A SYNOPSIS OF LOPHOSTACHYS (ACANTHACEAE) IN MEXICO AND CENTRAL AMERICA

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ABSTRACT. Four species of the neotropical genus *Lophostachys* are recognized in Mexico and Central America: *L. chiapensis, L. guatemalensis, L. uxpanapensis,* and *L. soconuscana.* The latter species is newly described from southeastern Chiapas in southern Mexico. An introduction to *Lophostachys* and its subfamilial affinities is followed by a description of the genus and a key to the four middle American species. Notes on distributions, habitats, phenologies, and distinguishing morphological characters are provided for each species.

Nineteen species have been described in this poorly known American genus of Acanthaceae. Most of these are Brazilian, although one has been described from each of Bolivia, Peru, and Guatemala. Recently, Acosta C. (1985) described two new species from southern Mexico. While preparing a treatment of the Acanthaceae of Chiapas, the southernmost state of Mexico, I encountered additional collections of the two species described by Acosta C. and another collection that represents an undescribed species. In order to adequately delimit the latter, a review was undertaken of all species of Lophostachys in Mexico and Central America. Selected materials of South American species were also studied. In the synopsis that follows, a key to the four species of Lophostachys occurring in Mexico and Central America is provided; the new species is described; and notes on distribution, habitat, phenology, and morphology are provided for the three previously described species.

Although infrafamilial classification of the Acanthaceae has not been studied in detail since 1895 (Lindau 1895) and remains problematic at present, the coupling of Lophostachys with the large, pantropical genus Barleria has been consistent for almost 150 years. Nees (1847) treated Lophostachys in his tribe Barlerieae and Bentham (1876) included the genus in subtribe Barleriinae (as "Barlerieae") of his tribe Justicieae. Lindau (1895) placed the genus in his subfamily Acanthoideae, tribe Barlerieae and distinguished the genus on the basis of having thecae of the posterior pair of stamens unilocular or abortive, a four-parted calyx with the anterior lobe bifid, and tricolporate pollen covered with a network of ridges. Most recently, Bremekamp (1965) treated most of Lindau's Barlerieae as subtribe Barleriinae of his tribe Ruellieae.

Characteristics of the pollen have traditionally been important in delimiting *Barleria* and its relatives (Lindau 1895, Bremekamp 1965). Raj (1961) characterized pollen of three South Amer-

ican species of Lophostachys as prolate and tricolporate. In addition, he noted that the exine sculpturing of L. falcata Nees consists of a homobrochate reticulum, the lumina of which contain densely spaced processes. I examined pollen of each of the Mexican and Central American species with the scanning electron microscope. Pollen of these four species, like that of their South American counterparts so far examined, is prolate and tricolporate (FIGURE 1). The most conspicuous feature of the grains is the coarsely reticulate exine in which the mostly five to sevensided lumina contain baculae, pilae, and/or gemmae. Among Mexican and Central American Acanthaceae pollen with similar exine sculpturing is found in Ruellia (Ruelliinae), Teliostachva (Lepidagathidinae), and Barleria (Barleriinae), each of which would be included in a different subtribe utilizing the classification of Bremekamp (1965).

The closest relative of Lophostachys in Mexico and Central America is Barleria micans Nees, the sole species of this large genus native to the New World. In addition to having similar pollen, both genera have four-parted calyces with the anterior lobe bifid. These genera can be distinguished on the basis of corolla form (in Barleria. the lateral lobes of the lower lip of the corolla are in closer proximity to the upper lip than to the lower-central lobe during anthesis) and bract posture (secund in Lophostachys). Barleria micans can be further distinguished from Mexican and Central American species of Lophostachys by its bright yellow corollas (that become dark blue-black on drying), dentate bracts, and three staminodes.

The Mexican and Central American species of *Lophostachys* generally occur in regions of moist to wet forest (i.e., rain forest of Breedlove 1981; "bosque tropical perennifolio" of Rzedowski 1978). The three Mexican species are restricted to regions that receive an average annual rainfall of more than 3,000 mm. Acosta C. (1985) point-

FIGURE 1. Pollen of Lophostachys. a, L. soconuscana (Boege 1086), colpal view. b, L. uxpanapensis (Hernández G. 642), colpal view. c, L. uxpanapensis (Hernández G. 642), intercolpal view. d, L. chiapensis (Breedlove 30873), colpal view. e, L. guatemalensis (Heyde & Lux 4382), intercolpal view. f, L. soconuscana (Boege 1086), polar view. Scale in b-e same as in a.

ed out the disjunction between species of *Lophostachys* in South America and those in Mexico and Central America. He suggested that this distribution, like that of *Schaueria* (Hilsenbeck & Marshall 1983), exemplifies a southern floristic influence in the rain forests of Mexico. Such an influence has also been noted by Rzedowski (1978) and Wendt (1989). Other predominantly South American moist to wet forest Acanthaceae that attain the northernmost extent of their distributions in the rain forests of southeastern Mexico include *Mendoncia* Vell. ex Vand. and *Aphelandra aurantiaca* (Scheidw.) Lindl.

TAXONOMY

Lophostachys Pohl, Pl. Bras. 2: 93. 1831. TYPE: Lophostachys villosa Pohl. [Although C. Bremekamp cited L. villosa as the type of the genus in the original card Index nominum genericorum (plantarum) (see Farr et al. 1979), Pohl (1831) did not select a type in the protologue which included three species. Bremekamp's citation of L. villosa could be considered as a lectotypification of the genus (but see discussion by Farr et al. 1986).]

Perennial herbs or shrubs. Leaves petiolate, opposite, sometimes unequal at a node. Inflorescence of axillary and terminal, usually densely flowered spikes or racemes; bracts green or brightly colored, alternate, secund; bractlets 2 or absent; flowers solitary, sessile or pedunculate in axils of bracts. Calyx 4-lobed nearly to base, zygomorphic, outer (anterior and posterior) segments larger than inner (lateral) segments, anterior lobe bifid, posterior lobe entire to emarginate, lateral lobes entire. Corolla whitish to reddish to purplish, imbricate in bud with lateral lobes of lower lip outermost and upper lip innermost, tube somewhat ampliate distally, limb bilabiate with upper (posterior) lip shallowly bilobed and lower (anterior) lip deeply trilobed. Androecium of 2 stamens and 2 staminodes or 4 didynamous stamens and no staminodes, stamens inserted near middle of corolla tube, if 4 then with longer pair bithecous and shorter pair monothecous, if 2 then bithecous; thecae rounded to acute (but lacking appendages) at base; pollen prolate, 3-colporate, reticulate, the reticulum subhomobrochate with lumina mostly pentagonal or hexagonal and baculate, pilate, and/or

TABLE 1. Character states useful for distinguishing the Mexican and Central American species of Lophostachys.

– Taxa	Characters				
	Calyx length (mm)	Corolla length (mm)	Stamen number	Thecae length (mm)	Capsule length (mm)
L. chiapensis	11.5-15	16-29	4	1.7-2.5	9–10
L. guatemalensis	10-15	28-33	4	2-3	9.5-12
L. soconuscana	15-24	50-56	4	3.6-4	15.5
L. uxpanapensis	20-28	40-63	2	4-5.2	13-16

gemmate. Stigma appearing subcapitate (although usually minutely and asymmetrically bilobed). Capsule ellipsoid. Seeds 4, flattened.

Nineteen species; southern Mexico to southeastern Brazil.

Key to Lophostachys in Mexico and Central America

Additional characters useful in distinguishing among these species are presented in TABLE 1.

- 1. Anterior lobe of calyx obovate, divided 0.50–0.68 its length; bractlets spatulate, 6.5–10 mm long; capsule externally pubescent with eglandular trichomes 0.1–0.3 mm long over entire surface. 1. L. guatemalensis.
- 1. Anterior lobe of calyx elliptic, divided 0.01–0.31 its length; bractlets triangular to lanceolate to ovate, 2.5–7 mm long; capsule glabrous (rarely with a few eglandular trichomes at apex only).
 - Calyx 11.5–15 mm long, anterior lobe 3.2–4 mm wide, posterior lobe 3–3.5 mm wide; corolla 24– 29 mm long; stamens 8–12 mm long; thecae 1.7– 2.3 mm long; capsule 9.5–10 mm long. 2. L. chiapensis.
 - Calyx 15-27 mm long, anterior lobe 3.8-7 mm wide, posterior lobe 3.5-7 mm wide; corolla 50-63 mm long; stamens 21-33 mm long; thecae 3.6-5.2 mm long; capsule 13-16 mm long.
 - Calyx dark purplish red when dry; lobes of lower lip of corolla 4–7 mm long, 2.5–3.3 mm wide; stamens 2, bithecous, staminodes 2. 3. L. uxpanapensis.
 - 3. Calyx greenish when dry (although somewhat reddish near base); lobes of lower lip of corolla 11.5–12.5 mm long, 5.5–6.5 mm wide; stamens 4, longer pair bithecous, shorter pair monothecous, staminodes absent. 4. L. so-conuscana.
- Lophostachys guatemalensis J. D. Smith, Bot. Gaz. (Crawfordsville) 31: 119. 1901. TYPE: Guatemala, Santa Rosa, Casillas, January 1893, E. Heyde & E. Lux 4382 (US!, holotype; A!, GH!, K!, M!, MO!, US!, isotypes).

ADDITIONAL SPECIMENS EXAMINED. El Salvador. AHUACHAPAN: without specific locality, S. Padilla 25 (US). SAN VICENTE: vicinity of San Vicente, P. Standley 21673 (GH, US). DEPARTMENT UNKNOWN: summit of Cerro del Guayabal, S. Calderón 2016 (US). Guatemala. ESCUNTLA: below Las Lajas, P. Standley 64851 (F, US); San Antonio Jute, P. Standley 64915 (F, US); NE of Escuintla on road to Palín, P. Standley 89490 (F), 89504 (F, US); Río Burrión, NE of Escuintla, P. Standley 89566 (F, US). GUATEMALA: Amatillán, Moran, W. Kellerman 6727 (F), 6728 (F, US).

DISTRIBUTION AND HABITAT. Guatemala (Escuintla, Guatemala, Santa Rosa) and El Salvador (Ahuachapán and San Vicente); plants occur in moist or dry thickets or forests at elevations from 450–1,440 m.

PHENOLOGY. Flowering: January–March; fruiting: February–March.

A description of this species was provided by Gibson (1974). The following characteristics can be added to her description: bractlets spatulate; anterior lobe of the calyx obovate, divided 6–8.5 mm from the apex, the two resulting segments asymmetrically obovate-spatulate; seeds subcircular in outline, 2.6–3.6 mm long and 2.5–3.2 mm wide, covered with appressed trichomes up to 0.4 mm long. Lophostachys guatemalensis resembles L. chiapensis in stamen number and length of the calyx, corolla, thecae, and capsule (TABLE 1). These species are readily distinguishable by the characters of the calyx, bractlets, and capsule noted in the key above.

The habitat information from herbarium specimens noted above is rather sketchy. The distribution of the species as shown in FIGURE 2 reveals that plants occur in regions dominated by humid forests (Anonymous 1972, 1979).

 Lophostachys chiapensis S. Acosta C. Phytologia 57: 256. 1985. TYPE: Mexico, Chiapas, Mpio. Tumbalá, Agua Azul, 10 April 1984, *R. Fernández 2400* (ENCB!, holotype; MEXU, XAL, isotypes).

ADDITIONAL SPECIMENS EXAMINED. Mexico. CHIAPAS: Mpio. Berriozábal, near Finca El Suspiro and Pozo Turipache, 13 km N of Berriozábal, D. Breedlove & R. Thorne 30873 (C, DS, K, MEXU, MO, TEX, US), D. Breedlove et al. 66152 (CAS), T. Daniel & A. Ton 6183



FIGURE 2. Distribution of Lophostachys in Mexico and Central America.

(C, CAS, DUKE, ENCB, F, K, MEXU, MICH, MO, NY, SEL).

DISTRIBUTION AND HABITAT. Southern Mexico (Chiapas); plants occur in regions of lowland to montane rain forest at elevations from 350–1225 m.

PHENOLOGY. Flowering and fruiting: December-April.

The following characteristics augment the description provided by Acosta C. (1985): leaf blades 2–3.4 times longer than wide and seeds 2.2–2.6 mm long, 2–2.3 mm wide, covered with appressed trichomes up to 0.3 mm long. The species resembles *L. guatemalensis* in numerous characters (see above).

Lophostachys chiapensis was previously known only from the lowland to lower montane rain forests in the vicinity of Agua Azul in northeastern Chiapas. The specimens cited above extend its known range into a montane rain forest in northwestern Chiapas (FIGURE 2). The latter region, located to the north of Berriozábal, comprises an oak and laurel-dominated forest at an elevation approximately 800 meters higher than the somewhat more species-rich forests near Agua Azul. Other species of Acanthaceae that have been collected at both locales include: *Aphelandra aurantiaca* (Scheidw.) Lindl., *Justicia magniflora* (Blake) D. Gibson, and *Louteridium mexicanum* (Baill.) Standley.

 Lophostachys uxpanapensis S. Acosta C. Phytologia 57: 253. 1985. TYPE: Mexico, Veracruz, Mpio. Jesús Carranza, camino a Pancho Villa, 18 January 1975, B. Dorantes 3963 (ENCB!, holotype; MEXU, XAL, isotypes).

ADDITIONAL SPECIMENS EXAMINED. Mexico. OAXACA: Isthmo de Tehuantepec, Plantación Buena Ventura, C. Conzatti & S. Harvey K (US); Uxpanapa Region, between Esmeralda (17 km E of Sarabia) and Río Manea, 11.5–13.5 mi S of Esmeralda, 17°04'N, 94°45'W, T. Croat & D. Hannon 63248 (CAS, TEX); Mpio. Sta. María Chimalapa, Distr. Juchitán, Colonia Cuauhtemoc, KM 23 de la carr. Matías Romero-Acayucan, J. García P. 539 (CAS, DAV, F, LL, US); Mpio. Sta. María Chimalapa, Arroyo Sardina, ca. 7 km SE de Sta.



FIGURE 3. Lophostachys soconuscana (Boege 1086). a, habit, $\times 0.5$. b, leaf, $\times 0.5$. c, portion of inflorescence with bracts, bractlets, and calyx, $\times 0.9$. d, opened corolla showing androecium, $\times 1$. e, anthers, $\times 3.8$. f, partially opened capsule, $\times 2.5$. Drawn by Nancy King.

María, 16°54'N, 94°38'W, *H. Hernández G. 476* (CAS); Mpio. Sta. María Chimalapa, ca. 8 km N de Sta. María, por la vereda al Río Verde, 16°57'N, 94°41'W, *H. Hernández G. 642* (CAS). VERACRUZ: 26 km E and 8 km S of Jesús Carranza, Arroyo Azul, R. Baker 5 (US); Mpio. Hidalgotitlán, NE del Campamento de S.R.H., Hnos. Cedillo camino a La Laguna, B. Dorantes 2455 (K); Dos Ríos, C. Mell 513 (US); Mpio. Las Choapas, Río Grande, at and upstream from main gravel rd, of Uxpanapa Region, M. Nee & K. Taylor 29871 (F); Mpio. Hidalgotitlán, N side of Río Solosúchil, 2-3 km SE of Agustín Melgar, 17°14'N, 94°33'W, M. Nee & K. Taylor 29944 (F, TEX); Mpio. Hidalgotitlán, Breca Hnos. Cedillo-La Escuadra, 17°18'N, 94°38'W, B. Vazquez 56 (C); Mpio. Hidalgotitlán, Río Soloxúchil, camino a Pancho Villa, 17°16'N, 94°37'W, B. Vasquez 1306 (ENCB); Mpio. Hidalgotitlán, Río Soloxochil entre Hnos. Cedillo y la Escuadra, 17°17'N, 94°38'W, M. Vasquez et al. 346 (F, US); Mpio. Jesús Carranza, 2 km N del Poblado 2, Ejido F. J. Mina, 17°16'N, 94°40'W. M. Vasquez T. et al. 2422 (CAS); Mpio. Minatitlán, 13.7 km E de La Laguna, sobre la terracería a Uxpanapa, 17°19'N, 94°23'W, T. Wendt et al. 2840 (CAS, TEX).

DISTRIBUTION AND HABITAT. Southern Mexico (Oaxaca and Veracruz); plants occur in regions of lowland rain forest at elevations from 100–285 m.

PHENOLOGY. Flowering: October-April; fruiting: March-April.

Acosta C.'s (1985) description of this species can be augmented by the following information on the seeds: 3.7–4.8 mm long, 3.4–4 mm wide, and covered with inconspicuous trichomes 0.05– 0.2 mm long. *Lophostachys uxpanapensis* is unique among the Mexican and Central American species of the genus by its androecium which comprises two bithecous stamens (28–33 mm long) and two staminodes (12 mm long). The staminodes consist of apically flared filaments that are inserted in the corolla tube about 10 mm below the stamens.

This species, which occurs only in the Uxpanapa region of the Isthmus of Tehuantepec (FIGURE 2), attains the westernmost extent of the distribution of the genus. The Uxpanapa region has been described as a center for endemism and disjunct populations (Wendt 1989).

4. Lophostachys soconuscana T. F. Daniel, sp. nov. FIGURE 3.

Perennis. Folia petiolata, ovato-elliptica, 35– 170 mm longa, 10–55 mm lata, 2.2–3.6-plo longiora quam latiora. Bracteae et bracteolae triangulatae vel lanceolatae, 3.5–7 mm longae, 1–1.5 mm latae. Calyx in sicco viridis, 15–24 mm longus, lobo antico 0.14–0.31 diviso. Corolla in sicco rubens, 50–56 mm longa, lobis labii inferioris subellipticis, 11.5–12.5 mm longis, 5.5–6.5 mm latis. Stamina 4, didynama, antherae staminum longiorum biloculatae, antherae staminum breviorum uniloculatae. Staminodia nulla. Capsula glabra. Semina pubescentia.

TYPE. Mexico, Chiapas, Sta. Anita entre Huixtla y Tapachula, 700 m, 26 December 1968, *W. Boege 1086* (GH!, holotype).

Perennial of unknown height (at least 3.5 dm tall). Young stems subquadrate to quadrate-sulcate, pubescent with antrorse to antrorsely appressed eglandular trichomes 0.2-0.7 mm long concentrated in 2 vertical lines, soon glabrate. Leaves petiolate with petioles to 50 mm long, blades ovate-elliptic, 35-170 mm long, 10-55 mm wide, 2.2-3.6 times longer than wide, attenuate at base, acuminate at apex, surfaces glabrous, margin entire to subcrenate. Inflorescence of axillary and terminal pedunculate spikes to 120 mm long (including peduncle but excluding flowers), rachis conspicuously ridge-angled, pubescent like young stems, bracts alternate along rachis, flowers alternate and secund, sessile or subsessile (i.e., borne on peduncles to 1 mm long). Bracts triangular to lanceolate, 3.5-6 mm long, 1-1.5 mm wide (proximalmost often larger), abaxial surface glabrous, margin subciliate with a few cauline type trichomes, sterile bracts curved and appressed toward floriferous side of inflorescence. Bractlets triangular to lanceolate, 3.5-7 mm long, 1-1.5 mm wide, pubescent like bracts. Calyx drying greenish, 15-24 mm long, divided nearly to base, abaxially mostly glabrous (anterior and posterior lobes) or pubescent (lateral lobes) with cauline type trichomes, margins of lobes ciliate with cauline type trichomes, anterior lobe elliptic, 15-23 mm long, 3.8-6.2 mm wide, bilobed at apex (divided 0.14-0.31 its length) with lobes lance-subulate, 4-6.5 mm long, lateral lobes subulate, 9-14 mm long, 1-1.2 mm wide, posterior lobe elliptic, 15-22 mm long, 3.5-5.5 mm wide, entire to minutely bilobed at apex. Corolla reddish (when dry), 50-56 mm long, externally pubescent with flexuose eglandular trichomes 0.2-1 mm long, tubular portion 35-40 mm long, upper lip 15 mm long, bilobed with lobes 1 mm long, lower lip 15-16 mm long, trilobed with lobes subelliptic, 11.5-12.5 mm long, 5.5-6.5 mm wide, central lobe slightly larger than lateral lobes. Stamens 4, didynamous, more or less equally inserted near base of throat (17-19 mm above base of corolla), longer pair bithecous, 25 mm long, thecae parallel, 3.8-4 mm long, shorter pair monothecous, 21 mm long, theca 3.6-3.7 mm long, the other theca replaced by a sterile appendage 0.2 mm long. Style 50-53 mm long, glabrous, stigma subcapitate, 0.2 mm long. Capsule ellipsoid, 15.5 mm long, 4 mm across splitting face, externally glabrous. Seeds flattened, 3 mm long, 2.5 mm wide, surface and margin covered with inconspicuous trichomes to 0.2 mm long.

PARATYPE. Mexico. CHIAPAS: near Finca Irlanda, C. Purpus 7077 (UC).

DISTRIBUTION AND HABITAT. Southern Mexico (Chiapas); plants occur in a region of lower mon-

tane to montane rain forest at an elevation of about 700 m.

PHENOLOGY. Flowering and fruiting: December.

Lophostachys soconuscana resembles L. uxpanapensis in length of the calyx, corolla and capsule whereas it has an androecium more similar to that of L. guatemalensis and L. chiapensis (TABLE 1). The calyx differs from that of L. uxpanapensis by its color (greenish vs. dark purplish red), anterior lobe (divided at apex 0.14-0.31 its length with lobes 4-6.5 mm long vs. divided at apex 0.04-0.14 its length with lobes 0.5-4.5 mm long), and lateral lobes (9-14 mm long vs. 17-22 mm long). The corolla differs from that of L. uxpanapensis by the size of the lobes of the lower lip (11.5-12.5 mm long and 5.5-6.5 mm wide vs. 4-7 mm long and 2.5-3.3 mm wide). Although L. soconuscana has the same number of stamens as L. chiapensis and L. guatemalensis, those of the former species are considerably longer than those of the latter two species (21-25 mm vs. 8-12 mm).

The two known collections of *L. soconuscana* were made on adjacent coffee plantations in the Sierra Madre de Chiapas in the southeasternmost region of that state (FIGURE 2), within about 20 kilometers of the Guatemalan border (Helbig 1964). The epithet of this species is derived from the name of the former colonial district in Nueva España's Department of Guatemala that included this portion of Chiapas. Even today, this region is commonly known as "El Soconusco."

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