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The Genus *Sphinctospermum* (Leguminosae): Taxonomy and Tribal Relationships as Inferred from a Cladistic Analysis of Traditional Data

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ABSTRACT. The systematic position of the monotypic genus *Sphinctospermum* has been confused, being placed in either of two tribes, Robinieae or Millettieae, of the Leguminosae subfam. Papilionoideae. Originally allied with *Tephrosia* (Millettieae), subsequent studies revealed that *Sphinctospermum* has a base chromosome number of $x = 8$ and seeds that accumulate the non-protein amino acid canavanine. Such evidence was used to support its inclusion in Robinieae. A cladistic analysis of primarily morphological data is presented that incorporates new or newly interpreted characters, including anatomical and developmental features. These data do not support a sister group relationship of *Sphinctospermum* and *Coursetia*, as previously proposed by some workers. Furthermore, the results of this analysis of traditional data are equivocal and suggest that the probable affinities of *Sphinctospermum* are just as likely to be with genera of Millettieae than with those of Robinieae.

Sphinctospermum Rose was originally proposed (Rose 1906) to accommodate a morphologically distinct *Tephrosia constricta* (S. Watson) Rose that was considered distantly related to other *Tephrosia* Persoon by its annual habit, simple linear leaves, solitary flowers, and constricted seeds. Rose regarded *Sphinctospermum* as closely related to *Tephrosia*, a relationship maintained until Wood (1949) allied *Sphinctospermum* with the genus *Coursetia* DC. (then *Cracca* Benth.) because of its base chromosome number of $x = 8$, which was unlike that of *Tephrosia*, $x = 11$. This relationship was supported by Polhill and Sousa (1981) who considered the septate pods (with evident external constrictions) of *Sphinctospermum* to be homologous to those of *Coursetia* (then *Cracca*).

Lavin (1987) considered a closer relationship of *Sphinctospermum* to *Tephrosia* by postulating previously unconsidered homologies, in addition to pointing out its numerous dissimilarities with *Coursetia*. Putative homologies included seeds with a conspicuous radicular lobe, seedlings with falcate foliar cotyledons and linear-lanceolate eophylls, leaves with a parallel secondary venation, legume septa formed by expansion of the inner epidermis, and an inconspicuous floral hypanthium. Other characters considered very distinctive of *Sphinctospermum*, an annual habit in combination with linear entire leaves, and inflorescences consisting of solitary flowers, were matched very closely by species of *Tephrosia* subg. *Macronyx* (Dalz.)

Hooker, and Lavin proposed the transfer of *Sphinctospermum* from the tribe Robinieae to Millettieae and its alliance with *Tephrosia*.

Furthermore, *Sphinctospermum* lacked many synapomorphic traits diagnostic of the genera of Robinieae possessing a style brush. For example, the style of *Sphinctospermum* is slender and confluent with the placental margin of the mature legume, whereas in *Coursetia* and close relatives, *Robinia* L., *Olneya* A. Gray, *Peteria* A. Gray, and *Genistidium* I. M. Johnson (herein referred to the barbistyled Robinieae), the style base is bulbous and displaced to the carinal margin at maturity (the derived condition; Lavin 1987). Also, *Sphinctospermum* lacks other diagnostic synapomorphies of these genera of Robinieae, notably spinescent stipules and glandular indumentum. *Sphinctospermum* was thus considered as part of the Millettieae lineage rather than having undergone a series of reversals from a Robinieae-like ancestry (Lavin 1987).

This study fully enumerates the traditional evidence with which to assess the tribal relationships of *Sphinctospermum*. The data set includes new or newly interpreted anatomical and developmental evidence, as well as seed chemistry, chromosome, and phytochemical data. In addition, the taxonomy is discussed in order to clarify points concerning lectotypification, morphological circumscription, and geographical distribution.

TAXONOMY

SPHINCTOSPERMUM Rose, Contr. U.S. Natl. Herb. 10:107. 1906.—TYPE: *Sphinctospermum constrictum* (S. Watson) Rose. Figure 1.

Annual herbs. Stems erect to ascending, branching from the base, 1.5–7.5 dm tall. Tap roots often becoming lignescent. Leaves pulvinate, simple, entire, linear-lanceolate; petiole inconspicuous; blade (1)2–8(9) cm long, 1.5–2.5 mm wide at the middle, both surfaces glabrate to sparsely strigose; stipules subulate, persistent 1–2 mm long. Inflorescences of solitary flowers borne from a very short rachis, 0.1–1.0 mm long. Flowers with a proportionately well-developed hypanthium; pedicels ascending, glabrate to sparsely strigose, 1–2 mm long; floral bracts linear-lanceolate, usually caducous before anthesis, 1–2 mm long. Calyx tube campanulate, rounded to slightly attenuate at base, glabrous to sparsely strigose, 1.5–2.0 mm long; lobes narrowly triangular, 1.5–2.0 mm long. Petals clawed; standard orbicular, emarginate, 5–6 mm long, 5–6 mm wide, with calluses just below the nectar guide, lavender to mauve, the nectar guide yellowish; wings free from keel, 5–6 mm long, pale lavender; keel 5–6 mm long, pale lavender, with a blunt apex. Ovary glabrous, with 10–12 ovules, sessile or nearly so on the receptacle; style with a brush uniformly surrounding the distal end. Legumes glabrous, with parallel margins, septate between seeds, the septa formed by the expansion of the inner epidermis. Seeds uniformly brownish to gray, strongly constricted in the middle, 3–12 per legume. Seedlings with epigeal germination, cotyledons foliar, falcate, eophylls entire, linear-lanceolate, alternate, nearly identical to mature leaves. $x = 8$ (Lavin, in prep.; Wood 1949).

This monotypic genus is readily distinguished from other New World Papilionoideae by a combination of its annual growth habit, simple entire linear-lanceolate leaves, and seeds strongly constricted in the middle.

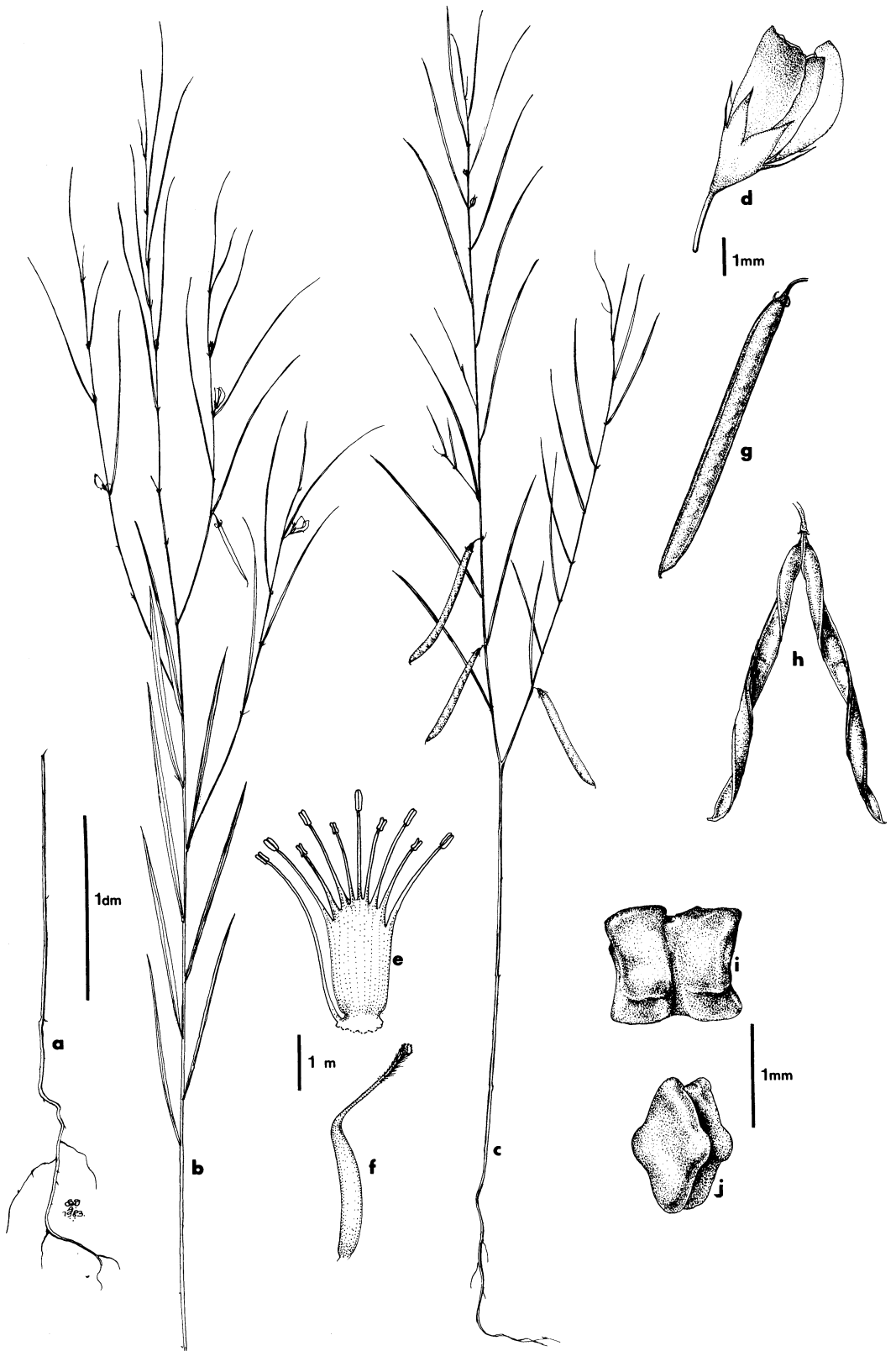
SPHINCTOSPERMUM CONSTRICTUM (S. Watson) Rose, Contr. U.S. Natl. Herb. 10:107. 1906.—*Tephrosia constricta* S. Watson, Proc. Amer. Acad. Arts 24:46. 1889.—*Cracca constricta* (S. Watson) Tidestrom, Proc. Biol. Soc. Wash. 48:40. 1935.—TYPE: Mexico, Sonora, "In ravines in the mountains about Guaymas,"

Oct 1887, Palmer 261 (lectotype here designated: GH!, photo: CAS; isotype: UC!).

Flowering occurs during the wet season, August through November; mature fruits persist throughout this time. Distribution (fig. 2) includes tropical deciduous forests, grasslands, and occasionally oak woodlands of Mexico (Sonora and Baja California del Sur south to Oaxaca) and Sonoran Desert shrublands of Arizona (Pima, Pinal, and Santa Cruz cos.) at elevations between 50–1700 m. With the exception of McVaugh (1987), most floras inaccurately list the distribution of *Sphinctospermum* as southern Arizona, U.S.A., and Sonora and Baja California del Sur, Mexico. However, this species is common, though poorly collected, in the seasonally dry forests of Pacific coastal Mexico south to Oaxaca. I have observed young individuals occasionally in Oaxaca during the beginning of the wet season (June–July), but they are very inconspicuous and readily go undetected.

Sphinctospermum constrictum is often found growing among grasses in fields and along roadsides, in open sandy areas of undisturbed forest and shrublands, and in disturbed areas such as at the edges of pastures. It is locally abundant during wet years; in dry years it may be scarce. Robust specimens bear numerous flowers although most often only a few flowers reach anthesis synchronously rendering most individuals very inconspicuous especially when growing among grasses.

Representative specimens examined. MEXICO. **Baja California del Sur:** San José del Cabo, 20 Sep 1890, Brandegee 134 (CAS, NY, UC); near Rancho del Cayuco, 6 Oct 1951, Carter & Kellogg 3097 (CAS, MICH, UC); Sol de Mayo, NW Santiago, 2 Nov 1986, Leon 2251 (MEXU); Arroyo Quisapol, 18 Nov 1959, Wiggins 15555 (ARIZ, CAS). **Guerrero:** Coyuca-Chacamerto, 20 Sep 1934, Hinton 6627 (F, MO, UC); 12 km S de Tonalapa, 18 Oct 1977, Ladd O. 116 (MEXU). **Jalisco:** 10 km N de S. Cristóbal de la Barranca, 14 Aug 1984, Hernández M. et al. 9579 (MEXU); Presa Santa Rosa, N of Amatitan, 10 Sep 1960, McVaugh 18554 (CAS, MICH); 3 km del Poblado de San Martín Bolanos, 20 Oct 1983, Rico et al. 659. **México:** Temascaltepec, Bejucos, 26 Aug 1932, Hinton 1470 (F, GH, MO, NY, TEX); Naranjo, 9 Oct 1933, Hinton 4732 (F). **Michoacan:** 75 mi N of Arteaga, 2 Oct 1984, Lavin & Sundberg 5120 (CAS, MEXU, MO, TEX); 1 mi W of San Juan toward Amatlan (Sta. Ana), 17 Sep 1957, McVaugh 17965 (MICH); 5 mi N of Nueva Italia, 19 Sep 1958, McVaugh 18025 (CAS, MEXU, MICH); 6 km SW de La Huacana, 27 Oct 81,



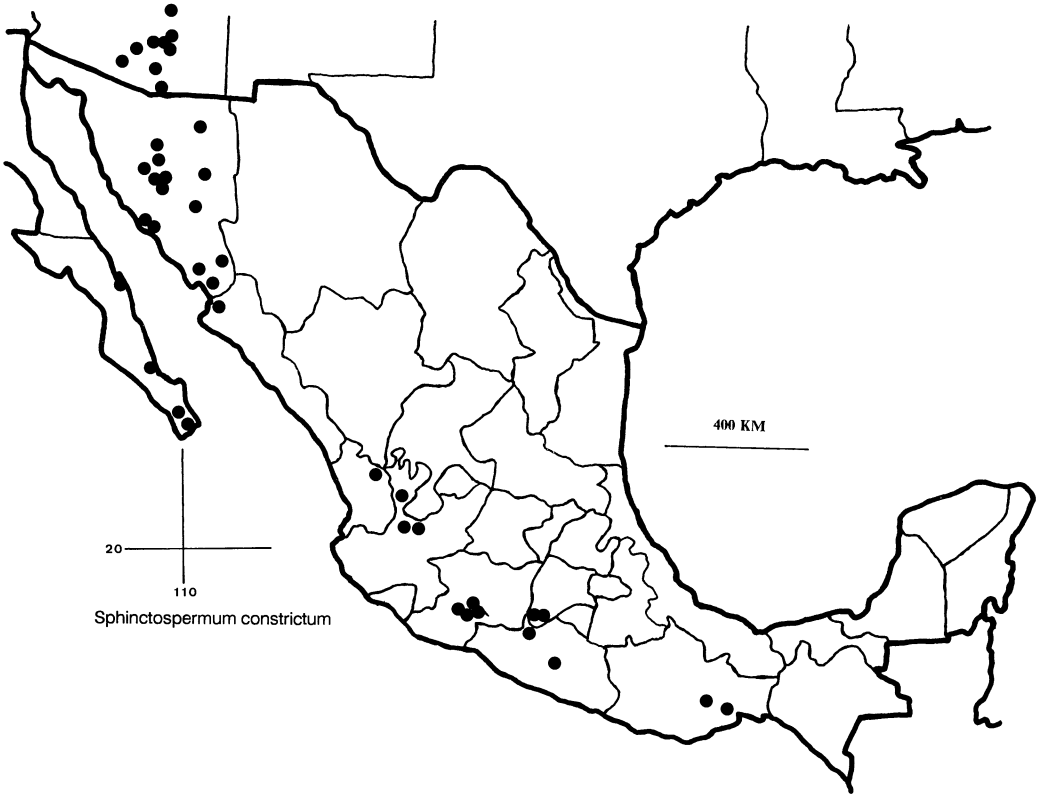


FIG. 2. Distribution of *Sphinctospermum constrictum*.

Soto 3558 (MEXU, MO); 5 km W de Zicuiran, 28 Oct 1981, *Soto* 3579 (MEXU). **Nayarit:** Near Jesus Maria, 18 Sep 1960, *Feddema* 1246 (MICH); 10 km E of Jesus Maria, 20–21 Sep 1960, *Feddema* 1344 (MICH). **Oaxaca:** Distr. Yautepec, 7 km SW de La Reforma, 19 Jun 1985, *Lavin & Torres s.n.* (TEX); 10 km W de Tehuantepec, 4 Oct 1975, *Sousa et al.* 5019 (MEXU). **Sinaloa:** 18–24 mi N of Los Mochis, 8 Nov 58, *Gentry* 17633 (ARIZ). **Sonora:** 5 km W of Pilares de Nacozari, 19 Nov 1939, *Drouet et al.* 3683 (F); 5.9 mi S of Benjamin Hill, 19 Aug 1960, *Felger* 3827 (ARIZ); 4 km N of Bahia San Carlos, 18 Nov 1985, *Felger & Straub* 85–1332 (ARIZ, TEX); San Bernardo, Rio Mayo, 31 Aug 1935, *Gentry* 1654 (ARIZ, F, MO, UC); 10 mi S of Hermosillo, 6 Sep 1939, *Gentry* 4559 (ARIZ, NY, UC); Guaymas, 22 Oct 1939, *Gentry* 4676 (ARIZ, CAS, F, MICH, MO, NY, UC, US); 40 mi S of Navojoa, 1–3 Oct 1954, *Gentry* 14396 (ARIZ, TEX); Cochuto, 2 Oct 1890, *Hartman* 97 (NY,

UC); Hermosillo, 29 Oct 1926, *Jones* 22485 (CAS); Guaymas, Sep 1887, *Palmer* 222 (GH); 10.7 mi from Hermosillo to Rio Matape, 20 Aug 1982, *Reichenbacher* 1035 (ARIZ); 10 mi S of Santa Ana, 15 Sep 1934, *Shreve* 6660a (MICH); 46 mi S of Moctezuma, 25 Sep 1934, *Shreve* 6768 (ARIZ); 10 mi N of Carbo, 16 Sep 1934, *Wiggins* 7260 (CAS, MICH); 14 mi S of Divisaderos, 26 Sep 1934, *Wiggins* 7468 (CAS, GH, MICH); 8 mi W of Hermosillo, 27 Aug 1941, *Wiggins & Rollins* 106 (ARIZ, CAS, MICH, MO, TEX, UC).

U.S.A. Arizona: Pima Co.: 3 mi S of Continental, Sierrita Mts., 6 Sep 1840, *Benson* 10392 (ARIZ); Tumamoc Hill, Tucson, 20 Oct 1983, *Bowers* 2775 (ARIZ); Fresnal Canyon, Baboquivari Mts., 6 Sep 1931, *Gilman* 121 (ARIZ, CAS); Tucson Mts., 8 Sep 1903, *Thornber s.n.* (CAS); Tumamoc Hill, Tucson Mts., 30 Aug 1906, *Thornber* 4851 (ARIZ); Santa Catalina Mts., 21 Aug 1914, *Thornber* 7590 (ARIZ, CAS); SE side of Coyote

FIG. 1. *Sphinctospermum constrictum*. a. Root system. b. Flowering stem. c. Fruiting stem. d. Flower. e. Androecium. f. Ovary. g. Pod. h. Pod after dehiscence. i, j. Seed. This drawing first appeared as figure 99 in volume 5 of *Flora Novo-Galiciana*, by Rogers McVaugh.

Mt., Sep 1939, *Gentry 4618* (CAS); Robles to San Fernando, 21 Aug 1932, *Harrison & Kearney 8932* (F); Tucson Mts., 5 Sep 1988, *Van Devender et al. 88-607* (ARIZ). Pinal Co.: N side of Table Mt., N of Galiuro Mts., 28 Aug 1980, *Warren & Anderson 342* (ARIZ). Santa Cruz Co.: near Nogales, Tumacacori Mission, 14 Sep 1929, *Harrison et al. 6023* (ARIZ, GH); Nogales, 7 Aug 1927, *Peebles et al. 4616* (ARIZ, US).

The inflorescence of *Sphinctospermum* is a solitary flower borne from a nearly inconspicuous rachis. This rachis is evident throughout floral development and is well demarcated from the pedicel either by a floral bract, which is present prior to anthesis, or by a conspicuous node (the scar of the fallen floral bract) that is evident at and after anthesis. Reference to the inflorescence as two flowers per axil actually refers to a developing shoot borne from the same axil as a solitary flower and itself also bearing a flower at the basal node.

TRIBAL RELATIONSHIPS

Sphinctospermum accumulates canavanine in seed (Lavin 1986), an important phylogenetic marker used by Polhill (1981) to characterize a major subgroup of Papilionoideae. Within this subgroup, the slender herbaceous habit of *Sphinctospermum* is reminiscent of that in temperate herbaceous tribes, such as Galegeae, but except for chromosome number, little other evidence suggests a relationship to these tribes; notably, *Sphinctospermum* lacks a major structural mutation of the chloroplast chromosome, the loss of the inverted repeat, that is known to occur in these temperate tribes (Lavin et al. 1990), as well as other diagnostic synapomorphies such as epulvinate leaves and stipules adnate to the petioles. The base chromosome number of *Sphinctospermum*, $x = 8$, is found in few tropical Papilionoideae tribes that also accumulate canavanine in seed (e.g., Indigofereae, Robinieae, and Millettieae). No other characters have been found that suggest a relationship of *Sphinctospermum* with Indigofereae, so potential relationships are narrowed down to Robinieae and Millettieae.

If placed in Millettieae, *Sphinctospermum* would be most closely related to *Tephrosia* as evinced by its style bearing a pollen brush, seeds with a conspicuous radicular lobe, seedlings with falcate foliar cotyledons and linear-lanceolate eophyll, leaves with parallel secondary

venation, ovaries with numerous ovules, and legume septa formed by expansion of the inner epidermis. *Tephrosia* subg. *Macronyx* matches *Sphinctospermum* very closely in its herbaceous annual habit, simple linear-lanceolate leaves, and inflorescences consisting of solitary flowers.

If allied with Robinieae, the relationships of *Sphinctospermum* would be with the barbistyled Robinieae because of its style with a pollen brush (Lavin 1987, 1988). The genus *Coursetia* of this group matches *Sphinctospermum* most closely in its superficially similar septate legumes and base chromosome number of $x = 8$.

Regardless of where *Sphinctospermum* is relegated, problems remain in discerning its relationships. If allied with *Tephrosia*, its canavanine accumulating seeds, free wing petals, and base chromosome number would be anomalous. If placed with the barbistyled Robinieae, its lack of many synapomorphic traits diagnostic of these genera (e.g., spinescent stipules, stipitate glandular vestiture, a bulbous style base that is displaced to the carinal margin in fruit, and standard petals with inflexed auricles) would be problematic in assessing its relationships to any particular genus of this group.

MATERIALS AND METHODS

Anatomical analyses of *Sphinctospermum* were conducted on leaf and legume tissue, while scanning electron micrographs were taken of the pollen brush throughout its development and of the androecium. Material was fixed in FAA for 24 hours and transferred to glycerol/ethanol (1:10) for storage. Prior to study, tissue was dehydrated with 100% ethanol. Legume and leaf tissues were taken to 100% tert-butyl alcohol (TBA) and embedded in parafin for thin sectioning. The 100% ethanol was removed from androecial and stelar tissues with a critical point dryer. This material was mounted on metal stubs and sputter-coated with gold in preparation for scanning electron microscopy using a JEOL JSM35 scanning electron microscope.

Cladograms were generated on a Zenith 80386 microcomputer with PAUP (D. Swofford, version 2.4.1) and CLADOS (K. C. Nixon, version 0.9). All characters were unordered and the branch and bound search option (BANDB) of PAUP was used to find the most parsimonious cladogram. Characters and taxa utilized in this

TABLE 1. Data matrix (11 taxa by 27 characters) for the cladistic analysis of *Sphinctospermum* and selected genera of Dalbergieae, Millettieae, and Robinieae. See description of character 3 for variations used in character coding. A "9" equals missing data.

<i>Dalbergia</i>	00000	00000	00000	00000	00000	00
<i>Kunstleria</i>	00000	01000	01110	00000	00010	10
<i>Lonchocarpus</i>	10000	21011	11111	00100	00110	11
<i>Piscidia</i>	10100	21011	11111	00100	00110	11
<i>Tephrosia</i>	11100	21111	11111	10110	00111	11
<i>Sphinctospermum</i>	11111	12110	00100	11110	00091	91
<i>Sesbania</i>	00001	10010	00000	01110	00000	11
<i>Hebestigma</i>	00001	10010	00000	19110	00110	11
<i>Robinia</i>	00001	10110	00000	11111	11111	11
<i>Peteria</i>	00011	10110	00000	11111	11111	11
<i>Coursetia</i>	00001	12110	00000	11110	11111	11

analysis are listed and discussed below. The polarization of putative synapomorphies was inferred by regarding that state in the outgroups *Dalbergia* L. f. (Dalbergieae) and *Kunstleria* Prain (Millettieae) as ancestral (see discussion of taxa below). For each character, the putative apomorphic state was coded "1" (and "2" in multistate characters) while the hypothetical ancestral condition was coded "0." A matrix consisting of 11 taxa by 27 characters is presented in table 1.

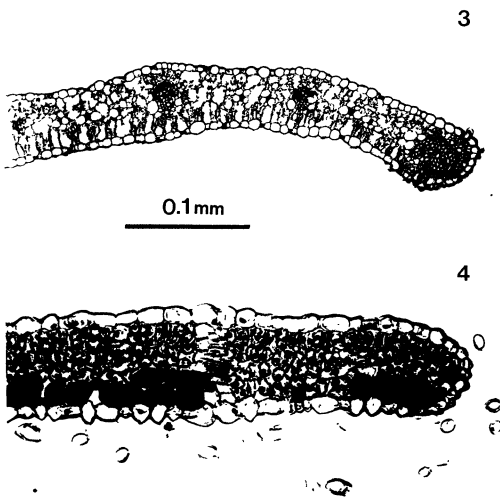
CHARACTERS

1. Leaves or leaflets with parallel secondary venation; hypothetical ancestral condition = reticulate secondary venation. A cross-section of the leaf of *Sphinctospermum* (fig. 3) shows the secondary venation itself also cut in cross-section; this is a result of this vasculature diverging at acute angles from the midrib and running parallel toward the leaf margin. This leaf venation is also distinctive of the genus *Tephrosia* (Wood 1949), as well as related genera of Millettieae. Robinieae have a reticulate secondary venation, and when leaflets are cut in cross-section, the secondary venation is mostly seen in longitudinal-section (fig. 4). It is possible that parallel venation in the case of *Sphinctospermum* is a physical constraint of a narrow leaf; however, Robinieae with narrow leaflets do not show it.

2. Seedling morphology comprising falcate foliar cotyledons; hypothetical ancestral condition = elliptic, bilaterally symmetrical cotyledons, as found in all members of Robinieae.

Seedling morphology of *Sphinctospermum* (fig. 5) is very similar to that of *Tephrosia* (fig. 6) and includes slightly asymmetrical falcate foliar cotyledons (also compare the illustration of the seedling of *Tephrosia leiocarpa* A. Gray in Sousa and de Sousa 1981, p. 274). Seedling morphology in Papilionoideae is generally considered evolutionarily conservative and phylogenetically informative because of the morphological uniformity often found among related genera and tribes (Duke and Polhill 1981). Lavin (1987), therefore, considered this character very informative in discerning the relationships of *Sphinctospermum*. Falcate cotyledons may be the result of seeds with recessed hila and this may always be true if the cotyledons are the storage type. However, I have observed species of *Lonchocarpus* Kunth and *Piscidia* L. that have seeds with recessed hila and seedlings with foliar, bilaterally symmetric cotyledons; therefore, if the cotyledons are of the foliar type, retaining an original falcate shape is tentatively regarded as derived from one that expands into bilateral symmetry.

3. Legume with cross-septa between seeds formed by expansion of the inner epidermis; hypothetical ancestral condition = cross-septa lacking. *Coursetia* (the only genus of the barbistyled Robinieae to have septate legumes) has cross-septa formed by the inflexion of the endocarp and only a slight connation of the inner epidermis (fig. 7); this condition is either not homologous with the apomorphic condition, as found in *Sphinctospermum* (fig. 8) and *Tephrosia*, or represents a transformation state from the putatively derived condition. Therefore, it was

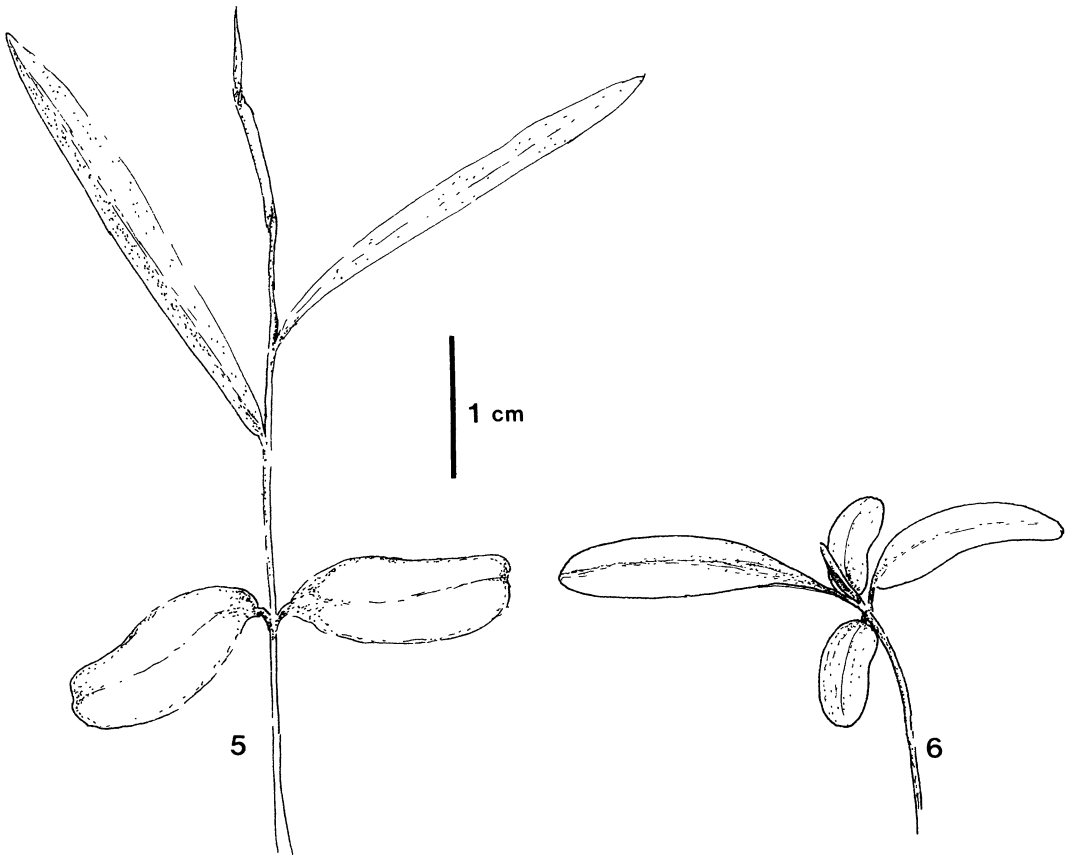


FIGS. 3, 4. Cross-section of leaves. 3. *Sphinctospermum constrictum* (Lavin 5120, TEX). 4. *Coursetia pumila* (Lavin & Sundberg 5006, TEX).

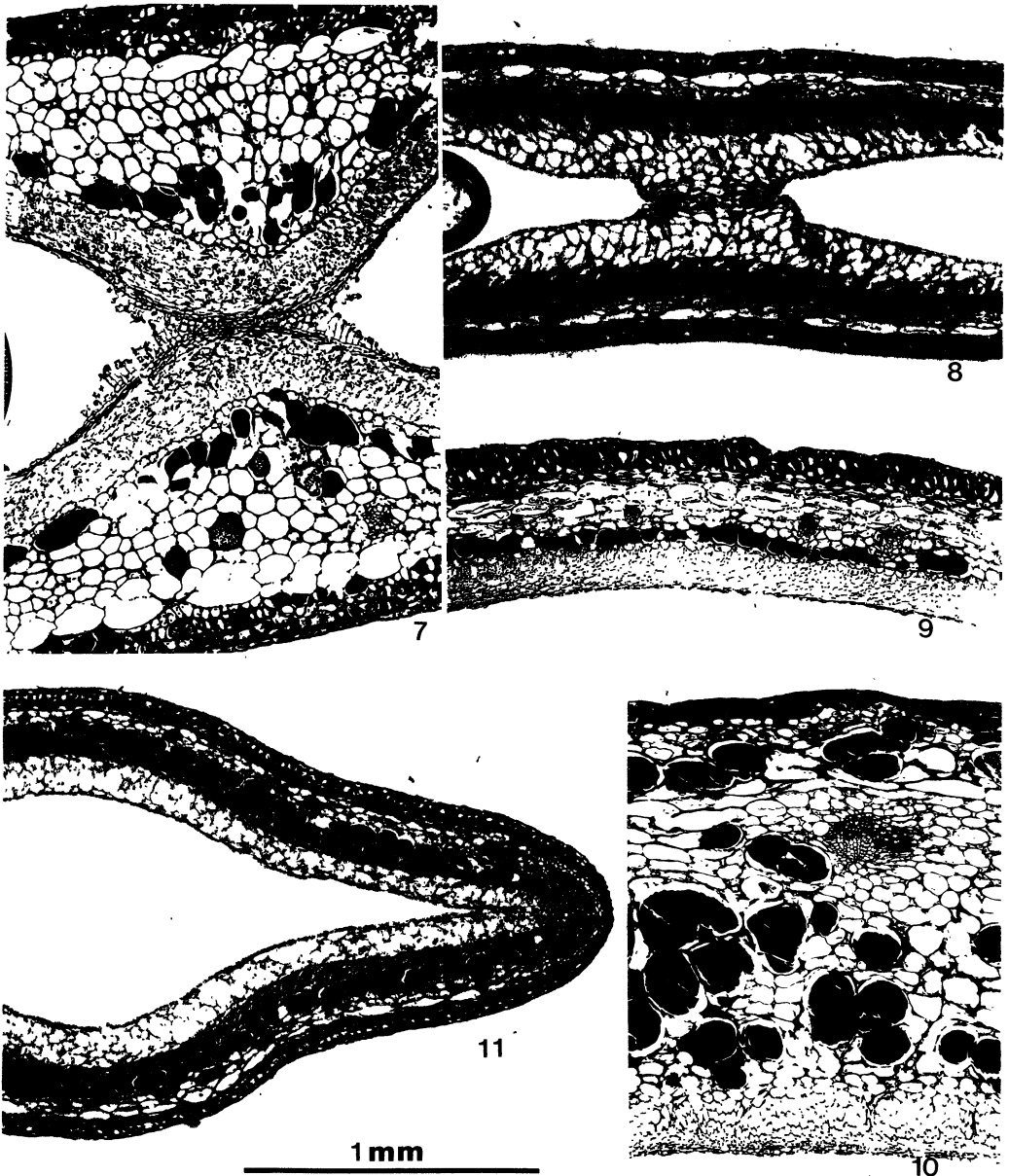
coded "0" in some computer runs and as part of an unordered multistate character ("2") in others.

4. Herbaceous growth habit; hypothetical ancestral condition = woody growth habit. *Sphinctospermum* has been allied with *Coursetia* (as *Cracca*) in part due to its completely herbaceous growth habit (Polhill and Sousa 1981; Wood 1949). Lavin (1988) suggested that the ancestral condition of *Coursetia* (including *Cracca*) included a woody growth habit; therefore, this genus is not coded for the apomorphic condition. Likewise, *Tephrosia* includes many species with herbaceous growth habits, but just as many have a woody habit; given its taxonomic position in a predominantly woody tribe, the ancestral condition of *Tephrosia* very likely includes a woody habit. Only *Peteria* of the tribe Robinieae consistently has a completely herbaceous growth habit.

5. Pericarp with large, thin-walled mesocarp



FIGS. 5, 6. Seedlings. 5. *Sphinctospermum constrictum* (Lavin 5120, TEX). 6. *Tephrosia rhodesica* Bak. f. (Lavin 6218, BH).



FIGS. 7-11. Anatomical sections of legumes. 7, 8. Longitudinal section of legume showing cross-septa between seed compartments. 7. *Coursetia caribaea* (Jacq.) Lavin (Lavin 5153, TEX). 8. *Sphinctospermum constrictum* (Lavin 5120, TEX). 9-11. Cross-sections of pericarp. 9. *Coursetia brachyrhachis* Harms (Lavin & Lavin 5806, TEX). 10. *Olneya tesota* A. Gray (Lavin & Lavin 4653, TEX). 11. *Sphinctospermum constrictum* (Lavin 5120, TEX).

cells accumulating tannins; hypothetical ancestral condition = tanniferous cells lacking. Anatomical surveys of pericarpal structure (Lavin 1988, in prep.) indicate that the anatomy shown in figures 9 and 10 is distinctive of the genera of Robinieae; this anatomical structure consists of a well-developed hypodermal layer, large

thin-walled cells of the mesocarp, and large tannin deposits most commonly adjacent to the endocarp. *Sphinctospermum* has a very similar structure (fig. 11). In contrast, species of *Tephrosia* and other Millettieae so far surveyed lack the thin-walled cells of the mesocarp and large tannin deposits (Lavin, in prep.).

6. The non-protein amino acids canavanine (coded "1") and γ -hydroxyhomoarginine (coded "2") accumulated in seed; hypothetical ancestral condition = non-protein amino acid accumulation lacking. The presence/absence of canavanine has been used at various taxonomic levels, from tribe to species (e.g., Kupicha 1981; Lackey 1981; Polhill 1981); in Robinieae and Millettieae, it has been shown to be informative at the generic and tribal level (e.g., Lavin 1986). *Dalbergia* and *Kunstleria* represent the only two groups in this analysis that presumably evolved before the advent of non-protein amino acid synthesis in Papilionoideae (Geesink 1984; Polhill 1981). The non-protein amino acid γ -hydroxyhomoarginine is reported by Evans et al. (1985) to be accumulated in many species of Millettieae. From the taxonomic distribution of non-protein amino acids in seeds of Papilionoideae, it is hypothesized that canavanine synthesis is ancestral to γ -hydroxyhomoarginine synthesis (e.g., see Polhill 1981). This multistate character was unordered during analysis, however.

7. $x = 11$ (coded "1") and 8 (coded "2"); hypothetical ancestral condition = $x = 10$. The base number of *Sphinctospermum* is $x = 8$ (Wood 1949; Lavin, in prep.), a number relatively uncommon in tropical Papilionoideae, although it is found in genera of Robinieae, including *Coursetia* (Lavin 1988) and *Genistidium* (Lavin, in prep.). The postulated base chromosome number of Dalbergieae and Robinieae is $x = 10$ (Goldblatt 1981; Lavin 1988), which is also found in other potential outgroup tribes (e.g., Aeschynomeneae and Amorpheae) that were not used in this analysis. Nearly all the genera of Millettieae have a base of $x = 11$ (Geesink 1981; Goldblatt 1981), including *Kunstleria*, *Lonchocarpus*, *Piscidia*, and *Tephrosia*. This base number is considered derived as it is restricted to a relatively specialized group of papilionoid tribes otherwise characterized by a pseudoracemose inflorescence (see Tucker 1987a). This multistate character was unordered during analysis.

8. Style with a pollen brush; hypothetical ancestral condition = style glabrous. The pollen brush occurs in at least eight unrelated groups of Papilionoideae (Lavin and Delgado, in prep.); two of these pertinent to this analysis are *Tephrosia* subg. *Barbistyla* Brummitt (Millettieae) and the barbistyled Robinieae (Robinieae). Although there exists much morphological vari-

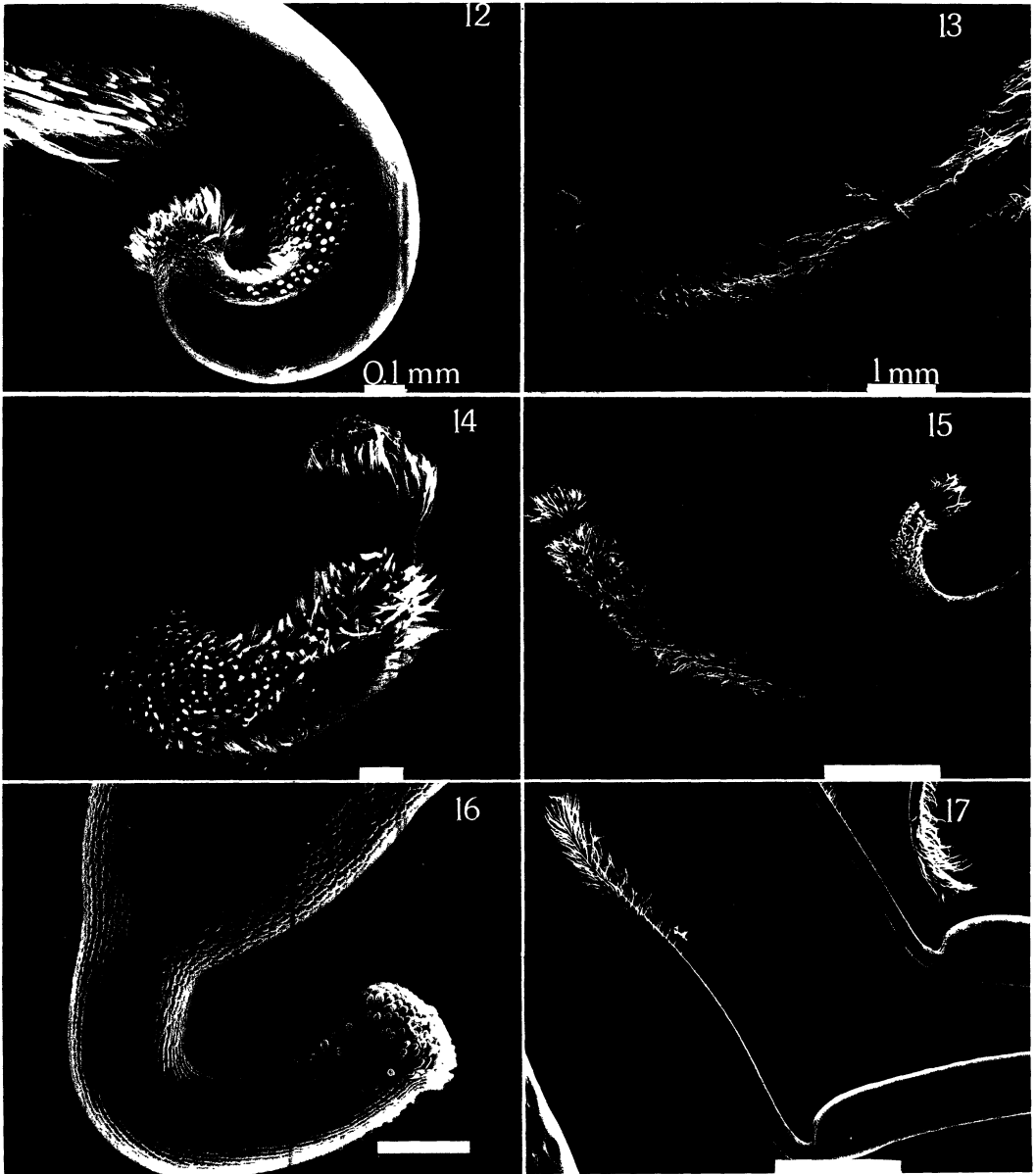
ation in the pollen brush, there are no specific attributes about the brush (or its development up through anthesis) of *Sphinctospermum* that suggest a closer relationship to either *Tephrosia* or the barbistyled Robinieae (figs. 12–17). *Tephrosia abbottiae* C. Wood (figs. 12, 13) has an introrse pollen brush, while *Sphinctospermum* (figs. 16, 17) has a pollen brush with trichomes more introrsely diffused. This similarity is not considered significant because the pollen brush is so variable in *Tephrosia* (ranging from introrse to latrorse to extrorse, or uniformly surrounding the style). The occurrence of the pollen brush in *Sphinctospermum*, the barbistyled Robinieae, and *Tephrosia* is hypothesized to be homologous prior to parsimony analysis.

9. Androecium with well-developed basal fenestrae often surrounded by a callus (sometimes with a papillate epidermis; figs. 18–20); hypothetical ancestral condition = absence of well-developed fenestrae. A staminal tube with basal fenestrae is well developed in all genera of Millettieae and Robinieae and the fenestrae are very conspicuous due to the growth of callus on the portions of the filaments that surround the openings. The systematic significance of a papillate epidermis on the callus, as shown in *Sphinctospermum* and *Coursetia* (figs. 18, 19, respectively), is not yet known.

Basal fenestrae are functional in allowing a floral visitor access to the hypanthial or disk nectaries. It is noteworthy that *Sphinctospermum*, with poorly developed nectaries and very small flowers (the standard measuring only 5–6 mm long) that are self-fertile (pers. obs. of both field and greenhouse specimens), has a staminal tube with very well-developed basal fenestrae. This trait is likely maintained by genetic canalization in a species that may be rarely visited by pollinators.

10. Pseudomonadelphous staminal tube; hypothetical ancestral condition = diadelphous staminal tube. In the putatively apomorphic condition, the vexillary filament is free at the base only (in the region of the basal fenestrae) and attached along most of its middle and distal length. In hypothetical ancestral condition, the vexillary filament is free its entire length. *Tephrosia*, with a variably fused or free vexillary filament, was coded for the apomorphic condition as outgroup comparisons suggest it to be ancestrally pseudomonadelphous.

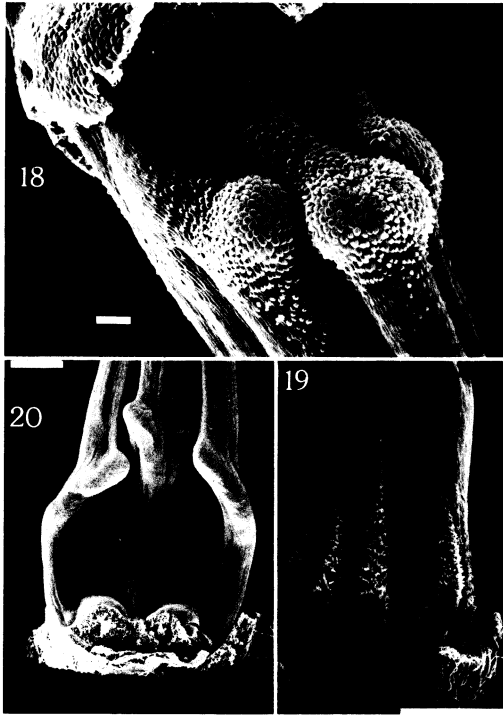
11. Pseudoracemose inflorescence; hypo-



FIGS. 12-17. Pollen brush development just after inception to maturity. 12, 13. *Tephrosia abbottiae* (Bruneau & Lavin 506, MONT). 14, 15. *Robinia pseudoacacia* L. (Lavin 6200, BH). 16, 17. *Sphinctospermum constrictum* (Lavin 5120, TEX). Scale = 0.1 mm in figures 12, 14, 16; and 1.0 mm in figures 13, 15, 17.

thetical ancestral condition = "simple" racemose inflorescence. Tucker (1987a) considers the pseudoraceme, one in which flowers are fascicled along an inflorescence rachis, as a homologous feature among the tribes Abreae, Millettieae, Phaseoleae, Psoraleeae, and Desmodieae. The "simple" raceme (in which flowers are borne

singly along the rachis) of Robinieae is considered by some authors as reduced from the pseudoraceme (e.g., Geesink 1984; Sousa and de Sousa 1981), although Lavin (1987, in prep.) considers this doubtful. Nearly all outgroups of Robinieae (i.e., Dalbergieae, as well as those not used in this analysis such as Aeschynomeneae, Sopho-



FIGS. 18–20. Basal fenestrae of the staminal tube. 18. *Sphinctospermum constrictum* (Lavin 5120, TEX). 19. *Coursetia heterantha* (Grisebach) Lavin (Lavin & Lavin 5800, TEX). 20. *Tephrosia abbottiae* (Bruneau & Lavin 506, MONT). Scale = 1.0 mm.

reae, and *Poecilanthus* Benth.) possess a simple raceme and it is most parsimonious to assume the hypothetical ancestor of Robinieae was also with a simple raceme.

12. Floral hypanthium absent; hypothetical ancestral condition = well-developed floral hypanthium. The condition in outgroup tribes, such as Sophoreae, Dalbergieae, and Aeschynomeneae, is a flower with a well-developed hypanthium. Only in the tribes with a pseudoraceme is the hypanthium so reduced as to be imperceptible. The reduction of the hypanthium corresponds to a reduction or loss of hypanthial nectaries and a gain of intrastaminal disk nectaries, although the correspondence is not perfect. The very small flowers of *Sphinctospermum* were first interpreted as lacking a hypanthium (Lavin 1987). However, closer examination reveals that the hypanthium and associated nectaries are indeed present in this small-flowered species.

13. Seed with a prominent radicular lobe and

recessed hilum; hypothetical ancestral condition = absence of such a lobe and the presence of an apical or subapical hilum. The very unusual seeds of *Sphinctospermum* have a recessed hilum in conjunction with a prominent radicular lobe. A prominent radicular lobe is correlated with the recessed hilum and therefore both are treated as a single character.

14. Wing petals adherent to the keel petals; hypothetical ancestral condition = wing petals that are free from the keel petals. In the apomorphic condition, the blade of the wing petal has a socket located near the junction of the claw, which fits over a corresponding callus or extrusion emanating from the adjoining keel petal. This feature occurs in nearly every genus of Millettieae, as well as tribes closely related, such as Phaseoleae. All of the basal tropical woody Papilionoideae tribes, such as Sophoreae, Dalbergieae, and Robinieae have flowers with free wing petals.

15. Standard densely sericeous on the abaxial surface; hypothetical ancestral condition = standard that is glabrous or at most strigose on the abaxial surface.

16. Floral bracteoles lacking; hypothetical ancestral condition = bracteoles present. Bracteolate flowers are predominant in most tropical woody tribes, including Sophoreae, Dalbergieae, and Millettieae. With the exception of the *Sesbania* Adanson, the entire tribe Robinieae lacks bracteoles subtending the flowers, except for the rare occurrence on flowers of *Olneya*. Lavin (1987) suggests that this is a synapomorphy of Robinieae.

17. The isoflavonoid compound, rotenone, not accumulated as a secondary metabolite; hypothetical ancestral condition = presence of rotenone as a constitutive component of roots and wood. Rotenone has long been known as a constitutive component of roots and wood in genera of Millettieae (summarized in Gomes et al. 1981; Harborne et al. 1971, 1975; Harborne and Mabry 1982). Although numerous flavonoids have been reported for genera of Robinieae, rotenoids or other isoflavonoids have never been. Even in areas where genera of Millettieae have been used as fish poisons (e.g., *Lonchocarpus*, *Piscidia*, and *Tephrosia*—see Wood 1949), species of Robinieae that grow in close proximity have not. Attempts at isolating rotenoids from roots and wood of *Sphinctospermum*, *Robinia*, *Peteria*, and *Coursetia* (Lavin, unpubl. data)

proved unsuccessful using the methods outlined in Harborne et al. (1971). *Hebestigma* Urban was scored as missing data for this character.

18. Ovary with more than two ovules; hypothetical ancestral condition = ovary with 1-2 ovules. This character is more qualitative than it may appear. Most genera in the tribe Dalbergieae (and some Millettieae) have one or two ovules per ovary with four being the maximum found rarely in some species. On the other hand, genera of Robinieae and Millettieae have more than six ovules per ovary, with *Kunstleria* being exceptional in having 1-2 (Geesink 1984).

19. Dehiscent legumes; hypothetical ancestral condition = indehiscent. At the level of the entire Leguminosae, the dehiscent legume would be considered the ancestral condition. At the level of Robinieae and Millettieae, the indehiscent legume is considered ancestral as it is found almost exclusively in potential outgroups to these tribes, such as Sophoreae, Dalbergieae, and Aeschynomeneae.

20. Spinescent stipules; hypothetical ancestral condition = herbaceous or non-spinescent stipules. Spinescent stipules are very uncommon in the subfamily Papilionoideae and within the tribes Millettieae and Robinieae are found in some species of Old World *Tephrosia*, as well as *Robinia*, *Olneya*, *Peteria*, *Genistidium*, and three species of *Coursetia*. The occurrence of spinescent stipules is regarded as a secondarily derived condition in *Coursetia* (Lavin 1988) and *Tephrosia* (given their occurrence in only a few specialized Old World species in this genus).

21. Stipitate glands; hypothetical ancestral condition = absence of these glands. Stipitate glands are relatively unusual among tropical woody Papilionoideae and within the tribes Robinieae and Millettieae are found only in the genera *Robinia*, *Olneya*, *Peteria*, and *Coursetia*.

22. Bulbous style base displaced to the carinal margin in fruit; hypothetical ancestral condition = slender style base that is confluent with the placental margin in fruit. In the derived condition, the style base is hollow.

23. Standards with inflexed auricles; hypothetical ancestral condition = standard without such auricles. Inflexed auricles are found toward the base of the blade near the juncture of the claw. In the presence of these auricles, the claw is usually short and abruptly bent perpendicular to the plane of the standard blade, and

callosities are often present on the face of the standard. In the absence of the auricles, the claw is relatively long and slender and not abruptly bent, and callosities are absent or weakly developed.

24. Nyctinastic leaf movements in which the leaflets simply drop to a vertical position without any rotational movement (the adaxial surfaces face outward after these evening movements have occurred); hypothetical ancestral condition = leaflets rotate 90° on the midrib axis with the adaxial surface facing the distal end of the leaf (the leaflets then fold forward against the leaf rachis with the abaxial surfaces facing outward). The hypothetical ancestral condition is found in such outgroup tribes as Dalbergieae and Aeschynomeneae, as well as *Sesbania* (see Lavin 1987, 1988, for a description of these movements).

25. Calyx with 4-5 subequal lobes as long or longer than the calyx tube; hypothetical ancestral condition = calyx truncate or with very short lobes. It is difficult to polarize this character with certainty, but most of the potential outgroups of Robinieae are with poorly developed calyx lobes; hence well-developed lobes are considered derived in those Robinieae in which they occur.

26. Leaves with opposite leaflets; hypothetical ancestral condition = alternate leaflets. In the apomorphic condition, there is a tendency toward canaliculate leaf rachises and stipellate leaflets; the tendency in the ancestral condition is toward a terete rachis and exstipellate leaflets.

27. Keel petals valvately connate at the distal ends; hypothetical ancestral condition = imbricate keel petals. Tucker (1987b) has shown that keel petals are adnate by various means; but in Robinieae they are consistently valvately connate, as opposed to other conditions such as in Aeschynomeneae where they are adnate due to clasping trichomes toward the distal end of the keel petals (Tucker 1987b).

TAXA

The taxa chosen in this analysis are genera selected from the tribes Dalbergieae, Robinieae, and Millettieae. As this is not intended to be a comprehensive analysis of the generic relationships within and among these tribes, only one to several genera are discriminately selected from each tribe. The purpose of this analysis is

rather to assess the congruency of all hypotheses of homology that pertain to the tribal relationships of *Sphinctospermum* in an attempt to reveal the higher taxonomic relationships of this morphologically unusual genus.

Representative genera chosen from Millettieae include *Lonchocarpus*, *Piscidia*, and *Tephrosia* (see Geesink 1984, for a discussion of these genera). *Tephrosia* was scored for the traits of subg. *Barbistyla* because, as in *Sphinctospermum*, this group is marked by a pollen brush. *Lonchocarpus* and *Piscidia* were included as they are, among the genera of Millettieae, closely related to *Tephrosia*, as indicated by their seeds that accumulate γ -hydroxyhomoarginine, leaves with parallel secondary venation, and a similar chloroplast DNA molecule (Lavin and Doyle, in prep.). A relationship of *Tephrosia* with *Piscidia* is further supported by their legumes with seed compartments formed by an expansion of the inner epidermis (Lavin, in prep.). *Dalbergia* (Dalbergieae) and *Kunstleria* (Millettieae) are included as the outgroups based on previous analyses (Geesink 1984; Lavin 1987), which reveal their potential sister group relationship with an unspecialized character complement relative to genera of Robinieae (e.g., these outgroups are characterized by such unspecialized traits as free wing and keel petals, a diadelphous androecium lacking basal fenestrae, and seeds not accumulating non-protein amino acids).

Genera chosen from Robinieae include *Coursetia*, *Peteria*, *Robinia*, *Hebestigma*, and *Sesbania*. *Coursetia* was included as it has been suggested that *Sphinctospermum* is most closely related to this genus (Polhill and Sousa 1981; Wood 1949). *Robinia* and *Peteria* were included as they are, among the genera of Robinieae, very closely related to *Coursetia* (Lavin 1988). The additions of *Hebestigma* and *Sesbania* were made to include diverse lineages of Robinieae (see Lavin 1987).

RESULTS AND DISCUSSION

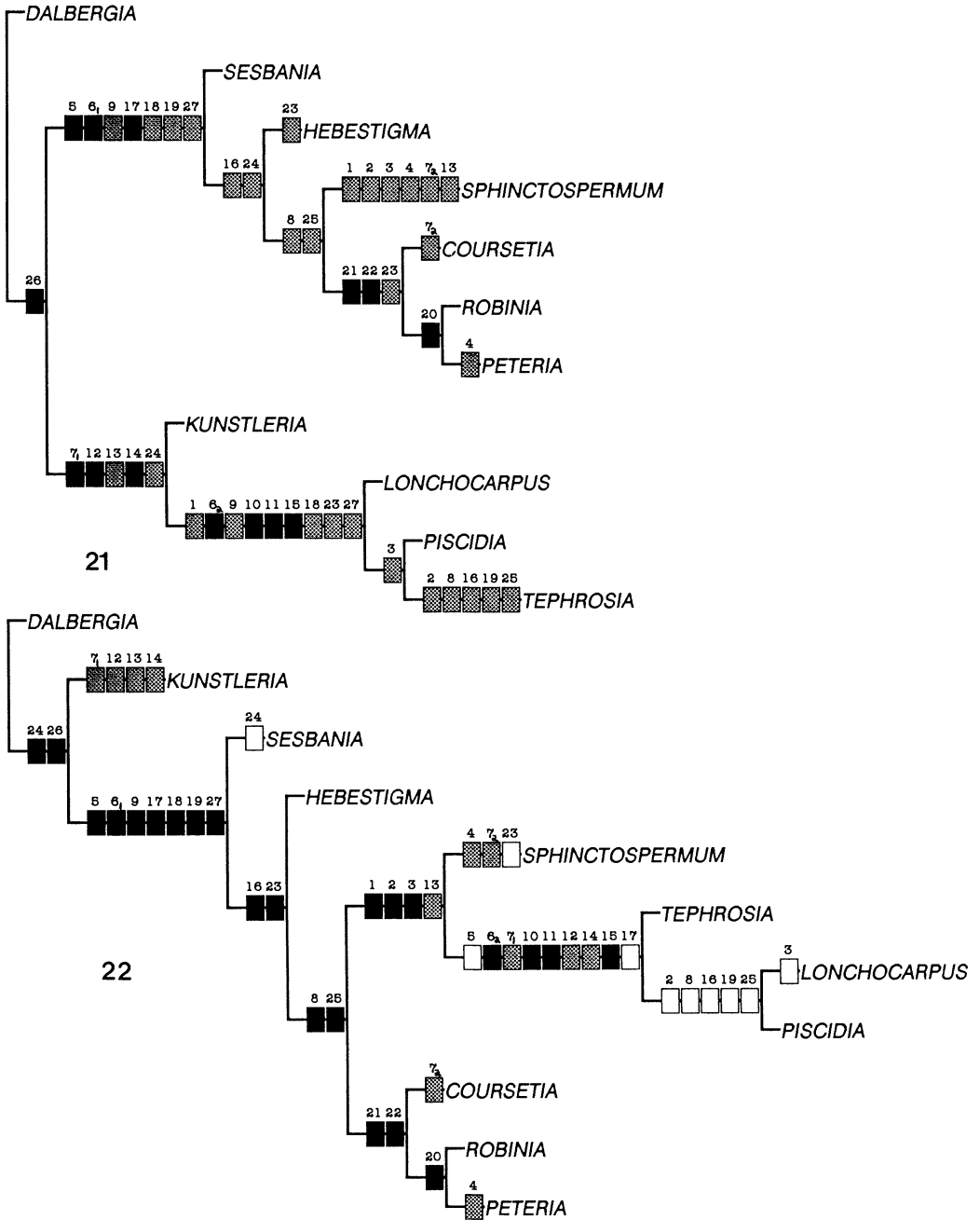
Two most parsimonious cladograms generated from the data matrix (table 1) are shown in figures 21 and 22. The branch and bound search option in PAUP (BANDB) resulted in these cladograms of 45 steps and a consistency index of 0.644. The topologies of these cladograms were unaffected by the variations in coding character 3 (legume cross-septa) as either a multistate or binary character. All computer runs

consistently depicted *Sphinctospermum* as a sister group to either the clade comprising *Robinia*, *Peteria*, and *Coursetia* (i.e., the barbistyled Robinieae) or that comprising *Tephrosia* and close relatives. The hypothesis that *Sphinctospermum* is most closely related to Robinieae (Polhill and Sousa 1981; Wood 1949) is not strongly supported in this analysis as an alternative hypothesis, a close relationship of the genus with genera of Millettieae, is equally likely.

The Relationship between *Tephrosia* and the Barbistyled Robinieae. Does the similarity of *Sphinctospermum* with both *Tephrosia* (Millettieae) and *Coursetia* (Robinieae) indicate a close relationship among these taxa, as suggested by Sousa and de Sousa (1981)? Probably not. A relationship of *Tephrosia* with other genera of Millettieae is well supported (see also Geesink 1984) by the following shared derived characters considered diagnostic of the Millettieae-Phaseoleae tribal alliance: a pseudoracemose inflorescence, an intrastaminal disk, an inconspicuous floral hypanthium, wing petals adherent to the keel petals, a standard densely sericeous on the abaxial surface, a diversity of non-protein amino acids accumulated in seeds (Evans et al. 1985), a diversity of isoflavonoid compounds accumulated as secondary metabolites (Gomes et al. 1981), and a base chromosome number of $x = 11$. Furthermore, within Millettieae, *Tephrosia* is considered a derived element as evinced by its ovary with many ovules, thinly woody elastically dehiscent legumes, and a predominantly shrubby to herbaceous habit (Geesink 1984). Additionally, chloroplast DNA data (Lavin and Doyle, in prep.) suggest *Tephrosia* is very closely related to *Lonchocarpus* and *Piscidia*.

None of the genera of Robinieae possess those derived traits diagnostic of Millettieae. *Coursetia* belongs to the barbistyled Robinieae group (Lavin 1987), which is characterized by such derived traits as spinescent stipules, stipitate glands, bulbous style base displaced to the carinal margin in fruit, and standards with inflexed auricles. The barbistyled Robinieae are regarded as a derived element of the tribe Robinieae (Lavin 1987) and, therefore, a wide phylogenetic gap is postulated between them and *Tephrosia* and close relatives.

Relationship of *Sphinctospermum*. The topology of the two most parsimonious cladograms are equivocal with regard to the relationships of *Sphinctospermum*. The inference of



FIGS. 21, 22. Most parsimonious cladograms of 45 steps and a consistency index of 0.644. Solid box = forward change; hatched box = parallelism; open box = reversal. 21. Cladogram depicting *Sphinctospermum* as a sister group to genera of the barbistyled Robinieae. 22. Cladogram depicting *Sphinctospermum* as a sister group to *Tephrosia* and closely related to genera of Millettieae.

relationships depicted in figure 22 supports many of the hypotheses of homology between *Sphinctospermum* and *Tephrosia*, such as leaves or leaflets with a parallel secondary venation (character #1), falcate foliar cotyledons (#2), legumes with seed chambers formed by the expansion of the inner epidermis (#3), a style with a pollen brush (#8), seeds with prominent radicular lobe and recessed hilum (#13), ebracteolate flowers (#16), dehiscent legumes (#19), and calyx with well-developed lobes (#25). However, an equally parsimonious cladogram in figure 21 depicts these same putative homologies as having arisen by parallel evolution in *Tephrosia* and *Sphinctospermum*, a topology supporting relationships proposed by Polhill and Sousa (1981) and Wood (1949). That the two most parsimonious cladograms depict such different relationships reveals that the data set is equivocal with regard to the generic or tribal affinities of *Sphinctospermum*. Thus, a close relationship of this genus with Millettieae is a viable alternative hypothesis to the one suggesting a close relationship with Robinieae.

One previously proposed relationship, that of *Coursetia* and *Sphinctospermum* (Polhill and Sousa 1981; Wood 1949), is not supported in this analysis. The chromosome number, herbaceous habit, and septate legumes have been used to suggest a close relationship of these two genera. But the evidence provided here suggests these are similarities arising independently; for example, the structural differences in the legume cross-septa (figs. 8, 9; see description of character 3) are not considered homologous. Even in those computer runs where the legume condition in *Coursetia* was coded "2," cladograms were consistently generated that refuted a hypothesis of homology between the legume cross-septa of *Coursetia* and those of *Sphinctospermum*.

SUMMARY

Although the previously proposed relationship of *Sphinctospermum* with *Coursetia* (Polhill and Sousa 1981; Wood 1949) is refuted in this analysis, the actual relationships of *Sphinctospermum* are difficult to determine using primarily morphological data. Although equivocal, the choice of potential relationships of the genus is limited; it is either a sister group of the barbistyled Robinieae or *Tephrosia* and closely related genera of Millettieae. *Sphinctospermum* is

a morphologically very unusual genus of Papilionoideae, one that has undergone a very rapid rate of morphological evolution relative to other genera of Millettieae and Robinieae. Hypotheses of homology are difficult to postulate for its most distinctive features, such as its pollen brush, ebracteolate flower, septate legume, and linear entire leaf. However, an enumeration of a primarily morphological data set does provide a foundation for interpreting newly acquired data that may bear on the relationships of this unusual genus.

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