

REVISION OF SPATHACANTHUS (ACANTHACEAE)

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INTRODUCTION

Spathacanthus Baill. is treated as comprising three species occurring in moist to wet forests of Mexico and Central America. This genus of large shrubs and small trees is distinctive among neotropical Acanthaceae by its very large capsules and seeds, both of which are among the largest known in the family. Few collections of the genus had been made until relatively recently. There is no previous comprehensive treatment of the genus; however, Daniel (1995a) treated two of the species in Mexico.

The generic affinities of *Spathacanthus* have never been adequately addressed. Lindau (1895) placed the genus in the tribe Asystasieae, which he characterized as having “Rahmenpollen” (i.e., 3-colporate and 6-pseudocolpate pollen with the pseudocolpi in each mesocolpium fused near the poles to form pseudocolpal ellipses), four stamens usually with ditheous anthers, and two seeds per capsule valve. Bremekamp (1965) included Lindau’s Asystasieae within subfamily Ruellioideae, tribe Justicieae, subtribe Odontoneminae.

Examination of pollen in *Spathacanthus* (*S. hahnianus*: Breedlove & Smith 21618, Hernández G. 1777, Hernández G. & González L. 1855, Wendt et al. 2769; *S. hoffmannii*: Liesner et al. 15444, Skutch 3325; *S. parviflorus*: Matuda 1696, Ramírez-Marcial & Quintana-Ascencio 507, Skutch 961, Steyermark 46632) reveals grains that are similar to most others in Bremekamp’s (1965) Odontoneminae. They are usually 3-colporate and 6-pseudocolpate (Fig. 1). The two pseudocolpi in each mesocolpium are sometimes fused near one or both poles, but with equal frequency they are not. Similar variation in fusion of pseudocolpi is commonly encountered among American genera of Odontoneminae (Daniel 1998); however, two features of pollen in *Spathacanthus* are noteworthy. Unlike most American Odontoneminae, the interapertural surfaces of the exine (excluding the pseudocolpi) are not conspicuously reticulate. Rather, they vary from being foveolate to fossulate to verrucate to rugulate. The absence of a conspicuously reticulate exine is treated as a derived character in *Spathacanthus* relative to other American Odontoneminae. Secondly, variation in aperture number was noted in *S. parviflorus* (Fig. 1g–i). Pollen of Skutch 961 and Steyermark 46632 has four colpi and eight pseudocolpi; pollen of Matuda 1696 consists of grains with four colpi and eight pseudocolpi together with grains having three colpi and six pseudocolpi; and pollen of Ramírez-Marcial & Quintana-Ascencio 507 (although consisting of poorly formed grains) has pollen with three colpi and six pseudocolpi. Among Mexican Acanthaceae, variation of aperture number within a species has been encountered only in *Stenandrium dulce* (Daniel 1998). Even variation of aperture number within a genus is uncommon among American Odontoneminae; it has been noted

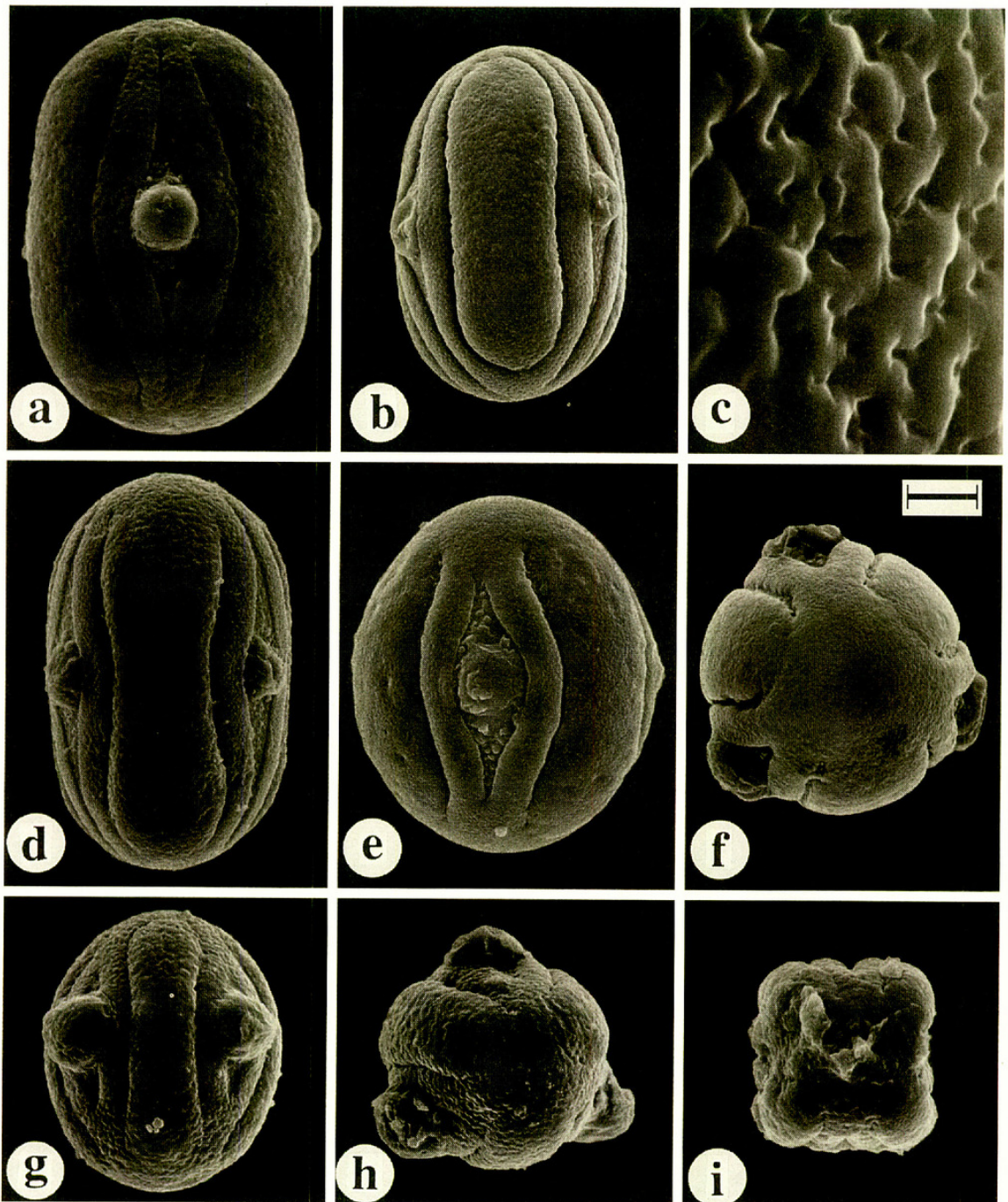


FIG. 1. Pollen of *Spathacanthus*. a. *S. hahnianus* (Hernández G. & González L. 1855), apertural view. b. *S. hahnianus* (Hernández G. & González L. 1777), interapertural view. c. *S. hahnianus* (Wendt et al. 2769), interapertural surface. d. *S. hoffmannii* (Liesner et al. 15444), interapertural view. e. *S. hoffmannii* (Skutch 3325), apertural view. f. *S. hoffmannii* (Skutch 3325), polar view. g. *S. parviflorus* (Matuda 1696), interapertural view. h. *S. parviflorus* (Matuda 1696), polar view of 3-aperturate grain. i. *S. parviflorus* (Steiermark 46632), polar view of 4-aperturate grain. Scale: a, i, bar = 10 μm ; b, d–h, bar = 12.5 μm ; c, bar = 1.5 μm .

only in *Odontonema* (Daniel 1995b). Additional sampling of pollen in *Spathacanthus* is clearly warranted.

The presence of four stamens is not common among Bremekamp's *Odontoneminae*. The only other American genus with four ditheous stamens in this subtribe is *Chalarothyrsus* Lindau. *Chalarothyrsus* is a unispecific genus occurring in the dry forests of western Mexico. Pollen of *Chalarothyrsus* resembles that of

Spathacanthus in sometimes having pseudocolpal ellipses in the mesocolpia; however, it resembles that of most other American Odontoneminae by having a reticulate exine. These two genera can be distinguished by the following couplet:

- Perennial herbs or small shrubs to 1.5 m tall; calyx small (to 5 mm long), 5-lobed, the lobes homomorphic; corolla red, 13–16 mm long; capsule 12–18 mm long; seeds permanently retained in capsule and partially fused to inner capsule wall. *Chalarothyrsus*.
 Large shrubs or small trees to 8 m tall; calyx large (15–40 mm long), 2-parted, the 2 segments entire or variously lobed at apex; corolla white to yellow, 23–95 mm long; capsule 40–85 mm long; seeds expelled from mature capsule, not fused to inner capsule wall. *Spathacanthus*.

PHYLOGENY

A cladistic analysis of *Spathacanthus* using PAUP 3.1.1 (Swofford 1993) was conducted to reveal possible phylogenetic relationships of the species. *Chalarothyrsus* was designated as the outgroup and ten characters were used (Table 1), four of which (2–5) were potentially informative. A branch-and-bound search was performed using equal weighting and unordered character states. Both ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) optimization methods were utilized. A discussion of each character, which includes information from other Odontoneminae (if known), follows:

1. Calyx color: 0 = green; 1 = yellow. Colored calyces are rare among Acanthaceae in general and among Odontoneminae in particular. The bright yellow calyx exhibited by *S. parviflorus* when the corolla is mature is highly unusual and probably attracts floral visitors to the relatively small flowers of this species.

2. Calyx division: 0 = spathaceous and with major divisions equal; 1 = spathaceous and with major divisions unequal; 2 = not spathaceous and equally 5-parted. The feature from which the genus takes its name is a calyx that is fused proximally and comprises two large, spathelike segments distally. This type of calyx is unique to *Spathacanthus* among Odontoneminae. Whether the divisions of the major segments are equal or unequal varies in the genus. The pentamerous and deeply divided calyx of *Chalarothyrsus* is typical of other Odontoneminae. This multi-state character could be treated as two binary characters: calyx lobes fused into two major segments vs. calyx lobes not fused into two major segments, and major calyx segments equally divided vs. major calyx segments unequally divided. The latter character would apply solely to the ingroup.

3. Corolla length: 0 = short (15–29 mm long); 1 = long (46–97 mm long). Corollas of both *S. hahnianus* and *S. hoffmannii* are exceptionally large among Odontoneminae.

4. Corolla color: 0 = white; 1 = yellow; 2 = red. These and other colors are known for corollas among Odontoneminae. Because this character is likely very labile and because corolla color of the outgroup is not represented among species of *Spathacanthus*, it is not possible to determine directionality of the states represented *a priori*.

5. Length of lobes of lower lip: 0 = short (1–6 mm long); 1 = long (8–20 mm long). It is possible that this character is linked to corolla length (character 3). However, using the measurement ranges noted herein, there are taxa that have short corollas with long lobes (e.g., *Mexacanthus mcvaughii* T. F. Daniel) and long corollas with short lobes (e.g., *Dicliptera anomala* Leonard) elsewhere in the Odontoneminae.

6. Number of apertures in pollen: 0 = 3; 1 = 3–4. Triaperturate pollen is widespread among Odontoneminae. See discussion above concerning pollen of *Spathacanthus*.

TABLE 1. Data matrix for species of *Spathacanthus* and the outgroup *Chalarothyrsus*.

	1	2	3	4	5	6	7	8	9	10
<i>S. hahnianus</i>	0	1	1	1	1	0	0	1	1	0
<i>S. hoffmannii</i>	0	0	1	0	1	0	0	1	1	0
<i>S. parviflorus</i>	1	1	0	0	0	1	1	1	1	0
<i>Chalarothyrsus</i>	0	2	0	2	0	0	0	0	0	1

7. Polar diameter of pollen: 0 = 54–67 μm ; 1 = 39–51 μm . In *Chalarothyrsus* the polar diameter of pollen varies from 54–59 μm and overlaps measurements of this diameter in *S. hahnianus*. Although large pollen might be correlated with large corollas within *Spathacanthus*, this is obviously not the case in the outgroup where the corollas are relatively small and the pollen is relatively large.

8. Exine surface: 0 = reticulate; 1 = foveolate to verrucate to rugulate. Exine of interapertural surfaces in *Chalarothyrsus* and most other Odontoneminae is conspicuously reticulate. In species of *Spathacanthus*, the exine varies from foveolate to fossulate to verrucate to rugulate.

9. Capsule length: 0 = short (4–30 mm long); 1 = long (40–90 mm long). Capsules of *Spathacanthus* are the longest known among American Odontoneminae (which otherwise vary in length from 4 to 27 mm). Capsules of *Chalarothyrsus* vary from 12–18 mm in length.

10. Seed fusion: 0 = seeds not fused to capsule valves; 1 = seeds fused to capsule valves. Fusion of the seed coat to the inner wall of the capsule, as observed in *Chalarothyrsus*, has been reported previously in the family only in the unspecific Mexican genus *Aphanosperma* (Daniel 1988). This latter genus is also treated in the Odontoneminae, but it has pseudopapilionaceous corollas and an androecium of two stamens. Therefore, it does not appear to be particularly closely related to *Chalarothyrsus*.

The phylogenetic analysis resulted in a single most parsimonious tree (Fig. 2) of 12 steps (CI = 1.0, HI = 0, RI = 1.0, RC = 1.0). No differences in character state changes resulted from the ACCTRAN vs. DELTRAN optimization. Even if one of the possibly linked characters noted above (i.e., 3 and 5) is deleted from the analysis, a tree with the same topology (but with one less step) is obtained. Dividing character 2 into two binary characters, as noted above, also results in a single tree with the same topology.

On the basis of character states in other Odontoneminae, most characters at the base of the tree in Fig. 2 can be unambiguously mapped onto one of the clades. Given their absence elsewhere in the subtribe, the exceptionally long capsules (9), the two-parted and spathe-like calyces (2), and the non-reticulate exine of pollen grains (8) likely are synapomorphic for *Spathacanthus*. Permanent retention of seeds in the capsular valves (10) would appear to represent a derived condition in *Chalarothyrsus*. As noted above, corolla color cannot be polarized on the basis of character states occurring in other Odontoneminae. The change to red corollas in *Chalarothyrsus* (as mapped) could with equal likelihood have been shown as a change to white corollas in *Spathacanthus*.

Within *Spathacanthus*, *S. hahnianus* and *S. hoffmannii* comprise a clade defined by long corollas with long lobes on the lower lip. *Spathacanthus parviflorus*, which has white corollas like *S. hoffmannii* but spatheous calyces with unequal segments like *S. hahnianus*, is sister to this clade.

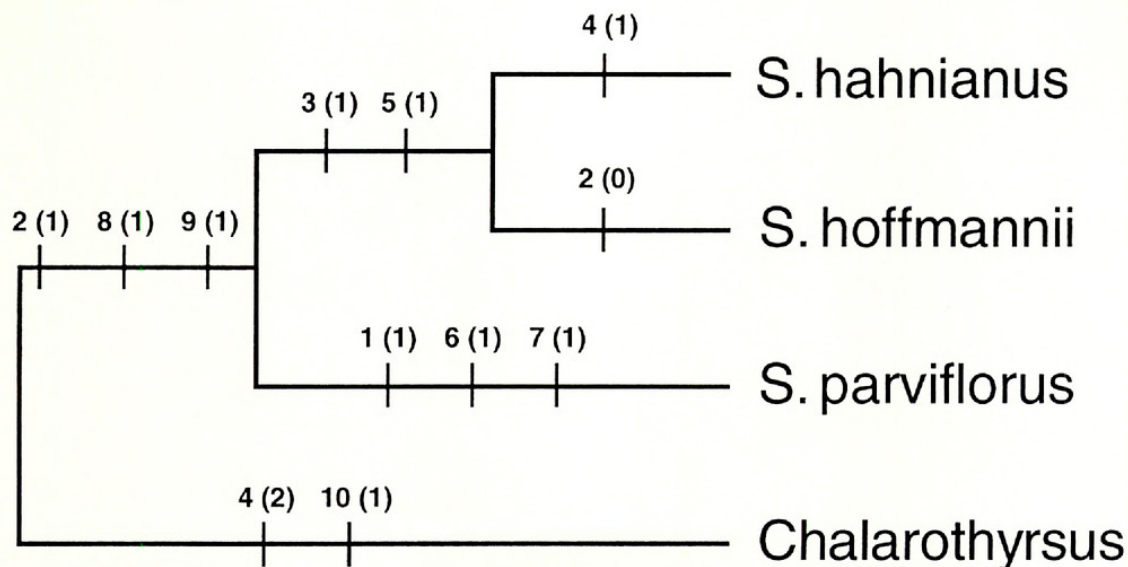


FIG. 2. Cladogram of hypothesized phylogenetic relationships of species of *Spathacanthus*; *Chalarothyrsus* is the outgroup.

TAXONOMY

Spathacanthus Baill., Hist. pl. 10: 444. 1891.—TYPE: *Spathacanthus hahnianus* Baill.

Shrubs or small trees with cystoliths, stems sometimes with conspicuous protruding or blisterlike lenticels. Leaves opposite, subsessile to petiolate, entire. Inflorescence of terminal dichasiate racemes (or thyrses); dichasia opposite, mostly 1-flowered, sessile (to pedunculate), subtended by a bract. Bracts opposite, green, $\pm$ inconspicuous, entire. Flowers subtended by 2 homomorphic bracteoles, pedicellate, pedicels usually enlarged in fruit. Calyx green or yellowish, spathaceous, beaked in bud, equally or unequally divided into 2 segments, 1 segment comprising 2 fused lobes, apically entire to 2-lobed, the other segment comprising 3 fused lobes, apically entire to 3-lobed. Corolla white or yellow, externally glabrous (although margins of lobes sometimes ciliolate), tube expanded distally into a $\pm$ distinct throat, limb bilabiate (or appearing $\pm$ regular), upper lip deeply 2-lobed, lower lip deeply 3-lobed, corolla lobes imbricate (ascending cochlear) in bud. Stamens 4, didynamous, inserted at base of corolla throat, included in corolla tube, anthers 2-thealous, thecae equal in size, parallel, equally inserted, lacking basal appendages, direction of dehiscence (as observed in 2 specimens): anterior pair dehiscing toward upper lip and posterior pair dehiscing toward lower lip; pollen prolate spheroidal to euprolate, 3 (–4)-colporate, 6 (–8)-pseudocolpate, pairs of pseudocolpi sometimes fused near 1 or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, exine foveolate to fossulate to verrucate to rugulate; staminodes 0. Style included in corolla tube, glabrous, stigma 2-lobed, lobes equal. Capsule stipitate, very large, glabrous. Seeds 4, homomorphic, borne on retinacula, flattened, lacking trichomes.

Spathacanthus is a genus of three species occurring in moist to wet forests in southern Mexico and Central America.

KEY TO THE SPECIES OF SPATHACANTHUS

1. Calyx at anthesis equally or subequally divided into 2 prominent segments; corolla 73–97 mm long; capsule 50–89 mm long; Costa Rica. *S. hoffmannii*.
1. Calyx at anthesis unequally divided into 2 (rarely more) prominent segments; corolla 23–70 mm long; capsule 40–62 mm long.
 2. Corolla white, 23–29 mm long, throat 5–7.5 mm in diameter, limb 5–8 mm in diameter with lobes 1–3 mm long; calyx yellow prior to fruiting; Mexico and Guatemala on the Pacific slope. *S. parviflorus*.
 2. Corolla yellow, 46–70 mm long, throat 9.5–16 mm in diameter, limb 22–45 mm in diameter with lobes (5–) 8–15 mm long; calyx green prior to fruiting; Mexico, Guatemala, and Honduras on the Gulf and Caribbean slopes. *S. hahnianus*.

Spathacanthus hahnianus Baill., Hist. pl. 10: 444. Jan–Feb 1891.—TYPE: MEXICO. Veracruz: Misanthla, forêt de la montays Santa Rita, 3 Jul 1866, L. Hahn 349 (holotype: P!); see discussion in Daniel (1995a: 130).

Macfadyena simplicifolia Donn. Sm., Bot. Gaz. (Crawfordsville) 16: 198. Jul 1891. *Spathacanthus simplicifolius* (Donn. Sm.) Lindau ex Bureau & K. Schum. in C. Martius, Fl. bras. 8(2): 294. 1897 [combination also proposed by Leonard, Proc. Biol. Soc. Wash. 50: 16. 1937]. *Spathacanthus donnell-smithii* Lindau ex Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 293. Jul 1895, nomen superfl. (new name for *M. simplicifolia* but latter cited as synonym and “specific name dropped as inappropriate”). *Spathacanthus donnell-smithianus* Lindau, Bull. Herb. Boissier 3: 371. Aug 1895, nomen superfl. (*M. simplicifolia* cited in synonymy).—TYPE: GUATEMALA. Alta Verapaz: Pansamalá, 3800 ft, Aug 1886, H. von Türckheim 1030 (holotype: US!; isotypes: GH! K! M! US!).

Ruellia macrocarpus Sessé & Moc., Fl. mexic., ed. 2. 148. 1894, non *Ruellia macrocarpa* Wall., 1830.—TYPE: not designated; see discussion in Daniel (1995a: 130).

Branched shrubs or small trees to 8 m tall, often with many stilt roots. Young stems quadrate to somewhat compressed, pubescent (especially at nodes where trichomes often form dense tufts) with flexuose to antrorsely appressed eglandular trichomes to 1 mm long, soon glabrate. Leaves petiolate, petioles to 45 mm long, blades elliptic to broadly elliptic to obovate-elliptic, (36–) 45–250 mm long, (9–) 17–143 mm wide, 1.3–3.1 (–4) times longer than wide, (rounded to acute to) acuminate at apex, acute at base, adaxial surface glabrous, abaxial surface glabrous or pubescent along major veins with flexuose to appressed eglandular trichomes to 0.5 mm long, margin glabrous. Inflorescence of terminal racemes or a basally branched panicle of racemes to 5 cm long (excluding flowers), rachis nearly glabrous or pubescent with flexuose-appressed eglandular trichomes, often enlarged in fruit; dichasia 1-flowered, sessile (sometimes becoming subsessile in fruit with peduncles to 2 mm long). Bracts triangular to subulate, 1.5–6 mm long, 1–2.3 mm wide, abaxial surface nearly glabrous or pubescent like rachis. Bracteoles triangular to subulate to linear-lanceolate, 1–6 mm long, 0.8–1.5 mm wide, abaxial surface nearly glabrous or pubescent like rachis. Flowers subsessile to pedicellate, pedicels to 7 mm long, 3–3.7 mm in diameter in fruit, glabrous. Calyx green, (18–) 22–43 mm long, 8–14 mm in diameter (measured flat), abaxially glabrous, beaked in bud with beak to 2 mm long, divided into 2 elliptic to ovate-elliptic segments with unequal incisions 16–30 mm long on 1 side and (0.5–) 3–15 mm long on the

other, longer incision 0.56–0.87 times as long as calyx (when shorter incision less than 1 mm long the calyx then appearing particularly spathe-like), 1 segment generally with 2 triangular lobes 0.4–2 mm long, other segment generally with 3 triangular lobes 0.4–4 mm long, lobes rarely longer and calyx then appearing unequally 5-lobed. Corolla yellow (white fide *Ventura 19361* from Veracruz and *Holmes 4392* from Honduras), 46–70 mm long, narrow proximal portion of tube 13–20 mm long, 2.5–4 mm in diameter, densely pubescent internally, throat 19–33 mm long, 9.5–16 mm in diameter at widest expanse, limb 22–45 mm in diameter, upper lip 12–19 mm long, lobes elliptic, (5–) 9–10.5 mm long, 4.5–8.5 mm wide, lower lip 15–18 mm long, lobes linear-elliptic to elliptic, 8–15 mm long, (3.5–) 7–8.5 (–11) mm wide. Stamens with longer pair 16–18.5 mm long and shorter pair 12–14.5 mm long, thecae 3.3–4.2 mm long; pollen subprolate to euprolate, 3-colporate, polar diameter 56–64 μm , equatorial diameter 42–43 μm , P:E = 1.31–1.51, exine foveolate to fossulate to rugulate. Style 28–35 mm long, stigma lobes 0.7 mm long. Capsule 43–62 mm long, stipe 27–34 mm long, head 25–28 mm long, retinacula 7–10 mm long. Seeds subcircular to somewhat squarish to deltate in outline, 6.3–9 mm long, 5.7–8 mm wide, 2–2.3 mm thick, surfaces with low verrucose ridges or bumps.

Illustrations. Fig. 3; Bot. Gaz. (Crawfordsville) 16: pl. 18, 1891.

Phenology. Flowering: throughout the year; fruiting: December–June.

Distribution (Fig. 4). Mexico (Chiapas, Oaxaca, Puebla, and Veracruz), Guatemala (Alta Verapaz), and Honduras (Yoro); in floodplains and along arroyos in lowland rain forests, lower montane rain forests, mesophytic montane forests, and oak forests; 100–1350 m.

This species of the Gulf slope of southern Mexico and the Caribbean slope of northern Central America was not included by Standley (1926) in his account of the ligneous flora of Mexico. Until recently, the species was known from few Mexican collections, and it is still poorly known in Central America. A nearly sterile specimen from Guatemala (mountains E of Tactic on road to Tamahú, *P. Standley 71343* at F) was annotated as this species by Leonard and cited by Gibson (1974). The condition of the specimen does not allow for its identification using my key, and I am therefore hesitant to include it. Thus, the type of *Macfadyena simplicifolia* represents the only known occurrence of this species in Guatemala. A single collection, noted as having white corollas, is also known from Honduras. White corollas were also noted on *Ventura A. 19361* from Veracruz. It remains to be verified whether notations on these two specimens accurately portray a difference in corolla color on some individuals of the species.

The racemose inflorescences of *S. hahnianus* sometimes become more or less thyrsoid in fruit by slight elongation of the region between the bracts and bracteoles (i.e., forming a peduncle).

ADDITIONAL SPECIMENS EXAMINED. **Honduras.** YORO: ca. 16 km from Yarucha [=Yaruca?] on Quebrada de Oro to Cerro Búfalo, *W. Holmes 4392* (NY, TEX). **Mexico.** CHIAPAS: Mpio. Berriozábal, 13 km N of Berriozábal near Pozo Turipache and Finca El Suspiro, *D. Breedlove & A. Smith 21618* (DS, DUKE, F, MO, NY, RSA, TEX, US, WIS), *D. Breedlove & R. Thorne 30868* (DS, ENCB, MO); Mpio. Berriozábal, a 12 km N de Berriozábal, *E. Martínez S. & M. Soto M-24241* (CAS, MEXU); Mpio. Berriozábal, La Aduana, cerca de Rancho Flor de Corazón, hacia el Cairo, *E. Palacios E. 1726* (CAS, CHIP, MEXU).—OAXACA: Mpio. San Felipe Usila, Campamento Cerro Verde, carr. para Arroyo Tambor, *J. Calzada et al. 16596* (MEXU); Mpio. Santiago Lachigüiri, Distr. Tehuantepec, Cerro de Buenavista, 2 km SO de Crucero Buenavista, 16°45'N, 95°30'W, *A. Campos V. & R. Torres 4103* (MEXU); Uxpanapa Region, between Esmeralda (17 km E of Sarabia) and Río Verde, 1.1 mi S of



FIG. 3. *Spathacanthus hahnianus* (fig. 33 from *Flora of Chiapas, Pt. 4*, used with permission). a. Habit. b. Inflorescence node. c. Flower. d. Calyx split open. e. Corolla split open showing stamens. f. Capsule. g. Seed. Scale: a, bar = 2 cm; b, bar = 3 mm; c, bar = 1 cm; d, bar = 8 mm; e, bar = 6 mm; f, bar = 1 cm; g, bar = 2.5 mm. (Based on: a, b, *Hernández G. & González L. 1855*; c-e, *Hernández G. & González L. 1777*; f, g, *Wendt et al. 3773*.) Drawn by Ellen del Valle.

Esmeralda, 17°10'N, 94°45'W, *T. Croat & D. Hannon 63303* (BM, CAS, ENCB, MO, TEX); Mpio. Sta. María Chimalapa, Arroyo Matzpac, N de Sta. María por la vereda al Río Verde, 16°58'N, 94°41'W, *H. Hernández G. & C. González L. 1777* (CAS, MEXU, MO, TEX); Mpio. Sta. María Chimalapa, Río Verde por la vereda a la cabecera, ca. 7 km N de Sta. María, 16°59'N, 94°40'W, *H. Hernández G. & C. González L. 1855* (CAS, MEXU, MO, TEX); Mpio. San Felipe Usila, Nueva

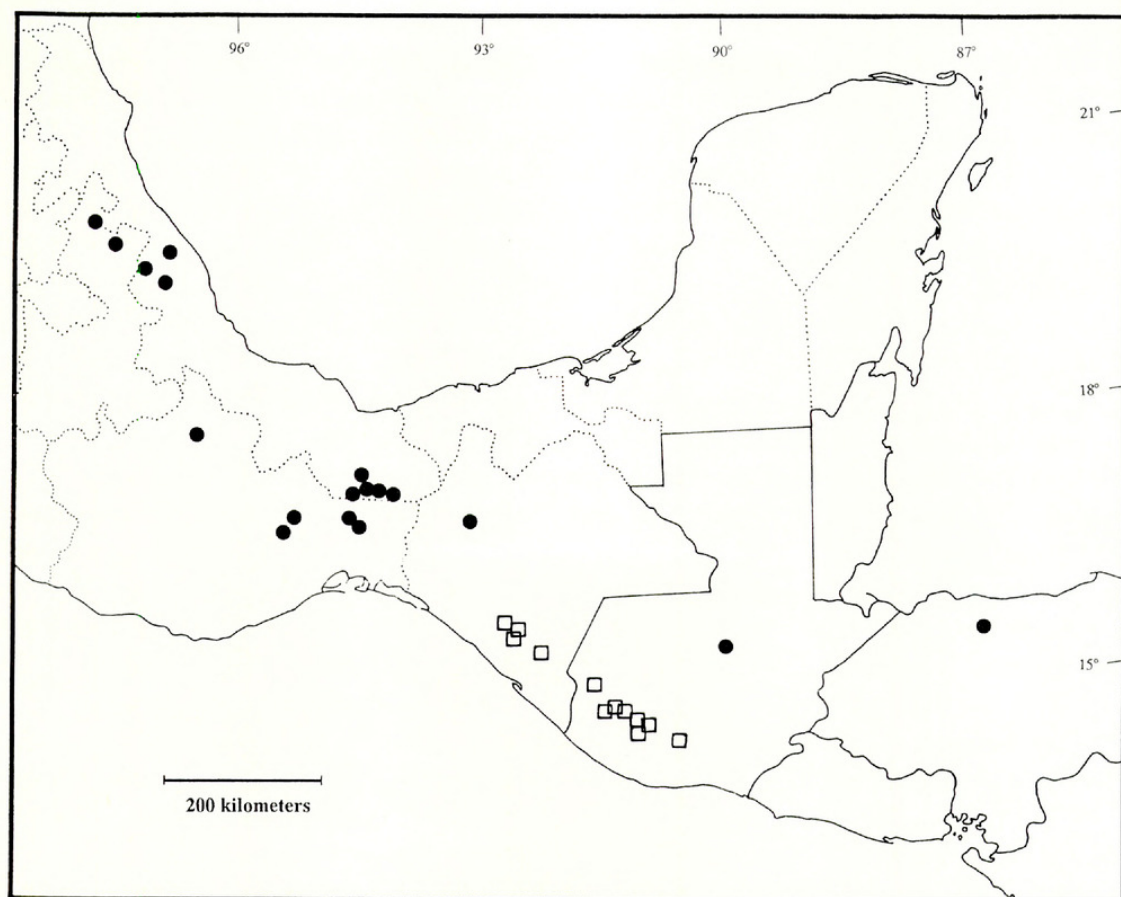


FIG. 4. Distribution of *S. hahnianus* (dots) and *S. parviflorus* (open squares).

Santa Flora, *R. de Santiago & A. María H.* 247 (MEXU); Mpio. Guevea de Humboldt, Distr. de Tehuantepec, recorrido La Cumbre–arroyo seco, 13.4 km N de Guevea de Humboldt, 16°52'N, 95°25'W, *R. Torres C. & A. Campos V.* 13897 (MEXU).—PUEBLA: Tzitzinapan, Yancuictlalpan, Cuetzalán, *F. Basurto & R. Patrón* 454 (MEXU); cerca de Atexcaco, *D. Gold* 324 (MEXU); Patla/Necaxatal, *C. Troll* 325 (M).—VERACRUZ: Colonia Melchor Ocampo, Cerro del Chiquihuite, *C. Conzatti* 4 (GH); Mpio. Hidalgotitlán, Km 4 camino Cedillo–La Escudra, 17°00'N, 94°40'W, *J. Dorantes et al.* 3766 (ENCB); Mpio. Hidalgotitlán, Km 4 del camino Hnos. Cedillo–La Hulera, *J. Dorantes et al.* 4058 (ENCB); SW de Esfuerzo Nuevo en la cascada, Minatitlán, 17°10'N, 94°21'W, *J. Rivera H. & F. Gómez* 8 (CAS); 3 km E de Río Chalchijapa por la carretera Sarabia–Cedillo, Jesús Carranza, *M. Vázquez et al.* 1584 (ENCB); Mpio. Hidalgotitlán, Río Soloxuchil, 1.5 km O del Campamento Hnos. Cedillo, 17°16'N, 94°36'W, *M. Vázquez et al.* 1611 (ENCB, MEXU); Mpio. Atzalan, La Calavera, *F. Ventura A.* 11601 (ENCB, MEXU); Mpio. San Andrés Tlalnehuayocan, *F. Ventura A.* 19361 (ENCB); Mpio. Minatitlán, Río Uxpanapa, cerca del límite con Oaxaca, 17°11'N, 94°08'W, *T. Wendt et al.* 2769 (CAS, MEXU, MO, TEX); Mpio. Hidalgotitlán, Arroyo Mazate al S de Ejido Agustín Melgar al SE de Paso de Moral, 17°13'N, 94°35'W, *T. Wendt et al.* 3773 (CAS, MEXU, MO, TEX); Mpio. Minatitlán, 4.5 km O de Uxpanapa, sobre terracería a La Laguna, 17°12'N, 94°14'W, *T. Wendt & I. Almaráz G.* 4194 (CAS, MEXU, MO, NY, TEX).—State Undetermined: without locality, *M. Sessé & J. Mociño* 302 (MA, US); *M. Sessé et al.* 2146 (F, MA, US).

Spathacanthus hoffmannii Lindau, Bull. Herb. Boissier 3: 370. 1895.—TYPE: COSTA RICA. Alajuela: prope Aguacate, Aug 1857, *C. Hoffmann* 842 (holotype: B, destroyed, photos: F! GH! US!).

Shrubs to small trees to 8 m tall, trunk (often with multiple trunks) up to 10 cm in diameter. Young stems quadrate to somewhat flattened, glabrous (or the nodes pubescent with brownish, flexuose eglandular trichomes). Leaves subsessile to petiolate, petioles to 15 mm long, blades elliptic to elliptic-obovate to obovate,

89–285 mm long, 25–109 mm wide, 1.8–5.2 times longer than wide, abruptly acuminate to apiculate at apex, acute to attenuate at base, surfaces and margin glabrous. Inflorescence a terminal raceme to 35 mm long (excluding flowers), rachis pubescent like young stems; dichasia 1-flowered, sessile. Bracts triangular to lanceolate, 2–8 mm long, 1–1.3 mm wide, abaxial surface glabrous. Bracteoles lance-subulate, 2–5 mm long, 1–1.5 mm wide, abaxial surface glabrous. Flowers pedicellate, pedicels to 9 mm long, 3.1 mm in diameter in fruit, glabrous. Calyx green, 25–40 mm long (somewhat accrescent in fruit), (8–) 10–16 mm in diameter (measured flat), abaxially glabrous, beaked in bud with a beak 0.6–1.2 mm long, equally or subequally divided into 2 ovate to elliptic to obovate-elliptic segments, incisions 11–22 (–28) mm long (rupturing further when capsules dehisce), 0.34–0.73 times as long as calyx, 1 segment apically entire, other segment apically entire or 2-lobed, lobes triangular, to 1.5 (–5) mm long. Corolla white, 73–97 mm long, narrow proximal portion of tube 18–30 mm long, 2–5 mm in, internally pubescent, throat 35–50 mm long, 9–18 mm in diameter near midpoint, limb 30–42 mm in diameter, upper lip 15–26 mm long, lobes ovate to elliptic, 10–20 mm long, 11–18 mm wide, lower lip 18–25 mm long, lobes ovate to elliptic, 15–20 mm long, 12–16 mm wide. Stamens with longer pair 24–34 mm long and shorter pair 18–28 mm long, thecae 4–6 mm long; pollen subprolate to euprolate, 3-colporate, polar diameter 65–71 μm , equatorial diameter 44–56 μm , P:E = 1.16–1.62, exine foveolate to foveolate-verrucate to subrugulate. Style 44–59 mm long, stigma lobes 0.3–0.6 mm long. Capsule 50–89 mm long, stipe 20–40 mm long, head 27–39 mm long, retinacula 7–12 mm long. Seeds somewhat irregularly shaped to subcordate to subelliptic in outline, 7.5–13 mm long, 7.5–11 mm wide, 3–5 mm thick, surface with shallow subconcentric ridges (especially toward margin).

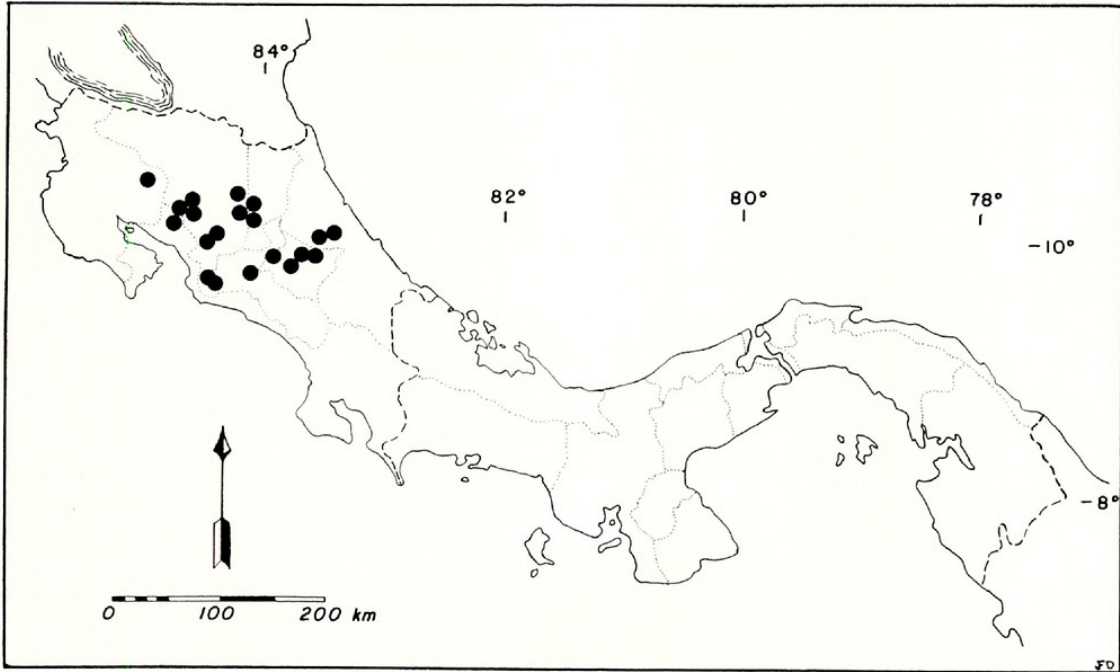
Illustration. Fieldiana, Bot. (n.s.) 18: 19, fig. 17, 1986.

Phenology. Flowering: January–March and May–October; fruiting: December–March, and May–September.

Distribution (Fig. 5). Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, and San José); along streams in regions of humid forests, rain forests, and cloud forests on both the Caribbean and Pacific escarpments; 80–1700 m.

Based on the cladistic analysis *Spathacanthus hoffmannii* is more closely related to *S. hahnianus* than to *S. parviflorus*. The former two species both have long corollas with the lower lip terminating in relatively long lobes. Like *S. parviflorus*, however, *S. hoffmannii* has white corollas.

ADDITIONAL SPECIMENS EXAMINED. **COSTA RICA.** ALAJUELA: Est. Biol. Reserva Forestal de San Ramón, valley of Río Lorencito, 10°13'N, 84°37'W, W. Burger et al. 12439 (F); Bajos de Jamaical, Reserva de San Ramón, I. Chacón 1768 (CR, DUKE); Buena Vista, San Carlos, D. Cox 5 (DUKE); Finca Los Ensayos ca. 11 mi NW of Zarcero, T. Croat 43516 (MO); San José de Naranjo, I. García 1 (CR, F); Río San Lorencito, límite E de la Reserva Forestal de San Ramón, J. Gómez-Laurito 10263 (CR, F); Est. Biol. Res. Forestal de San Ramón, valley of Río Lorencito on Caribbean slope, 10°13'N, 84°37'W, J. Gómez-Laurito & K. Swangel 12439 (CR); Reserva Forestal de San Ramón, Río San Lorencito, 10°14'13"N, 84°36'22"W, G. Herrera Ch. 362 (CAS, MEXU, US); Buena Vista de San Carlos, L. Holdridge 6790 (CR); Quebrada Lajas, Finca Los Ensayos, Buena Vista de San Carlos, A. Jiménez M. 2319 (BM, CR, F, MO, NY); near road to Laguna Hule, 10°17'N, 84°12'W, R. Lent 3243 (CR, F, MO); along Río Sarapiquí, 1 mi S of Cariblanco, R. Primack & D. Stone 44 (DUKE); Cordillera de Tilarán, Río La Balsa, 10°15'N, 84°31'W, V. Ramírez & Q. Jiménez 273 (NY); rd to Colonia Virgen del Socorro, barranca of Río Sarapiquí, 10°15'N, 84°10'W, W. Stevens 13547 (DUKE, F, MEXU).—CARTAGO: above La Suiza, ca. 0.5 mi behind town, S of Turrialba, G. De Wolf 307 (K, NY); carretera entre Turrialba y Siquirres, a la vera del Río Chitaría, J. Gómez-Laurito 6801 (CR, USJ); along Río Chitaría, R. Lent 1414 (F, US); Cerros de La Carpintera, 9°53'N, 83°59'W, R. Lent

FIG. 5. Distribution of *S. hoffmannii*.

3657 (CR, F, MO); 13 km E of Turrialba on hwy to Limón, canyon of Río Chitaría, 9°55'N, 83°36'W, R. Liesner *et al.* 15444 (CR, DUKE, MEXU, WIS); ca. 10 mi from Turrialba along road to Siquirres, L. McDade 233 (DUKE); above Turrialta Restaurant, 36.5 km from Turrialba, R. Read & G. Daniels 74-63 (US); vicinity of Pejivalle, P. Standley & J. Valerio 46759 (F, US); forêts de Las Vueltas, Tucurrique, A. Tonduz 12943 (BM, GH, K, M, US, W); Río Chitaría, 9.5 mi E of Turrialba, 9°55'N, 83°36'W, G. Webster 22253 (DAV, DUKE, F, MEXU).—GUANACASTE: El Silencio, near Tilarán, P. Standley & J. Valerio 44745 (F, US).—HEREDIA: Virgen del Socorro, Río Sarapiquí, Cariblanco, I. Chacón & G. Herrera 1211 (CAS, CR, DUKE); barranca del Río Sarapiquí, Colonia Virgen del Socorro, J. Gómez-Laurito 9868 (CR, F); canyon of Río Sarapiquí, just upstream from bridge on rd to La Virgen del Socorro, B. Hammel 13304 (CR, DUKE, F, MO); camino a la Colonia de la Virgen del Socorro, rumbo a Pto. Viejo, L. Poveda 985 (CR, USJ); Vara Blanca de Sarapiquí, N slope of Central Cordillera, A. Skutch 3325 (A, K, MO, NY, US); above Río Sarapiquí near crossing of road to La Virgen de Socorro, D. Smith *et al.* 1181 (DUKE).—LIMÓN: La Florida, voie ferrée atlantique, H. Pittier 11286 (US); Río Hondo, H. Pittier 16641 (K).—PUNTARENAS: Quebrada Seca, Cerro Zapotal, Miramar, L. Gómez *et al.* 23990 (CAS, CR, DUKE).—SAN JOSÉ: Nordhänge der Cerros de Escazú, Wege kurz südlich oberhalb Matinilla (Verlängerung der Strasse 126 Santa Ana-Salitril-Matinilla), P. Döbbeler s.n. (USJ); Zona Protectora La Cangreja, Santa Rosa de Puriscal, Q. Jiménez M. 482 (CR, K); Zona Protectora Cerro Turrubares, 9°49'10"N, 84°29'10"W, Q. Jiménez M. 543 (CR); ca. 5 mi. past Santiago on CR 239 towards Parrita, L. McDade 249 (DUKE); Tiquires, M. Valerio 1685 (F). Province undetermined: El Rosario de Orosí, H. Pittier 16631 (K, P, US, W).

Spathacanthus parviflorus Leonard, Proc. Biol. Soc. Wash. 50: 15. 1937.—TYPE: GUATEMALA. Quezaltenango: Volcán Zunil, 7 Aug 1934, A. Skutch 961 (holotype: US!; isotypes: A! BM! L! NY! US!).

Branched shrubs or small trees to 7.6 m tall. Young stems subquadrate to somewhat compressed, internodes glabrous or sparsely bifariously pubescent with antrorsely appressed eglandular trichomes 0.2–0.5 mm long, nodes usually with a few stiff, straight to flexuose eglandular trichomes to 0.5 mm long. Leaves petiolate, petioles to 45 mm long, blades ovate-elliptic to elliptic to obovate-elliptic, 18–205 mm long, 11–100 mm wide, 1.6–3.7 times longer than wide, (rounded to) acute to acuminate (often abruptly

so) to subfalcate at apex, acute at base, surfaces and margin glabrous (or with antrorse eglandular trichomes along major veins on abaxial surface). Inflorescence usually of terminal racemes or thyrses to 12 cm long (excluding flowers), sometimes with racemes or pedunculate dichasia in axils of distalmost pair of leaves as well (see discussion), rachis glabrous or bifariously pubescent with antrorse to antrorse-appressed eglandular trichomes 0.2–0.3 mm long; dichasia 1-flowered (except for those sometimes borne in axils of distalmost leaves, which are often 3-flowered), sessile or pedunculate, peduncles to 18 mm long, glabrous. Bracts triangular to subulate, 1.3–6 mm long, 0.8–1.4 mm wide, abaxial surface glabrous or with antrorsely appressed eglandular trichomes (especially along midvein), proximalmost pair often subfoliose and larger. Bracteoles and secondary bracteoles triangular to subulate to linear, 1–2.7 (–4) mm long, 0.6–1 mm wide, abaxial surface glabrous or pubescent like bracts. Flowers pedicellate, pedicels to 13 mm long, 1–2.5 mm in diameter in fruit, glabrous. Calyx greenish yellow to pale yellow prior to fruiting (becoming green as fruit matures), 15–26 (–31) mm long, 6.5–11 mm in diameter (measured flat), abaxially glabrous, beaked in bud with a beak 1–3.5 mm long, divided into 2 lance-ovate to ovate segments with unequal incisions of 7–17 (–20) mm on 1 side and 1–6 (–16) mm on the other, longer incision 0.45–0.89 times as long as calyx, 1 segment apically (entire to) 2-lobed, lobes triangular, 0.3–0.7 mm long, other segment apically (entire to) 3-lobed, lobes triangular, 0.6–0.8 mm long. Corolla white, 23–29 mm long, narrow proximal portion of tube 7–14 mm long, 1.8–4 mm in diameter, densely pubescent internally with coarse eglandular trichomes, throat 12–18 mm long, 5–7.5 mm in diameter at widest expanse, limb 5–8 mm in diameter, upper lip 2–3 mm long, lobes rounded, 1.5–3 mm long, 1.5–2 mm wide, lower lip 2.5–3.5 mm long, lobes rounded, 1–3 mm long, 1.5–2.5 mm wide. Stamens with longer pair 11–15 mm long and shorter pair 8–12 mm long, thecae 3–4.5 mm long; pollen prolate spheroidal to euprolate, 3–4-colporate, polar diameter 39–51 μm , equatorial diameter 28–43 μm , P:E = 1.14–1.40, exine foveolate to fossulate to verrucate to rugulate. Style 10–17 mm long, stigma lobes 0.4–0.9 mm long. Capsule 40–54 mm long, stipe 20–25 mm long, head 17–25 mm long, retinacula 5–7 mm long. Seeds subcircular to $\pm$ squarish in outline, 7–10 mm long, 6.5–8 mm wide, 2.7 mm thick, surface with low verrucose ridges or bumps or becoming smooth.

Illustration. Fieldiana, Bot. 24(10): 446, fig. 101, 1974.

Phenology. Flowering: throughout the year; fruiting: September–February.

Distribution (Fig. 4). Mexico (Chiapas) and Guatemala (Chimaltenango, Quezaltenango, San Marcos, Sololá, and Suchitepéquez); plants occur along streams, on slopes, and on ridges in rain forests and cloud forests; 730–2030 m.

Local names. “Huesco de pollo” (Heath & Long MA84); “aritas de montaña” (Steyermark 33507); “violeta de montaña” (White 5419).

This species is restricted to the Pacific escarpment in southern Mexico (Sierra Madre de Chiapas) and Guatemala (along the volcanic axis). The above description has been augmented with data from many more collections than were studied by Daniel (1995a).

The inflorescence of *Spathacanthus parviflorus* is commonly a terminal raceme (i.e., dichasia sessile and flowers pedicellate). Sometimes racemes arise from the axils of the distalmost pair of leaves resulting in what appears as a basally branched panicle of racemes. Other times, pedunculate dichasia arise from one or both axils of the distalmost pair of leaves. In some specimens (e.g., Steyermark 46632) the inflorescence is a thyrses (i.e., dichasia pedunculate more or less throughout the inflorescence).

In addition to the distinctions noted above in the key to species, *S. parviflorus* further differs from other species of the genus by its smaller pollen, which has a tendency to be 4-aperturate (see discussion above).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Jaltenango, Reserva del Triunfo, Cañada del Pavón al NO del Triunfo, *J. Calzada et al.* 8738 (NY, UC); Mpio. Jaltenango, camino del Triunfo para La Finca Prusia, *J. Calzada et al.* 8935 (CIES); El Triunfo Biosphere Reserve, vicinity of Deslave along trail from El Pavál to Camp. El Triunfo, ca. 15°38'N, 92°50'W, *T. Daniel et al.* 8403 (CAS, CIES, ENCB, K, MEXU, MICH, MO, NY, US); Mpio. Jaltenango, El Triunfo Reserve, 1–3 km from El Triunfo camp toward Palo Gordo camp, 15°39'N, 92°50'W, *R. Hampshire et al.* 522 (BM, MEXU); Mpio. Jaltenango/Mapastepec, Reserva el Triunfo, near campamento El Triunfo, 15°39'N, 92°48'W, *M. Heath & A. Long* MA84 (BM, CHIP); Mpio. Jaltenango, Reserva El Triunfo, campamento/HQ–Finca Prussia, 15°39'N, 92°48'W, *M. Heath & A. Long* 491 (CHIP, MEXU); Mpio. La Concordia, camino entre Finca Custepec and San Antonio Miramar (pass), 15°42'N, 92°59'W, *M. Heath & A. Long* 834 (CHIP); Mpio. Jaltenango, Reserva El Triunfo, Palo Gordo–Finca Catarrinas, 15°39'N, 92°48'W, *M. Heath et al.* 738 (CHIP); Mt. Paxtal (“Pasitar”), *E. Matuda* 1696 (A, F, GH, LL, MEXU, MICH, MO, NY, US); Mpio. Jaltenango, Reserva de la Biosfera El Triunfo, 15°39'28"N, 92°49'27"W, *N. Ramírez-Marcial & P. Quintana-Ascencio* 507 (CAS, CIES, MEXU); between Cañada Honda and El Triunfo, s slopes of Sierra de Soconusco, *E. Xolocotzi & A. Sharp* 338 (DS, MEXU). **Guatemala.** CHIMALTENANGO: SW slope of Volcán Fuego above Finca Montevideo, *J. Steyermark* 52100 (F, US).—QUEZALTENANGO: Pacific escarpment, 3 km S of Santa María Planta Eléctrica on Hwy 9S, 14°40'N, 91°30'W, *K. Roe et al.* 715 (BM, US, WIS); Volcán Zunil, *A. Skutch* 961 (BM, F); Colomba, *A. Skutch* 1290 (A); along Quebrada San Gerónimo, Finca Pirineos, lower S-facing slopes of Volcán Sta. María, between Sta. María de Jesús and Calahuaché, *J. Steyermark* 33359 (F); lower S-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuache, *J. Steyermark* 33507 (F).—SAN MARCOS: La Trinidad, ca. 2 km from Finca Armenia above San Rafael, *T. Croat* 40846 (CAS, MO); Finca Armenia, Rafael de Cuesta, *J. Dwyer* 14412 (CAS); Finca Armenia, San Rafael pie de la cuesta to Carrizal, past Finca Africa, *J. Dwyer* 15340 (LL, MO); Volcán Tajumulco, above Finca Porvenir on “Todos Santos Chiquitos,” *J. Steyermark* 37204 (F); Finca El Porvenir, *S. White* 5419 (MICH).—SOLOLÁ: Finca Mocá, Guatalón, S slope of Volcán Atitlán, *W. Hatch & C. Wilson* 342 (F); Presa Forest, Finca Mocá Guatalón, S slope of Volcán Atitlán, *W. Hatch & C. Wilson* s.n. (F); S-facing slope of Volcán Atitlán above Finca Mocá, *J. Steyermark* 47897 (US).—SUCHITEPÉQUEZ: Mpio. Sta. Bárbara, Finca Sta. Adelaida, *K. Lind* 69 (F); Volcán Sta. Clara, between Finca El Naranjo and upper slopes, *J. Steyermark* 46632 (CAS, F, NY, US).—Department undetermined: Inter Sta. Lucia et S. Miguelito, *Bernoulli & Cario* 2255 (K).

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