blake (1913) lectotypified S. exaristata with Wright 1224 (also unaware of the achene variation of this collection), and cited Wright 331 as representative material. He also discovered (by a letter from DeCandolle) that the type collection of S. lagascaeformis had pubescent, awned achenes, not glabrous as originally described. Blake (1917) later independently rediscovered the polymorphic nature of this trait in Wright 331, and validly but superfluously described S. exaristata var. perplexa, based on that portion of this collection with pubescent, awned achenes. Blake (1917, p. 45) by this time realized the tenuous nature of the features separating S. lagascaeformis and S. exaristata, but maintained them as weak segregates on the basis of other characters, the "longer narrower phyllaries, narrower pales, longer disc florets, fewer larger heads, and leaves not at all glandular beneath" of S. exaristata. He suggested, however, that S. exaristata might be better treated as a variety of S. lagascaeformis were it not due to a "striking gap in their ranges". This range gap has been closed with subsequent collections (Fig. 25). A critical examination of the features mentioned above indicates that they vary

considerably throughout the range of the species, and are not taxonomically useful, even at the varietal level. The only discernable trend is for some plants in the northern part of the range to have less gradate phyllaries. While this is pronounced in some individuals, it is far from constant and specimens with less graduate phyllaries are also found farther south.

In addition to this nomenclatural confusion, there are problems regarding the localities of the types of these taxa. Wright's collections have partial or ambiguous locality data, which is complicated by subsequent place name or boundary changes. Another ambiguity is that even though Wright maintained his own collection numbers, these rarely appear on his collections, as they were subsequently distributed by A. Gray under new numbers. Also, these new distribution numbers may incorporate more than one of Wright's collections. Wooten (1906), however, provides data that help clarify the collection localities of Wright 331 and 1224. As no more than one locality each is mentioned in the respective protologues, it is very possible that each number represents a single collection. "El Paso" refers to a town in Mexico, not Texas, but the most likely locality for Wright 331 made in September at "mountains E of El Paso" is in El Paso Co., Texas. Regarding Wright 1224, even though some of Wright's specimens labelled "Sonora" were collected in the United States, the best match for "valley of a tributary of the San Pedro" is in N Sonora, collected in Sep 1849.

Due to the variation in achene morphology in both Wright 331 and 1224, only holotypes are here designated for their respective taxa,

and the others are here listed as potential isotypes. They are Wright 331: BM, GH, OXF; Wright 1224: CGE, G, GH, MO, NY, PH, US, photo: TEX. Blake (1913) cited both GH and US for Wright 1224, but an annotation by Blake on one of the sheets at GH indicates it is his lectotype.

Rose (1895) designated Palmer 1105 as the type of Encelia purpurea. He worked at US, but two sheets of this collection are deposited there, so one of these has been chosen as a lectotype. Blake (1913, p. 383) commented that this species "seems to be merely a peculiarly branched and perhaps somewhat teratological condition, with very numerous capitula and somewhat flattened branches". The branches are mostly terete, but this collection has a normal morphology for S. lagascaeformis. Its small leaves suggest it is new growth from a damaged plant or perhaps a dwarf individual.

The lectotype of Encelia pilosa, Holway 3747 has only Oaxaca for the locality. The only published itinerary of Holway in Mexico (McVaugh, 1972), adds no additional locality data.

Simsia lagascaeformis is almost always an herbaceous species. In some habitats, however, such as along irrigation ditches (e.g., Spooner 2831, 2836b) the plant may persist and become woody. The latter specimen had a woody base to 8 cm diameter and was apparently persistent for quite some time. The leaves of this species are usually unlobed with no wings on the petioles, and lack nodal discs. Rarely, however, lobed leaves and/or petioles with basal wings or nodal discs occur (e.g., some sheets of Spooner & Dorado 2646).

Simsia lagascaeformis is apparently able to hybridize naturally with S. amplexicaulis. Intermediates (Spooner & Villaseñor 2491)

occur with S. lagascaeformis (2489) and S. amplexicaulis (2490). The intermediates possess amplexicaulate leaves of S. amplexicaulis and purple subequal phyllaries of S. lagascaeformis.

14. Simsia eurylepis S.F. Blake, Proc. Amer. Acad. Arts 49: 382.

1913.-TYPE: MEXICO. San Luis Potosí: Distr. Ciudad del Maíz, near Gallinas, Feb 1888, C. & E. Seler 684 (holotype: GH!; isotypes MO! US!).

Simsia submollicoma S.F. Blake, Proc. Amer. Acad. Arts 49: 381.

1913.-TYPE: MEXICO. Tamaulipas: vicinity of Tampico, 10 Mar-18 Apr 1910, Palmer 250 (holotype: GH!; isotypes: BM! F! K! MO! NY! US!).

Annuals. Stem erect, 0.5-3 mm tall, green to purple, 0.5-1 cm diameter, glabrous to sparsely pilose. Leaves with petioles 1-8 mm long, 1 mm diameter, at base often long-pilose, unwinged or with stipules minute-3.2 cm high, these often united from opposite leaves to form nodal discs; blades broadly to narrowly ovate, herbaceous, unlobed to deeply 3-lobed, 3-15 mm long, 2-13 mm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins dentate to crenate, puberulent above and below, sometimes intermixed with hispid hairs and longer pubescent hairs. Capitulescence corymbiform to paniculate, tightly to loosely branched; peduncles subsessile-10 cm long, 1 mm diameter, sparsely to moderately pilose and puberulent. Heads eradiate, 13-16 mm tall; involucre urceolate,

10-13 mm tall, 6-12 mm diameter. Phyllaries 3-seriate, unequal, 19-32, appressed, purple and green, moderately to densely sericeous to pilose; outer series ovate, apex acute to acuminate, 3.7-6.5 mm long, 1.6-2.5 mm wide; inner series ovate to lanceolate, apex acute to acuminate, 8.7-10.7 mm long, 1.5-2.6 mm wide. Ray florets absent. Disc florets 19-41, orange-yellow, corollas 6.3-8.5 mm long, 1.1-1.3 mm diameter, tubes 1.5-2.5 mm long, 0.6-0.7 mm diameter, the lobes 1.5-1.8 mm long, 0.6-0.7 mm wide; anthers yellow, 2.6-3.6 mm long, with terminal appendages stramineous; achenes ovate to obovate, 4.2-5.8 mm long, 2.2-3.6 mm diameter, awns absent or 0.3-5 mm long. Pales stramineous to purple, acute to acuminate at the tips, 7.4-9.8 mm tall, 1.8-3.1 mm wide, antrorsely pubescent apically.

Phenology. Flowering throughout the year.

Distribution. (Fig. 25). Common along roadsides, old fields and other disturbed sites; 0-825 m; along the Gulf coastal lowlands from Tamaulipas to Campeche.

REPRESENTATIVE SPECIMENS. MEXICO. CAMPECHE: along Campeche-Uxmal Rd, 0.5 mi E of jct with Rt 180, Spooner 2799* ** (LE, MEXU, OS, P, TEX, WIS); 3 mi W of Tikirmul, Spooner 2800** (MEXU, MO, OS, WIS); Ichek, Spooner 2801** (MEXU, OS, TEX); W side of Escarcega, Spooner 2812** (MEXU, NY, OS). NUEVO LEÓN: SE side of El Cercado, Spooner 2481* ** (CHAPA, COL, ENCB, F, LE, MASS, MEXU, OS, RSA, TENN, TEX, UC, US, WIS). SAN LUIS POTOSÍ: valley of Río Tampoán, Chase 7494** (ARIZ, CAS, F, GH, MICH, MO, NY); 8 mi S of Valles, Crutchfield & Johnston 5206** (MEXU, MICH, TEX); Cd. Valles, Hansen & Nee 7359 (MO); 9 mi E

of Cd Valles, McGregor 16325 (MSC); El Abra, Rzedowski 7440 (ENCB, MEXU, MICH); Rt 85, 5.1 mi N of jct of Rt 86, Spooner & Brandenburg 2209* ** (GH, MEXU, OS, TEX, US, WIS); 30-40 mi W of Cd. Valles on Rt 86, Stuessy & Gardner 4039** (ASU, CHAPA, ENCB, MO, OS, WIS); 25 mi. E. of Río Verde, Stuessy & Gardner 4041** (ASU, ENCB, MO, OS, WIS); 12 mi E of Cd. Valles, Turner & Turner 80-26M ** (TEX); 19 mi [S] of Antiquo Morelos, Whiffin & Rodriguez 206 (TEX). TAMAULIPAS: along Hwy 85, 111 km NW of Cd. Victoria, Croat 39215 (F, MO); 15 mi from Tampico on the Mante Hwy, Graham & Johnston 4089 (MICH, TEX); 3 mi. E of Casas, Johnston 5776 (MEXU, MICH, TEX); El Bordo, Rzedowski May 19, 1966 (ENCB, WIS); N side of Tampico, Spooner 2884** (MEXU, OS, P, RSA, WIS); along Tampico-Cd Victoria Rd, 14.6 mi SE of jct of rd in town of Manuel to Cd Mante, Spooner 2885** (OS, OSH, TENN, US); along Rt 180, 3.1 mi N of jct of rd to Aldama, Spooner 2886* ** (CHAPA, F, MEXU, OS, WIS); 4 mi S of Los Lavaderos, Spooner 2887** (MEXU, OS) 8.1 mi NE of Manuel, Stuessy and Roberts 3635 (NY, OS, UC). VERA CRUZ: Jalapa-Veracruz Rd, turnoff to Los Baños de Carrizal, Calzada 2052 (ENCB, F, LE, MEXU, NY), Spooner 2882* ** (MEXU, OS); 1 km N of Poza Rica, Hansen & Nee 7414 (MO); 10.8 mi SW of Panuco, Keil & Canne 9231** (OS); banks of Río Plano, Rt 140, 39 km S of Jalapa, Long & Burch 3225 (F, NY); Ídolos, Paray 2881 (ENCB); valley of the Río Pánuco, 15 mi SW of Tampico, Worth 23 (PH).

Simsia eurylepis is a distinctive species that has overall resemblance to *S. lagascaeformis* and is a likely derivative. It differs from the latter by being self-compatible with anthers yellow

throughout (without a purple apical band), prevalence of lobed leaves, and possession of nodal discs. Blake (1913) distinguished this species from S. submollicoma largely by the possession of nodal discs, but this feature varies within populations. Also variable is peduncle length, with some capitulescences tightly aggregated, and others more open with peduncles to 10 cm long. While this character is taxonomically useful in some species, as S. steyermarkii, it has no diagnostic value here. Simsia eurylepis is the only eradiate species of the genus, but it is visited by diverse pollinators (bees, beetles, pers. obser.) and is probably partly outcrossing. The possible hybridization of S. eurylepis with S. foetida to produce S. chaseae has been discussed earlier (see Artificial Hybridizations)

Two anomalous specimens of possible relationship to S. eurylepis are noteworthy: Tamaulipas, vicinity of Tampico, Palmer 52 (BM), which has subequal phyllaries, rays, and black anthers; and Nuevo León, vicinity of Horsetail Falls, El Cercado, Duke 3992 (MO), which has harsh pubescent leaves, partly subequal phyllaries and brownish anthers. Neither population has been located in the field despite extensive searches. These are possibly of hybrid origin involving some other species of Simsia, or they may represent extremely local undescribed taxa. More material is needed before proper affinities can be determined.

IIb. Simsia series Simsia.

Base of petioles and nodes glabrous or strigose or hispid. Phyllaries unequal (subequal in some populations of S. chaseae), usually yellow or black.

15. Simsia chaseae (Millspaugh in Millspaugh & Chase) S. F. Blake, Proc. Amer. Acad. Arts 49: 385. 1913.- Encelia chaseae Millspaugh in Millspaugh & Chase, Publ. Field Columbian Mus., Bot. Ser. 3: 125. 1904.-TYPE: MEXICO. Yucatán: ruins of Kobah, 26 Nov 1865, Schott 911 (lectotype, designated by Blake, 1913: F-1760201; isoelectotype: F1).

Annuals, but occasionally persisting and woody at base. Stems erect, 0.3-3 m tall, green to purple or yellow, 2-20 mm diameter, glandular-puberulent and hispid. Leaves with petioles 1-7 cm long, 1-2 mm diameter, without wings or discs; blades broadly to narrowly ovate to deltate, herbaceous, unlobed to 3-lobed one-half way to the midrib, 3-18 cm long, 2-15 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenate to dentate, with both sides glandular-puberulent, sometimes with thinly scattered scabrous or hirsute hairs. Capitulescence corymbiform, loosely branched; peduncles 1-6.5 cm long, 1 mm diameter, glandular-puberulent and hirsute. Heads radiate, 12-16 mm tall, 10-15 mm diameter; involucre urceolate, 11-15 mm tall, 7-12 mm diameter. Phyllaries 3-seriate, unequal to almost subequal, 16-32, 3-seriate, appressed to slightly

reflexed apically, green to yellow or brown, acute to acuminate at the tips, glandular-puberulent and hispid; outer phyllaries ovate to lance-ovate, 5-9.5 mm long, 1.1-2 mm wide; inner phyllaries lanceolate, 7.8-10.2 mm long, 1.2-2.2 mm wide. Ray florets 6-13, ligules light lemon-yellow, 4.2-9 mm long, 1.5-3.2 mm wide; tubes 1-1.6 mm long, 0.3-0.5 mm diameter; ovaries 5-7.4 mm long, 0.4-0.5 mm diameter. Disc florets 21-67; corollas 5.3-6.3 mm long, 0.8-1 mm diameter; tubes 0.8-1.6 mm long, 0.4-0.6 mm diameter; lobes 0.4-0.8 mm long, 0.4-0.8 mm wide; anthers yellow, rarely blackish apically, 2.2-3.2 mm long, with terminal appendages stramineous; achenes 4.2-6.1 mm long, 2.5-3.8 mm diameter, awns absent or 1.8-3.2 mm long. Pales stramineous, sometimes flecked greenish-black apically, acute or acuminate at the tips, 7.5-9.3 mm long, 1.8-3 mm wide, scabrous apically.

Phenology. Flowering June-November.

Distribution. (Fig. 25). Roadsides, borders of agricultural fields, and other weedy areas; 0-600 m; along the Gulf coastal lowlands in central and southern Veracruz, and in the northern part of the Yucatan Peninsula.

REPRESENTATIVE SPECIMENS: MEXICO. CAMPECHE: Rt 261, 5.1 mi S of Campeche-Yucatán border, Spooner 2802* ** (MEXU, OS, OSH, TEX, UC, US). QUINTANA ROO: Santa Rosa, jct of rd to Peto and rd to Tzucacab, Spooner 2811* ** (GH, MEXU, MO, OS, P, TEX, UC, US). VERACRUZ: Cerro Gordo, Dorantes, Acosta, Calles, & Marquez 1743 (ENCB, MEXU, MO), Spooner 2880** (F, MEXU, OS, TENN, TEX, UC); Zacuapan, Purpus 7472

(UC), 11121** (F, NY, US), 13085 (MO), 13095 (F, K), 15002 (F); crossing of Jalapa-Huatusco Rd & Río Pescado, Turner & Tapia 15522 (TEX); 13.4 mi W of Rt 140, near Puente Nacional, on rd to Huatusco, Spooner 2859** (OS); Jalapa-Veracruz Rd, at jct of rd to Carrizal, Spooner 2881* ** (MEXU, OS); 3.8 mi E of Tuzamapan, Zola 12 (TEX). YUCATAN: Uxmal, Degener 26757 (US), Gustafsson 1471 (US); Izamal, Gaumer 910 (CAS, F, G, GH, MO, NY, S); Chichankanab, Gaumer 2045** (B, BM, C, F, GH, MO, NY, S, US); Calotmul Gaumer 2046 (CAS, LE, W); Ruins of Kobah, Spooner 2803 (GH, LE, MEXU, OS); Rt 180, just NW of Santa Elena, Spooner 2804* ** (MEXU, OS); 2.7 mi SE of town square of Muna on rd to Ticul, Spooner 2805** (MEXU, OS); 4.9 mi S of town square of Uman on Rt 180, Spooner 2806 (OS); Progreso-Mérida Rd, 4.4 mi S of rd to Yukalpetén, Spooner 2807a* (OS); 6.1 mi NW of town square of Motul, on rd to Baca, Spooner 2807b (OS); 1.2 mi E of Temax, Spooner 2808 (OS); Motul-Tizimin Rd, 6.7 mi W of rd to Cenotillo, Spooner 2809* ** (OS); Chichén Itzá, Steere 1026 (GH, LL, MICH, TEX), 1625 (MICH); Progreso, Steere 3027 (LL, MICH).

Simsia chaseae is remarkably similar to S. dombeyana, and it often is difficult to distinguish these species (see Numerical Taxonomy of S. chaseae and S. dombeyana). The former usually has outer phyllaries 3/4 or less the size of the inner phyllaries, and the latter almost always has subequal phyllaries. This character, in addition to the obvious distributional and phenological differences simplifies many identifications. Some individuals of S. chaseae, however, have more subequal phyllaries, but S. dombeyana generally has

larger heads and associated head parts.

Simsia chaseae is intermediate in many features between S. eurylepis and S. foetida, and possibly has been produced by diploid hybrid speciation between them (see discussion under Artificial Hybridizations). Its overall resemblance is closer to S. foetida, sharing its yellowish color, highly glandular nature, and foetid odor. It is best distinguished from this species, however, by its sparingly glandular-pubescent leaves that often appear almost glabrous to the naked eye, the usually shorter outer phyllaries, and its urceolate heads.

16. Simsia dombeyana DeCandolle, Prodr. 5: 578. 1836.-Encelia hirsuta f. radiata Kuntze, Revis. gen. pl. 3(2): 145. 1898., nomen superfl.-TYPE: PERU. Lima, [1778-1788, fide Ruiz, 1940], Dombey 12 (holotype: P!, photo: OSI, fragment: US!; isotypes: B, destroyed, photos: CMI GH! TEX!; G-DC, photos: IDC. 800. 946. III. 8! GH! MO! NY! TEX!, tracing: GH! MPU!).

Encelia hirsuta Kuntze, Revis. gen. pl. 3(2): 145. 1898.-Simsia hirsuta (Kuntze) S. F. Blake, Proc. Amer. Acad. Arts 49: 389. 1913.-TYPE: ARGENTINA. Córdoba: Dique near Córdoba, Dec 1841, Kuntze s.n. (lectotype, here designated: US-701505!; isoelectotypes: NY [2]! US!, fragment: GH!).

Annuals. Stems erect, 0.4-3.5 m tall, green to purple or yellow, 3-30 mm diameter, glandular-puberulent and hispid. Leaves with

petioles 1-8 cm long, 1-2 mm diameter, without wings or discs; blades ovate to deltate, herbaceous, usually unlobed but sometimes slightly lobed to lobed one-half way to the midrib, 3-15 cm long, 2-12 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenate to dentate, with both sides glandular-puberulent, with intermixed scabrous and hirsute hairs. Capitulescence corymbiform, loosely branched; peduncles 2-15 cm long, 1-2 mm diameter, glandular-puberulent and hirsute. Heads radiate, 12-18 mm tall; 9-17 mm diameter; involucre urceolate, 10-16 mm tall, 9-15 mm diameter. Phyllaries 3-seriate, subequal, 16-32, appressed to slightly reflexed at the tips, green to yellow or brown, lanceolate, acute or acuminate at the apex, glandular-puberulent and hispid; outer phyllaries 8-12 mm long, 1.6-3.1 mm wide; inner phyllaries 8-12.5 mm long, 1.2-2.9 mm wide. Ray florets 6-13, ligules light lemon-yellow, 2.5-10 mm long, 1.3-2.9 mm wide; tubes 0.5-2.3 mm long, 0.2-0.5 mm diameter; ovaries 3.7-8.2 mm long, 0.4-0.5 mm diameter. Disc florets 23-82; corollas 4.2-8.4 mm long, 0.7-1.1 mm diameter; tubes 0.7-2.3 mm long, 0.4-0.6 mm diameter; lobes 0.3-0.7 mm long, 0.4-0.6 mm wide; anthers yellow to black, 1.8-3.5 mm long, with terminal appendages stramineous; achenes 5-7.5 mm long, 2.5-3.9 mm diameter, awns 1.2-4.6 mm long. Pales stramineous, sometimes purple or speckled black apically, acute or acuminate at the tips, 7.7-10.5 mm tall, 1.8-2.8 mm wide, scabrous apically.

Phenology. Flowering specimens can be found throughout the year, but most flower from December-May.

Distribution. (Fig. 20). Roadsides and disturbed ground; 40–2020 m; throughout the Andean chain from Ecuador, Peru, Bolivia, and the northern parts of Argentina, east to Entre Rios, Argentina, and in eastern Brazil in the states of Bahia and Minas Gerais.

REPRESENTATIVE SPECIMENS: ECUADOR. GUAYAS: along rd. to Daule, 17 km E of Palestina, King & Garvey 7008 (F, MO, NY, UC, US); 2 km N of Daule, Spooner 2907* ** (OS, TENN, UC); 3.5 km NE of Durán, Spooner 2908* ** (OS, TEX, US). LOJA: slopes of Cerro Villonaco, Harling & Andersson 13338** (US). PERU. CAJAMARCA: 15 km E of Chilete on Cajamarca–Pacasmayo Rd., Dillon & Dillon 4618* (MO, OS); km 124 of Pacasmayo–Cajamarca Rd., near Choropampa, Sánchez 2368 (CHAPA, SI). LAMBAYEQUE: Pampa de Olmos, between Motupe & Piura, Ferreya 12369 (MO). LA LIBERTAD: Cerro Cabezón, Sagástegui & Cabanillas 8740 (F, SI). LIMA: km 56, Central Rd, Ferreya 10482 (MO). PIURA: 32 km S of Piura, Piura–Chiclayo Rd, Ferreya 5902** (US); Hacienda Pabur, Piura–Huancabamba Rd, Ferreya 6037** (F, NY, US); Cabo Blanco, Haught 249** (BM, GH, NY, US); between Piura & Nomala, Weberbauer 5934** (F, G, GH, US). TUMBES: Lechugal, Ferreya 10662 (MO); Mancora Valley, 50 mi N of Tumbes, Haught 155 (NY, US). BRAZIL. BAHIA: 12 km W of Irecê, Coleman 505 (US); valley of Rio Formoso, 40 km SE of Correntina, Harley 21718 (K, US); 5 km N of Tobocas, Harley, Bromley, DeCarvalho, Hage & Brito 21987 (K, NY, US); 32 km S from rd between Itaberaba & Ibotirama, along rd to Andaraí, King & Bishop 8704 (US). MINAS GERAIS: 2 km along rd N of Mato Verde towards Monte Azul, King & Bishop 8586** (K, US). ARGENTINA. CATAMARCA: between Alijilán & El Alto, Cristóbal

328** (UC); Andalganá, Jørgensen 1286** (BAB, GH, MO, SI, UC), Turner 9232 (LL); Santa María, Morello 280** (LIL). CÓRDOBA: near Córdoba, Castellanos, 94 (SI), Stuckert 6403 (SI); Pampas, Reise, Kuntze Jan, 1982 (NY); Quebrada de Las Rosas, Lanfranchi 1314 (SI). ENTRE RÍOS: Paraná, Burkhart 22337** (SI); Diamante, Burkhart 22323 (SI). JUJUY: Alto de la Vina, Cabrera & Kiesling 24908** (SI). SALTA: aeropuerto, Dept. Capital, Krapovickas & Schinini 35947 (OS); Prov. Cafayate, Rodríguez 1442** (BAB, SI). SANTIAGO DEL ESTERO: Dept. Guasayán, El Cevillar, Pierotti Mar, 1944 (U). TUCUMÁN: Vipos, Dinelli 812 (BAB), Lillo 7951 (BAB), 25375 (GH, US), Venturi 4999 (US); San Pedro de Colalao, Venturi 6277** (US). BOLIVIA. COCHABAMBA: Mizque, Prov. Campero, Steinbach 711 (GH, MO, NY, WIS). TARIJA: Prov. Avilés, Chocloca, Beck & Saenz 724 (LPB, SI, US).

The holotype information of Simsia dombeyana comes from diverse sources. The protologue and holotype sheet of Simsia dombeyana mention only "Perou" for the locality. A specimen at MPU, a repository for many Dombey duplicates (Stafleu & Cowan, 1976) has "Lima au Perou" but no other data and is considered isotype material. A probable isotype at G-DC has the collection number 12.

Kuntze (1898) cited three specimens for Encelia hirsuta f. radiata, including a Dombey specimen at B. As this sheet is probably the holotype of Encelia hirsuta, this is an illegitimate name.

Blake (1913) cited and annotated two specimens at US as type material for Encelia hirsuta without designating a specific holotype. A lectotype is selected herein.

Simsia dombeyana is one of the three self-compatible species in the genus and is so similar to S. chaseae that a combination of features often is necessary to distinguish them. It may have originated from S. chaseae from long-distance dispersal from Mexico (see Artificial Hybridizations).

Simsia dombeyana also possesses much floral variation. For example, Ferreyra 6037 has disc corollas 8.4 mm long and tubes 2.3 mm long, while Burkhart 22337 has measurements of 4.2 and 1.0, respectively, a range of size variation that partly separates varieties in S. foetida. These variants show no geographical correlation, however. One feature that does exhibit some geographic correlation is anther color which is yellow in the northern part of the range and is often black in the southern part (e.g., in the south Beck & Saénz 724, Cabrera & Kiesling 24908, Cristóbal 328, Dinelli 812, and Jørgensen 1286). Black anthers are rare in Simsia section Simsia and this trait has likely undergone a reversal in this southern part of the range.

One collection of ambiguous identity cited by Kuntze (1898) as a representative of Encelia hirsuta f. radiata (COLOMBIA. Bolívar: Cartagena, 1825-1826, Billberg s. n. (S, 4 specimens), has sinuate phyllaries more typical of S. foetida but with an overall appearance of S. dombeyana. It may be of hybrid origin.

Burkhart (1974) and Cabrera (1978) concluded that many specimens of S. dombeyana were eradiate. All specimens examined in this study have ray ovaries indicative of the radiate nature of this species. Some specimens have very small rays not or only slightly exerted

beyond the phyllaries, and the rays in this species as in all others in the genus are readily deciduous; features which likely misled them to interpret the species as eradiate.

17. Simsia amplexicaulis (Cavanilles) Persoon, Syn. pl. 2: 478. 1807.

Coreopsis amplexicaulis Cavanilles, Descr. pl. 226. 1802.

Encelia amplexicaulis (Cavanilles) Hemsley, Biol. cent.-amer.,

Bot. 2: 183. 1881. Simsia amplexicaulis var. genuina, S. F.

Blake, Contr. Gray Herb, 52: 46. 1917, nomen superfl.-TYPE:

MEXICO. cultivated in the Royal Botanic Garden of Madrid, from unvouchered seed of the Sesse and Mocino expedition.

(holotype: MA1, photo: OS!).

Ximenesia cordata Kunth in Humboldt, Bonpland & Kunth, Nov. gen.

sp. 4 [folio]: 178. 1818; 4 [quarto]: 228. 1820.-Simsia

cordata (Kunth in Humboldt, Bonpland & Kunth) Cassini, Dict.

sci. nat., 59: 137. 1829. Encelia cordata (Kunth in Humboldt,

Bonpland & Kunth) Hemsley, Biol. cent.-amer., Bot. 2: 183.

1881.-TYPE: MEXICO. Michoacán: "Valladolid de Mechoacan" [=

Morelia fide Sprague, 1924] "et prope Capula Mexicanorum"

[Aug-Sep 1803 fide Sprague, 1924], Bonpland 2350 (holotype:

P-HBK, IDC 6209. 109. I. 31; isotype: P!).

Ximenesia heterophylla Kunth in Humboldt, Bonpland & Kunth, Nov.

gen. sp. 4 [folio]: 178. t. 380. 1818; 4 [quarto]: 227. 1820.

non Simsia heterophylla (Cavanilles) Persoon, Syn. pl. 2: 478.

1807. Simsia kunthiana Cassini, Dict. sci. nat. 59: 137. 1829,

nomen superfl. Simsia heterophylla (Kunth in Humboldt, Bonpland & Kunth) DeCandolle, Prodr. 5: 577. 1836. Encelia heterophylla (Kunth in Humboldt, Bonpland & Kunth) Hemsley, Biol. cent.-amer., Bot. 2: 184. 1881, -TYPE: MEXICO. Michoacán: near "Zinapequaro" [= Zinapécuaro] "alt 960 hex" [5808 ft, Sep-Oct, 1803, fide Sprague, 1924], Bonpland 4360 (holotype: P-HBK, IDC 6209. 109. I. 21).

Helianthus trilobatus Link, Enum. hort. berol. alt. 2: 352. 1822 [fide Blake, 1917, p. 46].-TYPE: MEXICO. exact locality unknown, cultivated in the Botanic Garden at Berlin (holotype: B, destroyed).

Simsia auriculata DeCandolle, Prodr. 5: 577. 1836. sub Encelia mexicana Martius ex Hemsley, Biol. cent.-amer., Bot. 2: 184. 1881, nomen superfl.-TYPE: MEXICO. [Distrito Federal?]: near Mexico City, Sep 1827, Berlandier 927 (lectotype, chosen by Blake, 1913: G-DC, IDC 800. 946. III. 41; isolectotypes: BM! FI FII G[3]! LE! MO! OXF! PI W [3]!).

Encelia mexicana Martius ex DeCandolle, Prodr. 5: 578. 1836, pro syn. sub Simsia auriculata, based on: MEXICO. locality unknown, Jan 1822, Karwinski s.n. (BR!)

Ximenesia hirta Martius ex DeCandolle, Prodr. 5: 578. 1836, pro syn. sub Simsia auriculata.

Helianthus amplexicaulis DeCandolle, Prodr. 5: 589. 1836.-TYPE: MEXICO. Guanajuato: Province of León, W of the town of "Guanaxuato" [= Guanajuato] 1829, Mendez s.n. (holotype: G-DC, IDC 800. 951. I. 61).

Simsia schaffneri Schultz-Bipontinus ex A. Gray, Proc. Amer. Acad.

Arts 19: 8. 1883., pro syn. sub Encelia mexicana Martius ex Hemsley, based on: MEXICO. [Distrito Federal?]: valley of Mexico, Aug 1854, Schaffner 162 (GH!, B, destroyed, photos: GH! TEX!).

Helianthus sericeus Sessé and Mociño, Pl. nov. Hisp. 147.

1890.-TYPE: MEXICO. [Morelos]: "Ayacapixtla" [= Yecapixtla], "Sep" [probably Nov 1788, fide McVaugh, 1977], Sessé & Mociño s.n. (holotype: MA, not seen, probable isotype: OXF!).

Simsia foetida (Cavanilles) S. F. Blake var. decipiens S. F.

Blake, Proc. Amer. Acad. Arts 49: 387. 1913. Simsia amplexicaulis (Cavanilles) Persoon var. decipiens (S. F. Blake) S. F. Blake, Contr. Gray Herb 52: 46. 1917.-TYPE: MEXICO. Chihuahua: "SW Chihuahua, Aug-Nov 1885" [Norogachic, 13-25 Nov, fide McVaugh, 1956], Palmer 440, (holotype: GH!; isotypes: K!, LE! LL! MEXU! MO! NY [2]! UC!).

Annuals. Stems ascending or erect, sometimes decumbent at the base and rooting at the nodes, 0.1-3 m tall, green to yellow, brown, or purple, 1-10 mm diameter, glandular-puberulent and scabrous with intermixed hirsute hairs. Leaves with petioles 1-11 cm long, 1-2 mm diameter, often winged throughout and clasping at the dilated base, or only partially winged, or entirely unwinged; blades ovate to deltate, herbaceous, narrowly to deeply 3-lobed or unlobed, 2-18 cm long, 1-14 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenate to dentate, with both sides scabrous

and strigose, sometimes hirsute, usually eglandular. Capitulescence corymbiform to paniculate, loosely branched; peduncles 1-12 cm long, 1-1.5 mm diameter, glandular-puberulent, scabrous and hirsute. Heads radiate, 12-14 mm tall, 22-35 mm diameter; involucre ovoid-campanulate, 10-12 mm tall, 7-13 mm diameter. Phyllaries 2-3 seriate, nearly subequal, with the outer series usually slightly shorter than the inner, 15-22, moderately to greatly reflexed, acute to caudate at the tips, dark green to black, rarely purple, scabrous and hirsute, sometimes glandular; outer phyllaries lanceolate, 5-14 mm long, 1-2.5 mm wide; inner phyllaries lanceolate to linear, 6.1-14 mm long, 1.3-2.2 mm wide. Ray florets 8-14, ligules orange-yellow, 8-16 mm long, 3.7-7.5 mm wide; tubes 0.7-1.7 mm long, 0.3-0.5 mm diameter; ovaries 4.6-6.5 mm long, 0.5-0.9 mm diameter. Disc florets 23-55; corollas 5.2-6.5 mm long, 1-1.5 mm diameter; tubes 0.8-1.3 mm long, 0.5-0.7 mm diameter; lobes 0.8-1.3 mm long, 0.6-0.8 mm wide; anthers yellow below, usually purple (often drying bronze) apically, 3.2-4.2 mm long, with terminal appendages stramineous; achenes 3.5-5.5 mm long, 1.8-3 mm diameter, pappus 2.2-3.8 mm long or more rarely absent. Pales stramineous, usually flecked with black, especially above, rarely purple, acute to acuminate at the tips, 6.7-10.2 mm tall, 1.2-3.2 mm wide, antrorsely pubescent apically.

Phenology. Flowering specimens can be found throughout the year, but most flower from September-November.

Distribution. (Fig. 26). Mostly in areas of oak-pine forests, along roadsides, agricultural fields, wet alpine meadows, and in oak-pine woodlands; 1350-2990 m, but usually above 1600 m; northern

Fig. 26. Distribution in Mexico and adjacent United States and
Central America of Simsia amplexicaulis.

Figure 26.

Chihuahua to Nuevo Leon, SW to Honduras.

REPRESENTATIVE SPECIMENS. MEXICO. AGUASCALIENTES: Hwy 70, 3 mi E of La Sauz, Sundberg & Lavin 2922 (OS, TEX); CHIAPAS: N edge of San Cristóbal de las Casas, Breedlove & Raven 12434 (CAS, DUKE, MEXU, MICH), 13283 (DS, ENCB, F, LL, MICH, NY, US); Tuxtla Gutiérrez, Spooner 2780* (MEXU, OS); Rt. 195, 0.6 mi E of footpath to Pinabeto, Spooner 2794 (COL, MEXU, OS, UC, US); Rd to Zinacantan, 2 mi N of San Cristóbal de las Casas, Stuessy & Gardner 4304 (ASU, CHAPA, ENCB, MO, OS, WIS). CHIHUAHUA: 1/2 mi W of Cuauhtémoc, Powell & Edmondson 998 (TEX); 15 mi SW of Buenaventura, Spooner & Schilling 2453* (BM, COL, G, GH, LL, MEXU, MICH, NY, OS, OSH, P, TEX, UC, US); E of Cuauhtémoc, Spooner & Schilling 2455* (LE, MEXU, MICH, NY, OS, P, UC, US). COAHUILA: Saltillo, Palmer 422 (BM, C, F, G, GH, MSC, MO, NY, S, US); Parras, Palmer 427 (BM, C, F, G, GH, MEXU, MO, MSC, NY, UC, US); Hwy 57, 6 mi SE of turnoff to Arteaga, Spooner & Schilling 2463* (BM, COL, G, GH, LE, MEXU, MICH, NY, OS, TEX, UC). DISTRITO FEDERAL: near México City, Berlandier 850 (BM, G, LE, OKF, W); Xochimilco, Rzedowski 1062 (CHAPA, ENCB, LJ, MEXU, OS). DURANGO: Durango, Palmer 657 (C, CAS, F, G, GH, MEXU, MICH, MO, NY, UC, US); Rt 45, 19.7 mi N of traffic circle on N side of Durango, Spooner & Brandenburg 2326 (CHAPA, OS). GUANAJUATO: "Guanaxuato" Hartweg 145 (BM, CGE, G, OKF, P); 1 km W of San Luis de La Paz, García 64 (CHAPA, MEXU). HIDALGO: Rt 105, 10 mi SE of Pachuca, Spooner & Brandenburg 2229* (CHAPA, OS); Municipio de Tepeapulco, Ranchería Los Cides, Ventura 1723 (ARIZ, CAS, CHAPA, ENCB, MEXU, OS). JALISCO: fields near Guadalajara, Pringle 4266 (BM, BR, F,

G, GH, GOET, JE, LE, M, MASS, MEXU, MO, MSC, NY, S, TEX, UC, US, W); Rt 80, bypass around Tepatitlán, Spooner & Brandenburg 2302* (CHAPA, OS); Rt 80, W limits of Jalostotitlan, Stuessy & Gardner 4095 (ASU, MO, OS, WIS); Rt 80, between Lagos de Moreno & Ojuelos, Stuessy & Gardner 4083 (ASU, MO, OS). MEXICO: Rt 85, 20 mi N of rd to pyramids (Rt 30), Powell & Edmondson 599, (MICH, TEX), 603 (MICH, TEX); 1 mi W of Tepetlaoxtoc, on rd to Jalopan, Spooner & Brandenburg 2232* (CHAPA, OS); Rt 15, 7 mi W of Toluca, Stuessy & Gardner 4192 (OS); Rt 55, 0.5 mi S of Tenancingo, Stuessy & Gardner 4196 (ASU, ENCB, MO, OS, WIS). MICHOACÁN: Rt 15, 14 mi W of Zamora, Powell & Edmondson 840 (MICH, TEX); Rt 15, near intersection of rd to Zinapécuaro, Spooner & Villaseñor 2557 (MEXU, OS, OSH, US). MORELOS: Coajomulco, Díaz 153 (DS, ENCB, MICH, NY). NUEVO LEÓN: 8.7 mi NW of San Rafael, Sundberg, Nixon, Grimes, & Dorr 1744 (OS, TEX). OAXACA: Rt 190, 1 mi SE of Asunción Nochixtlán, Spooner & Dorado 2654* (B, G, LE, MEXU, MO, OS, UC, US); Rt 190, 10 mi SE of Nochixtlán, Stuessy & Gardner 4259 (OS). PUEBLA: Rt 190, just E of San Martín Texmelucan, King 2239 (TEX, US); Rt 140, 22 mi NE of Tepeaca, Powell & Edmondson 640 (F, MEX, MICH); 3 mi SE of Cd Serdán, Spooner & Triplehorn 2048 (CHAPA, OS, UC, US, WIS). QUERETARO: Cadereyta, Kelly 672 (UC). SAN LUIS POTOSÍ: 2 mi S of Venado, Spooner & Brandenburg 2195* (OS). TLAXCALA: San Juan Quetzalcoapan, Vibrans 410 (ARIZ, MEXU, OS, U). VERACRUZ: Guadalupe Victoria, Turner 15197 (TEX). ZACATECAS: 8 mi E of Zacatecas on rd to Aguascalientes, Garcia 805 (CAS, CHAPA, TEX); Rt 85, 10 mi SE of Arriaga, Spooner & Villaseñor 2488 (OS). GUATEMALA. BAJA VERAPAZ: Purulhá, Spooner & Dorado 2751* (MEXU, OS, TENN, UC). CHIMALTENANGO:

Aldea El Parcelamiento, near Chocoyos, Spooner & Dorado 2684* (MEXU, OS, UC). EL QUICHÉ: Utatlán Ruins, Molina & Molina 25095 (C, P, NY, US). HUEHUETENANGO: Rt 9N, 3 mi S of Huehuetenango, King 3415 (DS, MICH, NY, TEX, UC). JALAPA: between Jalapa & Montaña Miramundo, Steyermark 32894 (F, GH). QUEZALTENANGO: vicinity of Zunil, Standley 83164 (F). SACATEPÉQUEZ: Volcan de Agua near Santa María de Jesús, Spooner & Dorado 2687 (F, MEXU, MO, OS). SAN MARCOS: near Castalia, Spooner & Dorado 2673* (MEXU, OS). SOLOLÁ: near Nahuala, Williams, Molina, & Williams 41437 (F, NY). TOTONICAPÁN: jct of Rt CA-1 & rd to San Francisco el Alto, Stuessy & Gardner 4335 (ENCB, OS). HONDURAS. MORAZÁN: Cerro de Uyuca, Sauer 1582 (UC, WIS).

Simsia amplexicaulis is an extremely variable species. Some plants may be profusely branched and attain a height of three meters, while others within the same population may be stunted, unbranched individuals flowering at 0.1 meter tall. Leaf shape is especially variable, with petiolar wings absent or present, and leaves lobed or not.

The species is one of the dominant weeds in upland areas in Mexico (Rzedowski, 1983), and is frequently found along the borders of agricultural fields, along irrigation ditches, about human dwellings, and even growing from cracks in asphalt along roads. In a more natural setting it is a component of pine-oak forests.

It sometimes is difficult to distinguish specimens of *Simsia amplexicaulis* from *S. foetida* var. *foetida* and var. *guatemalensis*. In some cases this may be due to hybridization between the two species

(see discussion under S. foetida). Both have subequal to nearly subequal phyllaries, often with caudate tips. Simsia amplexicaulis generally has green, non-glandular leaves and dark green to blackish phyllaries, whereas S. foetida var. foetida generally has yellowish, densely stipitate-glandular leaves and yellowish phyllaries. These differences are very pronounced in the field, where the glandular, spicy-smelling and viscid leaves of the latter are easily distinguished from those of the former. Additionally, these species grow in very different habitats. Although there is considerable overlap in their absolute elevational tolerances throughout their ranges, S. foetida grows in the hot lowlands and S. amplexicaulis grows in the cool uplands, and they rarely co-occur. Also, S. amplexicaulis apparently hybridizes with S. lagascaeformis (see discussion under that species).

The type specimens for Simsia amplexicaulis and S. foetida were grown from seed from the Sessé and Mociño expedition, probably sent by Vincente Cervantes (Cavanilles, 1791; McVaugh, 1977). No specific locality is provided by Cavanilles, and this expedition covered much of central, western, and southern Mexico (McVaugh, 1977); the exact locality of these plants, therefore, is uncertain. A mixed sheet bearing four fragmentary specimens, labelled Coreopsis amplexicaulis and C. foetida in Cavanilles's handwriting (comparison from Burdet, 1973) represents a possible isotype, but no designation as such is made here because of historical uncertainty. Further, they may represent hybrids (see S. foetida var. foetida for a discussion of this problem.)

The holotypes of Ximenesia cordata and X. heterophylla do not bear Bonpland's name on the collections, but it is included in the type citations as Stearn (1956) documents that most of the specimens made during the travels of Humboldt and Bonpland were collected by the latter.

Cassini (1829) published Simsia kunthiana as a substitute for Ximenesia heterophylla Kunth 1818 which he accepted as a Simsia. He published this name due to the existence of the earlier Simsia heterophylla (Cavanilles) Persoon (1807), which is today accepted as an Iostephane (Strother, 1983).

Encelia mexicana and Simsia mexicana have been commonly used epithets, and these names appear on many specimens of S. amplexicaulis. Encelia mexicana was originally published by DeCandolle under synonymy with S. auriculata. The specimen upon which E. mexicana Martius ex DeCandolle is based has a printed label "Herbarium Martii" with "Simsia auriculata" written by DeCandolle on a fragment packet. The name was later validly but superficially published by Hemsley (1881) and accepted by Gray (1883) and later authors. It was misapplied to S. fruticulosa by Klatt (1887), and it was accepted and utilized until Blake (1913) placed it in synonymy with S. foetida and later with S. amplexicaulis Blake (1917).

The specimen upon which Simsia schaffneri is based, J. G. Schaffner 162, "valley of México" was most likely collected in the Distrito Federal or the state of México. Even though the valley of Mexico encompasses parts of Hidalgo, the Distrito Federal, México, and Morelos, Rzedowski (1959) documents that most of Schaffner's

collections during this time were in areas near México City.

The locality of Helianthus sericeus, "Ayacapixtla", was given various spellings in Pl. nov. Hisp. (Sessé & Mociño, 1890) but refers to Yecapixtla in Morelos (not Mexico fide Sprague, 1926), that was visited by the Sessé and Mociño expedition in Nov 1788 (McVaugh, 1977). The protologue says "flowers in Sep", but flowering times earlier than November are commonly given for these collections in this publication (McVaugh, 1977). The probable isotype at OXF bears "Helianthus sericeus" in Mociño's handwriting (comparison from Burdet, 1977). Duplicates of the Sessé and Mociño collections were distributed in many herbaria, including OXF (Stafleu and Cowan, 1985). There are other fragments of S. amplexicaulis and S. lagascaeformis from MA at F that bear names that apparently never were published. These fragments apparently were taken from specimens when the entire Sessé and Mociño herbarium was sent to F on a long-term loan in the 1930's (McVaugh, 1977).

The holotype of Simsia amplexicaulis var. decipiens has the calvous achenes that were used to distinguish this variety, but the US isotype bears awned achenes, an intrapopulational variation pattern common within many populations of various Simsia taxa.

18. Simsia foetida (Cavanilles) S. F. Blake, Proc. Amer. Acad. Arts 49: 385. 1913. Coreopsis foetida Cavanilles, Icon. 1: 55. t. 77. 1791. Simsia ficifolia Persoon, Syn. pl. 2: 478. 1807, nomen. superfl. Ximenesia foetida (Cavanilles) Sprengel, Syst.

veg. 3: 606. 1826. Encelia foetida (Cavanilles) Hemsley, Biol. cent.-amer., Bot. 2: 183. 1881. ~TYPE: MEXICO. cultivated in the Royal Botanic Garden of Madrid, from unvouchered seed from the Sessé & Mocino expedition (holotype: MA!, photo: OSI; isotype: MA!).

Encelia adenophora Greenman, Proc. Amer. Acad. Arts 39: 109. 1903.

Simsia adenophora (Greenman) S. F. Blake. ~TYPE: MEXICO.

Jalisco: Tequila, fields and copses, Sep-Oct 1893, Pringle 4602 (lectotype, chosen by Blake, 1913: GH!; isolectotypes: BM! BR! F! G [2]! GOET! JE! K! LE! MI MEXU [2]! MSC! NY! SI UC! US! [2]!).

Annuals, occasionally persisting and woody at base. Stems erect, 0.5-4 m tall, yellow-green to green or purple, 0.2-2 cm diameter, usually copiously glandular-puberulent, setose or pilose, sometimes hispid. Leaves with petioles 1-10.5 cm long, 0.5-1.5 mm diameter, naked, winged, or sometimes auriculate-clasping, at base with stipules of opposite leaves absent or present, unfused or fused with those of opposite leaves to form nodal discs 0-3.5 cm long and wide; blades ovate to deltate, herbaceous, unlobed, rarely narrowly to more rarely deeply 3-lobed from the base, 3-18 cm long, 2-15 cm wide, at base cordate to truncate or cuneate, at apex acute to acuminate, with margins crenate-dentate, with both sides hirsute or sericeous, intermixed glandular-puberulent with stipitate or sessile glands. Capitulescence of monocephalous or of loosely and sparingly branched peduncles arising from many nodes; peduncles 1-14 cm long, 1-2 mm

diameter, densely glandular-puberulent and hirsute. Heads radiate, 10-20 mm tall; 20-35 mm diameter; involucre campanulate to ovoid-campanulate, 8-17 mm tall, 8-22 mm diameter. Phyllaries 2-4 seriate, subequal, 11-66, greatly reflexed to appressed except slightly reflexed apically, yellow-green to light-green, linear to linear-ovate, sinuate, acute to caudate at the tips, hirsute or velutinous and densely glandular-puberulent; outer phyllaries 6-20 mm long, 1.2-3.5 mm wide; inner phyllaries 7.1-20 mm long, 0.5-3.2 mm wide. Ray florets 7-45, ligules light lemon-yellow to orange-yellow, 3.8-11.5 mm long, 1.5-7 mm wide; tubes 1.1-2.1 mm long, 0.3-0.9 mm diameter; ovaries 3.4-9.5 mm long, 0.7-1 mm diameter. Disc florets 20-172; corollas 5.2-8.7 mm long, 1-1.5 mm diameter; tubes 0.6-1.9 mm long, 0.5-0.8 mm diameter; lobes 0.5-1.5 mm long, 0.7-1 mm wide; anthers yellow, 2.7-4.5 mm long, with terminal appendages stramineous, achenes 3.1-7.4 mm long, 1.7-4 mm wide, pappus 1.7-7.4 mm long. Pales stramineous, acute to attenuate at the tips, 7-14 mm tall, 1.3-3.8 mm wide, scabrous apically.

Simsia foetida is a highly variable species here interpreted to comprise six varieties distributed in Mexico from Jalisco to Queretaro, then south to Panama, with a disjunct variety in Jamaica and disjunct populations in Bolivia and Venezuela. These varieties differ mainly by overlapping quantitative features, but previous treatments have ignored this overlap and have described these differences in a qualitative fashion or in a more discrete quantitative way. Considerable intergradation of these varieties

makes identifications difficult, especially in transitional areas. For a fuller discussion of these problems, see the Numerical Taxonomy section and discussions under individual varieties below.

18a. Simsia foetida var. foetida.

Stems 1-3 m tall. Leaves with petioles 1-7 cm long, naked; blades 3-12 cm long, 2-9.5 cm wide, on both sides densely glandular-puberulent with stipitate glands, setose, sometimes hispid. Peduncles 1-8.5 cm long. Heads 10-17 mm tall, 20-30 mm diameter; involucre 8-15 mm tall, 8-13 mm diameter. Phyllaries 13-23, 2-3-seriate, hirsute and glandular-puberulent; outer phyllaries 6-14 mm long, 1.2-2.8 mm wide; inner phyllaries 7.2-14.5 mm long, 1.5-3.2 mm wide. Ray florets 7-13, ligules light lemon-yellow, 5.8-11 mm long, 2.8-4.6 mm wide; ovaries 3.4-9.5 mm long. Disc florets 20-76, corollas 5.2-8.2 mm long, tubes 0.6-1.8 mm long; achenes 3.5-6.6 mm long, 1.8-4 mm diameter, awns 2.6-5.6 mm long. Pales 8-12 mm long, 1.8-3.8 mm wide.

Phenology. August-December.

Distribution. (Fig. 27). Open grassy fields and roadsides in areas of tropical deciduous forests; 700-2150 m, but most populations rarely occurring above 1700 m; from southern Nayarit east to Querétaro, southeast to eastern Oaxaca.

Fig. 27. Distribution in Mexico, Central America, and Jamaica of the six varieties of S. foetida. See Fig. 18 for the distribution of the Venezuelan and Bolivian populations of S. foetida var. panamensis.

Figure 27.

REPRESENTATIVE SPECIMENS: MEXICO: Guanajuato: 23 mi N of Celaya on rd to Querétaro, Crutchfield & Johnston 5951A (TEX). GUERRERO: Coyuca, Hinton 5538** (BM, G, K, US); Cañón de Zopilote, 4 km N of Milpillas, Rzedowski 23516** (CHAPA, ENCB, MEXU, OS); Rt 95 toll rd on N side of Iguala, Spooner 2846** (MEXU, OS). JALISCO: Rt 80 to Guadalajara, 0.5 mi E of jct of rd to Acatlán, Spooner & Brandenburg 2292* (MEXU, OS, US); Rt 80, 37 mi SW of Guadalajara, Spooner & Brandenburg 2300* (MEXU, OS, UC); S limits of Atenquique on short rt to Guadalajara, Stuessy & Gardner 3088 (F, MEXU, MSC, NY, OS, UC); 26 mi NW of Tequila on Rt 15, Stuessy & Gardner 4111** (ASU, ENCB, MO, OS); 2 mi N of Guadalajara on rd to Saltillo, Villareal 1264** (MICH). MÉXICO: Rincón del Carmen, Hinton 1741** (BM, G, GH, K, MEXU, NY, US); Volcán, Hinton 2216** (F, GH, K, LL, MO, NY, PH); Acatitlán, Hinton 8582** (K, LL, GH, K); 6 km N of Huehuetoca, Rzedowski 29500** (ARIZ, ASU, CAS, COL, ENCB, US); Rt 130, 4 mi SW of Tejupilco de Hidalgo, Spooner & Brandenburg 2264* (MEXU, OS); Valle de Bravo-Tingambato Rd, 1 mi NE of rd to Zacazonapan, Spooner & Villaseñor 2569* (MEXU, MICH, F, OS, TENN), Villaseñor & Spooner 772 (MEXU, OS). MICHOACÁN: near Barranca Hondo, 47 km S of Uruapan, Cronquist & Fay 10816** (CAS, DUKE, ENCB, F, MEXU, MICH, MSC, NY, RSA, TEX, US); Zitácuaro-Los Guajes, Hinton 13289** (ARIZ, ENCB, GH, K, LL, MICH, TEX, US). MORELOS: Xochitepec, Lyonet 845** (MEXU, LL, US); limestone hills near Yautepec, Pringle 9898** (CM, F, GH, MO, NY, US). NAYARIT: Ahuacatlán, Gentry, Barclay, & Arguelles 19532** (DES, LL, US). OAXACA: Monte Albán ruins, Smith 236 (MO, NY, TEX, US), Solano 384 (TEX), Spooner 2822** (MEXU, OS, TEX); Rt 195, 61 mi SE of Oaxaca, Spooner & Dorado

2664** (COL, MEXU, NY, OS, P, US); Rt 195, 3 mi SW of San José Viejo, Spooner & Dorado 2666** (MEXU, OS, UC); 1 mi N of Jayacatlán, Spooner 2829** (MEXU, OS); 1 mi N of Monte Albán Park on rd to Cd Oaxaca, Stuessy & Gardner 4261 (OS, WIS). PUEBLA: Rt 190, 3 mi N of Tehuitzingo, Olsen & Lane 389 (LL), Spooner & Dorado 2637* ** (MEXU, OS, TEX); QUERÉTARO: Álamos, Arguelles 271** (ENCB, MEXU, NY).

Putative hybrids with S. amplexicaulis: HIDALGO: municipio of Huehuetoca, W side of Cerro Sincoque, Rzedowski 34445 (CAS, CHAPA, ENCB, MEXU, NY, OS); just E of México-Hidalgo state line on toll rd 57 to Queretaro, Stuessy & Gardner 4578 (ASU, ENCB, MO, OS, WIS). JALISCO: 48 mi S of Guadalajara, Cronquist 10290 (ENCB, MEXU, MICH, NY); Rt 15, 11 mi W of Jalisco-Michoacán state line, Lane & Olsen 2144 (TEX); 15 km SSE of Acátlan de Juárez, McVaugh & Koelz 341 (ENCB, MICH); km 18-9 of rd to Sahuayo-Tizapán, Panero & Schilling 459 (OS, TENN); 2 mi W of S. L. Soyotlán, Spooner & Villasenor 2535 (BM, MEXU, MICH, OS, TENN, TEX, UC); MICHOACÁN: km 543, 8 mi NW of Sahuayo, McVaugh 18185 (DUKE, ENCB, MICH, US); rd to Jiquilpan de Juárez, 8 mi. SE of Tizapán El Alto, Spooner & Villasenor 2538 (MEXU, OS).

Putative hybrids with S. lagascaeformis: MEXICO. OAXACA: along rd from Huahuapan de León to Mariscala de Juárez, via Amatitlán, 26.2 mi from the intersection of rd to San Agustín Atenango, Spooner & Dorado 2644* (BM, COL, F, LE, MEXU, MICH, NY, OS, OSH, RSA, TENN, TEX, UC, US, WIS), same but 29.4 mi S, Spooner 2645 (OS). PUEBLA: km 170, 6.4 mi NE of center of Tehuitzingo on rd to Izúcar, Spooner & Dorado 2635* (BM, MEXU, OS, TENN, TEX, UC, US); 12 mi SE of Tehuitzingo on rd to Oaxaca, Spooner & Dorado 2639 (MEXU, MICH, OS, TEX, UC).

The exact locality of the type of Simsia foetida var. foetida is unknown, subject to the same difficulties of determining the type locality of Simsia amplexicaulis (see discussion under that species).

Blake (1913) confused this taxon nomenclaturally with Simsia amplexicaulis, which he treated under the name of S. foetida. He treated the concept of S. foetida under Simsia adenophora. Blake (1917) later reported having seen an "authentic specimen" of Coreopsis foetida at G-DC and corrected his nomenclatural error.

The holotype of Simsia foetida var. foetida is easily identified as such, as it bears a label in Cavanilles's handwriting (comparison from Burdet, 1973), and also bearing an appended copy of the illustration from the protologue, and with a form which closely approximates the illustration. The identification of isotype material at MA is problematical, however. One mixed sheet with four fragmentary specimens bears a single annotation label in Cavanilles's handwriting listing both Coreopsis amplexicaulis and C. foetida. All bear amplexicaulate leaves as in S. amplexicaulis yet with intermediate glandularity of the leaves and phyllaries. As both of the species were grown in the Royal Botanic Garden at Madrid, and as both are capable of hybridizing, some or all may represent hybrids or may be subsequent collections. Another collection at MA, one at F, and one at G-DC (photograph: IDC 800. 946. III. 1) are potential isotypes, but as their identity and dates of collections are similarly uncertain, they are not here so designated.

Almost all collections of S. foetida var. foetida have non-lobed leaves with naked petioles. Lobed leaves are rarely found, however,

including the type specimen. Also, some individuals of one collection from the northern part of the range in Querétaro, Arguelles 271, have petioles winged at the base. This collection could be confused with S. megacephala.

Simsia foetida var. foetida apparently is able to hybridize naturally with various species within the genus. Apparent hybrid swarms between this variety and S. lagascaeformis are found with the co-occurring parents and are listed below. These hybrids are quite variable, exhibiting various combinations of intermediate features. Some have more unequal phyllaries tinged with purple as in S. lagascaeformis, but all have the glandular leaves and lemon-yellow ligules as in Simsia foetida var. foetida. This variety apparently also can hybridize with S. amplexicaulis. Many of these occur about Lake Chapala in Jalisco and adjacent Michoacán and were noted by McVaugh (1984). Others occur in Hidalgo (see above). These hybrids, like those with S. lagascaeformis, have the densely glandular leaves like S. foetida var. foetida, yet possess heads like S. amplexicaulis with its darker phyllaries and orange-yellow ligules. These hybrids are interesting because they are apparently stabilized derivatives that do not co-occur with the putative parents as is the case of the hybrids with S. lagascaeformis mentioned above. Also of interest is that the Lake Chapala populations all occur between 1480-1650 m elevation, which is transitional between the elevational ranges of the two parents. The Hidalgo populations grow in higher elevations, however, from 2250-2500 m. In addition to these hybrids, a more hypothetical hypothesis of possible hybridization of this variety with

S. annectens var. *grayi* is mentioned under the discussion of *S. annectens* var. *annectens*.

18b. *Simsia foetida* var. *jamaicensis* (S. F. Blake) D. M. Spooner, *comb. et stat. nov.* *Simsia jamaicensis* S. F. Blake, Proc. Amer. Acad. Arts 49: 388. 1913.-TYPE: JAMAICA. Vicinity of Kingston, 500 ft, 29 Jan-4 Feb 1900, Clute 2 (holotype: GH!; isotypes: FI KI MO! NY! US [2]!, fragment: GI!).

Stems 1-3 m tall. Leaves with petioles 1-5.5 cm long, naked, blades 3-17 cm long, 2-16 cm wide, on both sides densely glandular-puberulent with subsessile glands, setose, sometimes hispid. Peduncles 1-6 cm long. Heads 10-18 mm tall, 20-30 mm diameter; involucre 8-17 mm tall, 8-12 mm diameter. Phyllaries 11-18, 2-3 seriate, hirsute and glandular-puberulent; outer phyllaries 6.5-11.4 mm long, 1.7-2.5 mm wide; inner phyllaries 8-10.8 mm long, 1.6-2.2 mm wide. Ray florets 7-10, ligules light lemon-yellow, 3.8-6.8 mm long, 1.5-3.8 mm wide; ovaries 6.5-8.7 mm long. Disc florets 25-54, corollas 6.3-7 mm long, tubes 1.7-1.9 mm long; achenes 5.8-7.5 mm long, 2.5-3.5 mm diameter, awns 3.3-5.4 mm long. Pales 8.2-10.6 mm long, 2-2.6 mm wide.

Phenology. November-February.

Distribution. (Fig. 27). Open dry limestone slopes; 30-200 m; all sites within 20 km radius of Kingston Harbor, Jamaica.

SPECIMENS EXAMINED: JAMAICA. MIDDLESEX: St. Catherine Parish: upper slopes of Port Henderson Hill, Proctor 32765** (ENCB, LJ, LL, MASS, NY, RSA); Rodney's Lookout near Port Henderson, Wunderlin 5081** (NY, F). SURREY: Kingston Parish: base of Long Mountain behind Rennock Lodge, Proctor 24496** (GH, LJ, LL, MICH, NY, US). St. Andrew Parish: valley of Hope River, University Rd to Hope Rd, Adams 8766** (BM, DUKE, M); Kings House Grounds, Harris 6953 (NY, F), 6989** (B, BM, F, K); Hope Grounds, Harris 8228** (BM, F, NY); Long Mountain Road, Harris 10001** (BM, C, F, G, NY, US); 1 mi SSE of Papine, Proctor 21945** (LJ, LL). St. Thomas Parish: Four-mile wood near milepost 13, Proctor 38472** (LJ); on Hwy A-4, 2 mi W of Albion, Pruski 1269** (LJ, K, NY, OS, US).

Simsia foetida var. jamaicensis can be difficult to distinguish and appears to combine some features of vars. foetida and grandiflora. It has the naked petioles (although some sheets of Proctor 24496 have minute wings at the base), small heads, and lemon-yellow ligules of var. foetida, and the darker green-yellow leaves with sessile glands of var. grandiflora. It has statistically significant and consistently larger tubes of the disc florets than other varieties, however. While these are not obvious morphological markers, they are consistent and taxonomically useful features. This variety also has the least amount of morphological variability than any other within this species (Fig. 8), which is possibly the result of the origin from a single introduction, perhaps from historical times, from some intermediate population from the mainland. The occurrence of all

sites within 20 km from Kingston Harbor, an active port for hundreds of years (Long, 1774), and the fact that the island has traditionally been an active horticultural center (Adams, 1972), supports this hypothesis. Many other natural disjunct patterns of distribution of closely related taxa between Jamaica and tropical America are well documented, however (Howard, 1973), and combined with the morphologically distinct nature of var. jamaicensis (Table 7) suggests this as a distinct and indigenous variety.

18c. Simsia foetida var. megacephala (Schultz-Bipontinus ex S. F.

Blake) D. M. Spooner, comb. et stat. nov. Simsia megacephala Schultz-Bipontinus ex S. F. Blake, Proc. Amer. Acad. Arts 49: 391. 1913.--TYPE: MEXICO. Oaxaca: cultivated plant grown in the Botanic Garden of Deidsheim, Rhine-Palatinate, 25 Nov 1859, Schultz-Bipontinus s.n., grown from seed of Liebmann 546 (holotype: GH!, photo: ENCB!).

Simsia cronquistii H. Robinson & R. D. Brettell, Phytologia 24:

370. 1972.--TYPE: MEXICO. Oaxaca: 97 mi SE of Oaxaca and 54 mi NW of Tehuantepec, 3100 ft, along the Pan-American Hwy in small-forest region, 13 Oct 1962, Cronquist 9661** (holotype: US!, isotypes: GH! MO! MICH! MSC! NY! SMU! TEX!).

Stems 1-3 m tall. Leaves with petioles 1-5.5 cm long, some leaves, especially the upper, often winged throughout with wings often 1 cm wide or more, at base often cordate-clasping, sometimes united from those of opposite leaves to form nodal discs, blades

3-12.5 cm long, 2-9 cm wide, on both sides densely glandular-puberulent with stipitate glands, setose, sometimes hispid. Peduncles 1-14 cm long. Heads 10-16 mm tall, 25-35 mm diameter; involucre 8-13 mm tall, 8-15 mm diameter. Phyllaries 19-29, 3-seriate, hirsute and glandular-puberulent; outer phyllaries 10-20 mm long, 1.6-3.2 mm wide; inner phyllaries 11.6-20 mm long, 1.4-2.7 mm wide. Ray florets 7-14, ligules light lemon-yellow, 5.3-10 mm long, 2.3-4.8 mm wide; ovaries 2.3-4.8 mm long. Disc florets 35-55, corollas 5.6-8.7 mm long, tubes 0.8-2.5 mm long; achenes 4.4-7.4 mm long, 2.6-4.1 mm diameter, awns 4.4-7.4 mm long. Pales 9.2-14 mm long, 1.9-3.1 mm wide.

Phenology. June-November.

Distribution. (Fig. 27). Roadsides and disturbed fields in areas of tropical deciduous forest; 0-950 m; confined to eastern Oaxaca in the lower slopes of the eastern end of the Sierra Madre del Sur and adjacent lowlands about the Isthmus of Tehuantepec.

SPECIMENS EXAMINED: MEXICO. OAXACA: 12 mi NW of Tehuantepec, Hartman & Funk 4190** (MO, OS, TEX); Jalapa del Marqués, Hernandez M.118** (MEXU), Spooner & Dorado 2669** (BM, MEXU, OS, UC); Rt 190, 0.9 mi NW of Las Majadas, Jansen & LaDuke 403** (ASU, ENCB, OS); Rt 190, 6.9 mi NE of Juchitán de Zaragoza, Keil & Luckow 15553** (OB, OS); Rt 190, 10-15 km NW of Tehuantepec, King 768 (MICH); Sta. Cruz, Liebmman 546 (C, P); Salina Cruz, Ortega 25 (MEXU); Rt 195, 1 mi W of bridge over Río Tehuantepec, Spooner 2814** (MEXU, OS, UC); Rt 195, 4.8 mi SE of Coyula, Spooner 2815** (MEXU, OS); Rt 195, 3 mi SW

of town center of La Coyula, Spooner & Dorado 2667* ** (BM, GH, MEXU, MICH, NY, OS, TENN, US, WIS); Rt 195, 3.3 mi SW of La Reforma, Spooner & Dorado 2668** (MEXU, OS, P, TEX); 8 mi NW of Tehuantepec, Webster & Arnbruster 21031 (TEX); Huazantlán del Río, Mpio San Mateo del Mar, Zizumbo & Colunga 288 (CAS, TEX); ex Hort Cantab., from seeds Hort Paris, collector unknown, 1866 (GH, MO, NY).

Blake cited two syntypes for Simsia megacephala (Dugès 12, Schultz-Bipontinus 25 Nov 1859), but a note on the latter at GH indicates it is the type. Dugès 12 is a rather typical specimen of S. amplexicaulis.

The type of S. foetida var. megacephala is a cultivated plant grown from seed of Liebmann 546 collected in Dec 1841 at "Sta. Cruz". This is a common place name in much of Mexico and Oaxaca, with at least two localities within the likely range of S. megacephala. The name also is a possible transcription error for "Salina Cruz", also in Oaxaca within its range. Liebmann's itineraries (Oersted 1869, 1887; Hemsley, 1887) make no mention of Sta. Cruz. Also, while his exact location in Dec 1841 is unclear, he was possibly in northern Oaxaca, outside the known range of this variety. His later excursions in 1842, however, traversed much of the range of the variety, and 1841, therefore, is possibly a transcription error for 1842.

Simsia foetida var. megacephala grades into var. foetida to the northwest and var. guatemalensis to the southeast, and intermediates occur in these areas (e.g., Funk & Ramos 257, King 768, Ortega 25).

Most specimens, however, are well distinguished by the wide, frequently hourglass-shaped petioles, especially in the upper nodes, but some petioles are widened only at the base and sometimes fused to form nodal discs. In addition, the pales of this variety are slightly longer than those of all the others, often slightly extending above the flowers. Although this variety is narrowly restricted in its range, it is a dominant and abundant weed at some sites.

18d. Simsia foetida var. guatemalensis (H. Robinson & R. D. Brettell)

D. M. Spooner, comb. et stat. nov. Simsia guatemalensis H.

Robinson & R. D. Brettell, *Phytologia* 24: 372. 1972.—TYPE:

GUATEMALA. GUATEMALA: Amatitlán: Amatitlán, 1200 m, Oct 1904,

Tuerckheim 8701 (holotype: US!).

Stems 1-4 m tall. Leaves with petioles 1-10.5 cm long, naked or narrowly winged, sometimes auriculate-clasping, at base stipules 0-2 cm long, sometimes united with those of opposite leaves to form nodal discs, blades 3-11.5 cm long, 2-11 cm wide, on both sides densely glandular-puberulent with stalked glands, setose, sometimes hispid. Peduncles 1-9.5 cm long. Heads 11-16 mm tall, 20-30 mm diameter; involucre 8-17 cm tall, 9-13 mm diameter. Phyllaries 17-26, 3-seriate, hirsute and glandular-puberulent; outer phyllaries 7-11.5 mm long, 1.5-2.5 mm wide; inner phyllaries 7-10.3 mm long, 1.2-2.7 mm wide. Ray florets 8-14, ligules light lemon-yellow, 5.5-9.7 mm long, 2.9-4.5 mm wide; ovaries 4.5-6.7 mm long. Disc florets 31-70, corollas 5.6-6.9 mm

long, tubes 0.6-1.3 mm long; achenes 4-5.2 mm long, 1.8-3.2 mm diameter, awns 1.7-4 mm long. Pales 7-10.1 mm long, 1.5-2.6 mm wide.

Phenology. July-March.

Distribution. (Fig. 27). Dry weedy thickets and streamsides in areas of tropical deciduous forests; 300-1600 m; Chiapas to El Salvador.

REPRESENTATIVE SPECIMENS: MEXICO. CHIAPAS: Municipio of Tenejapa, paraje of Sibani Ha', near schoolhouse of Pokolum, Breedlove 9437 (DS, ENCB, LL, MICH, NY); at Mirador of El Sumidero, Breedlove 41483 (DS, MO, TEX), Spooner 2787** (MEXU, OS); Rt. 190, 0.3 mi S of San Gregorio, Spooner 2768* ** (MEXU, OS, P, TEX, UC, US); rd into Parque Natural Ejidal Lagos de Colón, 3 mi E of Rt 190, just N of San Gregorio, Spooner 2769** (BM, COL, LE, MEXU, MICH, OS, OSH, TENN, UC, US, WIS); Hwy 190, 4.6 mi S of rd into La Trinitaria, Spooner 2770* (MEXU, OS); pull-off area for Mirador El Roblar on rd to El Sumidero from Tuxtla Gutiérrez, Spooner 2786** (MEXU, OS); N of Arriaga to Tuxtla Gutiérrez, 1.9 mi S of jct to Santa Elena, Spooner 2792** (F, GH, MEXU, MICH, NY, TEX); Municipio of Tenejapa, paraje of Mahbenchauk, barrio of Tih Ha', Ton 2033 (DS, ENCB, F, MICH, MSC, NY, US). GUATEMALA. BAJA VERAPAZ: 4 mi E of town square of Salamá, Spooner & Dorado 2747* F, MEXU, MICH, OS, UC); near town square of San Miguel Chicaj, Spooner & Dorado 2749** (MEXU, OS, UC, US). CHIQUIMULA: Rt 20, lower and middle slopes of Cerro Sillón, 5 mi N of Guatemala-Honduras border, Stuessy & Gardner 4377 (OS). EL PROGRESO: Guatemala-El Progreso rd (Rt 4), 8.4 mi NE of RR station at Agua Caliente Spooner &

Dorado 2691* (GH, LE, MEXU, OS, TENN, WIS); Guatemala City-Puerto Barrios Rd, 0.9 mi NE of intersection to Sanarate, Spooner & Linder 2758 (MEXU, OS). ESCUINTLA: near El Llano, Harmon 4668 (ENCB). GUATEMALA: near Amatitlán, Holway 624** (GH), Standley 61469** (F); along Guatemala City-Puerto Barrios Rd, by bridge over river, 5.4 mi SW of Agua Caliente, Spooner & Dorado 2688* ** (F, GH, MEXU, OS, OSH, TENN, UC, US); 1.4 mi SW of S entrance to Amatitlán, Spooner & Dorado 2693** (BM, COL, MEXU, MICH, NY, OS, OSH, RSA, UC, US, WIS). HUEHUETENANGO: mountains near El Reposo, 8 km from Mexican border, Williams, Molina, & Williams 41109 (MICH, F), 41366 (MICH, F). JALAPA: vicinity of Jalapa, Standley 46514 (F). SANTA ROSA: Cerro Redondo, Heyde & Lux 6160 (BR, F, G, GH, MO, NY, US). EL SALVADOR. CHALATENANGO: along Tejutla Creek, hwy to La Palma, Molina & Montalvo 21575** (F, NY, US).

Simsia foetida var. guatemalensis is polymorphic in many characters, including the taxonomically diagnostic petiole, nodal, and head characters. Because of this, some plants, especially the smaller ones, or collections from smaller side branches may be confused with S. foetida var. foetida. In addition, this variety exhibits much intergradation with var. grandiflora to the southeast, especially in central and eastern Guatemala, and many of these specimens are difficult to assign to one or the other of these varieties. These patterns of variation led Nash (1972), based on her primary focus on Guatemalan material, to consider S. foetida var. foetida (as S. foetida) native to Guatemala and to consider S. foetida var.

guatemalensis (as S. guatemalensis) as a synonym of S. grandiflora.

In light of the intrapopulational variability of the diagnostic characters separating these varieties, and the considerable intergradation over much of Guatemala, this would be a defensible taxonomic position, but present data more strongly suggest varietal status.

18e. Simsia foetida var. grandiflora (Bentham in Oersted) D. M.

Spooner, comb. et stat. nov. Simsia grandiflora Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn. 1852: 92. 1853. Encelia grandiflora (Bentham in Oersted) Hemsley, Biol. cent.-amer., Bot. 2: 184. 1881.-TYPE: [NICARAGUA: Chinandega]: In dry fields at foot of mont El Viejo [= Volcán El Viejo, = Volcán San Cristóbal], 1851, Oersted 100 (holotype: K!, photo and fragment: US!, photos: GH! OS!; isotype: CI).

Simsia polycephala Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1852: 93. 1853. Encelia polycephala (Bentham in Oersted) Hemsley, Biol. cent.-amer., Bot. 2: 184. 1881.-TYPE: [COSTA RICA]. Guanacaste: In dry fields between Sapoá and Tortuga, 1851, Oersted 160 (holotype: K!, photos: GH! OS! US!; isotypes: C, [2]!).

Stems 1-4 m tall. Leaves with petioles 1-10 mm long, naked or winged, at base sometimes auriculate-clasping, or with stipules 0-2 cm long, these sometimes united with those of opposite leaves to form

nodal discs; blades 3-14 cm long, 2-15 cm wide, on both sides moderately to densely glandular-puberulent with subsessile glands, setose, sometimes hispid. Peduncles 1-14 cm long. Heads 13-19 mm tall, 25-45 mm diameter; involucre 9-13 mm tall, 10-22 mm diameter. Phyllaries 21-66, 3-4 seriate, hirsute and glandular-puberulent; outer phyllaries 8-14 mm long, 1.9-3.5 mm wide; inner phyllaries 8.4-14.5 mm long, 1.2-3 mm wide. Ray florets 11-45, ligules light lemon-yellow in the northwestern part of the range in Guatemala to orange-yellow farther south, 7.6-12 mm long, 3-7 mm wide; ovaries 6.1-8 mm long. Disc florets 66-172, corollas 6.1-7.4 mm long, tubes 0.9-1.7 mm long; achenes 4-6.2 mm long, 2.5-3.4 mm diameter, awns 2.7-6 mm long. Pales 8-11.7 mm long, 1.8-2.8 mm wide.

Phenology. October-March.

Distribution. (Fig. 27). Dry weedy thickets and streamsides in areas of tropical deciduous forests; 0-1700 m; Guatemala to Costa Rica.

REPRESENTATIVE SPECIMENS: GUATEMALA. CHIQUIMULA: between Jocatán & Camotán, Molina & Molina 25217** (C, F, NY, US); Esquipulas-Chiquimula Rd, 5 mi SE of bridge over river at San Jacinto, Spooner & Dorado 2740** (B, BM, GH, MEXU, MICH, NY, OS, TENN, UC). JUTLAPA: along Pan-American Hwy, 3 mi W of San José Acatempa, Spooner & Dorado 2695** (MEXU, OS, TEX, UC, US); 2.5 mi N of Pan-American Hwy on rd to Chiquimula, Spooner & Dorado 2697** (MEXU, OS, TEX). SANTA ROSA: along rd SE of Barberena, Standley 77857 (F). EL SALVADOR. AHUACHAPÁN: vicinity of Ahuachapán, Standley 19947 (NY, US). LA LIBERTAD: Colón,

Williams & Molina 15188** (F, GH). LA UNIÓN: Gulf of Conchagua,
Barclay 2600 (BM, MICH, US). SAN SALVADOR: vicinity of Tonacatepeque,
Calderón 250 (GH, NY, US), Standley 19483** (GH, MO, US); airport at
 San Salvador, Heiser R7 (IND). SAN VINCENTE: vicinity of San Vincente,
Standley & Padilla 3549** (F). SANTA ANA: vicinity of Metapán,
Standley & Padilla 3179 (F). HONDURAS. CHOLUTECA: between El Espino &
 San Marcos de Colón, Molina 23238** (G, NY); along Pan-American Hwy,
 between El Chinchayote & Comalí, Molina & Molina 24566** (DUKE, F, NY,
 US). EL VALLE: along Pan-American Hwy, 6 mi S of Jícaro Galán, Spooner
 & Dorado 2699* ** (EAP, MEXU, OS, TENN, US). NICARAGUA. ESTELÍ: 4 km
 on way to San Juan Limay, Molina 23157** (F, MO, NY, S); Paso León, 5
 km from Estelí on rd to Mirafior, Moreno 22322 (MO, OS); Pan-American
 Hwy, 2 mi. N of center of Estelí, Spooner & Dorado 2700** (OS, MEXU,
 TEX, UC); Pan-American Highway, 14.6 mi N of bridge over Río Estelí on
 N side of Estelí, Spooner & Dorado R. 2702** (OS, MEXU, TEX). GRANADA:
 Niquinohomo, Baker 2419** (G, GH, MO, MSC, NY, TEX, UC, US, W); km 54,
 rd to Diria, Moreno & Stevens 22882 (MO, OS). LEÓN: Cañón of Río
 Sinecapa, near Santa Rosa, Williams & Molina R. 42449 (F, MICH).
 MANAGUA: Sierra de Managua, Grant 7339 (F, GH); Along Hwy 2, 2 km SSW
 of Hwy 12, Stevens 4768 (MO, OS). MATAGALPA: Pan-American Hwy, 0.9 mi.
 S. of rd to Jinotega, Spooner & Dorado, 2703** (C, MEXU, OS, OSH, US);
 Pan-American Highway, 7.0 mi. S of bridge over Río Grande at Sébaco,
Spooner & Dorado 2723* ** (MEXU, OS, US); 27.6 mi S. of Sébaco,
Stuessy & Gardner 4552 (CHAPA, ENCB, MO, OS, WIS). COSTA RICA.
 CARTAGO: Ojos de Agua, ex herb. Klatt 352 & 382 (GH). GUANACASTE: Río
 Guapote, Santa Rosa National Park, Janzen 10652** (MO); between

Capalchi & La Cruz, 29 Jan 1909, Brenes s. n. (NY); PUNTARENAS: Isla de Chira, Valerio 1507** (F).

The previous citations by other workers of Simsia grandiflora Benth. ex Oersted, and S. polycephala Benth. ex Oersted likely have resulted from an incorrect translation of the protologue title "Bestemmelser og Beskrivelser af G. Benth." [= determined and described by G. Benth. (italics mine)].

Simsia foetida var. grandiflora is a distinctive taxon, possessing the largest heads of any variety within the genus. This variety, and var. panamensis also differ from all other varieties in S. foetida by the prevalence of orange-yellow ligules, and phyllaries that tend to be more indurate below. These characters intergrade considerably with var. guatemalensis to the northwestern part of the range, however, as discussed above under that variety.

- 18f. Simsia foetida var. panamensis (H. Robinson & R. D. Brettell) D. M. Spooner, comb. et stat. nov. Simsia panamensis H. Robinson & R. D. Brettell, Phytologia 24: 372. 1972.—TYPE: PANAMA.
Panama: Bella Vista, "Silvulaca", brushy field, 28 Nov 1923, Standley 25386 (holotype: US!).

Stems 1-4 m tall. Leaves with petioles 1-8 cm long, naked throughout or with stipules at the base minute-1.5 cm long, these sometimes united with those of opposite leaves to form nodal discs; blades 3-18 cm long, 2-14 cm wide, on both sides pilose to

subsericeous and glandular-puberulent with subsessile glands. Peduncles 1-13 cm long. Heads 12-16 mm tall, 25-35 mm diameter; involucre 9-13 mm tall, 9-18 mm diameter. Phyllaries 30-44, 3-seriate, pilose and glandular-puberulent; outer phyllaries 6-10 mm long, 1.9-3.5 mm wide; inner phyllaries 7.2-10.5 mm long, 1-2.8 mm wide. Ray florets 12-25, ligules varying from orange-yellow to light lemon-yellow, 5.1-11 mm long, 2.2-5.2 mm wide; ovaries 3.5-6.4 mm long. Disc florets 40-151, corollas 5.2-6.9 mm long, tubes 0.7-1.5 mm long; achenes 3.1-5.1 mm long, 1.7-2.5 mm diameter; awns 2.2-5 mm long. Pales 6.5-8.9 mm long, 1.3-2.8 mm wide.

Phenology. November-April.

Distribution. (Fig. 27). Roadsides and old fields in area of tropical deciduous forests; sea level-500m; from Panama City SW to the Azuero Peninsula.

REPRESENTATIVE SPECIMENS: PANAMA. COCLÉ: entrance to Río Hato airbase, Blum & Tyson 1866** (MO); Río Hato Airstrip, Dwyer 1146** (MO, GH, UC, US); Aguadulce, Pittier 4847** (US); 6.5 km SW of Penonomé, Spooner 2904* ** (OS, PMA, QCA); 4 mi W of Anton, Tyson & Blum 2595** (MO). HERRERA: outskirts of Pesé on rd to La Avena, Burch. Oliver & Robertson 1312** (F, MO, UC, US); 4 mi S of Los Pozos, Dwyer 2697** (MO); along dirt rd near Pan-American Highway, 2.5 mi W of Divisa, Spooner 2905* ** (OS, QCA). LOS SANTOS: 7 mi S of Chitré, Croat 9703** (MO); 17.8 mi S of Macaracas, Lewis. MacBryde. Oliver & Ridgeway 1616** (GH, MO, US); Monagre Beach, 5 mi SE of Chitré, Tyson. Dwyer & Blum 3024** (MO); 12 mi S of Macaracas, Tyson. Dwyer & Blum

3069** (MO). PANAMA: 1 mi W of Río Coton, D'Arcy 9756** (MO); El Valle, Harvey 5166** (F); Sabanas, Paul 595** (LL, US); Punta Paitilla, Piper 5427** (NY, US); Pan-American Highway, 2 km NE of turnoff to La Chorrera, Spooner 2902* ** (OS, PMA, QCA, UC); 1 km SW of San Carlos, Spooner 2903** (OS, PMA, QCA, US). VERAGUAS: Pan-American Hwy, 10.9 km W of jct with rd to Chupampa, Spooner 2906* ** (OS, QCA). VENEZUELA. GUARICO: Guardatinajas, Crespo 1983** (OS, MY). BOLIVIA. SANTA CRUZ: between Charagua & Izozog, Cardenas 2666 (US). TARIJA: Fortín Crevaux, Fries 1645 (S).

Simsia foetida var. panamensis shares many characters with var. grandiflora, and is obviously closely related to it. It is generally easily identified, however, by its pilose leaves and smaller achenes. An apparent intergrade with var. grandiflora from Costa Rica, Brenes s. n., listed under var. grandiflora, combines these characters. The Venezuelan collection appears to be an isolated disjunct, but is from a large population, and is not a waif. As it occurs in an agricultural area, it may have been recently introduced. The two collections from Bolivia are very similar to this variety but have more gray-green leaves, dark brown to black anthers, and achenes up to 7 mm long. Although dark anthers are rarely found within S. foetida, they are commonly variable in other species (see Morphological Criteria). While these Bolivian populations may represent a new taxon in Simsia, they are not so treated here due to their similarity to var. panamensis and because little material exists for adequate comparative purposes.

DOUBTFUL AND EXCLUDED NAMES

Simsia anethifolia R. Brown, Trans. Linn. Soc. London 10: 153.

1810.-TYPE: AUSTRALIA: Victoria: southern coast, "Lewins Land"
[= on the southern mainland adjacent to Bass Strait fide
Brown, 1810], [1802 fide Stearn, 1960], Brown, s. n. (not
located). = Stirlingia tenuifolia (R. Brown) Steudel, fide
Jackson, 1895.

Simsia canescens Torrey & A. Gray ex. A. Gray (A. Gray), Mem. Amer.

Acad. Arts 1 (Pl. fendl.): 85. 1849.-TYPE: U.S.A. CALIFORNIA:
interior of California, 1844, Fremont 393 (lectotype, GH, seen
and designated by Curtis Clark, 1987). = Geraea canescens
Torrey & A. Gray ex A. Gray, fide Blake (1913) and Clark (1987,
pers. comm.).

Simsia frutescens A. Gray in Torrey, Rep. U. S. Mex. bound (House ed.)

2: 89. 1859 [1858, see Stafleu and Cowan, 1976, entry 1670
under Emory, W. H.].-TYPE: U.S.A. CALIFORNIA: Sierra Prieta,
near Fort Yuma, Dec 1854, Schott s. n. (lectotype, GH, seen
and designated by Curtis Clark, 1987) = Encelia frutescens (A
Gray) A. Gray, fide Blake (1913) and Clark (1987, pers.
comm.).

Simsia sect. Geraea A. Gray, Mem. Amer. Acad. Arts 1 (Pl. fendl.): 85.

1849.-TYPE: Simsia canescens Torrey & A. Gray ex A. Gray (A.

Gray). = Geraea Torrey & A. Gray ex A. Gray, fide Blake (1913) and Clark (1987, pers. comm.).

Simsia heterophylla (Cavanilles) Persoon, Syn. pl. 2: 478. 1807, non.
Simsia heterophylla (Kunth in Humboldt, Bonpland & Kunth)
 DeCandolle, Prod. 5: 577. 1836. Coreopsis heterophylla
 Cavanilles, Icon. 3: 34 t. 268. 1795. Ximenesia cavanillesii
 Sprengel, Syst. veg. 16(3) 605. 1826, ~~nom nov.~~ Echinacea
heterophylla (Cavanilles) D. Don in Sweet, Brit fl. gard. ser.
 2. 1: pl. 32. 1831 [1830].-TYPE: MEXICO. cultivated in the
 Royal Botanic Garden of Madrid, from unvouchered seed from the
 Sesse' and Mociño expedition; the plate fixes the application
 of the name = Iostephane heterophylla (Cavanilles) Benthham ex
 Hemsley, fide Strother (1983a).

Simsia hispida (Kunth in Humboldt, Bonpland & Kunth) Cassini, Dict.
 Sci. Nat. 59: 137. 1829. Ximenesia hispida Kunth in Humboldt,
 Bonpland & Kunth, Nov. gen. sp. 4 [folio]: 178. 1818; 4
 [quarto]: 227. 1820. Encelia hispida (Kunth in Humboldt,
 Bonpland & Kunth) Hemsley, Biol. cent.-amer., Bot. 2: 183.
 1881.-TYPE: MEXICO. Michoacán: Valladolid [= Morelia, 6200
 ft., Sep 1803, fide Sprague, 1924], Bonpland 4277. (holotype:
 P-HBK, IDC 6209. 109. I. 1!). = Viguiera sessilifolia
 DeCandolle, fide Blake, 1918.

Simsia latifolia R. Brown, Suppl. prod. fl. Nov. Holl. 9. 1830.-TYPE:

AUSTRALIA. WESTERN AUSTRALIA: King Georges's Sound, 1823,

Baxter s. n. (not located). = Stirlingia latifolia (R. Brown)

Steudel, fide Jackson, 1895.

Simsia scaposa A Gray, Smithsonian Contr. Knowl. 5, Art 6 (Pl. wright.

2): 88. 1853.-TYPE: U.S.A. NEW MEXICO: between the Mimbres and the Rio Grande, Oct 1851, Wright s.n. (holotype GH, not seen)

= Encelia scaposa (A. Gray) A. Gray, fide Blake, 1913.

Simsia tenuifolia R. Brown, Trans. Linn. Soc. London 10: 152.

1810.-TYPE: AUSTRALIA. Victoria: southern coast, "Lewins Land"

[= on the southern mainland adjacent to Bass Strait fide

Brown, 1810] [1802 fide Stearn, 1960], Brown s. n. (not

located). = Stirlingia tenuifolia (R. Brown) Steudel, fide

Jackson, 1895.

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