TAXONOMIC REVISION OF THE ANT-ACACIAS (FABACEAE, MIMOSOIDEAE, *ACACIA*, SERIES GUMMIFERAE) OF THE NEW WORLD[1]

David S. Seigler[2] *and John E. Ebinger*[3]

ABSTRACT

Detailed descriptions, habitat preferences, geographic ranges, and representative specimens are given for the 13 ant-acacia species and hybrids from Mexico, Central America, and South America. A principal component analysis (PCA) of vegetative and floral features shows these species form discrete groups in plots of the first three principal components. Taxa were found to be relatively homogeneous, as indicated by the tight clusters formed in the PCA plots. The data suggest that there is very little gene flow between species, and hybrids are extremely uncommon. Of the 13 species in this group, *Acacia ruddiae* is only marginally a myrmecophyte, rarely being inhabited by acacia-ants, and apparently never producing Beltian bodies on the tips of the leaflets. The remaining taxa have stipular spines that usually are inhabited by obligate acacia-ants of the genus *Pseudomyrmex*, produce Beltian bodies, and have enlarged petiole and rachis glands.

There are about 50 species of the genus *Acacia* Miller series *Gummiferae* Benth. (Fabaceae: Mimosoideae) in the New World. The taxa of this series are quite distinct and are diverse in habitat, habit, morphology, and chemistry. Most authors agree that the series *Gummiferae* is a natural, monophyletic unit composed of trees and shrubs that lack prickles but have stipular spines, bipinnately compound leaves, globose heads or cylindrical spikes that are solitary or borne in axillary fascicles, and legumes that are dehiscent or indehiscent, mostly with uniseriate seeds (Bentham, 1875; Pedley, 1978; Vassal, 1969–1972). Britton & Rose (1928), however, subdivided this series into a number of genera. Most of these "genera" currently are not accepted, but they often circumscribe groups of species at the level of subgenus or section. *Tauroceras* and *Myrmecodendron* are two such segregates proposed by Britton & Rose (1928) that are separated from other *Acacia* species by various fruit characteristics, the involucre of the flowering peduncle, and the large, ant-inhabited stipular spines.

The 13 ant-acacias are restricted to relatively dry to wet, lowland habitats from the coastal regions of central Mexico to northwestern Colombia. This group of neotropical myrmecophytes shares many adaptive ecological and morphological traits, most of which appear to be related to their mutualistic association with acacia-ants of the genus *Pseudomyrmex* (Janzen, 1966, 1974). All have: enlarged stipular spines that are usually inhabited by ants (Fig. 1A, B, C); Beltian bodies, which are used as a food source by the ant larvae, on the tip of many leaflets (Fig. 1D); and enlarged petiolar glands (Fig. 1E, F, G). Many have rachis glands that continuously secrete nectar, many produce new leaves throughout the year, and some have lost chemical and structural traits that protect other *Acacia* species from herbivores (Rehr et al., 1973).

For the most part, ant-acacia species are distinct units that are clearly delimited by a number of morphological traits. Furthermore, in areas where two or more species grow side by side, intermediate plants seldom are encountered (Janzen, 1974), indicating that these species hybridize only rarely with each other (Ebinger & Seigler, 1992).

MATERIALS AND METHODS

More than 2000 specimens from 14 herbaria (A, CM, EIU, F, GH, ILL, LL, MEX, MINN, MO,

[1] We thank the curators of the many herbaria which sent plant material for study and acknowledge support by the National Science Foundation (NSF BSR 82-15274) and the U.S. Department of Agriculture OICD research agreement (58-319R-0-011), and a grant from the American Philosophical Society.

[2] Department of Plant Biology, University of Illinois, Urbana, Illinois 61801, U.S.A.

[3] Botany Department, Eastern Illinois University, Charleston, Illinois 61920, U.S.A.

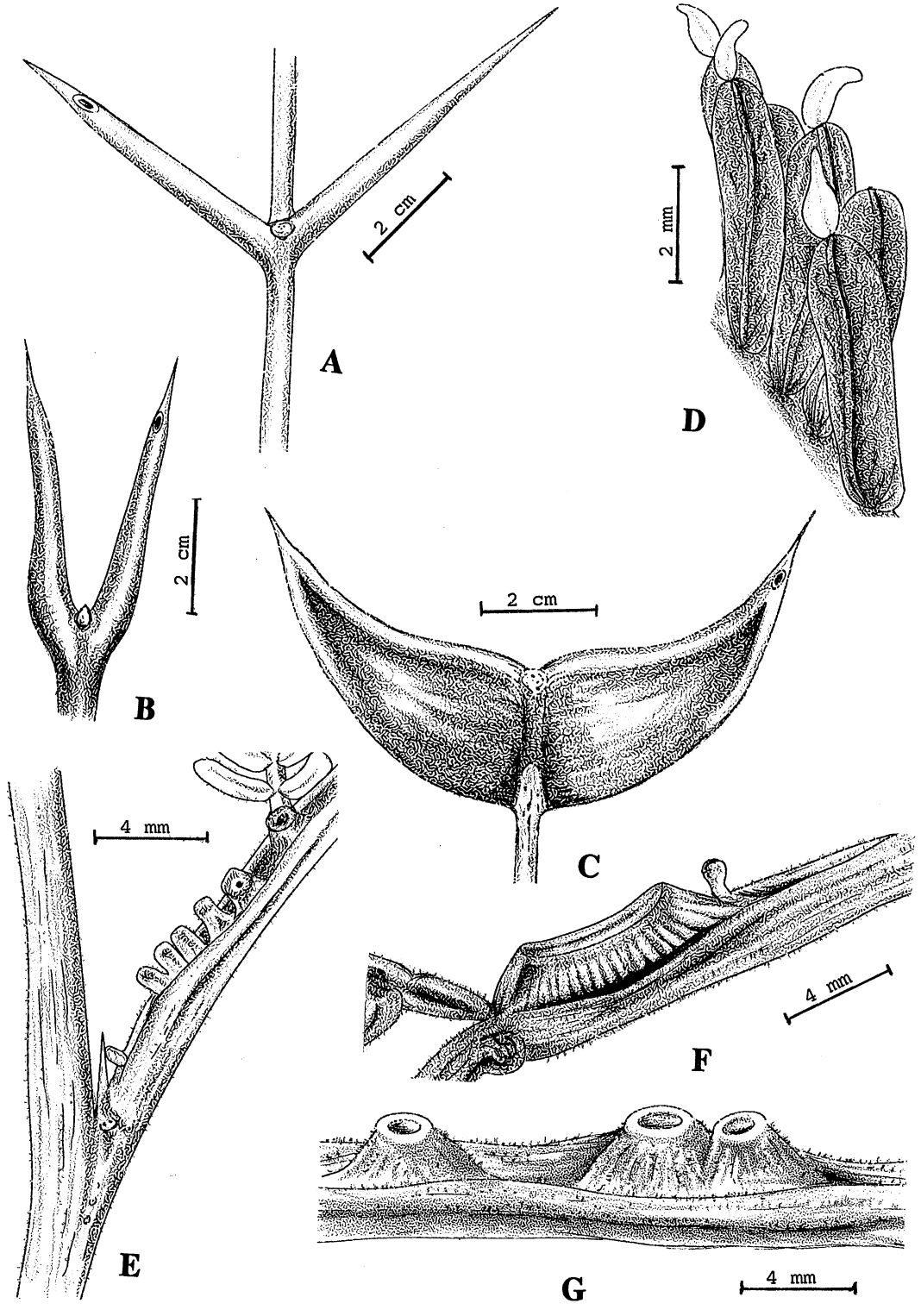

FIGURE 1. A–C, Examples of enlarged stipular spines of ant-acacia species.—A. *A. chiapensis.*—B. *A. globulifera.*—C. *A. hindsii.*—D. Beltian body on a leaflet of *A. chiapensis.* E–G, Examples of petiole glands of some ant-acacia species.—E. *A. chiapensis.*—F. *A. cornigera.*—G. *A. globulifera.*

TABLE 1. Characters scored for the principal component analysis of the 13 species of ant-acacias.

1. Stipular spines inhabited by ants: 1 = not inhabited, 2 = inhabited.
2. Stipular spine pubescence: 1 = glabrous to lightly puberulent, 2 = densely puberulent, 3 = pubescent with yellowish hairs.
3. Stipular spine surface: 1 = smooth, 2 = longitudinal ridges and grooves, 3 = longitudinal flanges.
4. Stipular spine symmetry: 1 = symmetrical, 2 = asymmetrical.
5. Leaf length: 1 = most less than 200 mm long, 2 = most more than 200 mm long.
6. Average number of pairs of pinnae per leaf.
7. Rachis glands: 1 = absent, 2 = present.
8. Petiolar glands: 1 = one present, 2 = two or more present, 3 = absent.
9. Petiolar and rachis gland shape: 1 = volcano- to columnar-shaped, 2 = narrow and elongated to canoe-shaped.
10. Beltian bodies: 1 = absent, 2 = present.
11. Leaflet length: 1 = less than 5.9 mm long, 2 = more than 6 mm long.
12. Secondary veins of leaflets: 1 = not obvious, 2 = obvious.
13. Thickness of flowering peduncle: 1 = less than 1.9 mm thick, 2 = more than 2 mm thick.
14. Inflorescences per node: 1 = 1–8, 2 = 9 or more.
15. Inflorescence shape: 1 = globose, 2 = cylindrical.
16. Floral bract apex shape: 1 = circular, 2 = tailed.
17. Calyx/corolla ratio: 1 = calyx about half the length of the corolla, 2 = calyx nearly as long as the corolla.

NY, TEX, UC, and US) were studied to determine the geographic range and morphological variation of the ant-acacia taxa. These specimens were sorted into groups based on similarity of morphological characteristics. Virtually all of the specimens could be placed in groups corresponding to the taxa listed below; only a few intermediate individuals were found (Ebinger & Seigler, 1992). Ninety-three specimens representing the geographical and morphological range of each taxon were scored for 12 vegetative and five floral characters (Table 1). All characters were measured (three or more measurements from each specimen) and plotted to confirm that gaps existed in order to enable the use of scored characters. These differences were observed in all cases. The data were then analyzed by principal components analysis (PCA) with the BMDP Statistical Software Package (Dixon, 1983) and by NTSYS-pc (Rohlf, 1990). Groups were analyzed separately and in various combinations, as were apparently hybrid specimens and their putative parental taxa. Subsequently all taxa were analyzed simultaneously.

All specimens used in this study were tested for the presence of cyanogenic compounds by the Feigl-Anger method (Feigl & Anger, 1966; Tantisewie et al., 1969; Brinker & Seigler, 1989). A few leaflets from each specimen were crushed, placed in a small vial, and moistened with distilled water. A strip of filter paper impregnated with copper ethylacetoacetate and tetra base (4,4′-tetramethyldiaminodiphenylmethane) was added to the vial so as not to touch the sample, and the vial sealed with a cork. The presence of cyanide was indicated if the filter paper turned a deep blue color.

RESULTS AND DISCUSSION

When the entire set of 93 specimens was analyzed, the first three principal components accounted for 38%, 17%, and 12% respectively, or 67% of the total variance. The amount of variance contributed by the remaining components diminished slowly from the third principal component onward. Plots of all pairs of the first three principal components indicated that the only phenetic groupings were those found in the ordination based on the first two components.

A plot of the first two principal components revealed 13 distinct groups corresponding to the previously defined species (Fig. 2). Calyx/corolla length ratio, inflorescence shape, and the presence or absence of rachis glands (characters 17, 15, and 7) were the most important characters for determining the component score of the first principal component. Stipular spine symmetry, number of inflorescences per node, and stipular spine pubescence (characters 4, 14, and 2) were the most important in determining the second principal component (Table 1).

Distinct OTUs can be recognized in the PCA plot (Fig. 2). The clusters do not seem to contain recognizable subgroups, and each cluster is separated from the others. Also, the points for specimens in each group are closely spaced, indicating that the species are homogeneous. Similar results were obtained when the entire complex was divided into smaller species groups and analyzed by PCA.

TAXONOMIC TREATMENT

The present systematic treatment is based on herbarium specimens as well as extensive collections and observations of these taxa in Mexico and Central America by the first author (DSS) on 13 trips during 1975–1993. Only important diagnostic characteristics were used to distinguish the taxa, and only enough representative specimens to indicate the distribution of each species are included. Most specimens used in the PCA analysis also are included in the list of representative specimens.

FIGURE 2. Plot of axis 1 vs. 2 for principal component analysis, using 12 vegetative and five floral variables, of 93 specimens of ant-acacia species.

For most accepted names and synonyms, the type specimens are readily available. For some, however, particularly for names proposed by Schenck (1913) and Schlechtendal & Chamisso (1830), the types, which were probably located at B, have been destroyed (H. Ern, pers. comm.). For these species, lectotypes have been designated.

The ant-acacias are closely related to the *Acacia macracantha* Humb. & Bonpl. ex Willd, *A. cochliacantha* Humb. & Bonpl. ex Willd., and *A. pennatula* (Schltdl. & Cham.) Benth. group in the series *Gummiferae*. In addition to the myrmecophyte characteristics of enlarged stipular spines, enlarged petiolar glands, and the usual production of Beltian bodies, the ant-acacias are shrubs or small or medium-sized trees with bipinnately compound leaves that bear one or more extrafloral nectaries on the petiole and/or rachis. The inflorescences are spicate or capitate and fascicled or solitary in the axils of the leaves, or sometimes on leafless shoots. The flowers are small (2–5 mm long) and subtended by a small, peltate bract. The sepals and petals are connate and 4–5-merous. The stamens are numerous (50 or more) and exserted. There is a single carpel which develops into a dehiscent or indehiscent legume.

KEY TO THE SPECIES OF ANT ACACIAS

1a. Petiolar glands usually saddle-shaped or canoe-shaped, or long and narrow, lower than the petiolar groove and nearly as long as the petiole.

2a. Petiolar glands long and narrow, lower than the petiolar grooves and nearly as long as the petiole ..... 4. *A. cookii*

2b. Petiolar glands saddle-shaped or canoe-shaped.
3a. Spines with two longitudinal flanges; leaflets more than 10 mm (usually 12–18 mm) long ..... 10. *A. mayana*
3b. Spines lacking longitudinal flanges; leaflets less than 10 mm long.
4a. Leaflets with 2–3 veins from the base, lateral veins obvious; inflorescence more than 3 times longer than wide ..... 5. *A. cornigera*
4b. Leaflets with one vein from the base, lateral veins not obvious; inflorescence subglobose, less than 2 times longer than wide ..... 13. *A. sphaerocephala*
1b. Petiolar glands dome-shaped, volcano-shaped, or columnar, rarely absent.
5a. Inflorescence cylindrical, more than 5 times longer than wide.
6a. Leaflets with one vein from the base, lateral veins not obvious; enlarged stipular spines flattened at the base ..... 8. *A. hindsii*
6b. Leaflets with 2–5 veins from the base, lateral veins obvious; enlarged stipular spines terete or oval in cross section.
7a. Petiolar glands usually solitary; rachis glands scattered along the leaf rachis ..... 6. *A. gentlei*
7b. Petiolar glands 3–5; rachis glands absent ..... 3. *A. collinsii*
5b. Inflorescence globose, never more than 2 times longer than wide.
8a. Leaflets more than 1.8 mm wide, with 2–3 veins from the base, lateral veins obvious ... 1. *A. allenii*
8b. Leaflets mostly less than 1.8 mm wide, with one vein from the base, lateral veins not obvious.
9a. Adaxial surface of the petiole flattened (on well-developed leaves) with numerous petiolar glands (6–30) present on the flattened surface ..... 11. *A. melanoceras*
9b. Adaxial surface of the petiole grooved with fewer than 13 petiolar glands present in the groove.
10a. Stipular spines asymmetrical, commonly curved around the stem, pubescent with yellowish hairs ..... 9. *A. janzenii*
10b. Stipular spines symmetrical, glabrous to puberulent.
11a. Rachis glands cylindrical and narrowing toward the base; most stipular spines not enlarged, those that are usually not inhabited by acacia-ants ..... 12. *A. ruddiae*
11b. Rachis glands narrowly volcano-shaped, or columnar and not narrowing toward the base; most stipular spines enlarged and inhabited by acacia-ants.
12a. Petiolar and rachis glands columnar; inflorescences in clusters of 10–40; fruit margins ridged ..... 2. *A. chiapensis*
12b. Petiolar and rachis glands narrowly volcano-shaped; inflorescences in clusters of 4–8; fruit margins not ridged ..... 7. *A. globulifera*

1. Acacia allenii D. H. Janzen, Smithsonian Contr. Bot. 13: 53. 1974. TYPE: Costa Rica. Puntarenas: Osa Peninsula, bank of tributary of Río Agua Buena, 3.5 mi. SW of Rincón, 9 Mar. 1967, *D. H. Janzen 1769* (holotype, US; isotypes, F, GH, K, MEXU, MICH, MO, NY, UC).

Tree to 25 m tall with widely spreading branches, young twigs dark brown to dark reddish brown, lightly puberulent. Stipular spines black to dark brown, commonly grooved and with low, rounded longitudinal ridges, glabrous to lightly puberulent, nearly terete in cross section, sometimes slightly reflexed, symmetrical, broadly V-shaped with an angle of 90–120°, to 45 mm long, 8–12 mm wide near the base. Leaves 150–400 mm long, pinnae 10–22 pairs per leaf, 60–110 mm long, 15–22 mm between pinna pairs; rachis grooved, lightly puberulent, rachis glands puberulent, lightly striate, narrowly volcano-shaped, 1 or 2 located at the node of each pinna pair, sometimes scattered along the rachis between the pinna pairs; petiole grooved, lightly puberulent, 14–30 mm long. Petiolar glands narrowly volcano-shaped, usually 4–10, scattered along the petiole, puberulent, lightly striate, apex 0.4–0.7 mm across, base 0.8–1.2 mm across. Leaflets 15–25 pairs per pinna, glabrous, linear, 6–12 mm long, 1.8–3.9 mm wide, lateral veins obvious, 2–3 veins from the base, apex obtuse to rarely acute. Inflorescence a densely flowered globose head, 5–7 mm across, in axillary clusters of 5–15 in the axil of reduced leaves, commonly on short axillary branches 40–150 mm long; peduncles lightly puberulent, 10–15 mm long, 0.6–0.9 mm thick, nearly the same thickness throughout; involucre located on the lower ⅓ of the peduncle, puberulent, 5-lobed. Floral bracts peltate, apex circular, ciliate, stalk 0.8–1.0 mm long. Flowers sessile; calyx 5-lobed, puberulent on the lobes, 0.9–1.2 mm long; corolla 5-lobed, glabrous, pale yellow, 1.2–1.5 mm long.. Legumes (only one specimen, *Janzen 11051*, with fruits seen) slightly curved, flattened, 65–110 mm long, 15–20 mm wide, glabrous, longitudinally striate, dark brown to black, dehiscent along two sutures, base not stipitate, the apex acute. Flowering April–July.

Distribution. Heavily shaded understory at lower elevations (to 160 m) in wet forests, in moist disturbed stream banks, at forest edge, and on roadsides, in Puntarenas Province, Costa Rica.

Representative specimens. COSTA RICA. **Puntarenas:** forested hills near Golfito de Golfo Dulce, *Allen 5997* (F, GH, MO, US); 5 mi. SW of Rincón, Osa Peninsula, *Janzen 791* (F, GH, MEX, MO).

The narrow geographic range of *Acacia allenii* is typical of many of the ant-acacia species of Central America. Its normal habitat appears to be at lower elevations in heavily shaded understory of wet tropical forests. In general, it reacts fairly well to disturbances, and most present-day collections are from roadsides, recent landslides, disturbed stream banks, and secondary successional areas after logging. It is rarely found in open pastures, and according to Janzen (1974) will not survive fire.

As is typical of many wet forest ant-acacias, Beltian body production in *Acacia allenii* is not particularly extensive. However, the Beltian bodies are much larger (to 3 mm long) than those found in dry area ant-acacias. In *A. allenii*, these relatively large Beltian bodies are formed only on the lower 3–6 leaflets of each pinna, and occasionally the lower leaflet of a pinna has been replaced by a large Beltian body. None of the individuals tested positive for cyanide production.

Acacia allenii is most closely related to *A. melanoceras* and possibly *A. collinsii*. The globose inflorescences and the presence of rachis glands easily separate this species from *A. collinsii*, which has elongated inflorescences and usually lacks rachis glands. It is easily separated from *A. melanoceras*, since its leaflets are nearly twice as large and have obvious secondary veins. Also, well-developed leaves of *A. allenii* have only 4–10 widely scattered petiolar glands, while *A. melanoceras* commonly has 6–30 closely spaced petiolar glands on the flattened adaxial surface of the petiole. Furthermore, the fertile branches of *A. allenii* are commonly less than 150 mm long, are scattered along major branches throughout the crown, and have 5–15 inflorescences in the axis of reduced leaves. In *A. melanoceras*, the fertile branches are to 350 mm long, tend to be bunched near the ends of the sterile branches, and have 2–6 inflorescences at each leafless node.

2. Acacia chiapensis Safford, J. Wash. Acad. Sci. 5: 356. 1915. TYPE: Mexico. Chiapas: near San Fernando, between Tuxtla and Chicoasén, 12 Jan. 1907, *G. N. Collins 164* (holotype, US; photo, F).

Shrub or small tree to 10 m tall, young twigs brown to reddish brown, usually densely puberulent. Stipular spines (Fig. 1A) usually dark brown to black, smooth, terete, usually densely puberulent (rarely glabrous), symmetrical, V-shaped with an angle of 70–100°, straight to slightly reflexed near the apex, 30–80 mm long, 4–7 mm thick near the base. Leaves 100–250 mm long; pinnae 12–30 pairs per leaf, 30–70 mm long, 5–12 mm between pinna pairs; rachis grooved, densely puberulent, a columnar gland commonly present between each pinna pair (sometimes absent); petiole grooved, densely puberulent, 7–17 mm long. Petiolar glands (Fig. 1E) columnar, densely puberulent, striate, apex 0.5–0.8 mm across, base 0.6–1.2 mm across, usually 6–13 scattered along the petiole. Leaflets 22–50 pairs per pinna, glabrous, linear, 3–8 mm long, 0.7–1.6 mm wide, lateral veins not obvious, only one vein from the base, apex acute to obtuse. Inflorescence a densely flowered globose head 5–9 mm across, in clusters of 10–40 in the axil of slightly reduced leaves, or in clusters of 10–40 in the axil of much reduced leaves on axillary branches; peduncles glabrous to lightly puberulent, 10–35 mm long, 0.6–1.1 mm thick, nearly the same thickness throughout; involucre located near the middle of the peduncle, glabrous to puberulent, 4-lobed. Floral bracts peltate, apex circular, stalk 0.8–1.5 mm long. Flowers sessile; calyx 5-lobed, glabrous, 1.0–1.3 mm long; corolla 5-lobed, glabrous, pale yellow, 1.6–1.9 mm long. Legume nearly straight, flattened, 65–90 mm long, 8–10 mm wide, glabrous, longitudinally striate, black to dark brown, tardily dehiscent, stipe less than 5 mm long, the apex narrowing to a very short spinelike beak, margins ridged. Flowering January–May.

Distribution. Usually rare in dry lowland sites, and along and near watercourses in heavily disturbed vegetation in extreme southern Mexico.

Representative specimens. MEXICO. **Chiapas:** steep slope with montane rainforest, 18–20 km N of Ocozocoautla along road to Mal Paso, 800 m, *Breedlove 23862* (MEX, MICH, MO, NY, TEX). **Oaxaca:** gravel pit, second growth vegetation, 1 mi. W of Temascal, *Janzen 185* (F, MEX, MO). **Veracruz:** Dos Ríos, *Mell 506* (NY).

Acacia chiapensis appears to be most closely related to *A. globulifera* in its morphology and habit. These two species are easily separated, because in *A. chiapensis* there are usually 6–13 columnar petiolar glands scattered along the petiole, the globose inflorescences are in axillary clusters of 10–40, and the legume has a distinct marginal ridge. *Acacia globulifera*, in contrast, usually has only 3–6 narrow, volcano-shaped petiolar glands on a petiole, the globose inflorescences rarely exceed 8 in a cluster, and the legume lacks marginal ridges. The only other species with which *A. chia-*

pensis could be sometimes confused is *A. collinsii*, but this species has elongated inflorescences, fewer petiolar glands, and its leaflets have obvious secondary veins.

Acacia chiapensis is usually shrubby, but can reach a height of 10 m (Janzen, 1967b). When repeatedly cut it commonly forms a dense bush, but rarely produces root sprouts. In many respects this species has a life form similar to that of non-ant-acacias such as *A. farnesiana* and *A. macracantha*. It is similar to these species in seed dispersal, seedling ecology, low Beltian body production, and the fact that many leaves on elongated lateral branches are not subtended by swollen spines (Janzen, 1974).

It appears that *A. chiapensis* is a marginal host for obligate acacia-ants. Janzen (1974) indicated that this species can sometimes survive in the absence of ants. Most specimens of this species retain cyanogenic glycosides in the leaves, which probably limits herbivory (Seigler & Ebinger, 1987). Low Beltian body production in this species may also indicate that it is a marginal host for acacia-ants. Beltian bodies of this species are generally less than 0.6 mm long, commonly are not well developed, and usually occur only on the lower 3–9 pairs of leaflets on some of the pinnae.

According to Janzen (1974), *Acacia chiapensis* occasionally hybridizes with *A. cornigera* and with non-ant-acacias such as *A. macracantha*. During the present study, no specimens were found that would indicate hybridization involving these species. Hybrids involving *A. pennatula* and *A. chiapensis*, however, have been observed.

3. Acacia collinsii Safford, Science N. S. 31: 677. 1910. *Myrmecodendron collinsii* (Saff.) Britton & Rose, N. Amer. Fl. 23: 92. 1928. TYPE: Mexico. Chiapas: between Chicoasén and San Fernandino, 1005 ft., 13 Jan. 1907, *G. N. Collins & C. B. Doyle 180* (holotype, US; photo, F). [Safford (1910) listed Guy N. Collins as the only collector, and cited 14 Jan. 1907 as the date collected; on the label of the herbarium specimen G. N. Collins and C. B. Doyle are listed as the collectors, and 13 Jan. 1907 is given as the date of collection.]

Acacia costaricensis Schenck, Repert. Spec. Nov. Regni Veg. 12: 361. 1913. *Myrmecodendron costaricensis* (Schenck) Britton & Rose, N. Amer. Fl. 23: 93. 1928. TYPE: Costa Rica. Alajuela: Alajuela, 900 m, 1896, *J. D. Smith 6488* (lectotype, designated here, US [B destroyed]; isotypes, BM, GH, K, MO).

Acacia yucatanensis Schenk, Repert. Spec. Nov. Regni Veg. 12: 361. 1913. TYPE: Mexico. Yucatan: 1895, *G. F. Gaumer 353* (lectotype, designated here, US [B destroyed]; isotypes, BM, GH, F, MO).

Acacia panamensis Schenck, Repert. Spec. Nov. Regni Veg. 12: 362. 1913. TYPE: Panama. Aljahuela: Prof. Alex. Koch (holotype, B destroyed).

Acacia nelsonii Saff., J. Wash. Acad. Sci. 4: 363. 1914. TYPE: Mexico. Guerrero: Acapulco, sea level, 30 Apr. 1903, *E. W. Nelson 7024* (holotype, US; isotypes, GH, F).

Acacia penonomensis Saff., J. Wash. Acad. Sci. 4: 363. 1914. TYPE: Panama. Coclé: Penonomé, 50–1000 ft., 23 Feb.–22 Mar. 1908, *R. S. Williams 113* (holotype, NY; photo, F; fragment and photo, US; isotype, US).

Tree to 10 m tall; young twigs reddish brown to dark brown, glabrous. Stipular spines shiny, light reddish brown to dark brown, rarely ivory to yellowish, smooth, glabrous, terete in cross section, mostly symmetrical, V- to U-shaped with an angle of 50–180°, 20–50 mm long, 4–13 mm wide at the base, sometimes reflexed near the tip. Leaves 40–195 mm long; pinnae 3–15 pairs per leaf, 30–90 mm long, 7–17 mm between pinna pairs; rachis grooved, glabrous to lightly puberulent, rachis glands usually absent; petiole grooved, glabrous to lightly puberulent, 4–18 mm long. Petiolar glands 3–5 (rarely 2), dome-shaped to broadly volcano-shaped, usually near the base of the petiole, puberulent, striate, apex 0.3–0.8 mm across, base 1–2.5 mm across. Leaflets 11–29 pairs per pinna, glabrous, linear, 6–13 mm long, 1.3–3.1 mm wide, 2–3 veins from the base, lateral veins obvious, apex obtuse, margins usually not ciliate. Inflorescence of densely flowered cylindrical obtuse spikes, 15–35 mm long, 4–6 mm thick, commonly in short, leafy racemes with 1–3 (rarely 5) spikes per node; peduncles glabrous to lightly puberulent, 6–20 mm long, 0.8–1.8 mm thick, nearly the same thickness throughout; involucre located near the base to lower third of the peduncle, glabrous to lightly puberulent, 4-lobed, the lobes unequal. Floral bracts peltate, apex circular and usually puberulent, stalk 0.6–1.1 mm long. Flowers sessile; calyx 5-lobed, glabrous, 1–1.4 mm long; corolla 5-lobed, glabrous, yellowish, 1.1–1.5 mm long, slightly longer than the calyx. Legumes nearly straight, elliptical in cross section, 30–60 mm long, 7–13 mm wide, glabrous, not striate, dark brown to black, dehiscent along both sutures, not stalked, the apex acute with a short beak 1–6 mm long. Flowering January–August.

Distribution. In shrubby vegetation of pastures and on rocky ridges, in habitats ranging from moderately wet to very dry, at lower elevations (below 1000 m) along the west coast of Mexico from Guerrero east to the Yucatán Peninsula, south

through the dry lowland of Central America to the lowlands of northern Colombia.

Representative specimens. BELIZE. Maskall, *Gentle 1112* (GH, WIS). COLOMBIA. **Bolívar:** Municipio de Arenal, *Forero G. & Jaramillo M. 496* (F). COSTA RICA. **Alajuela:** El Coyolar, 240 m, *Standley 40026* (US). **Guanacaste:** vicinity of Cañas, Finca La Pacífica, *Daubenmire 449* (F). **Puntarenas:** ca. 10 mi. NE of Palmar Sur on the Inter-American hwy., *Janzen 1852* (US). **San José:** Villa Colón, *Janzen 1862* (F, US). EL SALVADOR. **La Unión:** 7.1 mi. W of El Amatillo, *Janzen 1801* (F). GUATEMALA. **Zacapa:** Jones Bridge, 5.8 mi. NE of Río Hondo on hwy. 9, *Janzen 1797* (MEX). HONDURAS. **Colón:** 4.5 mi. NE of Trujillo on old road to Castilla, *Saunders 1040* (F, MO). **Comayagua:** on slope down to Río Selguapa, Comayagua valley, ca. 600 m, *Burch 6033* (MEX, MO). **Olancho:** vicinity of Juticalpa, 380–480 m, *Standley 17522* (F). **Valle:** 28.4 mi. SE of El Amatilla on Inter-American hwy., *Janzen 1841* (F, MEX, US). MEXICO. **Campeche:** 0.8 mi. E of Campeche on hwy. 180, *Janzen 428* (MEX, F). **Chiapas:** along hwy. 190, 13 mi. S of La Trinitaria, 3000 ft., *Breedlove & Raven 8448* (F). **Guerrero:** Petatlán, Montes de Oca, *Hinton 10333* (MO). **Oaxaca:** 11.4 mi. W of Tehuantepec, *Janzen 1780* (F). **Quintana Roo:** 32 mi. N of jct. 307 & 186, N of Chetumal on hwy. 307, *Seigler et al. 11595* (MEX, ILL). **Yucatán:** Chichén Itzá, *Seigler et al. 11599* (EIU, ILL). NICARAGUA. **Esteli:** 1 mi. N Condega, *Janzen 1810* (F). **Rivas:** Peña Blanco, *Janzen 1830* (F, MEX). **Zelaya:** in vicinity of La Luz-Siuna, 150–200 m, *Bunting & Licht 666* (US). PANAMA. **Canal Zone:** Victoria fill, near Miraflores Locks, *Allen 1743* (US). **Coclé:** roadside pasture 20 mi. S of Nata, *Croat 9643* (MO).

Acacia collinsii has the most extensive geographical distribution of all New World ant-acacias and is the only ant-acacia that occurs in South America. It also has the widest ecological distribution, growing in dry to moderately wet pastures and fields and in open shrubby vegetation from sea level to 1000 m. It is a common component of early successional areas. This wide ecological and geographical distribution has resulted in a relatively broad morphological diversity, which is reflected in the extensive synonymy. Though morphologically diverse, it can easily be distinguished from all other ant-acacias by the following combination of characters: elongated cylindrical inflorescences, 3–5 petiolar glands that are broadly dome-shaped, absence of rachis glands, leaflets with obvious lateral veins, and relatively small stipular spines that are terete in cross section.

As is typical of most xerophytic ant-acacias, Beltian body production in *Acacia collinsii* is relatively extensive. In this species the nearly globose Beltian bodies are 0.4–0.8 mm long and usually are found on more than 50% of the leaflets of developing leaves. As most individuals of this species are inhabited by obligate acacia-ants, the Beltian bodies are generally "harvested" soon after development.

Cyanide tests of more than 400 specimens of *Acacia collinsii* indicate that this species is not cyanogenic. Herbarium material of this species was reported to be cyanogenic (Seigler et al., 1978), but reinvestigation of these same specimens failed to confirm activity (Seigler & Ebinger, 1987). Janzen (1981) did not report cyanogenesis for this species.

Acacia collinsii probably hybridizes with *A. hindsii*. These species are sympatric in parts of their ranges in Mexico and Central America, and occasionally occur at the same site. *Acacia collinsii* also hybridizes with the non-ant-acacia *A. pennatula* (Ebinger & Seigler, 1992).

4. Acacia cookii Safford, Science N. S. 31: 677. 1910. *Myrmecodendron cookii* (Saff.) Britton & Rose, N. Amer. Fl. 23: 93. 1928. TYPE: Guatemala. Alta Verapaz: Finca Trece Aguas, near Secanguím, 300 m, 8 Mar. 1907, *G. P. Goll 102* (holotype, US).

Acacia bucerophora B. L. Rob., Proc. Amer. Acad. Arts 49: 502. 1913. TYPE: Belize. Belize: about Toledo, 4 mi. from the coast and 5 mi. from Punta Gorda, sea level, 29 Mar. 1907, *M. E. Peck 632* (holotype, GH; fragment and photo, F, US; isotype, F, K).

Tree to 12 m tall, young twigs dark reddish brown to black, densely puberulent. Stipular spines dark brown to black, smooth, terete, densely puberulent, asymmetrical, U-shaped with an angle of 25–50°, usually curved around the stem, 60–100 mm long, 3.5–5.5 mm thick near the base. Leaves 275–500 mm long, pinnae 18–40 pairs per leaf, 10–15 mm between pinna pairs; rachis grooved, densely puberulent; a depressed, elongated gland 1–3 mm long present between each pinna pair; petiole grooved, densely puberulent, 9–16 mm long. Petiolar glands elongate, located in the groove of the petiole, lower than the top of the groove and nearly the same length as the petiole, not striate, glabrous to lightly puberulent, apex 6–13 mm long. Leaflets 50–70 pairs per pinna, glabrous, linear, 6–8 mm long, 0.9–1.2 mm wide, lateral veins not obvious, only one vein from the base, apex acute. Inflorescences of densely flowered globose heads 6–8 mm across, in axillary clusters of 20–70 subtended by normal to slightly reduced leaves; peduncles glabrous to lightly puberulent, 15–30 mm long, 0.8–1 mm thick, slightly thicker near the apex; involucre located near the middle of the peduncle, 4- to 7-lobed, the lobes unequal in length. Floral bracts peltate, apex circular, stalk 0.8–1.1

mm long. Flowers sessile; calyx 5-lobed, glabrous, 1–1.3 mm long; corolla 5-lobed, glabrous, pale yellow, 1.5–1.8 mm long, about ⅓ longer than the calyx. Legumes slightly curved, flattened, 250–300 mm long, 10–16 mm wide, glabrous to lightly puberulent, not striate, dark brown to black, dehiscent along both sutures, stipe 10–40 mm long, the apex narrowing to a terminal point 10–30 mm long. Flowering November–April.

Distribution. In naturally disturbed sites along rivers and in wet forests with a very mild dry season, sea level to 400 m elevation, in Belize and Guatemala.

Representative specimens. BELIZE. Big Rock, Toledo, 200 ft., *Schipp 1072* (F, GH, MICH, MO, NY, UC). GUATEMALA. **Alta Verapaz:** near the Finca Sepacuite, road from Secanguím to Sepacuite, *Cook & Griggs 374* (US). **Izabal:** 2.8 mi. W of Puerto Matías de Gálvez on road to Escobas, *Janzen 1524* (F, GH, MEX, MICH, MO, NY, UC).

Acacia cookii is separated easily from other ant-acacias by its usually asymmetrical, thin, densely puberulent stipular spines that are curved around the stem. The one other species with similar spines, *A. janzenii*, is probably its nearest relative. Though similar, plants of these two species are easily separated. The stipular spines of *A. cookii* are relatively long (60–100 mm), fairly thin (3.5–5.5 mm), and densely puberulent with short gray hairs. *Acacia janzenii*, in contrast, has shorter (30–60 mm), relatively broad (6–9 mm) stipular spines that are densely pubescent with straight, yellowish hairs to 0.5 mm long. In *A. cookii*, the puberulent petioles are 9–16 mm long with a gland to 13 mm long, while in *A. janzenii* the pubescent petioles are less than 8 mm long and lack a gland. The rachis glands that are located between each pair of pinnae also differ in these two species, being elongate (1–3 mm) in *A. cookii* and much smaller (0.5–0.7 mm) and circular in *A. janzenii*. Further, the leaflets of *A. cookii* are 6–8 mm long, usually more than 1 mm wide, and have glabrous margins, while in *A. janzenii* they are shorter (3–5.5 mm), narrower (0.6–0.9 mm), and have ciliate margins. The arrangements of the inflorescences also differ. In *A. cookii* the inflorescences are in axillary clusters of 20–70 on typical branches and are subtended by normal to slightly reduced leaves. In *A. janzenii* some of the inflorescences are on thin fertile branchlets to 250 mm long, with 16–42 inflorescences in each of 6–12 fascicles that are usually not subtended by leaves (Ebinger & Seigler, 1987).

Originally *Acacia cookii* was probably a wet forest species and was commonly found in naturally disturbed sites along rivers in very wet forests (Janzen, 1974). Presently, it is also found along roadsides, in areas of recent landslides, and occasionally in pastures and other sites after human disturbance. According to Janzen (1974), however, this species generally disappears after a forest is cut. Like those of most wet forest ant-acacias, specimens of *A. cookii* generally have relatively low Beltian body production. Commonly only the lower 6–12 pairs of leaflets on a pinna produce Beltian bodies, but usually the bodies are 1–2 mm long. As in most ant-acacias, none of the specimens of this species tested positive for cyanide production.

5. Acacia cornigera (L.) Willdenow, Sp. Pl. 4: 1080. 1806. *Mimosa cornigera* L. Sp. Pl. 520. 1753. *Tauroceras cornigerum* (L.) Britton & Rose, N. Amer. Fl. 23: 86. 1928. TYPE: in the Linnean Herbarium, from a cultivated plant grown in the garden of George Clifford, between Haarlem and Leyden, Holland, collected by Linnaeus (No. 4) and bearing his label "*Mimosa cornigera*," presumably grown from Mexican seed (Rudd, 1964) (holotype, BM; fragment and photo, US).

Acacia cornigera (L.) Willd. var. *americana* DC. Prodr. 2: 460. 1825.

Acacia spadicigera Schltdl. & Cham., Linnaea 5: 594. 1830. *Tauroceras spadicigerum* (Schltdl. & Cham.) Britton & Rose, N. Amer. Fl. 23: 85. 1928. TYPE: Mexico. Veracruz: near La Laguna Verde, Mar. 1828, *Schiede & Deppe 685* (lectotype, designated here, US, fragment [B destroyed]).

Acacia campecheana Schenck, Repert. Spec. Nov. Regni Veg. 12: 361. 1913. TYPE: Mexico. Campeche: von Chrismar (holotype, B destroyed).

Acacia cubensis Schenck, Repert. Spec. Nov. Regni Veg. 12: 360. 1913. TYPE: Cuba. N coast, 21 Apr. 1863, *C. Wright 2402* (lectotype, designated here, US fragment and photo [B destroyed]; isotypes, G, GOET, HAL, JE, K, MO, US). A note on the herbarium sheet (JE) indicates that the seeds he grew came from Martinique.

Acacia interjecta Schenck, Repert. Spec. Nov. Regni Veg. 12: 361. 1913. TYPE: *Engler 3870a* (lectotype, designated here, JE [B destroyed]). Material growing in the Singapore and Kew Botanical Gardens (Janzen, 1974).

Acacia nicoyensis Schenck, Repert. Spec. Nov. Regni Veg. 12: 360. 1913. TYPE: Costa Rica. Guanacaste: shore of the Gulf of Nicoya, sea level, Feb. 1900, *A. Tonduz 13538* (lectotype, designated here, US [B destroyed]; isotypes, BM, GH, K, NY, US).

Acacia rossiana Schenck, Repert. Spec. Nov. Regni Veg. 12: 361. 1913. TYPE: Mexico. Veracruz: Santa Lucrezia, Isthmus of Tehuantepec, 8 Oct. 1906, *H. Ross 918* (lectotype, designated here, M, photo, US).

Acacia furcella Saff., J. Wash. Acad. Sci. 4: 359. 1914. TYPE: Mexico. Veracruz: shore of Lake Catemaco,

southern Veracruz, 1000 ft., 26 Apr. 1894, *E. W. Nelson 427* (holotype, US).

Acacia hernandezii Saff., J. Wash. Acad. Sci. 4: 358. 1914. TYPE: Mexico. San Luis Potosí: vicinity of Rascón, 19–22 July 1905, *E. Palmer 699* (holotype, US; isotypes, F, GH, MO, NY).

Acacia turgida Saff. in W. M. Wheeler, Bull. Mus. Comp. Zoology Harvard Coll. 90: plate 45, 1942 (holotype, plate 45 in Wheeler, 1942).

Shrub or small tree to 10 (rarely 15) m tall, young twigs dark gray to reddish brown, lightly to densely puberulent. Stipular spines light to dark brown to sometimes ivory to yellow, glabrous to densely puberulent, smooth, terete to slightly flattened, symmetrical, commonly V-shaped with an angle of 60–150°, straight to slightly reflexed near the apex, 30–100 mm long, 4–10 mm thick near the base. Leaves 40–160 mm long; pinnae 3–14 pairs per leaf, 30–70 mm long, 7–17 mm between pinna pairs; rachis grooved, glabrous to densely puberulent, rachis glands usually absent; petiole grooved, usually puberulent, 5–20 mm long. Petiolar gland (Fig. 1F) canoe-shaped, usually solitary, glabrous, striate on the sides, apex 1–4 mm long, located near the middle to top of the petiole, sometimes a small tubular gland below. Leaflets 15–40 pairs per pinna, glabrous, oblong, 4–11 mm long, 1.3–2.7 mm wide, 2–3 veins from the base, lateral veins obvious, apex usually mucronate. Inflorescence a densely flowered, cylindrical spike, 20–35 mm long, 8–11 mm thick near the base and narrowing slightly toward the blunt apex, solitary in the leaf axil, or solitary or in clusters of 2–4 in the axil of small spines on short, lateral, usually leafless, axillary branches; peduncles glabrous to lightly puberulent, 5–15 mm long, 2–4 mm thick, thickest just below the inflorescence; involucre usually puberulent, 4-lobed, the lobes spreading, located near the base of the peduncle. Floral bracts peltate, the apex tailed on one side, the stalk 0.7–1.3 mm long. Flowers sessile; calyx shallowly 5-lobed, glabrous to lightly puberulent on the lobes, 1–1.4 mm long; corolla glabrous, pale yellow, 1.1–1.5 mm long, only slightly longer than the calyx. Legume usually straight, mostly terete, 50–90 mm long, 13–18 mm thick, glabrous to minutely puberulent, usually not strongly longitudinally striate, mostly red to maroon, indehiscent, stipe to 10 mm long, the apex narrowing to a spinelike beak 20–50 mm long. Flowering January–July.

Distribution. Wet to relatively dry, mostly disturbed habitats at lower elevations from southern Mexico to Costa Rica.

Representative specimens. BELIZE. Mile 42.5 on Northern Hwy., N of Maskall River, *Dwyer 11023* (F). COSTA RICA. **Guanacaste:** NW of Paloverde, Barbudal Hills, *Garwood et al. 570* (F). EL SALVADOR. Banks of Río Acelhuate, SE part of San Salvador, 690 m, *Carlson 55* (F). GUATEMALA. **Alta Verapaz:** near Pancajche, about 360 m, *Standley 70768* (F). **El Petén:** 2 mi. E of Melchor, roadside, *Croat 24623* (MO). **Escuintla:** near San José at sea level, *Standley 64241* (F). **Retalhuleu:** 9 mi. N of Champerico, *Harmon 2298* (MO). **San Marcos:** 2 mi. E of the border between Mexico (Puente Talisman) on hwy. 2, *Janzen 1045* (F, MEX, MO). **Suchitepéquez:** S of Alotenango Farm, 7 mi. S of Tiquisate along rd. within 3 mi. of ocean, 30–50 m, *Steyermark 47739* (F). HONDURAS. Vegas del Río Agua, 3 km de Yoro, 1000 m, *Molina R. 6807* (F). MEXICO. **Campeche:** 30 km E of Campeche on hwy. 261, *Seigler et al. 11603* (ILL, MEX). **Chiapas:** Ciudad Cuauhtemoc on hwy. 190, *Janzen 499* (F, MEX). **Guerrero:** 1 mi. NW Cuajinicuilapa, *Johnson 740-79* (WIS). **Oaxaca:** Capilla, N end of lake behind Presa Alemán, W of Tierra Blanca, *Janzen 1937* (F, MO, WIS). **Quintana Roo:** 52 mi. W of jct. of Mexico 307 & 186 on hwy. 186, *Seigler et al. 11594* (ILL, MEX). **San Luis Potosí:** Barrio de San Juan, Tamazunchale, *Edwards 600* (F, MO). **Tamaulipas:** Tampico, Rujal rd., *Kenoyer 791* (F). **Veracruz:** Zacuapán, *Purpas 7748* (GH, MO). **Yucatán:** Izarnal, *Greenman 379* (GH). NICARAGUA. Laguna de Masaya, a 2 km de la entrada, *Araquistain & Moreno 593* (MEX).

Acacia cornigera is probably the best known of the ant-acacias. It is easily separated from other ant-acacias by having peltate floral bracts in which the apex is tailed on one side. Also, the presence of canoe-shaped petiolar glands separates this taxon from all ant-acacias except *A. mayana* and *A. sphaerocephala*. The presence of obvious secondary venation in the leaflets and the relatively thick cylindrical inflorescences separate this taxon from *A. sphaerocephala*, while the smaller leaflets and the lack of longitudinal flanges on the stipular spines separate it from *A. mayana*.

Acacia cornigera is a highly variable species that occurs in a wide range of habitats. This morphological diversity has resulted in an extensive synonymy, which is discussed by Rudd (1964). It is the most common of the ant-acacias, and its geographic range is almost as extensive as that of *A. collinsii*. It is relatively common in riparian and swamp habitats and is the common ant-acacia in fallow fields, pastures, roadsides, and other disturbed sites from sea level to about 1200 m (Janzen, 1967a, b). Some of its present distribution has been caused by the dissemination of seeds by birds, people, and cattle into secondary growth vegetation. The present distribution of this species into the drier parts of the Yucatán peninsula is probably due to introduction by humans, since most collections are from around settlements, cattle corrals, and Indian ruins. It has also become naturalized on the Caribbean islands of Martinique, Guade-

loupe, and Cuba, as well as in extreme southern Florida.

Beltian body production in *Acacia cornigera* is typical of that found in ant-acacias that inhabit more open sites. Generally, these bodies are relatively small, 0.5–0.9 mm long, 0.4–0.6 mm wide, and are present on more than half of the leaflets. Since individuals of this species are usually occupied by obligate acacia-ants, the Beltian bodies are rarely seen because they are usually "harvested" as soon as the young leaves develop.

Of the more than 250 herbarium specimens of this species examined, none tested positive for cyanide production. Also, numerous living specimens have been tested, usually with negative results. Leaves of *Acacia cornigera* have been reported to contain a β-glucosidase (Rehr et al., 1973). It appears that the hydrolytic enzyme necessary for the liberation of HCN is present, but the cyanogenic glycoside is absent. Living material from two populations of this species collected near Cañas, Guanacaste Province, Costa Rica, gave a very weak positive test for cyanide (Seigler & Ebinger, 1987). Dried material from these same individuals gave a negative test with and without emulsin.

Janzen (1974) reported seeing a single plant of *A. cornigera* × *A. sphaerocephala* on the dunes south of Veracruz, Mexico, and suggested that *A. cornigera* may occasionally hybridize with *A. chiapensis*. It is also possible that this species may occasionally hybridize with the non-ant-acacia *A. pennatula* (Ebinger & Seigler, 1992).

6. Acacia gentlei Stand., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 77. 1940. TYPE: Belize. *P. Gentle 185* (holotype, F).

Small tree to 20 m tall; young twigs dark reddish brown, densely puberulent. Stipular spines dull, red to dark brown, most commonly black, usually lightly puberulent, terete, commonly symmetrical to slightly asymmetrical, U-shaped with an angle of 30 to 60°, suberect to recurved around the stem, 35–80 mm long, 3.5–6 mm thick near the base. Leaves 70–180 mm long; pinnae 5–12 pairs per leaf, 55–90 mm long, 13–20 mm between pinna pairs; rachis grooved, puberulent, a narrow, volcano-shaped gland located on the rachis internodes between each pinna pair; petiole grooved, densely puberulent, 9–20 mm long. Petiolar glands narrowly volcano-shaped, usually laterally compressed, solitary (rarely 2), puberulent, lightly striate, apex 0.6–1.2 mm across, base 2–3 mm long, located near the base to middle of the petiole. Leaflets 20–35 pairs per pinna, glabrous, linear, 7–14 mm long, 1.8–3.1 mm wide, lateral veins obvious, 3–5 veins from the base, apex obtuse to acute, margins ciliate. Inflorescence a densely flowered, cylindrical spike 15–40 mm long, 4–6 mm thick, nearly the same thickness throughout, apex blunt, in racemes on fertile branchlets with usually one (occasionally 2–4) spike at a node in the axil of a reduced leaf; peduncles puberulent, 16–22 mm long, 0.7–1.1 mm thick, nearly the same thickness throughout; involucre located near the middle of the peduncle, puberulent, 4-lobed with 2 lobes longer. Floral bracts peltate, apex circular, puberulent, the stalk less than 1 mm long. Flowers sessile; calyx 5-lobed, puberulent, 0.5–0.8 mm long; corolla 5-lobed, puberulent, yellowish, 1.3–1.8 mm long, twice as long as the calyx. Legumes straight to slightly curved, flattened, 160–300 mm long, 9–14 mm wide, glabrous, longitudinally striate, black to dark brown, dehiscent along both sutures, stipe 10–30 mm long, the apex narrowing to a spikelike beak 10–40 mm long. Flowering January–May.

Distribution. Rainforests, wet successional areas where the vegetation is 15–20 years of age, wet disturbed sites, swamps, and river edge vegetation in the lowlands of Belize, northern Guatemala, and extreme southern Mexico.

Representative specimens. BELIZE. 3–6 mi. S of Belmopan, *Dwyer 12544* (F, GH, MO); Southern Hwy., 14 mi. N of Punta Gorda, San Antonio, *Gentry 8072* (MEX, MO); Maskall, *Gentle 1121* (F, GH, MICH, MO, NY); Hummingbird Hwy., *Gentle 9078* (F, MICH, MO, NY); Mountain Pine Ridge, Blancaneaux Lodge, *Wiley 457* (MO). GUATEMALA. **Alta Verapaz:** along Río Sebol between Sebol and Carrizal, N of Sebol, 200–300 m, *Steyermark 45762* (F). **Izabal:** El Zapotillo, 1 km E El Estor (Lake Izabal), *Janzen 657* (F, GH, MEX, MICH, MO, US). **El Petén:** Uaxactun, *Bartlett 12578* (NY, TEX, UC). Tikal National Park, Tikal, in ramonal, *Ibarra 16* (LL). MEXICO. **Chiapas:** a 3 km al S de Frontera Corozal, sobre el Río Usumacinta, 120 m, *Martínez S. 11433* (MEX, MO, NY). **Quintana Roo:** a 2 km al N de Estero Franco, carretera Chetumal–La Unión, *Cabrera & Cabrera 2512* (MEX, MO). **Tabasco:** Carretera W–O por El Poblado de Apatzingan, Balancán, 150 m, *Calzada 2345* (F, MEX, MO).

Acacia gentlei is a common species in wet sites at lower elevations in Belize, Guatemala, and extreme southeastern Mexico. It is distinguished easily from all other ant-acacias by the combination of its elongate inflorescence, laterally compressed, volcano-shaped glands scattered along the leaf rachis, very thin spines (usually less than 6 mm thick), and relatively large leaflets (7–14 mm long) with obvious secondary veins.

Unlike many of the wet forest ant-acacias, *Acacia gentlei* is a common species in areas of human

disturbance. It appears as a successional species after logging, and in many parts of its range is found along roadsides. Unlike most wet forest ant-acacias, it has relatively large Beltian bodies (1–2 mm long) on most of the leaflets. Like most of the other ant-acacias, it usually lacks cyanogenic glycosides in the leaflets. Of the specimens examined, only one, *Lundell 16903*, from Guatemala, was weakly cyanogenic.

7. Acacia globulifera Saff., J. Wash. Acad. Sci. 4: 360. 1914. *Myrmecodendron globuliferum* (Saff.) Britton & Rose, N. Amer. Fl. 23: 93. 1928. TYPE: Mexico. Yucatán: at the port of Silam (Tzilam), N coast of Yucatán, Apr. 1895, *G. F. Gaumer 1909* (holotype, F, fragment and photo, US; isotypes, GH, MO, NY, US).

Acacia donnelliana Saff., J. Wash. Acad. Sci. 4: 361. 1914. *Myrmecodendron donnellianum* (Saff.) Britton & Rose, N. Amer. Fl. 23: 93. 1928. TYPE: Honduras. Santa Bárbara: San Pedro de Sula, Cortes, 600 ft., Mar. 1888, *C. Thieme 5216* (holotype, US).

Shrub or small tree usually less than 3 (rarely 10) m tall, young twigs brown to reddish brown, glabrous to lightly puberulent. Stipular spines (Fig. 1B) usually dark brown to black (sometimes yellow to ivory), smooth, terete, glabrous to lightly puberulent, symmetrical, V-shaped with an angle of 40–120°, straight to reflexed near the apex, 25–60 mm long, 4–7 mm thick near the base. Leaves 60–250 mm long; pinnae 6–26 pairs per leaf, 30–65 mm long, 6–11 mm between pinna pairs, rachis grooved, glabrous to lightly puberulent, a small volcano-shaped gland present between each pinna pair; petiole grooved, glabrous to lightly puberulent, 8–18 mm long. Petiolar glands (Fig. 1G) volcano-shaped, commonly laterally compressed, densely puberulent, usually lightly striate, apex nearly circular, 0.3–0.9 mm across, base 1–2 mm across, usually 2–5 glands scattered along the petiole. Leaflets 20–50 pairs per pinna, glabrous, linear, 4–6 mm long, 0.6–1.2 mm wide, lateral veins not obvious, only one vein from the base, apex mostly acute. Inflorescence a densely flowered globose head 4–7 mm across, in clusters of 4–8 in the axil of slightly reduced leaves, or in small clusters in the axil of small spines on lateral, usually leafless branches; peduncles glabrous to lightly puberulent, 6–25 mm long, 0.5–1.0 mm thick, nearly the same thickness throughout; involucre located on the lower ¼ of the peduncle, glabrous to lightly puberulent, 4-lobed. Floral bracts peltate, apex circular, the stalk about 1 mm long. Flowers sessile; calyx 5-lobed, glabrous, 1–1.5 mm long; corolla 5-lobed, glabrous, pale yellow, 1.5–2.0 mm long. Legumes slightly curved, elliptical to nearly terete in cross section, 50–90 mm long, 9–12 mm wide, glabrous, not striate, black to dark brown, dehiscent along one suture, stipe less than 5 mm long, the apex narrowing to a terminal spinelike beak usually less than 10 mm long. Flowering January–April.

Distribution. In riparian and swamp successional stages as well as open, dry habitats, from sea level to about 1200 m, in southern Mexico (Campeche, Oaxaca, Yucatán), Belize, Guatemala, and Honduras.

Representative specimens. BELIZE. **El Cayo:** Vaca, *Gentle 2275* (AA, F, MICH, MO, NY). GUATEMALA. **Amatitlán:** Laguna (Lake Amatitlán), 1200 m, *Kellerman 5042* (UC). **Guatemala:** 20.5 mi. NE Guatemala City on hwy. 9, *Janzen 1565* (F, GH, MEX, MICH, MO, US). **El Petén:** in Mananche, *Contreras 5480* (F, MICH, US). **Zacapa:** along Río Teculután, above Teculután, 250–275 m, *Steyermark 42146* (F, NY). HONDURAS. Cut over river valley lands, Yoro 2800 ft., *Edwards P-748* (AA, F); 26 mi. SW of San Pedro Sula on hwy. 18, *Janzen 1608* (F); 10.4 mi. SW of Santa Rosa on hwy. 18, *Janzen 1634* (F, MICH, MO, UC, US). MEXICO. **Campeche:** 48 mi. NE of Puerto Real (Isla Aguada) on hwy. 180, *Janzen 611* (F, MICH, US). **Oaxaca:** 11.3 mi. N of intersection of Mexico hwy. 185 and 190, on hwy. 185, *Janzen 1502* (F, GH, MEX, MICH, MO, NY, UC, WIS). **Quintana Roo:** en San José de la Montaña, km 8 de la carreterra a Tomás Garrido, *Cabrera et al. 4504* (MEX). **Yucatán:** Silám, *Gaumer 655* (F, GH, US).

Acacia globulifera is easily distinguished from most ant-acacias by its spherical inflorescences, small leaflets that lack obvious secondary veins, and 2–5 narrow volcano-shaped petiolar glands. It is most closely related to *A. chiapensis* and has been occasionally combined with it (Janzen, 1974). These two species differ, however, in petiolar glands, inflorescence clusters, and fruit characteristics (see discussion under *A. chiapensis*). *Acacia globulifera* is commonly found in riparian or relatively dry sites from sea level to about 1200 m, which is the upper elevation limit of ant-acacias. It usually grows in open, fully insolated habitats, rarely exceeds 3 m in height, and is usually restricted to young successional habitats (Janzen, 1974).

Beltian body production in *Acacia globulifera* is typical of that found in most ant-acacias that inhabit more open sites. These bodies, which are less than 0.8 mm long, usually are present on more than half of the leaflets of a developing leaf. The bodies are rarely seen, as they are usually "harvested" soon after development by obligate acacia-ants.

Acacia globulifera is similar to *A. chiapensis*

in that many individuals of both species are cyanogenic; the cyanogenic glycoside of *A. globulifera* is (*R*)-epiproacacipetalin, whereas that of *A. chiapensis* is (*S*)-proacacipetalin. Of the specimens of *A. globulifera* tested, most gave a positive test for HCN. Of these specimens, however, nearly one-third required the addition of emulsin to give a positive test. This suggests that many individuals of this species either lack the enzyme capable of hydrolyzing the cyanoglycoside, or that the enzyme is inactivated by drying and storage (Seigler & Ebinger, 1987).

Janzen (1974) suggested that *Acacia globulifera* may occasionally hybridize with a non-ant-acacia of the *A. macracantha* complex. During the present study no specimens were found that would indicate hybridization involving this species.

8. Acacia hindsii Benth., London J. Bot. 1: 504. 1842. *Myrmecodendron hindsii* (Benth.) Britton & Rose, N. Amer. Fl. 23: 91. 1928. TYPE: Mexico. Jalisco: shore of Manzanilla Bay, sea level, 1841, *R. B. Hinds 248* (holotype, K, photo, F).

Acacia bursaria Schenck, Repert. Spec. Nov. Regni Veg. 12: 363. 1913. TYPE: Guatemala. Amatitlán: Laguna Amatitlán, 3900 ft., Feb. 1890, *J. D. Smith 2304* (lectotype, designated here, US [B destroyed]; isotypes, GH, K).

Acacia tepicana Saff., J. Wash. Acad. Sci. 4: 366. 1914. TYPE: Mexico. Nayarit: thickets, vicinity of Acaponeta, Tepic, 30 m, 10 Apr. 1910, *J. N. Rose, P. C. Standley & P. G. Russell 14357* (holotype, US, photo, F; isotype, NY).

Acacia sinaloensis Saff., J. Wash. Acad. Sci. 4: 365. 1914. TYPE: Mexico. Sinaloa: vicinity of Villa Unión, growing about a pond, 2 Apr. 1910, *J. N. Rose, P. C. Standley & P. G. Russell 13972* (holotype, US; isotype, NY).

Tree to 10 m tall; young twigs reddish brown to dark brown, glabrous to rarely lightly puberulent. Stipular spines (Fig. 1C) shiny, light brown to nearly black (sometimes light gray), smooth, glabrous to lightly puberulent, flattened at the base, symmetrical, nearly flat to broadly U-shaped across the top at an angle of 90–180°, 30–55 mm long, 10–20 mm wide at the base. Leaves 45–180 mm long; pinnae 10–18 pairs per leaf, 20–45 mm long, 6–12 mm between pinna pairs; rachis grooved, usually puberulent, a small narrow volcano-shaped gland located at the node between each pinna pair; petiole grooved, usually densely puberulent, 7–14 mm long. Petiolar glands narrow volcano-shaped (to almost columnar), usually 3–7 (rarely 1) scattered along the petiole, puberulent, lightly striate, apex 0.4–0.7 mm long, base 0.8–1.2 mm long. Leaflets 12–30 pairs per pinna, glabrous, linear, 3–7 mm long, 0.9–1.4 mm wide, one vein from the base, lateral veins not obvious, apex obtuse, margins lightly ciliate. Inflorescence a loosely flowered, cylindrical spike, 20–50 mm long, 4–7 mm thick, nearly the same thickness throughout, apex blunt, in racemes with 1–3 (rarely 4–8) spikes at each node in the axil of a reduced leaf; peduncles glabrous to lightly puberulent, 10–20 mm long, 0.6–1.1 mm thick, nearly the same thickness throughout; involucre located at the base to the lower third of the peduncle, puberulent, 4-lobed with 2 lobes longer. Floral bracts peltate, apex circular, stalk 0.4–0.7 mm long. Flowers sessile; calyx 5-lobed, puberulent, 0.5–0.9 mm long; corolla 5–6-lobed, puberulent, yellowish, 1.6–2.0 mm long, usually more than twice as long as the calyx. Legumes curved, elliptical in cross section, 40–100 mm long, 8–12 mm wide, glabrous to lightly puberulent, usually not striate, black to dark brown, dehiscent along one suture, short stalked, base narrowly cuneate, the apex narrowing to a beak 10–15 mm long. Flowering January–July.

Distribution. Disturbed, usually wet sites of the Pacific lowlands and foothills from extreme southern Sinaloa, Mexico, south to Nicaragua.

Representative specimens. EL SALVADOR. **La Unión:** vicinity of La Unión, 150 m or less, *Standley 20663* (NY, UC, US). **San Vicente:** vicinity of Apastepeque,, *Standley 21333* (NY). **Sonsonate:** vicinity of Acajutla, 30 m or less, *Standley 21942* (US). GUATEMALA. **Alta Verapaz:** near Pancajche, about 360 m, *Standley 70648* (F). **Escuintla:** S of Río Burrion, NE of Escuintla, about 700 m, *Standley 89619* (F). **Retalhuleu:** vicinity of Retalhuleu, 240 m, *Standley 88846* (F). **San Marcos:** Sands, Ocos, 1–2 m, *Steyermark 37779* (F). HONDURAS. Encinales del Valle de El Espino cerca de San Jerónimo, 350 m, *Molina R. 8059* (F, MO, US). MEXICO. **Chiapas:** 13 mi. NE of the border of Chiapas & Oaxaca on hwy. 190, *Seigler et al. 11583* (ILL). **Colima:** Manzanillo, *Palmer 1395* (MO, NY, US). **Guerrero:** sandy river bank, Tecpan–El Verde, 20 m, *Hinton 14120* (MO, TEX, US). **Jalisco:** just E of Barra de Navidad in sandy soil near sea level, in thickets about margin of palm forest, *McVaugh 11847* (US). **Michoacán:** a 10 km aprox. al N de Playa Azul, carr. a Nueva Italia, *Nuñez & Boom 2115* (MO). **Nayarit:** 4 mi. S of intersection to Acaponeta on hwy. 15, *Seigler et al. 11797* (ILL). **Oaxaca:** sand dunes behind the beach at Salina Cruz, *King 2461* (TEX, US). **Sinaloa:** near Colomas, in the foothills of the Sierra Madre, *Rose 1766* (NY).

Like *Acacia collinsii* and *A. cornigera*, *A. hindsii* has an extensive geographical range. Unlike these species, however, *A. hindsii* is restricted to the Pacific lowlands and foothills in Central America. Before the existence of extensive agri-

culture in the region it was probably common along rivers, in semideciduous and deciduous forests, and in mangrove swamps (Janzen, 1974). Presently it is a common element of shrubby regeneration, particularly in wetter habitats such as river banks, where it commonly forms dense thickets by means of root sprouts.

Acacia hindsii is easily separated from all other ant-acacias by its stipular spines, which are flattened at the base and nearly flat to broadly U-shaped across the top. It is morphologically very similar to *A. collinsii* and *A. gentlei*, both of which have relatively small leaves and cylindrical spikes, but differs in leaflets that lack obvious secondary venation.

As is typical of most ant-acacias that inhabit more open sites, Beltian body production in *Acacia hindsii* is relatively extensive. In this species the small, slightly elongated Beltian bodies usually are less than 1 mm long, and are found commonly on more than 60% of the leaflets of developing leaves. As most individuals of this species are inhabited by obligate acacia-ants, the Beltian bodies generally are not seen, being "harvested" soon after development.

Acacia hindsii is polymorphic with respect to HCN production (Seigler & Ebinger, 1987), being reported acyanogenic by Rehr et al. (1973), while Seigler et al. (1978) found individuals that are strongly cyanogenic. Of more than 300 herbarium specimens tested, 123 were positive for HCN production. In general, many of the specimens from Mexico tested positive for cyanide, while most of the acyanogenic specimens are from Guatemala, El Salvador, and Honduras. The glycoside in this species is proacacipetalin.

Acacia hindsii probably hybridizes with the ant-acacia *A. collinsii*. It also has been reported to hybridize with non-ant-acacias of the *A. macracantha* complex, particularly *A. pennatula* (*Acacia* × *standleyi* Safford), and *A. cochliacantha* (*Acacia* × *gladiata* Safford).

9. Acacia janzenii Ebinger & Seigler, Southw. Naturalist. 32: 245. 1987. TYPE: Mexico. Tabasco: 9.8 mi. W of Lázaro Cárdenas on hwy. 180, 17 June 1966, *D. H. Janzen 515* (holotype, MO; isotypes, BM, CAS, F, GH, MICH, MO, UC, US).

Tree to 12 m tall, young twigs dark reddish brown, lightly puberulent. Stipular spines dark brown to black, smooth, terete, densely pubescent with straight, yellowish hairs to 0.5 mm long, asymmetrical, U-shaped with an angle of 30–70°, usually curved around the stem, 30–60 (rarely 80) mm long, 6–9 mm thick near the base. Leaves 150–370 mm long; pinnae 30–60 pairs per leaf, 6–9 mm between pinna pairs; rachis grooved, densely pubescent with yellowish hairs, a columnar to narrowly volcano-shaped gland located at the node of each pinna pair, its apex 0.5–0.7 mm across; petiole densely pubescent, 5–8 mm long. Petiolar glands absent. Leaflets 40–70 pairs per pinna, glabrous, linear, 3–5.5 mm long, 0.6–0.9 mm wide, lateral veins not obvious, only one vein from the base, apex acute, margins ciliate. Inflorescence a densely flowered globose head 4–6 mm across, in clusters of 16–42 in the axil of slightly reduced leaves on normal branches, also located on fertile branchlets to 250 mm long with 16–42 inflorescences in each of 6–12 fascicles that may not be subtended by leaves; peduncles glabrous to lightly puberulent, 7–16 mm long, 0.3–0.7 mm thick, the same thickness throughout; involucre located near the middle of the peduncle, usually 4-lobed. Floral bracts peltate, apex circular, stalk 0.4–0.7 mm long. Flowers sessile, calyx 5-lobed, glabrous, 0.6–1.1 mm long; corolla 5-lobed, glabrous, 1.2–2.1 mm long, about twice as long as the calyx. Legumes not seen, but probably very similar to those of *Acacia cookii*. Flowering May–July.

Distribution. Disturbed habitats, roadsides, pastures, and moist disturbed forests, to 400 m elevation, in Chiapas, Tabasco, and Veracruz, Mexico.

Representative specimens. MEXICO. **Chiapas:** stream bank, lower montane rainforest ridge above Ixtacomitán, 300 m, *Breedlove 35053* (MEX, MICH, MO). **Tabasco:** 9.8 mi. W of Cárdenas on hwy. 180, *Janzen 515* (MEX). **Veracruz:** Las Cruces, 250 m, *Nevling & Gómez-Pompa 1555* (F).

Acacia janzenii is easily distinguished from all other ant-acacias by its asymmetrical stipular spines, which usually curve around the stem and are covered with straight, yellowish hairs to 0.5 mm long. The only other species that commonly has asymmetrical thorns is *A. cookii*. These two closely related species differ in the petiolar and rachis glands, the type of pubescence on the spines, the leaflet length and width, and the flowering branchlets (see discussion under *A. cookii*).

Janzen (1974) considered this taxon a part of *Acacia cookii*. However, he noted that specimens from Tabasco and Chiapas, Mexico (herein referred to *A. janzenii*) differ from typical *A. cookii*. In particular, he noted that progressing from north (Mexico) to south (Belize, Guatemala, Honduras),

there is a change in spine length, a shortening of the fertile branchlets, an increase in the number of inflorescences per axil, an increase in the number of Beltian bodies per leaf, and a higher percentage of plants occupied by ants. Although he suggested that the extremes are clinally connected, our principal component analysis (PCA) suggests that these two species are specifically distinct. No intermediate plants were found, and the characters used for separation (petiolar and rachis glands, spine size, pubescence, leaflet size, fertile branchlets) are as significant as those characters used to distinguish other taxa of ant-acacias.

Originally, *Acacia janzenii* probably was a species of disturbed sites in open forests, particularly landslide scars and stream banks. Most recent collections seen are from roadsides and pastures.

Beltian body production in this species is relatively low; usually less than ¼ of the leaflets contain these bodies. Also, these bodies are usually less than 0.7 mm long. None of the specimens tested positive for cyanide production.

10. Acacia mayana Lundell, Publ. Carnegie Inst. Wash. 478: 210. 1937. TYPE: Guatemala. El Petén: near San Diego on the Río Pasión, 10 Apr. 1935, *M. Aguilar H. 495* (holotype, MICH; isotypes, GH, NY, US).

Shrub or small tree to 10 m tall; young twigs gray to light brown, glabrous. Stipular spines shiny, dark black, glabrous, symmetrical, V-shaped with an angle of 70 to 150°, the upper half strongly reflexed, 30–75 mm long, 5–12 mm thick near the base, two bladelike longitudinal flanges extending from the base to the apex along each side of the spine. Leaves 150–400 mm long; pinnae 6–19 pairs per leaf, 75–120 mm long, 15–30 mm between pinna pairs; rachis grooved, glabrous to puberulent, a small, elongated gland present between each pinna pair; petiole grooved, glabrous to puberulent, 15–35 mm long. Petiolar glands canoe-shaped, solitary (rarely 2), glabrous, striate on the sides, apex 1.2–5 mm long, located just below the first pinna pair. Leaflets 25–40 pairs per pinna, glabrous, linear, 10–23 mm long, 1.8–3.5 mm wide, lateral veins obvious, 3–5 veins from the base, apex obtuse. Inflorescence a densely flowered spike, 30–50 mm long, 7–10 mm near the base, narrowing toward the elongated and pointed apex, solitary or in small racemes on short, leafless, axillary branches; peduncles glabrous, 5–15 mm long, 4–6 mm thick, nearly the same thickness throughout; involucre located near the base of the peduncle, glabrous to lightly puberulent, with 4–5 irregular, shallow lobes. Floral bracts peltate, apex circular, the stalk 0.9–1.2 mm long. Flowers sessile; calyx shallowly 5-lobed, glabrous, 0.9–1.2 mm long; corolla 5-lobed, glabrous, pinkish, 1–1.3 mm long, only slightly longer than the calyx. Legume slightly curved, nearly terete, 90–120 mm long, 12–15 mm thick, glabrous, longitudinally striate, dark reddish brown, indehiscent, stipe to 25 mm long, the apex narrowing to a long spinelike beak 7–20 mm long. Flowering January–June.

Distribution. Apparently a species of lowland, wet forests and forest margins in the departments of Alta Verapaz and El Petén, Guatemala, and the states of Chiapas, Oaxaca, Tabasco, and Veracruz, Mexico.

Representative specimens. GUATEMALA. **Alta Verapaz:** along Río Icuolay, N and NW of Finca Cubilguitz to Quebrada Diablo, 300–350 m, *Steyermark 44726* (F). **El Petén:** high forest in zapotal & corozal, Chinchila, Sebol road, *Contreras 10691* (F). MEXICO. **Chiapas:** near Lacanjá, Mpio. Ocosingo, *Breedlove 34505* (MEX). **Oaxaca:** San Felipe, a 7 km al N-NW de Macedonio Alcalá, Distr. de Tuxtepec, 80 m, *Sousa et al. 7286* (MEX, MICH, NY). **Tabasco:** Retiro, above Tenosique, in virgin forest, *Matuda 3410* (F, GH, LL, MEX, MICH, MO, NY). **Veracruz:** Estación de Biología Tropical Los Tuxtlas, 200 m, *Ibarra M. 1449* (MO, NY).

According to Janzen (1974), *Acacia mayana* probably represents a "wet-forest edition" of *A. cornigera*. Undoubtedly, the two taxa are very closely related, having many vegetative and floral characteristics in common. However, the large leaflets (more than 10 mm long), the rachis glands between each pinna pair, and the inflorescence, which narrows toward the elongated and pointed apex, separate this species from the closely related *A. cornigera* and *A. sphaerocephala*. Also, the pair of bladelike longitudinal flanges extending from the spine base to apex separates *A. mayana* from all other species of ant-acacia.

Acacia mayana is one of the rarest of the ant-acacias. Collecting data from the few collections observed indicate that it has pinkish flowers and varies in size from a shrub to a small tree to 10 m tall. Most collections indicate that it occurs as widely scattered individuals in moist lowland forests. Janzen (1974) reported an individual from an old second growth cornfield regeneration where the forest was about 15 m tall.

Unlike most wet forest ant-acacias, Beltian body production in *Acacia mayana* is extremely high. On developing leaves, nearly all of the leaflets contain Beltian bodies, and these bodies are usually about 2 mm long and up to 0.8 mm wide. As is typical of most ant-acacias, none of the individuals

of *A. mayana* tested positive for cyanide production.

11. Acacia melanoceras Beurl., Kongl. Svenska Vetensk. Acad. Handl. 1854: 123. 1856. *Myrmecodendron melanoceras* (Beurl.) Britton & Rose, N. Amer. Fl. 23: 93. 1928. TYPE: Panama. Colón: Portobello, sea level, Apr. 1826, *J. G. Billberg 289* (lectotype, designated here, S, photo, F).

Acacia multiglandulosa Schenck, Repert. Spec. Nov. Regni Veg. 12: 362. 1913. TYPE: Panama. Colón: Portobello, *J. G. Billberg 1825 (lectotype, designated here, US, photo [B destroyed])*.

Tree to 15 m tall; young twigs dark brown to dark reddish brown, puberulent. Stipular spines shiny, dark reddish brown to black, grooved and with low, rounded longitudinal ridges, rarely with two narrow, bladelike longitudinal flanges, glabrous to lightly puberulent, terete in cross section, symmetrical, broadly V-shaped with an angle of 80–120°, 20–55 mm long, 5–9 mm wide near the base, abruptly tapering to a narrow, sharp-pointed tip, many spines not enlarged, usually less than 5 mm long and 0.4 mm wide. Leaves 150–290 mm long; pinnae 12–28 pairs per leaf, 20–50 mm long, 6–11 mm between pinna pairs; rachis grooved, puberulent; rachis glands puberulent, striate, columnar to narrowly volcano-shaped, one located at the node of each pinna pair, its apex 0.2–0.6 mm across; petiole grooved to flattened on the adaxial surface, densely puberulent, (5)10–28 mm long. Petiolar glands columnar to narrowly volcano-shaped, usually numerous (6–30) on the flattened adaxial surface of the petiole, reduced to 0–5 on petioles of smaller leaves, puberulent, striate, apex 0.3–1.1 mm across, base 0.4–1.5 mm across. Leaflets 12–29 pairs per pinna, glabrous, linear, 4.5–7.6 mm long, 1.0–1.7 mm wide, lateral veins not obvious, only one vein from the base, apex acute. Inflorescence a densely flowered globose head 5–6.5 mm across, solitary or in clusters of 2–6 in the axil of small spines on lateral, usually leafless, axillary branches to 350 mm long; peduncles densely puberulent, 5–10 mm long, 0.5–0.8 mm thick, nearly the same thickness throughout; involucre located near the base of the peduncle, puberulent, 5-lobed. Floral bracts peltate, apex circular, ciliate, stalk 0.8–1.2 mm long. Flowers sessile; calyx 5-lobed, glabrous, 0.9–1.1 mm long; corolla 5-lobed, glabrous, pale yellow, 1.5–1.8 mm long. Legumes curved, particularly at the narrowing apex, inflated to slightly flattened, 65–110 mm long, 10–20 mm wide, glabrous, longitudinally striate, dark brown to black, indehiscent, stipe absent, the apex narrowing and usually acuminate. Flowering April–July.

Distribution. Wet, relatively undisturbed forests on the Atlantic lowlands of central Panama (Colón Province) and the Canal Zone.

Representative specimens. PANAMA. **Colón:** Río Boquerón, about 6–8 km upstream from Peluca Hydrographic Station, *Dressler 4657* (F, GH, MO); 500 m upstream from mouth of Río Piedras, *Janzen 1641, 1912, 1913, 1915, 1916* (F, GH, MEX, MO). **Canal Zone:** Barro Colorado Island, *Aviles 20b* (F, MO); along Río Mendosa near Pipeline Road bridge, 8 km NW of Gamboa, 95 m, *Nee 7739* (MO).

Acacia melanoceras has the most restricted range of all ant-acacias and is relatively rare throughout this range. According to Janzen (1974), rarely more than two individuals are found per acre in forest communities. Also, this species, which is usually restricted to lowland wet forests, disappears from any habitat subjected to disturbances that are any more catastrophic than infrequent cutting.

This species can easily be distinguished from all other ant-acacias by the extremely high number (6–30) of volcano-shaped petiolar glands on the flattened adaxial surface of the petiole. Also, the large leaves (to 300 mm) and the rachis glands at the node of each pinna pair help to separate it from most other ant-acacias.

Beltian body production is relatively low in *Acacia melanoceras*, rarely more than half of the leaflets on mature plants producing these structures, which vary from 1 to 1.6 mm long. This characteristic, which is typical of most wet forest ant-acacias, is probably due to the high cost to the plant of Beltian bodies in a habitat with low solar energy input and perhaps somewhat reduced herbivore loads (Janzen, 1974). None of the individuals of this species tested positive for cyanide production.

12. Acacia ruddiae D. H. Janzen, Smithsonian Contr. Bot. 13: 34. 1974. TYPE: Costa Rica. Limón: ferry landing, Moin River, Moin, 13 Feb. 1965, *D. H. Janzen 828* (holotype, US; isotypes, CAS, F, GH, MEXU, MICH, MO, NY, UC).

Tree to 30 m tall; young twigs dark brown to dark reddish brown, glabrous to puberulent. Stipular spines dull, dark reddish brown to black, smooth, glabrous to lightly puberulent, nearly terete in cross section, symmetrical, broadly V-shaped

with an angle of 70–180°, to 9.5 mm long, 4–9 mm wide, abruptly tapering to a narrow, sharp-pointed tip; many spines not enlarged, usually less than 8 mm long and to 0.4 mm wide. Leaves 130–400 mm long; pinnae 17–40 pairs per leaf, 30–55 mm long, 5–13 mm between pinna pairs; rachis grooved, densely puberulent; rachis glands glabrous, striate, cylindrical, commonly narrowing toward the base, to 1 mm long, one located at the node of each pinna pair, its apex 0.4–0.9 mm across; petiole grooved, densely puberulent, 6–25 mm long. Petiolar glands commonly absent, rarely 1 or 2 present, identical to the rachis glands. Leaflets 25–75 pairs per pinna, glabrous, ciliate along the margins, linear, 3.5–6.5 mm long, 0.6–1.1 mm wide, lateral veins not obvious, only one vein from the base, apex acute. Inflorescence a densely flowered globose head 6–7 mm across, in clusters of 1–8 in the axil of normal leaves; peduncles densely puberulent, 8–11 mm long, 0.5–0.7 mm thick, nearly the same thickness throughout; involucre located near the middle of the peduncle, puberulent, 5-lobed. Floral bracts peltate, apex circular, ciliate, stalk less than 0.8 mm long. Flowers sessile; calyx 5-lobed, glabrous, 0.7–1.0 mm long; corolla 5-lobed, glabrous, pale yellow, 1.3–1.6 mm long. Mature legumes not seen. Flowering July.

Distribution. Very wet rainforest, particularly in primary succession along rivers, at edge of swamps, and on landslide scars in the Caribbean lowlands, from Puerto Barrios area of Guatemala to northern Panama.

Representative specimens. COSTA RICA. **Alajuela:** 11 mi. N Florencia, *Janzen 1883* (F), *1885* (F), *1886* (F, MICH). **Heredia:** Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 100 m, *Hammel & Trainer 12918* (MICH, MO); 16 mi. N of Vara Blanca on rd. from Heredia to Puerto Viejo, *Janzen 819* (F, GH, MICH, NY, US). **Limón:** 1 km W of La Lola (on Limón–Siquirres railroad), *Janzen 1868* (F, NY), *1872* (F), *1874* (F), *1875* (F), *1877* (F, NY, US), *1881* (F). GUATEMALA. **Izabal:** 1.9 mi. W of Puerto Matias de Gálvez (on rd. to Escobas), *Janzen 1582* (F, GH, MEX, MICH, US). HONDURAS. **Atlántida:** Lancetilla Valley, near Tela, 20–600 m, *Standley 54627* (F). NICARAGUA. **Zelaya:** Municipio de Rama, *Robleto 664* (MO). PANAMA. **Bocas del Toro:** Campamento forestal, Boca Chica, *Correa A. et al. 3581* (MO, NY); along Changuinola River, Changuinola Valley, *Dunlap 462* (F).

Acacia ruddiae is probably most closely related to *A. cookii* and *A. janzenii*, which it resembles in having small globose inflorescences, large leaves with numerous small leaflets, and rachis glands between each pinna pair. However, both *A. cookii* and *A. janzenii* have asymmetrical stipular spines that usually curve around the stem, whereas *A. ruddiae* has symmetrical spines. Also, the rachis glands of *A. ruddiae* are urn-shaped, narrowing slightly toward the base, whereas in *A. cookii* and *A. janzenii* they are elongated to volcano-shaped.

Though *Acacia ruddiae* has a relatively extensive geographical range in the Caribbean lowlands from Guatemala to Panama, it has rarely been collected. The presence of this species in Costa Rica was discussed by Calvert & Calvert (1917) who mentioned a bull-horn acacia with swollen thorns and urn-shaped rachis glands that lacked Beltian bodies and obligate acacia-ants. Though referring to this species as *Acacia campeachiana* Miller (= *A. cochliacantha*), there is little doubt that the taxon discussed is *A. ruddiae*.

This wet forest species is only marginally an ant-acacia. Janzen (1974) found that relatively few of the stipular spines were swollen, none were occupied by obligate acacia-ants, and Beltian bodies were not formed on the leaflets. During the present study, no indication of Beltian bodies was found on developing leaves; all of the mature leaves examined lacked the scar left by these bodies. However, a characteristic entrance hole made by ants was observed on two specimens (*Correa A. et al. 3581* and *Janzen 819*). These probably represent chance encounters, as none of the other spines on the specimens had entrance holes.

Of the specimens of *Acacia ruddiae* examined, none tested positive for HCN production. Seigler & Ebinger (1987) obtained similar results, finding one individual that was weakly cyanogenic while the rest tested negative.

13. Acacia sphaerocephala Schltdl. & Cham., Linnaea 5: 594. 1830. TYPE: Mexico. Veracruz: Actopan, sea level, Mar. 1829, *Schiede & Deppe 684* (holotype, HAL, fragment and photo, F, US).

Acacia veracruzensis Schenck, Repert. Spec. Nov. Regni Veg. 12: 362. 1913. TYPE: Mexico. Veracruz: sand dunes S of Veracruz, sea level, 13 Oct. 1908, culta in hort. bot. Darmstadt., *H. Schenck 916* (lectotype, designated here, M, fragment and photo, US [B destroyed]; isotypes, F, HAL).

Acacia dolichocephala Saff., J. Wash. Acad. Sci. 5: 355. 1915. TYPE: Mexico. Veracruz: along the shore N of the city of Veracruz, 24 Jan. 1906, *J. M. Greenman 87* (holotype, F; isotypes, GH, NY, US, photo, K).

Small, spreading, much-branched shrub to 2 (rarely 5) m tall; young twigs dark gray to reddish brown, glabrous to lightly puberulent. Stipular spines ivory to yellow or rarely reddish to dark brown,

glabrous to lightly puberulent, smooth, terete, mostly symmetrical, V-shaped, straight to slightly reflexed, 20–80 mm long, 6–16 mm thick near the base. Leaves 40–140 mm long; pinnae 5–15 pairs per leaf, 20–55 mm long, 7–17 mm between pinna pairs; rachis grooved on the upper surface, glabrous to lightly puberulent, rarely a few glands present; petiole grooved, glabrous to lightly puberulent, 6–13 mm long. Petiolar glands canoe-shaped, solitary, glabrous, striate on the sides, apex 1.4–4.5 mm long, located near the middle of the petiole, sometimes a small tubular gland below. Leaflets 16–48 pairs per pinna, glabrous, oblong, 4–10 mm long, 1.4–2.2 mm wide, lateral veins not obvious, apex mucronate. Inflorescence a densely flowered, subglobose spike less than 2× longer than wide, 7–14 mm long, 5–7 mm wide, apex blunt, solitary or in clusters of 2–6 in the axil of small spines on short, usually leafless, axillary branches; peduncles glabrous to lightly puberulent, 7–18 mm long, 0.8–1.1 mm thick, nearly the same thickness throughout; involucre located at the base of the peduncle, glabrous to lightly puberulent, 4-lobed. Floral bracts peltate, apex circular, the stalk 0.9–1.5 mm long. Flowers sessile; calyx 5-lobed, glabrous to lightly puberulent, 1–1.5 mm long; corolla 5-lobed, glabrous, pale yellow, 1.2–1.8 mm long, only slightly longer than the calyx. Legumes straight, nearly terete, 30–80 mm long, 12–15 mm thick, glabrous, longitudinally striate, red to maroon, indehiscent, stipe to 10 mm long, the apex narrowing to a spinelike beak 10–30 mm long. Flowering December–April.

Distribution. Native on sand dunes and in dry places near the coast in Tamaulipas, San Luis Potosí, and Veracruz. Naturalized elsewhere in southern Mexico.

Representative specimens. MEXICO. **Colima:** 2 km S of Rancho Blanca, *Iltis et al. 681* (WIS). **Michoacán:** a 2 km al NE de El Ranchito, 100 m, *Soto N. et al. 2794* (MEX). **Oaxaca:** 13 mi. E of Pinotepa Nacional on Mexican hwy. 200, *Hansen et al. 1531* (WIS). **San Luis Potosí:** 10.3 mi. NE of Ciudad Valles on hwy. 110, *Janzen 1923* (F). **Tamaulipas:** vicinity of Tampico, 15 m, *Palmer 133* (F, MO, NY, US). **Veracruz:** 5.1 mi. SE of Jalapa on hwy. 140, *Janzen 1921* (F, MEX, NY).

It is very possible that *Acacia sphaerocephala* represents a dry-land derivative of the widespread *A. cornigera* (Janzen, 1974). These two taxa are closely related, and with sterile material the only reliable diagnostic characteristic is the lack of secondary venation in the leaflets of *A. sphaerocephala*. With fertile material, the subglobose inflorescence less than 2× longer than wide, the circular apex of the peltate floral bracts, and the longitudinally striate legumes separate this species from *A. cornigera*.

Native populations of *Acacia sphaerocephala* are restricted to a relatively small area along the east coast of Mexico from the southern part of the state of Tamaulipas to just south of the city of Veracruz. Naturalized populations, probably resulting from seed dispersal by cattle and humans, have also been found in Colima, Michoacán, Morelos, and Oaxaca, and will undoubtedly be found elsewhere in Mexico where there is suitable habitat.

Janzen (1974) suggested that this species can be divided into a beach ecotype and an inland ecotype. The beach ecotype occurs on new dunes in the vicinity of the city of Veracruz, and the inland one throughout the remainder of the range of this species. The beach ecotype commonly forms dense stands of flat-topped shrubs mostly less than 1.5 m tall; the spines usually are not occupied by obligate acacia-ants, and the leaflets usually lack Beltian bodies. The inland ecotype, in contrast, occurs as scattered individuals that may reach 5 m in height; its spines are commonly inhabited by obligate acacia-ants, and its leaves produce numerous small Beltian bodies. These inland plants are morphologically very similar to *A. cornigera*, but usually grow on slightly drier sites. All specimens of both the inland and the beach ecotypes tested negative for cyanide production, as did fresh material of a population of 10 plants from the coastal dunes, just south of Veracruz (Seigler & Ebinger, 1987). During the present study, all beach populations of this species examined contained numerous acacia-ants.

Reported Hybrids

Hybrids between ant-acacia species and between ant-acacias and non-ant-acacias have been discussed by Janzen (1974) and more recently by Ebinger & Seigler (1992). Presently only three probable hybrids between ant-acacias have been reported. Hybrids between ant-acacias and non-ant-acacias are somewhat more common. Past studies indicate that at least four ant-acacia species hybridize with various species of the *Acacia macracantha* complex, including *A. macracantha* Humb. & Bonpl. ex Willd., *A. cochliacantha* Humb. & Bonpl. ex Willd., and *A. pennatula* (Schltdl. & Cham.) Benth. In addition to these hybrids, Janzen (1974) suggested that *A. globulifera* rarely may hybridize with non-ant-acacias, but did not list the non-ant-acacia parent.

Acacia collinsii × *A. hindsii.* These two species are sympatric in parts of their ranges and are sometimes found at the same sites on soils and in climates that are suitable for seasonal agriculture (Janzen, 1974). One sterile specimen was encountered that is intermediate between these two species. This specimen is similar to *A. collinsii* in having relatively large leaflets (7–11 mm long, 1.6–3.1 mm wide) with obvious secondary veins, and with less than 25 pairs of leaflets per pinna. It is similar to *A. hindsii* in that rachis glands are common at many of the pinnae nodes, the stipular spines are slightly flattened, and the petiolar glands are narrowly volcano-shaped. The rachis glands, for the most part, are broadly dome-shaped, typical of the petiolar glands of *A. collinsii.* Intermediate rachis and petiolar gland shapes also are common on this specimen and are slightly compressed volcano-shaped, but not as narrow as those of *A. hindsii.* The specimen is weakly cyanogenic, typical of many specimens of *A. hindsii,* but not of *A. collinsii.* Final determination of the status of this probable hybrid must await flowering and fruiting material (Ebinger & Seigler, 1992).

Representative specimen. MEXICO. **Guerrero:** Lok. 7, Mirador, 5 km S de la Base Naval de Icacos, *Brimer s.n.* (ILL).

Acacia cornigera × *A. sphaerocephala.* Janzen (1974) reported seeing a single plant of this hybrid on the dunes south of the city of Veracruz, Mexico. No specimen was cited, and none were located during this study. These species are similar morphologically, and it is probable that they hybridize.

Acacia chiapensis × *A. cornigera.* Janzen (1967a, 1974) suggested that some of the morphological variation of *Acacia chiapensis* is probably an expression of the introgression of *A. macracantha* and *A. cornigera* genes into the *A. chiapensis* population. He found hybrids to be common in a permanently wet site below the dam at Temascal, Río Chichicazapa, and at Arroyo Enmedio, between Temascal, Oaxaca and La Granja, Veracruz, Mexico. On a recent trip (May 1991) to Temascal both *A. cornigera* and *A. chiapensis* were common in disturbed sites, but no hybrid individuals were observed.

Acacia chiapensis × *A. pennatula.* Shrub or small tree to 5 m tall; twigs brown to dark reddish brown, puberulent. Enlarged stipular spines shiny, reddish brown, puberulent, usually terete in cross section, sometimes ridged or striate, broadly V-shaped with an angle of 160–180° (sometimes slightly reflexed), to 70 mm long, 4.0–5.5 mm wide near the base. Leaves 70–160 mm long; pinnae 14–30 pairs per leaf; rachis densely puberulent, rachis glands absent except between the terminal 1–3 pinna pairs; petioles grooved, densely puberulent, 4–8 mm long. Petiolar glands 1–3, nearly circular and with a depressed apex, puberulent, striate, apex 0.9–1.5 mm across. Leaflets 28–36 pairs per pinna, lightly puberulent, linear, 1.9–2.8 mm long, 0.5–0.7 mm wide, one vein from the base, lateral veins not obvious, margins ciliate. Flowers and fruits not observed.

Representative specimen. MEXICO. **Oaxaca:** edge of road near large dam at Temascal, in pasture near degraded evergreen forest, *Seigler et al. 13544* (EIU, ILL).

Janzen (1974) observed that at two sites (below the dam at Temascal, Río Chichicazapa, and at Arroyo Enmedio, between Temascal, Oaxaca and La Granja, Veracruz, Mexico) *Acacia chiapensis* may hybridize with non-ant-acacias such as *A. macracantha.* At this site, numerous plants occurred that were intermediate in spine, leaf, and branching morphology between these two species. During the present study no hybrids involving *A. chiapensis* and *A. macracantha* were found; however, on a recent trip to Temascal (May 1991) the authors collected hybrid specimens of *A. chiapensis* × *A. pennatula.* Both parents were common in the pasture where the hybrid was collected and, except for *A. cornigera,* were the only acacias in the area.

Acacia collinsii × *A. pennatula.* Shrub or small tree to 5 m tall; twigs reddish brown, glabrous to lightly puberulent. Enlarged stipular spines shiny, dark brown to black, glabrous to lightly puberulent, terete in cross section, usually abruptly narrowing at the base, symmetrical, straight, V-shaped with an angle of 80–160°, to 40 mm long, 3–5.5 mm wide near the base, some of the spines not enlarged, puberulent at least near the base, less than 6 mm long. Leaves 80–160 mm long; pinnae 13–30 pairs per leaf, 25–45 mm long, 5–9 mm between pinna pairs; rachis lightly puberulent, rachis glands absent; petiole grooved, puberulent, 8–10 mm long. Petiolar glands 2–4, scattered along the petiole, broadly dome-shaped, the apex depressed, puberulent, striate, apex 1.4–2.5 mm across, sometimes the glands overlapping and continuous to 4.5 mm long. Leaflets 23–32 pairs per pinna, usually glabrous, linear, 4.5–5.5 mm long, 0.9–1.2 mm wide, one vein from the base, lateral veins sometimes obvious. Inflorescence a densely flowered cylindrical spike, 10–14 mm long, 6–7 mm wide, in

clusters of 2–6 in the axil of slightly reduced leaves; peduncles densely puberulent, to 35 mm long; involucre usually located just below the spike, puberulent, usually 4-lobed, Floral bracts spatulate to nearly peltate with a circular apex. Corolla yellowish, about ⅔ as long as the calyx. Fruit straight, elliptical in cross section, to 80 mm long, 13–16 mm wide, glabrous, not striate, dark brown, probably dehiscing along one suture, short-stalked, base broadly cuneate, apex narrowing to a short beak.

Representative specimens. GUATEMALA. **Guatemala:** 16.2 mi. NE of Guatemala City on rd. to Puerto Barrios, *Janzen 744* (EIU, ILL). MEXICO. **Chiapas:** El Chorreadero, 5.6 mi. E of Chiapa de Corzo along Mexican hwy. 190, 2500 ft., *Breedlove 9638* (F, US); 8.5 mi. S of La Trinitaria on hwy. 190, *Janzen 571* (EIU, ILL). **Oaxaca:** 50 mi. E of Tehuantepec on hwy. 190, *Seigler & Holstein 9782* (ILL). NICARAGUA. **Esteli:** 15.8 mi. W of Sebaco, 550 m, *Janzen 742* (EIU, ILL).

The puberulent stipular spines, petioles, rachises, peduncles, and bracts of these hybrids strongly suggest that *A. pennatula* is the non-ant-acacia parent. Also, the young leaves are densely yellowish puberulent, a characteristic of young leaves of *A. pennatula.* The cylindrical spikes, the enlarged stipular spines, the presence of Beltian bodies on the lower 1–2 leaflets of most pinna pairs, the broadly dome-shaped petiolar glands, and the absence of rachis glands on the hybrid specimens indicate *A. collinsii* as the most probable ant-acacia parent.

Acacia cornigera? × *A. pennatula:* Small shrub to 2 m tall; twigs reddish brown, puberulent. Enlarged stipular spines light grayish brown, puberulent, terete to oval in cross section, symmetrical, straight, V-shaped with an angle of 80–160°, to 30 mm long, 3–4 mm wide near the base, most spines not enlarged, puberulent, less than 4 mm long. Leaves 70–120 mm long; pinnae 12–23 pairs per leaf, 22–34 mm long, 2–5 mm between pinna pairs; rachis puberulent, a nearly circular columnar gland with a depressed apex located near the node between each pinna pair; petiole grooved, puberulent, 4–7 mm long. Petiolar glands columnar, the apex depressed, usually 1 just below the first pinna pair, puberulent, lightly striate, apex 0.8–1.2 mm long. Leaflets 15–26 pairs per pinna, lightly puberulent, ciliate, linear, 2.2–4.5 mm long, 0.6–1.3 mm wide, one vein from the base, lateral veins usually not obvious. Flowers and fruits not observed.

Representative specimen. MEXICO. **Veracruz:** 24.3 mi. from Veracruz on hwy. 140, *Seigler et al. 12224* (ILL).

The wide-ranging ant-acacia *Acacia cornigera* may rarely hybridize with the non-ant-acacia *A. pennatula.* The only specimen seen of this probable hybrid was a 2-m-tall sapling collected in a pasture where both parent species were common. The only other acacia species present was *Acacia macracantha.* The dense pubescence of this hybrid, however, suggests that *A. pennatula* is the non-ant-acacia parent. Not only are the twigs and spines densely puberulent, but the leaflets are lightly puberulent and ciliate, while the columnar rachis glands with a depressed apex are similar to those found in *A. pennatula.* The enlarged spines, the presence of Beltian bodies on the lower 1–2 leaflets of some pinnae, and the well-developed rachis and petiolar glands indicate a relationship to an ant-acacia species. Because *A. cornigera* is the only ant-acacia known to occur in this part of Mexico, it is probably the ant-acacia parent. However, the relatively small leaflets generally lack secondary veins, and the petiolar glands differ from the canoe-shaped glands of typical *A. cornigera.* Final determination must await flowering and fruiting material (Ebinger & Seigler, 1992).

Acacia hindsii × *A. cochliacantha.*

Acacia ×gladiata Saff., J. Wash. Acad. Sci. 5: 359. 1915. *Myrmecodendron gladiatum* (Saff.) Britton & Rose, N. Amer. Fl. 23: 92. 1928. TYPE: Mexico. Sinaloa: vicinity of Rosario, 1849, *J. Gregg 1135* (holotype, MO; photo, F, NY; fragment and photo, US).

Shrub or small tree to 4 m tall, twigs dark reddish brown, nearly glabrous. Stipular spines light brown to reddish brown, glabrous, flattened (sometimes oval in cross section), symmetrical, widely spreading with an angle of 160 to 180°, linear-lanceolate, constricted toward the base, to 60 mm long, 5–13 mm wide. Leaves 70–130 mm long; pinnae 8–16 pairs per leaf, 15–35 mm long, 5–10 mm between pinna pairs; rachis puberulent, a columnar gland with a depressed apex located near the node between each pinna pair (sometimes absent); petiole grooved, puberulent, 7–10 mm long. Petiolar glands columnar to volcano-shaped, 1–2 scattered along the petiole, glabrous, striate, apex 0.4–1.5 mm across. Leaflets 14–20 pairs per pinna, glabrous, linear, 2.5–4.5 mm long, 0.7–1.2 mm wide, one vein from the base, lateral veins not obvious. Inflorescence a loosely flowered, cylindrical spike, 8–17 mm long, 3.5–5 mm thick, in clusters of 2–6; peduncles to 13 mm long, puberulent; involucre located at or above the middle of the peduncle, 4-lobed, puberulent. Floral bracts spatulate. Flow-

ers sessile; calyx 0.6–0.9 mm long, the lobes puberulent; corolla puberulent, maroon, 5–6-lobed, about twice as long as the calyx. Fruits not seen.

Representative specimens. MEXICO. **Oaxaca:** 3 mi. N of Puerto Escondido, *Seigler et al. 11566 (ILL)*. **Sinaloa:** 14.4 mi. NW of Rosario on hwy. 15, *Janzen 1720* (EIU, ILL), *Ortega 4884* (US).

The narrow cylindrical inflorescences, the small leaflets, and the presence of rachis glands indicate that *A. hindsii* is the ant-acacia parent, while the enlarged, flattened stipular spines suggest that *A. cochliacantha* is the non-ant-acacia parent. In many of its characteristics this hybrid is intermediate between the parents. The large, compressed stipular spines are similar to those of *A. cochliacantha*, although these spines are not spoon-shaped as in typical *A. cochliacantha*. No specimens were found on which the spines exhibited the characteristic entrance holes made by acacia-ants. Overall, the leaves are similar to those of *A. cochliacantha* in that they are relatively short and narrow. The leaflets, however, are similar to those of *A. hindsii*, being 3.0–4.5 mm long and 0.7–1.2 mm wide. In *A. cochliacantha*, in contrast, the leaflets are typically 0.8–2.4 mm long and 0.3–0.6 mm wide (Seigler & Ebinger, 1988). Furthermore, the presence of rachis glands indicates a relationship to *A. hindsii*, as does the presence of Beltian bodies on the lower 1–4 leaflet pairs of most pinnae.

Acacia hindsii × *A. pennatula.*

Acacia ×standleyi Saff., J. Wash. Acad. Sci. 4: 367. 1914. *Myrmecodendron standleyi* (Saff.) Britton & Rose, N. Amer. Fl. 23: 92. 1928. TYPE: Mexico. Nayarit: along the river in the vicinity of Acaponeta, Territory of Tepic, W Mexico, 11 Apr. 1910, *J. N. Rose, P. C. Standley & P. G. Russell 14374* (holotype, US; photo, F).

Acacia ×hirtipes Saff., J. Wash. Acad. Sci. 4: 367. 1914. *Myrmecodendron hirtipes* (Saff.) Britton & Rose, N. Amer. Fl. 23: 92. 1918. TYPE: Guatemala. Santa Rosa: along the Río de las Cañas, 3000 ft., Apr. 1892, *Heyde & Lux 3299b* (holotype, US; photo, NY).

Myrmecodendron oaxacanum Britton & Rose, N. Amer. Fl. 23: 92. 1928. TYPE: Mexico. Oaxaca: Fonameca, 110 m, 3 July 1925, *E. Makrinius 488* (holotype, US).

Shrub or small tree to 10 m tall; twigs reddish brown, glabrous to lightly puberulent. Enlarged stipular spines shiny, light gray to black, glabrous to lightly puberulent, terete to oval in cross section, the base usually flattened, symmetrical, straight, V-shaped with an angle of 80–180°, to 40 mm long, 3–7 mm wide near the base, some of the spines not enlarged, puberulent at least at the base, less than 5 mm long. Leaves 90–150 mm long; pinnae 16–31 pairs per leaf, 20–46 mm long, 4–7 mm between pinna pairs; rachis puberulent, a columnar gland with a depressed apex located near the node between each pinna pair (rarely some absent); petiole grooved, puberulent, 6–11 mm long. Petiole glands solitary, columnar to elongated, the apex depressed, puberulent, apex 1–2 mm across. Leaflets 26–40 pairs per pinna, glabrous to lightly puberulent, ciliate, linear, 2.4–3.8 (rarely 5.0) mm long, 0.7–1.1 mm wide, one vein from the base, lateral veins not obvious. Inflorescence a densely flowered cylindrical spike, 13–20 mm long, 6–8 mm thick, slightly thicker near the apex, in clusters of 1–8 in the axis of slightly reduced leaves; peduncle densely puberulent, 10–27 mm long; involucre located near the middle of the peduncle, puberulent, usually 4-lobed. Floral bracts spatulate. Corolla yellowish to reddish, about twice as long as the yellowish calyx. Fruit straight, elliptical in cross section, 40–100 mm long, 8–12 mm wide, glabrous, not striate, black to dark brown, dehiscent along one suture, short stalked, base broadly cuneate, apex narrowing to a short beak.

Representative specimens. GUATEMALA. **Escuintla:** in pasture above Palín, 1500 m, *Standley 60100* (F). **Guatemala:** 19 km S of Guatemala City on C. A. 8, *Janzen 764* (EIU, ILL). HONDURAS. **Comayagua:** tree in dry gulch near San Luís, close to the river, *Hazlett 1445* (MO). MEXICO. **Chiapas:** a unos 3 km de Ocosingo, por la orilla de la carretera que va a Tonina, *Shapiro & Elliott 471* (MICH, MO); 3.9 mi. NE of Arriaga, *Janzen 758* (EIU, ILL). **Jalisco:** Reserva Biosfera de la Sierra de Manantlán, 16 km by new dirt road WSW of El Terrero, *Cochrane et al. 11730* (WIS). **Nayarit:** 16 mi. E of San Blas, *Johnson 109-73* (MO). **Oaxaca:** Nejapa, a 5 km al S-SW de Santa Maria Zacatepec, *Sousa et al. 10587* (MEX); 46.7 mi. W of Tehuantepec, along hwy. 190, *Janzen 748* (EIU, ILL).

The densely puberulent stipular spines, petioles, rachises, peduncles, and bracts are similar to those found in *A. pennatula*. Also, the spatulate floral bracts are typical of *A. pennatula*, as are the columnar petiolar glands with a depressed apex. These hybrid specimens also have numerous characteristics of *A. hindsii*. The presence of enlarged stipular spines, Beltian bodies on the lower 1–2 leaflets of most pinnae, the well-developed rachis glands, and the elongated spikelike inflorescence all indicate a relationship to *A. hindsii*. Considering the distribution of this hybrid, the only other possible ant-acacia parent is *A. collinsii*. The lack of obvious secondary veins in the leaflets, the presence of rachis glands, and the small size of the leaflets, however, indicate that *A. collinsii* is not the ant-

acacia parent. Of the specimens of this hybrid tested for cyanide production, four gave a weak to moderate positive reaction.

Literature Cited

Bentham, G. 1875. Revision of the order Mimoseae. Trans. Linn. Soc. London 30: 335–664.

Brinker, A. M. & D. S. Seigler. 1989. Methods for the detection and quantitative determination of cyanide in plant materials. Phytochem. Bull. 21(2): 24–31.

Britton, N. L. & J. N. Rose. 1928. Mimosaceae. N. Amer. Fl. 23(2): 1–194.

Calvert, A. S. & P. P. Calvert. 1917. A Year of Costa Rican Natural History. MacMillan, New York.

Dixon, W. J. 1983. BMDP Statistical Software. Univ. California Press, Berkeley.

Ebinger, J. E. & D. S. Seigler. 1987. A new species of ant-acacia (Fabaceae) from Mexico. SouthW. Naturalist 32: 245–249.

——— & ———. 1992. Ant-acacia hybrids of Mexico and Central America. SouthW. Naturalist 37: 408–414.

Feigl, F. & V. A. Anger. 1966. Replacement of benzidine by copper ethylacetoacetate and tetra base as spot-test reagent for hydrogen cyanide and cyanogen. Analyst 91: 282–284.

Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20: 249–275.

———. 1967a. Interaction of the Bull's Horn Acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Univ. Kansas Sci. Bull. 47: 315–558.

———. 1967b. Fire, vegetation structure, and the ant × *Acacia* interaction in Central America. Ecology 48: 26–35.

———. 1974. Swollen-thorn acacias of Central America. Smithsonian Contr. Bot. 13: 1–131.

———. 1981. The defenses of legumes against herbivores. Pp. 952–977 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Royal Botanical Gardens, Kew.

Pedley, L. 1978. A revision of *Acacia* Mill. in Queensland. Austrobaileya 1: 75–337.

Rehr, S. S., P. P. Feeny & D. H. Janzen. 1973. Chemical defense in Central American non-ant-acacias. J. Animal Ecol. 42: 405–416.

Rohlf, F. J. 1990. NTSYS-pc. Numerical Taxonomy and Multivariate Analysis System, Version 1.50. Exeter Software, Setauket, New York.

Rudd, V. E. 1964. Nomenclatural problems in the *Acacia cornigera* complex. Madroño 17: 198–201.

Safford, W. E. 1910. Bull-horn acacias in botanical literature, with a description of two new species. Science (N.S.) 31: 676–677.

Schenck, H. 1913. Acaciae myrmecophilae novae. Repert. Spec. Nov. Regni Veg. 12: 360–363.

Schlechtendal, D. & A. Chamisso. 1830. Plantarum Mexicanarum a cel. viris Schiede et Deppe collectarum recensio brevis. Linnaea 5: 72–174, 206–236, 554–625.

Seigler, D. S. & J. E. Ebinger. 1987. Cyanogenic glycosides in ant-acacias of Mexico and Central America. SouthW. Naturalist 32: 499–503.

——— & ———. 1988. *Acacia macracantha*, *A. pennatula*, and *A. cochliacantha* (Fabaceae: Mimosoideae) species complex in Mexico. Syst. Bot. 13: 7–15.

———, J. E. Dunn, E. E. Conn & G. L. Holstein. 1978. Acacipetalin from six species of *Acacia* of Mexico and Texas. Phytochemistry 17: 445–446.

Tantisewie, B., H. W. L. Ruijgrok & R. Hegnauer. 1969. Die Verbreitung der Blausäure bei den Cormophyten. 5. Mitteilung: Über cyanogene Verbindungen bei den Parietales und bei eingen weiteren Sippen. Pharm. Weekbl. Ned. 104: 1341–1354.

Vassal, J. 1969–1972. Apport des recherches ontogénetique et séminologique a l'étude morphologique, taxonomique et phylogénique du genre *Acacia*. Trav. Lab. Forest. Toulouse 8: 1–416.

Wheeler, W. M. 1942. Studies of neotropical ant-plants and their ants. Bull. Mus. Comp. Zoology Harvard Coll. 90(1).