

# ZAPOTECA: A NEW GENUS OF NEOTROPICAL MIMOSOIDEAE<sup>1</sup>

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## ABSTRACT

The existence of consistent variation patterns in polyad characteristics, seedling morphology, chromosome numbers, and several reproductive features within the American species of *Calliandra* Benth. has revealed the presence of two well defined taxonomic units, the first one including the species of ser. *Laetevirentes*, and the second the remaining neotropical species. The lack of intermediate forms between the two units suggests that *Calliandra*, as originally conceived by Bentham, is polyphyletic. Therefore, the creation of the genus *Zapoteca*, consisting of ca. 25 taxa distributed from southwestern United States and northern Mexico to northern Argentina, is proposed to include the species of ser. *Laetevirentes*. New combinations are presented for *C. caracasana*, *C. formosa*, *C. lambertiana*, *C. media*, *C. mollis*, *C. portoricensis*, and *C. tetragona*.

## RESUMEN

La existencia de patrones estables de variación en las características de las políades, morfología de las plántulas, números cromosómicos, así como en varios rasgos reproductivos en especies americanas de *Calliandra* Benth. ha revelado la presencia de dos unidades taxonómicas bien definidas. La primera de éstas incluye a las especies de la ser. *Laetevirentes*, y la segunda al resto de las especies neotropicales. La ausencia de formas intermedias entre las dos unidades sugiere que el género *Calliandra*, como fue concebido originalmente por su autor, es polifilético. En consecuencia, se propone la creación del género *Zapoteca* para incluir a los miembros de la ser. *Laetevirentes*. El género está constituido por aproximadamente 25 taxa distribuidos desde el suroeste de los Estados Unidos y el norte de México hasta el norte de Argentina, con un claro centro de diversificación en el sur de México. Se presentan también nuevas combinaciones para *C. caracasana*, *C. formosa*, *C. lambertiana*, *C. media*, *C. mollis*, *C. portoricensis* y *C. tetragona*.

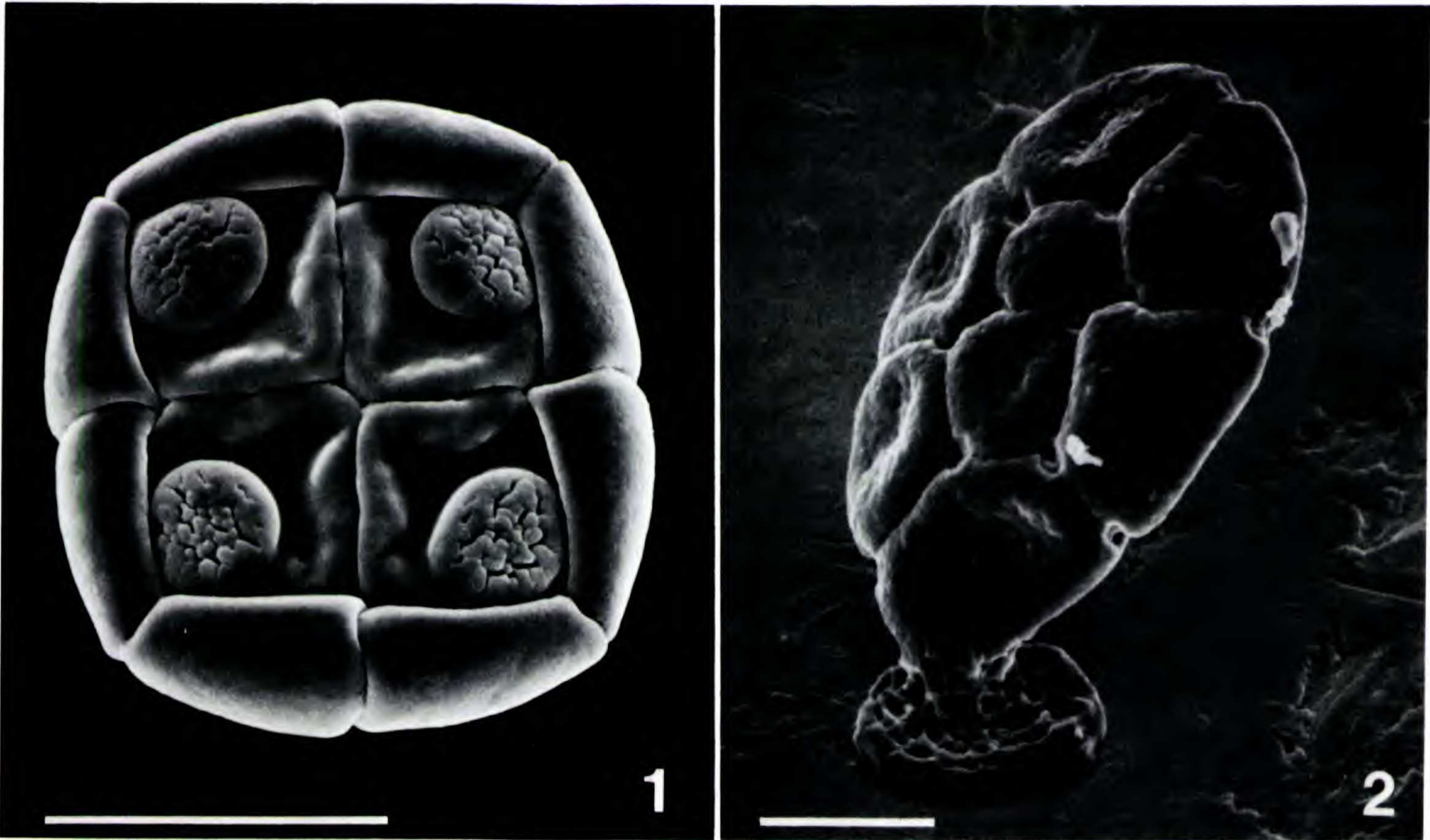
This paper reports part of a biosystematic study of the genus *Calliandra* (Leguminosae: Mimosoideae, tribe Ingeae). As currently circumscribed, this genus includes a relatively heterogeneous assemblage of about 150 species native predominantly in tropical and sub-tropical regions in the Americas. In addition, a few species are found in continental Africa (Thulin et al., 1981), Madagascar, and India (Paul, 1979). The genus was originally described by G. Bentham in 1840, who subsequently (1844), and more formally in his monograph of the Mimosoideae (1875), subdivided it into five series based on leaf and inflorescence characteristics: ser. *Macrophyllae*, *Laetevirentes*, *Pedicellatae*, *Nitidae*, and *Racemosae*. Since then, many new species have been described, and the genus has been included

in a number of floras; nevertheless, Bentham's original concept of the genus remains unchanged.

Palynological studies have contributed substantially to the understanding of the infrageneric relationships in *Calliandra* (Guinet, 1965, 1969, 1981; Guinet & Barth, 1969; Sorsa, 1969; Niezgodá et al., 1983). The New World species may be classified into two basic pollen groups, according to their contrasting polyad features. The first group (Type IB in Guinet, 1965) includes all the species of ser. *Laetevirentes*, and two species placed by Bentham into ser. *Macrophyllae*. Polyads in this group are 16-grained, radially symmetrical, acalymmate, with granular ectexine structure. These polyad characteristics are found in all the other genera of the tribe Ingeae; however, species in this portion of *Calliandra* have

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FIGURES 1, 2. Polyad types of *Zapoteca* and *Calliandra*.—1. Unacetolysed 16-grained polyad of *Z. tetragona* (cult. at MO from: Mexico, Veracruz, *Johnson 1582*).—2. Unacetolysed 8-grained polyad of *C. houstoniana*. The sticky appendage on the basal cell is attached to the SEM stub (cult. at MO from: Mexico, Chiapas, *Johnson 363-78*). Scales = 50  $\mu$ m.

very distinctive circular thickenings in the central cells generally on one side of the polyad (Fig. 1), which are an excellent diagnostic character. The remaining species of the genus, in contrast, have specialized 8-grained, bisymmetric, calymmate polyads, with columellar/granular exine structure. In addition, the 8-grained polyads have a mucilaginous structure on the “basal” cell (on the narrow part of the polyad), which is associated with transfer by pollinators (Fig. 2). The nature of polyad cohesion (calymmate), the characteristics of the ectexine, and the presence of the sticky appendage in the “basal” cell of the 8-grained polyads in *Calliandra*, form a combination of features found nowhere else in the Mimosoideae. It is important to mention that no intermediate forms have been found between the two pollen groups (Ph. Guinet, pers. comm.).

The outstanding differences between the 16- and 8-celled polyads have provided evidence to suggest that the genus should be subdivided (Guinet, 1969). Moreover, Niezgodá et al. (1981) have suggested a separate generic or even tribal status for the species of *Calliandra* with 8-celled polyads, in light of their great distinctiveness in the whole subfamily.

On the basis of this evidence, several studies were initiated in order to test the general validity of this relationship within *Calliandra*. These studies, the results of which will be outlined below, include surveys on seedling morphology, reproductive biology, and chromosome numbers of species throughout the genus. Although these investigations are still in progress, they show the same variation pattern found in the palynological work. The dichotomy resulting from the analysis of these characters acquires a special meaning when it is considered that the identity of *Calliandra* has been traditionally based on the presence of a single morphological feature: the elastically dehiscent pods. All other evidence indicates that ser. *Laetevirentes* and the rest of *Calliandra* species do not constitute a monophyletic assemblage and suggests that these taxonomic units must be placed into separate genera.

The genus name *Calliandra* Benth. has been conserved over *Anneslia* R. A. Salisbury (Int. Code Bot. Nomencl. p. 267, no. 3444. 1961), with *C. houstonii* (L'Hér.) Benth., nom. illeg. [*Gleditsia inermis* L., *C. inermis* (L.) Druce] as the type species. Bunting (Taxon 16: 469–472. 1967) has proposed amending the conservation

of *Calliandra* with *C. grandiflora* (L'Hér.) Benth. as the type species, because of the difficulty of typifying *C. inermis*; however, this proposal was rejected (Taxon 17: 466. 1968). Bentham (1875) considered *C. houstonii* as belonging to his ser. *Racemosae*. Similarly, the synonyms of *Calliandra*, *Clelia ornata* Casar. [= *Calliandra harrissii* (Lindley) Benth.], and *Codonandra purpurea* Karsten. [= *Calliandra codonandra* (Karsten.) Benth.] were included in sers. *Macrophyllae* and *Nitidae* respectively. Consequently, as no published generic name seems to be available for any member of ser. *Laetevirentes*, the following new name is proposed.

*Zapoteca* H. Hernández, gen. nov. (Leguminosae—Mimosoideae, trib. Ingeae). TYPE: *Z. tetragona* (Willd.) H. Hernández, comb. nov. *Acacia tetragona* Willd. Species Plantarum 4(2): 1069. 1806. Venezuela, Caracas, in ripis arenosis fluvii Guairito, *Bredemayer 17* [lectotype: B (Herbar Willdenow no. 19147) here designated; phototypes MO!, MEXU!].

*Calliandra* Benth. ser. *Laetevirentes* Benth. Hook. J. Bot. 3: 97. 1844.

Frutices ramosi, erecti vel scandentes, inermes, ramis teretibus vel tetragonis. Stipulae saepe conspicuae, foliaceae, persistentes. Folia bipinnata, foliolis saepe membranaceis vel interdum coriaceis. Inflorescentia capitata, pedunculata, axillaris vel in pseudopanicula, homomorpha, heterogama vel homogama, bracteata. Flores sessiles, actinomorphi, 5-meri vel rarius 6-meri. Calyx cupulatus, dentatus, glaber vel pubescens. Corolla infundibuliformis vel campanulata, petalis revolutis. Stamina numerosa (ca. 30–60); filamentis longe exsertis, 19–43 mm longis, albis, roseis vel purpureis; staminum tubo incluso; antheris eglandulosis. Pollinia 16-cellularia, discoidea, heteromorpha; cellulis centralibus papillatis. Ovarium breviter stipitatum, 10–15 ovulatum; stylo filiformi, 18–45 mm longo; stigmate apicali, cupulato. Legumen membranaceum ad coriaceum, siccum, lineare, rectum, plano-compressum, margine incrassato, valvis ab apice ad basin elasticè dehiscentibus. Semina indurata, exarillata.  $x = 13$ .

Shrubs ramose, erect or scandent, unarmed, glabrous or pubescent, with the young branches terete or 4-angled. Phyllotaxy distichous. Stipules usually conspicuous, leafy, usually persistent in mature leaves. Leaves bipinnate; petiole rarely with nectariferous glands; leaflets opposite, sessile, usually membranous or rarely coriaceous, usually glaucous underneath, glabrous or pubescent. Inflorescences axillary and/or pseudopaniculate, pedunculate, capitate, densely flowered, homomorphic, heterogamic or homogamic, bracteate. Flowers sessile, actinomorph-

ic, 5- rarely 6-merous; calyx cup-shaped, dentate, glabrous or pubescent; corolla campanulate or infundibuliform, membranous, with the petals revolute, valvate in bud; nectariferous disk present in all flowers; stamens numerous (ca. 30–60), filaments long-exserted, ca. 19–43 mm long, white, pink, or purple, staminal tube inserted; anthers dithecal, dorsifixed, eglandular, every anther containing eight polyads; polyads 16-grained, discoid, heteromorphic, with eccentric lens-shaped thickenings on central cells; ovary 1, shortly stipitate, with ca. 10–15 ovules; style filiform, ca. 15–56 mm long in fertile pistils; stigma apical, cup-shaped. Legume dry, membranaceous to coriaceous, linear, straight, plano-compressed, with the margins thickened, usually with constrictions in interseminal areas, valves dehiscent elastically from the apex to the base. Seeds in one series, hard, ovate to rhomboid, non-arillate, non-alate usually with irregular or regular 90 percent pleurogram. Seedlings phaneroepigeal, with the cotyledons ephemeral, foliaceous, sessile, elliptic to elliptic-ovate; the first and second eophylls opposite, the third and fourth alternate; leaflets usually membranous.  $x = 13$ .

*Z. caracasana* (Jacq.) H. Hernández, comb. nov. *Mimosa caracasana* Jacq., Collectanea 4: 142. 1791. Fig. Jacq., Icon. pl. rar. 3: 20, t.632. 1793.

*Z. formosa* (Kunth) H. Hernández, comb. nov. *Acacia formosa* Kunth, Mim. p. 102, t. 32. 1822.

*Z. lambertiana* (G. Don) H. Hernández, comb. nov. *Acacia lambertiana* G. Don, Edwards Bot. Reg. 9: t. 721. 1823. TYPE: México, locality unknown; cultivated by G. Don, from material sent to him by Mr. Lambert from Boyton, where plants of this species had been raised from seeds collected in México (lectotype, K!, here designated).

*Z. media* (M. Martens & Galeotti) H. Hernández, comb. nov. *Acacia media* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10: 316. 1843. TYPE: México, Hidalgo, Hacienda de Guadalupe près Mextitlán *Galeotti 3362* pro parte (lectotype, BR!, here designated).

*Z. mollis* (Standley) H. Hernández, comb. nov. *Calliandra mollis* Standley, Contr. U.S. Natl. Herb. 17: 431. 1914. TYPE: Costa Rica, Puntarenas, near Nicoya, *Tonduz 13536* [holotype, US! (sheet no. 578114); isotypes, BM!, F!, G!, GH!, K!, NY!, US!].

**Z. portoricensis** (Jacq.) H. Hernández, comb. nov.  
*Mimosa portoricensis* Jacq., Collectanea 4:  
 143. 1791. Fig. Jacq., Icon. pl. rar. 3: 20, t.  
 633. 1793.

This genus is named to pay homage to the Zapotec people, who since 500 B.C. (Flannery & Marcus, 1983) to the present have inhabited the varied lands of Oaxaca, Mexico, the center of diversity of this group of plants.

*Zapoteca* is a rather homogeneous assemblage morphologically, consisting of about 25 taxonomically difficult taxa, distributed from northern Mexico and southwestern United States to northern Argentina, ranging from sea level to ca. 2,150 m. The greatest concentration of species is in southern Mexico, especially in the state of Oaxaca. Natural populations occur primarily in disturbed habitats derived from a variety of vegetation types, from semi-arid scrub to relatively wet forests; however, the greatest diversification has occurred in tropical dry forests. Several species have very wide ranges (e.g., *Z. formosa*, *Z. portoricensis*, *Z. tetragona*) and evidently have outstanding ability to colonize new habitats. Other species are narrow endemics (e.g., *Z. mollis*).

The totality of published specific epithets (45) included within *Calliandra*, ser. *Laetevirentes* is clearly comprised in *Zapoteca*. As mentioned above, 25 taxa are currently recognized in the genus, and new combinations are proposed here for seven of them. The remaining ones will be treated in a future revision, due to the fact that their taxonomic status—whether species or subspecies—is still unclear. Because the species of *Zapoteca* are quite uniform morphologically, the genus is easy to identify. There are, however, some *Calliandra* species, not members of ser. *Laetevirentes*, that must also be taken into consideration because they have some features typical of *Zapoteca*. These are *C. amazonica* Benth. and *C. aculeata* Spruce ex Benth., both placed by Bentham (1875) in his ser. *Macrophyllae*, who, however, had previously noted similarity between the structure of the inflorescence of *C. amazonica* and that of *Z. portoricensis* (Bentham, 1844). Subsequently, Guinet (1965) found that the polyad characteristics of these two species are essentially the same as those of Bentham's ser. *Laetevirentes*. The small number and larger size of the leaflets in *C. amazonica* and *C. aculeata*, and the presence of stipular spines in *C. aculeata*, are the main characters differentiating

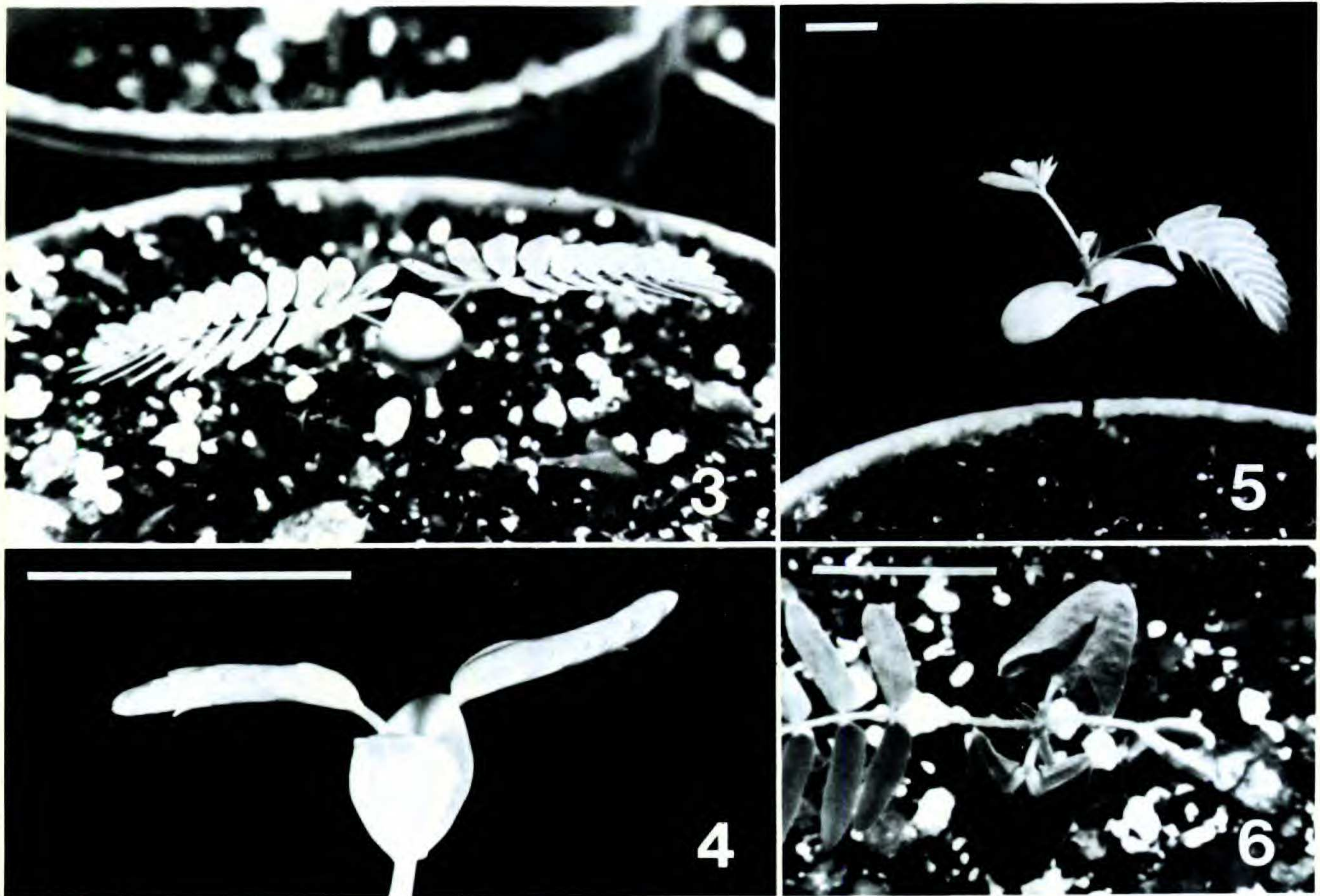
them from the species of *Zapoteca*. In the light of present evidence, it seems clear that these two species do not fit within the limits of *Calliandra* as proposed in this paper; however, their inclusion within *Zapoteca* or another genus needs further study.

#### DESCRIPTION OF SOME CRITICAL CHARACTERS IN *ZAPOTECA* AND *CALLIANDRA*

This section provides the supporting evidence that reflects the heterogeneous nature of *Calliandra* as structured by G. Bentham. The characters analyzed are described concisely; comprehensive accounts will be provided in a subsequent paper.

*Seedling morphology.* A total of 95 seedling samples have been studied, representing nine species of *Zapoteca* and 31 of *Calliandra*. In describing the seedlings I have selected four main characters: 1) degree of persistence of cotyledons, 2) morphology of cotyledons, 3) type of succession of eophylls, and 4) number of leaflets. Of these, cotyledon features revealed the most striking contrast between the *Zapoteca* seedlings and those of *Calliandra*. All the species of *Zapoteca* have seedlings with elliptic or elliptic-ovate, sessile, foliaceous, and ephemeral cotyledons (Figs. 3, 4). In contrast, *Calliandra* seedlings have sagittate, petiolate, fleshy, and relatively persistent cotyledons as common characters (Figs. 5, 6). While the type of succession of the eophylls and the leaflet characteristics were remarkably constant in the *Zapoteca* seedlings, these characters display a high degree of variation in *Calliandra*. This variation allows a further grouping into five subtypes, which correspond to a certain extent with Bentham's series. In sum, the morphological characteristics in the seedlings of *Zapoteca*, which are notably homogeneous, differ from those of *Calliandra* primarily in the basic features of the cotyledons. The absence of intermediate seedling forms between *Zapoteca* and *Calliandra* reflects the lack of close relationships between the two genera.

*Reproductive biology.* The species of *Zapoteca* differ from those of *Calliandra* in a number of aspects of their reproductive behavior. In *Zapoteca* the individual flowers are always arranged in compact, homomorphic, spherical inflorescences (Fig. 7). In *Calliandra*, in contrast, there are more diverse patterns of inflorescence organization. The basic type seems to be the axillary, obconiform inflorescence (Fig. 8) from which other types have been derived. The racemose



FIGURES 3–6. Seedling types of *Zapoteca* and *Calliandra*.—3. *Z.* sp. nov. (cult. at MO from: Mexico, Oaxaca, Torres 4167).—4. *Z. tetragona* (cult. at MO from: Mexico, Veracruz, H. Hernández 167).—5. *C. calothyrsus* (cult. at MO from: Panama, David, Johnson 929-79).—6. *C. eriophylla* (cult. at MO from: Mexico, Oaxaca, Torres 4192). Scales = 10 mm.

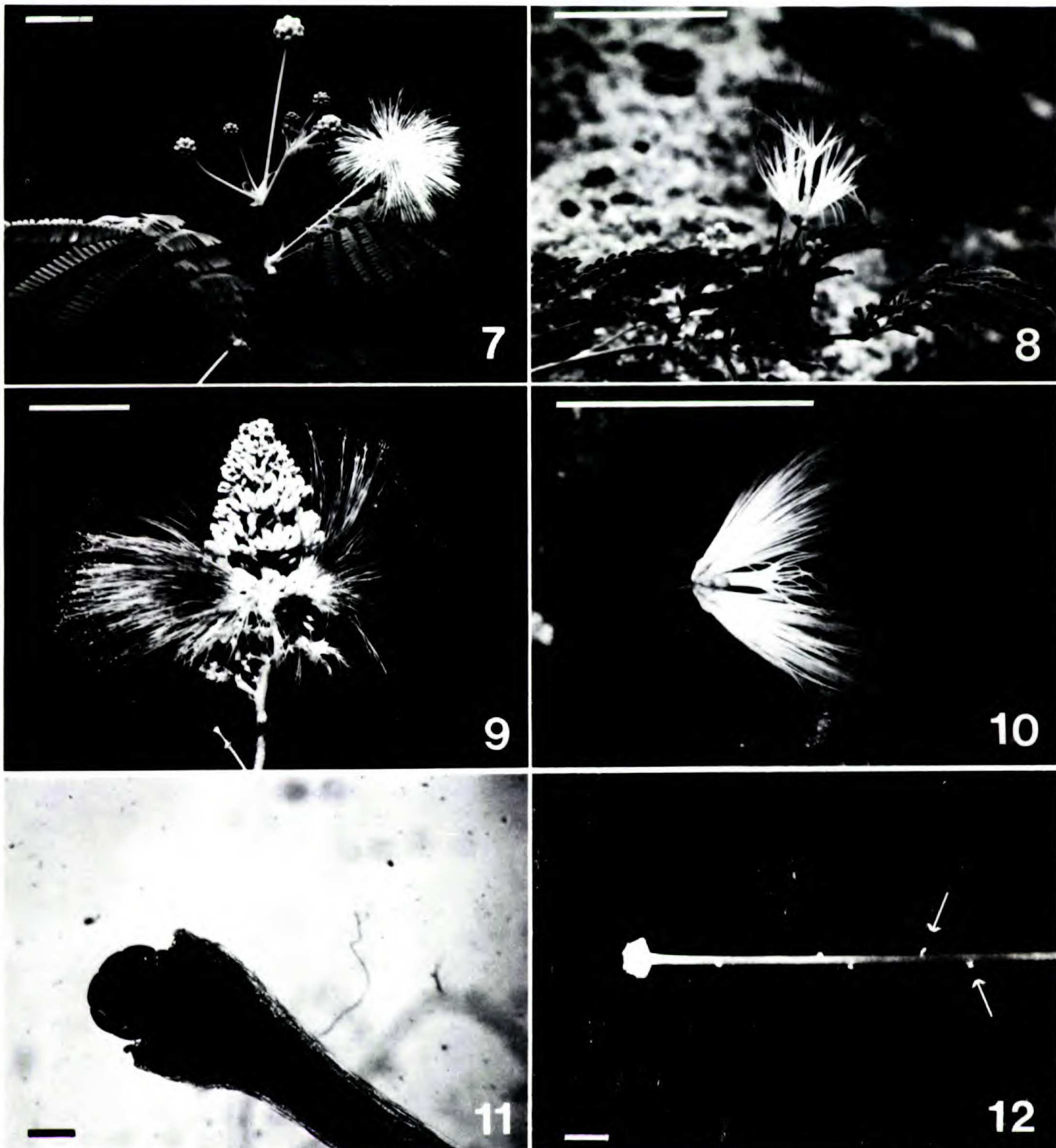
inflorescences of the species of ser. *Racemosae* (Fig. 9), a group basically endemic to Mexico and Central America, represent the type that has departed most from the ancestral type of inflorescence.

An interesting reproductive feature found in most species of *Calliandra* ser. *Nitidae*, *Macrophyllae*, and in some of the *Pedicellatae* is the presence of heteromorphic inflorescences (Fig. 10). In general, these have one to several central flowers whose morphology is modified in relation to the peripheral ones. The central flowers are the only ones bearing nectaries; these are larger and have the staminal tube well exerted from the corolla apex. This floral specialization, which is also found in other genera of the tribe Ingeae (e.g., *Albizia*), has important consequences on the foraging behavior of flower visitors. Because the central flowers are more conspicuous and provide nectar rewards, the visitors forage actively on them, seeking them out and therefore increasing the possibilities of pollinating a higher number of hermaphroditic flowers in the inflorescence in the course of a single visit.

A detailed analysis of sex expression carried

out on flower material collected in natural populations has shown that andromonoecy, expressed morphologically by gynoeceium abortion, is widespread in both genera. In contrast to the opinion of Nevling and Elias (1970), this study has shown that variation in the presence of andromonoecy is not consistent with the variation patterns found in other characters (e.g., polyads, seedlings, chromosome numbers).

Another reproductive feature characteristic of *Zapoteca* species is the stigma type. All the species in this genus have delicate, cup-shaped stigmas, with a very narrow area of receptivity that can hold just a single 16-celled polyad (Fig. 11). As far as it has been possible to observe, this stigma type is found in all the genera of the tribe Ingeae, except *Calliandra* (see for example, Koptur, 1983; Hoc, 1981), and in 17 genera of the Mimosoideae (Lewis, pers. comm. via Polhill; see also Simpson et al., 1977; Nevling & Niezgoda, 1978; Kenrick & Knox, 1981; Lewis & Elias, 1981; Hopkins, 1984). In contrast, the species of *Calliandra* have very distinctive expanded, fungiform, discoid, or capitate stigmas with a much wider area of polyad receptivity (Fig. 12). The stigma types in *Cal-*



FIGURES 7-12. Reproductive characters of *Zapoteca* and *Calliandra*.—7. Spherical, homomorphic inflorescence of *Z. tetragona* (cult. at MO from: Mexico, Veracruz, *Johnson 1582*).—8. Obconiform, heteromorphic inflorescence of *C. rubescens* (Mexico, Veracruz, *H. Hernández 156*).—9. Racemose inflorescence of *C. calothyrsus* (Mexico, Chiapas, *H. Hernández 519*).—10. Heteromorphic inflorescence of *C. rubescens* (Mexico, Veracruz, *H. Hernández 156*).—11. Cup-shaped stigma of *Z. caracasana* with a 16-grained polyad in the stigmatic cavity (cult. at MO from: *Johnson 2494-82*).—12. Fungiform stigma of *C. houstoniana*. The arrows indicate polyads attached to the style (cult. at MO from: Mexico, Chiapas, *Johnson 363-78*). Scales = 40 mm in Figures 7-10; 50  $\mu$ m in Figure 11; and 1 mm in Figure 12.

*liandra* are clearly a derived condition with important reproductive consequences; however, an analysis of their adaptive significance is out of the scope of this paper.

The specific set of morphological and behav-

ioral reproductive characteristics in *Zapoteca* and *Calliandra* is associated with particular classes of pollinators. Field and greenhouse observations, in conjunction with some literature reports, have allowed us to characterize these

TABLE 1. Chromosome numbers in *Zapoteca* and *Calliandra*. The asterisk (\*) indicates first report for the species.

Species	Chromosome Number		Reference
	<i>n</i>	<i>2n</i>	
<i>Zapoteca tetragona</i> *		26	México, Veracruz, Mun. Catemaco, a 1 km de Sontecomapan por camino a Coxcoapan, <i>H. Hernández 167</i> (MO, MEXU)
		26	México, Veracruz, Mun. Córdoba, sobre la autopista Fortín-Córdoba, <i>H. Hernández 827</i> (MO, MEXU)
		26	Costa Rica, Cartago, Finca Perla, entre Reserva de Vida Silvestre Tapantí y Purisil, <i>H. Hernández 675</i> (MO, MEXU)
<i>Z. portoricensis</i> *		26	México, Veracruz, 6.8 km N de Xalapa por camino a Naolinco, <i>H. Hernández 154</i> (MO, MEXU)
<i>Z. formosa</i> *		26	México, Oaxaca, Dist. Tehuantepec, 11.1 km SW del entronque carr. Tehuantepec-Oaxaca, por camino a Buenos Aires, <i>R. Torres 4262</i> (MO, MEXU)
		26	México, Yucatán, 20 km S of Progreso, <i>D. Johnson 483-78</i> (MO)
<i>Z. media</i> *		26	México, Hidalgo, Mun. Metztlán, Paso del León, Barranca de Venados, <i>A. Delgado 53</i> (MEXU)
<i>Z. sp. nov. (1)</i> *		26	México, Oaxaca, Dist. Mixe, 6 km N de Mitla por camino a Totontepec, <i>R. Torres 3947</i> (MO, MEXU)
<i>Z. sp. nov. (2)</i> *		26	México, Oaxaca, Dist. Tehuantepec, El Manguito, SW de El Limón, <i>R. Torres 4167</i> (MO, MEXU)
Ser. Nitidae			
<i>Calliandra surinamensis</i>		16	Atchinson (1949) <sup>1</sup> ; Goldblatt (1981b)
<i>C. surinamensis</i>	8		Bir et al. (1980)
<i>C. magdalenae</i>		16	Goldblatt (1981b)
<i>C. haematocephala</i>		16	Atchinson (1951)
<i>C. tweedyi</i>		16	Bir and Kumari (1978, 1979)
<i>C. pittieri</i>		32	Shibata (1962)
Ser. Macrophyllae			
<i>C. tergemina</i> *		16	México, Jalisco, Mun. la Huerta, Estación de Biología Chamela, <i>E. Lott 1686</i> (MO, MEXU)
Ser. Racemosae			
<i>C. houstoniana</i>	8		Bir et al. (1980)
<i>C. calothyrsus</i>		22	Goldblatt (1981b) <sup>2</sup>
<i>C. rusbyi</i> *		22	México, Guerrero, Mun. Coyuca, Torre de Microndas, 5 km NW de El Zapote, por carr. Atoyac-Cayuca, <i>H. Hernández 865</i> (MO, MEXU)
<i>C. sp. nov.*</i>		22	México, Oaxaca, Dist. Putla, 11.5 km NE de Putla por carr. a Tlaxiaco, <i>H. Hernández 465</i> (MO, MEXU)

<sup>1</sup> Referred to as *C. haematocephala*.<sup>2</sup> Referred to as *C. confusa*.

genera in terms of their pollination mechanisms. The pollination of species of *Zapoteca* appears to be exclusively nocturnal, and a number of settling moth species (families Noctuidae, Pyralidae, and Geometridae, etc.) consistently have been observed foraging on inflorescences of *Z. portoricensis*, *Z. formosa*, *Z. media*, and *Z. tet-*

*ragona* (pers. obs.). *Calliandra*, however, is more diverse in its pollination systems. Several species of the genus have been reported as hawkmoth-pollinated (Cruden et al., 1976; Haber & Frankie, 1984; pers. obs.), whereas others are hummingbird-pollinated (Snow & Snow, 1972; Arroyo, 1981; pers. obs.). Interestingly, as was noted by

TABLE 2. Comparative characters of *Zapoteca* and *Calliandra*.

	<i>Zapoteca</i>	<i>Calliandra</i>
Leaflets	thin membranaceous, rarely coriaceous	chartaceous to coriaceous
Inflorescence	spherical heads; homomorphic	obconiform, racemose, rarely spherical; homomorphic or heteromorphic
Polyads	16-grained, discoid	8-grained, bisymmetric, with viscid appendage in "basal" grain
Stigmas	cup-shaped, with narrow area of polyad receptivity	expanded; fungiform, discoid, or capitate
Legume	membranaceous to coriaceous	more rigid; coriaceous, ligneous, rarely membranaceous
Seedlings	cotyledons ovate, sessile, foliaceous, ephemeral	cotyledons saggitate, petiolate, fleshy, persistent
Chromosome numbers	$x = 13$	$n = 8, 11$

Arroyo (1981) for other genera of the Mimosoideae, the limits between sphingophily and ornithophily are not well established in a number of species of *Calliandra* [e.g., *C. magdalenae* (Bertero ex DC.) Benth., *C. grandiflora* (L'Hér.) Benth., *C. houstoniana* (Miller) Standley]. In these species the filaments are red or a combination of white and red, and the flowers remain in anthesis during the night and the first hours of the day, allowing a succession of sphingid moth and hummingbird visits. The relative effectiveness of each pollinator class will be analysed elsewhere. A similar situation is probably found in *C. calothyrsus* Meissn. (= *C. confusa* Sprague & Riley, and *C. similis* Sprague & Riley), whose flowers have been reported to be visited by honeycreepers (Coerebidae; Skutch, 1981), bats (Holdridge & Poveda, 1975), and sphingid moths (pers. obs.). Visitors of high energetic requirements often seek such flowers with their copious nectar product if the nectar is relatively accessible.

*Cytogenetics.* Although *Calliandra* sensu Bentham is a large genus, very little information on its chromosome numbers has been published (Table 1). The counts I have obtained so far in the hitherto cytologically unknown *Zapoteca* are  $n = 13$  (Table 1), which is consistent with the basic chromosome numbers reported for all the genera of the Ingeae ( $x = 13$ ; Goldblatt, 1981a). *Calliandra* sensu stricto, in contrast, represents the only known exception to  $x = 13$ , with several species distributed in sers. *Nitidae*, *Macrophyllae*, and *Racemosae* having  $n = 8$  (Table 1). Furthermore, *C. calothyrsus* (Goldblatt, 1981b) and other members of ser. *Racemosae* are known to be  $n = 11$ , and *C. pittieri* is polyploid,  $n = 16$

(Shibata, 1962). Table 2 shows a summary of the basic characters of *Zapoteca* and *Calliandra*.

#### GENERAL REMARKS

The segregation of the species of *Calliandra* ser. *Laetevirentes* into the genus *Zapoteca* as proposed in this paper constitutes the first step toward a comprehensive study of *Calliandra* (Forero, 1984; Hernández, 1984; Romeo, 1984). The *Calliandra* species from Madagascar and India must be studied critically in the same way as the *Zapoteca* species because these are palynologically dissimilar to the remaining species (Guinet, 1965). The neotropical species of *Calliandra* as circumscribed here, however, are certainly monophyletic. We must pursue an integral infrageneric classification of this genus in order to improve Bentham's taxonomic framework. Several taxa, primarily South American, do not fit into this classification, and evidence indicates that sers. *Macrophyllae* and *Pedicellatae* are artificial.

The presence of two species of *Calliandra* in restricted areas of eastern Africa provides an interesting phytogeographic pattern. These species, which are clearly related to the neotropical ones (Thulin et al., 1981), probably represent remnants of more diversified taxa that existed in Africa before the widespread extinction that has taken place in this continent since the close of the Oligocene (Raven & Axelrod, 1974). The polyad characteristics of these species are basically the same as those of the neotropical *Calliandra* (Thulin et al., 1981) with the exception that the cells are free from one another (acalym-



mate). The existence of this feature is a further indication of the primitive nature of these species.

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