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MONOGRAPH OF LEUCAENA (LEGUMINOSAE-MIMOSOIDEAE)

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ABSTRACT. The neotropical genus *Leucaena* comprises 22 species, 6 infraspecific taxa, and two named hybrids. A morphological data set is analyzed cladistically to determine species relationships. The comparative morphology of species of *Leucaena* and closely related genera is investigated and presented. This includes detailed studies of bark anatomy, nyctinastic leaf movements, morphology of extrafloral nectaries, seedlings, inflorescences, pods, anther, and pollen morphology. Scanning Electron Microscopy was used to investigate micromorphology. Criteria for the assessment of primary homology, including the problems of character coding in relation to inapplicable data and continuous characters, are discussed. A total of 29 binary and multistate characters are analyzed. A preliminary analysis of sister group relationships amongst the genera of the informal *Leucaena* and *Dichrostachys* groups and two outgroup genera, *Parkia* and *Xylia,* revealed no support for these groups and suggested that *Schleinitzia*, the only other genus traditionally placed in the *Leucaena* group, may not be the sister group of *Leucaena*. Instead, three resolved clades are found: a monophyletic *Leucaena*; a clade containing *Schleinitzia, Desmanthus,* and *Neptunia;* and a clade containing the remaining genera of the *Dichrostachys* group, including *Calliandropsis, Alantsilodendron, Gagnebina,* and *Dichrostachys*. This analysis was used to select different combinations of outgroups for the species-level analysis. The 22 species of *Leucaena* are delimited using the phylogenetic species concept. The difficulties posed by hybrids for cladistic analysis and the evidence for hybridization in *Leucaena* are reviewed. Analysis of species relationships omitting the four known tetraploid species showed no support for division of *Leucaena* into two recently recognized sections. The morphological analysis showed broad concordance with results from cpDNA restriction fragment analysis. A combined analysis was not pursued here due to a number of limitations, including intraspecific polymorphism due to introgressive hybridization, associated with the cpDNA data. A full taxonomic account of *Leucaena* is presented; all taxa are illustrated and their distributions mapped. One hybrid, *L.* ×*mixtec*, is described as new.

INTRODUCTION

Leucaena is here shown to comprise 22 species, six infraspecific taxa, and two named hybrids, and is placed in the tribe Mimoseae of the subfamily Mimosoideae of the family Leguminosae. All species are native to the New World, although one, *L. leucocephala*, is cultivated pantropically and has become naturalized and weedy in many areas (Hughes & Styles 1989; Hughes 1998). The greatest diversity of species is in Mexico (17 species, 10 endemics) and in northern Central America (9 species, 4 endemics). The genus extends north into southern Texas (U.S.A.), sporadically across the Caribbean and into South America as far south as Peru. All species are small to medium-sized trees, which grow mainly in seasonally dry deciduous tropical forests, and to a lesser extent in semi-arid thorn scrub forest, dry mid-elevation matorral, and, in the north, subtropical or warm temperate habitats (Fig. 1).

The economic importance of *Leucaena* species, and particularly *L. leucocephala*, for the production of livestock feed, green manure, small wood products, and for soil conservation is well known and widely documented (Pound & Martínez-Cairo 1983; National

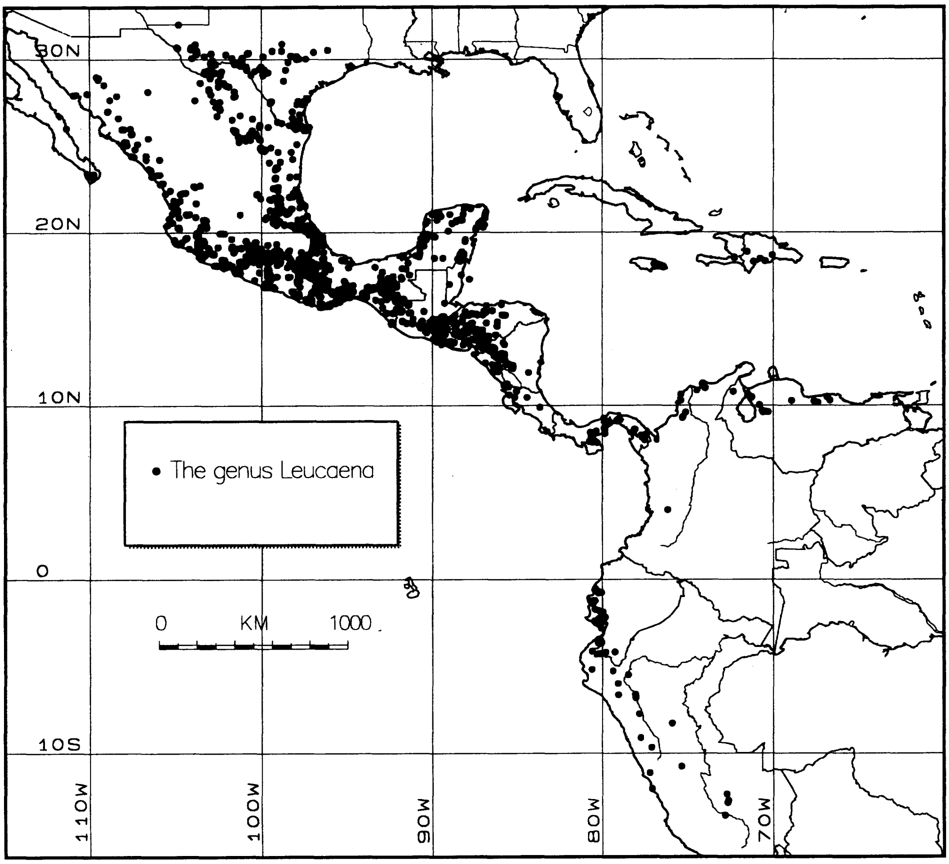


FIG. 1. Distribution of all *Leucaena* species in the New World. Data points are 2393 herbarium specimen collection sites with verifiable localities (88% of the total specimens examined). The distribution shows clearly the occurrence of species of *Leucaena* in seasonally dry tropical habitats and their virtual absence from the cold arid deserts of north-central Mexico, and the non-seasonal wet lowland forests of the southern Gulf of Mexico (Tabasco and northern Chiapas), the Petén region of Guatemala, the Atlantic zone of Honduras, Nicaragua, Costa Rica, and Panama, and the perhumid forests of the Darién/Chocó coastal zones of Colombia and northwestern Ecuador.

Academy of Sciences 1984; Brewbaker 1987b; Shelton & Jones 1995; Hughes 1998). *Leucaena leucocephala*, and more recently, other species of *Leucaena* (Brewbaker & Sorensson 1994) have been widely promoted and introduced into cultivation by national and international development agencies throughout the tropics as fast-growing exotics for reforestation. As well as being a useful plant, *L. leucocephala* is a known invasive weed in some areas (Cronk & Fuller 1995; Hughes 1998) and is currently the focus of biological control efforts in southern Africa (Neser 1994). As potential sources of germplasm for genetic improvement of an important tree and agricultural crop, *Leucaena* species have been the focus of considerable applied agronomic research over the last two decades (summarized in Brewbaker 1987b; Hughes 1998). This means that comprehensive seed collections of *Leucaena* species are available (Hughes et al. 1995; Hughes 1998). It also means that much is known about interspecific crossability (Sorensson 1993; Sorensson

& Brewbaker 1994), hybridization, both spontaneous (Hughes & Harris 1994, 1998; Hughes 1998) and artificial (Brewbaker & Sorensson 1990), chromosome numbers (González et al. 1967; Pan & Brewbaker 1988; Sorensson 1989; Palomino et al. 1995), and breeding systems (Sorensson 1989) compared to most tropical woody genera. Wider agronomic characteristics including *Rhizobium* affinities (Halliday & Somasegaran 1983), Bruchidae host records (Hughes & Johnson 1996), psyllid (*Heteropsylla cubana* Crawford) tolerance (Muddiman et al. 1992; Sorensson & Brewbaker 1987), cold tolerance and site adaptability (e.g., Brewbaker et al. 1988; Stewart et al. 1991; Hughes 1998), and leaf chemical composition (e.g., Norton et al. 1995; Wheeler et al. 1995), including presence of mimosine (Bray 1995), are well studied for most species.

Indigenous use of *Leucaena* has concentrated not on leaf and wood products, but on the unripe pods and seeds, which are used as a minor food for human consumption throughout south-central Mexico (Whitaker & Cutler 1966; Zárate 1984b, 1987a, 1994, 1997; Casas & Caballero 1996; Hughes 1998). Ethnobotanical and archaeological data indicate that indigenous food use is prevalent over a wide geographic area, has involved at least 13 species, and has probably been continuous over the last 7000 years (Hughes 1998). This has resulted in a series of highly sophisticated and finely differentiated local cognitive systems (e.g., Berlin et al. 1974; Casas & Caballero 1996). Indigenous use has involved a complex process of incipient domestication (Zárate 1984b; Casas & Caballero 1996) that has resulted in widespread artificial sympatry facilitating spontaneous hybridization (Hughes 1998). Despite its indigenous and wider economic importance, the taxonomy of the genus remains confused; the most recent complete taxonomic revision of *Leucaena* is that by Britton and Rose (1928).

Recent investigation of the systematics of *Leucaena* has focused on three main problems: generic relationships, species delimitation (including hybrids), and species relationships. In their preliminary arrangement of the 36 genera of the Mimoseae as 12 informal groups, Lewis and Elias (1981) placed *Leucaena* with the Pacific genus *Schleinitzia* Warb. ex Nevling & Niezgoda in the *Leucaena* group. They suggested that the *Leucaena* group is closely related to both the *Dichrostachys* group, comprising *Desmanthus* Willd., *Dichrostachys* (DC.) Wight & Arn., *Gagnebina* Necker, and *Neptunia* Lour., and the *Xylia* group, containing *Xylia* Benth. and *Calpocalyx* Harms. Within the confines of the *Leucaena* group the boundaries between *Leucaena* and *Schleinitzia* appear entirely satisfactory. However, when the relationships amongst the genera of the *Leucaena* and *Dichrostachys* groups are considered together, difficulties arise because the characters used to circumscribe the groups and their constituent genera do not stand up to cladistic analysis (Luckow 1995, 1997). Understanding of the sister group relationships of the genera of the Mimoseae, and the *Leucaena* and *Dichrostachys* groups in particular, has been confounded by poorly circumscribed genera and over-reliance on a small number of characters (Luckow 1995). Recent work by Luckow (1997) has provided the first explicit phylogenetic hypothesis of generic relationships within the Mimoseae that includes *Leucaena* and *Schleinitzia*.

Different approaches to species delimitation have resulted in widely differing numbers of species recognized within *Leucaena* by different authors (Britton & Rose 1928; Brewbaker 1987a; Zárate 1994), and this has been the main cause of taxonomic confusion within the genus. Species delimitation is complicated by polyploidy, with four known tetraploid species, and by putative interspecific hybridization resulting from the indigenous domestication of *Leucaena* species as minor food plants in Mexico (e.g., Hughes & Harris 1994, 1998; Casas & Caballero 1996; Hughes 1998). There is also lack of agreement about species relationships within *Leucaena* with two competing hypotheses. The sectional classification of Zárate (1994) is based on a small number of morphological characters and disagrees with results from the chloroplast DNA restriction fragment analysis of Harris et al. (1994a).

The taxonomic account presented here is based on a cladistic analysis of a new morphological data set and on re-evaluation of the cpDNA data set of Harris et al. (1994a). Assembly of the morphological data set and the resultant taxonomic account are based on study of over 2700 herbarium specimens and on field work in the U.S.A., Mexico, Central America, and northern South America. Some material from cultivated and naturalized Old World populations has been examined and identified; however, the identities of some of this material, particularly from parts of southeast Asia, are complicated by spontaneous interspecific hybridization (Dijkman 1950; Howcroft 1994; Hughes & Harris 1994, 1998). Further work will be required to unravel fully hybrid identities in these areas. A herbarium specimen database for *Leucaena* has been assembled using the botanical database system BRAHMS (Botanical Research and Herbarium Management System) (Filer 1996), and data are available on request from the author. Through previous involvement in applied research on the genetic resources of *Leucaena*, I am in the fortunate and unusual position, for a monographer, of having seen and collected all of the known taxa of *Leucaena* from wild populations or cultivated trees. This means that not only is there a large collection of *Leucaena* specimens and associated material at FHO, but also that several new characters, including nyctinastic leaf movements, bark morphology, and flowering shoot development, could be observed and scored from living trees either in the field or from cultivated plants in the greenhouse or field plots established in Honduras.

TAXONOMIC HISTORY

The taxonomic history of *Leucaena* is complex. At the time of Bentham's 1846 treatment *Leucaena* included another genus, *Schleinitzia*, and it was later split into three genera, *Leucaena, Ryncholeucaena* Britton & Rose, and *Caudoleucaena* Britton & Rose. However, the greatest source of confusion has surrounded the delimitation of species.

As part of his revision of the Mimosoideae, Bentham (1842) established the genus *Leucaena*, with four species: *L. glauca*, *L. pulverulenta*, *L. diversifolia,* and *L. trichodes*, all transferred from *Acacia* L. and placed in his tribe Eumimoseae. Bentham (1846) added three more species, including *L. forsteri*, a species with glands on the anther tips, although this was not a character of the genus *Leucaena* nor of his tribe Eumimoseae. The absence of anther glands was used by Bentham (1875) to separate the Eumimoseae, containing *Neptunia, Desmanthus, Mimosa* L., *Schrankia* Willd., and *Leucaena*, from the Adenanthereae, but Bentham (1875) already knew of several species amongst these genera that possess anther glands and was aware of how unreliable that character could be (Bentham 1875: 337). Today *L. forsteri* is referred to *Schleinitzia*, a genus whose species have been variously ascribed to *Leucaena, Piptadenia* Benth., and *Prosopis* L., but which was judged to have closest affinities to *Leucaena* (Verdcourt 1977, 1979; Nevling & Niezgoda 1978; Lewis & Elias 1981).

After *Leucaena* was described by Bentham (1842), initially with four, and later six (Bentham 1846), then nine species (Bentham 1875), four botanists, Nathaniel Britton and Joseph Rose, James Brewbaker, and Sergio Zárate, have figured prominently in the classification of *Leucaena*. These authors have had distinct approaches to delimiting species, and the number of species recognized has varied from 10 to 39.

After Bentham's (1875) revision, field exploration, principally by the prolific plant collectors Edward Palmer, Cyrus Pringle, Joseph Rose, and Karl Purpus, led to the description of many supposed new species. Standley (1922) recognized 15 species, and Britton and Rose (1928), who alone added 24 species, recognized 39. Neither of these revisions included taxonomic and nomenclatural synonyms beyond those of Bentham (1875). Britton and Rose (1928) based their species delimitation on characters that are now viewed as unreliable, either because they present continuous patterns of variation across species or because they vary within and among populations. Inadequate sampling resulted in failure to detect the continuities and population variation that are now obvious. The result was a proliferation of new species, most of which are here treated as conspecific.

Britton and Rose (1928) were the only workers to depart from the traditional circumscription of *Leucaena*. They described two segregate genera *Ryncholeucaena* and *Caudoleucaena*, each monotypic, and based on the unusual species *L. greggii* and *L. retusa,* respectively. *Ryncholeucaena* was distinguished by its narrow linear pods and longitudinal alignment of seeds, and *Caudoleucaena* by its long caudate floral bracts, narrow linear pods, and oblique seed alignment. These two species also share several other unusual characters, including long peduncles and yellow flowers. While all subsequent authors have treated these segregate genera as congeneric with *Leucaena* (Brewbaker 1987a; Harris et al. 1994a; Zárate 1994), some have recognized their unusual characteristics and emphasized their possible close relationship to each other, a relationship supported by cpDNA restriction fragment data (Harris et al. 1994a). The distinction of these species as possible segregate genera has remained largely untested.

Taxonomically provincial treatments of *Leucaena* have accumulated over the 60 years following the revision by Britton and Rose (1928); however, these have provided only limited taxonomic synthesis. Such treatments have been made for Peru (Macbride 1943), Guatemala (Standley & Steyermark 1946), Panama (Schery 1950), western Mexico (McVaugh 1987), and Nicaragua (Zárate, in press).

James Brewbaker and colleagues at the University of Hawaii made the first attempt to synthesize this proliferation of species based on genetic improvement studies that involved breeding and hybridization experiments over a 30-year span. They reduced the number of species initially to ten (Brewbaker & Ito 1980), with gradual re-acceptance of additional species to 16 as they were added to the Hawaii collection (Brewbaker 1987a, b; Brewbaker & Sorensson 1994).

Sergio Zárate, of the Universidad Nacional Autónoma de México, worked on *Leucaena* initially for the Flora of Oaxaca, but expanded this study to include the taxonomy, ethnobotany, and indigenous domestication of the Mexican species of *Leucaena* as minor food plants (Zárate 1982, 1984a, b, 1987a, 1997). In his revision of the Mexican species (Zárate 1994) he added six new taxa and proposed various new combinations at infraspecific rank. Zárate adopted a different approach to species delimitation that relied on extensive use of subspecies. The differing approaches to species delimitation by Britton and Rose, Brewbaker, and Zárate have resulted in widely differing numbers of recognized species and are the main cause of taxonomic confusion within *Leucaena* today. Species delimitation in *Leucaena* was further discussed by Hughes (1997c), who described one new species and two new subspecies, and proposed four new combinations in advance of this monograph in order to expedite use of these new names in a series of publications on genetic resources (Bray et al. 1997; Hughes 1998).

Early efforts to understand species relationships within *Leucaena* relied on variation in quantitative leaf characters. These prominent characters were used by Bentham (1875) to divide the genus into two informal groups based on leaflet size, shape, and the related number of pairs of pinnae. Zárate (1984a, 1994) was the first to formalize the two divisions, again based on leaflet size and number and the related number of pinnae but including shape of extrafloral nectary as an additional character to support these two groups. This division was claimed by Zárate (1984a: 27) to be "somewhat natural," although the problematic position of *L. shannonii* with its polymorphic leaflets, which are intermediate between the two sections, was recognized. The two sections were formally designated by Zárate (1994) as section *Macrophylla*, typified by *L. macrophylla* and comprising *L. macrophylla, L. lanceolata, L. shannonii, L. retusa*, and *L. trichodes*, and section *Leucaena*, typified by *L. leucocephala* and comprising the remaining species.

Harris et al. (1994a) produced the first explicitly phylogenetic hypothesis of relationships within *Leucaena* based on chloroplast DNA restriction site variation. The results of this analysis (summarized in Fig. 31) do not support the sectional classification of Zárate.

Known polyploidy (Sorensson 1989), confirmed and unconfirmed reports of natural or spontaneous hybridization (Hughes & Harris 1994, 1998; Hughes 1998), evidence of cpDNA introgression (Harris et al. 1994a), and high artificial crossability (Sorensson & Brewbaker 1994) indicate that hybridization (including introgression) has been important in *Leucaena*. Two spontaneous hybrids have been identified using a combination of morphological, molecular, geographic, and ethnobotanical data (Hughes & Harris 1994, 1998), and hybrid origins have been proposed for three of the four known tetraploid species (Pan 1985; Harris et al. 1994a).

There has been considerable doubt and confusion over the correct application of the name *Leucaena* and its generic type. That type is listed as *"non designatus"* in Index Nominum Genericorum (Farr et al. 1979) and as *Mimosa glauca* L. by Greuter et al. (1993) in *Names in Current Use*. These doubts arose following the research of de Wit (1961, 1975), who showed that the species commonly called *Leucaena glauca* (L.) Benth.—the lectotype species designated by Britton and Shafer (1908)—is not the species to which the basionym *M. glauca* applies. *Mimosa glauca* L. belongs to the genus *Acacia*; the correct name for "*Leucaena glauca*" is *L. leucocephala* (Lam.) de Wit (see Taxonomy for details). Subsequent discussion and confusion over the generic type of *Leucaena* (see Williams 1964; Wilbur 1965; Isely 1970; Wilbur 1981; Isely 1986) was resolved by Hughes (1997b), who proposed formal conservation of the name *Leucaena* with a new type, *L. diversifolia* (Schltdl.) Benth.

MORPHOLOGY

Habit. All species of *Leucaena* are woody, forming small to medium-sized trees ranging from 4–5 m (e.g., *L. greggii, L. retusa, L. confertiflora*, and *L. cuspidata*) to 20–25 m (e.g., *L. salvadorensis, L. multicapitula, L. esculenta*, and *L. diversifolia*). Tree form varies from consistently single-stemmed (e.g., *L. macrophylla* subsp. *istmensis*) to strongly multiple-stemmed (e.g., *L. matudae*). Herbaceous habit is rare in the Mimosoideae and occurs in the genera of the *Dichrostachys* and *Leucaena* groups only in *Neptunia* and in some species of *Desmanthus*, where it was shown to be the derived condition by Luckow (1993, 1995). Habit is thus variable at generic (character #1 in generic analysis) but not species level.

Bark. "Bark" is not a technical term but is taken to include all the tissues outside of the vascular cambium, i.e., the rhytidome, the periderm, and the phloem (Trockenbrodt 1990; Junikka 1994). Data on bark surface pattern are usually either lacking or dismissed as too variable for use in systematics; few attempts have been made to correlate bark surface pattern with internal structure (Whitmore 1962; Junikka 1994) and hence define characters based on anatomy and structure that meet the criteria of topographic and compositional correspondence for primary homology assessment. However, bark has been used as a character in systematic studies of a number of taxa, e.g., *Eucalyptus* L'Hérit. (Chattaway 1953), Dipterocarpaceae (Whitmore 1962), and *Inga* Miller (Trockenbrodt & Parameswaran 1986). The variable bark morphology in *Leucaena* warrants systematic investigation.

In *Leucaena* there are two basic bark surface patterns (character #2 in species analysis). The majority of species have thin, mid-grey-brown bark, with shallow rusty orange-brown vertical boat-shaped fissures, which become deeper, more pronounced, and rougher with age; the inner bark or slash is pale cream or creamy pinkish and fibrous (type A, Fig. 2A, C). *Leucaena esculenta* and closely related species have bark that is thick, corky, lustrous pale metallic grey, like galvanized zinc, smooth when young, sometimes with an irregular "semaphore" pattern of horizontally aligned pale brown raised lenticels, becoming horizontally or irregularly gnarled with age; the inner bark is orange-red to deep blood-red and corky in texture (type B, Fig. 2B, D). Within type B, there is a specialized scalloped surface pattern with sinuous ridges dividing depressions formed when scallop-shaped scales are detached; this is found in *L. matudae*, which has bark otherwise similar to *L. esculenta* (Fig. 2D). Although Zárate (1994) attributed this pattern to injury due to removal of bark by humans, I believe it is a natural phenomenon; the pattern is too regular, fine-scale, and ubiquitous, occurring on all older trees and even inaccessible larger branches, to have been caused by bark stripping by humans. These two bark surface patterns correspond to different internal structures (Fig. 3A, B). Type A is distinguished by the presence of a series of periderms formed below the surface and the formation of a thick rhytidome or outer bark. This contrasts with type B in which a single superficial periderm forms with almost no outer bark or rhytidome. In type A, tangential stresses associated with increased tree girth are accommodated by the formation of a series of periderms, fissuring of the outer bark, and limited formation of expansion tissue or phloem proliferation tissue in the inner living bark. In bark type B, expansion occurs through abundant formation of intercalary expansion tissue, mainly in the rays of the secondary phloem and as a thick phelloderm outside the secondary phloem, with little or no fissuring of the outer bark; the epidermis often remains substantially intact even on larger trees (Fig. 2B).

Two exceptions to the exact correlation between surface pattern and internal structure were observed in *L. pallida* and *L.* ×*mixtec*, which have an intermediate bark type with limited development of a series of periderms, but also with abundant intercalary expansion tissue and a largely intact epidermis. This intermediacy is attributed to putative hybridity. Pan and Brewbaker (1988) hypothesized *L. pallida* to be an amphidiploid hybrid between *L. esculenta* (bark type B) and *L. trichandra* (bark type A). Similarly (Hughes & Harris 1994) showed *L.* ×*mixtec* to be a hybrid between *L. esculenta* (bark type B) and *L. leucocephala* (bark type A). This type of blurring of otherwise discrete character states due to hybridity is discussed further below.

Shoots. Species of *Leucaena*, and indeed the majority of genera in the *Leucaena* and *Dichrostachys* groups, are unarmed. Spines are present only in species of *Dichrostachys*

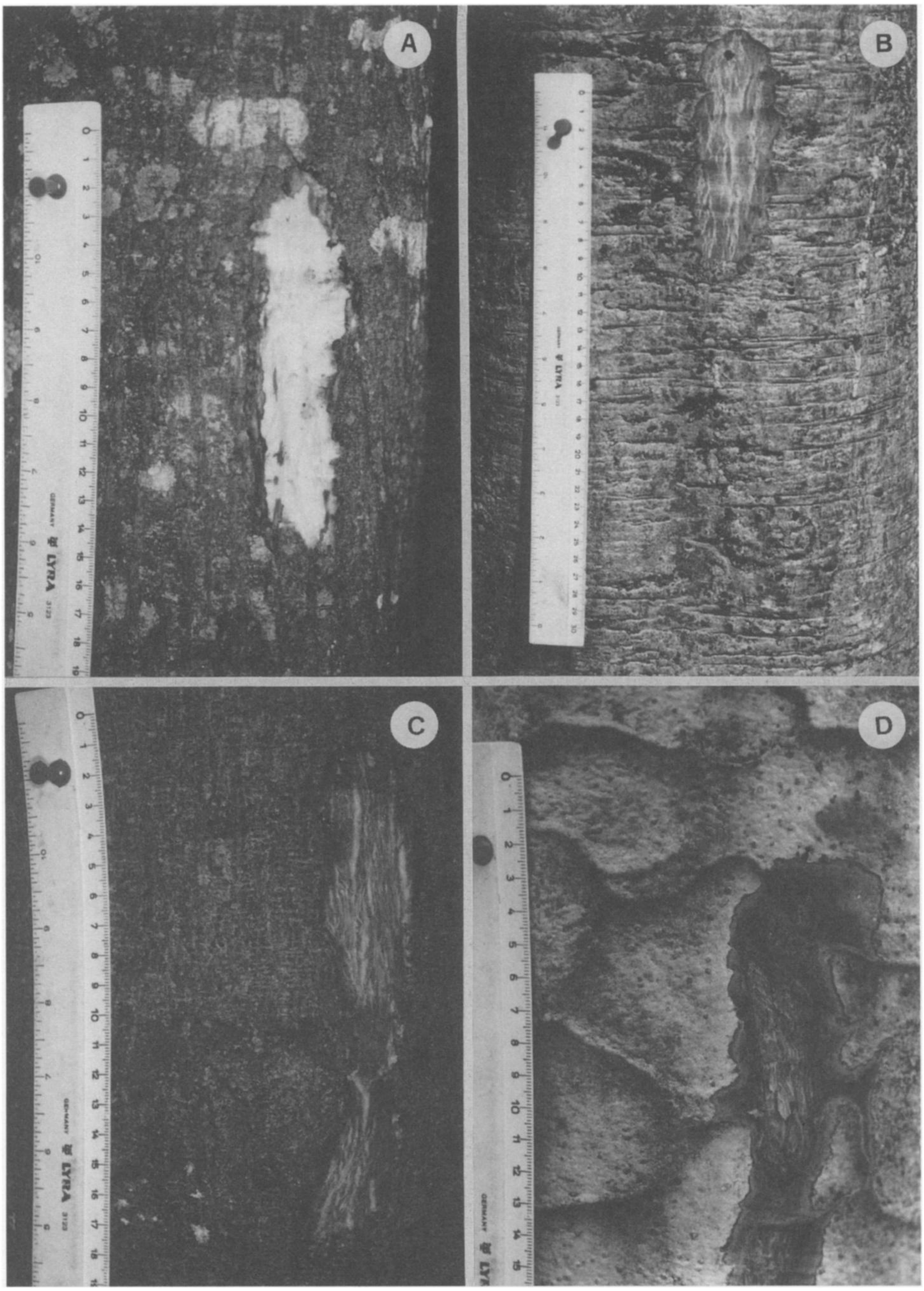


FIG. 2. Bark surface pattern and slash; species character #2. A. Bark type A, *L. leucocephala* subsp. *glabrata*. B. Bark type B, *L. esculenta*. C. Bark type A, *L. diversifolia*. D. Bark type B, *L. matudae*. Rulers in cm and inches. (Based on: A, *Hughes 1805*; B, *Hughes 1779*; C, *Hughes 1876*; D, *Hughes 1821*.)

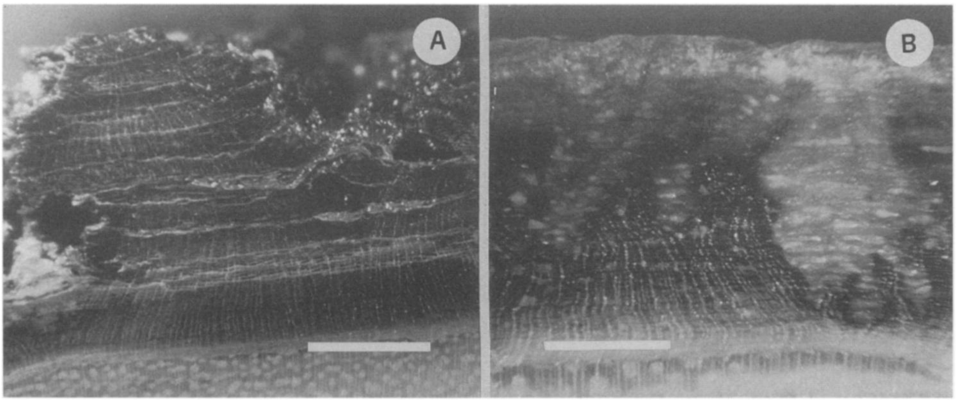


FIG. 3. Bark internal structure (transverse sections); species character #2. A. Bark type A, *L. collinsii* subsp. *zacapana*. B. Bark type B, *L. esculenta*. Scale bars = 0.25 cm. (Based on: A, *Hughes 1754*, B, *Hughes 1779*.)

sensu stricto [i.e., *Dichrostachys cinerea* (L.) Wight & Arn. and allies] and provide a unique synapomorphy (character #2 in generic analysis) for that group (Luckow 1995). Terminal shoots of *Leucaena* species are either terete or angled with conspicuous fiber bundles forming ridges on the stem (character #1 in species analysis; #3 in generic analysis). Angled stems are most striking in *L. esculenta*, which has five or six marked longitudinal corky ridges on the young stems (Fig. 4A). They also occur in *L. pueblana, L. pallida,* and *L.* ×*mixtec*, although only weakly and variably in the last two species, again possibly due to their hybrid origins (see above). The remaining species have terete stems. Angled shoots with similar corky ridges occur in all species of *Desmanthus, Neptunia,* and *Gagnebina* in the *Dichrostachys* group (Luckow 1993, 1995), in one species of *Schleinitzia*, and weakly in *Kanaloa kahoolawensis* Lorence & Wood. In Luckow's (1995) cladistic analysis of the *Dichrostachys* group, angled shoots are derived independently in *Gagnebina* and *Desmanthus/Neptunia*.

Many woody plants of dry habitats possess short shoots or brachyblasts, characterized by short, congested internodes and usually covered with persistent fused stipules, stipule bases, or bracts, both in the Mimosoideae and in the Leguminosae as a whole (Hallé et al. 1978). Within the *Dichrostachys* group, presence of brachyblasts has been used to infer the monophyly of *Dichrostachys* (Lewis & Guinet 1985), but Luckow (1993, 1995) showed that this character is not unique to *Dichrostachys* but occurs also in *Calliandropsis* H. M. Hern. & Guinet and the woody species of *Desmanthus*. Though brachyblasts (character #3 in species analysis; #4 in generic analysis) are uniformly absent in *Leucaena*, their occurrence is potentially informative at generic level (Luckow 1993, 1995).

Leaves. All species of *Leucaena* have bipinnate, alternate, stipulate leaves. The leaf rachis is strongly or weakly canaliculate with two parallel ridges on the adaxial side and terminates in a short mucro or spicule. The pinnae and leaflets are opposite; the leaflets are inserted contiguously, adaxially on the pinna, and nearly sessile or short-petiolate with small wedge-shaped petiolules. The bases of the petiolules, petioles, and pinnae have

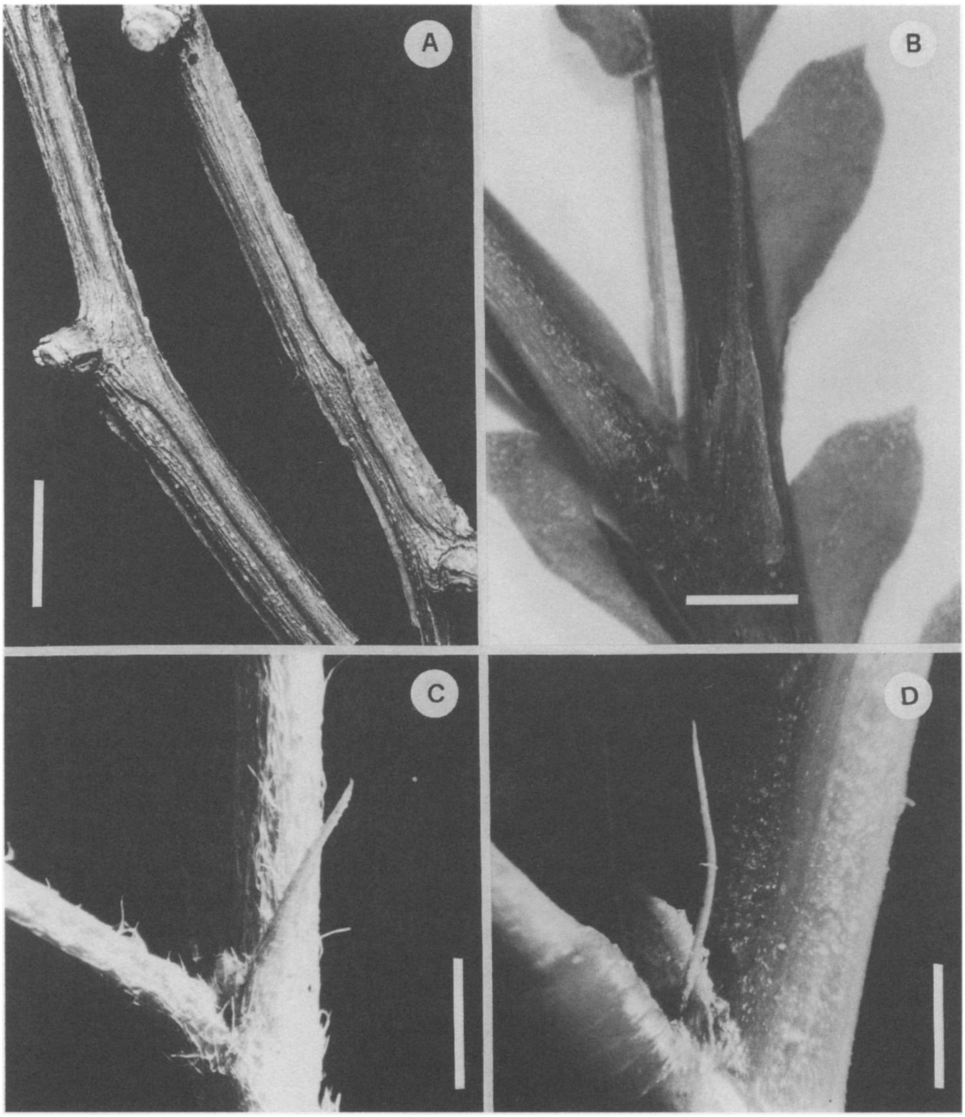


FIG. 4. Shoots and stipules. A. Angular shoots with longitudinal corky ridges, *L. esculenta*, species character #1. Stipule shape, species character #4: B. Stipule, *L. greggii*, seedling progeny derived from *Hughes 1056*. C. *Calliandropsis nervosus*, ovate, striate stipule. D. *Desmanthus fruticosus*, setiform/subulate stipule. Scale bars: A = 2 cm, B = 1 mm, C = 0.5 cm, D = 0.5 cm. (Based on: A, *Hughes 1779*; C, *Hughes 1784*; D, *Hughes 1532*.)

well-developed pulvini and the leaves are nyctinastic (i.e., undergo sleep movements; see below), but not seismonastic (i.e., sensitive). There is considerable quantitative variation in leaflet size, number of leaflets per pinna, and number of pinnae per leaf; reduction in number of leaflets is strongly correlated with increased leaflet size (see below). Variation also occurs in stipules, leaflet shape, venation, and vestiture, the occurrence of glandular trichomes, and the number, position, and morphology of extrafloral nectaries.

Stipules. Stipules occur in all genera of the *Leucaena* and *Dichrostachys* groups and in the Mimoseae more generally. Stipules in *Leucaena* are uniformly simple, ovate to lanceolate, 0.2–0.7 mm long with irregular membranous basal wings (Fig. 4B), and a prominent midrib. They may be deciduous or persistent with age, sometimes becoming stiff and dry when old, but they are never modified into spines. Although invariant within *Leucaena*, stipule shape was included in the species analysis (character #4), because there is considerable variation across the genera of the *Dichrostachys* and *Leucaena* groups (character #5 in generic analysis) (Fig. 4C, D). This was described and illustrated for the genera of the *Dichrostachys* group by Luckow (1993: 6, 1995), who demonstrated the usefulness of this character at generic level. Across the genera of the *Leucaena* and *Dichrostachys* groups, including *Leucaena*, stipules are united at the base, at least in the early stages of development, except in *Neptunia* and *Kanaloa* Lorence & Wood. Free stipules also occur in *Xylia* and *Parkia* R. Br., the outgroup used by Luckow (1995). Stipule fusion was included in the preliminary analysis of generic relationships (character #6 in generic analysis).

Stipels. Stipels occur frequently on the compound leaves in the Leguminosae, and have been observed and recorded from a few species of *Desmanthus* (Luckow 1993: 63) and all species of *Schleinitzia* (Nevling & Niezgoda 1978: 355), either in place of the first pair of pinnae or subtending the base of the first pair of pinnular rachises with the petiolar nectary between them. Stipels have not been observed in *Leucaena*. Occurrence of stipels was found to be variable within *Desmanthus bicornutus* S. Watson (Luckow 1993) and does not appear to provide a useful character.

Leaflet shape and venation. Leaflets in *Leucaena* have consistently entire margins, and shape varies from narrow oblong/lorate to elliptic/ovate/lanceolate (Figs. 5, 6). Species with narrow-oblong leaflets are always strongly asymmetric particularly at the base, which is always cordate or truncate, except in *L. leucocephala*, which has acute leaflet bases (Fig. 5I). In contrast, species with ovate or elliptic, lanceolate leaflets are only very weakly asymmetric (Fig. 6). Although shape is a function of the ratio of length to width and asymmetry and is thus a quantitative character, the variation in leaflet shape within *Leucaena* divides clearly into two discrete types (Figs. 5, 6) and thus meets the criteria for character selection for primary homology assessment (character #5 in species analysis; #7 in generic analysis). Across the genera of the *Leucaena* and *Dichrostachys* groups, small, asymmetric, linear-oblong leaflets predominate, occurring in all species of *Alantsilodendron* Villiers (Villiers 1994: 68), *Calliandropsis* (Hernández & Guinet 1990: 611), *Desmanthus* (Luckow 1993), *Neptunia*, *Schleinitzia* (Nielsen 1992a: 192), *Dichrostachys* (Brenan & Brummitt 1970: 41), and *Gagnebina*. Only *Kanaloa* and *Xylia* have species with large elliptic/ovate nearly symmetric leaflets that are similar to the large leaflets found in some species of *Leucaena*.

In the majority of species with narrow leaflets only the primary vein or midrib is visible externally. In all these species the primary vein is displaced towards the anterior margin (Fig. 5). Although larger leaflet size is clearly associated with an increase in the degree of organization of leaflet venation, this is not a simple correlation. For some species with small leaflets and all species with large leaflets secondary and tertiary venation is externally visible and is consistently brochidodromous. The secondary veins depart from the primary vein at an acute or right angle, curving abruptly to join superadjacent secondaries to form a loop. In addition loops are enclosed by arches formed by higher order veins (Fig. 6).

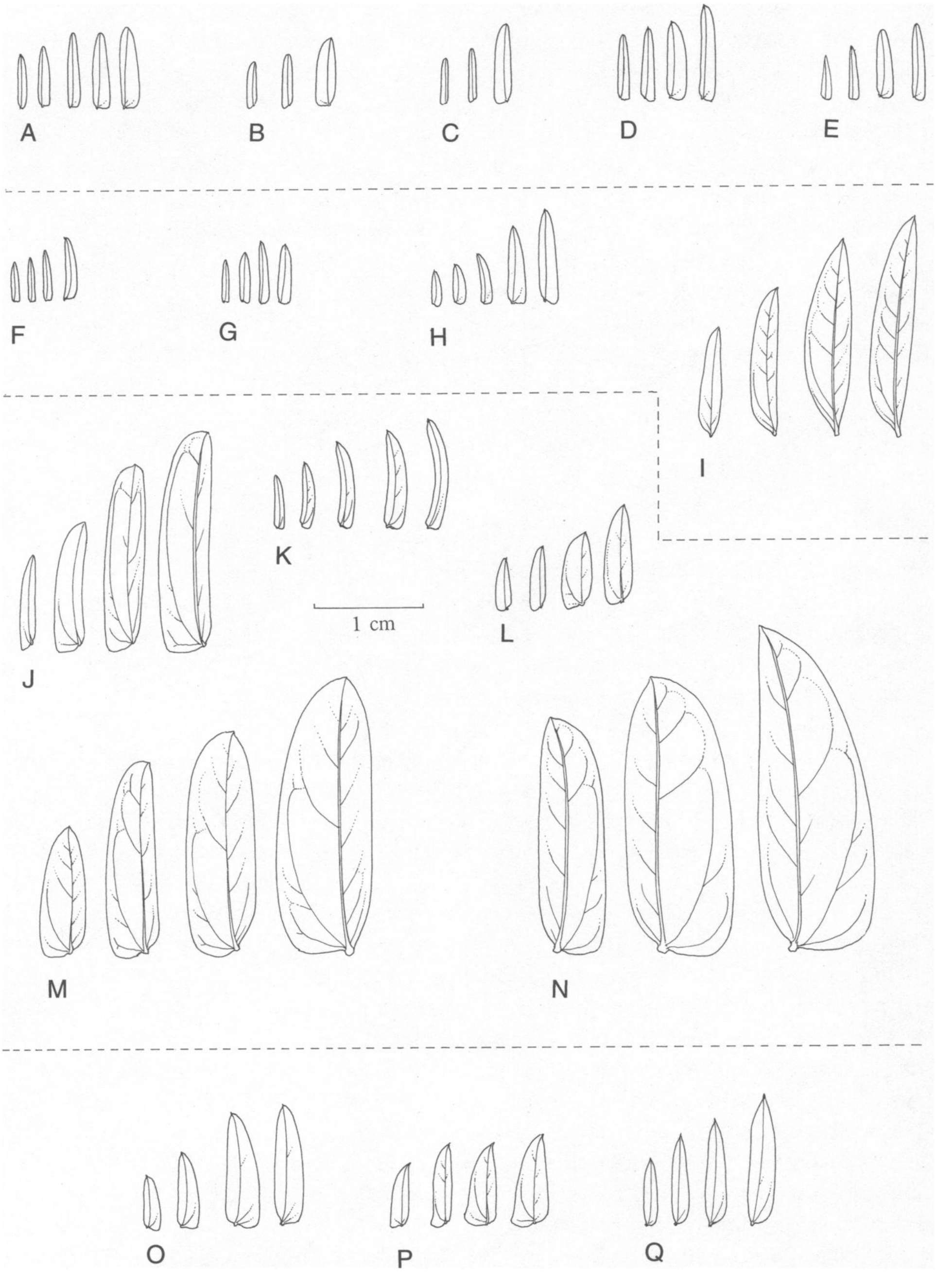


FIG. 5. Leaflet shape and venation, species characters #5 and #6; species with linear or linear-oblong leaflets with strongly asymmetric bases. A. *L. esculenta*. B. *L. involucrata*. C. *L. pueblana*. D. *L. pallida*. E. *L. matudae*. F. *L. trichandra*. G. *L. pulverulenta*. H. *L. diversifolia*. I. *L. leucocephala*. J. *L. salvadorensis*. K. *L. collinsii*. L. *L. lempirana*. M. *L. shannonii*. N. *L. magnifica*. O. *L. confertiflora*. P. *L. cuspidata*. Q. *L. greggii*. Leaflets were sampled to represent range of leaflet size and shape variation within species, including variation across intraspecific taxa where they exist.

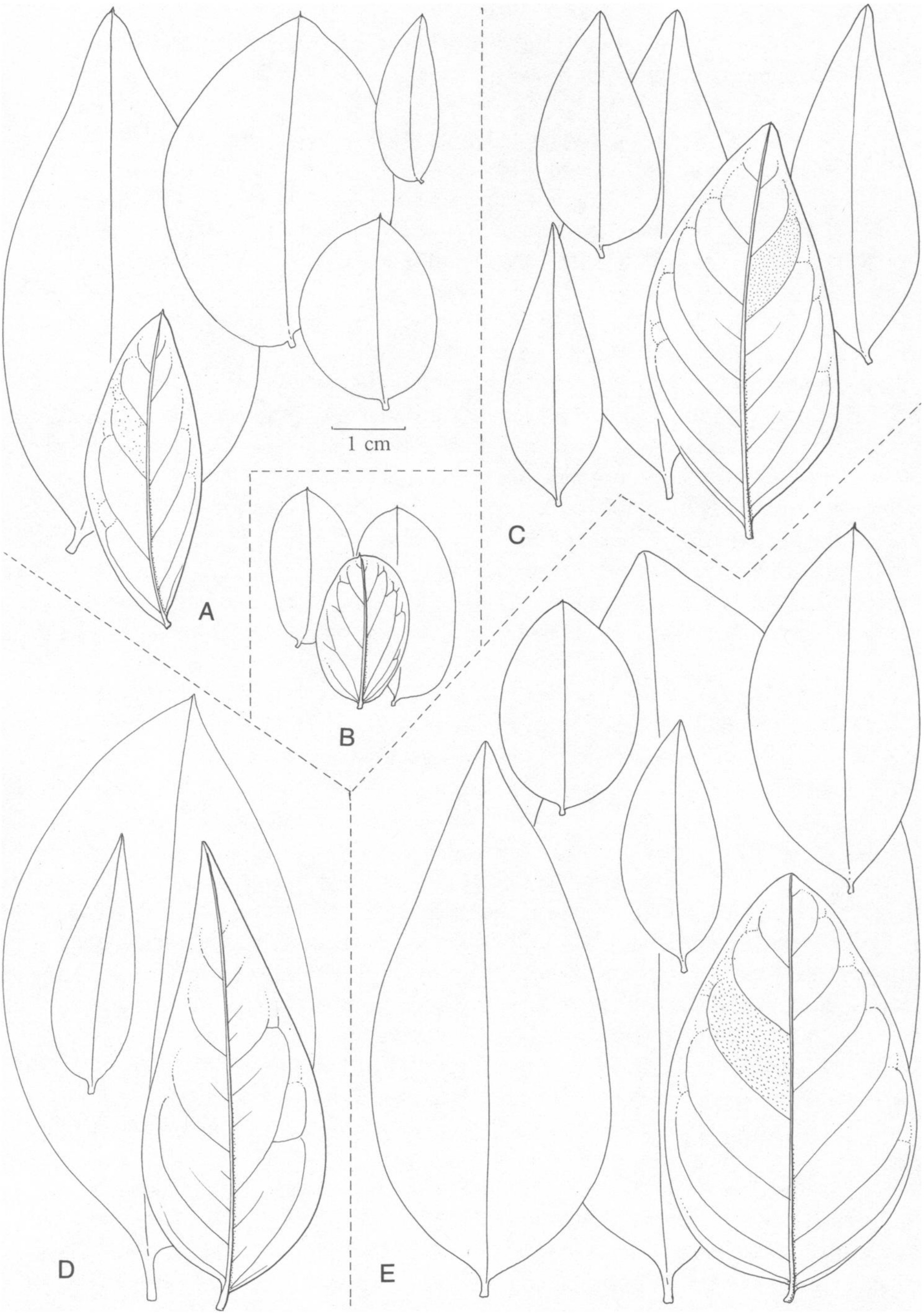


FIG. 6. Leaflet shape and venation, species characters #5 and #6; species with ovate or elliptic leaflets and weakly asymmetric bases. A. *L. lanceolata*. B. *L. retusa*. C. *L. multicapitula*. D. *L. macrophylla*. E. *L. trichodes*. Leaflets were sampled to represent range of leaflet size and shape variation within species, including variation across intraspecific taxa where they exist.

The most notable variation in leaflet venation is thus in the presence or absence of visible secondary and tertiary venation (character #6 in species analysis). Similar variation in leaflet venation occurs across the closely related genera.

Vestiture. Leaves of *Leucaena* are either glabrous or pubescent. Hairs are simple, unicellular, and erect or curled and appressed. The occurrence of pubescence on the leaves is highly variable, between and within species, such that fixed differences are infrequent. Although useful in some cases for delimitation of infraspecific taxa, leaf pubescence does not provide any reliable taxonomic characters for analysis.

Glandular trichomes. Glandular trichomes (colleters sensu Bell, 1991) occur on the leaves of all species of *Leucaena* and on the seedling shoots and peduncles of some species. These trichomes are generally scattered on the adaxial surface of the leaf rachis and occasionally on the pinnular rachis, and clustered around the bases of the pinnae and leaflets and sometimes around the bases of extrafloral nectaries. They are small, wedge-shaped, and generally brown, orange-brown, or amber-colored, and apparently secrete exudate. In common with extrafloral nectaries, the trichomes develop rapidly in early leaf expansion, becoming full-sized and active when the leaf is still small. Abundant exudate from these trichomes has been observed coating the young expanding leaves on several species. On older leaves the exudate appears as amorphous, red or orange-brown granules scattered on the leaf rachis, bases of the leaflets, and pinnae, and sometimes on the peduncles.

Quantitative leaf variation: number and dimensions of pinnae and leaflets. Despite the great variation in and clear importance of quantitative leaf variation for species identification, number and dimensions of pinnae and leaflets are rarely used in cladistic analysis of legume genera as they suffer from the problems of all continuous variables (see below); however, in *Leucaena*, more detailed analysis of leaf morphology is justified for three reasons. 1) Leaf morphology has been used as the primary indicator of species relationships in the past, providing two of the three characters used by Zárate (1984a, 1994) to divide the genus into two sections. Investigation of quantitative leaf variation is needed to assess the basis for Zárate's sectional classification. 2) Leaf morphology is very variable amongst species of *Leucaena* (Figs. 5–8), has been used to delimit infraspecific taxa (see Taxonomy), and in the construction of identification keys (Bentham 1875; Standley 1922; Britton & Rose 1928; Zárate 1984a, 1994); leaf morphology is the most conspicuous feature used by foresters and agronomists to identify species. 3) Sorensson (1993) created a set of artificial *Leucaena* hybrids and demonstrated that hybrid leaf morphology in *Leucaena* can be accurately predicted from parental leaf morphology based on a series of simple geometric models. There is potential to use these models to identify putative natural, semi-natural, or artificial interspecific hybrids (e.g., Hughes & Harris 1994, 1998) and to provide additional evidence on the hybrid background of amphidiploid species. Thus for *Leucaena*, unlike many other genera, detailed analysis of leaf morphology is justified.

The bipinnate leaf provides an unusually diverse array of quantitative traits (e.g., number of pairs of pinnae per leaf, number of pairs of leaflets per pinna, leaflet length, leaflet width, length of rachis or pinnular rachis, distances between pinnae or leaflets), although in many cases strong correlations between traits are likely. Choosing what traits to measure and how to measure them are important decisions given the range of possible traits and the fact that there may be variation between populations and individuals and within individual trees and individual leaves. Analyzing putative spontaneous hybrids with the hybrid leaf models of Sorensson (1993) (see Hughes & Harris, 1998) I have measured four traits: number of pairs of pinnae per leaf, number of pairs of leaflets per pinna, leaflet length, and leaflet width. Measurements came from the mid-pinna on a leaf and the mid-leaflet on a pinna; five leaves per tree were measured. Heavily shaded leaves or those on recently resprouted shoots were not measured. Because of my interest in detecting absolute gaps in variation across species as the basis for defining character states (see below), data are presented as ranges between maximum and minimum values (means of five leaves) ordered by ascending midpoint, following the convention of Stevens (1991) (Figs. 7, 8).

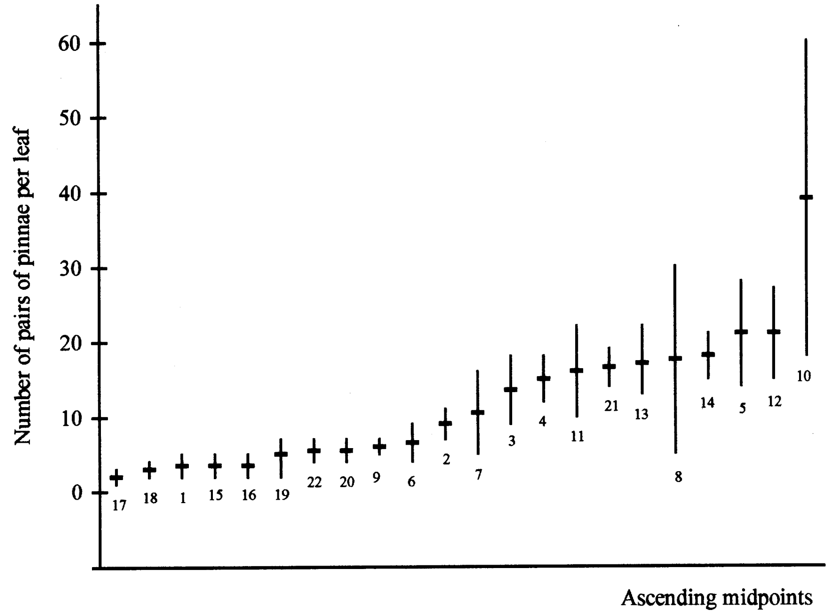
There is significant variation in all four quantitative leaf traits between species of *Leucaena* (e.g., number of pairs of pinnae ranges from 1–3 to 20–60, number of pairs of leaflets from 2–6 to 40–85, and leaflet length from 3–5 to 20–80 (–118) mm). However, there are no absolute gaps that could be used to define different character states. Quantitative leaf variation within *Leucaena* appears to be truly continuous. This could, in part be due to inclusion of putative hybrids, which may blur otherwise distinct character states (see below). Removal of the known tetraploids from the leaf trait data results in formation of a gap, albeit a barely detectable one, in one trait, leaflet length, when *L. leucocephala* is omitted (Fig. 8, species #6). Given these data, there appears to be no objective basis for Zárate's (1994) division of *Leucaena* into two sections based on leaflet traits (see below).

Extrafloral nectaries. Extrafloral nectaries are glands on the vegetative organs of plants from which nectar is secreted (Metcalfe & Chalk 1979). They are present in many diverse legume groups but are most commonly found in the subfamily Mimosoideae, especially in the tribes Acacieae and Ingeae and in 24 out of 37 genera of the Mimoseae (Lewis & Elias 1981). Exudation of nectar is presumed to attract ants in exchange for protection, although there are few quantitative ecological studies of these interactions and the exact physiological function of extrafloral nectaries is still obscure (Bentley 1977; Elias 1983; McKey 1989). No such relationship between ants and extrafloral nectaries in *Leucaena* has been demonstrated, although copious nectar exudation has been observed both in natural populations and greenhouse-grown plants.

In this study, fresh specimens or those preserved in FAA were used in addition to dried herbarium specimens. Nectaries can be distorted or broken off, as in the case of long stipitate glands, during drying and pressing of specimens. Nectary morphology was also observed on leaves at different stages of seedling development for all species.

Nectary morphology on the first leaves of seedlings of *Leucaena* may be quite different from that on later adult leaves. The eophylls generally have either no visible nectary formed or very small rudimentary glands. The nectaries on the first leaves are almost uniform across all species of *Leucaena*. They are small and cylindrical, reduced versions of the stipitate peg-shaped nectaries found on adult leaves of some species. The variable morphology of nectaries found on adult leaves starts to become apparent by the third or fourth seedling leaf.

On adult leaves of all species of *Leucaena*, petiolar, inter- and infra-pinnal nectaries are present. Nectaries in *Leucaena* belong to the "Hochnektarien" (elevated nectaries) of Zimmermann (1932); they are vascularized and elevated above the ground tissue. The petiolar nectary is the most conspicuous and morphologically variable within *Leucaena*



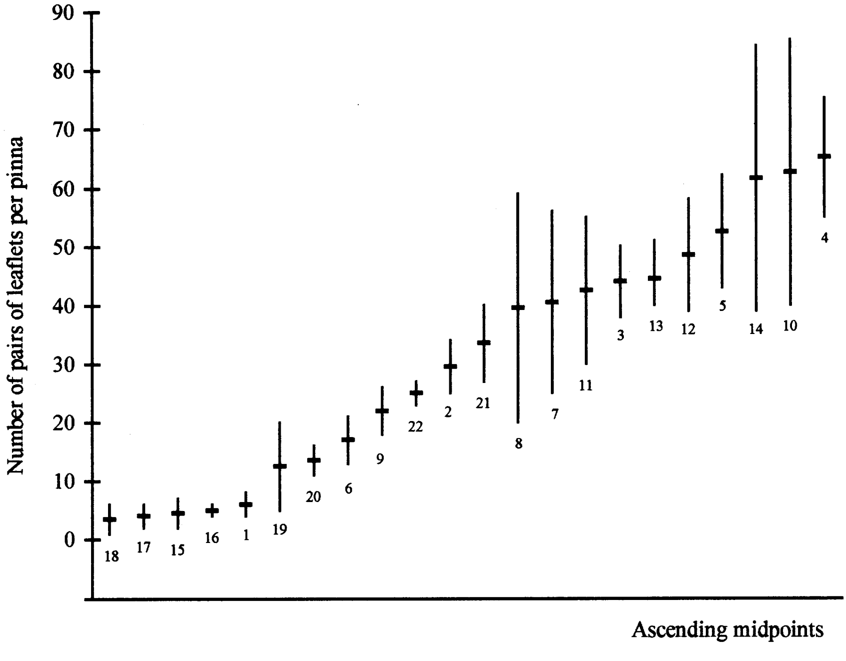


FIG. 7. Variation in quantitative leaf traits across species: number of pairs of pinnae per leaf and numbers of pairs of leaflets per pinna. Species are ordered by ascending midpoints. Numbers refer to phylogenetic sequence (listed under Numerical List of Species).

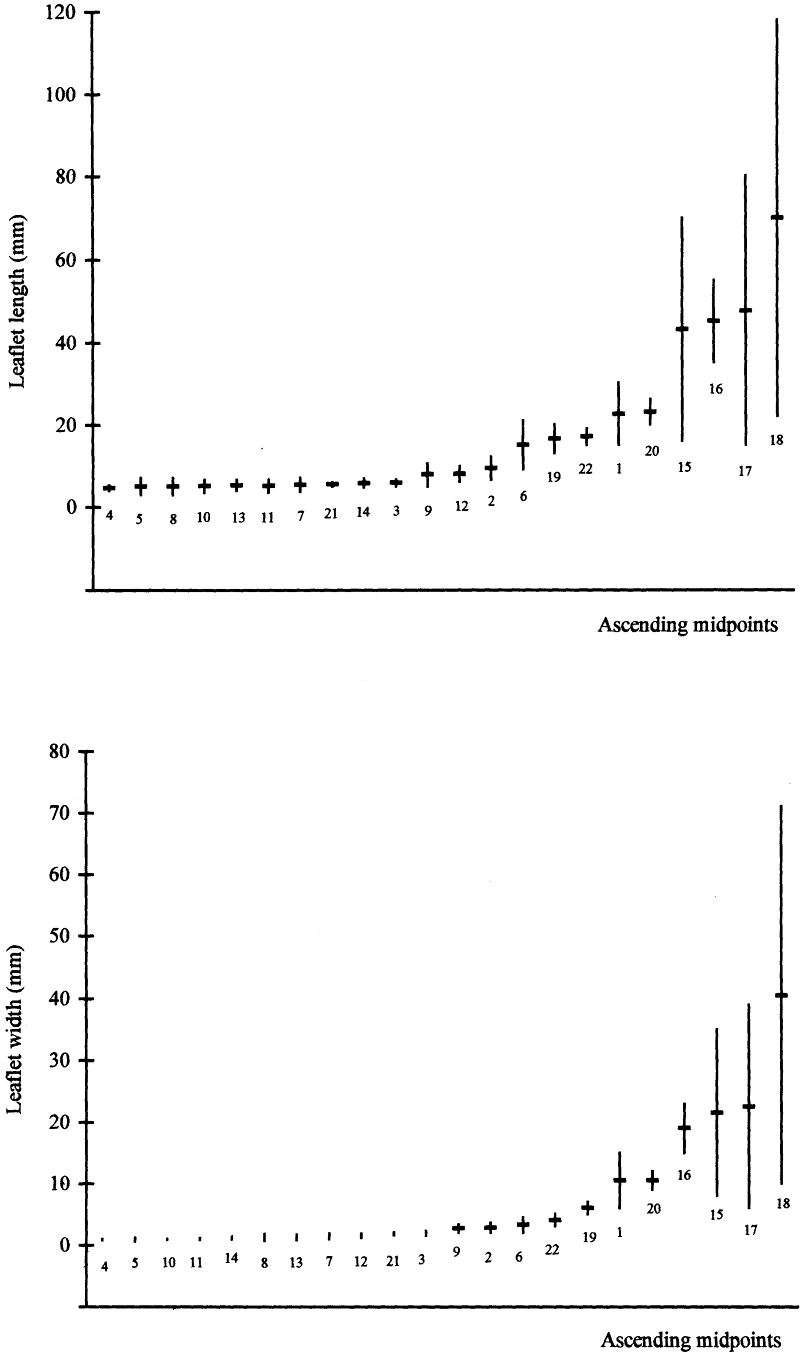


FIG. 8. Variation in quantitative leaf traits across species: leaflet length and leaflet width. Species are ordered by ascending midpoints. Numbers refer to phylogenetic sequence (listed under Numerical List of Species).

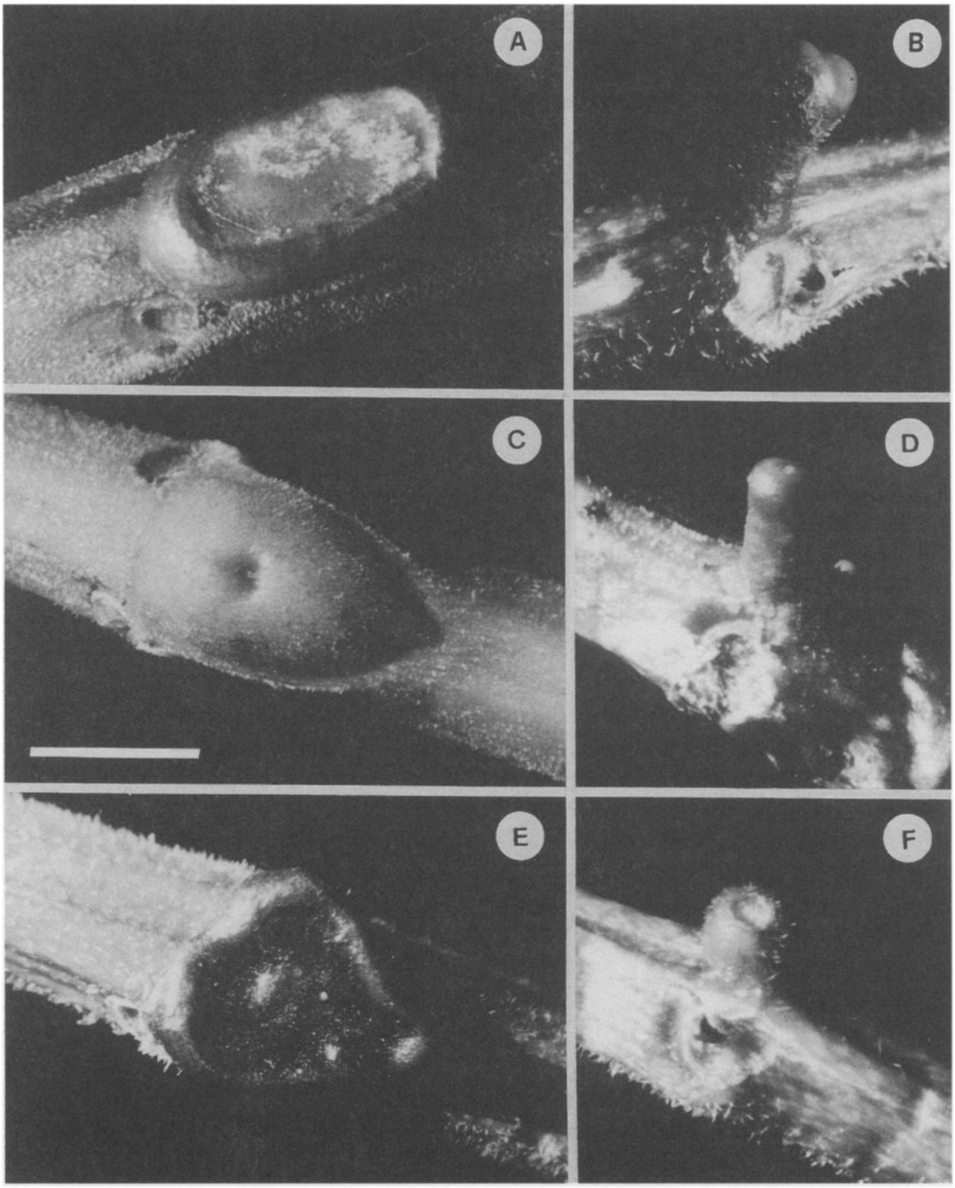


FIG. 9. Petiolar nectaries, species character #7, photographed from fixed material from cultivated trees derived from progeny of accessions as indicated. A. *L. esculenta*. B. *L. greggii*. C. *L. collinsii* subsp. *collinsii*. D. *L. matudae*. E. *L. diversifolia*. F. *L. retusa*. Scale bar = 3 mm. (Based on: A, *Hughes 903*; B, *Hughes 1057*; C, *Hughes 662*; D, *Hughes 879*; E, *Hughes 923*; F, *Hughes 1361*.)

(Fig. 9A–F) and three types of glands can be recognized: 1) short- or long-stipitate, erect, peg-shaped nectaries (Fig. 9B, D, F); 2) sessile crateriform or patelliform, concave nectaries with a broad orifice (Fig. 9A, E); 3) sessile convex, shallow conical or truncate conical, poriform, or sometimes verruciform nectaries, the orifice a narrow pore (Fig. 9C) (character #7 in species analysis; #8 in generic analysis). Type of nectary is generally constant on mature leaves within the majority of each *Leucaena* species, but there is some variation in form within *L. diversifolia*, *L. trichandra*, and *L. confertiflora* (see Fig. 47 in Taxonomy). Nectaries occur on the ventral face of the petiole below the point of insertion of the first pair of pinnae. Occasionally a double nectary is present on the petiole with two nectaries immediately adjacent to each other at the base of the leaf rachis. In addition, interpinnal nectaries are present in some species, most notably in species with stipitate nectaries (e.g., *L. greggii* and *L. retusa*), which usually have a nectary on the leaf rachis at the base of each pair of pinnae. Other species have 1–4 nectaries at the base of the distal pairs of pinnae, whereas in *L. lempirana* additional nectaries are found at the base of the basal pinnae pairs. One or sometimes up to three small infrapinnal glands are also present in most species at the tips of the pinnular rachis and the bases of the distal pairs of leaflets, and, in *L. retusa*, at the base of all leaflet pairs.

Extrafloral nectaries have been described from all the closely related genera in the *Dichrostachys* and *Leucaena* groups, except in two species of *Desmanthus* and some species of *Neptunia* that lack nectaries (Luckow 1993). Similar diversity of nectary morphology to that found within *Leucaena* occurs in *Desmanthus*, *Dichrostachys* (Luckow (1993, 1995), and *Schleinitzia* (Nevling & Niezgoda 1978). Luckow's (1993) cladistic analysis suggested that stipitate nectaries are plesiomorphic and sessile nectaries derived within *Desmanthus* and *Neptunia*, and that sessile nectaries have evolved more than once within the *Dichrostachys* group as a whole.

Nyctinasty. Nyctinasty refers to "night-time" or "sleep" movements of leaves in response to light quality and has been observed and investigated in the Leguminosae ever since Darwin and Darwin (1880). Nyctinasty differs from seismonasty or "sensitive" movements. Movement in the bipinnate leaves of *Leucaena* can potentially occur at three positions: the primary pulvinus at the base of the petiole whereby the petiole or whole leaf moves, the secondary pulvini at the base of the pinnae whereby the pinnae or rachillae move, and the tertiary pulvinules at the base of the individual leaflets that can move. Research into nyctinasty has concentrated on the mechanisms and physiology (e.g., Satter & Galston 1981) with only limited survey of the systematic value of nyctinastic leaf movements as taxonomic characters (e.g., Lasseigne 1980; Lavin 1988, 1993; Luckow 1993; Lewis 1994).

Leaf movements were observed in both adults and seedlings of all *Leucaena* species. Seedlings grown in a greenhouse under a uniform light regime were observed from dusk until five hours after dark to ensure that the plants had completed their movements for the night. A minimum of ten seedling plants were observed for each species. Leaf movements were also observed on adult plants 3.5 years old in a field trial in Honduras. Leaf movements were the same on seedlings and adult plants.

Nyctinasty is basipetal in all species, the youngest leaves undergoing movement first. As the leaves age they often cease to undergo nyctinastic movements. The primary pulvinus, at the base of the petiole shows little or no movement in any *Leucaena* species. In contrast, the primary pulvinus in *Desmanthus* and *Neptunia* can cause upward or downward movement of the leaf rachis (Luckow 1993). Movement of the tertiary pulvinus is also uniform within *Leucaena.* Leaflets on opposite sides of the pinnae come into contact either above the pinnular rachis or parallel with it and are directed forward toward the apex of the leaf, thus exposing the abaxial sides of the leaflets (Fig. 10A–C). Similar movements of the leaflets have been observed in species of *Desmanthus* and *Neptunia* (Luckow 1993).

It is the movements of the pinnae that vary within *Leucaena.* In most species, the pinnae move down at the same time as the leaflets close up. The secondary pulvinus moves in two planes, downwards and inwards, pivoting so that at complete rest, the pinnae are at an angle of 60–90° to the rachis and in some species each pinna is flush with its counterpart (Fig. 10A, B). In contrast, a small number of species (*L. cuspidata, L. confertiflora, L. greggii, L. matudae, L. retusa*) show little or no movement of the pinnae (Fig. 10C) (character #9 in species analysis). Movement of the pinnae also occurs in the closely related genera of the *Dichrostachys* and *Leucaena* groups, although data are far from complete pending observation of a wider range of species. In addition to downward or no movement of the pinnae, the pinnae of some species of *Desmanthus* move upwards, and in some species of *Neptunia* and *Dichrostachys* the pinnae move perfectly forward flush with the rachis and parallel to it (Luckow 1993). Variation in movement of the pinnae was found to be lacking within species across the limited material tested in this study. Luckow (1993) found that nyctinastic leaf movements were similarly conservative at the population and species level.

Flowering shoots. Given the very variable terminology that has been applied to Mimosoid inflorescence structure by different authors, some explanation of terms is necessary. In *Leucaena* individual flowers are tightly massed into globose or subglobose heads or capitula. Capitula are here referred to as inflorescences, the term often used for the capitate or spicate groups of flowers that are frequent in Mimosoideae (e.g., Robbertse 1974). Other authors have applied the term inflorescence to the whole flowering shoot, with the capitula (or spikes) described in this case as partial inflorescences [e.g., Weberling (1989), Barneby (1991), Grimes (1992), and others]. The compound inflorescence sensu Grimes (1992) is here simply termed the flowering shoot. In this section the arrangement of capitula on flowering shoots is described and discussed. The morphology of the individual capitula and flowers are discussed below.

As pointed out by Grimes (1992), the architecture of the flowering shoot is a reflection of three properties: first, the organization of the components and their relative positions; second, the hierarchical relationship of the axes of the shoot and the position they assume in total tree architecture, and third, the heterochronic development of the components of the shoot. The flowering shoots in *Leucaena* are described in relation to these properties and terminology broadly follows Grimes (1992), who developed a system for recognition of homologies and definition of character states in relation to arrangement of capitula/inflorescences (termed partial inflorescences by Grimes, 1992) in the *Pithecellobium* Mart. complex.

Each capitulum in *Leucaena* is borne at the apex of an unbranched, leafless, usually terete peduncle articulated at its base. If a particular capitulum fails to produce pods, the peduncle and the remains of the capitulum abscise at this point. In all species of *Leucaena* the capitula occur in fascicles of 2–5 (–7) per node subtended either by a leaf, an incipient leaf, or by a reduced and usually early caducous bract.

The flowering shoot ends in a vegetative apex with a lateral capitulum and would thus be described according to the system of Weberling (1989) as a homothetic compound raceme and in this sense may be considered indeterminate or polytelic. Examination of the post-anthesis development of the flowering shoot, however, shows that the apical meristem can be either indeterminate or determinate in *Leucaena*. Briggs and Johnson (1979) introduced a more specific nomenclature to subdivide indeterminate polytelic flowering shoots into two categories, which are adopted here: auxotelic with indeterminate meristems, which continue to grow beyond the flowering region, and anauxotelic with

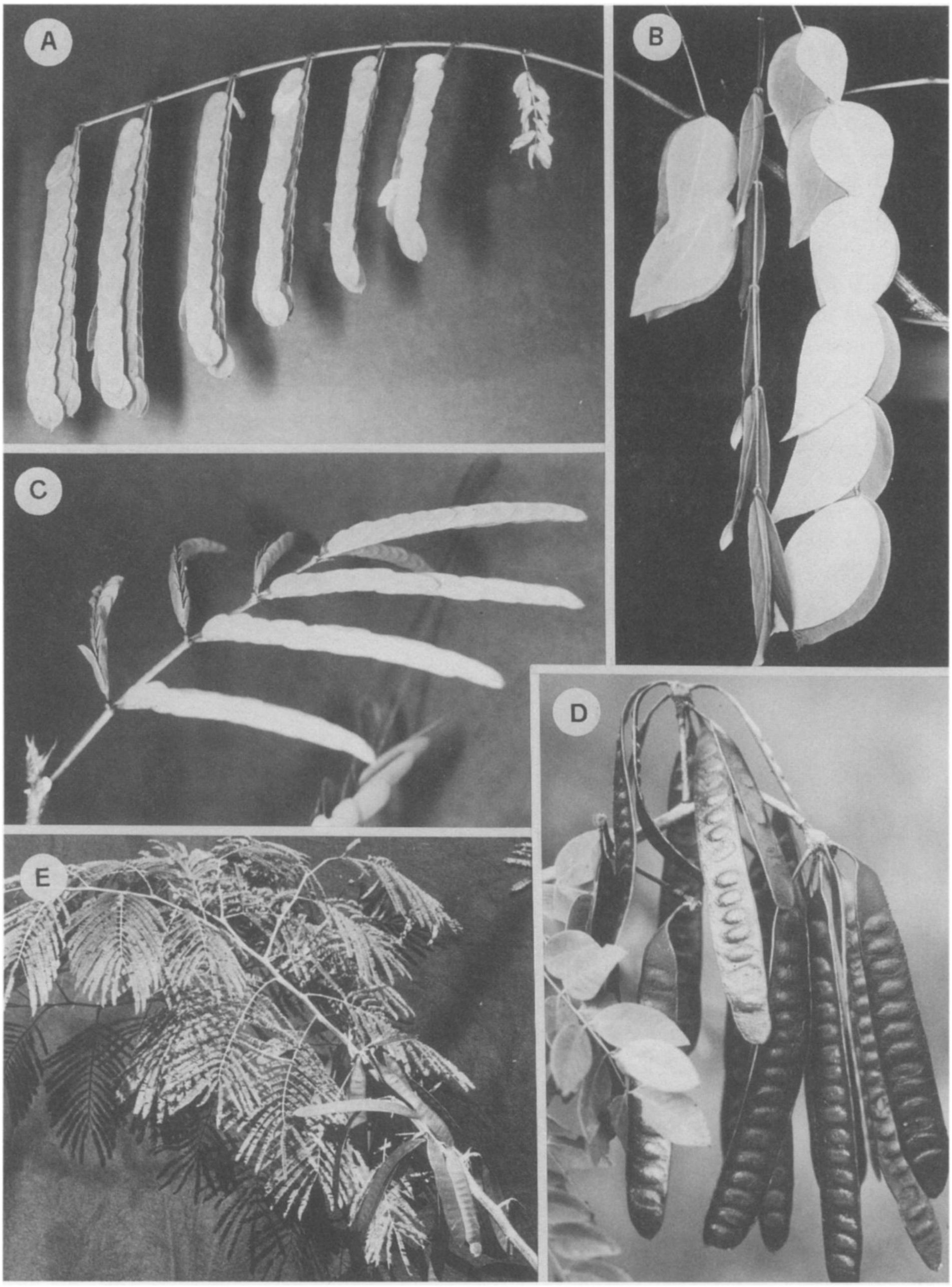


FIG. 10. Nyctinasty, species character #9: leaflet movements; all species showing upward or forward movement of leaflets along pinnular rachis. Photographed from seedlings derived from seed collected from accessions as indicated. A. *L. magnifica*. B. *L. macrophylla*. C. *L. greggii*. Variation in position of pods on shoots: D. Pods borne at tips of determinate shoots on periphery of tree crown, *L. lanceolata*. E. Pods borne on older wood on indeterminate shoots inside the tree crown, *L. collinsii* subsp. *collinsii*. (Based on: A. *Hughes 1093*; B, *Hughes 1179*; C, *Hughes 1050*; D, *Hughes 1544*; E, *Hughes 1760*.)

determinate meristems, which end in an abortive vegetative apex, future growth arising from a bud below the position of the lowest abscised peduncle. In *Leucaena*, meristems may be auxotelic (Figs. 11A, 12A) or anauxotelic (Figs. 11B–D, 12B–D) (character #10 in species analysis).

Differences in branching of the flowering shoot also occur within *Leucaena*. The simplest arrangement of capitula is in fascicles of peduncles borne on an unbranched primary shoot (Figs. 11A, B, 12A, B), which may be persistent or ephemeral as above. In three species the flowering shoot includes branched subunits or paraclades (sensu Weberling) formed from sylleptic buds (Figs. 11C, D, 12C, D). In one species, *L. multicapitula*, two orders of branching occur (Figs. 11D, 12C). This twice-branched flowering shoot is unique within the genus and was used by Schery (1950) to distinguish *L. multicapitula* from *L. trichodes,* although the original description of *L. multicapitula* refers to a thrice-branched panicle, presumably including the peduncles as the third order branches. Once-branched flowering shoots occur in two species, *L. esculenta* and *L. magnifica* (Figs. 11C, 12D) (character #11 in species analysis).

Heterochrony plays an important role in determining the aspect of the different arrangements of capitula on the flowering shoots found in *Leucaena*, notably in the difference between initiation of leaves and that of the axillary fascicles of capitula. In the majority of species the leaves and capitula develop together. The leaves in this case are termed coeval (Fig. 12A). In some *Leucaena* species the formation and/or development of leaves is delayed with either partial or total leaf suppression (only bracts form) (Fig. 12B–D). The degree of leaf suppression is variable within species in some cases. In *L. salvadorensis* a third heterochronic pattern is apparent: fascicles of capitula form on older branches, often in the axils of older leaves or at nodes after leaf fall, as well as on developing shoots with simultaneous leaf development.

As pointed out by Wyatt (1982) and Hopkins (1986), differences in the arrangement of inflorescences on flowering shoots influence overall crown architecture and the position of flowers and fruits in relation to the foliage (Fig. 10D, E), and hence pollinator attraction and seed dispersal and predation. For species with auxotelic meristems and coeval leaf development, the capitula are held within the crown amongst the leaves, so that pods develop and ripen on the older wood often well inside the tree crown (Fig. 10E). In species with anauxotelic meristems and partial or total suppression of leaf development, capitula are exposed beyond the foliage, so that pods ripen on terminal shoots on the periphery of the tree crown (Fig. 10D). Species with auxotelic meristems tend to have fan-shaped crowns with long unbranched primary branches and few secondary branches, whereas those with anauxotelic meristems have more rounded crowns with reticulate secondary branching.

Similar patterns of variation in the arrangement of capitula on flowering shoots have been described in several other genera of woody Mimosoideae (Luckow, 1993, for *Desmanthus*; Grimes, 1992, for the *Pithecellobium* complex; Barneby, 1991, for *Mimosa*; Derstine & Tucker, 1991, for *Acacia*; Hernández, 1989, for *Zapoteca* H. M. Hern.; Hopkins, 1986, for *Parkia*). For *Mimosa* and *Zapoteca*, Barneby (1991) and Hernández (1989) interpreted the variation as an "evolutionary trend" from the basic pattern of a series of capitula that develop on a single axis with the new foliage towards progressive reduction of the subtending leaves and increased second order branching, hypothesizing a continuum of flowering shoot specialization whereby flowers are temporarily displayed to greater advantage. That partial or total suppression of leaves on flowering shoots is the

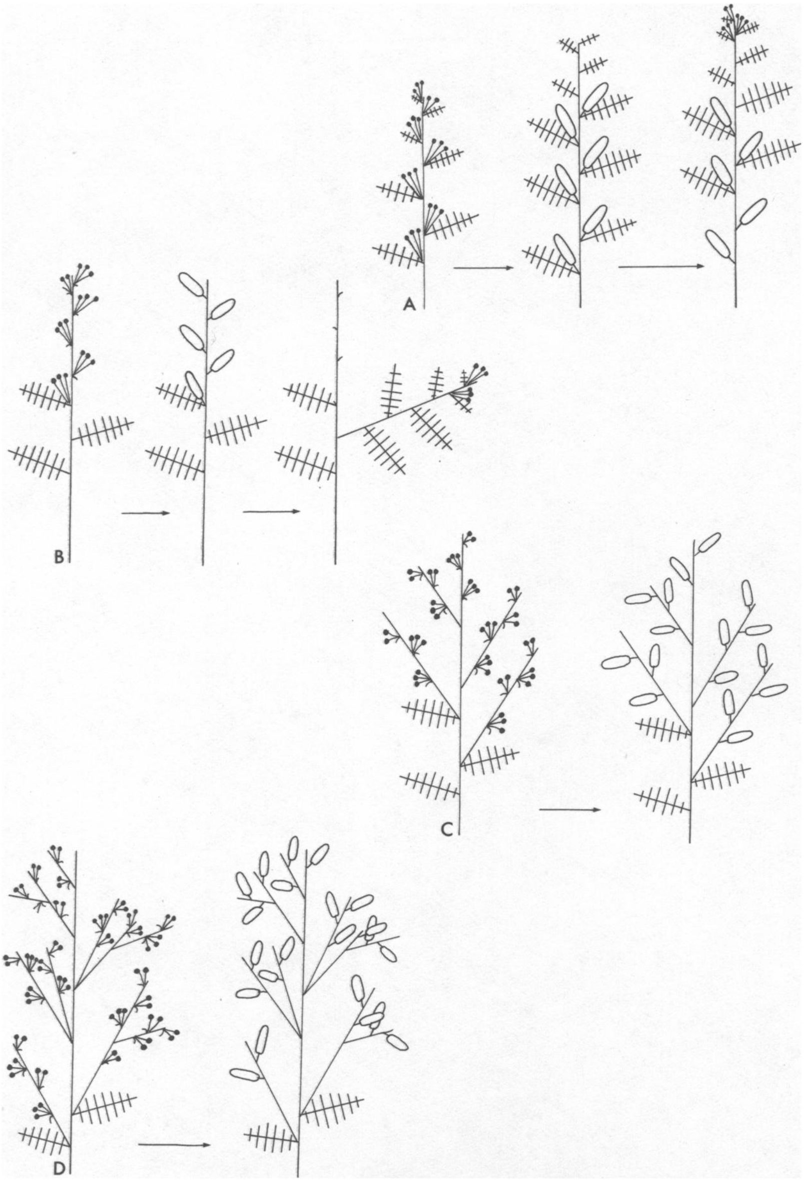


FIG. 11. Flowering shoots, species characters #10 and #11. A. Meristem auxotelic, the main axis persistent, i.e., continuing to grow beyond the flowering region, partial inflorescences axillary, leaves coeval (i.e., leaves and partial inflorescences developing together), pods borne on older wood away from the branch tips inside the tree crown; clearly manifest in *L. collinsii, L. diversifolia, L. leucocephala,* and *L. pulverulenta*. B. Meristems anauxotelic, the main axis ephemeral ending in an abortive vegetative apex that breaks off after pod dehiscence, partial inflorescences axillary, leaves partially or totally suppressed (variable within species) but leaves never forming at the youngest nodes, subsequent growth from proleptic buds below the position of the lowest abscised peduncle, pods borne at branch tips on the periphery of the tree crown; clearly developed in *L. esculenta, L. lanceolata, L. lempirana, L. macrophylla, L. shannonii,* and sometimes in *L. trichodes*. C. Meristems anauxotelic, partial inflorescences axillary, leaf development partially or totally suppressed, axillary branch buds sylleptic forming singly branched subunits from the main axis of the inflorescence; clearly developed in *L. macrophylla* subsp. *istmensis, L. magnifica,* and sometimes in *L. trichodes*. D. Same as C but with twice-branched subunits arising from the main axis of the inflorescence; only manifest in one species, *L. multicapitula*.

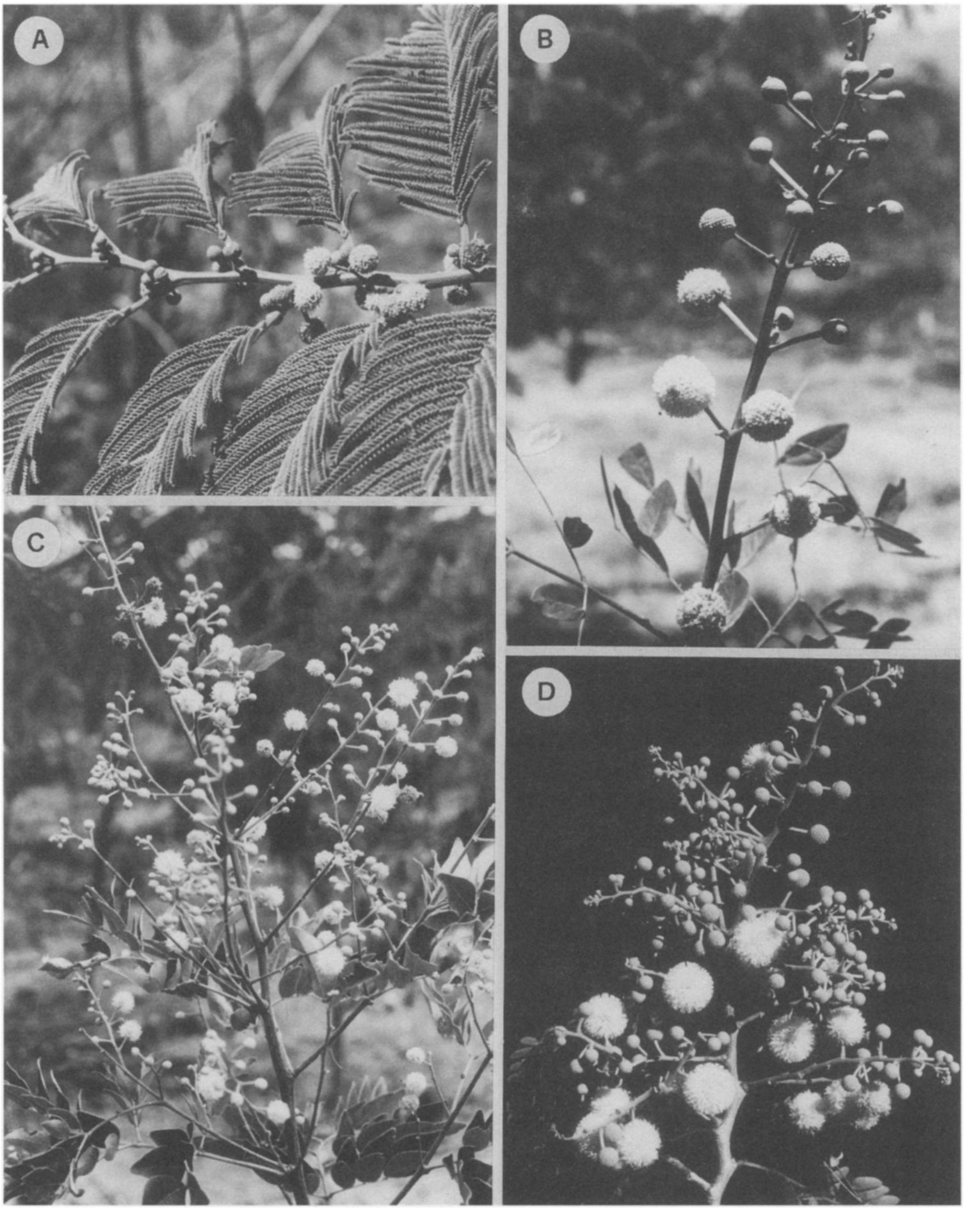


FIG. 12. Flowering shoots, species characters #10 and 11. A. Flowering shoot with auxotelic (indeterminate) meristem, *L. trichandra*. B. Flowering shoot with anauxotelic (determinate) meristem and strong suppression of leaf development, *L. lanceolata*: unbranched flowering shoot. C. *L. multicapitula*, twice-branched flowering shoot. D. *L. magnifica*, once-branched flowering shoot. (Based on: A, *Hughes 1107*; B, *Hughes 613*; C, *Hughes 1041*; D, *Hughes 1748*.)

derived condition in *Leucaena* is indicated by the presence of paired stipules at the base of every node along the flowering shoot.

Capitula. Individual flowers are arranged in tightly packed globose or subglobose capitula (Fig. 13A–D) borne in fascicles of 2 to 7 per node on peduncles that vary in length from 10 to 90 mm. Similar globose heads or capitula occur in some genera of the *Leucaena* and *Dichrostachys* groups, whereas others have spikes or compressed spikes (character #10 in generic analysis). Although capitula are invariant within *Leucaena*, inflorescence was included in the preliminary generic analysis of sister group relations of *Leucaena*. Like in the majority of Mimosoideae with small flowers, it is the capitulum of *Leucaena* that is the unit of pollinator attraction, and it is the numerous and exposed stamen filaments and anthers that determine the size, shape, color, and overall appearance of the capitulum. Flowers open largely synchronously within a capitulum, and there are generally one or two capitula open per flowering shoot at any time, each lasting only one to two days. Occasionally secondary capitula arising directly from within another capitulum have been observed in individuals of *L. retusa, L. esculenta,* and *L. leucocephala* (Murty & Murty 1989), but this phenomenon is considered to be an abnormal variant. Zárate (1994) also observed sporadic variants with secondary apical capitula in hybrid material (*L. leucocephala* × *L. diversifolia*). All species have an involucre of united bracts on the peduncle, usually immediately below the base of the capitulum, sometimes variably below the capitulum, but never less than halfway below the distal end of the peduncle. The subdistal position of the involucre is most pronounced in *L. cuspidata* (Fig. 13B) and was noted by Standley (1919) in the original description of that species, but even within *L. cuspidata*, the position of the involucre is variable. The involucre generally has between two and four acute or blunt lobes. An involucel also occurs in *Schleinitzia* and some species of *Desmanthus*, but is absent in the remaining genera of the *Dichrostachys* group (character #9 in generic analysis; #8 in species analysis). The number of flowers per capitulum varies across species of *Leucaena* from 35 to 50 in *L. multicapitula* and *L. pulverulenta* where the flowers are widely and distinctively separate in bud (Fig. 13D), to 400 to 450 in *L. lanceolata* where the flowers are tightly packed in bud (Fig. 13A). The number of flowers per head varies both within and between species, providing a quantitative and continuous character that is not amenable to division into character states for cladistic analysis.

Staminate flowers occurring at the base of the capitulum were first noted in a few species of *Leucaena* by Zárate (1994); limited survey of capitula from herbarium specimens indicates that staminate flowers with a reduced or vestigial gynoecium occur sporadically, generally in small numbers (less than 5%) in the majority of species but consistently in *L. cuspidata, L. leucocephala, L. confertiflora,* and *L. pulverulenta.* Similar occurrence of morphologically detectable andromonoecy is common across the Mimosoideae in general (Arroyo 1981). As in *Leucaena*, andromonoecy is usually highly variable within species, populations, and even individuals, and it is not a useful taxonomic character. In other respects the flowers are monomorphic. No terminal heteromorphic flowers, as found for some Ingeae, have been recorded from *Leucaena*. More importantly, no sterile flowers or flowers with showy staminodia, as found in the closely related genera *Desmanthus, Gagnebina, Neptunia*, and *Dichrostachys* sensu stricto, occur in any *Leucaena* species.

The presence of sterile flowers with showy staminodia at the base of the inflorescence was used by Lewis and Elias (1981) to distinguish their informally recognized

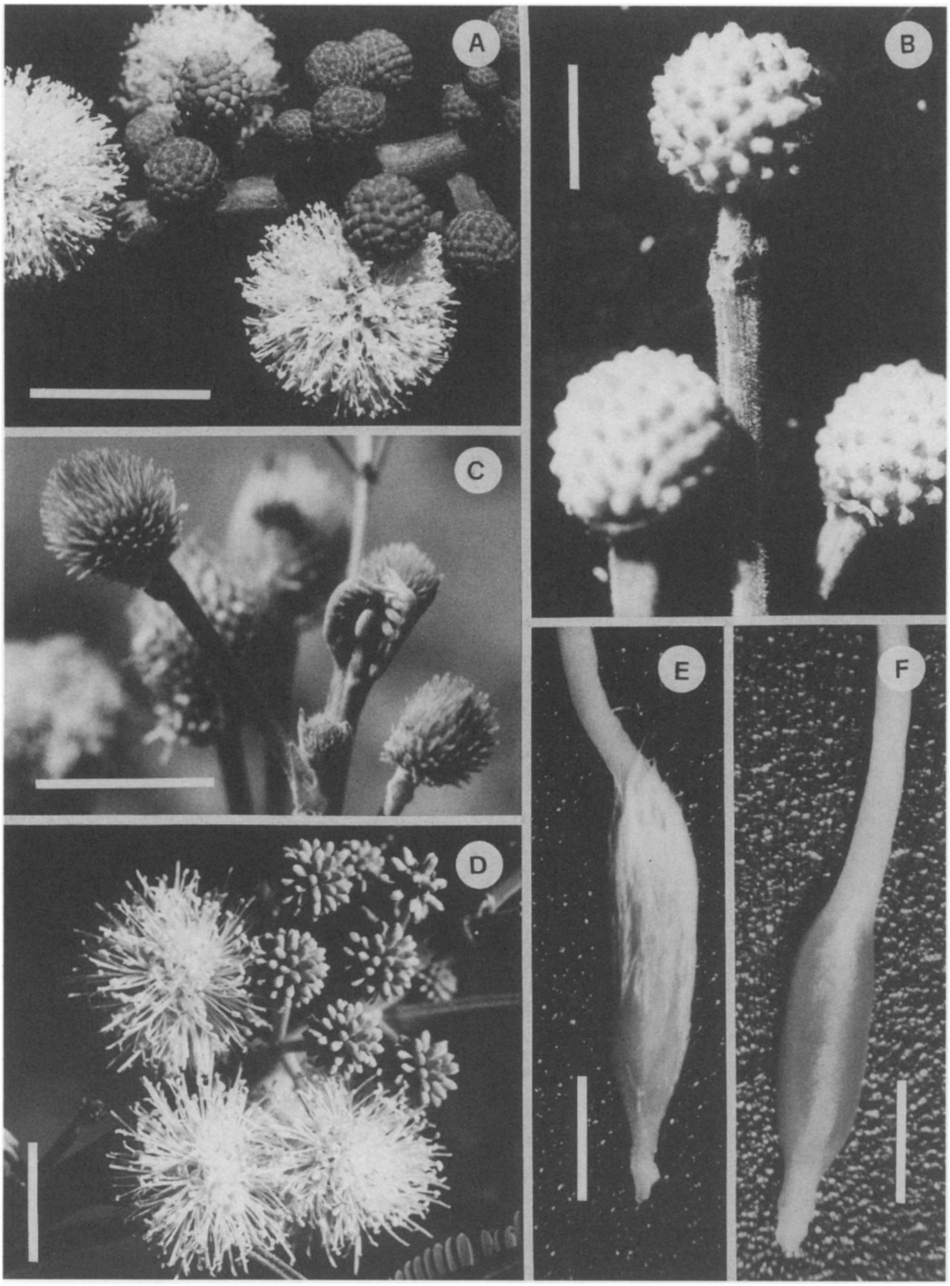


FIG. 13. Floral bracts, species characters #13 and #14; capitula and ovary vestiture, species character #18. A. Round bracts and "moriform" developing capitula (see text), *L. shannonii*. B. "Moriform" developing capitula showing variable and occasionally subdistal position of involucre, *L. cuspidata*. C. Long-caudate floral bracts and "conelike" developing capitula (see text), *L. retusa*. D. *L. pulverulenta*, few flowers per capitulum, widely separated in bud (progeny derived from *Hughes 1053*). E. Ovary showing long-pilose pubescence on distal half, *L. pulverulenta*. F. Glabrous ovary, *L. esculenta*. Scale bars: A = 1 cm, B = 0.5 cm, C = 1 cm, D = 0.5 cm, E = 0.5 mm, F = 0.5 mm. (Based on: A, *Hughes 1389*; B, *Hughes 1856*; C, *Hughes 1361*; E, *Hughes 1587*; F, *Hughes 1779*.)

Dichrostachys group. Luckow (1993, 1995) showed that not all members of the *Dichrostachys* group have staminodial flowers in the inflorescence. The three species of *Desmanthus* that lack sterile flowers were interpreted as derived within the genus (Luckow 1993), although this was not used as a character in her analysis of *Desmanthus*. Later analysis of the entire *Dichrostachys* group (Luckow 1995) included presence or absence of staminodial flowers as a character in the analysis and showed that the clade containing *Alantsilodendron* and *Calliandropsis* (called the "*Dichrostachys humbertii* clade" by Luckow) was distinguished by lack of staminodial flowers and capitate inflorescences. Although invariant within *Leucaena*, presence of staminodial flowers in the inflorescence was included in both the generic and species analyses given its potential importance at generic level and as a test of the monophyly of *Leucaena* (character #12 in species analysis; #11 in generic analysis).

Flowers. All species of *Leucaena* have radially symmetric, pentamerous flowers with ten stamens, which are always free to the base and free from the corolla, i.e., lacking a stemonozone. The anthers are introrse or, in two species, *L. macrophylla* and *L. trichodes*, markedly latrorse, dorsifixed, or nearly basifixed. The calyx and petals are valvate in bud, and the calyx is campanulate to tubular with small lobes. The ovary is subsessile and with a narrow-funnelform or tubular stigma. Limited investigation of floral ontogeny of *L. leucocephala* by Tucker (1987) and Ramírez-Domenech and Tucker (1990) showed that sepal initiation is helical and that petals and stamens initiate in a simultaneous whorl. Although when casually observed the small flowers of *Leucaena* may appear monotonously uniform, closer examination reveals important variation in a number of flower characters, including bracts, petal fusion, anther hairiness, anther glands, ovary vestiture, filament and style length.

Floral bracts. Individual flowers in *Leucaena* are subtended by peltate bracts, which conceal the flower bud completely only in early stages of development. They are pushed aside as the flowers develop and are marcescent within the capitulum after anthesis. The floral bracts of *Leucaena* are always peltate, short-pedicellate, except at the base of the capitulum where bracts are sessile and fused into an involucre. Bracts in most *Leucaena* species are approximately round (Fig. 13A, B), sometimes weakly deltate and truncate, but lanceolate in *L. greggii*, and long-caudate in *L. retusa* (Fig. 13C) (character #14 in species analysis) and often hairy and at least ciliate on margins. The long-caudate bracts of *L. retusa* are conspicuous in bud and conceal the flowers through initial development (Fig. 13C). Barneby (1991: 500, Fig. 21) described such developing capitula with imbricate, long-caudate bracts as "conelike," contrasting this with the smoother spherical developing capitulum in which bracts are rapidly surpassed by the developing flowers as "moriform" in reference to the resemblance to the syncarp of *Morus* or *Rubus*. These terms accurately describe variation in the developing capitula of *Leucaena* species. Similar peltate, pedicellate bracts with similarly variable shape (deltate to caudate) occur in the genera *Desmanthus, Kanaloa,* and *Schleinitzia*. Bracts in the remaining genera of the *Dichrostachys* group are sessile, carinate, and generally lanceolate (*Alantsilodendron, Calliandropsis, Dichrostachys, Gagnebina,* and *Neptunia*) and those of *Xylia* and *Parkia* spathulate or clavate and either elongate or truncate (character #13 in species analysis; #12 in generic analysis). Luckow (1993: 8) treated floral bracts as homologous to stipules in her analysis of *Desmanthus*, but over a wider range of genera, this appears to be an oversimplification, given that the morphology of bracts is not simply correlated with that of stipules. For example, the floral bracts of *Xylia* and *Parkia* are both spathulate, but *Parkia* has lanceolate and *Xylia* filiform stipules. It therefore seems reasonable to treat floral bracts and stipules as independent characters.

Corolla. Most generic descriptions of *Leucaena* describe the five petals as free to the base (Bentham 1875; Britton & Rose 1928; Elias 1974; Brenan & Brummitt 1970; Brewbaker 1987a). Zárate (1994) was the first to point out that in some species the petals are united either at the base or along the middle portion. Survey of the corolla across species is complicated by the need to examine flowers at different stages of development, given that petal fusion may be temporary or permanent; petals may be initially united and later split at anthesis. The fact that the petals are only weakly united and readily broken during dissection also complicates assessment. Careful dissection of flowers at different stages of development was undertaken across all species of *Leucaena*. Petals, as assessed at anthesis, are basally connate in only one species, *L. pulverulenta*. In this species petals are united in bud and remain firmly united along 75% of their length at anthesis. In six other species (*L. cuspidata, L. leucocephala, L. diversifolia, L. lempirana, L. magnifica,* and *L. salvadorensis*), the petals are partially and weakly united along the middle portion of the petals, but are free at the base. Petals are free along their entire length in the remaining species of *Leucaena* (character #16 in species analysis).

The comparative floral ontogeny, including the initiation and development of the corolla, of a selection of species of Mimosoideae was investigated by Tucker (1987) and Ramírez-Domenech and Tucker (1990). They demonstrated that corolla initiation occurs synchronously from free, equidistant radial primordia along the meristem, the petals enlarging simultaneously. Fusion of the petals to form a corolla tube or partial, looser form of conation occurs at mid-stage flower development, probably as a result of interprimordial and basal intercalary growth and/or epidermal appression. In *Mimosa albida* Ramírez-Domenech and Tucker (1990) showed that the initially free margins of the petals become appressed and the marginal epidermal cells interlock with adjacent petal epidermal cells at the tips of the petals. Zárate (1994) also concluded that petal fusion is secondary during flower development, based on the spongy appearance of the margin, which appears as a suture. Thus in the Mimosoideae that have been examined, petal initiation is free and synchronous in a simultaneous whorl, whereas time to fusion varies; the fused or partially fused petals found in some species of *Leucaena* are thus likely to be the result of exactly this sort of ontogenetic pattern of secondary fusion from initially free primordia.

Degree of petal fusion varies across the genera of the *Dichrostachys* and *Leucaena* groups (character #13 in generic analysis). Petals are consistently free to the base in *Desmanthus* and *Neptunia* (Luckow 1993), *Schleinitzia*, *Kanaloa* (Lorence & Wood 1994), some species of *Xylia,* and most species of *Parkia* (Luckow 1995; Luckow & Hopkins 1995). The corolla is basally connate in *Alantsilodendron, Calliandropsis, Dichrostachys* sensu stricto (Luckow 1995), some species of *Xylia* and *Gagnebina* although in the latter petals may later split on one side. Hernández and Guinet (1990) pointed out that petal fusion is highly variable in *Calliandropsis nervosus* (Britton & Rose) H. M. Hern. & Guinet within populations and even within individuals, with some petals free from the base and others fused for approximately half their length. Despite this variation, Luckow (1995) scored *Calliandropsis* as having fused petals.

The individual petals in *Leucaena* are one-veined and variably hairy or glabrous. Similar one-veined petals occur in the genera of the *Dichrostachys* group except *Alantsilodendron*, which has striate petals with 3–6 raised veins (Luckow 1995) (character #14 in generic analysis). Petals of *Schleinitzia* and *Kanaloa* are one-veined also. Despite this comparative lack of variation, petal venation was included in the preliminary analysis of generic relationships.

Style and stigma. Variation in the length of the style in relation to the stamen filaments and anthers is marked within *Leucaena.* In common with many Mimosoideae, the flowers of the majority of species of *Leucaena* are protogynous, i.e., stigma receptivity precedes pollen donation (Zárate 1994), whereas *L. lanceolata, L. macrophylla, L. trichodes,* and to a lesser extent *L. leucocephala* are protandrous with a dichogamy of one day (Brewbaker 1983). Taking pattern of development into account, the style may be exserted beyond the anthers, held at the same level as the anthers, or included below. Although the division between style exserted and included appears to be discrete and non-arbitrary, variation across species is in fact continuous. Variation in style length in relation to the anthers has also been observed within species [e.g., for *L. salvadorensis* where the style may be included or exserted (Boshier, pers. comm.)]. Although the variable position of the style in relation to the anthers is likely to be significant in terms of pollination, as a continuous and non-fixed variable, it was not included as a character in this analysis.

The stigma in *Leucaena* species is uniformly narrow-funnelform (sensu Luckow, 1995) or tubular (sensu Lewis and Elias, 1981), but is somewhat variable across the genera of the *Dichrostachys* and *Leucaena* groups in terms of width. Luckow (1995) used stigma morphology as a character in her analysis of the *Dichrostachys* group, delimiting three character states, porate, narrow-funnelform, and broad-funnelform. Variation at the generic level appears to divide into discrete states quite satisfactorily, even when *Xylia, Leucaena,* and *Schleinitzia* are added to the data set of Luckow (1995). Although the stigma is invariant within *Leucaena,* it was included as a character in both the generic and species analyses and as a test of the monophyly of *Leucaena* (character #17 in species analysis; #15 in generic analysis).

Ovary. The ovary in *Leucaena* is consistently sessile or subsessile and varies in length from (1.0–) 1.2 to 2.7 (–3.0) mm. Luckow (1995) included stipitate versus sessile ovary as a character in her analysis of the *Dichrostachys* group, but this character is only useful at generic level (character #17 in generic analysis). Ovary variation within *Leucaena* occurs in the indumentum; the ovary may be glabrous in the majority of species, long-pilose (in *L. cuspidata, L. diversifolia, L. greggii, L. retusa, L. leucocephala,* and *L. trichandra*) (Fig. 13E, F), or densely covered in short-velutinous pubescence in three species (*L. salvadorensis, L. lempirana,* and *L. shannonii*) (character #18 in species analysis; #16 in generic analysis). The degree of hairiness varies from sparsely hairy, with hairs usually restricted to the distal 50% of the ovary, to densely hairy over the whole ovary.

Stamen filaments. The common pentamerous ground plan of legume flowers includes ten stamens in two whorls with members alternating radially (Tucker 1987). In common with the majority of genera of the Mimoseae, *Leucaena* species have ten stamens, which are free to the base. Stamens are in two ranks, those opposite the petals sometimes shorter and slower to mature than those alternate to the sepals. Sorensson (1993: 45) suggested that bimodal anther length was unique to *L. lanceolata* and *L. collinsii*; however, although ranks of two different lengths are particularly pronounced in those two species, they are present to a lesser degree in most species. In a few species of *Desmanthus* and some species of *Neptunia,* as well as *Calliandropsis nervosus,* there are only five stamens

(Luckow 1993) (character #18 in generic analysis). Tucker (1987) showed for *Desmanthus illinoiensis* (Michx.) MacMill. ex B. L. Rob. & Fernald that the inner whorl of stamens opposite the petals is not initiated. Although constant within *Leucaena*, and the majority of closely related genera, stamen number was included as a character in the preliminary analysis of generic relationships.

Anthers. The anthers of *Leucaena* are uniformly ovate-oblong and dorsifixed, although in some species they are dorsifixed so near the base as to appear basifixed. Luckow (1995) included anther shape and fixation as a character in her analysis of the *Dichrostachys* group, and, although invariant within *Leucaena*, it is maintained as a character here in my preliminary analysis of generic relationships (character #19 in generic analysis). Anthers of *Leucaena* vary in size from 0.3 to 1.2 mm long and have two C-shaped thecae bound together by a variable connective, with two microsporangia per theca (Fig. 14) (see also Jain and Vijayaraghavan, 1992, for description and illustration of anthers of *L. leucocephala*). In two species, *L. macrophylla* and *L. trichodes*, the thecae are displaced laterally, such that the connective is visible on the ventral side of the thecae and the stomia are lateral rather than ventral (Fig. 14A). Of immediate interest here is the presence or absence of hairs on the anthers and variation in the occurrence of an extension of the connective, which affords the anther with an apiculum. Fuller discussion of anther morphology and the variable nature of the tapetal membrane and stage at which the tapetum is broken during anther development is presented in Hughes (1997a).

Anthers bearing hairs are relatively infrequent among legumes (Tucker 1987), occurring only in the genera *Bauhinia* L., *Moldenhauera* Schrad. (Caesalpinioideae); *Crotalaria* L., *Indigofera* L., *Harleyodendron* R. Cowan, *Mucuna* Adans. (Papilionoideae); and *Leucaena* (Mimosoideae). Thus, within the subfamily Mimosoideae, *Leucaena* is the only genus with hairy anthers making this a particularly notable field character, as the hairs are visible to the naked eye or at least with a hand lens. Within *Leucaena* anthers may be hairy, sometimes described as pilose (most species), or glabrous (*L. pulverulenta, L. greggii,* and *L. retusa* only) (Fig. 14B) (character #19 in species analysis; #20 in generic analysis). For the species with hairy anthers, hairiness varies from sparsely hairy in *L. cuspidata, L. esculenta, L. pallida,* and *L. diversifolia* to moderately or densely so in the remaining species. The hairs arise mainly on the ventral face of the anthers from the epidermis of the unopened thecae, sometimes concentrated along the stomial furrow, and are uniformly distributed from base to tip or, in some species, concentrated on the distal half or around the apex of the anther. The hairs range from 0.3 to 0.7 mm in length, and in some species are longer than the anthers.

In five species of *Leucaena, L. pulverulenta, L. cuspidata, L. retusa, L macrophylla,* and *L. trichodes* the anthers have a short distal protrusion of the connective between the thecae, termed an apiculum by Lewis and Guinet (1985); such anthers are described as apiculate, whereas in the remaining species the apiculum is absent (Fig. 14A–D). The apiculum in the Mimoseae has variously been described as "a short point" or "glandular prolongation" (Villiers 1994), or a "sub-cylindrical apical gland" (Hernández & Guinet 1990), and the anthers as "appendiculate" (thus referring to an "appendage") (Luckow 1995). More generally apicula have been simply described as "short connective protrusions" (Parkin 1951; Hufford & Endress 1989). The apiculum in *Leucaena* varies from a small pointed or rounded extension of the connective (as in *L. pulverulenta, L. cuspidata,* and *L. retusa*, Fig. 14B, D) to a relatively larger, broader, dorsi-ventrally flattened lip that extends forward over the ventral face of the anther in the form of a small "hood," as in

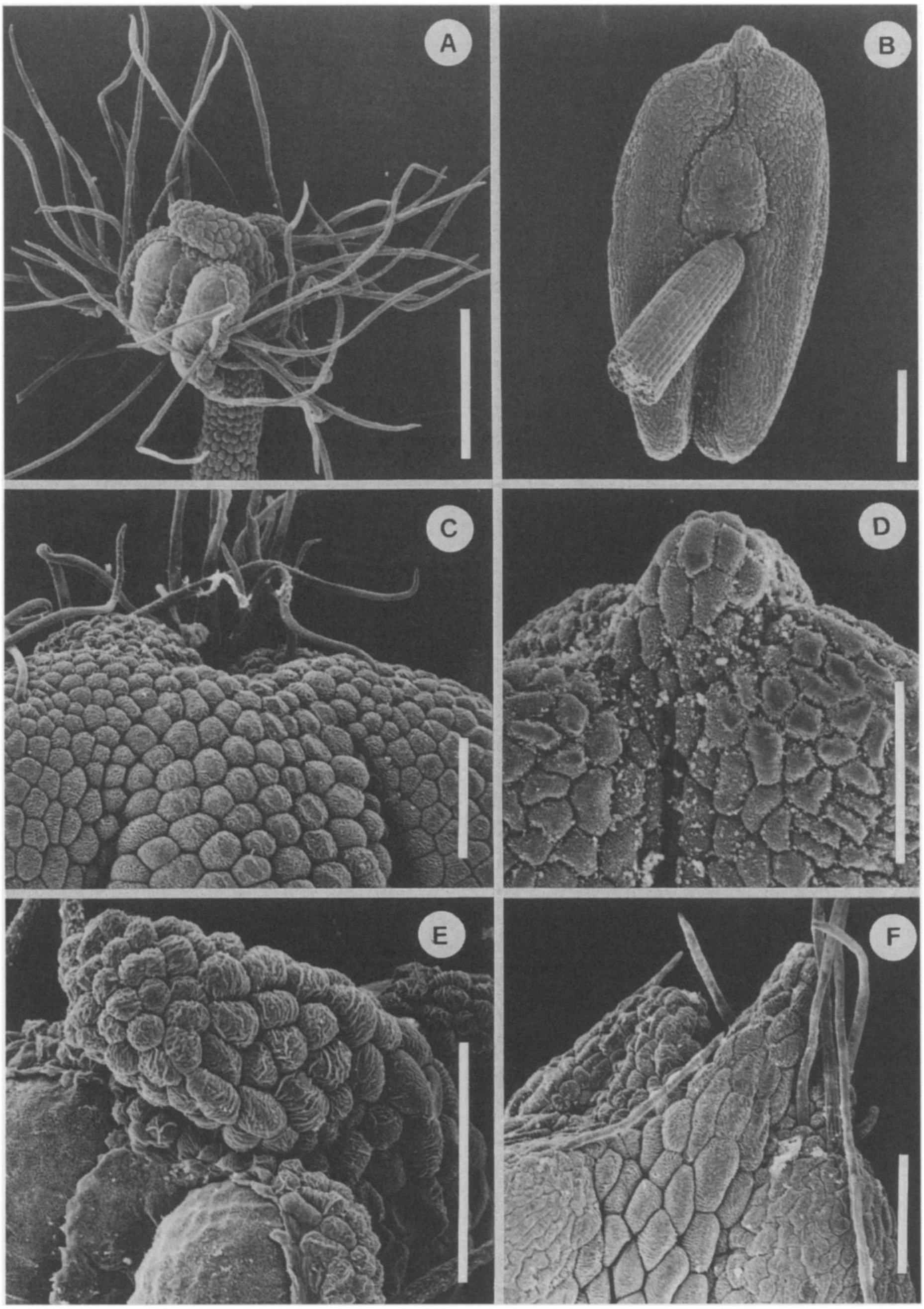


FIG. 14. Anther morphology, apicula, and hairiness in *Leucaena*, species characters #19 and #20. A. Hairy anther of *L. macrophylla*, view from above left side. B. Anther with small rounded apiculum, *L. pulverulenta*, dorsal view. C. Anther lacking distal protrusion of the connective, *L. esculenta*, dorsal view. D. Small rounded apiculum, *L. pulverulenta*, dorsal view. E. Short dorsiventrally flattened apiculum forming a small "hood" over the ventral face of the anther, *L. macrophylla*, view from above left side. F. Short, pointed apiculum, *L. cuspidata*, dorsal view. Scale bars: A = 0.25 mm, B = 0.25 mm, C = 0.1 mm, D = 0.1 mm, E = 0.1 mm, F = 0.1 mm. (Based on: A, *Hughes 1830*; B, *Hughes 1859*; C, *Hughes 1779*; D, *Hughes 1859*; E, *Hughes 1830*; F, *Hughes 1856*.)

L. macrophylla and *L. trichodes* (Fig. 14A, E) (character #20 in species analysis). The apiculum arises directly from the connective with no disjunction, and consists of closely packed fusiform cells with marked reticulate thickening. Luckow and Grimes (1997) surveyed variation in anther glands across virtually all the genera of the tribes Parkieae and Mimoseae and divided anther glands into four types: the *Piptadenia*-type, spherical, ellipsoid, or clavate and usually stipitate; the *Gagnebina*-type, apiculate; the *Prosopis africana*-type, forming a triangular flap; and the *Pentaclethra*-type, large, dorsally furrowed, with a specialized conical structure on the ventral surface. The apicula observed on the anthers of some species of *Leucaena* fall into the *Gagnebina*-type sensu Luckow and Grimes (1997). *Gagnebina*-type apicula have only been recorded on the anthers of some species of *Alantsilodendron* (Villiers 1994: 68–69; Luckow 1995: 66; Luckow & Grimes 1997; Hughes 1997a), all species of *Gagnebina* (Lewis & Elias 1981; Lewis & Guinet 1985: 468; Luckow 1995; Luckow & Grimes 1997; Hughes 1997a), some species of *Mimosa* (Barneby 1991), and very occasionally in *Calliandropsis* (Hernández & Guinet 1990: 614) (characters #21 and 22 in generic analysis). Luckow and Grimes note the unusual occurrence of cells at different angles in the apicula of *Gagnebina*; this was not observed in *Leucaena*. The function of the apiculum in *Leucaena* is unknown, as indeed it appears to be in other Mimosoid legume genera. The only investigation of similar swollen anther tips found in some species of *Caesalpinia* sect. *Poincianella* (Caesalpinioideae) by Rudall et al. (1994), showed that the tip has mucilage-filled secretory ducts forming discrete regions of secretory tissue, justifying the description of the apiculum as a type of gland, but it is doubtful if this can be extended to other genera without detailed examination.

Luckow (1995) treated the appendiculate tips of the anthers of *Alantsilodendron* and *Gagnebina* as homologous with the stipitate anther glands (*Piptadenia*-type sensu Luckow and Grimes, 1997) that are commonly found in a wide range of genera in the Mimoseae. This appears to be justified based on the similarity criterion of topographic correspondence in that both are appendages that arise at the apex as direct extensions of the connective. The glandular nature of these stipitate appendages was demonstrated for *Prosopis juliflora* (Sw.) DC. (Chaudhry & Vijayaraghavan 1992) and more recently for more genera (Luckow & Grimes 1997). Bentham (1875) relied on the presence or absence of stipitate anther glands to characterize tribes, and more recently Lewis and Elias (1981) used this as one character to separate *Schleinitzia* and *Leucaena*. Within the *Dichrostachys, Xylia,* and *Leucaena* groups sensu Lewis and Elias (1981), stipitate, terminal, often caducous, anther glands are found in species of *Schleinitzia* (Nevling & Niezgoda 1978: 347; Hughes 1997a), some species of *Xylia* (Hughes 1997a), *Calpocalyx*, one species of *Desmanthus* (Luckow 1993: 7), some species of *Neptunia* and *Dichrostachys* sensu stricto (Lewis & Elias 1981; Luckow 1995: 66).

The anthers of *Leucaena*, and other Mimoseae, dehisce along a simple, linear, longitudinal, stomial furrow, dividing the thecae into two almost equal halves. In most plant species, and apparently most species of *Leucaena*, the interlocular zone, consisting of the septum and the tapetum, is disrupted prior to dehiscence along the stomium (Keijzer 1987), thereby creating a single pollen-containing chamber prior to dehiscence with the pollen grains free within that chamber at the time of dehiscence. Breakdown of the septum and tapetum prior to dehiscence was ascertained and illustrated for *L. leucocephala* by Jain and Vijayaraghavan (1992). In *L. macrophylla* and *L. trichodes*, the locules remain separate, as discrete elliptical "units" surrounded by what appears to be an intact tapetal membrane, until after dehiscence of the anther (Fig. 14A). In the case of *L. macrophylla*, the tapetum apparently remains intact until after dehiscence of the anther and forms a "sac," which holds the whole locular contents together as a unit. The intact tapetal membrane of *L. macrophylla* was observed on fixed flower material prior to critical-point drying, and is not therefore an artifact of the drying procedure. Anther dehiscence in relation to the tapetal membrane is further discussed in Hughes (1997a). Variation in anther morphology and dehiscence within *Leucaena* is summarized in Table 1.

Flower color. Field notes that record flower color in *Leucaena* usually refer to the color of the stamen filaments and anthers (and occasionally the style), which are the most conspicuous parts, and not the color of the calyx or corolla, which are largely hidden within the capitulum. Color of the filaments, anthers, and style is often poorly preserved in dried specimens and is of little practical use in assessing color variation, which must be observed from living material. Color also varies as flowers develop and fade; in particular the anthers commonly fade from white to pale tangerine-yellow or orange or from pink to dull mauve, and freshly opened flowers must be observed to allow comparisons. Flower color was recorded and photographed for all *Leucaena* species from freshly opened flowers. Color was recorded separately for calyx, corolla, filaments, anthers, and style.

The color of the calyx and corolla in *Leucaena*, and all the closely related genera, is largely pale green, whitish green or yellow-green, sometimes with a reddish maroon tinge on the lobe tips of the corolla. Color variation in the filaments, anthers, and style is however striking in *Leucaena*. Three colors, white, pink/purple, and yellow occur in the genus. The majority of *Leucaena* species have white or pale cream-white filaments, anthers, and style, although the anthers vary from cream-white to pale creamy yellow. Two species, *L. greggii* and *L. retusa*, have consistently bright yellow filaments, anthers, and styles. The remaining species have pink or purple-pink anthers, and variably pink, white-pink, or reddish filaments and styles (character #15 in species analysis). Of the pink-flowered species, variation is most pronounced within *L. diversifolia* and *L. trichandra* where filament/anther/style color ranges from pale white-pink to strong shocking pink, dull purple-pink (fading dull mauve), and occasionally bright scarlet. Flowers of closely related genera in the *Dichrostachys* and *Leucaena* groups present the same range in color seen within *Leucaena*. Indeed, white, yellow, and pink flowers are dominant throughout the Mimosoideae.

Pollen. Variation in apertural type, the structure of the exine and particularly the tectum and its ornamentation, and the high frequency of compound grains (polyads and tetrads) have provided useful characters in systematic studies of the Mimosoideae (Guinet 1981a, b; Guinet & Ferguson 1989). The pollen of *Leucaena* was first studied in depth by Guinet (1966), who examined pollen of 17 species (although several of these are here treated as conspecific) using light microscopy and was the first to show the occurrence of both polyads and eumonads within the genus. Guinet's (1966) study was limited by reliance on light microscopy, by taxonomic confusion surrounding the material used, and incomplete sampling of species within the genus. Voucher specimens were cited later in Guinet (1969), and the majority of these have been seen and identified during the present work.

Pollen of all 22 species of *Leucaena*, as well as two species of *Xylia* and one of *Schleinitzia*, was surveyed (summarized in Table 1) and discussed within a wider systematic context by Hughes (1997a). Pollen in the majority of *Leucaena* species occurs in symmetric tricolporate eumonads (Fig. 15A, C). Pollen occurs in polyads in three *Leucaena* species, one of which, *L. multicapitula*, has individual pollen grains that are tricolporate (Fig. 15B), while the other two (*L. trichodes* and *L. macrophylla*) have pantoporate monad units (Fig. 15D–F). Thus in *Leucaena* there are two basic types of apertures, colporate and

TABLE 1. Summary of anther and pollen data for *Leucaena*. Vouchers are cited in Hughes (1997a).

	Anthers			Pollen		
Species	Vestiture	Apiculum	Dehiscence	Monads/polyads	Apertures	Tectum
L. collinsii	hairy	absent	normal	monads	tricolporate	psilate
L. confertiflora	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. cuspidata	sparsely hairy	small-pointed	normal	monads	tricolporate	perforate, punctate
L. diversifolia	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. esculenta	sparsely hairy	absent	normal	monads	tricolporate	perforate, punctate
L. greggii	glabrous	absent	normal	monads	tricolporate	sparsely punctate
L. involucrata	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. lanceolata	hairy	absent	normal	monads	tricolporate	psilate
L. lempirana	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. leucocephala	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. macrophylla subsp. *macrophylla*	hairy	broad, flattened	tapetal membrane	polyads (acalymmate monads)	pantoporate	finely punctate
L. macrophylla subsp. *istmensis*	hairy	broad, flattened	tapetal membrane	polyads (acalymmate monads)	pantoporate	finely punctate
L. magnifica	hairy	absent	normal	monads	tricolporate	psilate
L. matudae	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. multicapitula	hairy	absent	normal	polyads (acalymmate tetrads)	tricolporate	perforate, punctate
L. pallida	hairy	absent	normal	monads	tricolporate	finely reticulate
L. pueblana	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. pulverulenta	glabrous	small, rounded	normal	monads	tricolporate	perforate, punctate
L. retusa	glabrous	small, rounded	normal	monads	tricolporate	perforate, punctate
L. salvadorensis	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. shannonii	hairy	absent	normal	monads	tricolporate	perforate, punctate
L. trichandra	hairy	absent	normal	monads	tricolporate	finely reticulate
L. trichodes	hairy	broad, flattened	tapetal membrane	polyads (acalymmate monads)	pantoporate	sparsely punctate

porate (Table 1) (character #21 in species analysis; #23 in generic analysis). Pollen of *Leucaena* material from Hispaniola, originally described as *L. pseudotrichodes*, shows unusual variation in aperture type; some grains are clearly colporate; others show only weak development of the colpi and would be described as colpoidorate. Tricolporate eumonads or monad units were considered by Guinet (1981a) to be the *basic* (my emphasis) pollen aperture type in the Leguminosae. In species of the *Dichrostachys* and *Leucaena* groups, both porate (*Dichrostachys, Gagnebina,* and some species of *Xylia*) and colporate (*Calliandropsis, Desmanthus, Kanaloa, Neptunia, Schleinitzia,* and some species of *Xylia*) apertures occur. In her phylogenetic analyses of both *Desmanthus* and the *Dichrostachys* group Luckow (1993, 1995) postulated porate apertures to be plesiomorphic and tricolporate apertures to be independently derived at least twice in both groups.

The occurrence of compound grains (polyads and tetrads) is a most conspicuous feature of Mimosoid pollen. As pointed out by Guinet (1981a, b), the compound grain is a more or less compact unit made by the permanent assemblage of a variable number of individual cells remaining more or less independent of each other. The degree of asymmetry in shape and exine development of the individual grains is a function of the closeness of the grouping. Within the Mimosoideae, there is a complete spectrum from calymmate (the external layer of the exine is common to all the grains) to acalymmate (polyads in which the ectexine is not completely continuous around members of the dispersal unit) compound grains. This means that simply distinguishing between monads and polyads does not properly account for the morphological variation encountered. Luckow (1995) recognized this problem in relation to variation in types of compound grain within the *Dichrostachys* group, and divided polyads into three types, calymmate, acalymmate tetrads (where individual cells are tightly bound within tetrads and the tetrads are loosely associated into larger compound grains), and acalymmate monads where monad units are themselves loosely associated into compound grains. The number of cells per compound grain is sometimes extremely variable and also of limited value due to intraspecific variation (Guinet 1981a, b). The tetrad represents in most genera only a sporadic variant, occurring along with 1-, 8- and 16-celled grains, often in the same anther. The polyads found by Guinet (1966) in *Leucaena* were all acalymmate, corresponding to the category of acalymmate monads of Luckow (1995), but Guinet further differentiated *Leucaena* polyads as more or less loosely associated. For the species with very loosely associated grains (which disintegrate following normal acetolysis or even modified procedures of Wodehouse, 1935, and taking great care in dissecting the anthers), Guinet (1966) deduced their occurrence in polyads from the asymmetry of the individual monads. In this survey, polyads were found in three species of *Leucaena* (Fig. 15B, D–F): *L. multicapitula, L. trichodes,* and *L. macrophylla*, but these are of two very different types. In *L. multicapitula*, pollen occurs in calymmated tetrahedral tetrads composed of tricolporate monad units. The tetrads are loosely aggregated into 16-celled polyads, equivalent to the acalymmate tetrads sensu Luckow (1995) (Fig. 15B). In *L. trichodes* and *L. macrophylla*, pollen occurs in acalymmated polyads with 1–26 irregularly asymmetric porate monad units per polyad. These compound grains are loosely attached and therefore difficult to observe intact. Evidence for their occurrence comes from the asymmetry of the monad units (Fig. 15D, F), broken polyad fragments after acetolysis that contain several monad units in regular, non-random arrangements (Fig. 15D), and observation of more or less intact polyads when pollen is extracted with care from the anthers and observed without acetolysis (Fig. 15E). The occurrence of species with pollen in monads and others with polyads in the same genus is not uncommon in the Mimosoideae and has been reported for *Newtonia* Baill., *Entada* Adans.,

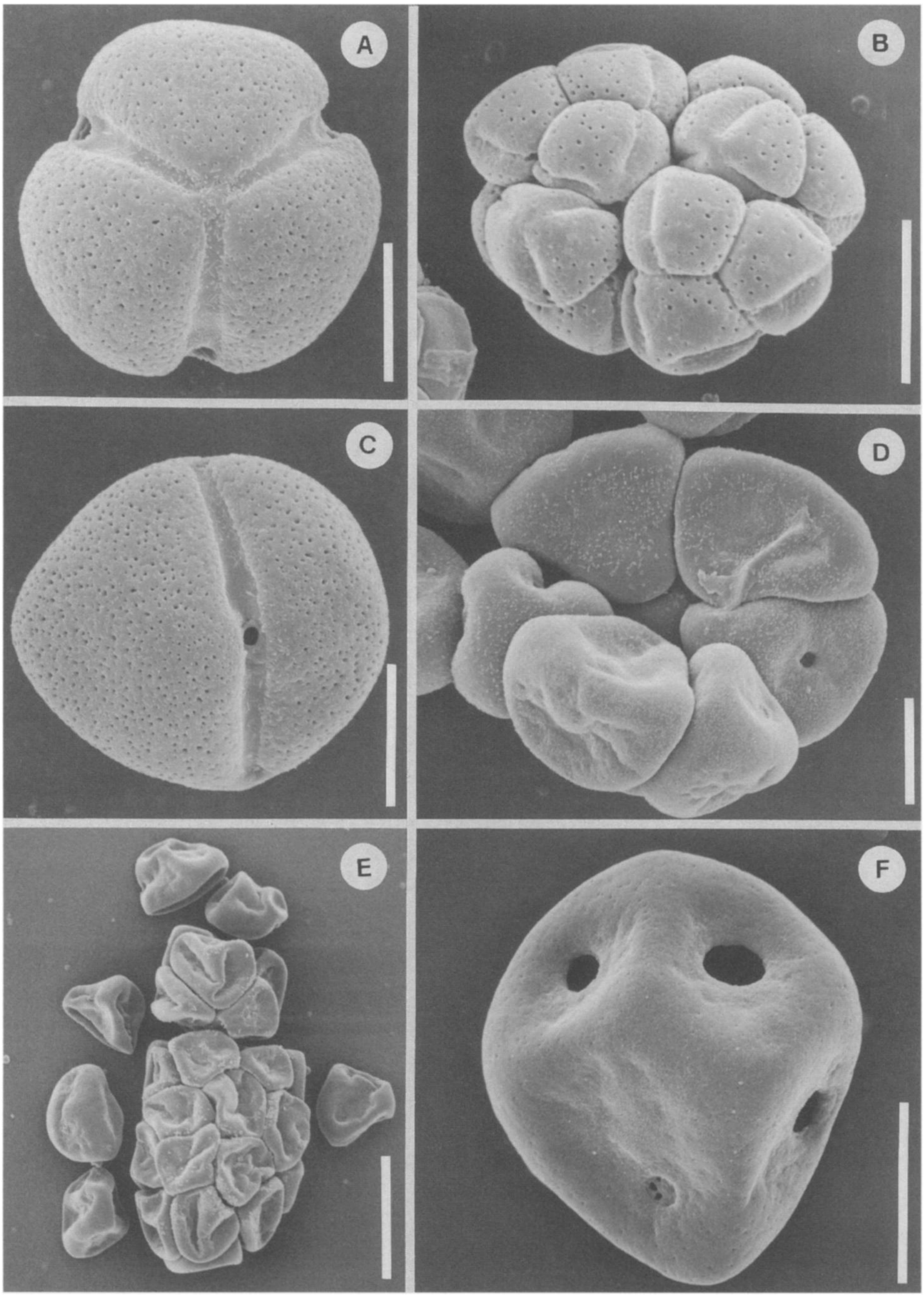


FIG. 15. Pollen variation in *Leucaena*, species characters #21 and #22. A. *L. salvadorensis*, polar view. B. *L. multicapitula*, showing 16-grained polyads of the acalymmate tetrad type (see text). C. *L. salvadorensis*, equatorial view. D. Partially disintegrated acalymmate polyad, *L. macrophylla* subsp. *istmensis*. E. *L. macrophylla* subsp. *istmensis*, showing loosely associated acalymmate polyads prepared without acetolysis. F. *L. macrophylla* subsp. *istmensis*, monad unit derived from acalymmate polyad. Scale bars: A = 15 µm, B = 25 µm, C = 15 µm, D = 15 µm, E = 25 µm, F = 15 µm. (Based on: A, C, *Hughes & Styles 37*; B, *Hughes 795*; D–F, *Macqueen 277*.)

Dichrostachys, *Dinizia* Ducke, as well as *Leucaena* (Guinet 1981b), and recently for *Desmanthus* (Luckow 1993). Across the genera of the *Dichrostachys, Xylia,* and *Leucaena* groups, there is great diversity of the pollen unit. Calymmate polyads occur in *Gagnebina* and some species of *Dichrostachys* and *Xylia*. Acalymmate tetrads occur in some species of *Dichrostachys, Xylia,* and *Schleinitzia*, one species of *Leucaena*, and one species of *Desmanthus*. Acalymmate monads occur in both *Dichrostachys* and *Leucaena*. Eumonads occur in *Neptunia, Calliandropsis, Kanaloa,* and most species of *Desmanthus* and *Leucaena* (character #22 in species analysis; #24 and 25 in generic analysis).

Many terms associated with pollen wall architecture, and particularly categories used to describe tectal ornamentation, are arbitrary and have not been consistently applied. Terms used here to categorize tectal ornamentation follow Walker and Doyle (1975, their Figs. 7–9). The exine in *Leucaena* has well-developed columellae (Fig. 16F) and is tectate, or occasionally semi-tectate. In *Leucaena*, the external surface of the tectum is devoid of raised ornamentation and ranges from tectate, smooth, almost psilate (without perforations) in a few species (Fig. 16A) to smooth, perforate, punctate, or finely foveolate (scattered isodiametric channels ≤1 μm in diameter) in the majority of species (Fig. 16B–D), to semi-tectate, finely reticulate with small lumina (≥1 μm in diameter) (Fig. 16E) in two species. This variation appears to be quantitative and continuous (Fig. 16A–E). The division between tectate perforate with large perforations and semi-tectate reticulate with small lumina is arbitrary and difficult to define (Moore et al. 1991). Although variation in tectal ornamentation within *Leucaena* is continuous and therefore cannot be readily divided into discrete character states (sensu Stevens, 1991), discrete variation is encountered between genera and tectal ornamentation was included as a character in the preliminary generic analysis and the species-level analysis to test the monophyly of *Leucaena* (character #23 in species analysis; #26 in generic analysis). Across the genera of the *Dichrostachys, Xylia,* and *Leucaena* groups, only a few species of *Desmanthus* share the psilate/punctate/finely foveolate tectal ornamentation found in *Leucaena*. Considerable variation in tectal ornamentation occurs in the remaining genera (Luckow 1993, 1995; Hernández & Guinet 1990).

Fruits. Pods in *Leucaena* occur in groups of 1–4, but in some species there can be 6–15 and occasionally up to 45 pods per capitulum. Variation in pod set has been attributed in part to breeding system, with high numbers of pods per capitulum associated with self-fertility (e.g., *L. leucocephala* and *L. diversifolia*). Similar variation occurs in closely related genera such as *Desmanthus*, where self-compatibility has also been related to high pod set per capitulum (Luckow 1993).

In *Leucaena*, pods are short-stipitate, strongly pendent, and either narrow, linear, and slightly thickened, or broad, linear-oblong or oblong, and broadly to narrowly plano-compressed and flat (Fig. 17A–D). Similar variation in pod shape occurs in the majority of the closely related genera, except for *Kanaloa,* which has small obovate or subcircular compressed, apparently monospermous pods, which are unusual within the Mimoseae (Lorence & Wood 1994) but similar to those of *Neptunia dimorphantha* Domin. (illustrated in Gunn, 1984: 121). Variation in pod shape (linear vs. linear-oblong or oblong) although clear-cut at the extremes varies continuously and is largely a function of the continuously variable pod width and not readily amenable to division into anything but arbitrary character states. For this reason, pod shape was not included as a character in the analysis. The apex may be acuminate or obtuse, sometimes with a beak that is apparently easily broken off when fruits ripen. The pod valves have variably raised sutural ribs along the margins but are never winged. The presence of a wing on the fruit (character #27 in

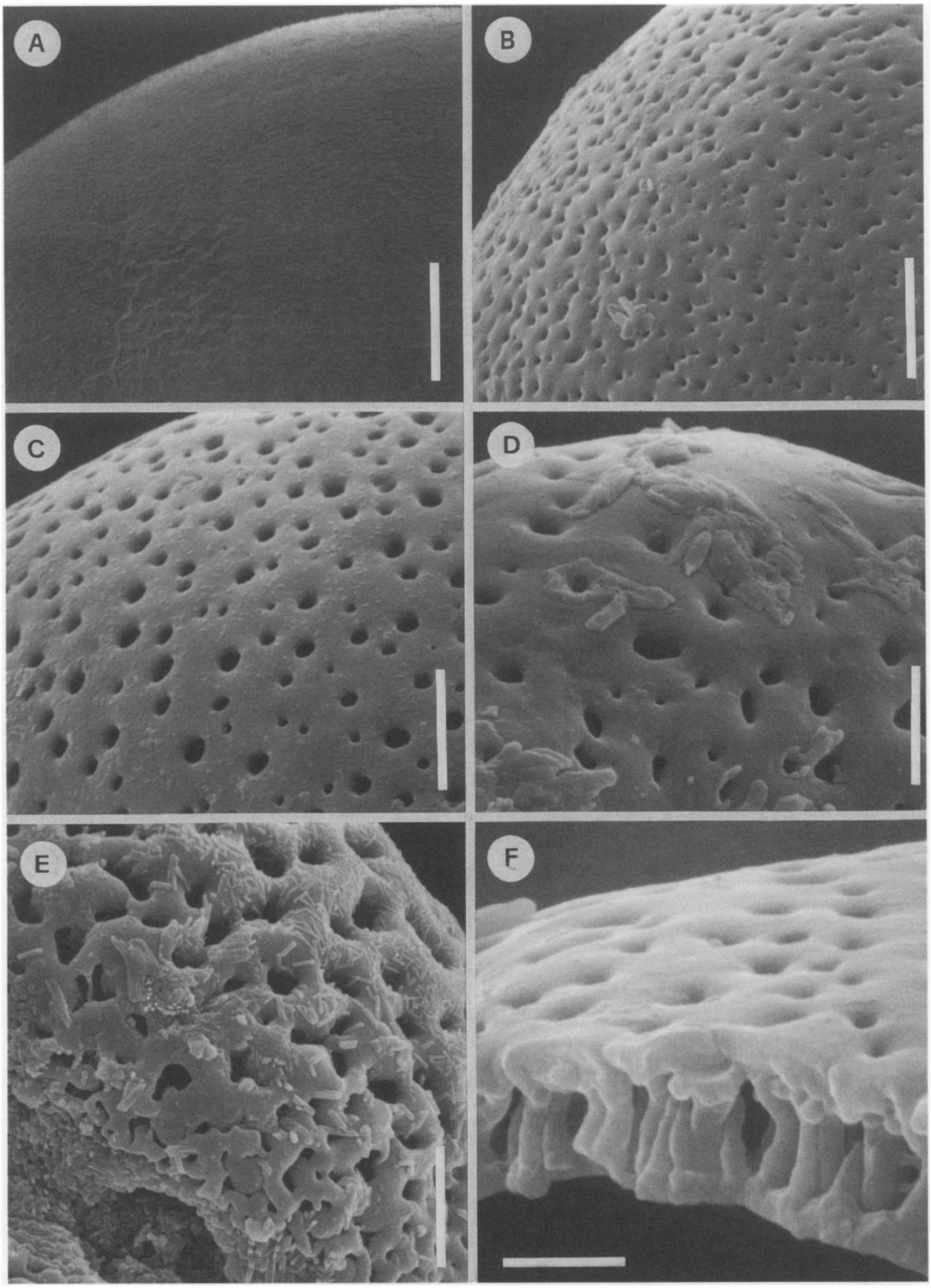


FIG. 16. Continuous variation in tectal ornamentation within *Leucaena*, species character #23. A. *Leucaena collinsii* subsp. *zacapana*, showing psilate tectum. B. *L. leucocephala*, showing punctate tectum with micro-perforations. C. *L. pueblana*, showing punctate/perforate tectum. D. *L. pallida*, showing foveolate tectum. E. *L. trichandra*, showing finely reticulate tectum. F. *L. leucocephala*, approximate transverse section through ectexine showing columellae. Scale bars A–E = 3 µm, F = 1 µm. (Based on: A, *Hughes 1137*; B, F, *Hughes 1547*; C, *Hughes 1803*; D, *Hughes 1506*; E, *Hughes 1094*.)

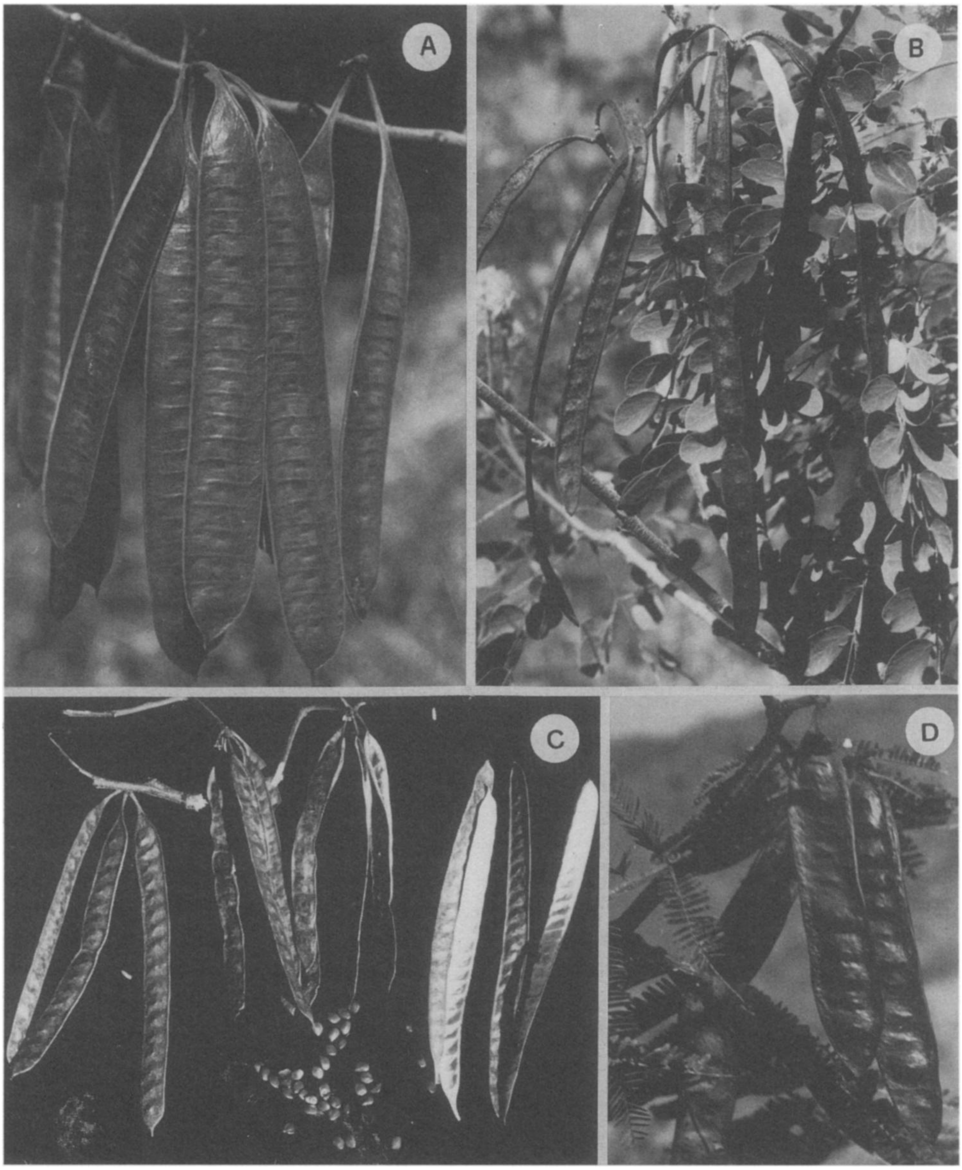


FIG. 17. Variation in pod shape within *Leucaena*, species character #24. A. Linear-oblong, flat, chartaceous to weakly coriaceous pods, *L. lanceolata*. B. Linear, coriaceous or weakly lignified pods, *L. retusa*. C. Linear, thickened pods tardily dehiscent along both sutures with oblique seed alignment, *L. involucrata*. D. Ripe pods tardily dehiscent along both sutures, *L. pueblana*. (Based on: A, *Hughes 1300*; B, *Hughes 1361*; C, *Hughes 1572*; D, *Hughes 1327*.)

generic analysis) was used to separate *Schleinitzia* from *Leucaena* (Lewis & Elias 1981); however, the wing on *Schleinitzia* is variable. It is well developed in *S. novoguineensis* (Warb.) Verdc. and *S. insularum* (Guill.) Burkart, but rudimentary in *S. megaladenia* (Merrill) Guinet & Nielsen (Nielsen 1992a). The presence of a pod wing was also traditionally used to distinguish *Gagnebina* from *Dichrostachys*, but again the wing on pods of *Gagnebina* species is variable and sometimes lacking altogether (Lewis & Guinet 1985). *Tetrapleura* Benth., *Gagnebina,* and *Schleinitzia* are the only genera reported with winged fruits in the subfamily Mimosoideae (Gunn 1984). Although invariant within *Leucaena* "winged fruits" was included as a character in the analysis of generic relationships because of its use to delimit *Schleinitzia* from *Leucaena.*

The exocarp in *Leucaena* varies from thin and membranous to chartaceous, subcoriaceous, or, in a few species, coriaceous (character #24 in species analysis). Similar variation occurs in the closely related genera of the *Leucaena* and *Dichrostachys* groups (character #28 in generic analysis). The mesocarp is uniformly absent from these genera (Gunn 1984). The surface of the exocarp in *Leucaena* can be densely pubescent (velutinous) or glabrous, sometimes with crosswise or mosaic-like cracks, dull or lustrous, and in some species with irregular veins. Pod vestiture has been used as an important character to distinguish a number of intraspecific taxa in *Leucaena*, including *L. leucocephala* subsp. *leucocephala* (Zárate 1987a), *L. lanceolata* var. *lanceolata*, and *L. cuspidata* subsp. *jacalensis* (Zárate 1994). Although pods are consistently covered in dense velutinous pubescence in a number of taxa, including *L. magnifica, L. shannonii,* and *L. leucocephala* subsp. *leucocephala,* occurrence of pubescence on pods is variable in other taxa, including *L. lempirana, L. lanceolata* (both varieties), *L. esculenta* (Zárate 1994), *L. cuspidata,* and *L. diversifolia,* and pods may be either pubescent or glabrous (see Taxonomy). Similar variation in pod vestiture was described by Luckow (1993) for species of *Desmanthus.* Given the intraspecific variability and lack of fixed differences, pod vestiture was not included as a character in the cladistic analysis. The endocarp is smooth, white or tan, sometimes with rudimentary septa of a spongy consistency, which weakly partition the pods into separate seed chambers (termed subseptate by Gunn. 1984). In the partitioned pods the seed chambers are visible on the outside of the pods (Fig. 17C, D) (character #25 in species analysis; #29 in generic analysis).

Mode of dehiscence of fruits of Mimosoideae is highly variable and has been widely included as character in cladistic analysis of different groups (e.g., Luckow, 1993, for *Desmanthus*; Luckow, 1995, for the *Dichrostachys* group; and Grimes, 1995, for the Ingeae). Fruits of all species of *Leucaena* are dehiscent, either along one suture or both. Fruits of most species are dehiscent along both sutures (Fig. 18C), although some are more tardily dehiscent than others. In the majority, dehiscence is rapid along both sutures and is medial (starts in the middle portion of the legume), the valves remaining attached initially at both apex and base and later only at the base. In a few species both margins split before the valves separate completely (Fig. 17C), but dehiscence is never more than slightly tardy in *Leucaena.* The valves of species opening along both sutures tend to twist slightly and reflex transversely, curling back after dehiscence (Fig. 18C). In two species, *L. cuspidata* and *L. confertiflora*, pods dehisce initially along only one suture (Fig. 18A, B, D, E), and in *L. cuspidata* the valves twist strongly after dehiscence forming tight spirally twisted rolls (Fig. 18B, E) (characters #26 and 27 in species analysis; #30 and 31 in generic analysis). In the genera of the *Leucaena* and *Dichrostachys* groups a wider range of dehiscence types occurs including indehiscent, dehiscent initially through one suture, inertly dehiscent simultaneously through two sutures, and elastically dehiscent through

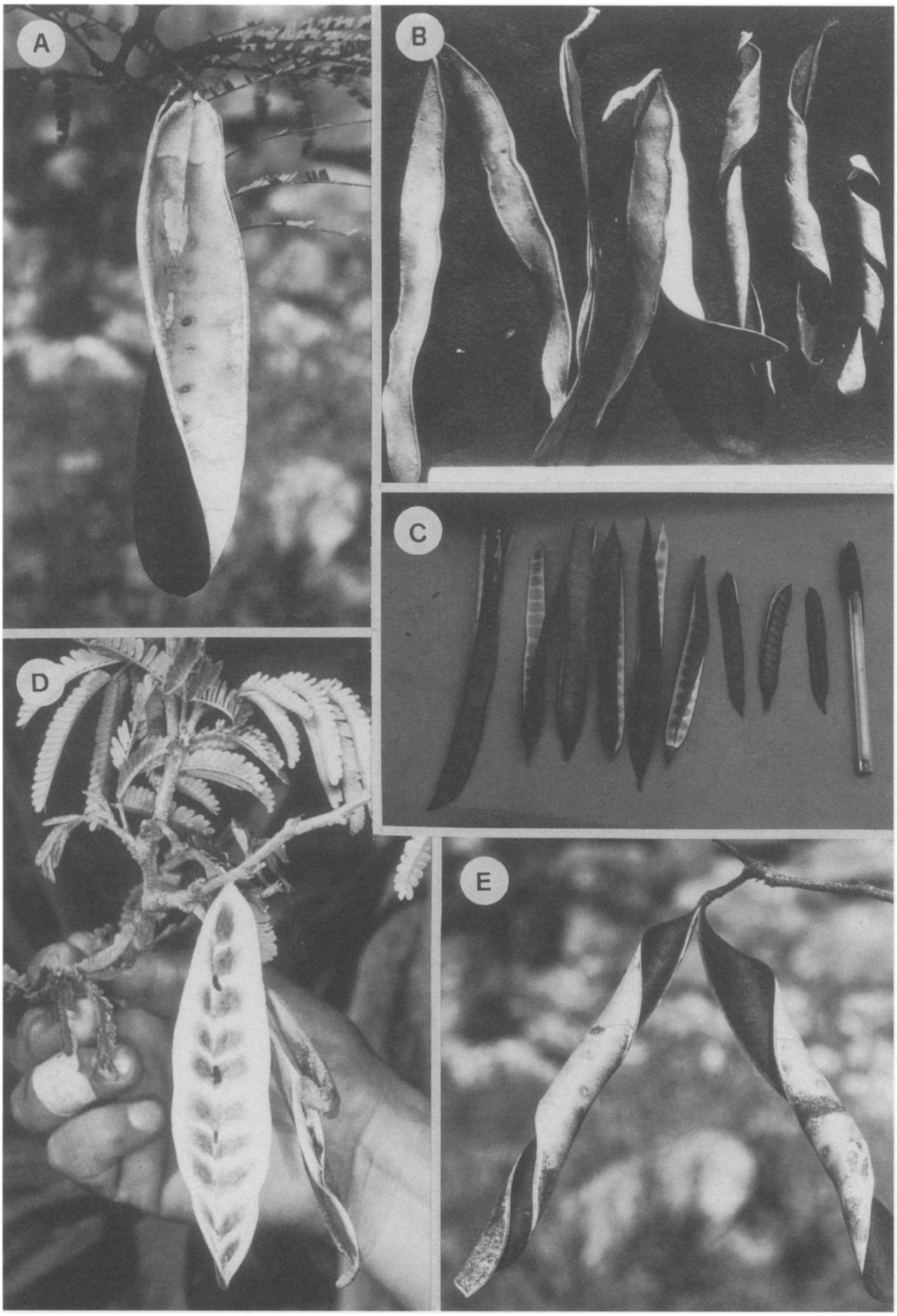


FIG. 18. Pod dehiscence, species characters #26 and #27. A. Pod dehiscence along one suture, *L. cuspidata*. B. Flat oblong pods, dehiscent along one suture, the valves twisting in tight spirals after dehiscence, *L. cuspidata*. C. Linear-oblong flattened pods readily dehiscent along both sutures, *L. collinsii* subsp. *zacapana*. D. Linear-oblong pods, transverse seed alignment, dehiscent along one suture, *L. confertiflora*. E. Flat oblong pods, dehiscent along one suture, the valves twisting in tight spirals after dehiscence, *L. cuspidata*. (Based on: A, B, E, *Hughes 1850*; C, *Hughes 299*; D, *Hughes 1321*.)

two sutures. Indehiscent pods occur in some species of *Dichrostachys* sensu stricto and in *Schleinitzia*, although in the latter there has been some controversy and disagreement in the literature about the mode of dehiscence. Breteler (1960), Verdcourt (1977), Nielsen (1992a), and Gunn (1984) point out that although the pods of *Schleinitzia* split along both sutures, they are only dehiscent along the margins or wings, the remainder of the pod valves remaining firmly attached until much later. *Schleinitzia* pods are coded here as partially dehiscent. This character was used by Lewis and Elias (1981) as a further character (along with winged pods and anther glands) to separate *Schleinitzia* from *Leucaena*. Pods that are initially dehiscent along only one suture occur in *Xylia*, some species of *Gagnebina* and *Neptunia,* and pods opening inertly along both sutures in *Kanaloa* and most species of *Desmanthus*. Elastic dehiscence, where the pods open from the apex to base along both sutures, occurs in *Alantsilodendron* and *Calliandropsis*.

Seeds. *Leucaena* seeds are generally circular to ovate or ellipsoid, dorsi-ventrally flattened, and lentiform in cross section. Some species, such as *L. retusa* and *L. greggii*, consistently have rhomboidal seeds and yet others, such as *L. involucrata, L. matudae, L. pallida,* and *L. pueblana*, are intermediate with weakly rhomboidal seeds. This variation in seed shape is apparently correlated with pod width and shape (see below). The testa is uniformly rich chestnut-brown and glossy and is marked on two sides by a horseshoe- or U-shaped pleurogram. In the majority of *Leucaena* species the pleurogram is uniformly horseshoe- or U-shaped, with 90–95% arm extension (sensu Gunn, 1984) and open towards the hilum. Only two species, *L. matudae* and *L. pueblana*, show significant variation from this pattern with only 50–75% arm extension, and *L. pueblana* has a bell-shaped pleurogram. There is similar variation in the degree of arm extension of the pleurogram amongst the closely related genera, but this appears to be continuous and not amenable to division into character states. Seeds of species of *Leucaena* contain endosperm, which is variable in thickness and adnate to the testa (Gunn 1984). Endosperm is recorded as present in seeds of all the closely related genera (Gunn 1984), except *Xylia, Calliandropsis,* and one species of *Dichrostachys* sensu stricto (Luckow 1995), but the taxonomic significance of endosperm cannot be assessed due to lack of data for many species of *Alantsilodendron* and *Gagnebina* from Madagascar (Luckow 1995). Seeds of all species, except *L. salvadorensis* and *L, esculenta,* require a scarification pretreatment to promote rapid germination (Hawkins & Ochoa 1991). Bruchids are recorded as feeding on seeds of almost all *Leucaena* species (Hughes & Johnson 1996; see below). Seed characters are of very limited value in species circumscription or as characters for cladistic analysis within *Leucaena*, other than the distinctive pleurogram of *L. matudae* and *L. pueblana*.

In *Leucaena*, seeds are discharged passively from the pods. The variable alignment of seeds in the pods has been noted by several authors and was used by Britton and Rose (1928) as a distinguishing character in their segregation of the two monotypic genera *Caudoleucaena* and *Ryncholeucaena* from *Leucaena*. Seed alignment is transverse in the majority of *Leucaena* species, but becomes markedly oblique in *L. pallida, L. matudae,* and *L. involucrata*, and longitudinal in *L. greggii* and *L. retusa* (character #28 in species analysis). Similar variation has been noted in other genera in the Mimoseae, such as *Mimosa* (Barneby 1991) and *Desmanthus* (Luckow 1993).

Seedlings. Twenty seedlings of each of the species and varieties of *Leucaena, Desmanthus fruticosus* Rose, *Schleinitzia novoguineensis,* and *Xylia torreana* Brenan were grown in greenhouse conditions to examine seedling morphology and nyctinastic leaf movements. Seeds were mechanically scarified to promote rapid and uniform germination and *Rhizobium* inoculum applied (NifTAL, strain TAL 1145).

Seedlings of most *Leucaena* species are phaneroepigeal with foliar cotyledons. One species, *L. cuspidata*, is unique within the genus with phanerogeal seedlings, i.e., with very little or no extension of the hypocotyl and its foliar cotyledons held at or slightly below ground level. Germination rates are usually high (50–90%) with the taproot emerging from the micropylar pole of the seed. In most species the cotyledons open, and the testa splits and is dropped as the hypocotyl extends. Hypocotyl extension varies across species (Table 2) with the greatest extension in *L. matudae* with its cotyledons held 50 mm or more above ground level. Although it was tempting to include the degree of elongation of the hypocotyl as a character in the cladistic analysis, particularly as similar variation occurs in the closely related genus *Desmanthus*, more detailed analysis reveals that this is simply a continuous character that is not amenable to division into character states except on an arbitrary basis. Further, as found by Luckow (1993), hypocotyl length was found to be variable within species.

Many features of the seedlings are uniform throughout the genus (Table 2). Cotyledons are short-petiolate, basally auriculate or cordate, and apically obtuse or rounded. Cotyledon shapes and dimensions are closely correlated to seed shape and size (Table 2) and are ovate to orbicular. In most species three faint veins are visible at the base of the cotyledons, but in some species only one vein is visible and in a few up to five veins can be seen. The number of primary veins in cotyledons across the Mimosoideae as a whole was investigated by Smith and Scott (1995), who found a range from 1 to 7 with no obvious phylogenetic pattern. The two species of *Leucaena* observed by them both had cotyledons with three primary veins.

Eophylls are uniformly pinnate with 2–26 leaflets and in most cases lack a petiolar nectary; a nectary is however present on the eophyll of *L. cuspidata*. The first leaf is bipinnate usually with one pair of pinnae, occasionally with two pairs in some species, and consistently with two to three pairs in *L. esculenta*. The first leaves are stipulate and possess petiolar nectaries. Unlike the closely related genus *Desmanthus* (Luckow 1993), all species of *Leucaena* show some extension of the epicotyl.

Seedlings of species of *Desmanthus, Neptunia, Calliandropsis, Schleinitzia,* and *Dichrostachys* are similar to those found in *Leucaena* with short-petiolate, ovate to orbicular, three-veined cotyledons auriculate at the base, a single once-pinnate eophyll, and a bipinnate second leaf usually with one pair of pinnae.

CHROMOSOME NUMBERS

The occurrence of polyploidy in *Leucaena* has long been known following early reports of chromosome counts for *L. leucocephala* (2n = 104) (Tjio 1948; Frahm-Leliveld 1957; Shibata 1962; González et al. 1967). Interest in the cytology of *Leucaena* has been driven by breeding and artificial hybridization, and chromosome counts are now available for more than half the species in the genus (Appendix 2). These studies show that both diploids and tetraploids occur and that within each ploidy level there are two chromosome numbers (2n = 2x = 52; 2n = 2x = 56; 2n = 4x = 104; 2n = 4x = 112) (character #29 in species analysis). Recent studies have reported considerable variation within species and even within individuals (e.g., Palomino et al. 1995), and some counts although clearly either diploid or tetraploid are imprecise beyond that and remain to be verified by

TABLE 2. Seedling characteristics of species of *Leucaena, Desmanthus,* and *Schleinitzia* (vouchers cited in Appendix 1).

	Cotyledons		Hypocotyl	Epicotyl	1st Leaf		2nd Leaf
Species	Mean Lgth. (mm)	Mean Wdth. (mm)	Mean Length (mm)	Mean Length (mm)	pinnate/ bipinnate	no. pairs leaflets	no. pairs pinnae
L. collinsii subsp. *collinsii*	13.9	11.4	21.7	11.8	pinnate	9–12	1
L. collinsii subsp. *zacapana*	13.2	12.7	27.6	11.7	pinnate	12–17	1–2
L. confertiflora	11.7	9.0	5.7	8.7	pinnate	6–7	1
L. cuspidata	14.2	12.2	0	14.9	pinnate	12–17	1–2
L. diversifolia	11.6	7.6	13.7	6.3	pinnate	6–9	1
L. esculenta	18.1	17.2	20.8	21.2	pinnate	18–26	2–3
L. greggii	14.2	11.8	9.0	12.7	pinnate	7–10	1
L. involucrata	15.2	12.9	9.5	13.2	pinnate	8–9	1
L. lanceolata	13.8	11.4	11.8	18.0	pinnate	3–7	1
L. lempirana	17.0	10.8	17.0	8.7	pinnate	6–12	1
L. leucocephala subsp. *leucocephala*	12.9	10.5	11.2	6.4	pinnate	6–7	1
L. leucocephala subsp. *glabrata*	15.5	11.7	24.2	10.9	pinnate	7–8	1
L. macrophylla subsp. *macrophylla*	16.0	11.5	14.2	17.4	pinnate	3–4	1
L. macrophylla subsp. *istmensis*	12.5	11.0	7.5	12.1	pinnate	4	1
L. magnifica	15.3	12.5	39.3	11.0	pinnate	6–8	1
L. matudae	14.4	15.6	52.6	21.2	pinnate	10–15	1–2
L. multicapitula	12.2	7.2	21.5	5.1	pinnate	3–5	1
L. pallida	12.0	11.0	21.9	14.8	pinnate	12–13	1
L. pulverulenta	10.9	6.4	8.7	7.0	pinnate	9–16	1
L. retusa	13.6	12.7	10.0	12.8	pinnate	3–4	1
L. salvadorensis	16.4	13.4	42.8	11.8	pinnate	9–12	1
L. shannonii	15.6	13.4	18.0	7.8	pinnate	6–8	1
L. trichandra	11.3	8.0	13.0	8.5	pinnate	7–8	1
L. trichodes	14.3	11.1	48.7	15.3	pinnate	2–3	1
Desmanthus fruticosus	9.6	8.7	23.0	0	pinnate	5	1
Schleinitzia novo–guineensis	11.3	6.0	20.3	3.7	pinnate	6	1

examination of more material (e.g., Sorensson 1989). Given the small size of the chromosomes, the tendency for chromosomes to clump, and the difficulties of obtaining good contrast between chromosomes and cytoplasm in *Leucaena* (De Freitas et al. 1991), some of this variation may reflect inaccuracies in counts. In addition, taxonomic confusion means that plants used to derive counts may, in some cases, have been misidentified; I have not been able to see all the voucher material cited by Palomino et al. (1995). Finally, variation could be due to hybridization, particularly given the variation in number of chromosomes reported in F_2, F_3, and F_4 progeny material of some artificial hybrids (e.g., González et al. 1967; De Freitas et al. 1991). Further work is needed to verify extant counts and investigate those species for which no count is available.

Goldblatt (1981) reported a base number of x = 7 and early establishment of x = 14 in the evolution of the Leguminosae. The Mimosoideae are thus fundamentally tetraploid with x = 14. Within the Mimoseae, base numbers x = 14 (8 genera), x = 13 (14 genera), and x = 12 (one genus, *Xylia*) have been reported (Goldblatt 1981). Although a base number of x = 13 or 14 indicate that *Leucaena* species should be considered tetraploids and octoploids, the terms diploid and tetraploid are used because inheritance studies (Pan 1985; Sorensson 1989) indicate that *Leucaena* species may be secondary polyploid derivatives. Polyploidy has been reported for three genera within the Mimoseae, *Leucaena, Schleinitzia,* and *Dichrostachys* (Lewis & Elias 1981; Goldblatt 1981), but chromosome counts are lacking for most species of the genera of the *Leucaena* and *Dichrostachys* groups.

INSECTS

Bruchids. Current information on bruchid-host records for *Leucaena* is summarized in Appendix 3 based on Johnson (1981) (who summarized previous records), additional records from Johnson (1983, 1984, 1989, 1990), and new records presented by Hughes and Johnson (1996).

Of the Bruchidae feeding on seeds of *Leucaena*, the two species of *Stator* are known omnivores that feed on a wide range of Mimosoid legume genera, although they have been recorded from only a few species of *Leucaena* (Johnson 1984). In contrast, the five species of *Acanthoscelides* feed exclusively on *Leucaena* seeds and so far have not been recorded on any other host plant genus (Johnson 1989). Based on morphology, Johnson (1983, 1990) considered these five species of *Acanthoscelides* to be in the Mexicanus species group with *A. boneti, A. macrophthalmus,* and *A. suramerica* closely related to each other. Most species in this group feed on seeds of Mimosoid legumes. That all five are in the same species group could mean that their ancestors exploited *Leucaena* early and that co-speciation occurred between the plants and insects.

Johnson (1981, 1989) showed that there are few examples of one-to-one bruchid-plant specificities, but that most bruchids have few hosts and the seeds of most legume species that are hosts of Bruchidae are fed upon by only one species of bruchid. This is not the case for the Bruchidae from *Leucaena*; the five species of *Acanthoscelides* have been recorded from between two and eighteen *Leucaena* host species, and some *Leucaena* species are food plants for four of the five species of *Acanthoscelides.* Two bruchids, *A. macrophthalmus* and *A. mankinsi,* are notably catholic, feeding on 18 and 15 *Leucaena* species respectively, whereas *A. boneti* and *A. leucaenicola* are both recorded from only eight host species, and *A. suramerica* has been found on only two. This may be due in part to differences in geographic distribution and concurs with the view put forward by Johnson and Slobodchikoff (1979) that bruchid species that feed on more than one species have wider distributions than those that feed on only one host. *Acanthoscelides macrophthalmus* and *A. mankinsi* are both widely distributed species occurring across the range of most, if not all, *Leucaena* species from Texas and northern Mexico south to Nicaragua and Venezuela respectively, whereas *A. boneti* and *A. leucaenicola* are more restricted, occurring from south-central Mexico to Honduras in Central America and sympatrically with only a proportion of *Leucaena* species. *Acanthoscelides suramerica*, although widely distributed in northern South America, and reported from Puerto Rico, overlaps with only one native *Leucaena* species, *L. trichodes*, and the widely cultivated *L. leucocephala*, and is thus only found on these two species. The *Acanthoscelides* species feeding on *Leucaena* hosts are thus generalists. Indeed, *A. macrophthalmus*, out of 340 species in the genus, is, after *A. aureolus*, the species with most recorded host species and a true generalist.

In parts of the south-central Mexican States of Oaxaca and Puebla, four of the five species of *Acanthoscelides* have been found at the same locality, often where several *Leucaena* species are cultivated in close proximity, but sometimes on a single host species and in one case on a single tree. The sympatric occurrence of four *Acanthoscelides* species at some localities in Oaxaca and Puebla is possibly the result of particularly active indigenous domestication of *Leucaena* as minor food plants in these areas (Zárate 1984a; Hughes & Harris 1994, 1998; Casas & Caballero 1996; Hughes 1998).

There is, to date, only one record of *Acanthoscelides* species feeding on seeds of *Leucaena* species outside their native ranges in Latin America, and this following accidental introduction of *A. macrophthalmus* to Australia (Jones 1996). There is clear evidence that several *Acanthoscelides* species have transferred to new *Leucaena* hosts following their transportation and cultivation within the region. For example, *A. suramerica* feeds on introduced *L. leucocephala* in northern South America and *A. macrophthalmus* feeds on seeds of *L. trichodes* cultivated in a research trial in Honduras. In addition, deliberate release of *A. macrophthalmus* as a biocontrol agent is under consideration in South Africa (Neser 1994).

Outside Latin America, *Leucaena* seeds may still be heavily attacked by other seed beetles. Records include the square-necked grain beetle *Cathartus quadricollis* (Guerin-Meneville) reported on *L. leucocephala* in the Dominican Republic (Pound & Martínez-Cairo 1983), *Araecerus levipennis* Jordan (Coleoptera: Anthribidae) in Hawaii (Sherman & Tanashiro 1956), *Araecerus fasciculatus* De Geer (Coleoptera: Anthribidae) on *L. leucocephala* in India (Singh et al. 1981), and the Philippines (Braza & Salise 1988).

Psyllids. The dramatic spread of the psyllid, *Heteropsylla cubana*, from Central America through the Pacific, Asia, and East Africa as a pest of the pantropically cultivated *L. leucocephala* is well documented by Muddiman et al. (1992) and prompted fresh taxonomic investigation of *Heteropsylla*. Although some specificities were detected at generic level the host preferences of psyllids at species level are blurred. *Heteropsylla cubana* has been recorded from *L. leucocephala, L. diversifolia, L. salvadorensis, L. pulverulenta,* and *L. trichodes* (Muddiman et al. 1992). Considerable variation among *Leucaena* species in resistance to attack by *Heteropsylla cubana* has been documented (e.g., Sorensson & Brewbaker 1987), but not all taxa of *Leucaena* presently recognized have been evaluated. Patterns are not complete enough as yet to derive any insights into relationships within *Leucaena* based on psyllid resistance.

HYBRIDIZATION AND CROSSABILITY

Hybridization. Polyploidy (see above), confirmed and unconfirmed reports of natural or spontaneous hybridization (Hughes & Harris 1994, 1998), evidence for cpDNA introgression (Harris et al. 1994a), and high artificial crossability within *Leucaena* (Sorensson & Brewbaker 1994), taken together, indicate that hybridization, or reticulate evolution, has played a significant role in the evolution of the genus. Although most authors suggest that natural hybridization is infrequent in *Leucaena*, precluded by ecological and geographic separation (Sorensson & Brewbaker 1994, Brewbaker & Sorensson 1994), it is apparent that indigenous domestication and use of *Leucaena* species as minor food plants (Standley 1922; Whitaker & Cutler 1966; Smith 1967; Zárate 1984a, b; McVaugh 1987; Casas & Caballero 1996; Hughes 1998) has resulted in artificial sympatry and significant spontaneous hybridization (Hughes 1998). The identities of two putative spontaneous hybrids (*L. leucocephala* × *L. esculenta* and *L. leucocephala* × *L. diversifolia*) have been confirmed beyond doubt using a suite of morphological, geographic, molecular, and other data (Hughes & Harris 1994, 1998). A further seven unconfirmed putative hybrids have been postulated (Sorensson & Brewbaker 1994; Hughes 1998), although neither their hybridity nor identities are certain.

Although there is ample data to show that, in general, allopolyploidy is much more common than autopolyploidy (Soltis & Soltis 1993), evidence about the origins of the four known tetraploid species in *Leucaena* remains inconclusive. Pan (1985, 1988) suggested that *L. diversifolia* was a possible autotetraploid derived from *L. trichandra*, but this has been refuted by the cpDNA data that do not show these as sister taxa (Harris et al. 1994a). Hybrid (amphidiploid) origins have been proposed for three of the four known tetraploid species, *L. pallida* (Pan 1985), *L. leucocephala,* and *L. diversifolia* (Harris et al. 1994a). The origin of the poorly known tetraploid, *L. confertiflora*, remains unknown.

Further evidence for hybridization within *Leucaena* comes from the cpDNA analysis of Harris et al. (1994a), which showed that two accessions (*Hughes 924* and *Hughes 1317*) did not group according to their gross morphology. Re-analysis of the cpDNA data including only the diploid taxa and with all accessions as terminal taxa revealed three further examples of incongruence suggestive of cytoplasmic introgression (Harris, unpubl. data). One of these accessions (*Hughes 239*), which has the morphology of *L. shannonii* and grouped with other *L. shannonii* in the analysis of isoenzymes, was placed quite separate from the remaining five accessions of *L. shannonii* in the cpDNA analysis.

Evidence from any one of these three sources would be sufficient to suggest that hybridization may have been important in *Leucaena*. Taken together there is overwhelming evidence that hybridization, recent and possibly ancient, has been a significant process in the evolution of *Leucaena*.

Crossability. Artificial crossability studies undertaken in Hawaii (Sorensson 1993; Sorensson & Brewbaker 1994) indicate that there are few genetic barriers to crossing amongst the 15 species of *Leucaena* included in that study, with 77% of 118 possible two-way combinations and 61% of 232 one-way combinations producing viable seed. Although Sorensson (1993) attempted to use degree of crossability to estimate closeness of relationships amongst species of *Leucaena*, Rosen (1979) considered the ability to form hybrids a shared primitive (plesiomorphic) feature between two taxa and the evolution of reproductive barriers to be a derived or apomorphic state in one or the other taxon. In other words "reproductive compatibility is a primitive attribute for the members of a lineage and has, therefore, no power to specify relationships within a genealogical framework" (Rosen 1979: 277). Crossability data treated in this way can thus only be compared with hypotheses of relationships derived from other data (e.g., as discussed in studies of *Glycine* by Doyle et al., 1990).

ANALYSIS OF SISTER GROUP RELATIONSHIPS IN THE INFORMAL DICHROSTACHYS AND LEUCAENA GROUPS

INTRODUCTION

Within the Mimoseae, Lewis and Elias (1981: 157) suggested that *Leucaena* and *Schleinitzia*, as the only members of their informal *Leucaena* group, are sister groups; however, a number of more recent studies question this. The *Leucaena* group was distinguished by Lewis and Elias (1981) by the presence of flowers in heads, persistent spathulate or peltate floral bracts, and an involucel on the peduncle. Within the *Leucaena* group, they separated *Schleinitzia* from *Leucaena* by the presence of anther glands, unusual pod dehiscence (opening only along the margins), and often winged pods. The presence of neuter flowers with showy staminodia provided a putative synapomorphy for a monophyletic *Dichrostachys* group comprising *Dichrostachys*, *Desmanthus*, *Neptunia,* and *Gagnebina*, and distinguished the *Dichrostachys* group from the *Leucaena* group. Since Lewis and Elias's (1981) study, three new genera that have affinities to the genera of the *Leucaena* and/or *Dichrostachys* groups have been described. First, Hernández and Guinet (1990) established the monotypic genus *Calliandropsis* to account for the unusual morphological features of *Desmanthus nervosus*, a move supported in subsequent cladistic analyses of *Desmanthus* (Luckow 1993) and the *Dichrostachys* group (Luckow 1995). In her analysis of the genera of the *Dichrostachys* group, Luckow (1995) showed that *Dichrostachys* is polyphyletic and proposed the segregation of a subset of the Madagascan species with capitate inflorescences, lacking sterile flowers, and having elastically dehiscent pods into a new genus designated as the "*Dichrostachys humbertii* clade." This work was anticipated by Villiers (1994), who established the new genus *Alantsilodendron* for these species. Finally, another new genus, the Hawaiian *Kanaloa*, with possible affinities to genera of the *Leucaena* and *Dichrostachys* groups, was described by Lorence and Wood (1994). They showed that *Kanaloa* shares certain morphological features with members of both the *Leucaena* and *Dichrostachys* groups, but that its unique combination of characters precluded placement in any known genus. *Kanaloa* remains poorly known; only two plants have been collected and hermaphrodite flowers are unknown. That neither Hernández and Guinet (1990), nor Villiers (1994), nor Lorence and Wood (1994) were able to place any of their new genera *Calliandropsis, Alantsilodendron,* and *Kanaloa* firmly within either of the informal groups of Lewis and Elias (1981) is indicative of the confusion over the higher level taxonomic boundaries and relationships amongst the genera of the *Leucaena* and *Dichrostachys* groups. Furthermore, the putative synapomorphy supporting the *Dichrostachys* group varies within that group. Several species of *Desmanthus*, *Calliandropsis,* and *Alantsilodendron* lack neuter flowers with showy staminodia (Luckow 1995). Similarly, the characters supporting the *Leucaena* group (flowers aggregated into in heads, spathulate or peltate floral bracts, and an involucel on the peduncle) are present in some members of the *Dichrostachys* group. *Desmanthus, Calliandropsis,* and *Alantsilodendron* have capitate inflorescences; *Desmanthus* and *Neptunia* have peltate floral bracts; an involucel is present on the peduncle of some species of *Desmanthus*.

Since the treatment of Lewis and Elias (1981), the relationships of the genera of the *Dichrostachys* group have been analyzed in detail (Luckow 1993, 1995), and a preliminary analysis including one species each of *Leucaena* and *Schleinitzia* and a selection of genera from the *Dichrostachys* group has been carried out (Luckow 1997). In her monograph of *Desmanthus*, Luckow (1993) pointed out the close palynological and morphological similarity of *Desmanthus balsensis* J. L. Contr. to *Schleinitzia*. *Schleinitzia* differs from *Desmanthus* in lacking sterile flowers and having partially dehiscent pods. Luckow (1993) speculated that the absence of sterile flowers in *Leucaena* and *Schleinitzia* may be secondarily derived, and that the *Leucaena* and *Dichrostachys* groups should be treated as one, concluding that "the relationships between the *Dichrostachys* and *Leucaena* groups should be reevaluated" (Luckow 1993: 16). Harris et al. (1994a) included *Desmanthus fruticosus* and *Schleinitzia novoguineensis* as out-group species in their cladistic analysis of *Leucaena* cpDNA restriction fragment data. In that analysis, *Schleinitzia* was placed as the sister group to *Desmanthus*, a relationship maintained in trees up to 26 steps longer than the minimal tree, providing further evidence that *Schleinitzia* may not be the sister group of *Leucaena*, but may rather be part of the *Dichrostachys* group, or that the *Leucaena* and *Dichrostachys* groups might be better considered as a single group.

Luckow (1997) used a combination of morphological and cpDNA restriction site data to re-examine relationships in the *Dichrostachys* group, and specifically the relationships of *Desmanthus* and *Neptunia*, including one species each of *Leucaena* and *Schleinitzia*. That analysis showed that the *Dichrostachys* group sensu Lewis and Elias (1981) is not monophyletic with *Schleinitzia* placed as sister group to a monophyletic *Desmanthus*, and *Leucaena* as sister group to a combined *Schleinitzia/Desmanthus* clade. This analysis undersampled the variation within *Leucaena* and *Schleinitzia*, employed only a single outgroup, and did not include all the genera of the *Dichrostachys* group. Regardless of these limitations, Luckow suggested recircumscribing the *Leucaena* group to include *Desmanthus, Schleinitzia,* and *Leucaena*, and the *Dichrostachys* group to include *Calliandropsis, Dichrostachys, Gagnebina,* and *Alantsilodendron.*

In order to test the monophyly of *Leucaena* and provide a hypothesis on which to choose an outgroup for a subsequent species-level cladistic analysis of *Leucaena*, an analysis of sister group relations of the genera of the informal *Leucaena* and *Dichrostachys* groups is undertaken here. Data on numbers of species and geographic distribution of these genera are presented in Table 3.

METHODS

The analysis carried out here builds directly on and utilizes the data matrix of Luckow (1995) for the genera of the *Dichrostachys* group, which included 24 characters. Changes to that data matrix include the addition of data for *Leucaena, Schleinitzia, Kanaloa,* and *Xylia*, omission of two characters (extent of arm extension of the pleurogram and staminode color), and addition of nine characters. Four of these (leaflet shape, presence or absence of an involucel, anthers glabrous or hairy, and fruit winged or not) were added to account for additional variation observed in the genera *Leucaena, Schleinitzia, Xylia,* and *Kanaloa*. Three of the characters are the result of different approaches to partitioning and coding characters. First, the protrusion of the connective of the anther is here treated as two characters (presence/absence and type of presence) as opposed to a single multistate character. Similarly, pod valve morphology and dehiscence, which was treated by Luckow (1995) as a single multistate character, is here divided into three independent characters (pod valves woody/coriaceous; dehiscence type; and mode of twisting of valves after dehiscence). Number of stamens was dismissed by Luckow (1995), because her earlier analysis of *Desmanthus* had shown that the state of five stamens was derived within *Desmanthus*. Because number of stamens varies elsewhere in the *Dichrostachys* group I have

TABLE 3. Genera of the informal *Leucaena* and *Dichrostachys* groups.

Informal Group (Lewis & Elias 1981)	Genus	Authority	Number of Species and Distribution
Dichrostachys Group	*Desmanthus*	Willdenow (1806)	ca. 24 spp. New World, USA to Argentina (Luckow 1993)
	Dichrostachys	Wight & Arnott (1834)	ca. 12 spp. Madagascar, NE Africa; 1 sp. pantropical; 1 sp. Australia
	Gagnebina	Necker (1790)	4–5 spp. Madagascar, Mascarene and Comoros Islands
	Neptunia	Loureiro (1790)	11 spp. pantropical, mainly tropical America and Australia
Leucaena Group	*Leucaena*	Bentham (1842)	22 spp. New World from Texas to Peru
	Schleinitzia	Warburg ex Nevling & Niezgoda (1891)	3–4 spp. W Pacific basin (New Guinea, Melanesia, Micronesia, and Polynesia)
Named since Lewis and Elias (1981)	*Calliandropsis*	segregated from *Desmanthus* by Hernández and Guinet (1990)	monotypic, endemic to central Mexico
	Alantsilodendron	segregated from *Dichrostachys* by Villiers (1994)	8 spp. endemic to Madagascar
	Kanaloa	Lorence and Wood (1994)	monotypic, endemic to Kaho'olawe Island, Hawaii

included it. Finally, stipule shape and shape of floral bracts were included as putatively independent characters in contrast to Luckow (1993, 1995), who hypothesized stipules and floral bracts to be homologous.

Morphological data were partitioned into 22 bistate and 9 multistate morphological characters:

1. Habit: 0 = woody; 1 = herbaceous.
2. Spines: 0 = absent; 1 = present.
3. Terminal shoots: 0 = terete; 1 = angled with corky ridges.
4. Brachyblasts: 0 = present; 1 = absent.
5. Stipule shape: 0 = lanceolate fleshy; 1 = linear (with very narrow membranous wings); 2 = ovate (with broader wings); 3 = filiform (lacking membranous wings).
6. Stipule union: 0 = not united; 1 = united at base.
7. Leaflet shape: 0 = oblong, narrow-oblong or lorate, strongly asymmetric; 1 = ovate, elliptic, lanceolate, symmetric or weakly asymmetric.
8. Extrafloral nectaries: 0 = short- or long-stipitate, cylindrical, erect, peglike, cup-shaped; 1 = sessile concave, crateriform or patelliform, the orifice as broad or broader than the base; 2 = sessile, convex, conical, truncate conical or verruciform, the orifice smaller than the base; 3 = club-shaped.

9. Involucel: 0 = absent; 1 = present.
10. Inflorescence: 0 = spike; 1 = compressed spike; 2 = capitulum.
11. Flower types in inflorescence: 0 = staminodial flowers present; 1 = staminodial flowers absent.
12. Floral bracts: 0 = peltate; 1 = sessile, carinate; 2 = clavate or spathulate.
13. Petal union: 0 = free at the base; 1 = basally connate.
14. Petals: 0 = one-veined; 1 = striate (with 3–6 raised veins).
15. Stigma: 0 = porate; 1 = tubular (= narrow-funnelform); 2 = funnel-shaped (= broad-funnelform).
16. Ovary indumentum: 0 = glabrous; 1 = hairy.
17. Ovary: 0 = sessile or subsessile; 1 = stipitate.
18. Number of stamens: 0 = ten; 1 = five.
19. Anther shape: 0 = ovate, dorsifixed; 1 = linear-elongate, basifixed.
20. Anthers: 0 = glabrous; 1 = hairy.
21. Protrusion of the connective of the anther: 0 = absent; 1 = present.
22. Protrusion of the connective of the anther: 0 = apiculate; 1 = stipitate; ? = absent.
23. Pollen apertures: 0 = simple porate; 1 = colporate.
24. Pollen unit: 0 = polyads; 1 = monads.
25. Polyads: 0 = calymmate polyads; 1 = acalymmate tetrads; 2 = acalymmate monads; ? = monads.
26. Pollen exine: 0 = reticulate; 1 = verrucate, scabrate, fossulate, coarsely foveolate; 2 = striate; 3 = psilate, punctate (smooth); 4 = rugulate.
27. Wing on fruit: 0 = absent; 1 = present.
28. Pod valves: 0 = woody; 1 = coriaceous or chartaceous.
29. Fruit endocarp: 0 = forming a partition between seeds; 1 = not forming a partition between seeds.
30. Pod dehiscence: 0 = indehiscent; 1 = dehiscent along one suture (pod valves eventually splitting along both sutures); 2 = dehiscent along both sutures; 3 = partially dehiscent along both sutures only along the margins, the valves remaining firmly attached.
31. Pod valves: 0 = curling transversely after dehiscence; 1 = twisting spirally after dehiscence; 2 = recurving longitudinally after dehiscence; ? = indehiscent.

Choice of outgroups is limited by lack of a well-resolved corroborated hypothesis of sister group relationships within the Mimoseae as a whole and is based on shared characters that permit primary homology assessment to proceed. *Parkia* (justified by Luckow, 1995, as outgroup in her analysis of the *Dichrostachys* group) and *Xylia* were chosen as outgroups. *Xylia* shares a number of characters with both the *Leucaena* and the *Dichrostachys* groups. Like members of the *Leucaena* group, *Xylia* lacks brachyblasts, has flowers in heads, lacks staminodial flowers at the base of the inflorescence, and has anther glands that closely resemble those of *Schleinitzia*. With members of the *Dichrostachys* group, *Xylia* shares pollen in polyads with similar exine ornamentation, absence of an involucel, and similar anther glands. *Xylia* is distinguished from members of the *Dichrostachys* and *Leucaena* groups by its unusual woody dolabriform fruits, free filiform stipules, and clavate floral bracts. Although *Neptunia* and *Kanaloa* have free stipules, they are quite different from those of *Xylia*. These choices are consistent with the broad results found by Chappill (1995) in her preliminary analysis of the Leguminosae as a whole.

Terminal taxa were determined by the distribution of characters used in the analysis. The number of terminal taxa representing *Alantsilodendron* and *Gagnebina* was reduced compared to the analysis by Luckow (1995) to two and three respectively. This reduction was determined by the distribution of characters, but where taxa differed only because of missing data, they were eliminated. This is justified on the basis that in the analysis of Luckow (1995) both genera formed well-supported monophyletic groups.

For *Xylia, Leucaena, Schleinitzia,* and *Kanaloa*, all species except one were examined in the present study and terminal taxa selected to represent the variation in the characters included. For *Xylia*, five taxa [*X. evansii* Hutch., *X. hoffmanii* Drake, *X. torreana, X. xylocarpa* (Roxb.) Taub. var. *xylocarpa,* and *X. xylocarpa* var. *kerrii* (Craib & Hutch.) I. Nielsen] were examined and are here represented by two species. *Xylia schliebenii* Harms was found to be poorly known and was not examined in this study. All four recognized species of *Schleinitzia* were examined; *S. fosbergii* is doubtfully distinct from *S. insularum*, showed no character differences in this study, and was not included in the analysis. The 22 species of *Leucaena* are represented by 8 species, again based on distribution of characters.

The data matrix is presented in Table 4. It contains 0.5% missing values mainly due to the lack of collections of *Kanaloa* with hermaphrodite flowers (Lorence & Wood 1994). Inapplicable data account for a further 3% of the values in the data matrix.

Parsimony analysis was carried using Hennig86 (Farris 1988), using the *mh* bb** command, and PAUP (Swofford 1990) under both closest and random stepwise addition sequence (with 100 replicates) options, combined with tree-bisection and reconnection (TBR) branch swapping. Character optimization and tree printing were carried out using CLADOS (Nixon 1992). Successive approximations weighting was applied to choose amongst equally parsimonious solutions according to the following criteria (Farris 1969; West & Faith 1990; Swofford & Begle 1993): 1) the weighted tree(s) should be amongst the original set of unweighted trees; 2) tree length (when all characters have weight = 1) should be the same as the original trees; 3) stability of the results of successive weighting should be tested using different character reliability measures and according to best, mean, and worst fit across trees. In this analysis, weighting by *rc* and *ci* and by best, worst, and mean fits was implemented using PAUP.

RESULTS

Analysis using PAUP with either the random addition sequence or closest options and TBR resulted in 32 equally parsimonious solutions of length 131 steps with a consistency index of 0.344 and a retention index of 0.730. The *mh* bb** option on Hennig86 produced 28 equally parsimonious cladograms, which are a subset of those found using PAUP. The strict consensus tree of the 32 trees from PAUP is shown in Fig. 19 and differs from the strict consensus of the 28 trees from Hennig86 only in the placement of one species within *Schleinitzia*. The combinable components consensus tree was virtually the same as the strict consensus differing only with respect to the monophyly of the outgroup genus *Parkia* and the placement of *Kanaloa*.

Application of successive weighting on the 32 equally parsimonious solutions using *rc* under best fit, scaled between 0 and 1000, resulted in two equally parsimonious cladograms of length when weights equal one of 131 steps, i.e., the same length as the original trees. These two solutions differed only in the placement of one polymorph of *Calliandropsis nervosus* and were the same as two of the original cladograms. One of these two

TABLE 4. Data matrix for generic analysis (missing data indicated by "?", inapplicable data points by "_").

		1		2		3	
	12345	67890	12345	67890	12345	67890	1
Parkia bicolor	00010	00300	02100	11000	0_000	00000	0
Old World *Parkia*	00010	00300	02001	01000	0_000	10010	0
Parkia multijuga	00010	00301	12001	00000	11000	00010	0
Parkia velutina	00010	00301	12001	00000	11000	10112	0
Parkia ulei	00010	00301	12001	00000	11000	00112	0
Parkia platycephala	00010	00301	02001	01000	0_000	10100	0
Xylia torreana	00013	01102	12100	10000	11100	10012	1
Xylia xylocarpa	00013	01202	12001	10000	0_001	10012	1
Alantsilodendron alluaudiana	00002	10102	11111	10000	10001	10?1?	2
Alantsilodendron humbertii	00002	10102	11111	10000	0_001	10112	2
Desmanthus arborescens	00002	10101	01002	00000	0_000	00112	0
Dichrostachys perrieriana	00002	10100	01002	00000	0_000	00112	0
Dichrostachys tenuifolia	00002	10101	01002	10000	0_000	00112	2
Gagnebina bernieriana	00111	10101	01001	11000	0_000	00102	2
Dichrostachys richardiana	00002	10001	01101	11000	0_000	10112	2
Gagnebina pervilleana	00111	10101	01001	11010	10000	11102	2
Gagnebina commersoniana	00111	10101	01001	11010	10000	11100	0
Dichrostachys cinerea	01002	10000	01102	11000	11002	10010	0
Dichrostachys kirkii	01002	10000	01102	11000	11002	10112	0
Calliandropsis nervosus a	00002	10102	11001	10100	0_11_	10112	2
Calliandropsis nervosus b	00002	10102	11001	10100	1011_	10112	2
Calliandropsis nervosus c	00002	10102	11101	10100	0_11_	10112	2
Calliandropsis nervosus d	00002	10102	11101	10100	1011_	10112	2
Neptunia 1	10112	00101	00002	00000	1111_	20111	1
Neptunia 2	10112	00101	00002	00100	0_11_	20111	1
Desmanthus balsensis	00101	100?2	00002	00000	11101	10112	2
Desmanthus fruticosus	00101	10102	00002	00000	0_11_	20112	0
Desmanthus virgatus	00111	10112	00002	00000	0_11_	20112	0
Desmanthus leptolobus	10111	10102	10002	00100	0_11_	20102	0
Leucaena cuspidata	00012	10012	10001	10001	1011_	30111	1
Leucaena diversifolia	00012	10112	10001	10001	0_11_	30112	0
Leucaena esculenta	00112	10112	10001	00001	0_11_	30112	0
Leucaena greggii	00012	10012	10001	10000	0_11_	30102	0
Leucaena macrophylla	00012	11212	10001	00001	10002	30112	0
Leucaena multicapitula	00012	11112	10001	00001	0_101	30112	0
Leucaena pulverulenta	00012	10212	10101	10000	1011_	30112	0
Leucaena retusa	00012	11012	10001	10000	1011_	30102	0
Kanaloa kahoolawensis	00110	01102	1000?	??000	0_11_	401?2	0
Schleinitzia insularum	00011	10112	10002	00000	11101	11113	_
Schleinitzia megaladenia	00011	10112	10002	00000	11001	10113	_
Schleinitzia novoguineensis	00011	10112	10002	00000	11101	40113	_

original cladograms is presented in Fig. 20. Successive weighting using *rc* and mean fit resulted in six equally parsimonious cladograms of length with weights equal one the same as the original solutions at 131 steps. The strict consensus of these six weighted cladograms is the same as one of the original cladograms and is presented in Fig. 21, where it can be seen to differ from the result using best fit of *rc* (Fig. 20).

The most striking result is that there is no support for the *Dichrostachys* and *Leucaena* groups sensu Lewis and Elias (1981), in line with the findings of Luckow (1997). Instead of two groups, three clades are supported in all 32 cladograms (Fig. 19).

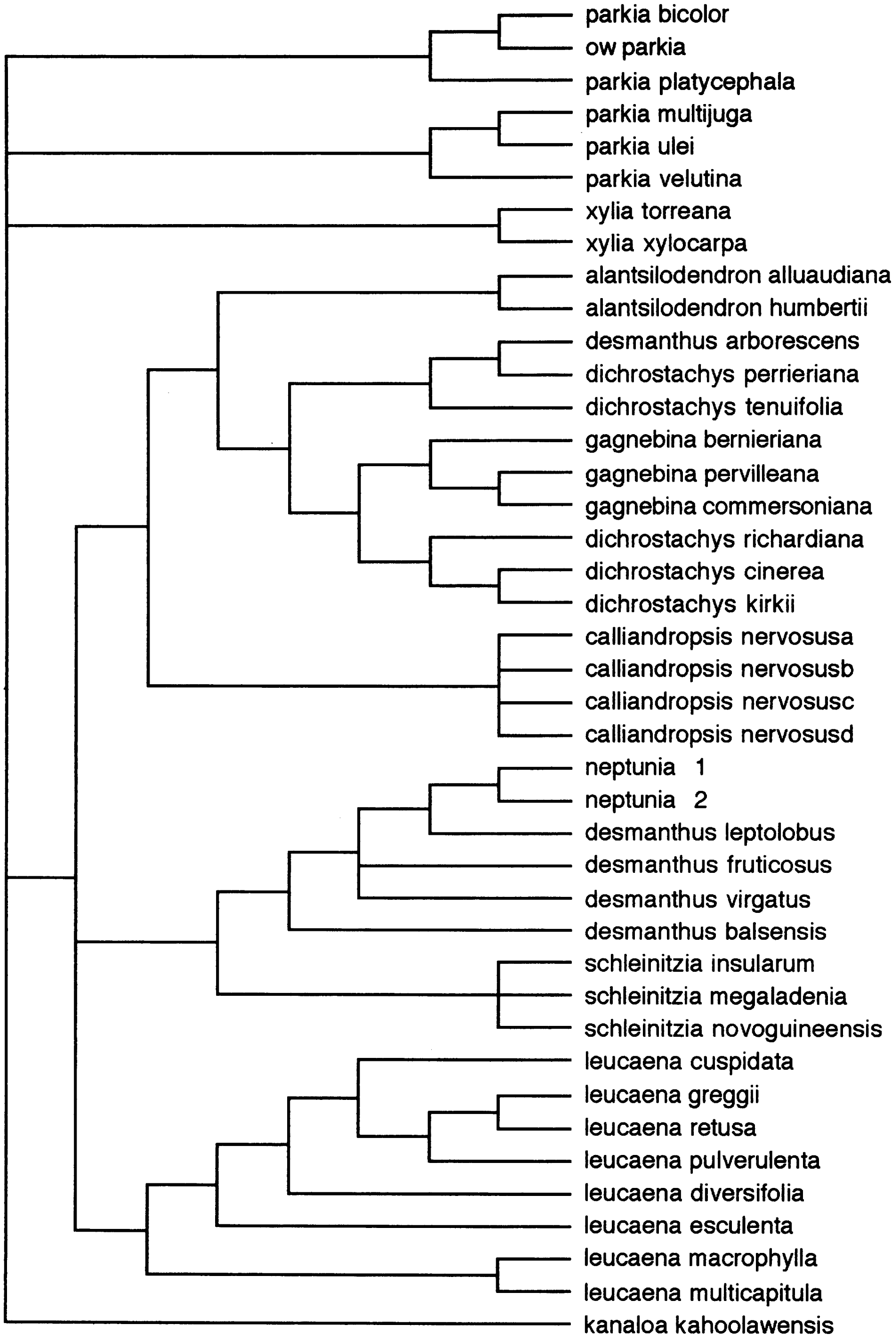


FIG. 19. Strict consensus tree of 32 equally parsimonious cladograms (131 steps, CI = 0.344, RI = 0.730) obtained from preliminary analysis of sister group relationships in the informal *Leucaena* and *Dichrostachys* groups sensu Lewis and Elias (1981).

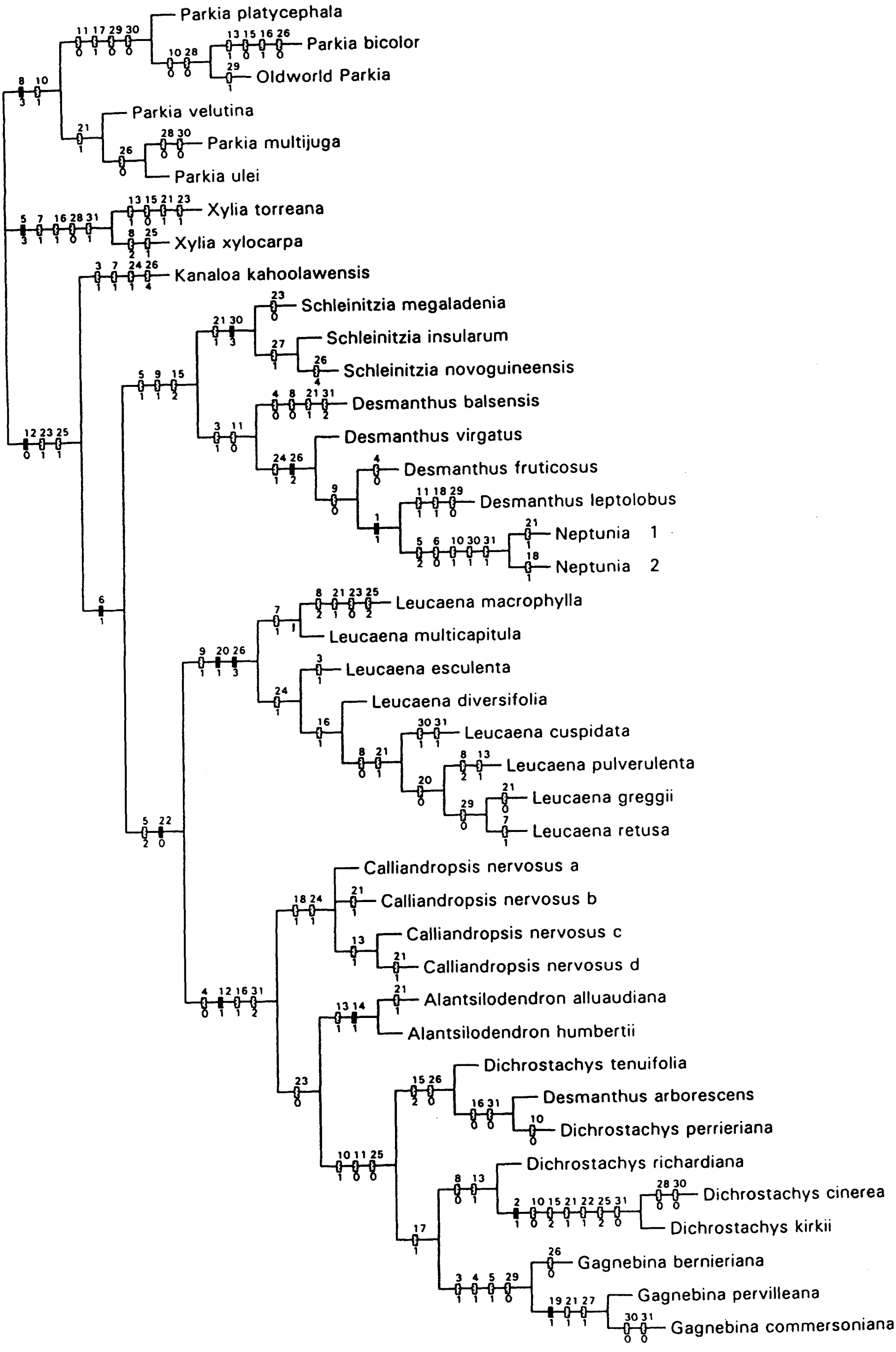


FIG. 20. One of the 32 equally parsimonious trees from the unweighted analysis (131 steps, CI = 0.344, RI = 0.730) chosen based on successive approximations weighting using *rc* with best fit across trees. Black bars represent forward changes, the stippled bars parallelisms and reversals. The number above each bar corresponds to the character, and the number below each bar is the character state at that node.

FIG. 21. One of the 32 equally parsimonious trees from the unweighted analysis (131 steps, CI = 0.344, RI = 0.730) chosen as the same as the strict consensus tree of six trees produced by successive approximations weighting using *rc* with mean fit across trees. Black bars represent forward changes, the stippled bars parallelisms and reversals. The number above each bar corresponds to the character, and the number below each bar is the character state at that node.

The first, here termed the "*Dichrostachys* clade," comprises the genera *Calliandropsis, Alantsilodendron, Gagnebina,* and *Dichrostachys*, as well as the poorly understood *Desmanthus arborescens* Bojer ex Benth. This clade corresponds to the re-defined *Dichrostachys* group of Luckow (1997). The topology within this clade is constant across all cladograms. The second clade, here referred to as the "*Desmanthus/Schleinitzia* clade," comprises the genera *Desmanthus, Schleinitzia,* and *Neptunia*. This clade is supported by a single homoplasious character state, funnel-shaped stigma. *Schleinitzia* is placed as sister group to *Desmanthus* and *Neptunia*, not to *Leucaena,* as suggested by Lewis and Elias (1981). This result confirms the earlier findings of Harris et al. (1994a) and Luckow (1997). The monophyly of *Leucaena* is supported in all cladograms, and *Leucaena* itself forms the third clade distinguished by two synapomorphies, pollen with punctate/psilate tectal ornamentation and hairy anthers, although this second character is reversed within the *Leucaena* clade.

The relationships between the three clades are unresolved in the strict consensus tree. Unlike the analysis of Luckow (1997), which placed *Leucaena* as sister group to *Schleinitzia* and *Desmanthus*, the 32 original solutions differ in the placement of *Leucaena* either as the sister group to the "*Dichrostachys* clade" or to the "*Desmanthus/ Schleinitzia* clade" (Figs. 20, 21). Application of successive weighting to choose among these solutions failed to resolve this ambiguity because of the instability of the results from different weighting options. Swofford and Begle (1993) pointed out that successive weighting should be treated with caution because of the range of options under which it can be applied. The results here bear this out. Weighting using the *rc* under best/worst and mean fit gave different placements of *Leucaena* either as sister group to the "*Dichrostachys* clade" or to the "*Desmanthus/Schleinitzia* clade" (Figs. 20, 21), providing inconclusive evidence about the sister group of *Leucaena*. What is clear is that *Schleinitzia* is not the sister group of *Leucaena,* and that a wider range of genera including *Desmanthus* and *Calliandropsis* need to be considered.

ANALYSIS OF SPECIES RELATIONSHIPS

METHODS

Choice of outgroup. Donoghue and Cantino (1984) maintained that, even in the face of uncertainty over sister group relationships, as is the case for *Leucaena*, outgroup comparison (Watrous & Wheeler 1981; Clark & Curran 1986; Nixon & Carpenter 1993) can still be used in a rigorous and explicit manner by adopting the outgroup substitution approach. In the analysis of species relationships in *Leucaena* three combinations of outgroups were used to take account of the uncertainty encountered in the higher-level analysis. These are: 1) *Calliandropsis nervosus* alone selected as basal within the "*Dichrostachys* clade"; 2) an outgroup comprising *Desmanthus balsensis, D. fruticosus,* and *Schleinitzia novoguineensis* selected as exemplar taxa from the "*Desmanthus/ Schleinitzia* clade" for which adequate data were available; 3) a combination of 1) and 2) including all four taxa.

Species delimitation. My aim in delimiting species within *Leucaena* has been to name, as species, all the diagnosable entities based on available character evidence. Such an objective must emphasize distinctions rather than similarities as pursued by Zárate (1994). The delimitation of *Leucaena* species presented here is based on the phylogenetic species concept (Rosen 1979; Eldredge & Cracraft 1980; Nelson & Platnick 1981; Cracraft 1983; Nixon & Wheeler 1990) using the characters and character states defined below. Species delimitation in *Leucaena* and implications of application of the phylogenetic species concept are discussed in detail by Hughes (1997c). Many of the species recognized by Britton and Rose are treated as conspecific, whereas some of the subspecies recognized by Zárate (1994) qualify as distinct species.

A number of species groups within *Leucaena*, such as the *L. shannonii* alliance, initially presented difficulties in the delimitation of species. As additional characters have been discovered and particularly as field characters have been added, most of these problems have been solved. In these cases molecular evidence, where available, has been found to support delimitation of species or alternatively to delimit subspecies where discrete boundaries cannot be discovered. The cpDNA analysis of Harris et al. (1994a) and the isozyme analyses of Chamberlain et al. (1996) were directly applicable in this way. Additional evidence from isozymes of *L. leucocephala* (Harris et al. 1994b) as well as the analysis of variation in seed storage proteins (Chamberlain 1993) provided some circumstantial evidence.

I have used quantitatively varying leaf and pod traits to recognize a number of subspecies and varieties. Subspecies are used for entities that are distinguished by several quantitative traits and that are clearly correlated with geography (e.g., *L. collinsii*, see Fig. 44). Varieties are used for entities that differ in several quantitative traits but that are not correlated with geography (e.g., *L. lanceolata*, see Fig. 59) or for which the geographic limits of the variants are poorly known. An exception to strict application of the phylogenetic species concept is the retention of *L. trichodes* and *L. macrophylla* as distinct species in the absence of clear character state differences pending more detailed examination of variation within this widely distributed group (see Taxonomy for full discussion).

Cladistics and hybrids. Inclusion of hybrids, which are common in *Leucaena*, in cladistic analyses may be problematic (Bremer & Wanntorp 1979; Wagner 1983; Humphries 1983; Funk 1985; McDade 1990, 1992, 1995; Rieseberg & Ellstrand 1993; Rieseberg 1995). First, hybrid intermediacy will often blur otherwise clear-cut boundaries between character states (Wagner 1983; McDade 1990, 1992), making it difficult to partition characters into states and tending to reduce the number of characters available for analysis. Second, inclusion of hybrids, which express a mixture of parental, intermediate, and extreme character states (McDade 1990, 1995; Rieseberg & Ellstrand 1993; Rieseberg 1995), in cladistic analysis can cause distortion of species relationships among nonhybrid species, an increase in the number of equally parsimonious solutions, and unresolved consensus trees (Humphries 1983; Funk 1985; McDade 1992; Rieseberg & Ellstrand 1993; Rieseberg 1995). In this analysis, known tetraploid and hybrid taxa were removed, as advocated by Wagner (1983) and McDade (1992). Initial analysis was carried out including only the diploid species. The tetraploid species were included one-by-one in subsequent analyses (McDade 1992) to examine their placement and effect on the diploid tree in relation to existing evidence about origins of the tetraploid species. This approach offers an effective compromise and permits the full character set to be maintained in an initial diploid analysis. The tetraploid species when added in later analyses were scored as missing in cases where character state boundaries were blurred.

Characters and character states. There is widespread agreement that cladistic characters should show uniform and consistent occurrence among terminal taxa, i.e., they should not show great environmental plasticity and their pattern of occurrence in a population should suggest that differences among populations are fixed (Sneath & Sokal 1973; Crisp & Weston 1987; Lavin 1987, 1993; Farris 1983; Riggins & Farris 1983; Felsenstein 1982). Characters should also be independent of each other (Farris 1983; Riggins & Farris 1983; Felsenstein 1982; Hawkins et al. 1997), i.e., not be related logically with one another, such that they are different descriptions of a single variable. I have taken care to avoid combining independent characters as character states under one loosely defined character, or conversely, coding of a single character as if it were two or more "independent" characters, either by treating character states of multistate characters as independent binary characters or, in a more extreme form, treating a binary character as two independent characters with states present or absent (termed nominal variables by Pimental and Riggins, 1987). In the absence of any hypotheses of character evolution, multistate characters are treated as unordered, thereby minimizing assumptions built into the analysis (Scotland 1992; Scotland & Williams 1993; Smith 1994). Coding of character states for attributes of a structure that is lacking altogether in some of the taxa under study is also problematic (Riggins & Farris 1983; Pimental & Riggins 1987; Maddison 1993; Smith 1994). Although a two-character conceptualization is the theoretically robust way to code such variation (Hawkins et al. 1997), many authors have advocated use of single multistate characters with absence as one state (Pimental & Riggins 1987; Maddison 1993; Smith 1994) due to the problems caused by inapplicable data for character optimization (see characters #20 and #22).

Character states used in cladistic analysis should be discrete and without overlap. The problem with most continuous characters (measured as non-integers) is that they show variation that is overlapping between species (Stevens 1991) and therefore of doubtful cladistic significance or utility (Cranston & Humphries 1988; Stevens 1984, 1991; Crisp & Weston 1987; Farris 1990; Bateman et al. 1992). One approach to quantitative variation is to rely on simple graphical techniques to define states based on absolute gaps (i.e., with zero overlap in ranges amongst subdivisions) (Almeida & Bisby 1984). For the vast majority of continuous data absolute gaps simply do not exist when the full range of within species variation is sampled (Stevens 1991). This is the case for quantitative leaf variation in *Leucaena* (see above, Figs. 7, 8). Such characters are excluded from the analysis.

In summary, all characters must be subjected to detailed morphological study to establish topographical correspondence under the similarity criterion (sensu De Pinna, 1991; Hawkins et al. 1997). Characters that do not show uniformity and consistency of occurrence (fixed differences) are here avoided. Quantitative characters can be included only where absolute gaps are detected without statistical manipulation of the data. Use of nominal variables is avoided and care taken to ensure independence of characters as far as possible. Multistate characters, rather than division into sets of bistate characters, are used where the similarity test reveals a set of topographically correspondent character states. Multistate characters are treated as unordered. Finally, morphological variation that is nested (physically), although more correctly coded as two independent characters, is coded as single multistate characters because of the problem of impossible character optimizations.

Morphological data were partitioned into 18 bistate and 11 multistate characters:

1. Terminal shoots: 0 = terete; 1 = angled with corky ridges (Fig. 4A). As previously discussed, shoots of *L. pallida* and *L.* ×*mixtec* were found to be slightly angular with incipient, poorly developed corky ridges. This blurring of otherwise distinct

character states due to hybridity was circumvented by omitting these two taxa from the initial analysis of diploid non-hybrid species and coding *L. pallida* as missing for this character when it was included in a later analysis.

2. Bark: 0 = bark with a succession of internal periderms, formation of a thick rhytidome, little intercalary expansion tissue, and vertical fissuring on the surface; 1 = bark with a single superficial periderm formed, little or no rhytidome, abundant formation of intercalary expansion tissue, and an intact epidermis. Although there is marked variation in a number of different features of the internal bark structure (rhytidome, number of periderms, fissuring, intercalary expansion tissue) these appear to be almost perfectly correlated, occurring as complexes of related characters that correspond almost exactly to the two surface pattern types A and B described above (Figs. 2, 3). Given the apparent lack of independence of the individual bark structure features, a single character combining this information was defined that corresponds to the two bark types. Given that scoring of bark characters requires field observation and/or collection of bark samples, variation could not be assessed for any of the outgroup taxa. Intermediate bark type, attributed to hybridity, was observed for *L. pallida* and *L.* ×*mixtec* and treated as for character #1.
3. Brachyblasts: 0 = present; 1 = absent.
4. Stipule shape: 0 = linear (with very narrow membranous wings); 1 = ovate (with broader wings) (Fig. 4B). Luckow (1995) distinguished linear stipules and subulate stipules with an elaborated base as separate character states. I prefer to treat subulate and linear as one character state. The auricle or elaborated base found in some species of *Desmanthus* would be treated as a separate character, if such species of *Desmanthus* were included in the analysis.
5. Leaflet shape: 0 = oblong, narrow-oblong, or lorate, strongly asymmetric; 1 = ovate, elliptic, lanceolate, symmetric or weakly asymmetric (Figs. 5, 6). Blurring of otherwise clear-cut character states due to hybridity (see above) was encountered when scoring *L. leucocephala* for leaflet shape, which was observed to be intermediate between states 0 and 1 (Fig. 5I). When *L. leucocephala* was included in a later analysis this character was scored as missing. Intermediate leaflet shape suggests a hybrid origin for *L. leucocephala* between a species with narrow-oblong leaflets and one with ovate/elliptic leaflets.
6. Leaflet venation: 0 = only primary (mid-rib) visible externally; 1 = secondary and tertiary veins visible externally (Figs. 5, 6).
7. Extrafloral nectaries: 0 = short- or long-stipitate, cylindrical, erect, peg-shaped; 1 = sessile, concave, crateriform or patelliform, the orifice as broad or broader than the base; 2 = sessile, convex, conical, truncate conical or verruciform, the orifice smaller than the base (Fig. 9A–F).
8. Involucel: 0 = absent; 1 = present (Fig. 13B).
9. Nyctinasty: 0 = pinnular rachis shows no nyctinastic movement; 1 = pinnular rachis moves downward and inward to 60–90° (Fig. 10A–C). Luckow (1993) pointed out that the movements of the rachis, pinnae, and leaflets are not independent and cannot be treated unquestioningly as separate characters. However, given that the only variation observed within *Leucaena* is in the movements of the pinnae, this has been used as the character in this analysis, despite some loss of information for the species in other closely related genera, which show variation in movement of the leaf rachis.

10. Flowering shoots: 0 = auxotelic (as defined by Briggs & Johnson, 1979), the shoot continuing to develop beyond the flowering region; 1 = anauxotelic, the shoot ending in an abortive vegetative apex (Figs. 11, 12).
11. Flowering shoots: 0 = unbranched; 1 = once-branched; 2 = twice-branched (Figs. 11, 12).
12. Flower types in inflorescence: 0 = staminodial flowers absent; 1 = staminodial flowers present.
13. Floral bracts: 0 = peltate; 1 = sessile, carinate.
14. Floral bracts: 0 = round; 1 = lanceolate or caudate (Fig. 13A–C).
15. Color of staminal filaments, anthers, and style: 0 = white or pale cream; 1 = bright yellow; 2 = pink-purple (occasionally red).
16. Petal fusion: 0 = basally connate; 1 = partially united along mid-portion of petals, free at base; 2 = free. Given the variation in degree of fusion of petals, character delimitation and coding requires precise description of character states. Luckow (1995) reduced the variation to basally connate or free, thereby ignoring additional information on other forms of connation. Luckow and Hopkins (1995) divided petal fusion into four character states: free, loosely connate, united in the middle, and basally connate, thereby making the distinction between petals free in bud and at anthesis. In this analysis, petal fusion as assessed at anthesis, is divided into three character states. *Calliandropsis nervosus* is reported to be polymorphic for two of the characters used in this analysis. Hernández and Guinet (1990) showed that petal union is highly variable. In some cases petals are free to the base, in others the petals are united to approximately half their length, and variation occurs within populations and even within individual inflorescences. Similarly, anther glands (see below) are very occasionally present (Hernández & Guinet 1990). Although it has not been possible to examine sufficient material during the present study to confirm that all four combinations of these two characters occur, *Calliandropsis nervosus* is here divided into four separate terminal units (as suggested by Nixon and Davis, 1991, more generally for polymorphic taxa) representing the four possible combinations of character states (Table 5).
17. Stigma: 0 = tubular (= narrow-funnelform); 1 = funnel-shaped (= broad-funnelform). The character definition and coding followed Luckow (1995), except that the terms were altered to be more descriptive of the variation encountered.
18. Ovary: 0 = glabrous; 1 = pilose; 2 = short-velutinous (Fig. 13E–F). Luckow (1995) used ovary vestiture as a character in her analysis of the *Dichrostachys* group, defining two states, glabrous and hairy. A third character state, short dense velutinous is added, here treated as a homologous transformation of long-pilose.
19. Anthers: 0 = glabrous; 1 = hairy (Fig. 14A–F).
20. Protrusion of the connective of the anther: 0 = absent; 1 = apiculate, small rounded or cylindrical; 2 = apiculate, dorsi-ventrally flattened, hooded; 3 = stipitate (Fig. 14A–F). A protrusion of the connective on the anther may be present or absent and, if present, either stipitate, apiculate-rounded, or apiculate-flattened. Such variation may be coded either as two independent characters, with the consequent problems of character optimization resulting from scoring taxa lacking protrusions as inapplicable "?," or as a single multistate character with "absence" as one character state. As previously discussed, although the theoretically correct way to partition such variation is as two independent characters (as for characters #21 and #22 in the generic analysis), a single multistate character was used

here to avoid impossible character optimizations (Pimental & Riggins 1987; Platnick et al. 1991; Maddison 1993; Smith 1994) despite loss of primary homology information and the theoretical problems of combining two independent characters (presence/absence of anther protrusion and type of protrusion) into one. For a data matrix with "?" entries attributable to inapplicable data points, such spurious resolutions are not even potentially supported by any conceivable character states that are quite simply "impossible." There are two ways to view such "impossible" optimizations. Either they can be viewed as just that—impossible optimizations, thereby encouraging recasting the character definition as a single multistate character, or such optimizations may be viewed as meaningless, simply because the taxa involved lack the structure for which the character is being optimized.

21. Pollen apertures: 0 = simple porate; 1 = colporate (Fig. 15A–D, F).
22. Pollen unit: 0 = monads; 1 = polyads of acalymmate tetrads; 2 = polyads of acalymmate monads (Fig. 15A–F). Although pollen unit could arguably be treated as two independent characters (polyads present/absent and type of polyad), as pursued in the higher level analysis, I prefer to treat pollen unit as a single character because of the problem of inapplicable data (see above), given that, in this case, independence of characters is not clear-cut.
23. Pollen exine: 0 = verrucate, scabrate, fossulate, coarsely foveolate; 1 = striate, rugulate; 2 = psilate, punctate (smooth) (Fig. 16A–E). Partitioning tectal ornamentation into discrete character states is complicated by a number of difficulties. First, several of the categories commonly used to describe tectal ornamentation represent arbitrary limits imposed on a continuum. For example, it may be difficult to separate punctate or perforate from foveolate, foveolate from fossulate, scabrate from verrucate, or striate from rugulate tectal patterns. Second, variation in tectal ornamentation has been reported within species and even within individuals. For example, Luckow (1993) reports the occurrence of both fossulate and striate pollen within a single individual of *Desmanthus pubescens* B. L. Turner, showing that this is at least partly related to differences between male and hermaphrodite flowers. Third, tectal ornamentation can vary on different parts of the pollen grain, particularly in the case of monad units derived from polyads, where tectal ornamentation varies between proximal and distal faces. For example, in *Schleinitzia novoguineensis*, the tectum is coarsely rugulate on the poles, but fossulate on the equatorial region. These difficulties led Luckow (1995) to code verrucate and foveolate tectal ornamentation as a single character state from which she was able to separate reticulate and striate states. I have added one more character state, "psilate/punctate," to incorporate the variation observed in *Leucaena*. In addition, I group "fossulate, coarsely foveolate, verrucate, scabrate," and "striate, rugulate" as single character states, because they represent arbitrary points along a continuum.
24. Pod valves: 0 = lightly woody or coriaceous; 1 = chartaceous.
25. Endocarp: 0 = forming a partition between seeds; 1 = not forming a partition between seeds.

26–27. Partitioning and coding of pod dehiscence presents a number of problems given the great variation in pod morphology across genera and consequent uncertainty over whether apparent homologies in mode of dehiscence are truly homologous under strict scrutiny of compositional and topographic correspondence. Luckow

(1993) resorted to coding dehiscence as three separate characters using a nominal variables approach, whereas Luckow (1995) included two pod characters within a single multistate character. Here dehiscence is coded as two separate characters, the first describing the mode of dehiscence and the second the mode of twisting of the pod valves after dehiscence. This is not an entirely satisfactory solution, because these two characters are not completely independent. A better approach to primary homology assessment of pod characters would be to examine comparative anatomy of the pod valves in detail. 26. Pod dehiscence: 0 = dehiscent along one suture (pod valves eventually splitting along both sutures); 1 = dehiscent along both sutures; 2 = partially dehiscent along both sutures only along the margins, the valves remaining firmly attached (Figs. 17, 18). 27. Pod valves: 0 = reflexing longitudinally after dehiscence; 1 = curling transversely or spirally after dehiscence; ? = pod valves not separating, dehiscing only along margin (Fig. 18B, E).

28. Seed alignment in pods: 0 = transverse; 1 = oblique or longitudinal. The problem of defining seed shape and alignment as characters is twofold. First, it is unclear whether seed shape and alignment, and pod width and shape represent independent characters or functional complexes of related characters. Second, can they be defined as discrete characters? Variation in mode of seed insertion in the pods is strongly correlated with pod width and linearity and with seed shape. Thus it may be that seed shape and orientation are quite simply adaptable to the constraint of the enveloping pod valves and sometimes distorted thereby. In a broad linear-oblong or oblong fruit, the seeds are ovate, ellipsoid, or sometimes more circular and transversely oriented; in narrow linear pods the seeds are rhomboidal, apparently distorted by mutual pressure, and oblique or longitudinal in orientation. Barneby (1991) interpreted similar variation within *Mimosa* as secondary mechanical adjustments without phylogenetic significance beyond the basic variation in pod morphology. Seed shape in *Leucaena* appears to be perfectly correlated with alignment and was not included as a separate character. The second problem is whether any of these characters are discrete and amenable to anything but arbitrary division into character states. As discussed above, variation in pod shape appears to be continuous. Although seed alignment and shape are similarly quantitative in nature, variation falls into readily recognizable and discrete categories, and seed alignment was therefore included as a character in the analysis.

29. Chromosome number: 0 = 2n = 52; 1 = 2n = 56; ? = tetraploid or missing.

Morphological data were scored from herbarium material at FHO, field observations in natural populations (characters such as bark structure, arrangement of flowering shoots, and flower color), from SEM (pollen and anthers), and from a living collection of seedling material of *Leucaena* species maintained in glasshouses at Oxford. Data for the outgroup taxa (*Calliandropsis, Desmanthus,* and *Schleinitzia*) were derived from herbarium material, limited living material and field observations, and from Luckow (1993) for *Desmanthus*, Nevling and Niezgoda (1978) for *Schleinitzia,* and Hernández and Guinet (1990) for *Calliandropsis*. A few characters had to be coded as missing for some outgroup taxa. The data matrix is presented in Table 5; it contains 5% missing values mainly due to lack of chromosome data (character #29).

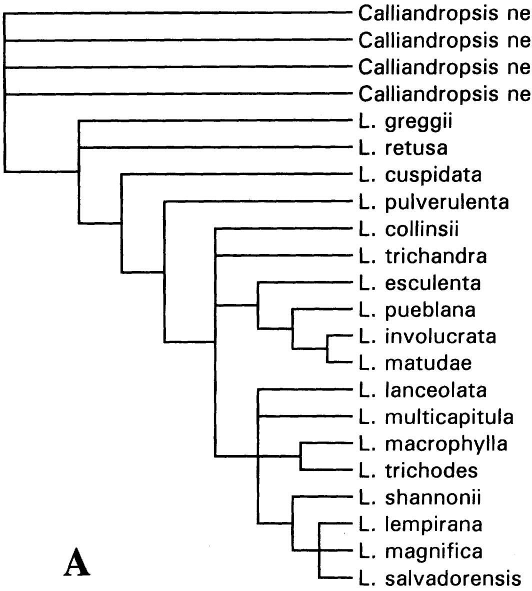
TABLE 5. Data matrix for species analysis (missing values indicated by "?").

		1		2		
	12345	67890	12345	67890	12345	6789
Calliandropsis nervosus 1	0?010	010?0	00112	00100	10010	101?
Calliandropsis nervosus 2	0?010	010?0	00112	00101	10010	101?
Calliandropsis nervosus 3	0?010	010?0	00112	20100	10010	101?
Calliandropsis nervosus 4	0?010	010?0	00112	20101	10010	101?
Schleinitzia novoguineensis	0?100	01101	10012	21003	11100	2?0?
Desmanthus balsensis	1?000	00?00	01010	21003	11010	101?
Desmanthus fruticosus	1?000	01000	01010	21000	10111	111?
Leucaena collinsii	00110	02110	00000	20010	10211	1100
Leucaena cuspidata	0?110	00100	00000	10111	10210	010?
Leucaena esculenta	11110	01111	10000	20010	10211	1100
Leucaena greggii	00110	00100	00011	20100	10210	1111
Leucaena involucrata	01110	00111	00000	20010	10200	111?
Leucaena lanceolata	00111	12111	00000	20010	10211	1100
Leucaena lempirana	00110	12111	00000	10210	10211	110?
Leucaena macrophylla	00111	12111	10000	20012	02211	1100
Leucaena magnifica	00110	12111	10000	10210	10211	110?
Leucaena matudae	01110	00101	00000	20010	10200	111?
Leucaena multicapitula	00111	11111	20000	20010	11211	110?
Leucaena pueblana	11110	01111	00000	20010	10200	110?
Leucaena pulverulenta	00110	02110	00010	00101	10211	1101
Leucaena retusa	0?111	10100	00011	20101	10210	1111
Leucaena salvadorensis	00110	12110	00000	10210	10211	110?
Leucaena shannonii	00110	12111	00000	20210	10211	1100
Leucaena trichandra	00110	01110	00002	20010	10211	1100
Leucaena trichodes	00111	12111	00000	20012	02211	1100
Leucaena confertiflora	00110	10100	00002	20010	10211	010?
Leucaena diversifolia	00110	01110	00002	10110	10211	110?
Leucaena leucocephala	0011?	11110	00000	10110	10211	110?
Leucaena pallida	1?110	0111?	00002	20?10	10200	11??

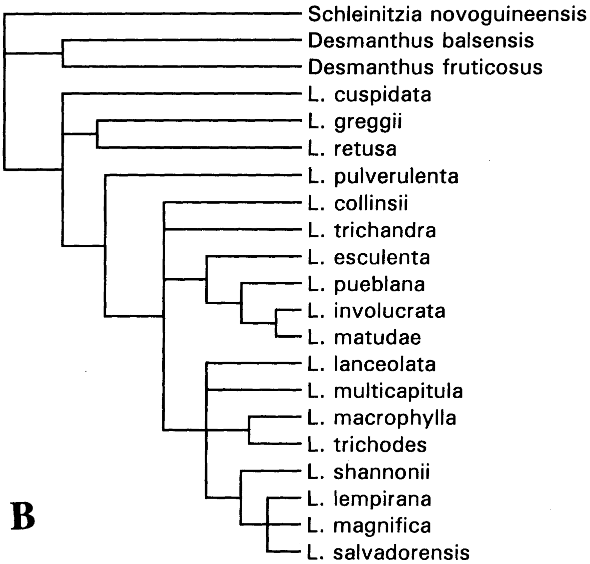
Parsimony analysis. Parsimony analysis was carried out using Hennig86 (Farris 1988) employing the heuristic search procedure *mh** *bb** (multiple hennig, which generates several starting trees, and branch breaker, which performs branch swapping on the starting trees) and using NONA (Goloboff 1994), which facilitates random taxon entry. Where multiple equally parsimonious trees were found, a strict consensus tree was generated using the nelsen option of Hennig86. Character optimization and tree printing were carried out using CLADOS (Nixon 1992).

RESULTS

Diploid species. The strict consensus trees generated by heuristic searches of the morphological data set using three alternative combinations of outgroup taxa, and including only the diploid species of *Leucaena*, are shown in Figs. 22A, 22B, and 26. All three outgroup combinations support the monophyly of *Leucaena*. Within *Leucaena*, the hypothesized topologies with different outgroups are virtually identical (Figs. 22A, 22B, 26) apart from minor differences in the relationships amongst the three basal species *L. retusa,*



A



B

FIG. 22. Strict consensus trees of equally parsimonious trees generated from analyses of morphological data using different outgroups. A. Strict consensus of 118 trees using *Calliandropsis nervosus* as outgroup. B. Strict consensus of 44 equally parsimonious trees generated using *Schleinitzia/Desmanthus* as outgroup.

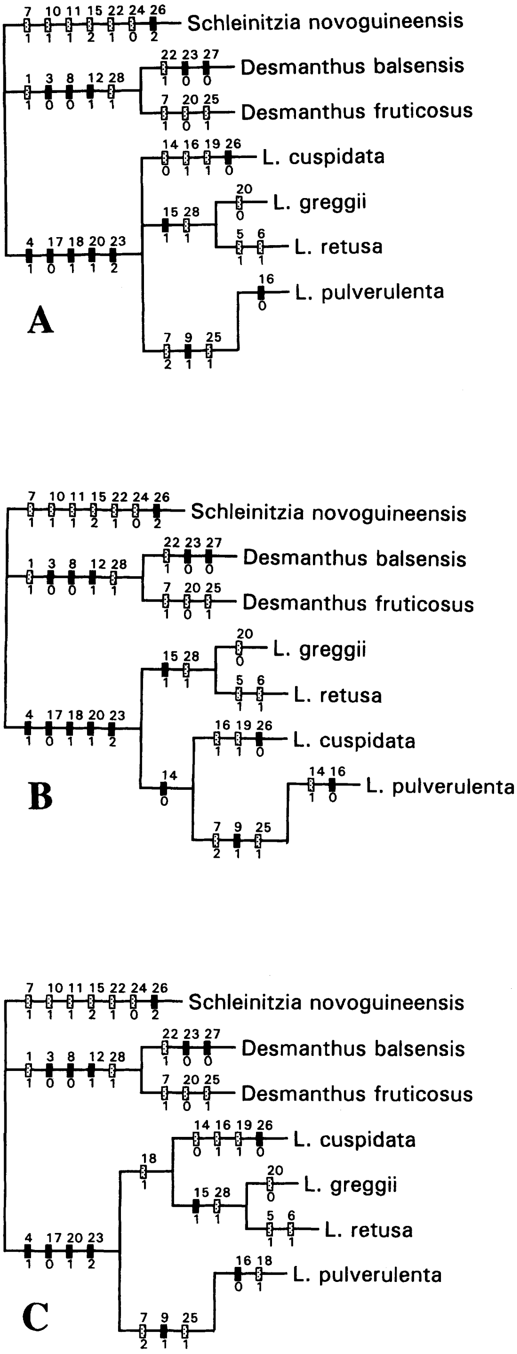


FIG. 23. Three equally parsimonious topologies showing alternative placements of *L. greggii, L. retusa, L. cuspidata,* and *L. pulverulenta* using *Schleinitzia/Desmanthus* as outgroup. Black bars represent forward changes, stippled bars parallelisms or reversals. The number above the bar corresponds to the character number, and the number below is the character state at that node.

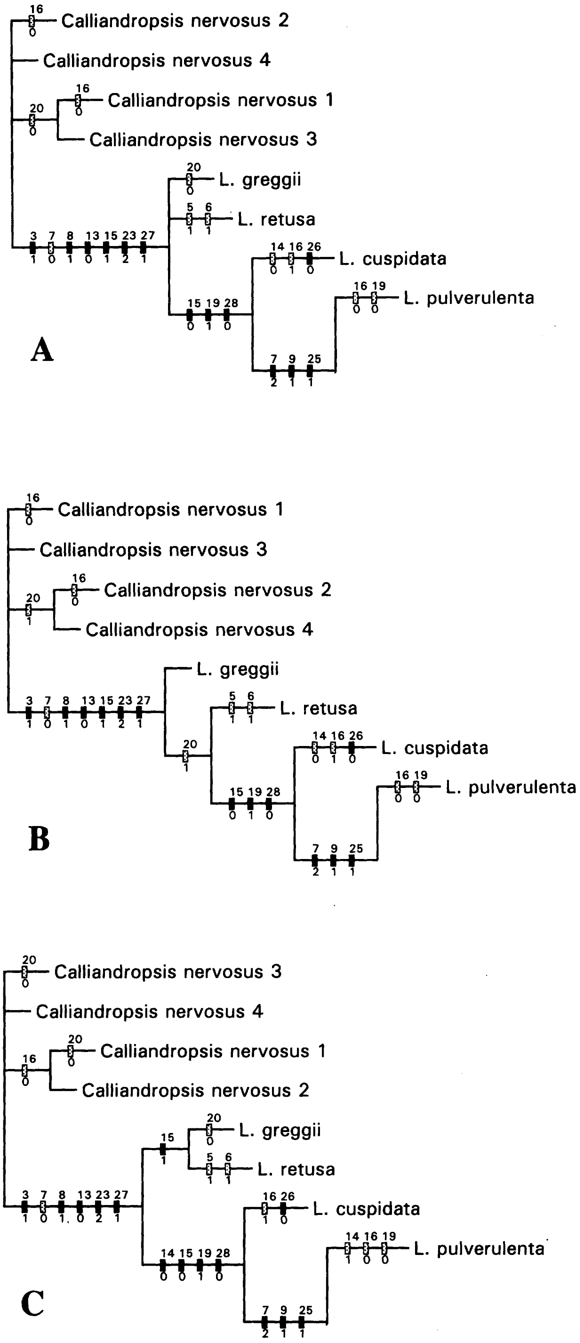


FIG. 24. Three equally parsimonious topologies showing alternative placements of *L. greggii, L. retusa, L. cuspidata*, and *L. pulverulenta* using *Calliandropsis nervosus* as outgroup. Black bars represent forward changes, stippled bars parallelisms or reversals. The number above the bar corresponds to the character number, and the number below is the character state at that node.

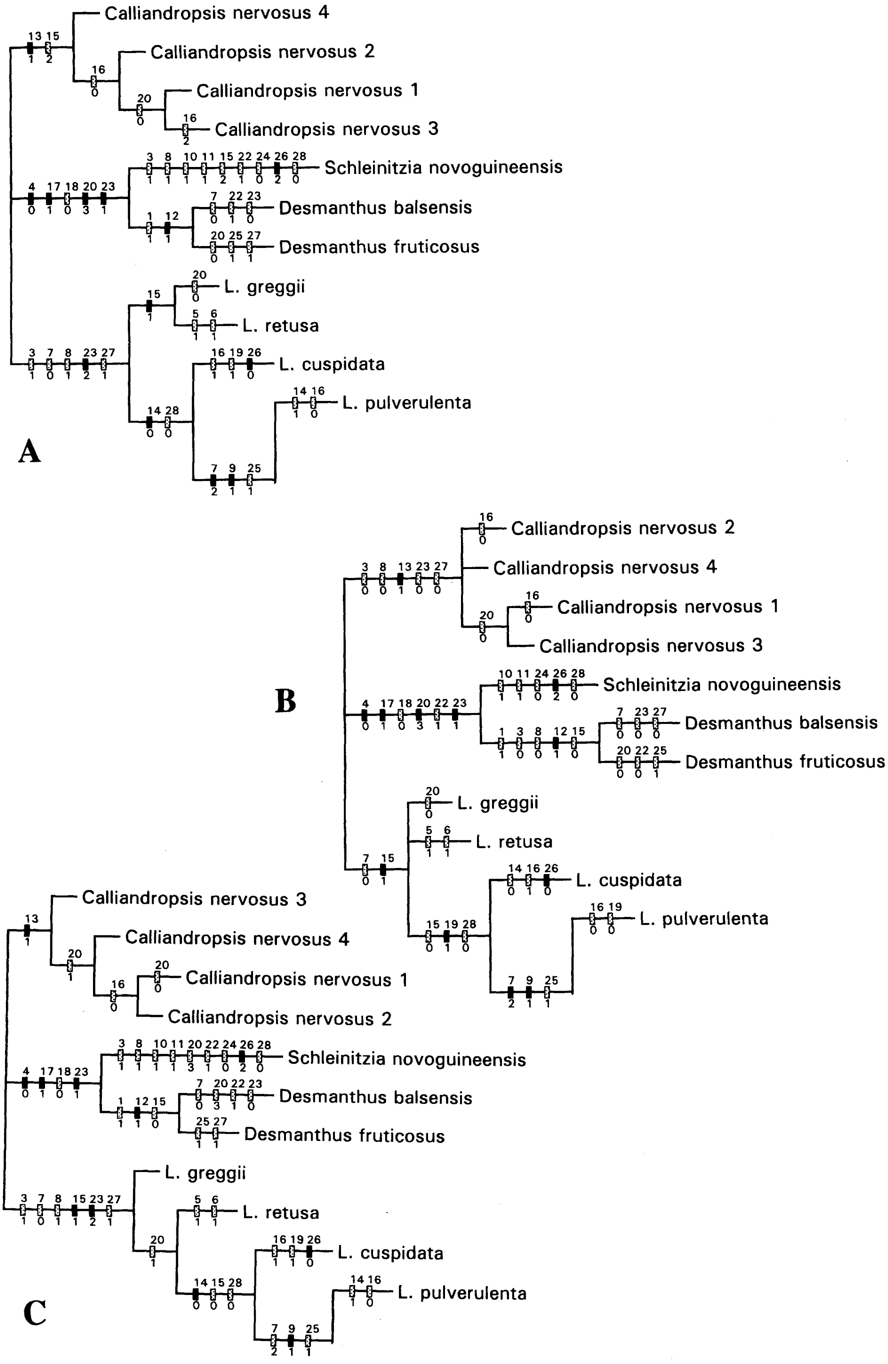


FIG. 25. Three equally parsimonious topologies showing alternative placements of *L. greggii, L. retusa, L. cuspidata,* and *L. pulverulenta* using both *Schleinitzia/Desmanthus* and *Calliandropsis* as outgroups. Black bars represent forward changes, stippled bars parallelisms or reversals. The number above the bar corresponds to the character number, and the number below is the character state at that node.

L. greggii, and *L. cuspidata*; however, character support for *Leucaena* is strikingly influenced by which outgroups are used (Figs. 23–25). Inclusion of more outgroup taxa (within limits, Donoghue & Cantino, 1984) increases global parsimony and will lead to greater stability in future studies (Nixon & Carpenter 1993; De Pinna 1994; Weston 1994). The analysis with *Desmanthus, Schleinitzia,* and *Calliandropsis* as outgroups is more globally parsimonious and is preferred. In that analysis, psilate or punctate tectal ornamentation of pollen is the only non-homoplasious character state supporting *Leucaena.*

A heuristic search of the morphological data set using both outgroups and including only the diploid species using Hennig86, CLADOS, and NONA, following procedures of Coddington and Scharff (1994) to eliminate trees with zero-length branches, resulted in 50 equally parsimonious cladograms of length 75 steps with a consistency index of 0.52 and a retention index of 0.75. Three groups within *Leucaena* are maintained in all 50 solutions (Fig. 26). The *L. esculenta* clade comprising *L. esculenta, L. pueblana, L. involucrata,* and *L. matudae* is supported by one non-homoplasious character state, thick corky metallic-grey bark. A larger group, the *L. lanceolata* clade is supported by two homoplasious character states, ovate, elliptic leaflets and visible secondary leaflet venation, with a smaller *L. shannonii* clade nested within it supported by one non-homoplasious character state, short velutinous ovary pubescence. *Leucaena macrophylla* and *L. trichodes* form a group within the *L. lanceolata* clade supported by three non-homoplasious character states, hooded apicula on the anthers, porate pollen apertures, and polyads composed of acalymmate monads. A representative cladogram showing character support is shown in Fig. 27.

The strict consensus (Fig. 26) shows consistent resolution except in three areas. First, three equally parsimonious hypotheses of relationships amongst the basal species *L. retusa, L. greggii,* and *L. cuspidata* were found (Fig. 25A–C). *Leucaena retusa* and *L. greggii* are placed either together as a group that is sister group to the remainder of the genus, or separately at the base of the cladogram, or unresolved at the base. Second, the relationships of *L. trichandra* are ambiguous, again with three equally parsimonious placements. *Leucaena trichandra* is placed either unresolved with *L. collinsii*, resolved as sister to *L. collinsii,* or as sister to the "*L. esculenta* clade." Finally, the relationships between *L. multicapitula, L. lanceolata, L. macrophylla,* and *L. trichodes* are equivocal with three equally parsimonious arrangements. *Leucaena trichodes* and *L. macrophylla* always form a group supported by three homologies, but the relationships of *L. multicapitula* and *L. lanceolata* with respect to this group are ambiguous. Four equally parsimonious topologies showing alternative placements of *L. trichandra* and arrangements of *L. lanceolata, L. multicapitula, L. trichodes,* and *L. macrophylla* are shown in Fig. 28.

Tetraploid species. Results of adding the four known tetraploid species, *L. pallida, L. leucocephala, L. diversifolia,* and *L. confertiflora,* individually, one-by-one into the diploid morphological data set are presented in terms of numbers of equally parsimonious trees in Table 6 and as strict consensus trees in Figs. 29A, B, 30A, B. In all cases the number of equally parsimonious trees increased compared to the diploid analysis. For *L. pallida* and *L. diversifolia* this resulted in no loss of resolution in the strict consensus. *Leucaena pallida* was placed within the "*L. esculenta* clade" unresolved with respect to *L. pueblana*, the two forming the sister group to *L. involucrata* and *L. matudae*. *Leucaena diversifolia* was placed as sister species to *L. trichandra*. In contrast, inclusion of either *L. leucocephala* or *L. confertiflora* resulted in substantial loss of resolution in the strict consensus trees (Figs. 29B, 30B). This was particularly striking in the case of *L. confertiflora*,

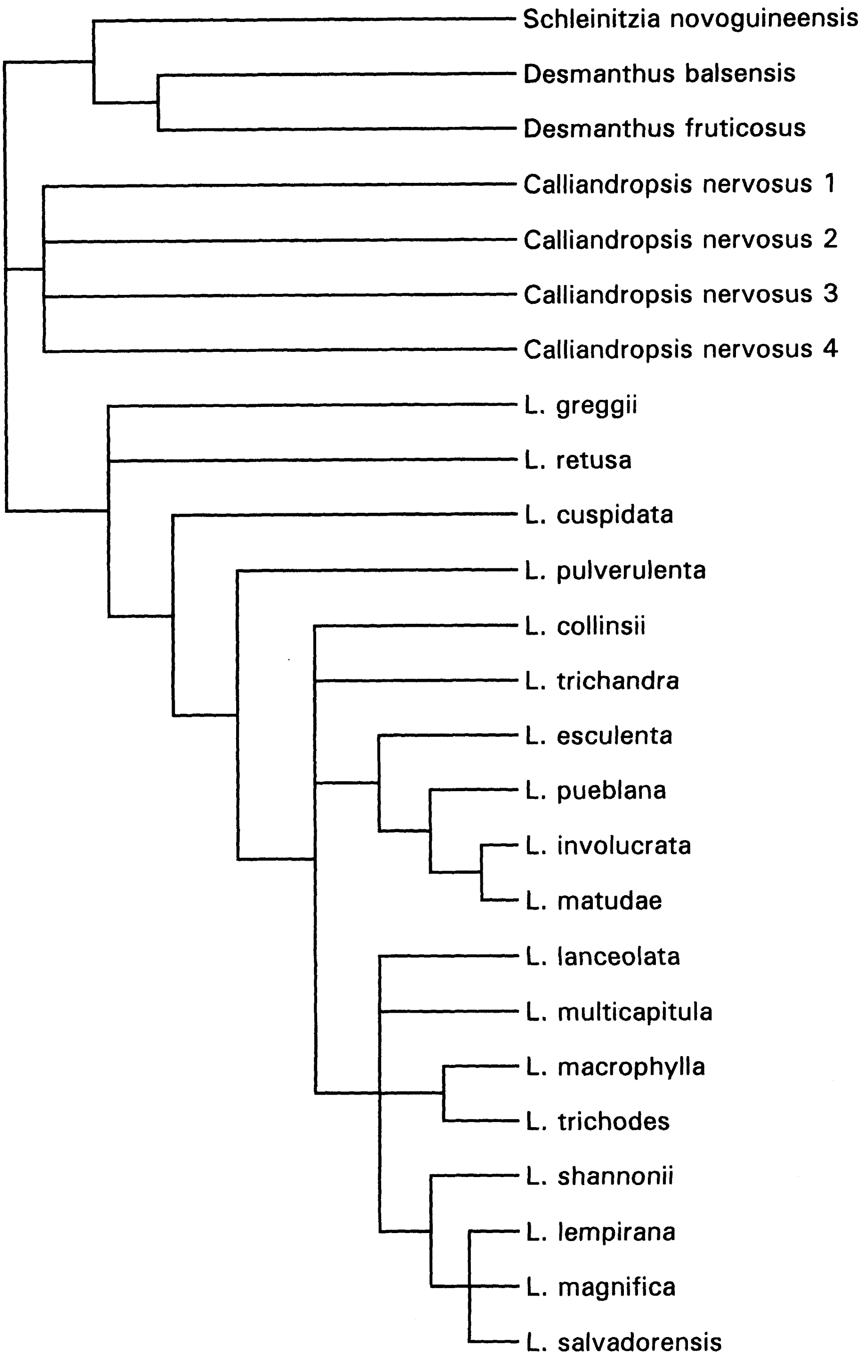


FIG. 26. Strict consensus tree of 50 equally parsimonious trees generated from a heuristic search of the morphological data set of diploid species of *Leucaena*, including both *Calliandropsis* and *Schleinitzia/Desmanthus* as outgroups.

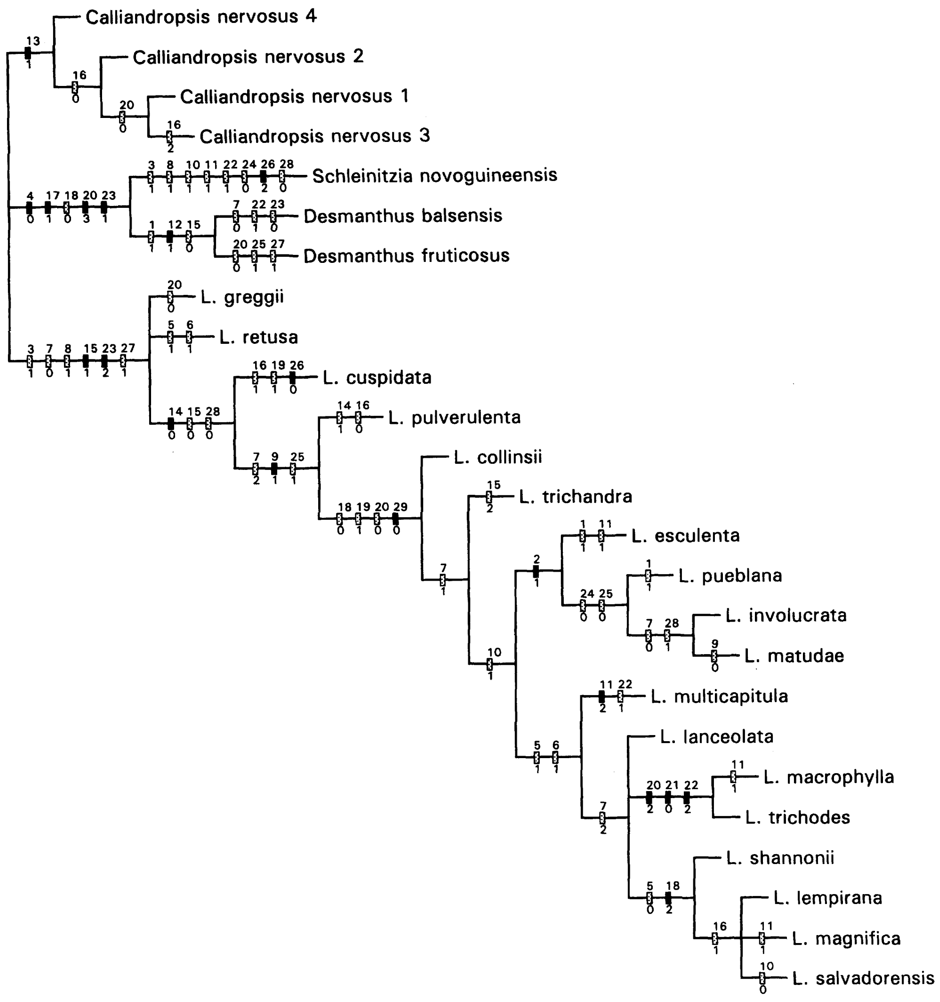


FIG. 27. One of the 50 equally parsimonious trees generated by heuristic search of the morphological data set for diploid species of *Leucaena*. Black bars represent forward changes, stippled bars parallelisms or reversals. The number above the bar corresponds to the character number, and the number below is the character state at that node.

which caused major loss of resolution at the base of the cladogram and collapse of a monophyletic *Leucaena*. When *L. leucocephala* was included, resolution within the "*L. lanceolata* clade" was completely lost (Fig. 29B).

CHLOROPLAST DNA

Harris et al. (1994a) produced the first explicitly phylogenetic analysis of *Leucaena* based on chloroplast DNA restriction fragment variation. Their cpDNA study analyzed 102 accessions, including all the known species and subspecies and multiple accessions of the majority of taxa. A total of 342 cladistically informative restriction fragments were used in parsimony analysis. This resulted in 411 equally parsimonious trees of 1058 steps

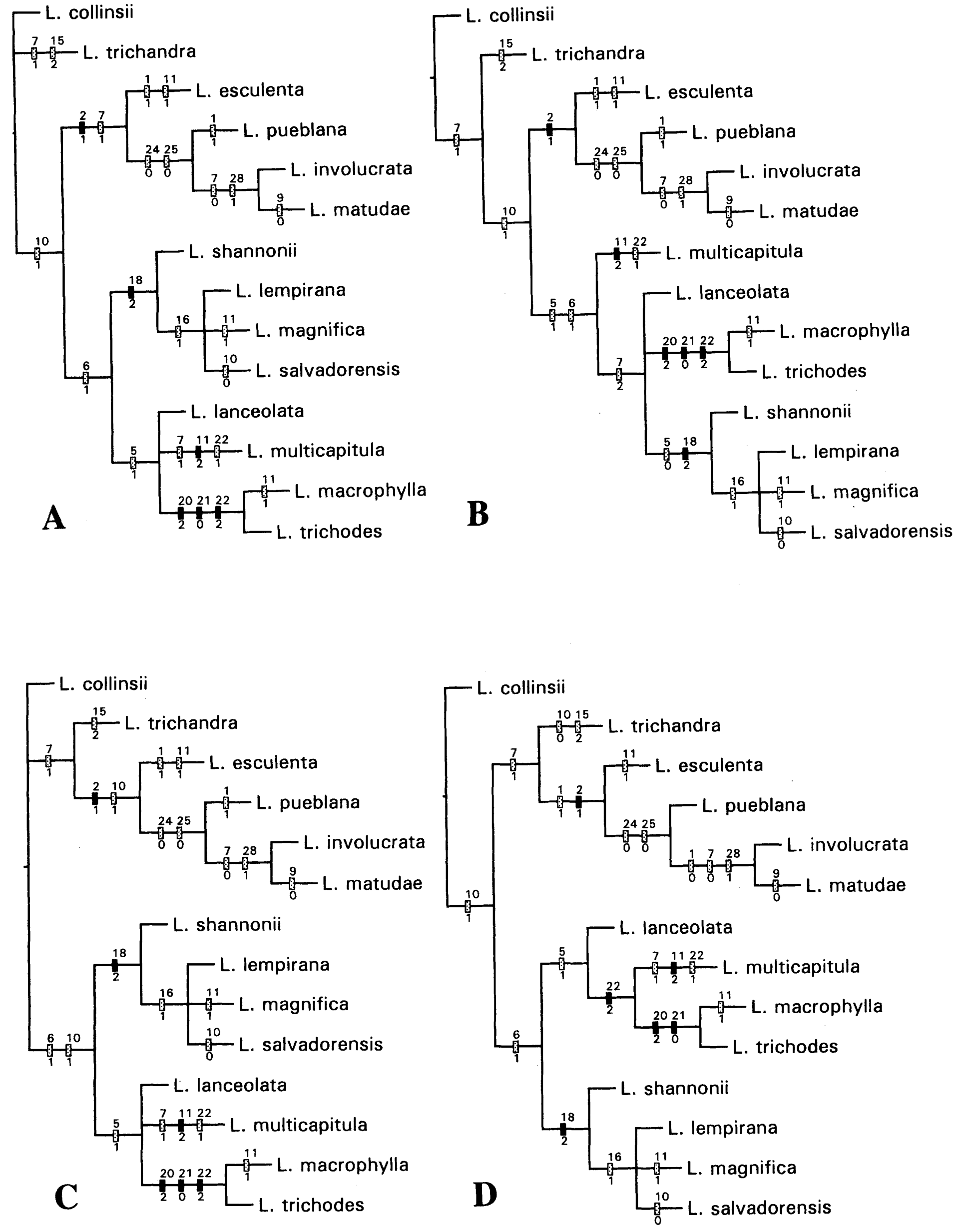


FIG. 28. Four equally parsimonious topologies showing alternative placements of *L. trichandra* and arrangements of *L. lanceolata, L. multicapitula, L. trichodes,* and *L. macrophylla.* Black bars represent forward changes, stippled bars parallelisms or reversals. The number above the bar corresponds to the character number, and the number below is the character state at that node.

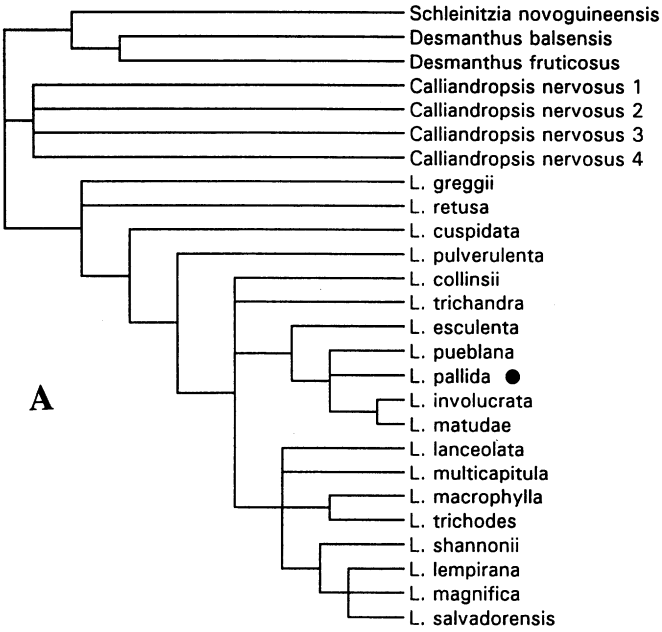
TABLE 6. Analyses of tetraploid species of *Leucaena.*

Tetraploid species	Number of equally parsimonious trees	Tree length	Consistency Index	Retention Index
L. pallida	276	76	0.51	0.75
L. leucocephala	366	78	0.50	0.74
L. diversifolia	140	78	0.50	0.74
L. confertiflora	526	80	0.48	0.73

and a consistency index of 0.428. The strict consensus tree from Harris et al. (1994a) is shown in Fig. 31 with names updated according to the taxonomy used here. The cpDNA data resolve three major clades within *Leucaena* (Fig. 31).

There are several limitations associated with interpretation of the cpDNA analysis of Harris et al. (1994a) as a scheme of species relationships for *Leucaena.* First, fragment occurrence (presence/absence) was used rather than mapping of restriction sites. It was adopted because of the complexity of the fragment banding patterns. Harris et al. (1994a) argued that an artificial increase in homoplasy resulting from non-independence of fragments would be unlikely to obscure phylogenetic relationships. This may be true for the three major clades, which were strongly supported, being maintained in suboptimal trees up to 32 steps longer than the shortest trees (Harris et al. 1994a). However, such data are less useful for elucidating the more complex relationships within clades, which were weakly supported. The inclusion of a distantly related outgroup taxon, *Microlobius foetidus,* in the cpDNA study was in large part the cause of complex banding patterns. New work (Luckow 1997) and the generic analysis (Figs. 19–21) indicate that *Calliandropsis* as well as *Desmanthus* and *Schleinitzia* would be more suitable outgroups for a cpDNA restriction site study of *Leucaena.*

Second, Palmer (1985), Rieseberg and Soltis (1991), Doyle (1992), Avise (1994), and Rieseberg (1995) pointed out that apart from ambiguity or incongruence due to sampling error, incongruence between gene/genome trees and species trees can result from introgression, lineage sorting, and gene duplication. Harris (unpubl.) showed that cpDNA is maternally inherited in *Leucaena.* Thus the cpDNA analysis of *Leucaena* (Harris et al. 1994a), a group where there is significant evidence of hybridization and introgression, should be viewed not strictly as an estimate of a species tree for *Leucaena.* Faulty phylogenetic conclusions from cpDNA restriction site data can be avoided by employing adequate population sampling within species in order to detect cytoplasmic geneflow (Lavin et al. 1991; Rieseberg & Soltis 1991; Rieseberg 1995). In fact, the clonal transmission of the cpDNA molecule, although potentially limiting its usefulness in estimating species trees, makes it particularly useful for detecting cases of reticulation (Avise 1994) and for determining the maternal parent of putative hybrids and amphidiploid species (see, e.g., Harris et al. 1994a; Hughes & Harris 1994, 1998). Multiple accessions of the majority of *Leucaena* species were included in the cpDNA analysis of Harris et al. (1994a). In their original analysis two accessions that failed to group with the remaining accessions of that species were detected, indicating probable cytoplasmic geneflow in *Leucaena.* However, Harris et al. (1994a) simplified their data matrix by coding variation between



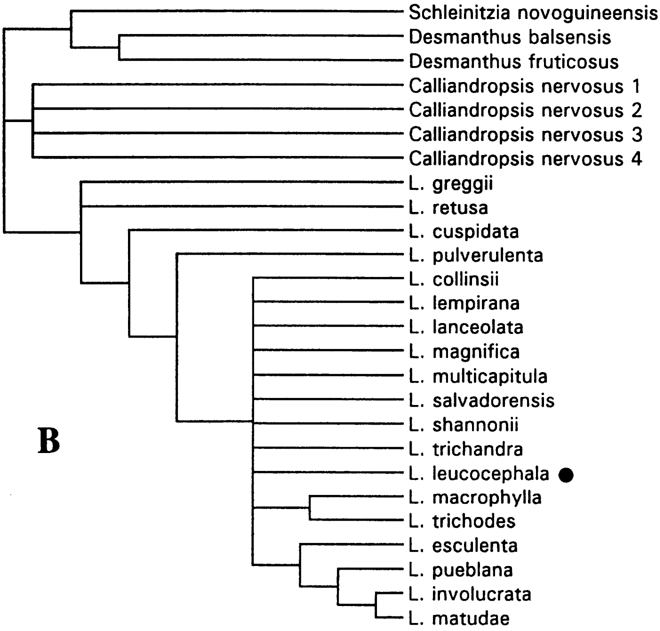


FIG. 29. Strict consensus trees. A. Strict consensus tree of 276 equally parsimonious trees generated by a heuristic search of the morphology data set of diploid species of *Leucaena* with inclusion of the tetraploid species *L. pallida*. B. Strict consensus tree of 366 equally parsimonious trees following inclusion of the tetraploid species *L. leucocephala*. Tetraploids are indicated by black dots.

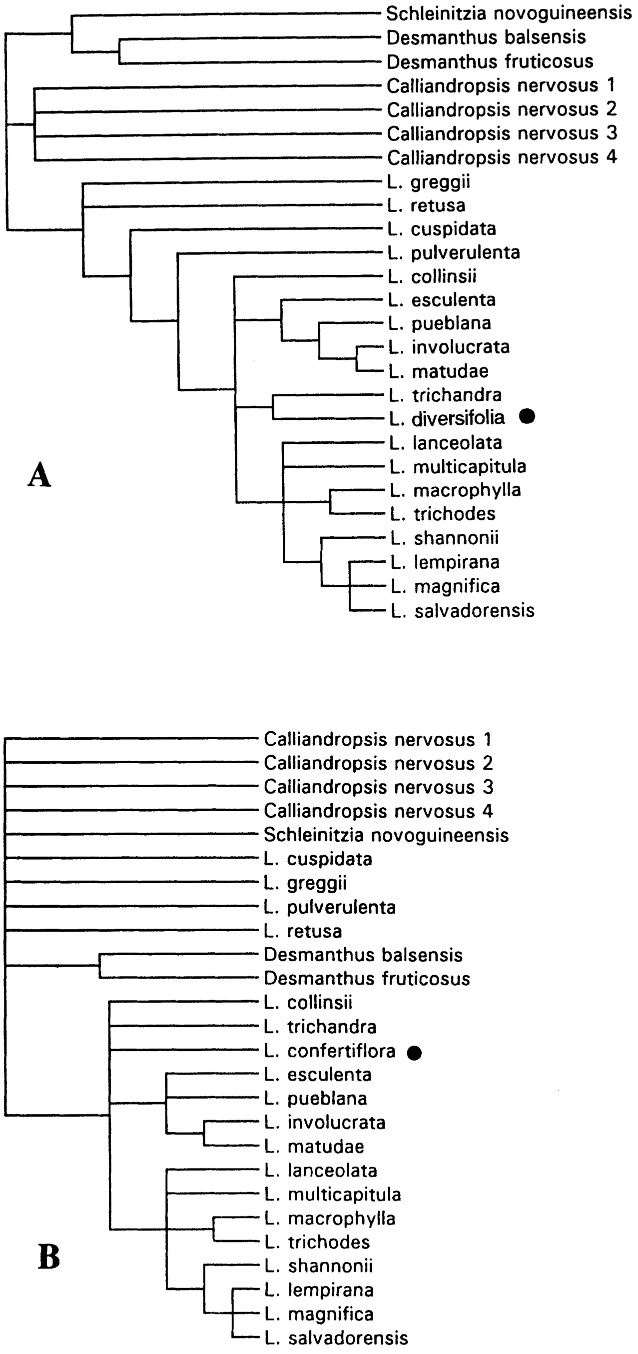


FIG. 30. Strict consensus trees. A. Strict consensus tree of 140 equally parsimonious trees generated by a heuristic search of the morphological data set of diploid species of *Leucaena* with inclusion of the tetraploid species *L. diversifolia*. B. Strict consensus tree of 526 equally parsimonious trees following inclusion of the tetraploid species *L. confertiflora*. Tetraploids are indicated by black dots.

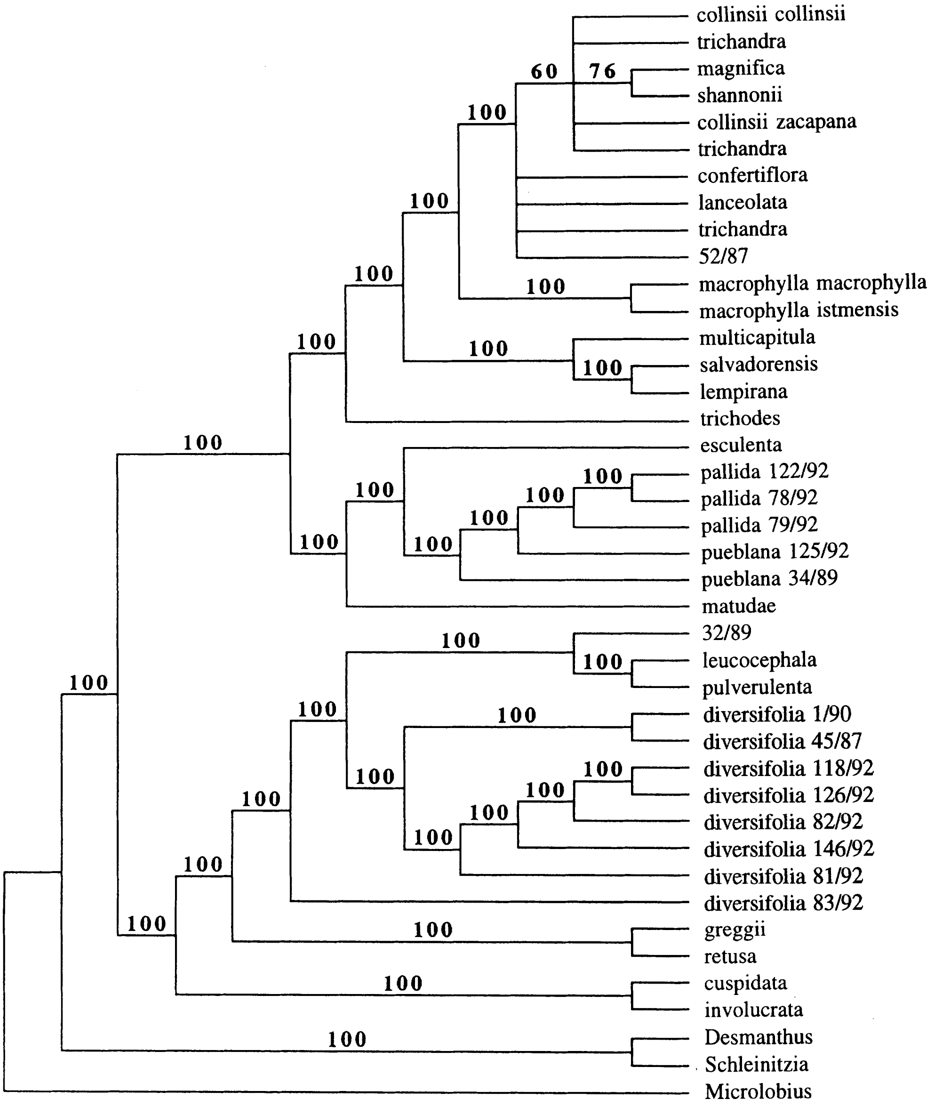


FIG. 31. Strict consensus tree of 411 equally parsimonious trees generated by a heuristic search of the complete *Leucaena* cpDNA fragment data set. Figures in brackets refer to the number of times a particular clade was obtained in 100 bootstrap replicates from Harris et al. (1994a), with names updated to current taxonomy. Variation within species was coded as polymorphic characters, except for *L. pallida, L. diversifolia,* and *L. trichandra.* Accession numbers are Oxford Forestry Institute seedlot identity numbers (see Hughes, 1998).

accessions within a taxon as polymorphic character states for all taxa, except *L. diversifolia, L. pallida,* and *L. pueblana,* to facilitate computation. This means that the opportunity to detect cases of reticulation was largely forfeited.

Introgression in *Leucaena* confounds the cpDNA data set, and integration with the morphological data set is therefore not undertaken; however, morphological analysis allows a test of the three major cpDNA groups.

DISCUSSION

The analysis of morphology shows that under all outgroup combinations tested *Leucaena* represents a well-defined monophyletic group within the Mimoseae. Different outgroup combinations cause only minor changes to hypothesized relationships within *Leucaena*; however, important differences in character support for a monophyletic *Leucaena* using alternative outgroup combinations were found. This is a consequence of the lack of decisiveness encountered in the analysis of sister group relationships amongst the closely related genera of the *Leucaena* and *Dichrostachys* groups and the ambiguity surrounding the sister group of *Leucaena* in that analysis. One non-homoplasious character state, pollen with psilate or punctate tectal ornamentation, and five homoplasious character states, pod valves curling transversely or twisting spirally after dehiscence (also found within *Desmanthus),* yellow flowers, presence of an involucel (also found in *Schleinitzia* and some species of *Desmanthus*), stipitate extrafloral nectaries, and absence of brachyblasts are the character states supporting a monophyletic *Leucaena* (Fig. 27).

There is broad agreement between the schemes of species relationships derived from morphology and cpDNA (Figs. 26, 31) although there are also some differences. The two schemes of relationships hypothesize a number of the same groups with broadly similar relationships. The *L. esculenta* alliance (see below) is common to both. *Leucaena retusa, L. greggii, L. cuspidata,* and *L. pulverulenta* comprise a paraphyletic assemblage at the base of the morphological cladogram and a basal group on the cpDNA cladogram. A large derived group comprising the remaining diploid species is also common to both analyses.

It is immediately apparent that the hypothesized schemes of relationships (Figs. 26, 27, 31) show no support for the two sections, *Macrophylla* and *Leucaena*, formally designated by Zárate (1994). Zárate (1994) placed *L. shannonii* in section *Macrophylla* because of its sessile dome-shaped petiolar nectary, despite its intermediate leaflets. When the additional variation in leaf characters within the *L. shannonii* alliance (comprising *L. lempirana, L. magnifica, L. salvadorensis,* and *L. shannonii*), which was treated as one variable species by Zárate, is observed, leaflet size and the related number of pinnae show continuous variation across the genus as a whole with no gaps to allow other than arbitrary division (see Figs. 7, 8). Second, while morphology of the extrafloral petiolar nectary is highly variable within *Leucaena*, the observed variation is not satisfactorily partitioned into two character states, as pursued by Zárate (1994), but in fact represents three distinct types (see Fig. 9). Thus although Zárate (1984a, 1994) had suggested that *Leucaena* comprised two sections, based on leaflet size and shape of nectary, his partitioning of these characters oversimplified the observed variation. Furthermore, although variation in leaflet size is visually striking, it may be evolutionarily insignificant (Sorensson 1990). Analysis of a wider set of character evidence reveals a more complex scheme of species relationships.

Leucaena retusa and *L. greggii*, although unresolved in the morphological consensus tree, are closely related and together with *L. pulverulenta* and *L. cuspidata* comprise a paraphyletic assemblage that is sister group to the remainder of the genus. These four species are all northerly, cool-climate, subtropical or subtemperate species distributed in northeastern Mexico and Texas with unusual phenology (flowering February–May, fruiting September–November). The placement of *L. retusa*, along with *L. greggii* and *L. pulverulenta* as sister group to the rest of the genus is supported by a number of character states. These are the only species in the genus that have glabrous anthers and a chromosome number of $2n = 56$. Hairy anthers, which are unique to *Leucaena* within the

Mimosoideae as a whole, characterize the remaining species of *Leucaena,* and this is certainly the derived condition.

Neither the higher-level analysis of the *Leucaena* and *Dichrostachys* groups nor that of species relationships within *Leucaena* support the view of Britton and Rose (1928) that *L. retusa* and *L. greggii* should be placed in segregate monotypic genera. That these two species are placed within *Leucaena* reflects my view that all species represent a geographically distinct and well-defined monophyletic lineage within the Mimoseae. Nevertheless, a close relationship between *L. retusa* and *L. greggii* is strongly supported by cpDNA restriction fragment data (Harris et al. 1994a) and morphology. Both species share a number of unusual character states, including erect peg-shaped extrafloral nectaries, one at the base of each pair of pinnae, yellow flowers, long-caudate or lanceolate floral bracts that are exserted in bud (Fig. 13C), very long peduncles compared to all other species, thick woody pods, and rhomboidal seeds, which are longitudinally or obliquely aligned. The distinction of *L. retusa* and *L. greggii* from all other *Leucaena* species is further revealed by their northerly distribution (Fig. 33), an ability to withstand low winter temperatures (Glumac et al. 1987), and very slow growth in field trials compared to other species (Stewart et al. 1991). These two species, and *L. retusa* in particular, are thus highly distinctive within the genus.

The *L. esculenta* alliance comprises *L. esculenta, L. involucrata, L. pueblana,* and *L. matudae* along with the tetraploid species *L. pallida.* Diverse evidence from morphology and cpDNA data suggests that the *L. esculenta* alliance is a monophyletic lineage of closely related species characterized by thick, corky, metallic-grey bark. This group was also revealed in the cpDNA consensus tree (Fig. 31), although in that analysis the position of *L. involucrata* (designated by Harris et al., 1994a, as "*Leucaena sp nov 2*") was unstable. Apart from *L. involucrata*, which is restricted to the mountains of Sonora and Sinaloa in northwestern Mexico, this group is distributed in the dry, inland valleys and mountains of central Mexico.

The large and only partially resolved *L. lanceolata* alliance includes all the species with large ovate or elliptic leaflets except *L. retusa*, along with the group, here designated as the *L. shannonii* alliance, nested within it. Many authors have considered the four large-leaflet species *L. lanceolata, L. macrophylla, L. multicapitula,* and *L. trichodes* to be closely related, although some have doubted the distinction of *L. multicapitula* from *L. trichodes* (Zárate 1984a, 1994; Brewbaker 1987a). A close relationship between these four species is supported here. Within this group, *L. macrophylla* and *L. trichodes* are sister species, supported by three unique phylogenetic markers: porate pollen apertures, pollen in polyads composed of acalymmate monads, and anthers with a hooded apiculum. The distinction of *L. multicapitula* is not in doubt. It has polyads composed of calymmated tetrads, which are unique within *Leucaena*, tricolporate monad units, and lacks anther glands (Hughes 1997a). However, its exact relationships are uncertain and differ in the morphological and cpDNA analyses. As with other genera of the Mimoseae, characters of the pollen and anthers are highly variable within *Leucaena*, even, as in the *L. lanceolata* alliance, within groups of closely related species.

A final group, here referred to as the *L. shannonii* alliance, comprising *L. lempirana, L. magnifica, L. salvadorensis,* and *L. shannonii,* is characterized by velutinous ovary indumentum. It is notable for its Mesoamerican and mainly Central American distribution south of the Isthmus of Tehuantepec and the main center of *Leucaena* species diversity.

Harris et al. (1994a) used the placement of three of the four known tetraploid species in the cpDNA analysis to hypothesize the likely maternal parent species of

L. leucocephala and *L. diversifolia*, as *L. pulverulenta*, and of *L. pallida*, as *L. esculenta*. Recognition of *L. pueblana* as a distinct species since the study by Harris et al. (1994a) reveals that *L. pueblana* is the sister species of *L. pallida* in the cpDNA analysis and therefore a putative maternal parent species of *L. pallida*. Although placement of hybrids on a morphological cladogram is unpredictable, hybrids between sister, or closely related, taxa generally cause only minor changes in topology in weakly supported areas of the cladogram that include the parents, whereas hybrids between distantly related species on divergent clades can cause major restructuring of relationships and collapse of consensus trees (Humphries 1983; Funk 1985; McDade 1992; Rieseberg 1995). This means that inclusion of the four tetraploid species, one-by-one into the morphological data set may provide some additional insights about their likely parentage. The cpDNA data (Harris et al. 1994a) suggested that *L. leucocephala* and *L. diversifolia*, which were placed as sister species to *L. pulverulenta* in that analysis (Fig. 31), had *L. pulverulenta*, or a species with the cpDNA type of *L. pulverulenta*, as the maternal parent. Assuming an allotetraploid origin of *L. leucocephala*, the loss of resolution caused by inclusion of that species in the morphological analysis indicates that the paternal parent was probably distantly related to *L. pulverulenta*. Leaflet morphology suggests that one of the species with elliptic leaflets, and probably *L. lanceolata* or *L. macrophylla*, was the paternal parent. The collapsed consensus tree (Fig. 29B) is compatible with this hypothesis. *Leucaena diversifolia* was placed as sister species to *L. trichandra* in the morphological analysis (Fig. 30A), suggesting that species as a possible paternal parent species with *L. pulverulenta* as the maternal parent species. *Leucaena pallida* was unresolved with *L. pueblana* as sister species to *L. matudae* and *L. involucrata* in the morphological analysis, a placement consistent with the cpDNA data and with *L. pueblana* as the likely maternal parent of *L. pallida*. Finally, the morphological analysis suggests that *L. confertiflora*, if of allotetraploid origin, is a hybrid between distantly related species, including one of the basal taxa, and possibly *L. trichandra*. A close relationship between *L. confertiflora* and *L. cuspidata* has been postulated (Zárate 1994), suggesting that species as a possible parent species; however, the origin of *L. confertiflora*, with two subspecies and evidence of cytoplasmic introgression in one accession from Santa Catalina Oxolotepec, Puebla (Hughes, unpubl.), is not obvious and demands further investigation. Indeed the effects of reticulation in *Leucaena* in general remain to be fully understood. Future research to determine chromosome numbers for all species, recode and analyze the cpDNA data as restriction sites rather than fragment occurrences, and seek additional molecular markers is needed to fully unravel reticulate from phylogenetic relationships in *Leucaena*.

The order of species in the Taxonomy presented below reflects the scheme of species relationships derived from morphological data (Fig. 26). Tetraploid species are placed adjacent to their likely maternal progenitors based on currently available evidence.

TAXONOMY

Leucaena Bentham, Hook. J. Bot. 4: 416. 1842.—Lectotype, designated by Hughes, 1997b: *Leucaena diversifolia* (Schlechtendal) Bentham.

Ryncholeucaena Britton & Rose, Fl. N. Amer. 23: 130. 1928.—Type: *Ryncholeucaena greggii* (S. Watson) Britton & Rose [=*Leucaena greggii* S. Watson].

Caudoleucaena Britton & Rose, Fl. N. Amer. 23: 130. 1928.—Type: *Caudoleucaena retusa* (Bentham) Britton & Rose [=*Leucaena retusa* Bentham].

Unarmed small or medium-sized trees 2–15 (–20) m in height, sometimes branched from the base, more often with a short 3–5 (–10) m bole and an open spreading crown. Bark either mid- to dark grey-brown with shallow rusty orange-brown vertical fissures or smooth, sometimes gnarled or scalloped but without fissures, pale to mid-metallic-grey, inner bark cream, rarely streaked pink, deep orange, or blood-red. Young stems usually terete, but sometimes angled with corky ridges; older stems terete, often weakly geniculate (strongly geniculate in *L. matudae* and *L. pueblana*). Stipules ovate, subulate or long-pointed at apex with small asymmetric striately nerved basal wings, persistent or tardily deciduous. Brachyblasts absent. Leaves bipinnate, paripinnate, the rachis adaxially canaliculate, pubescent or glabrous, with a single or rarely double acropetiolar sessile or stipitate nectary and 1–many nectaries at the base of the terminal and subterminal pairs of pinnae, extending beyond the distal pair of pinnae in a short pointed mucro; (1–) 2–many pairs of pinnae, triangular in cross section, usually ridged adaxially between leaflets and often bearing 1–several minute nectaries between distal pairs of leaflets; leaflets few to numerous, opposite or subopposite, short-petiolate or nearly sessile, inserted contiguously from near the base of the pinna, very variable in size, linear, oblong, or elliptic, weakly or strongly oblique at base, acute, rounded, retuse, or cuspidate at apex, venation sometimes obscure except for eccentric visible midvein but sometimes brochidodromus secondary and tertiary veins visible, glabrous or pubescent, often ciliate on margins. Inflorescence capitate, pedunculate, the peduncle with an involucel of united bracts at distal end or sometimes subdistal, the capitula occurring in fascicles of 1–several in leaf axils on 0–2-branched shoots that may be auxotelic or anauxotelic, with coeval leaf development or leaf suppression on flowering shoots, composed of mainly perfect flowers, sometimes with a few male flowers at base but lacking sterile flowers bearing showy staminodia. Flowers pentamerous, subtended by peltate bracts that are exserted in bud and persistent after anthesis, round, lanceolate, or caudate; calyx broadly to narrowly obconic, tubular or campanulate, united for 2/3 of its length with 5, blunt, usually ciliate teeth, pale green or whitish green; petals 5, 1-nerved, oblanceolate or linear, attenuate, glabrous or hairy, usually free, but occasionally united at the base or united along the mid-portion but free at the base; stamens 10, usually arranged in 2 distinct ranks, usually white or cream-white but occasionally yellow or pink to reddish, anthers ovate to oblong, dorsifixed to nearly basifixed, bilocular, caducous, usually sparsely or densely pilose but in a few species glabrous, usually eglandular, but in some species the connective bearing a small rounded or dorsiventrally flattened hooded apiculum, usually white or cream-white, rarely yellow or pink; ovary ovate, sessile or subsessile, glabrous or hairy, cream, the style exserted or included at anthesis, stigma narrow-funnelform or tubular. Pollen in monads, acalymmate polyads or, in 1 species, calymmated tetrahedral tetrads, tricolporate or, in 2 species, pantoporate, the tectum smooth psilate or punctate to finely perforate. Fruits short-stipitate, pendulous, linear, linear-oblong, or occasionally oblong, the base acute, the apex rounded or acute and usually with a small beak, more or less compressed, the valves usually membranous or chartaceous, in some species coriaceous or slightly woody, mid- to dark orange or sometimes reddish brown, glabrous or pubescent, sometimes lustrous, in most species opening simultaneously along both sutures, but, in 2 species, initially along 1 suture, the valves either curling transversely, twisting spirally, or reflexing longitudinally after dehiscence, the endocarp pale tan, sometimes partitioned between seeds by pithy walls; seeds usually transversely, but in a few species, longitudinally or obliquely aligned in pods, circular, ovate, or weakly rhomboidal in outline, compressed, rich chestnut-brown and glossy, with a U-shaped, generally symmetric pleurogram on both sides. Base chromosome numbers: x = 26 or 28.

KEY TO THE SPECIES OF LEUCAENA

1. Leaflets elliptic, ovate, or lanceolate, only weakly asymmetric at base, large (usually >1 cm wide), (1–) 2–6 (–8) pairs per pinna.
  2. Petiolar nectary stipitate, erect, columnar, peg-shaped, 1–3 mm tall; peduncles 25–90 mm long; floral bracts long-subulate or caudate and strongly exserted in bud; filaments, anthers, and style bright yellow; anthers glabrous; pods 11–13 mm wide, linear, the valves strongly coriaceous or slightly woody; seeds rhomboidal with strongly oblique or longitudinal alignment in pods; northeastern Mexico (Chihuahua, Coahuila) and southwestern U.S.A. (New Mexico, Texas). 1. *L. retusa.*
  2. Petiolar nectary sessile, crateriform, conical, or verruciform, <1 mm tall; peduncles <20 mm long; floral bracts round and only superficially exserted in bud; filaments, anthers, and style white; anthers hairy to densely pilose; pods ≥13 mm wide, linear-oblong, the valves membranous or chartaceous; seeds ovate or elliptic, transversely aligned in pods.
    3. Petiolar nectary crateriform; flowering shoots 2-branched; capitula ≤8mm in diameter at anthesis, ≤60 flowers per capitulum; pollen in polyads composed of calymmated tetrads arranged in acalymmated polyads; southern Nicaragua, Costa Rica, and Panama. 16. *L. multicapitula.*
    3. Petiolar nectary convex, conical, or truncate conical; flowering shoots unbranched or 1-branched; capitula ≥7mm in diameter at anthesis, ≥90 flowers per capitulum; pollen in monads or acalymmated polyads composed of loosely associated monads.
      4. Capitula (15–) 20–40 mm in diameter at anthesis with ≥250 flowers per head; anthers lacking a protrusion of the connective; pollen tricolporate in monads. 15. *L. lanceolata.*
      4. Capitula 7–12 (–15) mm in diameter at anthesis with 90–190 flowers per head; anthers with a small dorsiventrally flattened, hooded protrusion or apiculum on the connective; pollen pantoporate in acalymmated polyads of loosely associated monads.
        5. Flowering shoots usually 1-branched; Mexico. 17. *L. macrophylla.*
        5. Flowering shoots usually unbranched; South America. 18. *L. trichodes.*
1. Leaflets linear, narrow-oblong, or lorate, strongly asymmetric at base, ≤1 cm wide, with (5–) 7-many pairs per pinna.
  6. Young shoots angled with corky ridges, these visible as distinct striations on the stem (Fig. 4A).
    7. Leaves with ≥25 pairs of pinnae and ≥55 pairs of leaflets per pinna; fruits oblong or broadly linear-oblong, ≥23 mm wide, not forming a partition between seeds, the seed chambers not or barely visible on exocarp; seeds ≥9 mm long. 10. *L. esculenta.*
    7. Leaves with ≤27 pairs of pinnae and ≤58 pairs of leaflets per pinna; fruits linear or narrowly linear-oblong, ≤18 mm wide, forming a partition between seeds, the seed chambers clearly visible on exocarp; seeds ≤8 mm long.
      8. Shoots strongly geniculate; leaflets ≤6 mm long; anthers pale cream-white or creamy yellow. 11. *L. pueblana.*
      8. Shoots scarcely geniculate; leaflets ≥6 mm long; anthers pale pink or dull purplish mauve. 12. *L. pallida.*
  6. Young shoots terete.
    9. Petiolar nectary sessile, convex, shallow-conical, truncate-conical, verruciform, the orifice a narrow pore, or sometimes invisible.
      10. Anthers glabrous and with a small rounded protrusion (apiculum) on the connective; petals connate at base; ovary pilose; capitula lax in bud (Fig. 13D) with 45–65 flowers; young leaves densely white-puberulent or tomentose; northeastern Mexico (Veracruz–Tamaulipas) and U.S.A. (Texas). 4. *L. pulverulenta.*
      10. Anthers hairy and lacking an apiculum; petals free at the base; ovary glabrous or very short-velutinous; capitula with (55–) 90–220 flowers and densely packed in bud; young leaves without whitish grey tomentum; southern Mexico (Chiapas, Yucatán) and Central America.
        11. Leaflets 3–8 (–10) mm long, 1–2 mm wide; pairs of pinnae per leaf (6–) 10–20; pairs of leaflets per pinna 25–60.

12. Flowering shoots continuing to grow beyond the flowering region (auxotelic), with coeval leaf development on flowering shoots and with pods borne on older wood away from shoot tips; ovary glabrous; petals free; pods 7–19 mm wide; Mexico (Chiapas) and Guatemala. 7. *L. collinsii.*

12. Flowering shoots determinate, ending in an abortive vegetative apex (anauxotelic), leaf development suppressed on flowering shoots, pods and flowers borne on naked terminal shoots; ovary densely short-velutinous; petals weakly connate along mid-portion; pods (18–) 20–26 (–32) mm wide; Honduras (Yoro). 21. *L. lempirana.*

11. Leaflets 13–26 mm long, 3–10 (–12) mm wide; pairs of pinnae per leaf 2–7; pairs of leaflets per pinna 5–27.

13. Pairs of leaflets per pinna >20; leaflets ≤5 mm wide; pods strongly coriaceous, pod valves always glabrous; eastern El Salvador, southern Honduras, and northern Nicaragua. 22. *L. salvadorensis.*

13. Pairs of leaflets per pinna <20; leaflets >5 mm wide; pods chartaceous, valves often velvety to the touch.

14. Leaves (6–) 10–15 cm long; leaf rachis 3–9 cm long; (2–) 4–6 (–7) pairs of pinnae per leaf; (5–) 7–13 pairs of leaflets per pinna; leaflets (13–) 16–18 (–20) mm long, 5–7 mm wide, adaxial surface not glossy; flowering shoots unbranched; capitula 11–12 mm in diameter with 80–140 flowers per head; pods (11–) 14–16 (17) mm wide; widespread in southern Mexico and Central America to central Nicaragua. 19. *L. shannonii.*

14. Leaves (18–) 20–30 cm long; leaf rachis 12–18 cm long; 4–7 pairs of pinnae per leaf; 11–16 pairs of leaflets per pinna; leaflets (20–) 22–26 mm long, 9–12 mm wide; adaxial surface glossy; flowering shoots 1-branched; capitula 21–26 mm in diameter with 200–220 flowers per head; pods (19–) 22–24 (–26) mm wide; Guatemala (Chiquimula). 20. *L. magnifica.*

9. Petiolar nectary stipitate peg-shaped or sessile concave, cupulate, crateriform or patelliform with a broad orifice.

15. Petiolar nectary concave, broad-cupulate, or crateriform, elliptic or circular.

16. Pinnae 4–9 pairs per leaf, leaflets 13–21 pairs per pinna. 6. *L. leucocephala.*

16. Pinnae 9–30 pairs per leaf, leaflets (20–) 30–60 pairs per pinna.

17. Leaflets 8–21 mm long, 1.2–2.7 mm wide; filaments, anthers, and style cream-white or white tinged very pale pink.

18. Bark pale metallic grey and unfissured or very weakly fissured; flowering abundantly throughout the year but sterile and lacking pods. 23. *L.* ×*mixtec.*

18. Bark mid-grey-brown with shallow rusty orange-brown vertical fissures; pod set abundant. 24. *L.* ×*spontanea.*

17. Leaflets 2.9–7 mm long, 0.6–1.8 mm wide; anthers (and sometimes filaments and style) usually tinged strong pink or reddish, occasionally pale cream or pale pink.

19. Leaflets ≥43 pairs per pinna; anthers sparsely hairy at distal end only; corolla with petals weakly fused along mid-portion although free at base; ovary hairy on distal half; moist Gulf- or E/NE-facing slopes of eastern Mexico and northernmost Guatemala. 5. *L. diversifolia.*

19. Leaflets ≤30 pairs per pinna; anthers densely pilose throughout; petals completely free; ovary glabrous; seasonally dry central mountains of Mexico and Central America. 8. *L. trichandra.*

15. Petiolar nectary cylindrical, subsessile or stipitate, peg-shaped, circular.

20. Peduncles 60–90 mm long; floral bracts lanceolate and slightly exserted in bud; anthers glabrous; staminal filaments, anthers, and style bright yellow; pods woody, with thickened margins and terminating in a thickened pointed persistent style; seeds aligned longitudinally in pods; northeastern Mexico (Coahuila, Nuevo León). 2. *L. greggii.*

20. Peduncles <40 mm long; floral bracts round, scarcely exserted in bud, anthers hairy; anthers cream-white or pinkish purple, filaments cream-white; pods coriaceous or chartaceous, lacking a thickened woody pointed apex; seeds aligned transversely or obliquely in pods.

21. Leaves with 5–16 (–18) pairs of pinnae; leaflets 1.5–3.5 mm wide, oblong, often cuspidate, usually with midrib and secondary veins externally visible; pods 16–30 mm

wide, oblong or linear-oblong, flat, endocarp not forming a partition between seeds, seed chambers not visible on exocarp, pods dehiscent initially along one suture only, seeds circular or elliptic and transversely aligned in pods.

22. Leaves with 5–7 pairs of pinnae and (18–) 22–26 pairs of leaflets per pinna; pod valves chartaceous; Mexico (Oaxaca, Puebla). 9. *L. confertiflora.*

22. Leaves with (9–) 11–16 (–18) pairs of pinnae and (38–) 40–45 (–50) pairs of leaflets per pinna; pod valves strongly coriaceous or weakly lignified; Mexico (Hidalgo, Querétaro, San Luis Potosí). 3. *L. cuspidata.*

21. Leaves with (13–) 16–22 pairs of pinnae; leaflets 0.9–1.7 mm wide, linear, acute at apex, only midrib visible externally; pods 9–15 (–17) mm wide, linear, sometimes slightly constricted, slightly thickened, endocarp partitioned between seeds, the seed chambers clearly visible on exocarp, pods tardily dehiscent along both sutures, seeds weakly rhomboidal, obliquely aligned in pods.

23. Pods 9–13 mm wide, not constricted; bark smooth, inner bark thin; Mexico (Sinaloa, Sonora). 13. *L. involucrata.*

23. Pods 12–15 (–17) mm wide, weakly constricted between the seeds, bark scalloped on surface with thick corky deep blood-red inner bark; Mexico (Balsas Depression in Guerrero). 14. *L. matudae.*

1. Leucaena retusa Bentham in Gray, Plantae Wrightianae 1: 64. 1852. *Caudoleucaena retusa* (Bentham) Britton & Rose, N. Amer. Fl. 23: 131. 1928.—TYPE: U.S.A. Texas: bottom of the Rio Nueces, 29°26′N, 100°05′W, Jun 1849, *Wright 171* (lectotype, here designated: K!; isolectotypes: BM! GH! NY! OXF! US!).

Acacia sabeana Buckley, Proc. Acad. Nat. Sci. Philadelphia 453. 1861.—TYPE: U.S.A. Texas: banks of San Saba River, N of Fort Mason, rd to Camp Colorado, 13°52′N, 98°48′W, Jun 1861, *Buckley s.n.* (holotype: PH!).

Shrub or small tree, 2–5 (–8) m tall, 10–15 cm stem diameter, typically slow-growing, with brittle branches and a small round crown. Bark on young branches smooth, mid-brown with pale orange-brown lenticels, on bole darker blackish brown and rougher with shallow orange-brown vertical fissures. Shoots terete, mid-brown. Stipules 7.3–7.5 mm long, ovate, long-pointed or subulate at apex, with asymmetric membranous basal wings, striate, midrib prominent, venation inconspicuous, glabrous, persistent. Leaves (15–) 18–25 cm long, (15–) 19–22 cm wide; petioles (including pulvinus) 40–50 mm long; rachis 7–9 cm long, villose-pubescent when leaves first appear, soon sparsely pubescent then glabrous at maturity, with a series of cylindrical, columnar, peg-shaped nectaries, 1 mm long, 1 mm wide, 1–3 mm tall, on ventral side of petiole and rachis at base of each pair of pinnae, densely covered in short white hairs on young leaves, later glabrous, the rachis extending beyond the terminal pinnae as a pointed thornlike mucro, 3.2–3.9 mm long, thickened at base and densely covered in white hairs; pinnae (2–) 3–4 (–5) pairs; pinnular rachis 9–11 cm long, angled, sparsely white-puberulent, with minute, round, knoblike nectaries at base of each pair of leaflets; leaflets (4–) 5–6 (–8) pairs per pinna, (15–) 20–26 (–30) mm long, (8–) 10–12 (–15) mm wide, short-petiolate, weakly asymmetric, obliquely obovate or elliptic-lanceolate, rounded and apiculate, rarely slightly retuse-apiculate, obliquely rounded or cuneate at the asymmetric base, entire, villose-pubescent, like the rachis and petiole, when leaves first appear, soon glabrous and at maturity thin blue-green, with a slender midrib and prominent veins extending obliquely towards the apex of the leaflet. Capitula 20–25 mm in diameter at anthesis, in fascicles of (1–) 2–4 in leaf axils on actively growing shoots, each capitulum with 150–190 flowers; peduncles 25–90 mm long, angled, villose, densely covered with yellow-green hairs, with a pair of caudate bracts at the distal end. Flowers subtended by peltate, ovate, long-subulate or caudate, villose bracts, 5–7 mm long, conspicuously exserted in bud (Fig. 13C); calyx 4.2–4.5 mm long, glabrous, ciliate on lobe margins, pale yellow-green; petals 5.4–6.6 mm long, free, glabrous, minutely ciliate on lobe margins, the lobe margins markedly thickened, pale yellow-green; filaments 12–13.5 mm long, bright yellow; anthers glabrous, yellow, with a small rounded protrusion or apiculum on the connective; ovary 2 mm long, pilose on distal half, pale yellow-green, with 16–28 ovules, style 12.5–14 mm long, bright yellow, narrowing to a tubular stigma, held level with anthers. Pods (Fig. 17B) 1–2 (–5) per capitulum, (12–) 16–20 (–25) cm long, 11–13 mm wide, pendulous on sturdy 4–5 mm long stipes, linear, sometimes slightly falcate, basally cuneate, straight, acuminate, terminating in the thickened persistent style, compressed, 13–15-seeded, valves green and fleshy when unripe, turning mid- to reddish brown, glabrous, with pronounced reticulation, strongly coriaceous, almost lignified, the margins markedly thickened, tardily dehiscent along both sutures. Seeds 7.3–8.5 mm long, 4.8–6.5 mm wide, compressed, rhomboidal, deep chestnut-brown, glossy, aligned strongly obliquely or longitudinally in pods; pleurogram visible, deeply U-shaped, 90%, symmetrical. Chromosome number: 2n = 56 (Pan & Brewbaker 1988; Sorensson 1989). Fig. 32.

Phenology. Flowering (March–) April–June (–August); fruiting (July–) August–October (–November); leafless during the cold winter season from December–February.

Distribution (Fig. 33). *Leucaena retusa* is the most northerly species in the genus, occurring from 26°43′N to 31°52′N, and extends into mountains as high as 1900 m and is thus the most cold-tolerant species, occupying a warm temperate climate with cold winters. It occurs in the extreme north of Mexico, mainly in Coahuila, and in the southern U.S.A., mainly in south-central and western Texas. Single collections from Chihuahua, Mexico, and New Mexico, U.S.A., are clearly outliers; the species is apparently rare in those states. *Leucaena retusa* occupies a wide range of habitats from moist to semi-arid and montane to deep canyon sites, mainly in rocky places and predominantly on limestone but in some areas also on igneous rocks. It occurs as an understory shrub or small tree in a range of open vegetation types, including mixed pine-oak forest with *Pinus ponderosa*, scrub oak-juniper forest with *Quercus* species, including *Q. fusiformis, Q. grisea,* and *Q. intricata, Juniperus ashei* and other *Juniperus* spp., *Eysenhardtia texana, Fraxinus greggii, Cassia orcuttiana, Juglans, Rhus, Berberis, Pistacia, Cercis,* and *Platanus occidentalis,* and chaparral and semi-arid thorn scrub forest with *Acacia berlandieri, A. roemeriana, Mimosa, Prosopis, Parthenium incanum, Opuntia, Agave lechiguilla,* and *Yucca carnerosana*; (120–) 400–1900 m.

Vernacular names. *Cafecillo, planta de patro* (Coahuila); *little-leaf lead tree, goldenball lead tree* (Vines 1960), *lead tree, woohoo, hiusache* (Texas).

Representative Specimens. **U.S.A.** New Mexico: nr Queen, Guadelupe Mtns, 31°59′N, 104°50′W, *P. J. Leyendecker s.n.* (US).—Texas: Brazos Co., high bottoms Little Brazos River, nr College Stn, 30°31′N, 96°08′W, *Demaree 50883* (BM, GH, MO). Brewster Co., mtns 46 km E of Alpine, 30°10′N, 97°57′W, *Correll 14085* (NY, TEX); Green Gulch, Chisos Mtns, Big Bend National Park, 29°18′N, 103°18′W, *Correll 30625* (NY, TEX); several miles from mouth of Heath Canyon in E facing canyon, *Correll 32630* (GH, TEX, UC); 91 km SE of Marathon, 30°10′N, 103°19′W, *Cory 28622* (A); Reagan Canyon, 2 km above the mouth, 29°44′N, 102°41′W, *McVaugh 7813* (CAS, F, GH, TEX), Black Gap Wildlife Management Area, 80 km S of Marathon, 29°34′N, 102°55′W, *Rowell 11245* (TEX); arroyo, 24 km S of Persimmon Gap, 29°21′N, 103°07′W, *Sperry 1375* (GH, US); Buena Vista Canyon, 7 km W of Alpine, 30°17′N, 103°48′W, *Steiger 921* (NY); nr Alpine, 30°19′N, 103°45′W, *Studhalter 1063* (NY, US); Box Canyon, 9 km NW of Alpine, Kolernot Ranch, 30°29′N, 103°46′W, *Warnock 5575* (TEX). Crockett Co., *Goodrum 78* (GH, TEX). Edwards Co., Ranch Exp. Stn., Pasture, *Cory 3018* (GH), *Cory 3023* (GH); 11 km N of Barksdale, rd to Rocksprings, 29°30′N, 100°00′W, *M.C. Johnston 54653* (TEX). Jeff Davis Co., 8 km W of Fort Davis nr Limpia Creek, 30°37′N, 104°01′W, *Andrews 22* (A),

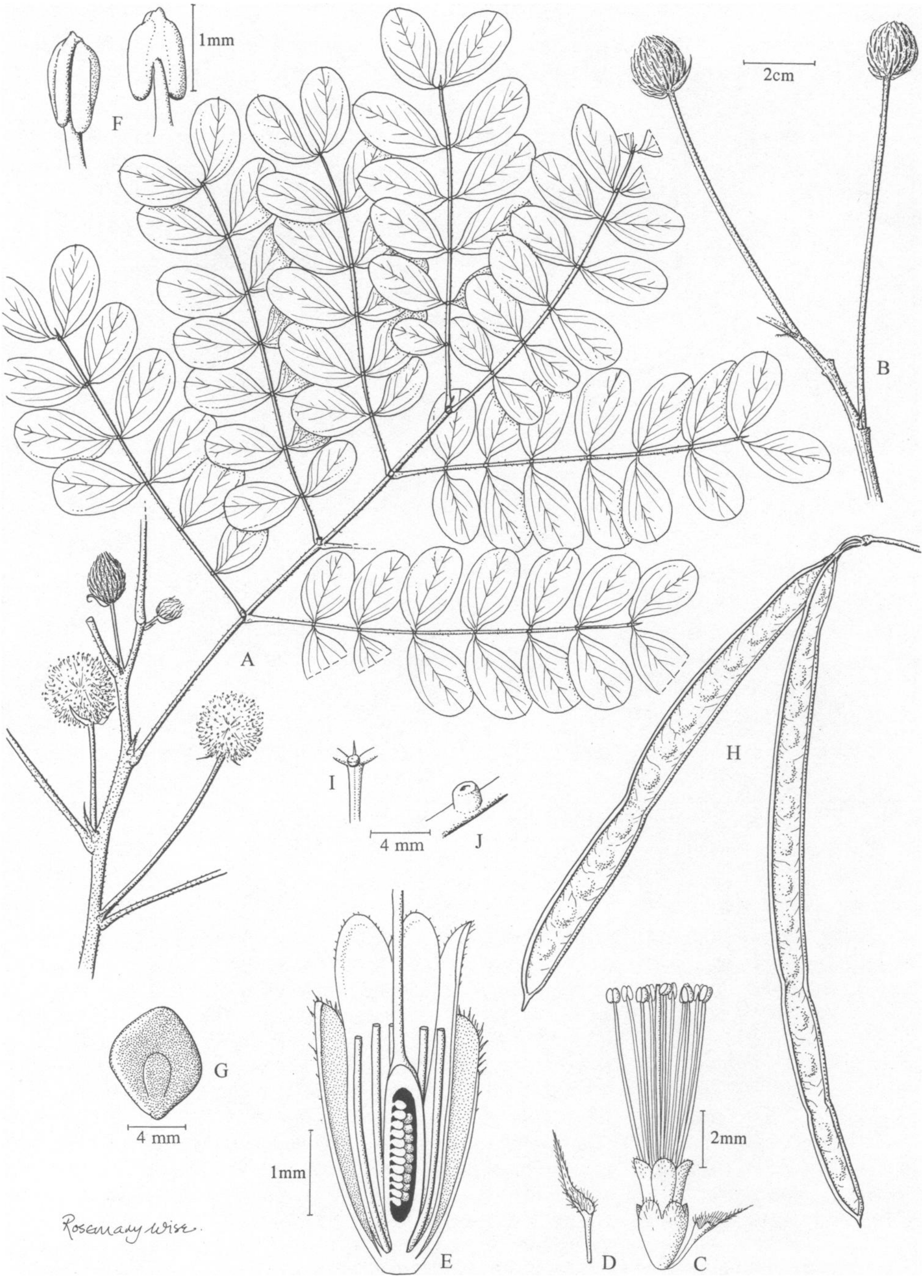


FIG. 32. *Leucaena retusa*. A. Leaf, flowering shoot. B. Unopened flower heads. C. Flower. D. Bract. E. Longitudinal section of flower. F. Anther. G. Seed. H. Pods. I. Nectary between terminal leaflets. J. Petiolar nectary. (Based on: A–G, *Hughes 1361*; H–J, *Wright 170*.)

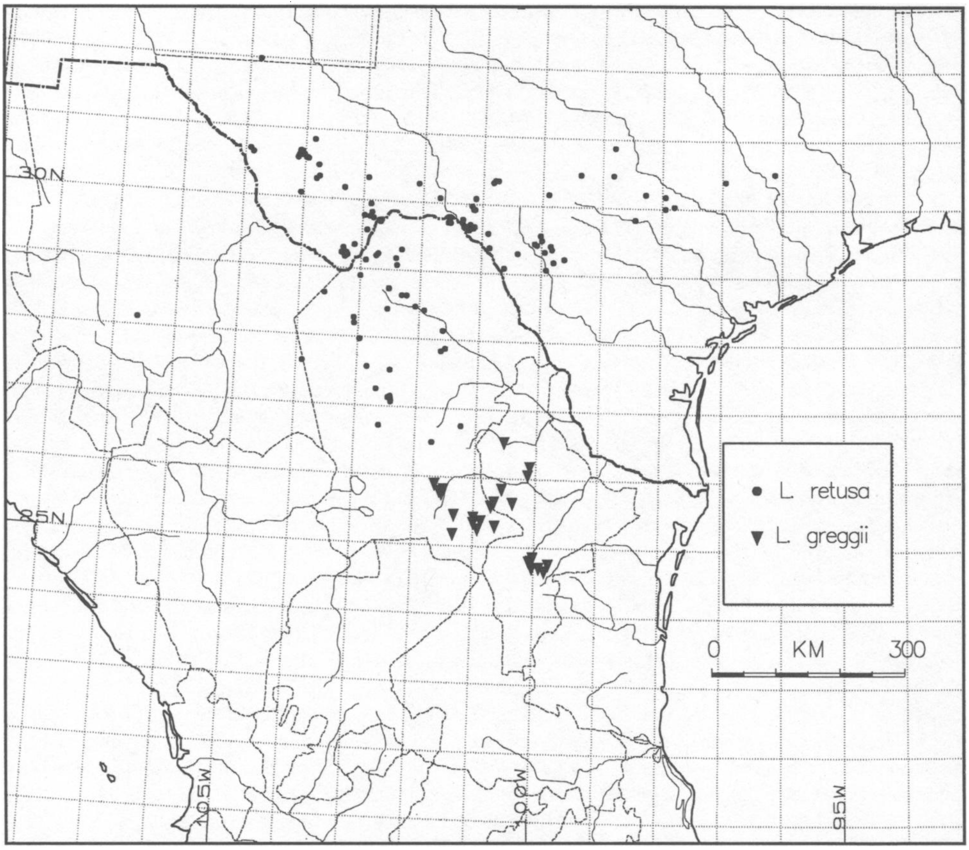


FIG. 33. Distribution of *L. retusa* and *L. greggii.*

Andrews 33 (A), *Cory 53095* (CAS, NY, UC, US); Caldwell Ranch, Davis Mtns, 30°24′N, 96°57′W, *L. C. Hinckley s.n.* (GH, TEX); below MacDonald Observatory, Davis Mtns, 30°41′N, 104°55′W, *Innes 1121* (GH); S of Toyahvale, 30°51′N, 103°51′W, *Kiltz 799* (A); Little Aguja Canyon, Davis Mtns, 30°40′N, 104°03′W, *J. A. Moore 3062* (A, CAS, NY); Davis Mtns, 30°38′N, 104°52′W, *Steiger 1740* (NY); Limpia Canyon, N of Wild Rose Pass, Rokernot Ranch, Davis Mtns, 30°37′N, 104°02′W, *Warnock 7743* (TEX); Lower Madera Canyon, nr old Hunsaker resort, N of Timber Mountain, *Weedin & Crabtree 531* (TEX). Kimble Co., Junction City, 30°10′N, 99°54′W, *Reverchon 1262* (A, CAS, F, MO, NY, US). Kinney Co., 32 km NE of Brackettville, W Nueces River, 29°27′N, 100°07′W, *Correll 14106* (NY, TEX); 40 km N of Del Rio, 29°22′N, 100°52′W, *Cory 41653* (A, TEX); creek canyon, US 277, 45 km S of Del Rio, 29°05′N, 100°37′W, *Isely 10737* (BM, MO, NY, US). Pecos Co., canyon, 32–56 km S of Ft. Stockton, Sanderson Hwy, 30°20′N, 102°56′W, *Warnock 13338* (TEX). Presidio Co., ridge nr mouth of Goat or Merrill Canyon, *Hinckley 3154* (NY), *Hinckley 3475* (NY). Real Co., lookout over Frio River, rte 83, several km NE of Leakey, 29°25′N, 99°51′W, *Correll 29599* (TEX); 9 km S of Camp Wood, 29°34′N, 100°01′W, *Hubricht 1844* (A, MO); 5 km S of Leakey, 29°20′N, 99°57′W, *M. C. Johnston 54643* (TEX). Sutton Co., 2 km W of Sonora, 30°21′N, 100°48′W, *Barneby 17958* (NY), *M. C. Johnston 6400* (TEX), *6401* (NY, TEX). Terrell Co., 14 km N of Sanderson, Hwy 285, 29°57′N, 102°52′W, *M. C. Johnston 6467* (NY, TEX), *Warnock 14840* (TEX); nr Feodora, *Palmer 33556* (A, NY); Ligan Canyon, 32 km S of Sheffield, 30°16′N, 102°05′W, *Webster 291* (TEX). Travis Co., central parts of Austin, 30°00′N, 97°57′W, *Nee 27126* (F, NY); Univ. of Texas, Brackenfield Field Lab., Lake Austin Boulevard, Austin, 30°02′N, 97°48′W, *Pratler 1243* (TEX). Uvalde Co., Garner State Park, 29°11′N, 99°48′W, *Correll 15757* (TEX); divide between Frio and Sabinal watersheds, 16 km W of Utopia, 29°14′N, 99°37′W, *M. C. Johnston 54642* (TEX); 10 km SE of Concam, 29°04′N, 99°55′W, *E. B. Kincaid s.n.* (TEX); nr Laguna by Nueces River, 29°26′N, 100°05′W, *McKelvey 1883* (GH). Valverde Co., Devils River, 8 km above Fort Hudson, *W. V. Brown s.n.* (TEX); 13 km W of Comstock, rte 90, 29°40′N, 101°12′W, *Correll 20717* (TEX); Fielder Draw, 12 km SW of Pandale, 30°04′N, 101°43′W, *Cory 39569* (TEX); Devils River, banks of Rio Grande, 29°35′N, 100°54′W, *H. Eggert s.n.* (MO); 7.5 km E of entrance to Seminole Canyon State Park, Hwy 90 W of Comstock, 29°43′N, 101°34′W, *Ertter 5411* (CAS, NY); nr Langtry, 29°48′N, 101°34′W, *Grant 61* (US); nr Rio Grande River, nr Comstock, 29°37′N, 101°13′W, *Hastings 34* (US); 3 km N of Comstock, Hwy 163, 29°42′N, 101°12′W, *Hess 3177* (NY, US); Hwy 90, 16 km E of Pecos River, 29°48′N, 101°32′W, *Isely 10761* (NY); Seminole Canyon State Park above the S rim of Canyon R.8, 29°40′N, 101°17′W, *Labus 57* (TEX); Devils River Valley, 48 km N of Comstock, 29°58′N, 101°11′W, *C. H. Muller 8106* (TEX); 29°40′N, 101°08′W, *Palmer 11067* (A, CAS, MO, US); nr Pecos River, 29°43′N, 101°20′W, *Tharp 3453* (US); 5 km E of Shulma, 29°46′N, 101°20′W, *Warnock 9918* (TEX).

Mexico. CHIHUAHUA: 40 km SE of Cuauhtémoc, 28°07′N, 106°37′W, *Correll 21602* (CAS, MEXU, NY, TEX).—COAHUILA: 22 km ESE of La Cuesta del Plomo, Múzquiz to Boquillas del Carmen rd, 28°38′N, 102°18′W, *Chiang 7543C* (MEXU); La Cuesta del Plomo, rd from Múzquiz to Boquillas del Carmen, 28°44′N, 102°31′W, *Chiang 9228* (MEXU, TEX); Sierra San Marcos y Pinos, 56 km SW of Monclova, 26°30′N, 101°43′W, *H. S. Gentry 23115* (MEXU); 32 km NNW of Palos Blancos, 32 km N of Ocampo, 27°32′N, 102°27′W, *Graber 115* (TEX); 35 km WNW of Cuatro Ciénegas, upper portion Canyon de la Hacienda, Sierra de la Madera, 27°04′N, 102°25′W, *Henrickson 13631* (TEX); 48 km WNW of Cuatro Ciénegas, Cañón Los Pozos, 5–7 km W of Rancho Cerro de la Madera, trail to Cañón Desiderio, 27°08′N, 102°28′W, *Henrickson 15947* (TEX); Cañón de los Arboles nr the Río Grande, *Jermy 9* (TEX, US); W base of Picacho del Fuste, NE of Tanque Vaionetta, 27°34′N, 102°50′W, *I. M. Johnston 8406* (GH); Aguaje del Pajarito, canyon W end Sierra de la Fragua, 3 km N of Puerto Colorado, 26°43′N, 102°36′W, *I. M. Johnston 8689* (GH, TEX); lower N end Cañón de la Hacienda, N side Sierra de la Madera, 27°06′N, 102°25′W, *M. C. Johnston 10986* (CAS, MEXU, NY, TEX); La Noria, end of rd from T. Armendaiz N into Sierra del Pino, 28°12′N, 103°04′W, *Johnston & Muller 510* (GH, TEX); Rancho El Almagre, Sierra Almagre, border between Coahuila and Chihuahua, 27°37′N, 103°54′W, *Johnston & Muller 1189* (GH, TEX); Cañón del Indio Felipe, nr Chihuahuan boundary, NE from Rancho El Tule beyond Puerto del Aire in Sierra de Hechiceros, 28°38′N, 103°35′W, *Johnston & Muller 1334* (GH, TEX), *Stewart 122* (GH, TEX); nr Múzquiz, 27°52′N, 101°33′W, *Marsh 51* (GH, TEX); Sorpresa Spring nr Múzquiz, *Marsh 325* (GH, MEXU, TEX); Sierra de Santa Rosa, S of Múzquiz, 27°50′N, 101°37′W, *Marsh 1241* (GH, TEX); Sierra de la Gloria SE of Monclova, 26°45′N, 101°15′W, *Marsh 1924* (GH, TEX); opposite Los Fresnos, NE slope Sierra de San Marcos, *Pinkava 5996* (TEX); Cañón Espantosa, W slopes Sierra de San Vicente, 20 km ESE of Cuatro Ciénegas, 28°54′N, 103°00′W, *Schroeder 144* (GH); Cañón de San Enrique, E side Sierra de la Encantada, 5 km W of Rancho Buena Vista, 28°25′N, 102°32′W, *Stewart 1393* (GH, TEX); Hwy 53, 50 km W from rd to La Babia Hacienda, 28°43′N, 102°31′W, *Vankat 6* (TEX); Sierra Santa Rosa, E of Rancho La Peña, 135 km on Hwy 53, Múzquiz to Boquillas del Carmen, 28°38′N, 102°13′W, *Wehbe 93* (MEXU, TEX); Cañón del Diablo E side Sierra del Carmen, 29°14′N, 102°43′W, *Wendt 145A* (MEXU, TEX); "Slump Spring," Rincón de María, Hacienda La Babia, 112 km NW of Múzquiz, 28°28′N, 102°04′W, *Wendt 930* (TEX); Rancho Agua Dulce, lower slopes Sierra San Manuel, Múzquiz, 28°25′N, 101°55′W, *Wynd & Mueller 317* (A, K, NY, US); Villa Acuña, nr Santo Domingo, 29°04′N, 102°24′W, *Wynd & Mueller 479* (A, K, NY, US).

Honduras. COMAYAGUA: Cultivated in field trial, La Soledad Exp. Stn. El Taladro, 10 km WSW of Comayagua, *Hughes 1361* (FHO).

Neither the analysis of sister group relationships in the *Leucaena* and *Dichrostachys* groups nor that of species relationships within *Leucaena* supports the view of Britton and Rose (1928) that *L. retusa* should be placed in the segregate monotypic genus *Caudoleucaena*. Nevertheless, the placement of *L. retusa*, along with *L. greggii* and *L. pulverulenta,* as a paraphyletic sister group to the rest of the genus is supported by a number of character states. These are the only species in the genus that have glabrous anthers and a chromosome number of 2n = 56. A close relationship between *L. retusa* and *L. greggii* is hypothesized in the analysis of species relationships and is strongly supported in the analysis of cpDNA restriction site data (Harris et al. 1994a). Both species share a number of unusual character states, including erect peg-shaped extrafloral nectaries, one at the base of each pair of pinnae, yellow flowers, long-caudate or lanceolate floral bracts that are exserted in bud (Fig. 13C), very long peduncles compared to all other species, thick woody pods, and rhomboidal seeds longitudinally or obliquely aligned. The distinction of

L. retusa and *L. greggii* from all other species of *Leucaena* is further revealed by their northerly distribution (Fig. 33) and an ability to withstand low winter temperatures (Glumac et al. 1987), unusual *Rhizobium* affinities (Halliday & Somasegaran 1983), and their very slow growth in field trials compared to other species (Stewart et al. 1991). These two species, and *L. retusa* in particular, are thus highly distinctive within the genus.

Leucaena retusa is readily distinguished from *L. greggii* on leaf characters alone. It has few pairs of large elliptic or ovate leaflets, whereas *L. greggii* has many pairs of small linear-oblong leaflets.

In the protologue, Bentham cites three specimens, *Wright 171* and *170,* and an additional collection from 1851. The first of these, a specimen with flowers is here chosen as the lectotype. *Wright 170* (BM! GH! MO! OXF! UC! US!) is fruiting material collected on the same expedition in Texas at Pass of the Limpia in August, 1849.

2. Leucaena greggii S. Watson, Proc. Amer. Acad. Arts 23: 272. 1888. *Ryncholeucaena greggii* (S. Watson) Britton & Rose, N. Amer. Fl. 23: 130. 1928.—TYPE: MEXICO. Nuevo León: dry ravine E of Rinconada, 25°41′N, 100°40′W, 25 May 1847, *Gregg s.n.* (lectotype, here designated: NY!; isolectotype: GH!).

Shrub or small tree, (2–) 3–5 (–8) m tall, 10–15 cm bole diameter, typically slow-growing, with brittle branches and a small round crown. Bark on young branches smooth, mid-brown with pale orange-brown lenticels, on bole darker blackish brown and rougher with shallow orange-brown vertical fissures. Shoots terete, rich orange-brown, with small pustular orange lenticels, glabrous or very sparsely pubescent. Stipules 4–5.5 mm long, ovate, with a subulate or long-pointed apex, persistent (Fig. 4B). Leaves (15–) 17–22 cm long, (13–) 15–18 (–19) cm wide; petioles (including pulvinus) (16–) 20–24 (–27) mm long; rachis 8–12 cm long, glabrous, extending beyond the terminal pinnae as a slender pointed mucro, 3–6 (–8) mm long, often broken on dried specimens, rachis with a series of slender, cylindrical, columnar, peg-shaped nectaries, 0.5 mm in diameter, 2–2.5 (–3.2) mm tall, on ventral side of petiole and rachis at base of each pair of pinnae (Fig. 9B); pinnae (7–) 8–10 (–11) pairs; pinnular rachis 8–11 (–13) cm long, weakly canaliculate or striate, glabrous, with 2–4 round, knoblike nectaries, 0.3 × 0.3 mm, at base of terminal pairs of leaflets; leaflets (25–) 27–34 pairs per pinna, (6.5–) 8–11.5 (–12.1) mm long, (2–) 2.5–3.0 (–3.6) mm wide, short-petiolate, slightly asymmetric, linear-oblong, attenuate at apex, truncate at the asymmetric base, entire, glabrous, waxy blue-green, midrib and 2 secondary veins visible. Capitula 24–26 mm in diameter at anthesis, in fascicles of 1–3 in leaf axils on actively growing shoots, each capitulum with (120–) 150–200 flowers; peduncles 60–90 mm long, angled, glabrous or sparsely pubescent, with a prominent subapical involucre of bracts. Flowers subtended by peltate, lanceolate bracts, 5–6 mm long, slightly exserted in bud; calyx 4.8–5.5 mm long, densely pubescent on upper half of lobes, yellow-green; petals 6.0–6.5 mm long, free, glabrous, sparsely ciliate on lobe margins, the lobe margins slightly thickened, pale yellow-green; filaments 11.5–12 mm long, bright yellow; anthers glabrous, yellow, apiculum absent; ovary 3 mm long, hairy on distal half, pale yellow-green, with 18–26 ovules, style 12.5–13 mm long, bright yellow, narrowing to a tubular, funnelform stigma, held level with anthers. Pods 1–3 (–5) per capitulum, (12–) 15–18 (–21) cm long, 9–15 mm wide, pendulous, almost sessile, narrowly linear, sometimes slightly falcate, basally cuneate, straight, acuminate, terminating in the thickened persistent style, compressed, 11–15-seeded, valves green and fleshy when unripe, turning mid- to orange-brown, glabrous, with faintly visible reticulation, slightly woody, the margins markedly thickened, tardily dehiscent along both sutures. Seeds 4.9–6.9 mm wide, 7.5–9.0 mm long, compressed, variably circular to strongly rhombic, deep chestnut-brown, glossy, longitudinally aligned in pods; pleurogram visible, deeply U-shaped, 90%, symmetrical. Chromosome number: 2n = 56 (Sorensson 1989). Fig. 34.

Phenology. Flowering April–June (–August); fruiting (September–) October–November, the pods sometimes persistent on tree for several months after ripening; detailed phenological study reported in Bendeck and Foroughbakch (1988).

Distribution (Fig. 33). *Leucaena greggii* is restricted to the mountains of northeastern Mexico in northern and central Nuevo León and southeastern Coahuila. Although it was reported from southern Texas, U.S.A., by Sargent (1921), Britton and Rose (1928) (as *Ryncholeucaena*), and Cory and Parks (1937), this was questioned by Isely (1970) and Turner (1959). I have seen only one specimen from the U.S.A. (*M. B. Johnson s.n.*) and that is from cultivated material. *Leucaena greggii* occurs mainly on steep mountain slopes, in canyons, ravines, and on cliffs, mainly on north- and northeast-facing slopes, on limestone or gypsum, often on shallow rocky calcareous soils. It is most often found in submontane matorral or thorn scrub as a small canopy tree with diverse woody legumes, including *Acacia berlandieri, Bauhinia macracantha, Cercis canadensis, Prosopis laevigata, Sophora secundiflora*, and species of *Agave, Bouvardia, Ceanothus, Dodonaea, Eysenhardtia, Fendlerella, Fraxinus, Opuntia, Pistacia, Ptelea, Rhus*, and *Vauquelinia*, but also as an understory tree or shrub in dry oak-pine forest with *Pinus arizonica, P. cembroides*, and *P. pseudostrobus*; (680–) 1400–1800 (–2200) m.

Vernacular Names. *Guajillo, Gregg lead tree.*

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARIZONA: Tuscon, cultivated trees from College Station campus, Tuscon, *M. B. Johnson s.n.* (FHO).

Mexico. COAHUILA: General Cepeda, Cañón del Tejocote, Sierra la Concordia, 25°12′N, 101°20′W, *Andrés 837* (MEXU); Mina la Abundancia, upper reaches of Cañón Corazón del Toro, SW quadrant Sierra de Paila, 25°55′N, 101°39′W, *Chiang 10117* (CAS, MEXU, NY, TEX); San Lorenzo Canyon, 8 km SE of Saltillo, 5 km E of hwy 54, Sierra Poliname, 25°17′N, 100°56′W, *Hess 4343* (MEXU); Sierra Paila above Carrera, distr. of G. Cepeda, 25°49′N, 101°34′W, *Hinton 16592* (GH, NY, US); nr Saltillo, 25°22′N, 101°00′W, *Hinton 16695* (US); nr Morillo, close to Saltillo, 25°27′N, 101°00′W, *Lyonnet 3487* (MEXU, US); El Chiflón, nr General Cepeda, 25°29′N, 101°19′W, *Lyonnet 3524* (MEXU, UC, US); Sierra de Paila, 25°47′N, 101°32′W, *Purpus 4850* (GH, US); rd to Estación Viga, main Saltillo to Torreón rd, Buenavista, *L. E. Rodríguez 514* (TEX); Cañón Loma Prieta, 12 km NE of Hipólito, rd to Valle Loma Prieta, Sierra de Pailla, 25°51′N, 101°30′W, *Villarreal 3088* (MEXU, TEX); nr Las Vigas, Cañón de la Carbonera, Sierra de Arteaga, 25°20′N, 100°39′W, *Villarreal 3787* (MEXU, TEX).—NUEVO LEÓN: Higueras, N side of rd to short-wave mast at Mamulique, 36 km S of Sabinas Hidalgo, 26°12′N, 100°06′W, *Bridges 13144* (TEX); below grotto of Villa de García, 25°52′N, 100°33′W, *Clausen 7603* (GH, K, MEXU, NY); nr Rancho Resendez, Lampazos, *Edwards 359* (CAS, GH, NY, TEX, UC); turnoff to La Colorada, rd Iturbide to Linares, 24°42′N, 99°51′W, *Estrada 1024* (MO); Puerto Pastores, rd Iturbide to Galeana, 24°47′N, 100°02′W, *Estrada 1494* (MEXU, NY, TEX); nr Galeana, N of Linares to San Roberto rd, 24°49′N, 100°05′W, *J. M. Gillett 17090* (MEXU); nr San Pedro Iturbide, 24°43′N, 99°53′W, *Hinton 17795* (GH, MEXU, NY, TEX); La Poza to Río de San José, nr Galeana, 24°44′N, 100°02′W, *Hinton 22044* (TEX), *Hinton 21733* (TEX); 4 km S of Galeana, jctn with Linares-San Roberto rd, 24°48′N, 100°04′W, *Hughes 695* (FHO, K, MEXU); El Barrial, rd between Iturbide and San Roberto, 3 km E of jctn to Galeana, 24°47′N, 100°01′W, *Hughes 696* (FHO, K, MEXU); rd 47 km W of Linares into the Sierra Madre Oriental, 5 km W of Iturbide, 24°47′N, 99° 46′W, *Hughes 1048* (FHO, K, MEXU); El Barrial, rd 60 km W of Linares into Sierra, 24°53′N, 100°01′W, *Hughes 1050* (FHO, K, MEXU), *Hughes 1056* (FHO, K, MEXU), *Hughes 1057* (FHO, K, MEXU); mtns W of Bustamante, 26°33′N, 100°32′W, *LeSeur 176* (GH); rd Linares to Galeana, half way up canyon nr Iturbide, 24°41′N, 99°50′W, *Manning & Manning 53297* (GH, MEXU); 5 km above Iturbide, rd to Galeana, 24°44′N, 99°55′W, *McVaugh 10567* (CAS, NY); La Cuesta de Mamulique, hills nr Monterrey, 26°05′N, 100°08′W, *Muller & Muller 29* (F); Monterrey, Cuesta de Mamulique, 26°05′N, 100°08′W, *Muller & Muller 529* (A, MEXU, TEX), *C. S. Sargent s.n.* (A); Hwy 85 at Mamulique Pass, N of Monterrey, 26°12′N, 100°06′W, *Peterson 1240* (TEX); 11 km ESE of Galeana off Hwy 57 to Linares, 24°46′N, 100°03′W, *Thomas*

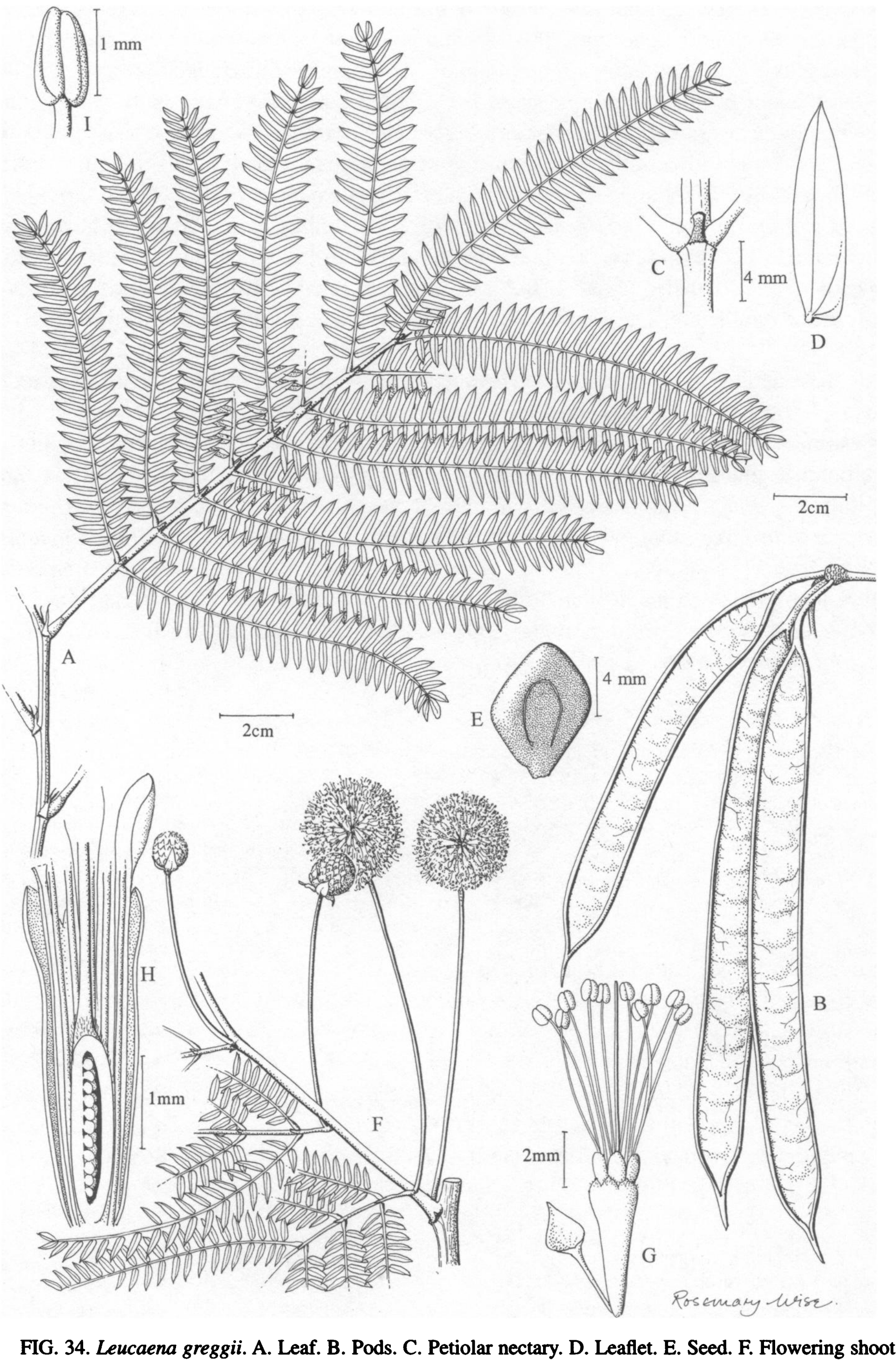


FIG. 34. *Leucaena greggii*. A. Leaf. B. Pods. C. Petiolar nectary. D. Leaflet. E. Seed. F. Flowering shoot. G. Flower. H. Longitudinal section of flower. I. Anther. (Based on: A–E, *Hughes 1056*; F–H, *Hughes 696*; I, *Hughes 695*.)

2755 (MEXU, NY); 18 km SE of Rayones towards Galeana, 24°53′N, 100°04′W, *R. Torres 1012* (MEXU); Cañada Cortinas, SE of Casablanca Villa de García, 25°37′N, 100°43′W, *Villarreal 2036* (MEXU, TEX); 14 km W of Iturbide, Hwy 60, 24°44′N, 99°58′W, *Weaver 2074* (MEXU); 3 km SE of Galeana, Linares to San Roberto rd, 24°47′N, 100°03′W, *Zárate 362* (MEXU).

Zárate (1984a) placed *L. greggii* and *L. retusa* in separate sections within *Leucaena* (section *Leucaena* and section *Macrophylla,* respectively), suggesting a distant relationship between these two species. This was also the view of Britton and Rose (1928), who placed the two species in separate segregate genera (*Ryncholeucaena* and *Caudoleucaena,* respectively). My analysis shows that *L. greggii* is most closely related to *L. retusa* and shares a suite of diagnostic characters with that species, including yellow flowers held on long peduncles, pointed or caudate floral bracts that are slightly or conspicuously exserted in bud, thickened, narrow, linear, lignescent pods with thickened margins, longitudinal seed alignment, and erect columnar, peg-shaped nectaries (Fig. 9B, F) that are distributed along the length of the leaf rachis. In addition to shared morphological characters, cpDNA analysis showed these two species to be very closely related, a relationship that appeared in 100% of bootstrap replicates in that analysis (Harris et al. 1994a). *Leucaena greggii* and *L. retusa* are both restricted to the mountains of northeastern Mexico and Texas (Fig. 33), with cold winter climates, in dry matorral or mixed dry oak-pine forest, usually on calcareous soils. The foliage of *L. greggii* is apparently highly palatable and, in some areas, grazing pressure has reduced populations to scattered remnants in inaccessible gullies.

Despite its clear morphological distinction and affinities with *L. retusa, L. greggii* has been confused with *L. leucocephala*. The drawing labelled *L. greggii* in Sargent (1921: 597, Fig. 547), which appears to be of *L. leucocephala* has been cited by several authors (e.g., Brewbaker 1987a). Presumably confusion is due to the broad similarity in leaflet number, size, and shape (Brewbaker 1987a).

Watson cites three specimens in the protologue, *Gregg s.n., Palmer 307,* and *C. S. Sargent s.n.* The first is chosen as the lectotype as the epithet *greggii* clearly refers to the *Gregg* collection.

3. Leucaena cuspidata Standley, Contr. U.S. Natl. Herb. 20: 189. 1919.—TYPE: MEXICO. San Luis Potosí: Minas de San Rafael, 22°12′N, 100°16′W, May 1911, *Purpus 5183* (holotype: US!; isotypes: GH! MO! NY! UC!).

Leucaena cuspidata subsp. *jacalensis* S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65(2): 144. 1994.—TYPE: MEXICO. Hidalgo: 7 km NE of Jacala, 21°03′N, 99°10′W, 15 Aug 1964, *Quintero 1292* (holotype: MEXU!).

Small, often multiple-stemmed tree, 2–4 (–6) m tall, 10–15 cm bole diameter, with an open, irregular, spreading crown. Bark on young branches smooth, mid-grey-brown with pale brown lenticels, on bole darker blackish brown and rougher with shallow, orange-brown, vertical fissures. Shoots terete, grey-brown with pale orange-brown, slightly raised lenticels. Stipules 4.9–6 mm long, lanceolate, membranous with asymmetric basal wings, persistent, becoming hard and stiff when dry. Leaves (17–) 18–22 cm long, (10–) 12–15 cm wide; petioles (including pulvinus) 26–30 mm long; rachis 8–15 cm long, variably glabrous or densely covered in short white pubescence, extending beyond the terminal pinnae as a pointed, curling mucro, 2.9–4.5 mm long, variably covered in white hairs or glabrous, rachis with 1–2 usually cylindrical, columnar, peg-shaped nectaries, 1–1.5 mm long, 1 mm wide, 1 mm tall, or sometimes flatter discoid nectaries, on ventral side of petiole and rachis at base of the lower pinnae pairs, and sometimes with 1 or 2 additional nectaries at base of terminal pinnae pairs; pinnae (9–) 11–16 (–18) pairs; pinnular rachis 7–10 cm long, with a double ridge on ventral side, variably white-pubescent, with 1 or 2 minute round knoblike nectaries at base of terminal pairs of leaflets; leaflets (38–) 40–45 (–50) pairs per pinna, sessile, (5–) 5.2–6.6 mm long, 1.5–2.3 mm wide, strongly asymmetrically truncate at base, linear-oblong, acuminate, cuspidate at apex, the cusp sometimes strongly curved towards apex of pinnae, entire, glabrous or sparsely pubescent, thickened, subcoriaceous, strongly discolorous, dark glossy green above, paler mid- or grey-green below, only midrib visible on ventral side, venation prominent below. Capitula 13–16 mm in diameter at anthesis, in fascicles of (1–) 2–4 in leaf axils on actively growing shoots, each capitulum with 135–150 flowers; peduncles variable, 26–35 mm long, angled, variably pubescent or glabrous, with an involucre of basally united bracts, often below distal end of peduncle, sometimes at distal end, but never less than halfway along peduncle (Fig. 13B). Flowers subtended by peltate bracts, 3 mm long, 1 mm in diameter; calyx 2.5–3 mm long, glabrous, ciliate on lobe margins, pale green; petals 3.8–4.2 mm long, free at base, weakly connate along mid-portion, glabrous, ciliate on lobe margins, the lobe margins markedly thickened, pale green; filaments 5.5–7.5 mm long, pale creamy white; anthers sparsely hairy, usually with a small tuft of short hairs at distal end (Fig. 14F), cream or cream-white, with a small pointed protrusion or apiculum on the connective (Fig. 14F); ovary 2 mm long, pilose, pale cream-white, with 12–16 ovules, style 6.5–8 mm long, pale cream-white, with a porate, tubular stigma, held level with or very slightly exserted beyond anthers. Pods 1–2 (–3) per capitulum, (10–) 14–22 (–28) cm long, 20–30 mm wide, pendulous, sessile, linear-oblong, slightly falcate, acute at base and apex, compressed, 13–15-seeded, valves thick, green and fleshy when unripe, turning mid- to dark reddish brown, glabrous or pubescent, strongly coriaceous, almost lignified, the margins thickened, dehiscent initially along one suture (Fig. 18A, B, E), the valves later twisting, sometimes forming tight spirals (Fig. 18 B, E). Seeds 9.4–11.8 mm long, 8.1–10.6 mm wide, compressed, circular, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, regular, U-shaped, with 75–90% arm extension, symmetrical. Chromosome number unknown. Fig. 35.

Phenology. Flowering February–May; fruiting (October–) November–December (–February).

Distribution (Fig. 36). *Leucaena cuspidata* is restricted to the drier mid-elevation slopes on the western side of the Sierra Madre Oriental in the Mexican states of Hidalgo, Querétaro, and San Luis Potosí. It is common only in Hidalgo, where the majority of collections have been made, although even here most are from a restricted set of localities. It is apparently rare in Querétaro and San Luis Potosí. It occurs as an understory shrub or small tree in mixed pine-oak-juniper forest and scattered in mixed dry and low matorral. Associated canopy species include *Pinus cembroides, P. pinceana, Juniperus deppeana, J. flaccida,* and *Quercus mexicana,* and other woody shrubs, such as *Acacia subangulata, Hybosema ehrenbergii,* and *Sophora secundiflora,* and species of *Bauhinia, Brongniartia, Buddleja, Dodonaea, Eysenhardtia, Pistacia,* and *Tecoma* along with *Agave, Yucca,* and many Cactaceae. *Leucaena cuspidata* occurs mainly on steep rocky calcareous slopes, sometimes where sulphur deposits occur (e.g., type locality in San Luis Potosí); (1400–) 1600–2200 (–2400) m.

Vernacular names. *Efe* (= *guaje* in Otomi), *efe de cerro, gauche (guaje) de cerro, guachito, huaxi (guaje), guaje de cerro* (Hidalgo).

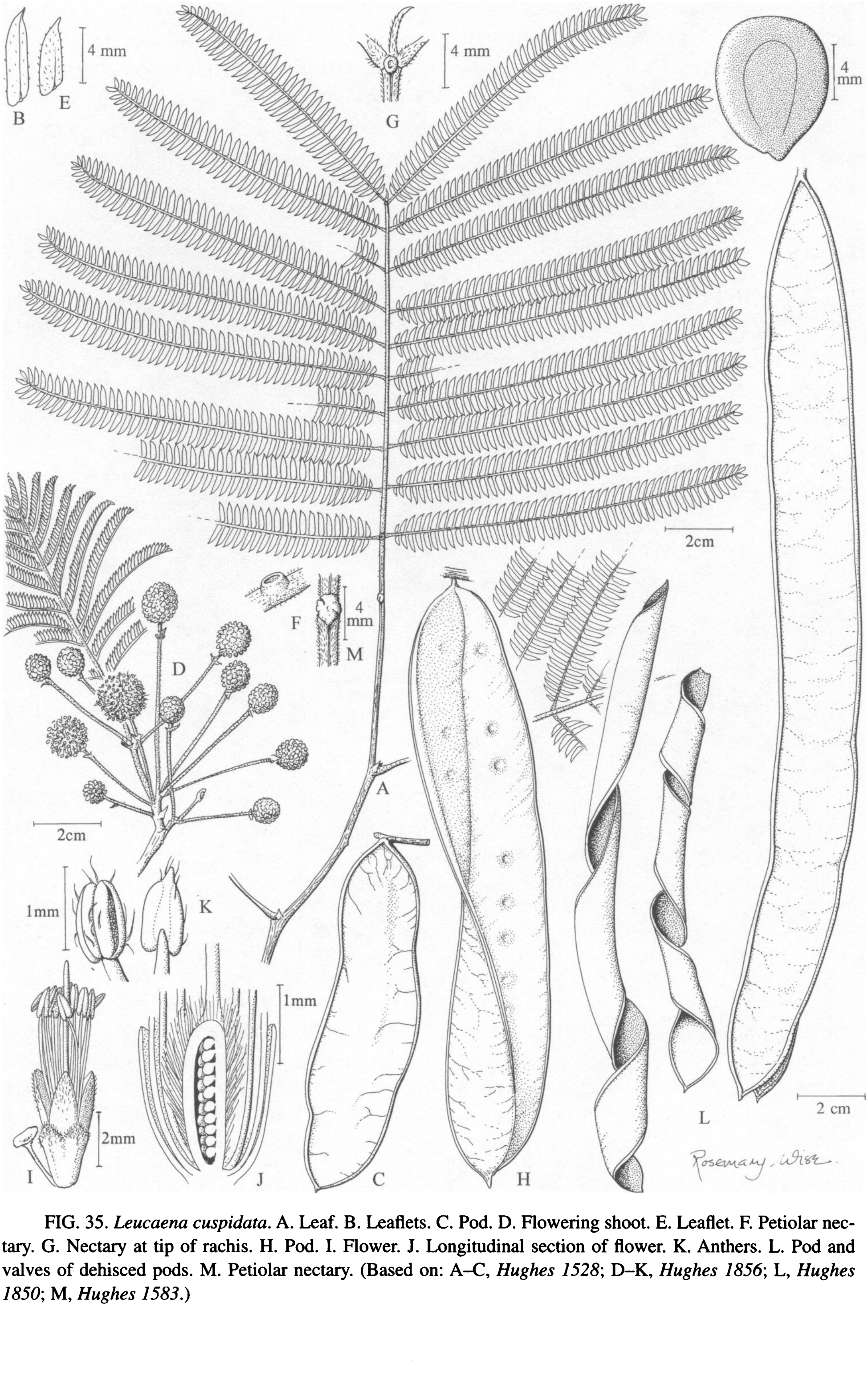


FIG. 35. *Leucaena cuspidata.* A. Leaf. B. Leaflets. C. Pod. D. Flowering shoot. E. Leaflet. F. Petiolar nectary. G. Nectary at tip of rachis. H. Pod. I. Flower. J. Longitudinal section of flower. K. Anthers. L. Pod and valves of dehisced pods. M. Petiolar nectary. (Based on: A–C, *Hughes 1528*; D–K, *Hughes 1856*; L, *Hughes 1850*; M, *Hughes 1583*.)

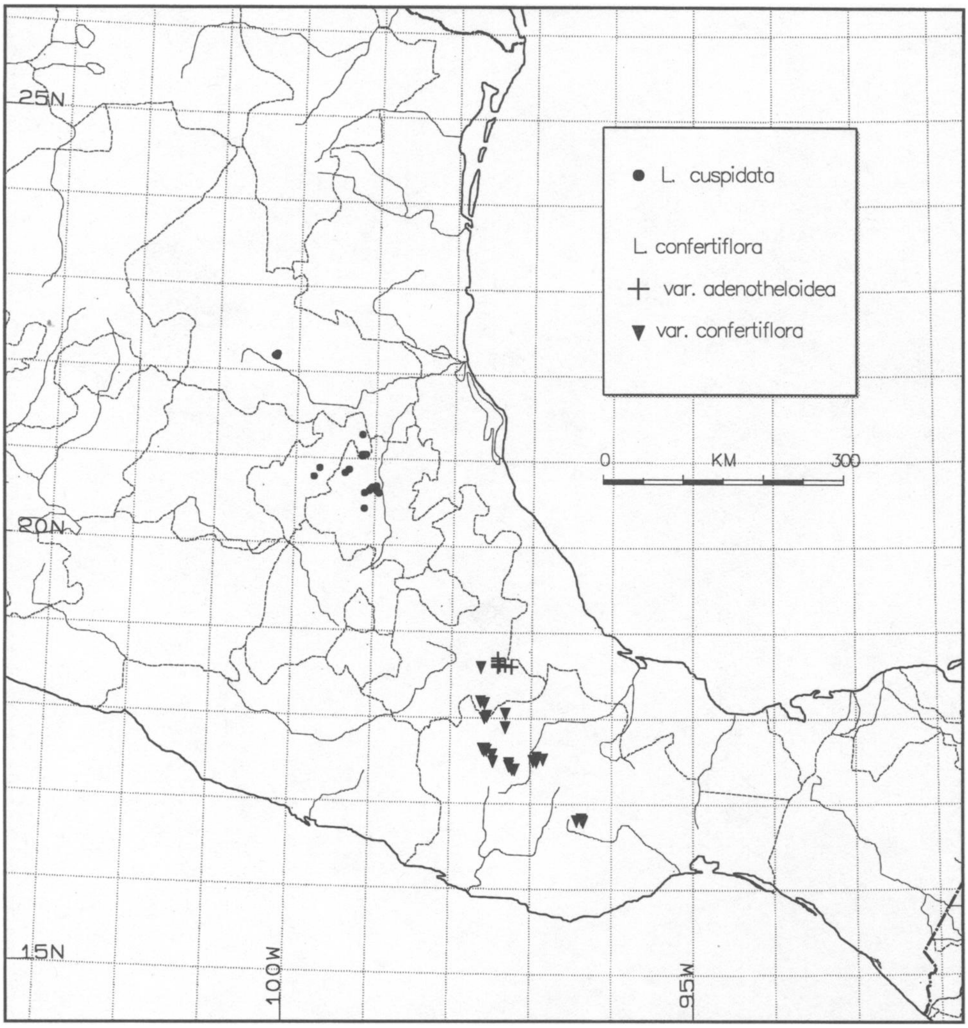


FIG. 36. Distribution of *L. cuspidata* and *L. confertiflora.*

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** HIDALGO: 10 km NE of Jacala, rd to Tamazunchale, 21°03'N, 99°07'W, *Chase 7397* (GH, MO, NY), *Hughes 1586* (E, FHO, K, MEXU, MO, NY), *Hughes 1587* (E, FHO, K, MEXU, MO, NY), *Hughes 1856* (CAS, FHO, K, MEXU, MO, NY), *Zárate 408* (MEXU); Cardonal, Barranca of Tolantongo, 2 km SW of Molanquito, 20°39'N, 98°59'W, *Hughes 1528* (FHO, K, MEXU, MO, NY), *Hughes 1580* (E, FHO, K, MEXU, MO, NY), *Medraño 9390* (MEXU), *Medraño 9458* (MEXU), *Medraño 9460* (MEXU), *Medraño 9490* (MEXU), *Medraño 9517* (MEXU), *Medraño 9534* (MEXU), *Téllez 307* (MEXU); slopes above Camarones, 5 km E of Cieneguilla, 15 km ENE of Cardonal, S of track from La Laguna, 20°41'N, 98°59'W, *Hughes 1581* (E, FHO, K, MEXU, MO, NY); Arroyo Hondo at bottom of barranca between Cuesta Blanca and La Mesa, rd 6 km NW from Cardonal to Cieneguilla, 20°39'N, 99°03'W, *Hughes 1582* (E, FHO, K, MEXU, MO, NY); close to Shote, 15 km N of Zimapán, rd to Mina San Miguel, 20°50'N, 99°23'W, *Hughes 1583* (E, FHO, K, MEXU, MO, NY); Barranca Tolantongo, rd NE from Cardonal to Cieneguilla, between Cuesta Blanca and La Mesa, 20°39'N, 99°03'W, *Hughes 1850* (FHO, K, MEXU, MO, NY, TEX); hills above Camarones, 8 km SE of Cieneguilla, 55 km NE of Ixmiquilapan, N of Barranca de Tolantongo, 20°41'N, 98°59'W, *Hughes 1851* (FHO, K, MEXU, MO, NY, TEX); 10 km NE of Cardonal, rd to Cuesta Blanca and

Cieneguilla, 40 km NE of Ixmiquilapan, 20°38′N, 99°04′W, *Hughes 1854* (FHO, K, MEXU, MO, NY, TEX); close to Cajay, 15 km N of Zimapán towards Mina San Miguel, 20°52′N, 99°20′W, *Magaña 6568* (CAS); 10 km SE of Ixmiquilapan, 20°25′N, 99°08′W, *F. Martínez 4210* (MEXU); 2 km W of Cardonal, 20°36′N, 99°08′W, *Medraño 8860* (MEXU); Puerta de la Zorra, Km 284 rd NE of Jacala, 21°03′N, 99°07′W, *H. E. Moore 2661* (GH), *H. E. Moore 3797* (MEXU); 21.5 km E of turnoff to Tolantongo, 43 km NE of Ixmiquilapan, rd to las Grutas, 200 m W of rd, 20°38′N, 98°59′W, *Zárate 550* (MEXU); 21 km E of turnoff to Tolantongo, 43 km NE of Ixmiquilapan, rd to las Grutas, 200 m W of rd, 20°38′N, 98°59′W, *Zárate 551* (CAS, MEXU, MO).—QUERÉTARO: Cadereyta, 7 km NE of Vizarrón, 20°53′N, 99°42′W, *Fernández & Zamudio 962* (MEXU); rd W from Tamazunchale to Jalpan de la Sierra, 51 km from turnoff, 25 km SW of Xilitla, 21°17′N, 99°10′W, *Hughes 1594* (E, FHO, K, MEXU, MO, NY); Cadereyta, NE slope of Sierra Peña Azul, 6.5 km SW of Vizarrón, 20°47′N, 99°46′W, *Zamudio 2751* (TEX).—SAN LUIS POTOSÍ: 1 km N abandoned mine of Guascama before mines of San Rafael, 27 km from Paraíso by the turnoff towards Guascama, 22°10′N, 100°17′W, *Zárate 330* (MEXU); nr Minas de Guascama, 42.5 km N of Mojarras de Arriba, 4.5 km from Buena Vista, 22°11′N, 100°18′W, *Zárate 585* (CAS, MO), *Zárate 586* (CAS, MEXU, MO).

Leucaena cuspidata was distinguished by Standley because of its unusual cuspidate subcoriaceous leaflets, which are quite unlike those of other species in the genus apart from *L. confertiflora.* The type material seen by Standley lacked mature pods. The unusually broad, slightly falcate pods with their initially fleshy and later thick coriaceous or lignescent valves, which dehisce initially along one suture, the valves then twisting and forming tight spirals (Fig. 18B, E), confirm the distinction of *L. cuspidata* as an unusual species within the genus. The subdistal position of the involucre of basally united bracts on the peduncle (Fig. 13B), which is marked on the type specimen and was noted by Standley in his original description, although quite variable within *L. cuspidata*, is also unusual within *Leucaena*. Finally, the phanerogeal seedling morphology, with very little or no extension of the hypocotyl and the cotyledons held at, or slightly below, ground level is also unique within the genus; all other species have phaneroepigeal seedlings with extension of the hypocotyl. The affinities of *L. cuspidata*, with so many unusual characters, remain uncertain. In the analysis of morphology its placement was ambiguous but always amongst the group of basal species comprising *L. greggii, L. retusa,* and *L. pulverulenta*, a position supported by possession of a small apiculum on the connective of the anther. In the analysis of cpDNA restriction site data *L. cuspidata* was placed next to *L. involucrata.*

Zárate (1984a, 1994) indicated a close relationship between *L. cuspidata* and *L. confertiflora*. Indeed, *L. confertiflora* was first considered to be a subspecies of *L. cuspidata* by Zárate (1984a). These two species share unusual pod dehiscence, initially along one suture (Fig. 18 A, D), and they occupy similar habitats immediately north (*L. cuspidata*) and south (*L. confertiflora*) of the volcanic axis of central Mexico (Fig. 36) further suggesting that they may be closely allied. However, this relationship is not apparent in either the cpDNA or morphological analyses, but this may be attributable to the likely hybrid origin of *L. confertiflora*, as discussed below.

Variation in a number of characters has been observed within *L. cuspidata* as treated here. The petiolar nectary, although usually short-stipitate, columnar, and circular, may be asymmetrically elliptic and crateriform, as on material from the Tolantongo area of Hidalgo. Leaf and pod pubescence also varies within *L. cuspidata*. Zárate (1984a, 1994) used pubescence to distinguish subsp. *jacalensis,* which he described as a strongly pubescent variant occurring as a restricted endemic around the town of Jacala, an area falling within the geographic range of *L. cuspidata* as a whole. My observations indicate that leaf and particularly pod indumentum are very variable. Although trees from around Jacala are indeed more pubescent, even in this area glabrous individuals also occur. Elsewhere sparsely pubescent individuals occur alongside glabrous ones. Pending more detailed studies, I am therefore placing subspecies *jacalensis* in synonymy.

Leucaena cuspidata is heavily grazed by goats and in some areas is now rare and restricted to steep cliffs and gullies that are inaccessible to browsing animals. Unripe pods are harvested, and the seeds consumed and marketed locally, e.g., in Ixmiquilapan (Hidalgo). *Leucaena cuspidata* is occasionally cultivated for its edible seeds within its natural range (e.g., around Cardonal and above Jacala, Hidalgo).

4. Leucaena pulverulenta (Schlechtendal) Bentham, Hooker J. Bot. 4: 417. 1842. *Acacia pulverulenta* Schlechtendal, Linnaea 12: 571. 1838.—TYPE: MEXICO. Veracruz: "ad ripam fluminis Misantlensis, pr. San Antonio, reg. calidae," 19°56′N, 96°52′W, Feb, *Schiede & Deppe s.n.* (holotype: HAL; isotypes: OXF! US!; photo of isotype formerly at B: NY!)

Small to medium-sized tree, 5–18 (–20) m tall, 20–50 cm bole diameter, usually slender with a clear bole up to 10 m and a light feathery crown. Bark on young branches smooth, pale orange-brown, pale yellow, or grey-brown, on bole with shallow rusty orange-brown vertical fissures, the inner bark green. Shoots terete, thickly coated with puberulent, whitish grey, caducous tomentum, older shoots pale orange-brown. Stipules 2.3–2.5 mm long, triangular, pointed with a prominent midrib, margins ciliate, deciduous. Leaves 18–22 cm long, 7–9.5 cm wide, young foliage whitish puberulent; petioles (including pulvinus) 27–35 mm long; rachis 11–17 cm long, densely covered in short white pubescence, with an oblong, slightly asymmetric, irregularly lumpy or verrucate, dark reddish brown nectary, 3 mm long, 1.5 mm wide, 1 mm tall, on ventral side of petiole between the lower pair of pinnae, sometimes with an additional nectary between terminal pair of pinnae, apex of rachis extending beyond the terminal pinnae in a pointed, curling mucro, 2.2–3 mm long, covered in white hairs; pinnae (12–) 14–16 (–18) pairs; pinnular rachis 5–6.5 cm long, markedly canaliculate on ventral side, densely white-pubescent, with 1 (–2) round nectaries between terminal pairs of leaflets, 0.2 mm in diameter; leaflets (55–) 61–69 (–75) pairs per pinna, (4–) 4.4–4.9 (–5.2) mm long, 0.8–1 mm wide, sessile or very short-petiolate, oblong, slightly acute at base, entire, glabrous, the margins ciliate, only midrib visible on ventral side, slightly displaced. Capitula 15–20 mm in diameter at anthesis, in fascicles of (3–) 4–7 in leaf axils, often densely packed on actively growing shoots, the buds lax (Fig. 13D), each capitulum with 45–65 flowers; peduncles 25–35 mm long, slender, angled, densely pubescent, with an involucre of fused bracts at the distal end. Flowers subtended by small peltate bracts, 1.3–1.5 mm long, 1 mm in diameter; calyx 1.3–1.5 mm long, pilose on outer surface, ciliate on lobe margins, pale whitish green; petals 3.8–4.1 mm long, united from base forming a corolla tube 3 mm long, pilose, ciliate on lobe margins, pale green; filaments 5.5–6.3 mm long, pale cream-white; anthers glabrous (Fig. 14B), pale cream-white, with a small rounded protrusion or apiculum on the connective (Fig. 14B, D); ovary 1.7–1.8 mm long, pilose on distal end (Fig. 13E), pale cream-white, with 28–34 ovules, style 6.2–6.8 mm long, pale cream-white, with a narrow-funnelform stigma, slightly exserted beyond the stamens. Pods 1–2 (–3) per capitulum, (12–) 14–18 (–21) cm long, (14–) 16–23 (–24) mm wide, pendulous, on short stipes, narrowly linear-oblong, acute at base, rounded at tip, usually with a short straight or recurved point, narrowly planocompressed, 16–24 (–26)-seeded, valves thin, chartaceous, dark brown, slightly lustrous, glabrous, the margins slightly thickened, dehiscent along both sutures. Seeds 6.5–7.9 mm long, 3.2–4.2 mm wide, narrowly oblong, slightly compressed, dark glossy chestnut-brown, aligned transversely in pods; pleurogram visible, regular, U-shaped, 95%, symmetrical. Chromosome number: 2n = 56 (Turner & Fearing 1960; González et al. 1967). Fig. 37.

Phenology. Flowering (November–) February–July (–August); fruiting August–November.

Distribution (Fig. 38). *Leucaena pulverulenta* is distributed primarily along the wet, east-facing slopes of the Sierra Madre Oriental in northeastern Mexico from around Misantla in central Veracruz, north through Hidalgo, San Luis Potosí, and Tamaulipas to around Monterrey, Nuevo León. It is also found in some areas on the lower coastal plains surrounding the Gulf of Mexico, extending north into Texas, U.S.A. In Texas, *L. pulverulenta* is commonly cultivated as an ornamental in towns, especially in southern Texas in Cameron and Hidalgo Counties, but also further north, for example in Kingsville. It was also reported as an ornamental from New Orleans, Louisiana, by Sargent (1921). In parts of southern Texas it is abundant and weedy, forming thickets along roadsides, canal banks, and on waste ground. Because *L. pulverulenta* is both cultivated and weedy, it has been speculated that this species may be introduced to Texas, but Sargent (1889) and Isely (1973) report large trees to 20 m tall that are apparently indigenous in the lower Rio Grande Valley. More northerly occurrences in Texas may indeed be introductions, with trees killed back following occasional severe frosts (Glumac et al. 1987; Correll & Johnston 1970). *Leucaena pulverulenta* occurs as an understory tree in a variety of forest types from moist evergreen submontane *Liquidambar-Podocarpus* forest to drier oak or pine-oak forest and extending into dry matorral in some areas. It also occurs abundantly in secondary vegetation, along roadsides, and in bush fallows (milpas). *Leucaena pulverulenta* also occurs spontaneously in parts of western Java, Indonesia, especially around Bandung (Nielsen 1992b), where it is introduced in cultivation (Dijkman 1950); 0–1400 (–1850) m.

Vernacular names. *Barba de chivo* (San Luis Potosí); more widely in Mexico: *guache, guache de monte, guaje, guaje de monte, guajillo, huash, huaxe*; *liliakiwi* (Totonaco, considered a wild form of *liliak, L. leucocephala*); *thuk* (Huastec) San Luis Potosí and Veracruz; *timbre, tzuqui, palo seco* (San Luis Potosí); *tze* (= *guaje* in Mazateco); *tepeguaje* in Texas.

REPRESENTATIVE SPECIMENS. **U.S.A.** CALIFORNIA: Los Angeles, Elytian Park, Los Angeles, *J. R. Brown s.n.* (CAS); Santa Barbara, UCLA Botanical Garden, *E. McClintock s.n.* (CAS).—TEXAS: Cameron Co., 3 km SE of Southmost along the Rio Grande, *Correll 17924* (GH, TEX); Ray's Ranch below Southmost in Palm Hammock, *Correll 27665* (NY, TEX); Las Palmas Ranch, nr Brownsville, 25°54′N, 97°30′W, *Ferris & Duncan 3157* (CAS, MO, NY), *Lundell & Lundell 8690* (MO, TEX, UC, US), *Runyon 202* (US); Resaca Levee, 26°02′N, 97°45′W, *M. C. Johnston s.n.* (TEX); nr Point Isabel, 26°04′N, 97°13′W, *Runyon 5859* (GH, TEX, UC); Rio Grande Valley below Donana, around Brownsville, 25°55′N, 97°31′W, *A. Schott s.n.* (US); 1122 E Polk Street in Harlingen, 26°12′N, 97°45′W, *Traverse 1114* (F, GH, MO, TEX, US); Santa Maria, 26°05′N, 97°51′W, *J. G. Tucker s.n.* (US). Hidalgo Co., along the Rio Grande S of Alamo, 26°05′N, 98°07′W, *Clover 455* (NY); Progreso, 25°04′N, 97°57′W, *Parks 2458* (MO); 5 km N of Edinburg, 26°18′N, 98°09′W, *Whitehouse 44262* (GH). Kenedy Co., 70 km S of Kingsville, off Hwy 77, 26°48′N, 97°47′W, *Stanford 497* (TEX). Kleberg Co., W of barricade on King St., W of Nimitz St., Naval Air Station, Kingsville, Ricardo Quadrangle, 27°29′N, 97°49′W, *Carr 12080* (TEX). Willacy Co., Farm rd 186, 8 km W of Raymondville, 26°21′N, 97°56′W, *Rios & Cavazos 276* (TEX).

Mexico. HIDALGO: Km 178, rd from Pachuca to Tampico via corta, 13 km S of Tepemaxac, *Grethur 592* (MEXU); rd NE from Jacala towards Tamazunchale, 7 km NE of Chapalahuacan, 22 km SW of Tamazunchale, 21°11′N, 98°53′W, *Hughes 1590* (E, FHO, K, MEXU, MO, NY), *Hughes 1857* (FHO, K, MEXU, MO, NY); rd 12 km SW from Huejutla de Reyes towards Pachuca and Zacualtipán, 21°05′N, 98°29′W, *Hughes 1611* (E, FHO, K, MEXU, MO, NY); nr Huejutla, 21°07′N, 98°25′W, *Seler & Seler 891* (GH); 24 km NW of Huejutla rd to San Felipe Orizatlán, 21°10′N, 98°31′W, *R. Torres 3084* (MEXU, TEX); 64 km NE of Jacala, 10 km SW of the limit

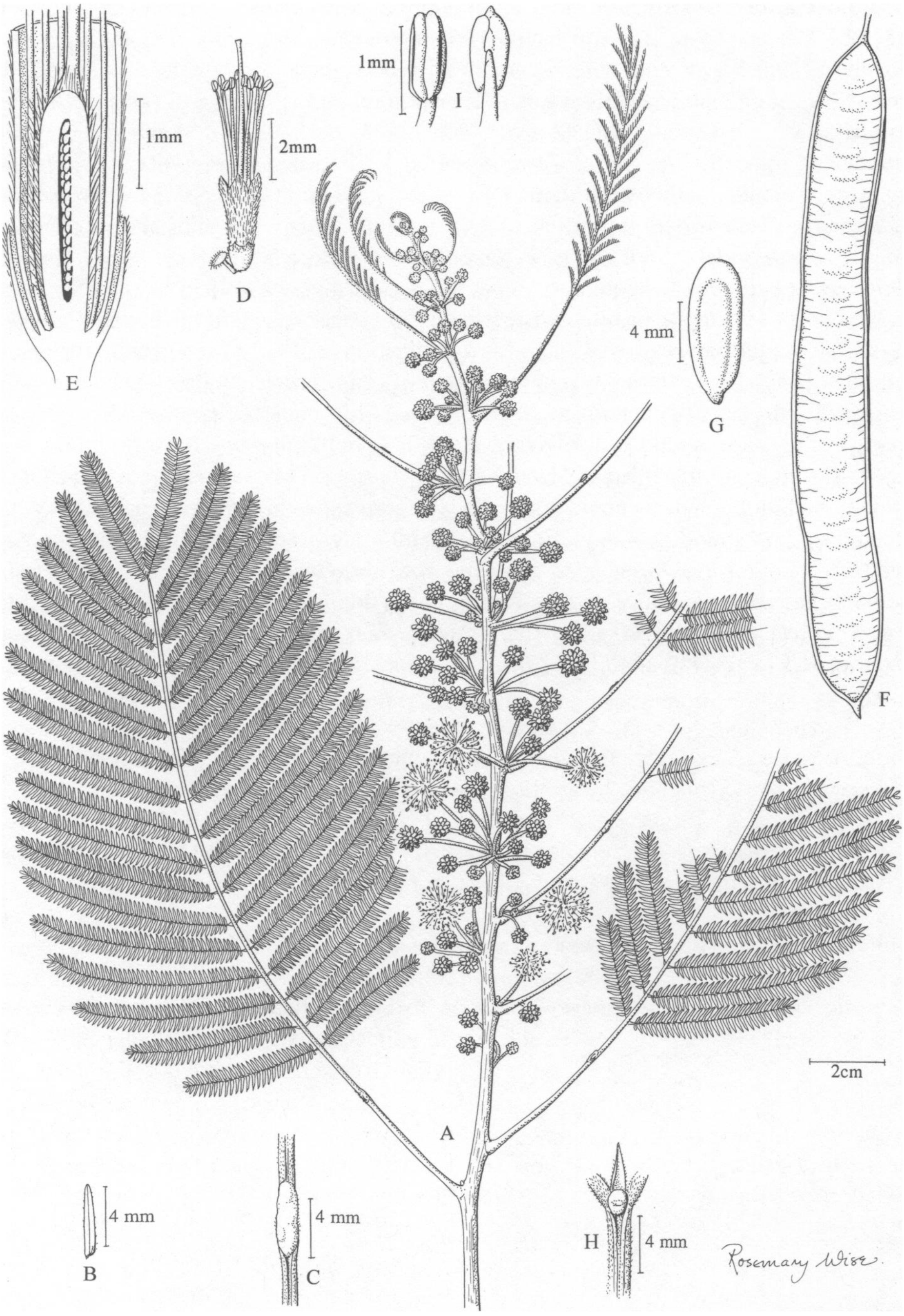


FIG. 37. *Leucaena pulverulenta*. A. Flowering shoot and leaves. B. Leaflet. C. Petiolar nectary. D. Flower. E. Longitudinal section of flower. F. Pod. G. Seed. H. Rachis nectary and mucro. I. Anthers. (Based on: A–E, *Hughes 1593*; F, G, *Hughes 1052*; H, *Hughes 1866*; I, *Hughes 1859*.)

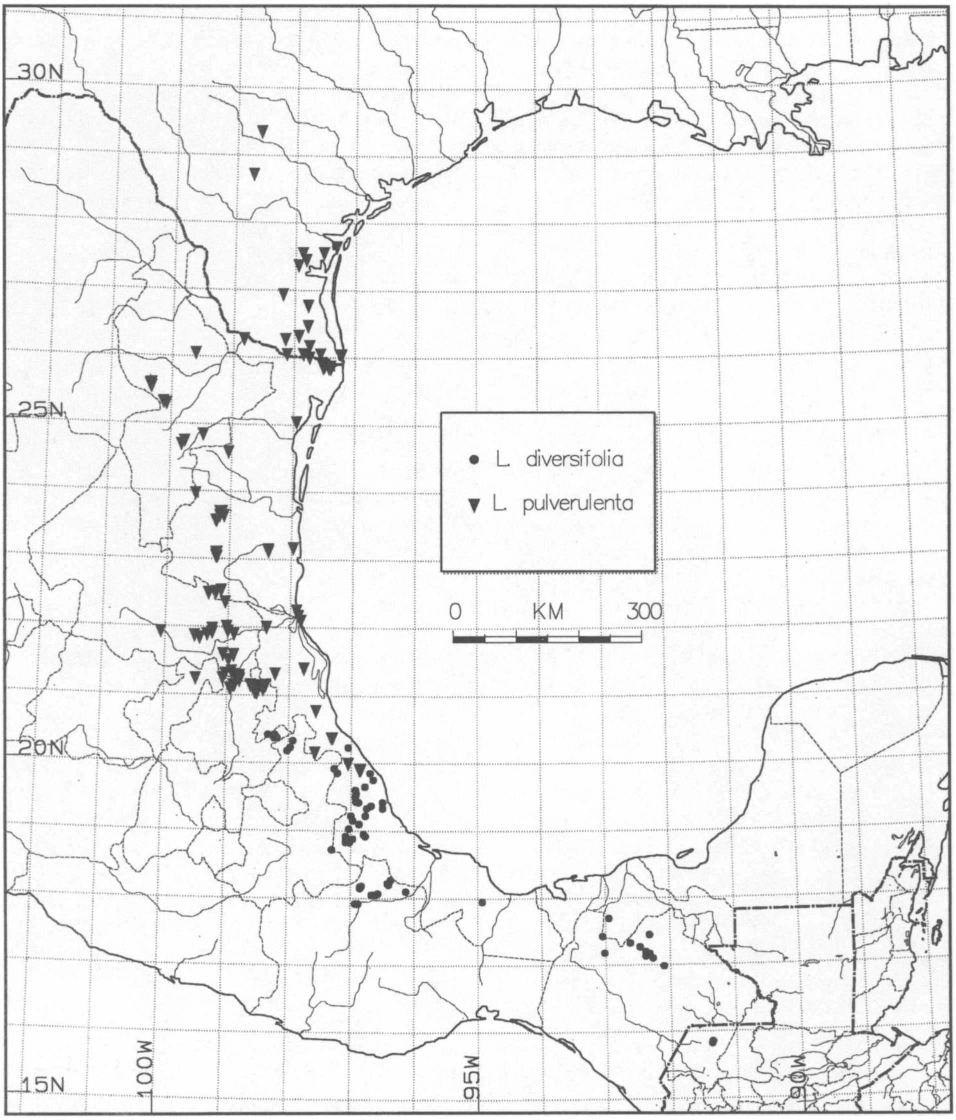


FIG. 38. Distribution of *L. pulverulenta* and *L. diversifolia.*

with San Luis Potosí, rd Jacala to Tamazunchale, 21°08′N, 98°57′W, *Zárate 314* (MEXU).—NUEVO LEÓN: Horse Tail Falls nr Santiago, 25°21′N, 100°08′W, *Chase 7797* (GH, MO, NY, TEX); Ejido Guadelupe nr Linares, 24°53′N, 99°28′W, *Estrada 378* (MEXU, MO); Ejido Santa Rosa, nr Iturbide, 24°44′N, 99°49′W, *Estrada 1518* (MEXU, TEX); rd W from Linares into Sierra Madre Oriental to San Roberto, 10 km E of Iturbide, 24°47′N, 99°46′W, *Hughes 1047* (FHO, K, MEXU); Dulces Nombres, Sierra Madre Oriental just E of border with Tamaulipas, 24°00′N, 99°34′W, *Meyer & Rogers 2958* (GH, MO); Sierra Madre nr Monterrey, 25°37′N, 100°21′W, *Pringle 2510* (F, GH, K, MEXU, MO, NY, US), *Pringle 11430* (CAS, F, GH, K, US), *Pringle 2090* (A, F, US); rd to Los Cuñados, nr Chipinque, Monterrey, *R. F. Smith M281* (TEX); just below Chipinque Mesa, 5 km SW of Monterrey, 25°37′N, 100°21′W, *B. L. Turner 3979* (TEX); 32 km NW of Montemorelos, 25°20′N, 100°05′W, *Weaver 541* (GH, TEX).—QUERÉTARO: rd 10 km NNE from Jalpan de la Sierra towards Río Verde, 21°16′N, 99°30′W, *Hughes 1600* (E, FHO, K, MEXU, MO, NY).—SAN LUIS POTOSÍ: San Antonio, 21°37′N, 98°54′W, *Alcorn 2951* (MEXU, TEX); nr Tamazunchale, 21°16′N, 98°48′W, *Edwards 603* (F); 85 km E of San Luis Potosí, rd to Río Verde, 21°57′N, 100°04′W, *A. Gentry 20460* (US); rd W towards Jalpan de la Sierra and Xilitla, 6 km from Tamazunchale to Valles rd nr Axtla de Terrazas, 21°23′N, 98°56′W, *Hughes 1593* (E, FHO, K, MEXU, MO, NY); rd E from San Luis Potosí towards Ciudad Valles, 50 km E of Río Verde, 10 km E of turnoff to Rayón, 21°54′N, 99°32′W, *Hughes 1603* (E, FHO, K, MEXU, MO, NY); outskirts of Ciudad Valles, 3 km from city, rd S towards Tamazunchale 500 m from jctn to Tampico, 21°58′N, 99°00′W, *Hughes 1605* (E, FHO, K, MEXU, MO, NY); 12 km E of Ciudad Valles, rd to Tamiun Abra Mtns, 21°56′N, 98°54′W, *M. C. Johnston 5398* (MEXU, TEX); mtns along rd to Jalpan, 14 km NE of Xilitla, 21°17′N, 99°04′W, *King 4316* (NY, TEX, US); Rascón, 21°57′N, 99°15′W, *Purpus 5278* (UC); hills 48 km W of Ciudad Valles, Hwy 86, 21°55′N, 99°20′W, *Roe 195* (NY); 4 km NW of Estación Rascón, nr Tamasopo, 22°00′N, 99°15′W, *Rzedowski 6994* (TEX); Chupaderos, nr Cd. del Maíz, 22°32′N, 99°19′W, *Rzedowski 7412* (MEXU); 2 km W of Aquismón, 21°38′N, 99°04′W, *Rzedowski 10175* (MEXU); N outskirts of Ciudad Valles, 22°02′N, 99°01′W, *Wiggins 13347* (MEXU, NY); 73 km NE of Ciudad Valles, rd to San Luis Potosí, 21°52′N, 99°27′W, *Zárate 326* (MEXU); "El Picacho," km 26 rd from Cd. Victoria to San Luis Potosí, *Zárate 398* (MEXU).—TAMAULIPAS: La Vegonia, nr San José, 22°24′N, 99°03′W, *Bartlett 10527* (MEXU, US); Pico del Diablo, nr Marmolejo, Sierra de San Carlos, 24°37′N, 99°03′W, *Bartlett 10935* (CAS, F, GH, NY, US); from Victoria to Tula, canyons nr Palonilla, 23°44′N, 99°08′W, *Berlandier 2227* (F, GH, K); 8 km W of jctn of Hwys 80 and 85 on Hwy 80, W of Antiguo Morelos, 22°34′N, 99°07′W, *Dunn 17585* (MEXU); Wartenberg, nr Tantoyuca in the Huasteca, 21°21′N, 98°14′W, *Ervendberg 6* (GH, NY); rd 30 km SW from Cd. Victoria to Tula and San Luis Potosí about 30 km, nr Altas Cumbres, E slope of Sierra Madre Oriental, 23°36′N, 99°14′W, *Hughes 1051* (FHO, K, MEXU), *Hughes 1052* (FHO, K, MEXU), *Hughes 1053* (FHO, K, MEXU); Sierra de Tamaulipas, rd from Rancho Las Yucas to Santa María de los Nogales and Hacienda Acuña, nr Villa de Casas, 23°11′N, 98°22′W, *F. M. Martínez F-2040* (TEX); 10 km NW of Gómez Farías mid E slopes, Sierra de Guatemala, 23°05′N, 99°13′W, *McCarter & Hughes 89* (FHO, MEXU); 42 km NE of Aldama, 23°12′N, 97°58′W, *Medraño 3162* (MEXU); between Torrecillas and Pénjamo, nr González, 23°09′N, 98°22′W, *Medraño 7293* (NY).—VERACRUZ: Silo Súchil, nr Tantoyuca, 21°21′N, 98°17′W, *Alcorn 2310* (TEX); rd from Misantla to Martínez de la Torre, 7 km from Santa Cruz, 20°01′N, 97°03′W, *Castilleja 15* (F, MEXU); Cerro del Carbón, nr Papantla, 20°24′N, 97°18′W, *M. E. Cortés 471* (MEXU); Chaca, 25 km W of Pánuco, 22°02′N, 98°23′W, *C. Gutiérrez 2518* (MEXU); 12 km NW of Naranjos, 0.5 km W of Hwy 180, Brecha Microwave stn, 21°26′N, 97°46′W, *Hansen & Nee 1781* (MEXU, TEX, US); 13 km N of Tihuatlán, Hwy 130 S from Álamo to Poza Rica, 20°48′N, 97°34′W, *Hughes 1862* (CAS, FHO, K, MEXU, MO, NY); 1 km S of El Chote, rd from Poza Rica SE to Martínez de la Torre, 20°24′N, 97°19′W, *Hughes 1863* (FHO, K, MEXU, MO, NY, TEX); 6 km N of Misantla, 37 km SE of Martínez de la Torre, 19°56′N, 96°51′W, *Hughes 1866* (FHO, K, MEXU, MO, NY, TEX); nr Congregación Buenos Aires, Alto Lucero, *Márquez 577* (K, MEXU, NY); 3 km NE of Huejutla, rd to Plantón Sánchez nr Chalma, 21°11′N, 98°23′W, *Nee 18424* (F, GH, MEXU); Tampico, 22°12′N, 97°52′W, *Palmer 413* (GH, K, MO, NY, US); Cerro Akgmuxni, W of Chapultepec, nr Coxquihui, 20°11′N, 97°35′W, *Tenorio 8545* (MEXU, MO); Cerro Monte de Oro, *C. Vázquez 591* (MEXU).

Brazil. SÃO PAULO: Campinas, cultivated, *Lima 7281* (UC).

Leucaena pulverulenta is unique within the genus in possessing basally connate petals, a character state associated with other genera such as *Alantsilodendron, Dichrostachys,* and *Calliandropsis*. Other unusual character states include glabrous anthers, a chromosome number of $2n = 56$ (shared with *L. retusa* and *L. greggii*), and presence of a small rounded apiculum on the connective of the anther (shared with *L. retusa* and *L. cuspidata*). In addition, Zárate (1994) pointed out the unusual spiral phyllotaxy found in *L. pulverulenta* (shared with *L. diversifolia* and *L. leucocephala*). Although detailed investigation of phyllotaxy has not been carried out, most other species in the genus appear to have distichous patterns. Finally, the young shoots and developing leaves of *L. pulverulenta* are densely covered in a white or whitish grey tomentum, which is also unique within the genus. Thus *L. pulverulenta* is an extremely unusual species within the genus. Its affinities lie first with *L. retusa* and *L. greggii*, as discussed above for those species, but also with the two tetraploid species *L. leucocephala* and *L. diversifolia* (see below).

Evidence from the analysis of cpDNA restriction site data suggests a close relationship among the cpDNA genomes of *L. pulverulenta, L. leucocephala,* and *L. diver-*

sifolia (Fig. 31) (Harris et al. 1994a; Hughes & Harris, 1998). This suggests *L. pulverulenta* as the most likely maternal parent for these two tetraploids, given the maternal inheritance of the chloroplast genome in *Leucaena* (Harris, unpubl.). The sympatric occurrence of all three species in central Veracruz, Mexico, is consistent with this hypothesis.

A close relationship between *L. pulverulenta* and *L. diversifolia* is also suggested by morphological similarities, and *L. diversifolia* is the species most likely to be confused with *L. pulverulenta,* particularly in areas where the two occur sympatrically (see Fig. 38, e.g., around Misantla in Veracruz, Mexico; *Hughes 1865, 1866*). The two species have very similar leaves in terms of numbers of pairs of pinnae, number of pairs of leaflets and size of leaflets, the pods are almost identical, and the inflorescence is similarly lax as seen in bud with few flowers per capitulum. These similarities have resulted in significant confusion over the identity of material from northern Oaxaca, which Zárate (1984a) attributed to *L. pulverulenta* subsp. *brachycarpa*, a taxon he later hypothesized to be of hybrid origin between *L. diversifolia* and *L. leucocephala* (Zárate 1994). All material south of Misantla is here referred to *L. diversifolia. Leucaena pulverulenta* is distinguished from *L. diversifolia* by its characteristic whitish grey tomentum, its lumpy verrucate, as opposed to cupulate, elliptic, extrafloral nectary, its glabrous anthers, and cream-white, as opposed to pinkish, flowers (see also discussion under *L. diversifolia*).

A number of putative hybrids between *L. pulverulenta* and *L. leucocephala* have been reported from Indonesia (Dijkman 1950; Lowry et al. 1984) and Texas (Correll & Johnston 1970). The identity of these putative hybrids has not been confirmed, and I have seen no material of them. Hybrids are most likely to be the result of artificial sympatry following cultivation of one or both parents, as hypothesized by Correll and Johnston (1970). The hybrids, being triploid, are weakly fertile and, in Indonesia, have been propagated by grafting for use as shade trees over tea, where seedless varieties are preferred to avoid regeneration and weed problems (Dijkman 1950).

Leucaena pulverulenta is known for food and medicinal use (Alcorn 1984). Zárate (1994) reports that the unripe seeds and flower buds are eaten raw with enchiladas.

5. Leucaena diversifolia (Schlechtendal) Bentham, Hook. J. Bot. 4: 417. 1842. *Acacia diversifolia* Schlechtendal, Linnaea 12: 570. 1838.—TYPE: MEXICO. Veracruz: "in sylvis prope Jalapam," Aug 1828, 19°26′N, 96°55′W, *Schiede 693* (holotype: HAL!; isotypes: GH! NY!).

Leucaena laxifolia Urban, Symb. antil. 2: 266. 1900.—TYPE: MEXICO. Without locality data, 1833, *Sommerschuh s.n.* (holotype: B, destroyed; isotypes: US! NY!).

Leucaena brachycarpa Urban, Symb. antil. 2: 265. 1900. *Leucaena pulverulenta* var. *brachycarpa* (Urban) S. Zárate, Bull. Intern. Group Study of Mimosoideae 12: 131. 1984.—TYPE: MEXICO. Veracruz: Tuspango nr Córdoba, 18°50′N, 97°01′W, 2 Jun 1865, *Bourgeau 2401* (lectotype, designated by Zárate, 1994: BR; isolectotypes: F! K! US!).

Small to medium-sized tree, 5–18 (–20) m tall, 20–50 cm bole diameter, usually slender with a clear bole up to 10 m and a light feathery but spreading crown. Bark on young branches smooth, rougher on bole, mid-grey-brown with shallow rusty orange-brown vertical fissures (Fig. 2C), the inner bark green then cream. Shoots terete, mid-orange-brown, thickly covered with dense white velutinous pubescence. Stipules 3.4–4.4 mm long, ovate with a subulate or long-pointed apex, with a prominent midrib and broad asymmetric basal wings, margins ciliate, persistent. Leaves (17–) 19–24 (–28) cm long, (6–) 8–11 (–13) cm wide; petioles (including pulvinus) (16–) 18–23 (–30) mm long; rachis (12–) 16–19 (–23) cm long, strongly canaliculate and densely covered in velutinous white pubescence, with a single sessile, discoid or shallowly crateriform, elliptic or sometimes rounded-triangular nectary (Fig. 9E), (2.2–) 3–4.5 (–5.4) mm long, 1.4–2.6 mm wide, 1 mm tall, on ventral side of petiole at base of the lower pair of pinnae, with an additional 1 or 2 similar but smaller nectaries 1–1.8 (–2.3) mm long, 0.7–1.3 mm wide, at base of terminal pair of pinnae, apex of rachis extending beyond the terminal pinnae in a slender pointed mucro, (2.5–) 3–4 (–4.7) mm long, covered in white hairs; pinnae (14–) 16–24 (–28) pairs; pinnular rachis (3.5–) 5–7 (–8) cm long, markedly canaliculate on ventral side, densely white-pubescent, with 1 or 2 elliptic nectaries, 0.4–0.5 × 0.2–0.3 mm, at base of terminal pairs of leaflets; leaflets (43–) 48–58 (–62) pairs per pinna, (2.9–) 4–5.5 (–7) mm long, (0.6–) 0.8–1 (–1.2) mm wide, sessile or very short-petiolate, linear-oblong, acute at apex, cordate/cuneate and strongly asymmetric at base, entire, glabrous, the margins strongly ciliate, only midrib visible on ventral side, strongly asymmetric. Capitula 11–15 mm in diameter at anthesis, in fascicles of (1–) 4–5 (–7) in leaf axils, on actively growing auxotelic shoots with coeval leaf development, the buds lax, each capitulum with (45–) 50–70 (–90) flowers; peduncles (12–) 17–23 mm long, slender, angled, densely pubescent, with an involucre of fused bracts at the distal end. Flowers subtended by squat peltate bracts, (1–) 1.1–1.5 (–1.9) mm long, densely hairy; calyx (1.5–) 1.7–2 (–2.6) mm long, pilose on outer surface, ciliate on lobe margins, pale green; petals 3.4–4.1 (–4.4) mm long, partially connate along mid-portion of petals but free at the base, pilose, ciliate on lobe margins, pale green, the lobe tips strongly tinged reddish; filaments (4–) 5.5–7.2 (–8.5) mm long, white, sometimes tinged pink and occasionally bright scarlet; anthers sparsely hairy at distal end or occasionally glabrous, pale cream-white, pale pink, bright shocking pink, or occasionally bright scarlet, occasionally with a small rounded apiculum (usually absent); ovary (1.5–) 1.8–2.1 (–2.2) mm long, pale cream-white, hairy on distal half, with 18–22 ovules, style (7.4–) 8–9.8 mm long, white, white tinged pink, pink, or occasionally bright scarlet, with a narrow funnelform stigma, exserted beyond the anthers. Pods (1–) 3–6 (–7) per capitulum, (7–) 10–13 (–15.5) cm long, (11–) 13–16 (–17) mm wide, pendulous, on 3–11 mm long stipes, narrowly linear-oblong, acute at base and apex, usually with a short, straight or recurved point, flat, (6–) 10–18 (–20)-seeded, valves thin, membranous, dark brown or reddish brown, sometimes lustrous, glabrous or covered in dense velutinous pubescence, the margins slightly thickened, dehiscent along both sutures. Seeds 2.7–3.4 mm long, 4.3–5.5 mm wide, narrowly oblong, slightly compressed, dark glossy chestnut-brown, aligned transversely in pods; pleurogram visible, regular, U-shaped, with 95% arm extension, symmetrical. Chromosome number: $2n = 104$ (Pan & Brewbaker 1988). Fig. 39.

Phenology. Flowering (February–) May–June (–December); fruiting (June–) August–February (–April).

Distribution (Fig. 38). *Leucaena diversifolia* is distributed along a narrow belt at mid-elevations on the moist Gulf-facing slopes of the Sierra Madre Oriental of central and southern Mexico from Hidalgo south through Veracruz, northern Oaxaca, and Tabasco to northern Chiapas, and the northern fringes of the Guatemalan Department of Huehuetenango on the wet north-facing slopes of the Sierra de los Cuchumatanes. Taxonomic confusion and misidentification have meant that most previous authors have considered *L. diversifolia* to be much more restricted than this, occurring only in central Veracruz, around Jalapa (Brewbaker 1987a; Zárate 1994). *Leucaena diversifolia* has been introduced outside its native range in historical times into Jamaica, Martinique (from where it was

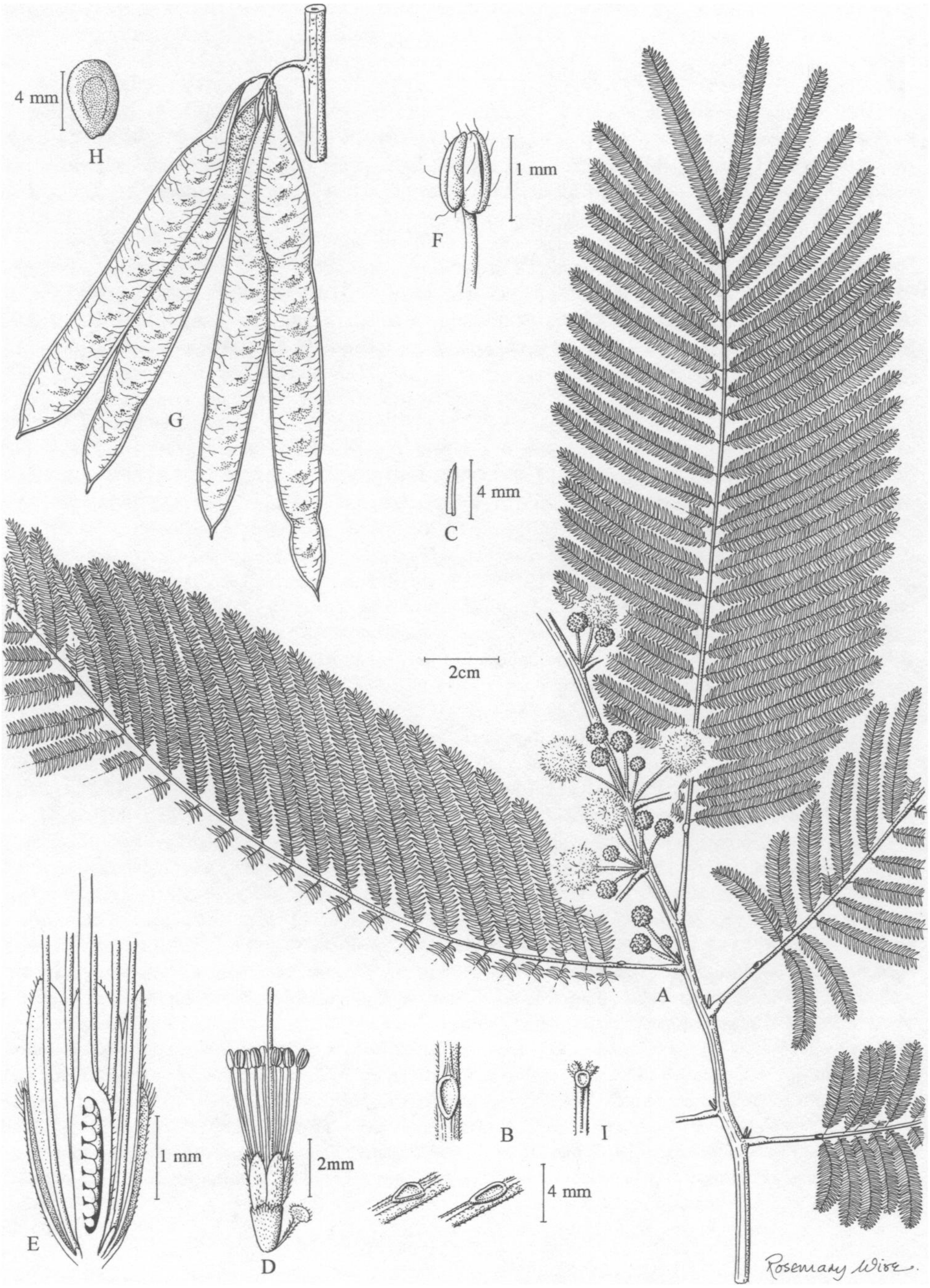


FIG. 39. *Leucaena diversifolia*. A. Leaves and flowering shoot. B. Extrafloral nectaries. C. Leaflet. D. Flower. E. Longitudinal section of flower. F. Anther. G. Pods. H. Seed. I. Nectary at apex of rachis. (Based on: A–C, *Hughes 1864*; D–F, *Hughes 1867*; G– I, *Hughes 1733*.)

described as *L. brachycarpa*, see below; Adams 1972: 338), Indonesia, usually for use as a shade tree for coffee, and much more widely in the last two decades. The natural distribution of *L. diversifolia* corresponds to a narrow belt of moist or very moist submontane evergreen forest, subject to frequent mist and cloud cover. Associated trees include *Albizia purpusii, Alnus acuminata, Liquidambar styraciflua, Platanus mexicana, Pinus chiapensis, P. maximinoi, Brosimum alicastrum, Cordia alliodora,* and species of *Quercus, Salix, Lonchocarpus*, and *Cecropia*. *Leucaena diversifolia* also grows, sometimes abundantly, in secondary vegetation with other small woody leguminous trees and shrubs, including *Acacia angustissima, A. pennatula, Calliandra calothyrsus, C. houstoniana, Desmanthus pubescens, Gliricidia sepium,* and *Zapoteca tetragona*. Towards the northern limits of the distribution, around Misantla and María de la Torre in Veracruz, it is sympatric with *L. pulverulenta*. *Leucaena leucocephala* is found cultivated throughout the range of *L. diversifolia*; 30–1500 (–1740) m.

Vernacular names. *Chalíp, guash* (Huehuetenango, Guatemala), *shashíb, shashíbte* (Tzeltal, Chiapas, Mexico), *guache, guashí* (Hidalgo, Mexico), *guaje* (Oaxaca, Veracruz), *guaje blanco, guajillo, guaje del río* (Veracruz, Mexico), *wild tamarind* (Jamaica: not distinguished from *L. leucocephala*).

REPRESENTATIVE SPECIMENS. **Jamaica.** ST. ANDREW: nr Hope, 18°00′N, 76°45′W, *Campbell 6425* (NY); below Content Gap, 18°02′N, 76°40′W, *W. Harris 12342* (K, NY, US); below Guava Ridge, 18°01′N, 76°40′W, *W. Harris 12451* (CAS, GH, K, NY, US); rd Kingston towards Guava Ridge and N to Content Gap and St. Peters, 21.6 km from jctn. off Kingston to Newcastle rd, just above Wallenford Factory, 18°04′N, 76°41′W, *Hellin & Lewis 1* (FHO, UCWI); same locality, 24 km from jctn. off Kingston to Newcastle rd, just above Wallenford Factory, 18°04′N, 76°41′W, *Hellin & Lewis 2* (FHO, UCWI), *Hellin & Lewis 10* (FHO, UCWI); S slope of Silver Hill Gap, 18°06′N, 76°41′W, *Proctor 23721* (TEX); St. Thomas, 17°57′N, 76°27′W, *Proctor 24021* (GH); Wistphalia, *Watt 8835* (NY). **Martinique.** Introduced, cultivated in Botanic Garden of St Pierre, reported to be of Mexican origin, *Duss 1163b* (NY).

Mexico. CHIAPAS: nr rd 15 km NNW from Ocosingo towards Palenque, 4 km ESE of the turnoff to Yajalón, 16°59′N, 92°06′W, *Hughes 1733* (E, FHO, K, MEXU, MO, NY); Solusuchiapa, 20 km SE of Pichucalco, Hwy 195 from Villahermosa to Tuxtla Gutiérrez, 17°26′N, 93°03′W, *Hughes 1886* (CAS, FHO, K, MEXU, MO, NY); 10 km WNW of Yajalón, rd 4 km E of Petalcingo, valley of the Río Grande, 17°12′N, 92°23′W, *Hughes 1887* (CAS, FHO, K, MEXU, MO, NY); 1 km N of Yajalón, nr rd to Petalcingo, 17°10′N, 92°19′W, *Hughes 1889* (CAS, FHO, K, MEXU, MO, NY); Kakate, nr Yajalón, 17°16′N, 92°28′W, *Shilom Ton 4444* (CAS, MEXU, MO); rd to Colonia E. Zapata, nr Yajalón, 17°08′N, 92°23′W, *Shilom Ton 5547* (MEXU); Venustiano Carranza, Finca Carmen, nr Sabanilla, 17°20′N, 92°37′W, *Shilom Ton 6328* (CAS, MEXU); Rancho Pulpitillo, nr Yajalón, 17°27′N, 92°19′W, *A. Shilom Ton s.n.* (MEXU).—HIDALGO: Calinola, rancheria of San Bartolo Tutotepec, 20°22′N, 98°11′W, *Gimate 908* (MEXU); rd 3 km NE from Tenango de Doria to San Bartolo Tutotepec, above Río Pantepec, 20°22′N, 98°14′W, *Hughes 1612* (E, FHO, K, MEXU, MO, NY); track 8 km N from San Bartolo Tutotepec towards Tuto and San Jerónimo, N side of Río Pantepec, 20°25′N, 98°13′W, *Hughes 1613* (E, FHO, K, MEXU, MO, NY).—OAXACA: rd SW to Temascal from rd between Tierra Blanca and Tuxtepec, 10 km NE of Temascal, 18°16′N, 96°22′W, *Hughes 1310* (CR, FHO, K, MEXU, NY); Presa Miguel Alemán, 2 km NW of Temascal or 35 km N of Tuxtepec, 18°13′N, 96°24′W, *Hughes 1311* (FHO, K, MEXU, NY); rd W from Jalapa de Díaz to Huautla, N side of Río Santo Domingo, 50 km W of Tuxtepec, 18°03′N, 96°36′W, *Hughes 1314* (FHO, K, MEXU, NY); Río Santo Domingo gorge, nr rd ENE from Cuicatlán through Santiago Quiotepec to San Isidro Buenos Aires, 2 km W of San Juan Coyula, Sierra Mazateca, 17°55′N, 96°56′W, *Hughes 1649* (E, FHO, K, MEXU, MO, NY); gorge Río Santo Domingo, nr track from Cuicatlán ENE through Santiago Quiotepec to San Isidro Buenos Aires, 2 km NE of San Juan Coyula, Sierra Mazateca, 17°55′N, 96°53′W, *Hughes 1651* (E, FHO, K, MEXU, MO, NY); nr San Bartolomé Ayautla, 22 km W of Jalapa de Díaz, rd to Huautla de Jiménez, 18°03′N, 96°39′W, *Hughes 1669* (E, FHO, K, MEXU, MO, NY); 9 km E of San Jerónimo Tecoatl, 2 km NW of Puente de Fierro, distr. of Teotitlán del Camino, 18°10′N, 96°51′W, *Sousa 9342* (CAS, MEXU, MO, UC); María Luisa, 5 km SW of Santa María Chichotla, Teotitlán del Camino, 18°11′N, 96°50′W, *Sousa 9353* (MEXU); Temascal, next to the dam, 18°12′N, 96°24′W, *Sousa 8837* (UC); Huautla de Jiménez, 1 km NE of Puente de Fierro in the canyon, distr. of Teotitlán del Camino, 18°09′N, 96°51′W, *Sousa 9350* (CAS, MEXU, MO, UC); María Luisa, 5 km SW of Santa María Chichotla, distr. of Teotitlán del Camino, 18°11′N, 96°50′W, *Sousa 9352* (UC); N side of

Tuxtepec, exit to Cd. Alemán, 18°06′N, 96°08′W, *Sousa 11663* (K).—PUEBLA: 2 km S of Nuevo Necaxa, 20°11′N, 98°01′W, *Basurto & Durán 476* (MEXU, MO); mid E escarpment of Sierra Madre Oriental, 4 km NE of Villa Juárez, Mex Hwy 130 to Poza Rica, 20°20′N, 97°56′W, *Marcks 815* (TEX).—TABASCO: 40 km S of Villahermosa, rd to Teapa, 17°42′N, 92°57′W, *Hughes 1885* (CAS, FHO, K, MEXU, MO, NY); 34 km N of turnoff to Pichucalco, 17°11′N, 93°01′W, *Téllez 651* (MEXU).—VERACRUZ: 2 km N of Atoyac, 18°55′N, 96°46′W, *Acavedo 381* (XAL); nr El Trapiche and Teocelo, 19°22′N, 96°58′W, *Barrera 134* (MEXU); 5 km W of Fortín de las Flores, 12 km E of Córdoba, 18°52′N, 97°04′W, *Brewbaker 22* (MEXU); 3 km W of Córdoba, 18°53′N, 96°58′W, *Brewbaker 23* (MEXU); Tonayán, Congregación de Ixtapan, Sierra de Chiconquiaco, 19°39′N, 96°55′W, *Calzada 2102* (F, TEX); Tepetlán, between Pactapec and San Pablo Coapa, 19°39′N, 96°47′W, *Cházaro 1280* (F); Cerro Gordo, nr Dos Ríos, 19°27′N, 96°41′W, *Dorantes 368* (F, K, MEXU, MO); 6.5 km W of Tlapacoyan, rd to Teziutlán, 19°55′N, 97°16′W, *Gómez-Pompa 1134* (CAS, F, GH, MEXU); nr Paso de las Milpas, rd from El Rinconada towards Actopan, 19°25′N, 96°30′W, *Hughes 910* (FHO, K, MEXU); nr La Bocana, 45 km SE of Xalapa rd to Veracruz, 19°25′N, 96°25′W, *Hughes 912* (FHO, K, MEXU); nr Corral Falso, 25 km from Xalapa to Veracruz, 19°27′N, 96°41′W, *Hughes 916* (FHO, K, MEXU); 6 km SE of Xalapa, nr rd to Veracruz a few km from Las Trancas, 19°32′N, 96°55′W, *Hughes 921* (FHO, K, MEXU); 12 km N of María de la Torre, rd NW from Martínez de la Torre through El Chote to Poza Rica, 20°14′N, 97°03′W, *Hughes 1864* (FHO, K, MEXU, MO, NY, TEX); 7 km N of Misantla, 36 km SE of Martínez de la Torre, 19°57′N, 96°52′W, *Hughes 1865* (FHO, K, MEXU, MO, NY, TEX); 8 km SSW of Tuzanapan, 4 km WNW of Jalcomulco on the Coatepec-Huatusco rd, in the valley of the Mesa Olivera, 19°21′N, 96°49′W, *Hughes 1871* (CAS, FHO, K, MEXU, NY, TEX); 3 km ENE of Acultzingo, 20 km SW of Orizaba rd from Orizaba to Tehuacán, 18°43′N, 97°18′W, *Hughes 1884* (FHO, K, MEXU, MO, NY, TEX); 16 km E of Acayucan, 17°57′N, 94°56′W, *C. D. Johnson 115-68* (MO); 9 km NE of Atzalan towards Tlapacoyan, edge of the Río Alseseca, 19°51′N, 97°13′W, *Lot 261* (NY); 1.5 km from Plan de Las Hayas, transect from Plan de Las Hayas to Palma Sola, 19°45′N, 96°39′W, *Lot 2042* (CAS, F, MO); Puente Nacional, 1 km SE of Palmillas, rd to barranca, 19°13′N, 96°46′W, *Medina & Vázquez 401* (XAL); nr Ingenio, Sierra de la Cruz, nr Orizaba, 18°50′N, 97°05′W, *F. Muller s.n.* (NY); nr Jalcomulco, 19°20′N, 96°45′W, *Nee 22448* (F, GH, MO, NY, TEX); Orizaba, 19°06′N, 96°52′W, *Nevling & Gómez-Pompa 2255* (F, K, MO); Jilotepec, 19°36′N, 96°56′W, *Ortega Ortíz 280* (F, MEXU, NY, UC); hills nr Jalapa, 19°30′N, 96°56′W, *Pringle 7759* (MO); Zacualpan, Veracruz, 20°25′N, 98°20′W, *Purpus 10674* (NY, US), *Purpus 10795* (NY, US); Monte Rey, Ejido Coetzalán, nr Axocuapam, 19°18′N, 96°42′W, *Robles 227* (MEXU); Cerro de Escarmela N of Orizaba, 18°52′N, 97°03′W, *Rosas 988* (F, GH, MEXU); Zapata, nr La Laja, between Corral Falso and Pinoltepec, rd from Veracruz to Jalapa, 16 km SE of Jalapa, 19°26′N, 96°45′W, *Sousa 4828* (MEXU); 3 km E of Tuzamapan, nr Coatepec, 19°22′N, 96°50′W, *M. Vázquez 2207* (F, NY); past Chasmán, rd from Orizaba to Huatusco about 16.5 km from Fortín, 19°02′N, 97°02′W, *Zárate 345* (MEXU); nr turnoff to Poxtla, rd from Xalapa to Huatusco, 19°13′N, 97°00′W, *Zárate 348* (MEXU); Col. Martires de Chicago nr Jalapa, 19°34′N, 96°54′W, *Zárate 357* (MEXU); La Concepción, 19°36′N, 96°56′W, *Zola Baez 450* (F, TEX).

Guatemala. HUEHUETENANGO: about 4 km NW of Barillas, track towards Florída, 15°51′N, 91°22′W, *Hughes 1693* (E, FHO, K, MEXU, MO, NY); rd 15 km E from San Mateo Ixtatán to Barillas, on hills 3–4 km W of Barillas, 15°49′N, 91°23′W, *Macqueen 357* (EAP, FHO, K, MEXU).

Brazil. SÃO PAULO: introduced, cultivated, Hacienda Santa Elisa, Campinas, *A. Daniel s.n.* (NY).

There has been considerable confusion over the identity, status, and relationships of *L. diversifolia*. The known tetraploid and diploid taxa are here treated as separate species, *L. diversifolia* (tetraploid) and *L. trichandra* (diploid). Most recent authors recognized the two cytotypes as subspecies of *L. diversifolia* (e.g., Brewbaker 1987a; Pan & Brewbaker 1988; Zárate 1994). Pan (1985, 1988) postulated that the tetraploid subspecies, which he designated as subsp. *diversifolia*, is an autotetraploid derived from diploid subspecies *trichandra*. The correct name for the diploid taxon was complicated by further confusion over the identity of *L. trichandra*. Zárate (1994) treated *L. trichandra* as a synonym of *L. diversifolia* subsp. *diversifolia*, and used the name *stenocarpa* for the diploid subspecies, a combination subsequently taken up by Hughes (1993) and Harris et al. (1994a). It is now clear that *L. trichandra* is not conspecific with *L. diversifolia* but corresponds to the widespread and variable diploid species as recognized by Pan (1988); as the older name, *L. trichandra* takes precedence over *L. stenocarpa*. The analysis of cpDNA of *Leucaena* by Harris et al. (1994a), placed *L. diversifolia* and *L. trichandra*, represented by 21 accessions, in two distinct clades (Harris et al. 1994a: 9; Fig. 31) separated by 63 synapomorphies, 17 of which were unique, and each supported by a 100% bootstrap value. The cpDNA analysis thus casts doubt on Pan's (1985) hypothesis that *L. diversifolia* is an autopolyploid derivative of diploid *L. trichandra,* whereby the two taxa would be expected to appear as sister taxa within the cpDNA tree (Soltis et al. 1992; Harris et al. 1994a).

Although the morphological differences between *L. diversifolia* and *L. trichandra* are limited largely to quantitative characters, treatment as separate species is justified not only on the results of the cpDNA analysis but also on other molecular data. Harris (unpubl. data) has shown that *L. diversifolia* and *L. trichandra* are readily separated by both isozyme and RAPD markers in addition to cpDNA markers. Pan (1988) described the differences between *L. diversifolia* and *L. trichandra* in quantitative leaf and flower characters, showing that *L. diversifolia* has larger leaves with more pairs of pinnae per leaf, longer pinnae, and more pairs of leaflets per pinna, larger stomatal guard cells, and larger flowers and pollen than *L. trichandra.* In addition, the anthers of *L. diversifolia* are only very sparsely hairy and occasionally have a minute cylindrical protrusion of the connective compared to the dense pilose anthers lacking any apiculum in *L. trichandra.* The corolla of *L. diversifolia* is generally partly connate along the mid-portion of the petals, whereas petals of *L. trichandra* are free.

The inclusion of *L. diversifolia* within the same plastome clade as *L. pulverulenta* indicates the other parental lineage of *L. diversifolia* (Harris et al. 1994a). Morphological data also show a number of similarities that suggest a close relationship between these two species. The leaves of *L. diversifolia* and *L. pulverulenta* are very similar in terms of size, number of pinnae pairs, and number of leaflets, the pods are almost identical, the inflorescence is similarly lax as seen in bud with few flowers per capitulum, and the minute apiculum on the anthers is similar, although not always present in *L. diversifolia.* The sympatric occurrence of *L. diversifolia* and *L. pulverulenta* in north-central Veracruz (e.g., around Misantla, *Hughes 1865, 1866*) (Fig. 38) is consistent with a possible origin that involved *L. pulverulenta. Leucaena pulverulenta* is distinguished from *L. diversifolia* by its characteristic whitish grey tomentum on the young developing leaves and shoots, its irregular, lumpy-verrucate as opposed to discoid or shallow-crateriform petiolar extrafloral nectary, its pale cream-white as opposed to pink flower color, basally connate petals, and its glabrous as opposed to sparsely hairy anthers.

In the original description of *L. brachycarpa*, Urban (1900) cited three specimens: from near Córdoba, central Veracruz, Mexico, from Hope, Jamaica, and from Martinique. Zárate (1984a) suggested combining *L. brachycarpa* as a subspecies of *L. pulverulenta* to account for the unusual material from around Temascal in northern Oaxaca. Later, Zárate (1994) treated *L. brachycarpa* as a distinct species, selected the Mexican syntype, *Bourgeau 2401*, as the lectotype and postulated the species to be of hybrid origin (*L.* ×*brachycarpa* Urban pro. sp.) between *L. diversifolia* (*L. diversifolia* subsp. *diversifolia* of Zárate, 1994) and *L. leucocephala. Leucaena brachycarpa* is here treated as conspecific with *L. diversifolia* based on thorough examination of the isolectotype and other material from Jamaica, Martinique, and Veracruz, Mexico. Analysis of cpDNA, isozymes, and RAPD markers showed that material from Jamaica, as well as from throughout the range of *L. diversifolia*, including accessions from near Córdoba (*Hughes 1881*) and Temascal (*Hughes 1666*), is identical to *L. diversifolia* and quite distinct from hybrids between *L. diversifolia* and *L. leucocephala* (Harris, unpubl.; Hughes & Harris 1998). The occurrence of *L. diversifolia* in Jamaica (at least since 1896) and Martinique (at least since 1887) is almost certainly the result of early introduction from Veracruz for use as a coffee shade tree with limited subsequent naturalization (Urban 1900; Adams 1972). The present-day distribution of *L. diversifolia* in Jamaica is restricted to the western parishes of St. Andrew and St. Thomas, and is consistent with this hypothesis.

Putative hybrids between *L. diversifolia* and *L. leucocephala* have been reported on a number of occasions (Sorensson & Brewbaker 1994). Recently new material of putative *L. diversifolia* × *L. leucocephala* hybrids has been collected from central Veracruz, Mexico, Huehuetenango, Guatemala, Jamaica, Indonesia, and Papua New Guinea. The identity and characteristics of these putative hybrids have been investigated in detail and confirmed by Hughes and Harris (1998), who named this hybrid as *L.* ×*spontanea* (see below). These hybrids have been facilitated by artificial sympatry in cultivation. The unripe pods and seeds of *L. diversifolia* are occasionally harvested and consumed, but not on the same scale as those of some other species of *Leucaena*. However, it is mainly cultivated as a shade tree in coffee plantations along with other trees, including species of *Erythrina, Grevillea,* and *Inga. Leucaena leucocephala* is also widely cultivated in Mexico and elsewhere (see below). The ease with which these hybrids apparently occur wherever the two parents are cultivated together, along with increasing use of *L. diversifolia* and the artificial hybrid in tropical reforestation (Brewbaker & Sorensson 1994; Sorensson 1995), suggests that the hybrid may already be more common than has been realized, and that it may become even more common in the future. After *L. leucocephala*, *L. diversifolia* is now probably the most widely cultivated species of *Leucaena* with a virtually pantropical, albeit somewhat scattered, distribution.

6. Leucaena leucocephala (Lamarck) de Wit, Taxon 10: 53. 1961. *Mimosa leucocephala* Lamarck, Encycl. Méth. Bot. 1: 12. 1783. *Acacia leucocephala* (Lamarck) Link, Enum. hort. berol. 2: 444. 1822.—TYPE: "Mimosa latisiliqua," "Mimosa leucocephala" (holotype: P-LA, microfiche: K!).

Small to medium-sized tree, 3–15 (–20) m tall, 5–50 cm bole diameter, variably shrubby and highly branched to arborescent with a short clear bole to 5 m, upright angular branching, and a narrow open crown. Bark on young branches smooth, mid-grey-brown, inner bark salmon pink, on older branches and bole darker grey-brown and rougher with shallow rusty orange-brown vertical fissures and deep red inner bark (Fig. 2A). Leafy shoots terete, pale to mid-brown, densely white-pubescent or glabrous. Stipules 3.5–4.1 mm long, ovate or lanceolate, with asymmetric wings at base, venation and midrib prominent, persistent but shrinking and inconspicuous on older shoots. Leaves (10–) 12–25 cm long, (5–) 7–16 cm wide; petioles (including pulvinus) 13–34 mm long, glabrous or densely white-pubescent, with a single nectary, 2–3 × 1.2–1.5 mm, at the distal end on adaxial side of petiole, green or yellow-green, sessile, elliptic, concave, crateriform; rachis (5–) 7–15.5 cm long, glabrous or densely white-pubescent, with 1–2 (–4) small, sessile, elliptic, concave nectaries distally, apex extending beyond the terminal pinnae as a pointed, glabrous or pubescent mucro 1.9–5 mm long, curling when dry; pinnae (4–) 6–8 (–9) pairs; pinnular rachis 5–10.2 cm long, angled, sparsely puberulent on adaxial side or densely white-puberulent, with 1–2 (–3) minute sessile, elliptic, discoid nectaries at base of terminal pairs of leaflets; leaflets 13–21 pairs per pinna, 9–16 (–21) mm long, 2–4.5 mm wide, nearly sessile, strongly asymmetric, linear-oblong to weakly elliptic, acute or acuminate apically, rounded to obtuse basally, glabrous, mid-green, slightly discolorous, margins variably ciliate especially near the base, primary vein asymmetric, secondary venation brochidodromous and clearly visible. Capitula 12–21 mm in diameter at anthesis, in fascicles of 2–6 in leaf axils arising on actively growing young shoots, the leaves developing simultaneously with the capitula, each capitulum with 100–180 flowers; peduncles 15–20 mm long, angled, glabrous or pubescent, with an involucre of dentate bracts at the distal end. Flowers subtended by peltate bracts, 2.3–3 mm long, 0.7 mm in diameter; calyx 2.3–3.8 mm long, pubescent on lobes, pale greenish cream; petals 4–5.6 mm long, free at base, free or partially united above, puberulent on lobes, pale green; filaments 6.2–11.1 mm long, white; anthers sparsely hairy especially at distal end, pale cream-white, apiculum absent; ovary 1.8–2.7 mm long, covered in white hairs especially at distal end, cream-white, with 18–28 ovules, style 7.8–11.9 mm long, white, with a terminal narrow tubular stigma, variably exserted beyond the anthers or included. Pods (3–) 5–20 (–45) per capitulum, (9–) 11–19 cm long, (13–) 15–21 mm wide, pendulous on sturdy 4–14 mm long stipes, linear-oblong, acute or rounded apically, sometimes with a short curled beak, narrowly planocompressed, 8–18-seeded, valves mid- to orange-brown, glabrous and slightly lustrous or densely white-velutinous, chartaceous, the margins slightly thickened, dehiscent along both sutures. Seeds 6.7–9.6 mm long, 4–6.3 mm wide, compressed, ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, 90–95% arm extension, symmetrical. Chromosome number: 2n = 104 (Tjio 1948, and others); self-compatible tetraploid. Figs. 40, 42.

Typification of *Leucaena leucocephala* (Lam.) de Wit has been the result of intensive nomenclatural detective work by de Wit (1961) and colleagues, who determined the correct basionym to be *Mimosa leucocephala* Lam. (1783, Encycl. Méth. Bot. 1: 12). *Leucaena leucocephala* had been in collections and gardens in Europe much earlier. Prior to de Wit's study, the species was called *L. glauca* (L.) Benth. with the basionym *Mimosa glauca* L. (1763, Sp. pl., ed. 2, vol. 2: 1504). However, Linnaeus (1753, Sp. pl. 1: 520) had previously applied the epithet *M. glauca* to a specimen of van Royen in Holland; de Wit (1961, 1975) clearly shows the van Royen specimen to be an acacia, now *Acacia glauca* (L.) Moench. The later 1763 Linnaean reference is to a specimen of *Leucaena leucocephala*, but it was misidentified as *M. glauca*. Bentham established the genus *Leucaena* and applied it to this 1763 material [*L. glauca* (L.) Benth.; basionym *M. glauca* L., 1763]; de Wit (1961) showed that this name could not be applied to a species of *Leucaena*, because it was based on the 1753 *M. glauca* L. that is now correctly seen to be an acacia.

An article by Gillis and Stearn (1974) challenging those conclusions led de Wit (1975) to detail nomenclatural evidence for the typification of *Lysiloma latisiliqua* (L.) Benth. (syn. *L. bahamensis* Benth.) based on *Mimosa latisiliqua* L. (1753, Sp. pl. 1: 519), citing Plumier's "spec. 17." A specimen at LINN (1228.19) labelled "21 latisiliqua" is considered by de Wit (following Bentham) to be *Leucaena leucocephala* (Lam.) de Wit. Gillis and Stearn (1974) argued that Linnaeus, having no wild tamarind (*Lysiloma*) material in 1753, published the binomial *latisiliqua* in reference to *Leucaena,* and they proposed the combination *Leucaena latisiliqua* (L.) Gillis and Stearn for the common leucaena ("jumbie bean" in the Bahamas). De Wit (1975) showed clearly, however, that Linnaeus did not use the LINN "21. latisiliqua" for his most precise description of *Mimosa latisiliqua*, but rather the plate of Plumier (Pl. Amer. fasc. primus, tab VI). Polhill and Stearn (1976) accepted that Linnaeus had seen the Plumier plates, citing notes made by him, and showed that the plate does in fact represent *Lysiloma*. Shaw and Schubert (1976), studying the problem, came to the same conclusions leading to the re-instatement of the names *Leucaena leucocephala* and *Lysiloma latisiliqua*.

Variation within *L. leucocephala* was first noted by agronomists, who were evaluating the performance of different accessions for fodder production in field trials (e.g., Hutton & Gray 1959; Brewbaker et al. 1972). Two main variants, based primarily on habit, branchiness, and vigor were recognized. First, a shrubby, low-growing, highly branched, seedy, and often weedy variant was designated the '*Common*' type (previously referred to inappropriately as the '*Hawaiian*' type: Brewbaker 1997; Bray 1997). Second, an erect, arborescent, lightly branched, less seedy variant was designated the '*Giant*' or '*Salvador*' type (Hutton & Gray 1959; Gray 1967; Brewbaker et al. 1972; Brewbaker 1980, 1987b).

Although it was realized from the start that the '*Giant*' or '*Salvador*' type corresponded to the type material of *L. glabrata* (*Palmer 386* from the vicinity of Acapulco, Guerrero, Mexico) (e.g., González et al. 1967), Brewbaker (1980) initially treated *L. glabrata* as a synonym of *L. leucocephala* and only later alluded to the distinction of two varieties, "var. *leucocephala*" corresponding to the shrubby '*Common*' type and "var. *glabrata*" corresponding to the '*Giant*' or '*Salvador*' type (Brewbaker 1987a). The formal recognition of two infraspecific taxa within *L. leucocephala* was discussed by Zárate (1987a), who raised their rank to subspecies and published the new combination: *L. leucocephala* subsp. *glabrata* (Rose) S. Zárate. The two subspecies recognized by Zárate (1987a) correspond directly to the agronomic "types," viz.: subsp. *leucocephala* = '*Common*' type; subsp. *glabrata* = '*Giant*' or '*Salvador*' type. A third agronomic variant, the so-called '*Peru*' type is further discussed under subsp. *glabrata*.

Zárate (1987a) listed the characters, in addition to habit, branchiness, and vigor, that distinguish subspecies *leucocephala* and *glabrata*. These included leaf size, leaflet size, pod and seed size, habit, and most notably vestiture of the shoot, leaf rachis, leaflets, and pod. Subspecies *glabrata* has larger leaves, leaflets, and pods, and is almost entirely glabrous, compared to the smaller leaves, leaflets, pods and densely puberulent, canescent shoot, leaf rachis, and pods of subsp. *leucocephala* (Figs. 40, 42). The two subspecies were further distinguished on the basis of multi-enzyme phenotypes in a preliminary study of variation within *L. leucocephala* (Harris et al. 1994b). The distributions of the two subspecies are largely allopatric, albeit with limited sympatry in northern Veracruz, Mexico, and the Isthmus of Tehuantepec (Fig. 41), where some intermediates are encountered suggesting geneflow between the two subspecies (Zárate 1987a). The distribution of *L. leucocephala* and in particular subsp. *glabrata*, within Mexico, has been greatly altered by its movement and cultivation for pod production (see subspecies accounts below).

During recent exploration by Hughes and collaborators in northern Guatemala, an additional variant, which differed from both subsp. *leucocephala* and *glabrata*, was encountered in a localized area around the town of Ixtahuacán in the highlands of Huehuetenango. This variant has the small leaves, leaflets, and pods of subsp. *leucocephala* but is glabrous like subsp. *glabrata*. This material was described as a third subspecies named subsp. *ixtahuacana* (Hughes 1997c).

Leucaena leucocephala is known to be a self-compatible tetraploid ($2n = 4x = 104$) (Tjio 1948; Frahm-Leliveld 1957, 1960; Turner & Fearing 1960; Shibata 1962; González et al. 1967; Hutton 1981; Brewbaker 1983; De Freitas et al. 1991; Sorensson & Brewbaker 1994). Patterns of natural variation within *L. leucocephala* have been greatly disrupted by the widespread indigenous domestication of the species as minor food plants in Mexico (Whitaker & Cutler 1966; Smith 1967; Zárate 1984a, 1984b, 1994; Casas & Caballero 1996; Hughes 1998). It is now impossible to identify a "center" of morphological diversity, or any unequivocally *natural* populations, although the widespread and abundant occurrence of subsp. *leucocephala* throughout the Yucatán Peninsula has led some to conclude that it is native there (e.g., Brewbaker 1987b). Despite its economic importance the origin of *L. leucocephala* remains unknown. It is widely suspected to be an amphidiploid between two sympatric diploid species, but the likely parents have until recently remained largely unknown. Brewbaker et al. (1972) suggested that *L. leucocephala* originated in southern Mexico or Guatemala as a hybrid between "diploid *L. diversifolia*" (= *L. trichandra*) and *L. collinsii*, or in eastern El Salvador (Brewbaker 1980), whereas Brewbaker (1983) and Pan and Brewbaker (1988) suggested "diploid *L. diversifolia*" (= *L. trichandra*) and *L. shannonii* as more likely putative parent species. Harris et al. (1994a) showed that the cpDNA of *L. leucocephala* is very similar to that of *L. pulverulenta,* suggesting this species as the most likely maternal parent of *L. leucocephala* and placing the putative origin in eastern Mexico, possibly in northern Veracruz. Clearly, any explanation of the origin of *L. leucocephala* must account for the three recognized subspecies. Interestingly, both subspecies *leucocephala* and *glabrata* occur sympatrically with *L. pulverulenta* in parts of north-central Veracruz. The lack of natural populations of *L. leucocephala,* along with increasing realization of the extent and importance of indigenous domestication of *Leucaena* as a minor food source in Mexico, led Harris et al. (1994a) to speculate that *L. leucocephala* might have arisen in pre-Columbian times following cultivation and consequent artificial sympatry of the parent species. Additional ethnobotanical evidence supports a possible anthropogenic origin (Hughes 1998).

Leucaena leucocephala has been, and still is, the most important species in both the indigenous domestication (for pods in food production) and the exotic domestication (as a tropical tree for fodder, wood, and soil conservation) of the genus *Leucaena* (Pound & Martínez-Cairo 1983; National Academy of Sciences 1984; Brewbaker 1987b). Although some aspects of the history of introduction of *L. leucocephala* across the tropics remain obscure and debatable (see subspecies accounts below), there is broad consensus that subsp. *leucocephala* was introduced, initially to the Philippines and later more widely, much earlier (possibly as early as the 16th Century–see below under subspecies) than subsp. *glabrata,* which was spread across the tropics only in the last few decades. Thus, all early agronomic investigation and most Flora treatments (e.g., Brenan 1959, Fl. Tropical East Africa; Brenan & Brummitt 1970, Fl. Zambesiaca; Ross 1975, Fl. Southern Africa; Elias 1974, U.S.A.; Barreto Valdéz & Yakovlev 1982, Cuba; Merrill 1912, Fl. Manila, Philippines; Nielsen 1992b, Fl. Malesiana) and references to naturalization and weediness (summarized in Cronk & Fuller, 1995; Hughes 1998), refer to subsp. *leucocephala,* which is pantropically distributed and more widely naturalized than subsp. *glabrata.* As far as is known, subsp. *ixtahuacana* has not been introduced outside its very restricted distribution in Guatemala and Mexico.

KEY TO THE SUBSPECIES OF LEUCAENA LEUCOCEPHALA

1. Habit upright arborescent, to 20 m; leaves ≥19 cm long, ≥12 cm wide, pinnular rachis ≥8 cm long, leaflets (11–) 16–21 mm long; capitula >18 mm in diameter at anthesis, with ≥120 flowers per capitulum; pods 12–19 cm long, 18–21 mm wide. 6b. *L. leucocephala* subsp. *glabrata.*
1. Habit shrubby, branchy, generally ≤10 m; leaves ≤20 cm long, ≤12 cm wide, pinnular rachis ≤8 cm long, leaflets 9–13 mm long; capitula 12–17 mm in diameter at anthesis, with ≤125 flowers per capitulum; pods 9–13 cm long, 13–18 mm wide.
    2. Young shoots, leaves, and unripe pods with dense whitish velutinous pubescence, ripe pods sparsely pubescent. 6a. *L. leucocephala* subsp. *leucocephala.*
    2. Shoots, leaves, and pods glabrous. 6c. *L. leucocephala* subsp. *ixtahuacana.*

6a. Leucaena leucocephala subsp. leucocephala.

Small tree, 3–5 (–7) m tall, 5–10 cm bole diameter, shrubby and highly branched with an irregular crown. Leafy shoots canescent, densely covered in short white pubescence reminiscent of *L. pulverulenta*. Leaves 12–17 (–19) cm long, (5–) 7–10 cm wide; petioles (14–) 16–25 mm long, densely white-pubescent, petiolar nectary 2.1–2.3 × 1.3–1.4 mm; rachis 5–7.5 cm long, densely white-pubescent, mucro 2.2–3.1 mm long, pubescent; pinnae (5–) 6–8 pairs; pinnular rachis 5–7.5 cm long, densely white-puberulent; leaflets 13–17 pairs per pinna, 10–13 mm long, 2.4–3.2 mm wide, ciliate along leaflet margins especially near the base. Capitula 12–14 mm in diameter at anthesis, in fascicles of 2–6, each capitulum with 100–110 flowers; peduncles 18–20 mm long, pubescent. Flowers subtended by peltate bracts, 2.4–2.5 mm long; calyx 2.4–2.6 mm long; petals 4.7–5.1 mm long, free at base, partially united above; filaments 7.3–8.7 mm long; ovary 1.8–2.1 mm long, with 18–22 ovules, style 10.3–10.9 mm long. Pods 4–12 per capitulum, 10–13 cm long, 13–16 mm wide, linear-oblong, rounded apically, with a short curled beak, 12–16-seeded, valves mid-brown, sparsely white-velutinous. Seeds 6.7–7.2 mm long, 4–4.3 mm wide. Fig. 42A–C.

Phenology. Flowering and fruiting throughout the year as long as moisture permits.

Distribution (Fig. 41). Within Mexico, *L. leucocephala* subsp. *leucocephala* is distributed mainly in the Yucatán Peninsula, in the States of Tabasco, Campeche, Quintana Roo, and Yucatán, including the Island of Cozumel, and extending south into northern Belize around Corozal and Orange Walk. Outlying occurrences include an area of north-central Veracruz, between Tampico and Papantla, and infrequently across the Isthmus of Tehuantepec into the State of Oaxaca (Fig. 41). In the Yucatán Peninsula, it occurs primarily as a ruderal weed of disturbed sites, including roadsides, waste ground, particularly around towns and cities, in abandoned milpas and neglected sisal plantations, along the coastal fringe, including the mangrove edge, and frequently on and around Mayan ruins (Brewbaker 1979). It grows on shallow limestone soils and coastal sand, often forming shrubby and sometimes dense thickets. Associated woody species are dominated by legumes and include *Lysiloma latisiliqua, Piscidia piscipula, Mimosa bahamensis, Gliricidia maculata, Caesalpinia gaumeri, Haematoxylon campechianum, Leucaena shannonii,* and species of *Acacia*. Despite its great abundance and widespread occurrence throughout the Yucatán, McClay (1990) doubted that subsp. *leucocephala* is native there because of the poverty of its phytophagous insect fauna and particularly absence of the insect defoliator *Heteropsylla cubana*, which was not found in that area despite exhaustive sampling (Waage 1990). McClay (1990) went on to speculate that *L. leucocephala* subsp. *leucocephala* might have been introduced to the Yucatán from elsewhere in Mexico, and possibly from Veracruz, in pre-Columbian times for the production of edible seeds and pods, although Brewbaker (1979) speculates that its main use in the Yucatán might have been as a green manure for soil nitrogen. The capacity of subsp. *leucocephala* to become naturalized, spread rapidly, and dominate secondary vegetation on limestone soils has been amply demonstrated on many Pacific islands (see below) and parts of Southeast Asia, and may provide a possible explanation for its abundance in the Yucatán today. *Leucaena leucocephala* subsp. *leucocephala* was introduced in historic times to Asia and is now pantropical (see below for discussion of the history of introduction); 0–250 (–500) m.

Vernacular names. *Guaje* (Mexico); *guaslim, tumbapelo* (Campeche, Mexico); *guaxin, huaxe, huaxin, huaxim, uaxi, uaxim, uaxin, waxim, xaxim* (Maya; Yucatán, Campeche, Quintana Roo, Mexico); *liliak* (Totonaco; Veracruz, Mexico); *lead tree* (Florida, Texas, U.S.A.); *koa-haole, false koa* (Hawaii); *wild tamarind* (Corozal, Belize); *jumbie bean* (Bahamas); *aroma blanca* (Cuba); *lamtoro* (Indonesia, Malaysia); *ipil-ipil* (Philippines); *tangan-tangan* (Guam); *kanthum thect, kratin* (Cambodia); *kan thin* (Laos); *kra thin* (Thailand); *bo chet, schemu* (Vietnam); *subabul* (India).

Representative Specimens (material from the Old World and South America not cited). **U.S.A.** Florida: Dade Co., S Miami off US 1 in the vicinity of Sunset Drive, *Lakela 31947* (MO); Black Point, E of Goulds, *Semple & Semple 1704* (CAN, MO, USF, WAT); Brickell Hammock, Miami, *Small 5459* (US); in pinelands nr Miami, *Small & Carter s.n.* (F). Hillsborough Co., Himes Ave. N of Gandy Boulevard, Tampa, *Burch 6846* (MO). Lee Co., vicinity of Marco, *Standley 12734* (US). Monroe Co., Key Largo, *Correll & Correll 40286* (MO); Hammock, Big Pine Key, *Killip 32883* (UC); old rd NE of Inn, *Killip 40763* (K); Big Pine Key, *Killip 42029* (F); Cudjoe Key, off US 1, *Lundell & Lundell 17513* (TEX); Upper Matecombe Key, Isla Morada, *Lundell & Lundell 17540* (TEX); nr Hwy 1, 3 km S of Key Largo, *Perdue 4454* (TEX).—Texas: Kleberg Co., vacant lot in Kingsville off Hwy 77, *Stanford 489* (TEX). Willacy Co., 29 km N of Raymondville, *Cory 51497* (UC).

Bermuda. *Brown & Britton 260* (K, UC); *Collins 205* (K). **Bahamas.** nr Nassau, *Curtiss 123* (TEX); S Bimini Island, *Stimson 1116* (UC). **Cuba.** Las Villas: between Tierra Roja and mangrove at Gavilán, *R. Howard 8* (UC).—Santa Clara: Gavilán, Soledad, *Jack 5705* (UC). **Grenada.** Nr Grand Etang, *A. C. Smith 10119* (UC). **Jamaica.** St. Thomas: just N of Grant Pen, off the rd A44, *Crosby 830* (UC); Hotel Shevlin grounds, May Pen, *Orcutt 330* (UC). **Virgin Islands.** St. Croix, *Ricksecker 178* (UC).

Mexico. Campeche: 15 km N of Escárcega, rd to Champotón, 18°43′N, 90°45′W, *Cabrera 2002* (MEXU); 8 km SE of Conhuas, rd to the Centro Regional de Calakmul, Km 99 rd Escárcega to Chetumal, 18°30′N, 89°52′W, *Cabrera 10977* (MEXU, MO); 3 km beyond Remate, Calkiní, 20°30′N, 90°22′W, *Chan 276* (MEXU); 3 km S of Champotón, nr rd to Escárcega, turnoff to Yohaltún, 2 km from coast, 19°20′N, 90°44′W, *Hughes 1286* (BR, FHO, K, MEXU, NY, US); nr rd 2 km W of Francisco Escárcega to Villahermosa, nr short-wave radiomast at La Tormenta, 18°35′N, 90°46′W, *Hughes 1734* (E, FHO, K, MEXU, MO, NY); 16 km N of Campeche, 19°53′N, 90°17′W, *Janzen 1109* (MEXU); Xcutoc, nr Holpechén, 19°44′N, 89°50′W, *Labat 1901* (MEXU); Xiquichak, E of Seybaplaya, 19°38′N, 90°36′W, *Lot 2551* (MEXU, MO); between Campeche and Mérida, *McCarter & Styles 338* (FHO, MEXU); turnoff to Sabancuy, rd from Escárcega to Palenque, 18°39′N, 90°58′W, *Sousa 12239* (MEXU); 3 km SW of Trez Brazos, 24 km SW of bridge over the Río Candelaria, 18°14′N, 91°26′W, *Sousa 12242* (MEXU); 2 km N of José Maria Morelos and Pavón, S of Champotón, 19°05′N, 90°43′W, *Sousa 12419* (MEXU).—Chiapas: Ocozocoautla, Camp. Bajada del Macho, SE on Río Cintalapa, Reserva del Ocote, *Calzada 10022* (F).—Oaxaca: nr Puente Sta. Cruz, rd Salina Cruz to Pochutla, 45 km E of Pochutla, 15°47′N, 96°01′W, *Hughes 834* (FHO, K, MEXU); El Barrio, Track crucero (8 km S of Matias Romero) to Lagunas, 16°49′N, 95°04′W, *Martines 1361* (MEXU); Tehuantepec, 5 km W of Jalapa de Márquez, 2 km E of Llano Grande, 16°26′N, 95°30′W, *Sousa 6878* (F, MEXU); 5 km N of La Ventosa, N of Juchitán, 16°34′N, 94°56′W, *Sousa 8723* (MEXU); El Mezquite, 5 km SE of Chivela, NE of Juchitán, 16°40′N, 95°01′W, *Sousa 10208* (MEXU); 3 km E of Lagunas, nr El Barrio, N of Juchitán, 16°47′N, 95°05′W, *Sousa 10223* (MEXU).—Quintana Roo: Humay, 9 km towards Felipe Carillo Puerto, 19°28′N, 88°04′W, *Balam 509* (K); junction at Bacalar, 18°41′N, 88°22′W, *Cabrera 1575* (MEXU); 2 km E of Calderitas nr Chetumal, 18°34′N, 88°15′W, *Cabrera 1578* (MEXU); area S of the Parque Chankanab, Isla de Cozumel, 20°17′N, 87°00′W, *Cabrera 9835* (MEXU); 4 km S of Tulum, rd Tulum to Boca Paila, 20°10′N, 87°26′W, *Grethur 443* (MEXU); Felipe Carillo Puerto, 19°35′N, 88°03′W, *Janzen 1116* (MEXU, TEX); rd 6 km W of Chetumal towards Francisco Escárcega, 1 km E of turnoff to Belize border, 18°31′N, 88°24′W, *Hughes 1735* (E, FHO, K, MEXU, MO, NY); rd to Xcaret off rd Cancún to Tulum, nr Playa del Carmen, 20°36′N, 87°07′W, *Moreno 277* (MEXU); Km 334–335, rd Tulum to Cancún, 20°35′N, 87°08′W, *Moreno 339* (MEXU); 1 km SW of airport at Cancún, rd Cancún to Tulum, 21°02′N, 86°53′W, *Moreno 839* (MEXU, TEX); Zona Hotelera Norte, Isla de Cozumel, 20°25′N, 86°55′W, *Pérez 1658A* (MEXU); Km 323 rd Chetumal to Cancún, nr Benito Juárez, 20°30′N, 87°15′W, *Pulido 586* (MEXU); outskirts of Puerto Morelos, 20°50′N, 86°53′W, *Sousa 10883* (MEXU); 5 km N of Playa del Carmen, 20°39′N, 87°05′W, *Téllez 1811* (MEXU); Isla Mujeres, colonial ruins of La Mundaca, 21°11′N, 86°50′W, *Ucan 1041* (F, UC).—Tabasco: 20 km NE of Ciudad del Carmen, rd to Champotón, Isla del Carmen, 18°41′N, 91°41′W, *Cabrera 15100* (MEXU); Hwy 30 nr Ojo de Agua, N of Balancán, 17°52′N, 91°33′W, *Calzada 2339* (MEXU); 13 km NE of Tenosique, 17°32′N, 91°21′W, *Téllez 927* (MEXU).—Tamaulipas: 1 km S of El Abra, 10 km S of Cd. Mante, 22°36′N, 99°02′W, *Medraño 12206* (MEXU).—Veracruz: El Salto de Eyipantla, 8 km from Sihuapán, San Andrés Tuxtla, 18°23′N, 95°13′W, *Calzada 1525* (MEXU, TEX); Cerro del Carbón, SE of Papantla, 20°24′N, 97°18′W, *M. E. Cortés 375* (MEXU), *M. E. Cortés 423* (MEXU); 13 km N of Tihuatlán, Hwy 130 S from Alamo to Poza Rica, 20°48′N, 97°34′W, *Hughes 1861* (CAS, FHO, K, MEXU, MO, NY); 30 km S of Tampico, rd to Cerro Azul, 21°55′N, 97°46′W, *McKee 10957* (MEXU); 8 km from Barra de Tuxpan, 20°57′N, 97°20′W, *Monroy 146* (MEXU); 7 km S of Tatahuicapan, nr Mecayapan, 18°12′N, 94°46′W, *Nee 25151* (F, MEXU).—Yucatán: nr Dzibilchaltún, 21°06′N, 89°36′W, *Bradburn & Darwin 1251* (F, MEXU); Pixoy, nr Valladolid, 20°42′N, 88°18′W, *Chan 1080* (F); hills nr Tzucacab, rd to Becanchén, 20°04′N, 89°03′W, *Darwin 2492* (EAP); Fraccionamiento Jardines de Mérida, Mérida, 20°59′N, 89°37′W, *J. S. Flores 8078* (MEXU); rd from Umán to Hotzuc, 20°42′N, 89°43′W, *Gongora 387* (UC); 23 km N of Colonia Yucatán, 16.5 km S of El Cuyo, rd El Cuyo to Colonia Yucatán, 21°21′N, 87°44′W, *Grethur 459* (MEXU); 6 km S of Yuxcaba, 20°30′N, 88°50′W, *Guzmán 7* (MEXU); 19 km S of Río Lagarteros, 21°21′N, 88°07′W, *C. D. Johnson 1744* (MEXU); nr Xtun, Campeche to Mérida rd, *Miranda 8024* (MEXU); rd from Mérida to Progreso, 21°07′N, 89°39′W, *Miranda 8225* (MEXU); archaeological zone of Dzibilchaltún, nr Mérida, 21°05′N, 89°35′W, *Ordoñez 184* (F, MEXU); nr Progreso, 21°07′N, 89°39′W, *Rita 166* (MEXU); 3 km from Sisal towards Mérida, 21°01′N, 90°00′W, *Schubert 1609* (A, MEXU); ruins of Cich'en Itzá nr the Casa de las Monjas, 20°41′N, 88°34′W, *Seler & Seler 4908* (GH); Ruinas Xtanciakaj, 6 km SE of Oxkutzcab, *Sima 696* (K); rd San Pedro to the Cayma-Tinum rd, 20°43′N, 88°23′W, *Ucan 2447* (UC); Chacmay, nr Ozocauich, 21°02′N, 88°57′W, *Yam 20* (MEXU, UC).

Belize. BELIZE: Calabash section, Turneffe Island, 17°16′N, 87°50′W, *Egler 42-29* (F, TEX); 3 km W of Belize River Bridge, N hwy, 17°32′N, 88°18′W, *Liesner 1449* (TEX).—COROZAL: Wilson's Motel, Corozal, beach rd, 18°23′N, 88°23′W, *Dwyer 14501* (MEXU); Corozal, 18°23′N, 88°23′W, *Gentle 291* (F); 3 km N of Corozal nr the Mexican border at Santa Elena, 18°25′N, 88°23′W, *Hughes 485* (FHO, K, MEXU); Orange Walk Rd, Corozal, 18°23′N, 88°23′W, *Lundell 4893* (A, F); 18 km W of Santa Elena nr the Mexican border, 18°27′N, 88°30′W, *Sousa 12037* (MEXU). **Panama.** CANAL ZONE: Exp. Gdns, Canal Zone, *Lindsay 255* (MO); nr Balboa, Canal Zone, *Allen 2756* (GH, MO); Summit Gdns, *Mori 2230* (MO).—LOS SANTOS: La Honda, *McDaniel 8058* (MO).

Leucaena leucocephala subsp. *leucocephala* corresponds to the shrubby '*Common*' type and is reported to have been introduced to the Philippines during the Spanish occupation aboard one of the annual Spanish government galleons that sailed between Acapulco and Manila between 1521 and 1815 (Merrill 1912). All communications between Spain and the Philippines during this period (almost 300 years) were via Mexico and led to the introduction of nearly 200 tropical American species, including other well-known legume trees such as *Acacia farnesiana, Gliricidia sepium, Pithecellobium dulce, Prosopis juliflora,* and *Samanea saman* (Merrill 1912). *Leucaena leucocephala* is recorded in Blanco's (1845) Flora of the Philippines (cited in Merrill, 1918), but beyond this the precise date of introduction is not known, although some speculate that it may have been introduced before 1600 (Brewbaker et al. 1972; Brewbaker & Hutton 1979; Pound & Martínez-Cairo 1983). *Leucaena leucocephala* is indeed found today abundantly around Acapulco, the area alluded to as the source of the original introductions of subsp. *leucocephala* by Brewbaker et al. (1972), but all trees from that area, and indeed most from the western Pacific coast of Mexico, belong not to subsp. *leucocephala* but to subsp. *glabrata.* However, it is quite possible that seed and/or pods of subsp. *leucocephala* were transported to Acapulco from elsewhere in Mexico by the Spanish, who were undoubtedly aware of the indigenous use of *Leucaena* as a food plant there. This seems a more likely motivation for the introduction than as feed and bedding for horses accompanying the Spanish, as suggested by Brewbaker et al. (1972).

By the late 19th Century subsp. *leucocephala* had spread or been introduced throughout Asia and Africa, and it is now pantropical, recorded from the majority of tropical and subtropical countries (e.g., Lock 1989, for Africa; Nielsen 1992b, for Malesia). That spread of subsp. *leucocephala* preceded subsp. *glabrata* was confirmed during testing of accessions from around the world for forage potential during the 1950's, which revealed all non-Mesoamerican accessions to be of subsp. *leucocephala* (Hutton & Gray 1959; Brewbaker et al. 1972; Batson et al. 1984). Herbarium records confirm the general pattern of introduction and demonstrate that subsp. *leucocephala* has been widespread in the Caribbean, Africa, and Asia at least since the latter part of the 19th Century.

Leucaena leucocephala subsp. *leucocephala* is an aggressive colonizer of ruderal sites and secondary or disturbed vegetation in many places, such as the Philippines where Merrill (1912) observed that it "is now so thoroughly naturalized, common and widely distributed that the casual observer would consider it a native species." This has been attributed to its precocious year-round flowering and fruiting, abundant seed production, self-fertility, hard seed coat, and ability to resprout after fire or cutting. It is now naturalized and weedy in more than 20 countries on all continents except Europe and Antarctica (e.g., Smith 1989, Hawaii; Henderson 1989, Wells et al. 1989, Neser 1994, South Africa; Merrill 1912, Philippines; Debell & Whiteswell 1993, Guam; Cock 1984, Vanuatu; Sheil 1994, Tanzania; Gordon & Thomas 1997, Florida, U.S.A.; additional references in Cronk & Fuller, 1995, and Hughes, 1998). On some Pacific islands, spread was accelerated by aerial seeding for rehabilitation of eroded lands (e.g., on Guam, Debell & Whitesell 1993), and on some islands, such as Hawaii, subsp. *leucocephala* now forms extensive dense monospecific thickets. In Hawaii it is classified amongst the 12 worst pests out of 86 serious alien invaders. Biological control has been contemplated in Hawaii (Smith 1985) and South Africa (Neser 1994), but is frustrated by the taxon's economic importance, although proposals to release the seed-eating bruchid *Acanthoscelides macrophthalmus* in South Africa are still being pursued (Neser 1994).

6b. Leucaena leucocephala subsp. **glabrata** (Rose) S. Zárate, Phytologia 63(4): 305. 1987. *Leucaena glabrata* Rose, Contrib. U.S. Natl. Herb. 5(3): 140. 1897.—TYPE: MEXICO. Guerrero: vicinity of Acapulco, Oct 1894–Dec 1895, *Palmer 368* (holotype: US!; isotypes: GH! F! MO! NY! UC!).

Small tree, 5–15 (–20) m tall, 10–35 (–50) cm bole diameter, arborescent with a short clear bole to 3–5 m and an open irregular crown. Leafy shoots glabrous. Leaves (17–) 19–25 cm long, 12–16 cm wide; petioles 24–34 mm long, glabrous, petiolar nectary 2–3 × 1.4–1.5 mm; rachis 11–15.5 cm long, glabrous, mucro 3–5 mm long, very sparsely puberulent; pinnae (4–) 6–8 (–9) pairs; pinnular rachis 8–10.2 cm long, glabrous; leaflets (15-) 16–19 (–21) pairs per pinna, 11–16 (–21) mm long, (2.4–) 3–4.5 mm wide, very sparsely ciliate along leaflet margins near base. Capitula 18–21 mm in diameter at anthesis, in fascicles of 2–6, each capitulum with 120–180 flowers; peduncles 17–20 mm long, glabrous. Flowers subtended by peltate bracts, 2.4–3 mm long; calyx 2.3–3.2 mm long; petals 4–5.6 mm long, free; filaments 7–11.1 mm long; ovary (2–) 2.4–2.7 mm long, with 24–28 ovules, style 10.8–11.9 mm long. Pods 6–20 (–45) per capitulum, 12–19 cm long, 18–21 mm wide, linear-oblong, rounded apically, with a short curled beak, 13–18-seeded, valves mid-orange-brown, glabrous and slightly lustrous. Seeds 7.6–8.2 mm long, 5.4–5.6 mm wide. Fig. 40.

Phenology. Flowering and fruiting throughout the year as moisture permits.

Distribution (Fig. 41). The natural distribution of *L. leucocephala* subsp. *glabrata* remains unknown. Within Mexico and Central America it is extremely widely distributed (Fig. 41) as a cultivated tree (sometimes locally naturalized, as around Acapulco) but no natural populations are known to date. It is a very common backyard, street, and orchard (*guajal*) tree cultivated for the production of unripe pods and seeds, which are consumed and widely marketed throughout Mexico. Indeed, *L. leucocephala* subsp. *glabrata* is found in the majority of villages and towns in Mexico, in all tropical and subtropical areas (wet, seasonally dry, and semi-arid), except at higher elevations (above 2000 m) and in the northern States, where regular frost limits its cultivation. *Leucaena leucocephala* subsp. *glabrata* has been widely introduced outside Mexico and Central America only in the last few decades, but its active promotion in tropical reforestation means that it is now in

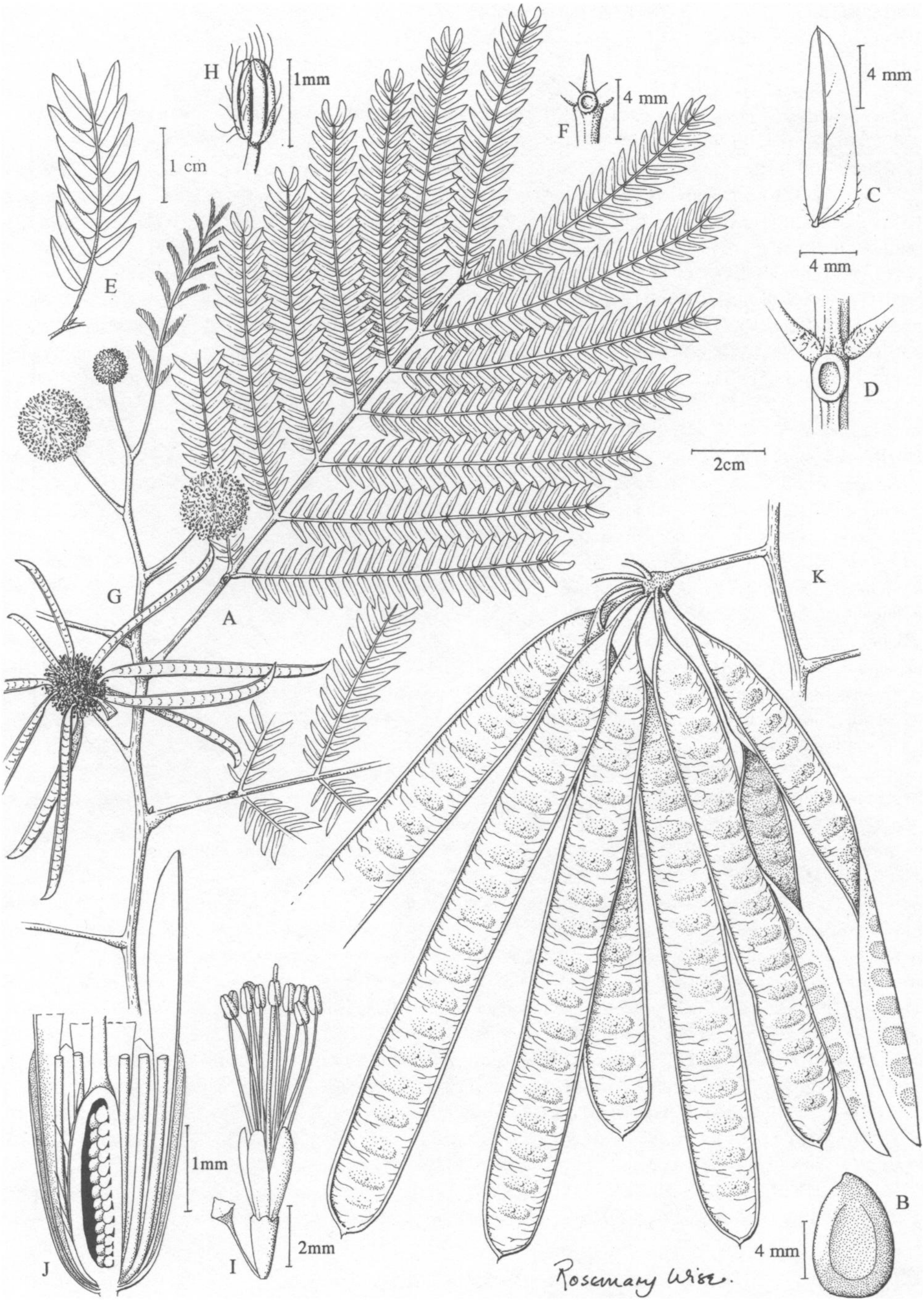


FIG. 40. *Leucaena leucocephala* subsp. *glabrata*. A. Leaf. B. Seed. C. Leaflet. D. Petiolar nectary. E. Inset pinna. F. Rachis nectary. G. Flowering shoot. H. Anther. I. Flower. J. Longitudinal section of flower. K. Pods. (Based on: A, B, K, *Hughes 905*; C–F, *Hughes & Styles 133*; G, H, *Hughes 639*; I, J, material fixed in spirit derived from University of Hawaii accession K636.)

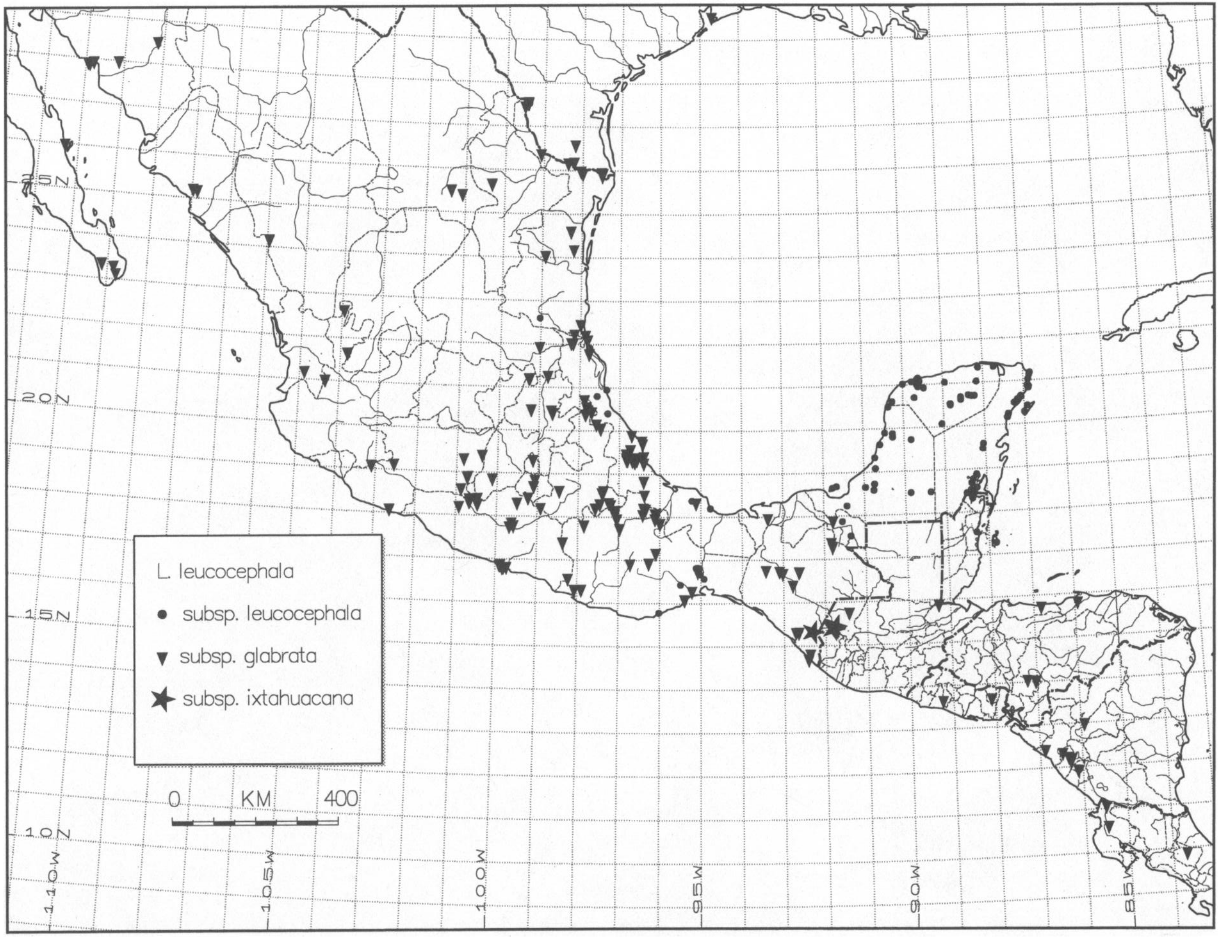


FIG. 41. Distribution of *L. leucocephala.*

cultivation pantropically (see below for detailed discussion of the history of introduction); 0–500 (–2100) m.

Vernacular names. *Guaje, guaje blanco, guaje verde, calguaje* (Mexico); *dormilón* (Tamaulipas, Mexico); *efe, guache, guache de tierra caliente* (Hidalgo, Mexico); *guas, guash, guashe, guash de castilla* (Chiapas, Mexico), indicative of cultivation/introduction of material; *chalip* (Guatemala); *barba de león* (El Salvador); *frijol guaje* (Honduras).

REPRESENTATIVE SPECIMENS. **U.S.A.** ARIZONA: A.S.U., N of Rainbow Bridge, Maricopa, *Lehto 5628* (CAS).—CALIFORNIA: Santa Barbara, Cliff Drive, nr Miramontes Drive, *C. F. Smith 3755* (CAS).—FLORIDA: Dade Co., SW 8th Street, Miami, *Duckett 8169* (CAS, F, UC). Monroe Co., Key Largo, *Seigler 10260* (MEXU).—TEXAS: Cameron Co., cemetery, Brownsville, 25°54′N, 97°30′W, *Runyon 2123* (F, UC); Brownsville, Lower Río Grande Valley, 25°57′N, 97°29′W, *Runyon 5029* (TEX). Galveston Co., S side of Pine Drive, E side of Geisler's Gully, Dickinson, *Waller 3606* (MO, TEX). Harris Co., Seabrook Yacht Basin, 150 m W of S.H. 146 drawbridge, 29°33′N, 94°42′W, *Waller 2812* (TEX). Hidalgo Co., NW part of county W of Linn, 26°36′N, 98°12′W, *M. C. Johnston s.n.* (TEX); in McAllen, 26°12′N, 98°14′W, *Nee 24049* (F); nr entrance to Bentsen-Rio Grande State Pk, 6 km S of Mission, 26°11′N, 98°23′W, *Nee 24062* (F, MEXU); Santa Ana National Wildlife Refuge, 26°00′N, 98°03′W, *Solomon 5653* (MO). Kenedy Co., base of Juidas Windmill, Norias Division, King Ranch, 25 Jun 1953, *M. C. Johnston s.n.* (TEX); Travis Co., grounds of Capt. R.W. Aldrich, 5 km E of Austin, 30°01′N, 97°25′W, *Tharp 46019* (TEX). Webb Co., cult., motel in Laredo, 27°33′N, 99°27′W, *Cox 2874* (TEX).

Bahamas. BIMINI ISLAND: N Bimini Island, *R. A. Howard 9984* (UC).

Mexico. BAJA CALIFORNIA NORTE: ornamental, Ensenada, 31°51′N, 116°35′W, *Saiz 43* (MEXU).—BAJA CALIFORNIA SUR: in El Pescadero, 9 km S of Todos Santos, rd S towards Cabo San Lucas, 23°22′N, 110°09′W, *Hughes 1547* (FCME, FHO, K, MEXU, MO, NY); Loreto, E coast, 26°00′N, 111°21′W, *Hughes 1557* (FHO, K, MEXU, MO, NY); nr Santa Catarina, 10 km N of San José del Cabo 10 km inland from coast, 23°09′N, 109°47′W, *Hughes & Styles 160* (FHO, MEXU); Santiago, Presa Ensolvada, SW of Boca de la Sierra, 23°19′N, 109°51′W, *Tenorio 12834* (MEXU, MO).—CHIAPAS: rd 40 km E from Cintalapa de Figueroa to Ocozocuautla and Tuxtla Gutiérrez, at jctn. El Gavilán, 16°46′N, 93°26′W, *Hughes 1679* (E, FHO, MEXU, NY); Chiapa de Corzo, 16°42′N, 93°01′W, *Laughlin 790* (CAS, F); rd 36 km SE of Palenque towards Chancalá, 17°18′N, 91°48′W, *Macqueen 328* (EAP, FHO, K, MEXU); Ococingo, 5 km S of Crucero Corozal, *E. Martínez 12238* (MEXU); 35 km SE of Palenque, rd to Chancalá, 17°24′N, 91°50′W, *E. Martínez 13370* (CAS, MEXU); Acacoyagua, 15°20′N, 92°39′W, *Matuda 16785* (EAP, MEXU); Escuintla, cult. Rancho Soconusco, 15°20′N, 92°43′W, *Matuda 17928* (CAS, MEXU, NY), *Matuda 18403* (CAS, F, MEXU, NY); Tuxtla Gutiérrez, cult., 16°45′N, 93°06′W, *Miranda 5871* (MEXU); purchased in market, San Cristóbal de las Casas, 16°44′N, 92°37′W, *Schubert 1758* (A); Yajalón, Arroyo Banca de Grava, *Shilom Ton 7002* (CAS, MEXU, MO); Venustiano Carranza, Planta Angostura, Presa Belisario Domínguez, 16°25′N, 92°47′W, *Sousa 11342* (CAS, MEXU, MO); Pto. Madero, S of Tapachula, 14°42′N, 92°25′W, *Ventura 1443* (MEXU, TEX), *Ventura 3707* (MEXU, TEX); Cantón Palo Seco, nr Tapachula, 14°49′N, 92°23′W, *Ventura 2033* (MEXU).—COAHUILA: 9 km W of Saltillo off Hwy 40 at jctn to short-wave radio mast at La Vega, 25°26′N, 101°05′W, *Yatskievych 86-244* (UC); in "La Rosa," 45 km W of Saltillo, rd to Torreón, 25°31′N, 101°22′W, *Zárate 366* (MEXU).—DISTRITO FEDERAL: Valle de México, 19°20′N, 99°08′W, *Urbina 209* (MEXU).—DURANGO: nr El Cico, 10 km NE of Toyaltita, 24°11′N, 105°57′W, *Tenorio 6308* (MEXU).—GUERRERO: nr Lago Tres Palos, 16°50′N, 99°44′W, *Boege 433* (MEXU); La Cabana Motel, nr Iguala, Hwy 95, 18°20′N, 99°30′W, *Freeland & Spetzman 15* (MEXU); Coyuca, Pungarabato, 18°20′N, 100°40′W, *Hinton 7287* (A, F, K, NY); 8 km SW of Mezcala, nr track to Carrizalillo, 17°52′N, 99°38′W, *Hughes 887* (FHO, MEXU); 2.5 km W of Puerto Marques, nr Acapulco, 16°49′N, 99°50′W, *W. López 706* (MEXU); Acapulco, rocky headland, Hotel Mirador, 16°53′N, 99°54′W, *MacDaniels 155* (F); Tlalchapa, 18°25′N, 100°28′W, *Orozco 1* (MEXU); nr Pie de la Cuesta, rd to Zihuatenejo, *Pennington 9436* (A); Adama, Achótla, *Reko 5008* (NY); nr Acapulco to México rd, 1 km W of Milpillas, side rd to Fila de Caballo, 17°48′N, 99°35′W, *Soto 5148* (MEXU); Amapilca, nr Alcozauca, 17°25′N, 98°22′W, *Viveros & Casas 98* (MEXU).—HIDALGO: in San Pedro, on rd to Metztitlán, 20°29′N, 98°42′W, *A. Delgado 63* (MEXU); 2 km N of Ixmiquilapan in San Nicolás, nr rd to Cardonal and Grutas de Tolantongo, 20°30′N, 99°12′W, *Hughes 1578* (E, FHO, MEXU, NY); 8.6 km S of Venados, rd to Pachuca, 20°25′N, 98°40′W, *R. Torres 3034* (MEXU).—JALISCO: nr El Ojo de Aguacaliente, rd to Ahuijullo, nr Tecalitlán, 19°06′N, 103°06′W, *Magallanes 1602* (MEXU, MO); Sierra Madre nr Bolanos, 21°40′N, 103°49′W, *Rose 1215* (NY), *Rose 1218* (GH); Arroyos del Agua, 10 km NW of Huejuquilla, 22°39′N, 103°57′W, *Rzedowski 17617* (MEXU, TEX).—MÉXICO: Nanchititla, Temascaltepec, *Hinton 3119* (K); Temascaltepec, Rincón del Carmen, 18°53′N, 100°07′W, *Hinton 5408*

(A, F, K).—Michoacán: 30 km W of Playa Azul, rd to Manzanillo, 18°06′N, 102°37′W, *Hughes 639* (FHO, K, MEXU); 2 km N of Tacupa, 8 km N of Ciudad Altamirano, rd to Huetamo, 18°17′N, 100°28′W, *Hughes 905* (FHO, K, MEXU); Tiquicheo exit to Limón de Papatzindan, 18°55′N, 100°43′W, *Soto 52* (MEXU); Los Bancos, 7 km N of Cd. Altamirano, 18°24′N, 100°40′W, *Soto 657* (MEXU); El Manguito, 11 km SE of El Devanador rd Temazcal to Huetamo, 19°20′N, 100°50′W, *Soto 813* (MEXU, MO); nr Amatitlán, 23 km NW of Apatzingán, 19°09′N, 102°33′W, *Soto 2123* (MEXU); in Placeres de Oro SW of Coyuca de Catalán, 18°13′N, 100°55′W, *Soto 2304* (K, MEXU, TEX); in La Garita, 3 km SW of Zitácuaro, 19°25′N, 100°23′W, *Soto 7303* (MEXU, MO); 13 km SW of Xochipala, rd to Fila de Caballo, 17°47′N, 99°41′W, *Soto 5167* (MEXU).—Morelos: Miacatlán, 500 m N of Laguna "El Rodeo," 18°47′N, 99°20′W, *Dorado 858* (MEXU, MO); P. de Ixtla, 5 km W of Tilzapotla, 18°27′N, 99°14′W, *Dorado 898* (MEXU); in Temilpa Nuevo, in valley of Río Yautepec, 2 km NNE of Tlaltizapán, 10 km NNE of Jojútla de Juárez, 18°43′N, 99°06′W, *Hughes 1728* (E, FHO, K, MEXU, MO, NY); N part of dam of Río Yautepec, nr Yautepec, 18°52′N, 99°04′W, *G. Salgado s.n.* (MEXU).—Nayarit: Pátzcuaro nr Compostela, 21°12′N, 104°53′W, *L. M. González 658* (MEXU); El Trapiche SE of Yxtlan, 21°01′N, 104°21′W, *Mexía 810* (F, GH, UC).—Nuevo León: in Monterrey, 25°41′N, 100°20′W, *Estrada 357A* (MEXU).—Oaxaca: Villa Hidalgo, Yalalag, 17°11′N, 96°06′W, *Alatorre 31* (MEXU); nr the Presa Temazcal, W of Tuxtepec, 18°13′N, 96°24′W, *L. Cortés 106* (MEXU); 3 km on rd to San Mateo del Mar, nr Tehuantepec, 16°18′N, 95°13′W, *A. R. García 2823* (MEXU, TEX); 2 km E of Tomellín, nr Cuicatlán, 17°45′N, 96°59′W, *A. R. García 3406* (MEXU, TEX); Carrizal, 2 km SW of Morro de Mazatán, 35 km SW of Salina Cruz, rd to Pochutla, 16°06′N, 95°24′W, *S. González 385* (MEXU, TEX); San Bartolo Albarradas, 20 km E of Villa de Mitla rd to Zacatepec, 16°57′N, 96°16′W, *Hughes 1659* (E, FHO, MEXU, NY); 86.5 km S of Tehuacán towards Oaxaca, 7 km S of San Juan de los Cues towards Cuicatlán, lower Tehuacán Valley, 17°58′N, 97°03′W, *Hughes 1805* (FHO, K, MEXU, NY); Santiago Apóstol, nr Ocotlán, 16°56′N, 96°43′W, *Robinson 84-40-10* (NY); Alto de la Mesa, 6 km NW of Ixcapa, 16°35′N, 98°14′W, *Sousa 5904* (MEXU); Cafetal Segundo, 4 km E of San Lucas Ojitlán, nr Tuxtepec, 18°05′N, 96°25′W, *Sousa 7268* (MEXU, MO); 7 km NW of Reforma, nr Chiltepec, nr Tuxtepec, 17°59′N, 96°07′W, *Sousa 7273* (MEXU, MO); San Antonio Nanahuatipan, nr Teotitlán del Camino, 18°08′N, 97°07′W, *Sousa 8855* (MEXU, UC); San Jerónimo Silacayoapilla, nr Huajuapan de León, 17°49′N, 97°51′W, *Sousa 9821* (MEXU); in San Andrés Nuaxpaltepec, nr Jamiltepec, 16°20′N, 97°54′W, *Sousa 9927* (MEXU); Pinotepa Nacional, 16°20′N, 98°04′W, *G. Torres s.n.* (MEXU); 10.4 km S of El Barrio, rd to Almaloya, N of Juchitán, 16°45′N, 95°05′W, *R. Torres 9757* (MEXU).—Puebla: in Santiago Yancuictlalpan, nr Cuetzalán, 20°04′N, 97°28′W, *Basurto 54* (MEXU); 2 km W of Villa Lázaro Cárdenas, nr Venustiano Carranza, 20°27′N, 97°42′W, *Basurto & Durán 43* (MEXU); 4 km NE of Villa Avila Camacho, nr Jalpan, 20°24′N, 97°51′W, *Basurto & Durán 524* (MEXU); 9 km E of Mecapalapa, nr Pantepec, 20°30′N, 97°48′W, *Basurto & Durán 559* (MEXU); 5 km E of Metlaltoyuca, nr Francisco Z. Mena, 20°44′N, 97°53′W, *Basurto & Durán 696* (MEXU); cult., Zapotitlán Salinas, 30 km SW of Tehuacán, rd to Huajuapan de León, 18°19′N, 97°28′W, *Hughes 1618* (E, FHO, MEXU, NY); nr rd 6 km N from Teotitlán del Camino towards Tehuacán, 1 km N of San José Tilapa, 18°10′N, 97°07′W, *Hughes 1640* (E, FHO, MEXU, NY); Santiago Acatepec, Tehuacán-Huajuapan de León rd, Hwy 125, about 25 km SW of Zapotitlán Salinas, 18°13′N, 97°35′W, *Hughes 1791* (FHO, K, MEXU, MO, NY); Francisco I. Madero, 2 km SW of San Pedro Chapulco, 14 km NE of Tehuacán, rd to Orizaba, 18°35′N, 97°25′W, *Hughes 1883* (FHO, K, MEXU, NY, TEX); 4 km S of Calipan, towards Tehuacán, 18°18′N, 97°12′W, *Medraño 1180* (MEXU); 7 km S of Chilac, rd to San Mateo Tlacoxcalco, *Salinas 3095* (MEXU, TEX); in Mitepec, nr Jolalpan, 18°13′N, 98°55′W, 27 Sep 1983, *R. Vázquez 15* (MEXU); 200 m from Cerrito Coatepec, side rd 4 km from Ajalpan and 3 km NW of Zinacatepec, 18°21′N, 97°15′W, *Zárate 613* (MEXU, MO), *Zárate 614* (MEXU, MO); market, Izúcar de Matamoros from Tejalpa, 18°37′N, 98°28′W, *Zárate 701* (MEXU).—Querétaro: nr rd 35 km SE from Jalpan de la Sierra to Xilitla, 1 km E of the village of Lagunita, 21°14′N, 99°15′W, *Hughes 1596* (E, FHO, MEXU, NY).—San Luis Potosí: nr rd 10 km NNW from Tamazunchale to Ciudad Valles, nr Ixtiamel, 21°17′N, 98°48′W, *Hughes 1591* (E, FHO, MEXU, NY); nr Ciudad Valles, 21°57′N, 99°01′W, *R. Rojas s.n.* (MEXU).—Sinaloa: Guamuchil, 4 km S of Caitime, Hwy 15 76 km N from Culiacán to Los Mochis, 25°13′N, 107°59′W, *Hughes 1519* (FHO, K, MEXU, MO, NY); nr Miramar at Guaymas, 27°55′N, 110°57′W, *C. E. Smith 4730* (US).—Sonora: E outskirts of Empalme, nr rd to Barcenas, 15 km E of Guaymas, 27°57′N, 110°48′W, *Hughes 1568* (FHO, K, MEXU, NY); nr rd ESE from Hermosillo towards Chihuahua, 51 km ESE of Tónichi nr Tecupa, 28°31′N, 109°10′W, *Hughes 1574* (FHO, K, MEXU); nr Miramar at Guaymas, 27°55′N, 110°57′W, *C. E. Smith 4730* (US); rd to short wave radio mast, Cerro del Vigía, N of Guaymas, 28°00′N, 110°09′W, *R. M. Turner 75-27* (UC).—Tabasco: rd from Triunfo to San Pedro, *Espejo 1035* (MEXU); forest of Colegio Superior de Agric. Tropical de Cárdenas, nr Cárdenas, 17°59′N, 93°22′W, *Ricárdez 287* (MEXU); 11 km NE of Chablé, 32 km SE of Balacán at crossroads, 17°54′N, 91°47′W, *Sousa 12377* (MEXU).—Tamaulipas: Nuevo Laredo, Ave. Juárez, 27°28′N, 99°31′W, *Calzada 4598* (MEXU); Km 232 rd from Soto la Marina to jctn with rd from Cd. Victoria to Matamoros, 500 m S of turnoff to San Fernando, 24°12'N, 98°12'W, *Grethur 603* (MEXU); 7 km ESE of Cd. Bravo, Km 79 rd from Matamoros to Reynosa, 25°57'N, 98°00'W, *Grethur 610* (MEXU, TEX); La Servilleta, 4 km W of La Charca, nr Gómez Farías, *Mahinda Martínez 583* (MEXU); Río Purificación, bridge at Hwy 101, 42 km NE of Cd. Victoria, nr Nueva Cd. Padilla, 24°03'N, 98°55'W, *Nee 24465* (MEXU, TEX); Las Norias, 30.5 km S of San Fernando, Hwy 101, 24°37'N, 98°17'W, *Nee 27115* (F); banks of Río Pánuco nr Tampico, 22°13'N, 97°53'W, *Nee 28689* (F); 2 km E of Cd. Miguel Alemán, rd from Laredo to Reynosa, 26°23'N, 99°05'W, *Zárate 386* (MEXU).—VERACRUZ: rd Jalapa to Veracruz at turnoff to Baños de Carrizal, nr Emiliano Zapata, 19°22'N, 96°38'W, *Calzada 2195* (F, MEXU, TEX); Tampico–El Alto, La Rivera, entrance to Laguna de Tamiahua, 22°07'N, 97°49'W, *Calzada 6327* (F); Méndez, 22°15'N, 98°09'W, *Chiang 148* (F, MEXU); Cerro Achichuca between Tuzamapan and Jalcomulco, 19°21'N, 96°48'W, *Castillo & Tapia 653* (MEXU); 3.8 km from Tuzamapan on rd to Totutla, nr Coatepec, 19°24'N, 96°50'W, *Corral 17* (MEXU, TEX); N side of Cerro Monte de Oro, 19°25'N, 96°24'W, *Dorantes 909* (MEXU); nr Laguna Verde, E of Alto Lucero, 19°43'N, 96°26'W, *Dorantes 5127* (MEXU); El Zapote 2 km SWW of Coxquihui, 20°10'N, 97°35'W, *Grimes 2725* (F, MEXU, TEX); Colonia López Mateos, nr Tepalzingo, *Guerrero 1494* (MEXU); rd 5 km S of Pánuco to Miradores and El Olvido, 22°03'N, 98°14'W, *Gutiérrez Baez 1960* (MEXU); nr Rinconada, nr Emiliano Zapata, 19°21'N, 96°34'W, *Gutiérrez Baez 16* (F); 8 km SSW of Tuzamapan, 4 km WNW of Jalcomulco, Coatepec-Huatusco rd, valley of Mesa Olivera, 19°21'N, 96°49'W, *Hughes 1875* (FHO, K, MEXU, NY); Hwy 140 40 km SE of Xalapa towards Veracruz, between Cerro Gordo and Plan del Río, 1 km N of Plan del Río, 19°24'N, 96°38'W, *Hughes 1878* (FHO, K, MEXU, NY); 49 km S of Tampico, Hwy 180 to Tuxpan, 21°48'N, 97°47'W, *Lasseigne 4900* (MEXU); Est. Exp. Cotaxtla, CIASE, nr Tlalixcoyan, 18°51'N, 96°24'W, *S. Ochoa 1733* (K, MEXU); in Tolomé, nr Paso de Ovejas, 19°16'N, 96°24'W, *A. Santiago s.n.* (MEXU); La Victoria, S side of Laguna de Catemaco, 18°21'N, 95°07'W, *Sousa 2889* (CAS, F, MEXU); 6 km from jctn Tierra Blanca-Acatlán, Las Margaritas, 18°32'N, 96°23'W, *Téllez 335* (MEXU); rd to Plan de Las Hayas, 2.5 km from turnoff, 19°47'N, 96°27'W, *C. Vázquez 713* (MEXU); 0.5 km from El Limón, nr Apazapam, 19°20'N, 96°41'W, *G. Williams 27* (F, MEXU); Jalapa, 19°29'N, 96°50'W, *Zola Baez 849* (F, MEXU).

Costa Rica. GUANACASTE: Liberia, 10°37'N, 85°28'W, *Liesner 5228* (F).—TURRIALBA: cult., Instituto Interamericana de Ciencias Agrícolas, 9°54'N, 83°41'W, *J. Léon 2860* (EAP). **El Salvador.** LA LIBERTAD: Ladera La Laguna, volcanic crater above Jardín Botánico La Laguna, 13°40'N, 89°15'W, *P. Lemus s.n.* (FHO, K).—MORAZÁN: Caserio El Tiangue, rd to San Francisco Sotera, 13°41'N, 88°06'W, *Reyna 1436* (K). **Guatemala.** HUEHUETENANGO: cult. close to Florída to Soledad rd, 10 km NW Barillas, 15°48'N, 91°48'W, *Hughes 1698* (E, FHO, K, MEXU, MO, NY).—IZABAL: rd 2 km from Modesto Méndez to Poptún, 15°54'N, 89°17'W, *Macqueen 73* (EAP, FHO, K, MEXU, MO). **Honduras.** ATLÁNTIDA: nr La Ceiba, rd E by Río Cangrejal, 15°45'N, 86°49'W, *Macqueen 31* (EAP, FHO, K, MEXU, MO).—COLÓN: Hacienda El Tumbador, nr Trujillo, 15°49'N, 85°56'W, *Saunders 469* (F).—FRANCISCO MORAZÁN: Loma Linda Norte nr Tegucigalpa, 14°04'N, 87°14'W, *Audato Paz 126* (NY); cult., Escuela Agrícola Panamericana, El Zamorano, 14°03'N, 87°01'W, *Molina 5888* (EAP, GH); nr El Zamorano, 14°02'N, 87°02'W, *Valerio 3021* (EAP). **Nicaragua.** CHONTALES: Ometepe Island, Lago de Nicaragua, 11°05'N, 85°30'W, *Shimek & Smith 254* (F).—LEÓN: W side Isla Momotombito, Lago de Managua, 12°21'N, 86°28'W, *Araquistain & Moreno 1034* (MO); nr León, rd to Poneloya nr Parque Arlen Siu and Presa El Clavo, 12°26'N, 86°53'W, *E. García 90* (MO).—MANAGUA: nr Escuela Nacional de Agric. y Ganadería, 12 km E of Managua, 12°13'N, 86°17'W, *Atwood 2550* (MO), *Zelaya 2266* (MO); Sierra de Managua, 12°09'N, 86°17'W, *Garnier 60* (F); nr Managua, 12°13'N, 86°17'W, *Garnier 4062* (A, F); Cerros Cuapes, SE of Hacienda El Tamagas on Peninsula Chiltepe, 12°15'N, 86°20'W, *Moreno 1721* (MO).—MASAYA: nr W shore of Laguna de Masaya, Parque Nacional de Masaya, 11°57'N, 86°07'W, *Neill 3042* (MO).—MATAGALPA: Finca Armonia, Hotel Selva Negra, 7 km N of Matagalpa, 13°00'N, 85°55'W, *Sousa 12941* (MEXU). **Panama.** COCLÉ: Panamerican Hwy, 2 km SE of turnoff to Cerro Campana, 8°24'N, 79°52'W, *Nee 9224* (MO, TEX).—VERAGUAS: Divisa, *Lao 311* (MO).

Bolivia. SANTA CRUZ: 7 km SSE of Santa Cruz, *Nee 37031* (MEXU, TEX). **Brazil.** BAHIA: Bahia, *Glocker 169* (OXF). **Colombia.** VALLE: Tulua, Corregimiento Mateguadua, natural reserve, 4°02'N, 76°10'W, *Devia 3191* (TEX). **Peru.** OXAPAMPA: Pasco, old Villa Rica rd between Puente Paicaratambo and Cedropampa, 10°45'S 75°22'W, *D. N. Smith 5410* (TEX). **Surinam.** Lower Commewijne River, nr plant Mon Souci, *Hekking 1116* (TEX). **Venezuela.** BARINAS: nr Barinitas, *Breteler 4232* (EAP).

Unripe pods and seeds of *L. leucocephala* subsp. *glabrata* are highly preferred over other species of *Leucaena* for food use, due to very abundant and virtually year-round production of large pods, large seed size, and its "sweeter" flavor. It has become—alongside *L. esculenta*—the most widely cultivated and marketed *Leucaena* within Mexico. There is some evidence to suggest that its distribution within Mexico has expanded over the last few millennia and is still expanding. Based on investigation of plant remains from archaeological excavations of cave settlement sites in the Tehuacán Valley, Zárate (1994) suggests that it was introduced to that area as late as 200 B.C. to 700 A.D. In many areas, new attempts by local residents to establish trees or small *guajales* at the extreme climatic limits of the species—for example in mid-elevation (2000 m) frost-prone villages in Puebla and Oaxaca—are evidence of continued expansion of the range. Finally, the recent prominence given to this taxon as an agroforestry or fodder tree has prompted wider cultivation within Mexico and Central America; in some areas, such as in the Comayagua Valley of Central Honduras where it was unknown 25 years ago (Molina 1974), it is now one of the commonest trees and could easily be taken to be native there despite its recent introduction.

Leucaena leucocephala subsp. *glabrata* corresponds to the '*Giant*' or '*Salvador*' type recognized by agronomists in the 1950's and 1960's (Zárate 1987a). Its superior vigor, erect habit, and branching characteristics, compared to the previously tested shrubby subsp. *leucocephala* type, were recognized following introduction of material collected near Jocóro, in Morazán Province, El Salvador, to Hawaii in 1945 (Brewbaker et al. 1972; Brewbaker 1980). The '*Salvador*' designation, which refers to this original collecting locality, led to subsequent confusion with *L. salvadorensis*, which was treated, until recently, as conspecific with *L. leucocephala* by Brewbaker. After visiting El Jocóro in 1967 and failing to locate any trace of *L. salvadorensis*, but encountering only cultivated *L. leucocephala* in the town square, Brewbaker consigned *L. salvadorensis* to synonymy (Brewbaker 1980; see also Hellin & Hughes, 1993). Following agronomic trials in Hawaii (Brewbaker et al. 1972) and in Australia (Gray 1967), one variety of *L. leucocephala*, designated K8, was formally released by the University of Hawaii (Brewbaker 1975), and a handful of others followed. These cultivars have subsequently been widely promoted and used throughout the tropics for reforestation (Pound & Martínez-Cairo 1983; National Academy of Sciences 1984; Hughes 1998), despite concerns over the genetic vulnerability of a handful of highly self-fertile lines, several of which originate from cultivated material from El Salvador, in single variety plantations (Brewbaker 1980, 1985; Hughes 1998).

A third agronomic variant, the so called '*Peru*' type, was recognized (Gray 1968; Brewbaker & Hutton 1979; Brewbaker 1980) based on material introduced to Australia from Argentina, but of supposed Peruvian origin, and characterized by the erect habit of the '*Giant*' type but the greater branchiness of the '*Common*' type. The '*Peru*' type apparently belongs within subsp. *glabrata*, although the original material has not been traced to verify this. The bred line '*Cunningham*,' released and widely planted in Australia (Gray 1967), is a cross between the '*Salvador*' and '*Peru*' types, and is therefore also attributable to subsp. *glabrata*.

6c. Leucaena leucocephala subsp. **ixtahuacana** C. E. Hughes, Contr. Univ. Michigan Herb. 21: 285. 1997.—TYPE: GUATEMALA. Huehuetenango: 1 km ENE of San Miguel, track running WSW from Ixtahuacán into the valley of the Río Cuilco, 15°23′N, 91°50′W, *Hughes 1689* (holotype: FHO!; isotypes: E! K! MEXU! MO! NY!).

Small tree, (3–) 5–7 m tall, 5–20 cm bole diameter, arborescent with a short clear bole to 2 m and a rounded compact crown. Leafy shoots glabrous. Leaves (10–) 13–16 cm

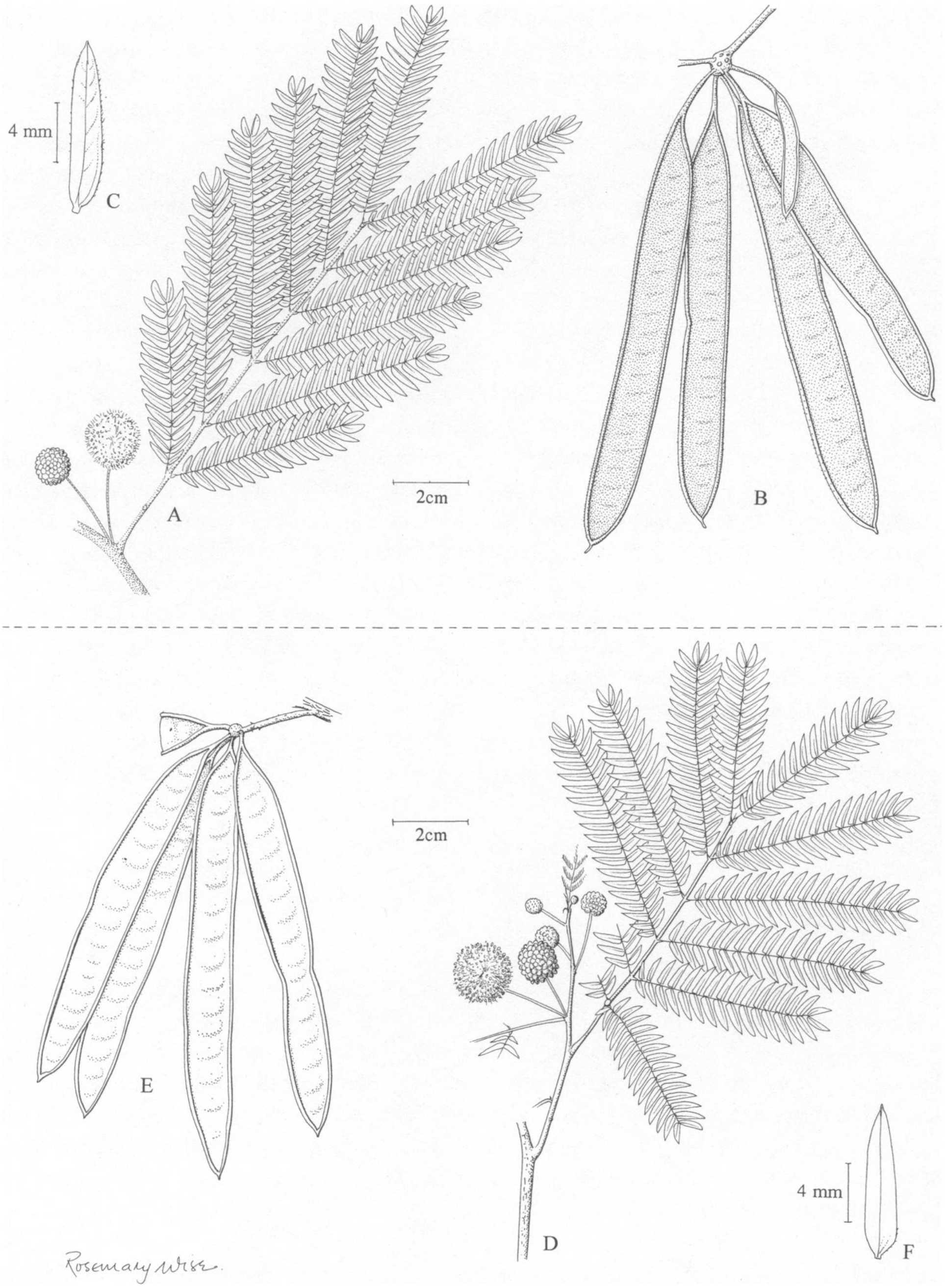


FIG. 42. *Leucaena leucocephala* subsp. *leucocephala* and subsp. *ixtahuacana*. *L. leucocephala* subsp. *leucocephala*: A. Leaf and capitula. B. Pods. C. Leaflet. *L. leucocephala* subsp. *ixtahuacana*: D. Leaf and capitula. E. Pods. F. Leaflet. (Based on: A–C, *Hughes 1286*; D–F, *Hughes 1469*.)

long, 8–11 cm wide; petioles 13–23 mm long, glabrous, petiolar nectary 2–2.4 × 1.2–1.5 mm; rachis (5–) 7–12 cm long, glabrous, mucro 1.9–3.6 mm long, very sparsely puberulent; pinnae (4–) 6–8 pairs; pinnular rachis 5–8 cm long, glabrous; leaflets 16–20 pairs per pinna, 9–11 mm long, 2–2.6 mm wide, glabrous or very sparsely ciliate along leaflet margins near base. Capitula 12–17 mm in diameter at anthesis, in fascicles of 2–6, each capitulum with 110–120 flowers; peduncles 15–19 mm long, glabrous. Flowers subtended by peltate bracts, 2.3–2.4 mm long; calyx 2.8–3.8 mm long; petals 5–5.2 mm long, free at base, partially united above; filaments 6.2–8.8 mm long; ovary 2–2.3 mm long, with 20–26 ovules, style 7.8–8.8 mm long. Pods (3–) 6–12 per capitulum, (9–) 10–13 cm long, (13–) 15–17 mm wide, linear-oblong, acute apically, 8–14-seeded, valves mid-reddish brown, glabrous and slightly lustrous. Seeds 8–9.6 mm long, 4.7–6.3 mm wide. Fig. 42D–F.

Phenology. Flowering February–April; fruiting November–April (data based on very few collections or observations and incomplete).

Distribution (Fig. 41). *Leucaena leucocephala* subsp. *ixtahuacana* is restricted to a small area of northern Guatemala and the immediate border zone in Mexico around Motozintla, largely in the valleys of the Río Cuilco and Río Seleguá, Department of Huehuetenango and Chiapas (Fig. 41). It apparently occurs only in cultivation in fields and around houses; 1350–2000 m.

Vernacular names. *Guash criollo* (Ixtahuacán, Huehuetenango); the local name *criollo* indicates the distinction made by local people between it and either of the two introduced species *L. leucocephala* subsp. *glabrata* (*guaje*) and *L. collinsii* (*guash*), which are cultivated nearby.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: 2 km SE of Tolimán rd to Ojo de Agua and Berriozábal, nr Motozintla de Mendoza, 15°19′N, 92°19′W, *Sousa 11827* (CAS, K, MEXU).

Guatemala. HUEHUETENANGO: rd from Huehuetenango NW to La Mesilla, 10 km WNW of Colotenango, valley of Río Seleguá, 15°27′N, 91°46′W, *Hughes 1132* (FHO, K, MEXU); rd W from Colotenango to Cuilco, 5 km W of Ixtahuacán, above Río Cuilco, 15°25′N, 91°48′W, *Hughes 1469* (EAP, FHO, K, MEXU, NY); 1 km ENE of village of San Miguel, track running WSW from Ixtahuacán, into valley of Río Cuilco, 15°23′N, 91°50′W, *Hughes 1689* (E, FHO, K, MEXU, MO, NY); Huehuetenango, *Skutch 1631* (A).

Leucaena leucocephala subsp. *ixtahuacana* is cultivated for the production of unripe pods and seeds, which are locally consumed and marketed in the nearby villages of San Miguel, Colotenango, and Ixtahuacán. The primary use appears to be medicinal, as a cure for stomach parasites; the unripe seeds are eaten with lemon and salt. The characteristics and distribution of this subspecies remain poorly known. Further field exploration will be needed to assess whether this variant is as localized as current collections suggest. Subspecies *ixtahuacana* is named with reference to its very localized distribution centered on the small town of Ixtahuacán.

7. Leucaena collinsii Britton & Rose, N. Amer. Fl. 23: 126. 1928. *Leucaena esculenta* subsp. *collinsii* (Britton & Rose) S. Zárate, Bull. Intern. Group Study of Mimosoideae 12: 30. 1984.—TYPE: MEXICO. Chiapas: "Castla Gutiérrez" (Tuxtla Gutiérrez), 6 Jan 1907, *Collins & Doyle 157* (holotype: NY!; isotype: US!).

Small to medium-sized tree, 10–15 (–20) m tall, 20–40 cm bole diameter, typically branchy when young, older trees with a short clear bole to 3–5 m, upright angular branching, and a spreading, open crown. Bark on young branches smooth, mid-grey or grey-brown, inner bark cinnamon brown then pale salmon pink, on older branches and bole darker grey-brown and rougher with shallow rusty orange-brown vertical fissures (Fig. 3A). Shoots terete, slightly striate, mid-orange-brown, puberulent. Stipules 3.2–4 mm long, ovate or lanceolate, with asymmetric membranous wings at base, venation and midrib prominent, caducous. Leaves (7–) 14–20 (–23) cm long, (3–) 5–13 cm wide; petioles (including swollen green or slightly blackened pulvinus) (11–) 14–28 mm long, sparsely puberulent, with a single yellow-green or green, sessile, rounded, elliptic, dome-shaped or truncate-conic nectary with a narrow central pore (Fig. 9C), 2 × 1 mm, at the distal end on adaxial side of petiole; rachis 3.7–17 cm long, sparsely pubescent, sometimes with a small elliptic conic nectary at the distal end, apex of rachis extending beyond the terminal pinnae as a pointed dark brown mucro (1–) 1.5–2.8 mm long, curling when dry; pinnae (5–) 6–16 pairs; pinnular rachis (3.7–) 4–8.7 cm long, angled, puberulent, with 1 or 2 minute elliptic nectaries at base of terminal pairs of leaflets; leaflets 25–56 pairs per pinna, 3.7–7 mm long, 1–1.9 mm wide, nearly sessile, smaller at base and apex of pinnular rachis, asymmetric about midvein, broadly linear, acuminate apically, rounded to truncate basally, sparsely puberulent along margins but otherwise glabrous, a few secondary veins visible. Capitula 9–24 mm in diameter at anthesis, in fascicles of 2–3 (–6) in leaf axils on actively growing shoots, the leaves developing with the capitula, the flowering shoot auxotelic with pods borne on older wood within crown (Fig. 10E), each capitulum with 55–170 flowers; peduncles (14–) 16–21 mm long, angled, pubescent with an involucre of bracts at the distal end. Flowers subtended by peltate bracts, 3–4 mm long, 0.7 mm in diameter; calyx 1.9–3.9 mm long, glabrous, finely ciliate along lobe margins, pale whitish green; petals 3–4.9 mm long, free, glabrous, pale whitish green; filaments 7.8–12.2 mm long, white; anthers hairy especially distally, white, apiculum absent; ovary 1.6–2.3 mm long, glabrous, white, with 13–20 ovules, style 4.2–10.5 mm long, white, with a terminal tubular stigma, exserted slightly beyond the anthers or included. Pods 1–2 (–4) per capitulum, 11–18.5 cm long, (7–) 10–19 mm wide, pendulous on sturdy 10–15 mm long stipes, linear-oblong or oblong, acuminate or sometimes obtuse apically, sometimes with a short beak, apparently readily broken off when dry, narrowly planocompressed, 9–20-seeded, valves mid-brown, glabrous, with reticulate venation most pronounced close to margins, membranous, the margins slightly thickened, dehiscent along both sutures. Seeds 6.5–8.8 mm long, 4–6.2 mm wide, compressed, circular to ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, symmetrical. Chromosome number: 2n = 52 (Pan & Brewbaker 1988; Sorensson 1989). Fig. 43.

Leucaena collinsii was described from material collected near Tuxtla ("Castla") Gutiérrez, Chiapas, Mexico. Until recently, it was thought to be restricted to the central depression of Chiapas in southern Mexico. It is now known to extend a short distance into the northern fringe of Guatemala in the department of Huehuetenango in the upper extension of the watershed of the Río Grijalva, which flows into Mexico. A distinct variant occurs further south and east in Guatemala in the Motagua valley system. Standley and Steyermark (1946), having seen only limited material without flowers, misidentified material from the Motagua Valley as *L. trichandra*. Confusion persisted due to the broad similarity between this material and *L. trichandra* in leaf and pod morphology. With collection of flowering material, the affinities of this material to *L. collinsii* became clear; a new subspecies of *L. collinsii*, subsp. *zacapana*, was recognized by Hughes (1991), based on a suite of quantitative leaf and pod characters that show discontinuous variation and on the geographic discontinuity between the two. Subspecies *collinsii* ranges from 400 to 900 m elevation in the central depression of Chiapas in Mexico and the fringes of northern Guatemala, whereas subspecies *zacapana* ranges from 100 to 800 m in the Motagua Valley system in Guatemala. The intervening mountains of central and northern Guatemala, rising to between 2000 and 3000 m, effectively isolate the two subspecies.

Zárate (1982, 1984a) treated *L. collinsii* as a subspecies of *L. esculenta*, but subsequently retained it at species rank (Zárate 1994) although still maintaining a close relationship to *L. esculenta*. In fact, *L. collinsii* is not closely related to *L. esculenta* but groups closely with *L. trichandra* in both the cpDNA analysis (Harris et al. 1994a) (Fig. 31) and in the cladistic analysis of morphological data, although in the latter a number of equally parsimonious hypotheses of relationships were discovered (Fig. 28A–D). *Leucaena collinsii* is easily distinguished from *L. trichandra* by its convex, truncate, conical nectary with a narrow pore compared to the cupulate concave broad nectary of *L. trichandra* and by its whitish green as opposed to pink flowers.

KEY TO THE SUBSPECIES OF LEUCAENA COLLINSII

1. Leaves ≥14 cm long with ≥7 pairs of pinnae and ≥45 pairs of leaflets per pinna, capitula ≥15 mm in diameter at anthesis with ≥140 flowers per capitulum, pods >16 cm long and ≥17 mm wide. 7a. *L. collinsii* subsp. *collinsii.*
1. Leaves ≤12 cm long with ≤8 pairs of pinnae and ≤40 pairs of leaflets per pinna, capitula ≤16 mm in diameter at anthesis with ≤85 flowers per capitulum, pods ≤13.5 cm long and ≤12 mm wide. 7b. *L. collinsii* subsp. *zacapana.*

7a. **Leucaena collinsii** subsp. **collinsii.**

Leaves 14–20 (–23) cm long; rachis 8–17 cm long, (7–) 12–16 pairs of pinnae per leaf; leaflets 45–56 pairs per pinna, 4.3–7 mm long, 1.1–1.9 mm wide. Capitula (15–) 20–24 mm in diameter at anthesis, each capitulum with 140–170 flowers; calyx 3.3–3.9 mm long, petals 4.2–4.9 mm long, filaments (8–) 9.6–12.2 mm long, ovary with 18–20 ovules, style 4.2–5.6 mm long. Pods 16.5–18.5 cm, 17–19 mm wide, with 14–20 seeds per pod (Fig. 43A–I).

Phenology. Flowering (July–) August–November (–December); fruiting March–April; deciduous during the prolonged dry season, December–April.

Distribution (Fig. 44). *Leucaena collinsii* subsp. *collinsii* is restricted to the central depression of Chiapas in southern Mexico and immediately adjacent areas in Guatemala on the border fringes of the department of Huehuetenango in lower lying areas of the Río Grijalva watershed. It occurs in remnant tropical dry deciduous forest, secondary dry thorn scrub, along fencelines, and is frequently cultivated around houses and in villages. Associated trees include species of *Acacia, Albizia, Caesalpinia, Calicophyllum, Enterolobium, Haematoxylon, Piptadenia, Pithecellobium, Prosopis, Swietenia,* and *Taxodium*; 450–800 (–1210) m.

Vernacular names. *Chalip (chilip)* (Huehuetenango, Guatemala), *chijlip* (La Trinitaria, Chiapas, Mexico) (*"chij"* = sweet; Tojolabal), *guash (huash)* (Huehuetenango and Chiapas), *guash de monte* (as opposed to *guash de castilla* = *L. leucocephala*), *guaxin* (La Chacona and Tuxtla Gutíerrez, Chiapas), *guaje, guaje colorado, páka sasib* (Tzeltal) (Municipio of Tenejapa) (Berlin et al. 1974).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: 9 km N of Tuxtla Gutiérrez, rd to El Sumidero, 16°48′N, 93°07′W, *Breedlove 13889* (CAS, F, TEX, US); slopes above Chicoasén, 16°58′N, 93°06′W, *Breedlove 37257* (CAS, MEXU, MO); Río Cuilco, between Nuevo Amatenango and Frontera Comalapa, 15°33′N,

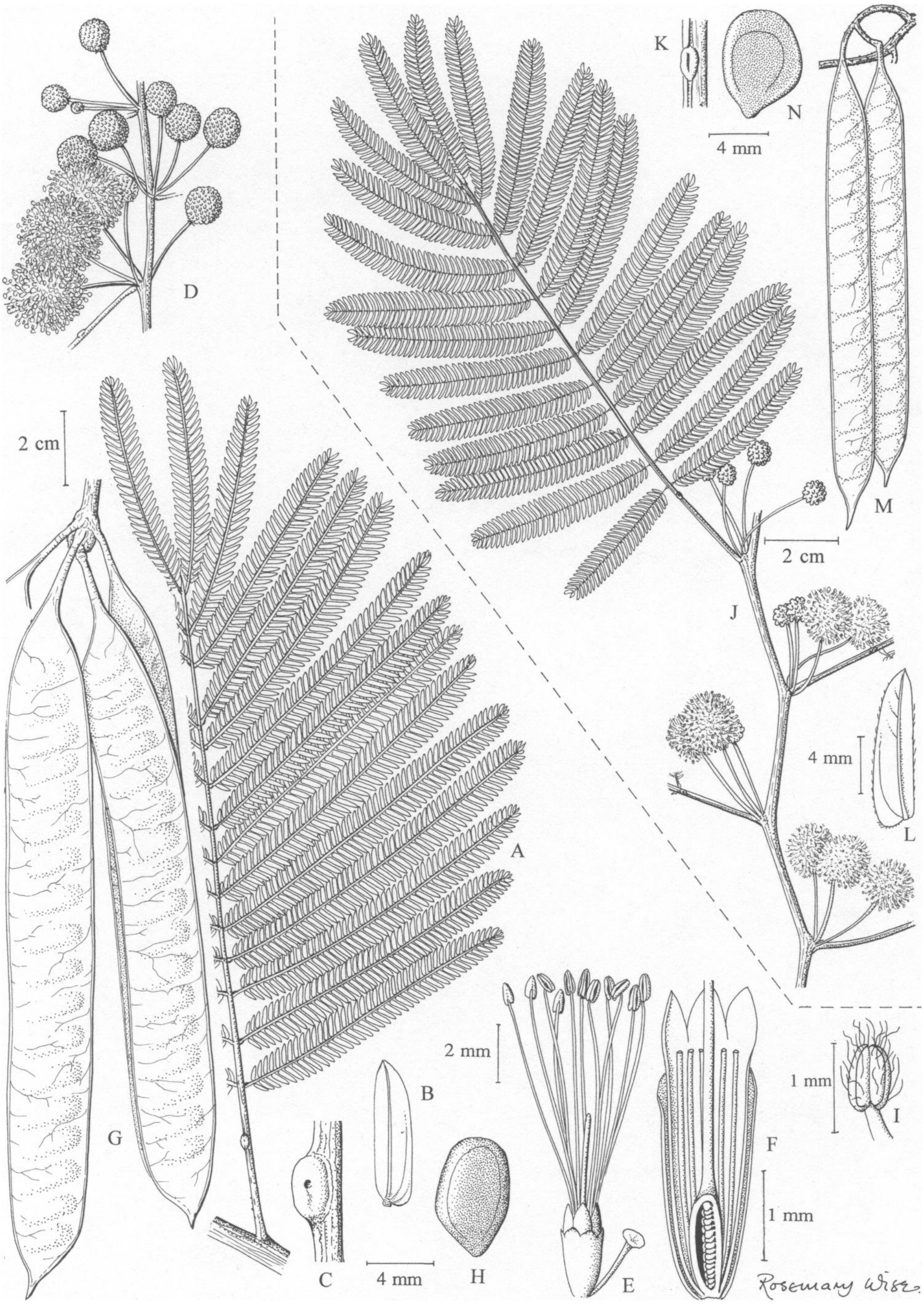


FIG. 43. *Leucaena collinsii*. A–I, subsp. *collinsii*: A. Leaf. B. Leaflet. C. Petiolar nectary. D. Flowering shoot. E. Flower. F. Longitudinal section of flower. G. Pods. H. Seed. I. Anther. J–N, subsp. *zacapana*: J. Leaf and flowering shoot. K. Petiolar nectary. L. Leaflet. M. Pods. N. Seed. (Based on: A–E, ***Hughes 1137***; F, ***Hughes 1138***; G, ***Hughes 538***; H, ***Hughes 531***; I, ***Hughes 1760***; J–N, ***Hughes 1125***.)

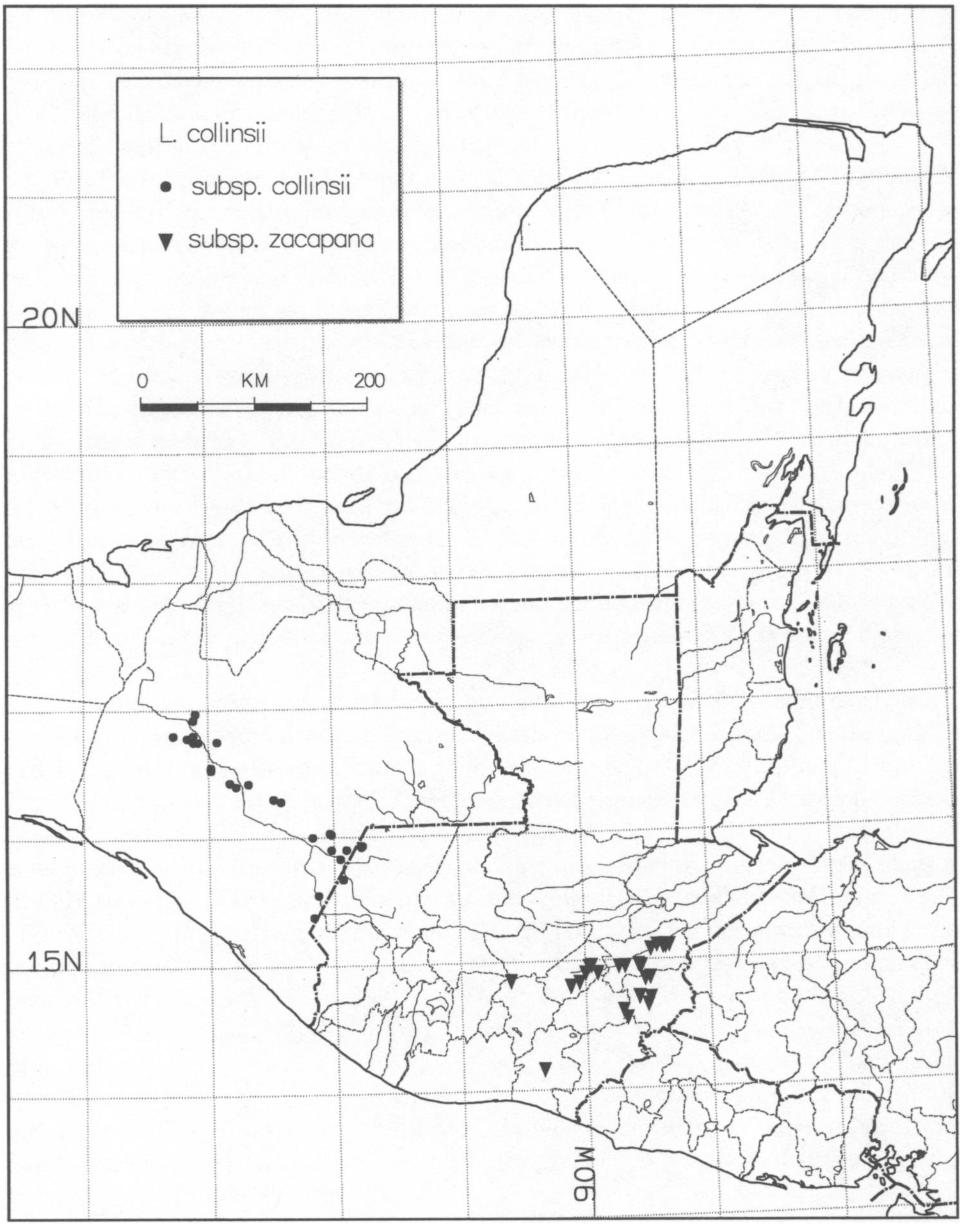


FIG. 44. Distribution of *L. collinsii.*

92°08'W, *Breedlove 41777* (CAS, MEXU); rd to Boquerón and Ejido Mujica W of Hwy 190, 18 km SW of La Trinitaria, 16°00'N, 92°10'W, *Breedlove 42131* (CAS, MEXU, MO, NY); Lagos de Colón Parque Natural, nr the ruins of Lagarteros, *Breedlove 47125* (CAS, MEXU); 12 km S of La Trinitaria, nr Panamerican Hwy, 16°02'N, 92°02'W, *Hughes 377* (FHO, K, MEXU); 15 km S of La Trinitaria, side rd to Morelos, 16°01'N, 92°01'W, *Hughes 378* (FHO, K, MEXU); 5 km W of Ingénio Pujiltíc, 16°18'N, 92°29'W, *Hughes 513* (FHO, K, MEXU); 5 km S of Narcisco Mendoza, rd between Tuxtla Gutiérrez and Villa Flores, 16°32'N, 92°59'W, *Hughes*

527, Hughes 530–539 (all FHO, K, MEXU); 20 km SSW of Tuxtla Gutiérrez nr Narcisco Mendoza, 16°33'N, 92°59'W, *Hughes 662* (FHO, K, MEXU); close to Santa Elena, rd from Comitán to Ciudad Cuauhtémoc, 20 km SE of La Trinitaria, 15°54'N, 92°01'W, *Hughes 1141* (FHO, K, MEXU); rd N from Tuxtla Gutiérrez to Chicoasén, 6 km NE of San Fernando, nr tunnel to Sumidero Canyon, 16°55'N, 93°07'W, *Hughes 1290* (BR, FHO, K, MEXU, NY); 15 km SE of La Trinitaria, rd to Ciudad Cuauhtémoc, 15°50'N, 91°57'W, *Hughes 1485* (FHO, K, MEXU, MO, NY); outskirts of Mazapa rd N from Huixtla to Motozintla and Ciudad Cuauhtémoc, 10 km N of Motozintla, 15°23'N, 92°10'W, *Hughes 1759* (CAS, FHO, K, MEXU, MO, NY); 8 km WNW of Presa Angostura, nr rd from Tuxtla Gutiérrez through Narcsico Mendoza to dam, 16°26'N, 92°50'W, *Hughes 1760* (CAS, FHO, K, MEXU, MO, NY); Tuxtla Gutiérrez, 16°45'N, 93°07'W, *C. D. Johnson 1056* (MO); El Chorreadero, 9 km E of Chiapa de Corzo along Mexican Hwy 190, 16°45'N, 92°56'W, *Laughlin 1275* (CAS, F, US); Venustiano Carranza, nr Soyatitán, rd from Pinola Las Rosas to Pujiltíc, 16°17'N, 92°25'W, *Laughlin 1991* (CAS, US); NW of Tuxtla Gutiérrez, 16°47'N, 93°09'W, *Miranda 5415* (MEXU, US); N of La Chacona, 16°47'N, 93°10'W, *Miranda 6411* (MEXU, US); Jeríco, on the rd to Parral and Aguaje del Cimarrón, *Miranda 6907* (MEXU); nr La Chacona, 16°47'N, 93°10'W, *Miranda 7575* (MEXU, US); Berriozábal–Las Vistas, 16°48'N, 93°17'W, *Miranda 5869* (MEXU); Venustiano Carranza, above Finca Carmen, rd from Acala to Pujiltíc, 16°25'N, 92°41'W, *Shilom Ton 3229* (CAS, MO, NY, TEX, US); 3 km E of Tuxtla Gutiérrez, 16°45'N, 93°05'W, *Sousa 6683* (CAS, MEXU, MO, TEX); Venustiano Carranza, Planta Angostura, Presa Belisario Domínguez, 16°24'N, 92°47'W, *Sousa 11343* (MEXU), *Sousa 11346* (MEXU, MO); Lagostero San Jerónimo 6 km NE of San Gregorio, 15°54'N, 91°54'W, *Sousa 11596* (CAS, MEXU).

Guatemala. HUEHUETENANGO: 1 km SE of Aldea Chacáj, valley of the Río Lagartero, 15 km NW of Nentón, 15°55'N, 91°47'W, *Hughes 1137* (FHO, K, MEXU); track from Chacáj to Ojo de Agua, plains nr Río Lagartero, 15 km NW of Nentón nr Mexican border, 15°56'N, 91°46'W, *Hughes 1138* (FHO, K, MEXU); Chacaj, nr the Río Lagartero, 12 km NW of Nentón 2 km E of the Mexican border, 15°56'N, 91°47'W, *Hughes 1187* (FHO, K, MEXU); rd 6 km N of Camojá Grande towards Nentón, 15°40'N, 91°56'W, *Hughes 1355* (AAU, FHO, K, MEXU, NY).

Leucaena collinsii subsp. *collinsii* is particularly abundant in certain villages, such as Chacáj in Guatemala, where it is widely cultivated for pod production. The unripe seeds are consumed locally and marketed in nearby towns and also further afield in adjacent areas outside the natural distribution in the northern highlands of Guatemala (e.g., market of Todos Santos los Cuchumatanes) and the central highlands of Chiapas (e.g., market of San Cristóbal de las Casas).

7b. **Leucaena collinsii** subsp. **zacapana** C. E. Hughes, Kew Bull. 46(3): 553. 1991.—

TYPE: GUATEMALA. Zacapa: Estanzuela in dry thorn forest, 1 Mar 1988, *Hughes 1102* (holotype: FHO!; isotypes: K! MEXU!).

Leaves 7–12 cm long; rachis 3.7–4.9 cm long, 5–8 pairs of pinnae per leaf; leaflets 25–40 pairs per pinna, 3.7–6 mm long, 1–1.3 mm wide. Capitula 9–16 mm in diameter at anthesis, each capitulum with 55–85 flowers; calyx 1.9–2.2 mm long, petals 3–3.7 mm long, filaments 7.8–9.1 mm long, ovary with 13–16 ovules, style 8.2–10.5 mm long. Pods 11–13.5 cm long, (7–) 10–12 mm wide, with 9–15 seeds per pod (Fig. 43J–N).

Phenology. Flowering (August–) September–October (–December); fruiting February–April; deciduous during the prolonged dry season, December–April.

Distribution (Fig. 44). *Leucaena collinsii* subsp. *zacapana* is restricted to the middle and lower dry or semi-arid Río Motagua Valley system in southeastern Guatemala. It is most frequent in the departments of Chiquimula, Progreso, and Zacapa, with outlying occurrences in the fringes of the departments of Jalapa and Guatemala. A single collection, *C. D. Johnson 1972*, from near Cuilapa in the department of Santa Rosa outside the Motagua valley, is apparently an outlier, possibly resulting from cultivation; the subspecies is not common in that area. It occurs abundantly in dry thorn scrub and secondary vegetation including bush fallow after cultivation, sometimes dominating such stands and occasionally as pure stands when managed on a coppice rotation. Associated trees include species of *Acacia, Albizia, Apoplanesia, Caesalpinia, Guaiacum, Haematoxylon, Cordia, Phyllocarpus,* and *Pithecellobium,* and Cactaceae, including species of *Pereskia,* and these are abundant throughout the range; 110–600 (–900) m.

Vernacular names. *Guaje* (*yaje*).

Additional Specimens Examined. **Guatemala.** Chiquimula: 3 km E of Vado Hondo, rd to Jocotán, 14°43′N, 89°29′W, *Hughes 438* (FHO, MEXU); above El Carrizal, rd from Chiquimula to Quetzaltepeque and Esquipulas, 5 km NW of Quetzaltepeque, 14°40′N, 89°30′W, *Hughes 1096* (FHO, K, MEXU), *Hughes 1097* (FHO, K, MEXU); 2 km NE of San José la Arada, track to Chiquimula nr the Monumento Batalla de la Arada, 14°44′N, 89°34′W, *Hughes 1114* (FHO, K, MEXU); rd N from Agua Blanca, 5 km S of Ipala, lower W slopes of Volcán de Ipala, 14°34′N, 89°40′W, *Hughes 1390* (EAP, FHO, K, MEXU, NY); gorge of the Río Chiquimula between Santa Barbara and Petapilla, 9 km N of Chiquimula, 14°53′N, 89°29′W, *Steyermark 30269* (A, F).—Guatemala: 3 km S of Río Motagua bridge at Concuá, old rd from Guatemala City to Cobán via San Juan Sacatepéquez, 14°52′N, 90°36′W, *Hughes 1108* (FHO, K, MEXU).—Jalapa: 5 km W of Ipala towards San Luís Jilotepeque, 14°38′N, 89°42′W, *Hughes 410* (FHO, K).—Progreso: Km 49 on CA-9 from Guatemala City nr El Progreso, 14°49′N, 90°07′W, *Harmon 5902* (NY), *Harmon & Dwyer 3498* (F, GH, US); 3 km E of El Rancho, rd to San Agustín Aguascatlán, 14°55′N, 90°00′W, *Hughes 263* (FHO, MEXU); 2 km S of Puerto de Golpe nr San Agustín Aguascatlán, 14°58′N, 89°58′W, *Hughes 299* (FHO); 4 km W of Cabanas on the rd to El Rancho, 1 km E of El Rancho, S side of Río Motagua, 14°55′N, 89°54′W, *Hughes 1754* (CAS, FHO, K, MEXU, MO, NY); San Agustín Acuascatlán, 3 km S of Puerto de Golpe, 14°59′N, 89°57′W, *McCarter & Hughes 36* (FHO, K, MEXU); San Agustín, 14°51′N, 90°03′W, *Molina 24970* (EAP, F, NY, US); 10 km N of El Rancho and the Guatemala-Puerto Barrios rd, on rd to Cobán, *Téllez 8919* (MEXU).—Santa Rosa: 14 km SE of Cuilapa, 14°11′N, 90°21′W, *C. D. Johnson 1972* (CAS).—Zacapa: 20 km E of Zacapa, rd to Puerto Barrios, 15°06′N, 89°28′W, *A. R. García 1355* (MEXU, MO); nr San José, lower Motagua Valley, 14°58′N, 89°41′W, *Hughes 297* (FHO, MEXU); 1.5 km E of Mayuelas, nr Río Motagua, downstream from Gualán, 15°07′N, 89°21′W, *Hughes 462* (FHO, MEXU); El Porvenir sawmill, immediately N of the Río Motagua, 2.5 km NW of Gualán, 15°08′N, 89°22′W, *Hughes 1120* (FHO, K, MEXU); Los Achiotes, 159 km E Guatemala City, 6 km W of Gualán, 15°08′N, 89°25′W, *Hughes 1122* (FHO, K, MEXU); 1 km E of Gualán, S side of Río Motagua, rlwy line E to Puerto Barrios, 15°08′N, 89°21′W, *Hughes 1123* (FHO, K, MEXU); 4 km E of Gualán, track to Biafra and Vainilla, S side of Río Motagua, 15°08′N, 89°19′W, *Hughes 1125* (FHO, K, MEXU), *Hughes 1126* (FHO, K, MEXU); 1 km N of Estanzuela, S side of Río Motagua Valley, 5 km NW Zacapa, 14°59′N, 89°34′W, *Hughes 1705* (E, FHO, K, MEXU, MO, NY); nr station, Gualán, 15°07′N, 89°22′W, *Record G102* (NY, US); nr Zacapa, 14°58′N, 89°33′W, *Standley 72008* (F); vicinity of Zacapa, 14°58′N, 89°33′W, *Standley 73562* (A, F), *Standley 73641* (F, US); divide between Zacapa and Chiquimula, 14°52′N, 89°31′W, *Standley 73837* (EAP, F); Río Motagua, 2 km W of Teculatán, 14°58′N, 89°44′W, *Steyermark 29191* (F).

Leucaena collinsii subsp. *zacapana* is distinguished from subsp. *collinsii* by its smaller leaves, fewer pinnae per leaf, fewer leaflets per pinna, smaller leaflets, smaller flowers, fewer flowers per capitulum, and smaller pods. In addition, the style is long in subsp. *zacapana*, protruding beyond the anthers, compared to subsp. *collinsii,* which has shorter styles that are included below the anthers.

Unlike subsp. *collinsii* there is no record of use of pods or seeds of subsp. *zacapana* as food. It is however highly valued because of its extremely dense wood with abundant formation of heartwood, which makes it ideal for fence posts and house construction, as well as one of the highest quality firewoods available. Because of these qualities secondary stands are managed in parts of the Motagua Valley on a four-year coppice rotation specifically for fuelwood production.

8. Leucaena trichandra (Zuccarini) Urban, Symb. antil. 2: 267. 1900. *Acacia trichandra* Zuccarini, Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 2: 349. 1837[?]. *Leucaena diversifolia* subsp. *trichandra* (Urban) F. J. Pan, Quart. J. Chinese For. 21: 89. 1988.—Type: Cultivated "in horto Monacensi a. 1835, crescit in imperio mexicano, unde semina communicavit clar. de Karwinski," Herb. Regium Monacense (holotype: M!, fragment and tracing ex M: US!).

Leucaena stenocarpa Urban, Symb. antil. 2: 266. 1900. *Leucaena diversifolia* subsp. *stenocarpa* (Urban) S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65: 152. 1994.—TYPE: MEXICO. Oaxaca: foothills of Sierra San Felipe, N of Oaxaca, 1900 m, 17°07′N, 96°43′W, 26 May 1894, *Pringle 4656* (holotype: B, destroyed; isotypes: A! F! K! MEXU! MO! NY! UC! US!).

Leucaena guatemalensis Britton & Rose, N. Amer. Fl. 23: 126. 1928.—TYPE: GUATEMALA. Guatemala: on plains nr Guatemala City, 14°37′N, 90°31′W, Jul 1860, *Hayes 23* (holotype: NY!; isotypes: K! GH! MO! US!).

Leucaena revoluta Britton & Rose, N. Amer. Fl. 23: 127. 1928.—TYPE: MEXICO. Chiapas: mountain slopes nr Fenix, 17 May 1900, *Purpus 10158* (holotype: NY!; isotype: US!).

Leucaena standleyi Britton & Rose, N. Amer. Fl. 23: 128. 1928.—TYPE: EL SALVADOR. Santa Ana: vicinity of Santa Ana, 750 m, 13°59′N, 59°32′W, *Standley 20409* (holotype: NY!; isotypes: GH! US!).

Senegalia albanensis Britton & Rose, N. Amer. Fl. 23: 117. 1928.—TYPE: MEXICO. Oaxaca: Monte Albán, 5 Sep 1894, *C. L. Smith 320* (holotype: NY, photo ex NY at K!).

Small to medium-sized tree, 5–15 (–18) m tall, 20–50 cm bole diameter, tree form very variable, usually slender with a clear bole up to 3 m and a light feathery but spreading and irregular crown, often modified by lopping. Bark on young branches smooth, rougher on bole, mid-grey-brown to dark blackish brown with shallow rusty orange-brown vertical fissures, the inner bark green and further in cream, sometimes streaked pink or reddish. Shoots terete, mid-orange-brown, variably glabrous or thickly covered with dense white velutinous pubescence. Stipules 3.9–4.8 mm long, ovate, with a subulate or long-pointed apex, with small asymmetric basal wings, midrib prominent, margins ciliate, persistent. Leaves (9–) 12–20 (–25) cm long, (4–) 7–11 (–13.5) cm wide; petioles (including pulvinus) (8–) 12–22 (–26) mm long; rachis (7–) 9–13 (–20) cm long, strongly canaliculate and variably glabrous or densely covered in velutinous white pubescence, with a sessile, strongly cupulate or deeply crateriform, round or sometimes rounded-triangular, occasionally elliptic nectary, or rarely a pair of adjacent nectaries, 1.6–3.4 (–4.8) mm long, 1–1.7 (–2.2) mm wide, 1–2 mm tall, on ventral side of petiole at base of the lower pair of pinnae, with an additional 1–2 (–15) sessile, cupulate or shallowly discoid, circular, or weakly elliptic nectaries, 0.8–1.4 mm long and 0.7–1.2 mm wide, at base of terminal and subterminal pairs of pinnae and where many, at the base of all pairs of pinnae, apex of rachis extending beyond the terminal pinnae in a slender pointed mucro, 2.6–3.5 (–4.4) mm long, variably glabrous or covered in white hairs; pinnae (5–) 11–22 (–30) pairs; pinnular rachis (3–) 4–6 (–8.4) cm long, strongly canaliculate on ventral side, varying from sparsely pubescent on adaxial side to densely white-pubescent throughout, with 1 (–2) sessile, discoid or circular nectaries, 0.2–0.3 × 0.1–0.2 mm, at base of terminal pairs of leaflets; leaflets (20–) 30–40 (–59) pairs per pinna, (3–) 3.8–5.2 (–7) mm long, (0.7–) 1–1.4 (–1.8) mm wide, sessile or very short-petiolate, linear-oblong, acute at apex, cordate/cuneate and strongly asymmetric at base, entire, variably glabrous, sparsely pilose or villose, the margins strongly ciliate, strongly asymmetric midrib visible. Capitula 7–10 (–12) mm in diameter at anthesis, in fascicles of (1–) 3–5 in leaf axils, on actively growing auxotelic shoots with coeval leaf development (Fig. 12A), each capitulum with (60–)

70–130 (–165) flowers; peduncles 12–23 mm long, slender, angled, variably glabrous or densely pubescent, with an involucre of basally united bracts at the distal end. Flowers subtended by slender peltate bracts, (1.6–) 1.8–2.2 (–2.4) mm long, round and densely ciliate; calyx (1.8–) 2–2.4 (–2.9) mm long, densely hairy on lobes, ciliate on lobe margins, pale green; petals (2.6–) 2.9–3.2 (–4) mm long, free, sparsely hairy on lobes, ciliate on lobe margins, pale whitish green, the lobe tips sometimes tinged dark green or maroon; filaments (2.9–) 3.1–4 (–5.1) mm long, white, sometimes tinged pink; anthers densely pilose, pale cream-white, very pale pinkish grey, pale, dull or bright rose pink, or occasionally pale violet, apiculum absent; ovary 1.4–1.8 (–2.1) mm long, glabrous, pale cream-white, with 14–24 ovules, style (4.7–) 5.1–6.2 (–7.3) mm long, white, white tinged pink, or occasionally deep pink or scarlet, with a narrow-funnelform stigma, exserted beyond the anthers. Pods (1–) 2–4 (–15) per capitulum, (5–) 7–11 (–16.5) cm long, (13–) 15–23 (–29) mm wide, pendulous, on (3–) 5–10 (–15) mm long stipes, narrowly or broadly linear-oblong, occasionally oblong, acute at base, acute or rounded at apex, usually with a short straight or recurved point, flat, 5–20-seeded, valves thin, chartaceous, yellow-green or reddish green often deep maroon and very glossy when unripe, turning pale yellow- or deep reddish brown, sometimes lustrous, glabrous or sometimes covered in dense velutinous pubescence, the margins slightly thickened, dehiscent along both sutures, borne on older wood within the crown and often crowded along branches. Seeds 4.5–6.5 (–7.3) mm long, 2.8–3.7 (–4.2) mm wide, slightly compressed, narrowly oblong, dark glossy chestnut-brown, aligned transversely in pods; pleurogram visible, regular, U-shaped, 95% arm extension, symmetrical. Chromosome number: 2n = 52 (Hutton 1981; Pan & Brewbaker 1988; Sorensson 1989). Fig. 45.

Phenology. Flowering (May–) June–September; fruiting (February–) March–May.

Distribution (Fig. 46). *Leucaena trichandra* has the most extensive native distribution (after *L. leucocephala*, which is extensively cultivated), occurring from northern Nicaragua at 13°06′N, through Honduras, El Salvador, Guatemala, Belize, southern Mexico in Chiapas and Oaxaca, and sporadically through south-central and western Mexico as far north as Durango at 25°25′N. It occurs primarily as a small understory tree or shrub in pine, mixed pine-oak, and oak forest at mid-elevations throughout the dissected mountains of this region. It also extends at lower elevations into dry deciduous forest, dry matorral, and dry secondary forest, and occurs on a wide range of soils from shallow calcareous over limestone to shallow infertile more acid soils over volcanic ignimbrites and tuffs. Associated trees include a selection of pines, e.g., *Pinus oocarpa, P. maximinoi, P. tecunumanii, P. devoniana,* and occasionally *P. caribaea*, a wide range of species of *Quercus* as well as other tree species, including *Liquidambar styraciflua, Alnus acuminata, Piscidia grandifolia, Acacia angustissima, Calliandra grandiflora, C. houstoniana, Diphysa americana,* and *Hybosema ehrenbergii,* as well as species of *Rhus, Fraxinus, Lysiloma, Albizia,* and *Eysenhardtia.* It occurs sympatrically with other species of *Leucaena* including *L. esculenta* and *L. pallida*, and often contiguously with other species such as *L. confertiflora, L. collinsii,* and *L. shannonii*; (200–) 700–2000 (–2500) m.

Vernacular names. *Barba león* (Huehuetenango, Guatemala), *chalí* (Guatemala, Guatemala), *frijolillo* (Intibuca, Honduras), *guaje (huaje)* (widely in Guatemala, El Salvador, Honduras, and Mexico), *guaje chiquito, guaje flojo* (México, Mexico), *guaje rojo* (Ahuachapán, El Salvador), *shashíb (shashíl, shaskíb, xaxíb, shashíbtez, k'ushabil shashíb* = edible *sasib*) (Tzeltal; Chiapas, Mexico), *quebracho (quebrachillo)* (names normally applied to *Lysiloma* spp.) (Paraíso and Lempira, Honduras, Guatemala, Guatemala), *tze* (Mazateco; Oaxaca, Mexico), *vainillo* (Chiquimula and Honduras).

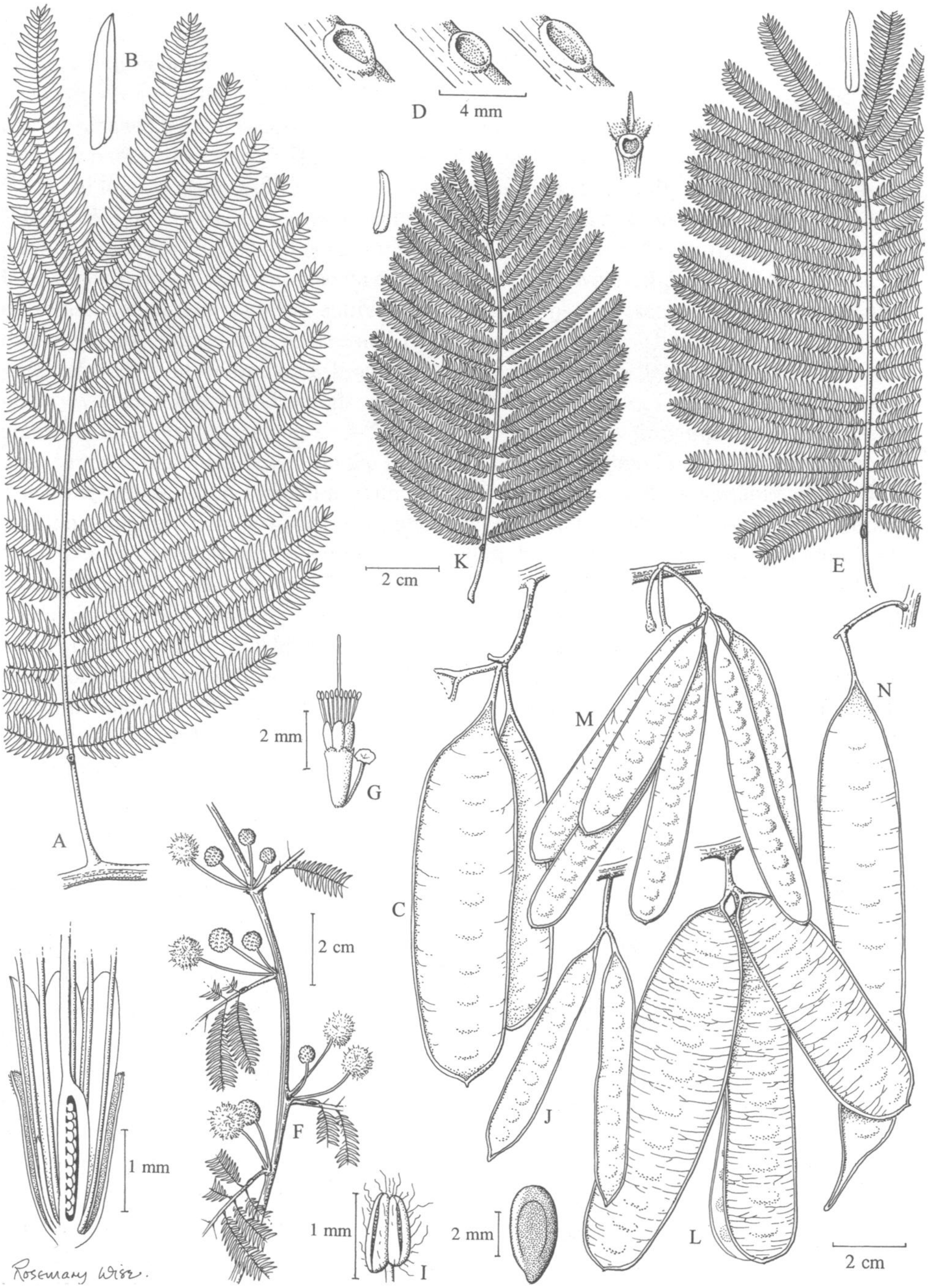


FIG. 45. *Leucaena trichandra*. A. Leaf. B. Leaflet. C. Pods. D. Extrafloral nectaries. E. Leaf and leaflet. F. Flowering shoot. G. Flower. H. Longitudinal section of flower. I. Anther. J. Pods. K. Leaf and leaflet. L. Pods. M. Pods. N. Pod. (Based on: A–D, *Hughes 1422*; F–J, *Hughes 1419*; K, L, *Hughes 1350*; M, *Hughes 1701*; N, *Hughes 1474*.)

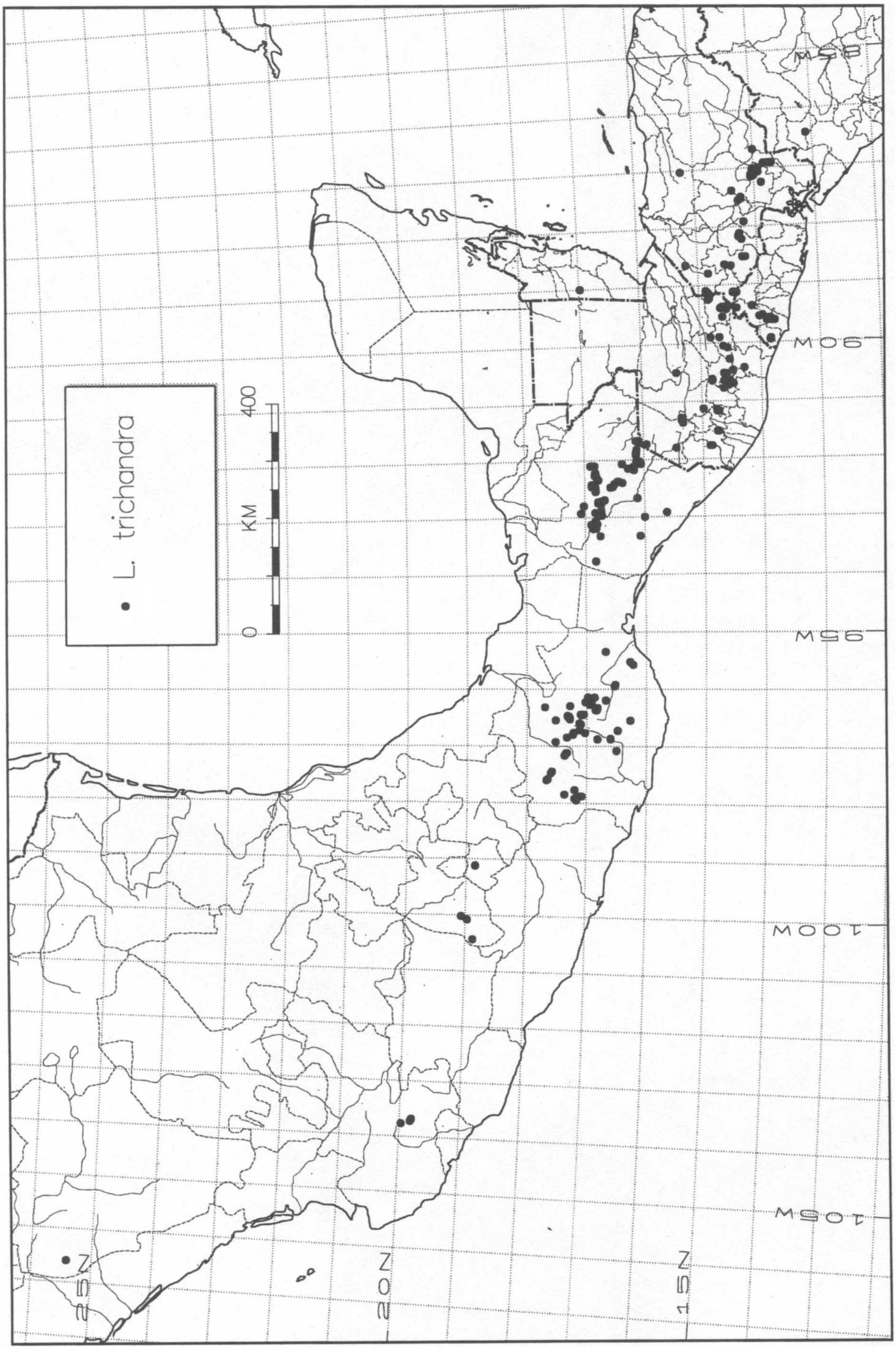


FIG. 46. Distribution of *L. trichandra*.

Berlin et al. (1974) provide the variant *bac'il sasib* (= genuine *sasib*) and point out that *sasib* is a polytypic generic tree name containing at least five species in four genera, all of which are Mimosoid legumes with finely divided leaves. Zárate (1994) lists two additional Zapotec names used in Oaxaca: *la-aye-ti* (= *guaje chiquito*) and *lobadaviyia* (= *guaje de pájaro*).

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: nr Laguna Juenaján, 16 km NE of Comitán de Domínguez, 16°22′N, 92°04′W, *Alexander 1270* (MEXU, NY); nr Habenal, paraje of Mahben Chauk, nr Tenejapa, *Breedlove 7646* (CAS, NY, US); Paraje of Kulak'tik, nr Tenejapa, 16°49′N, 92°29′W, *Breedlove 10962* (CAS, US); nr center of Amatenango, 16°30′N, 92°25′W, *Breedlove 12125* (CAS, US); canyon above El Chorreadero, nr Chiapa de Corzo, 16°45′N, 92°56′W, *Breedlove 20430* (CAS, MEXU, MO, NY); nr large double waterfall 6–8 km W of Jitotol, 17°04′N, 92°56′W, *Breedlove 23261* (CAS); 15 km E of La Trinitaria, rd to Montebello, 16°08′N, 91°55′W, *Breedlove 42057* (CAS, MO, NY); nr Colonia Vicente Guerrero, nr Villa Corzo, 16°00′N, 93°00′W, *Breedlove 48581* (CAS, MEXU); 6–10 km NNE of La Soledad, logging rd from Las Margaritas to Campo Alegre, nr La Independencia, *Breedlove 53187* (CAS, MEXU); 3 km S of Aguacatenango, rd to Las Rosas, 16°27′N, 92°23′W, *Breedlove 53249* (CAS, MEXU, NY); 3 km NW of Comitán de Domínguez, Hwy 190, 16°16′N, 92°09′W, *Breedlove 53695* (CAS, MEXU, NY, TEX); 3 km W of Tziscao, Parque Natural Lagunas de Montebello, 16°06′N, 91°41′W, *Cabrera 2986* (MEXU, MO, NY); 32 km SW of Ocosingo on Hwy 199, 16°48′N, 92°18′W, *Croat 40410* (MO); 8 km N of Bochíl, Hwy 195 from Ixtapa to Pichucalco, 17°01′N, 92°48′W, *Croat 47695* (MEXU, MO); 3 km SW of Tzimol, 16°10′N, 92°11′W, *A. R. García 1311* (MEXU, MO, TEX); 13 km SW of Angel Albino Corzo, 16°05′N, 93°20′W, *A. R. García 1428* (MEXU, MO); Ejido 21 de Marzo, nr Mapastepec, 15°38′N, 92°55′W, *C. Graham s.n.* (MEXU); Ixtapa, 6 km NW of Zinacantán, 16°47′N, 92°44′W, *Grethur 1739* (MEXU); 5 km S of Villa Las Rosas, central depression of Chiapas, 16°22′N, 92°24′W, *Hughes 512* (FHO, K, MEXU); nr rd 25 km N from Tuxtla Gutiérrez N to Chicoasén, 5 km NE of San Fernando, 16°49′N, 93°12′W, *Hughes 1185* (FHO, K, MEXU), *Hughes 1289* (BR, CR, FHO, K, MEXU, NY, US); nr rd N Francisco I. Madero to Adolfo López Mateos, 20 km N of Cintalapa de Figueroa, 16°50′N, 93°46′W, *Hughes 1350* (BR, FHO, K, MEXU, NY); Zinacantán Paraje of Muctajoc on Hwy 190, 16°44′N, 92°53′W, *Laughlin 1582* (CAS, F, US); trail from Zinacantán paraje of Paste' to San Lucas, nr Zapotal, 16°40′N, 92°42′W, *Laughlin 2558* (CAS, MEXU, US); between turnoff to Pichucalco and San Cristóbal de las Casas, 16°44′N, 92°46′W, *Sousa 2697* (MEXU, NY, TEX, UC); 5 km NW of Teopisca, 16°34′N, 92°29′W, *Sousa 6704* (MEXU, MO, UC); nr Muctajo, Ixtapa, 16°44′N, 92°53′W, *Sousa 6759* (CAS); Mirador "El Roblar," El Sumidero, 17 km N of Tuxtla Gutiérrez, 16°50′N, 93°04′W, *Sousa 11408* (MEXU); 5 km SW of Nuevo Vicente Guerrero, rd to San Juan Custepeque, nr Jaltenengo de la Paz, 16°00′N, 93°00′W, *Sousa 11529* (MEXU); 7 km SSE of La Trinitaria, 16°04′N, 92°04′W, *Sousa 11576* (MEXU); 4 km E of Ocozocuautla, 16°45′N, 93°20′W, *Sousa 11917* (K, MEXU).—DURANGO: nr Tabahueto (al catorce) 196 km W of Tepehuanes, 25°25′N, 106°36′W, *R. Torres 3569* (MEXU).—GUERRERO: 4 km E of Yextla nr El Espinalito, *V. Blanco 860* (MEXU).—JALISCO: 20 km W of Sayula, rd to Venustiano Carranza, 19°48′N, 103°41′W, *Magallanes 2277* (TEX); Salto de Agua El Nogal, 5 km N of Tapalpa, 19°58′N, 103°46′W, *Magallanes 2904* (K, TEX).—MÉXICO: nr to Tenería, nr Tejupilco, 18°58′N, 100°05′W, *Guizar 621* (MEXU); nr Nanchititla, Temascaltpec, 18°52′N, 100°26′W, *Hinton 3970* (K, NY, TEX, UC); nr Carboneras, Temascaltepec, 19°04′N, 100°01′W, *Hinton 7993* (K, NY, TEX).—MORELOS: Cañón de Lobos, nr Amador Salazar, 18°51′N, 99°07′W, *M. Z. Fernández s.n.* (MEXU).—OAXACA: 6 km N of turnoff to Lachivelde, rd from Totolapan to Tehuantepec, 16°41′N, 96°12′W, *Acosta-Solis 890* (MEXU, NY); Km 232 rd from Oaxaca to Tuxtepec, 17°42′N, 96°19′W, *Brenan 14324* (K); nr Guelatao, 17°18′N, 96°30′W, *E. García 550* (MEXU); Km 35 rd from Teotitlán del Camino of Huitzo to Oaxaca, *Grethur 700* (CAS, MEXU); nr Cerro Zempoaltepetl, trail from Santo Domingo Albarradas to Mitla 25–30 km SW of summit, 16°56′N, 96°16′W, *Hallberg 1031* (US); nr rd 45 km SE from Oaxaca and Tlacolula to Tehuantepec, 3 km NW of turnoff to San Baltazar Guelavila, 16°50′N, 96°22′W, *Hughes 1499* (FHO, K, MEXU, MO, NY); nr rd 10 km NNE from Oaxaca towards Tuxtepec, 5 km SSW of Tierra Colorada, SW slopes, Sierra de Juárez, 17°06′N, 96°37′W, *Hughes 1654* (E, FHO, K, MEXU, MO, NY); nr rd 10 km E from San Pablo Villa de Mitla between Corral del Cerro and San Bartolo Albarradas, 16°57′N, 96°16′W, *Hughes 1657* (E, FHO, K, MEXU, MO, NY); rd SE from Oaxaca to Tehuantepec below Cerro Nueve Puntas, 12 km SE of Matatlán, 16°49′N, 96°20′W, *Hughes 1661* (E, FHO, K, MEXU, MO, NY); Portillo de Nejapa, 107 km NW of Tehuantepec rd to Oaxaca, 17 km NW of El Coyul, 16°32′N, 95°57′W, *Hughes 1772* (CAS, FHO, K, MEXU, MO, NY); Río Culebra nr Macuiltianguis, 17°31′N, 96°33′W, *Lucero 93* (MEXU); 2 km N of rd between Huajuapan de León and Oaxaca, side rd to Santa María Tinú, 17°22′N, 97°10′W, *Magallanes 126* (CAS); 5 km N Yucunama, Teposcolula Mixteca Alta, 17°36′N, 97°29′W, *Mendoza 1067* (MEXU, MO); 2 km S of jctn of Putla to Juxtlahuaca and Putla to Tlaxiaco rds, 17°09′N, 97°53′W, *Mendoza 3120* (MEXU); 12 km NW of San Juan Mixtepec or "El Palenque," 17°22′N, 97°51′W, *J. Reyes 139* (MEXU); nr El Carrizal, nr Cuilapan de Guerrero, *Robles 78* (MEXU); Monte Albán, nr Oaxaca, 17°02′N, 96°46′W, *Rose 4567* (K, NY, US); S of Santiago Matatlán, distr. of Tlacolula, 16°51′N, 96°22′W, *Solano & Vara 195* (CAS, MEXU); 30 km NE of Etla, nr San Juan Guelache, 17°14′N, 96°48′W, *Solano & Vara 375* (MEXU); 67 km NW of Tequisistlán, rd to Tehuantepec, *Sousa 2692* (MEXU, TEX, UC); S slopes of Cerro San Felipe, Oaxaca, 17°07′N, 96°43′W, *Sousa 5642* (MEXU); 18 km SE of Nochistlán, 2 km NW of Cuesta Blanca, 17°20′N, 97°07′W, *Sousa 5980* (CAS, MEXU, UC); nr El Estudiante, *Sousa 6102* (CAS, TEX); nr San Bernardo Mixtepec, 4 km N of Santa Cruz Mixtepec, Zimatlán, 16°49′N, 96°53′W, *Sousa 6270* (CAS, MEXU, UC); in Barranca Larga 23 km SW of Ocotlán, 7 km S of Ejutla, 16°29′N, 96°44′W, *Sousa 6526* (CAS, MEXU); Cerro el Veinte, 5 km S of Tonaltepec, Cuicatlán, 17°31′N, 96°56′W, *Sousa 7796* (MEXU, UC); 8 km N of Díaz Ordaz, rd to Cuajimaloya, nr Tlacolula, 17°05′N, 96°27′W, *Sousa 7806* (MEXU, UC); 12 km E of Mitla, Tlacolula, 16°55′N, 96°15′W, *Sousa 7834* (CAS, MEXU, UC); nr El Zacatal, 14 km SW of San Pedro and San Pablo Ayutla, Mixe, 16°59′N, 96°09′W, *Sousa 7858* (CAS, MEXU, UC); 20 km NE of Sola de Vega, 16°36′N, 96°52′W, *Sousa 9992* (CAS), *Roe 604a* (NY); 5 km SW of Tamazulapan, rd to Chilapa de Díaz, distr. of Teposcolula, 17°40′N, 97°36′W, *Sousa 10369* (MEXU); 4 km WNW of turnoff to Copala, nr Putla, 17°10′N, 97°57′W, *Sousa 10602* (MEXU); 9 km N of El Cerezal, nr Ixtepeji, nr Ixtlán, 17°17′N, 96°32′W, *Sousa 12619* (CAS, MEXU); 11 km NW of Lachivíza, track to Lachiguiri, nr Guienagati, Tehuantepec, 16°41′N, 95°21′W, *Tenorio 11124* (MEXU); nr El Vado, 1 km W of jctn rd from Oaxaca to Puerto Escondido, Sola de Vega, 16°36′N, 96°53′W, *R. Torres 429* (MEXU); Cerro Tres Cruces S of El Limón, 11.1 km SW of jctn with main Tehuantepec to Oaxaca rd, *R. Torres 4275* (MEXU, MO); 18 km SW of Buenos Aires towards Tenango entering by Hierba Santa, 10 km NW of Tehuantepec, 16°13′N, 95°35′W, *R. Torres 7404* (MEXU, MO, TEX); 3 km N of San Juan Lajarcia, nr Yautepec, 16°31′N, 95°56′W, *R. Torres 7894* (MEXU, MO); nr Santa Lucía, Miahuatlán, 16°16′N, 96°33′W, *Vásquez 98* (MEXU); 7 km SW of Guelatao, 17°17′N, 96°32′W, *Zárate 629* (MEXU, MO).—PUEBLA: Barrancas nr the Río San Francisco, *Purpus 3865* (MO, UC).

Belize. EL CAYO: San Luis rd nr Augustine, Mountain Pine Ridge, 16°59′N, 89°00′W, *Hunt 112* (US). **El Salvador.** AHUACHAPÁN: nr La Mirador, Finca San Benito, 30 km WNW of Acajutla, nr El Imposible forest reserve, 13°50′N, 89°57′W, *Hughes 1233* (FHO, K, MEXU, NY, US); San Francisco Menéndez, 150 m S of mirador El Mulo, Cerro Ishtepeque, El Imposible, 13°49′N, 89°57′W, *Reyna 1465* (K); San Francisco Menéndez, Hda. San Benito, W of bajadero los Escobos, El Imposible, 13°49′N, 89°56′W, *Sandoval 258* (K).—SANTA ANA: nr rd W from San Salvador to Santa Ana, 6 km E of Santa Ana, nr El Congo, 13°57′N, 89°32′W, *Hughes 1244* (FHO, K, MEXU, NY); Cerro Montecristo, above Hac. San José, 15 km N of Metapán, 14°23′N, 89°24′W, *Hughes 1259* (FHO, K, MEXU, NY).—SONSONATE: 3 km E of Volcán Izalco, 13°48′N, 89°37′W, *Allen 6922* (EAP, F, GH, NY, TEX, US); rd to Sonsonate, 13°45′N, 89°37′W, *Carlson 184* (F, UC); cloud forest of Cerro Verde, 13°49′N, 89°35′W, *Molina 21711* (EAP, F, NY, US). **Guatemala.** ALTA VERAPAZ: Canyon Río Chixoy, Sierra de Chamá 10–15 km W of San Cristóbal, 15°25′N, 90°30′W, *L. O. Williams 40538* (EAP, F).—CHIQUIMULA: nr Cruz Alta, rd from Esquipulas to Chiquimula, 3 km W of Esquipulas, 14°34′N, 89°23′W, *Hughes 1094* (FHO, K, MEXU); nr rd 12 km E from Ipala to Yerbabuena and Quetzaltepeque, 14°37′N, 89°33′W, *Hughes 1391* (EAP, FHO, K, MEXU, NY); nr rd 10 km SE from Quetzaltepeque to Esquipulas W slopes Montaña La Ruda, 14°37′N, 89°24′W, *Hughes 1456* (EAP, FHO, K, MEXU, NY); 5 km W of Honduran border post at El Florída, nr rd W to Jocotán, Camotán, and Chiquimula, 14°51′N, 89°15′W, *Hughes 1739* (CAS, FHO, K, MEXU, MO, NY); Quebrada Oscura nr Esquipulas, 14°33′N, 89°22′W, *Molina 25227* (EAP, F, MO, NY, US); Montaña Castilla, nr Montaña Cebollas, Río Santa Lucía Saso, 5 km SE of Quetzaltepeque, 14°07′N, 89°22′W, *Steyermark 31302* (F).—GUATEMALA: nr rd 21 km E from Guatemala City to El Progreso and Puerto Barrios, nr turnoff to Palencia, 14°41′N, 89°54′W, *Hughes 1105* (FHO, K, MEXU); between Montúfar and Los Guates, mtns S of the Río Motagua Valley, 15 km N of San Juan Sacatepéquez, 14°49′N, 90°39′W, *Hughes 1106* (FHO, K, MEXU); nr rd 20 km ESE from Guatemala City to Jutiapa, 14°28′N, 90°28′W, *Hughes 1270* (FHO, K, MEXU, NY); 20 km E of Guatemala City, rd to Antigua, 14°37′N, 90°39′W, *Molina 13533* (EAP, F, NY, TEX); 21 km NW of Guatemala City, 14°31′N, 90°39′W, *Molina 15962* (EAP, F, NY, US); nr La Aurora, 14°34′N, 90°32′W, *Morales 617* (US).—HUEHUETENANGO: 5 km E of Aguacatán nr Río Blanco at base of S slopes of Sierra Los Cuchumatanes, 15°21′N, 91°17′W, *Hughes 1130* (FHO, K, MEXU); nr rd 20 km N from Nentón to the Mexican border at Gracias a Dios, a few km past Finca El Carmen, 15°57′N, 91°44′W, *Hughes 1356* (FHO, K, MEXU, NY); Valley Río Bucá, nr rd 18 km E from Huehuetenango to Aguacatán, S slopes Sierra de Cuchumatanes, 15°20′N, 91°20′W, *Hughes 1474* (EAP, FHO, K, MEXU, NY); on Río Amelco, Sierra de los Cuchumatanes below Finca San Rafael, *Steyermark 49677* (F); Cumbre Papal, S-facing slopes between Cuilco and Ixmoqui, 15°27′N, 91°48′W, *Steyermark 50928* (F, NY).—JALAPA: nr rd 30 km E from San José Pinula to Mataquescuintla, 14°31′N, 90°17′W, *Hughes 1464* (EAP, FHO, K, MEXU, NY); ravine in mtns on rd from Jalapa to Paraíso, 14°37′N, 90°03′W, *Standley 77231* (F).—JUTIAPA: hills between

Jutiapa and Plan de Urrutia, N of Jutiapa, 14°50′N, 89°54′W, *Standley 75475* (F).—Quetzaltenango: nr rd 27 km N from Retalhuleu towards Quetzaltenango, 2 km N of Santa María, 14°45′N, 91°31′W, *Hughes 1386* (EAP, FHO, K, MEXU, NY); above Santa María de Jesús, 14°44′N, 91°31′W, *Standley 87031* (F).—Quiché: Pascual Abaj nr Chichicastenanago, 14°59′N, 91°08′W, *Molina 15309* (EAP, F).—Sacatepéquez: San Mateo del Milpar 10 km from Antigua, 14°29′N, 90°42′W, *Molina 15514* (EAP); nr Pastores, 14°38′N, 90°47′W, *Standley 59893* (A, F); nr Antigua, 14°33′N, 90°44′W, *Standley 63862* (F).—San Marcos: nr rd 20 km S from San Marcos towards Coatepeque, 23 km N of El Quetzal, 14°51′N, 91°46′W, *Hughes 1701* (E, FHO, K, MEXU, MO, NY); rd from Coatepeque to San Marcos, 20 km N of La Reforma, 14°53′N, 91°46′W, *Macqueen 353* (EAP, FHO, K, MEXU).—Santa Rosa: rd from Barberena to Ixpaco, 8 km S of second jctn from the main Guatemala-Cuilapa rd to Ixpaco, 14°17′N, 90°26′W, *Macqueen 367* (EAP, FHO, K, MEXU).—Sololá: Sololá, *Holway 147* (NY, US); nr rd 2 km N Panajachel to Sololá above Lago Atitlán, 14°45′N, 91°10′W, *Hughes 1359* (BR, FHO, K, MEXU, NY); Panajachel waterfall, rd to Sololá, 14°45′N, 91°10′W, *Molina 16235* (EAP, F, NY, US). **Honduras.** Choluteca: rd to Morolica, 13°42′N, 86°55′W, *Molina 13068* (F, NY, TEX, US).—Comayagua: nr rd N from Tegucigalpa to Comayagua, 4 km S of Flores, above Comayagua Valley, 14°17′N, 87°33′W, *Hughes 1081* (FHO, K, MEXU); nr Presa del Coyolar, 5 km from El Rodéo, *Molina 10796* (F, NY).—Copán: between Guatemalan frontier post at La Florída and Copán, 9 km SW of Copán, 14°50′N, 89°14′W, *Hughes 991* (FHO, K, MEXU); nr rd S from La Entrada to Santa Rosa de Copán, about 5 km N of Santa Rosa, 14°50′N, 88°48′W, *Hughes 1419* (EAP, FHO, K, MEXU, NY); 4 km from Copán Ruins, rd to Santa Rita, 14°53′N, 89°06′W, *Molina 24647* (EAP, F, MO, NY, US); 3 km NW of Copán, 14°51′N, 89°10′W, *L. O. Williams 42961* (F, US).—El Paraíso: nr Candelaria, rd S from El Zamorano and San Lucas to Morolica and Choluteca, 13°45′N, 86°55′W, *Hughes 1075* (FHO, K, MEXU).—Francisco Morazán: NE flanks of Cerro Uyuca nr rd 20 km E from Tegucigalpa to El Zamorano and Danlí, 14°01′N, 87°06′W, *Hughes 1079* (FHO, K, MEXU); gully behind Suyapa, 14°03′N, 87°09′W, *Lorena 163* (MO); Barranco nr Zambrano, 14°23′N, 87°23′W, *Molina 5767* (F, US); Cuesta de los Muertos, Monte Obscuro, Cordillera Azacualpa, *Molina 14522* (EAP, F, NY, TEX); hills nr Río Rancho Quemado, 25 km SE of Tegucigalpa, rd to Sabana Grande, 13°53′N, 87°15′W, *Molina 18630* (F, GH, NY, US); nr El Zamorano, 14°01′N, 87°01′W, *Standley 4367* (EAP, F, GH, US); El Chile nr Tegucigalpa, 14°03′N, 87°07′W, *Standley 26716* (F); slopes of Cerro Uyuca, trail between La Labranza and Carratera above El Jicaríto, 13°59′N, 87°03′W, *Standley 28762* (F, GH).—Intibucá: nr Ologosi, 6 km E of La Esperanza, rd to Otoro and Siguatepeque, 14°17′N, 88°07′W, *Hellin & Hughes 18* (EAP, FHO, K, MEXU, NY); nr rd 12 km SW from La Esperanza towards Concepción and the El Salvador border, 14°15′N, 88°13′W, *Hellin & Hughes 19* (EAP, FHO, K, MEXU, NY); Intibucá, 14°18′N, 88°10′W, *Standley 25446* (EAP, F).—La Paz: Agua Blanca River between Chinacla and Planes de Mulle, 14°12′N, 87°55′W, *Molina 24322* (F, NY).—Lempira: 5 km WNW of Erandique, hills NW of Cerro La Laguna, nr track S towards Candelaria, 14°15′N, 88°31′W, *Hellin & Hughes 24* (EAP, FHO, K, MEXU, NY), *Hughes 1421* (EAP, FHO, K, MEXU, NY); Quebrada El Mecatal, 8.8 km SE of Gracias, Celaque Nat. Park, path between the Electric Plant and Don Tomás, 14°33′N, 88°39′W, *D. Mejía 74* (EAP, FHO, MO, TEFH); 0.5 km E of San Manuel Colohete, 14°27′N, 88°40′W, *D. Mejía 263* (EAP, FHO, MO, TEFH).—Ocotepeque: rd to Guisayote Biological Reserve, 8 km NE of Nuevo Ocotepeque, 14°25′N, 89°07′W, *Hawkins 268* (EAP, FHO, MO, TEFH); nr El Portillo, 14°26′N, 89°08′W, *Hughes 369* (FHO, K, MEXU); La Montañita, Cordillera Merendón, 14°22′N, 89°08′W, *Molina 22544* (F, NY).—Santa Bárbara: nr rd from San Pedro Sula S and W to Santa Rosa de Copán, 15 km S of turnoff to Macuelizo, 25 km N of La Entrada, 15°12′N, 88°39′W, *Hughes 1087* (FHO, K, MEXU).—Yoro: Yoro, nr rd 20 km NE from Yoro towards Jocón, nr Puentecita, 15°13′N, 87°02′W, *Hellin & Hughes 3* (EAP, FHO, K, MEXU, NY). **Nicaragua.** Estelí: cloud forest N side of Cerro Quiabú, 10 km W of Estelí, 13°06′N, 86°26′W, *Bockus 7749* (GH).

Indonesia. West Java: At Pondok Gedeh, 25 km S of Bogor. Experimental station of the Indonesian Biotechnology Research Institute for Estate Crops, IBRIEC, *Hughes 1899* (FHO, K, NY).

Leucaena trichandra is here treated as a distinct species in contrast to the work of recent authors, who treated it as a subspecies of *L. diversifolia* (Pan 1985, Pan & Brewbaker 1988, as subsp. *trichandra*; Zárate 1994, as subsp. *stenocarpa*). Viewing *L. trichandra* as a subspecies of *L. diversifolia* was based not only on morphological similarity of the two taxa, but also on the hypothesis that tetraploid *L. diversifolia* is an autotetraploid derivative of diploid *L. trichandra* (Pan 1985, 1988). Harris et al. (1994a) showed that this hypothesis was incorrect. As discussed in the account of *L. diversifolia*, Bentham (1842, 1875) and Zárate (1994) believed *L. trichandra* to be conspecific with *L. diversifolia*, prompting Zárate (1994) to use the name *L. diversifolia* subsp. *stenocarpa*. The type of *L. trichandra* is unusual, with few pairs of pinnae per leaf and few leaflets per pinna casting doubt on its identity. The depauperate state of the type specimen may be attributed to cultivation in a greenhouse at the Munich botanic garden. It clearly does not belong with *L. diversifolia* and must be assigned to the widely distributed diploid taxon. The precise origin within Mexico of the Munich material remains unknown.

Harris et al. (1994a: 9) (Fig. 31), in their analysis of cpDNA, showed that rather than grouping with *L. diversifolia*, *L. trichandra* (designated as *L. diversifolia* subsp. *stenocarpa*) was placed in a largely unresolved clade with *L. collinsii, L. confertiflora, L. magnifica, L. lanceolata,* and *L. shannonii*. Re-analysis of the cpDNA data set (Hughes, unpubl.) resulted in greater resolution and showed that most accessions of *L. trichandra* group with *L. collinsii*, a relationship supported by the analysis of morphology. Three Mexican accessions of *L. trichandra,* however, were placed in a separate clade from the remaining accessions, a result as yet unexplained but possibly attributable to hybridization and cytoplasmic introgression.

Leucaena trichandra here includes the types of *L. stenocarpa, L. guatemalensis, L. standleyi,* and *L. revoluta*, species formerly recognized along with *L. trichandra* by Britton and Rose (1928). Although *L. trichandra* is a very variable species, the characters used by Britton and Rose to distinguish the segregates, which include leaf and shoot pubescence, ciliate or eciliate leaflet margins, eccentricity of the leaflet midrib, and pod pubescence, are all highly variable, show no correlation with other characters or with geography, and often vary within populations. In addition to variation in these characters, there is also considerable variation in quantitative traits, such as leaf size, number of pairs of pinnae, number of pairs of leaflets, leaflet size, and pod dimensions across the range of *L. trichandra* (Fig. 45). Harris (unpubl. data) has shown that this morphological diversity is matched by high levels of diversity as detected by molecular markers including isozymes and cpDNA. Although recognition of infraspecific taxa to describe this variation might be desirable, patterns of variation correlated with geography or other characters remain to be found. *Leucaena trichandra* is thus one of the most variable species in the genus, variability that may be expected given its very extensive distribution scattered across highly dissected mountainous territory in a series of highly disjunct and often isolated populations. Two variants stand out amongst this mosaic of variation. Material from around Aguacatán in the valley of the Río Blanco and from San Marcos in the northern Guatemalan Departments of Huehuetenango and San Marcos (*Hughes 1130, 1131, 1473, 1691*) is characterized by having much broader, oblong pods than other material, but this variant also occurs sporadically elsewhere in the southern Honduran Departments of Intibucá and Lempira. A high elevation population in the mountains of Lempira in Honduras, near the small town of Erandique, is unusual in having large leaves with fewer pairs of pinnae, fewer leaflets per pinna, large glossy leaflets, and often white flowers (*Hughes 1421, 1424, 1427, 1708–1710, Hellin & Hughes 24*). Further study of material from these two populations might allow recognition of infraspecific taxa to document formally this variation.

Leucaena trichandra is sporadically cultivated as a shade tree over coffee, often with species of *Inga* and *Erythrina*. The unripe pods, seeds, and flower buds are widely consumed in southern Mexico, but because the seeds of other species are larger, those are generally preferred. Seeds are harvested and occasionally marketed in July through September. In Chiapas, trees are sometimes planted and frequently protected when land is cleared (Berlin et al. 1974).

9. Leucaena confertiflora S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65: 148. 1994.—TYPE: MEXICO. Oaxaca: Matatlán, Cerro Nueve Puntas nr short-wave relay mast, 5 km S of Matatlán, 16°49′N, 96°21′W, 2050 m, 11 Jan 1980, *Zárate 428* (holotype: MEXU!).

Small, often multiple-stemmed, branchy shrub or small tree, 2–4 (–6) m tall, 10–15 cm bole diameter, with an open irregular, often spreading umbrella crown. Bark smooth, mid-grey-brown, with horizontally aligned pale rusty orange-brown lenticels and shallow rusty orange-brown vertical fissures, inner bark green then cream. Shoots terete, mid-orange or reddish brown, with pale brown, slightly raised lenticels, glabrous. Stipules 2.8–3.1 mm long, lanceolate, long-pointed, membranous basal wing asymmetric, ciliate on margins, persistent, becoming hard and stiff when dry. Leaves (8–) 10–17 cm long, (7.6–) 9–11 cm wide; petioles (including pulvinus) 9–23 mm long; rachis 4–10 cm long, variably sparsely puberulent or densely covered in short white pubescence, with 1–3 small variably cylindrical, columnar, peg-shaped or discoid, shallowly crateriform nectaries, 0.5–1.5 mm long, 0.5–1.5 mm wide, 1–1.5 mm tall, on ventral side of petiole and rachis at base of the lower pinnae pairs, sometimes at base of all pinnae pairs along rachis, and always with 1 or 2 additional nectaries at base of terminal pinnae pairs, sometimes a pair of nectaries at base of some pinnae pairs, apex of rachis extending beyond the terminal pinnae as a deltate, pointed, curling mucro, 1.5–3 mm long, variably covered in white hairs; pinnae 5–7 pairs; pinnular rachis 4–8 cm long, with a double ridge on ventral side, variably pubescent with white hairs, with 1 (–2) minute elliptic concave nectaries at base of terminal pairs of leaflets; leaflets (18–) 22–26 pairs per pinna, (5–) 7–10.5 mm long, 2–3.4 mm wide, sessile, asymmetrically truncate at base, linear-oblong, acuminate, sometimes cuspidate at apex, the cusp slightly curved towards apex of pinnae, entire, glabrous except ciliate on margins, thickened, subcoriaceous, strongly discolorous, dark glossy bottle-green above, paler mid-green below, only midrib visible on ventral side, two primary veins visible on abaxial side. Capitula 13–20 mm in diameter at anthesis, in fascicles of (1–) 2–5 in leaf axils on older shoots and on actively growing shoots with coeval leaf development, each capitulum with 55–70 flowers; peduncles 4–6 mm long, angled, variably pubescent or glabrous, with a subapical involucre of basally united bracts. Flowers subtended by small peltate pedicellate bracts, 2.3–2.6 mm long, 1 mm in diameter; calyx 2.5–2.7 mm long, glabrous or sparsely hairy on lobes, pale green; petals 4.1–4.5 mm long, weakly united at tips in bud, free to base at anthesis, glabrous, the lobe margins slightly thickened, pale green; filaments 4.5–6.5 mm long, arranged in two distinct ranks, pale creamy white; anthers densely pilose, dull pinkish grey or dull greenish brown fading dull mauve, apiculum absent; ovary 1.8–2 mm long, glabrous, pale cream-white, with 18–20 ovules, style 8.5–9 mm long, pale cream-white, with a porate, tubular or narrow-funnelform stigma, strongly exserted beyond anthers. Pods 1–4 (–7) per capitulum, 9–15 cm long, 16–26 mm wide, pendulous, nearly sessile, linear-oblong or oblong, the base acute, the apex rounded, sometimes retuse, often with a short pointed beak, compressed, 10–15-seeded, valves chartaceous, deep maroon and slightly glossy when unripe, turning dark reddish brown, glabrous or occasionally sparsely pubescent, the margins slightly thickened, dehiscent initially along one suture, the valves reflexing transversely, sometimes forming tight rolls after dehiscence (Fig. 18D). Seeds 6.5–8.3 mm long, 5–6.8 mm wide, compressed, circular to ovate, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, regular, U-shaped, 90% arm extension, symmetrical. Chromosome number: 2n = 112 (Sorensson & Brewbaker 1994; Palomino et al. 1995). Fig. 47.

Leucaena confertiflora was discovered by Sergio Zárate and Robert Reid in cultivation in the small village of San Pedro Chapulco northeast of Tehuacán in Puebla in 1980, and it is only in the last decade that its identity, distribution, and ecology have been investigated in detail. Zárate (1984a) initially considered, but did not formally describe, *L. confertiflora* as a subspecies of *L. cuspidata*, but later treated it as a distinct species (Zárate 1994). The material from Chapulco, the surrounding area near the village of Azumbilla, and the northern fringes of the Sierra Zongolica differs in the shape of the extrafloral petiolar and leaf rachis nectaries from specimens distributed further south in Puebla and Oaxaca. Zárate (1994) thus divided *L. confertiflora* into two subspecies: *confertiflora* with sessile, discoid or shallowly crateriform, concave nectaries on the petiole and rachis, and subspecies *adenotheloidea* with stipitate, erect, peg-shaped, cylindrical nectaries, usually occurring at the base of each pair of pinnae (Fig. 47I, J). No other distinguishing features were found between these two subspecies. While the nectary shape is clearly distinct at the extremes and fixed in most areas, variation within populations and even within individuals has been observed. First, material from the mountains northwest of Huajuapan de León, around Santa Catarina Zapoquila and Membrillos (*Hughes 1812*) has both gland types within populations, indicating the presence of both infraspecific taxa in this area. Second, in the village of Santa Catalina Oxolotepec, in the Sierra Zongolica, both nectary types and intermediate forms are found within the cultivated material there and even on single individuals (*Hughes 1616, 1731, 1799*). At Santa Catalina Oxolotepec, variation may be the result of interspecific hybridization with *L. pallida*. This hypothesis is supported by the findings of the re-analysis of cpDNA data (Hughes, unpubl.), which showed that one accession of *L. confertiflora* from Santa Catalina Oxolotepec was placed outside the clade containing the remaining accessions of *L. confertiflora*. The extent of artificial sympatry amongst species of *Leucaena* in villages such as Santa Catalina Oxolotepec means that unravelling the identities of some hybrids may be difficult. Despite inconstancy of nectary shape in some areas and the lack of other distinguishing features two infraspecific taxa may still be recognized, albeit at varietal rather than subspecific rank (Hughes 1997c).

Leucaena confertiflora shows some morphological affinities to *L. cuspidata* (similar leaf morphology, cuspidate leaflets, pod dehiscence initially along one suture, flower color), as recognized by Zárate (1984a, 1994), who considered the two to be closely related. In addition, these two species occupy similar ranges and habitats, at higher elevations in dry upland matorral, inland and west of the Sierra Madre Oriental, separated by the central Mexican volcanic axis, *L. cuspidata* to the north and *L. confertiflora* to the south, suggesting vicariant isolation following recent volcanic activity. *Leucaena confertiflora* may be distinguished from *L. cuspidata* by its chartaceous as opposed to lignescent pod valves, which reflex transversely rather than twist spirally after dehiscence. *Leucaena confertiflora*, designated as *L. "glossy,"* was listed as tetraploid (2n = 112) by Sorensson and Brewbaker (1994), a count confirmed for var. *adenotheloidea* by Palomino et al. (1995); the chromosome number of var. *confertiflora* remains to be ascertained. If tetraploid, its origin remains unknown. However, given that *L. confertiflora* (most accessions) was placed as sister species to *L. trichandra* in the cpDNA analysis, that species is the most likely maternal parent species. Inclusion of *L. confertiflora* in the morphological analysis of diploid species resulted in an increase in the number of equally parsimonious trees and significant loss of resolution in the strict consensus tree (Fig. 30B).

KEY TO THE VARIETIES OF LEUCAENA CONFERTIFLORA

1. Extrafloral petiolar and leaf rachis nectaries sessile, discoid, round, weakly concave (crateriform); usually only petiolar or with 1–2 rachis nectaries. 9a. *L. confertiflora* var. *confertiflora.*
1. Extrafloral petiolar and leaf rachis nectaries stipitate, erect, peg-shaped, cylindrical or pointed, occasionally double; usually petiolar and 2–5 nectaries along rachis, sometimes at base of each pair of pinnae. 9b. *L. confertiflora* var. *adenotheloidea.*

9a. Leucaena confertiflora var. confertiflora.

Nectaries sessile, round, discoid or shallowly crateriform, always shorter than wide, borne on the petiole and at the base of the terminal pinnae pair at the apex of the leaf rachis, rarely with additional nectaries along the leaf rachis (Fig. 47A–H).

Phenology. Flowering November–February; unripe pods July–December, ripe pods November–February; leafless during the cold/dry season November–March.

Distribution (Fig. 36). *Leucaena confertiflora* var. *confertiflora* is restricted to the high, dry, inland hills and plateaus of Oaxaca and southern Puebla, between the coastal Sierra Madre Oriental and the Sierra Madre Sur. It occurs mainly in a belt extending from Cerro Nueve Puntas about 50 km east of Oaxaca to western Oaxaca around Tamazulapan, and north into southern Puebla in the mountains south of the Tehuacán Valley around Caltepec. It is an understory shrub or small tree in dry oak forest and in dry matorral, almost always on rocky calcareous slopes with shallow black soils. Associated species include *Quercus segoviensis, Q. affinis, Q. magnolifolia, Arctostaphylos polifolia, Rhus chondroloma, R. mollis, Acacia subangulata, Calliandra grandiflora, Rhynchosia pringlei, Senna galeottiana, Brahea dulcis, Salvia candicans, Krameria cytisoides,* and *Pistacia mexicana,* as well as species of *Juniperus, Dodonaea, Dasylirion, Eysenhardtia, Desmodium, Harpalyce, Sophora,* and *Vauquelinia*; (1500–) 1750–2430 m.

Vernacular names. *Huaje, guaje, guaje del cerro, guaje de venado.*

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** OAXACA: Cerro Solo, 7 km NE of Tepelmeme de Morelos, 17°55′N, 97°19′W, *Cisneros 2113* (CAS); 4.5 km W of Nochistlán, Km 95 rd Huajuapan de León to Oaxaca, 17°28′N, 97°16′W, *Grethur 721* (MEXU); rd N from Oaxaca to Tehuacán, 8 km N of El Moral, 35 km N of San Francisco Telixtlahuaca, 160 km S of Tehuacán, 17°31′N, 96°56′W, *Hughes 1151* (FHO, K, MEXU); rd N from Oaxaca to Tehuacán, 8 km N of El Moral, 35 km N of San Francisco Telixtlahuaca, 160 km S of Tehuacán, 17°31′N, 96°56′W, *Hughes 1152* (FHO, K, MEXU), *Hughes 1153* (FHO, K, MEXU), *Hughes 1653* (E, FHO, K, MEXU, MO, NY), *Hughes 1780* (CAS, FHO, K, MEXU, MO, NY); nr shortwave radio stn at Nueve Puntas, 5 km SSE of Santiago Matatlán, 2 km SW of Oaxaca to Tehuantepec rd, 16°51′N, 96°22′W, *Hughes 1501* (FHO, K, MEXU, MO, NY), *Hughes 1660* (E, FHO, K, MEXU, MO, NY), *Hughes 1777* (CAS, FHO, K, MEXU, MO, NY); Teposcolula, 5 km SW of Tamazulapan, rd to Chilapa de Díaz on N slopes of Cerro Yocondodo, 17°40′N, 97°34′W, *Hughes 1510* (FHO, K, MEXU, MO, NY); 5 km SW of Tamazulapan, rd to Chilapa, distr. of Teposcolula Mixteca Alta, 17°40′N, 97°36′W, *Hughes 1631* (E, FHO, K, MEXU, MO, NY), *Mendoza 706* (MEXU), *Medraño 10586* (MEXU), *Sousa 9312* (MEXU, TEX), *R. Torres 6670* (MEXU), *Zárate 434* (MEXU); 1 km N of San Pablo Guilá, SE flanks of the Cerro Piedra del Sol, 15 km SW of Matatlán, 16°50′N, 96°26′W, *Hughes 1778* (FHO, K, MEXU, MO, NY, TEX); track SE from Santa Catarina Zapoquila, valley of the Río Grande, nr Membrillo, mtns 23 km NE of Huajuapan de León, 18°03′N, 97°33′W, *Hughes 1812* (CAS, FHO, K, MEXU, MO, NY); 3 km S of Matatlán, 16°51′N, 96°22′W, *Medraño 11444* (MEXU, MO); Cerro El Peñasco, 3 km NE of Teposcolula, 17°31′N, 97°28′W, *Mendoza 305* (MEXU); 4 km N of Yucunama, Teposcolula Mixteca Alta, 17°36′N, 97°29′W, *Mendoza 862* (MEXU), *Mendoza 1048* (MEXU, NY); nr Tamazulapan, 17°40′N, 97°36′W, *Rzedowski 34870* (MEXU); Loma, S of Yucuita in the Nochistlán Valley, 17°30′N, 97°16′W, *C. E. Smith 5026* (US); nr shortwave radio pylon, 10 km SE of Mitla, Tlacolula, 16°49′N, 96°21′W, *Sousa 6528* (MEXU); 24 km SE of Cañón del Tomellín, Cuicatlán, 17°33′N, 96°51′W, *Sousa 6895* (MEXU, TEX); Nueve Puntas, 5 km SE of Matatlán, 16°49′N, 96°21′W, *Sousa 8546* (MEXU), *9406* (MEXU); Cañada de Carrizalillo, Cerro Verde, N of Tepelmeme, watershed of the Río Hondo Alta Mixteca, 18°05′N, 97°19′W, *Tenorio 7008*

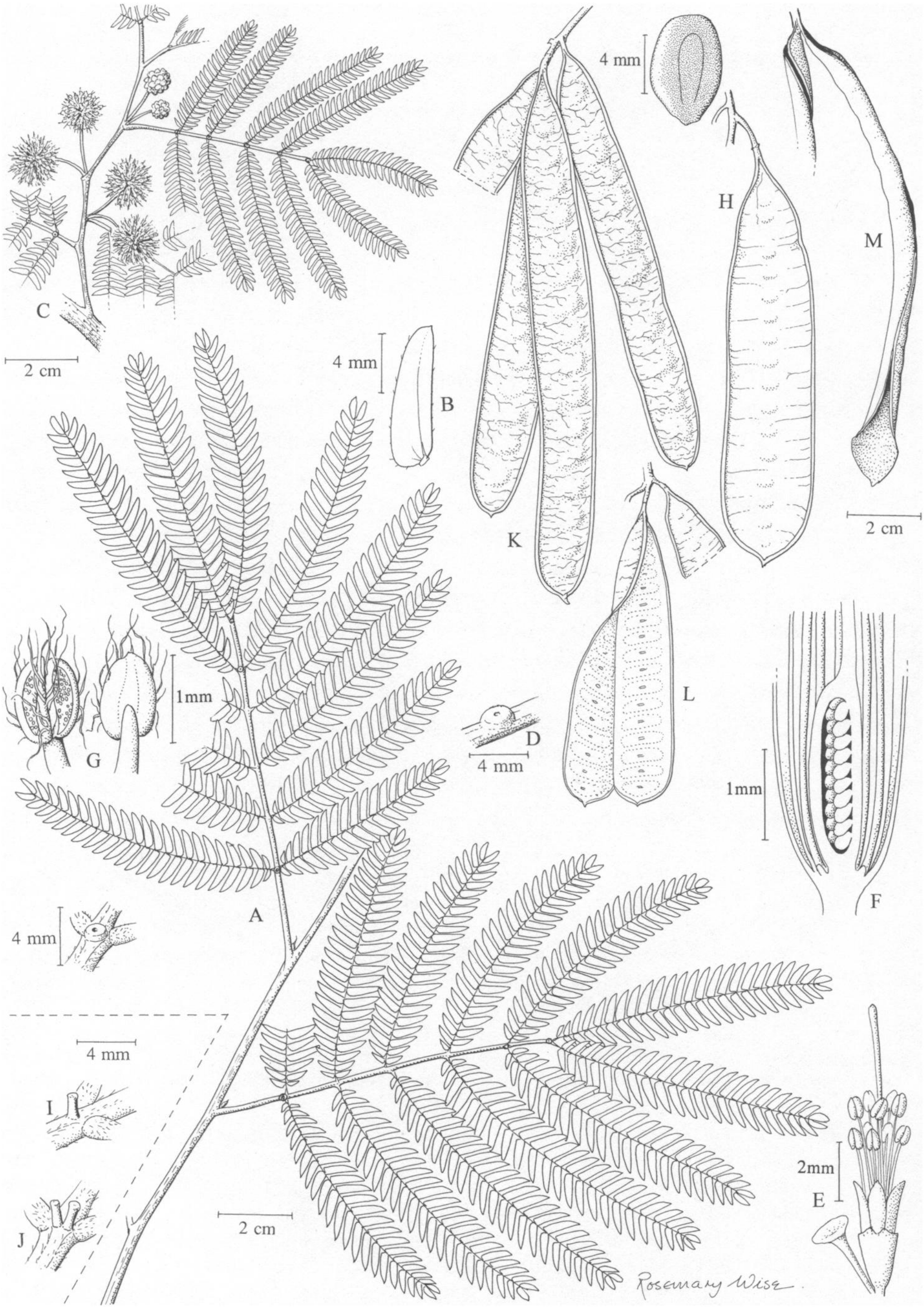


FIG. 47. *Leucaena confertiflora*. A–H, var. *confertiflora*: A. Leaves and enlargement showing rachis nectary. B. Leaflet. C. Flowering shoot. D. Extrafloral nectary. E. Flower. F. Longitudinal section of flower. G. Anthers. H. Pod. I–M, var. *adenotheloidea*: I, J. Extrafloral petiolar nectaries. K. Pods. L, M. Valves of dehisced pods. (Based on: A, B, *Hughes 1780*; C–H, *Hughes 1152*; I, *Hughes 1796*; J–M, *Hughes 1797*.)

(MEXU); 4 km SE of Nochistlán, 17°26′N, 97°14′W, *Zárate 635* (CAS, MEXU, MO), *433* (MEXU).—PUEBLA: 8 km NE of Santiago Acatepec, 18°37′N, 97°38′W, *Chiang 1955* (MEXU), *1957* (MEXU); Cañada San Lorenzo, SW of Los Membrillos, SW of Caltepec, 18°02′N, 97°35′W, *Tenorio 4968* (TEX); Río Jahuey, E of Estanzuela, nr Atzumba, 18°12′N, 97°35′W, *Tenorio 7373* (MEXU).

Trees of *L. confertiflora* are often very scattered. Extensive natural populations are infrequent, and the species is threatened by grazing. Variety *confertiflora* is used as a minor food source, the unripe pods and seeds harvested from natural populations, often several kilometers distant from villages, e.g., on the slopes of Cerro Piedra del Sol above the village of San Pablo Guilá in Oaxaca. There are no reports of widespread marketing of pods or cultivation of var. *confertiflora*, but harvesting from natural populations is still intensive.

9b. Leucaena confertiflora var. **adenotheloidea** (S. Zárate) C. E. Hughes, Contr. Univ. Michigan Herb. 21: 287. 1997. *Leucaena confertiflora* subsp. *adenotheloidea* S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65(2): 149. 1994.—TYPE: MEXICO. Puebla: San Pedro Chapulco, 13 km NE of Tehuacán on rd towards Orizaba, 18°36′N, 97°25′W, 2100 m, 7 Dec 1981, *Zárate 610* (holotype: MEXU!).

Nectaries stipitate, erect, peg-shaped, cylindrical, always taller than wide, borne on the petiole and at the base of the majority of pinnae pairs along the leaf rachis (Fig. 47I–M), double nectaries occasionally at the base of some pinnae pairs (Fig. 47J).

Phenology. Flowering December–March; fruiting July–November (unripe), November–February (–March) (ripe); leafless during the cold/dry season December–March.

Distribution (Fig. 36). *Leucaena confertiflora* var. *adenotheloidea* is restricted to a small area of central Puebla at the northern end of the Sierra Zongolica, to the northeast of the northern end of the Tehuacán Valley. It is found in similar dry upland matorral, mixed dry oak matorral, and degraded dry pine matorral (*Pinus pseudostrobus*) as variety *confertiflora*. It has also been found in cultivation in villages northeast of Tehuacán, including San Pedro Chapulco, Azumbilla, and Santa Catalina Oxolotepec; 2000–2550 m.

Vernacular names. *Guaje zacatzin* (San Pedro Chapulco and Azumbilla), *guaje de huerta* (in cultivation), and *guaje de monte* (in natural populations) (in and around Santa Catalina Oxolotepec, Puebla).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** PUEBLA: nr San Pedro Chapulco, 13 km NE of Tehuacán, rd to Orizaba, 18°40′N, 97°25′W, *Hughes 932* (FHO, K, MEXU), *Hughes 1321* (AAU, CR, FHO, K, MEXU, NY), *Hughes 1614* (E, FHO, K, MEXU, MO, NY), *Hughes 1796* (CAS, FHO, K, MEXU, MO, NY, TEX), *Zárate 604* (MEXU), *Zárate 605* (MEXU), *Zárate 709* (MEXU); track above and N of Santa Catalina Oxolotepec, Sierra Zongolica, 20 km NE of Tehuacán, 1 km S of rd from Azumbilla to Vicente Guerrero, 18°36′N, 97°15′W, *Hughes 1616* (E, FHO, K, MEXU, MO, NY); slopes above rd Azumbilla E to Nicolás Bravo and Vicente Guerrero, 3 km from Azumbilla, 2 km from Nicolás Bravo, Sierra Zongolica, NNE of Tehuacán, 18°37′N, 97°20′W, *Hughes 1730* (E, FHO, K, MEXU, MO, NY), *Hughes 1797* (CAS, FHO, K, MEXU, MO, NY); Santa Catalina Oxolotepec, Sierra Zongolica 15 km NE of Tehuacán, 27 km S of Azumbilla towards Vicente Guerrero, 18°36′N, 97°15′W, *Hughes 1731* (E, FHO, K, MEXU, MO, NY), *Hughes 1799* (CAS, FHO, K, MEXU, MO, NY); 25 km S of La Esperanza, rd to Azumbilla, 18°42′N, 97°25′W, *Salinas 4206* (MEXU).

The variable nectary morphology at Santa Catalina Oxolotepec (*Hughes 1616, 1731, 1799*) is notable and as yet unexplained. These trees are also notably larger (to 12 m in height) than normal for var. *confertiflora* (usually 2–4 m), and pods are extremely variable in size. The most likely explanation for this variation is interspecific hybridization with *L. pallida*.

In the villages of San Pedro Chapulco, Azumbilla, and Santa Catalina Oxolotepec, Puebla, *L. confertiflora* var. *adenotheloidea* is cultivated in informal orchards (*guajales*) as a source of food (unripe pods and seeds). It occurs with other species of *Leucaena*, most notably *L. pallida*, other fruit trees including *Persea americana, Prunus persica, Prosopis laevigata,* species of *Ficus* and *Opuntia,* along with *Schinus molle*, and with species of *Agave* and *Eysenhardtia*. The cultivation of var. *adenotheloidea* has been investigated by Zárate (1984b), who showed that cultivated material is derived directly from adjacent natural populations in the nearby hills surrounding the villages mentioned, probably only in the last century; Zárate (1984b) described var. *adenotheloidea* as undergoing a process of "incipient domestication." The unripe pods from San Pedro Chapulco and Santa Catalina Oxolotepec are consumed locally and also sold in nearby markets such as Tehuacán. Growing at between 2000 to 2550 m, *L. confertiflora* var. *adenotheloidea* is the highest elevation taxon in the genus and survives occasional moderate frosts.

10. Leucaena esculenta (Sessé & Mociño ex DC.) Bentham, Trans. Linn. Soc. 30: 442. 1875. *Acacia esculenta* Sessé & Mociño ex DC., Prodr. 2: 470. 1825. *Mimosa esculenta* Sessé & Mociño, Pl. Nov. Hisp. 178. 1890.—TYPE: Plate 6331.627 (photo!) of the Torner Collection of Sessé & Mociño Biological Illustrations based on a painting made by the artists of the Sessé & Mociño Real Expedición (Fig. 48), "in temperatis Novae Hispaniae locis," probably derived from specimens seen near Mexico City.

Leucaena confusa Britton & Rose, N. Amer. Fl. 23: 128. 1928.—TYPE: MEXICO Jalisco: hills nr Tequila, 18 Oct 1893, *Pringle 4534* (holotype: NY!; isotypes: BM! GH! MO! UC! US!).

Leucaena doylei Britton & Rose, N. Amer. Fl. 23: 128. 1928.—TYPE: MEXICO. Chiapas: nr "Castla" Gutiérrez (Tuxtla Gutiérrez), 6 Jan 1907, *Collins & Doyle 161* (holotype: NY!; isotype: US!, photo: F!).

Small to medium-sized tree, (3–) 10–15 (–20) m tall, 20–70 cm bole diameter, typically multiple-stemmed and branchy when young, older trees with a short clear bole to 5 m, heavy spreading branches, and an open spreading rounded crown. Bark thick and corky, pale silvery grey, with a metallic sheen, smooth becoming horizontally gnarled, inner bark bright green then deep orange-red (Figs. 2B, 3B). Shoots strongly 5–6-angled (Fig. 4A), mid-grey-brown with pale orange-brown lenticels and marked orange-brown corky ridges, glabrous and slightly shiny. Stipules 3.9–4.8 mm long, lanceolate, with asymmetric basal wings, midrib prominent, persistent, shrinking when dry. Leaves (15–) 20–40 (–44) cm long, 15–22 cm wide; petioles (including pulvinus) 17–20 mm long, young developing leaves often covered in glossy clear exudate, with a single (or occasionally double) maroon-red, sessile, elliptic, shallowly concave, crateriform nectary, 5.5–8.0 × 3.1–3.9 mm (Fig. 9A), at the distal end on adaxial side of petiole; rachis 30–35 cm long, with 2–3 elliptic crateriform nectaries, 2.5 × 1.7 mm, at base of distal pairs of pinnae, apex of rachis extending beyond the terminal pinnae as a pointed glabrous reddish brown mucro 4–7 mm long, curling when dry; pinnae (25–) 30–40 (–60) pairs; pinnular rachis 9.5–12 cm long, angled, glabrous, with 3–4 elliptic nectaries, 0.6 × 0.4 mm, at base of terminal pairs of leaflets; leaflets (55–) 60–75 (–85) pairs per pinna, 3.5–6.6 mm long, 0.9–1 mm wide, nearly sessile, asymmetric, linear, acute or subacute, glabrous, only the

FIG. 48. *Leucaena esculenta*. Reproduced from the painting by the artists of the Sessé & Mociño Real Expedición to Mexico, which is the type of *L. esculenta*. Courtesy of the Torner Collection (accession number 6331.627) of Sessé & Mociño Biological Illustrations; Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, PA.

asymmetric midrib visible. Capitula 25–28 mm in diameter at anthesis, in fascicles of 2–7 at nodes on long (20–35 cm), often 1-branched terminal anauxotelic shoots with complete or partial suppression of leaf development, globose or sometimes subelliptic, each capitulum with 150–170 flowers; peduncles 25–30 mm long, angled, glabrous, with an involucre of bracts. Flowers subtended by peltate bracts, 2.9–3.4 mm long; calyx 2.6–4 mm long, with ciliate teeth, pale greenish white, lobe tips tinged mid-green; petals 4.2–5.5 mm long, free, glabrous, pale greenish white; filaments 12–13.8 mm long, white; anthers sparsely pilose, pale yellow-green, apiculum absent; ovary 1.5–1.6 mm long, glabrous (Fig. 13F), reddish, with 16–20 ovules, style 12–13 mm long, white, with a narrow tubular stigma. Pods 1–2 per capitulum, (10–) 15–25 (–30) cm long, 23–26 mm wide, pendulous on sturdy 15–20 mm long stipes, oblong to linear-oblong, acuminate, narrowly planocompressed, (few–) 15–20-seeded, valves glossy reddish maroon when unripe, turning mid-orange-brown, glabrous, with reticulate venation close to margins, chartaceous, the endocarp not forming partitions between the seeds, the margins slightly thickened, dehiscent along both sutures. Seeds 9.1–10.9 mm long, 7–9 mm wide, compressed, flattened, circular to ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, symmetrical. Chromosome number: 2n = 52 (Hutton 1981; Pan & Brewbaker 1988). Fig. 49.

Phenology. Flowering (August–) October–November (–January); fruiting (January–) February–March (–April); deciduous January–April.

Distribution (Fig. 50). *Leucaena esculenta* is widely cultivated in Mexico for its edible pods and seeds (Casas & Caballero 1996; Zárate 1984a, 1994, 1997). It is often found abundantly in and around centers of population, and in some towns and villages it is the dominant tree in gardens and backyards. The present-day distribution is therefore probably more extensive than its natural distribution, and there has been some debate over the true extent of its natural range. Zárate (1984a, 1994, 1997) postulates that it may be native only in the upper Balsas depression in Guerrero, Morelos, and possibly parts of Puebla, México, and Michoacán, where it occurs abundantly and apparently naturally in mid-elevation tropical dry deciduous forest (see below); (400–) 600–1800 (–2080) m; occasionally cultivated at lower elevations.

Vernacular names. The long and widespread history of cultivation of *L. esculenta* has given rise to numerous vernacular names; these are fully described by Zárate (1994) and Casas and Caballero (1996). The most widely used names are *guaje (huaje, uaxin, oaxin), guaje rojo (oaxin chichiltic), guaje colorado, guashe, guashi, guaje grande (hueyoaxin)* and *guaje mihuateco*, all names that derive from the Nahuatl *huaxin* (Standley 1922; Casas & Caballero 1996). The names *colorado* and *rojo* refer to the reddish maroon unripe pods. Other names include: *diiwa, tondua cuuha* (Mixteco), *libad-lo* (Mixteco de la costa), *lya kures* (*guaje de sequia*, Zapoteco de Mitla), *yaga-la* (Zapoteco) *al-pa-la* and *pa-la* (probably Chontal names for *guaje*) (Zárate 1994), *uachi* (*guaje*, Chiapas, the named used for the more widespread *L. collinsii* of that area).

REPRESENTATIVE SPECIMENS. **U.S.A.** CALIFORNIA: Santa Barbara, 604 Santa Barbara Street, *Blakely 2935* (CAS), *Muller & Broder 2358* (CAS).—FLORIDA: Dade Co., Univ. of Miami, Coral Gables, *Read 2069* (US); USDA Plant Introduction Station in Miami, cultivated. M-12545, from Tuxtla Gutiérrez, Chiapas (from Faustino Miranda), *Gillis 9997* (MO).

Mexico. CHIAPAS: S outskirts of Tuxtla Gutiérrez, N side of by-pass rd, backyard of the property Quinta Querem No. 4355, 1 km from intersection of ring rd and rd running E to Chiapa de Corzo, 16°44′N, 93°05′W, *Hughes 1764* (CAS, FHO, K, MEXU, MO, NY), *Miranda 5889* (MEXU, US).—GUERRERO: nr El Tomatal, Iguala, 18°19′N, 99°30′W, *G. Camarillo s.n.* (MEXU); Cañón de la Mano between Los Amates and El Naranjo, 10 km N of Iguala, 18°24′N, 99°30′W, *Catalán & Vázquez 331* (MEXU); nr Limones, Temascaltepec, 19°02′N, 100°01′W, *Hinton 1905* (A); 15 km SW of Mezcala, track towards Carrizalillo, 17°52′N, 99°38′W, *Hughes 888* (FHO, K, MEXU); 5 km N of San Martín Pachívia, rd to Ixcateopan de Cuauthémoc, 18°24′N, 99°43′W, *Hughes 894* (FHO, K, MEXU); Los Aguajes, main Iguala to Ciudad Altamirano rd, 15 km W of Teloloapan, 18°25′N, 99°58′W, *Hughes 1829* (CAS, FHO, K, MEXU, MO, NY); rd from Chilpancingo, 18 km W towards Chichihualco, 17°38′N, 99°37′W, *Macqueen 434* (EAP, FHO, K, MEXU); Adama, nr Achótla, trail to Suriana, Sierra Madre Sur N of the Río Balsas, 18°08′N, 100°09′W, *Mexía 8820* (CAS, F, GH, K, MO, NY, UC, US); nr Taxco El Viejo, Taxco to Iguala rd, 18°28′N, 99°35′W, *Rico 1* (CAS, MEXU); 14.1 km SE of the turnoff to Chichi-

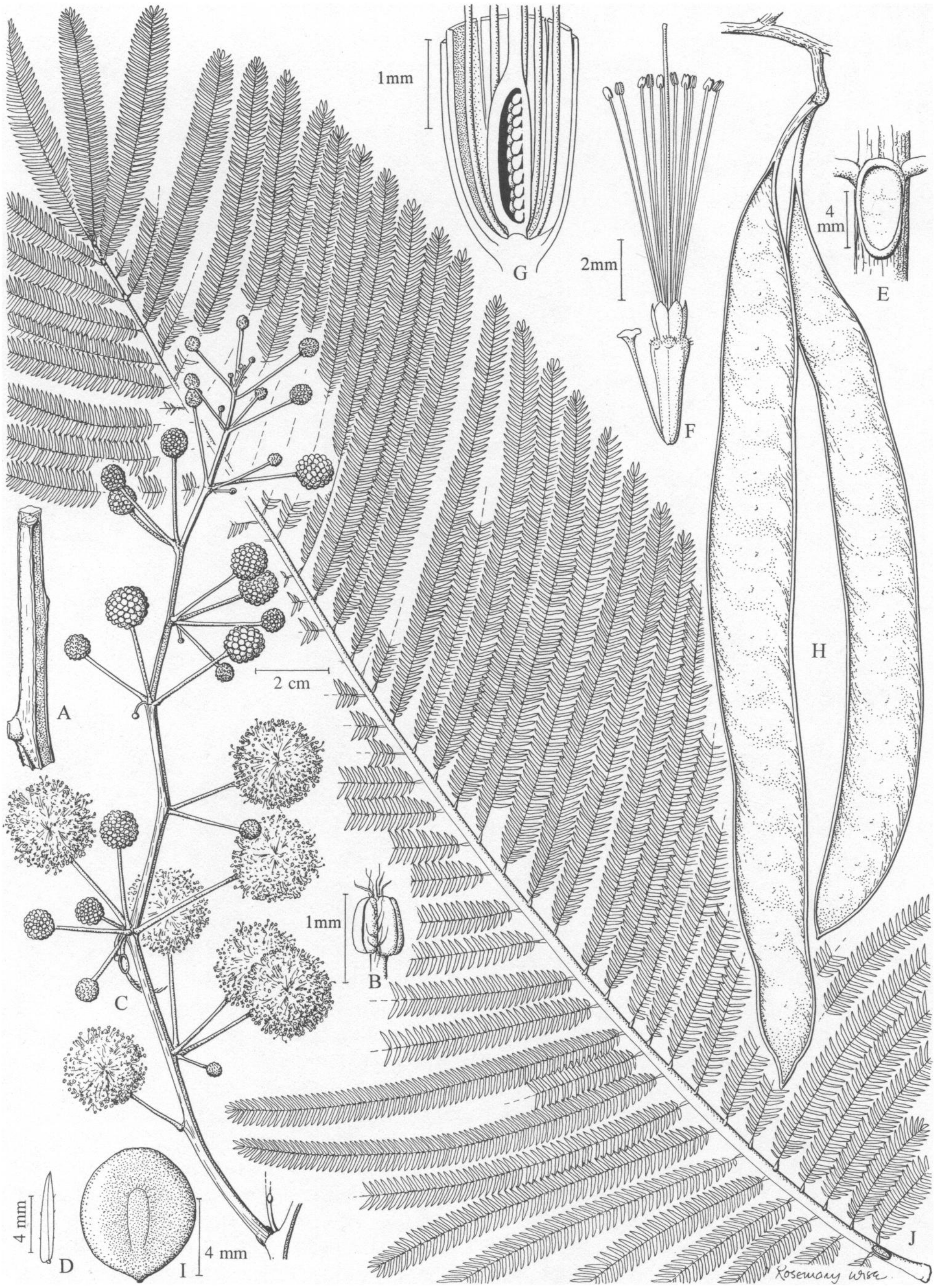


FIG. 49. *Leucaena esculenta*. A. Angled shoot with corky ridges. B. Anther. C. Flowering shoot. D. Leaflet. E. Petiolar nectary. F. Flower. G. Longitudinal section of flower. H. Pods. I. Seed. J. Leaf. (Based on: A–G, *Hughes 1779*; H–J, *Hughes 888*.)

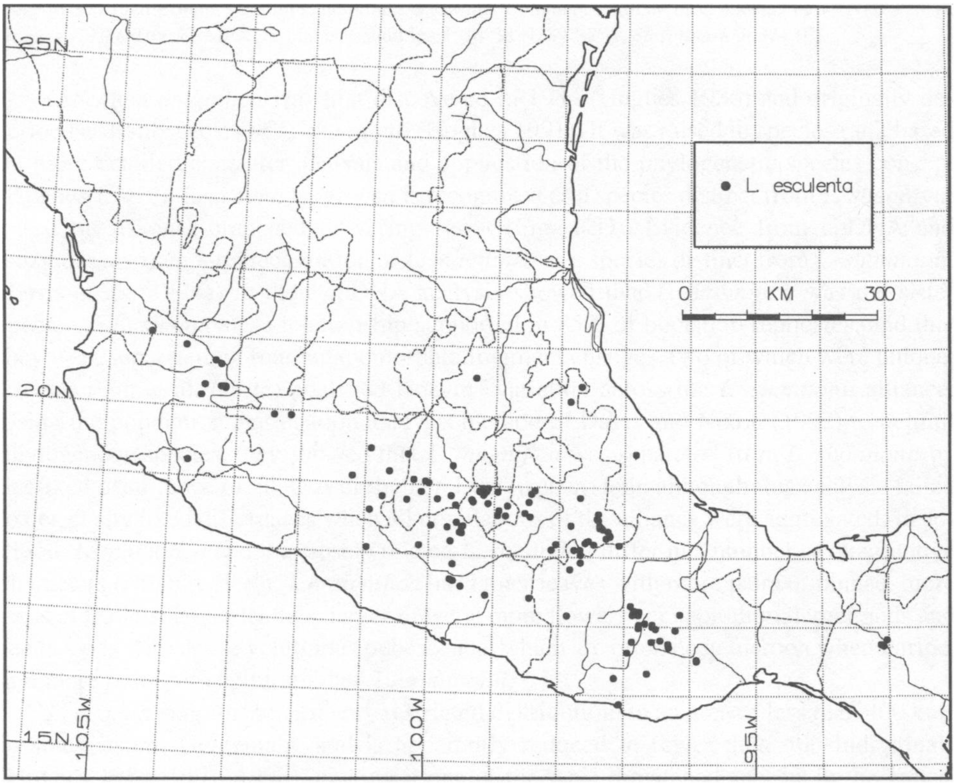


FIG. 50. Present-day range of *L. esculenta*. Outlying localities in Sonora, Hidalgo, Chiapas, and coastal Oaxaca represent records of cultivated trees. The presumed native range is in the central area of Guerrero, Morelos, and southern Puebla.

hualco from the rd between Fila de Caballo and Col. Helizondo de Castillo, 17°39′N, 99°40′W, *Rico 208* (CAS, MEXU); nr Atzcala, Cocula, 18°12′N, 99°40′W, *Soto 8880* (CAS, MEXU, MO); 3 km from Tlamacazapa, entrance to Taxco, *Terán 409* (K); San José Laguna, Alcozauca nr Barranca Grande, 17°24′N, 98°27′W, *Viveros & Casas 245* (CAS, MEXU); Grutas de Juxtlahuaca, 7 km NE of Colotlipa, Quechultenango, 17°26′N, 99°07′W, *Xelhuantzi 5319* (MEXU).—HIDALGO: Puente de Tasquillo, main rd from Mexico City to Nuevo Laredo, 20°33′N, 99°19′W, *L. G. Quintero s.n.* (MEXU).—JALISCO: 8 km S of Zacoalco, 20°10′N, 103°34′W, *C. D. Johnson 348-73* (MO); rd Chapala to Ajijic by Lago Chapala, 5 km W of Chapala, 20°17′N, 103°12′W, *Macqueen 224* (EAP, FHO, K, MEXU); Cuesta de San Marcos above and E of Laguna de San Marcos, 15 km SSE of Acatlán de Juárez, 20°19′N, 103°31′W, *McVaugh & Koelz 310* (CAS, NY); nr Chapala, 20°18′N, 103°12′W, *Rose 7654* (NY, US); San Pedro, nr Guadalajara, 20°37′N, 103°17′W, *Safford 1413* (US).—MÉXICO: Km 138, rd from Toluca to Zihuatanejo, 18°47′N, 100°21′W, *I. García 274* (MEXU); Temascaltepec, *Hinton 2349* (K); 1 km NW of Rancho El Naranjo nr Tejupilco, 18°54′N, 100°08′W, *Medraño 4990* (MEXU); 2 km NE of Ixtapan de la Sal, 18°51′N, 99°40′W, *J. Rzedowski s.n.* (MEXU); side rd just beyond Ixtapanpongo, 19°04′N, 100°15′W, *Schubert 2133* (MEXU).—MICHOACÁN: El Souse nr Zitácuaro, 19°26′N, 100°21′W, *Hinton 13371* (CAS, GH, K, MEXU, NY, US); 2 km N of Tiringucha, rd 18 km N from Huetamo de Núñez towards Zitácuaro, 18°37′N, 100°55′W, *Hughes 903* (FHO, K, MEXU); Cerro Colotepec nr Xochiltepec, *Lyonnet 1183* (MEXU, US); 17.5 km from Temascal, rd to Huetamo, 19°30′N, 100°55′W, *H. E. Moore 5713* (BM, GH, UC); Cerro la Beata nr Zamora, 19°56′N, 102°10′W, *R. Palacios s.n.* (CAS, MEXU); El Tiquicheo, 18°49′N, 100°44′W, *Soto 53* (MEXU); Santiago Tangamandapio, rd from Jiquilapán to Zamora, 19°56′N, 102°26′W, *Soto 2900* (TEX); Nocupetaro, 2 km NW of San Antonio de las Huertas, 19°06′N, 101°12′W, *Soto 10670* (CAS); 9 km SW of Tuzantla, 19°11′N, 100°38′W, *Soto 12012* (CAS, MEXU, MO).—MORELOS: 2 km track to Santa Catarina Civac (Texcal), Tepoztlán, 18°58′N, 99°06′W, *A. Burgos 101* (MEXU); Amayuca, 18°43′N, 98°48′W, *Converse 24*

(UC); 8 km W of Yautepec, Hwy 138, 18°56′N, 99°07′W, *Dunn 18700* (NY); Río Yautepec rd from Tlaltizapán towards Yautepec, 3 km SE of Ticumán, 18°45′N, 99°06′W, *Hughes 1729* (E, FHO, K, MEXU, MO, NY); 500 m E of the Colonia López Mateos, Tepalcingo, 18°39′N, 98°56′W, *R. Monroy 2076* (MEXU); Tejalpa, N of the main garden, Juitepec, 18°54′N, 99°09′W, *M. Reyes s.n.* (K, MEXU); 2 km from Miacatlán, 18°46′N, 99°20′W, *A. Rodríguez 5* (MEXU); nr Cuernavaca, 18°55′N, 99°14′W, *Rose 4353* (US); nr the water tank, above Oaxtepec, 18°55′N, 98°57′W, *Zárate 90* (MEXU).—NAYARIT: Ojos de Agua nr Yxtlán del Río, 21°03′N, 104°22′W, *Mexía 736* (CAS, GH, UC, US).—OAXACA: nr Oaxaca, 17°03′N, 96°41′W, *Bruff 1272* (MEXU); Barranca de Xochimilco, Oaxaca Valley, *Conzatti 5209* (MEXU, NY); Tequixtepec, Chinango, Huajuapan de León, 18°06′N, 97°46′W, *L. Hernández 79* (MEXU); San Juan Guelache, 17°13′N, 96°49′W, *Holway 5413* (US); a few km S of Miahuatlán, rd to Pochutla, 16°19′N, 96°39′W, *Hughes 843* (FHO, K, MEXU); rd NW from San Pedro Totolapan to Tlacolula and Oaxaca, 8 km from Totolapan above Arroyo Seco, 16°42′N, 96°19′W, *Hughes 1496* (FHO, K, MEXU, MO, NY); 3 km N of Teotitlán del Camino towards Tehuacán, lower Tehuacán Valley, 18°10′N, 97°05′W, *Hughes 1639* (E, FHO, K, MEXU, MO, NY); 9 km NNW of Etla side track to San Pedro and San Pablo Etla, about 15 km NNW of Oaxaca, close to Oaxaca to México rd, 17°12′N, 96°48′W, *Hughes 1779* (FHO, K, MEXU, MO, NY); nr Guadalupe Cuautepec, 18°02′N, 97°40′W, *Magallanes 3* (MEXU); El Coyul, rd between Tehuantepec and Oaxaca, 16°30′N, 95°54′W, *McCarter & Hughes 70* (FHO, MEXU); "Turpentine" camp, rd to Puerto Escondido, *Orr 8* (US); in Nazareno Xoxocotlán, 17°11′N, 96°50′W, *Robles 1* (MEXU); nr Monte Albán, 17°02′N, 96°46′W, *C. L. Smith 322* (EAP, MO, NY, UC, US); Zona Pie de Monte, San Miguel Tilquialpán, 16°47′N, 96°35′W, *B. Solano 43* (CAS, MEXU, MO); Cuilapan de Guererro, Barrio San Juán, 16°59′N, 96°47′W, *Solano & Vara 150* (CAS); San Pablo Guilá S of Tlacolula, 16°48′N, 96°27′W, *Solano & Vara 190* (CAS, MO); Rancho del Toro, *Solano & Vara 461* (MEXU); Concepción Guerrero, 14 km N of Putla, 17°09′N, 97°52′W, *Sousa 5841* (MEXU, NY); Santa Cruz Mixtepec, 7 km W of Valdeflores, Zimatlán, 16°47′N, 96°53′W, *Sousa 6254* (MEXU); 16 km NE of Sola de Vega, 16°37′N, 96°57′W, *Sousa 7190* (BM, MEXU); 10 km N of Huajuapan de León, 17°55′N, 97°40′W, *Sousa 9816* (CAS, MEXU, MO); San Jerónimo Silacayoapilla, Huajuapan de León, 17°49′N, 97°50′W, *Sousa 9820* (CAS, MEXU); 8 km SW of San Pedro Juchatengo, Juquila, 16°15′N, 97°09′W, *Sousa 9958* (CAS, MEXU); 10 km N of the turnoff to Guadalupe Huautepec, rd Huajuapan de León to Tehuacán, 18°06′N, 97°41′W, *R. Torres 790* (CAS); nr Valalag, Villa Alta in the Sierra Norte, 17°11′N, 96°09′W, *Vásquez 2* (MEXU); 2 km NW of the ruins of Lambiteyco, 4 km NW of Tlacolula, 16°58′N, 96°31′W, *Zárate 631* (BM, CAS, MEXU, MO).—PUEBLA: 2 km SW of Villa Lazaro Cárdenas, Venustiano Carranza, 20°27′N, 97°41′W, *Basurto & Durán 387* (TEX); Tequezquitla, Zihuatuetla, 20°14′N, 97°51′W, *Basurto & Durán 458* (CAS, MEXU, MO); 7 km before Atlixco, rd from Puebla to Matamoros, 18°57′N, 98°23′W, *Boege 584* (CAS, MEXU); 20 km N of Izúcar de Matamoros, 18°47′N, 98°28′W, *Brewbaker 14* (MEXU); outskirts of Ixcaquixtla nr San Juan Ixcaquixtla, 18°27′N, 97°49′W, *Cházaro 714* (MEXU); San Diego Chalma, 6 km S of Tehuacán, rd towards Teotitlán and Oaxaca, Tehuacán valley, 18°25′N, 97°23′W, *Hughes 1180* (FHO, K, MEXU); Santiago Acatepec, rd 50 km SW from Tehuacán towards Huajuapan de León, 18°13′N, 97°35′W, *Hughes 1325* (FHO, K, MEXU, NY); Hwy 150, 6 km SE of Tecamachalco, 18°51′N, 97°41′W, *King 2293A* (TEX); Cañada, slopes of the Sierra Tzentzo, *Medina 399* (MEXU); La Pedrera at the turnoff to Santa Cruz de Bravo, 18 km SW of Acatlán, Petlalcingo, 18°06′N, 98°07′W, *Medraño 47* (MEXU); 54 km SE of Acatlán on Hwy 190, 18°11′N, 98°03′W, *Siegler 9722* (MEXU); in ranchos at Calipa, Zapotitlán Valley, rd from Chazumba to Acatepec, 18°12′N, 97°36′W, *C. E. Smith 3985* (MEXU, US); S outskirts of San Diego, Tehuacán, 18°25′N, 97°21′W, *Sousa 5128* (MEXU); Portezuelo de los Negritos, N of Caltepec, 18°11′N, 97°28′W, *Tenorio 3900* (TEX); nr Cerrito Coatepec, side rd 3 km NW of Zinacatepec or 4 km from Ajalpan, 18°22′N, 97°15′W, *Zárate 616* (BM, CAS, MEXU, MO); 5 km E of Zinacatepec on the rd from Tehuacán to Teotitlán, 18°18′N, 97°13′W, *Zárate 619* (BM, CAS, MEXU, MO); San Pedro Chapulco, 13.5 km NE of Tehuacán, rd to Orizaba, 18°37′N, 97°24′W, *Zárate 686* (MEXU); Miahuatlán, 18°33′N, 97°25′W, *Zárate 689* (MEXU).—SONORA: E outskirts of Empalme close to the rd to Barcenas, 27°57′N, 110°48′W, *Hughes 1567* (FCME, FHO, K, MEXU, NY).—VERACRUZ: 11 km on the rd from Xalapa towards Veracruz, 19°29′N, 96°50′W, *Zola Baez 850* (MEXU, TEX).

Leucaena esculenta is readily distinguished by its gnarled thick corky pale metallic grey bark, strongly angled shoots, long elliptic sessile petiolar nectary, and very large leaves with many pinnae pairs and numerous pairs of very small leaflets per pinna, large flower heads, and large pods and seeds. Its close relatives are *L. pallida, L. pueblana, L. matudae,* and *L. involucrata*, all of which share the silvery corky bark with a single subepidermal periderm and lack of vertical fissuring (Figs. 2B, 3B). This group was consistently resolved in the cladistic analyses of morphology and cpDNA, although the position of *L. involucrata* in the cpDNA analysis was unstable. Zárate (1984a, 1994) agreed that these taxa are closely related but treated *L. esculenta* as a very variable species and included *L. matudae* and *L. pallida* (treated by him as *L. paniculata*) as subspecies within *L. esculenta*. The characters used to distinguish these as separate species are discussed under the individual species accounts.

Britton and Rose (1928) distinguished *L. confusa* by its glabrous anthers, but this was clearly an error, and the type is referable to *L. esculenta* and was determined as such originally. Britton and Rose (1928) also described *L. doylei* based on its narrower pods and the presence of a subulate beak on the pods. A pointed beak is present on most pods on specimens of *L. esculenta* and where it is absent, the beak may apparently have been broken off during handling of the dry material; this character provides no basis for species delimitation of *L. doylei,* which is treated here as conspecific with *L. esculenta.*

Leucaena esculenta is by far the best-known and most common species of *Leucaena* in the highlands of south-central Mexico, where it is very extensively cultivated for its edible unripe pods and seeds. Indeed, in some areas, it is one of the commonest tree species dominating many settlements in Oaxaca, Puebla, and parts of Guerrero. Its use, cultivation, and incipient indigenous domestication are discussed by Casas and Caballero (1996), Zárate (1984a, 1994, 1997), and Hughes (1998). This means that *L. esculenta* has been moved, cultivated, and in some areas possibly been naturalized, casting doubt over the extent of its native range. It is extremely abundant in the Tehuacán and Oaxaca Valleys, in the vicinity of Tuxtla Gutíerrez, Chiapas, and in parts of Jalisco. However, Zárate (unpubl.) postulates that it was introduced into these areas in pre-Columbian times. Casas and Caballero (1996) and Hughes and Harris (1994) followed Zárate and agreed that it occurs naturally only in parts of the Balsas depression, particularly in parts of Guerrero and Morelos. McVaugh (1987) discusses its occurrence in Nueva Galicia and concludes that in large part it is introduced into western Mexico, but that in the barrancas around Guadalajara it is abundant and apparently native. Observation of trees in and around Tuxtla Gutíerrez, Chiapas, strongly suggests that it is introduced there. It continues to be cultivated in the suburbs of Tuxtla with limited spread into the immediately surrounding area. The four cited collections from Chiapas (*Miranda 5889, Hughes 519, 1764*, and *Collins & Doyle 161*, the type of *L. doylei* from "castla" = Tuxtla) are all from the immediate vicinity of Tuxtla Gutíerrez. The *Collins & Doyle 161* collection shows that *L. esculenta* has been present in the area at least since 1907. The abundance of *L. esculenta* around Guadalajara could also be the result of a similar early introduction and subsequent naturalization. A number of other outlying occurrences, where collections have been clearly made from single isolated cultivated trees, include: Puerto Escondido, Oaxaca, *Sousa 9938*; Orizaba, Veracruz, *Rosas 268*; Empalme, near Guaymas, Sonora, *Hughes 1567*; Santa Barbara, California, U.S.A., *Blakely 2935* and *Muller & Stroder 2358*; Coral Gables, Florida, U.S.A., *Read 2069. Leucaena esculenta* is also reported from Sénégal (Berhaut 1956; Lock 1989).

Leucaena esculenta is known to hybridize with *L. leucocephala* subsp. *glabrata* (Hughes & Harris 1994) almost certainly as a result of the sympatry created by cultivation. These triploid hybrids, here described as *L.* ×*mixtec*, are uniformly sterile, morphologically intermediate, and readily distinguished from either parent species (see *L.* ×*mixtec*, no. 23).

Previous authors mistakenly have cited material other than the painting made by the artists of the Sessé & Mociño expedition as the type of *L. esculenta*. This painting is no. 185 of the *Icones Florae Mexicanae*, represented at G-DC by plate 209 of de Candolle's collection (McVaugh 1980, 1987); neg. 30593 F! A specimen at OXF (!, ex herb. Lambert), labelled by Pavón "*Mimosa esculenta*" and by Bentham "*Leucaena esculenta,*" was mistakenly taken as the lectotype of *M. esculenta* (McVaugh 1987).

11. Leucaena pueblana Britton & Rose, N. Amer. Fl. 23: 126. 1928.—TYPE: MEXICO. Oaxaca: west side of the valley of Cuicatlán, 17°47′N, 96°58′W, 9 Nov 1894, *E. W. Nelson 1886* (holotype: NY!; isotype: US!).

Small tree, 5–10 m tall, 5–20 (–30) cm bole diameter, sometimes multiple-stemmed and typically branchy when young, with an open rounded crown when older. Bark whitish, pale to mid-metallic grey, smooth with horizontally aligned, raised, orange-brown pustular lenticels, thick, corky, inner bark bright green then deep orange to blood-red. Young shoots with abundant glandular trichomes, especially on seedlings; leafy shoots angular with 4–6 longitudinal corky ridges, deep orange-brown, strongly geniculate, glabrous or sparsely puberulent. Stipules 5.1–5.4 mm long, lanceolate, long-pointed, with asymmetric wings at base, weakly striate, midrib prominent, ciliate on margin, persistent. Leaves (13–) 15–17 (–19) cm long, 5–9.5 (–11.5) cm wide; petioles (including pulvinus) 12–16 mm long, the pulvinus markedly swollen and often tinged bright scarlet, with a single, reddish green or brown, sessile, elliptic, shallowly crateriform or discoid nectary, 2.4 × 1.6 mm, at the distal end on adaxial side of petiole immediately below the first pair of pinnae; rachis 9–15 cm long, with 2–3 small elliptic discoid or shallowly concave nectaries at the distal end, apex of rachis extending beyond the terminal pinnae as a pointed glabrous or sparsely puberulent mucro 2.5–3.0 (–4.5) mm long; pinnae (10–) 16–20 (–22) pairs; pinnular rachis 4–8 cm long, angled, puberulent, with 2–3 minute elliptic nectaries at base of terminal pairs of leaflets; leaflets (30–) 40–55 pairs per pinna, 4.7–5.8 mm long, 0.9–1.1 mm wide, nearly sessile, slightly asymmetric, linear, rounded at apex, rounded to truncate at base, sparsely puberulent, ciliate on margins, single unequal midvein only. Capitula 18–25 mm in diameter at anthesis, in fascicles of 2–6 at nodes on unbranched terminal, strongly geniculate, often twisted, anauxotelic shoots, the development of leaves suppressed on flowering shoots, with the capitula exposed on the periphery of the tree crown, each capitulum with 100–140 flowers; peduncles 21–27 mm long, angled, glabrous or very sparsely puberulent, with an involucre of dentate bracts at the distal end. Flowers subtended by peltate bracts, 2.3–2.6 mm long, 0.7 mm in diameter; calyx 3.6–4 mm long, glabrous but the lobe tips ciliate on margin, pale whitish green; petals 4.7–5.2 mm long, free, glabrous, pale whitish green; filaments 11.4–13 mm long, white; anthers sparsely hairy, pale cream-white or creamy yellow, apiculum absent; ovary 1.4–1.6 mm long, glabrous, pale green, with 16–20 ovules, style 11.6–12.7 mm long, white, with a terminal narrow-tubular stigma, included. Pods 1–2 per capitulum, (10–) 13–15 cm long, 13–15 mm wide, pendulous on sturdy 4–7 mm long stipes, linear, acute apically, sometimes with a short beak, apparently readily broken off when dry, compressed, the seed chambers raised and clearly visible on exocarp (Fig. 17D), 12–16-seeded, valves green, strongly tinged scarlet when unripe, turning rich orange-brown, glabrous, slightly lustrous when ripe, with reticulate venation most pronounced close to margins, coriaceous and slightly lignified, the margins thickened, tardily dehiscent along both sutures, the seed chambers weakly partitioned by papery or spongy septa. Seeds 7.5–8 mm long, 5.8–6.1 mm wide, compressed, circular to ovoid or slightly rhomboid, deep chestnut-brown, glossy, aligned obliquely in pods; pleurogram visible, U- or sometimes bell-shaped, symmetrical, with 70% arm extension. Chromosome number unknown. Fig. 51.

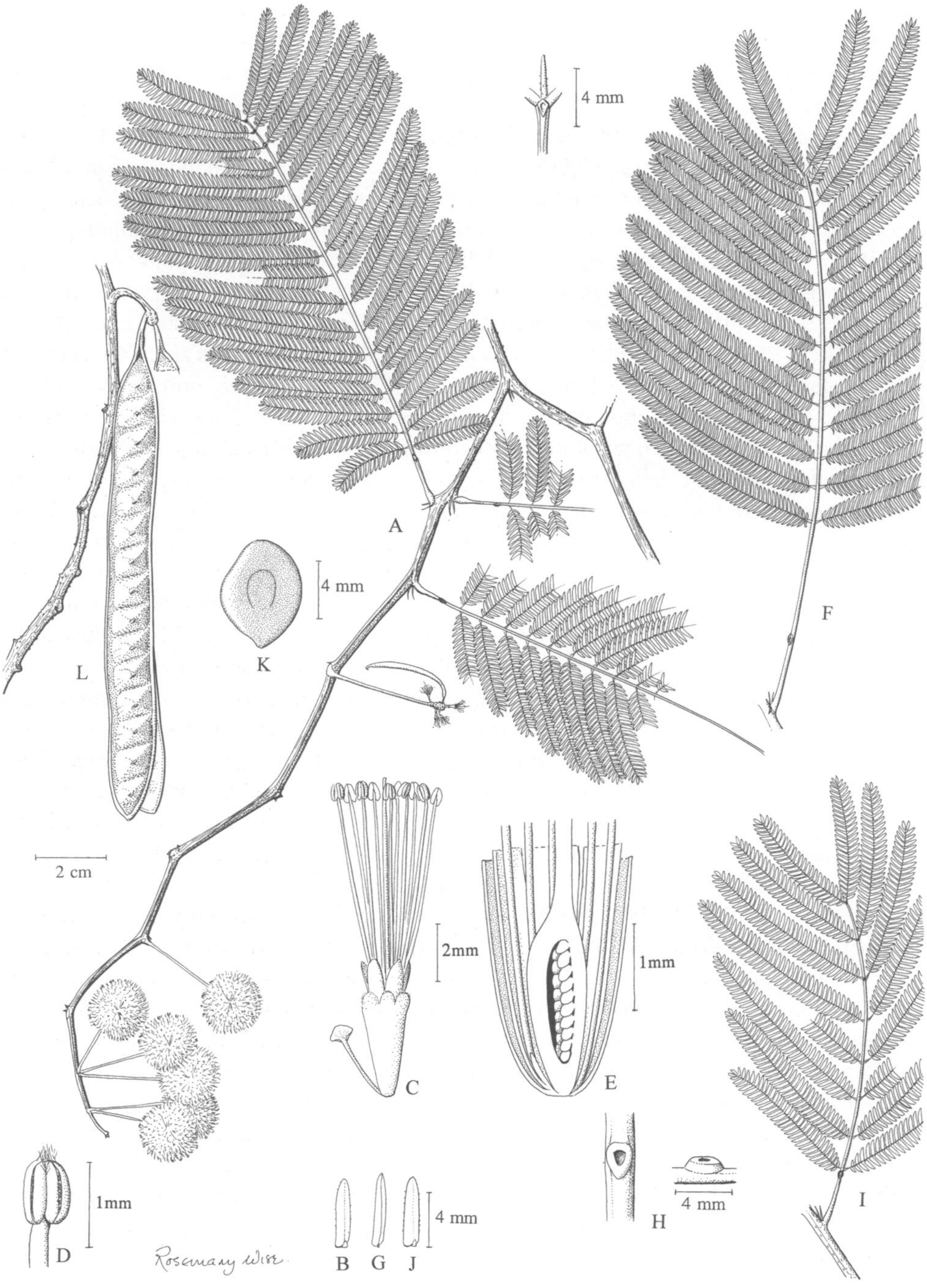


FIG. 51. *Leucaena pueblana*. A. Flowering shoot with leaves. B. Leaflet. C. Flower. D. Anther. E. Longitudinal section of flower. F. Leaf. G. Leaflet. H. Petiolar nectaries. I. Leaf. J. Leaflet. K. Seed. L. Pod. (Based on: A–E, *Hughes 1782*; F–H, *Hughes 1803*; I–L, *Hughes 1182*.)

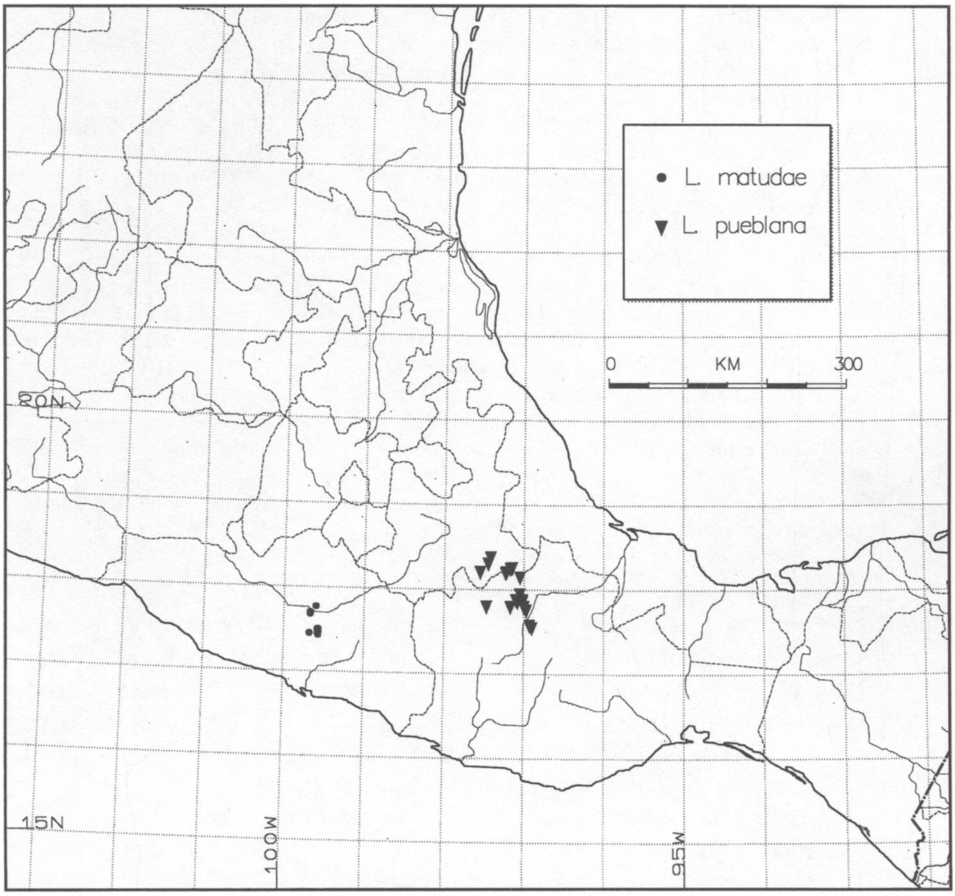


FIG. 52. Distribution of *L. matudae* and *L. pueblana*.

Phenology. Flowering November–December; fruiting (December–) January–February (–March); deciduous December–May.

Distribution (Fig. 52). *Leucaena pueblana* is restricted to the Tehuacán and Cuicatlán Valley systems of southern Puebla and northern Oaxaca. It forms a canopy tree in the prevalent dry thorn scrub forest of the mid and lower Tehuacán Valley. Associated woody species include many Leguminosae, such as *Acacia bilimekii, A. subangulata, A. pringlei, A. sericea, A. farnesiana, Caesalpinia melanadenia, Cercidium praecox, Coursetia glandulosa, Pithecellobium dulce, Prosopis laevigata, Zapoteca formosa*, and species of *Brongniartia*, several other species of *Leucaena* (see below), species of other woody genera including *Ceiba, Bursera, Jatropha, Zizyphus,* and many species of Cactaceae; 580–2000 m.

Vernacular names. *Guaje*. The ethnobotany of *L. pueblana* remains little studied and poorly known (see below).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** OAXACA: Huichica, 7 km NE of Teotitlán del Camino, rd to Huautla, 18°10′N, 97°03′W, *Cedillo 1607* (CAS, MEXU, MO); 4 km N of Tonaltepec, rd to Teotitlán del

Camino, 17°36′N, 96°56′W, *Cedillo 1880* (CAS, MEXU, MO, NY); Teotitlán del Camino, 12 km S of Dominguillo or 3 km E of Tonaltepec, Cañón de Tomellín, 17°34′N, 96°54′W, *A. Delgado 578* (CAS, MEXU, MO, NY); rd Tehuacán S to Oaxaca, 10 km S of Santiago Dominguillo, 30 km S of San Juan Bautista Cuicatlán, 17°36′N, 96°56′W, *Hughes 1182* (FHO, K, MEXU); outskirts of Magdalena Jicatlán, track 21 km NE from Villa Tamazulapan to Tepelmeme, 17°49′N, 97°28′W, *Hughes 1633* (E, FHO, K, MEXU, MO, NY); rd 35 km S of Teotitlán del Camino towards Oaxaca, lower Tehuacán Valley, 17°53′N, 97°01′W, *Hughes 1648* (E, FHO, K, MEXU, MO, NY); 20 km N of Cuicatlán, rd Oaxaca to Tehuacán, lower Tehuacán Valley, 17°54′N, 97°01′W, *Hughes 1782* (CAS, FHO, K, MEXU, MO, NY); 86.5 km S of Tehuacán towards Oaxaca, 7 km S of San Juan de los Cues towards Cuicatlán, lower Tehuacán Valley, 17°58′N, 97°03′W, *Hughes 1803* (FHO, K, MEXU, MO, NY, TEX); Teotitlán, Río Seco–Río Santiago, SSW of Tecomavaca, 17°53′N, 97°05′W, *Salinas 7215* (K); Cuicatlán, Cerro El Castillo, N of San Pedro Nodón, 17°49′N, 97°10′W, *Tenorio 17773* (MEXU); 33 km S of turnoff to San José Cues, rd from Teotitlán to Huitzó, 17°49′N, 97°00′W, *Zárate 621* (MEXU).—PUEBLA: 1 km SW of Zapotitlán Salinas, 18°20′N, 97°27′W, *Bannett 919* (MEXU); E slopes Sierra Mazateca above Tehuacán valley, rd 3 km E Coxcatlán towards Zoquitlán and Coyomeapan, 18°16′N, 97°10′W, *Hughes 1327* (BR, CR, FHO, K, MEXU, NY); 7 km ENE of Coxcatlán, E side of the Tehuacán Valley, rd up into Sierra Mazateca, 18°17′N, 97°09′W, *Hughes 1808* (FHO, K, MEXU, MO, NY); 8 km ENE of Santiago Acatepec, Hwy 125 Tehuacán–Huajuapan de León, 16 km SW of Zapotitlán Salinas, 18°14′N, 97°33′W, *Hughes 1787* (FHO, K, MEXU, MO, NY, TEX); San Jose Miahuatlán, 4 km S of Axusco, rd to Cerro Tepetroja, 18°13′N, 97°14′W, *Salinas 4217* (MEXU), *F. Chiang s.n.* (MEXU); W of Río Salado, around Petlanco, a travertine hill with numerous salt springs and salt domes, nr Tehuacán, 18°24′N, 97°25′W, *C. E. Smith 3647* (US).

Leucaena pueblana was treated as conspecific with *L. trichandra* (*L. diversifolia* subsp. *stenocarpa*) by Brewbaker (1987a) and Zárate (1994). Detailed examination of the type material of *L. pueblana* reveals a set of characters that clearly distinguish it from *L. trichandra* and indicate that the distinctive *Leucaena* material from the lower Tehuacán Valley is attributable to *L. pueblana*. The type material of *L. pueblana*, although in poor condition and incomplete, is clearly distinguished by its angular shoots with longitudinal corky ridges, the arrangement of the capitula on exposed terminal shoots on which leaf development is suppressed, the strongly geniculate shoots, the longer peduncles, larger flowers, glabrous ovary, and rounded leaflet tips, none of which are characters of *L. trichandra*. Moreover, detailed field exploration by the author and others over the last few years of the west side of the Cuicatlán Valley between 600 and 1300 m, where the type specimen was collected, has failed to reveal any occurrence of *L. trichandra* in that area. The small leaves and leaflets of the type material, which broadly resemble *L. trichandra*, and which undoubtedly led to its confusion with that species, are not typical of *L. pueblana* as a whole, but this is no more than a depauperate collection.

The true affinities of *L. pueblana* lie with the *L. esculenta* alliance, and with *L. pallida* and *L. matudae* in particular. *Leucaena pueblana* shares the characteristic thick, corky, pale metallic grey bark of the *L. esculenta* group and groups with these species in the cladistic analysis of morphology. It also groups closely with these species in the cpDNA analysis (Harris et al. 1994a), although in that analysis it was not recognized as distinct from *L. pallida* (accession ident. nos. 125/92 and 34/89). *Leucaena pueblana* is distinguished from *L. pallida* by its white or cream-white flowers, its smaller leaves with more pinnae pairs and smaller leaflets, and by its geniculate shoots.

In addition, *L. pueblana* occupies a clearly defined range, below 2000 m restricted to the Tehuacán and Cuicatlán Valley system, an area well-known for its high endemism (Smith 1965). Several other species of *Leucaena*, including *L. confertiflora, L. esculenta, L. leucocephala,* and *L. pallida* also occur in or around the fringes of the Tehuacán Valley. Of these, *L. confertiflora* and *L. pallida* occur at higher elevations, sometimes in cultivation but generally above *L. pueblana*. *Leucaena esculenta* is very widely cultivated but doubtfully native (Zárate 1994), especially in the mid-elevation zone (1000–2000 m), and *L. leucocephala* is very abundant but almost certainly introduced (Zárate 1994) and only in cultivation in the lower valley [500–1500 (–2000) m]. By contrast *L. pueblana* appears to be native throughout the lower to middle zone (500–1500 m), occurring scattered in undisturbed dry thorn scrub. It has not been recorded in cultivation, and it is likely that it is the only species of *Leucaena* native in these lower reaches of the valley. Perhaps because it is not widely cultivated, or because it has remained poorly known, the ethnobotany of *L. pueblana* has not been widely investigated. Nevertheless, Smith (1967) mentions the occurrence of *L. pueblana* seed and pod fragments in some of the pre-Columbian cave settlement deposits of the valley. These findings indicate that seeds and unripe pods may have been harvested from the dry thorn scrub, possibly as early as 5,000–3,500 B.C., and more definitely from 200 B.C. onwards. Given that *L. pueblana* may have been the only *Leucaena* species locally available in the earliest phase of occupation, at least in the mid-lower Tehuacán Valley, re-examination of the archaeological remnants in the light of its recognition as a valid species would be worthwhile.

12. **Leucaena pallida** Britton & Rose, N. Amer. Fl. 23: 126. 1928.—TYPE: MEXICO. Jalisco: nr Huejuquilla, 22°36′N, 103°52′W, 25 Aug 1897, *Rose 2569* (holotype: NY!; isotypes: US! GH!). [The flowering shoot mounted with the US isotype is *L. leucocephala*.]

Leucaena dugesiana Britton & Rose, N. Amer. Fl. 23: 127. 1928.—TYPE: MEXICO. Guanajuato: Guanajuato, 21°01′N, 101°15′W, 11 Jul 1899, *Rose & Hough 4841* (holotype: NY!; isotype: US!).

Leucaena oaxacana Britton & Rose, N. Amer. Fl. 23: 127. 1928.—TYPE: MEXICO. Oaxaca: nr the city of Oaxaca, 17°03′N, 96°41′W, 18 Jun 1899, *Rose & Hough 4648* (holotype: NY!; isotype: US!).

Leucaena paniculata Britton & Rose, N. Amer. Fl. 23: 128. 1928. *Leucaena esculenta* subsp. *paniculata* (Britton & Rose) S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65(2): 133. 1994.—TYPE: MEXICO. Morelos: nr Cuernavaca, 18°53′N, 99°16′W, 15 Aug 1906, *Rose & Rose 11090* (holotype: NY!; isotype: US!).

Small, often multiple-stemmed tree, 3–7 (–15) m tall, 10–15 (–30) cm bole diameter, with an open irregular spreading crown. Bark smooth, mid-metallic grey, blotched lighter grey with horizontally aligned pale brown lenticels, inner bark greenish. Shoots scarcely geniculate, subterete, slightly angular with incipient longitudinal corky ridges, rich mid-orange-brown, glabrous or sparsely puberulent, young shoots and seedling shoots with scattered thornlike glandular trichomes (as in *L. pueblana*). Stipules 4–5.9 mm long, ovate, with a subulate or long-pointed apex, with asymmetric membranous basal wings, persistent. Leaves (17–) 20–28 (–32) cm long, (12–) 14–19 (–22) cm wide; petioles (including pulvinus) (10–) 13–31 mm long; rachis 14–25 cm long, sparsely puberulent, with a single, sessile, shallowly crateriform, elliptical nectary, 3.2–4 mm long, 1.8–3.2 mm wide, on ventral side of petiole at base of the basal pair of pinnae, and 1 or 2 additional, sessile, discoid or shallowly crateriform, elliptical nectaries at base of terminal pinnae pairs, 1.3–2.2 mm long, 0.8–1.8 mm wide, apex of rachis extending beyond the terminal pinnae as a slender pointed, curling mucro, 3.5–4.2 mm long, variably puberulent; pinnae 15–25 pairs; pinnular rachis 7.5–10.5 (–13.5) cm long, sparsely pubescent, with 1 or 2 minute sessile elliptical nectaries at base of terminal pairs of leaflets; leaflets 39–50 (–58) pairs per pinna, 6.1–8 (–9.8) mm long, 1.2–1.6 (–1.9) mm wide, sessile, asymmetrically truncate at base, linear or linear-oblong, acuminate, entire, ciliate on margins, otherwise glabrous, slightly discolorous, glossy bottle-green above, paler mid- or grey-green below, only midrib visible when dried. Capitula 14–16 mm in diameter at anthesis, in fascicles of 3–5 in leaf axils on actively growing shoots, sometimes with suppression of the leaves on the flowering shoot, each capitulum with 95–110 flowers; peduncles variable, 20–23 mm long, angled, sparsely puberulent, with scattered amber-colored exudate (termed "glands" by Britton & Rose, 1928), with an involucre of basally united bracts at distal end. Flowers subtended by small peltate bracts, 2.7–2.9 mm long, 1 mm in diameter; calyx 2.9–3.1 mm long, sparsely hairy on lobe tips, pale whitish green; petals 4.5–4.7 mm long, free, glabrous, pale green; filaments 7.4–8.7 mm long, creamy white; anthers sparsely hairy on ventral side, pale pink or dull purplish mauve, apiculum absent; ovary 2–2.2 mm long, sparsely hairy at distal end, pale cream-white, with 16–22 ovules, style 9.8–11.1 mm long, cream-white, with a narrow funnelform stigma, held level with or slightly exserted beyond anthers. Pods (1–) 3–5 per capitulum, 12–18.5 cm long, 14–18 mm wide, pendulous, with a short stipe, linear, cuneate at base and apex, often with a short beak at apex, compressed, (7–) 16–22-seeded, valves thickened coriaceous, glossy maroon when unripe, turning mid-reddish or orange-brown, glabrous or occasionally pubescent, the margins slightly raised, the endocarp forming a weak partition between seeds, the seed chambers visible on exocarp, somewhat tardily dehiscent along both sutures. Seeds 6.2–7.7 mm long, 5.1–6.5 mm wide, compressed, circular or slightly rhombic, deep chestnut-brown, glossy, aligned transversely or oblique-transversely in pods; pleurogram visible, regular, U-shaped, with 75–90% symmetrical arm extension. Chromosome number: 2n = 104 (Pan & Brewbaker 1988; Sorensson 1989). Fig. 53.

Phenology. Flowering (April–) May–October (–December); fruiting (October–) December–March (–April); leafless during part of the dry season December–March.

Distribution (Fig. 54). *Leucaena pallida* is distributed mainly in the mid-interior highlands of south-central Mexico in the States of Oaxaca, Puebla, Morelos, and eastern Guerrero, with sporadic outlying occurrences in Jalisco, Zacatecas, and Guanajuato, each represented by one or two collections, mostly from the last century. *Leucaena pallida* is extensively cultivated for its edible pods and seeds (almost half the extant botanical collections are stated to be from cultivated trees), and these outliers almost certainly represent locations where it has been introduced in cultivation. McVaugh (1987) suggests that nothing similar to *L. pallida* has been collected in Nueva Galicia since the type specimen in 1897. As for other widely cultivated species, such as *L. esculenta* and *L. leucocephala*, the natural distribution of *L. pallida* is now difficult to ascertain. In parts of Oaxaca, in and around many towns and villages, *L. pallida* is extremely abundant in cultivation. In other situations, it occurs, apparently naturally, often on shallow calcareous soils, in disturbed dry thorn forest, dry matorral, oak forest, oak-pine forest, and particularly in the oak-dry thorn forest transition zone. Associated trees include species of *Acacia, Arctostaphylos, Bursera, Brahea, Eysenhardtia, Dodonaea, Lindleyella, Lysiloma, Neopringlea, Prosopis, Quercus, Rhus,* and *Vauquelinia*; (850–) 1300–2200 (–2480) m.

Vernacular names. Most commonly *guaje, guaje colorado*, or *guaje rojo*, names that are applied equally frequently to *L. esculenta*, which is perceived to be closely related; *guaja, guajal, guajal de castilla, guaje barbero, guaje delgado* (in reference to its narrower pods than those of *L. esculenta*), *guaje de risa* (Guerrero), *ndwan duchi* (Mixteco, zona La Montaña, Guerrero; Casas & Caballero 1996), *lobada le-eg* (Zapoteco; Guelatao, Oaxaca; Zárate 1994), *lya gusgih* (Zapoteco de Mitla = *guaje de lluvias*; Zárate 1994), *guajentudi, huaje, texcalera*, and *timbre*.

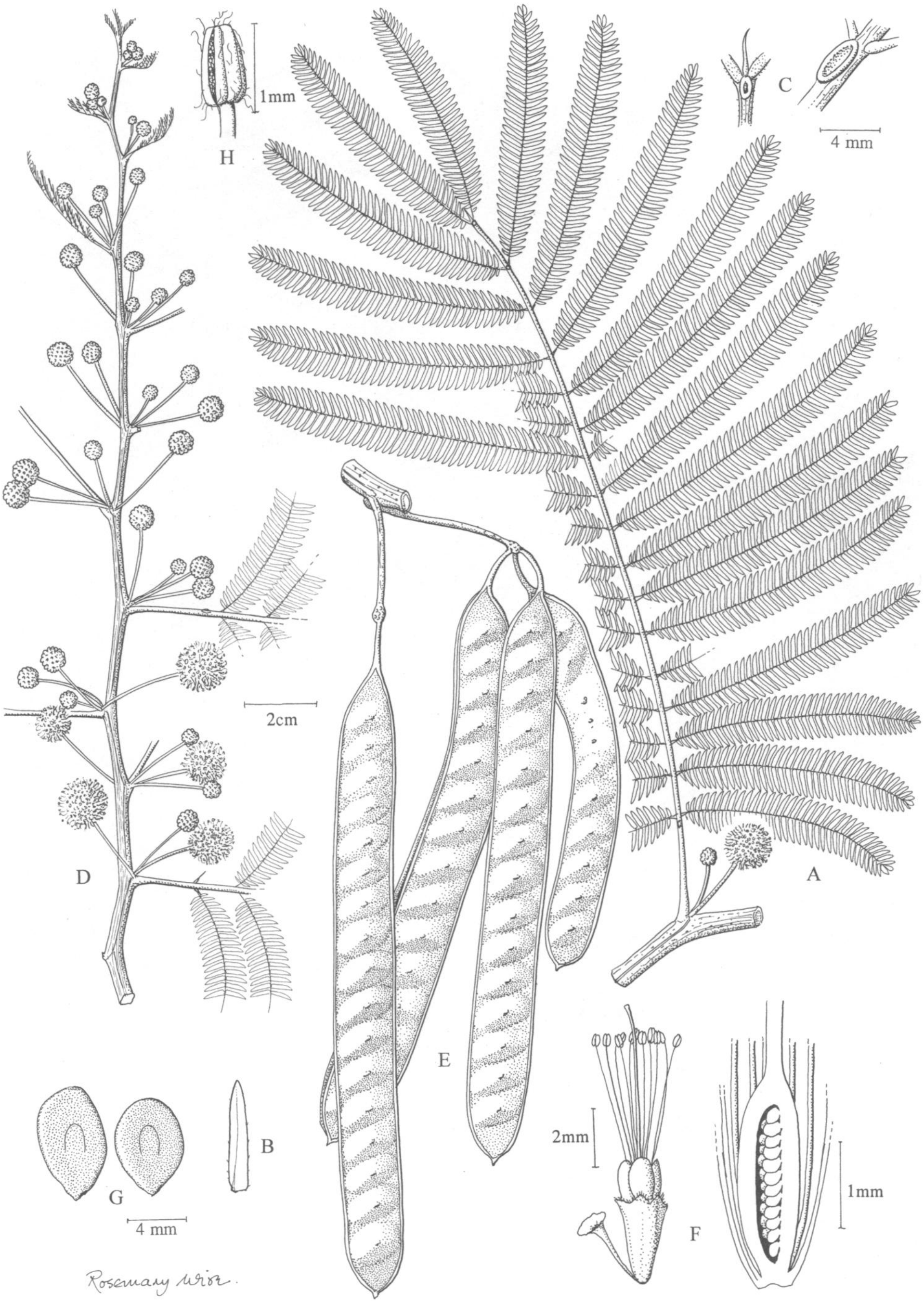


FIG. 53. *Leucaena pallida*. A. Leaf. B. Leaflet. C. Petiolar and rachis tip nectaries. D. Flowering shoot. E. Pods. F. Flower and longitudinal section of flower. G. Seeds. H. Anther. (Based on: A–C, *Hughes 1795*; D–F, *Hughes 1506*; G, *Hughes 1629*; H, *Hughes 1775*.)

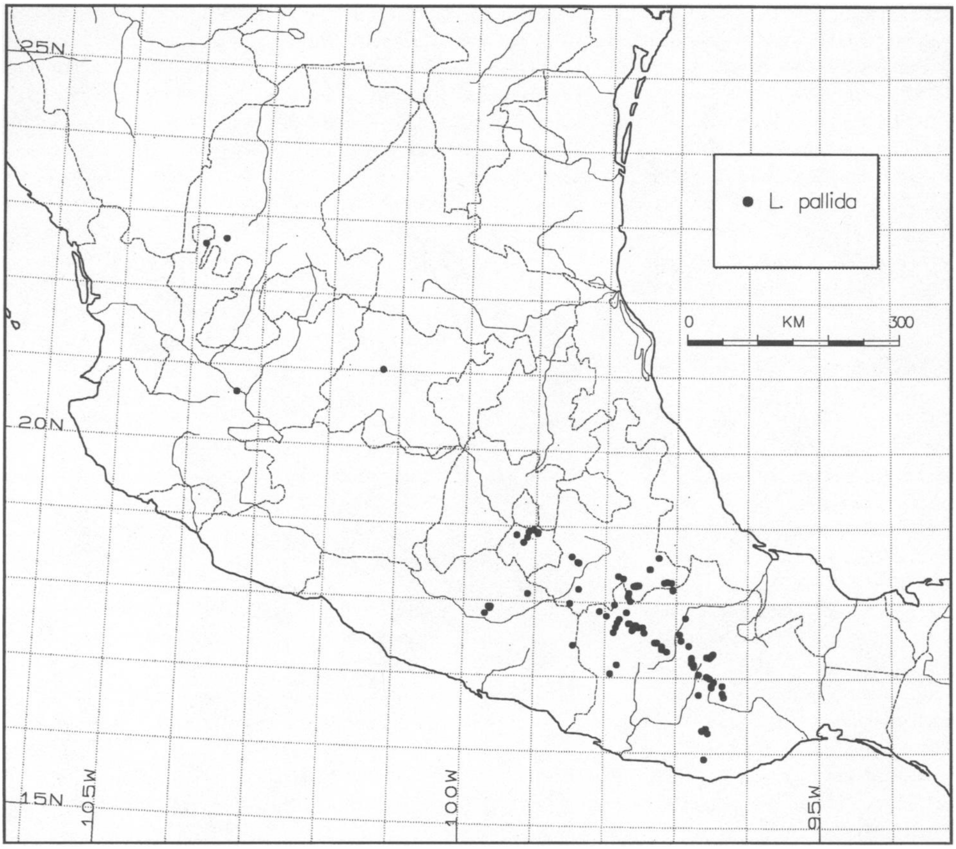


FIG. 54. Distribution of *L. pallida.*

Representative Specimens. **Mexico.** Guerrero: 4 km SE of Mezcala, hills above Río Balsas W of Zumpango del Río, 17°54′N, 99°38′W, *Contreras 427* (MEXU); Cerro Xilotín, 3 km NW of Xilotepec, nr Xochihuehuetlán, 17°59′N, 98°30′W, *Contreras 995* (MEXU); 1.5 km from Atenango del Río, 18°06′N, 99°06′W, *A. Delgado 180* (CAS, MEXU, MO); 4 km SW of Mezcala, lower slopes of Cordillera de la Encinera Amarilla, nr track to Mezapa, 17°55′N, 99°37′W, *Hughes 884* (FHO, K, MEXU); San José Lagunas, nr Joya de Soyaixtlahuaca and Alcozauca, 17°25′N, 98°27′W, *Viveros & Casas 144* (CAS, MEXU).—Jalisco: nr Guadalajara, 20°39′N, 103°20′W, *Rose 7448* (GH).—Morelos: side of gully running S to San José Laureles from Amatlán, 18°57′N, 99°02′W, *Miranda 941* (MEXU); Amador Salazar, Cañón de Lobos nr Yautepec, 18°51′N, 99°07′W, *J. Vázquez 2913* (MEXU); 3 km SE of San Andrés de la Cal, foot of Cerro de la Cal, nr Tepoztlán, 18°55′N, 99°06′W, *Zárate 72* (CAS, MEXU, NY); centro vacacional Oaxtepec, 18°54′N, 98°58′W, *Zárate 94* (MEXU).—Oaxaca: Río La Junta, 4 km SW of Santa María Mixtlepilco, 12 km SW of Huajuapan de León, 17°44′N, 97°50′W, *Cedillo 1417* (MEXU, MO); Valley of Oaxaca, N of Tlacolula and E of Tule, nr Mitla, 17°00′N, 96°32′W, *Ernst 2408* (BM, MEXU, US); in Guelatao, 17°18′N, 96°30′W, *E. García 438* (CAS, MEXU); 4.5 km W of Nochistlán, Hwy 95 to Oaxaca, 17°28′N, 97°16′W, *Grethur 720* (MEXU); San Andrés Sinaxtla, rd 5 km W of Nochixtlán towards Huajuapan de León, 17°28′N, 97°18′W, *Hughes 1508* (FHO, K, MEXU, MO, NY); track SW from lower Tehuacán Valley towards Santa María Ixcatlán, 12 km from main Teotitlán to Oaxaca rd, 17°54′N, 97°06′W, *Hughes 1635* (E, FHO, K, MEXU, MO, NY); 7 km SE of Nueve Puntas, 1 km SE of Portillo San Dionisio, rd 55 km SE of Oaxaca, from Matatlán to Totolapan, 16°45′N, 96°20′W, *Hughes 1775* (CAS, FHO, K, MEXU, MO, NY); San Juan Guelache, nr Etla, 17°12′N, 96°47′W, *Holway 5408* (US); 14 km N of Oaxaca, 17°11′N, 96°45′W, *C. D. Johnson 285–78* (MO); 5 km SW of Tamazulapan, rd to Chilapa, Teposcolula Mixteca Alta, 17°39′N, 97°36′W, *Mendoza 710* (CAS, MEXU, MO); rd from Cuicatlán to

Reyes Papalo, 17°48′N, 96°52′W, *Miranda 4629* (MEXU); 10 km above Dominguillo, 17°35′N, 96°57′W, *E. W. Nelson 1835* (US); nr San Juan del Estado, 17°16′N, 96°47′W, *Rila 321* (MEXU); San Antonio Castillo Velazco, nr Ocotlán, 16°47′N, 96°41′W, *Robles 3* (MEXU); nr San Bartolomé Quialana, Oaxaca Valley, nr Tlacolula, 16°53′N, 96°30′W, *Robles 39* (MEXU); Santa Catarina Cuixtla, nr Miahuatlán, 16°18′N, 96°38′W, *Robles 76* (MEXU); La Loma Pechona, 6 km NE of Giusepe Cuautepec, 1 km E of jctn Huajuapan de León to Tehuacán rd to Giusepe Cuautepec, 18°01′N, 97°39′W, *Salinas 3693* (MEXU, MO); nr Jayacatlán, 17°26′N, 96°49′W, *L. C. Smith 116* (US); in San Pablo, nr Etla, about 10 km NW of Oaxaca, 17°09′N, 96°45′W, *Solano & Vara 313* (MEXU); Rancho del Toro, *Solano & Vara 460* (F, MEXU); N of Putla, Sierra Madre del Sur, 17°03′N, 97°55′W, *Sousa 2674* (MEXU); Tierra Blanca, 23 km SW of Suchixtepec, nr Pochutla, 15°55′N, 96°36′W, *Sousa 6500* (MEXU, MO); 8 km NNE of Teotitlán del Camino, 18°10′N, 97°03′W, *Sousa 9332* (CAS, MEXU); Río de Oro, 7 km NW of Tamazulapan, nr Teposcolula, 17°42′N, 97°34′W, *Sousa 9851* (CAS, MEXU, MO); Yosososumha, 21 km SW of Tlaxiaco, 17°10′N, 97°50′W, *Sousa 9863* (CAS, MEXU, MO); 14 km SW of San Marcos Arteaga, rd Huajuapan de León to Juxtlahuaca, 17°36′N, 97°53′W, *Tenorio 3627* (MEXU); 6.7 km W of Miahuatlán, rd to Piedra Larga (Coatlanes), 16°20′N, 96°35′W, *R. Torres 1722* (MEXU, MO); 6 km N of Chilapa, nr Teposcolula, 17°38′N, 97°37′W, *R. Torres 6678* (MEXU); 34 km S of Cuicatlán, 17°30′N, 96°56′W, *Zárate 622* (MEXU); 0.5 km along rd towards Chicomezuchitl, SW side of Río Grande, 4 km SW of Guelatao, 17°17′N, 96°31′W, *Zárate 625* (BM, CAS, MEXU, MO); 6 km NNW of Huajuapan de León, off Hwy 190, 10 km S of the Puebla-Oaxaca boundary, 17°52′N, 97°42′W, *Zárate 639* (BM, MEXU, MO).—PUEBLA: 4 km NE of Acatepec, rd from Huajuapan de León to Tehuacán, 18°14′N, 97°32′W, *Chiang 422* (MEXU); 3 km N of Axusco, track to the main Tehuacán to Oaxaca rd, 18°16′N, 97°10′W, *Chiang 2490* (MEXU); rd 17 km ENE from Teotitlán del Camino to Huautla, W flanks of the Sierra Mazateca, above Tehuacán valley, 18°16′N, 97°04′W, *Hughes 1318* (CR, FHO, K, MEXU, NY); W flanks of Sierra Mazateca, above the Tehuacán valley, nr rd 15 km E from Coxcatlán, towards Zoquitlán and Coyomeapan, 18°17′N, 97°08′W, *Hughes 1329* (BR, FHO, K, MEXU, NY); in Santa Catalina Oxolotepec, upper NW flanks of Sierra Zongolica, 25 km NE of Tehuacán, 18°36′N, 97°15′W, *Hughes 1800* (CAS, FHO, K, MEXU, MO, NY); rd from Acatlán to Huajuapan, 21 km NW of Huajuapan de León, 17°58′N, 97°52′W, *Koch 73172* (MEXU, MO); 9 km NE of Santiago Chazumba, 1 km after Oaxaca-Puebla boundary, 18°13′N, 97°36′W, *Medraño 701* (MEXU, MO); 9 km SW of Santa Cruz Nuevo, rd to San Juan Ixcaquistla, nr Totoltepec, 18°21′N, 97°49′W, *Medraño 1247* (CAS, MEXU, MO); 4 km NE of Santo Tomás Otlaltepec, nr San Martín Atexcal, 18°19′N, 97°45′W, *Medraño 1291* (CAS, MEXU, MO); Tlanislatepec, *Purpus 3864* (UC); 11 km SE of Izúcar de Matamoros, 18°32′N, 98°24′W, *Sousa 8197* (CAS, MEXU); La Vega, 2 km SE of Tehuacán, 18°27′N, 97°22′W, *Sousa 9314* (CAS, MEXU, UC); 7 km SE of Raboso, rd from Izúcar de Matamoros to Huajuapan de León, 18°10′N, 98°23′W, *Zárate 673* (MEXU).—ZACATECAS: 11 km W of Valparaiso, 22°41′N, 103°35′W, *Taylor & Taylor 6169* (NY).

Honduras. COMAYAGUA: cult. La Soledad field stn, nr El Taladro, 10 km WSW of Comayagua, *Hughes 1369* (FHO).

Britton and Rose (1928) distinguished four species, here treated as conspecific (*L. pallida, L. dugesiana, L. oaxacana, L. paniculata*), largely on leaflet size and particularly leaflet pubescence. *Leucaena dugesiana* was distinguished from *L. pallida* based on the supposed occurrence of glands on the peduncle, but these glandular trichomes occur in all four species. Although Brewbaker (1985), Hughes (1993), and Zárate (1994) all agreed that the four species described by Britton and Rose (1928), *L. dugesiana, L. oaxacana, L. pallida,* and *L. paniculata*, are conspecific, there has been a lack of agreement about which is the accepted name for this taxon, and about the rank at which it should be treated. This has led to confusion in the agronomic and forestry literature about the correct name to be used, particularly given the recent interest in this species for germplasm introduction, evaluation, and artificial hybridization programmes (Brewbaker 1987b; Shelton, pers. comm.). Brewbaker (1985) informally placed *L. dugesiana, L. oaxacana,* and *L. paniculata* in synonymy, selecting *L. pallida* as the valid name. The very wide use of the name *L. pallida* in the agronomic literature, as cited above, supports acceptance of this decision, despite the persistent preference of Zárate (1984a, 1994) for the epithet *paniculata*, albeit at subspecific rank. *Leucaena pallida* is the name chosen here based on Brewbaker (1985) and the wide acceptance of this name in the agronomic literature.

Leucaena pallida belongs in the *L. esculenta* alliance along with *L. esculenta, L. matudae, L. involucrata,* and *L. pueblana,* and it shows particular affinities with *L. pueblana* and *L. matudae*. It is distinguished from *L. pueblana* by lack of geniculate shoots and its pink or purple anthers, larger leaves and leaflets, and from *L. matudae* by its sessile, shallowly crateriform petiolar nectary.

Pan (1985) and Pan and Brewbaker (1988) showed *L. pallida* to be a tetraploid (2n = 104) and hypothesized an amphidiploid origin, with *L. esculenta* and *L. trichandra* as the putative parent species, based on a preliminary investigation of cytology, morphology, and phytogeography. The cpDNA analysis of Harris et al. (1994a) supported a hybrid origin for *L. pallida* with *L. esculenta* as the maternal parent. However, subsequent field work carried out after the cpDNA analysis was completed and published, showed that two of the accessions attributed by Harris et al. (1994a) to *L. pallida* (designated by them as *L. esculenta* subsp. *paniculata*) (seed accession numbers 125/92 and 34/89) are in fact attributable to *L. pueblana*. Given that these two accessions have similar cpDNA to *L. pallida*, this would suggest that *L. pueblana*, not *L. esculenta*, is the most likely maternal parent of *L. pallida*. Several morphological characters, including bark type, shoots, and nyctinasty, were difficult to score for *L. pallida* due to "blurring" of otherwise discrete character states (see above), perhaps as a result of its hybrid origin. As in the cpDNA analysis, inclusion of *L. pallida* in the morphological analysis of diploid species placed it next to *L. pueblana*, again suggesting a close relationship between these two species.

Material collected from immediately around the village of San Pedro Chapulco in Puebla was originally referred to *L. pallida*. Harris et al. (1994a) showed that the cpDNA of this material (represented in their study by accession 52/87) did not group with other *L. pallida* accessions, and concluded that the material from San Pedro Chapulco does not have the cpDNA of *L. pallida* and could be of hybrid origin. The cpDNA study did not shed further light on the identity of this material, which remains unknown, but is likely to be of hybrid origin. Detailed morphological study revealed that this material (*Hughes 924, 929, 930, 985, 1615*) has circular as opposed to elliptical petiolar nectaries, slightly larger leaves and leaflets, and dense pubescence on the young shoots, leaf rachis, and pinnular rachis. Given that *L. esculenta, L. leucocephala, L. confertiflora,* and possibly *L. pallida* as well as another putative hybrid (*Hughes 1882*) all occur in close proximity in cultivation in and around Chapulco, the origin of this material may be complex. The unusual growth performance, psyllid resistance, and leaf chemical composition of accession 52/87 and other seed accessions from San Pedro Chapulco (University of Hawaii accessions K806 and K953), documented by Shelton (pers. comm.), supports the distinction of this material from typical *L. pallida.*

Variants of *L. pallida* with pubescent pods have been collected on hills around Mezcala in central Guerrero (*Hughes 884, 886, 1826, 1827*).

Leucaena pallida is cultivated in "guajales," often along terrace boundaries, often with *L. esculenta, L. confertiflora,* and species of *Schinus, Agave,* and *Opuntia*, particularly in parts of Oaxaca and Puebla in Mexico. In these areas, it is valued particularly because it produces unripe pods earlier than *L. esculenta*, thereby extending the overall pod production period. Unripe pods, seeds, and flower head buds are harvested and consumed locally as well as being transported and sold in local and regional markets. In some of these areas *L. pallida* appears to be naturalized and ruderal following cultivation, e.g., in and around Guelatao de Juárez, northern Oaxaca.

13. Leucaena involucrata S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65(2): 138. 1994.—TYPE: MEXICO. Sonora: El Novillo, 28°55′N, 109°28′W, 19 Aug 1991, *Hughes 1522* (holotype: MEXU!; isotypes: FHO! K! NY! MO!).

Small, often multiple-stemmed tree, 2–5 (–8) m tall, 10–15 (–25) cm bole diameter, with an open irregular spreading crown, the branches often slightly pendulous. Bark smooth, mid-metallic grey, blotched lighter grey with horizontally aligned pale brown lenticels, inner bark greenish, then dark red. Shoots terete, rich mid-orange-brown, glabrous or sparsely puberulent. Stipules 4–5.9 mm long, ovate, with a subulate or long-pointed apex, with asymmetric membranous basal wings, persistent. Leaves (15–) 18–22 (–24) cm long, 8–13 cm wide; petioles (including pulvinus) (18–) 20–29 mm long; rachis 14–19 cm long, glabrous or sparsely puberulent, with a single, cylindrical, short, peg-shaped nectary, 1–1.5 × 1.2–1.5 mm and raised 1 mm above petiole, on ventral side of petiole at base of the basal pair of pinnae, and 1–4 (–5) additional cylindrical nectaries, 0.4 × 0.4 mm, at base of terminal pinnae pairs, apex of rachis extending beyond the terminal pinnae as a slender, pointed, curling mucro (2–) 3.5–4.6 mm long, variably puberulent; pinnae (13–) 16–22 pairs; pinnular rachis 5.5–8.3 cm long, sparsely pubescent, with 1–3 (–4) sessile circular nectaries, 0.1–0.2 mm in diameter, at base of terminal pairs of leaflets; leaflets (32–) 40–51 pairs per pinna, (3.9–) 5–6.6 mm long, 0.9–1.7 mm wide, virtually sessile on rudimentary wedge-shaped petiolules, asymmetrically truncate at base, linear or linear-oblong, acute, entire, ciliate on margins, otherwise glabrous or sparsely puberulent, only midrib visible. Capitula 16–20 mm in diameter at anthesis, in fascicles of 4–6 in leaf axils on actively growing shoots, sometimes with suppression of the leaves on the flowering shoot, each capitulum with 140–180 flowers; peduncles variable, 25–36 mm long, angled, glabrous, with scattered amber-colored glandular exudate and an involucre of basally united bracts at distal end in bud. Flowers subtended by small peltate bracts, 2.6–2.7 mm long, 1 mm in diameter; calyx 3–3.2 mm long, hairy on lobe tips, pale cream; petals 4.5–5 mm long, free, sparsely hairy on lobes, pale creamy green; filaments 6.4–7.9 mm long, pale creamy white; anthers with a distal tuft of hairs, pale yellow turning dull orange, apiculum absent; ovary 2–2.2 mm long, glabrous, pale cream-white, with 16–22 ovules, style 8.8–10 mm long, cream-white, with a narrow-funnelform stigma, held level with or slightly exserted beyond anthers. Pods 1–4 (–6) per capitulum, 11–18 cm long, 9–13 mm wide, pendulous, with a short stipe, linear, not constricted between seeds, cuneate at base and apex, often with a short beak at apex, compressed, 12–19-seeded, exocarp coriaceous, glossy reddish brown when unripe, turning lustrous rich orange-brown, glabrous, the margins slightly raised, endocarp subseptate forming weak partitions between seeds, the seed chambers clearly visible on exocarp, somewhat tardily dehiscent along both sutures (Fig. 17C). Seeds 7–8 mm long, 4.9–5.9 mm wide, compressed, weakly rhombic, deep chestnut-brown, glossy, strongly oblique seed alignment in pods; pleurogram visible, regular, U-shaped, 90%, symmetrical. Chromosome number unknown. Fig. 55.

Phenology. Limited data indicate flowering (June–) July–September (–?), fruiting (August–) September–January.

Distribution (Fig. 56). *Leucaena involucrata* is restricted to the mountains of the northwestern Mexican states of Sonora and northern Sinaloa. Even within these states it occurs rarely and very sporadically. Given that these areas are probably very undercollected, it may be more widespread and common than current collections suggest. At present, *L. involucrata* is known from only two areas, in the hills east of Hermosillo southeast of the dam at El Novillo and in the northern fringes of the Sierra de Surotato. Field

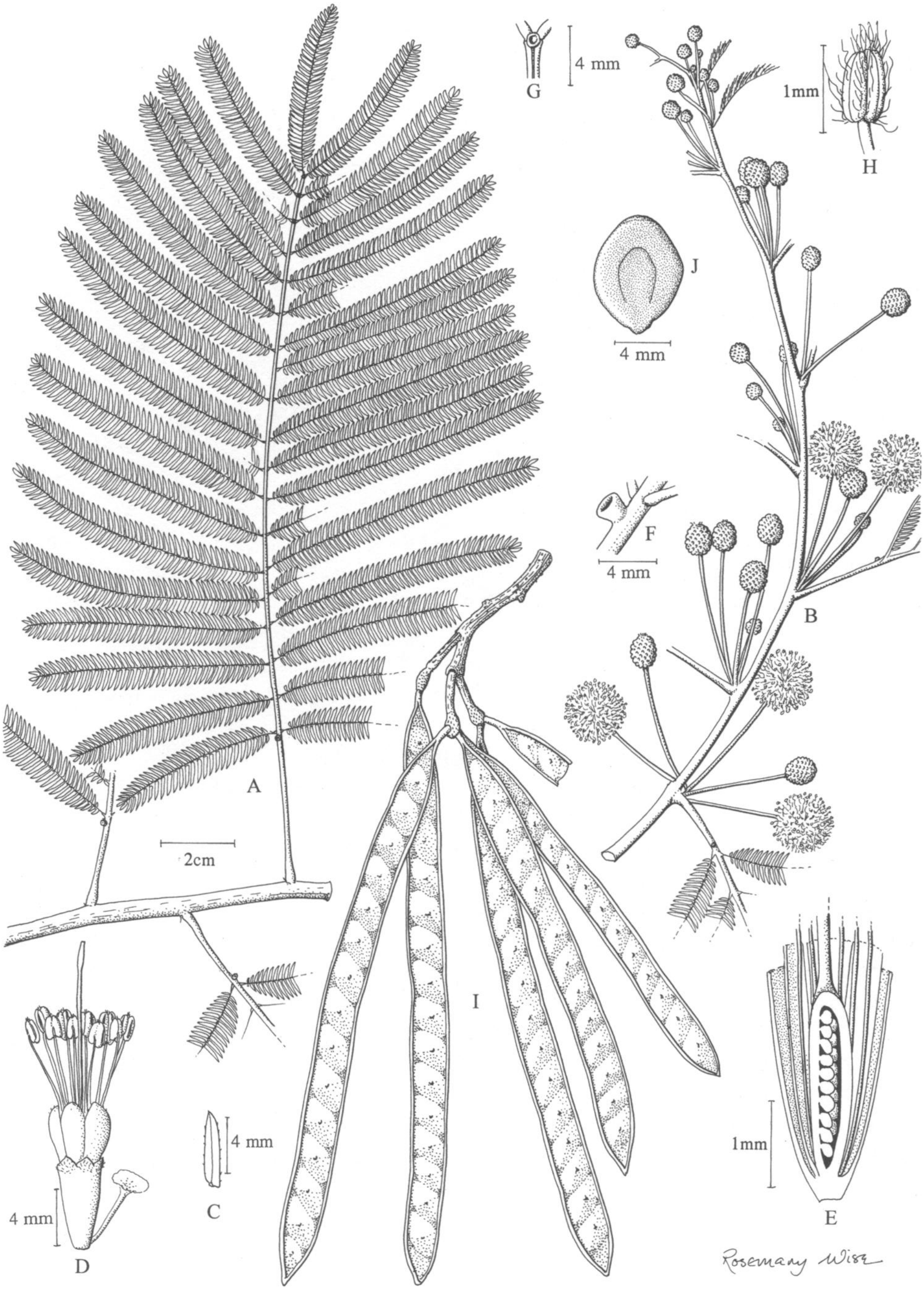


FIG. 55. *Leucaena involucrata*. A. Leaf. B. Flowering shoot. C. Leaflet. D. Flower. E. Longitudinal section of flower. F. Petiolar nectary. G. Rachis tip nectary. H. Anther. I. Pods. J. Seed. (Based on: A–E, *Hughes 1523*; F–J, *Hughes 1522*.)

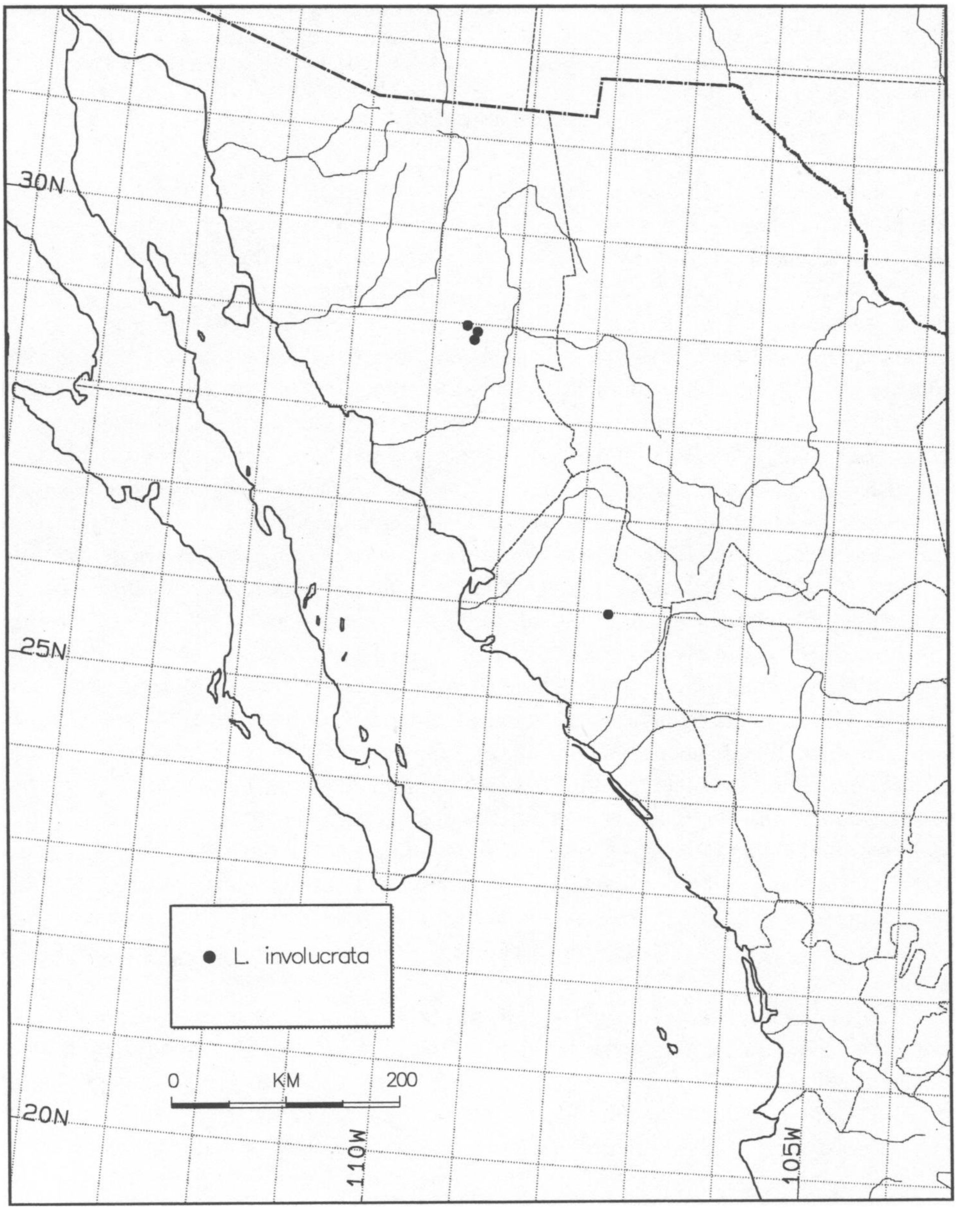


FIG. 56. Distribution of *L. involucrata*.

exploration in 1991 in the Sierra Surotato, where it was collected in 1941, failed to relocate *L. involucrata*. In the area of El Novillo, it occurs in dry thorn scrub forest where it appears to be restricted to rocky calcareous outcrops. Associated trees include species of *Acacia, Lysiloma, Mimosa, Desmanthus, Piscidia, Tecoma, Rhus, Alvaradoa, Dodonaea,* and *Yucca*. In the Sierra de Surotato it was described as an understory tree in mixed pine-oak forest; 400–1500 m.

Vernacular names. *Barra blanca* (Sonora).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** SINALOA: in the Quebrada de Mansana, Sierra Surotato, 25°59′N, 107°38′W, *H. S. Gentry 6481* (CAS, GH, NY).—SONORA: between Sahuaripa and Tónichi, 150 km E of Hermosillo, 28°52′N, 109°30′W, *R. Hernández 2389* (CAS, MEXU, UC); rd E from Hermosillo to Sahuaripa, 10 km ESE of El Novillo in mtns between El Novillo dam and Bacanora, 28°56′N, 109°36′W, *Hughes 1523* (FHO, K, MEXU, MO, NY), *Hughes 1572* (CU, FCME, FHO, K, MEXU, MO, NY).

My attention was first drawn to *L. involucrata* by the field notes on *Hernández 2389,* which describe the flowers as yellow, a flower color known elsewhere in *Leucaena* only in *L. greggii* and *L. retusa*, two other northerly species. Given that *Hernández 2389* was clearly not *L. greggii* nor *L. retusa* and was collected from northern Sonora, I suspected that this material belonged to an as yet unnamed taxon with affinities to these two species. Field exploration in 1991 and 1992 allowed complete material to be collected for the first time and revealed that the staminal filaments and anthers are cream-white not yellow (the anthers fade dull yellow-orange). Although several other characters, including the narrow coriaceous pods, strongly oblique seed alignment, and cylindrical extrafloral nectaries suggested affinities with *L. greggii* and *L. retusa*, the Sonoran trees also show affinities with the *L. esculenta* alliance and *L. pallida* and *L. matudae* in terms of bark, leaf, and inflorescence characters. Thus the true affinities of *L. involucrata*, as yet, remain uncertain. Zárate (1994) named *L. involucrata* in reference to what he described as a large involucre of basally united bracts at the distal end of the peduncle, without dentation and enveloping the whole bud in early development. I can see no basis for this, as the involucre is dentate and not unusually large. Despite this, *L. involucrata* does represent a species distinct from *L. pallida* and is recognized by its unusual narrow pods, cream-white staminal filaments, and small peg-shaped nectaries. In the cladistic analysis of morphology, *L. involucrata* is placed as the sister taxon to *L. matudae* within the "*L. esculenta* clade" along with *L. esculenta, L. pueblana,* and *L. pallida.* The position of *L. involucrata* (designated as *L. sp nov 2*) in the cpDNA analysis was equivocal and unstable (Harris et al. 1994a); it was placed at the base of the *L. esculenta* clade in 50% of bootstrap replicate trees but in the minimal tree as the sister taxon to *L. cuspidata* at the base of the tree along with *L. greggii* and *L. retusa*. More characters will be needed to assess better the relationships of *L. involucrata.*

Leucaena involucrata remains one of the least understood species in the genus with only five known collections, four of which are from the same locality in northern Sonora. Further field exploration will be needed to establish the true extent of the natural distribution. The *Gentry 6481* collection from the Sierra Surotato is here attributed to *L. involucrata*, based solely on leaf characters, given the lack of flowers and immaturity of the fruits on that collection. This material differs from the Sonoran collections in being more pubescent. Complete exploration of the mountains between the northern outliers of *L. pallida* in the States of Jalisco and Zacatecas and the occurrence of *L. involucrata* in Sonora will be needed to delimit these species properly.

14. Leucaena matudae (S. Zárate) C. E. Hughes, Contr. Univ. Michigan Herb. 21: 286. 1997. *Leucaena esculenta* subsp. *matudae* S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65(2): 134. 1994.—TYPE: MEXICO. Guerrero: Casa Verde, nr Venta Viejo in the Cañón de Zopilote, "*guaje chismoso*," 17°50′N, 99°34′W, 12 Dec 1978, *Halbinger 288* (holotype: MEXU!; isotypes: ENCB, MO! NY!).

Small tree, (5–) 8–10 m tall, 20–30 cm bole diameter, typically multiple-stemmed and very branchy when young, older trees with a short clear bole to 2–3 m, upright angular branching, and a narrow open crown. Bark pale whitish metallic grey, gnarled, thick corky, shedding in thick circular plates to leave a very distinctive scalloped surface, inner bark green then deep blood-red, corky (Fig. 2D). Leafy shoots terete, smooth or slightly striate, glabrous, rich mid-reddish brown, strongly geniculate. Stipules 4.2–6 mm long, lanceolate, with a long-pointed tip and a prominent midrib, with asymmetric wings at base, persistent. Leaves 18–26 cm long, 12–19 cm wide; petioles (including pulvinus) (11–) 14–22 (–31) mm long, with a maroon-tinged, short-stipitate, peg-shaped, cylindrical nectary, 1.5 × 1 mm, at the distal end on adaxial side of petiole (Fig. 9D); rachis 12–23 cm long, with 3 small asymmetric concave elliptic nectaries at the distal end below terminal pairs of pinnae, apex of rachis extending beyond the terminal pinnae as a pointed glabrous or sparsely puberulent mucro 3–3.5 (–4) mm long, curling when dry; pinnae (15–) 16–18 (–21) pairs; pinnular rachis 8.5–13 cm long, canaliculate, sparsely puberulent on adaxial side, with 5–7 round nectaries, 0.2 × 0.2 mm, at base of terminal pairs of leaflets; leaflets (39–) 60–75 (–84) pairs per pinna, (4.7–) 5.5–6.3 (–6.8) mm long, 1–1.3 (–1.4) mm wide, nearly sessile, asymmetric, linear, acute at apex, asymmetrically truncate at base, glabrous, margins ciliate, only asymmetric midrib visible. Capitula 18–22 mm in diameter at anthesis, in fascicles of 1–3 in leaf axils arising on actively growing shoots with synchronous leaf development, each capitulum with 90–120 flowers; peduncles 29–38 mm long, angled, glabrous, reddish brown with an involucre of bracts at the distal end. Flowers subtended by peltate bracts, 2.1–2.3 mm long, 0.7 mm in diameter, the stalk thickened; calyx 2.7–2.9 mm long, pale yellow or creamy green; petals 3.9–4.3 mm long, free, glabrous, pale green; filaments 5.9–9.4 mm long, arranged approximately in two distinct ranks, cream; anthers sparsely hairy at apex, pale creamy yellow, apiculum absent; ovary 1.4–1.5 mm long, glabrous, white, with 16–20 ovules, style 8–9.6 mm long, white, with a terminal tubular stigma, exserted slightly beyond the anthers. Pods 1–2 per capitulum, 14.8–19 cm long, 12–15 (–17) mm wide, pendulous on sturdy 4–5 mm long stipes, linear to linear-oblong, weakly constricted between seeds, acute or sometimes obtuse apically, sometimes with a short beak, apparently readily broken off when dry, narrowly planocompressed, 8–17-seeded, valves dark maroon or maroon-brown, glabrous, with reticulate venation most pronounced close to margins, coriaceous, the margins thickened, the seed chambers prominent on exocarp and weakly partitioned between the seeds, tardily dehiscent along both sutures. Seeds 7.8–9.4 mm long, 6.1–9 mm wide, compressed, circular or rhombic and angular, deep chestnut-brown, glossy, aligned obliquely in pods; pleurogram visible, U-shaped, symmetrical, 50–70% arm extension. Chromosome number: 2n = ?52 (Sorensson 1989). Fig. 57.

Phenology. Flowering July–August (–October); fruiting (November–) December–February (–March); strongly deciduous during the long dry season (November–April).

Distribution (Fig. 52). *Leucaena matudae* is endemic to a restricted part of the Río Balsas Depression in Guerrero, Mexico, in the area around Mezcala, the Cañón de Zopilote, and Xochipala. All the known collections are from a very restricted area, but it is likely that it also occurs further east along the Río Balsas (J. L. Contreras, pers. comm.). *Leucaena matudae* occurs as a canopy tree in the dry deciduous tropical forest and dry thorn scrub forest, usually on freely drained dry rocky calcareous slopes. Associated trees include *Acacia acatlensis, A. velvae, Bauhinia andrieuxii, Caesalpinia hintonii, Conzattia multiflora, Desmanthus balsensis, Lysiloma tergemina, Microlobius foetidus*, and species of *Mimosa, Bursera, Bourreria,* and many Cactaceae; 500–860 m.

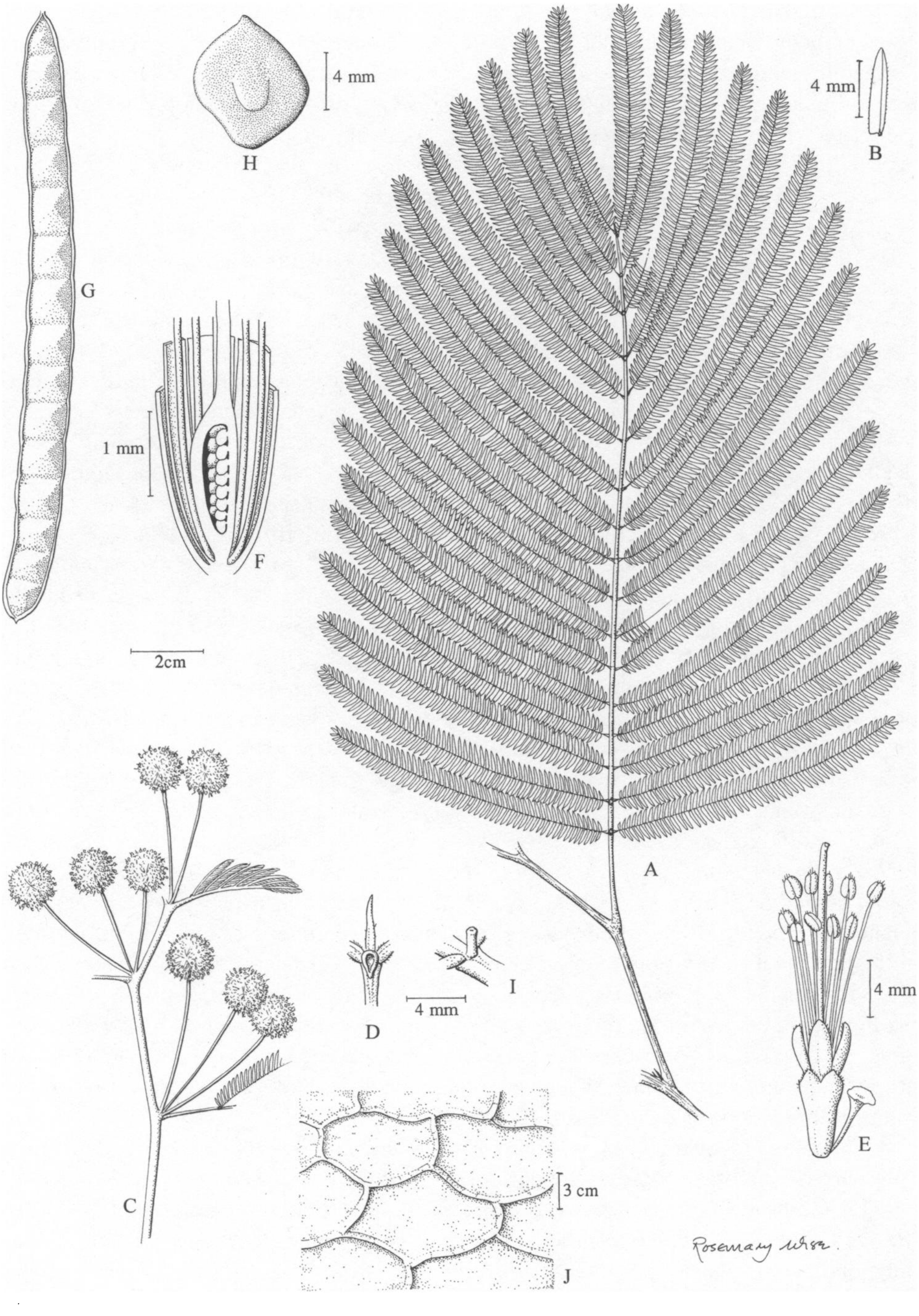


FIG. 57. *Leucaena matudae*. A. Leaf. B. Leaflet. C. Flowering shoot. D. Rachis nectary and mucro. E. Flower. F. Longitudinal section of flower. G. Pod. H. Seed. I. Petiolar nectary. J. Scalloped bark surface pattern (drawn from photograph). (Based on: A, B, *Hughes 1821*; C–F, *Hughes 1511*; G, H, *Hughes 883*; I, fixed material of progeny derived from *Hughes 879*.)

Vernacular names. *Guaje, guaje brujo, guaje chismoso, guaje jilguero, guaje retinto, guaje risueño* (Cañón de Zopilote, Guerrero); *tlapaloaxin* (*guaje escarlata, mexicano*) (information largely from Zárate, 1994).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** GUERRERO: rd above Cañón de Zopilote, 8 km E of Xochipala towards Fila de Caballo from Milpillas, 17°47'N, 99°41'W, *Breedlove 35999* (CAS, MEXU, MO, NY); Zumpango del Río, 500 m N of Venta Vieja, Km 64 rd Iguala to Chilpancingo, 17°48'N, 99°34'W, *Contreras 632* (MEXU); track 6 km SSW from Mezcala towards Carizalillo and Amatitlán, dry valley of the Río Xochipala, 17°51'N, 99°40'W, *Hughes 1511* (FHO, K, MEXU, MO, NY), *Hughes 1821* (CAS, FHO, K, MEXU, MO, NY, TEX); 4 km SW of Mezcala, track to Carrizalillo, valley of the Río Xochipala, 17°56'N, 99°36'W, *Hughes 879* (FHO, K, MEXU), *Hughes 883* (FHO, K, MEXU), *Rzedowski 22604* (CAS, MEXU, TEX); area of Chilpancingo, *E. Matuda s.n.* (MEXU); 12 km S of Mezcala, 17°50'N, 99°35'W, *Rico 425* (MEXU); side rd to Fila de Caballo, 2 km off main Acapulco to Mexico City rd, 17°47'N, 99°35'W, *Zárate 505* (MEX, MEXU, TEX).

Leucaena matudae was originally described as a subspecies of *L. esculenta* (Zárate 1994), but was raised to species rank by Hughes (1997c) in recognition of its clear morphological and molecular distinction from *L. esculenta.* Although the analysis of morphology and cpDNA support the placement of *L. matudae* in the *L. esculenta* clade, *L. matudae* is distinguished by a number of discrete character states. Most notably, the petiolar nectary of *L. matudae* is stipitate, erect, cylindrical, and quite unlike the large, sessile, elongate, concave, crateriform nectary of *L. esculenta.* In addition, *L. matudae* may be distinguished by its terete shoots, fewer pinnae pairs and leaflets per pinna, fewer flowers per capitulum, smaller, weakly constricted pods, which are partitioned between the seeds, and oblique alignment of seeds in the pods. Although *L. matudae* shares the same bark type as the remaining species in the *L. esculenta* clade (thick corky bark with a single periderm, a pale metallic grey surface, and deep blood-red inner bark) (Fig. 2D), the bark surface pattern in *L. matudae* is quite distinct and unique within the genus in having a scalloped surface resulting from shedding of small circular plates. Zárate (1994) mentioned use of the bark for medicinal purposes and attributed the unusual surface pattern to local harvesting of bark for that use, but given that there is no evidence of harvesting in most areas, that the patterns are extremely regular, and that they are found on inaccessible branches as well as boles, it seems clear that this is the natural state. In fact *L. matudae* shares most character states not with *L. esculenta* but with *L. involucrata* and *L. pueblana*, but is still readily distinguished by its distinctive bark and unusual slightly constricted pods; however, there is little doubt that *L. involucrata, L. matudae,* and *L. pueblana* are closely related.

In addition to these morphological distinctions, *L. matudae* occupies a distinct and highly restricted range. It is endemic to the dry canyon area of the central Balsas Depression, in an area of known high endemism with a number of other woody legume species with similar restricted distributions, such as *Desmanthus balsensis* and *Acacia velvae*.

15. Leucaena lanceolata S. Watson, Proc. Amer. Acad. Arts 21: 427. 1886.—TYPE: MEXICO. Chihuahua: Batopilas, Hacienda San Miguel, SW Chihuahua, 27°53'N, 108°26'W, Sep 1885, *Palmer 6* (holotype: GH!; isotypes: NY! UC! US!).

Small to medium-sized tree, 5–15 (–20) m tall, 20–50 cm bole diameter, typically branchy when young, older trees with a short clear bole to 5 m, upright angular branching, and a narrow open crown. Bark on young branches smooth, mid-grey or grey-brown, on bole darker grey-brown and rougher with shallow rusty orange-brown vertical fissures, often exuding gum, inner bark pale cream or pale salmon pink. Leafy shoots terete, pale to mid-brown, glabrous or densely pubescent. Stipules 4–4.3 mm long, lanceolate, striate, with asymmetric wings at base, venation and midrib prominent, early deciduous. Leaves (10–) 15–25 (–35) cm long, 9–23 cm wide; petioles (including pulvinus) 15–28 mm long, with a yellow-green or green, sessile, rounded, elliptic, dome-shaped or truncate-conic, convex nectary, 2.5–3.5 × 1.5–2 mm, at the distal end on adaxial side of petiole; rachis 5–16 cm long, extending beyond the terminal pinnae as a pointed mucro 2–2.4 mm long, curling when dry; pinnae 2–5 pairs; pinnular rachis 4.5–9 cm long, angled, puberulent or glabrous, with 2 sessile elliptic conical nectaries, 1–2 × 0.7–1 mm, at base of terminal pairs of leaflets; leaflets 3–6 pairs per pinna, 16–70 mm long, 8–35 mm wide, short-petiolate, slightly asymmetrical, broadly elliptic or elliptic-ovate, apex obtuse or acute (occasionally rounded), abruptly apiculate, base obtuse, variably glabrous to densely puberulent, primary and secondary venation visible on dried leaflets, secondary venation brochidodromous. Capitula (15–) 20–40 mm in diameter at anthesis, in fascicles of 1–2 (–3) in leaf axils on unbranched terminal anauxotelic shoots on which leaf development is variably suppressed (Fig. 12B), each capitulum with (250–) 300–450 flowers; peduncles 8–15 mm long, angled, glabrous or pubescent with an involucre of basally united bracts at the distal end. Flowers sweetly scented, often reported as smelling of papaya, melon, or plantain, subtended by peltate bracts, 3.9–4.1 mm long; calyx 3.7–4.1 mm long, glabrous, pale whitish green; petals 4.8–5.3 mm long, free, glabrous, pale whitish green; filaments 7.1–9.9 mm long in two distinct ranks, white or cream-white; anthers hairy, cream-white, apiculum absent; ovary 2.4–2.6 mm long, glabrous, cream, with 18–20 ovules, style 7–8.4 mm long, cream-white, with a narrow tubular stigma, included. Pods 1–6 per capitulum, 10–30 (–37) cm long, 13–32 mm wide, pendulous on slender 15–30 mm long stipes, oblong to linear-oblong, acute, obtuse or rounded apically, sometimes with a short beak, apparently readily broken off when dry, narrowly planocompressed, 13–18-seeded, valves pale to dark orange-brown, glabrous or with dense velutinous pubescence, membranous or chartaceous, the margins slightly raised, passively dehiscent along both sutures (Fig. 17A), borne on shoot tips (Fig. 10D). Seeds 6.3–11.1 mm long, 3.8–8.7 mm wide, compressed, circular to ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, symmetrical, with 90% arm extension. Chromosome number: 2n = 52 (González et al. 1967; Pan & Brewbaker 1988; Sorensson 1989). Fig. 58.

Leucaena lanceolata is an extremely variable species across its extensive and largely continuous distribution along the Pacific coast of Mexico from Sonora to Chiapas, with outlying occurrences in Baja California and Veracruz (Fig. 59). This great morphological variation in quantitative leaf and pod traits and leaf and pod pubescence has been treated by different authors in different ways. Britton and Rose (1928), who saw only limited material mainly from the northern and less variable portion of the distribution in Sonora and Sinaloa along with material from Veracruz, recognized nine segregate species based on leaflet size, shape, and vestiture, and pod size, shape, and vestiture. In contrast, McVaugh (1987: 185) described *L. lanceolata* as a single wide-ranging species, "not convincingly divisible on the basis of pubescence, nor the width of the legume." Later Zárate (1994) treated all the Britton and Rose segregate species as conspecific, in agreement with

McVaugh (1987), but he also described a new subspecies *sousae* to account for the variation encountered further south in Michoacán and Oaxaca.

A detailed study of morphological variation within *L. lanceolata* was undertaken here to investigate the basis for subdivision of *L. lanceolata* and see whether variation is truly clinal without discontinuities and whether variation in different traits is congruent. This study shows that there are no clear discontinuities in quantitative leaf or pod traits across the range of *L. lanceolata* that might be used to divide the species unambiguously. This study does not support recognition of any of the nine segregate species described by Britton and Rose (1928), and these are treated as conspecific with *L. lanceolata*. Despite this, there is some evidence to support the recognition of subspecies *sousae*. Variation in leaflet and pod traits shows some correlation with geography and with leaflet and pod vestiture, and two broad groups can be distinguished as recognized by Zárate (1994). Furthermore, Harris et al. (1994a) found two cpDNA plastome types among accessions of *L. lanceolata*. Additional analysis shows that cpDNA variation within *L. lanceolata* is not restricted to two plastome types, but that the two accessions of subsp. *sousae* did group together. Pending further detailed analysis, subsp. *sousae* was tentatively recognized by Hughes (1997c) but at the varietal rank.

Discontinuities in quantitative leaf and pod traits between var. *lanceolata* and var. *sousae* are clear-cut except in three specific areas. Pods, which are generally pubescent in var. *lanceolata* and glabrous in var. *sousae*, are exceptional in several areas. In Baja California, pods are glabrous on what is clearly var. *lanceolata* (e.g., *Hughes 1544*). In the transition area between var. *sousae* and var. *lanceolata* in a well-defined zone around Bahias de Santa Cruz in south-central Oaxaca (e.g., *Hughes 587, 835, 836, 841*), pods are pubescent on specimens that otherwise are referable to var. *sousae*. At slightly higher elevation and drier sites in southern Oaxaca (e.g., *Hughes 556, 1345, 1724*) pods are glabrous, with an unusual glossy or "basted" surface. This same Oaxacan material from the Municipios of San Bartolo Yautepec, Jalapa de Márquez, and Santiago Lachiguiri, also has pods wider than typical for var. *lanceolata* and that are slightly falcate (Fig. 58P). In the coastal zone 20–40 km west of Playa Azul in Michoacán, it is difficult to separate the two varieties, which appear to grow together there.

These difficulties were recognized by Zárate (1994) in his discussion of var. *sousae* (as subsp. *sousae*) when he stated that although readily distinguished at the type locality, in other areas it may be more difficult to define. Zárate (1994) attributed this to his hypothesis that var. *sousae* is of hybrid origin between *L. macrophylla* (*L. macrophylla* subsp. *nelsonii* sensu Zárate) and *L. lanceolata* var. *lanceolata*, although he did not provide evidence to support this hypothesis. I prefer to view *L. lanceolata* simply as a widespread and variable species and tentatively to recognize var. *sousae*, despite the blurring of discontinuities between the two varieties in a few specific areas.

Because of the broad similarity between *L. macrophylla* and *L. lanceolata* in leaf and pod traits, these two species are sometimes confused and considered to be closely related. In practice, *L. lanceolata* can be readily distinguished from *L. macrophylla* by its much larger flower heads. In addition, *L. lanceolata* is separated from the remaining species with equally large leaflets (*L. macrophylla, L. multicapitula,* and *L. trichodes*) by its pollen, which occurs as tricolporate eumonads, compared to the polyads of the other species. The true affinities of *L. lanceolata* are uncertain but apparently lie with the *L. shannonii* alliance and *L. collinsii*.

KEY TO THE VARIETIES OF LEUCAENA LANCEOLATA

1. Pods usually with dense velutinous pubescence, occasionally glabrous in a few areas, generally <18 cm long and <22 mm wide, leaflets generally <20 mm wide; widely distributed. 15a. *L. lanceolata* var. *lanceolata.*
1. Pods usually glabrous, usually lustrous or glossy, occasionally pubescent in a few areas, generally >20 cm long and >20 mm wide, leaflets generally >20 mm wide; restricted to Michoacán, Guerrero, and Oaxaca. 15b. *L. lanceolata* var. *sousae.*

15a. Leucaena lanceolata var. lanceolata.

Leucaena microcarpa Rose, Contr. U.S. Natl. Herb. 5: 141. 1897.—TYPE: MEXICO. Baja California Sur: nr Miraflores, 23°21′N, 109°47′W, 13 Oct 1890, *Brandegee 186* (holotype: US!; isotype: UC!).

Leucaena brandegeei Britton & Rose, N. Amer. Fl. 23: 128. 1928.—TYPE: MEXICO. Baja California Sur: nr La Mesa, Cape region, 31 Oct 1902, *T. S. Brandegee s.n.* (holotype, NY!; isotypes: US! UC!).

Leucaena cruziana Britton & Rose, N. Amer. Fl. 23: 123. 1928.—TYPE: MEXICO. Veracruz: Barranca de Panoaya, 19°18′N, 96°25′W, Dec 1919, *Purpus 8387* (holotype: NY!; isotypes: US! UC! GH!).

Leucaena palmeri Britton & Rose, N. Amer. Fl. 23: 123. 1928.—TYPE: MEXICO. Sonora: nr Alamos, 26°59′N, 108°57′W, 20 Sep 1890, *Palmer 718* (holotype: NY!; isotype: US!).

Leucaena pubescens Britton & Rose, N. Amer. Fl. 23: 122. 1928.—TYPE: MEXICO. Sinaloa: nr Mazatlán, 23°14′N, 106°24′W, 1925, *J. G. Ortega 5988* (holotype: NY!; isotypes: US! GH!).

Leucaena purpusii Britton & Rose, N. Amer. Fl. 23: 123. 1928.—TYPE: MEXICO. Veracruz: rim of barranca nr Remudadero, 19°15′N, 96°34′W, Jan 1926, *Purpus 10607* (holotype: NY!; isotype: US!).

Leucaena sinaloensis Britton & Rose, N. Amer. Fl. 23: 124. 1928.—TYPE: MEXICO. Sinaloa: vicinity of Palmar, 22°13′N, 105°36′W, 15 Apr 1910, *Rose et al. 14650* (holotype: NY!; isotype: US!).

Leucaena sonorensis Britton & Rose, N. Amer. Fl. 23: 122. 1928.—TYPE: MEXICO. Sonora: Sierra de Alamos, nr Alamos, 26°58′N, 108°57′W, 14 Mar 1910, *Rose et al. 12821* (holotype: NY!; isotype: US!).

Leucaena nitens M. E. Jones, Contrib. West. Bot. 15: 136. 1929.—TYPE: MEXICO. Sinaloa: nr Mazatlán, 23°14′N, 106°24′W, 20 Nov 1926, *Jones 22465* (holotype: POM; isotypes: MO! US!).

Leaf rachis (5–) 8–16 cm long, with (2–) 3–5 pairs of pinnae and (3–) 4–6 pairs of leaflets per pinna; leaflets (16–) 22–36 (–45) mm long, 8–20 (–27) mm wide, frequently densely puberulent, sometimes glabrous in southern part of range. Pods 10–18 (–22) cm long, 13–22 (–24) mm wide, generally covered in dense orange-brown velutinous pubescence, occasionally glabrous. Fig. 58A–L.

Phenology. Flowering (August–) September–October (–December); fruiting (November–) December–March; deciduous during the dry season from December to April.

Distribution (Fig. 59). *Leucaena lanceolata* var. *lanceolata* is distributed from Sonora and Chihuahua southeast along the Pacific coast of Mexico through Sinaloa, Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca, and into the extreme western corner of Chiapas, with outlying occurrences near the southern tip of Baja California and in central

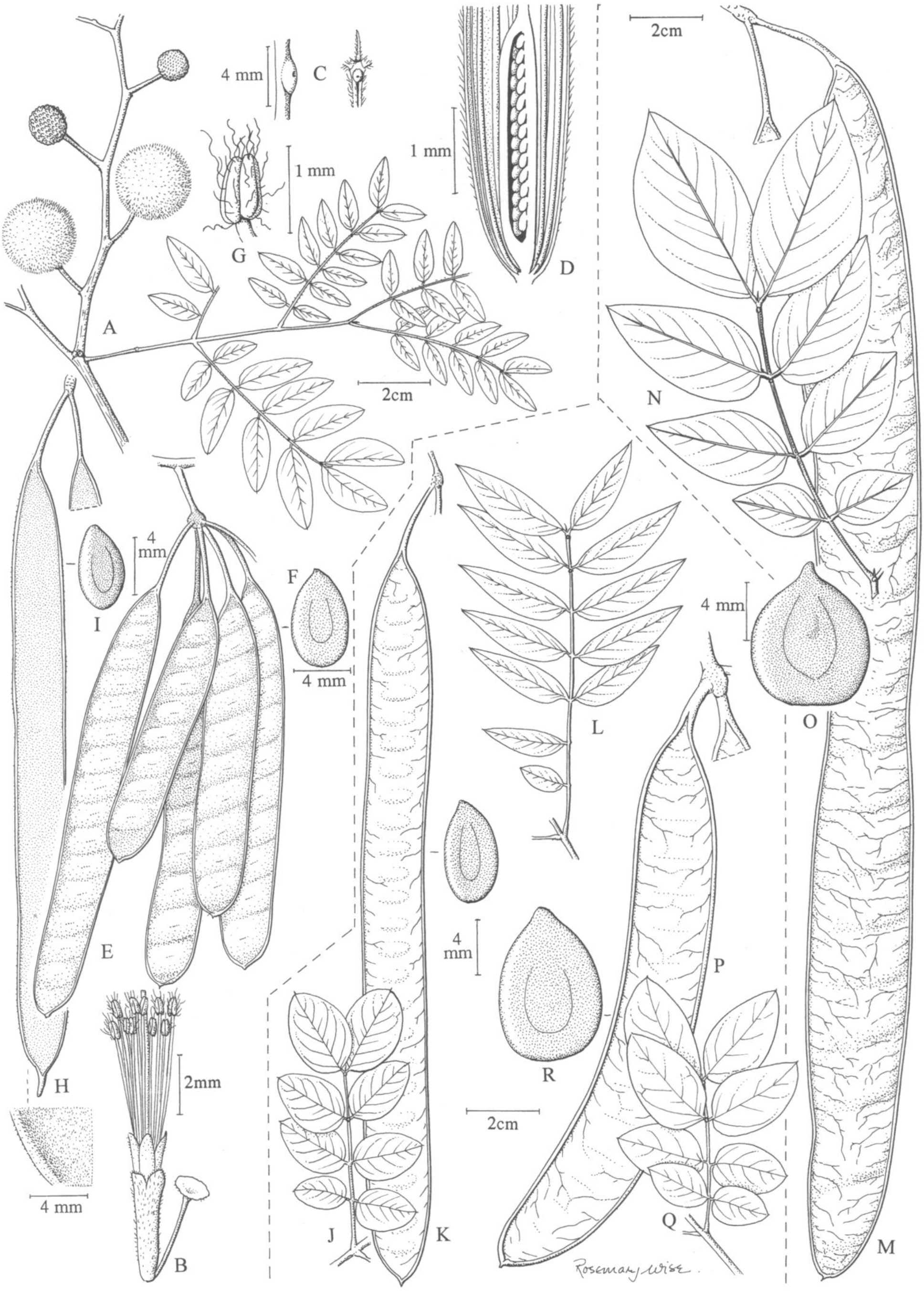


FIG. 58. *Leucaena lanceolata*. A–L, var. *lanceolata*: A. Leaf and flowering shoot. B. Flower. C. Petiolar and rachis nectaries. D. Longitudinal section of flower. E. Pods. F. Seed. G. Anther. H. Pod and enlargement showing pod indumentum. I. Seed. J. Pinna. K. Pod. L. Pinna. M–R, var. *sousae*: M. Pod. N. Pinna. O. Seed. P. Pod. Q. Pinna. R. Seed. (Based on: A–F, *Hughes 568*; G, J, *Hughes 1767*; H, I, *Hughes 604*; L, *Hughes 1345*; M–O, *Hughes 857*; P–R, *Hughes 637*.)

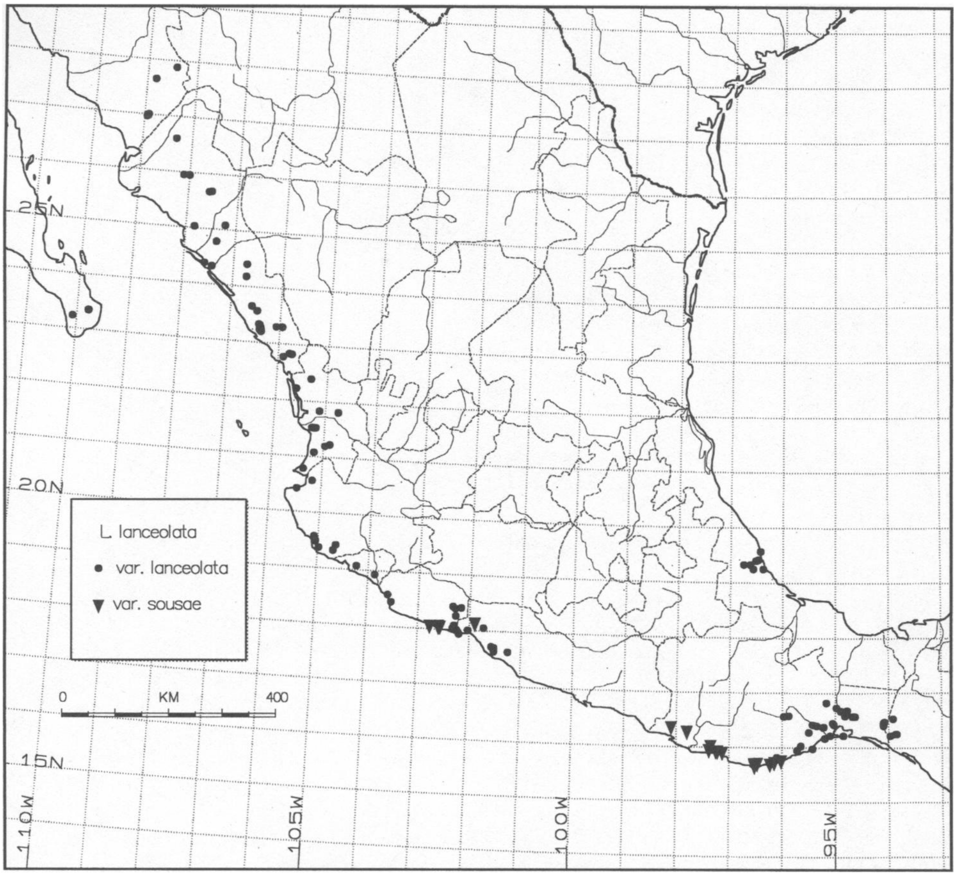


FIG. 59. Distribution of *L. lanceolata*.

Veracruz. It occurs primarily in the seasonally dry deciduous tropical forest, which forms a more or less continuous belt along the Pacific coast of Mexico. It also occurs in secondary dry forest, dry thorn scrub forest, and in some areas as a dominant element in secondary regrowth after cultivation of milpas. It evidently thrives on disturbance and can be very abundant and weedy along roadsides (e.g., in parts of the Isthmus of Tehuantepec around Juchitán, Oaxaca), or in coastal vegetation and on dunes (e.g., around Huazantlán del Río, east of Salina Cruz, Oaxaca). Associated trees include species of a wide range of legume genera (*Acacia, Albizia, Caesalpinia, Gliricidia, Lonchocarpus, Lysiloma, Piptadenia, Pithecellobium, Poeppigia, Pterocarpus,* and *Senna*). Other common trees are species of *Bursera, Calicophyllum, Capparis, Cordia, Coccoloba, Cochlospermum, Crataeva, Guazuma,* and *Thouinidium*; 0–700 (–1100) m, but mainly below 400 m.

Vernacular names. *Balillo* (Sonora), *guaje (palo de guaje, palo de huaje)* (all areas), *guaje blanco, guaje indio* (Veracruz), *guaje de monte, guaje de zopilote* (Oaxaca), *guajillo* (Sinaloa, Guerrero, Michoacán, Oaxaca), *palo blanco* (Oaxaca), *flor de canela* (Chiapas), *ejote, da-yuh* (Chatino, Oaxaca), *naj-py-team, yaga-la-sha-xi* (Oaxaca).

Representative Specimens. **U.S.A.** California: cult. Shasta City, *M. E. Jones s.n.* (UC).

Mexico. Baja California Sur: 6 km WSW of Miraflores, 70 km N of San José del Cabo, off rd to La Paz, 23°21′N, 109°46′W, *T. S. Brandegee s.n.* (UC), *Hughes 1544* (CU, FCME, FHO, K, MEXU, MO, NY).—Chiapas: 10 km W of Arriaga, main rd to Tepanatepec, 16°13′N, 93°58′W, *Hughes 523* (FHO, K, MEXU); nr the Río Cintalapa close to the Chiapas/Oaxaca border, 16°27′N, 94°06′W, *Sousa 2695* (CAS, GH, MEXU, UC); Humoa, 14 km NE of San Pedro Tepanatepec, rd to Tuxtla Gutiérrez, 16°24′N, 94°06′W, *Sousa 11303* (MEXU).—Colima: 48 km W of Colima, 18°56′N, 103°52′W, *H. S. Gentry 18331* (US); 8 km E of Manzanillo, Hwy 200, 19°04′N, 104°14′W, *Hill 1835* (MEXU, NY).—Guerrero: Microondas Las Rocas, Petatlán, *Diego 6537* (K); José Azueta, 17°42′N, 101°31′W, *Gallard 255* (K); hill opposite Hotel Sotovento, Zihuatanejo, 17°38′N, 101°31′W, *Germán 251* (MEXU, MO, NY); torrent de Chula, 20 May 1898, *Langlassé 185* (GH, K, US); nr Chavita, *Langlassé 513* (GH, US); rd to Camolote and Ejido Río Frio, 10 km N of Petatlán, 17°38′N, 101°15′W, *Macqueen 165* (EAP, FHO, K, MEXU); 15 km S of Zacatula, 18°00′N, 102°02′W, *Soto 151* (MEXU); 9 km N of La Unión, rd to Coahuayutla, 18°03′N, 101°44′W, *Soto 6001* (CAS, MEXU, MO).—Jalisco: 3 km SE of Puerto Vallarta along the Canyon of the Río Cuale, 20°34′N, 105°11′W, *Feddema 2527* (CAS, NY); 28 km N of Barra de Navidad, 19°26′N, 104°39′W, *C. D. Johnson 19-73* (MO); La Huerta, 1 km N of Est. de Biología de Chamela, rd Chamela to Melaque, 19°30′N, 105°03′W, *Lott 576* (NY, TEX); Cabo Corrientes, 15 km W of El Tuito nr Chacala, 20°25′N, 105°28′W, *Magallanes 1521* (MEXU).—Michoacán: campus of the Siderujica "Las Truchas" nr Ciudad Lázaro Cárdenas, 17°56′N, 102°12′W, *Granados 22* (MEXU); 30 km W of Playa Azul, rd. to Manzanillo, 18°04′N, 102°34′W, *Hughes 633* (FHO, MEXU); 5 km WNW of Arteaga, rd to Tumbiscatio del Ruíz, 18°25′N, 102°20′W, *Hughes 1172* (FHO, K, MEXU); El Mirador, 3 km W of turnoff to Aquila, rd from Tecomán to Playa Azul, 18°35′N, 103°36′W, *E. Martínez 4504* (MEXU, MO); 22 km NE of Arteaga, 18°24′N, 102°10′W, *Soto 132* (MEXU).—Nayarit: nr the jctn of Río Grande de Santiago and Hwy 15, 21°50′N, 105°07′W, *A. Gentry 19645* (US); 30 km S of Las Varas, rd to Puerto Vallarta, 21°05′N, 105°11′W, *Hughes 615* (FHO, K, MEXU); 70 km SW of Compostela, 21°14′N, 104°53′W, *C. D. Johnson 274-73* (EAP, MO); 12 km S of Acaponeta, 22°24′N, 105°19′W, *C. D. Johnson 480-73* (MEXU, MO); nr San Blas, 21°32′N, 105°15′W, *Rudd 3026* (GH, MEXU, MO, US); Km 20–40, dirt rd to Presa de Aguamilpa, 21°49′N, 104°45′W, *Téllez 11187* (MEXU, MO).—Oaxaca: rd between San Pedro Tepanatepec and Cinco Cerros, 16°25′N, 94°06′W, *Brenan 14473* (MEXU); Santiago Astata, rd to Estero or Banco de Sal nr Tehuantepec, 15°59′N, 95°40′W, *Calzada 8488* (F); Km 30 rd to La Venta Santo Domingo Niltepec, rd to Shortwave Stn, nr Juchitán, 16°35′N, 94°49′W, *Cedillo 508* (CAS, MEXU, NY); 50 km E of Juchitán, rd to Tepanatepec, 16°34′N, 94°41′W, *Hughes 540* (FHO, MEXU); 15–20 km E of Salina Cruz, rd to San Mateo del Mar, 16°13′N, 95°06′W, *Hughes 546* (FHO, K, MEXU); 2 km E of El Coyul, rd Tehuantepec to Oaxaca, 15°49′N, 96°06′W, *Hughes 556* (FHO, K, MEXU); between Rincón Bamba and San Jon, 30 km W of Salina Cruz, rd to Pochutla, 16°02′N, 95°39′W, *Hughes 559* (FHO, K, MEXU); 3 km E of Puente Huamelula, 12 km E of S. Astata, rd Salina Cruz to Pochutla, 15°53′N, 95°41′W, *Hughes 831* (FHO, K, MEXU); rd 2 km WNW from Ixtepec through Chihuitán to Santiago Laollago, 16°35′N, 95°11′W, *Hughes 1299* (BR, FHO, K, MEXU, NY); rd N from Presa Benito Juárez and Santa María Jalapa de Marques, 3 km S of Santiago Lachiguiri, 55 km NW of Tehuantepec, 16°40′N, 95°32′W, *Hughes 1345* (FHO, K, MEXU, NY); rd 12 km S Matías Romero across isthmus to La Ventosa and Juchitán, 16°46′N, 95°03′W, *Hughes 1672* (E, FHO, K, MEXU, MO, NY); Ixtaltepec, rd from Mazahua, which lies 8 km NE of La Ventosa, to Mezquite, 6 km along Hwy 185, 16°22′N, 94°57′W, *Martines 2088* (MEXU); 2 km W of Santo Domingo Petapa above El Barrio, 16°49′N, 95°10′W, *McCarter & Hughes 108* (FHO, MEXU); 6 km E of El Camarón, rd from Oaxaca to Tehuantepec, distr. of Juquila, 16°34′N, 95°58′W, *Sousa 6566* (MEXU); 3 km NE of Juchitán, 16°27′N, 95°03′W, *Sousa 6595* (MEXU); 9 km ENE of La Ventosa, Juchitán, 16°35′N, 95°53′W, *Sousa 7358* (MEXU); Salina Cruz, N side of port, 16°10′N, 95°12′W, *Sousa 8630* (CAS, MEXU, UC); nr Playa de Chipehua, Tehuantepec, 15°58′N, 95°34′W, *Sousa 8662* (MEXU, MO, UC); San Miguel Chimalapa, nr Las Anonas Chimalapa, 4 km SW of San Miguel Chimalapa, Juchitán, 16°41′N, 94°47′W, *Sousa 8693* (MEXU, MO, UC); 1 km NW of Río Hondo, Yautepec, 16°25′N, 95°51′W, *Sousa 9472* (MEXU, TEX); 14 km ENE of Totolapan, Tlacolula, 16°40′N, 96°13′W, *Sousa 10072* (CAS, MEXU, MO); 5 km SE of Lachiviria Guienagati, 12 km SE of Santa María Guienagati, 16°38′N, 95°18′W, *Sousa 10186* (CAS, MEXU, MO); 7 km S of Chiviza, nr Santiago Laollaga, 16°40′N, 95°18′W, *Tenorio 11117* (MEXU); nr Ruinas of Cerro Guiengola, Tehuantepec, 16°22′N, 95°20′W, *M. L. Torres 581* (MEXU); 17 km NW of La Reforma, rd to Tehuantepec, 16°26′N, 95°52′W, *R. Torres 3419* (MEXU, TEX); 10 km SW of Coyol, rd from Salina Cruz to Pochutla, 15°54′N, 95°51′W, *R. Torres 5214* (MEXU); Barrio, nr shortwave tower at Palma Sola, 11.4 km W of Almaloya, Juchitán, 16°46′N, 95°07′W, *R. Torres 6172* (MEXU); Km 165 on Oaxaca-Tehuantepec rd NW of Puerto San Bartolo, 16°27′N, 95°53′W, *R. Torres 7874* (MEXU, MO); 1.6 km N of Lachivizia, rd to Guevea de Humboldt nr Santa María Guienagati, 16°42′N, 95°22′W, *R. Torres 8820* (MEXU); 5.3 km SW of Buenos Aires, rd to San Miguel Tenango, by Hierba Santa, 16°18′N, 95°28′W, *R. Torres 10493* (CAS, MEXU, MO); 16 km W of Morro Mazatán, rd to Pochutla from Salina Cruz, 16°02′N, 95°25′W, *R. Torres 10733* (MEXU); 8 km N of San Pedro Huilotepec, track to San Mateo del Mar, rd to Juchitán, 16°13′N, 95°11′W, *Zárate 667* (MEXU); nr San Mateo del Mar, 16°13′N, 94°51′W, *Zizumbo 62* (MEXU).—SINALOA: 30 km from Cosala, rd to Guadalupe de los Reyes, 24°11′N, 106°44′W, *Armenta 116* (MEXU); 3 km N of Concordia, rd to lagoon, 23°18′N, 106°04′W, *Beltrán 1033* (MEXU); nr Cofradía, *Brandegee 1904* (K); Cerro Tecomato W of Pericos, 25°02′N, 107°50′W, *H. S. Gentry 5756* (CAS, GH, MEXU, MO, NY); W foothills, Sierra Surotato, 25°41′N, 107°32′W, *H. S. Gentry 18384* (TEX, US); 16 km from entrance to Peninsula de Lucenilla, Culiacán, 24°20′N, 107°26′W, *F. Hernández 106* (MEXU); 1 km S of Escuinapa de Hidalgo, rd to Acaponeta, 22°46′N, 105°54′W, *Hughes 605* (FHO, MEXU); 10 km N of Mazatlán nr beach, 23°20′N, 106°25′W, *C. D. Johnson 217-73* (MO); Km 268, rd N of Mazatlán past Concordia towards El Salto and Durango, 23°18′N, 105°57′W, *Macqueen 220* (EAP, FHO, K, MEXU); nr Los Labrados, *Mexía 925* (CAS, F, MO, NY, UC); nr Coacoyolitos, *J. G. Ortega 5845* (GH, US); nr El Norote, *J. G. Ortega 5920* (US); nr Culiacán, 24°47′N, 107°22′W, *J. G. Ortega 6627* (CAS, GH, NY, US); El Quelite off rd 15, 55 km S of Elota, 23°34′N, 106°28′W, *Ozment 115* (MO); nr Guadelupe, 26°36′N, 108°19′W, *Rose 14782* (US); nr Bagrecitos, 27 km NE of Tepuche, Culiacán, 25°05′N, 107°13′W, *Tenorio 3030* (CAS, MEXU, MO, TEX); 9 km E of Agua Caliente nr Sinaloa de Leyva, 25°57′N, 108°00′W, *Tenorio 10288* (CAS, MEXU, MO, NY).—SONORA: Arroyo Guajaray, Río Mayo, Lower Sonora Desert, *H. S. Gentry 1138* (F); Canyon above Aduana, nr Alamos, 26°59′N, 108°56′W, *H. S. Gentry 4819* (CAS, GH, MEXU, MO, NY, UC); 7 km S of Alamos, nr rd to San Vicente 1 km past municipal dump, lower slopes of Sierra de Alamos, 26°59′N, 108°57′W, *Hughes 1577* (FCME, FHO, K, MEXU, MO, NY); 4 km E of Alamos, 27°00′N, 108°55′W, *C. D. Johnson 188-77* (MO).—VERACRUZ: Emiliano Zapáta, track to Los Baños de Carrizal, 19°19′N, 96°38′W, *Calzada 2201* (F, NY); 4 km after Jalcomulco, rd to Apazapan, 19°20′N, 96°45′W, *Castillo & Tapia 938* (F, MEXU); Cerro Sur of the Cerro de los Metates, *Dorantes 941* (F, MEXU); Dos Ríos, Cerro Gordo, rd Jalapa to Veracruz, 19°27′N, 96°41′W, *Dorantes 1644* (F, MEXU); 1 km E of La Bocana, rd Jalapa to Veracruz, Actopan, 19°21′N, 96°39′W, *Dorantes 1814* (F, MEXU); area around Laguna Verde, Alto Lucero, 19°43′N, 96°27′W, *Dorantes 5175* (F, MEXU); Apazapan, rd Baños de Carrizal to Emiliano Zapáta, 4 km SE of Emiliano Zapáta, 19°20′N, 96°38′W, *Hansen & Nee 7476* (F, MO); nr El Rinconada, rd 45 km SE of Xalapa to Veracruz, 19°25′N, 96°28′W, *Hughes 913* (FHO, K, MEXU); Puente Nacional, 6 km SW of Conejos jctn rd to Tututla, 19°17′N, 96°32′W, *Nee 23064* (F, MEXU, TEX); Paso de Ovejas, El Panteón, 19°15′N, 96°23′W, *Ventura 18007* (MEXU).

15b. Leucaena lanceolata var. **sousae** (S. Zárate) C. E. Hughes, Contr. Univ. Michigan Herb. 21: 288. 1997. *Leucaena lanceolata* subsp. *sousae* S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65(2): 117. 1994.—TYPE: MEXICO. Oaxaca: 17 km WNW of Puerto Escondido, dist. of Juquila, 15°57′N, 97°13′W, 21 Oct 1976, *Sousa 6390* (holotype: MEXU!; isotype: UC!).

Leucaena rekoi Britton & Rose, N. Amer. Fl. 23: 122. 1928.—TYPE: MEXICO. Oaxaca: nr Pochutla, close to the Pacific coast, 15°44′N, 96°28′W, 28 Sep 1917, *Reko 3632* (lectotype, here designated: flowering shoot and leaves only, US!).

Leaf rachis 5–8 (–12) cm long, with 2–3 (–4) pairs of pinnae and 3–4 (–5) pairs of leaflets per pinna; leaflets (26–) 30–50 (–70) mm long, (16–) 20–35 mm wide, glabrous. Pods (16–) 20–30 (–37) cm long, (16–) 20–32 mm wide, glabrous, mid-reddish brown. Fig. 58M–R.

Phenology. Flowering (September–) October–December; fruiting January–March; deciduous during the dry season (December–April).

Distribution (Fig. 59). *Leucaena lanceolata* var. *sousae* is restricted to the Pacific coastal zones of southeastern Michoacán, with sporadic occurrences in Guerrero and the coast of Oaxaca as far east as Bahias de Santa Cruz. This is a more restricted distribution than that depicted by Zárate (1994). Like var. *lanceolata*, var. *sousae* occurs in dry deciduous tropical forest, sometimes forming a canopy tree, and in coastal scrub forest as well as secondary dry forest and along disturbance sites such as roadsides (e.g., road running east from Pochutla, Oaxaca). Associated trees are similar to those associated with var. *lanceolata*; 0–400 m.

Vernacular names. *Ejote*, *guaje*, *guaje de monte*, *guaje de zopilote* (Oaxaca), *guajillo* (Michoacán, Guerrero, Oaxaca), *da-yuh* (Chatino, Oaxaca).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** GUERRERO: 34 km N of Feliciano rd to Presa El Infiernillo between Cañoncitos and San Diego, about 20 km S of the Infiernillo dam, 18°09′N, 101°54′W, *Hughes 1844* (FHO, K, MEXU, MO, NY, TEX).—MICHOACÁN: 30 km W of Playa Azul, rd to Barra de Navidad, 18°04′N, 102°34′W, *Hughes 631* (FHO, MEXU); 8 km NW of Caleta de Campos, Playa Azul to Coahuayana rd, 18°05′N, 102°46′W, *Soto 3757* (CAS, MEXU, MO).—OAXACA: 7 km N of Pinotepa Nacional, 16°23′N, 98°06′W, *Boege 3342* (MEXU); 7 km S of Pochutla, rd to Salina Cruz, 15°43′N, 96°25′W, *A. Delgado 669* (CAS, MEXU, MO); nr Santa Cruz, 42 km NE of Pochutla, rd to Salina Cruz, 15°45′N, 96°09′W, *S. González 684* (MEXU); 10 km E of Puerto Angel, low hills close to the Pacific coast, 15°46′N, 96°28′W, *Hughes 389* (FHO, K, MEXU), *E. S. Blanco 110* (MEXU), *Zárate 653* (MEXU); 40 km E of Pochutla, rd to Salina Cruz, 15°51′N, 95°57′W, *Hughes 587* (FHO, K, MEXU); nr Bahias de Santa Cruz, 40 km E of Pochutla on the Pacific coast, 15°47′N, 96°01′W, *Hughes 835* (FHO, K, MEXU); 1 km inland from Playa Cipolite, track 4 km W of Puerto Angel, 15°41′N, 96°33′W, *Hughes 842* (FHO, K, MEXU), *Hughes 849* (FHO, K, MEXU), *Hughes 850* (FHO, K, MEXU) *Hughes 851* (FHO, K, MEXU), *Hughes 857* (FHO, K, MEXU), *Hughes 858* (FHO, K, MEXU); 5 km E of Cacalote between Río Grande and San Isidro Llano Grande, 40 km W of Puerto Escondido, 16°03′N, 97°21′W, *Hughes 866* (FHO, K, MEXU), *Hughes 867* (FHO, K, MEXU), *Hughes 872* (FHO, K, MEXU); nr Playa de San Agustín on Pacific coast, 15°43′N, 96°14′W, *Liebmann 4357* (F, UC, US); San Pedro Hauamelula, turnoff to Barra de la Cruz, rd Salina Cruz to Pochutla, 15°52′N, 95°57′W, *R. López 227* (MEXU); Arroyo Cruz, 7 km SW of Pochutla, 15°43′N, 96°32′W, *Sousa 4370* (CAS, MEXU, MO); nr to Playa Cipolite, 2 km W of Puerto Angel, 15°41′N, 96°31′W, *Sousa 5359* (MEXU); 13 km SE of El Río, rd Pinotepa Nacional to Puerto Escondido, *Sousa 5554* (MEXU, MO); Tututepec, nr Hidalgo, 21 km WNW of Puerto Escondido, 15°57′N, 97°15′W, *Sousa 6403* (MEXU); 11 km ESE of Pochutla, 15°43′N, 96°29′W, *Sousa 7582* (MEXU); nr to Laguna de los Bajos de Chila, Juquila, 15°56′N, 97°08′W, *Sousa 8426* (CAS, MEXU); 11 km W of San Isidro Llano Grande, 32 km WNW of Puerto Escondido, distr. of Juquila, 15°58′N, 97°23′W, *Sousa 12554* (MEXU); 3.5 km NW of Jamiltepec, 16°18′N, 97°48′W, *Zárate 644* (MEXU); 9.5 km ENE of Pochutla, 1.5 km past the Río Aguacate, rd Pochutla to Salina Cruz, 15°43′N, 96°22′W, *Zárate 657* (MEXU).

The type specimen of *L. rekoi* is a mixed collection, the leaves and flowers are of *L. lanceolata*, the pods are of *Caesalpinia (Brasilettia) velutina*, a species known to be sympatric in the Pochutla area.

The distribution presented for var. *sousae* (cf. Zárate 1994: 112) is more consistent with the characters defining the two varieties and the pattern of geographic variation encountered. Identification of material from the particular areas identified above (coastal Michoacán and Bahias de Santa Cruz, coastal Oaxaca) may be difficult. The pods (40 cm long) and capitula (4 cm in diameter) of var. *sousae* from parts of coastal Oaxaca are extremely large, exceeding the dimensions of any other *Leucaena* taxon encountered so far.

16. Leucaena multicapitula Schery, Ann. Missouri Bot. Gard. 37: 302. 1950.—TYPE: PANAMA. Canal Zone: Río Cocolí, Miraflores, 09°05′N, 79°38′W, 20 Jun 1938, *P. White 135* (holotype: GH!; isotypes: MO! US!).

Small to medium-sized tree, (10–) 15–25 (–30) m tall, 20–60 (–80) cm bole diameter, typically with a short clear bole to 5–7 m, upright angular branching, and a spreading open crown. Bark on young branches smooth, mid-grey or grey-brown, inner bark salmon pink, on bole mid-grey-brown with shallow rusty orange-brown vertical fissures and pale cream-pink inner bark. Shoots terete, pale to mid-brown, variably pubescent, sometimes glabrous. Stipules 2–2.3 mm long, lanceolate, with glabrous, asymmetric, membranous wings at base, early caducous. Leaves 20–30 cm long, 14–18 cm wide; petioles (including pulvinus) 30–50 mm long, with a single mid-green, sessile, elliptic, crateriform nectary, 3–5 × 1–2 mm, at the distal end on adaxial side of petiole; rachis 14–16 cm long with a small round cupulate nectary at the distal end, apex of rachis extending beyond the terminal pinnae as a pointed glabrous mucro 2.0–3.2 mm long, curling when dry; pinnae (2–) 3–4 (–5) pairs; pinnular rachis 7–10 cm long, angled, sparsely pubescent, with 1–2 minute rounded crateriform nectaries at base of terminal pairs of leaflets; leaflets 4–5 (–6) pairs per pinna, (35–) 40–50 (–55) mm long, (15–) 18–20 (–23) mm wide, with 2 mm long pulvinules, ovate, slightly asymmetric, rounded to obtuse at base, apically lanceolate, densely pubescent with short whitish hairs, mid- to dark green abaxially, paler grey-green adaxially, primary and secondary venation visible on dried material, secondary venation brochidodromous. Capitula 5–8 mm in diameter at anthesis, in fascicles of 2–5 on exposed 2-branched terminal anauxotelic shoots with leaf development suppressed (Fig. 12C), twice-branched subunits arising from sylleptic axillary branch buds, each capitulum with (35–) 40–50 (–60) flowers; peduncles 5–10 mm long, angled, pubescent with an involucre of basally united bracts, ciliate at margin. Flowers subtended by peltate bracts, 1.5–2.0 mm long, 0.6 mm in diameter; calyx 1.3–1.5 mm long, glabrous but sparsely ciliate on lobe margins, pale whitish green, lobe tips tinged yellow; petals 2.0–2.2 mm long, free, glabrous, pale whitish green; filaments 3.0–5.5 mm long, white; anthers hairy, cream-white, apiculum absent; ovary 1–1.2 mm long, glabrous, green, with 12–14 ovules, style 4.3–5.7 mm long, white, with a terminal tubular stigma, exserted slightly beyond the anthers. Pods 1–2 (–3) per capitulum, 8–16 cm long, 23–35 mm wide, pendulous on slender 11–15 mm long stipes, linear-oblong, apically obtuse or acuminate, sometimes with a short beak, apparently readily broken off when dry, narrowly planocompressed, 12–14-seeded, valves mid-orange-brown, glabrous, with reticulate venation most pronounced close to margins, chartaceous, the margins slightly thickened, dehiscent along both sutures. Seeds 7–9 mm long, 3.5–5.4 mm wide, compressed, flattened, ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, symmetrical. Chromosome number: 2n = 52 (Sorensson 1989). Fig. 60.

Phenology. Flowering (May–) June–August (–October); fruiting (July–) August–October.

Distribution (Fig. 61). *Leucaena multicapitula* is the only species of *Leucaena*, apart from *L. diversifolia*, that grows in wet tropical lowland forest. It occurs sporadically in southern Nicaragua, northern Costa Rica, and Panama. In Nicaragua it is restricted mainly to southern parts of the Department of Rívas around the southwestern corner of Lago de Nicaragua where it is abundant; elsewhere in Chontales and Zelaya it appears to be rare and very scattered. It is also restricted in Costa Rica, occurring abundantly only in northern Guanacaste, in a moist area 5–10 km south of the Nicaraguan border at Peñas Blancas (Janzen & Liesner 1987). It occurs only rarely in Alajuela (Holdridge & Poveda 1975). *Leucaena multicapitula* is most widespread in Panama, from the Azuero Peninsula across central Panama into the eastern province of Darién. It is common in parts of the Azuero, in the provinces of Los Santos and Herrera, and in Coclé and the Canal Zone. On Barro Colorado Island it is rare, occurring only at the northern end of the island (Croat 1978). It occurs particularly along river banks, streams, and gullies, the shoreline on Barro Colorado Island, and other gap sites or secondary forest; 100–200 (–400) m.

Vernacular names. *Frijolillo* (Panama and Nicaragua).

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** ALAJUELA: rd between Cañas and Upala nr the Río Zapote, 1.8–2.7 km S of the Río Canalete, 10°49′N, 85°03′W, *Croat 36344* (MO); Ciudad Quesada on the way to Terrón Colorado, 10°28′N, 84°26′W, *Poveda 612* (MO).—GUANACASTE: 5 km S of the Nicaraguan frontier at Peñas Blancas rd S to Liberia, 11°10′N, 85°37′W, *Hughes 1024* (FHO, K, MEXU); Río Zonzapote nr rd N from

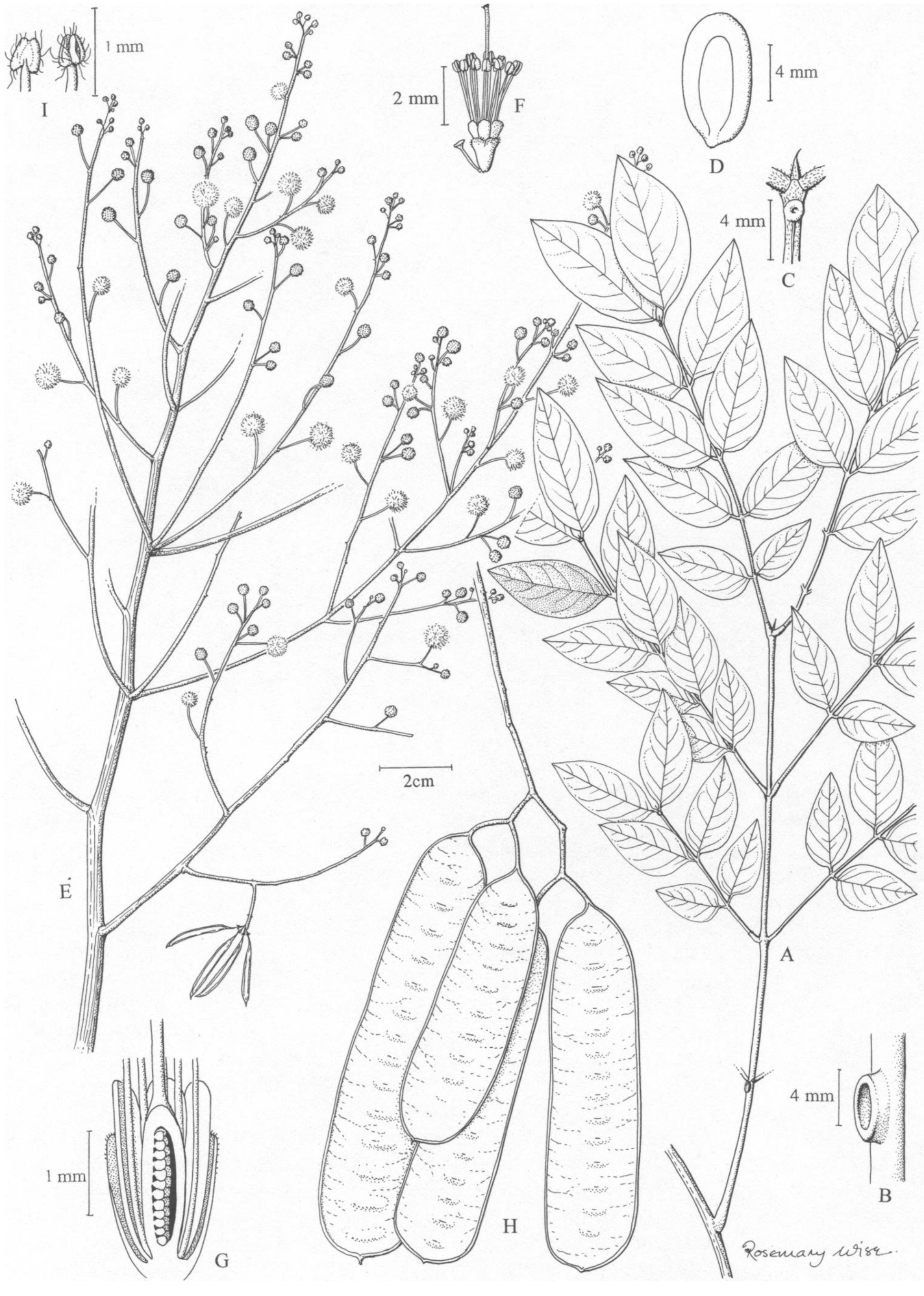


FIG. 60. *Leucaena multicapitula*. A. Leaf. B. Petiolar nectary. C. Nectary at tip of leaf rachis. D. Seed. E. Twice-branched flowering shoot. F. Flower. G. Longitudinal section of flower. H. Pods. I. Anthers. (Based on: A–D, *Hughes 1037*; E–G, *Hughes 1035*; H, *Hughes 1032*; I, *Hughes 795*.)

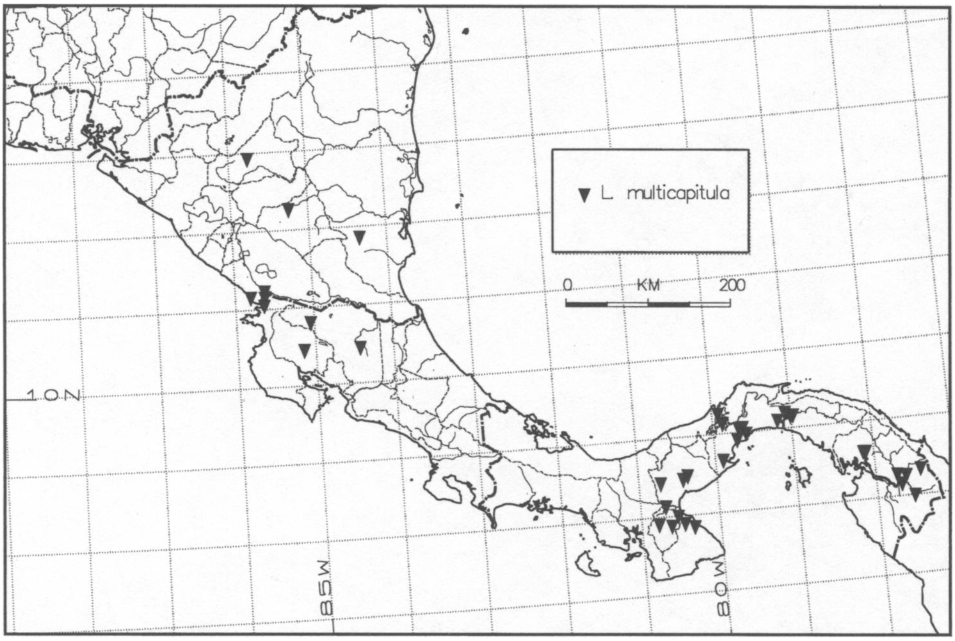


FIG. 61. Distribution of *L. multicapitula*.

La Cruz to Peñas Blancas 6 km S of the Nicaraguan frontier, 11°10′N, 85°37′W, *Hughes 1041* (FHO, K, MEXU), *Hughes 1042* (FHO, K, MEXU); 9 km S of Peñas Blancas, 11°10′N, 85°37′W, *Janzen 198* (MO); Cañas, La Pacífica, 4 km NW of Cañas, 10°28′N, 85°09′W, *Opler 1678* (MO), *Opler 1821* (F); 85 km N of Liberia nr La Cruz, 11°04′N, 85°38′W, *Webster 12487* (F, MO). **Nicaragua.** CHONTALES: 4.5 km S of Hwy 7 (from ca. 3.6 km E of La Gateada) rd to Nueva Guinea, 12°57′N, 85°45′W, *Stevens 2804* (MO, TEX); Hacienda San Martín, nr the confluence of the Río El Jordán and the Río La Pradera, 12°17′N, 85°15′W, *Stevens 21824* (MO, NY).—RÍVAS: 2 km N of the Costa Rican frontier at Peñas Blancas, rd to Rívas, 1 km from Lago de Nicaragua, 11°15′N, 85°37′W, *Hughes 1043* (FHO, K, MEXU); San Juan del Sur, Río Escameca Grande along rd SE from San Juan del Sur, 11°11′N, 85°48′W, *Stevens 3840* (MO).—ZELAYA: 0.5 km N of San Martín, 11°53′N, 84°21′W, *Nee 27835* (NY); Flor de Lis, 44 km W of El Recreo nr the limit between Zelaya and Chontales, *Sousa 13011* (CAS, K, MEXU, MO). **Panama.** CANAL ZONE: large cove, E side of Gross Peninsula, Barro Colorado Island, 9°09′N, 79°52′W, *Bailey & Bailey 281* (F, GH, MO), *Croat 11735* (MEXU, MO, NY), *D. Knight s.n.* (MO); shoreline of Miller Peninsula S of Orchid Isle on Barro Colorado Island, 9°09′N, 79°52′W, *Croat 6722* (F, MO, NY, US); Guillard Hwy, 0.5 km SE of Summit Gardens, 9°05′N, 79°37′W, *Croat 11056* (F, MO, NY, UC), *Croat 16656* (F, MO, NY); between Summit Gardens and Madden Wye, 9°05′N, 79°37′W, *Croat 14913* (F, MO, NY), *A. Gentry 1956* (F, GH, MO, NY); rd 6 km E of Arraiján, 8°56′N, 79°42′W, *Croat 15029* (F, MO, NY); nr Gatún Locks, 9°16′N, 79°55′W, *Dwyer 1782* (F, NY); shoreline E side of Gross Point, Barro Colorado Island, 9°09′N, 79°52′W, *Foster 1324* (MO); Empire Station, Panama Railrd, *Hayes 103* (K); 2 km S of Summit Gardens, 9°05′N, 79°37′W, *Lazor 5343* (F, MO); Fort Clayton, 9°00′N, 79°35′W, *Tyson 4169* (MO), *Tyson 4668* (MO).—COCLÉ: Patio of the Colégio Secundario Angel María Herrera, Penonomé, 8°31′N, 80°22′W, *Correa 4201* (PMA); nr the Río Coclé, W of Penonomé, 8°29′N, 80°26′W, *Folsom 2925* (MO); 3 km E of Divisa banks of the Río Santa María nr rd from Santiago to Panama City, 210 km W of Panama City, 8°09′N, 80°41′W, *Hughes 1037* (FHO, K, MEXU, PMA); El Copé, Penonomé, 8°27′N, 80°43′W, *Lao 301* (MO).—DARIÉN: headwaters of the Río Chico, 8°21′N, 77°26′W, *Allen 4642* (EAP, GH, MO); Río Chico nr Yaviza, 8°11′N, 77°41′W, *Allen 5088* (EAP, MO); vicinity of Santa Fe on the Río Sabana, 8°38′N, 78°08′W, *Duke 4128* (MO), *Tyson 4662* (MO); clearing at the confluence of the Río Chucunaque and the Río Canclones, *Duke 5113* (MO, NY); Santa Fe, 8°38′N, 78°08′W, *Duke 8406* (MO, NY, US); Río Pucro, below the village of Pucro, 8°01′N, 77°32′W, *Duke 13135(3)* (MO, NY); Lower Tuquesa Mining Camp called Charco Chiva

(=Quebrada Venado on Darién Radar map), 8°17′N, 77°37′W, *Mori 7000* (MO, US); Campamento Buena Vista on the Río Chucunaque above the confluence with the Río Tuquesa, 8°18′N, 77°44′W, *Stern 912* (GH, MO, UC, US), *Stern 934* (GH, MO, UC, US).—HERRERA: between Pesé and Los Pozos, 3 km SE of Pesé, 7°54′N, 80°37′W, *Hughes 795* (FHO, K, MEXU); 3 km W of Parita, rd towards Los Castillos and Ocú, 8°01′N, 80°32′W, *Hughes 1029* (FHO, K, MEXU, PMA); Río Chorro, Ocú, 7°56′N, 80°47′W, *Lao 145* (F, MO).—LOS SANTOS: Quebrada del Hato, 12 km SE of Los Santos, rd to Las Tablas, 7°52′N, 80°20′W, *Hughes 1025* (FHO, K, MEXU, PMA); *Hughes 1032* (FHO, K, MEXU, PMA); 3 km W of Los Santos, banks of the Quebrada Rebelo, rd to San Agustín and Bongo, 7°55′N, 80°27′W, *Hughes 1033* (FHO, K, MEXU, PMA), *Hughes 1034* (FHO, K, MEXU, PMA); 4 km W of Los Santos nr the Quebrada Rebelo, rd to San Agustín and Bongo, 7°55′N, 80°27′W, *Hughes 1035* (FHO, K, MEXU, PMA).—PANAMÁ: 5 km from the Carretera Interamericana, rd to Cerro Camapaña, 8°41′N, 79°54′W, *Correa 1031* (EAP, MO, PMA); vicinity of El Llano, nr Río Mamón, 9°11′N, 78°58′W, *Duke 5861* (MO, PMA); 5 km W of El Llano, 9°11′N, 79°00′W, *A. Gentry 1701* (F, GH, MO, NY); 2 km N of El Paraíso towards Gamboa, about 1 km E of the Panama Canal, 9°04′N, 79°38′W, *Hughes 1038* (FHO, K, MEXU, PMA); 8 km W of Chepo nr the Interamerican Hwy, 9°08′N, 79°10′W, *Tyson 6717* (MO, PMA); past Chepo and Río Manoni towards El Llano, 9°13′N, 79°04′W, *Tyson 6792* (MO, PMA); 8 km past Río Mamoni, rd towards El Llano, 9°10′N, 79°00′W, *Tyson 6794* (MO).

A close similarity in leaf and pod traits has led several authors to doubt the distinction of *L. multicapitula* from *L. trichodes* and *L. macrophylla* (Schery 1950; Zamora 1991). *Leucaena multicapitula* was treated as conspecific with *L. trichodes* by Janzen and Liesner (1980) and Brewbaker (1987a); Zárate (1994) suggested treating it as a subspecies of *L. trichodes*. Zamora (1991) followed Schery (1950) and maintained it as distinct from *L. trichodes* distinguishing it by its flowering shoots, which are consistently twice-branched and unique within the genus (Fig. 12C). However, *L. multicapitula* is also readily distinguished from *L. macrophylla* and *L. trichodes* by a number of other characters. First, the petiolar nectary is concave, cupulate with a wide orifice compared to the convex, conical narrow-pored nectaries of the other species. Second, the pollen of *L. multicapitula* is tricolporate and occurs in 16-grained polyads (Fig. 15B), composed of calymmated tetrahedral tetrads, which are again unique within the genus. It is very different from the porate pollen of *L. macrophylla* and *L. trichodes* (Fig. 15B, D–F), which is arranged in loosely aggregated polyads composed of acalymmate monads (Fig. 15D–F). Finally, the anthers of *L. multicapitula*, which lack an apiculum, are also quite distinct from those of *L. macrophylla* and *L. trichodes,* which have a small dorsiventrally-flattened "hooded" projection, or apiculum, on the connective (Fig. 14A, E). *Leucaena multicapitula* and *L. trichodes/L. macrophylla* may be distinguished by a suite of discrete character states that, taken together, leave no doubt about distinction of *L. multicapitula* as a separate species (Hughes 1997a). Given these differences there is even some doubt that *L. multicapitula* is closely related to *L. trichodes/L. macrophylla.* The cpDNA analysis of Harris et al. (1994a) consistently places *L. multicapitula* as sister species to *L. salvadorensis/L. lempirana* (Fig. 31). Thus the affinities of *L. multicapitula* remain uncertain as reflected by its ambiguous placement in the analysis of morphology (Fig. 28); a close relationship with *L. trichodes/L. macrophylla*, as was previously hypothesized, is not supported by any of the available morphological or molecular evidence.

Material of *L. multicapitula* from Costa Rica and Nicaragua shows some differences from the Panamanian material; the pods are consistently acuminate at the apex compared to the characteristic rounded (sometimes beaked) pod apices of the Panamanian material. Holdridge and Poveda (1975), although treating the Costa Rican material as *L. multicapitula*, pointed out that the few specimens they had seen from Alajuela lacked the branched flowering shoots that are consistently present in Panama. The identity of this material remains to be verified; so far, I have not seen flowering material from either

Nicaragua or Costa Rica, and pollen/anthers from these areas have not been examined. The cpDNA study of Harris et al. (1994a) included one accession from Guanacaste, Costa Rica, which grouped closely with *L. multicapitula* from Panama and not with *L. trichodes*. Pending further evidence, I am therefore treating the Costa Rican and Nicaraguan material as *L. multicapitula*.

In the absence of flowers, *L. multicapitula* has been frequently confused with *Albizia adinocephala* (Donn. Smith) Britton & Rose ex Record due to the broad similarity in leaf and pod morphology (Zamora 1991). The only notable difference in leaf morphology is in the position of the petiole gland, which in *L. multicapitula* is distally positioned immediately adjacent to the basal pair of pinnae, whereas in *A. adinocephala* it is always below mid-petiole and sometimes close to the pulvinus. The seeds of *A. adinocephala* are also distinctive in being pale yellow-brown and remain firmly attached to the pod valves after dehiscence; those of *L. multicapitula* are rich glossy chestnut-brown and are shed when the pods dehisce.

17. Leucaena macrophylla Bentham, Bot. Voy. Sulphur 90. 1844.—TYPE: MEXICO. Guerrero: Acapulco, 1841, *R. B. Hinds s.n.* (holotype: K!).

Small, single- or multiple-stemmed tree, 3–10 (–15) m tall, 10–15 (–40) cm bole diameter, with upright angular branching and an open irregular narrow crown. Bark pale to mid-grey-brown, smooth with pale brown slightly raised horizontally aligned lenticels on younger wood and shallow vertical rusty orange-brown fissures on older boles, inner bark cream. Shoots terete, mid-orange-brown, glabrous or occasionally densely covered in short white velutinous pubescence. Stipules 1.8–4.6 mm long, lanceolate, with a membranous basal asymmetric wing, caducous. Leaves 15–23 cm long, 17–28 cm wide; petioles (including pulvinus) 11–40 mm long; rachis 4.8–10.9 cm long, glabrous, with a single, sessile, convex or conical, elliptical nectary, 2.2–3 mm long, 1.4–1.6 (–2.3) mm wide, on ventral side of petiole at base of the basal pair of pinnae, apex of rachis extending beyond the terminal pinnae as a pointed, curling, glabrous mucro 2.1–3.2 mm long; pinnae (1–) 2–3 pairs; pinnular rachis (6–) 7–8.8 cm long, glabrous, with a sessile, conical, elliptical nectary, 0.7–1.7 × 0.7–1.5 mm, at base of terminal leaflet pair on pinnular rachis; leaflets 2–4 (–6) pairs per pinna, (15–) 23–55 (–80) mm long, (6–) 17–39 mm wide, short-petiolate, very slightly asymmetric, acute or cuneate at base, ovate-elliptic, apex acute or acuminate, margin entire, pubescence variable, sometimes densely pilose or villose or glabrous, slightly discolorous, mid-green above, paler below, midrib and secondary venation visible on both surfaces, secondary venation brochidodromous, tertiary venation reticulate. Capitula 7–11 (–15) mm in diameter at anthesis, in fascicles of 3–5 on long, naked, once-branched shoots arising in leaf axils, the leaves strongly suppressed on the flowering shoots, each capitulum with 140–180 (–190) flowers; peduncles variable, (3–) 10–19 mm long, angled, glabrous, with an involucre of basally united bracts at distal end. Flowers subtended by small peltate bracts, 1.7–2.3 mm long, 1 mm in diameter, densely pilose; calyx (1.9–) 2.3–2.5 mm long, hairy on lobe tips, pale green or greenish white; petals 2.5–3.4 mm long, free, glabrous, pale green; filaments 3.7–5.8 mm long, creamy white; anthers pilose, the hairs concentrated on the ventral side along the stomial furrow, cream-white, the connective with a pronounced dorsiventrally flattened or hooded protrusion or apiculum (Fig. 14A, E); ovary 1–1.6 mm long, glabrous, pale cream-white, with 12–18 ovules, style (3–) 5.5–7.4 mm long, cream-white, with a narrow-tubular or -funnelform stigma, held level with the anthers. Pods (1–) 2–4 (–8) per capitulum, (9–) 12–21

(–24) cm long, (9–) 14–23 (–26) mm wide, pendulous, with a stipe 9–15 mm long, linear-oblong, cuneate at base and apex, often with a short curled beak at apex, flattened, (7–) 10–16-seeded, valves thin, chartaceous or membranous, variably glabrous and slightly lustrous or with dense velutinous pubescence, green or dark maroon when unripe, turning mid-orange or reddish brown, the margins slightly raised, dehiscent along both sutures. Seeds 4.9–8.1 mm long, 3.5–5.7 mm wide, compressed, elliptic or circular, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, regular, U-shaped, with 90% arm extension, symmetrical. Chromosome number: 2n = ?52 (Sorensson 1989). Fig. 62.

Previous authors have considered the species of *Leucaena* with large leaflets—*L. lanceolata, L. macrophylla, L. multicapitula,* and *L. trichodes*—to form a closely related group based on the strong overall similarity in leaf and pod morphology (Brewbaker 1987a). These species, along with *L. shannonii* and *L. retusa,* were placed in section *Macrophylla* by Zárate (1994). Detailed survey of pollen and anther morphology shows that *L. lanceolata*, with tricolporate pollen in eumonads and anthers lacking an apiculum, and *L. multicapitula*, with tricolporate pollen in polyads of acalymmate tetrads and anthers lacking an apiculum, are clearly distinguished from *L. macrophylla* and *L. trichodes,* which have porate pollen in polyads of acalymmate monads and anthers with a prominent dorsiventrally flattened, "hooded" apiculum (Hughes 1997a). In addition, *L. lanceolata* is reliably distinguished from *L. macrophylla* by its large, many-flowered capitula (20–40 mm in diameter with 250–450 flowers) compared to the very small capitula of *L. macrophylla* (7–15 mm in diameter with 140–190 flowers). Additional characters used to distinguish *L. multicapitula* are discussed under that species (no. 16).

Leucaena macrophylla and *L. trichodes* thus form a closely related and widely, but disjunctly, distributed group that is supported by a suite of discrete pollen and anther characters unique within *Leucaena*. The study of relationships between these species has been neglected in most previous studies, which have focused either on the North American (Standley 1922; Britton & Rose 1928; Zárate 1994) or South American (Britton & Killip 1936) species alone. Within this group, there are no reliable discrete qualitative characters that distinguish these two species. In this treatment, *L. macrophylla* and *L. trichodes* are maintained as distinct species based on differences in the arrangement of flowering shoots, number of flowers per capitulum, and evidence from cpDNA restriction site data. They are also geographically isolated. The flowering shoots of *L. macrophylla* are consistently once-branched, arising in leaf axils and forming long, terminal, naked shoots with strong leaf suppression (Fig. 62), whereas those of *L. trichodes* are usually more compact with fascicles of axillary capitula on unbranched shoots in leaf axils. In their analysis of cpDNA, based on sparse sampling of this very widely distributed group (one accession of *L. macrophylla* subsp. *macrophylla*, and two each of *L. macrophylla* subsp. *istmensis* and *L. trichodes*), Harris et al. (1994a) showed that the two subspecies of *L. macrophylla* are clearly distinct from *L. trichodes*. Finally, *L. macrophylla*, from central and south-central Mexico is geographically isolated from *L. trichodes,* which occurs in northern and western South America. Although treatment of all three taxa as subspecies of *L. trichodes* is an alternative arrangement, they are maintained here within two separate species pending more detailed studies with more thorough rangewide sampling of variation.

Material of *L. macrophylla* from coastal Oaxaca and Veracruz, placed in subsp. *nelsonii* by Zárate (1994), differs from typical representatives of *L. macrophylla* in leaf and pod dimensions, habit, and cpDNA, meriting recognition as a distinct subspecies (Hughes 1997c). Given that the type of *L. nelsonii* belongs with typical *L. macrophylla* and not with the distinct Oaxacan material (see below), Hughes (1997c) had no alternative but to add a new subspecies, named *istmensis*, to account for this variation. Subspecies *istmensis* differs from subsp. *macrophylla* in its smaller leaflets and pods, shorter peduncles, and in its cpDNA (by 16 autapomorphic fragment changes, six of which are unique) (Harris et al. 1994a).

KEY TO THE SUBSPECIES OF LEUCAENA MACROPHYLLA

1. Petioles ≥30 mm long; leaflets ≥27 mm wide, 2–3 (–4) pairs per pinna; pods generally ≥20 mm wide.
17a. *L. macrophylla* subsp. *macrophylla.*

1. Petioles ≤22 mm long; leaflets ≤28 mm wide, 3–4 (–6) pairs per pinna; pods ≤23 mm wide.
17b. *L. macrophylla* subsp. *istmensis.*

17a. Leucaena macrophylla subsp. **macrophylla.**

Leucaena macrocarpa Rose, Contr. U.S. Natl. Herb. 1(9): 327. 1895.—TYPE: MEXICO. Jalisco: Río Blanco, Aug 1886, *Palmer 320 pro parte* (lectotype, designated McVaugh, 1987: US!, the flowering specimen only; the fruiting specimen is *Albizia occidentalis* Brandegee).

Leucaena houghii Britton & Rose, N. Amer. Fl. 23: 123. 1928.—TYPE: MEXICO. Morelos: Cuernavaca, 18°55′N, 99°16′W, 28 May 1899, *Rose & Hough 4362* (holotype: NY!; isotype: US!).

Leucaena nelsonii Britton & Rose, N. Amer. Fl. 23: 124. 1928. *Leucaena macrophylla* subsp. *nelsonii* (Britton & Rose) S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65(2): 113. 1994.—TYPE: MEXICO. Guerrero: between San Marcos and Copala, 16°45′N, 99°15′W, 8 Feb 1895, *E. W. Nelson 2286* (holotype: NY!; isotype: US!).

Small, generally multiple-stemmed tree, 3–10 m tall, 10–15 (–25) cm bole diameter. Leaves: petioles (including pulvinus) 30–40 mm long; rachis 4.8–9.8 cm long; pinnae (1–) 2 (–3) pairs; leaflets 2–3 (–4) pairs per pinna, (30–) 51–70 (–80) mm long, 27–39 mm wide. Capitula 9–11 (–15) mm in diameter at anthesis; peduncles (10–) 15–19 mm long. Flowers subtended by small peltate bracts, 2.1–2.3 mm long; calyx 2.3–2.5 mm long; petals 3.1–3.4 mm long; filaments 4.4–5.8 mm long; style 6.3–7.4 mm long. Pods (1–) 2–3 per capitulum, (12–) 16.5–21 (–24) cm long, (20–) 23–24 (–26) mm wide, glabrous and slightly lustrous. Seeds 6.3–8.1 mm long, 3.8–5.7 mm wide. Fig. 62A–I.

Phenology. Flowering (July–) September–December (–March); fruiting (January–) March–May (–June).

Distribution (Fig. 63). *Leucaena macrophylla* subsp. *macrophylla* is distributed throughout the highlands and coastal foothills of west-central Mexico in the States of Colima, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, the extreme northwest of Oaxaca, and the extreme southwest of Puebla. It is a small understory tree in a variety of forest types, including dry deciduous tropical forest, dry mattoral (mainly along streambanks), oak forest, and oak/pine/juniper forest, and is particularly abundant in the dry tropical forest-oak forest transition zone. It may occur abundantly following disturbance in secondary vegetation or on roadsides. Associated trees include species of *Quercus, Bursera, Ceiba, Ipomoea, Cordia, Tecoma, Dodonaea, Brahea, Guazuma, Tabebuia, Ficus, Bumelia, Casearia, Heliocarpus, Celtis,* and numerous woody legumes, including *Acacia, Caesalpinia, Conzattia, Diphysa, Lonchocarpus, Enterolobium, Lysiloma,* and sometimes other species of *Leucaena,* such as *L. esculenta*; (20–) 500–1900 m.

Vernacular names. *Frijolito* (Michoacán), *guaje* (Mexico, Guerrero, Puebla), *guaje amarillo* (Guerrero), *guaje blanco* (Guerrero and Michoacán), *guaje de venado* (Oaxaca), *guaje del cerro, guaje verde, calguaje, zarza guaje* (Guerrero), *guajillo* (Guerrero, Michoacán) and *guaje (huaje) brujo* (Morelos).

Representative Specimens. **Mexico.** Colima: Paso del Río, *Emrick 172* (F); Ixtlahuacán, 8 km E of Agua de la Virgen, nr Ixtlahuacán, 18°55′N, 103°37′W, *Magallanes 3508* (K, MEXU); N of Pihuamo, 19°19′N, 103°23′W, *Miranda 9061* (MEXU); Colima, Rancho El Jabalí, 20 km N of Colima, nr Hacienda San Antonio and El Ajuacate, towards Avenida de los Bambues, 19°26′N, 103°40′W, *Rico 992* (K, MEXU); Rancho El Jabalí, 22 km NNW of Colima, SW foothills of Volcán de Colima, 19°26′N, 103°43′W, *Sanders 10678* (K).—Guerrero: Cañón de La Mano, between Los Amates and El Naranjo, 10 km N of Iguala on railway, 18°24′N, 99°31′W, *Catalán 474* (MEXU); Hwy 95 between Km 39 and 40, 5 km N of El Rincón, 24 km N of Tierra Colorado, 17°20′N, 99°29′W, *Croat 45720* (CAS, MEXU, MO); 96 km N of Acapulco, Hwy 95, 17°12′N, 99°31′W, *Freeland & Spetzman 202* (MEXU); 1.4 km SW of Caserio La Vainilla, Mesa del Mango, nr José Azueta, 17°42′N, 101°31′W, *Gallardo 743* (K); rd from Zihuatanejo to Ixtla opposite the Escuela Agropecuaria, *Germán 222* (MEXU, MO); nr Atoyac, Galeana, 17°13′N, 100°26′W, *Hinton 10985* (K, NY, TEX, UC, US); Campo Morado, nr Otatlán and Mina, 17°40′N, 100°09′W, *Hinton 14840* (GH, MO, TEX, US); 9 km E of San Marcos, rd to Cuajinicuilapa, 69 km E of Acapulco, 16°46′N, 99°17′W, *Hughes 644* (FHO, K, MEXU); 6 km N of Ocotín, rd from Acapulco to Mexico City, 30 km S of Chilpancingo de los Bravos, 17°18′N, 99°28′W, *Hughes 876* (FHO, K, MEXU); 5 km SW of Mezcala, mtns between the Río Balsas to the N and track to Mezapa to the S, 17°55′N, 99°37′W, *Hughes 885* (FHO, K, MEXU); nr Bía de Ayala, rd 30 km W of Teloloapan to Ciudad Altamirano, 18°26′N, 100°00′W, *Hughes 900* (FHO, K, MEXU); rd W from Placeres de Oro 7 km E of Guayameo, hills S of Río Balsas, 18°19′N, 101°12′W, *Hughes 1168* (FHO, K, MEXU); rd SW from Ciudad Altamirano towards Pacific coast at Zihuatanejo, 15 km SW of Placeres de Oro, 18°08′N, 100°55′W, *Hughes 1169* (FHO, K, MEXU); S slopes of Sierra Madre del Sur, nr rd from Zihuatanejo to Ciudad Altamirano, 15 km N of Vallecitos, 15 km S of crest of the Sierra, 18°00′N, 101°18′W, *Hughes 1179* (FHO, K, MEXU); nr Balsas, *Lemmon 263* (UC); nr Oaxtepec, 18°54′N, 98°58′W, *Matuda 38249* (CAS, MEXU, US); Colotlipa, 17°25′N, 99°09′W, *Matuda 38250* (CAS, MEXU, MO, US); rd from Hwy 200 at San Marcos past Piedra Parada at Piedra Grande, 10 km from main rd, 16°51′N, 99°21′W, *Miller 549* (MEXU); Adama, nr Achótla, *Reko 5027* (A, NY, US); 16 km N of Limón de Papatzingán, nr Tiquicheo, 19°10′N, 100°47′W, *Soto 553* (MEXU, MO, NY); San Joaquín, 21 km NE of La Huacana, 19°06′N, 101°45′W, *Soto 582* (MEXU, MO, NY); 10 km SW of Placeres de Oro, Balsas watershed, 18°08′N, 100°55′W, *Soto 664* (MEXU, MO, NY); Coyuca de Catalán, El Cundancito, 85 km SW of Ciudad Altamirano, 18°04′N, 100°58′W, *Soto 8608* (MEXU, MO); Azueta, 3 km NW of Vallecito de Zaragoza, 17°55′N, 101°18′W, *Soto 11653* (MEXU, MO); 2 km NE of El Parotal, nr Petatlán, *Soto 12175* (K, MEXU, MO); 1 km from turnoff to shortwave radio station, 24 km from Taxco, *Zárate 16* (MEXU); 6 km W of Xalostoc, 33 km NW of Iguala, rd to Ciudad Altamirano, 18°25′N, 99°46′W, *Zárate 37* (MEXU); Acapulco, 21 km N of Acapulco, rd to Mexico, 17°04′N, 99°46′W, *Zárate 165* (MEXU).—Jalisco: Puente Barranquitas, rd from Guadalajara to Tepic, 21°03′N, 104°12′W, *A. Delgado 414* (CAS, MEXU, MO); Barranca de Colimilla, Tlaquepaque, 20°42′N, 103°14′W, *Díaz 2591* (MEXU); track from Talpa to La Cuesta, 20°17′N, 104°48′W, *Díaz 3674* (MEXU); Barranca de la Experiencia, Zapopan, 20°44′N, 103°23′W, *Díaz 9015* (MEXU); Los Angeles de Tenacatita, nr La Huerta, 19°19′N, 104°51′W, *L. M. González 940* (MEXU); 28 km W of Magdalena, 21°03′N, 104°12′W, *C. D. Johnson 64-73* (MEXU, MO, US); 12 km N of Tonila, 19°27′N, 103°31′W, *C. D. Johnson 361-73* (MO); Ahuijullo, nr Tecalitlán, 19°05′N, 103°05′W, *Magallanes 1605* (MEXU, MO); 15 km NW of Venustiano Carranza, rd to Tapalpa, 19°48′N, 103°48′W, *Magallanes 3221* (MEXU, MO, TEX); 6 km NE of La Cuesta, nr Talpa, 20°12′N, 104°47′W, *Magallanes 3434* (MEXU, MO); 14 km SW of Talpa de Allende above Aranjues, valley of Río Charco Verde nr headwaters, 20°17′N, 104°52′W, *McVaugh 14333* (K, MEXU, US); 5 km N of Pihuamo, 19°17′N, 103°22′W, *McVaugh & Koelz 1419* (CAS, NY); Barranca of Guadalajara, 20°43′N, 103°16′W, *Pringle 9758* (F, GH, K, MO, NY, US); El Cañón, 2 km NW of Hacienda San Antonio, Río Lumbre watershed, 19°26′N, 103°44′W, *Rico 1001* (K, MEXU); Bolanos, 21°40′N, 103°49′W, *Rose 2850* (NY, US); Tuxpan, Barranca, W of Atentique, 19°32′N, 103°28′W, *Rzedowski 21899* (TEX); Barranca de Atenquique, 2 km S of Pialla, Colima to Guadalajara rd, 19°31′N, 103°26′W, *Soto 2887* (CAS, MEXU); 21 km SW of Autlán, 19°38′N, 104°26′W, *Sousa 3860* (GH, MEXU).—México: Ixtapan, Temascaltepec, 18°50′N, 99°40′W, *Hinton 2256* (A, K, MO, US); Rincón del Carmen, Temascaltepec, 18°53′N, 100°07′W, *Hinton 8611* (A, F, K, MO, NY, TEX, US); Piedras Negras, nr Cacahuamilpa, 18°42′N, 99°36′W, *Matuda 29728* (MEXU); Los Bejucos, Tejupilco, 18°47′N, 100°26′W, *Matuda 31922* (MEXU); between San Pedro and Palmar Grande, 18°35′N, 100°21′W, *Matuda 32080* (F, MEXU, US); W of San Vicente, nr San Antonio, Tlatlayan, 18°37′N, 100°11′W, *Matuda 32121* (MEXU, US).—Michoacán: nr small Balneario, Arroyo Frio, Tocambaro, *Argüelles 2037* (MEXU); nr Ostula, Coalcomán, 18°30′N, 103°28′W, *Hinton 16182* (K, NY, TEX, UC, US); 10 km SSE of Arteaga, rd to La Mira, Playa Azul, and Lázaro Cárdenas, lower hills Sierra Madre del Sur, 18°18′N, 102°16′W, *Hughes 1176* (FHO, K, MEXU); Monte de Iguasán, *Langlassé 12* (GH, K, US); Aguililla, 12.5 km W of Aguililla, rd to Dos Aguas, 18°45′N, 102°52′W, *E. Martínez 5370* (MEXU, MO, NY); 25 km S of Arteaga, rd to Playa Azul, 18°10′N, 102°16′W, *McVaugh 22636* (CAS, MEXU, NY); 5.2 km N of El Limón, Temascal to Huetamo rd, 19°05′N, 100°47′W, *H. E. Moore 5652* (MEXU); 51 km from Temascal, rd to Huetamo de Núñez, 19°13′N, 100°48′W, *H. E. Moore 5704* (MEXU); 8 km S of Arío de Rosales, rd to La Huacana, 2 km before turnoff to Nuevo Urecho, 19°12′N, 101°43′W, *Rico 886* (K); 6 km S of Arío de Rosales, rd to La Huacana, 19°09′N, 101°43′W, *Rzedowski 37382* (MEXU); 9 km SW of Arío de Rosales towards Huacana, rd to Apatzingán, 19°07′N, 101°43′W, *R. Torres 346* (MEXU); 22 km SW of Zitácuaro at Las Trincheras, rd to Huetamo de Núñez, 19°17′N, 100°26′W, *Soto 120* (CAS, MEXU); 5 km W of Jacóna, 19°57′N, 102°21′W, *Soto 721* (CAS, MEXU, MO); 8 km NE of Coalcomán, rd to Aguililla, 18°51′N, 103°06′W, *Soto 2141* (CAS, MEXU, MO); in Tehuantepec, 27 km SW of Coalcomán, 18°41′N, 103°18′W, *Soto 2520* (K, MEXU, TEX); 1 km NW of Villa Victoria, nr Chinicuila, rd from Coalcomán to Pihuamo, 18°46′N, 103°22′W, *Soto 2530* (MEXU); El Ojo de Agua de Poturo, 30 km NW of Churumuco rd to La Huacana, 18°51′N, 101°38′W, *Soto 3517* (CAS, MEXU); 7 km N of Nocupétaro, rd to Villa Madero, 19°05′N, 101°11′W, *Soto 4646* (CAS, MEXU, MO); 2 km SE of Las Caranicuas, rd from Puruarán to Turicato, 19°04′N, 101°27′W, *Soto 4833* (MEXU); 5 km E of Guayameo, 18°18′N, 101°18′W, *Soto 4938* (CAS, MEXU, MO, TEX); 24 km SW of Coalcomán, nr Chinicuila, 18°43′N, 103°18′W, *Soto 8158* (MEXU).—Morelos: Palmira, 18°52′N, 99°12′W, *Dorado 16* (MEXU); 6 km on rd from Huitchila to Los Sauces, nr Tepalcingo, 18°36′N, 98°56′W, *Dorado 703* (MEXU); nr Cuernavaca, 18°56′N, 99°14′W, *Lemmon 47* (UC); Amatlán, 18°58′N, 99°03′W, *Miranda 938* (MEXU); L'Amagatall, *J. Vázquez 1928* (MEXU); 3 km SE of San Andrés de la Cal, foot of Cerro de la Cal, nr Tepoztlán, 18°57′N, 99°07′W, *Zárate 74* (MEXU); nr the water tank, Oaxtepec, rd to the tower, 18°55′N, 98°58′W, *Zárate 89* (MEXU).—Nayarit: 2 km SE of La Guera, nr Nayarit, 22°17′N, 104°26′W, *G. Flores 1550* (MEXU); 28 km S of Tepic, rd to Compostela, 21°18′N, 104°54′W, *A. Gentry 19496* (US); Choix, nr Aguajito, *J. González 676* (MEXU); 16 km NW of Tepic, 21°38′N, 104°58′W, *Grethur 804* (MEXU); Cerro Cangrejo, Cañada SE of Villa de Guadalupe rd from Herradura to El Canaveral and Jesús María nr Nayar, 22°15′N, 104°37′W, *Tenorio 16042* (MEXU).—Oaxaca: 19 km NE of Putla, Balsas watershed, 17°07′N, 97°53′W, *Sousa 5470* (MEXU); 6 km NW of San Jerónimo Silacayoapilla, nr turnoff to Cienaga Zahuatlán, Huajuapan de León, 17°51′N, 97°52′W, *Sousa 9826* (CAS, F, MEXU, MO).—Puebla: rd from Tehuixtle to Zacacuautla, nr Jolalpan, 18°21′N, 98°54′W, *Guizar 1488* (MEXU); E slopes of Sierra Mazateca above Tehuacán valley, rd 4 km E from Coxcatlán to Zoquitlán and Coyomeapan, 18°16′N, 97°09′W, *Hughes 1328* (BR, FHO, K, MEXU, NY); Cerro de Agua Fria, *Miranda 2593* (MEXU).

Britton and Rose (1928) distinguished *L. nelsonii* from *L. macrophylla* solely by its copiously pubescent leaflets and had not seen fruiting material at the time of their original description. Zárate (1994) combined *L. nelsonii* as a subspecies of *L. macrophylla* based on quantitative leaf and pod differences and leaflet pubescence, and assigned material from southeastern coastal Guerrero (type locality of *L. nelsonii*), coastal Oaxaca, and Veracruz to that subspecies. The type specimen of *L. nelsonii* does indeed have copious pilose or villose pubescence on both leaflet surfaces, a feature also noted by McVaugh (1987) to be present on trees from throughout the Balsas from eastern Jalisco to Guerrero. As noted by McVaugh (1987), even on typical specimens of *L. macrophylla* from the northern part of its range, leaflets are rarely completely glabrous, but often have stiff white hairs on the pulvinules and along the primary and secondary veins. Rangewide survey of leaflet pubescence reveals that while material from the Balsas is generally more pubescent, it is variable, and pubescent individuals also occur elsewhere (e.g., coastal Michoacán). At the type locality of *L. nelsonii* leaflet pubescence also varies with some very sparsely pubescent individuals present (e.g., *Hughes 644*). Material from coastal Oaxaca, assigned to subsp. *nelsonii* by Zárate (1994), is generally glabrous. Given this pattern of variation in leaflet pubescence and the close similarity of the material from coastal Guerrero to typical representatives of *L. macrophylla*, there appears to be no basis for maintaining *L. nelsonii* as a separate species or subspecies within *L. macrophylla*. The type specimen of *L. macrophylla* was collected from "Acapulco" and given that there is no record of typical *L. macrophylla* from the immediate vicinity of Acapulco, it is probable that the type was collected either further west along the coast (near the type locality of *L. nelsonii*) or inland close to the route to Mexico City. Similar variation in leaflet pubescence has been noted within the other large-leaflet species *L. lanceolata* and *L. trichodes*.

Although not as widely used as some other species of *Leucaena*, pods, seeds and young leafy shoots of *L. macrophylla* subsp. *macrophylla* are eaten either raw or cooked in some areas (Zárate 1994, 1997), and pods are sold in local markets, particularly in parts of the State of México (see notes on *Hinton* collections).

17b. Leucaena macrophylla subsp. **istmensis** C. E. Hughes, Contr. Univ. Michigan Herb. 21: 283. 1997.—TYPE: MEXICO. Oaxaca: 40 km W of Puerto Escondido, coast rd to Pinotepa Nacional, nr San Isidro Llano Grande, 2 km inland from Pacific coast, 15°58′N, 97°10′W, 26 Mar 1989, *Hughes 1338* (holotype: FHO!; isotypes: AAU! K! MEXU! NY!).

Small, generally single-stemmed tree 3–10 (–15) m tall, 10–15 (–40) cm bole diameter. Leaves: petioles (including pulvinus) 11–22 mm long; rachis (7–) 8.2–10.9 cm long; pinnae (2–) 3 pairs; leaflets 3–4 (–6) pairs per pinna, (15–) 23–56 (–64) mm long, (6–) 17–24 (–28) mm wide. Capitula 7–9 (–10) mm in diameter at anthesis; peduncles (3–) 4–10 mm long. Flowers subtended by small peltate bracts, 1.7–2.1 mm long; calyx 1.9–2.3 mm long; petals (2.5–) 2.6–3 mm long; filaments (3.7–) 4–5 (–5.2) mm long; style (3–) 5.5–6 mm long. Pods 2–4 (–8) per capitulum, (9–) 12–14 (–15.3) cm long, (9–) 14–18 (–23) mm wide, glabrous and slightly lustrous or with dense velutinous pubescence. Seeds 4.9–6.6 mm long, 3.5–4.6 mm wide. Fig. 62J–L.

Phenology. Flowering October–February; fruiting (February–) March– April.

Distribution (Fig. 63). *Leucaena macrophylla* subsp. *istmensis* is restricted to south-central Mexico along the coast, the Isthmus of Tehuantepec, the Pacific foothills in Oaxaca, and in a restricted area around San Andrés Tuxtla in southern Veracruz. It is essentially a lowland species of the dry deciduous tropical forest, although it does extend infrequently to mid-elevations in foothills in moister oak forest. Associated trees include species of *Guazuma, Cecropia, Bravaisia, Spondias, Brosimum*, numerous woody legumes, including species of *Acacia, Piptadenia, Pterocarpus, Enterolobium, Albizia, Gliricidia, Bauhinia, Calliandra, Zapoteca*, and one *Leucaena*, *L. lanceolata* var. *sousae*. It is most abundant in disturbed areas and in secondary vegetation where it is fast growing and can dominate early succession, later forming a subcanopy or understory tree; 0–400 (–1500) m.

Vernacular names. *Duva de cerro, ndwa de monte* (= *guaje de cerro*, Mixteco, Oaxaca), *guaje, guajito, punta de guaje, tepeguaje rojo, yuanda-tu-cu-u* (Mixteco de la costa), *chicaoaxin* (= *guaje de hormiga*, Zárate 1994) (all Oaxaca), *marinero, guaje de indio* (Veracruz).

REPRESENTATIVE SPECIMENS. **Mexico.** OAXACA: 3 km N of Santa María Chimalapa, track to Paso Mactaspac del Río del Corte, 16°55′N, 94°41′W, *H. M. Hernández 589* (CAS, MEXU, MO); 25 km S of Sola de Vega, rd to Puerto Escondido, Sierra Madre del Sur, 16°02′N, 97°09′W, *Hughes 386* (FHO, K, MEXU); 2 km E of San Isidro Llano Grande, coast rd between Pinotepa Nacional and Puerto Escondido, 15°59′N, 97°16′W, *Hughes 580* (FHO, K, MEXU); 10 km N of Candelaria, 40 km N of Pochutla, rd to Oaxaca, 15°51′N, 96°28′W, *Hughes 846* (FHO, K, MEXU); immediately S of El Arenal, 10 km E of Playa Coyula, nr the Pacific coast,

FIG. 62. *Leucaena macrophylla*. A–I, subsp. *macrophylla*: A. Leaf. B. Pod. C. Seed. D. Petiolar nectary. E. Rachis nectary. F. Flowering shoot. G. Flower. H. Longitudinal section of flower. I. Anther. J–L, subsp. *istmensis*: J. Leaf. K. Pods. L. Seed. (Based on: A–E, *Hughes 1179*; F, *Hughes 1823*; G, H, *Hughes 1338*; I, *Hughes 1830*; J–L, *Hughes 584*.)

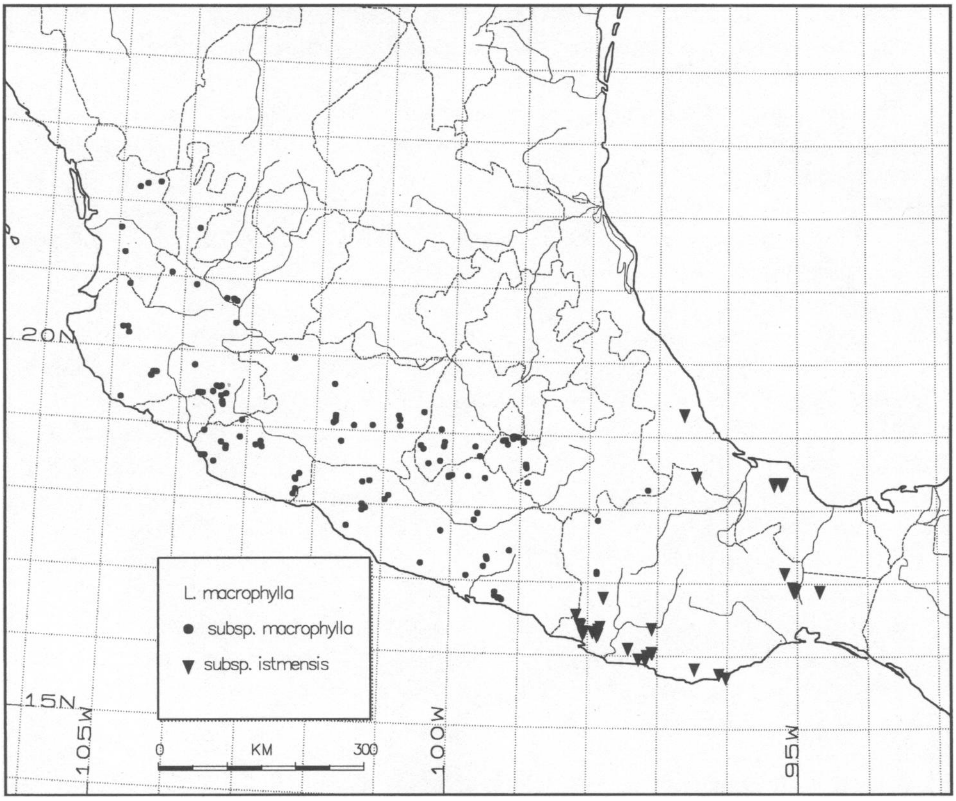


FIG. 63. Distribution of *L. macrophylla*.

15°44′N, 96°01′W, *Hughes 854* (FHO, K, MEXU); 6 km W of Pinotepa Nacional, rd to Acapulco, 16°21′N, 98°03′W, *Hughes 873* (FHO, K, MEXU); rd N from Juchitán to Acayucán 5 km N of Matías Romero, low windswept hills, Tehuantepec isthmus, 16°56′N, 95°01′W, *Hughes 1304* (CR, FHO, K, MEXU, NY); 2 km inland from Pacific coast, 10 km E of Coyula, 20 km E of Puerto Angel, dry valley between Coyula and Bahía de Santa Cruz, 15°47′N, 96°07′W, *Hughes 1340* (BR, FHO, K, MEXU, NY); 1 km E of Atoyaquillo, Putla, 16°49′N, 97°47′W, *E. Solano 70* (MEXU); Ranchería La Esmeralda, 6 km S of San Gabriel Mixtepec, 16°04′N, 97°04′W, *Sousa 5306* (MEXU); 8 km SE of Cacahuatepec, 3 km NW of Ixcapa, 16°35′N, 98°10′W, *Sousa 5507* (MEXU); 6 km NW of Pinotepa Nacional, distr of Jamiltepec, 16°23′N, 97°51′W, *Sousa 8453* (CAS, MEXU, UC); 11 km N of Matías Romero, 4 km S of Piedra Blanca, 16°55′N, 95°03′W, *Sousa 9225* (MEXU, MO, UC); Revolución, 16 km NW of Palomares, rd to Tuxtepec, 17°10′N, 95°11′W, *Sousa 9240* (MEXU, MO, UC); 5 km W of Jamiltepec, 16°18′N, 97°52′W, *Sousa 9928* (CAS, MEXU, MO); 3 km E of Ojo de Agua S of Sola de Vega, 16°24′N, 97°05′W, *Sousa 9986* (CAS, MEXU, MO); Acatlán, 1 km W of Tetela, distr of Tuxtepec, 18°29′N, 96°27′W, *Sousa 10306* (CAS, MEXU, MO); "El Tigre," 2 km N of San Agustín Chayuco, Jamiltepec, 16°25′N, 97°49′W, *Tenorio 234* (CAS, MEXU, MO); 1.2 km N of jctn to Vivero Guapinol towards San Agustín Chayuco, 24 km SE of Pinotepa Nacional, 16°19′N, 97°51′W, *R. Torres 1637* (CAS, MEXU, MO); Río Pacine, 3 km NE of San Juan Guichicovi, Juchitán, 16°58′N, 95°04′W, *R. Torres 12018* (MEXU); 14 km SE of Pinotepa Nacional, 4 km NW of Nuaxpaltepec, Jamiltepec, 16°21′N, 97°56′W, *Zárate 641* (MEXU).—VERACRUZ: Salto de Eyipantla, 8 km from Sihuapan, nr San Andrés Tuxtla, 18°24′N, 95°12′W, *Calzada 4245* (F); N side of Cerro de los Metates, *Dorantes 1011* (F, MEXU); Salto de Agua, 11 km S of Santiago Tuxtla, 18°23′N, 95°20′W, *Sousa 3007* (MEXU); nr Plan del Río and Emiliano Zapáta, 19°20′N, 96°38′W, *Villanueva 246* (NY).

As discussed above, Zárate (1994) assigned all material of subsp. *istmensis* to subsp. *nelsonii*. This approach was followed by Hughes (1993) in his rangewide seed collections of *Leucaena* and by Harris et al. (1994a).

The name *istmensis* refers to the occurrence of this subspecies across the Isthmus (*istmo*) of Tehuantepec. Pods of subspecies *istmensis* are usually glabrous and slightly lustrous, but pods of trees from one population from coastal Oaxaca, 20 km east of Pochutla near Coyula (*Hughes 854, 855, 1340*), have dense velutinous pubescence. *Leucaena lanceolata* var. *sousae*, which occurs sympatrically with *L. macrophylla* subsp. *istmensis*, shows similar variation in pod pubescence along the same stretch of coastal Oaxaca between Pochutla and Bahía de Santa Cruz. Zárate (1994) suggested that both the material here assigned to subsp. *istmensis* and *L. lanceolata* var. *sousae* may be of hybrid origin, but provided little evidence to support these hypotheses. What is clear is that, in this part of coastal Oaxaca, a number of unusual variants are found. It is perhaps no coincidence that a number of the best performing, fast-growing accessions of *Leucaena* in recent field trials (Stewart et al. 1991) were collected in this area. The dry forests of this stretch of coastal Oaxaca, which are well known for their high species diversity and endemism, have recently come under growing pressure from large-scale tourist development. This diversity within *Leucaena* adds weight to calls for conservation measures for these rapidly fragmenting forests.

Zárate (1994) reports sporadic food use of unripe seeds, but pods do not appear to be marketed or widely used. *Leucaena macrophylla* subsp. *istmensis* was found to be particularly fast growing and consistently single-stemmed in field trials in Honduras (Stewart et al. 1991).

18. Leucaena trichodes (Jacquin) Bentham, Hook. J. Bot. 4: 417. 1842. *Mimosa trichodes* Jacquin, Hort. Schoenbr. 3: 76 (plate 394; see Fig. 65). 1798. *Acacia trichodes* (Jacquin) Willdenow, Sp. pl. 4: 1063. 1805.—TYPE: VENEZUELA. Caracas, *Jacquin s.n.* (holotype: W, ex herb. Jacquin, photos: FHO! US!).

Leucaena canescens Bentham, Pl. hartw. 117. 1839.—TYPE: ECUADOR. Guayas: nr Guayaquil, *Hartweg 655* (holotype: K!, photo: MO!; isotypes: NY! OXF! W).

Acacia pseudotrichodes DC., Prodr. 2: 466. 1825. *Leucaena pseudotrichodes* (DC.) Britton & Rose, N. Amer. Fl. 23: 124. 1928.—TYPE: DOMINICAN REPUBLIC. Santo Domingo, 1821, *C. G. Bertero s.n.* (holotype: G-DC, photo: FHO!).

Leucaena colombiana Britton & Killip, Ann. New York Acad. Sci. 35: 146. 1936.—TYPE: COLOMBIA. Magdalena: north of Bonda, Santa Marta, 4 Aug 1898, *H. H. Smith 37* (holotype: NY!; isotypes: K! MO! US! CAS! UC!).

Leucaena bolivarensis Britton & Killip, Ann. New York Acad. Sci. 35: 147. 1936.—TYPE: COLOMBIA. Bolívar: nr Turbaco, Torecilla, 10 Nov 1926, *Killip 14239* (holotype: NY!; isotypes: K! US! GH!).

Leucaena trichodes var. *acutifolia* Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(3): 99. 1943.—TYPE: PERU: Piura: Pariñas valley, *Haught F119* (not located).

Small, sometimes multiple-stemmed tree or shrub, (1–) 3–10 (–15) m tall, 10–15 (–30) cm bole diameter, with upright angular branching and an open irregular narrow crown. Bark pale to mid-grey-brown, smooth with pale brown, slightly raised, horizontally aligned lenticels on younger wood, and shallow vertical rusty orange-brown fissures on older boles, inner bark cream. Shoots terete, pale grey-brown to rich mid-orange-brown, densely covered in short white velutinous pubescence or occasionally glabrous.

Stipules 2.8–3.1 mm long, lanceolate, long-pointed at apex, with a membranous basal asymmetric wing, early deciduous. Leaves 13–22 (–29) cm long, 10–14 (–20) cm wide; petioles (including pulvinus) (16–) 20–40 (–50) mm long; rachis 6.5–13 cm long, with dense white velutinous pubescence, with a single, sessile, convex or conical, elliptical nectary, 2–3.5 mm long, 1.2–1.6 mm wide, on ventral side of petiole at base of the basal pair of pinnae, apex of rachis extending beyond the terminal pinnae as a pointed, curling, sparsely pubescent mucro 2.1–2.8 mm long; pinnae 2–3 (–4) pairs; pinnular rachis 4.6–8.2 (–11) cm long, densely pubescent, with 1 or 2 sessile, conical, elliptical nectaries, 0.4–0.7 × 0.3–0.4 mm, at base of terminal leaflet pairs on pinnular rachis; leaflets (1–) 2–4 (–6) pairs per pinna, (22–) 28–60 (–118) mm long, (10–) 15–50 (–71) mm wide, short-petiolate, very slightly asymmetric, acute or cuneate at base, ovate-elliptic, apex variably acute or obtuse, sometimes rounded, entire, ciliate on margins, pubescence variable, sometimes densely pilose, sometimes sparse and occasionally glabrous, slightly discolorous, mid-green above, paler below, midrib and secondary venation visible on both surfaces, secondary venation brochidodromous, tertiary venation reticulate. Capitula 8–12 mm in diameter at anthesis, in fascicles of 3–5 in leaf axils on actively growing shoots, sometimes with suppression of the leaves on the flowering shoot and sometimes with once-branched flowering shoots, each capitulum with 90–170 flowers; peduncles variable, (6–) 10–18 mm long, angled, sparsely or densely pubescent, with an involucre of basally united bracts at distal end. Flowers subtended by small peltate bracts, 1.3–2.4 mm long, 1 mm in diameter, densely pilose; calyx 1.3–2.6 mm long, sparsely hairy on lobe tips, pale whitish green; petals 2.3–3.3 mm long, free, with short pubescence on lobes, pale green; filaments 4–6.2 mm long, creamy white; anthers long-pilose, the hairs concentrated on the ventral side along the stomial furrow, cream-white, the connective with a pronounced dorsiventrally flattened "hooded" protrusion or apiculum; ovary 1.1–1.8 mm long, glabrous, pale cream-white, with 12–16 ovules, style 4.5–6 (–7.4) mm long, cream-white, with a narrow-funnelform stigma, held level with or slightly exserted beyond anthers. Pods 1–3 (–4) per capitulum, (7–) 11–18 cm long, 18–24 mm wide, pendulous, with a short stipe, linear-oblong, cuneate at base and apex, often with a short beak at apex, flattened, 10–14-seeded, valves thin, chartaceous or membranous, variably glabrous and slightly lustrous or with dense velutinous pubescence, green or dark maroon when unripe, turning mid-reddish or orange-brown, the margins slightly raised, dehiscent along both sutures. Seeds 6.1–8.2 mm long, 4–5.8 mm wide, compressed, elliptic or circular, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, regular, U-shaped, 90–95%, symmetrical. Chromosome number: 2n = 52 (González et al. 1967; Pan & Brewbaker 1988). Figs. 64, 65.

Phenology. Flowering: Venezuela and Colombia: (August–) September–November; Ecuador and Peru: (February–) April–August (–October). Fruiting: Venezuela and Colombia: (November–) January–May (–June); Ecuador and Peru: (March–) June–September (–November). Partially deciduous.

Distribution (Fig. 66). *Leucaena trichodes* is the only species in the genus that grows naturally south of the equator or indeed in South America, where it occurs across the northern coastal regions of Colombia (Bolívar and Magdalena) and Venezuela (Aragua, Distrito Federal, Miranda, Trujillo, Yaracuy, and Zulia), and in coastal provinces of Ecuador and Peru as far south as 13°S in the departments of Cuzco and Apurimac. A 1905 collection (*Sargent 4*), labelled "expedition to Chile" was almost certainly collected in or near Callao, the port of Lima in Peru; *L. trichodes* has not been recorded from as far south as Chile. It is not clear whether the relatively common and widespread occurrence of

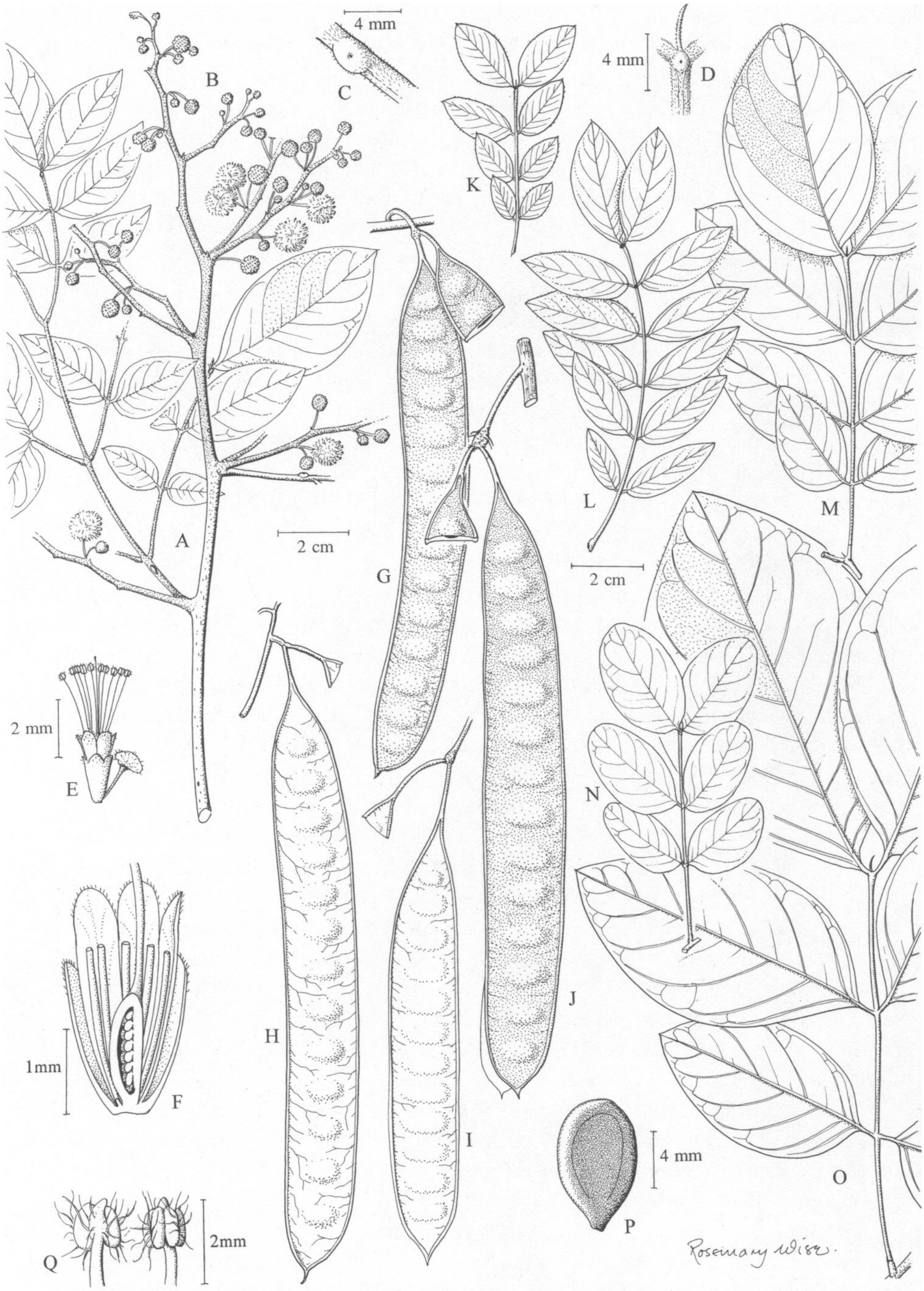


FIG. 64. *Leucaena trichodes*. A. Leaf. B. Flowering shoot. C. Petiolar nectary. D. Rachis nectary. E. Flower. F. Longitudinal section of flower. G. Pod. H. Pod. I. Pod. J. Pod. K–O. Pinnae showing variation in leaflet size and shape. P. Seed. Q. Anthers. (Based on: A–F, *Hughes 104*; G, M, *Hughes 1200*; H, L, *Hughes 760*; I, N, *Hughes 1021*; J, O, P, *Hughes 1195*; K, *Sargent 4*; Q, *Hughes 1017*.)

FIG. 65. *Leucaena trichodes*. Reproduced from Jacquin, *Hort. Schoenbr.* 3: 76 (Plate 394), 1798. a. Flower. b. Hairy anther. c. Calyx and corolla. d. Peltate bract. e. Capitulum and calyx. Courtesy of Royal Botanic Gardens, Kew.

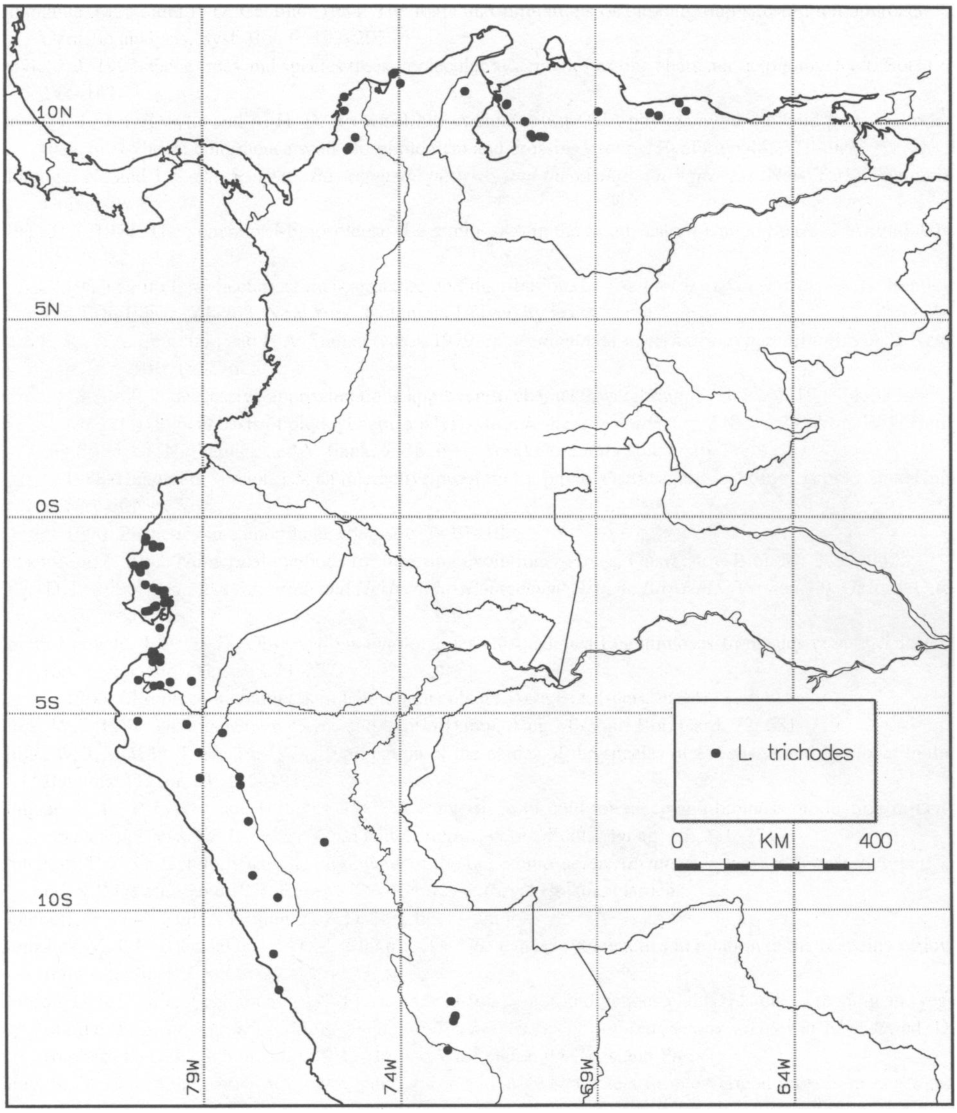


FIG. 66. Distribution of *L. trichodes*.

L. trichodes in Hispaniola (both in the Dominican Republic and Haiti) indicates that it is native there or is the result of an early (pre-1821) introduction and subsequent naturalization and spread. In both South America and Hispaniola, *L. trichodes* occurs primarily in dry deciduous tropical forest and dry thorn forest. Associated trees include species of *Albizia, Caesalpinia, Cedrela, Ceiba, Coursetia, Geoffroea, Guazuma, Mimosa, Myrospermum, Prosopis,* and *Senna*; 0–1500 (–2300) m.

Vernacular names. *Arabisco* (Peru: Huánuco), *beranero* (Colombia: Bolívar), *cañafistula de monte* (Colombia: Santa Marta), *capra (chapra)* (Ecuador: El Oro, Loja, Guayas), *chalón* (Ecuador: Guayas), *chamba* (Peru: Cuzco, Macbride 1943), *mihan (miham)*, *pela caballo* (Ecuador: Manabí), *platanito* (Colombia: Bolívar), *ramón* (Venezuela: Aragua, Trujillo), *vainita* (Venezuela: Trujillo), *veranero* (Colombia: Bolívar, Britton & Killip 1936), *yerba de la lancha* (Peru, Macbride 1943).

REPRESENTATIVE SPECIMENS. **Dominican Republic.** AZUA: Hato del Padre, nr San Juan, valley of San Juan N of Azua, 18°40′N, 70°03′W, *Ekman 13458* (GH, US); between Baní and Azua, 18°19′N, 70°29′W, *Liogier 25918* (NY); nr Loma Vieja, *M. Mejía 173* (NY); Azua, nr Santo Domingo, 18°28′N, 70°46′W, *Rose 4095* (NY, US).—BARAHONA: San Yaque nr Barahona, 18°18′N, 71°09′W, *Fuertes 685* (NY, US).—PERAVIA: 17 km W of Baní, or 2–3 km SE of Cruce de Ocoa on the Azua to Bani rd, 18°20′N, 70°28′W, *Zanoni 11823* (GH, NY).—SAN JUAN: Valle de San Juan, 0.5 km from Las Matas de Farfán, rd to El Cercado in garden, 18°52′N, 71°31′W, *Zanoni 27956* (GH, NY).—SANTO DOMINGO: in "manigua," rd from San José de Ocoa, *Liogier 20620* (NY, US); Santo Domingo, *Rose 3906a* (US). **Haiti.** Tout de Bolosse, *W. Bush s.n.* (US); on the Massif de la Pelle nr the Hospital in Port-au-Prince, 18°33′N, 72°17′W, *Ekman 2044* (GH, K, NY, US); Petionville, 18°30′N, 72°16′W, *Ekman 6460* (A).

Colombia. BOLÍVAR: nr small village of Pontezuela, 10 km inland, 25 km NE of Cartagena, 10°39′N, 75°24′W, *Hughes 760* (FHO, K); nr Palmitos, 9°22′N, 75°16′W, *Romero 9816* (F, MO, NY); nr Carmen de Bolívar, 9°37′N, 75°07′W, *Romero 10001* (MO).—MAGDALENA: nr Santa Marta, 11°14′N, 74°10′W, *Espina 85* (F); mule trail to Pueblito, Parque Nacional Tayrona, 11°00′N, 73°58′W, *Kirkbride 2532* (CAS, NY). **Ecuador.** EL ORO: nr Río Arenillas about 60 m from the Panamerican Hwy, 3°34′S 80°04′W, *Albert de Escobar 728* (NY); a few km SW of Arenillas, 3°34′S 80°04′W, *Albert de Escobar 1348* (NY); nr Huaquillas, 3°27′S 80°13′W, *Holm-Nielsen 22850* (AAU); nr main coast hwy between La Avanzada and Arenillas, 5 km E of Arenillas, 3°41′S 80°04′W, *Hughes 1013* (FHO, K, MEXU, QAME); Chacres, 3°32′S 80°11′W, *Paredes 6* (MO).—ESMERALDAS: nr Teaono, *Acosta Solís 12084* (F).—GUAYAS: rd from Guayaquil to Salinas, Santa Elena Peninsula, 2°15′S 80°11′W, *Anderson 2406* (MO); nr El Progreso, 2°24′S 80°26′W, *Asplund 15312* (NY); island of Puná, 2°49′S 80°05′W, *Barclay 447* (F, US); Guayaquil, nr the Escuela de Bellas Artes in Guayaquil, 2°10′S 79°54′W, *Alicia Delgado 63* (MO); nr the Río Chongón, nr Guayaquil, 2°17′S 80°13′W, *Alicia Delgado 89* (MO); Km 63, rd from Santa Elena to Guayaquil, 2°24′S 80°27′W, *Dodson 11020* (MO); 9 km SE of Cascol, rd to Guayaquil, Guayas-Manabí border, 1°43′S 80°27′W, *A. Gentry 12233* (US); Capeira, 22 km N of Guayaquil, rd to Daule, 2°00′S 79°58′W, *A. Gentry 54766* (MO, NY); nr Pedro Carbo, 1°48′S 80°14′W, *Haught 3014* (A, F, UC, US); rd N from Daule to Palestina, 5 km S of Santa Lucía, 1°52′S 80°06′W, *Hughes 1008* (FHO, K, MEXU, QAME); 34.5 km E of Cerecita, Km 16 Guayaquil to Playas rd, 2°11′S 79°58′W, *MacBryde 462* (MO, NY, US); nr Durán, 2°11′S 79°50′W, *Rose 23606* (GH, NY, US).—LOJA: 8 km from Malacaros, rd to El Tambo, 4°11′S 79°17′W, *Holm-Nielsen 22784* (AAU); nr rd S and W from Macará to Zapotillo, 15 km W of Macará, above Río Macará, 4°17′S 80°04′W, *Hughes 1017* (FHO, K, MEXU, QAME); Hacienda La Ceiba, 8 km N of Zapotillo, 4°18′S 80°14′W, *Samaniego & Vivar 12* (US).—MANABÍ: between Salina and Chone, 0°42′S 80°15′W, *Acosta Solís 10629* (F), *Rogers 14991* (MO); nr coast, outskirts of Peñas, Bahía de Caraquez, 0°37′S 80°27′W, *Cerón 6721* (K, NY); between San Vicente and Canoas, 0°32′S 80°26′W, *Cerón 6738* (NY); 15 km N of Chone, rd to El Carmen and Santo Domingo de los Colorados, coastal hills about 20 km inland from Pacific coast, 0°45′S 80°04′W, *Hughes 994* (FHO, K, MEXU, QAME); 1 km NW of Jipijapa immediately above bypass, 1°21′S 80°36′W, *Hughes 997* (FHO, K, MEXU, QAME); nr Cañitas, 6 km E of Sancán towards Sucre, 30 km S of Portoviejo, 1°13′S 80°27′W, *Hughes 1195* (FHO, K, MEXU, QAME); 2 km N of Manantiales, 10 km N of Puerto de Cayo, track through Motete to Montecristi, 23 km SW of Montecristi, 1°14′S 80°44′W, *Hughes 1197* (FHO, K, MEXU, QAME); nr Los Amarillos, main rd from Chone S and W through Tosagua to Rocafuerte and Portoviejo, 0°47′S 80°15′W, *Hughes 1200* (FHO, K, MEXU, QAME). **Peru.** AMAZONAS: nr Bagua, 10–10.5 km S of Mayo, 4 km S of Salinas, Km 489 Oleoducto Nor Peruano, 5°30′S 78°30′W, *Knapp 7570* (GH, K, MEXU, NY, TEX).—ANCASH: nr Anta, Fortaleza Valley, 9°41′S 77°07′W, *Anderson 475* (UC); between Carhuas and Caras, 9°07′S 77°45′W, *C. Vargas 10297* (US).—APURIMAC: Río Pachachaca, 20 km N of Abancay, *Goodspeed 11522* (K); Albancay, 20 km N of Albancay on the Río Pachachaca, 13°34′S 72°49′W, *Stork 10522* (F, UC).—CAJAMARCA: 0.5 km E of Pucará, 6°00′S 79°06′W, *A. Gentry 22700* (MO); Santa Cruz, Catache-Cumbil, 6°39′S 79°04′W, *López & Sagástegui 5193* (GH, MO); Celendín, between Limón and Balsas, 6°38′S 78°04′W, *J. G. Sánchez 5382* (MEXU, NY); Río Marañón Valley, Balsas to Celendín rd 7–13 km from Balsas, 6°50′S 78°03′W, *D. N. Smith 6186* (F, MO, NY, TEX); nr Mandanguia, *Woytkowski 6870* (CAS, F, GH, K, MO, NY, TEX, UC, US).—CUZCO: La Convención, on railroad tracks S of Quillabamba between Km 169 and 171, 12°20′S 72°44′W, *Croat 50954* (F, MO); Pawac Porterage, one hour float by raft below Hda Pomobamba, *E. W. Davis 1269* (F, K, MO, NY); before Echarate, Convención, 12°42′S 72°37′W, *C. Vargas 7419* (MO).—HUÁNUCO: nr Tingo María, Km

135 rd from Huánuco to Pucallpa, 8°17′S 75°56′W, *J. A. Burgos 38* (F, US).—LA LIBERTAD: Yataz, Marañón River across from Chaguay, Pataz, 7°45′S 77°51′W, *Young 1201* (F).—LIMA: Lima, *Cuming 985* (K); Chancay, nr Sayan, 11°07′S 77°14′W, *Ferreyra 3501* (US); Callao, 12°02′S 77°06′W, *Sargent 4* (A).—PIURA: Huancabamba, nr Ribera, left side of Río Huancabamba, 5°17′S 79°24′W, *Angulo 2107* (F); in the Pariñas Valley, *Haught 132* (NY, US).—TUMBES: Lechuagal, between Papayol and Matapalo, 3°41′S 80°15′W, *Ferreyra 10676* (MO, US); Piura, 5°12′S 80°38′W, *Schimpff 1156* (A); Zarumilla, bosque Nacional de Tumbes nr Campo Verde, 3°31′S 80°16′W, *D. R. Simpson 470* (F, GH, NY, US); Tumbes, between Ricaplaya and Casa Blanqueada, *Weberbauer 7739* (F, US). **Venezuela.** ARAGUA: Maracay, cerro behind Inst. de Botánica Agrícola in U.C.V in Maracay, 10°15′N, 67°37′W, *Cárdenas 1764* (F); nr La Vielón, *Curran 1949* (NY); between San Mateo and Victoria, old rd from Caracas to Maracay, 10°11′N, 67°24′W, *Hughes 768* (FHO, K); slopes above Maracay, 10°15′N, 67°37′W, *L. Williams 10324* (F, US).—DISTRITO FEDERAL: nr Cotiza, Caracas, *E. Delgado 255* (US); Jardín Botánico in Caracas on dry hillsides, 10°30′N, 66°52′W, *Steyermark 100210* (NY); Cotizo Alto, DF, *L. O. Williams 9955* (F, US).—MIRANDA: rd from Maracaibo to Altagracia, 6 km from the turnoff of the Maracaibo to Coro rd, 10°38′N, 71°29′W, *Bunting 5485* (NY); Hda. El Volcán, nr Santa Lucía, 10°18′N, 66°42′W, *Pittier 8253* (GH, NY, US); nr Los Mariaches, Miranda, *Pittier 11963* (A, NY, US).—TRUJILLO: Betijoque, rd from between Agua Viva and Valerita towards Carora, 9°37′N, 70°36′W, *Bunting 5850* (NY); rd between Carache and Cuicas, 9°38′N, 70°18′W, *Cárdenas 3181* (US); 15 km NE of Agua Viva, main rd to Barquisimeto, 9°42′N, 70°39′W, *Hughes 770* (FHO, K); 6 km SW of Cuicas, rd to Monay and Valera, 45 km NE of Valera, 9°39′N, 70°25′W, *Hughes 775* (FHO, K).—YARACUAY: W part of Cerro de Campo Elias, rd to Aroa, 10°17′N, 68°56′W, *Benítez 1038* (F).—ZULIA: 2 km S of El Guanabano, Bolívar, 10°29′N, 71°15′W, *Bunting 8149* (NY); 39 km E of El Venado, 10°02′N, 70°48′W, *C. D. Johnson 3853-85* (MO); E facing limestone slopes above Río Cachirí, between Cerro El Brillante and Cerro La Cruz, W of Hacienda La Carpa, or 12 km W of Parcelamiento Cachirí, 10°48′N, 72°20′W, *Steyermark 123403* (MO).

Hairy anthers (Figs. 14, 65) are a feature of the majority of species of *Leucaena*, and are unique within the Mimosoideae (Hughes 1997a). They were noted before the genus was established, as section *Trichodae* of Willdenow's *Acacia*, and in the descriptions of *Acacia trichandra* and *A. trichodes*, species later transferred to *Leucaena*, which were named with reference to their hairy anthers. The hairs on the anthers of *L. trichodes* are particularly conspicuous, accounting for its earlier description as the "hairy-anthered Acacia," *Acacia trichodes*.

Leucaena trichodes is one of a group of closely allied large-leaflet taxa that traditionally has been taken to include *L. macrophylla* and *L. multicapitula*. The distinction of *L. multicapitula* as a separate species from *L. trichodes*, which has very similar leaves and pods, was doubted by several authors (Janzen & Liesner 1980; Brewbaker 1987a; Zárate 1994). Detailed survey of anther and pollen morphology (Hughes 1997a) revealed a suite of discrete characters that distinguish these two species (discussed under *L. multicapitula*), fully justifying treatment of *L. multicapitula* as a separate species.

As discussed more fully under *L. macrophylla*, the distinction of *L. trichodes* from *L. macrophylla* is more problematic. Morphological analysis failed to reveal any discrete characters that distinguish these two species. They appear to form a widespread (northern Mexico to Peru) but highly disjunct and somewhat variable (in terms of leaf and pod dimensions) alliance, which shares a suite of pollen and anther characters (porate pollen apertures, polyads of acalymmate monads, hooded apicula on the anthers, and persistent tapetal membranes).

The origin, whether native or introduced, of *Leucaena* trees in Hispaniola described as *L. pseudotrichodes*, based on material from Santo Domingo, remains uncertain. What is clear is that this species has been present on Hispaniola at least since 1821 and is now widespread in both the Dominican Republic and Haiti. Most authors have treated *L. pseudotrichodes* as conspecific with *L. trichodes* (e.g., Bentham 1875; Brewbaker 1987a), but leaf and fruit morphology could indicate affinity equally with *L. macrophylla* or

L. multicapitula. The unusual pollen morphology of the one specimen examined (*Liogier 20620*), which has irregularly shaped, apparently loosely acalymmate monads that are colpoidorate, compared to the strongly asymmetric porate acalymmate monads of *L. trichodes,* casts doubt upon the identity of this little-known species from Hispaniola, and suggests possible affinities with the colporate pollen grains of *L. multicapitula*. However, *L. multicapitula* has pollen in calymmated tetrads (Fig. 15B), terminal twice-branched flowering shoots, concave petiolar nectaries, and anthers lacking an apiculum, characters absent from the material from Hispaniola. Given that *L. macrophylla* and *L. trichodes* are very closely related and are tentatively treated here as distinct species based on flowering shoots and disjunct distributions, pending more detailed studies (see *L. macrophylla*), it is difficult to consider *L. pseudotrichodes* as conspecific with one or the other with certainty. The treatment of *L. pseudotrichodes* as conspecific with *L. trichodes* should be seen in this light.

Segregation of the other species treated here as conspecific with *L. trichodes* (*L. canescens, L. bolivarensis,* and *L. colombiana*) relied heavily on shoot, leaflet, and pod pubescence, which are now seen to be highly variable locally and unreliable. In their taxonomic treatment of *Leucaena* for Colombia, Britton and Killip (1936) described *L. colombiana* and *L. bolivarensis* as new species from adjacent departments in northern Colombia, but made no reference to their possible affinities to *L. trichodes* from Venezuela or *L. canescens* from Ecuador.

Leucaena trichodes var. *acutifolia* was distinguished from typical *L. trichodes* solely by its acute or acuminate leaflets (Macbride 1943). Leaflet shape is highly variable within *L. trichodes* (Fig. 64), as it is within the other species with large leaflets (e.g., *L. lanceolata*). Acute, acuminate, and rounded leaflets can frequently be found within populations and use of this character alone does not constitute grounds for recognition of a distinct variety. Although the type of var. *acutifolia* could not be located, I am confident that var. *acutifolia* is no more than one extreme of the leaf variation. Leaflet size also varies greatly within *L. trichodes* (Fig. 64), with a clear trend from large leaflets in the north in Colombia, Venezuela, and central Ecuador, to smaller leaflets in the south in southern Ecuador (Provinces of Loja and El Oro) and Peru. Specimens from the extreme south of the distribution in the Departments of Apurimac and Cuzco in Peru have markedly smaller leaflets. More detailed studies will be required to see whether this variation merits recognition at the infraspecific level.

Leucaena trichodes is particularly common following disturbance, in secondary vegetation, and along roadsides; in some areas it is the dominant woody cover in abandoned milpas and forms weedy thickets on open ground. The wood is widely used for posts, poles, firewood, and occasionally sawtimber, and the leaves as fish poison (Cajamarca, Peru) or livestock feed, although toxicity leading to hair loss in animals (hence the vernacular name *pela caballo*) is frequently reported.

19. Leucaena shannonii Donnell Smith, Bot. Gazette 57: 419. 1914.—TYPE: EL SALVADOR. Cuscatlán: Cojutepeque, 13°42′N, 88°56′W, 900 m, Dec 1892, *Shannon 5032* (lectotype, here designated: US!).

Small to medium-sized tree, 10–12 (–15) m tall, 20–30 (–50) cm bole diameter, typically branchy when young, older trees with a short clear bole to 5 m, spreading angular branching, and an open rounded crown. Bark on young branches smooth, mid-grey or grey-brown, inner bark salmon pink, on bole darker grey-brown and rougher with shallow rusty orange-brown vertical fissures, inner bark cream. Shoots terete, pale to mid-brown. Stipules 2.8–3.9 mm long, lanceolate, with asymmetric basal wings, venation and midrib prominent, ciliate on wing margins, early caducous. Leaves (6–) 10–15 cm long, 8–12 cm wide; petioles (including pulvinus) 15–30 mm long, with a single, pale yellow-green, sessile, rounded, elliptic, dome-shaped or truncate-conic nectary, 2–3 × 1 mm, at the distal end on adaxial side of petiole; rachis 3–9 cm long, with a small elliptic conic nectary at the distal end, apex of rachis extending beyond the terminal pinnae as a pointed, pubescent, reddish brown mucro 1.5–2 mm long, curling when dry; pinnae (2–) 4–6 (–7) pairs; pinnular rachis 3–8 cm long, ridged, moderately pubescent, with 1 (–2) minute discoid nectaries at base of terminal pairs of leaflets; leaflets (5–) 7–13 pairs per pinna, (13–) 16–18 (–20) mm long, 5–7 mm wide, nearly sessile, the basal leaflets shorter, the distal pair shorter and wider, distinctly inequilaterally asymmetric about the midvein, the distal pair more extremely asymmetric, linear-oblong, obtuse to rounded apically, rounded to truncate basally, glabrous above, sparsely pubescent below with hairs concentrated at the base of main veins, secondary venation visible and brochidodromous. Capitula 11–12 mm in diameter at anthesis, in fascicles of 2–6 at nodes on long erect unbranched terminal shoots, often with the leaves suppressed and the flower heads and pods exposed on ends of otherwise naked shoots, each capitulum with 80–140 flowers (Fig. 13A); peduncles (14–) 18–19 mm long, angled, densely pubescent with an involucre of bracts at distal end. Flowers subtended by peltate bracts, 2–3 mm long, 0.7–1 mm in diameter, ciliate along margin; calyx 2.1–2.3 mm long, glabrous, finely ciliate along margins, pale whitish green; petals 3.3–3.8 mm long, free, glabrous, pale yellow-green; filaments 7.6–9.3 mm long, white; anthers with a distal tuft of hairs, white, apiculum absent; ovary (1.6–) 1.8–2 mm long, short-stipitate or subsessile, with short velutinous pubescence, with 18–20 ovules, style 6–9.5 mm long, white, with a terminal tubular stigma, included. Pods 1–2 (–3) per capitulum, (9–) 12–16 (–18) cm long, (11–) 14–16 (17) mm wide, pendulous on sturdy 6–10 mm long stipes, linear-oblong, acuminate, or sometimes obtuse apically, sometimes with a short beak, apparently readily broken off when dry, narrowly planocompressed, 12–20-seeded, valves mid- to reddish brown, glabrous or pubescent, chartaceous, the margins slightly thickened, dehiscent along both sutures. Seeds 6.2–7.5 (–8.5) mm long, (4.5–) 4.7–5.6 (–6.3) mm wide, compressed, flattened, ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, symmetrical. Chromosome number: 2n = 56 (Hutton 1981; Pan & Brewbaker 1988). Fig. 67.

Phenology. Flowering August–November (–February); fruiting February–March; partly or completely leafless February–March.

Distribution (Fig. 68). *Leucaena shannonii* occurs widely in dry deciduous tropical forest, secondary vegetation, and fencelines from southern Mexico (Campeche and Chiapas only) south through Guatemala (only in Jutiapa and Jalapa), El Salvador, Honduras to south-central Nicaragua as far south as Chontales. The distribution is highly disjunct with isolated occurrences in the southern Yucatán Peninsula and the central depression of Chiapas, and a scattered distribution through Central America, mainly in the seasonally dry inland valleys, and only rarely (in El Salvador) reaching the Pacific coast. Associated trees include species of *Albizia, Caesalpinia, Calicophyllum, Cassia, Cochlospermum, Cordia, Crescentia, Dalbergia, Enterolobium, Gliricidia, Guazuma, Gyrocarpus, Karwinskia, Lonchocarpus, Luehea, Lysiloma, Myrospermum, Platymiscium, Poeppigia, Simarouba, Swietenia, Tabebuia,* and *Thouinidium*; (5–) 400–1000 (–1450) m.

Vernacular names. *Barba de jelote* (Olancho, Honduras), *cascahuite* (San Miguel, El Salvador), *frijolillo* (Honduras and Nicaragua), *guacamayo* (Intibucá, Honduras), *guaje*

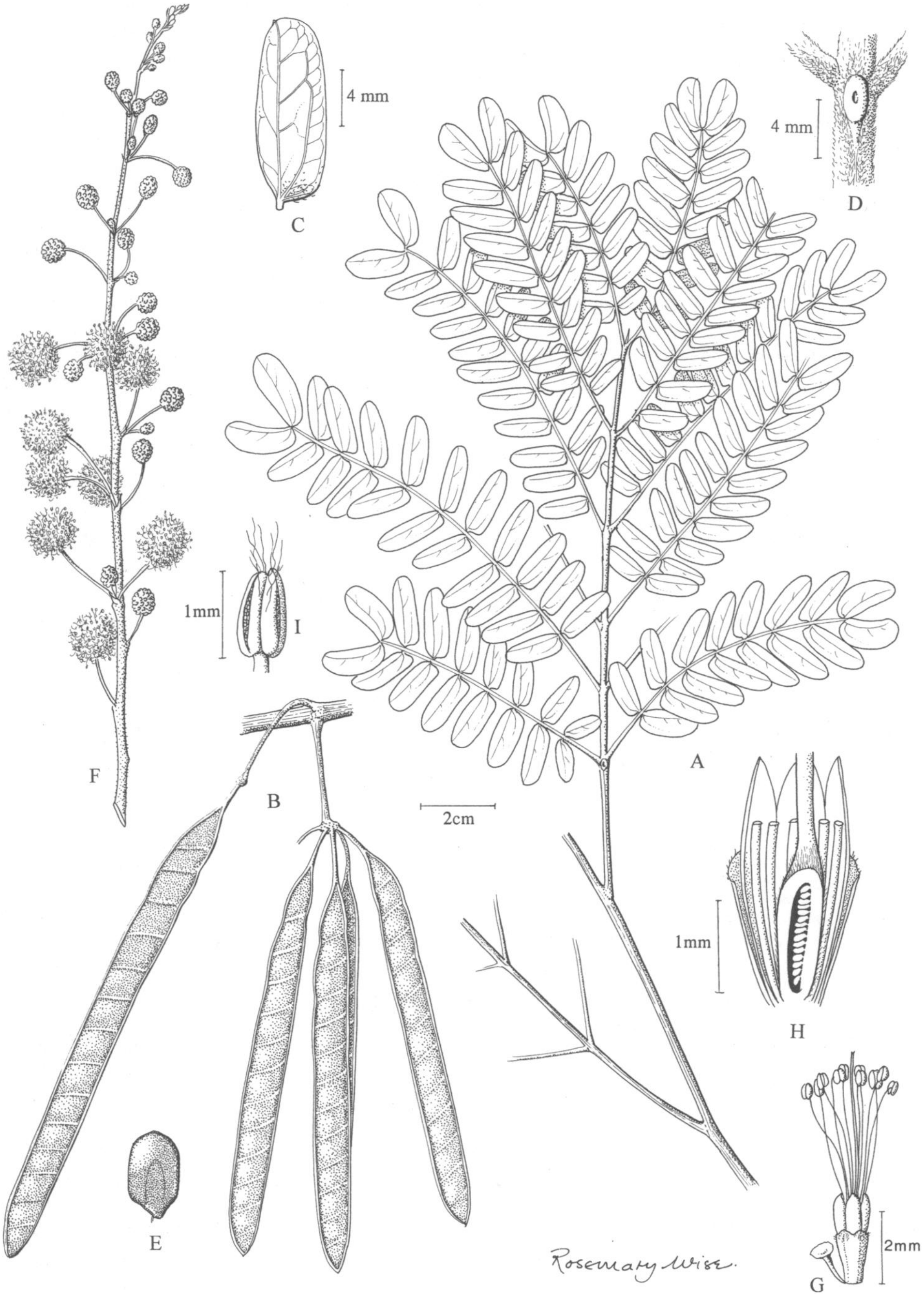


FIG. 67. *Leucaena shannonii*. A. Leaf. B. Pods. C. Leaflet. D. Petiolar nectary. E. Seed. F. Flowering shoot. G. Flower. H. Longitudinal section of flower. I. Anther. (Based on: A–E, *Hughes 933*; F–H, *Hughes 282*; I, *Hughes 1714*.)

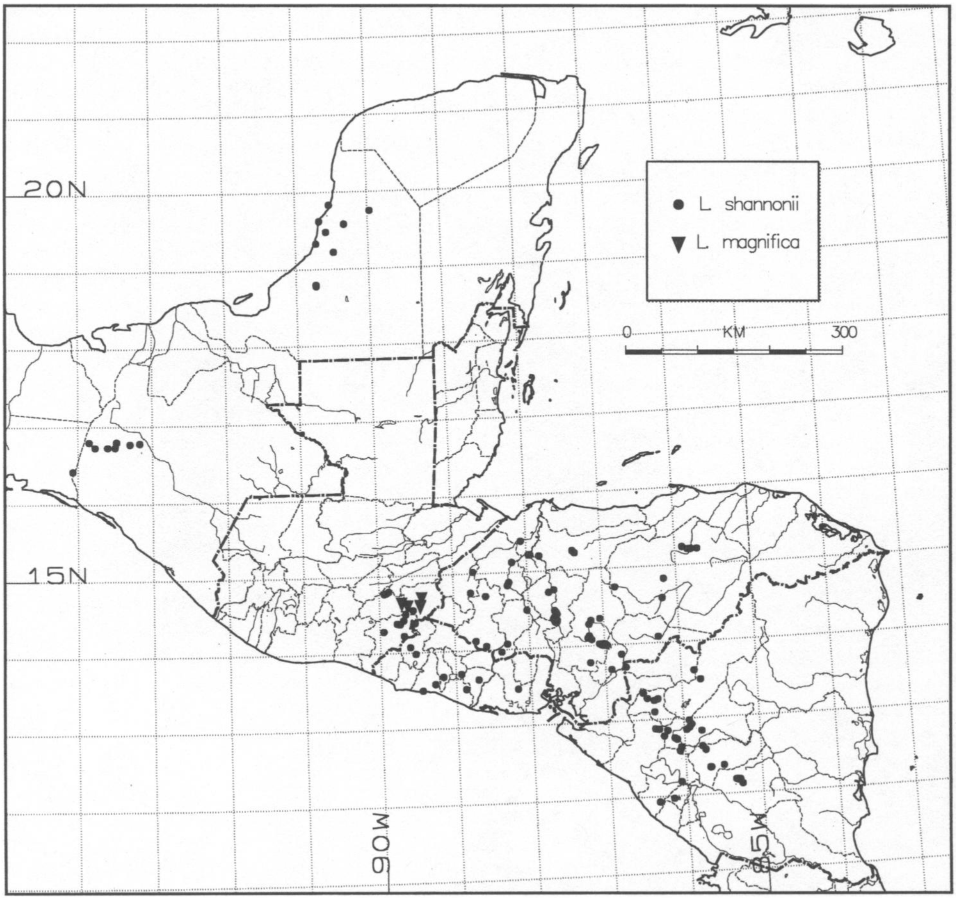


FIG. 68. Distribution of *L. shannonii* and *L. magnifica*.

(El Salvador, Guatemala, Honduras, Mexico, Nicaragua), *guash* (Chiapas, Mexico), *guashín* (Campeche, Mexico), *guajillo* (Jutiapa, Guatemala), *memblén* (Honduras, Francisco Morazán), *vainillo* (Jutiapa, Guatemala, and Estelí, Nicaragua).

REPRESENTATIVE SPECIMENS. **Mexico.** CAMPECHE: 28 km N of Escárcega, rd to Champotón, 18°47′N, 90°44′W, *Cabrera 2050* (CAS, MEXU, MO); rd to the Ingenio del Sol off the main Champotón to Campeche rd, 19°29′N, 90°35′W, *Cabrera 15204* (MEXU); Champotón, Xkeuil, 19°35′N, 90°20′W, *Chan 4243* (K); Pustunich, rd to Yacasay, nr Champotón, 19°13′N, 90°29′W, *Chan 4657* (K); 20 km W of Holpechén, rd to Campeche, 19°45′N, 89°58′W, *Hughes 506* (FHO, K, MEXU); close to the Caribbean coast, 3 km S of Champotón, 60 km S of Campeche, 19°20′N, 90°43′W, *Hughes 933* (FHO, K, MEXU).—CHIAPAS: steep ravine adjacent to Hwy 190, about 20 km W of Ocozocoautla, 16°41′N, 93°31′W, *Breedlove 28353* (CAS, MEXU, MO, NY); in large limestone sink called La Cima, about 15 km WNW of Ocozocoautla, 16°48′N, 93°29′W, *Breedlove 29020* (CAS, MEXU, MO, NY, TEX); 5 km N of Cintalapa, 16°44′N, 93°44′W, *Breedlove 36595* (CAS, MEXU, MO); nr Berriozabal, 16°48′N, 93°17′W, *Breedlove 49088* (CAS, MEXU); village of Francisco I. Madero, 15 km N of Cintalapa de Figueroa W of the central depression of Chiapas, 16°48′N, 93°51′W, *Hughes 1352* (AAU, FHO, K, MEXU, NY); rd 30 km from Tepanatepec NE towards Tuxtla Gutiérrez in hills immediately above the coastal plains nr the Chiapas-Oaxaca border, 16°25′N, 94°04′W, *Hughes 1492* (FHO, K, MEXU, MO, NY); rd E from Cintalapa de Figueroa towards Ocozocuautla and Tuxtla Gutiérrez nr the turnoff to Jiquipilas, 5 km from

Cintalapa, 16°41′N, 93°37′W, *Hughes 1676* (E, FHO, K, MEXU, MO, NY); above Encañada, old rd from La Chacona to San Fernando, 16°47′N, 93°10′W, *Miranda 5533* (MEXU, US); above Chacona, rd to San Fernando, 16°48′N, 93°13′W, *Miranda 6493* (MEXU); 3 km W of Los Amates, *Mosquin 6705* (GH); 2 km SW of Río de Oro nr Cintalapa de Figueroa, *Sousa 6637* (CAS, MEXU, MO, UC); entrance to the Parque "El Aguacero de Derna," 14 km W of Ocozocuautla, 16°44′N, 93°30′W, *Sousa 6850* (CAS, MEXU).

El Salvador. LA LIBERTAD: main rd running S from San Salvador towards the Pacific coast, 10 km N of La Libertad, 13°35′N, 89°17′W, *Hughes 1248* (FHO, K, MEXU, NY); coastal hwy running W from La Libertad to Acajutla 5 km W of El Zonte nr turnoff to Teotepique, about 1 km inland from Pacific coast, 13°30′N, 89°27′W, *Hughes 1251* (FHO, K, MEXU).—LA PAZ: Zacatecoluca, 13°30′N, 88°52′W, *Calderón 336* (GH, NY, US).—SAN MIGUEL: San Miguel, 13°29′N, 88°11′W, *Calderón 2105* (GH, NY, US).—SAN SALVADOR: Cerro San Jacinto, 13°40′N, 89°10′W, *Calderón 2245* (US).—SAN VICENTE: vicinity of San Vicente, 13°37′N, 88°42′W, *Standley 3477* (EAP, F).—SANTA ANA: 14 km NW of Santa Ana, 2 km along side track from San Cristóbal rd to La Parada and Piñalón, 14°04′N, 89°36′W, *Hughes 1245* (FHO, K, MEXU, NY); vicinity of Santa Ana, 13°59′N, 89°32′W, *Standley 19686* (GH, NY, US). **Guatemala.** JALAPA: 3 km N of San Manuel Chaparón, rd to San Luís Jilotepeque, 14°33′N, 89°33′W, *Hughes 733* (FHO, K).—JUTIAPA: 10 km W of Jutiapa, rd towards Cuilapa, 14°17′N, 89°57′W, *Hughes 402* (FHO, K); 6 km N of Asunción Mita, close to Estanzuela, 14°22′N, 89°44′W, *Hughes 408* (FHO, K); rd SE from Jutiapa to San Cristóbal Frontera and Guatemalan frontier, 6 km from San Cristóbal, nr N shore of Laguna Atescatempa, 14°13′N, 89°41′W, *Hughes 1267* (FHO, K, NY, TEX); S-facing slopes of Volcán Suchitán, 12 km E of Jutiapa nr Las Carboneras, 14°23′N, 89°46′W, *Hughes 1389* (EAP, FHO, K, MEXU, NY); rd nr Jutiapa, 14°46′N, 89°56′W, *C. D. Johnson 150-68* (MO); vicinity of Jutiapa, 14°47′N, 89°54′W, *Standley 75206* (F); plains and swampy ground along the railroad between Agua Blanca and Amatillo, 14°30′N, 89°39′W, *Steyermark 30435* (F). **Honduras.** COMAYAGUA: nr Yaramuela, 5 km E of La Paz, Comayagua valley, 14°19′N, 87°38′W, *Hughes 282* (FHO, MEXU); 5 km N of Lejamaní, rd towards El Taladro in the Comayagua Valley, 14°22′N, 87°40′W, *Hughes 310* (FHO, MEXU); 5 km E of La Paz nr the Río Humuya, Comayagua Valley, 14°19′N, 87°38′W, *Hughes 311* (FHO, MEXU); 2 km N of Meambar, rd to Palmital, 14°43′N, 87°43′W, *Hughes 396* (FHO, K); Comayagua Valley, 14°20′N, 87°39′W, *Molina 5755* (EAP, F); vicinity of Comayagua, 14°26′N, 87°37′W, *Standley 5217* (EAP, F).—COPÁN: 32 km from Sant Rosa de Copán in the valley of the Río Chamelecón, 15°01′N, 88°44′W, *Chaplin C433* (FHO); 5 km from Santa Rosa de Copán, valley of the Río Chamelecón, 14°45′N, 88°46′W, *Chaplin C436* (FHO); rd E and S from Santa Rosa de Copán towards Gracias about 15 km from Santa Rosa in the valley of the Río Licatuyo, 14°42′N, 88°34′W, *Hughes 1420* (EAP, FHO, K, MEXU, NY).—CORTÉS: nr Potrerillos, valley of the Río Ulúa, 15°13′N, 87°57′W, *Chaplin C430* (FHO); La Barca, valley of the Río Ulúa, 15°13′N, 87°58′W, *Chaplin C437* (FHO); nr Chamelecón, 15°24′N, 88°04′W, *Dickson 392* (EAP); Montaña El Carmen, *Molina 3521* (EAP, F).—EL PARAÍSO: 30 km NE of Danlí in the valley of Jamastrán, 14°05′N, 86°17′W, *Hughes 280* (FHO, MEXU); 12 km N of Morolica, rd to San Lucas, 13°41′N, 86°55′W, *Hughes 751* (FHO); 3 km N of Oropolí, 13°52′N, 86°47′W, *Hughes & Styles 127* (FHO).—FRANCISCO MORAZÁN: 30 km E of Tegucigalpa in the Valle Amarateca, 14°17′N, 87°12′W, *Hughes 32* (FHO, MEXU); rd from Sabana Grande E and S towards Nueva Armenia about 12 km NW of Nueva Armenia, nr Monte Grande, 13°47′N, 87°12′W, *Hughes 1204* (EAP, FHO); 4 km S of Talanga, slopes above Río Choluteca, 14°21′N, 87°03′W, *Hughes & Styles 116* (FHO); along Chaguite rd nr El Zamorano, 14°00′N, 87°00′W, *Molina 366* (EAP, F, GH, US); old rd from Suyapa to Tegucigalpa, 14°05′N, 87°10′W, *Molina 1468* (EAP, F, GH, MO, US); 2 km S of the Escuela Agrícola Panamericana EAP, campus at El Zamorano, 14°00′N, 87°00′W, *Pfeifer 1606* (US); 32 km from Tegucigalpa rd to Olancho, 14°20′N, 87°10′W, *Semple 80* (US); nr El Chile close to Tegucigalpa, 14°08′N, 87°12′W, *Standley 26739* (EAP, F, GH, US); region of Agua Amarilla above El Zamorano, 14°01′N, 87°04′W, *Standley & Williams 2199* (EAP); La Granja along the Río Choluteca nr Tegucigalpa, 14°06′N, 87°13′W, *L. O. Williams 10500* (EAP, F).—INTIBUCÁ: rd SSW, 25 km from La Esperanza towards Concepción and the El Salvador border nr Hoja Blanca, 14°04′N, 88°18′W, *Hellin & Hughes 20* (EAP, FHO, K, MEXU, NY); close to Caserio del Carrizal nr the rd running SW from Concepción and Camasca to San Juan de Dios and San Antonio, about 2 km NE of San Juan de Dios, 13°58′N, 88°23′W, *Hellin & Hughes 21* (EAP, FHO, K, MEXU, NY); 2 km W of Jesús de Otoro, 14°30′N, 88°01′W, *Hughes 716* (FHO, K, MEXU).—LEMPIRA: track SW from Candelaria towards Mapulaca, about 3 km from Candelaria or about 6–7 km N of the El Salvador border, 14°03′N, 88°35′W, *Hellin & Hughes 27* (EAP, FHO, K, MEXU, NY); track NW from La Virtud towards Valladolid in rough hills N of the El Salvador border, about 6 km from La Virtud, 14°07′N, 88°43′W, *Hellin & Hughes 28* (EAP, FHO, K, MEXU, NY).—OLANCHO: side rd W from San Estéban towards the Río Grande and Corral Viejo, about 1 km W of San Estéban, 15°12′N, 85°47′W, *Hellin & Hughes 16* (EAP, FHO, K, MEXU, NY); track W from San Estéban through the Agalteca Valley, 3 km W of El Ciruelo, or 15 km W of San Estéban, 15°14′N, 85°54′W, *Hellin & Hughes 17* (EAP, FHO, K, MEXU, NY); rd to San Francisco de la Paz, 10 km from San Estéban, 15°12′N, 85°42′W, *Macqueen 43* (EAP, FHO, K, MEXU, MO); vicinity of Juticalpa, 14°35′N, 86°12′W, *Standley 17947* (A, EAP).—Santa Bárbara: Monte Grande nr Santa Bárbara in the valley of the Río Chamelecón, 15°08′N, 88°12′W, *Chaplin C432* (FHO); turnoff to San Francisco nr Santa Bárbara in the valley of the Río Chamelecón, 14°52′N, 88°15′W, *Chaplin C434* (FHO); rd S and E from Santa Bárbara towards Taulabe, valley of the Río Otoro about 7 km S of Santa Bárbara, 14°50′N, 88°16′W, *Hughes 1453* (EAP, FHO, K, MEXU, NY).—Yoro: rd E from Santa Rita towards Yoro about 4 km E of Santa Rita in low hills above the Sula Valley, 15°12′N, 87°50′W, *Hughes 1410* (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro nr La Habana at the turnoff towards Locomapa and Yorito, 26 km W of Yoro, W extremity of the Yoro Valley, 15°13′N, 87°21′W, *Hughes 1451* (EAP, FHO, K, MEXU, NY). **Nicaragua.** Boaco: rd towards Camoapa, 12°22′N, 85°30′W, *Atwood 5404* (NY); rd ESE from Empalme Boaco towards Juigalpa about 10 km W of Tecolostote, 12°21′N, 85°40′W, *Hughes 1403* (EAP, FHO, K, MEXU, NY); El Mojón, Km 86 on the rd to Rama, 12°21′N, 85°41′W, *Moreno 18601* (MEXU); San José de los Remates, Lapita, on the rd to Malacatoya, 3.5 km E of San José de los Remates, 12°35′N, 85°44′W, *Moreno 24891* (MEXU); 1–2 km SE of Santa María along the Río Fonseca, 12°38′N, 85°46′W, *Nee 27971* (NY).—Chontales: 8–10 km N of Juigalpa, rd N towards Santo Domingo and La Libertad, nr La Puerta, 12°11′N, 85°19′W, *Hughes 1399* (EAP, FHO, K, MEXU, MO, NY); Cerro de los Andes, 10 km E of Juigalpa, 12°07′N, 85°16′W, *Neill 437* (GH, MEXU, MO); Hacienda Veracruz including Cerro La Batea and Cerro Los Charcos, 12°11′N, 85°21′W, *Stevens 22392* (CAS); nr Cerro Ana María, between Juigalpa and La Libertad, 12°10′N, 85°19′W, *Stevens 22434* (CAS).—Estelí: 15 km N of Estelí, close to Panamerican Hwy, 13°15′N, 86°23′W, *Hughes 451* (FHO, MEXU); rd NW from Estelí towards San Juan de Limay nr Regadío, about 19 km NNW of Estelí, 13°17′N, 86°28′W, *Hughes 1405* (EAP, FHO, K, MEXU, NY); 8 km W of Estelí, rd to El Sauce, 13°04′N, 86°22′W, *Hughes 1436* (EAP, FHO, K, MEXU, NY); 5 km W of Condega, rd to Pueblo Nuevo, 13°21′N, 86°25′W, *Hughes & Styles 30* (FHO); Piedra Azul, El Tular, 6 km N of Estelí, 13°12′N, 86°22′W, *Laguna 272* (MO); 4 km on way to San Juan de Limay, nr Estelí, 13°22′N, 86°29′W, *Molina 23154* (EAP, F, MO, NY); El Hondal, 4 km W of Estelí, 13°06′N, 86°23′W, *Moreno 19307* (MO); 24 km N of Estelí, 13°16′N, 86°20′W, *Moreno 25167* (MEXU); 3–7 km NW of Pueblo Nuevo, 13°22′N, 86°30′W, *L. O. Williams 42377* (EAP, F, US).—Jinotega: rd between Wiwilí and El Carmen on the banks of the Río Coco, 13°37′N, 85°50′W, *Araquistain & Moreno 1552* (MO); on the banks of the Quebrada Agua Amarilla on the rd from Jinotega to Wiwilí, 13°30′N, 85°45′W, *Araquistain & Moreno 1684* (MO); vicinity of Jinotega, *Standley 9650* (EAP, F).—León: nr Bordo las Tinajas, 5 km W of La India, rd from Sebaco to Telica, 12°47′N, 86°16′W, *Hughes & Styles 82* (FHO); Santa Rosa del Peñón at the entrance to the hydroelectric station Carlos Fonseca Amador (Santa Bárbara), 6 km from the San Isidro to León rd, "El Cacao," 12°52′N, 86°20′W, *Moreno 10454* (MEXU).—Managua: N of the Colégio Centroamericano on the rd to San Isidro de la Cruz Verde, Managua, *Guzmán & Castro 27* (MO); 5 km SW of El Crucero on the rd to San Rafael del Sur nr Finca El Socorro, 11°56′N, 86°22′W, *Soza & Vanegas 201* (MO); rd along ridge of the Sierra de Managua between Hwy 12 from Managua to León and Hwy 2 the Carratera Sur, 12°04′N, 86°22′W, *Stevens 5307* (MO).—Masaya: S side of the crater of Volcán Santiago in the Parque Nacional Volcán Masaya, 11°58′N, 86°11′W, *Grijalva 4088* (MEXU).—Matagalpa: 5 km N of Darío, 12°45′N, 86°08′W, *Harmon & Fuentes 5035* (MO); N edge of Sebaco Plains, rd from San Isidro to Telica, 12°51′N, 86°13′W, *Hughes 357* (FHO, K, MEXU); rd ESE from San Ramón to Yucúl, 10 km from San Ramón SE of Matagalpa, 12°50′N, 85°46′W, *Hughes 1374* (EAP, FHO, K, MEXU, NY); Laguna Tecomapa, on the Meseta de Estrada, 12°11′N, 86°04′W, *Hughes & Styles 78* (FHO); Terrabona, Km 86 carratera del Norte, 12°44′N, 86°06′W, *Moreno 7095* (MO); 2 km N of Puertas Viejas Panamerican Hwy nr San Vicente, 12°37′N, 86°03′W, *Moreno 18280* (MO); nr Santa María de Ostúma, rd from Matagalpa to Jinotega, 12°58′N, 85°56′W, *Neill 866* (MO); nr Matagalpa, 12°55′N, 85°54′W, *Zelaya 2313* (MO).—Nueva Segovia: track SSW from Santa María beyond Palo Verde towards Prisa, valley of the Río Choluteca, 5–10 km from the Honduran border, 13°42′N, 86°44′W, *Hughes 1443* (EAP, FHO, K, MEXU, NY).

In the cladistic analysis of morphology, *L. shannonii* grouped consistently with *L. lempirana, L. magnifica,* and *L. salvadorensis*. The distinction of these four species has been doubted by some authors and most notably by Zárate (1987b, 1994), who preferred to view *L. shannonii* as a widespread polymorphic species, although he only formally recognized one subspecies *L. shannonii* subsp. *salvadorensis*. I recognize four separate species based on a limited number of discrete character states, including type and branching of flowering shoots and ovary indumentum. This is supported by patterns of variation in quantitative leaf and pod characters and by virtually allopatric distributions through Central America. Detailed distinctions among these species are discussed in the accounts of *L. salvadorensis, L. magnifica,* and *L. lempirana.* Although not conclusive, a large isozyme study of these four species (Chamberlain et al. 1996) showed a number of fixed differences among aggregations of population allele frequencies for some species pairs, again supporting recognition of separate species. The analysis of cpDNA of Harris et al. (1994a) also supported the distinction of four separate species, but showed some disagreement with the morphological analysis in terms of hypothesized relationships. That analysis supported a close relationship between *L. magnifica* and *L. shannonii,* which were together placed as sister group to *L. collinsii,* and also between *L. salvadorensis* and *L. lempirana,* which grouped consistently with *L. multicapitula.* This discordance between morphology and cpDNA may be attributable to hybridization, but no further data to resolve this are currently available.

The analysis of cpDNA included six accessions of *L. shannonii* from throughout its scattered distribution. When the cpDNA data set was re-analyzed keeping all diploid accessions as terminals (Hughes, unpubl.), one accession (26/84) from Comayagua in Honduras was placed quite separately from the remaining accessions, again suggesting introgressive hybridization given that its morphology, isozymes, and seed proteins all confirmed its identity as *L. shannonii.*

In the protologue, Smith cites two specimens at US, *Shannon 5032* from Cuscatlán, El Salvador, and *Doyle 87a* from Chiapas, Mexico; the former is chosen here as the lectotype, given that the species was named in honor of *Shannon,* the collector of the specimen from El Salvador, and that the publication described new plants from Guatemala and other Central American republics and not Mexico.

Several other species of *Leucaena* grow in close proximity to but are rarely sympatric with *L. shannonii. Leucaena leucocephala* is now widely cultivated in areas where *L. shannonii* grows. *Leucaena shannonii* is occasionally invasive, occurring as a roadside weed or abundantly in secondary vegetation, often in bush fallows (*barbechos*) after cultivation (e.g., in Yoro, north-central Honduras).

20. Leucaena magnifica (C. E. Hughes) C. E. Hughes, Contr. Univ. Michigan Herb. 21: 286. 1997. *Leucaena shannonii* subsp. *magnifica* C. E. Hughes, Kew Bull. 46: 550. 1991.—TYPE: GUATEMALA. Chiquimula: Llano Grande, 1.5 km SW of Quetzaltepeque, rd towards Esquipulas, 14°37′N, 89°27′W, 26 Feb 1988, *Hughes 1093* (holotype: FHO!; isotypes: K! MEXU!).

Small to medium-sized tree, 10–15 (–20) m tall, 20–30 (–70) cm bole diameter, typically branchy when young, older trees with a short clear bole to 6 m, spreading angular branching, and an open rounded crown. Bark on young branches smooth, mid-grey or grey-brown, inner bark salmon pink, on older branches and bole darker grey-brown and rougher with shallow rusty orange-brown vertical fissures and deep red inner bark. Shoots terete, pale to mid-brown. Stipules 3.5–4.1 mm long, lanceolate, striate, with asymmetric basal wings, venation and midrib prominent, early caducous. Leaves (18–) 20–30 cm long, 14–20 (–22) cm wide; petioles (including pulvinus) 30–60 mm long, with a single, pale yellow-green, sessile, rounded, elliptic, dome-shaped or truncate-conic nectary, 3–4 × 1.5 mm, at the distal end on adaxial side of petiole; rachis 12–18 cm long, with a small elliptic conic nectary at the distal end, apex of rachis extending beyond the terminal pinnae as a pointed pubescent reddish brown mucro 1.5–2 mm long, curling when dry; pinnae 4–7 pairs; pinnular rachis 10–16 cm long, ridged, sparsely puberulent, with (1–) 2–5 (–8) minute discoid nectaries at base of terminal and lower pairs of leaflets; leaflets 11–16 pairs per pinna, (20–) 22–26 mm long, 9–12 mm wide, nearly sessile, the basal leaflets shorter, the distal pair shorter and wider, distinctly inequilaterally asymmetric about the midvein, the distal pair more extremely asymmetric, oblong, obtuse to rounded apically, rounded to truncate basally, glabrous and markedly glossy above, sparsely pubescent below with hairs concentrated at the base of main veins, secondary venation clearly visible and brochidodromous. Capitula 21–26 mm in diameter at anthesis, in fascicles of 2–6 at nodes on terminal, erect, singly branched, anauxotelic shoots on which leaf development is strongly suppressed leaving the capitula, and later the pods, exposed on the periphery of the tree crown (Fig. 12D), each capitulum with 200–220 flowers; peduncles (8–) 14–20 mm long, angled, sparsely pubescent with an involucre of bracts at distal end. Flowers subtended by peltate bracts, 3.5–4 mm long, 1 mm in diameter, ciliate along margin; calyx 3.1–3.8 mm long, glabrous, finely ciliate along margins, pale whitish green; petals 4.6–5.2 mm long, free, glabrous, pale yellow-green; filaments (8.8–) 10–13 mm long, arranged in two distinct ranks, white; anthers with a distal tuft of eglandular hairs, white, apiculum absent; ovary 1.8–2.6 mm long, short-stipitate, with short velutinous pubescence, with 18–24 ovules, style 4–7 mm long, white, with a terminal tubular stigma, included. Pods (5–) 11–16 per capitulum, (13–) 17–21 (–23) cm long, (19–) 22–24 (–26) mm wide, pendulous on sturdy 3–8 mm long stipes, linear-oblong, obtuse or rounded apically, sometimes with a short beak, 3–10 mm long, apparently readily broken off when dry, narrowly planocompressed, 14–22-seeded, valves deep maroon when unripe, turning mid-orange-brown, with dense velutinous pubescence, chartaceous, the margins slightly thickened, dehiscent along both sutures, borne in conspicuous clusters on branched terminal shoots on the periphery of the tree crown. Seeds 7.7–8.8 mm long, 4.5–5.2 mm wide, compressed, flattened, ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, symmetrical. Chromosome number: $2n = ?52$ (Sorensson 1989). Fig. 69.

Phenology. Flowering (September–) October–November (–December); fruiting February–March; partly deciduous January–March.

Distribution (Fig. 68). *Leucaena magnifica* is almost entirely restricted to the Department of Chiquimula in southeastern Guatemala in a 400 km^2 triangle bounded by the towns of Chiquimula, Quetzaltepeque, and Ipala. Although recorded from one collection (*P. H. Allen s.n.*) from an unknown locality in El Salvador, field exploration throughout eastern El Salvador in 1989 failed to locate any trees of *L. magnifica* in that area. *Leucaena magnifica* grows in degraded and highly disturbed mixed dry deciduous tropical forest with many woody Leguminosae, including species of *Acacia, Diphysa, Enterolobium, Gliricidia, Hymenaea, Lonchocarpus, Lysiloma,* and *Poeppigia,* and other trees, including species of *Alvaradoa, Cochlospermum, Cordia, Guazuma, Gyrocarpus, Simarouba, Swietenia, Tabebuia,* and *Tecoma*; 600–950 m.

Vernacular names. *Guaje, palo de guaje, vainillo.*

ADDITIONAL SPECIMENS EXAMINED. **El Salvador.** *P. H. Allen s.n.* (F, NY). **Guatemala.** CHIQUIMULA: nr El Rincón, 5–10 km N of Ipala, rd towards Chiquimula, 14°40′N, 89°42′W, *Hughes 412* (FHO, K), *Hughes 413* (FHO, MEXU), *Hughes 709* (FHO, K, MEXU), *Hughes 730* (FHO, MEXU), *Hughes 731* (FHO, MEXU), *Hughes & Styles 135* (FHO, K, MEXU); Km 194 rd from Esquipulas to Chiquimula, nr Quetzaltepeque, 14°38′N, 89°27′W, *Hughes 720* (FHO, MEXU), *Hughes 721* (FHO, K, MEXU), *Hughes 1748* (EAP, FHO, K, MEXU, MO, NY, TEX); 8 km S of Ipala, rd to Agua Blanca, nr El Amatillo, 14°32′N, 89°36′W, *Hughes 736* (FHO); close to Yerbabuena, 5 km W of the rd S from Chiquimula to Esquipulas, on connecting rd to Ipala, 14°38′N, 89°30′W, *Hughes 738* (FHO, MEXU); rd from Chiquimula to Esquipulas, 2 km SW of Quetzaltepeque, area of Llano Grande, 14°37′N, 89°27′W, *Hughes 1089* (FHO, K, MEXU), *Hughes 1090* (FHO, K, MEXU);

FIG. 69. *Leucaena magnifica*. A. Leaf. B. Petiolar nectary. C. Leaflet. D. Nectary between terminal leaflets and mucro. E. Once-branched flowering shoot. F. Longitudinal section of flower. G. Anther. H. Flower with peltate bract. I. Pods. J. Seed. (Based on: A–D, *Hughes 412*; E, F, *Hughes 709*; G–J, *Hughes 738*.)

close to San Juan Ermita, rd from Chiquimula E towards Comotán, 5 km W of Comotán, 14°44'N, 89°26'W, *Hughes 1220* (FHO, K, MEXU); plains around Ipala, 14°38'N, 89°37'W, *Steyermark 30314* (F).

Leucaena magnifica was first discovered in 1984 (Hughes 1986) and originally described as a subspecies of *L. shannonii* (Hughes 1991). It was raised to species rank based on more detailed character analysis and application of the phylogenetic species concept (Hughes 1997c). *Leucaena magnifica* is recognized as a species distinct from *L. shannonii* based on its once-branched flowering shoot (Fig. 12D). Evidence from cpDNA and isozymes also supports recognition of *L. magnifica* as a species distinct from *L. shannonii*. Harris et al. (1994a) in their cpDNA analysis showed that *L. magnifica* was the sister species to *L. shannonii*, a relationship supported in 85% of bootstrap replicates, and that they were separated by four autapomorphic fragment changes, two of which were unique. Chamberlain et al. (1996) analyzed isozyme variation across the *L. shannonii* alliance. Using the population aggregation analysis method of Davis and Nixon (1992) to delimit phylogenetic species, they showed that *L. magnifica* was separated from *L. shannonii* by the fixed occurrence of allele A of the Per-1 isozyme system, although this analysis failed to detect any fixed differences when all populations of the alliance were aggregated. In addition, *L. magnifica* and the closely related *L. shannonii* differ in a number of quantitative characters (Hughes 1991): *L. magnifica* has larger leaves with more pairs of pinnae, more pairs of leaflets, larger leaflets, larger flowers, more flowers per capitulum, larger pods and seeds, pods with dense velutinous pubescence, which are often deep maroon when unripe, and more pods per capitulum than *L. shannonii*.

Leucaena magnifica has a very restricted distribution, in an area of less than 400 km^2 in southeastern Guatemala, and is apparently reduced to fewer than 400 individuals (Hughes 1986, 1991, 1998), making it one of the most threatened species in the genus. It is also characterized by extremely low levels of diversity as measured using isozyme markers (Chamberlain et al. 1996). Its active protection and use by farmers in traditional indigenous agroforestry systems offers hope for increased circa-situm conservation (Hughes 1998).

21. Leucaena lempirana C. E. Hughes, Contr. Univ. Michigan Herb. 21: 279. 1997.—TYPE: HONDURAS. Yoro: 6 km SE of El Negrito, on side rd to Nueva Esperanza, nr Río Cuyamapa, on edge of Olomán Valley, 15°17'N, 87°40'W, 25 Feb 1991, *Hughes 1412* (holotype: EAP!; isotypes: FHO! MEXU! K! NY!).

Small, slender tree, 4–15 (–20) m tall, 10–40 cm bole diameter, typically with upright branching and a rounded crown above a short clear bole to 4 m. Bark light grey-brown with powdery orange-brown lenticels and shallow rusty orange-brown vertical fissures, inner bark green. Leafy shoots terete, pale orange-brown striped pale grey-brown covered in fine whitish velutinous pubescence. Stipules 3.5–3.8 mm long, ovate, with a subulate apex and small asymmetric wings at base, hairy, persistent. Leaves 19–24 (–26) cm long, 11–14 (–19) cm wide; petioles (including pulvinus) 25–35 mm long, with 1 or occasionally 2 pale yellow to orange-yellow, sessile, elliptic, dome-shaped or truncate-conic nectaries, 3 × 1.5 mm, at distal end on adaxial side of petiole; rachis 11–15 cm long with two narrow adaxial ridges and an elliptic conic nectary, 1 × 0.7 mm, at distal end, apex of rachis extending beyond the terminal pair of pinnae as a pointed hairy mucro 2.5–3.5 mm long, curling when dry; pinnae 14–19 pairs; pinnular rachis 7–10 cm long, densely covered in short white hairs, with a minute round nectary at distal end; leaflets (27–) 30–36

(–40) pairs per pinna, 5–6 mm long, 1.6–2 mm wide, nearly sessile, asymmetric, oblong, obtuse to rounded apically, rounded to truncate basally, densely white-pubescent, midrib strongly asymmetric, a few secondary veins visible. Capitula 16–18 mm in diameter at anthesis, in fascicles of 3–5 at nodes or in leaf axils on long, erect, unbranched, terminal, anauxotelic shoots on which leaf development is suppressed, the capitula exserted beyond the periphery of the tree crown, each capitulum with 100–130 flowers; peduncles 12–25 mm long, angled, pale orange-brown with velutinous white pubescence and an involucre of bracts. Flowers subtended by peltate bracts, 2.2–2.6 mm long, 0.6–0.9 mm in diameter, densely pubescent; calyx 2.4–2.7 mm long, glabrous, pale cream, the lobe tips tinged green; petals 3.5–4.5 mm long, weakly connate, glabrous, occasionally sparsely ciliate on lobe tips, pale green; filaments 10–12 mm long, white; anthers with a tuft of terminal hairs, cream-white, apiculum absent; ovary 2.3–3.4 mm long, sessile, densely short-white-velutinous, pale brown, with 24–25 ovules, style 10–11 mm long, white, with a terminal tubular stigma. Pods 1–2 (–3) per capitulum, (10–) 12–20 (–25) cm long, (18–) 20–26 (–32) mm wide, pendulous on sturdy 8–11 mm long stipes, oblong to linear-oblong, constricted where seed abortion has occurred, apex mucronate with a beak 5–15 mm long, base cuneate, narrowly planocompressed, 14–20-seeded, valves membranous, mid-orange-brown, pubescence variable from nearly glabrous to dense and velutinous, venation reticulate, most pronounced at margins, the margins slightly thickened, dehiscent along both sutures, borne on naked terminal shoots. Seeds 6.6–8.8 mm long, 3.8–5.2 mm wide, compressed, flattened, elliptic to ovate, deep chestnut-brown, glossy, aligned transversely in pods, pleurogram visible, deep U-shaped, symmetrical. Chromosome number unknown. Fig. 70.

Phenology. Flowering August–November and sporadically till February; fruiting March–April; semi-deciduous February–April.

Distribution (Fig. 71). *Leucaena lempirana* is the only species of *Leucaena* endemic to Honduras. It is restricted to two areas, the Aguán Valley system and the valleys of Olomán and Cataguana, both in the Department of Yoro in northern Honduras. It occurs in remnant semi-deciduous, subhumid tropical forest and dry thorn scrub forest, and scattered in secondary vegetation and pastures where trees are actively protected for production of fence posts. Associated woody species include *Acacia picachensis, Caesalpinia yucatanensis, Chloroleucon mangense, Diphysa carthagenensis, Guaiacum sanctum,* and *Haematoxylon brasiletto*; 150–500 m.

Vernacular names. *Guaje* (occasionally *frijolillo*) (around Cuyamapa, Olomán Valley), *hoja menuda* (occasionally *barba de jelote*) (in the Aguán Valley).

ADDITIONAL SPECIMENS EXAMINED. **Honduras.** YORO: 9 km SSE of Arenal, rd towards Jocón and Yoro, 15°22′N, 86°51′W, *Alvarado G/2/89* (HEH); rd E from Santa Rita to Yoro, nr Cuyamapa, 15°16′N, 87°27′W, *Hellin & Hughes 1* (EAP, FHO, K, MEXU, NY); 3 km WSW of Arenal, rd to Jocón, lower slopes of hills S side of the Aguán Valley, 15°22′N, 86°51′W, *Hellin & Hughes 4* (EAP, FHO, K, MEXU, NY); 3 km S of Zapamatepe, 8 km W of Arenal, S side of the Aguán Valley, 15°22′N, 86°54′W, *Hellin & Hughes 7* (EAP, FHO, K, MEXU, NY); N side of the Aguán Valley between Medina and Coyoles, rd 12 km W of Olanchito, 15°28′N, 86°28′W, *Hellin & Hughes 8* (EAP, FHO, K, MEXU, NY); 0.5 km SW of San Lorenzo, N side of the Aguán Valley, 47 km W of Olanchito, 15°25′N, 86°58′W, *Hellin & Hughes 11* (EAP, FHO, K, MEXU, NY); 15 km NW of Jocón, rd to the Aguán Valley in tributary valley of the Río Macora, between Macora and Sabana Larga, about 8 km NW of Macora, 15°21′N, 86°59′W, *Hellin & Hughes 14* (EAP, FHO, K, MEXU); rd E from Santa Rita to Yoro, 4 km E of Negrito immediately E of Valle Olomán above the Río Cuyamapa, 15°18′N, 87°40′W, *Hughes 1411* (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, 3 km SE of El Negrito or 2 km NW of the Río Cuyamapa in the Valle Olomán, 15°18′N, 87°41′W, *Hughes 1414* (EAP, FHO, K, MEXU, NY); W end of the lower Aguán Valley, rd W from Olanchito towards Sabana Larga, 1 km S of San Lorenzo, 15°25′N, 86°57′W,

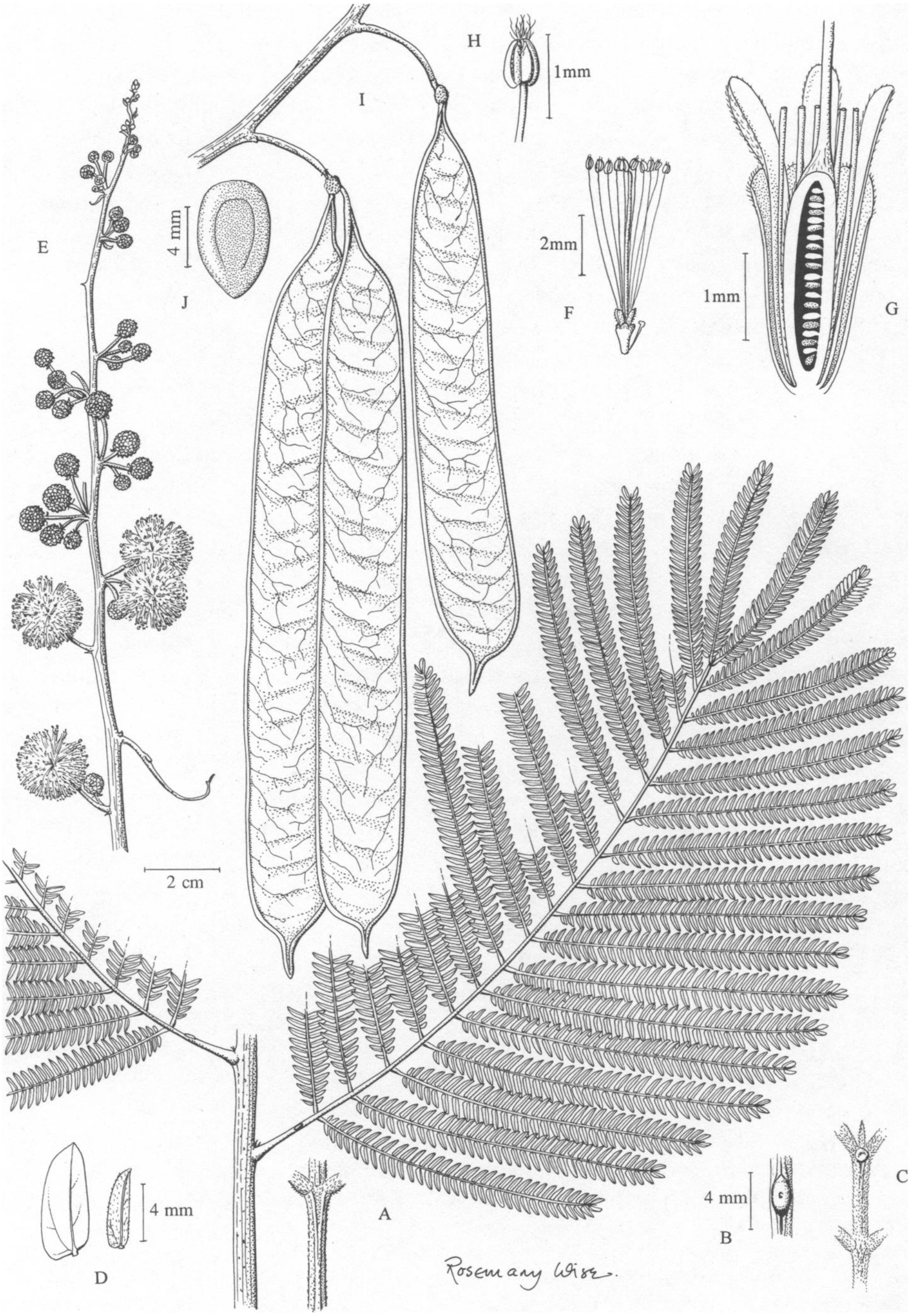


FIG. 70. *Leucaena lempirana*. A. Leaf and enlargment showing portion of rachis. B. Petiolar nectary. C. Rachis nectary. D. Leaflets. E. Flowering shoot. F. Flower. G. Longitudinal section of flower. H. Anther. I. Pods. J. Seed. (Based on the type, *Hughes 1412*.)

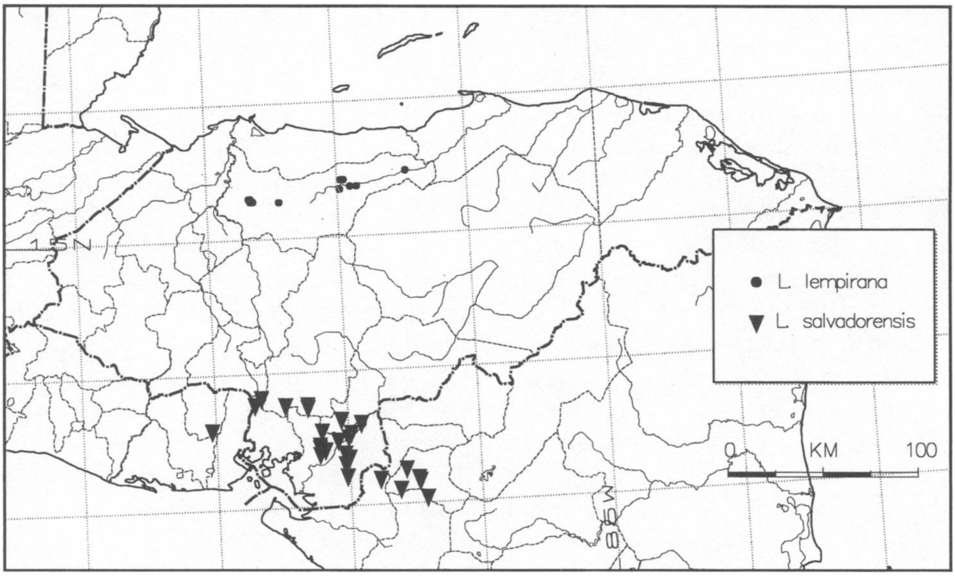


FIG. 71. Distribution of *L. salvadorensis* and *L. lempirana.*

Hughes 1447 (EAP, FHO, K, MEXU, NY); Santa Rita, 5 km ESE of El Negrito, side rd off the main El Negrito to Yoro rd to Nueva Esperanza, banks of the Río Cuyamapa, 15°17′N, 87°40′W, *Hughes 1479* (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, 4 km E of El Negrito, nr the turnoff over the Río Cuyamapa towards Morazán, 15°17′N, 87°39′W, *Hughes 1712* (E, FHO, K, MEXU, NY).

Leucaena lempirana shows closest affinities to *L. salvadorensis* and, to a lesser extent, *L. shannonii* (see *L. salvadorensis*). *Leucaena lempirana* is distinguished from *L. salvadorensis* by its long terminal anauxotelic flowering shoots on which the capitula and pods are borne on the periphery of the tree crown. These flowering shoots are strongly reminiscent of those of *L. shannonii*. *Leucaena lempirana* is distinguished from both *L. salvadorensis* and *L. shannonii* by its smaller and more numerous leaflets and pairs of pinnae per leaf. The pods are also similar to those of *L. shannonii* and are variably glabrous or pubescent as for that species. *Leucaena lempirana, L. salvadorensis,* and *L. shannonii* all occur in Honduras but occupy distinct and virtually allopatric distributions in different, isolated valley systems at low to mid-elevations (Figs. 68, 71).

22. Leucaena salvadorensis Standley ex Britton & Rose, N. Amer. Fl. 23: 125. 1928. *Leucaena shannonii* subsp. *salvadorensis* (Standley ex Britton & Rose) S. Zárate, Ann. Missouri Bot. Gard. 74: 449. 1987.—TYPE: EL SALVADOR. Morazán: nr Jocóro, 1924, *Calderón 2031* (holotype: NY!, fragment of holotype: US!).

Small to medium-sized tree, 10–15 (–20) m tall, 20–70 cm bole diameter, typically branchy when young, older trees with a short clear bole to 5 m, upright angular branching, and a narrow open crown. Bark on young branches smooth, mid-grey or grey-brown, inner bark salmon pink, on older branches and bole darker grey-brown and rougher with shallow rusty orange-brown vertical fissures and deep red inner bark. Leafy shoots terete, pale to mid-brown. Stipules 4.1–4.8 mm long, lanceolate, striate, with asymmetric wings at base, venation and midrib prominent, ciliate on margin, early deciduous. Leaves 20–30 cm long, 19–26 cm wide; petioles (including pulvinus) 19–25 mm long, with a single yellow-green or orange, sessile, rounded, elliptic, dome-shaped or truncate-conic nectary, 5 × 2.5 mm, at the distal end on adaxial side of petiole; rachis 7–14 cm long with a small elliptic conic nectary at the distal end, apex of rachis extending beyond the terminal pinnae as a pointed pubescent mucro 3.5–4.5 mm long, curling when dry; pinnae 4–7 pairs; pinnular rachis 13–16 cm long, angled, puberulent, with 1–2 minute elliptic nectaries at base of terminal pairs of leaflets; leaflets 23–27 pairs per pinna, 15–19 mm long, 3–5 mm wide, nearly sessile, asymmetric, linear-oblong, obtuse to rounded apically, rounded to truncate basally, glabrous, mid- to dark green abaxially, with sparse short pubescence on veins and margins, paler grey-green adaxially, midrib strongly asymmetric, secondary venation visible and brochidodromous. Capitula 23–25 mm in diameter at anthesis, in fascicles of 2–6 in leaf axils arising on older woody shoots, the leaves developing after the capitula, each capitulum with 90–140 flowers; peduncles 15–27 mm long, angled, pubescent with an involucre of bracts at the distal end. Flowers subtended by peltate bracts, 2.5–2.8 mm long, 0.7 mm in diameter; calyx 3–3.5 mm long, sparsely pubescent, pale whitish green, lobe tips tinged yellow; petals 4–5 mm long, free, glabrous, pale yellow-green; filaments 11–12 mm long, white; anthers sparsely hairy, cream-white, apiculum absent; ovary 2 mm long, covered in short white pubescence at distal end, reddish, with 22–25 ovules, style 12–13 mm long, white, with a terminal tubular stigma, exserted slightly beyond the anthers or included (varying from tree to tree). Pods 1–2 per capitulum, 14–18 cm long, 26–29 mm wide, pendulous on sturdy 7–15 mm long stipes, oblong to linear-oblong, acuminate or sometimes obtuse apically, sometimes with a short beak, apparently readily broken off when dry, narrowly planocompressed, 12–16-seeded, valves mid- to reddish brown, glabrous, with reticulate venation most pronounced close to margins, strongly coriaceous, the margins thickened, dehiscent along both sutures. Seeds 8.5–11.8 mm long, 5.2–6.7 mm wide, compressed, circular to ovoid, deep chestnut-brown, glossy, aligned transversely in pods; pleurogram visible, deeply U-shaped, symmetrical. Chromosome number: 2n = ?56 (Sorensson 1989). Fig. 72.

Phenology. Flowering March–April and sporadically May–October; fruiting February–March; deciduous December–March.

Distribution (Fig. 71). *Leucaena salvadorensis* is restricted to the seasonally dry Pacific slope watersheds of eastern El Salvador, southern Honduras, and northern Nicaragua. It occurs in remnant dry deciduous tropical forest and is often locally protected around settlements in fencelines and farmers' fields in traditional agroforestry systems outside remnant forest patches (Hellin & Hughes 1993). Recent field exploration in eastern El Salvador by Boshier suggests that it is restricted there to areas close to the Honduran border. It generally grows on young, skeletal, shallow soils of volcanic origin and freely drained. Associated woody plants include species of *Albizia, Bombacopsis, Caesalpinia, Calicophyllum, Cassia, Cochlospermum, Cordia, Crescentia, Dalbergia, Enterolobium, Gliricidia, Guazuma, Gyrocarpus, Karwinskia, Lonchocarpus, Luehea, Lysiloma, Myrospermum, Platymiscium, Poeppigia, Simarouba, Swietenia, Tabebuia,* and *Thouinidium*; (150–) 300–800 (–1080) m.

Vernacular names. In Honduras, *sepia (sepria)*, occasionally *frijolillo*, *aserillo* (Dept. Valle and El Salvador); in Nicaragua, *frijolillo*, occasionally *vaina*, *sepia* (Dept. Chinandega only).

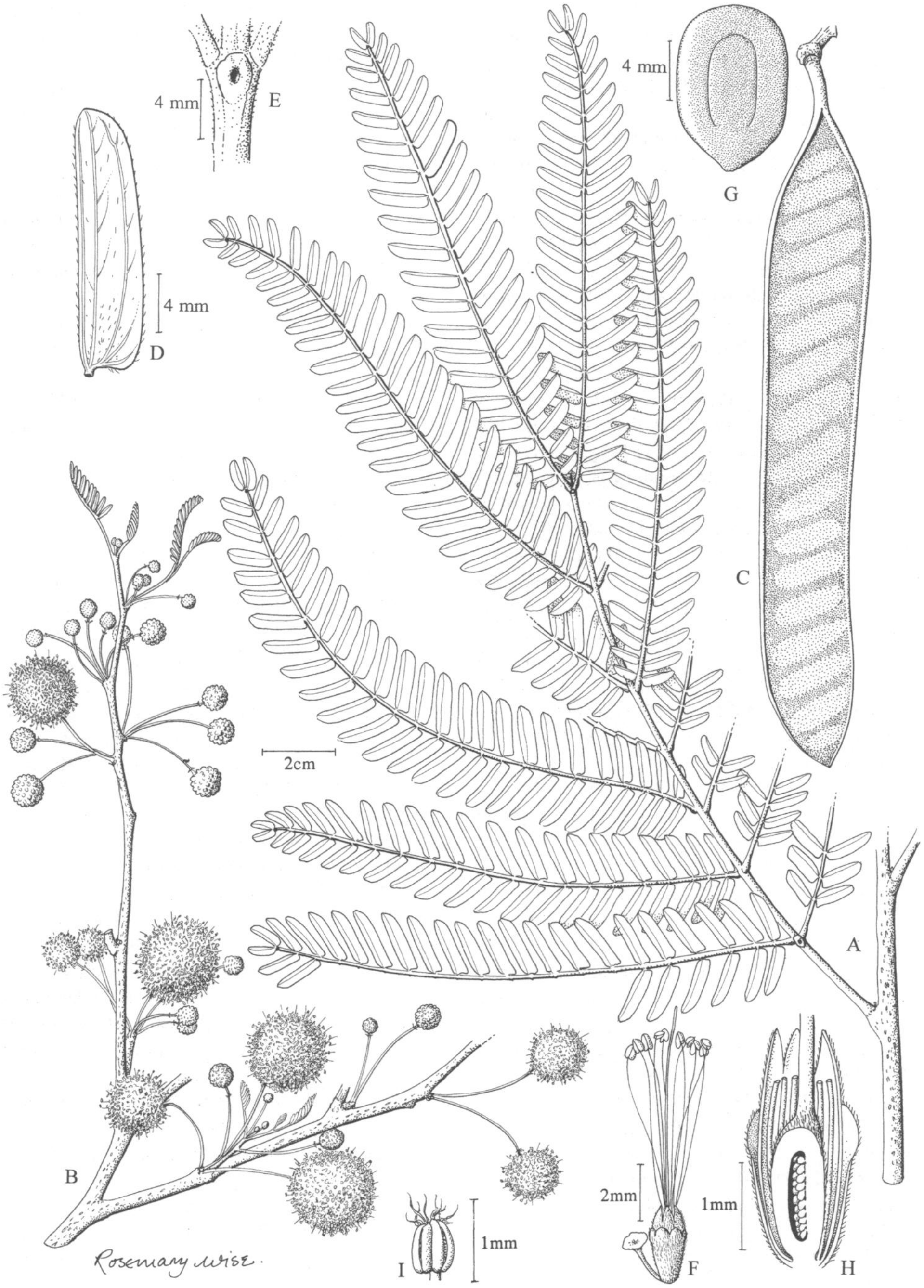


FIG. 72. *Leucaena salvadorensis*. A. Leaf. B. Flowering branch. C. Pod. D. Leaflet. E. Petiolar nectary. F. Flower. G. Seed. H. Longitudinal section of flower. I. Anther. (Based on: A–H, *Hughes 756*; I, *Hughes 1408*.)

Additional Specimens Examined. **El Salvador.** La Unión: 0.8 km from Nueva Esparta, rd to Poloros, 13° 48′N, 87° 50′W, *Boshier 71* (FHO). **Honduras.** Choluteca: 25 km NE of Choluteca, 13°22′N, 87°00′W, *Hughes 332* (FHO); 3 km S of Guayabillas rd to El Pillado, 13°24′N, 87°02′W, *Hughes 446* (FHO, MEXU); 3 km NW of Linaca, rd towards La Garita, about 20 km NW of Choluteca, 13°24′N, 87°13′W, *Hughes 742* (FHO, K); between El Corpus and Concepción de María, 9 km SE of El Corpus, about 25 km SE of Choluteca, 13°14′N, 87°01′W, *Hughes 746* (FHO, K); 5 km NNE of Apacilagua, rd to Morolica, beyond La Ceibita, nr the Río Choluteca, 13°31′N, 87°00′W, *Hughes 747* (FHO, K, MEXU); nr La Enea, rd 5 km N from Morolica towards San Lucas, 13°37′N, 86°54′W, *Hughes 750* (FHO, K, MEXU); 25 km NW of Choluteca in dry Pacific foothills above Linaca, close to Portillo del Viento, 13°27′N, 87°13′W, *Hughes 756* (FHO); 2 km E of La Garita, rd towards Linaca, 13°28′N, 87°13′W, *Hughes 824* (FHO, K), *Hughes 826* (FHO, MEXU); nr Carcha Verde, rd from Choluteca to Concepción de María about 15 km ESE of El Corpus, 13°14′N, 87°01′W, *Hughes 1062* (FHO, K, MEXU); nr Calaire on hills about 10 km E of Yusguare or 20 km E of Choluteca, 13°19′N, 87°02′W, *Hughes 1066* (FHO, K, MEXU); Portillo Grande, in hills about 4 km NE of Esquimay, 17 km E of Pespire, 13°34′N, 87°12′W, *Hughes 1211* (EAP, FHO); 1 km E of Orocuina, rd towards Morolica on the lower slopes of the valley of the Río Choluteca, 13°33′N, 86°59′W, *Hughes & Styles 102* (FHO, K, MEXU); gully between Tolobre and Los Achiotes on Montaña Tapahuasca, *Molina 14212* (EAP).—El Paraíso: close to El Pital on a ridge of mountains running S of the Río Texíguat, rd E from Nueva Armenia towards Texíguat about 3 km W of Texíguat, 13°39′N, 87°03′W, *Hughes 1206* (EAP, FHO); Cerro Las Golondrinas, 2 km S of Liure, 13°30′N, 87°05′W, *Repulski 534* (EAP).—Francisco Morazán: nr La Venta, 50 km S of Tegucigalpa, rd towards Choluteca, 13°46′N, 87°18′W, *Hughes 334* (FHO), *Hughes 739* (FHO, K, MEXU), *Hughes & Styles 129* (FHO, K, MEXU).—La Paz: 1 km SW of Lauterique, rd to Goascarán and Caridad, 13°50′N, 87°39′W, *Hughes 741* (FHO, K, MEXU).—Valle: 4 km S of La Caridad towards Aramecina rd from Goascarán to Lauterique, 13°47′N, 87°42′W, *Hughes 740* (FHO, K, MEXU); S slopes of Cerro El Camarón about 1 km S of Portillo El Camarón, rd N from San Francisco de Coray through San Miguelito to Alubarén and Reitoca, 13°46′N, 87°28′W, *Hughes 1214* (EAP, FHO). **Nicaragua.** Chinandega: 1 km E of San Francisco del Norte, rd to San Juan de Limay, 13°12′N, 86°46′W, *Hughes 1445* (EAP, FHO, K, MEXU, NY).—Estelí: 32 km NW of Estelí, rd through Regadío to San Juan de Limay nr Buena Vista, 13°11′N, 86°28′W, *Hughes 1407* (EAP, FHO, K, MEXU, NY); nr Los Jocotillos, 15 km SE of San Juan de Limay or 35 km NE of Estelí, rd from Estelí through Regadío to San Juan de Limay, 13°12′N, 86°29′W, *Hughes 1408* (EAP, FHO, K, MEXU, MO, NY), *Hughes 1431* (EAP, FHO, K, MEXU, NY); 10 km S of San Juan de Limay, rd to San Jose de Achuapa, nr Portillo de las Tablas, 13°07′N, 86°37′W, *Hughes 1434* (EAP, FHO, K, MEXU, NY); 18 km WSW of Estelí towards El Sauce, nr the departmental boundary between Estelí and León, 13°03′N, 86°25′W, *Hughes 1438* (EAP, FHO, K, MEXU, NY), *Hughes 1439* (EAP, FHO, K, MEXU, NY); 15 km NNE of San Juan de Limay, rd to Pueblo Nuevo, 13°16′N, 86°34′W, *Hughes 1444* (EAP, FHO, K, MEXU, NY); 10 km NE of San Juan de Limay, 13°16′N, 86°34′W, *Hughes & Styles 37* (FHO, MO); N of Estelí, *Laguna 427* (HNMN, MEXU).

Since 1928 the status of *L. salvadorensis* as a distinct species has been questioned and discussed by several authors. Standley and Steyermark (1946) treated it as conspecific with *L. shannonii*. Zárate (1984a) also treated it initially as conspecific with *L. shannonii* but later as a distinct subspecies of *L. shannonii* (Zárate 1987b). Brewbaker et al. (1972) and Brewbaker and Ito (1980) treated it initially as conspecific with *L. leucocephala*, but later accepted it as a distinct species (Brewbaker & Sorensson 1994). Excluding the type specimen, collected in 1924, only three further collections of *L. salvadorensis* were made prior to 1980. Taxonomic confusion was thus, at least in part, due to lack of material. It is only in the last fifteen years that *L. salvadorensis* has been collected more widely, mainly by Hughes and collaborators in Honduras and Nicaragua and by Boshier in El Salvador. This new material has allowed more detailed studies to be carried out (Hughes 1988; Hellin & Hughes 1993; Chamberlain et al. 1996). Results of these studies support recognition of *L. salvadorensis* as a distinct species.

Leucaena salvadorensis is most closely related to *L. lempirana*, a relationship supported by evidence from analysis of cpDNA (Harris et al. 1994a) (Fig. 31), in which the two were placed unequivocally as sister species, by seed protein data (Chamberlain 1993) and isozyme analysis (Chamberlain et al. 1996). In the analysis of morphological data alone, *L. salvadorensis* forms a trichotomy with *L. lempirana* and *L. magnifica,* which together with *L. shannonii,* form a group supported by two character state changes: ovary with short velutinous pubescence and linear-oblong leaflets with visible secondary venation. *Leucaena salvadorensis* is distinguished from *L. lempirana, L. magnifica,* and *L. shannonii* by the arrangement capitula on older wood on auxotelic shoots with the pods borne away from the ends of the shoots and by its coriaceous as opposed to chartaceous pods. In addition, leaflets of *L. salvadorensis* are longer than those of *L. lempirana.*

Forest cover has been reduced to scattered small remnants throughout the distribution of *L. salvadorensis.* As a result it is now rare and threatened in many parts of its range. Where it is more abundant, this is as a result of protection or cultivation by local communities that use the wood of *L. salvadorensis* for house construction (Hellin & Hughes 1993). *Leucaena salvadorensis* and *L. shannonii* occupy allopatric but contiguous distributions. *Leucaena leucocephala* is now frequently cultivated in areas of remnant *L. salvadorensis* stands, but no hybrids between the two have so far been encountered.

HYBRIDS

23. Leucaena ×mixtec C. E. Hughes & S. A. Harris [*L. leucocephala* subsp. *glabrata* (Rose) S. Zárate × *L. esculenta* (Sessé & Mociño ex DC.) Bentham], hyb. nov.—TYPE: MEXICO. Puebla: village of Santiago Acatepec, 50 km SW of Tehuacán, rd to Huajuapan de León, 18°14′N, 97°33′W, 16 Feb 1992, *Hughes 1622* (holotype: FHO!; isotypes: E! K! MEXU! MO! NY!).

Arbor inter *L. leucocephalam* (Lam.) de Wit et *L. esculentam* (Sessé & Moc. ex DC.) Benth. intermedia et verosimiliter ex hybridatione harum specierum orta, ab ambabus fructibus abortivis differt.

Small to medium-sized tree, 10–20 (–25) m tall, bole diameter 30–70 cm, with heavy branching and a wide, open, spreading crown (reminiscent of *L. esculenta*). Bark pale metallic grey, smooth, slightly corky, occasionally with very slight vertical fissures on lower boles of older trees, inner bark blood-red. Shoots terete or sometimes slightly angular, with incipient longitudinal corky ridges, mid-orange-brown. Leaves (20–) 22–28 (–30) cm long, 15–20 (–21) cm wide; petioles (including pulvinus) 22–28 mm long, with a single green or reddish green, sessile, elliptic or rounded, crateriform nectary, 3.2–4 × 2.5–2.7 mm, at the distal end on adaxial side of petiole; rachis 13–20 (–22) cm long, with 1 or 2 small elliptic discoid or shallowly crateriform nectaries at the distal end, apex of rachis extending beyond the terminal pinnae as a slender pointed glabrous mucro 4–5 mm long, curling when dry; pinnae 9–14 pairs; pinnular rachis 7–9 (–11) cm long, angled, puberulent, with 1–2 (–3) small elliptic or round nectaries at base of terminal pairs of leaflets; leaflets 9–14 mm long, 1.9–2.7 mm wide, 24–31 pairs per pinna, nearly sessile, slightly asymmetric, linear, acute or acuminate apically, rounded basally, glabrous, only the asymmetric midrib visible on dried leaflets. Capitula 24–26 mm in diameter at anthesis, in fascicles of 2–5 (–7) in leaf axils on actively growing shoots, the leaves developing with the capitula or somewhat suppressed leaving the flower heads exposed, each capitulum with 130–160 flowers; peduncles 24–33 mm long, angled, glabrous with an involucre of bracts at the distal end. Flowers subtended by peltate bracts, 2.5–4.0 mm long, 0.9 mm in diameter; calyx 2.8–3.3 mm long, sparsely pubescent, pale whitish green, lobe tips tinged yellow; petals 4.8–5.4 mm long, free, glabrous, pale whitish green;

filaments 9–11 mm long, white; anthers sparsely hairy, white, apiculum absent; ovary 3 mm long, covered in white hairs at distal end, pale greenish white, with 20–22 ovules, style 10–12 mm long, white, with a terminal tubular stigma, exserted slightly beyond the anthers. Pods almost always absent or misformed and lacking seeds. Fig. 73.

Phenology. Abundant flowering has been observed in January, April, August, and November, and is apparently year-round; fruiting nil, the hybrid is apparently highly sterile with little or no pod set.

Distribution (Fig. 74). *Leucaena* ×*mixtec* occurs frequently but sporadically in six states in south-central Mexico and is to be expected in any areas where *L. leucocephala* and *L. esculenta* are cultivated sympatrically in that region or elsewhere. It grows almost exclusively in suburbs of towns and villages, in gardens, backyards, and "guajales" (orchards) where the parent species are cultivated for pod production. Two individuals are known from Dakar, Senegal. Honduran collections are derived from cultivated material of artificial hybrids.

Vernacular names. The most widely used name, *guaje macho* (male Leucaena), refers to the lack of pod production by this sterile hybrid, a feature widely recognized by local residents. Occasionally this hybrid is called *guaje embra* (female Leucaena) and *guaje*, the generic Nahuatl name for *Leucaena*, or *guaje blanco*, a name usually applied to *L. leucocephala*.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: S outskirts of Tuxtla Gutiérrez, N side of bypass, backyard of the property Quinta Querem No. 4355, 1 km from the intersection of the ring rd and the rd E to Chiapa de Corzo, 16°44′N, 93°05′W, *Hughes 1762* (CAS, FHO, K, MEXU, MO, NY, TEX), *Hughes 1763* (CAS, FHO, K, MEXU, MO, NY).—GUERRERO: Almaloya, close to rd to Ciudad Altamirano, 50 km W of Teloloapan, 18°14′N, 100°06′W, *Hughes 902* (FHO, K, MEXU), *Hughes 1159* (FHO, K, MEXU), *Hughes 1741* (FHO, K, MEXU, MO, NY); outskirts of Ahuehuepan, 23 km W of Iguala, rd to Ciudad Altamirano, turnoff to Tonalapa del Río and Coatepec Costales, 18°20′N, 99°38′W, *Hughes 1828* (CAS, FHO, K, MEXU, MO, NY, TEX).—MORELOS: 500 m N of Laguna "El Rodeo," nr Miacatlán, 18°47′N, 99°20′W, *Dorado 858* (MEXU, MO); area of Rancho "El Limón," nr Tepalcingo, 18°31′N, 98°56′W, *Dorado 993* (MEXU); Temilpa Nuevo, valley of the Río Yautepec, 2 km NNE of Tlatizapan, 10 km NNE of Jojútla de Juárez, 18°43′N, 99°06′W, *Hughes 1727* (E, FHO, K, MEXU, MO, NY).—OAXACA: outskirts of Teotitlán del Camino, rd NW towards Tehuacán, 18°08′N, 97°04′W, *Hughes 1637* (E, FHO, K, MEXU, MO, NY).—PUEBLA: outskirts of Santiago Acatepec, rd 50 km SW of Tehuacán towards Huajuapan de León, 18°39′N, 97°35′W, *Hughes 1324* (BR, CR, FHO, K, MEXU, NY), *Hughes 1622* (E, FHO, K, MEXU, MO, NY), *Hughes 1624* (E, FHO, K, MEXU, MO, NY), *Hughes 1790* (FHO, K, MEXU); Esperanza Espinal, 15 km NNE of Huajuapan de León, rd SW from Tehuacán to Huajuapan, 17°52′N, 97°42′W, *Hughes 1628* (E, FHO, K, MEXU, MO, NY); outskirts of Coxcatlán, 30 km S of Tehuacán, rd to Oaxaca, 18°16′N, 97°09′W, *Hughes 1802* (CAS, FHO, K, MEXU, MO, NY); 57 km NW of Acatlán, Huajuapan to Izúcar rd, Hwy 190, just past the turnoff to Santa Cruz Tejalapa, 18°22′N, 98°18′W, *Hughes 1817* (FHO, K, MEXU, MO, NY, TEX).—QUERÉTARO: rd WNW from Xilitla towards Jalpan de la Sierra, 35 km SSE of Jalpan, about 1 km from Lagunita towards Jalpan, 21°13′N, 99°16′W, *Hughes 1597* (E, FHO, K, MEXU, MO, NY).

Honduras. COMAYAGUA: cult. La Soledad field station, Comayagua Valley nr El Taladro, 10 km WSW of Comayagua, 14°27′N, 87°41′W, *Hughes 1368* (FHO), *Hughes 1715* (E, EAP, FHO, K, MEXU, NY).

Senegal. DAKAR: Grounds of the IFAN Museum, Pl. Soweto, Dakar, *S. A. Harris 101* (FHO, K).

The identity of *L.* ×*mixtec* as a hybrid between *L. leucocephala* subsp. *glabrata* and *L. esculenta* was determined by Hughes and Harris (1994) using a combination of phytogeographical, morphological, molecular, and ethnobotanical evidence. In all eight hybrid individuals examined in their study, the female parent was *L. leucocephala,* but subsequently Hawkins and Harris (1998) encountered one hybrid individual with *L. esculenta* as the female parent. *Leucaena* ×*mixtec* shows broad, but not halfway, morphological intermediacy between the two parental species in a range of leaf, flower, shoot, and bark

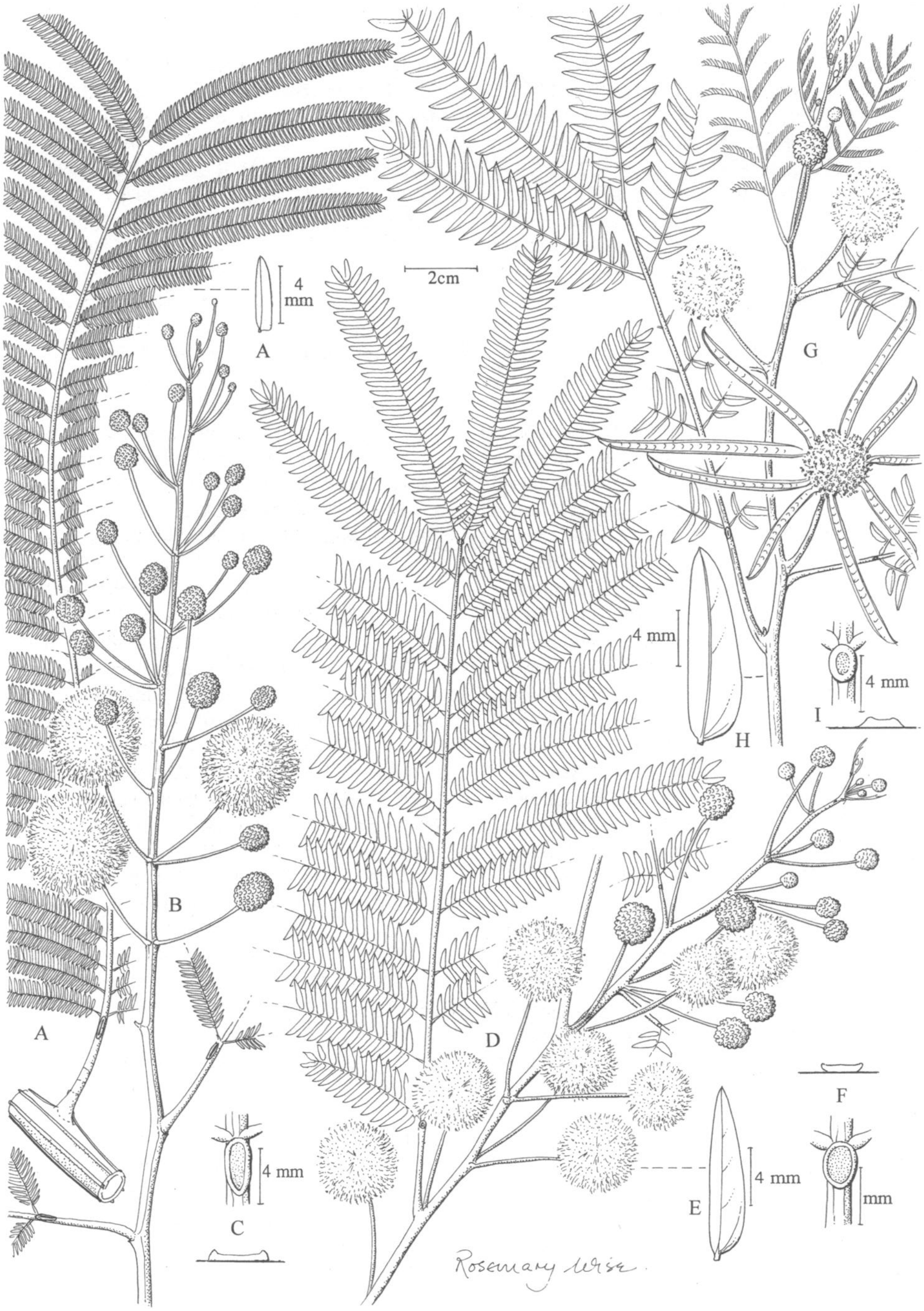


FIG. 73. *Leucaena esculenta, L.* ×*mixtec,* and *L. leucocephala* subsp. *glabrata.* A–C, *L. esculenta*: A. Leaf and leaflet. B. Flowering shoot. C. Petiolar nectary. D–F, *L.* ×*mixtec*: D. Leaf and flowering shoot. E. Leaflet. F. Petiolar nectary. G–I, *L. leucocephala* subsp. *glabrata*: G. Flowering shoot with leaf and unripe pods. H. Leaflet. I. Petiolar nectary. (Based on: A, *Hughes 895*; B, C, *Hughes 1180*; D–F, *Hughes 1715*; G–I, *Hughes 905*.) [First published in *Plant Systematics and Evolution.*]

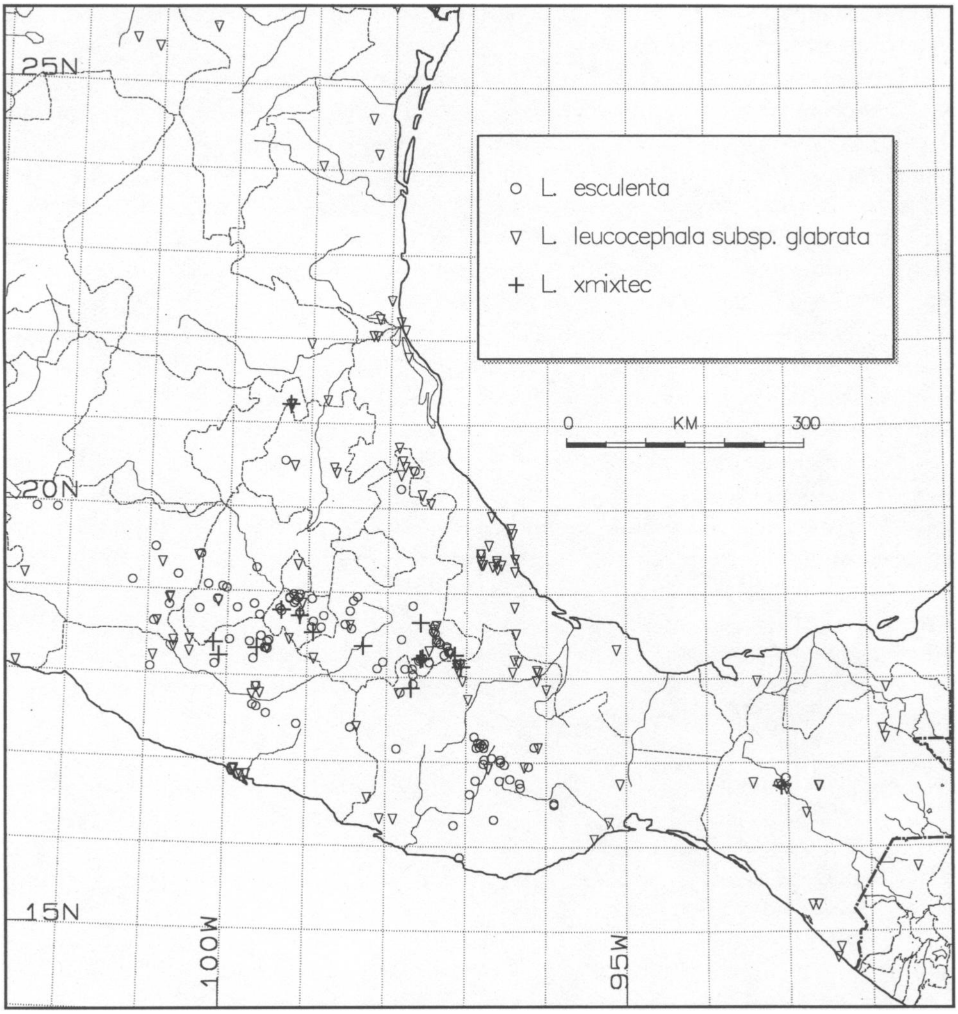


FIG. 74. Distribution of *L. leucocephala* subsp. *glabrata*, *L. esculenta*, and *L.* ×*mixtec* in Mexico.

characters. It is closer to *L. leucocephala* in quantitative traits due to the recognized dosage affect of ploidy (see Hughes & Harris, 1994, and Sorensson, 1993). *Leucaena* ×*mixtec* is easily recognized using leaf material alone (Fig. 73), and by its very striking lack of pod production despite virtual year-round and abundant flowering.

Leucaena ×*mixtec* is largely or completely sterile and, given that vegetative propagation is not known in the genus, each accession must have arisen as separate F_1 hybrids. Despite this lack of persistence, *L.* ×*mixtec* is relatively frequent and widespread albeit sporadic in occurrence. It was collected first in Morelos in 1982, and more than 25 individuals have now been recorded with only limited field exploration; it is undoubtedly more common than has been realized. Given the wide present-day sympatry of the two parent species (Fig. 74) and the apparent ease with which the hybrid occurs under these circumstances, *L.* ×*mixtec* is likely to become more common in the future and more widely represented in herbaria.

The name *mixtec* refers to the role that human interference by the Mixtec and other pre-Columbian people of central Mexico played in the origin of this hybrid species. By bringing *L. esculenta* and *L. leucocephala* into cultivation and into artificial sympatry, the opportunity was created for this hybrid to arise. Perhaps due to its lack of pod production, *L.* ×*mixtec* is widely recognized and known by local people in Mexico today. Sometimes trees are rogued because of the lack of pods, but in many cases trees are retained as attractive ornamentals.

Hutton and Tabares (1982) documented the occurrence of spontaneous hybrids between *L. leucocephala* and *L. esculenta* in research trials in Colombia. The recent discovery of two individuals of *L.* ×*mixtec* in Dakar, Senegal (*S. A. Harris 101*), was a surprise. While *L. leucocephala* is commonly cultivated and weedy throughout Dakar, *L. esculenta* is apparently rare, although it was recorded by Berhaut (1956) and cited by Lock (1989). Again this indicates the apparent ease with which this hybrid occurs. As *L. esculenta* is more widely introduced into areas where *L. leucocephala* is common and naturalized, *L.* ×*mixtec* may also become more common outside Mexico. The hybrid has been artificially recreated in Hawaii (Sorensson & Brewbaker 1994) and is artificially propagated there using rooted cuttings to supply known demand for seedless *Leucaena* for planting. It is an extremely vigorous and leafy tree, is likely to show good resistance to the psyllid defoliator *Heteropsylla cubana*, and being seedless poses low risk of invasion, making this one of the most attractive species of *Leucaena* for reforestation if the problems of propagation can be overcome (Hughes 1998).

24. Leucaena ×spontanea C. E. Hughes & S. A. Harris, Pl. Syst. & Evol. 212: 70. 1998. [*L. leucocephala* subsp. *glabrata* (Rose) S. Zárate × *L. diversifolia* (Schlechtendal) Bentham].—TYPE: MEXICO. Veracruz: Coatepec, 8 km SSW of Tuzamapan, 4 km WNW of Jalcomulco, rd Coatepec to Huatusco, 19°21′N, 96°49′W, 5 Dec 1995, *Hughes 1874* (holotype: FHO!; isotypes: K! MEXU! NY!).

Small to medium-sized tree, 5–15 (–20) m tall, bole diameter 30–40 cm, with a short bole, heavy branching, and a wide, open, spreading crown. Bark mid-grey-brown with shallow rusty orange-brown vertical fissures, inner bark green. Shoots terete, mid-orange-brown, glabrous or sparsely puberulent. Leaves (19–) 24–27 (–30) cm long, (10–) 11–14 cm wide; petioles (including pulvinus) (30–) 32–36 (–38) mm long, with a single green or reddish green, sessile, elliptic or rounded, cupulate nectary, 2.8–3.5 × 2–2.5 mm, often slightly wider at distal end than at the base, at the distal end on adaxial side of petiole; rachis 14–21 cm long, with 1 or 2 nectaries, 2.6 × 1.4 mm, elliptic, discoid, or shallowly crateriform, at the distal end, apex of rachis extending beyond the terminal pinnae as a slender pointed glabrous mucro 2.5–4 mm long, curling when dry; pinnae (10–) 11–16 (–18) pairs; pinnular rachis 6.5–9 cm long, angled, sparsely puberulent, with 1 or 2 (–3) sessile discoid elliptic nectaries, 0.3 × 0.7 mm, at base of terminal pairs of leaflets; leaflets (22–) 26–36 (–48) pairs per pinna, (6.2–) 8–10 (–11.9) mm long, 1.2–2 (–2.3) mm wide, nearly sessile, asymmetric, linear, acute or acuminate apically, rounded and strongly asymmetric basally, glabrous except ciliate at margins, asymmetric midrib and 1 or 2 secondary veins visible on dried leaflets. Capitula (17–) 20–24 (–28) mm in diameter at anthesis, in fascicles of (1–) 2–5 in leaf axils on actively growing shoots, the leaves developing with the capitula, each capitulum with 130–160 flowers; peduncles 24–33 mm long, angled, densely or sparsely pubescent with an involucre of bracts at the distal end. Flowers subtended by peltate bracts, 2.5–3 mm long, 0.8 mm in diameter; calyx 3–3.3 mm long, hairy on distal half and ciliate on lobe margins, pale whitish green; petals 4.7–5.4 mm long, free, hairy on distal half and ciliate on margin, pale whitish green; filaments 7.5–9.5 (–10) mm long, white or pale pink; anthers hairy, white or pale pink, apiculum absent; ovary 2.5–2.8 mm long, covered in white hairs at distal end, pale greenish white, with 18–24 ovules, style 12–13 mm long, white or pale pink, with a terminal tubular stigma, exserted strongly beyond the anthers. Pods (8–) 10–15 (–18) cm long, (12–) 15–20 (–22) mm wide, linear-oblong, the apex rounded with a short pointed beak, the base cuneate, 14–20-seeded, valves chartaceous or membranous, mid-green when unripe, turning mid-brown, glabrous, opening along both sutures, endocarp not partitioned between seeds. Seeds 6.5–7 mm long, 2.9–3.5 mm wide, compressed, oblong, dark reddish chestnut-brown, glossy, pleurogram visible, U-shaped with 95% arm extension. Chromosome number: 104 (rarely 86–103) (De Freitas et al. 1991). Fig. 75.

Phenology. Flowering December–March; fruiting December–March, but based on very limited observations or herbarium material.

Distribution (Fig. 76). *Leucaena* ×*spontanea* has been found in seven widely scattered countries: Mexico and Guatemala in Mesoamerica, the Dominican Republic, Haiti, and Jamaica in the Caribbean, and Papua New Guinea and the Philippines in Southeast Asia. This scatter reflects its spontaneous hybrid origin following wide introduction and cultivation of the two parent species. It is abundant, as far as is known, only in parts of the State of Veracruz in Mexico and elsewhere appears sporadically as scattered individuals. All the known trees occur in disturbed areas, including gardens or backyards (e.g., in Barrillas, Huehuetenango, Guatemala), in coffee plantations (e.g., in parts of Veracruz around Coatepec and in Jamaica), and in secondary vegetation on roadsides (e.g., near Plan del Río, Veracruz, Mexico). In Mexico and Guatemala, associated trees, other than the parent species, include *Pinus maximinoi, P. chiapensis, Liquidambar styraciflua,* and species of *Inga, Erythrina,* and *Grevillea.* Honduran collections are derived from cultivated material of artificial hybrids; 200–1000 (–1550) m.

Vernacular names. *Chalíp* (Guatemala); *guaje* (Mexico); *wild tamarind* (Jamaica); local names do not apparently differentiate between *L.* ×*spontanea* and its parents in these areas, although more detailed ethnobotanical investigation is needed to verify this.

ADDITIONAL SPECIMENS EXAMINED. **Dominican Republic.** SANTO DOMINGO: abandoned area in Santo Domingo (N Melo), 18°28′N, 70°46′W, *Liogier 23645* (MEXU). **Jamaica.** ST. ANDREW: rd Kingston towards Guava Ridge and N to Content Gap and St. Peters, 3.4 km from jctn off Kingston to Newcastle rd, *Hellin & Lewis 3* (FHO, UCWI); banks of Hope River, 18°00′N, 76°40′W, *A. Rehder s.n.* (A).

Mexico. VERACRUZ: 1 km NW of Tuzamapan, rd 12 km E from Coatepec, 19°25′N, 96°53′W, *Hughes 1868* (FHO, K, MEXU, NY), *Hughes 1869* (FHO, K, MEXU, NY); 8 km SSW of Tuzamapan, 4 km WNW of Jalcomulco on the Coatepec-Huatusco rd, in the valley of the Mesa Olivera, 19°21′N, 96°49′W, *Hughes 1872* (FHO, K, MEXU, NY), *Hughes 1873* (FHO, K, MEXU, NY), *Hughes 1874* (FHO, K, MEXU, NY); main Hwy 140, 40 km SE of Xalapa towards Veracruz, between Cerro Gordo and Plan del Río, 1 km N of Plan del Río, 19°24′N, 96°38′W, *Hughes 1876* (FHO, K, MEXU, NY), *Hughes 1877* (FHO, K, MEXU, NY); 3.1 km from Tuzamapan on the rd to Totutla, nr Coatepec, 19°21′N, 96°49′W, *Lorenzoni 17* (F).

Guatemala. HUEHUETENANGO: about 4 km NW of the small town of Barillas, track to Florída, 15°48′N, 91°48′W, *Hughes 1694* (E, FHO, K, MEXU, MO, NY), *Hughes 1695* (E, FHO, K, MEXU, MO, NY). **Honduras.** COMAYAGUA: cult., CONSEFORH experimental station nr El Taladro, 7 km SW of Comayagua, 14°27′N, 87°41′W, *Hughes 1892–1894* (all FHO, K, MEXU, NY).

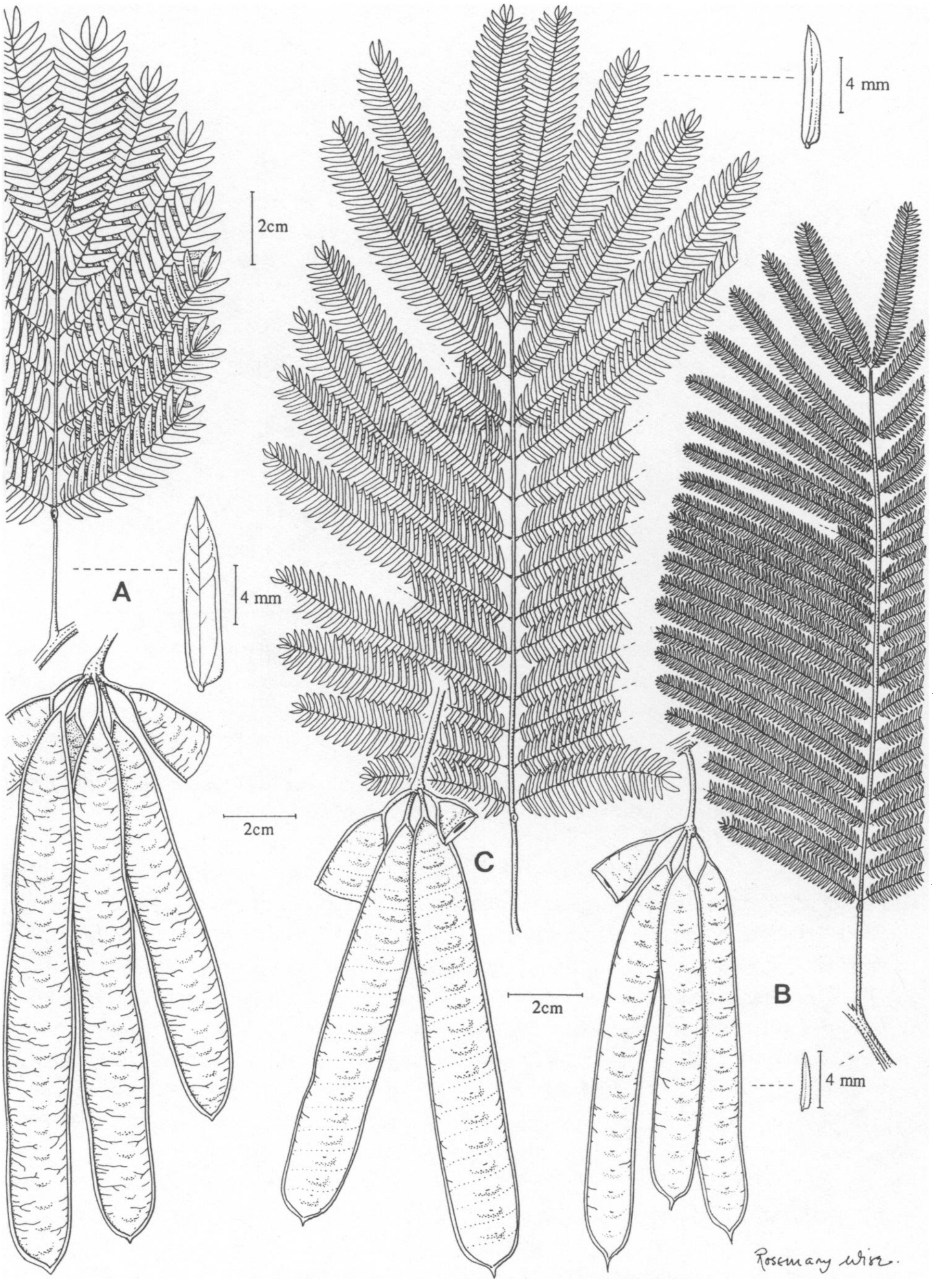


FIG. 75. *Leucaena leucocephala* subsp. *glabrata, L. diversifolia,* and *L.* ×*spontanea*. A, *L. leucocephala* subsp. *glabrata*: leaf, leaflet, and pods. B, *L. diversifolia*: leaf, leaflet, and pods. C, *L.* ×*spontanea*: leaf, leaflet, and pods. (Based on: A, *Hughes 1879*; B, *Hughes 1864*; C, *Hughes 1874*.) [First published in *Plant Systematics and Evolution.*]

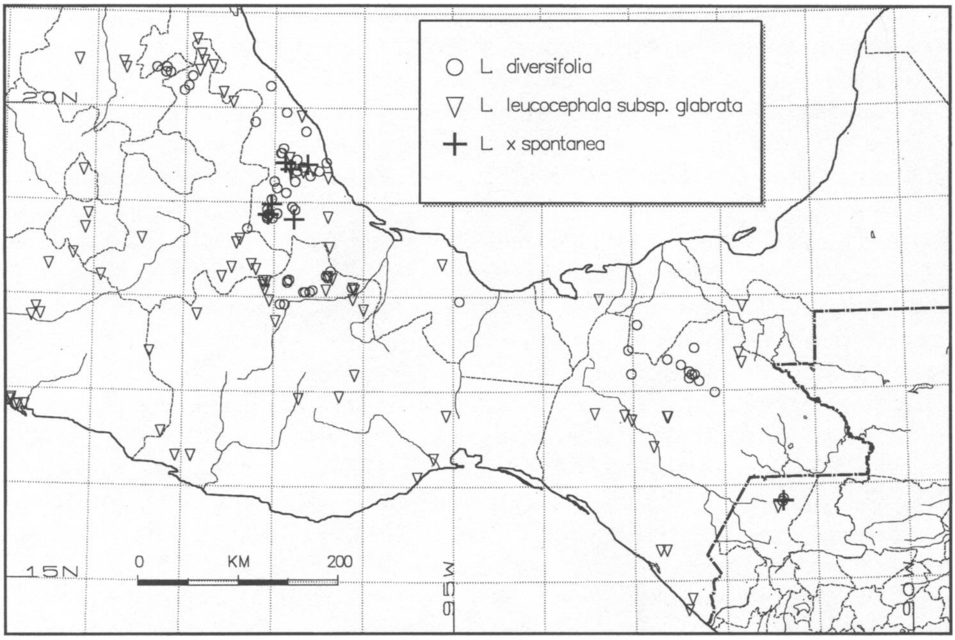


FIG. 76. Distribution of *L. leucocephala* subsp. *glabrata*, *L. diversifolia*, and *L.* ×*spontanea* in Mexico and northwestern Guatemala.

Papua New Guinea. KYNONTU: nr Aiyura, in the PNG highlands about 100 km from Gonoka, *H. M. Shelton s.n.* (FHO). **Philippines.** BATANGAS: S of Los Baños, *H. M. Shelton s.n.* (FHO).

The identity and characteristics of *L.* ×*spontanea* were investigated in detail by Hughes and Harris (1998) using combined geographical, morphological, and molecular evidence. Hybridity and the identity of the putative parent species *L. leucocephala* and *L. diversifolia* were supported by three of the criteria normally used to verify hybrids. First, it occurs in areas where the two parent species are always present. Second, it exhibits a high degree of morphological and molecular intermediacy in a suite of quantitative leaf and fruit traits (Fig. 75) and RAPD markers. Finally, and most convincingly, it closely resembles artificial hybrids created between the two putative parent species. Leaf morphology of the hybrids does not differ significantly from that predicted by hybrid leaf expression models developed from artificial hybrids by Sorensson (1993).

Zárate (1994) also noted the occurrence of what he believed were hybrids between *L. leucocephala* and *L. diversifolia* (treated as *L. diversifolia* subsp. *diversifolia* by him) from around Temascal, Oaxaca. He attributed these to *L.* ×*brachycarpa*, which was originally named from Jamaica, and as discussed in the account of *L. diversifolia*, is here treated as conspecific with *L. diversifolia*. The type of *L. brachycarpa*, and the material from Temascal in Oaxaca, are quite different from the hybrid material discussed here, and closely resemble *L. diversifolia* (formerly treated as *L. diversifolia* subsp. *diversifolia*), which is distributed from Veracruz south to northern Guatemala (Fig. 38). The occurrence of *L.* ×*spontanea* in Jamaica has perhaps contributed to the confusion surrounding the identity of *L. brachycarpa* and indeed all the material from Jamaica. For example, specimens of *L.* ×*spontanea* were often misidentified as either *L. brachycarpa* or *L. leucocephala* by different taxonomists (e.g., *A. Rehder s.n.*). All three taxa occur in close proximity to Hope in the Parish of St. Andrew.

Leucaena ×*spontanea* is named with reference to its spontaneous occurrence whenever the two parent species are brought together in cultivation. As discussed by Hughes and Harris (1998), it is very likely that *L.* ×*spontanea* has arisen following alteration of the distributions of the two parent species bringing them into artificial sympatry in cultivation. That this is the case for the hybrids in the Dominican Republic, Haiti, Jamaica, Papua New Guinea, and the Philippines, where both parent species are introduced, is not in doubt. In Mexico and Guatemala, both parent species are also cultivated, *L. leucocephala* for pod production (e.g., in informal *guajales* near Tuzanapan and Plan del Río, Veracruz, Mexico), and *L. diversifolia* primarily for coffee shade (e.g., widely around Jalapa and Coatepec, Veracruz, Mexico; near Barillas, Huehuetenango, Guatemala; in Jamaica). In all areas hybrids have thus apparently arisen spontaneously following cultivation. Given the very wide present-day cultivation of both *L. leucocephala* and *L. diversifolia*, particularly as exotics, it is extremely likely that *L.* ×*spontanea* is more widespread and abundant than current collections suggest, especially as wide cultivation of the two species is not entirely recent (e.g., *L.* ×*spontanea* collected in Jamaica in 1903, *A. Rehder s.n.*). Around Barillas, Huehuetenango, Guatemala, pods of *L.* ×*spontanea* are harvested for local food use.

The hybrid between *L. leucocephala* and *L. diversifolia* has been recreated artificially in Hawaii (University of Hawaii accession number KX3) (Brewbaker et al. 1988; Brewbaker & Sorensson 1990; Sorensson 1995) and has caused wide interest amongst those concerned with tropical tree planting. It has been shown to be a self-compatible tetraploid, is a prolific seeder, and can be very vigorous, particularly on mid-elevation sites where cooler conditions do not favor the growth of *L. leucocephala*. Seed of this hybrid has been widely distributed from Hawaii in the last decade, particularly to Asian countries for experimental field testing. The prolific seeding of this hybrid means that it has the potential to spread and become weedy.

Segregation has been observed among advanced generation progeny of the artificial hybrids (de Freitas et al. 1991; Sorensson 1995). No such segregation has been observed among the semi-natural hybrids, suggesting that most may be F_1 hybrids. Later generation material and backcross material are, however, to be expected under semi-natural conditions. De Freitas et al. (1991) observed considerable variation in flower color amongst F_2, F_3, and F_4 generation material, aneuploidy with 86–103 chromosomes as well as the normal 104, regular meiotic behavior, and high pollen stainability, confirming the fertility of this hybrid.

Continued spontaneous hybridization and cultivation of artificially produced hybrids mean that this hybrid is likely to become even more common and widely distributed in the future.

DOUBTFUL AND EXCLUDED NAMES

Leucaena blancii Ramírez Goyena, Fl. Nicaraguense 1: 379. 1911.—This name was previously considered a synonym of *L. leucocephala* subsp. *glabrata* (Brewbaker 1987a; Zárate 1994), based on the complete description and comparison with *L. glauca* (= *L. leucocephala* subsp. *leucocephala*) in the protologue. Lacking a type, the name cannot be assigned with certainty.

Leucaena boliviana Rusby, Bull. New York Bot. Gard. 8: 91. 1912.—TYPE: BOLIVIA. San Buena Ventura, *R. S. Williams 356* (holotype: NY!). = *Acacia glomerosa* Bentham vel. sp. aff., det. L. Rico & G. P. Lewis (K), 20/5/93, matched with *D. N. Smith et al. 13577* (K, LPB, MO).

Leucaena formosa Grisebach, Cat. pl. cubens. 82, 284 (addenda). 1866.—TYPE: CUBA. *Wright 2392* (holotype: ?GOET; isotypes: GH! NY!). = *Lysiloma sabicu* Bentham, Hook. J. Kew Gard. Misc. 6: 236. 1854; see also Shaw and Schubert (1976).

Leucaena forsteri Bentham, Lond. J. Bot. 5: 94. 1846.—TYPE: TAHITI. *Bertero & Moerenhout s.n.* (lectotype: P, not seen). = *Schleinitzia insularum* (Guillemin) Burkart, J. Arnold Arb. 57: 524. 1976; see also Verdcourt (1977) and Nevling and Niezgoda (1978).

Leucaena glauca (L.) Bentham, Hook. J. Bot. 4: 416. 1842. *Mimosa glauca* L., Sp. pl. 1: 520. 1753.—TYPE: Herb. A. van Royen (L, herb no. 908.132-54). = *Acacia glauca* (L.) Moench, Meth. pl. 466. 1794.—Linnaeus (1753) applied the name *M. glauca* to a specimen described by van Royen in Holland. De Wit (1961, 1975) clearly shows the van Royen specimen to be an acacia, now *A. glauca* (L.) Moench. In 1763 Linnaeus misapplied the name to material of *L. leucocephala* (Lam.) de Wit. Bentham established the genus *Leucaena* and applied it to this 1763 material [*L. glauca* (L.) Bentham, basionym *M. glauca* L., 1763].

Leucaena insularum (Guillemin) Däniker, Vierteljahrschr. Nat. Ges. Zürich Jahrg. 77 (Beibl. 19): 176. 1932. *Acacia insularum* Guillemin, Ann. Sci. Nat. ser. 2, 7: 360. 1837.—TYPE: TAHITI. *Bertero & Moerenhout s.n.* (lectotype: P, not seen). = *Schleinitzia insularum* (Guillemin) Burkart, J. Arnold Arb. 57: 524. 1976; see also Verdcourt (1977) and Nevling and Niezgoda (1978).

Leucaena insularum var. *guamensis* Fosberg & Stone, Micronesia 2: 67. 1965.—TYPE: MARIANA ISLANDS. Guam: Cocos Island, *Fosberg 43502* (holotype: US!; isotypes: BISH, F, L, NY). = *Schleinitzia fosbergii* Nevling & Niezgoda, Adansonia ser. 2, 18: 362. 1978.

Leucaena latisiliqua (L.) Gillis & Stearn, Taxon 23: 185. 1974. *Mimosa latisiliqua* L., Sp. pl. 1: 519. 1753. —TYPE: Plumier, Catalogus Plantarum Americanarum, 1703, 17, cum Plantarum Americanarum fasciculus primus, 1755, tab 6; Burman, J. (ed.). = *Lysiloma latisiliqua* (L.) Bentham, Trans. Linn. Soc. London 30: 534. 1875. De Wit (1975) showed that the basionym is clearly applicable to a species of *Lysiloma*.

Leucaena plurijuga Standley, Contrib. U.S. Natl. Herb. 20: 189. 1919.—TYPE: MEXICO. Michoacán: Monte León, 12 Nov 1892, *Pringle 5352* (holotype: US!). = *Albizia plurijuga* (Standley) Britton & Rosé.

Leucaena ulei Harms in Ule, Verh. Bot. Prov. Brandenburg 47: 162. 1907.—TYPE: BRAZIL. Amazónas: Cachoeira dos Marmellos, nr Rio Madero, Mar 1902, *Ule 6085* (holotype: B, destroyed; isotypes F, K, NY; photos ex B: FHO! US!). = *Parkia ulei* (Harms) Kuhlmann, Arch. Jard. Bot. Rio de Janeiro 4: 356. 1925; see also Hopkins (1986).

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APPENDIX 1

SEEDLING COLLECTIONS

Collections of species of *Leucaena*, grown from seed in the greenhouse, from which data for comparative seedling morphology (Table 2) were taken. Vouchers of seedlings are deposited in FHO and K.

L. collinsii subsp. *collinsii*: *Hughes 1137*
L. collinsii subsp. *zacapana*: *Hughes 1120*
L. confertiflora: *Hughes 1321*
L. cuspidata: *Hughes 1586*
L. diversifolia: *Hughes 921*
L. esculenta: *Hughes 894*
L. greggii: *Hughes 1057*
L. involucrata: *Hughes 1522*
L. lanceolata: *Hughes 559*
L. lempirana: *Hughes 1447*
L. leucocephala subsp. *leucocephala*: *Hughes 1671*
L. leucocephala subsp. *glabrata*: *Operation Double Harvest* nursery, Haiti
L. macrophylla subsp. *macrophylla*: *Hughes 1179*
L. macrophylla subsp. *istmensis*: *Hughes 580*
L. magnifica: *Hughes 412*
L. matudae: *Hughes 879*
L. multicapitula: *Hughes 1025*
L. pallida: *Hughes 924*
L. pulverulenta: *Hughes 1051*
L. retusa: seed collected by *Bendeck*, Univ. Auton. Nuevo León, Linares, unvouchered
L. salvadorensis: *Hughes 742*
L. shannonii: *Hughes 507*
L. trichandra: *Hughes 1106*
L. trichodes: *Hughes 1000*
Desmanthus fruticosus: *Hughes 1532*
Schleintizia novoguineensis: seed collected by *Chaplin*, Solomon Islands, unvouchered

APPENDIX 2

CHROMOSOME NUMBERS OF SPECIES OF LEUCAENA

L. collinsii, 2n = 52 (?56) (Pan & Brewbaker 1988; Sorensson 1988, 1989).
L. confertiflora, 2n = 112 (Sorensson 1988; Sorensson & Brewbaker 1994; Palomino et al. 1988, 1995).
L. diversifolia, 2n = 104 (Pan & Brewbaker 1988; Sorensson 1989).
L. esculenta, 2n = 52 (?56) (Hutton 1981; Pan & Brewbaker 1988; Sorensson 1989; Palomino et al. 1995).
L. greggii, 2n = 56 (Sorensson 1988, 1989).
L. lanceolata, 2n = 52 (González et al. 1967; Pan & Brewbaker 1988; Sorensson 1989).
L. leucocephala, 2n = 104 (Tjio 1948; Frahm-Leliveld 1957; Shibata 1962; González et al. 1967; Hutton 1981; Pan & Brewbaker 1988; De Freitas et al. 1991; Sorensson 1989).
L. macrophylla, 2n = ?52 (Sorensson 1989).
L. magnifica, 2n = ?52 (Sorensson 1989).
L. matudae, 2n = ?52 (Sorensson 1989).
L. multicapitula, 2n = ?52 (Sorensson 1989).
L. pallida, 2n = 104 (?110, 112) (Pan & Brewbaker 1988; Sorensson 1989; Palomino et al. 1988).
L. pulverulenta, 2n = 56 (Turner & Fearing 1960; González et al. 1967; Hutton 1981; Pan & Brewbaker 1988, Sorensson 1989).
L. retusa, 2n = 56 (Pan & Brewbaker 1988; Sorensson 1989).
L. salvadorensis, 2n = ?56 (Sorensson 1988, 1989).
L. shannonii, 2n = 52 (Hutton 1981; Pan & Brewbaker 1988; Sorensson 1989).

L. trichandra, 2n = 52 (?56) (Hutton 1981; Pan & Brewbaker 1988; Sorensson 1989; Palomino et al. 1988).
L. trichodes, 2n = 52 (González et al. 1967; Hutton 1981; Pan & Brewbaker 1988).

APPENDIX 3

SPECIES OF LEUCAENA AND ASSOCIATED SPECIES OF BRUCHIDS

Vouchers for bruchid host records are given in Hughes and Johnson (1996).
L. collinsii subsp. *collinsii*: *Acanthoscelides macrophthalmus, A. mankinsii.*
L. collinsii subsp. *zacapana*: *Acanthoscelides macrophthalmus, A. boneti.*
L. confertiflora sensu lato: *Acanthoscelides macrophthalmus, A. mankinsii, A. boneti, A. leucaenicola.*
L. cuspidata: *Acanthoscelides mankinsii.*
L. diversifolia: *Acanthoscelides macrophthalmus, A. mankinsii, A. boneti, A. leucaenicola.*
L. esculenta: *Acanthoscelides macrophthalmus, A. mankinsii, A. boneti, A. leucaenicola.*
L. greggii: *Acanthoscelides macrophthalmus.*
L. lanceolata: *Acanthoscelides macrophthalmus, A. mankinsii, A. leucaenicola.*
L. leucocephala subsp. *leucocephala*: *Acanthoscelides macrophthalmus, A. mankinsii.*
L. leucocephala subsp. *glabrata*: *Acanthoscelides macrophthalmus, A. mankinsii, A. suramerica, Stator pruinius, S. limbatus.*
L. macrophylla: *Acanthoscelides macrophthalmus, A. mankinsii, A. boneti, A. leucaenicola.*
L. magnifica: *Acanthoscelides macrophthalmus.*
L. multicapitula: *Acanthoscelides macrophthalmus, A. mankinsii.*
L. pallida: *Acanthoscelides macrophthalmus, A. mankinsii, A. boneti, A. leucaenicola.*
L. pueblana: *Acanthoscelides macrophthalmus, A. mankinsii.*
L. pulverulenta: *Acanthoscelides macrophthalmus, A. mankinsii, A. leucaenicola, Stator limbatus.*
L. retusa: *Acanthoscelides macrophthalmus.*
L. salvadorensis: *Acanthoscelides macrophthalmus, A. mankinsii.*
L. shannonii: *Acanthoscelides macrophthalmus, A. mankinsii, A. boneti.*
L. trichandra: *Acanthoscelides macrophthalmus, A. mankinsii, A. boneti, A. leucaenicola, Stator limbatus.*
L. trichodes: *Acanthosceilides macrophthalmus, A. suramerica.*

NUMERICAL LIST OF SPECIES

1. L. retusa
2. L. greggii
3. L. cuspidata
4. L. pulverulenta
5. L. diversifolia
6a. L. leucocephala subsp. leucocephala
6b. L. leucocephala subsp. glabrata
6c. L. leucocephala subsp. ixtahuacana
7a. L. collinsii subsp. collinsii
7b. L. collinsii subsp. zacapana
8. L. trichandra
9a. L. confertiflora var. confertiflora
9b. L. confertiflora var. adenotheloidea
10. L. esculenta
11. L. pueblana
12. L. pallida
13. L. involucrata
14. L. matudae
15a. L. lanceolata var. lanceolata
15b. L. lanceolata var. sousae
16. L. multicapitula
17a. L. macrophylla subsp. macrophylla
17b. L. macrophylla subsp. istmensis
18. L. trichodes
19. L. shannonii
20. L. magnifica
21. L. lempirana
22. L. salvadorensis
23. L. ×mixtec
24. L. ×spontanea
25. L. ? hybrid

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The numbers in parentheses refer to the corresponding species in the text and in the Numerical List of Species presented above. A herbarium specimen database for *Leucaena* has been assembled as the first in a series of *BRAHMS Monographs* using the Botanical Research and Herbarium Management System, BRAHMS (Filer 1996). This specimen database is available on request from the author.

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