

**STENOSTEPHANUS PURPUREUS (ACANTHACEAE: JUSTICIEAE:
ISOGLOSSINAE), A NEW SPECIES FROM COSTA RICA
AND PANAMA—OVERLOOKED FOR MORE THAN 150 YEARS**

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Abstract. Comparative studies of macromorphological and palynological characters of plants representing *Stenostephanus silvaticus* from southern Mexico and southern Central America reveal that those from the two geographically isolated regions represent different taxa. *Stenostephanus purpureus* is described as a new species from Costa Rica and Panama. It differs from *S. silvaticus* of Chiapas, Oaxaca, Tabasco, and Veracruz, Mexico by numerous characters, including: pyramidal inflorescences with rachises, dichasial peduncles, and floral pedicels glabrous; corollas blue-purple to purple with both lips recoiled; and pollen subspheroidal with a fossulate interapertural band of exine bearing a medial row of gemmae and baculae. We provide a description of *S. purpureus* and a key to, images of, and map showing the distributions of both species.

Keywords: *Stenostephanus silvaticus*, pollen, nototriby/sternotriby/pleurotriby

Resumen. Los estudios comparativos de caracteres macromorfológicos y palinológicos de plantas que representan a *Stenostephanus silvaticus* del sur de México y el sur de Centroamérica revelan que las de las dos regiones geográficamente aisladas representan taxones diferentes. *Stenostephanus purpureus* se describe como una especie nueva de Costa Rica y Panamá. Se diferencia de *S. silvaticus* de Chiapas, Oaxaca, Tabasco y Veracruz, México por numerosos caracteres, entre ellos: inflorescencias piramidales con raquis, pedúnculos bicaisales y pedicelos florales glabros; corolas azul-púrpura a púrpura con ambos labios retraídos; y polen subsferoidal con una banda interapertural fosulada de exina que lleva una fila medial de yemas y báculas. Proporcionamos una descripción de *S. purpureus* y una clave, imágenes y un mapa que muestra las distribuciones de ambas especies.

Palabras claves: *Stenostephanus silvaticus*, pollen, nototriby/sternotriby/pleurotriby

Stenostephanus Nees is a tropical American genus with some 90 currently accepted species (POWO, 2023) of perennial herbs and shrubs occurring from east-central Mexico (San Luis Potosí, ca. 21°31'N) to southeastern Brazil (São Paulo, ca. 23°47'S). Most species occur in moist to wet montane forests at relatively high elevations (usually above 1000 meters; e.g., cloud forests), with the highest concentration of species in the Andes Mountains of South America (Venezuela to Bolivia). Fifteen species occur in Mexico (Daniel, 1999) and 18 species are currently known from Central America (Daniel, 2005, 2010; Durkee, 1978; Hammel, 2020), three of which also occur in Mexico. These include taxa previously treated under several generic names, including: *Habracanthus* Nees, *Hansteinia* Oerst., *Kalbreyerella* Lindau, and *Razisea* Oerst. (Manzitto-Tripp et al., 2022). Costa Rican and Panamanian plants resembling *S. silvaticus* (Nees) T.F. Daniel of southern Mexico have been treated as pertaining to that species since 1855 (Oersted, 1855). Our studies comparing plants treated as *S. silvaticus* from these two regions reveal significant macro- and micromorphological differences indicating that they should be recognized as distinct species.

Much of the taxonomic history of *Stenostephanus* and related Neotropical genera was discussed by Wood (1988) and Daniel (1999). Based on morphology and preliminary molecular phylogenetic analyses (Kiel et al., 2006),

all Isoglossinae in the New World are now treated in *Stenostephanus* (except for the poorly known unispecific Brazilian *Sebastiano-Schaueria* Nees). Its closest relative appears to be the African/Malagasy genus *Brachystephanus* Nees (22 species, including *Oreacanthus* Benth.; Champluvier and Darbyshire, 2009). The combination of the following morphological characteristics distinguishes *Stenostephanus* from other Acanthaceae in the New World: corollas with ascending-cochlear aestivation, an androecium of two stamens and no staminodes, monothealous anthers, and biporate pollen with the ectoapertures greatly enlarged. Species of the genus exhibit corollas with diverse colors and shapes.

Nees (1847) described *Habracanthus silvaticus* based on two collections from southern Mexico in Hooker's herbarium at K: *Linden 181* from Chiapas and *Jurgensen 902* from Oaxaca. Oersted (1855) cited these collections in his account of *H. silvaticus* (as "sylvaticus"), and also indicated that he found the species in the dense forests at Turrialba on the eastern slope of Costa Rica with flowers in May. Subsequent floristic accounts have treated plants from Costa Rica (and Panama) as conspecific with those in Mexico (e.g., Lindau, 1900; Leonard, 1938; Gibson, 1974; Durkee, 1978, 1986; Daniel, 1995; Hammel, 2020). No collections of the species have been located between southern Mexico and Costa Rica, providing a gap of ca.

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1045 km between the nearest known locales for plants from the two regions (i.e., *Martínez S. 18041* in northeastern Chiapas and *Bello 2058* in west-central Alajuela). Plants from both regions share several taxonomically significant characteristics, such as: inflorescences consisting of open thyrses; corollas externally glabrous, with \pm cylindrical tubes up to 11 (to 16) mm long and one to two mm in diameter, and with the upper lip recurved to recoiled; stamens that do not dehisce toward the lower lip (i.e., flowers not nototribic); and glabrous capsules.

The advent of online color images of plants (e.g., iNaturalist, naturalista) often provides opportunities to

observe characteristics of living plants that are not readily apparent on herbarium specimens (e.g., colors and shapes). Indeed, images of plants identified as *S. silvaticus* from the two isolated regions revealed differences in colors of the inflorescence axes and corollas and in shapes of the corolla limb that were not always apparent on herbarium specimens studied. Reexamination of herbarium specimens of plants from both regions revealed additional differences. Altogether, the numerous distinctions coupled with the geographic distributions of plants previously treated as *S. silvaticus* strongly suggest that they do not represent the same taxon.

MATERIALS AND METHODS

Specimens were studied from the following herbaria: A, C, CAS, CR, DS, F, GH, LSU, MEXU, MO, NY, US. Specimens indicated as “image” were studied only via digital images from herbarium websites or data portals (e.g., SEINet, 2023). Pollen was studied as described by Daniel (1998), and imaged in the Scanning Electron Microscopy Laboratory at the California Academy of Sciences. Palynological terminology follows Walker and Doyle (1975) with some adjustments (e.g., pollen shapes) from Hesse et

al. (2009). Pollen was sampled from two collections of *S. purpureus* (*Solomon 19167*, CAS; *Burger & Visconti 10218*, CAS) and three collections of *S. silvaticus* (*Breedlove & Bartholomew 66948*, CAS; *Mexia 9273*, CAS; *Zuill 772*, DS). A provisional conservation assessment for *S. purpureus* is proposed based on IUCN (2022) guidelines, using herbarium specimen data and historical imagery (Google Earth Pro, 2023); extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCat (2023).

TAXONOMY

Stenostephanus purpureus T.F. Daniel & Kriebel, *sp. nov.*
 TYPE: COSTA RICA. Limón: Reserva Biol. Hitoy Cerere, cuenca superior del Río Hitoy, subiendo a Cerro Bitarkara, 09°38'25"N, 083°07'20"W, 27 February 1989 (fl, fr), *G. Herrera & M. Solís 2476* (Holotype: US [3213915]; Isotypes: CR, image [fl], CR, image [fr], F, MEXU, MO). Fig. 1.

Perennial herbs or shrubs to 2 m tall, erect to diffuse (or creeping), young stems subquadrate to quadrate-sulcate, bifariously pubescent (sometimes \pm inconspicuously so or only partially along distal portion of internodes, and sometimes only on one side; i.e., unifarious) with mostly retrorse to retrorsely appressed eglandular trichomes 0.05–0.30 mm long, internodes often soon glabrate. *Leaves* petiolate, petioles to 48 mm long, adaxially \pm u-shaped, pubescent (at least along margins) with antrorse to antrorsely appressed eglandular trichomes to 0.5 mm long, abaxially glabrous, blades ovate-elliptic to elliptic, 40–162 mm long, 14–68 mm wide, 2.0–3.7 \times longer than wide (the pair at a node sometimes anisophyllous), acuminate to caudate at apex, (rounded to) acute at base, adaxially glabrous except for retrorsely appressed eglandular trichomes along midvein, abaxially glabrous, margin \pm inconspicuously ciliolate with antrorse to antrorsely appressed eglandular trichomes to 0.1 mm long. *Inflorescences* of terminal, pedunculate, open, \pm pyramidally shaped (triangular when pressed), panicle-like thyrses 50–150 mm long (including peduncle and excluding flowers/fruits) and 30–70 mm wide (excluding flowers/fruits), peduncles to 28 mm long, pubescent like young stems, rachis often whitish or bluish, glabrous; dichasia opposite, pedunculate, (3–) 5–15 (or more)-flowered, dichasial peduncles 5–18 mm long, glabrous. *Bracts* subtending dichasia at base of inflorescence sometimes subfoliose, lance-ovate to lanceolate, 5–8 mm long, 0.7–

1.5 mm wide, pubescent like leaves, bracts distal to base of inflorescence subulate to lanceolate-linear, 1.5–3.5 mm long, 0.2–0.4 mm wide, abaxially and marginally glabrous. *Bracteoles* subulate to lanceolate-linear, 0.8–2.0 mm long, 0.2–0.4 mm wide, abaxially and marginally glabrous, secondary bracteoles similar to bracteoles or smaller. *Flowers* pedicellate, pedicels 1.5–2.5 mm long, glabrous. *Calyces* deeply 5-lobed, 3.5–6.5 (–8.0) mm long, lobes subequal, subulate to lanceolate-linear, 3.0–5.8 (–7.0) mm long, 0.4–0.8 mm wide, abaxially and marginally glabrous. *Corollas* pale blue-purple to purple (at least internally), (11–) 14–25 (–35) mm long, externally glabrous, tube cylindrical to subcylindrical, (5–) 7–11 (–16) mm long, 0.7–1.5 mm in diameter, limb (5–) 7–8 (–19) mm long, lips recoiled with lower lip usually more tightly so than upper lip, upper lip slender, 1.0–1.7 mm wide at base, tapered distally, lower lip \pm strap-shaped, 2.0–3.5 mm wide. *Stamens* (5.0–) 8.5–20 (–30) mm long, exerted beyond recoiled lips of corolla, filaments glabrous, sometimes spreading laterally away from central floral axis, anthers dehiscing toward upper lip (i.e., flowers sternotribic), thecae blue-purple, (1.3–) 1.9–2.5 mm long. Pollen 2-porate, subspheroidal (longer equatorial diameter [E]:shorter E = 1.02–1.08), apertural face circular in outline, 35–40 μ m in diameter, interapertural face circular in outline, 34–36 μ m in diameter, peripheral band continuous, 8 μ m wide, fossulate (with foveolae also present) and with a medial row of gemmae and baculae 1.6–3.2 μ m high, ectoaperture 31–34 μ m in diameter, with gemmae and baculae 0.7–1.9 mm high. *Styles* (9–) 15–20 (–39) mm long, glabrous; stigma subcapitate to minutely bilobed, 0.1 mm long. *Capsules* 12–17 mm long, externally glabrous, stipe 5–9 mm long, head ellipsoid with medial constriction (hourglass-shaped), 6.5–9.0 mm long. *Seeds* up to 4, 2.3–3.0 mm long, 1.7–2.1 mm wide, immature surfaces

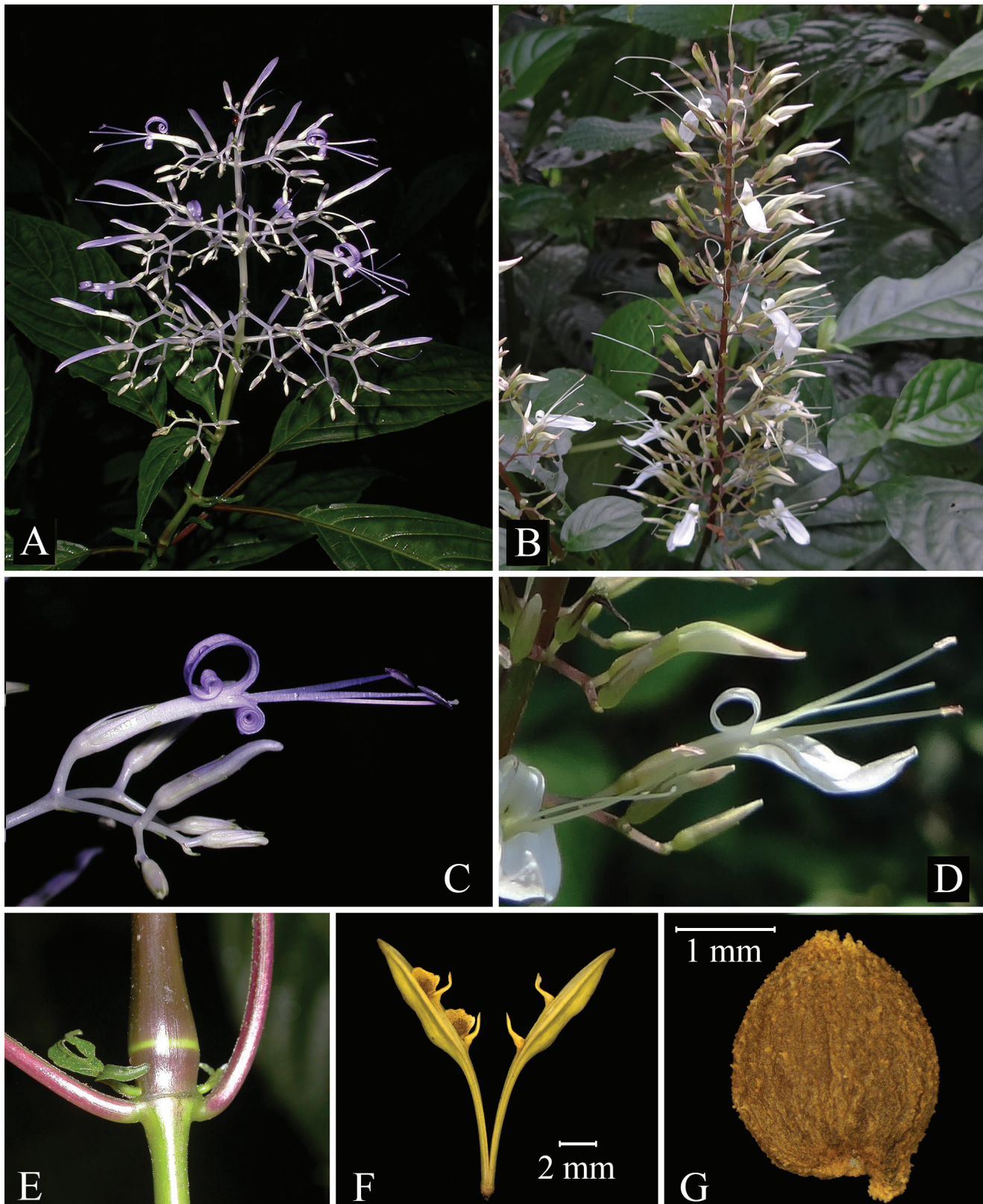


FIGURE 1. *Stenostephanus purpureus* (A, C, E–G) and *S. silvaticus* (B, D). A, inflorescence; B, cylindric inflorescence; C, flower and bud; D, flower and bud; E, vegetative node; F, capsule; G, seed. A, C, and E photos by M. Bonifacino from Costa Rica, used with permission; B and D photos by C. Davidson (Flora of the World website) of Martínez-Meléndez 3022 from Chiapas, used with permission; F from Taylor & Skotak 4841 (MO); G from Burger & Visconti 10218 (MO).

covered with \pm barbed and conical tubercles, mature surfaces smooth to slightly rugose with tubercles (if present) few and mostly restricted to margin.

Phenology: Flowering and fruiting throughout the year.

Distribution and habitats: Costa Rica (five provinces) and Panama (one province), primarily (or exclusively?) on the Caribbean escarpments of the Cordillera de Tilarán, Cordillera Central, and Cordillera de Talamanca (Fig. 2). Plants occur in low, damp sites; on slopes; and along watercourses, trails, and roads in tropical moist forests, semi-evergreen forests, evergreen premontane forests, wet montane forests, and cloud forests at elevations from (280–) 400–1800 (–2200) meters.

Illustrations: Ann. Missouri Bot. Gard. 65: 202, fig. 12. 1978; Fieldiana, Bot. (n.s.) 18: 8, fig. 6. 1986.

Local name: “Pavoncillo azul” (*Brenes 4938*).

Conservation: *Stenostephanus purpureus* has an extent of occurrence (EOO) of 7568 km² and an area of occupancy (AOO; cell width of 2 km) of 152 km². The geographic range of the species from northwest to southeast covers a distance of ca. 260 kilometers. At least 21 of the localities

from which collections were made lie within an international park, two national parks, and/or seven biological or forest reserves. Most of the numerous collections of this species are from undisturbed montane regions or reserves that show little or no change in vegetation cover during the past 50 years based on historical imagery (Google Earth Pro, 2023). Where plants occur they are sometimes noted to be locally common or abundant. While threats or potential threats to some populations of the species undoubtedly occur, none have been identified. Thus, despite both the EOO and AOO each suggesting a possible threatened category dependent on other criteria, we provisionally propose a conservation status of least concern (LC) for *S. purpureus*.

Discussion: *Stenostephanus purpureus* can be distinguished from other species of the genus in Costa Rica and Panama by its inflorescences of terminal, \pm pyramidal, and panicle-like thyrses bearing blue-purple to purple corollas with recoiled lips at maturity. Significant macromorphological and palynological differences between *Stenostephanus purpureus* and *S. silvaticus* are summarized in the following key:

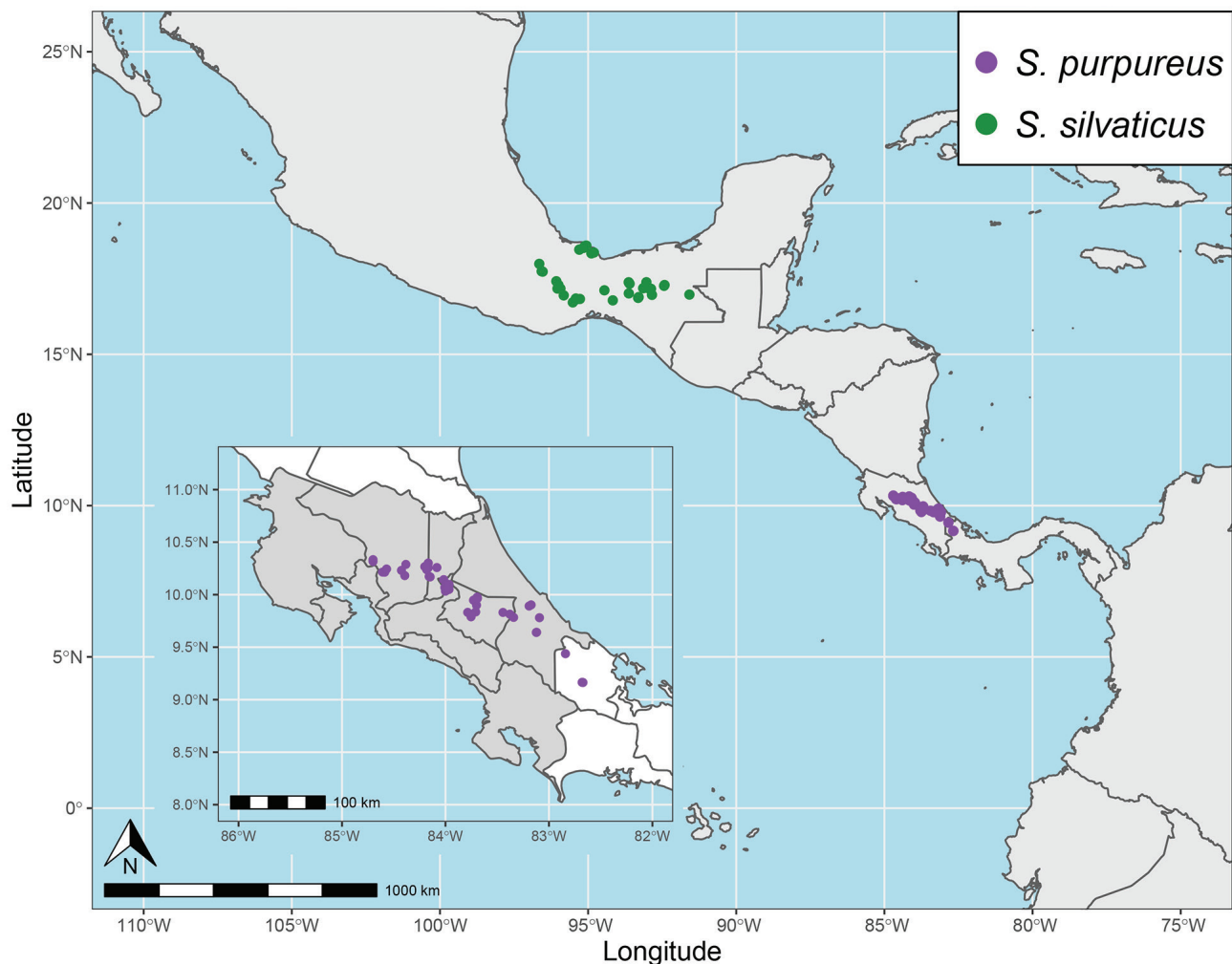


FIGURE 2. Map of Middle America showing distributions of *Stenostephanus purpureus* and *S. silvaticus*. Inset shows detailed distribution of *S. purpureus* in Costa Rica and adjacent western Panama.

- 1a. Cauline trichomes mostly retrorse to retrorsely appressed; abaxial surface of petioles glabrous; inflorescence usually \pm pyramidal (broadly triangular when flattened), 30–70 mm wide (excluding flowers and fruits), rachis, peduncles of dichasia, and pedicels of flowers glabrous and often white or purplish; corolla (at least internally) pale blue-purple to purple, upper and lower lips recoiled at maturity (lower lip more tightly so), lower lip 2–3 mm wide; anther thecae pale blue-purple to purple; pollen subspheroidal, interapertural face circular in outline, 34–36 μm across at equator, peripheral band of exine fossulate (with foveolae also present) and with a medial row of gemmae and baculae 1.6–3.2 μm high, ectoaperture 31–34 mm in diameter, covered with gemmae and baculae 0.7–1.9 μm high; Costa Rica and Panama *S. purpureus*
- 1b. Cauline trichomes mostly antrorse to antrorsely appressed; abaxial surface of petioles pubescent; inflorescence \pm cylindrical (oblong to lanceolate when flattened), 20–45 mm wide (excluding flowers and fruits), rachis, peduncles of dichasia, and pedicels of flowers pubescent, neither white nor purplish; corolla white (sometimes with pinkish markings or discoloration) internally, only upper lip recoiled at maturity, lower lip 3.0–5.5 mm wide; anther thecae pink; pollen discoid, interapertural face elliptical in outline, 10–17 μm across at equator, peripheral band of exine psilate to foveolate (with gemmae 0.4–0.6 μm high only at junction with ectoaperture on each apertural face), ectoaperture 14–22 μm in diameter, covered with gemmae 0.2–0.7 μm high; Mexico *S. silvaticus*

Flowers of *Stenostephanus purpureus* show a considerable range in size (by collection rather than on inflorescences). Corollas are usually 14 to 25 mm in length. Larger corollas, up to 35 mm long, were observed on several collections from both Costa Rica (e.g., Hammel et al. 17680, MO) and Panama (Monro et al. 6140, MO). These and other collections (including the type) also show atypically long stamens (to 30 mm) and styles (to 39 mm). At the other extreme, corollas 11 mm long, accompanied by atypically shorter stamens and styles were noted among other collections (e.g., Brenes 3706, NY). Collector's notes for *S. purpureus* indicate some variation in corolla color; in addition to purple, they include: "pale blue," "blue," "lavender-blue," "pastel violet," "pale violet," "violet-blue," "celeste," "celeste, parte central azul," "violeta," "pale purple," "morada," "lila," "white with lilac lobes," and "white." Buds, including the calyx, have been described as "green" or "white." White flowers were generally noted on specimens with only flower buds present. Thus, the internal surface of corollas is presumed always to be some shade of purple. Other parts of the inflorescence (e.g., rachis, bracts, dichasial peduncles, bracteoles, pedicels, calyces, and staminal filaments) are also sometimes noted to be white, blue-purple, or purple (Fig. 1A). By contrast, portions of the inflorescence in *S. silvaticus* were sometimes noted or observed to be greenish or pinkish to pink-red (Fig. 1C).

The differences in pollen shape and ornamentation between *S. purpureus* and *S. silvaticus* are substantial (Fig. 3). Pollen resembling each occurs elsewhere among Mexican and Central American species of the genus. Pollen of *S. azureus* (D.N. Gibson) T.F. Daniel, *S. gracilis* (Oerst.) T.F. Daniel, *S. latilabris* (D.N. Gibson) T.F. Daniel, *S. leiorhachis* (Lindau) Hammel, *S. madrensis* T.F. Daniel, and *S. purpusii* (Brandegge) T.F. Daniel (e.g., Daniel, 1999: fig. 1e, 2a, i; Daniel, 2010: fig. 9q, r) greatly resembles that of *S. purpureus*, whereas pollen of *S. monolophus* (Donn. Sm.) T.F. Daniel and *S. oaxacanus* T.F. Daniel (Daniel, 1999: fig. 2b–e) is nearly identical to that of *S. silvaticus*. Pollen of *S. chiapensis* T.F. Daniel and *S. guerrerensis* T.F. Daniel (Daniel, 1999: fig. 1c, f, g) appears to differ from that of *S. silvaticus* only by the sculpturing of the peripheral band of exine (verrucate in the former and shallowly fossulate in the latter vs. psilate to foveolate in *S. silvaticus*).

A flowering collection from Veraguas, Panama (vicinity of Santa Fé, slopes of Cerro Tute, [08.482220, -81.0981], P. Allen 4345, MO, US), was identified by E. C. Leonard,

treated by Durkee (1978), and annotated by T. F. Daniel as *S. silvaticus*. It has the blue-purple corollas, subspheroidal pollen, and other characteristics of *S. purpureus*, but differs from that species in several features, including cauline pubescence antrorse to antrorsely appressed; abaxial surface of the petioles sparsely pubescent; inflorescence rachis, peduncles, and pedicels pubescent; and anther thecae 2.5–3.0 mm long. This collection was made ca. 190 km southeast of the nearest locale for *S. purpureus* in Bocas del Toro. Whether it represents an outlier population of *S. purpureus* with at least atypical pubescence, a possible hybrid, or a different taxon awaits additional collections (including fruit) to assess its taxonomic status. It is not included in the information for *S. purpureus* presented above.

Daniel (1999) alluded to potential differences in the direction of anther dehiscence among species of *Stenostephanus* in Mexico, but noted the difficulty in interpreting this in several species, especially from herbarium specimens. Since then, from our observations of plants in the field and images on websites that show anther dehiscence, directionality often can be ascertained. Based on these observations we have determined the direction of dehiscence for several species of Mexican and Central American *Stenostephanus*. Species with nototribic flowers (i.e., anthers dehiscing toward the lower lip) include: *S. blepharorhachis* (Lindau) Hammel, *S. chiapensis*, *S. leiorhachis*, *S. monolophus*, *S. oaxacanus*, *S. reflexiflorus* (Leonard) J.R.I. Wood, *S. rostellatus* (Lindau) T.F. Daniel et al., *S. sessilifolius* (Oerst.) T.F. Daniel, *S. tacanensis* (Acosta & R. Fernández) T.F. Daniel, *S. ventricosus* (Donn. Sm.) Hammel & McDade and *S. villosus* (Gómez-Laur. & Hammel) McDade. Species with sternotribic flowers (i.e., anther dehiscing toward the upper lip) include *S. haematodes* (Schltdl.) T.F. Daniel, *S. latilabris*, and *S. purpureus*. *Stenostephanus silvaticus* appears to have pleurotribic flowers (i.e., anthers dehiscing toward each other). In this species, before either the corollas have fully expanded or the anthers have dehisced, the stamens are oriented so that the flowers would appear to be nototribic, but when mature, the stamens are spread apart laterally and the anthers open toward each other (or possibly in some instances, toward the upper lip?). Two other Mexican/Central American species, *S. azureus* and *S. harleyi* (Wassh.) T.F. Daniel, also appear to be pleurotribic (and/or possibly sternotribic in some instances). All three orientations of anther dehiscence appear to occur among South American species, as follows:

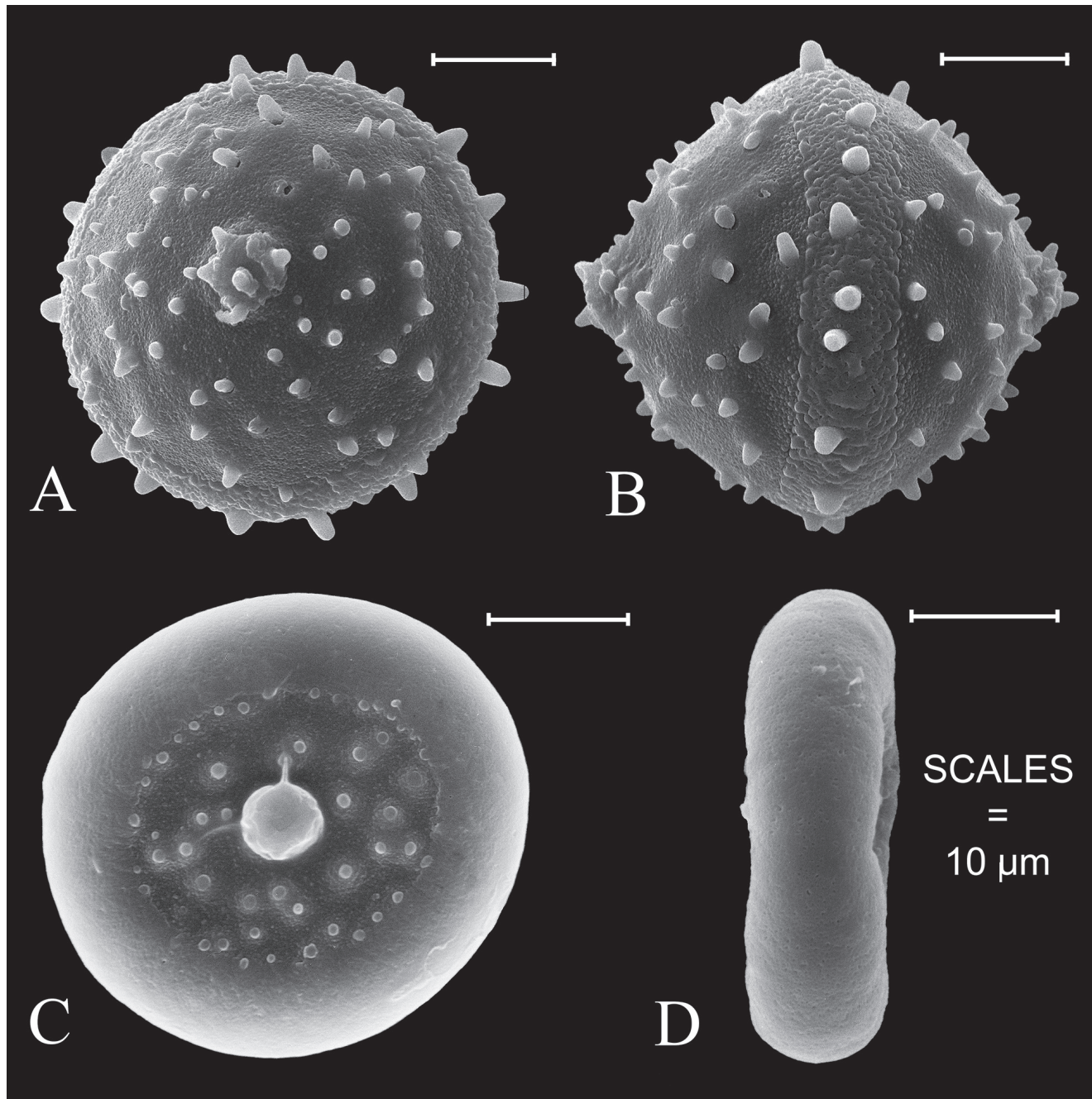


FIGURE 3. Pollen of *Stenostephanus*. **A–B**, *S. purpureus*. **A**, apertural view; **B**, interapertural view. **C–D**, *S. silvaticus*. **C**, apertural view; **D**, interapertural view. A–B from *Solomon 19167* (CAS); C from *Breedlove & Bartholomew 66948* (CAS); D from *Mexia 9273* (CAS).

nototribic (e.g., *S. ampelinus* (Leonard) J.R.I. Wood, *S. ericae* (Wassh.) J.R.I. Wood & R. Villanueva, *S. puberulus* Lindau, *S. sanguineus* (Nees) Wassh., and *S. tenellus* Wassh. & J.R.I. Wood), sternotribic (*S. lyman-smithii* Wassh.), and apparently pleurotribic (*S. spicatus* Wassh. & J.R.I. Wood). The direction of anther dehiscence plays an important role in pollination via the location of pollen deposition on floral visitors and/or pollinators. Pleurotribic flowers appear to be rare among Acanthaceae. Among them, the Mexican endemic *Mexacanthus mcvaughii* T.F. Daniel (Justicieae:

Tetrameriinae) has laterally spreading stamens with anthers opening toward each other, an androecial orientation similar to that of *S. silvaticus*. Field observations on *M. mcvaughii* (Holmqvist et al., 2005) reveal visitation by and pollen deposition upon hummingbirds and carpenter bees, and strongly suggest wing pollination by the latter. Floral visitors to and pollinators of *S. purpureus* and *S. silvaticus* remain undocumented; however, the difference in directionality of anther dehiscence between them suggests dissimilar pollen placement on floral visitors and/or pollinators. Another

difference in floral morphology between these two species also suggests pollination by different vectors. The presence of a large “landing pad” formed by the lower corolla lip in *S. silvaticus* (Fig. 1D) suggests pollination by insects. Conversely, the lack of a landing pad in *S. purpureus* suggests possible pollination by hummingbirds. Indeed, *S. purpureus* (as *Habracanthus silvaticus*) was grouped with hummingbird-pollinated species in an annotated checklist of the plants of Monteverde, Costa Rica (Haber, 2000).

Paratypes: COSTA RICA. Alajuela: Reserva Río San Lorenzo de UCR, headwaters of Río San Lorenzo below Finca Volcán Muerte, [ca. 10.229049°, -84.570844°], *K. Barringer & B. Perez 3855* (F); El Silencio de San Ramón, *Hb. Brenes 3685* (F); La Palma de San Ramón, *Hb. A. Brenes 3706* (F, NY), *23028* (NY); La Balsa de San Ramón, *Hb. A. Brenes 4938* (F); Cataratas de San Ramón, *Hb. A. Brenes 13462* (F, NY); Piedades Sur (La Palma) de San Ramón, *Hb. A. Brenes 17164* (F); Reserva Biológica Monteverde, Río Peñas Blancas, 10°20'N, 084°42'W, *E. Bello 2058* (MO); along upper Río Sarapiquí, near Cariblanco and along rd. to Colonia Virgen del Socorro, 10°18'N, 084°10'W, *W. Burger & T. Antonio 11144* (CAS, F, NY); valley of Río Sarapiquí, near bridge to La Virgen del Socorro, 10°18'N, 084°10'W, *W. Burger & T. Antonio 12055* (F); upper Río Sarapiquí, near Cariblanco and along road to Colonia Virgen del Socorro, 10°18'N, 084°10'W, *W. Burger et al. 11853* (F); canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, 10°16'N, 084°12'W, *M. Grayum et al. 6178* (MO); Reserva Forestal de S. Ramón, San Ramón, *J. Gómez-Laurito 9629* (F); Reserva Forestal de S. Ramón, ca. Colonia Palmareña, S. Ramón, [10.2444497, -84.569309], *J. Gómez-Laurito 10507* (F), *10607* (F); Virgen del Socorro, Cañón Río Sarapiquí, *L. Gómez et al. 20952* (MO); Reserva Biológica Monteverde, Río Peñas Blancas, 10°19'N, 084°42'W, *W. Haber & E. Bello 8377* (CAS), *8382* (CAS, MO); Reserva Forestal San Ramón, sender Miramar, 10°12'53"N, 084°36'28"W, *G. Herrera Ch. et al. 150* (CAS, MO); Cantón San Ramón, Los Angeles, Colonia Palmareña, Cuenca media de Río San Lorenzo, 10°12'50"N, 084°35'15"W, *G. Herrera et al. 4923* (MO); NW of Zarcero, ca. 2 km W of Zapote on road to Santa Elena, [10.2312286, -84.4254719], *D. Lellinger & J. White 1360* (F, US); bosques de Juan Viñas, *J. León 142* (F); San Ramón, Cuenca del San Carlos, Colonia Palmareña, R.B. Manuel Brenes, Estación San Lorenzo, 10°12'55"N, 084°35'20"W, *A. Rodríguez 1146* (MO); Cantón San Carlos, Cuenca del San Carlos, San Vicente, camino ruta al Parque Nacional Juan Castro Blanco, 10°17'17"N, 084°22'58"W, *A. Rodríguez et al. 3883* (MO); vicinity of Zarcero, [10.1814498, -84.3934938], *A. Smith H253* (F); Cantón Alfaro Ruiz, Zapote, *A. Smith P2252* (A, US); Cantón Alfaro Ruiz, La Peña de Zarcera, *A. Smith NY1008* (F, NY); near Cariblanco, 2.5–3.0 km from main road on road to Colonia Virgen de Socorro, [10.2383691, -84.18164], *C. Taylor & C. Skotak 4841* (MO); Naranjo, *Wendland 596* (F). Cartago: Río Jesús María near Santa Cruz on S slope of Volcán Turrialba, [9.947271, -83.7293089], *W. Burger & M. Burger 8160* (F, image); Cantón Turrialba, Valle del Reventazón, Moravia del Chirripó, 09°49'50"N, 083°26'40"W, *P. Campos*

& *M. Chavarría 11* (MO); Turrialba, Tayutic, 2 km W de Grano de Oro, camino a Llanos del Quetzal, 09°48'50"N, 083°22'40"W, *A. Cascante 656* (MO); stream valley E of Sta. Cruz, S slopes of Volcán Turrialba, *G. DeWolf 412* (LSU, image); Cantón Turrialba, Monumento Nacional Guayabo, 9.9721603, -83.6921981, *R. Kriebel 2955* (CR); Cantón Jiménez, Reserva El Copal, 9.9721603, -83.6921981, *R. Kriebel & D. Solano 2462* (CR); “taette Skove ved Turrialva paa den østlige Skraaning af Costa-Rica,” *A. Oersted 10656* (C); Sector Río Guayabo, El Ceibo, 09°57'50"N, 083°41'30"W, *G. Rivera & Y. Hoomans 1762* (F); Cantón Turrialba, Quebrada Barahona, 2 km W of Turrialba on CR 10, 09°54'N, 083°42'W, *J. Solomon 19196* (CAS, MO); Las Vueltas, Tucurrique, [9.8355261, -83.7081359], *A. Tonduz 13015* (US); ca. 2 km E of Cachí along rd. paralleling Río Naranjo towards Cerro Duán, [9.8311125, -83.7853432], *K. Utley 5883* (CAS); Cantón Turrialba, M.N. Guayabo, Cuenca del Reventazón, 09°58'30"N, 083°41'40"W, *L. Diego Vargas & V. Ramírez 232* (MO). Heredia: NW of Vara Blanca, N slope of Central Cordillera, [10°10'23.20"N, 084°09'27.85"W], *M. Chrysler 5103* (F); barranca del Río Sarapiquí, Colonia Virgen del Socorro, *J. Gómez-Laurito 9844* (F); Parque Nac. Braulio Carrillo, Atlantic slope of Volcán Barva, between Río Peje and headwaters of Río Sardinal, 10°15.5'N, 084°05'W, *M. Grayum & G. Herera 7826* (MO); Vara Blanca de Sarapiquí, N slope of Central Cordillera, [10.1689659, -84.1479663], *A. Skutch 3160* (A, MO, NY, US); Yerba Buena, NE of San Isidro, *P. Standley & J. Valerio 50069* (US); Sto. Domingo de Vara Blanca, *M. Valerio 286* (F). Limón: Cantón Limón, Faja Costeña de Limón, Asunción, 09°54'10"N, 083°10'20"W, *A. Estrada 376* (MO); Cantón Limón, Cordillera de Talamanca, headwaters of Quebrada Kakébeta, below divide between ríos Xikiari and Boyei, 09°47'00"N, 083°20'30"W, *M. Grayum 10950* (MO); Reserva Hitoy-Cerere, Río Hitoy y hasta la cima del Cerro Bitárkara, 09°38'30"N, 083°07'09"W, *B. Hammel et al. 17680* (MO); Cantón Limón, Cordillera de Talamanca, Cerro Muchilla, Fila Matama, 09°46'50"N, 83°05'30"W, *R. Robles & A. Chacón 2659* (MO); Cantón Talamanca, Fila de Matama, 09°53'30"N, 083°11'30"W, *A. Rodríguez 593* (MO). San José: Cantón Moravia, P.N. Braulio Carrillo, Cuenca del Sarapiquí, 10°03'40"N, 083°59'10"W, *L. Acosta & V. Ramírez 373* (MO); Río Claro Valley, below La Palma, NE of Jan Jeronimo, 10°03'N, 083°58'W, *W. Burger & M. Burger 7643* (CR, image, F, MO, NY); Río Clara Valley (Bajo La Hondura) below La Palma, NE of San Jerónimo, 10°03'N, 083°58'W, *W. Burger & R. Liesner 6276* (F, NY), *W. Burger et al. 9385* (F, NY); La Palma area, NE of San Jeronimo, above La Hondura Valley, 10°02'N, 084°00'W, *W. Burger & G. Visconti 10218* (CAS, CR, image, F, MO); vicinity of Bajo La Hondura, along road between Paracito and the Río Claro, [10.0625251, -83.9833999], *T. Croat 44505* (MO); Virgen del Socorro, Cañón Río Sarapiquí, [10.2546613, -84.1676727], *L. Gómez et al. 20952* (CAS); old cart road to Limón, 5.6 km N of San Jerónimo, near La Palma, 10°10'N, 084°00'W, *S. Hill et al. 17769* (NY); bajos de La Hondura, *A. Jiménez s.n.* (F); Bajo La Hondura, 10°04'N, 083°59'W, *H. Kennedy & P. DeVries 3814* (F); Cantón Vázquez de Coronado, P.N. Braulio Carrillo, cerca

del túnel, 10.0680556, -84.0069444, *R. Kriebel 4903* (CR); beside Río Hondura, *R. Lent 2040* (F); Parque Nac. Braulio Carrillo, 500 m before Zurquí tunnel, 10°08'35"N, 084°01'00"W, *P. Maas et al. 7800* (MO); Cantón Moravia, P.N. Braulio Carrillo, Cuenca del Sarapiquí, 10°03'35"N, 083°59'15"W, vicinity of La Palma on road to La Hondura, *W. Maxon & A. Harvey 8059* (US); *S. Salas et al. 188* (MO); Alto La Palma, [10.048574, -83.9889233], *C. Schnell 1087* (MO); Cantón Vázquez de Coronado, Parque Nac. Braulio Carrillo, trail from hwy. at La Ventana to Bajo La Hondura, 10°04'N, 083°59'W, *J. Solomon 19167* (CAS, CR, image, F, MO); Parque Braulio Carrillo, Río Bajo de Hondura, 25 km N de San José, *M. Sousa et al. 12666* (MEXU); La Hondura, *P. Standley 36540* (US), *37651* (US), *37859* (US); La Palma, *P. Standley 38237* (US); Peralta, *H. Stork 515* (US); below Bajo La Hondura, where Río Zurquí

flows into Río Hondura, 10°04'N, 083°59'W, *J. Taylor & C. Taylor 11928* (MO, NY); just above Río Hondura at Baja La Hondura, *J. Taylor 17887* (NY, US); La Palma, *A. Tonduz 7405* (GH, NY, US); La Hondura de San José, *M. Valerio 697* (F); La Palma, *M. Valerio 1404* (F); Moravia, San Gerónimo, Bajo de la Hondura, Parque Nacional Braulio Carrillo, 10°05'50"N, 083°58'00"W, *O. Valverde 949* (MEXU, image). Province undetermined: au dessus de Sta. Elena, *H. Pittier 13236* (US); Talamanca, *H. Pittier 9379* (US). PANAMA. Bocas del Toro: Caribbean slopes of Cerro Fábrega at foot of "Falso Fábrega" in Palo Seco Reserve, 09°09'54"N, 082°40'45"W, *A. Monro & S. Cafferty 4735* (MO); Changuinola, PILA, Punto 10, Falso Fábrega, 09°09'48.4"N, 082°40'17"W, *A. Monro et al. 6140* (MO); Changuinola, Parque Internacional La Amistad, Punto 3, 9.4376556, -82.8403107, *D. Solano et al. 5876* (MO).

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