

FLAVONOIDS IN *STROPHOSTYLES* SPECIES AND THE RELATED GENUS *DOLICHOPSIS* (PHASEOLINAE, FABACEAE): DISTRIBUTION AND PHYLOGENETIC SIGNIFICANCE

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ABSTRACT

Strophostyles Elliott is the only genus within the Phaseolinae with a center of distribution in the United States. It comprises three species, namely *S. helvula* (L.) Elliott, *S. umbellata* (Willd.) Britton, and *S. leiosperma* (Torrey & A. Gray) Piper, and it is considered as allied to *Dolichopsis* Hassler, a monotypic genus endemic to South America. This study analyses the leaf flavonoid content from the three *Strophostyles* species and *Dolichopsis paraguariensis* Hassler with the aim of examining the phylogenetic relationships among taxa. We isolated 38 glycosides based on kaempferol, quercetin and isorhamnetin. All *Strophostyles* species were characterized by the presence of isorhamnetin glycosides. However, *S. leiosperma* showed a distinctive profile while *S. helvula* and *S. umbellata* clustered together. In contrast, *D. paraguariensis* lacked isorhamnetin-based compounds. A cladistic analysis of flavonoid plus morphological data supported *Strophostyles* monophyly and showed *S. leiosperma* as the sister taxon of the clade *S. helvula*-*S. umbellata*.

RESUMEN

Strophostyles Elliott es el único género de las Phaseolinae con un centro de distribución en los Estados Unidos. Comprende tres especies: *S. helvula* (L.) Elliott, *S. umbellata* (Willd.) Britton y *S. leiosperma* (Torrey & A. Gray) Piper, y se considera afín a *Dolichopsis* Hassler, un género monotípico endémico de Sudamérica. Este estudio analiza el contenido de flavonoides foliares en las tres especies de *Strophostyles* y en *Dolichopsis paraguariensis* Hassler con el objeto de examinar las relaciones filogenéticas entre estos taxa. Se aislaron 38 glicósidos de kaempferol, quercetina e isoramnetina. Todas las especies de *Strophostyles* se caracterizaron por la presencia de glicósidos de isoramnetina. Sin embargo, *S. leiosperma* mostró un perfil distintivo mientras que *S. helvula* and *S. umbellata* se agruparon juntas. Por el contrario, *D. paraguariensis* no sintetizó compuestos basados en la isoramnetina. Un análisis cladístico conjunto de los datos de flavonoides y caracteres morfológicos apoyó la monofilia del género y mostró a *S. leiosperma* como el taxón hermano del clado *S. helvula*-*S. umbellata*.

INTRODUCTION

Strophostyles Elliott is the only genus within the Phaseolinae with a center of distribution in the United States. Its current taxonomic treatment follows the original generic concept (Elliott 1822), but it was previously

associated with unrelated species and reduced to a section of *Phaseolus* (de Candolle 1825; Bentham 1837, 1865) until it was restored as a separate genus including three species (Britton & Brown 1897; Piper 1926). A set of characters precludes merging *Strophostyles* with *Phaseolus*, namely erect style (not coiled), lack of hooked hairs, pedicels shorter than the calyx, and nodes of the inflorescence somewhat swollen (Maréchal et al. 1978). Moreover, *Strophostyles* plants can be recognized by their nearly asymmetric flowers arranged in subumbellate inflorescences, bracts and bracteoles persisting through seed maturation, cylindrical seeds (often pubescent), and linear pods.

Strophostyles has also been considered as allied to *Dolichopsis* Hassler (Maréchal et al. 1978; Lackey 1983). Nevertheless, both genera are easily distinguishable by many characters and their quite distinct geographical distributions. The monotypic genus *Dolichopsis*¹ resembles *Strophostyles* mainly in floral morphology (purplish corolla, keel with a not curved to somewhat curved beak, style slightly thickened distally, and stigma terminal oblique) and general appearance, but it is unlike the latter in having symmetric flowers clustered in elongate pseudoracemes and the unique fruit traits such as oblong, very flat pods with oblong seeds implanted through a very long funicle and with the hilum perpendicular to the placenta. The geographic range of *Dolichopsis* is Paraguay and Argentina, in South America, while *Strophostyles* occurs throughout eastern USA, eastern Canada up to south of Quebec and extreme northeastern Mexico.

Phytochemical data on *Strophostyles* species are scanty and include the absence of both leuco-anthocyanins (Baudet 1978) and canavanine (Lackey 1977), and a recent report of flavonoids (Williams et al. 1995). In this study, we expanded on the survey of foliar flavonoids by considering a larger number of samples of the three *Strophostyles* species, i.e. *S. helvula*, *S. umbellata* and *S. leiosperma*, and we added *Dolichopsis paraguariensis* for comparison.

MATERIALS AND METHODS

We analyzed the constitutive flavonoids present in the leaves of herbarium specimens belonging to the three *Strophostyles* species and *Dolichopsis paraguariensis*. Samples (100–200 mg) were powdered and extracted under reflux with 80% methanol (x 3). Concentrated methanolic extracts were two-dimensionally chromatographed on paper (BAW/ 15% acetic acid). Compounds were identified by standard methods (Mabry et al. 1970; Markham 1982). These included complete and controlled (3 min.) acid hydrolysis, enzymatic hydrolysis (β -glucosidase), co-chromatography with authentic markers and UV-Vis spec-

¹*Dolichopsis* was a genus with two species, *D. paraguariensis* and *D. monticola* (Lackey 1983, Lewis 1991), but recently Delgado Salinas & Lewis (1997) created the new genus *Oryxis* where they placed *D. monticola*. Therefore, *D. paraguariensis* has become the unique representative of the genus.

troscopy. Glucosides were separated from their galactosidic analogues by TLC in the appropriate system according to Budzianowski (1991).

Plant material.—Specimens were provided by the Instituto de Botánica Darwinion Herbarium (SI), San Isidro, and the Centro de Estudios Farmacológicos y Botánicos Herbarium (BACP), Buenos Aires.

Strophostyles helvula (L.) Elliott

U.S.A. Arkansas. Jefferson Co.: Arkansas river bottoms, 220 ft, 17 Sep 1937, *Demaree* 16245 (SI). Illinois. Mc Donough Co.: Argykle Lake, near Colchester, 2 Aug 1958, *Jones* 22335 (SI). Iowa. Dickinson Co.: N shore of Spirit Lake, sand (older beach), 5 Aug 1913, *Sinek* 14... (number illegible) (SI). Mississippi. Harrison Co.: near the coast on sand, 6 Jan 1951, *Demaree* 30675 (SI); Ship Island, P.O. Biloxi, in stabilized sand, moist, long trailing, *Demaree* 31059 (SI). Virginia. Prince George Co.: rich alluvial thicket back of sand-beach of James River, Jordan Point, SE Virginia, 16 Sep 1938, *Fernald & Long* 9353 (SI). *Unknown locality*: [Flora of the Western Reserve] 15 Aug 1897, *G.B. Aschcroft*, *Berea O. s.n.* (SI).

Strophostyles leiosperma (Torrey & A. Gray) Piper

U.S.A. Oklahoma: 5 mi NW of Breckenridge, 25 Jul 1941, *Gephardt* 747 (SI). Woods Co.: in waste place, hard soil, near Alva, 24 Sep 1913, *Stevens* 2824 (SI). Texas. Smith Co.: Amigo, neglected sandy field, 10–17 Aug 1945, *Moore, Jr.* 995 (SI). Morris Co.: Aug 1891, *Carleton* 420 (SI).

Strophostyles umbellata (Willd.) Britton

U.S.A. Virginia. Greensville Co.: dry pine and oak woods, about 1 mi N of Skipper's, 14–15 Jul 1938, *Fernald & Long* 8737 (SI).

Dolichopsis paraguariensis Hassler

ARGENTINA. Entre Ríos: Depto. La Paz, R 126, desvío a Ombúes, borde camino, 31 Jan 1981, fl. azul-violáceo, *Troncoso de Burkart & Bacigalupo* 3096 (SI). PARAGUAY. Depto. Pte. Hayes: Estancia Loma Pyta, 23° 40'S, 59° 35'W, 2 Apr 1974, enredadera casi rastrera, fl. violáceas, crece en pastizal, n.v. 'kekleichetas', *Arenas* 544 (BACP). Depto. Boquerón: Misión Santa Rosa, 21° 45'S, 61° 35'W, Feb 1981, enredadera, fl. violáceas, crece en pajonal, n.v. 'ceihlowéy', *Arenas* 1726 (BACP).

Data analysis.—A cluster analysis was performed on flavonoid data of 15 herbarium specimens. Similarity matrix was measured using Jaccard's coefficient and a dendrogram was constructed applying the unweighed pair-group method of arithmetic averages (UPGMA). All calculations were done using NT-SYS program (Rohlf 1993).

A cladistic analysis of the flavonoid data plus a set of morphological characters was carried out according to the maximum parsimony principle. Outgroup criterion was used for character polarization. *Vigna adenantha* was chosen as the external group which flavonoid data were obtained following the methods above mentioned (Pelotto, unpublished manuscript). For flavonoids, character states that occurred in the outgroup were scored as 0 and those in the ingroup (*D. paraguariensis* and the three *Strophostyles* species) were scored as 1 (see Appendix, Tables A and B). Morphological data were gathered from the literature and included some multistate characters that were treated as non-additive (see Appendix, Tables A and C). Cladograms were calculated

using the implicit enumeration routine (i.e.*) of the program Hennig86 (Farris 1988) with all characters equally weighted.

RESULTS AND DISCUSSION

Chromatographic properties of the identified flavonoid glycosides and its distribution in *Strophostyles* species and *D. paraguariensis* are shown in Tables 1 and 2, respectively. All detected compounds were O-glycosides of flavonols with sugars attached at positions 3 and 7 of the aglicone skeleton. This pattern of glycosilation is very common among the Phaseolinae (Zallocchi & Pomilio 1994; Williams et al. 1995, Pelotto unpublished manuscript).

All three *Strophostyles* species produced glycosides based on the methylated flavonol isorhamnetin plus kaempferol and quercetin. Notwithstanding *S. belvula* and *S. umbellata* showed very similar chromatographic patterns, while the flavonoid profile of *S. leiosperma* was quite distinctive. No rhamnosides were detected in *S. leiosperma* and it only shared the presence of monoglycosides with the other two species. Based on a three-sample analysis within a flavonoid survey of the Phaseolinae, Williams et. al (1995) have also reported the occurrence of isorhamnetin glycosides in *Strophostyles* species and noticed the same interspecific differences. In contrast with our results, Williams and co-workers isolated fewer compounds and did not detect kaempferol glycosides from leaves, although they did from stems and/or flowers.

In turn, *Dolichopsis paraguariensis* samples were characterized by the presence of kaempferol and quercetin glycosides, lacking isorhamnetin. Noticeably, Paraguayan samples contained only kaempferol glycosides while Argentinean one had kaempferol plus quercetin glycosides. However, in a previous work (Zallocchi et al. 1995) both kaempferol and quercetin glycosides were reported from one sample of *D. paraguariensis* from Paraguay, but of the eight flavonol glycosides the authors identified only rutin and kaempferol-3-O-rutinoside were also present in our samples. These differences may be due to the fact that Zallocchi and co-workers analyzed a whole plant extract and therefore their results are difficult to compare with ours.

After the cluster analysis *S. belvula* and *S. umbellata* are closer to *D. paraguariensis* than to *S. leiosperma* (Fig. 1). This is because *S. belvula* and *S. umbellata* have more glycosides (based on kaempferol and quercetin) in common with *D. paraguariensis* than with *S. leiosperma*, even though *D. paraguariensis* does not produce isorhamnetin glycosides.

Cladistic analysis resulted in two most parsimonious trees (length, L = 35, consistency index, CI = 91, retention index, RI = 70. Fig. 2). Both cladograms support *Strophostyles* monophyly but differ in the depicted relationships among *Strophostyles* species. One tree (Fig. 2.A) shows *S. belvula* and *S. leiosperma* as being sibling species, but this hypothesis needs the parallel gain of the characters 19, 22 and 31 on the *S. umbellata* and *S. belvula* branches. The other tree (Fig. 2.B) supports the clade *S. umbellata*-*S. belvula*

TABLE 1. Chromatographic characteristics of the identified compounds.

SPOT	IDENTITY	COLOUR [†]		Rf (× 100)	
		UV	+ NH ₃	BAW	15% aa
1	K-3-O-glucoside + K-3-O-galactoside	DP	Y	69	45
2	K-7-O-glucoside + K-7-O-galactoside	Y	Y	45	15
3	K-3-O-rutinoside + K-3-O-robinobioside	DP	Y	52	54
4	K-3-O-diglucoside + K-3-O-digalactoside	DP	Y	33.5	61.5
5	K-3,7-O-diglucoside	DP	Y	29	70
6	K-3-O-rutinoside-7-O-glucoside + K-3-O-robinobioside-7-O-glucoside	DP	Y	24	75
7	K-3,7-O-triglucoside	DP	Y	3	82
8	K-3,7-O-triglycoside (glu + rha + gal) [‡]	DP	Y	4	80
9	Q-3-O-glucoside + Q-3-O-galactoside	DP	Y	56	39
10	Q-7-O-glucoside + Q-7-O-galactoside	Y	YO	27	9
11	Q-3-O-rutinoside + Q-3-O-robinobioside	DP	Y	40	51
12	Q-3-O-diglucoside + Q-3-O-digalactoside	DP	Y	26	52
13	Q-3,7-O-diglucoside	DP	Y	23	63
14	Q-3-O-rutinoside-7-O-glucoside + Q-3-O-robinobioside-7-O-glucoside	DP	Y	15	70
15	Q-3,7-O-triglucoside	DP	Y	3	78
16	Q-3,7-O-triglycoside (glu + rha + gal)	DP	Yo	5	79
17	IR-3-O-glucoside + IR-3-O-galactoside	DP	Y	56	42
18	IR-7-O-glucoside + IR-7-O-galactoside	Y	Y	38	10
19	IR-3-O-rutinoside + IR-3-O-robinobioside	DP	Y	40	54
20	IR-3-O-diglucoside + IR-3-O-digalactoside	DP	Y	29	58
21	IR-3,7-O-diglucoside	DP	Y	25	68
22	IR-3-O-rutinoside-7-O-glucoside + IR-3-O-robinobioside-7-O-glucoside	DP	Y	19	74
23	IR-3,7-O-triglucoside	DP	Y	3	80

[†]DP: deep purple, Y: yellow, YO: yellow-orange[‡]glu: glucose, rha: rhamnose, gal: galactose

and requires three reversions (characters 1, 9 and 17). This scenario is preferable to that portrayed on Fig. 2.A since a mutation lost is a more probable event than the homoplastic acquisition of isorhamnetin glycosides. Even more, if we suppose reversal of characters 1, 9 and 17 on the *S. umbellata* branch as being a consequence of sampling error (undersampling), the cladogram becomes shorter with only 32 steps (CI= 100, RI= 100) and the unique solution of a similar analysis. Thus, we consider the tree depicted on Figure 2.B a more plausible ingroup phylogeny.

Flavonoid evolution shows methylation of the flavonol skeleton as an advanced character shared by all *Strophostyles* species and the absence of rhamnosides in *S. leiosperma* as an (aut)apomorphic loss.

Morphological traits are congruent with flavonoid data. Subumbellate inflorescence (character 24), persistent bracts and bracteoles (character 26), linear, terete pods (character 27) and seed pubescence (character 28) support *Strophostyles* monophyly, and are correlated with isorhamnetin monoglycoside production (characters 17 and 18). *Strophostyles belvula* strongly resembles

TABLE 2. Glycoside distribution in the analyzed samples. Compounds are numbered according to Table 1. K: kaempferol glycosides; Q: quercetin glycosides; IR: isorhamnetin glycosides; +: present; -: absent.

	K								Q								IR						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>S. belvula</i>																							
Jones 22335	-	+	+	-	-	+	-	-	-	+	+	-	-	+	-	-	-	+	+	-	-	+	-
Simek 14...	+	+	+	-	-	+	-	-	+	+	+	-	-	+	-	+	+	+	+	-	-	+	-
Aschroft & Berea s.n.	+	+	+	-	-	+	-	-	+	+	+	-	-	+	-	+	+	+	+	-	-	+	-
Demaree 30675	+	+	+	-	-	+	-	-	+	+	+	-	-	+	-	+	+	+	+	-	-	+	-
Demaree 16245	-	+	-	-	+	-	-	-	-	+	-	-	-	+	-	+	-	+	-	-	-	+	-
Demaree 31059	+	+	+	-	-	+	-	-	+	+	+	-	-	+	-	+	+	+	+	-	-	+	-
Fernald & Long 9353	-	+	+	-	-	+	-	-	-	+	+	-	-	+	-	+	-	+	+	-	-	+	-
<i>S. umbellata</i>																							
Fernald & Long 8737	-	+	+	-	-	+	-	-	-	+	+	-	-	+	-	+	-	+	+	-	-	+	-
<i>S. leioperma</i>																							
Moore Jr. 995	+	+	-	-	+	-	-	-	+	+	-	-	+	-	-	-	+	+	-	-	+	-	-
Carleton 420	+	-	-	+	+	-	+	-	+	-	-	+	+	-	+	-	+	-	-	+	+	-	+
Gephardt 747	+	-	-	+	+	-	+	-	+	-	-	+	+	-	+	-	+	-	-	+	+	-	+
Stevens 2824	+	-	-	+	+	-	+	-	+	-	-	+	+	-	+	-	+	-	-	+	+	-	+
<i>D. paraguayensis</i>																							
Arenas 1726	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arenas 544	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Troncoso & Bacigalupo 3096	-	+	+	-	-	+	-	+	-	+	+	-	-	+	-	+	-	-	-	-	-	-	-

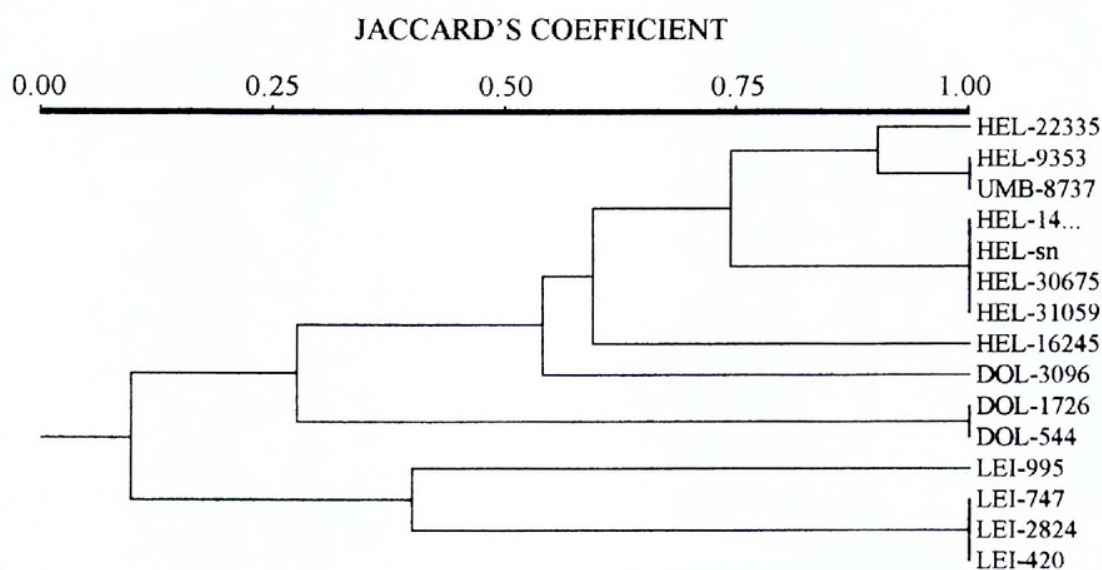


FIG. 1. Dendrogram of the *Strophostyles* and *Dolichopsis* specimens constructed from a similarity matrix (Jaccard's coefficient) using the UPGMA method. Cophenetic correlation coefficient, $r = 0.969$

S. umbellata, except for its more lobed leaflets and larger pods and seeds. *Strophostyles leiosperma* is rather different from the other two species because of the smaller flowers (character 25) arranged in more pauciflorous inflorescences and its seeds glabrous and shining at maturity (character 29).

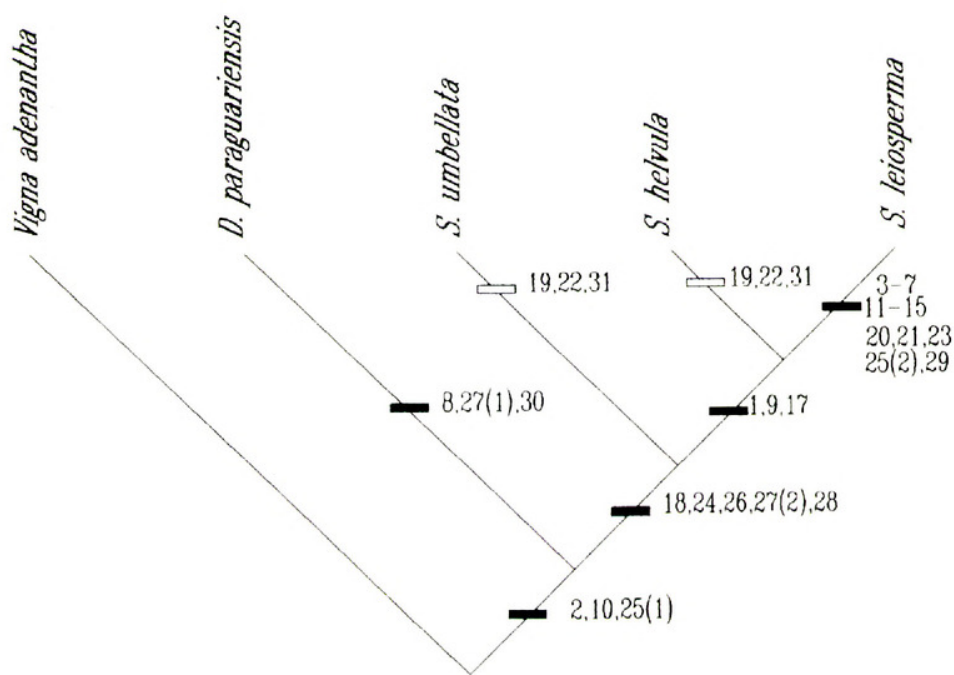
Similarly, both *S. helvula* and *S. umbellata* are more widespread and northerly distributed, with the first species reaching Canada, while *S. leiosperma* has a more limited distribution ranging from south of the United States to the extreme northeastern of Mexico (Britton & Brown 1897, Maréchal et al. 1978). Species divergence at chemical and morphological level also correlates with their ecological features; *S. helvula* and *S. umbellata* mostly grow in more mesic sites, while *S. leiosperma* is adapted to live into more xeric habitats.

Regarding the evolution of the growth form, overlapping this character onto our preferred topology suggests that annual growth would have evolved independently in both *S. leiosperma* and *S. helvula*, whereas perennation would be the plesiomorphic state shared by *D. paraguariensis* and *S. umbellata*.

In summary, universal occurrence of isorhamnetin-based compounds in *Strophostyles* species is a good chemical character in defining generic monophyly while individual glycosides are useful characters to trace species evolution. Within the Phaseolinae isorhamnetin glycosides have sporadically been recorded in four *Phaseolus* species (Pelotto, unpublished manuscript) and some *Vigna* and *Macroptilium* species (Zalocchi & Pomilio 1994; Williams et al. 1995). This fact suggests that flavonol methylation has appeared several times in the tribe, making it a valuable phylogenetic marker at the infrageneric level.

Beyond this contribution, flavonoid data from the related genera *Oxyrhynchus* and *Oryxis* are wanting for a complete view of this little group of American species around *Vigna*.

A-



B-

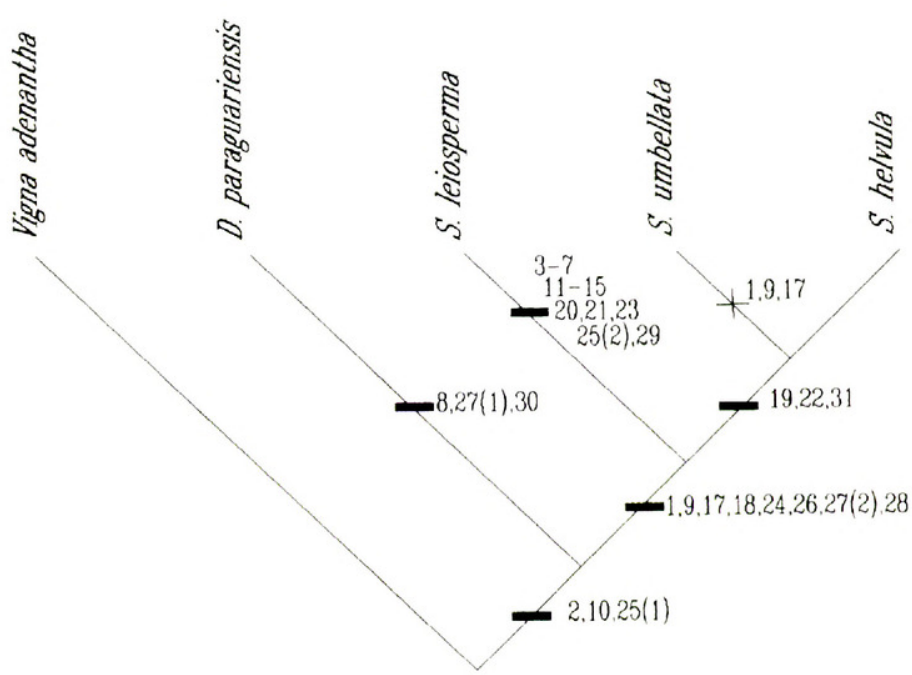


FIG. 2. The two most parsimonious trees (L = 35) generated using the data matrix (see Appendix, Table A) and *Vigna adenantha* as outgroup. Characters are mapped on the trees as follows: solid bar = non-homoplasious apomorphy, clear bar = homoplasious apomorphy, and cross = reversal. Numbers on the right of the character symbols stand for character numbers (and character state).

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APPENDIXES

TABLE A. Data matrix for the cladistic analysis including both flavonoid (characters 1–15, 17–23, codified according to Table B) and morphological (characters 24–31, codified according to Table C) data sets and using *Vigna adenantha* as outgroup.

Taxon	character number																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31		
<i>Vigna adenantha</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0		
<i>D. paraguariensis</i>	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	?	1	0	
<i>S. belvula</i>	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	2	1	0	0	1		
<i>S. umbellata</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	2	1	0	0	1		
<i>S. leiosperma</i>	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	1	2	1	2	1	1	0	0			

TABLE B. Flavonoids. Character numbers are as in Table 1. Character 16 was not included because no hypothesis about homology can be made on a partially identified compound.

Character states		
1. 0= absent, 1= present	8. 0= absent, 1= present	15. 0= absent, 1= present
2. 0= absent, 1= present	9. 0= absent, 1= present	17. 0= absent, 1= present
3. 0= present, 1= absent	10. 0= absent, 1= present	18. 0= absent, 1= present
4. 0= absent, 1= present	11. 0= present, 1= absent	19. 0= absent, 1= present
5. 0= absent, 1= present	12. 0= absent, 1= present	20. 0= absent, 1= present
6. 0= present, 1= absent	13. 0= absent, 1= present	21. 0= absent, 1= present
7. 0= absent, 1= present	14. 0= present, 1= absent	22. 0= absent, 1= present
		23. 0= absent, 1= present

TABLE C. Morphological characters, states and polarities.

character	states
24. inflorescence	0= pseudoracemose; 1= subumbellate
25. flower size	0= great (> 20 mm); 1= medium (7-15 mm); 2= small (< 7 mm)
26. bract and bracteole	0= persisting no longer anthesis; 1= persisting through seed maturation
27. pods	0= linear, compressed; 1= oblong, very flat, with false cellulosic septa; 2= linear, cylindrical
28. seed coat	0= smooth; 1= pubescent
29. seed pubescence	?= inapplicable; 0= persisting in mature seeds; 1= absent from mature seeds
30. hilum	0= parallel to the placenta; 1= perpendicular to the placenta
31. leaflets	0= entire; 1= lobed to somewhat lobed at base

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