REVISION OF STENOSTEPHANUS (ACANTHACEAE) IN MEXICO

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INTRODUCTION

Stenostephanus Nees is a neotropical genus of perennial herbs and shrubs comprising about 75 species that occur primarily at relatively high elevations from Mexico to Bolivia. The history of names applied to this genus and its current delimitation were addressed by Wood (1988, under *Habracanthus*) and Daniel (1995a). Most of the previously described Mexican species have been treated in either *Habracanthus* or *Hansteinia*. In this study, all Mexican species previously referred to *Habracanthus*, *Hansteinia*, and *Stenostephanus* were studied and are treated in the last genus. Combinations in *Stenostephanus* for most of the Central American and South American species that would also belong in this genus have yet to be made.

This study is based on examination of 460 herbarium specimens representing 167 collections from 32 herbaria, field observations, and laboratory studies of pollen and chromosomes. Fifteen species are recognized as occurring in Mexico. In the only previous account of Mexican species of *Stenostephanus*, Daniel (1995b) treated nine species in Chiapas. Descriptions of those species are repeated herein because, in most cases, they have been augmented substantially with additional data from either additional Chiapan collections (e.g., *S. gracilis*) or collections from other states of Mexico (e.g., *S. silvaticus*). Four species are newly described herein and two new combinations in *Stenostephanus* are proposed for species described in genera here treated as congeneric with it.

INFRAFAMILIAL AFFINITIES

Lindau (1895) treated most of the genera here recognized as constituting *Stenostephanus* in tribe Isoglosseae subtribe Isoglossinae. Lindau's subsequent (1922) placement of *Syringidium* in subtribe Porphyrocominae was likely a mistake on his part; the genus as described by him possesses the diagnostic characters of his Isoglossinae. Other genera of Isoglossinae treated by Lindau (1895) with two stamens and monothecous anthers consisted of the Old World genera *Brachystephanus* Nees and *Oreacanthus* Benth. Bremekamp (1965) retained Lindau's Isoglossinae, renaming it Rhytiglossinae, as a subtribe of his much-expanded tribe Justicieae. It is doubtful that Bremekamp intended to retain *Stenostephanus* (and those taxa here considered congeneric with it) within his subtribe, however; he noted that his Rhytiglossinae had bithecous anthers and consisted of genera confined to the Old World. Bremekamp (1965: 29) described pollen of his Rhytiglossinae as

"lenticular with a pore in the centre of each of the flattened sides, and a marginal zone differing in structure from the rest of the wall." He suggested that genera (e.g., Brachystephanus) with pollen differing from those types he described for the subtribes of Justicieae would probably need to be referred to subtribes of their own. Subsequent observations of additional pollen by various workers reveal grains like those described above by Bremekamp for his Rhytiglossinae in species of Stenostephanus (see below) and Oreacanthus (Scotland 1990), as well as diporate pollen like that of Stenostephanus in some species of Brachystephanus (Figueiredo & Keith-Lucas 1996). Thus, it would appear that Bremekamp's (1965) circumscription of pollen types was too narrow and that Stenostephanus and its relatives can be readily accommodated in subtribe Isoglossinae. Perhaps a more relevant question is whether Stenostephanus can be distinguished from its relatives in the subtribe. Other American genera that are obviously related to Stenostephanus, based on their macromorphological and palynological characteristics, include Razisea Oerst., Kalbreyeriella Lindau, and Cylindrosolenium Lindau. Lindau described the last two subsequent to his infrafamilial classification of 1895. Without knowledge of its palynological characteristics, Lindau (1895) treated Razisea in tribe Odontonemeae subtribe Odontoneminae. The genus comprises four species and is known from Central America and Colombia. Its androecium of two monothecous stamens and its diporate pollen that is similar to that of Stenostephanus (see below) confirm a close relationship between these genera. The genus is usually distinguished from those included here in Stenostephanus on the basis of such characters as its "spicate" (racemose as defined below) inflorescence, gradually expanded corolla tube, and abruptly bent upper lip of the corolla (Gibson 1974; Leonard 1958; Wood 1988). These features are all encountered among Mexican species of Stenostephanus, and it is doubtful that Razisea represents a distinct genus. Kalbreyeriella, which Lindau (1924) treated in subtribe Porphyrocominae, consists of three species occurring in Colombia and Panama that differ from Razisea primarily by their corollas with a rostrate tip in bud and a relatively long, narrow upper lip (Leonard 1958; Gibson 1974). Cylindrosolenium is a unispecific genus from Ecuador and Peru. Lindau (1897) included it in subtribe Isoglossinae and concluded that it differed from Stenostephanus by having looser and fewer-flowered inflorescences and corollas with a cylindrical tube and lingulate lobes. Additional studies will be necessary to determine whether these three genera should continue to be treated as distinct from Stenostephanus. Of the two paleotropical relatives of Stenostephanus noted above, Brachystephanus was purported to differ by its pollen and Oreacanthus was noted to differ by its short and broad corolla tube (Lindau 1895). If these genera are to be maintained as distinct from Stenostephanus, other characters will need to be found to distinguish them.

Stenostephanus is the only representative of subtribe Isoglossinae in Mexico and differs from other genera of Mexican Acanthaceae by its androecium of two stamens with monothecous anthers, which contain diporate pollen.

MACROMORPHOLOGY

Wood (1988) discussed variation in many of the characters traditionally used to distinguish both genera and species in this assemblage. Mexican species of *Stenostephanus* exhibit considerable morphological variation, particularly in pubescence, from locality to locality. This may be due, in part, to their rather isolated occurrences at high elevations (see below). Considerable variation in pubescence of the rachis was observed in several Mexican species (e.g., *S. glaber*, *S. haematodes*, *S. monolophus*, *S. oaxacanus*, and *S. tacanensis*). Wood (1988) noted similar variation in pubescence among some Colombian species (e.g., *H. charitopes* (Leonard) J. R. I. Wood).

Some aspects of inflorescence structure appear to be relatively stable and taxonomically useful characters among Mexican *Stenostephanus*. In most species, the distalmost pair of leaves is reduced in size and differs from other leaves in shape and attachment. In the following account, a terminal inflorescence (in which leaves are replaced by highly reduced bracts) is one that arises distal to this pair of leaves and axillary inflorescences arise in the axils of leaves proximal to this pair. Most inflorescences are terminal and many of those that superficially appear to be axillary are, in fact, also terminal. These latter inflorescences are borne on short branches in the leaf axils and are subtended by a pair of reduced leaves. Truly axillary inflorescences are not subtended by a pair of reduced leaves.

Because of the presence of both bracts and bracteoles, the basic unit of the inflorescence is considered to be a dichasium. In most species the dichasium is several- to many-flowered; however, in some, it comprises only a single flower. Terms denoting the arrangement of dichasia are primarily dependent on the presence of peduncles (i.e., stalks between the bract and the bracteoles) and pedicels (i.e., stalks between the bracteoles and the flower). In dichasiate spikes (not known among Mexican species), neither peduncles nor pedicels are present (i.e., the dichasia are sessile along the rachis). In dichasiate racemes, peduncles are absent but pedicels are present. In dichasiate thyrses, peduncles are present and pedicels may be present or absent. Panicles comprise branched inflorescences where the branches are indeterminate and consist of dichasiate spikes, racemes, or thyrses. Branching that results in a panicle is often exclusively from the basal node of the inflorescence (i.e., in one or both axils of the distalmost pair of leaves). Inflorescences are usually pedunculate; however, if either an indeterminate inflorescence axis or a dichasium occurs in the axil of one or both of the distalmost pair of leaves, then the inflorescence is considered to be sessile.

Sterile inflorescences with calyces differing in size and pubescence from those of fertile inflorescences, as noted by Wood (1988) in several Colombian species, were not observed among Mexican taxa. However, such inflorescences might be somewhat difficult to distinguish from juvenile ones, which were sometimes evident proximal to the fertile inflorescences.

Various structures of *Stenostephanus* tend to exhibit more color than those of many other Mexican Acanthaceae; however, colors are not always preserved on herbarium specimens nor noted on labels. Thus their usefulness for distinguishing taxa or assessing relationships remains unknown. Color of the corolla is generally known and is often a useful taxonomic character. For example, it appears to be the primary means for distinguishing *S. monolophus* from *S. glaber*. Colors such as red, maroon, and purple were also noted among trichomes (primarily the septae), calyces, and rachises of the inflorescence. Considerable variation in coloration was noted among calyces of herbarium specimens. Tips of the calyx lobes are often darker in dried material than the proximal portion of the lobes. Sometimes this darker coloration appears to be green and other times dark reddish or purplish.

The direction of dehiscence of the anthers was observed in most species to be in the direction of the lower lip. In some species (e.g., *S. latilabris*) the direction of dehiscence could not be determined with certainty from the herbarium specimens available. In *S. haematodes*, many collections have flowers with anthers that appear to dehisce toward the upper lip and other collections have flowers with anthers that appear to dehisce toward the lower lip. Whether such variation exists in the species (or in the genus) or whether determination of the direction of dehiscence is unreliable as viewed on herbarium specimens remains to be determined

Based on macromorphological characters, primarily features of the corolla, there appear to be at least two groups of species in Mexico. One consists of S. silvaticus and S. latilabris, which both have relatively short, bluish to white corollas with a well-developed and relatively long lower lip; a short, cylindrical corolla tube that lacks a distinct throat; a recurved to recoiled upper lip of the corolla; and stamens that are inserted in the distal 1/3 of the corolla tube. The remaining 13 species comprise a group characterized by having generally longer, reddish (at least in part and where known) corollas with a poorly developed (or absent) to relatively short lower lip; a mostly longer corolla tube that is gradually or abruptly expanded distally into a distinct (usually saccate) throat; a straightforward to erect upper lip of the corolla; and stamens that are inserted in the proximal 1/3 to 1/2 of the corolla tube. This latter group is readily divisible into those species with racemose inflorescences and those with thyrsoid inflorescences. It is not known whether this inflorescence character actually segregates species into natural groups. For example, S. chiapensis and S. monolophus, which greatly resemble each other in most features (including floral color and form), are distinguishable primarily by this difference in inflorescence structure. The ten species with thyrsoid inflorescences are not easily distinguishable by large suites of mutually exclusive characters. Their circumscriptions are sometimes confounded by lack of knowledge concerning some of their character states (e.g., corolla color, capsule pubescence, seed surface ornamentation).

POLLEN

Pollen of Mexican *Stenostephanus* was described by Daniel (1998). Examination of additional pollen for the present study confirms and elaborates on those observations. Pollen of all Mexican species was studied with a scanning electron microscope. Collections from which pollen was examined are listed in Appendix 1. The palynological terminology used herein follows Walker and Doyle (1975) with modifications of Daniel (1998). Pollen that illustrates most of the variation encountered among the Mexican species is shown in Figs. 1–3.

Pollen of *Stenostephanus* is 2-porate and varies in shape from globose-elliptic to globose-elongate (longer equatorial axis:shorter equatorial axis varies from 1.00–3.33). The longer equatorial axis is the diameter of the apertural face in all species except *S. gracilis* and *S. haematodes*, in which the diameter of the interapertural face is sometimes longer. Outline of grains in apertural view is subcircular to circular, and in interapertural view it varies from narrowly elliptic to circular to oblate. Using the size classes of Walker and Doyle (1975), pollen of Mexican *Stenostephanus* varies from medium-sized to large. *Stenostephanus silvaticus* (Fig. 2f, g) has the smallest grains (31 µm diameter in apertural view) and *S. gracilis* (Fig. 1e) has the largest (57 µm diameter in apertural view). The pores vary from 3–10 µm in diameter and from subpsilate to verrucate to gemmate to echinate in surface sculpturing. Each pore is surrounded by a \pm circular region 17–52 µm in diameter. The surface of the \pm circular regions varies from subpsilate to microverrucate to microrugulate and, additionally, is covered with gemmae, baculae, and/ or echinae. The two \pm circular regions of a grain are separated from one another

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FIG. 1. Pollen of Mexican Stenostephanus. a. S. alushii (Ton 5340), interapertural view. b. S. breedlovei (Breedlove 49644), interapertural view. c. S. chiapensis (Breedlove & Burns 72688), interapertural view. d. S. glaber (Daniel et al. 8405), interapertural view. e. S. gracilis (Croat 47536), interapertural view. f. S. guerrerensis (Breedlove 61946), apertural view. g. S. guerrerensis (Breedlove 36060), interapertural view. h. S. harleyi (Reveal et al. 4239), interapertural view. i. S. harleyi (Reveal et al. 4239), apertural view. Scale bar = 10 μm.

by a peripheral band 2–17 μ m in width. The band is continuous and encircles the grain in most species; in *S. alushii* (Fig. 1a) and some pollen of *S. haematodes* (Fig. 3e, f), *S. purpusii*, and *S. tacanensis* it is either broken into segments of varying lengths or does not completely encircle the grain. The surface sculpturing of the peripheral band varies among species and sometimes within a species. A central row of gemmae, baculae, and/or echinae running the length of the band was observed in six species.

Daniel (1998) noted two forms of pollen among the Mexican species of *Steno-stephanus*, globose-elongate (e.g., Fig. 1g) and globose-elliptic (e.g., Fig. 1a). Study of additional pollen reveals that these two forms based on shape are linked by globose-oblong pollen (e.g., Fig. 1b) found in several species. Because palynological variation was observed in the widespread and morphologically diverse species



FIG. 2. Pollen of Mexican Stenostephanus and Central American Razisea. a. S. madrensis (Campos V. 4736), interapertural view. b. S. monolophus (Matuda 3969), apertural view. c. S. monolophus (Matuda 3969), interapertural view. d. S. oaxacanus (Reko 3724), apertural view. e. S. oaxacanus (Carlson 4022), interapertural view. f. S. silvaticus (Breedlove & Bartholomew 66948). g. S. silvaticus (Mexia 9273), interapertural view. h. S. tacanensis (Nelson 3794), interapertural view. i. Razisea spicata (Daniel et al. 6231), interapertural view. Scale: a-h, bar = 10 µm; i, bar = 12.5 µm.

S. haematodes, pollen of numerous individuals of this species was studied. Some of the palynological diversity observed within *S. haematodes* is illustrated in Fig. 3 and is discussed under that species.

Pollen of Mexican *Stenostephanus* resembles that described and/or illustrated by Wasshausen (1985a, as *Kalbreyeracanthus*; 1984, 1985b, 1987a, 1987b, as *Habracanthus*; 1985c, as *Hansteinia*), Wood (1988, as *Habracanthus*), and Scotland (1990, as *Habracanthus*, *Hansteinia*, and *Stenostephanus*) for South American species. Among other genera from the New World, *Razisea* (Fig. 2i) and *Kalbreyeriella* (Scotland 1990) both have similar pollen. Pollen of the related genus *Cylindrosolenium* was described by Lindau (1897) as typical of Isoglossinae. Several genera from the Old World, including *Brachystephanus* and *Oreacanthus*, also have similar pollen (see Daniel 1998).



FIG. 3. Pollen of *Stenostephanus haematodes*. a. *Ventura A. 20491*, interapertural view. b. *Daniel & Acosta C. 8359*, interapertural view. c. *Hinton et al. 10758*, interapertural view. d. *Ventura A. 3425*, apertural view. e. *Ventura A. 4670*, interapertural view. f. *Ventura A. 4670*, detail of surface showing sculpturing and terminus of peripheral band. Scale: a-e, bar = 10 µm; f, bar = 2.2 µm.

While additional sampling of Mexican species that are known from few collections is still necessary, several palynological characters appear to be useful for characterizing species and will likely be useful in phylogenetic studies of the genus. Various palynological attributes of each species are provided in both the species descriptions and Table 1.

CHROMOSOME NUMBERS

No chromosome counts have been reported previously for species here treated in *Stenostephanus*. During this study, using methods noted by Daniel and Chuang (1993), counts were obtained for *S. glaber* and *S. haematodes* as well as for the Central American species currently known as *Hansteinia blepharorhachis* (Lindau) Durkee. Chromosomes in several cells were counted for each taxon and all counts were n = 18 (Fig. 4). The only known chromosome number in a related genus is n = 18, which was reported for *Razisea* (Daniel et al. 1990). From the preceding discussion of intergeneric relationships, it is evident that *Razisea* might not be distinct from *Stenostephanus*. A single chromosome number common to these two taxa further supports their close relationship. Additional chromosome counts in *Stenostephanus* and its relatives, especially the Old World genera *Brachystephanus* and *Oreacanthus*, are desirable.

DISTRIBUTION, HABITATS, AND FLOWERING TIMES

Stenostephanus occurs from east-central Mexico (Hidalgo, ca. lat. 21°00'N) southward through Central America and northwestern South America to Bolivia (ca. lat. 17°07'S). The genus is most species-rich in Andean South America, and its distribution is centered in Colombia where 34 species occur. The number of species drops off dramatically in other countries: Mexico (15), Venezuela (8),

| | Longer E: shorter E | Diameter of apertural face (µm) | Diameter of interapertural face (µm) | Outline of interapertural face | Width of peripheral band (µm) | |
|-----------------|------------------------|---------------------------------------|--|--|-------------------------------------|--|
| S. alushii | 1.06-1.20 | 41–48 | 40-44 | broadly elliptic to subcircular | 3–5 | |
| S. breedlovei | 1.66-1.81 | 38–46 | 23–24 | elliptic | 9–11 | |
| S. chiapensis | 2.11-2.77 | 46–56 | 20–24 | narrowly elliptic | 13–17 | |
| S. glaber | 1.16–1.21 | 46–50 | 38-42 | broadly elliptic | 9 | |
| S. gracilis | 1.00-1.05 | 50-54 | 50-57 | suboblate to circular | 11 | |
| S. guerrerensis | 2.60 | 46–55 | 20 | narrowly elliptic | 13 | |
| S. haematodes | 1.03-1.23 | 39–47 | 35-46 | broadly elliptic to subcircular to oblate | 2–10 | |
| S. harleyi | 1.46 | 47–48 | 32 | elliptic | 7 | |
| S. latilabris | 1.15 | 36 | 31 | subcircular | 6 | |
| S. madrensis | 1.10 | 44 | 40 | subcircular | 8 | |
| S. monolophus | 1.43–1.92 | 40–50 | 26–31 | elliptic to broadly elliptic | 15–17 | |
| S. oaxacanus | 1.48-2.27 | 38-50 | 22–27 | narrowly elliptic to elliptic | 12–13 | |
| S. purpusii | 1.04 | 38 | 36 | subcircular | 7 | |
| S. silvaticus | 1.85-3.33 | 31–39 | 10–17 | narrowly elliptic | 10–13 | |
| S. tacanensis | 1.03-1.12 | 50-52 | 44-49 | subcircular | 5–7 | |

TABLE 1. Palynological characteristics of species of *Stenostephanus* occurring in Mexico (E = equatorial axis).

Costa Rica and Ecuador (7), Guatemala (6), Peru (4), Panama and Bolivia (3), Brazil (2), and Nicaragua (1?, based on *Glockeria glandulosa* Oerst., the identity of which remains to be confirmed). Species likely occur in other mountainous countries of Central America (i.e., Honduras) but have yet to be collected there. *Stenostephanus* is represented in Central America by at least 13 species, most of which are currently treated in either *Habracanthus* or *Hansteinia*.



FIG. 4. Camera lucida drawings of meiotic chromosome preparations. a. *Hansteinia blepharorha*chis (Daniel & Almeda 6366), telophase I, n = 18. b. Stenostephanus glaber (Daniel et al. 8405), telophase I (chromosomes from only 1/2 of cell shown), n = 18. c. S. haematodes (Daniel & Acosta C. 8359), late diakinesis I, n = 18. Scale bar = 10 µm.

Most species are known from only a single country; this distribution pattern reflects the high degree of local endemism characteristic of many species. Of the 15 Mexican species of *Stenostephanus*, ten are endemic to Mexico, three occur only in Mexico and Guatemala, and two occur in Mexico and other Central American countries. Within Mexico, four species are endemic to Chiapas, two species are known only from Oaxaca, and two species occur only in Guerrero.

Wood (1988) noted that species of *Stenostephanus* are largely restricted to wet cloud forests between 1700 and 3000 meters elevation. This is generally true for Mexican species, which are found at elevations from (400) 1000 to 2875 meters. All Mexican species occur at or above 1000 meters, and the presence of *S. oaxacanus* at 2875 meters elevation represents the highest known occurrence of Acanthaceae in

Mexico. Plants generally occur in vegetation types that vary from mesic to wet: temperate deciduous forests, oak forests, pine-oak forests, pine-oak *Liquidambar* forests, mesophytic montane forests, montane rain forests, and cloud forests. Only three species, *S. gracilis*, *S. haematodes*, and *S. silvaticus*, can be found at elevations below 1000 meters where they occur in tropical deciduous forests (apparently rarely so and then always near water in these otherwise dry forests), lower montane rain forests, and mesophytic montane forests. The propensity of the majority of Mexican species to occur at relatively high elevations, particularly in relatively isolated, cloud forest habitats, likely contributes to the abundance of small-scale endemism noted above and undoubtedly helps explain the largely Andean character of the distribution of the genus.

Wood (1988) also noted that most species occur along streams or in swampy ground and that plants found apart from such situations are sterile. Indeed, most Mexican collections of *Stenostephanus* were noted to have been collected from near streams or springs. Of the two species that I studied in their native habitats, one (*S. haematodes*) occurred along a stream and the other (*S. glaber*) occurred on moist, level ground along a cloudswept ridge. Both were fertile.

Although flowering among Mexican species of *Stenostephanus* has been recorded during every month of the year, most species have been collected in flower between October and March. This corresponds to the end of the wet season and a major portion of the dry season in Mexico. Wood (1988) noted that species flower only at irregular intervals and for a short time. Plants of *S. chiapensis* that I propagated in a garden from seed of the type have failed to flower over a six-year period. Further studies of *Stenostephanus* might consider the possibility of gregarious flowering (not known among Acanthaceae from the New World) and the relationship between microhabitat and floral phenology.

TAXONOMY

Stenostephanus Nees in Martius, Fl. bras. 9: 91. (Jun) 1847.—Type: Stenostephanus lobeliiformis Nees.

- Habracanthus Nees in A. DC., Prodr. 11: 312. (Nov) 1847.—Type: Habracanthus silvaticus Nees [=Stenostephanus silvaticus (Nees) T. F. Daniel].
- Galeottia Nees in A. DC., Prodr. 11: 311. 1847, non Galeottia Rupr., 1842, nec Galeottia A. Rich., 1845. Glockeria Nees in A. DC., Prodr. 11: 728. 1847, non Glockeria Göpp., 1836.—TYPE: Galeottia gracilis Nees [=Stenostephanus haematodes (Schltdl.) T. F. Daniel].
- Hansteinia Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 142. 1855.—Type: Hansteinia gracilis Oerst. [=Stenostephanus gracilis (Oerst.) T. F. Daniel].
- Gastranthus Moritz ex Benth. & Hook. f., Gen. pl. 2(2): 1107. 1876, non Gastranthus F. Muell., 1868.—TYPE: Gastranthus schlechtendahlii Moritz ex Benth. & Hook. f. [=Stenostephanus lasiostachyus Nees, fide Lindau 1895]. The author and place of publication of G. schlechtendahlii are given as "Moritz ex Bentham (in Hooker, Ic. Pl. t. 1210. 1877)" by Bremekamp in Farr et al. (1979). The generic description followed by a citation of the name of the sole species in Genera plantarum fulfills the requirements of Article 42 of the International Code of Botanical Nomenclature (Greuter et al. 1994) for a descriptio generico-specifica.

Syringidium Lindau, Notizbl. Bot. Gart. Berlin-Dahlem 8: 142. 1922, non Syringidium Ehrenb., 1845. Kalbreyeracanthus Wassh., Taxon 30: 477. 1981.—Type: Syringidium atropurpureum Lindau.

Erect to spreading perennial herbs or shrubs with cystoliths and often with conspicuously multi-septate trichomes, septae usually dark (commonly maroon). Leaves opposite, petiolate or distalmost (i.e., subtending inflorescence) pair often sessile, margin entire to crenate to sinuate. Inflorescence of (axillary and) terminal (sessile and) pedunculate dichasiate spikes (i.e., dichasia and flowers sessile), racemes (i.e., dichasia sessile and flowers pedicellate), thyrses (i.e., dichasia pedunculate), or panicles (i.e., with indeterminate branches of dichasiate spikes, racemes, or thyrses); dichasia opposite or alternate, 1 (-3) per axil, 1-12 (-20 or more)flowered, sessile or pedunculate, subtended by a bract. Bracts opposite, green (or sometimes tinged with red or other colors), relatively small, often \pm conduplicate, margin entire. Flowers homostylous, subtended by 2 homomorphic bracteoles, sessile to pedicellate. Calyx often colored (e.g., reddish), deeply 5-lobed, often accrescent in fruit, lobes equal to \pm unequal in length, sometimes recurved at apex, apices often darker than proximal portions of lobes. Corolla 1- or 2-colored, colors various, tube cylindrical or distally gradually to abruptly expanded into a throat, narrow (i.e., unexpanded) proximal portion (if distinct) shorter than throat, throat (if present) often prominently saccate on ventral and/or dorsal side(s), urceolate to subcylindrical, limb 1-2-labiate, upper lip entire, 2-fid, or erose, straightforward (i.e., protruding forward in the same plane as the corolla tube), erect (i.e., bent upward in a plane ± perpendicular to the corolla tube), recurved (i.e., curved toward the base of the corolla tube), or recoiled, lower lip 3-lobed or truncate and minutely 3-fid or essentially absent, lobes of lower lip rounded to triangular, corolla lobes imbricate (ascending cochlear) in bud with lower-central lobe outermost and upper lip innermost. Stamens 2, inserted near apex of corolla tube or near base of throat, exserted from mouth of corolla, filaments often colored (commonly reddish), glabrous (in ours), anthers 1-thecous, often colored (commonly reddish), glabrous, usually dehiscing toward lower lip (i.e., flower nototribal; see discussion under Macromorphology); pollen globose-elliptic to globose-elongate, 2-porate, ± encircling peripheral band present, exine variously ornamented (see discussion); staminodes 0. Style exserted from mouth of corolla, often colored (commonly reddish), glabrous (in ours), stigma 2-lobed or lobes not evident. Capsule stipitate, head ovoid to ellipsoid (sometimes with a slight medial constriction), retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule wall. Seeds 4, homomorphic, discoid to lenticular to concavo-convex, whitish to tan when immature, dark brown when mature, lacking trichomes, usually tuberculate, tubercles usually less conspicuous or restricted to periphery on mature seeds. Base chromosome number: x = 18.

KEY TO THE MEXICAN SPECIES OF STENOSTEPHANUS

See Daniel (1995b) for a regional key to species in Chiapas [that does not include *S. alushii*], Appendix 2 for a key to Mexican species occurring in states other than Chiapas, and under *S. guerrerensis* for a key to species in Guerrero.

1. Corolla white to blue-purple, tube cylindrical (or expanded only at mouth), lacking a distinct or saccate throat, 3–10 mm long, 0.9–2 mm in diameter near midpoint, upper lip recurved to recoiled, 5–12 mm long, lower lip 6–12 mm long; stamens inserted in distal 1/2–1/3 of corolla tube, 6.5–15 mm long.

- Leaf margin ciliate; bracts triangular-linear to linear-elliptic, rounded at apex; calyx abaxially glabrous, lobes linear to lance-linear, margins eciliate; lower lip of corolla 5–8.5 mm wide; thecae 3–3.8 mm long.
 S. latilabris.
- Leaf margin eciliate or inconspicuously ciliate; bracts subulate, acute at apex; calyx abaxially puberulent (rarely pubescent with glands or nearly glabrous), lobes lance-subulate, margins ciliolate; lower lip of corolla 3–5.5 mm wide; thecae 1.3–2.5 mm long. S. silvaticus.
- 1. Corolla red, red and yellow, reddish and white, or purplish (color unknown in *S. harleyi* from Guerrero), tube gradually or abruptly expanded distally into a distinct (often saccate) throat, 10–30 mm long, 3–13 mm in diameter near midpoint, upper lip straightforward to erect, 1–8.5 mm long, lower lip absent or < 0.5–8 mm long; stamens inserted in proximal 1/3 to 1/2 of corolla tube, (12–) 14–38 mm long.
 - 3. Inflorescence of racemes or panicles of racemes, dichasia sessile to subsessile (i.e., borne on peduncles to 1 mm long except at base of inflorescence where peduncles to 6 mm long are sometimes present in *S. breedlovei*), 1–3 (–many)-flowered, lateral flowers of dichasia (if present) lacking secondary peduncles or borne on secondary peduncles to 1 mm long.
 - 4. Cauline trichomes retrorsely appressed; lobes of lower lip of corolla 3-3.5 mm long.

- 4. Cauline trichomes flexuose-retrorse to flexuose to antrorse to antrorsely appressed; lobes of lower lip of corolla absent or < 0.5 mm long.
 - Bracts lanceolate to ovate to ovate-elliptic, 2.5–11 mm long; corolla entirely red, externally pubescent with flexuose eglandular trichomes 0.2–1 (–2) mm long, upper lip 4.5–8.5 mm long, lower lip 3–6.5 mm long; capsule pubescent with eglandular trichomes 0.05–0.2 mm long.
 S. tacanensis.
 - 5. Bracts triangular to subulate, 1.2–2.5 mm long; corolla red dorsally and yellow ventrally, externally glabrous or inconspicuously puberulent with trichomes <0.1 mm long (sometimes also with a few flexuose eglandular trichomes to 0.4 mm long), upper lip 2.5–4 mm long, lower lip not evident or < 0.5 mm long; capsule glabrous.

S. chiapensis.

- Inflorescence of thyrses or panicles of thyrses, dichasia borne on peduncles (1-) 2-55 mm long, (1-) 3-many-flowered; lateral flowers of dichasia borne on secondary peduncles 1.5-30 mm long.
 - Cauline trichomes 1–1.3 mm long, bifariously disposed; flowers sessile to subsessile, pedicels (if present) to 1 mm long (calyx glabrous, corolla with narrow proximal portion 4–5 mm long and lips 4.5–8 mm long).
 - 6. Cauline trichomes absent or 0.1–0.8 mm long or if up to 1.2 mm long (as in *S. madrensis*) then ± evenly to quadrifariously disposed; flowers pedicellate, pedicels 1.5–7 mm long (or if flowers rarely subsessile, as in *S. oaxacanus*, and borne on pedicels as short as 0.7 mm long, then calyx pubescent and corolla with narrow proximal portion 1.5–2.5 mm long and lips up to 2 mm long).
 - 7. Capsule pubescent with eglandular trichomes.
 - 8. Corolla red and white, throat 6.5–9 mm in diameter; calyx 3.5–4.7 mm long during anthesis; pollen globose-elongate; Guerrero. *S. guerrerensis.*
 - 8. Corolla entirely red or yellow-orange with red to maroon distally, throat 3.6–6.2 mm in diameter; calyx 5.5–9.7 mm long during anthesis; pollen globose-elliptic; Chiapas.
 - Corolla entirely red, 22–29 mm long, lower lip 3–5.3 mm long with lobes 0.5– 0.7 mm long; calyx lobes linear, 0.6–1 mm wide; tubercles of seeds lacking barbs; Central Plateau.
 S. alushii.
 - Corolla yellow-orange with red to maroon distally, 15–20 mm long, lower lip 1.5–2.1 mm long with lobes 1–2 mm long; calyx lobes lance-ovate to lancelinear to elliptic to oblanceolate, 1.1–3.2 mm wide; tubercles of seeds bearing minute barbs; Sierra Madre de Chiapas.
 - 7. Capsule glabrous.
 - 10. Abaxial surface of calyx glabrous or pubescent with eglandular trichomes only.
 - Corolla 12–16 mm long, tube expanded from at or near base, the narrow (i.e., unexpanded) proximal portion (if distinct) up to 2 mm long (inflorescence rachis evenly public event with eglandular trichomes); stamens 12–16 mm long.

S. breedlovei.

- 11. Corolla 19–37 mm long, tube expanded distal to base, the narrow (i.e., unexpanded) proximal portion 2–11 mm long (if tube expanded from near base with the narrow proximal portion less than 2 mm long, as rarely in *S. haematodes*, then inflorescence rachis glabrous); stamens 22–37 mm long.
 - 12. Corolla concolorous, reddish, lower lip 3–8 mm long with lobes 0.8–4.5 mm long; states west of Chiapas. S. haematodes.
 - 12. Corolla bicolorous, reddish proximally and white distally, lower lip (if present) 0.5–0.7 mm long with lobes 0.2–0.5 mm long; Chiapas. *S. glaber*.
- 10. Abaxial surface of calyx pubescent with glandular trichomes.
 - 13. Corolla 25–32 mm long, tube with narrow (i.e., unexpanded) proximal portion 6–8 mm long, lower lip 3–4.5 mm long with lobes 2–4 mm long; thecae 3.5–4.5 mm long.
 S. haematodes.
 - 13. Corolla 13–26 mm long, tube with narrow (i.e., unexpanded) proximal portion 1–4 mm long, lower lip (if distinct) < 0.5–3 mm long with lobes (if present) 0.2–2 mm long; thecae 2.5–3.6 mm long.
 - 14. Corolla externally inconspicuously papillate to puberulent (to pubescent), upper lip 1–1.5 mm long. S. oaxacanus.
 - 14. Corolla externally glabrous, upper lip 1.8-5 mm long.
 - Calyx 2.3–3.3 mm long during anthesis; corolla with narrow (i.e., unexpanded) proximal portion of tube 1–1.5 mm long, lower lip 2–3 mm long with lobes 1.5–2 mm long; Oaxaca.
 S. madrensis.
 - 15. Calyx 3.5–8 mm long during anthesis; corolla with narrow (i.e., unexpanded) proximal portion of tube 2.5–4 mm long, lower lip absent or up to 0.7 mm long with lobes 0.2–0.5 mm long; Chiapas.
 - 16. Corolla red dorsally and yellow ventrally; young stems pubescent with flexuose-retrorse to flexuose-antrorse trichomes 0.3–0.8 mm long; calyx lobes lance-linear; montane rain forests at 1500–1900 m. S. monolophus.
 - Corolla reddish proximally and white distally; young stems mostly glabrous or sometimes with a few antrorse to antrorsely appressed trichomes to 0.3 mm long; calyx lobes lance-subulate; cloud forests at 1900–2120 m.
 S. glaber.

Stenostephanus alushii T. F. Daniel, sp. nov.—Type: MEXICO. Chiapas: Mpio. Tenejapa, Ojo del Río Yash Zanal, 1600 m, 5 Jan 1983, A. Ton 5340 (holotype: MEXU!; isotypes: CHIP! MO! NY!).

Herba perennis usque ad 1 m alta. Folia petiolata, laminae plerumque ovatae vel ellipticae, (18–) 29–130 mm longae, (8–) 14–58 mm latae, (1.6–) 2.1–2.2-plo longiores quam latiores. Inflorescentia thyrsi (vel paniculae thyrsorum) terminales (vel axillares) ex dichasiis constans; rachis pubescens trichomatibus eglandulosis et glandulosis; dichasia pedunculata, (1–) 3–multi-flora; flores pedicellati. Corolla rubra, 22–29 mm longa, extus pubescens; faux 14–17 mm longa et 4.5–6.2 mm diametro; labium superiorus 2.5–6.3 mm longum; labium inferiorus 3–5.3 mm longum lobis 0.5–0.7 mm longis. Capsula 13–15 mm longa, pubescens trichomatibus eglandulosis.

Perennial herbs to 1 m tall. Young stems subquadrate, bifariously pubescent for varying distances proximal to nodes with flexuose to retrorse eglandular trichomes 0.1–0.4 mm long. Leaves petiolate, petioles to 24 mm long, blades ovate to elliptic (distal pairs sometimes short-petiolate and broadly ovate to subcircular), (18–) 29–130 mm long, (8–) 14–58 mm wide, (1.6–) 2.1–2.2 times longer than wide, acuminate to caudate at apex, acute to attenuate (distal leaves sometimes \pm truncate) at base, surfaces nearly glabrous or pubescent with flexuose to antrorse eglandular trichomes along midvein, margin ciliate. Inflorescence of (axillary and)

terminal thyrses (or panicles of thyrses) to 21 cm long, rachis quadrate-sulcate to \pm flattened, densely and evenly pubescent with an understory of erect to flexuose eglandular trichomes 0.1-0.3 mm long and an overstory of flexuose glandular trichomes 0.3-0.7 mm long; dichasia opposite or alternate, (1-) 3-many-flowered, pedunculate, peduncles 2.5-13 mm long, pubescent like rachis. Bracts linear to subulate, 4.5-11 mm long, 0.5-0.9 mm wide, abaxial surface pubescent with antrorsely appressed eglandular trichomes 0.05-0.2 mm long. Bracteoles and secondary bracteoles linear-subulate to lance-subulate, 3.5-7.5 mm long, 0.4-0.7 mm wide, abaxial surface pubescent like bracts or like rachis. Flowers pedicellate, pedicels 2-5 mm long, pubescent like rachis, lateral flowers borne on secondary peduncles 2.5-4 mm long. Calyx 7-16 mm long, 7-9.7 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis, lobes linear, 6-15 mm long, subequal in length, 0.6-1 mm wide. Corolla subellipsoid to subfusiform in bud, red, 22-29 mm long, externally pubescent with flexuose eglandular trichomes 0.1-1 mm long (trichomes densest and longest proximally), tube 19-24 mm long, gradually to abruptly expanded distally into a throat, narrow proximal portion 5-7 mm long, 1.2-1.6 mm in diameter, throat subsaccate, 14-17 mm long, 4.5-6.2 mm in diameter, widest near midpoint, upper lip straightforward, 2.5-6.3 mm long, 3-3.5 mm wide, lower lip 3-lobed, 3-5.3 mm long, lobes 0.5-0.7 mm long, 0.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3-1/2 of tube), 25-28 mm long, thecae 3-3.5 mm long; pollen globose-elliptic, peripheral band not continuous, psilate to subpsilate and sometimes foveolate. Style 34 mm long, stigma 0.1 mm long. Capsule 13-15 mm long, pubescent with erect to flexuose eglandular trichomes <0.05-0.1 mm long, stipe 5-6 mm long, head subellipsoid. Seeds 2.3 mm long, 1.5 mm wide, immature surfaces \pm bubbly tuberculate to covered with subconical tubercles, tubercles lacking retrorse barbs.

Illustration. Fig. 5.

Phenology. Flowering and fruiting: January–March. Distribution. Mexico (Chiapas; Fig. 6); 1600 m.

PARATYPE. Mexico. CHIAPAS: Mpio. Tenejapa, Ojo de Agua Yashanal, A. Ton 7375 (MEXU).

Stenostephanus alushii is known only from the vicinity of a riverine spring on the northeastern escarpment of the Central Plateau of Chiapas in southern Mexico. Although the type of vegetation in which the species occurs was not recorded by the collector of the only known specimens, the possibilities at 1600 meters elevation in this portion of the Central Plateau comprise either montane rain forests, pine-oak-Liquidambar forests, or pine-oak forests (Breedlove 1981). Within one of these major vegetation types, it is likely that the species grows in a temperate riparian forest, as described by Berlin et al. (1974) for the Municipio of Tenejapa.

This species shares numerous morphological characteristics with *S. gracilis*, which also occurs in Chiapas, but differs from it in several characters of the flower and seed (see key to species for both shared characters and distinctions). *Stenostephanus breed-lovei* occurs in the vicinity of *S. alushii*, although at higher elevations, and resembles it in pubescence of the vegetative and inflorescence axes, floral form, and corolla color. These species can be distinguished by the following couplet:

Dichasia pedunculate, (1–) 3-many-flowered; bracts 4.5–11 mm long; bracteoles 3.5–7.5 mm long; calyx 7–16 mm long; corolla externally pubescent, lobes of lower lip 0.5–0.7 mm long; pollen globose-elliptic, peripheral band not continuous, psilate to subpsilate and sometimes foveolate. S. alushii.



FIG. 5. Stenostephanus alushii. a. Inflorescence with distal leaves. b. Proximal leaf. c. Flower. d. Calyx and dehiscing capsule. e. Capsule valve, interior view . f. Seed. Scale: a, b, bar = 15 mm; c, bar = 3.3 mm; d, bar = 2.3 mm; e, bar = 1.9 mm; f, bar = 0.7 mm. (Based on: a, d–f, *Ton 5340*; b, *Ton 7375*; c, *Ton 5430* and *Ton 7375*.) Drawn by Barnaby Hall.

Dichasia sessile (except at proximalmost nodes), 1-flowered; bracts 1.4–2.2 mm long; bracteoles 1.3–2.2 mm long; calyx 4.5–7.5 mm long; corolla externally glabrous, lobes of lower lip 3–3.5 mm long; pollen globose-oblong, peripheral band continuous, vertucate. S. breedlovei.

The epithet honors the collector of the only known specimens of this taxon, Alush Ton (Alonso Méndez Ton). Ton generously assisted me during field work in Mexico in 1989 and 1990. It is fitting that species honoring both Dennis Breedlove and Alush Ton both occur in the paraje of Yashanal near Tenejapa. These avid plant collectors and ethnobotanists worked together for many years in this and other regions of Chiapas. Their joint labors continue to bear significant fruit. Berlin et al. (1974) provided a brief biographical sketch of Ton.





Stenostephanus breedlovei T. F. Daniel, Proc. Calif. Acad. Sci. 48: 277. 1995.— TYPE: MEXICO. Chiapas: Mpio. Tenejapa, near paraje Yashanal, 2400 m, 5 Mar 1981, D. Breedlove 49995 (holotype: CAS!; isotypes: C! K! MEXU! MO! US!).

Shrubs to 1.2 m tall. Young stems quadrate to quadrate-sulcate, bifariously pubescent with retrorsely appressed eglandular trichomes 0.2-0.4 mm long. Leaves petiolate, petioles to 36 mm long, blades ovate-elliptic to elliptic to obovateelliptic, 32-140 mm long, 11-45 mm wide, 2.4-4.3 times longer than wide, acuminate to subfalcate at apex, acute to subattenuate at base, surfaces pubescent with antrorse to antrorsely appressed eglandular trichomes along major veins, margin entire to subcrenate, ciliate. Inflorescence of terminal racemes (to thyrses) to 200 mm long, rachis subquadrate-flattened to somewhat ridge-angled, evenly pubescent with an understory of erect mostly eglandular trichomes 0.05-0.2 mm long and an overstory of flexuose glandular trichomes 0.2-0.5 mm long; dichasia opposite or alternate, 1-flowered, sessile (or borne on peduncles to 6 mm long at proximalmost nodes). Bracts triangular-subulate to subulate, 1.4-2.2 mm long, 0.5-0.8 mm wide, abaxial surface glabrous or with a few antrorsely appressed eglandular trichomes or with flexuose glandular trichomes to 0.3 mm long. Bracteoles triangular-subulate to subulate, 1.3-2.2 mm long, 0.3-0.4 mm wide, abaxial surface pubescent like rachis. Flowers pedicellate, pedicels 2.5-5.5 mm long, pubescent like rachis. Calyx 4.5-7.5 mm long, abaxially pubescent like rachis, lobes lance-subulate, 3.5-6.2 mm long, equal to subequal in length, 0.6-0.9 mm wide. Corolla linear to subfusiform in bud, red, 25-29 mm long, externally glabrous (margins of lobes with a few flexuose eglandular trichomes evident at apex of buds), tube 20-25 mm long, ± gradually expanded distally into a throat, narrow proximal portion 4-8 mm long, 2-3 mm in diameter, throat not conspicuously saccate, 12.5-19 mm long, 5-7 mm in diameter, widest near midpoint, upper lip straightforward to erect, 4-4.7 mm long, 1.9-2.5 mm wide, lower lip 3-lobed, 4-5 mm long, lobes 3-3.5 mm long, 2-2.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of corolla tube), 22-31 mm long, thecae 3-3.4 mm long; pollen globose oblong, peripheral band continuous, verrucate. Style 29-33 mm long, stigma 0.2–0.3 mm long. Capsule not seen.

Illustrations. Proc. Calif. Acad. Sci. 48: 277, fig. 11. 1995; Flora of Chiapas 4: 137, fig. 35. 1995.

Phenology. Flowering: January-March.

Distribution. Mexico (Chiapas; Fig. 6); in cloud forests and pine-oak-Liquidambar forests; 1600–2460 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: Mpio. Tenejapa, near paraje Yashanal, D. Breedlove 49644 (CAS); Mpio. Jitotol, 5 km SE of Jitotol toward Bochil, D. Breedlove & B. Keller 49368 (CAS, MEXU, MICH, MO).

Stenostephanus breedlovei occurs in the vicinity of S. alushii on the Central Plateau of Chiapas. Differences between these species are noted under the latter taxon. No additional collections of S. breedlovei have been seen since I treated the species in 1995; however, the description above contains some information not previously provided.

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Stenostephanus chiapensis T. F. Daniel, Proc. Calif. Acad. Sci. 48: 278. 1995.— TYPE: MEXICO. Chiapas: ridge above Ejido Berriozábal near Cerro Boquerón, 2440 m, 29 Nov 1991, D. Breedlove & C. Burns 72688 (holotype: CAS!; isotypes: C! K! MEXU! MICH! MO! US!).

Shrubs to 1.5 m tall. Young stems quadrate-sulcate to ridge-angled, bifariously pubescent (for varying distances proximal to nodes) with flexuose to antrorse to antrorsely appressed eglandular trichomes 0.1-0.5 mm long. Leaves petiolate (distalmost pair often sessile), petioles to 95 mm long, blades ovate to ovate-elliptic, 13-200 mm long, 7-91 mm wide, 1.4-3 times longer than wide, acuminate to abruptly acuminate at apex, acute to attenuate at base (distalmost pair rounded to cordate at base), surfaces glabrous or pubescent with antrorse eglandular trichomes on major veins, margin entire to crenate, ciliate. Inflorescence of terminal (or sometimes appearing axillary) racemes or panicles of racemes to 28 cm long, rachis ridge-angled, (sparsely to) densely and evenly pubescent with an understory of erect to flexuose eglandular trichomes 0.2-0.5 mm long or erect to subflexuose subglandular to glandular trichomes 0.05-0.2 mm long and an overstory of flexuose glandular trichomes 0.1-2 mm long; dichasia opposite or alternate, 1-3 (-many)flowered, sessile to subsessile (i.e., borne on peduncles to 1 mm long). Bracts triangular to subulate, 1.2-2.5 mm long, 0.4-1 mm wide, abaxial surface pubescent like rachis or nearly glabrous. Bracteoles and secondary bracteoles triangular to subulate to linear, 0.8-2 mm long, 0.2-1 mm wide, abaxial surface pubescent like bracts or nearly glabrous. Flowers pedicellate, pedicels 1-4 mm long, pubescent like rachis, lateral flowers (if present) lacking secondary peduncles or borne on secondary peduncles to 1 mm long. Calyx 4-13 mm long, 4-8.7 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis, lobes linear-lanceolate to lance-subulate, 3.5-12 mm long, equal to subequal in length, 0.6-0.9 mm wide. Corolla ± c-shaped in bud, red (to orangish) dorsally and yellow ventrally, 18-23 mm long, externally glabrous or often appearing glabrous but inconspicuously puberulent with trichomes <0.1 mm long and sometimes also with a few flexuose eglandular trichomes to 0.4 mm long, tube 14-21 mm long, abruptly expanded distally into a throat, narrow proximal portion 2-4 mm long, 2-2.5 mm in diameter, throat saccate, 12-17 mm long, 5.5-7.5 mm in diameter, widest near base or midpoint and \pm narrowed distally, upper lip straightforward to erect, 2.5-4 mm long, 1-1.4 mm wide, lower lip absent (corolla truncate there) or consisting of lobes <0.5 mm long and wide. Stamens inserted at base of throat (i.e., in proximal 1/3 of corolla tube), 17-35 mm long, thecae 2.6-3.6 mm long, pollen globoseelongate, peripheral band continuous, verrucate. Style 22-31 mm long, stigma 0.2 mm long. Capsule 12-16 mm long, glabrous, stipe 3-5 mm long, head ellipsoid. Seeds 2.5–3.8 mm long, 1.6–2.2 mm wide, immature surfaces \pm bubbly tuberculate, mature surfaces tuberculate to \pm rugulate, tubercles mostly subconical to conical, lacking barbs.

Illustration. The illustration purporting to be this species in the protologue and in Daniel (1995b), based on *Nelson 3774*, is actually *S. tacanensis*, based on *Nelson 3794*. Figure 7 portrays *S. chiapensis*. The illustration of *S. tacanensis* is reproduced here (Fig. 14) in order to facilitate comparison between these species.

Phenology. Flowering and fruiting: November-May.

Distribution. Mexico (Chiapas; Fig. 6); in montane rain forests and cloud forests; 1500–2400 m.



FIG. 7. Stenostephanus chiapensis. a. Inflorescence with distal leaves. b. Proximal leaf. c. Inflorescence node with flower. d. Calyx and capsule. e. Seed. Scale: a, bar = 15 mm; b, bar = 16.7 mm; c, bar = 3.6 mm; d, bar = 3.1 mm; e, bar = 1.1 mm. (Based on *Breedlove 72688*.) Drawn by Hoc Kho.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: Mpio. Villa Corzo, E base of Cerro Tres Picos near Cerro Bola along road SW of Colonia Agronomos Mexicanos, *D. Breedlove 24984* (DS, ENCB, MO), *D. Breedlove & R. Thorne 30229* (DS, ENCB, MICH, MO, TEX); SE side of Cerro Tres Picos and ridges near summit, *D. Breedlove 34374* (DS, ENCB, MEXU, MICH, MO, TEX); from Chicharras [Las Chicharras, ca. 23 mi NE of Tapachula], *E. Nelson 3774* (GH, US); Mpio. Motozintla, track from Ejido Boquerón to Cerro Boquerón, 15°15'N, 92°17'W, *P. Stafford et al. 387* (BM, F).

Stenostephanus chiapensis is known from two regions in the Sierra Madre de Chiapas. Plants from near Cerro Tres Picos differ slightly from those collected nearer to the Guatemalan border by the understory pubescence of the inflorescence rachis, which consists of generally longer (0.2–0.5 mm long), eglandular trichomes in the former and generally shorter (0.05–0.2 mm long), subglandular to glandular trichomes in the latter. Pubescence in the inflorescence of *Strafford et al. 387* varies from very sparse on some shoots to rather dense on others.

Stenostephanus chiapensis resembles S. tacanensis in structure of the inflorescence and has been collected in the vicinity of that species (i.e., Nelson collections

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from near Chicharras). These species can be distinguished by the characters summarized in the key to species. Corollas of *S. chiapensis* resemble those of *S. monolophus* in color and form. *Stenostephanus monolophus* also occurs in the Sierra Madre de Chiapas. These species can be distinguished by the following couplet:

Inflorescence racemose, dichasia sessile to subsessile (i.e., borne on peduncles to 1 mm long), lateral flowers (if present) sessile or borne on secondary peduncles to 1 mm long; pollen globose-elongate. S. chiapensis.

Inflorescence thyrsoid, dichasia pedunculate, peduncles 6–28 mm long, lateral flowers borne on secondary peduncles 4.5–21 mm long; pollen globose-elliptic to globose-oblong. *S. monolophus.*

Stenostephanus glaber (Leonard ex Lundell) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 280. 1995, as "glabrus." *Glockeria glabra* Leonard ex Lundell, Contr. Univ. Michigan Herb. 6: 60. 1941. *Hansteinia glabra* (Leonard ex Lundell) D. N. Gibson, Fieldiana, Bot. 34: 62. 1972.—Type: MEXICO. Chiapas: "Mt. Pasitar" [Mt. Paxtal], 4 Aug 1937, *E. Matuda S-212* (holotype: US!; isotypes: GH! MICH! MO! NY! US!).

Perennial herbs or shrubs to 1.5 m tall. Young stems subquadrate to quadratesulcate, mostly glabrous, sometimes with a few scattered or bifariously disposed antrorse to antrorsely appressed eglandular trichomes to 0.3 mm long (especially near nodes or sometimes up to 25 mm proximal to a node). Leaves petiolate (distal pairs subsessile to sessile), petioles to 75 mm long, blades ovate to ovateelliptic, 19-152 mm long, 8-66 mm wide, 1.4-2.8 times longer than wide, acuminate at apex, attenuate at base, surfaces glabrous or with sparse coarse antrorse eglandular trichomes on midvein, margin entire to sinuate to subcrenate, ciliate or eciliate. Inflorescence of terminal thyrses to 17 cm long, rachis subquadrate to \pm flattened to ridge-angled, glabrous or puberulent with erect to flexuose subglandular to glandular trichomes 0.05-0.1 mm long (rarely with a few flexuose glandular trichomes to 0.5 mm long as well); dichasia opposite or alternate, 3-manyflowered, pedunculate, peduncles 4-13 mm long, glabrous or pubescent like rachis. Bracts triangular to linear to subulate, 1.5-3.5 mm long, 0.5-0.8 mm wide (proximalmost pairs sometimes foliose and larger), abaxial surface glabrous. Bracteoles and secondary bracteoles subulate, 1.3-3.1 mm long, 0.3-0.6 mm wide, abaxial surface glabrous (or sometimes sparsely puberulent). Flowers pedicellate, pedicels 1.5-4 mm long, glabrous or pubescent like rachis, lateral flowers borne on secondary peduncles 3-12 mm long. Calyx 4-11 mm long, 4-8 mm long during anthesis and accrescent in fruit, abaxially glabrous or with a few to many glandular trichomes 0.05-0.8 mm long, lobes lance-subulate, 3.5-9.5 mm long, subequal in length, 0.4-0.7 mm wide. Corolla c-shaped to s-shaped in bud, red to dark reddish purple proximally and white distally, 19-26 mm long, externally glabrous, tube 15-21 mm long, abruptly expanded distally into a throat, narrow proximal portion 2-3 mm long, 1-2 mm in diameter, throat saccate, 13-19 mm long, 6.5-10 mm in diameter, widest proximally and narrowed distally, upper lip straightforward to erect, 2.5-4.2 mm long, 1.2-2.2 mm wide, lower lip (sometimes not evident) 3-lobed, 0.5-0.7 mm long, lobes 0.2-0.5 mm long, 0.3-0.4 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 22-33 mm long, thecae 2.8-3.5 mm long; pollen globose-elliptic, peripheral band continuous, striate-rugulate. Style 26-35 mm long, stigma 0.2-0.3 mm long. Capsule 11.5-14 mm long, glabrous, stipe 3.5-5 mm long, head ellipsoid. Seeds 2-2.5 mm long, 1.7-21. mm wide, immature surfaces bubbly tuberculate, mature surfaces ± verrucate to rugulate, tubercles rounded to subconical, lacking barbs.

Illustration. Contr. Univ. Michigan Herb. 6: 61, fig. 4. 1941.

Phenology. Flowering and fruiting: August, November–January.

Distribution. Mexico (Chiapas; Fig. 6) and Guatemala; in cloud forests; 1900–2120 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: SE of El Triunfo Pass above Finca Prusia, J. Cloud 4 (CAS); El Triunfo Biosphere Reserve, between Deslave and Camp. El Triunfo along trail from El Paval to Camp. El Triunfo, ridgetop, ca. 15°39'N, 92°50'W, T. Daniel et al. 8405 (CAS, CIES, ENCB, K, MEXU, MICH, MO, NY, US); Mpio. Jaltenango, Reserva El Triunfo, Poligono 1, Palo Gordo–Nueva Alemania, ca. 15°39'N, 92°48'W, M. Heath & A. Long 515 (CHIP, MEXU); El Triunfo, Angel Albino Corzo, T. MacDougal s.n. (ENCB, NY); Mt. "Pasitar," E. Matuda 1656 (MEXU, MICH, US).

Daniel (1995b) noted variation in the presence and density of trichomes among collections of this species. All of the variation in pubescence of the rachis noted in the description above can be seen among individuals of *Daniel et al. 8405*. The distinctions between this species and *S. monolophus* were questioned by Daniel (1995b); the two are separable by the distinctions noted in the key to species.

Stenostephanus gracilis (Oerst.) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 280. 1995. Hansteinia gracilis Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 143. 1855, non Hansteinia gracilis (Nees) Lindau, 1893. Hansteinia oerstedii Lindau, Bot. Jahrb. Syst. 18: 58. 1893, nom. superfl.— TYPE: COSTA RICA. San José: Mt. Jaris [NE of Santiago de Puriscal, fide Durkee 1986] (fide protologue); prope San José (fide specimen labels), Nov 1846, A. Oersted 10660 (holotype: C!; isotype: CAS!; probable isotype: K!).

Shrubs to 2 m tall. Young stems subquadrate to quadrate-sulcate to \pm flattened, pubescent with flexuose to antrorse to antrorsely appressed eglandular trichomes 0.2-0.3 mm long, trichomes ± concentrated in 2 lines. Leaves subsessile to petiolate (distalmost pair sessile), petioles to 45 mm long, blades (lance-ovate to) ovate to elliptic, 37-270 mm long, 22-105 mm wide, 1.4-2.6 (-3.9) times longer than wide, acuminate at apex, attenuate (or distalmost pair cordate) at base, surfaces pubescent with antrorse eglandular trichomes (especially along major veins) and sometimes with scattered flexuose eglandular trichomes as well, margin entire to subsinuate to crenulate, ciliate. Inflorescence of terminal thyrses or panicles of thyrses to 50 cm long, rachis ± flattened to ridge-angled to subquadrate, densely and evenly pubescent with an understory of erect to flexuose eglandular trichomes 0.05-0.3 mm long and an overstory of flexuose glandular (sometimes appearing eglandular in Croat 47536) trichomes 0.2-1.5 mm long; dichasia opposite or alternate, (1-) 3-many-flowered, pedunculate, peduncles (1-) 2-52 mm long, pubescent like rachis, terminal (i.e., central) flower of a dichasium sometimes absent (caducous or suppressed ?) and the dichasium then appearing like an inflorescence branch. Bracts triangular to subulate to lance-subulate, (1.3-) 1.5-4 (-7.5) mm long, 0.8-1.5 mm wide, abaxial surface pubescent like rachis or glabrate. Bracteoles and secondary bracteoles triangular to subulate to lancelinear, (1-) 1.3-2.2 (-5) mm long, 0.6-0.9 mm wide, abaxial surface pubescent like rachis or glabrate. Flowers pedicellate, pedicels 2-7 mm long, pubescent like rachis, lateral flowers borne on secondary peduncles 2-21 mm long. Calyx 5.5-14 mm long, 5.5–7.5 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis, lobes lance-ovate to lance-linear to elliptic to oblanceolate, 5-12 mm long, subequal in length, 1.1-3.2 mm wide. Corolla subellipsoid to \pm c-shaped in bud, yellow-orange with red to maroon markings distally, 15–20 mm long, externally pubescent with flexuose eglandular (and a few glandular) trichomes 0.2–0.7 mm long, tube 14–17.5 mm long, gradually to abruptly expanded distally into a throat, narrow proximal portion, 3.5-5 mm long, 2-2.5 mm in diameter, throat not saccate to slightly saccate, 9–14 mm long, 3.6-4.8 mm in diameter, widest near midpoint, upper lip straightforward to erect, 2–3 mm long, 1–1.1 mm wide, lower lip 3-lobed, 1.5-2.1 mm long, lobes 1–2 mm long, 1.2-2 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of tube), 17–28 mm long, thecae 2.5-3mm long; pollen globose-elliptic, peripheral band continuous, irregularly subverrucate to rugulate and with a central row of gemmae to bacculae. Style 19–30 mm long, stigma 0.2-0.3 mm long. Capsule 10–14 mm long, pubescent with erect to flexuose eglandular trichomes <0.05-0.2 mm long, stipe 3–6 mm long, head subellipsoid. Seeds 2.5–3.7 mm long, 2–3.2 mm wide, immature surfaces tuberculate, mature surfaces subreticulate and with tubercles \pm restricted to periphery, tubercles subconical, bearing retrorse barbs.

Illustration. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: t. 4, figs. 23–26. 1855.

Phenology. Flowering: October-November and February; fruiting: October, February.

Distribution. Mexico (Chiapas; Fig. 8) and Costa Rica; in tropical deciduous forests (near springs) and montane rain forests; 400–1380 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: sitios of Unión Juárez, *D. Breedlove* 71524 (CAS); Mpio. Ocozocoautla de Espinosa, 13–15 km S of Ocozocoautla toward Villa Flores, *D. Breedlove & E. McClintock* 23469 (DS); between Finca California (at base of S slope of Monte Ovando and ca. 4 km N of Ovando Turquia) and summit of Cerro Ovando, *T. Croat* 47536 (MO, NY); Mpio. Mapastepec, Sierra de Soconusco, road toward Tuxtla Gutiérrez from Hwy 200 (5.5 mi NW turnoff to Mapastepec), 6.5–8.5 mi up road, ca. 15°32'N, 92°48'W, *T. Croat & D. Hannon* 63327 (CAS); Camino de Huixtla, *H. Green* 3 (DS); Madre Mía, El Rastrojo, Tonalá, *T. MacDougall s.n.* (MEXU); Finca Maravillas, *L. Quarles van Ufford* 164 (U).

Mexican collections cited below closely resemble a collection from Costa Rica (*Herrera Ch. et al. 292*, CAS and MEXU) that was annotated by Durkee as *Hansteinia stricta* (Leonard) D. N. Gibson. The Chiapan specimens differ from the type of *H. stricta* by their pedunculate (vs. sessile), mostly 3–many-flowered (vs. 1-flowered) dichasia and their capsules with eglandular (vs. glandular only) pubescence. Rather, they conform to the type of *H. gracilis*.

Daniel (1995b) treated *Breedlove & McClintock 23469* as similar to *Stenostephanus gracilis*, but differing by its apparently sessile and 1-flowered dichasia. Restudy of this collection reveals that it is probably best treated as a somewhat anomalous collection of *S. gracilis*. Although some dichasia are 1-flowered, all appear to be borne on peduncles of at least 1 mm in length. Other dichasia that appear to be sessile on lateral branches of the inflorescence likely represent secondary flowers of lateral, pedunculate dichasia of the thyrse (as noted in the description above). Such dichasia with the terminal (i.e., central) flower either caducous or suppressed sometimes appear as lateral branches (i.e., indeterminate axes) of the inflorescence in other specimens of the species as well. Contrary to the implication by Daniel (1995b: 140), capsules of *Breedlove & McClintock 23469* are pubescent with eglandular trichomes like those found elsewhere in *S. gracilis*.



FIG. 8. Distribution of S. gracilis and of S. oaxacanus in Mexico.

Stenostephanus guerrerensis T. F. Daniel, sp. nov.—Type: MEXICO. Guerrero: 1–3 km NW of Puerto El Gallo, 2500–2750 m, 11 Nov 1973, *D. Breedlove 36060* (holotype: CAS!; isotypes: ENCB! MEXU! MICH!).

Herba perennis vel frutex usque ad 1.5 m altus. Folia petiolata (vel folia summa plerumque sessilia), laminae lanceolato-ovatae vel ovatae vel ellipticae, 12–160 mm longae, 5–39 mm latae, 2–5.3-plo longiores quam latiores. Inflorescentia thyrsi vel paniculae thyrsorum terminales (vel axillares) ex dichasiis constans; rachis pubescens trichomatibus glandulosis et eglandulosis; dichasia pedunculata, 3–multi-flora; flores pedicellati. Corolla rubra et alba, 18–22 mm longa, extus puberula et pubescens; faux 13–16 mm longa et 6.5–9 mm diametro; labium superiorus 1.1–3.5 mm longum; labium inferiorus 1.3–3.5 mm longum lobis 1–3.5 mm longis. Capsula 9–13 mm longa, pubescens trichomatibus eglandulosis.

Perennial herbs or shrubs to 1.5 m tall. Young stems quadrate to quadratesulcate, \pm bifariously pubescent with flexuose-retrorse eglandular trichomes 0.3–0.7 mm long. Leaves petiolate (distalmost pair usually sessile), petioles to 25 mm long, blades lance-ovate to ovate to elliptic, 12-160 mm long, 5-39 mm wide (distalmost pair sometimes smaller), 2-5.3 times longer than wide, acute to acuminate to subfalcate at apex, (rounded to) acute to attenuate at base, surfaces pubescent (primarily along major veins) with flexuose-antrorse to antrorsely appressed eglandular trichomes, margin entire to subsinuate, often ciliate. Inflorescence of (axillary and) terminal thyrses or panicles of thyrses to 23 cm long, rachis quadrate-sulcate (to \pm flattened), densely and \pm evenly pubescent with an understory of erect to subflexuose eglandular trichomes 0.1-0.5 mm long and a sparser overstory of erect to flexuose glandular trichomes 0.3-1 mm long; dichasia opposite or alternate, 3-many-flowered, pedunculate, peduncles 6-45 mm long, pubescent like rachis. Bracts subulate, 1.2-5 mm long, 0.3-1 mm wide, abaxial surface pubescent with antrorse to acropetally pointed eglandular trichomes 0.1-0.2 mm long. Bracteoles and secondary bracteoles subulate, 1-3 mm long, 0.2-0.4 mm wide, abaxial surface pubescent like bracts. Flowers pedicellate, pedicels 2-6 mm long,

pubescent like rachis, lateral flowers borne on secondary peduncles 3-20 mm long. Calyx 3.5-9 mm long, 3.5-4.7 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis (or with the understory trichomes \pm antrorse), lobes lanceolate to lance-subulate, 3-8 mm long, subequal in length, 0.5-0.8 mm wide. Corolla subellipsoid to subfusiform in bud, red and white, 18-22 mm long, externally papillate-puberulent with inconspicuous trichomes to 0.05 mm long and pubescent (at least proximally) with flexuose eglandular trichomes to 1 mm long, tube 15-18.5 mm long, abruptly expanded distally into a throat, narrow proximal portion 1.7-2.8 mm long, 2-2.5 mm in diameter, throat saccate, 13-16 mm long, 6.5-9 mm in diameter, widest near base or midpoint, upper lip straightforward, 1.1-3.5 mm long, 1.5-3 mm wide, lower lip 3-lobed, 1.3-3.5 mm long, lobes 1-3.5 mm long, 1-2.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 23-27 mm long, thecae 2.9-3.5 mm long; pollen globose-elongate, peripheral band continuous, subpsilate to microverrucate. Style 22-31 mm long, stigma 0.2 mm long. Capsule 9-13 mm long, pubescent with flexuose eglandular trichomes 0.3-0.7 mm long, stipe 3-5 mm long, head ellipsoid. Seeds 2-3 mm long, 1.3-2 mm wide, immature surfaces bubbly tuberculate, mature surfaces rugulate to sparsely verrucate, tubercles rounded, lacking barbs.

Illustration. Fig. 9.

Phenology. Flowering: October-January; fruiting: November-January.

Distribution. Mexico (Guerrero; Fig. 10); in mesophytic montane forests, oak forests, and pine-oak forests; 2150–2650 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. GUERRERO: W slope of Cerro Teotepec, near Puerto El Gallo, *D. Breedlove 61946* (CAS, ENCB, MEXU); Mpio. Atoyac de Alvarez, 9 km SW de Puerto del Gallo, camino a Atoyac, *E. Martínez S. et al. 5087* (MEXU); estribaciones SW del Cerro Teotepec, ± 2 km NE del Campamento El Gallo, ca. 17°28'N, 100°13'W, *J. Rzedowski & R. McVaugh 183* (CAS, MICH).

Stenostephanus guerrerensis is known only from the slopes of Cerro Teotepec in the Sierra Madre del Sur of central Guerrero. It shares several characteristics with *S. gracilis* (e.g., inflorescence structure, corolla size and pubescence, and capsule pubescence) but differs from that species by its longer cauline trichomes, shorter calyces with narrower lobes, differently colored corolla with a shorter unexpanded proximal tube and a wider throat, differently shaped pollen, and differently ornamented seminal tubercles. *Stenostephanus guerrerensis* can be distinguished from the other species occurring in Guerrero, one of which (*S. harleyi*) also occurs on the slopes of Cerro Teotepec, by the following key:

- 1. Calyx 3.5–4.7 mm long, abaxial surface pubescent with eglandular and glandular trichomes; corolla externally papillate and pubescent with eglandular trichomes; capsule pubescent with eglandular trichomes; pollen globose-elongate. *S. guerrerensis.*
- 1. Calyx 4.5–9 mm long, abaxial surface glabrous or pubescent with eglandular trichomes only; corolla externally glabrous; capsule glabrous; pollen globose-elliptic.
 - Corolla 12–16 mm long, throat 3.9–5.5 mm in diameter; inflorescence rachis pubescent; calyx abaxially pubescent with eglandular trichomes (to nearly glabrous), lobes lance-subulate; stamens 12–16 mm long, thecae 2.4–3 mm long.
 S. harleyi.
 - Corolla 20–26 mm long, throat 6.5–8.5 mm in diameter; inflorescence rachis glabrous; calyx abaxially glabrous, lobes lance-linear to linear; stamens 24–27 mm long, thecae 3.2–3.8 mm long.
 S. haematodes.



FIG. 9. *Stenostephanus guerrerensis*. a. Habit. b. Leaf. c. Flower. d. Calyx and capsule. e. Seed. Scale: a, bar = 15 mm; b, bar = 12.5 mm; c, bar = 2.9 mm; d, bar = 2.5 mm; e, bar = 0.9 mm. (Based on: a, *Breedlove 61946*; b, c, *Rzedowski & McVaugh 183*; d, e, *Breedlove 36060*.) Drawn by Jenny Speckels.

Stenostephanus haematodes (Schltdl.) T. F. Daniel, comb. nov. Justicia haematodes Schltdl., Linnaea 7: 394. 1832. Habracanthus haematodes (Schltdl.) Nees in A. DC., Prodr. 11: 312. 1847. Glockeria haematodes (Schltdl.) Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 141. 1855.— TYPE: MEXICO. Veracruz: "In regione calidiore infra la Cuesta grande de Chiconquiaco," 29 Sep 1829, C. Schiede 76 (holotype: B, destroyed, photos: F! GH! NY! US!; isotypes: GOET (photo at US!), BM! NY! P! W!).
Galeottia gracilis Nees in A. DC., Prodr. 11: 311. 1847. Glockeria gracilis (Nees) Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 140. 1855. Hansteinia gracilis (Nees) Lindau, Bot. Jahrb. Syst. 18: 58. 1893, non Hansteinia gracilis Oerst., 1855.—Type: MEXICO. Veracruz: Mirador, Aug 1838, J. Linden 197 (lectotype, here designated: K!; isolectotype: MICH!).



FIG. 10. Distribution of S. guerrerensis, S. harleyi, and S. purpusii, and of S. silvaticus in Mexico.

Perennial herbs or shrubs to 2.5 m tall. Young stems terete to quadrate to quadrate-sulcate to \pm flattened, glabrous or (sometimes evenly to soon) \pm bifariously pubescent with (flexuose-retrorse to) flexuose to antrorse to antrorsely appressed eglandular trichomes 0.1-0.7 mm long, the lines of trichomes (if present) extending either the entire length of the internode or only for a short distance below the node. Leaves petiolate (distal pairs sometimes subsessile to sessile), petioles to 55 mm long, blades ovate to elliptic to obovate (distalmost pair sometimes subcordate to cordate), 23-240 mm long, 6-105 mm wide, 1.6-4.3 times longer than wide, acuminate to subfalcate (to caudate) at apex, acute to attenuate (distal pair sometimes rounded to cordate) at base, surfaces glabrous or pubescent with flexuose to antrorsely appressed eglandular trichomes to 1.1 mm long, trichomes usually restricted to major veins (at least on abaxial surface), margin entire to conspicuously crenate, often ciliate. Inflorescence of terminal thyrses (rarely panicles of thyrses) to 45 cm long, rachis (main axis sometimes suppressed and inflorescence expansion occurring by lateral growth) quadrate-sulcate to ridge-angled to \pm flattened, glabrous, pubescent like young stems, or evenly pubescent with an understory of erect to flexuose to antrorse eglandular trichomes 0.1-0.3 mm long and an overstory (sometimes sparse) of flexuose glandular trichomes 0.3-1 mm long; dichasia (alternate and) opposite, 3-many-flowered, pedunculate, peduncles (3-) 13-55 mm long, glabrous, sparsely pubescent with cauline type trichomes, or pubescent like rachis. Bracts triangular to subulate to linear, 0.5-3.5 (-9.5) mm long, 0.3-1.1 mm wide, abaxial surface glabrous or pubescent (sometimes sparsely so) with antrorse eglandular trichomes to 0.2 mm long. Bracteoles and secondary bracteoles

triangular to subulate to linear, 0.5-2.2 (-5) mm long, 0.2-0.6 (-1) mm wide, abaxial surface glabrous or pubescent like bracts and sometimes with a few flexuose glandular trichomes like those sometimes found on rachis as well. Flowers pedicellate, pedicels 1.5-7 mm long, glabrous or pubescent like rachis (or with glandular trichomes absent), lateral flowers borne on secondary peduncles 4-30 mm long. Calyx 1.5-9 mm long, 1.5-5.5 (-7) mm long during anthesis and often accrescent in fruit, abaxially glabrous or pubescent with erect to antrorse eglandular trichomes 0.05–0.2 mm long and sometimes with scattered flexuose glandular trichomes like those of rachis as well, lobes triangular to subulate to lance-linear to linear, 1-8.2 mm long, equal to unequal in length, 0.3-1 mm wide. Corolla subellipsoid to subfusiform (rarely \pm curved) in bud, red to reddish purple, 20–37 mm long, externally glabrous or rarely with a few flexuose eglandular trichomes to 0.2 mm long near apex (best observed in bud) and/or along ventral side, tube 16-30 mm long, \pm abruptly expanded into a throat, narrow proximal portion (1–) 4–11 mm long, 1.4-3.7 mm in diameter, throat slightly to prominently saccate (appearing urceolate when saccate both dorsally and ventrally), 11-25 mm long, 4.5-13 mm in diameter, widest near base (or midpoint), upper lip straightforward to erect, (1.5-) 2.6-8 mm long, 1.5-3 mm wide, lower lip 3-lobed, 3-8 mm long, lobes 0.8-2.5 (-4.5) mm long, 0.5-2 (-4) mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3–1/2 of corolla tube), 22–37 mm long, thecae 3–4.5 mm long; pollen globose-elliptic, peripheral band discontinuous or continuous, variously sculptured (see discussion). Style 25-46 mm long, stigma 0.1-0.2 mm long. Capsule 9-19.5 mm long, glabrous, stipe 3-11 mm long, head ellipsoid to subellipsoid with slight medial constriction. Seeds 1.5-3.3 mm long, 1.3-2.2 mm wide, immature surfaces rugulate to bubbly tuberculate, mature surfaces subpsilate to verrucate and with tubercles (rarely nearly completely suppressed) concentrated near or restricted to periphery, tubercles rounded to subconical, lacking barbs.

Illustrations. Figure 11; Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: t. 5, fig. 21. 1855; Biol. cent.-amer., Bot. 5: tab. 67, figs. 6–14. 1882.

Local name. "Ni" (Huastec, Alcorn 3195).

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

Distribution. Mexico (Hidalgo, Oaxaca, Puebla, San Luis Potosí, Veracruz; Fig. 12); in deciduous forests (apparently mesic or temperate), oak forests, meso-phytic montane forests, montane rain forests, and cloud forests; (600–) 800–2100 m.

Additional Specimens Examined. Mexico. Guerrero: Distr. Montes de Oca, Pilas-Pasion, G. Hinton et al. 10758 (ARIZ, K, BR, F, G, GH, LL, MO, NY, TEX, US).-HIDALGO: Mpio. Tlanchinol, 6 km S de Tlanchinol, R. Hernández M. 5335 (MEXU, NY, US); Mpio. Tlanchinol, Tlanchinol, R. Hernández M. et al. 6400 (MEXU); Mpio. Tlanchinol, 5 km E de Tlanchinol, I. Luna V. 14 (MEXU); Mpio. Tlanchinol, camino a Tierra Colorada, I. Luna & S. Ocegueda 509 (MEXU); Tlanchinol, H. Puig 3042 (ENCB).—OAXACA: Tepanaxtla, Cuicatlán, G. Aguirre B. 25 (NY); Mpio. Comaltepec, Cerro Redondo, above La Esperanza, path leading from Hwy 175 up to power lines, 17°37'N, 96°22'W, B. Boyle & A. Boyle 726 (CAS, MEXU); 80 km S of Tuxtepec near Vista Hermosa, D. Breedlove & F. Almeda 56747 (CAS, MO, NY, US); NNE slope of Cerro Humo Chico [N of Ixtlán de Juárez jct. on road to Valle Nacional], D. Breedlove & D. Mahoney 72407 (CAS); Mpio. Valle Nacional, Cerro Mirador, 15 km NNW de Valle Nacional, 17°93'N, 96°22'W, J. Meave del Castillo et al. 1527 (MEXU); between Teotitlán del Camino and Chilchotla [Santa María Chichotla], 3 mi past turnoff to Huatla de Jiménez, T. Croat 48357 (CAS, MEXU, MO); Distr. Ixtlán, between Km 84 and 85 on Hwy 175 SW of Tuxtepec, 71 km NE of Ixtlán, ca. 17°35'N, 96°23'W, T. Daniel & S. Acosta C. 8359 (CAS, ENCB, K, MEXU, MICH, MO, NY, OAX, US); Mpio. San Pedro Yaneri, 17.3 km S of La Esperanza and 40.3 km SE of Valle Nacional, G. Davidse et al. 30253 (CAS, MO); province d'Oaxaca, A. Ghiesbreght s.n. (BR, GH, S, US); Mpio. Comaltepec, La Esperanza, 17°45'N, 96°30'W, R. López L. 534



FIG. 11. Stenostephanus haematodes. a. Habit. b. Leaf. c. Flower. d. Capsule. e. Seed. Scale: a, bar = 18.8 mm; b, bar = 15 mm; c, bar = 4.3 mm; d, bar = 3.8 mm; e, bar = 0.9 mm. (Based on: a, López L. 534 and Breedlove 56747; b, López L. 534; c, Breedlove 72407; d, e, Breedlove & Almeda 56747.) Drawn by Jenny Speckels.

(CAS, MEXU); Ixtlán, La Esperanza, Comaltepec, T. MacDougall s.n. (NY); entre Vista Hermosa y Comaltepec, Km 136 carretera Tuxtepec a Oaxaca, Sierra Juárez, G. Martínez, C. 317 (CHIP, F, MEXU, MO, US); Distr. Ixtlán, 31 km S de Valle Nacional, camino a Oaxaca, E. Martínez S. et al. 8784 (MEXU, NY); O de Cuasimulco (Rancho Grande), F. Miranda 1114 (MEXU); Mpio. Comaltepec, 11.4 km S de La Esperanza, carr. Tuxtepec-Oaxaca, R. Torres C. & L. Cortes 8738 (MEXU).-PUEBLA: Mpio. Cuetzalán, Finca de Los Flores, SE de Xochical, 20°01'N, 97°29'W, A. Campos V. et al. 407 (CAS), 530 (CAS, MEXU), P. Tenorio L. et al. 13942 (CAS, MEXU); Mpio. Hueytamalco, Rancho Las Margaritas, Hueytamalco, W. Conradt 71 (MEXU), 76 (MICH); cercanías de Atexcaco, D. Gold 330 (MEXU); Huitamalco, F. Liebmann 10655 (CAS, K, P, US); Mpio. Teziutlán, Puente Colorado, F. Ventura A. 1879 (MEXU, MO); Mpio. Teziutlán, Arroyo Frio, F. Ventura A. 17649 (ENCB, MO); Mpio. Hueytamalco, Hueytamalco, F. Ventura A. 20491 (CAS, ENCB, MEXU); Mpio. Zacapoaxtla, La Escalera, F. Ventura A. 22176 (ENCB).-SAN LUIS POTOSÍ: Mpio. Aquismon, Tampaxal, J. Alcorn 3195 (TEX).-VERACRUZ: Mpio. Tonayan, Congregación Iztapan, S. Avendano R. 37 (ENCB, MEXU); Orizaba, M. Botteri 1097 (GH, K, US); Vallée de Cordova à la Grotte de la Coyaca, E. Bourgeau 2000 (B, BM, BR, G, GH, K, MO, NY, P, US); Ixhuatlancillo, M. Cabrera s.n. (ENCB); Fortín, 19°09'N, 96°58'W, J. Calzada 7967 (ENCB); Mpio. Xico, Cascada de Texolo, 19°26'N, 97°01'W, J. Calzada 8322 (MEXU, NY, WIS); Mpio. Jalapa, Puente Sedeño, carr. Jalapa-Banderilla, 19°34'N, 96°56'W, J. Calzada & R. Jiménez 4279 (ENCB, F); Mpio. Ixhuacán, al fondo de la barranquilla del Río Ixhuacán, entre El Aguacate y Patlanalan, Puebla, M. Cházaro & P. Hdz. de Ch. 4072 (CAS, F, NY, US); Mpio. Coatepec, La Cañada de Ramírez, M. Cházaro & H. Oliva 2023 (WIS); cordillera, H. Galeotti 7050 (BR, K, W); adelante de Cañada del Huérfano, A. Gómez-Pompa 1827 (MEXU); Mpio. Yecuatla, camino de Barranca del Maíz a Progreso de Juárez, 19°47'N, 96°47'W, C. Gutiérrez B. 2878 (MEXU); Santa Rita près Veracruz, L. Hahn s.n. (P); Mpio. Alto Lucero, Cerro del Sombrero, cerca de Plan de Las Hayas, R. Hernández M. 1623 (F, MEXU); barranca 3 km E of Tenejapa, I. Langman 3640 (US); Mirador, F. Liebmann 10658 (CAS, F, US), s.n. (GH, K); ca. 5 mi before Misantla along rd. from Banderilla, L. McDade 196 (DUKE, F); Mpio. Comapa, Barranca de Panoaya, 1.5 km NO de El Coyol, 19°12'N, 96°43'W, M. Medina A. & G. Castillo C. 865 (ENCB); Barranca Tenejapa, F. Miranda 4910 (MEXU); Engenio, Sierra de Ulnapa, F. Mueller 3034 (NY); vic. "La Calavera," 10 km N of Altotonga (13 km by road) on rd to Tlapacoyan, 19°15'N, 97°13'W, M. Nee & B. Hansen 18660 (F, MEXU); Sta. Rita, Sierra de Chiconquiaco, L. Nevling & A. Gómez-Pompa 7 (F); Barranca de Tenampa, Zacuapan, C. Purpus 2265 (F, GH, MEXU, MO, NY, UC, US);



FIG. 12. Distribution of S. haematodes, S. madrensis, and S. tacanensis.

Sierra Madre, Misantla-Naolineo, C. Purpus 6070 (GH, NY, UC, US); Barranca de Tenampa, C. Purpus 11068 (DS, F, MICH, MO, NY, UC, US); Barranca del Fortín near San Martín Tlacotepec, C. Purpus 16436 (F, GH); Mpio. Chiconquiaco, just N of Chiconquiaco on Xalapa-Misantla road in Sierra de Chiconquiaco, 19°44'N, 96°50'W, S. Reisfield 1224 (TEX, NY); Mpio. Tonayan, Congregación Iztapan, S. Reyes et al. 37 (CAS, F, US); ca. 3 km NW of Xico on trail to Perote at first bridge, 19°25'N, 97°03'W, S. Solheim & S. Reisfield 1475A (WIS); Mpio. Yecuatla, El Haya, F. Ventura A. 3425 (ENCB, MEXU, MO); Mpio. Acajete, Plan de Cedeño, F. Ventura A. 4670 (ARIZ, CAS, ENCB); Mpio. Yecuatla, Km 9, F. Ventura A. 5924 (ENCB, MEXU, MO, NY); Mpio. Huatusco, Dos Puentes, F. Ventura A. 7871 (ENCB, MEXU, MO); Mpio. Atzalan, La Calavera, F. Ventura A. 11605 (ENCB, GH, MEXU, MO); Mpio. Atzalan, La Calavera, F. Ventura A. 11605, MEXU, MO); Mpio. Atzalan, La Calavera, F. Ventura A. 11605 (ENCB, GH, MEXU, MO); Mpio. Atzalan, La Calavera, F. Ventura A. 18067 (ENCB, MEXU, MO, NY), 19294 (ENCB, MO); Mpio. San Andrés Tlalnehuayocan, San Antonio, F. Mpio. San Andrés Tlalnehuayocan, Otilpan, F. Ventura A. 19350 (ENCB, MO).—State undetermined: without locale, J. Linden 167 [=197?] (BR), M. Sessé & J. Mociño s.n. (OXF), M. Sessé et al. 289 (F, MA).

Nees's generic name *Galeottia* is a later homonym of *Galeottia* Rupr. (1842). In the addenda of his treatment of Acanthaceae for de Candolle's *Prodromus* (1847) Nees altered the generic name to *Glockeria* (a later homonym of *Glockeria* Goeppert, 1836) but did not effect a new combination for the only species, *Galeottia gracilis*. This species has usually been associated with the names *Glockeria gracilis* (Nees) Oerst. and *Hansteinia gracilis* (Nees) Lindau. The generic name of the former is illegitimate and the latter name is also illegitimate, being a later homonym of *Hansteinia gracilis* Oerst., a different species (see above). The new combination made above is based on an earlier name that also pertains to this species. In the protologue of *Galeottia gracilis* Nees (1847) cited *Linden 197* and *Galeotti 7050*, both from Veracruz, that he had seen in the herbaria of Hooker and Bentham. From these syntypes, the former collection at K is selected as the lectotype for this name.

Although endemic to Mexico, S. haematodes is among the most widely distributed species in the genus. At least three recognizable forms are included within the circumscription of this species at this time. Plants resembling the type represent the most commonly encountered and widely distributed form. In these plants the abaxial surfaces of the bracts, bracteoles, and calyces are glabrous (as are most of the inflorescence rachises); the bracteoles vary from 0.5 to 2.2 mm in length; the calyx lobes are triangular to triangular-subulate to lance-subulate; the narrow proximal portion of the corolla tube varies from 4 to 11 mm in length; and pollen grains have a variously sculptured peripheral band 2-5 µm wide that either lacks or possesses a central row of gemmae to baculae (Fig. 3a, d-f). Conspicuous morphological variation in this form of the species is mostly limited to numbers of flowers per dichasium (commonly more than three and sometimes more than 10) and form of the corolla throat (slightly to prominently saccate with saclike expansion(s) either ventral or both ventral and dorsal). The inflorescence rachis is usually glabrous, but in some individuals of Purpus 11068 it is sparsely pubescent like the young stems.

In northern Oaxaca, numerous collections (*Aguirre B. 25, Boyle & Boyle 726, Breedlove & Almeda 56747, Breedlove & Mahoney 72407, Daniel & Acosta C. 8359, Davidse et al. 30253, López L. 534, MacDougall s.n., Martínez C. 317, Martínez S. et al. 8784, Miranda 1114, Torres C. & Cortes 8738) differ in having the rachis, bracts, bracteoles, and calyces variously pubescent; the bracteoles vary from 2 to 5 mm in length; and the pollen grains have a verrucate peripheral band 4–7 µm wide that lacks a central row of gemmae to baculae (Fig. 3b). Collections of this form have been made in the Sierra Juárez, which lies to the southeast of most other localities of the species. In all other respects, these plants resemble the typical form. <i>Meave del Castillo et al. 1527*, also from the Sierra Juárez, resembles the typical form in lacking pubescence in the inflorescence.

Another geographically isolated form is represented by *Hinton et al. 10758* from central Guerrero (see below under *S. harleyi*). In this collection, the narrow proximal portion of the corolla tube varies from 1 to 2 mm in length (vs. 4 to 11 mm elsewhere in the species); the calyx lobes are lance-linear to linear (vs. triangular to subulate to linear-subulate elsewhere in the species); the upper lip of the corolla is 1.5-2 mm long (vs. 2.3-8 mm long elsewhere in the species); and the pollen grains have a peripheral band 10 μ m wide with a central row of gemmae to baculae (Fig. 3c). In all other respects, this collection resembles the typical form. Because the plants from Oaxaca and Guerrero noted above are more or less geographically isolated from the main distributional range of the species and because they differ from the commonly encountered form in several minor characters, one or both might eventually prove to be worthy of specific or infraspecific status.

The morphological diversity noted above and the relatively small number of characters found to be useful for distinguishing species of Mexican *Stenostephanus* can make identification of *S. haematodes* cumbersome with the key to species. In the key above it appears twice with the second entry (lead 13) referring to the form from Oaxaca, which sometimes has glandular trichomes on the calyx. Aside from being the only species known from eastern Mexico north of the Los Tuxtlas region of Veracruz, the typical (and most common) form of the species is distinctive by the following combination of characteristics: entirely red, often urceolate, and glabrous corollas; mostly glabrous and well-developed (i.e., each dichasium with many flowers) inflorescences often with the peduncles and pedicels somewhat wiry or capillary in appearance; and glabrous capsules.

Some of the diversity among pollen grains of *S. haematodes* is shown in Fig. 3. Further variation in sculpturing of the peripheral band was noted among collections representing the typical form of *S. haematodes*. For example, in *Ventura A.* 20491, the band is continuous, particularly narrow (2 μ m wide), psilate, and lacks a central row of gemmae to baculae (Fig. 3a). In other collections (e.g., *Hernández M. 5335, Luna & Ocegueda 509, Tenorio L. et al. 13942*) the band is similar (although sometimes discontinuous?) but somewhat wider (3–5 μ m). In other collections (e.g., *Ventura A. 4670, 7871*) the band is 5 μ m wide, discontinuous, and \pm reticulate to rugulate with a central row of gemmae to baculae (Fig. 3e, f).

Stenostephanus harleyi (Wassh.) T. F. Daniel, comb. nov. Hansteinia harleyi Wassh., Brittonia 43: 185. 1991.—Type: MEXICO. Guerrero: Sierra Madre del Sur, along Milpillas–Atoyac road via Puerto del Gallo, ca. 42.5 mi SW of Hwy 95, 11.5 mi SW of Filo de Caballo and 6.3 mi SW of Carrazal del Bravo, 16 Oct 1975, J. Reveal et al. 4239 (holotype: US!; isotypes: K! MARY, MEXU! NY! US!).

Perennial herbs to 3.5 dm tall. Young stems quadrate-sulcate to flattened, pubescent with flexuose-retrorse eglandular trichomes 0.3-0.7 mm long, trichomes \pm concentrated in 2 lines. Leaves petiolate (distal pairs sessile), petioles to 45 mm long, blades broadly ovate to ovate-elliptic, 13-95 mm long, 7-55 mm wide, 1.3-2.6 times longer than wide, acute to acuminate at apex, attenuate to rounded (distal leaves sometimes cordate) at base, surfaces sparsely pubescent with cauline type trichomes (especially along major veins), margin entire to subcrenate, usually ciliate. Inflorescence of (axillary and) terminal thyrses to 15 cm long, rachis ridgeangled to flattened, evenly pubescent with erect to flexuose eglandular trichomes 0.2-0.5 mm long; dichasia (alternate and) opposite, (1-) 3-many-flowered, pedunculate, peduncles 7-38 mm long, pubescent like rachis. Bracts subulate to linear, 1.4-2 mm long, 0.4-0.5 mm wide, abaxial surface nearly glabrous or pubescent with trichomes like those of rachis (or these \pm antrorse). Bracteoles and secondary bracteoles (if present) subulate to linear, 1.5-2.1 mm long, 0.3-0.4 mm wide, abaxial surface nearly glabrous or pubescent like bracts. Flowers pedicellate, pedicels 1.5-4.5 mm long, pubescent like rachis, lateral flowers (if present) borne on secondary peduncles 10-13 mm long. Calyx 4.5-11.2 mm long, 4.5-8 mm long during anthesis and accrescent in fruit, abaxially very sparsely pubescent with trichomes like those of rachis to nearly glabrous, lobes lance-subulate, 2.5-10.2 mm long, subequal in length, 0.5-0.7 mm wide. Corolla subellipsoid in bud, color unknown (appearing light yellowish in dried state), 12-16 mm long, externally glabrous, tube 10-13 mm long, expanded from at or near base (i.e., narrow proximal portion, if distinct, up to 2 mm long), throat ± saccate, 9-11 mm long, 3.9-5.5 mm in diameter, widest near midpoint, upper lip straightforward, 1.5-2 mm long, 1.5 mm wide, lower lip 3-lobed, 2-3 mm long, lobes 1.5 mm long, 1-1.1 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 12-16 mm long, thecae 2.4-3 mm long; pollen globose-elliptic, peripheral band continuous, \pm striate-rugulate and with a central row of baculae. Style 11–15 mm long, stigma 0.2 mm long. Capsule 10-13 mm long, glabrous, stipe 4.5-5 mm long, head subellipsoid. Seeds not seen.

Illustration. Brittonia 43: 186, fig. 1. 1991.

Phenology. Flowering and fruiting: October.

Distribution. Mexico (Guerrero; Fig. 10); in "mixed deciduous forest"; ca. 2575 m.

1999

This species was described by Wasshausen (1991) based solely on the type. As treated here, the species remains known only from that collection, which lacks information on corolla color. A collection, Hinton et al. 10758, with red corollas, from the same general region of central Guerrero is here treated in Stenostephanus haematodes (see discussion under that species) in spite of some similarities to S. harleyi. In both collections the narrow proximal portion of the corolla tube is either lacking or very short (up to 2 mm long) and inconspicuous. In most species of Stenostephanus, the narrow proximal portion of the corolla tube is conspicuous and longer. Interestingly, the only other species of the genus known from this region, S. guerrerensis, also has the narrow proximal portion of the corolla tube relatively short (1.8-2.8 mm long). The type of S. harleyi and Hinton et al. 10758 differ primarily in pubescence of the rachis (pubescent in the former vs. glabrous in the latter), corolla size (e.g., 12-16 mm long in the former vs. 20-26 mm long in the latter), stamen length (12-16 mm long in the former vs. 24-27 mm long in the latter), and thecae length (2.4-3 mm long in the former vs. 3.2-3.8 mm long in the latter). In all of these features, Hinton et al. 10758 resembles S. haematodes. The inclusion of Hinton et al. 10758 into that species is based on the totality of evidence available at this time rather than geographic proximity and a single shared, unusual feature. Because corollas of all collections, including those of S. guerrerensis, from central Guerrero resemble one another by their short or inconspicuous narrow proximal portion of the corolla tube, this feature may merely represent a common floral adaptation to a similar floral visitor among species in this region. Obviously, additional field studies in central Guerrero are desirable to sort out the taxonomy of Stenostephanus there.

Stenostephanus latilabris (D. N. Gibson) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. *Habracanthus latilabris* D. N. Gibson, Fieldiana, Bot. 34: 60. 1972.—Type: GUATEMALA. El Quiché: Cerro Putul, "Zona Reyna," 1640 m, 3 Dec 1934, A. Skutch 1836 (holotype: US!; isotype: A!).

Shrubs to 1.5 m tall. Young stems subquadrate to quadrate-sulcate, some internodes glabrous, others bifariously pubescent with flexuose eglandular trichomes 0.4-1.3 mm long (at least some internodes pubescent on each shoot). Leaves petiolate (distalmost pair often sessile to subsessile), petioles to 30 mm long, blades ovate to elliptic, 22-145 mm long, 10-63 mm wide, 2-2.8 times longer than wide, acuminate to subfalcate at apex, (rounded to) attenuate at base, surfaces sparsely pubescent with flexuose to antrorsely appressed eglandular trichomes, margin entire to crenate, ciliate. Inflorescence of (axillary and) terminal thyrses to 195 mm long, rachis quadrate-sulcate to ± flattened and ridge-angled, glabrous; dichasia opposite, expanded, (1-) 3-many-flowered, pedunculate, peduncles 6-17 mm long, glabrous. Bracts triangular-linear to linear-elliptic, 1-3 mm long, 0.7-1.2 mm wide, rounded at apex, abaxial surface glabrous. Bracteoles and secondary bracteoles triangular to linear, 0.8-2.2 mm long, 0.4-0.8 mm wide, abaxial surface glabrous. Flowers subsessile to pedicellate, pedicels 0.5-1.8 mm long, glabrous, lateral flowers borne on secondary peduncles 2.5-12 mm long. Calyx 4-6 mm long, abaxially glabrous, lobes linear to lance-linear, 3.5-5 mm long, 0.6-1 mm wide, margins eciliate. Corolla subfalcate to subfusiform in bud, blue-purple, 10-14.5 mm long, externally glabrous, tube cylindrical (or expanded only at mouth), lacking a well-defined or saccate throat, 4-6 mm long, 0.9-1.4 mm in diameter, upper lip recurved to recoiled, lance-linear, 5-10 mm long, 0.7-1.7 mm wide, lower lip 3-lobed, 6–10 mm long, 5–8.5 mm wide, lobes 0.7-1 mm long, 0.7-1 mm wide (lobes rarely divided nearly to base of lip on aberrant corollas). Stamens inserted in distal 1/2-1/3 of corolla tube, 8–13 mm long, thecae 3–3.8 mm long; pollen globose-elliptic, peripheral band continuous, subverrucate to irregularly rugulate and with a central row of gemmae to baculae. Style 11–14 mm long, stigma 0.1-0.2 mm long. Capsule not seen.

Illustration. Fieldiana, Bot. 34: 61, fig. 2. 1972.

Phenology. Flowering: August.

Distribution. Mexico (Chiapas; Fig. 6) and Guatemala; in montane rain forests; ca. 1700 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: Mt. Tacaná, *E. Matuda 2485* (A, CAS, K, MEXU, MICH, TEX); Mpio. Unión Juárez, 3 km NE de Unión Juárez, *E. Ventura & E. López 4078* (MEXU, MO).

The obvious affinities of this species are with *S. silvaticus* (see discussion under Macromorphology). Another blue-flowered species from Guatemala, *Habracanthus azureus* D. N. Gibson, superficially resembles both *S. silvaticus* and *S. latilabris*, but differs in form of the corolla (having a longer, conspicuously saccate throat) and insertion of the stamens (in proximal 1/3 of corolla tube). The type of *S. latilabris* from Guatemala is described as having whitish corollas.

Stenostephanus madrensis T. F. Daniel, sp. nov.—Type: MEXICO. Oaxaca: Mpio. San Jerónimo Coatlán, 36 km SE de Cruz de Honduras, brecha a San Jerónimo Coatlán, 16°14'N, 97°00'W, 2400 m, 11 Jul 1992, A. Campos V. 4736 (holotype: CAS!; isotypes: CAS! MEXU! TEX!).

Herba perennis usque ad 1 m alta. Folia petiolata (vel folia summa sessilia), laminae ovatae vel ellipticae (vel obovato-ellipticae), 40–170 mm longae, 15–67 mm latae, 2.5–3.2-plo longiores quam latiores. Inflorescentia thyrsi vel paniculae thyrsorum axillares vel terminales ex dichasiis constans; rachis pubescens trichomatibus glandulosis; dichasia pedunculata, 3–multi-flora; flores pedicellati. Corolla rubra (et alba?), 15–19 mm longa, extus glabra; faux 12.5–14.5 mm longa et 5–7.8 mm diametro; labium superiorus 1.8–2.2 mm longum; labium inferiorus 2–3 mm longum lobis 1.5–2 mm longis. Capsula 12–15 mm longa, glabra.

Perennial herbs to 1 m tall. Young stems quadrate-sulcate, pubescent with flexuose to retrorse to antrorse eglandular trichomes 0.3-1.2 mm long, trichomes \pm evenly to quadrifariously disposed. Leaves petiolate (distalmost leaves sessile), petioles to 45 mm long, blades ovate to elliptic (to obovate-elliptic), 40-170 mm long, 15-67 mm wide, 2.5-3.2 times longer than wide, acuminate to subfalcate at apex, acute to attenuate at base, surfaces pubescent with flexuose to antrorse eglandular trichomes, trichomes sometimes restricted to major veins on abaxial surface, margin entire to subsinuate, ciliate. Inflorescence of axillary and terminal thyrses or panicles of thyrses to 240 mm long, rachis quadrate-sulcate to flattened, very sparsely and evenly pubescent with flexuose glandular trichomes 0.6-1.3 mm long, sometimes becoming nearly glabrate proximally; dichasia opposite (or, at least opposite on an inflorescence branch), 3-many-flowered, pedunculate, peduncles 13-20 mm long, pubescent like rachis. Bracts (including those subtending inflorescence branches) linear to subulate, 1.5-2.5 mm long, 0.4-0.6 mm wide, abaxial surface glabrous or very sparsely pubescent with antrorse eglandular trichomes 0.1-0.2 mm long. Bracteoles and secondary bracteoles linear to subulate, (1-) 1.5-

2.5 mm long, 0.2-0.6 mm wide, abaxial surface glabrous or pubescent like bracts or with glands like those of rachis. Flowers pedicellate, pedicels 2-3.2 mm long, glabrous, lateral flowers borne on secondary peduncles 6-18 mm long. Calyx 2.3-4 mm long, 2.3-3.3 mm long during anthesis and slightly (if at all) accrescent in fruit, abaxially pubescent like rachis, lobes subulate, 2-3 mm long, equal to subequal in length, 0.6-0.9 mm wide. Corolla subfusiform in bud, red (and often appearing ± whitish distally in dried state), 15–19 mm long, externally glabrous, tube 13.5-16 mm long, abruptly expanded into a throat, narrow proximal portion 1-1.5 mm long, 1.3-2.2 mm in diameter, throat saccate, 12.5-14.5 mm long, 5-7.8 mm in diameter, widest near base, upper lip straightforward to erect, 1.8-2.2 mm long, 2-2.2 mm wide, lower lip 3-lobed, 2-3 mm long, lobes 1.5-2 mm long, 1.5-2.3 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 23–27 mm long, thecae 2.8–3.6 mm long; pollen globose-elliptic, peripheral band continuous, verrucate and with a central row of baculae to echinae. Style 24-28 mm long, stigma 0.2 mm long. Capsule 12-15 mm long, glabrous, stipe 5-6.5 mm long, head ellipsoid with slight medial constriction. Seeds 2.6-3 mm long, 1.9-2 mm wide, immature surfaces bubbly tuberculate, mature surfaces psilate and irregularly tuberculate at periphery, tubercles rounded, lacking barbs.

Illustration. Fig. 13.

Phenology. Flowering and fruiting: July.

Distribution. Mexico (Oaxaca; Fig. 12); in mesophytic montane forests; 2400 m.

This species is known only by the type collection from the Sierra Madre del Sur of south-central Oaxaca. Its affinities are with the large group of species (noted above under Macromorphology) that have reddish corollas with a straight-forward to erect upper lip and a distinct throat, stamens inserted in the proximal 1/3 to 1/2 of the corolla, and thyrsoid inflorescences. *Stenostephanus madrensis* occurs in the same region of Oaxaca as *S. oaxacanus*. Distinctions between these species are noted in the key in Appendix 2.

- Stenostephanus monolophus (Donn. Sm.) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. Glockeria monolopha Donn. Sm., Bot. Gaz. (Crawfordsville) 27: 439. 1899. Hansteinia monolopha (Donn. Sm.) D. N. Gibson, Fieldiana, Bot. 34: 62. 1972.—TYPE: GUATEMALA. Zacatepéquez: Capetillo, 1500 m, Nov 1889, E. Heyde & E. Lux 4556 (holotype: US!; isotypes: GH! K! US!).
 - Glockeria moralesii Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 47. 1930.— TYPE: GUATEMALA. Chimaltenango: San Martín, 1800 m, Nov 1928, J. Morales R. 1237 (holotype: F!).

Shrubs to 1.2 m tall. Young stems subterete to subquadrate to quadratesulcate, \pm bifariously pubescent with flexuose-retrorse to flexuose-antrorse eglandular trichomes 0.3–0.8 mm long. Leaves petiolate (or distalmost pair sessile), petioles to 95 mm long, blades ovate, 27–215 mm long, 20–112 mm wide, 1.4–2.1 times longer than wide, acuminate to subfalcate to caudate at apex, rounded to acute to subattenuate (or distalmost pair cordate) at base, surfaces sparsely pubescent with flexuose to flexuose-antrorse eglandular trichomes, margin entire to subcrenate, ciliate. Inflorescence of (axillary and) terminal thyrses (or panicles of thyrses) to 40 cm long, rachis subquadrate to quadrate-sulcate to ridge-angled, (nearly glabrous or) variously pubescent with glandular and eglandular trichomes (see discussion); dichasia opposite or alternate, 3–many-flowered, pedunculate,



FIG. 13. Stenostephanus madrensis. a. Habit. b. Leaf. c. Flower. d. Capsule. e. Seed. Scale: a, bar = 12.5 mm; b, bar = 15 mm; c, bar = 3.4 mm; d, bar = 3.3 mm; e, bar = 1.2 mm. (Based on *Campos V*. 4736.) Drawn by Jenny Speckels.

peduncles 6-28 mm long, nearly glabrous or pubescent like rachis. Bracts triangular (Matuda 1993) to lance-subulate to subulate, 1-3.5 mm long, 0.5-1.2 mm wide, abaxial surface pubescent with a few flexuose to antrorse eglandular trichomes 0.05–0.4 mm long (and/or sometimes with a few flexuose glandular trichomes to 0.3 mm long) or glabrous. Bracteoles and secondary bracteoles triangular to subulate, 0.8-1.7 mm long, 0.4-0.6 mm wide, abaxial surface either glabrous, pubescent like bracts, or sometimes with a few flexuose glandular trichomes to 0.3 mm long. Flowers pedicellate, pedicels 2-4.5 mm long, pubescent like rachis (or in Matuda 1993, pubescent like calyx), lateral flowers borne on secondary peduncles 4.5-21 mm long. Calyx 3.5-13.5 mm long, 3.5-7.5 mm long during anthesis and accrescent in fruit, abaxially pubescent with an understory of erect subglandular to glandular trichomes to 0.1 mm long and an overstory of flexuose glandular trichomes 0.4-2 mm long (most collections) or sparsely puberulent with eglandular and \pm sessile to stipitate glandular trichomes to 0.1 mm long (e.g., Breedlove & Smith 22692; or one sprig of Breedlove & Smith 22692 at MO sparsely glandular with subsessile to stipitate glands to 0.6 mm long) or evenly pubescent with flexuose glandular trichomes 0.1-0.6 mm long (e.g., Matuda 1993), lobes lance-linear, 3-12.5 mm long, subequal in length, 0.6-1 mm wide. Corolla c-shaped in bud, red (dorsally) and yellow (ventrally), 17-24 mm long, externally glabrous, tube 14-19 mm long, abruptly expanded distally into a throat, narrow proximal portion 2.5-4 mm long, 1.2-2.8 mm in diameter, throat 11-15 mm long, 3-7.5 mm in diameter, widest near base or midpoint, upper lip straightforward to erect, 2.5-5 mm long, 1-1.5 mm wide, lower lip absent or <0.5 mm long, lobes (if present) <0.5 mm long and wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 18-28 mm long, thecae 2.8-3.5 mm long; pollen globose-elliptic to globose-oblong, peripheral band continuous, psilate to subpsilate. Style 23-31 mm long, stigma 0.2 mm long. Capsule 9.5-13 mm long, glabrous, stipe 3-4 mm long, head ellipsoid. Seeds 2.5-3.9 mm long, 1.8-2.5 mm wide, immature surfaces evenly tuberculate, mature surfaces rugulate to tuberculate with tubercles sometimes concentrated at periphery, tubercles subconical to conical, lacking barbs.

Illustration. Fieldiana, Bot. 24(10): 371, fig. 83. 1974.

Phenology. Flowering and fruiting: November-January.

Distribution. Mexico (Chiapas; Fig. 6) and Guatemala; in montane rain forests; 1500–1900 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: Mpio. Motozintla de Mendoza, 45–50 km NE of Huixtla toward Motozintla, *D. Breedlove & A. Smith 22692* (DS, DUKE, ENCB, MICH, MO); Santa Rita, Mapastepec, *E. Matuda 1993* (MEXU, MICH); Mt. Ovando, *E. Matuda 3969* (F, GH, LL, MEXU, MICH, NY, US); de Tuxtla Gutiérrez a Montecristo (N Tuxtla G.), *F. Miranda 5693* (CHIP, MEXU).

All of the Mexican collections of *S. monolophus* are from the Sierra Madre de Chiapas except for *Miranda 5693*, which was presumably collected in the Northern Highlands (the imprecise locality was not located and is not shown in Fig. 6). It does not seem to differ significantly from other collections of this species in the characters observed; however, because *Miranda 5693* lacks well-preserved and open corollas, features of the lower lip could not be discerned for it.

Considerable variation in pubescence of the inflorescence rachis was noted among collections of S. monolophus: Miranda 5693 resembles the type from Guatemala by having rachises \pm evenly pubescent with an understory of erect to flexuose eglandular and subglandular trichomes 0.05-0.2 mm long and an overstory of \pm evenly to somewhat bifariously disposed flexuose eglandular and glandular (sometimes sparse) trichomes 0.3-0.8 mm long; in Matuda 3969 at MEXU the rachises are evenly pubescent with an understory like that described for Miranda 5693 and an overstory of flexuose glandular trichomes to 2 mm long; in Matuda 3969 at GH and F the rachises are evenly pubescent with erect to flexuose glandular and eglandular trichomes 0.1-0.5 mm long; in Matuda 3969 at NY and MICH the rachises are inconspicuously sparsely and \pm evenly puberulent with eglandular and glandular trichomes less than 0.05 mm long; in Breedlove & Smith 22692 at DS the rachises are evenly puberulent with an understory like that described for Matuda 3969 at NY and MICH and also possess a few flexuose eglandular trichomes to 0.9 mm long on some internodes; in Breedlove & Smith 22692 at MO, one shoot has a rachis with an understory of glandular and eglandular trichomes 0.05-0.3 mm long and an overstory of eglandular trichomes to 0.8 mm long, whereas another shoot on sheet has a rachis with some internodes pubescent like Matuda 3969 at NY and MICH and other internodes nearly glabrous or with a sparse overstory only; in Matuda 1993 the rachises are nearly glabrous. Thus pubescence of the rachis appears to vary within populations.

This species shows numerous similarities to *S. glaber*, which differs most conspicuously by its proximally reddish and distally white corollas. *Stenostephanus monolophus* also likely either occurs in Costa Rica or should be included within *Hansteinia sessilifolia* (Oerst.) Durkee. Most collections identified as *H. sessilifolia* from Costa Rica appear to differ from *S. monolophus* only by their generally shorter corollas and apically glandular-puberulent capsules. Other collections from Costa Rica (e.g., *Dryer 1671* at F) have longer corollas and lack glandular trichomes on the capsules. These latter collections appear to be indistinguishable from Mexican collections of *S. monolophus*. I refrain from making further taxonomic alterations until the Central American species of *Stenostephanus* have been adequately studied.

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Stenostephanus oaxacanus T. F. Daniel, sp. nov.—TYPE: MEXICO. Oaxaca: Hwy 190 to Hwy 175, left to La Cumbre, 17 mi from Oaxaca, left on lumber road to lumber camp (9 mi), crest of San Felipe range, 9,000–10,000 ft, 17 Jan 1965, *M. Carlson 4022* (holotype: F!; isotypes: MICH! NY! US!).

Herba perennis vel frutex usque ad 3 m altus. Folia petiolata (vel folia summa saepe subsessilia), laminae ovatae vel ellipticae vel anguste ellipticae, 20–175 mm longae, 8–57 mm latae, 1.9–4.3-plo longiores quam latiores. Inflorescentia thyrsi vel paniculae thyrsorum terminales (vel axillares) ex dichasiis constans; rachis pubescens trichomatibus glandulosis et eglandulosis; dichasia pedunculata, (1–) 3– multi-flora; flores subsessiles vel pedicellati. Corolla rubens (ad apice fuscata), 13–19 mm longa, extus inconspicuo papillato-puberula vel puberula et aliquando sparse pubescens; faux 9–14 mm longa et 4–7 mm diametro; labium superiorus 1–1.5 mm longum; labium inferiorus 0.5–2 mm longum lobis 0.5–1.8 mm longis. Capsula 9.5–15.5 mm longa, glabra.

Perennial herbs or shrubs to 3 m tall. Young stems subquadrate to quadratesulcate (to \pm flattened), bifariously pubescent with flexuose to antrorse to retrorse eglandular trichomes 0.2-0.7 mm long, sometimes soon glabrate. Leaves petiolate (distalmost pair often subsessile), petioles to 34 mm long, blades ovate to elliptic to narrowly elliptic, 20-175 mm long, 8-57 mm wide (distalmost pair sometimes smaller), 1.9-4.3 times longer than wide, acuminate to subfalcate to caudate at apex, acute to attenuate (distalmost pair rounded to truncate) at base, surfaces pubescent (mostly or entirely along major veins) with flexuose to antrorse to antrorsely appressed eglandular trichomes, margin entire to subcrenate, ciliate. Inflorescence of (axillary and) terminal thyrses or panicles of thyrses to 350 mm long, rachis subterete to quadrate to ± flattened, variously pubescent with eglandular and glandular (rarely inconspicuous) trichomes (see discussion below); dichasia alternate or opposite, (1-) 3-many-flowered, pedunculate, peduncles 4-25 mm long, pubescent with trichomes like those of rachis. Bracts (including those subtending inflorescence branches in panicles) linear to lanceolate to subulate, 1-5 mm long, 0.3-1.2 mm wide, proximalmost pair sometimes larger, abaxial surface pubescent like rachis or with antrorse eglandular trichomes to 0.2 mm long instead of, or in addition to, rachis-type trichomes. Bracteoles and secondary bracteoles subulate to linear-subulate to lanceolate, 0.7-2.6 mm long, 0.2-0.6 mm wide, abaxial surface pubescent like bracts. Flowers subsessile to pedicellate, pedicels (0.7-) 1.2-3 mm long, pubescent with trichomes like those of rachis, lateral flowers (if present) borne on secondary peduncles 1.5-10 mm long. Calyx 4.3-13 mm long, 4.3-8.8 during anthesis and accrescent in fruit, abaxially pubescent with flexuose to antrorsely appressed eglandular and glandular trichomes 0.05-0.2 mm long or pubescent with an understory of erect eglandular and glandular trichomes 0.05 mm long and an overstory of flexuose glandular trichomes to 1.2 mm long, lobes lanceolate to lance-linear to lance-subulate, 3.8-12 mm long, equal to subequal in length, 0.4-0.8 mm wide. Corolla subellipsoid to somewhat curved in bud, reddish and with a darker red or maroon coloration distally, 13-19 mm long, externally inconspicuously papillate-puberulent to puberulent (to pubescent) with eglandular trichomes to 0.05 (-0.2) mm long (on mature corollas) and sometimes also distally sparsely pubescent with flexuose glandular (and/or eglandular) trichomes (0.05-) 0.1-0.3 mm long (distal trichomes sometimes caducous and evident only on buds), tube 11.5-16 mm long, ± abruptly expanded into a throat, narrow proximal portion 1.5-2.5 mm long, 1.5-2.3 mm in diameter, throat saccate, 9-14 mm

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long, 4–7 mm in diameter, widest near base or midpoint, upper lip straightforward, 1–1.5 mm long, 1.3–2 mm wide, lower lip 3-lobed, 0.5–2 mm long, lobes 0.5– 1.8 mm long, 1–1.8 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of corolla tube), 14.5–25 mm long, thecae 2.5–3.3 mm long; pollen globose-elliptic to globose-elongate, peripheral band continuous, subpsilate. Style 16–32 mm long, stigma 0.1–0.2 mm long. Capsule 9.5–15.5 mm long, glabrous, stipe 3.5–6.5 mm long, head subellipsoid with a slight medial constriction. Seeds 1.5–3.1 mm long, 1.5–2.5 mm wide, immature surfaces bubbly tuberculate, mature surfaces sparsely tuberculate to irregularly roughened, tubercles \pm rounded, lacking barbs.

Phenology. Flowering: October-January, April; fruiting: October, January.

Distribution. Mexico (Oaxaca; Fig. 8); in mesophytic montane forests and pine-oak forests; 1000-2875 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. OAXACA: Distr. Juquila, Lacháo [San Juan Lacháo], Río Sal, *T. MacDougall s.n.* (CAS, MEXU); 20 km W de San Jerónimo Coatlán, *E. Martínez S. et al.* 2502 (CAS, MEXU); Cafetal Montecristo (Cerro Espino), *B. Reko 3724* (MEXU, US); Mpio. de Juquila, 4 km S de Lacháo, Km 183 carretera Oaxaca–Puerto Escondido, *J. Rzedowski 19543* (MEXU).

Stenostephanus oaxacanus is known both from the Sierra Madre del Sur (to the south of the Valley of Oaxaca) and the Sierra de San Felipe (to the north of the Valley of Oaxaca) in Oaxaca. Distinctions between this species and *S. madrensis*, which also occurs in the Sierra Madre del Sur in south-central Oaxaca, are summarized in Appendix 2.

The few known collections of S. oaxacanus differ from one another most conspicuously in pubescence of the rachis. In MacDougall s.n. and Carlson 4022 the rachis is densely and evenly pubescent with an understory of erect to appressed eglandular trichomes 0.05-0.2 mm long and an overstory of flexuose glandular trichomes 0.3-2 mm long; in Rzedowski 19543 it is pubescent with an understory of \pm evenly disposed flexuose to antrorsely appressed eglandular and glandular (sometimes inconspicuous) trichomes 0.1-0.4 mm long and an overstory of ± bifariously disposed antrorse eglandular trichomes 0.3-0.8 mm long; in Reko 3724 it is pubescent with an understory of evenly disposed \pm erect subglandular to glandular trichomes 0.05–0.1 mm long and an overstory of \pm evenly disposed flexuose glandular trichomes 0.2-0.8 mm long; in Martínez S. et al. 2502, the rachis of one sprig is \pm evenly pubescent with \pm flexuose glandular trichomes 0.1–0.5 mm long and \pm bifariously pubescent with antrorse eglandular trichomes 0.1-0.9 mm long, whereas the rachis of another sprig is pubescent with an understory of antrorse eglandular trichomes to 0.5 mm long (often inconspicuous) concentrated in 2 lines and erect to flexuose glandular subglandular and eglandular trichomes 0.05-0.1 mm long and an overstory of evenly disposed flexuose glandular trichomes 0.5-1.5 mm long. There appears to be no correlation between geography and pubescence type. Both MacDougall s.n. and Rzedowski 19543 were collected in the vicinity of Lacháo in the Sierra Madre del Sur. Inflorescence pubescence of the former collection appears more similar to that of Carlson 4022 from the Sierra de San Felipe, however. Indeed, the type of pubescence on the rachis is not always consistent even among individuals constituting a collection (e.g., Martínez S. et al. 2502).

Variation in pubescence of the external surface of the corolla was also noted among the collections of *S. oaxacanus*. Although mature corollas of all collections have an inconspicuous papillose-puberulence, most also have longer glandular (or eglandular) trichomes at or near the apex of the corolla. These trichomes are typically sparse, erect to flexuose, and sometimes apparently deciduous. Thus they are best observed on buds. In *MacDougall s.n.* and *Carlson 4022* these trichomes are conspicuous on the distal 1/3 of the corolla but can extend to the base of the throat. At the other extreme, in *Martínez S. et al. 2502*, most of the buds lack these longer trichomes altogether; rarely, a few are visible at the apex of the buds. Both of these extremes are evident in *Rzedowski 19543*.

Reko 3724 differs from other collections of *S. oaxacanus* by its narrower thyrses with one-flowered dichasia. Although one-flowered dichasia are sometimes encountered among other collections of the species, the presence of three or more flowers per dichasium is much more common.

Color of the corollas was stated to be red by *Martínez S. et al. 2502* and "blanco-moradas" by *Rzedowski 19543*. None of the other collections specifically noted color of the corolla when fresh. As preserved in the dried state, all of the corollas appear to be much darker distally than proximally. In several collections (i.e., *Reko 3724, Carlson 4022, and Martínez S. et al. 2502*) reddish coloration is preserved in the proximal portion of the corolla. The color of all corollas is assumed to be red with a darker reddish or maroon coloration distally. Some white coloration may be present as well, however.

Stenostephanus purpusii (Brandegee) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. Hansteinia purpusii Brandegee, Univ. Calif. Publ. Bot. 6: 67. 1914.— TYPE: MEXICO. Chiapas: Cerro del Boquerón, Aug 1913, C. Purpus 6842 (holotype: UC!; isotypes: BM! F! GH! MO! NY! US!).

Perennial herbs to 4 dm tall. Young stems terete to subquadrate, \pm densely bifariously pubescent with coarse flexuose eglandular trichomes 1-1.3 mm long. Leaves petiolate (distal pairs subsessile or sessile), petioles to 15 mm long, blades ovate to elliptic, 30-101 mm long, 13-37 mm wide, 2.3-3.2 times longer than wide, (acute to) acuminate at apex, (rounded to) acute to subattenuate at base, surfaces pubescent with cauline type trichomes, margin entire, ciliate. Inflorescence of (axillary and) terminal thyrses to 22 cm long, rachis subterete to quadrate, glabrous; dichasia opposite or alternate, 3-many-flowered, pedunculate, peduncles 6-16 mm long, glabrous. Bracts triangular to triangular-subulate to linear, 1-1.7 mm long, 0.3-0.6 mm wide, abaxial surface glabrous. Bracteoles and secondary bracteoles triangular to linear, 0.8-1.3 mm long, 0.3-0.5 mm wide, abaxial surface glabrous. Flowers sessile to subsessile (i.e., with pedicels to 1 mm long), lateral flowers borne on secondary peduncles 3-12 mm long. Calyx 4-7.7 mm long, abaxially glabrous, lobes lance-subulate, 3.8-6.9 mm long, subequal in length, 0.5-0.8 mm wide. Corolla subfusiform to linear-ellipsoid in bud, appearing purplish in dried state, 18-24 mm long, externally glabrous, tube 14-17 mm long, abruptly expanded distally into a throat, narrow proximal portion 4-5 mm long, 1.5-3 mm in diameter, throat saccate, 10-12 mm long, 3.5-6.5 mm in diameter, widest proximally and narrowed distally, upper lip straightforward to erect, 4.5-5.5 mm long, 0.6-1.5 mm wide, lower lip 3-lobed, 4.5-8 mm long, lobes 1.5-2 mm long, 1.2-1.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 14-24 mm long, thecae 3.2-3.5 mm long; pollen globose-elliptic, peripheral band discontinuous to continuous, \pm striate-rugulate and with a central row of gemmae to baculae. Style 20-28 mm long, stigma 0.1 mm long. Capsule not seen.

Phenology. Flowering: August and February. Distribution. Mexico (Chiapas; Fig. 10); in montane rain forests; 1000 m.

Additional Specimen Examined. Mexico. Chiapas: Finca Hamburg, L. Quarles van Ufford s.n. (U).

Stenostephanus purpusii is very similar to Habracanthus azureus D. N. Gibson from Guatemala. The latter differs most conspicuously from the former species by its less prominent vegetative pubescence (trichomes <1 mm long). Also, *H. azureus* has blue flowers (color unknown in *S. purpusii* but appearing purplish in dried state) and glabrous or glandular calyx lobes. Additional studies of *H. azureus* will be necessary to determine whether both of these taxa should continue to be recognized.

- Stenostephanus silvaticus (Nees) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. Habracanthus silvaticus Nees in A. DC., Prodr. 11: 312. 1847.— TYPE: MEXICO. Oaxaca: Sierra San Pedro Nolasco, Talea, etc., 1843–1844, C. Jürgensen 902 (lectotype, designated by Daniel, 1995a: K!; isolectotypes: BM! CGE!).
 - Stenostephanus lindenii Baill., Bull. Mens. Soc. Linn. Paris 2: 855. 1890, as "lindeni."—Type: MEXICO. Chiapas: entre San Bartolo et Pueblo Nuevo, 1840, J. Linden s.n. (holotype: P!; probable isotypes, i.e., J. Linden 181: G! K!).

Perennial herbs or shrubs to 2 m tall. Young stems subquadrate to quadratesulcate to \pm flattened, glabrous or \pm bifariously pubescent with antrorse to antrorsely appressed eglandular trichomes 0.05-0.2 (-0.3) mm long (puberulent). Leaves petiolate, petioles to 45 mm long, blades ovate to elliptic (to obovate), 35-185 mm long, 14-100 mm wide, 1.7-4.4 times longer than wide, often somewhat unequal in size at a node, acuminate to subfalcate at apex, acute to attenuate at base, surfaces glabrous or puberulent along major veins on abaxial surface, margin entire to irregularly subsinuate, eciliate or inconspicuously ciliate. Inflorescence of terminal thyrses (or panicles of thyrses) to 335 mm long, rachis quadrate to ± flattened, bifariously to \pm evenly puberulent or evenly pubescent with erect to antrorse eglandular trichomes 0.05-0.1 mm long (rarely with scattered erect to flexuose glandular trichomes to 0.8 mm long as well); dichasia opposite, (1-) 3-manyflowered, pedunculate, peduncles 2-11 mm long, pubescent like rachis. Bracts subulate, 1-5 mm long, 0.5-0.9 mm wide, acute at apex, abaxial surface glabrous or puberulent. Bracteoles and secondary bracteoles triangular to subulate, 0.6-2.5 mm long, 0.2-0.5 mm wide, abaxial surface glabrous or puberulent. Flowers pedicellate, pedicels 1-4 (-8) mm long, pubescent like rachis, lateral flowers borne on secondary peduncles 1.5-8 mm long. Calyx 2.2-6 mm long, 2.2-5.7 mm long during anthesis and slightly (if at all) accrescent in fruit, abaxially (nearly glabrous to) puberulent (sometimes with stipitate glands to 0.4 mm long as well), lobes lancesubulate, 1.5-4.7 mm long, equal to subequal in length, 0.3-0.6 mm wide, margins ciliolate. Corolla falcate to fusiform to \pm c-shaped in bud, white to blue-purple, 12-21 mm long, externally glabrous (marginal tips of the lobes puberulent-ciliate), tube cylindrical (or expanded only at mouth), lacking a well-defined or saccate throat, 3-10 mm long, 1-2 mm in diameter, upper lip recurved to recoiled, \pm linear (distal portion sometimes much narrower than proximal portion), 7.5-12 mm long, 0.5-2.5 mm wide, lower lip 3-lobed, 8-12 mm long, 3-5.5 mm wide, lobes 0.5-3 mm long, 0.2–1 mm wide. Stamens inserted in distal 1/3 of corolla tube, 6.5–15 mm long, thecae 1.3–2.5 mm long; pollen globose-oblong to globose-elongate, peripheral band continuous, psilate. Style 10–21 mm long, stigma 0.1–0.2 mm long. Capsule 10–17 mm long, glabrous, stipe 5–9 mm long, head ovoid to ellipsoid to obovoid (often with a medial constriction). Seeds 1.5–2.8 mm long, 1.5–2.5 mm wide, immature surfaces evenly tuberculate, mature surfaces rugulate to subpsilate and with tubercles \pm restricted to periphery, tubercles rounded to subconical, lacking barbs.

Illustrations. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: t. 4, fig. 20. 1855; Ann. Missouri Bot. Gard. 65: 202, fig. 12. 1978; Fieldiana, Bot. (n.s.) 18: 8, fig. 6. 1986; Flora of Chiapas 4: 142, fig. 37. 1995.

Phenology. Flowering: January-May; fruiting: February-May.

Distribution. Mexico (Chiapas, Oaxaca, and Veracruz; Fig. 10), Guatemala, Costa Rica, and Panama; in lowland rain forests, mesophytic montane forests, montane rain forests, and cloud forests; (400–) 780–2700 m.

Additional Specimens Examined. Mexico. Chiapas: Mpio. San Andrés Larrainzar, near summit of Chuchil Ton, NE of Bochil, D. Breedlove 34666 (DS, MEXU, MICH, MO); Mpio. Peltalcingo, Ahk'ulbal Nab above Petalcingo, D. Breedlove 49899 (CAS, GH, MEXU, MICH, MO, NY); Mpio. Berriozábal, near Pozo Turipache N of El Suspiro, D. Breedlove 67022 (CAS, MEXU); Hwy 195 near Pueblo Nuevo Solistahuacán, C. Broome 709 (DUKE); along Hwy 195 between Ixtapa and Pichucalco, ca. 1 mi below lookout, 9 mi NW of Pueblo Nuevo Solistahuacán, T. Croat 47805 (CAS, MO); Mpio. Solistahuacán, en la base del cerro de selva negra a 1 km antes del mirador el caminero, M. Magaña et al. 1059 (MO); Mpio. Rayón, 1 km E de la Selva Negra, E. Martínez S. et al. 3234 (CAS, K, MEXU, WIS); Mpio. Ocosingo, en Naha, 15 km N de Monte Líbano, camino a Chancala, E. Martínez S. 18041 (F, MEXU, MO, NY); Mpio. Rayón, 2.5 km NO de Rayón, camino a Tapalapa, E. Martínez S. & M. Soto A. 24153 (CAS); Ocozocuautla, reserva ecológia "El Ocote," J. Ortíz 985 (MEXU); Mpio. Ixtacomitán, 34 km S de Ixtacomitán, carr. a Tuxtla Gutiérrez, 17°23'N, 93°02'W, P. Tenorio L. et al. 5605 (MEXU); Mpio. Pueblo Nuevo Solistahuacán, along ridge above Pueblo Nuevo Solistahuacán, A. Ton 3970 (DS, ENCB, F, NY, US); Mpio. Tila, pie del Cerro Tak'abana, A. Ton 5765 (MEXU); Mpio. Tila, pie del Cerro Acavaina, A. Ton 7358 (MEXU); Yagalona Triunfo, L. Quarles van Ufford 472 (CAS, U); Mpio. Rayón, 9 mi NW of Pueblo Nuevo Solistahuacán along rd between Rincón Chamula and Rayón, H. Zuill 772 (DS) .- OAXACA: 11 km E of the Mitla to Choapam rd on rd to Zacatepec, NE slope of Cerro Zempoaltepetl, D. Breedlove & B. Bartholomew 66948 (CAS); Mpio. Guevea de Humboldt, Cerro de la Peña Blanca, al SO de la Cumbrela cual esta a 13.5 km N de G. de Humboldt, A. Campos V. 3597 (MEXU); Mpio. Santiago Lachiguiri, Arroyo Lagarto, 4 km SO de Crucero Buenavista, carr. a Lachiguiri, 16°43'N, 95°31'W, A. Campos V. 4313 (MEXU); Chinantla, H. Galeotti 510C (BR, W); Yelagago, B. Halberg s.n. (LL, MEXU); Mpio. Santa María Chimalapa, Cerros de los Pavos, ca. 47 km (línea recta) N de San Pedro Tapanatepec, 16°47'N, 94°10'W, S. Maya J. 4304 (CAS); Mpio. San Felipe Usila, Arroyo Lumbre, 3 km E de Santa Cruz Tepetotutla, 17°44'N, 96°32'W, J. Meave del Castillo et al. 1593 (MEXU); Distr. Choapam, Santa María, Montaña Santa María, Y. Mexia 9273 (ARIZ, B, CAS, F, LL, MO, NY, UC, US); Mpio. Totontepec, Santa María Tiltepec, P. Tenorio L. & R. Torres C. 5352 (MEXU); Distr. Mixe, 2 km N de Amatepec ó 5 km N de Totontepec, R. Torres C. & P. Tenorio L. 4584 (MEXU); Distr. Juchitán, 12 km N de Guevea de Humboldt, R. Torres C. et al. 2552 (MEXU); Mpio. Guevea de Humboldt, Cerro Picacho, 8.3 km N de Guevea de Humboldt, R. Torres C. et al. 9152 (MEXU); Mpio. Sta. María Chimalapa, Sierra de Tres Picos, ca. 17 km (línea recta) SSE of La Laguna, Ver, 17°07'N, 94°27'W, T. Wendt et al. 6794 (CAS).-VERACRUZ: Mpio. San Andrés Tuxtla, lado W de Cerro Mastagaga, ca. 13 km NE de San Andrés Tuxtla, J. Beaman 5556 (F); Km 15, orilla del camino al Vijía de Santiago Tuxtla, R. Cedillo T. 19 (MEXU); Mpio. San Andrés Tuxtla, Cumbres del Vigia, F. Ponce C. 71 (CAS); Distr. San Andrés Tuxtla, Santiago Tuxtla, C. Seler & E. Seler 5032 (GH, US); Mpio. San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, Lote 71, S. Sinaca C. 475 (MEXU), S. Sinaca C. et al. 522 (MEXU, MO).

Stenostephanus silvaticus is apparently the most widely distributed species in the genus, and it exhibits the broadest elevational range among Mexican Stenostephanus.

Its occurrences at lower elevations (i.e., 400–780 m) are all from the Los Tuxtlas region of Veracruz in lowland rain forests. The species is remarkably uniform in morphology throughout its range. Although corollas are generally described as white on specimen labels, the limb (especially along the margin) often has a reddish tinge in the dried state.

The protologue of *S. lindenii* notes that the inflorescence is entirely glabrous. Examination of the holotype reveals that its inflorescences are pubescent in a manner consistent with the above description. The rare occurrence of glands in the inflorescence (rachis, peduncles, pedicels, and calyx lobes) does not appear to be significant. In at least one specimen (*Martínez S. 18041* at MEXU) an inflorescence with glandular trichomes and one without glands occur on the same shoot.

The affinities of this species with S. latilabris are noted under Macromorphology.

Stenostephanus tacanensis (Acosta & R. Fernández) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. *Hansteinia tacanensis* Acosta & R. Fernández, Novon 3: 221. 1993.—Type: MEXICO. Chiapas: Mpio. Unión Juárez, SE side of Volcán Tacaná above Talquian, 23 Nov 1980, *D. Breedlove & F. Almeda* 47714 (holotype: MEXU!; isotypes: CAS! GH! TEX! US!).

Shrubs to 1.2 m tall. Young stems subquadrate to quadrate-sulcate, pubescent with flexuose-retrorse (to antrorsely appressed) eglandular trichomes 0.2-2 mm long, soon glabrate, trichomes concentrated in or restricted to 2 lines or \pm evenly disposed. Leaves petiolate (distalmost pair sometimes sessile), petioles to 53 mm long, blades ovate to elliptic, (15-) 34-190 mm long, (10-) 17-91 mm wide, 1.5-3 times longer than wide, \pm abruptly acuminate at apex, acute to attenuate at base (distalmost pair cordate at base), surfaces sparsely pubescent with antrorse to antrorsely appressed eglandular trichomes especially or exclusively along major veins, margin entire to subcrenate, ciliate. Inflorescence of axillary and terminal racemes (or panicles of racemes) to 25 cm long, rachis subterete to subquadrate to ridge-angled, densely pubescent either with an understory of evenly disposed erect to subflexuose eglandular and glandular trichomes to 0.3 mm long and an overstory of \pm evenly to somewhat bifariously disposed flexuose glandular trichomes 0.5–1.5 mm long or evenly pubescent with erect to flexuose eglandular and usually glandular trichomes 0.2-0.8 mm long (i.e., Breedlove & Almeda 47714); dichasia opposite or alternate, 1 (-3)-flowered, sessile to subsessile (i.e., borne on peduncles to 0.5 mm long). Bracts lanceolate to ovate to ovate-elliptic, 2.5-11 mm long, 0.8-4 mm wide, abaxial surface pubescent like rachis or with an understory of erect to antrorse eglandular trichomes 0.05-0.3 mm long and an overstory (sometimes absent) of flexuose glandular trichomes to 0.5 mm long. Bracteoles lance-subulate to lanceolate to lance-ovate to elliptic to linear, 2.5-5 mm long, 0.4-1.8 mm wide, abaxial surface pubescent like bracts. Flowers pedicellate, pedicels 2-5 mm long, pubescent like rachis or with mostly erect eglandular (and sometimes a few glandular) trichomes 0.1-0.3 mm long, lateral flowers (if present) not borne on secondary peduncles. Calyx 5.5-16 mm long, 5.5-8.5 mm long during anthesis and accrescent in fruit, abaxially pubescent like bracts (or with the overstory glands present when these mostly absent on bracts), lobes linear to lance-linear, 5-14 mm long, equal to subequal in length, 0.7–0.9 mm wide. Corolla subfusiform to \pm arched or c-shaped in bud, entirely red, 19-28.5 mm long, externally pubescent with

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FIG. 14. *Stenostephanus tacanensis.* a. Habit. b. Node. c. Flower. d. Distal portion of stamens with anthers. e. Distal portion of style. f. Calyx and capsule. g. Seed. Scale: a, bar = 15 mm; b, d, bar = 1.5 mm; c, bar = 3.3 mm; e, bar = 0.8 mm; f, bar = 2.4 mm; g, bar = 0.8 mm. (Based on *Nelson 3794.*) Drawn by Ellen del Valle.

flexuose eglandular trichomes 0.2–1 (–2) mm long, tube 14–21 mm long, gradually or abruptly expanded distally into a throat, narrow proximal portion 5–7 mm long, 0.8–3 mm in diameter, throat saccate, 8–14 mm long, 3.5–11 mm in diameter, widest near midpoint, upper lip straightforward, 4.5–8.5 mm long, 6–8 mm wide, lower lip 3–6.5 mm long, 7–8 mm wide, lobes (if distinct) <0.5 mm long and wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of corolla tube), 21–38 mm long, thecae 2–3 mm long; pollen globose-elliptic, peripheral band discontinuous or continuous, psilate or psilate-foveolate. Style 27–43 mm long, stigma 0.2 mm long. Capsule 9–13 mm long, pubescent with erect to flexuose to retrorse eglandular trichomes 0.05–0.2 mm long, stipe 2.5–4.5 mm long, head subellipsoid. Seeds 2.6–3.2 mm long, 1.8–2.8 mm wide, immature surfaces \pm bubbly tuberculate, mature surfaces rugulate to tuberculate, tubercles rounded to subconical, lacking barbs.

Illustrations. Fig. 14; Novon 3: 222, fig. 1. 1993; Proc. Calif. Acad. Sci. 48: 279, fig. 13 (as "*Stenostephanus chiapensis*"). 1995; Flora of Chiapas 4: 138, fig. 26 (as "*Stenostephanus chiapensis*"). 1995.

Phenology. Flowering and fruiting: November-February.

Distribution. Mexico (Chiapas; Fig. 12); in montane rain forests and cloud forests; 1300–2200 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: between Motozintla de Mendoza and Siltepec, 26–30 mi N of Motozintla, 9.5–11.5 mi S of Siltepec, *T. Croat* 47422 (CAS); Mt. Ovando, Escuintla, *E. Matuda* 16249 (MEXU, US); near Chicharras, *E. Nelson* 3794 (GH, US).

Variations in pubescence of the inflorescence rachis and form of the corolla among the few collections of *S. tacanensis* were noted by Daniel (1995b). The species resembles *S. chiapensis* by its racemose inflorescences. Its corollas, which are concolorous and have a well-developed lower lip, are more like those of *S. alushii*, *S. breedlovei*, and *S. purpusii*. Corollas of *S. tacanensis* differ from those of these last species by their often more prominently saccate throats and shorter lobes (if present at all) of the lower lip.

EXCLUDED NAME

Justicia paniculata Sessé & Moc., Pl. Nov. Hisp. 4. 1887, not of earlier authors.— TYPE: not designated.—The type locality of *J. paniculata* was given as "in montibus de *Tlacotzotillam* prope inter del Copalillo." According to McVaugh (1977), this is Tlalcozotitlán (ca. 30 km N of Chilapa), Guerrero. Plants labeled as *J. paniculata* in the Sessé and Mociño herbarium at MA (i.e., no. 289, CNHM neg. 49004) and at F pertain to typical *S. haematodes* but do not resemble the only other collection of this species from Guerrero (i.e., *Hinton et al. 10758*; see under *S. haematodes* for distinctions between the typical form of the species and this collection). Several morphological attributes noted in the protologue of *J. paniculata* (e.g., subvillose herb, lanceolate leaves, oval persistent bracts, corolla with lower lip entire and purple-spotted at base) do not conform to either the specimens of Sessé and Mociño or to other collections of *S. haematodes*. Given the absence of a type, and appropriate materials from which to designate one, it remains unknown to which species Sessé and Mociño's name applies.

ACKNOWLEDGMENTS

Funding for field and herbarium studies in Mexico was provided by the American Philosophical Society. Field studies in Costa Rica and travel to domestic herbaria were funded by the In-house Research Fund of the California Academy of Sciences. Permission to collect plants in Mexico was granted by the Instituto Nacional de Ecología (Secretaría de Medio Ambiente, Recursos Naturales y Pesca). I am grateful to Mario González E., Guadalupe Olalde R., Neptalí Ramírez M., and Miguel Martínez-Icó for facilitating my field and herbarium studies in Chiapas; T. I. and Fei Mei Chuang for assistance with the chromosome counts; Jenny Speckels, Ellen del Valle, Hoc Kho, and Barnaby Hall for illustrating several species; and the curators of the following herbaria for making specimens available: A, ARIZ, B, BM, BR, C, CAS, CGE, CHIP, DS, DUKE, ENCB, F, G, GH, K, LL, MA, MEXU, MICH, MO, NY, OXF, P, PH, S, TEX, U, UC, US, W, WIS.

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APPENDIX 1

Collections of Mexican Species of Stenostephanus from which Pollen was Examined

- S. alushii: Ton 5340
- S. breedlovei: Breedlove 49644
- S. chiapensis: Breedlove 34374; Breedlove & Burns 72688
- S. glaber: Cloud 4; Daniel et al. 8405
- S. gracilis: Breedlove 71524; Croat 47536; Croat & Hannon 63327
- S. guerrerensis: Breedlove 36060, 61946
- S. haematodes: Breedlove & Mahoney 72407; Daniel & Acosta C. 8359; Hernández M. 5335; Hinton et al. 10758; Ventura A. 4670, 20491
- S. harleyi: Reveal et al. 4239
- S. latilabris: Matuda 2485; Ventura & López 4078
- S. madrensis: Campos V. 4736
- S. monolophus: Breedlove & Smith 22692; Matuda 3969
- S. oaxacanus: Carlson 4022; MacDougall s.n.; Martínez S. et al. 2502; Reko 3724
- S. purpusii: Purpus 6842
- S. silvaticus: Breedlove & Bartholomew 66948; Mexia 9273; Zuill 772
- S. tacanensis: Breedlove & Almeda 47714; Nelson 3794

APPENDIX 2

KEY TO STENOSTEPHANUS IN MEXICAN STATES OTHER THAN CHIAPAS

See Daniel (1995b) for a key to species in Chiapas (excluding *S. alushii*) and under *S. guerrerensis* (above) for a key to species in Guerrero.

- Corolla white to blue-purple, tube cylindrical (or expanded only at mouth), lacking a distinct or saccate throat, 3–10 mm long, 1–2 mm in diameter near midpoint, upper lip recurved to recoiled, 7.5–12 mm long, lower lip 8–12 mm long; stamens inserted in distal 1/3 of corolla tube, 6.5–15 mm long.
- Corolla red or reddish, red and white, or color unknown in *S. harleyi* from Guerrero, tube gradually or abruptly expanded distally into a distinct (often saccate) throat, 10–30 mm long, 3.9–13 mm in diameter near midpoint, upper lip straightforward to erect, 1–8 mm long, lower lip 0.5–8 mm long; stamens inserted in proximal 1/3–1/2 of corolla tube, 12–37 mm long.
 - Capsule pubescent with eglandular trichomes 0.3–0.7 mm long.
 Capsule glabrous.
 - 3. Corolla 20–36 mm long, tube 16–30 mm long, narrow (i.e., unexpanded) proximal portion 4–11 mm long (or if only 1–2 mm long, then rachis glabrous). *S. haematodes.*
 - 3. Corolla 12–19 mm long, tube 10–16 mm long, narrow (i.e., unexpanded) portion (if distinct) up to 2.5 mm long (rachis pubescent).
 - 4. Abaxial surface of calyx pubescent with eglandular trichomes (to nearly glabrous); Guerrero. S. harleyi.

DANIEL: STENOSTEPHANUS

- 4. Abaxial surface of calyx pubescent with glandular trichomes; Oaxaca.
 - Calyx 2.3–3.3 mm long during anthesis; corolla externally glabrous, upper lip 2–3 mm long; peripheral band of pollen verrucate and with a central row of baculae to echinae.
 S. madrensis.
 - Calyx 4.3-8.8 mm long during anthesis; corolla externally inconspicuously papillate to puberulent (to pubescent), upper lip 0.5-2 mm long; peripheral band of pollen subpsilate.
 S. oaxacanus.



Daniel, Thomas Franklin. 1999. "Revision of Stenostephanus (Acanthaceae) in Mexico." *Contributions from the University of Michigan Herbarium* 22, 47–93.

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