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Phylogenetic Systematics of *Strophostyles* (Fabaceae): A North American Temperate Genus Within a Neotropical Diversification

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Abstract. A combined parsimony analysis of cpDNA *trnK*, nrDNA ITS/5.8S, and morphology reveals that the genus *Strophostyles* is monophyletic. In contrast to the conventional view of the geographic relationships of eastern North America, *Strophostyles* is most closely related to neotropical genera. Its sister is the South American genus *Dolichopsis*, which is endemic to the Chaco, a region characterized by having an annual frost interval. *Strophostyles* is apomorphically diagnosed by divergent stipules, persistent secondary floral bracts, calyces with four acute to sometimes attenuate lobes, and seed testa often with a cellular coat. The relationship with *Dolichopsis* is supported in part by a shared keel petal morphology involving a gibbous ventral margin proximal to the rostrum. Phylogenetic analysis of ITS/5.8S sequences and morphometric analysis of quantitative traits suggest that the three traditionally recognized species of *Strophostyles* can be recognized under the phylogenetic species concept. *Strophostyles umbellata* is the most genetically variable at the ITS locus and geographically centered in southern Appalachia. *Strophostyles helvola* shows the least amount of intraspecific genetic variation at this locus, suggesting a recent and rapid range expansion throughout eastern North America. Nucleotide sequence variation is intermediate in *Strophostyles leiosperma*, a species distributed primarily in central North America.

The genus *Strophostyles* Elliott is classified within the tribe Phaseoleae of the legume subfamily Papilionoideae. The liana habit of *Strophostyles* is common to papilionoid genera especially of this tribe. The asymmetric floral morphology of *Strophostyles*, whereby the rostrate keel petals curve to the right side of the flower, is characteristic of many genera in the tribe Phaseoleae subtribe Phaseolinae, a group of trifoliolate-leaved lianas comprising such well-known genera as *Phaseolus* L. and *Vigna* Savi. Indeed, the most recent higher level taxonomic treatment of Phaseoleae (Lackey 1981), in addition to phylogenetic analyses of nuclear ribosomal 5.8S and flanking internal transcribed spacers (the ITS region; Delgado-Salinas et al. 1999) and the chloroplast *trnK* locus (Delgado-Salinas et al. unpublished data), suggest that the closest relatives of the temperate *Strophostyles* are the primarily neotropical *Dolichopsis* Hassler, *Macroptilium* (Bentham) Urban, *Mysanthus* G.P. Lewis & A. Delgado, *Phaseolus*, *Oryxis* A. Delgado & G.P. Lewis, *Oxyrhynchus* Brandegee, *Ramirezella* Rose, and *Vigna* subgenus *Sigmoidotropis* (Piper) Verdcourt. Although these genera, collectively the New World Phaseolinae (Lackey 1983), form a strongly supported clade (Wojciechowski et al. in press; Delgado-Salinas et al. unpublished data), the putative monophyly and intergeneric relationships of most of them, including *Strophostyles*, has never been comprehensively addressed.

The New World Phaseolinae generally show a high degree of elaboration of petal morphologies, particularly in deviations from bilateral symmetry. In *Strophostyles*, the standard, wings, and keel petals are bilaterally symmetrical except for the distal end of the keel, which curves to the right side of the flower. This is similar to the floral morphology of *Dolichopsis*, *Oryxis*, *Oxyrhynchus*, *Ramirezella*, and some *Vigna* subgenus *Sigmoidotropis*. All other New World Phaseolinae genera have a keel beak that is abruptly hooked or coiled at least one-half turn to the right side of the flower. Although Maréchal et al. (1978) and Pelotto and del Pero Martínez (1998) have used overall similarity in morphology or secondary chemistry, respectively, to suggest a close relationship of *Strophostyles* with *Dolichopsis*, such analyses have not been comprehensive in taxon sampling, or have involved only limited data. The suggestion that the northern temperate *Strophostyles* is sister to *Dolichopsis*, which is endemic to the Chaco, is in need of independent verification with DNA sequence data.

At the species level, floristic treatments dealing with *Strophostyles* (e.g., Radford 1968; Correll and Johnston 1970; Isely 1998) have recognized at least three species, although species delimitation remains uncertain. Misidentification is common especially in the southeastern USA where the distributions of the traditionally recognized species broadly overlap. This difficulty arises because either the key morphologies are inadequate for diagnosing species identity, or species delimitations have been incorrectly drawn, or extensive introgressive hybridization is occurring.

This study was designed to determine the closest relatives of *Strophostyles* using nucleotide sequences from the cpDNA *trnK* and nrDNA ITS/5.8S regions, as well as morphological data. Such data were targeted because they have been shown to be highly informative in legumes from the level of closely related genera down to populations within an individual species (e.g., Delgado-Salinas et al. 1999; Hu et al. 2002; Lavin et al.

TABLE 1. Morphological characters scored for discrete states that are phylogenetically informative at the species and genus level. See Appendix A for character descriptions. An ''L'' designates a multistate taxon.

	Phylogenetically informative characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Ramirezella spp.	0	0	0	L	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxyrhynchus spp.	0	0	0	L	0	0	0	0	0	0	0	0	0	0	1	0	0
Macroptilium spp.	0	0	0	0	0	1	1	1	0	1	1	L	0	0	0	0	L
Mysanthus uleanus	0	1	0	1	0	1	1	1	0	1	1	1	0	0	0	0	1
Oryxis monticola	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1
Dolichopsis paraguariensis	1	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1
Dolichopsis ligulata	1	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1
Strophostyles umbellata	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1
Strophostyles helvola	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1
Strophostyles leiosperma	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1

2003; Schrire et al. 2003). The lack of a comprehensive taxonomic treatment of the genus at the species level and below warranted a reevaluation of the constituent taxa within *Strophostyles*. The goals of this study thus include a taxonomic monograph of the genus *Strophostyles*, which addresses the identity and relationships of species within the genus, as well as the relationships of the genus to putative neotropical relatives.

MATERIALS AND METHODS

Taxon Sampling. Each of the three species of *Strophostyles* was sampled as exhaustively as possible for sequences from the ITS region, as well as for morphological variation. Field and herbarium specimens of *Strophostyles* and related genera were sampled for morphological characters that included the many vegetative, floral, and fruiting traits that have been used traditionally to delimit the species and genera. At and below the species level in *Strophostyles*, quantitative characters that have been used in taxonomic and floristic treatments were sampled. Sampling was performed such that variation within and among the traditionally recognized species of *Strophostyles* and at the geographical extremes would be represented. From over 1,000 herbarium specimens of *Strophostyles*, 424 that possessed the greatest array of mature and healthy vegetative, floral, and fruiting characters were sampled for quantitative morphological variation. From these, 362 specimens with minimal missing parts were selected for morphometric analysis, and these were also selected to ensure they represented the distributional ranges of the traditionally recognized species.

Intergeneric relationships of *Strophostyles* and related New World Phaseolinae were studied by sampling qualitative morphology (Table 1 and Appendix A) and nucleotide sequences from both the ITS region and the *trnK* locus (Appendix B). The genera most closely related to *Strophostyles* include *Dolichopsis*, *Mysanthus*, *Oryxis*, and *Macroptilium*. Outgroups included exemplars from *Oxyrhynchus* and *Ramirezella*, two genera of the New World Phaseolinae with a sister relationship to the clade of above-named genera (Dalgado-Salinas et al. unpublished data).

DNA Sequence Data. DNA isolations, polymerase chain reaction (PCR) amplifications, and template purifications were performed with Qiagen Kits (i.e., DNeasy Plant Mini Kit, Taq PCR Core Kit, QIAquick PCR Purification Kit; Qiagen, Santa Clarita, California, USA). PCR and sequencing primers for the ITS region are described in Beyra-M. and Lavin (1999) and Delgado-Salinas et al. (1999). Primers for the *trnK* intron are as follows: from the 5′ *trnK* intron forward, TK1F: 5′-GGGTTGCTAACTCAATGGTAG-3′; middle of the *matK* coding region reverse, M4PF: 5′-CCTTCGA-TATTGGATAAAAGATG-3′; near 3′ end of *matK* coding region reverse, M7MR: 5′-CGGCTTACTAATAGGATGAC-3′; middle of *matK* coding region forward, M4PR: 5′-CATCTTTTATCCAATA-TCGAAGG-3′; and 3′ *trnK* intron reverse, TK2R: 5′-CCCGGAAC-TAGTCGGATGG-3′. DNA sequencing was performed on an automated sequencer at Northwoods DNA (Becida, Minnesota). Phylogenetic data are available from http://gemini.oscs.montana.edu/~mlavin/data/stroph.htm and TreeBase study accession number S1015. Missing entries accounted for 1.5% of the ITS sequence data set, and 8.3% of the combined data set. This last figure is high because *trnK* sequences were not obtained for *Oryxis* (if this genus is omitted, missing entries account for 2.9% of the combined data matrix).

Phylogenetic Analysis. Sequences were aligned manually with Se-Al (Rambaut 1996). Maximum parsimony analyses were performed with PAUP* (Swofford 2001). The combined data set was analyzed with the branch and bound search option, whereas the ITS data set required a heuristic search that included 100 random addition replicates and tree-bisection-reconnection branch swapping. In all analyses, the maximum number of trees was set at 10,000, which is sufficient to capture all topological variation (cf. Sanderson and Doyle 1993). Bootstrap resampling for clade support and a partition homogeneity test for data compatibility were each carried out on 10,000 replicate data sets. Each replicate was subjected to heuristic search options that included one random addition sequence, swapping with tree-bisection-reconnection, and invoking neither steepest descent nor retention of multiple parsimonious trees.

Morphometric Analysis. Ordination analyses of quantitative characters were performed with NTSYSpc (Rohlf 2000) following standard protocols outlined in that program. After standardization, a symmetric distance matrix was generated using the taxonomic distance option, and this was transformed using the double center module so that eigenvectors could be computed within the eigen module. The initial distance matrix and the first three eigenvectors were then subjected to multidimensional scaling. A variance-covariance matrix from the output of multidimensional scaling was input into the eigen module, and the recomputed eigenvectors were then graphically displayed in three dimensions.

Characters chosen for the morphometric analysis were ostensibly independent. For example, high trichome density on the undersurface of a leaflet could co-occur with low density on the upper surface, or long terminal leaflets could co-occur with short and narrow lateral leaflets. Seven vegetative traits were analyzed, including width and length of terminal leaflet, width and length of lateral leaflet, depth of sinus on lateral leaflet, and hair density on the upper and lower surface of the terminal leaflet. Six inflorescence and floral traits were measured, including lengths of standard petal, calyx tube, and bracteole, length and width of inflorescence rachis, and number of nodes per inflorescence. The remaining five characters were fruiting traits, including length and width of pod, number of ovules per ovary, hair density on the surface of the pod valve, and the presence of a cellular covering on mature seed testa. The last is derived from the cuticle of the seed (Martin 1937). With the exception of the presence or absence of a cellular covering on the seed, all traits were quantitative. Because all morphometric characters were scored from herbarium specimens, certain quantitative characters that vary among the traditionally recognized species were nearly impossible to measure and thus couldn't be included in this analysis. Such traits included annual versus perennial growth habit, degree of caudex branching, lateral compression of the pod, and the length and thickness of the keel beak.

RESULTS

Analysis of Sequences from the ITS Region. The ITS phylogram resolves a monophyletic *Strophostyles* with three constituent subclades each corresponding to the three traditionally recognized species of the genus (Figs. 1–3). *Dolichopsis* is determined to be the sister to *Strophostyles*. Although the monophyly of each *Strophostyles* subclade and the sister relationship with *Dolichopsis* are weakly to moderately supported by parsimony bootstrap analysis, these relationships are all resolved in the strict consensus. Although *Mysanthus* is resolved as the sister to the *Dolichopsis-Strophostyles* clade in some of the ITS phylograms (Fig. 1), this relationship is neither supported by parsimony bootstrap analysis nor resolved in the strict consensus (not shown).

Within *Strophostyles*, ITS sequence variation in *S. umbellata* was the greatest of the three species with 11 unique sequences obtained from 13 samples distributed throughout the range of this species (Fig. 2). Eight of the 13 substitutions distinguishing these 10 sequences are transversions, and the sequences are distinguished from each other commonly by more than one base substitution. The six ITS sequences from South Carolina samples are fairly divergent (Fig. 2), which contrasts to the ITS sequence variation found in the other two species of *Strophostyles* (Figs. 2, 3).

In contrast to the many divergent sequences of *Strophostyles umbellata*, only three ITS sequences were detected from 23 samples of *S. helvola*, distributed throughout eastern North America (Fig. 2). These three sequences differ from each other by only one or two nucleotide substitutions. The principal ITS lineages within *S. helvola* show no geographic structure, similar to the ITS lineages of *Strophostyles umbellata*.

The ITS sequences from *Strophostyles leiosperma* reveal an intermediate amount of genetic variation, with seven unique sequences detected from a sample of 32 accessions, and these taken from across the geographic range of this species (Fig. 3). Eastern Texas harbors a fair amount of this sequence diversity, as exemplified by two of the most divergent sequences (samples 1453 and 1462) occurring in Brazoria County (see Appendix A for voucher information). Some geographical structure to ITS variation is observed. That is, the southwestern-most samples from Kansas (DNA 1273), New Mexico (106), Oklahoma (446), and central Texas (197) form a fairly well-supported clade (Fig. 3). Furthermore, the northern-most samples from Nebraska (1334) and Wisconsin (1445) form a paraphyletic grade with respect to the southwestern-most clade (Fig. 3).

Analysis of Combined Data. Combined analysis of morphological data (Table 1; Appendix A) and DNA sequences from the ITS region and *trnK* locus reveals that the exemplars of the three species of *Strophostyles* form a strongly supported monophyletic clade that is sister to *Dolichopsis* (Fig. 4). The genus *Strophostyles* is apomorphically diagnosed by divergent stipules (character #2, independently reversed in *Macroptilium*), persistent secondary floral bracts (#3), calyx with four acute lobes (#5), and seeds with a cellular or waxy testa (#14). The last of these is inconsistently present in each of the three species of *Strophostyles*, but no other species in the New World Phaseolinae, except for the distantly related *Vigna latidenticulata* (Harms) A. Delgado, produces such a seed covering. The four closely related neotropical genera, *Dolichopsis*, *Oryxis*, *Mysanthus*, and *Macroptilium*, have appressed stipules (except *Macroptilium*), deciduous secondary floral bracts, calyces with five lobes (the upper two usually partially fused), and seeds with a consistently smooth testa. Overall, the 17 qualitative morphological characters added a length of 22 steps to the most parsimonious phylogram, and had a combined consistency index of 0.773 and a retention index of 0.929. These values are higher than for the total combined data when autapomorphies are excluded (Fig. 4).

The sister group relationship of *Dolichopsis* and *Strophostyles* is revealed morphologically by only the shared apomorphy of a gibbous upper margin of the keel petals just behind the beak (#9). The monotypic *Oryxis* is sister to the *Macroptilium-Mysanthus* clade, as suggested by the morphological apomorphies of deciduous bracteoles (#4; reversed in *Macroptilium*) and an arched ovary (#11). Such morphologies provide the only evidence yet for the relationship of *Oryxis*, a monotypic South American genus. Finally, *Mysanthus* is well resolved as sister to *Macroptilium*, which is consistent with the many shared floral similarities of these two genera, such as oblique standards (#6), long wing petals (#7), slender keel claws (#8), a keel rostrum abruptly hooked to coiled (#10), laterally compressed pods (#12—polymorphic in *Macroptilium* and independently gained in *Dolichopsis*), and an oblanceolate hilum (#15—independently gained in *Ramirezella*).

Morphometric Analysis. A total of 17 quantitative characters varying within and among *Strophostyles* species were sampled from 424 herbarium specimens (Table 2). A single qualitative trait, presence/absence of a cellular or waxy covering on the seed testa, was also sampled but not used in the morphometric analysis. Such seeds were most commonly observed in *S. umbellata* and *S. helvola*. Of 14 specimens of *S. umbellata* observed with mature seed, 13 possessed the cellular

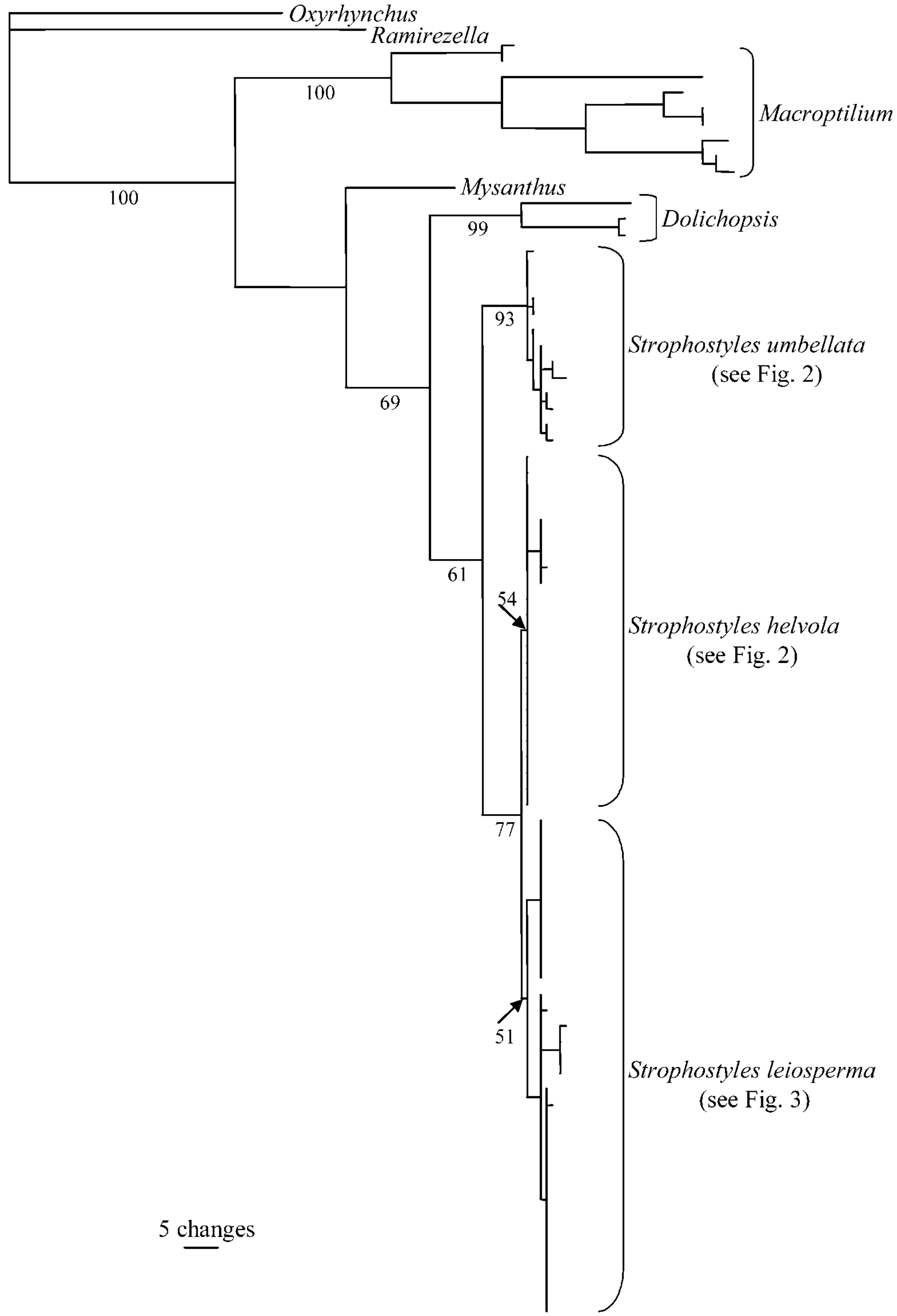

FIG. 1. One of 10,000 most parsimonious phylograms generated during a maximum parsimony analysis of nrDNA ITS/5.8S sequences. This data set contains 83 terminals and 676 aligned nucleotide sites, 157 of which are parsimony informative. The maximum parsimony trees have a length of 428, a consistency index of 0.736, and a retention index of 0.880. Bootstrap values greater than 50% are given below the branch only for those clades that were resolved in the strict consensus.

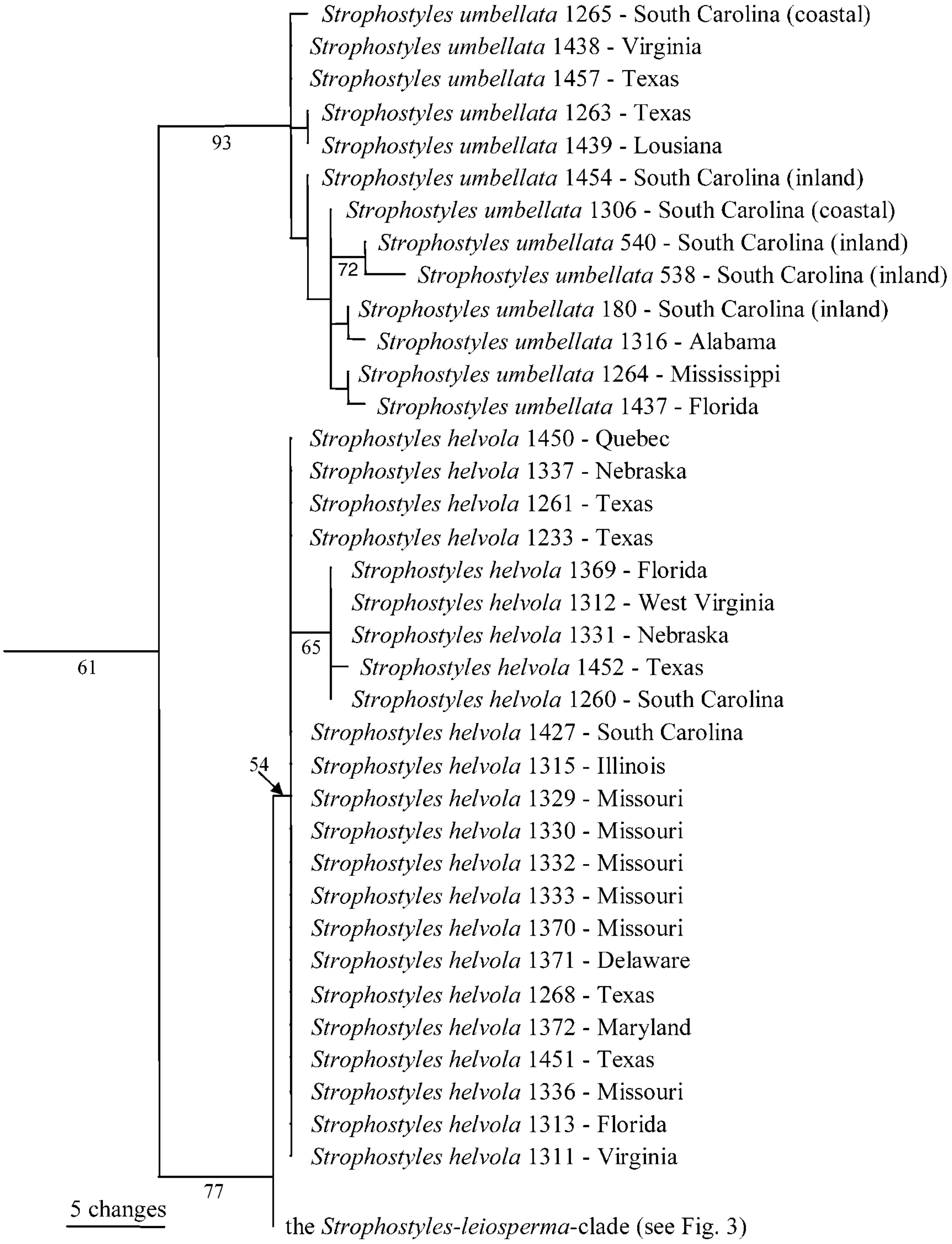

FIG. 2. The clades comprising accessions of *Strophostyles umbellata* and *S. helvola* expanded from Fig. 1 to show the identity of the terminal taxa. Bootstrap values greater than 50% are given below the branch only for those clades that were resolved in the strict consensus. Numbers after the species name refer to DNA accession numbers listed in Appendix B.

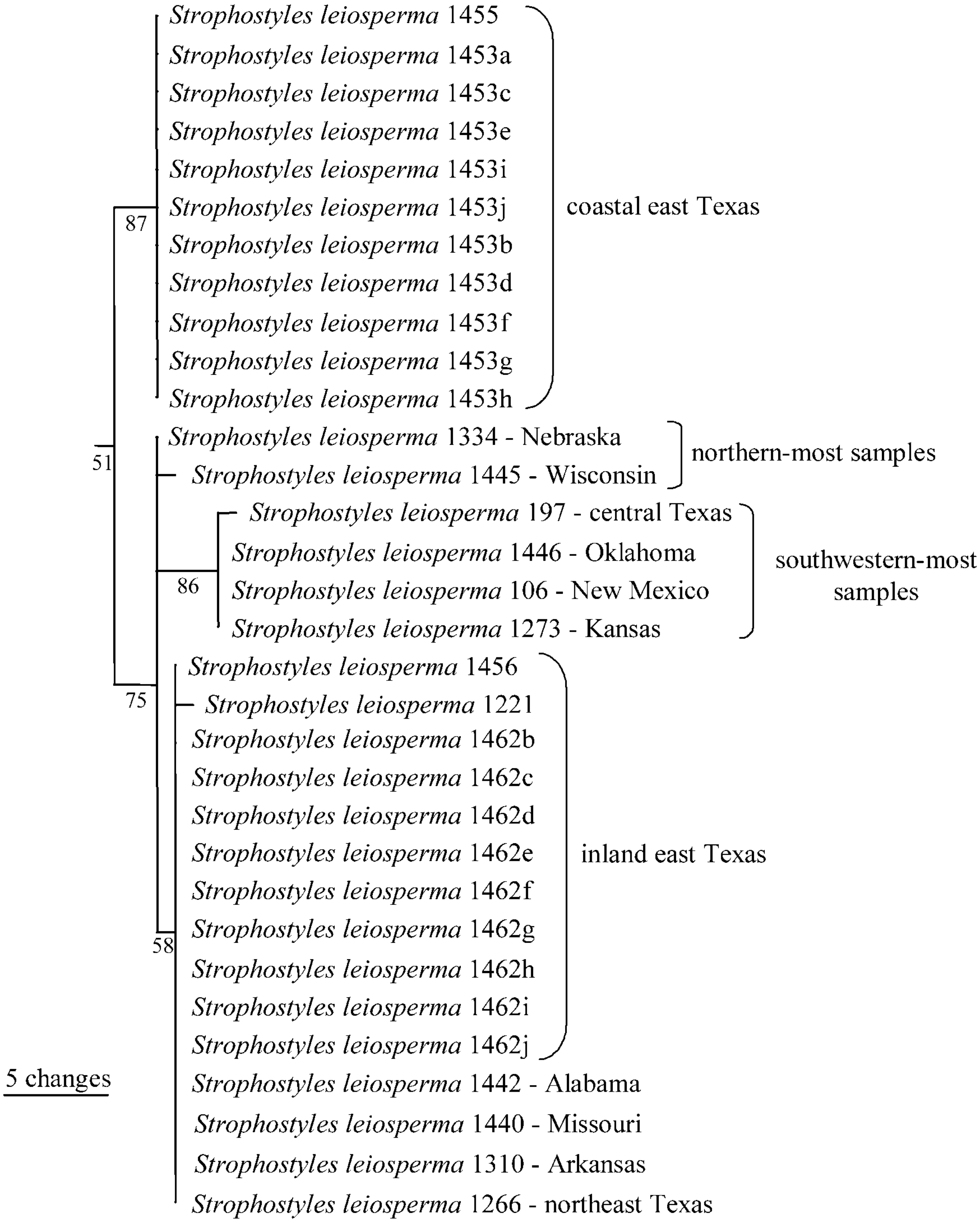

FIG. 3. The clade comprising accessions of *Strophostyles leiosperma* expanded from Fig. 1 to show the identity of the terminal taxa. Bootstrap values greater than 50% are given below the branch only for those clades that were resolved in the strict consensus. Numbers after the species name refer to DNA accession numbers listed in Appendix B.

coating on the testa. Of the 38 specimens of *S. helvola* with mature seed, 31 possessed the cellular coating. In contrast, of the 25 specimens of *S. leiosperma* with mature seed, only 8 had the cellular coat.

Of the 17 quantitative traits (Table 2), several trends were observed. *Strophostyles leiosperma* is the most phenotypically distinct of the three species, and is well marked by a high trichome density on the leaves (#'s

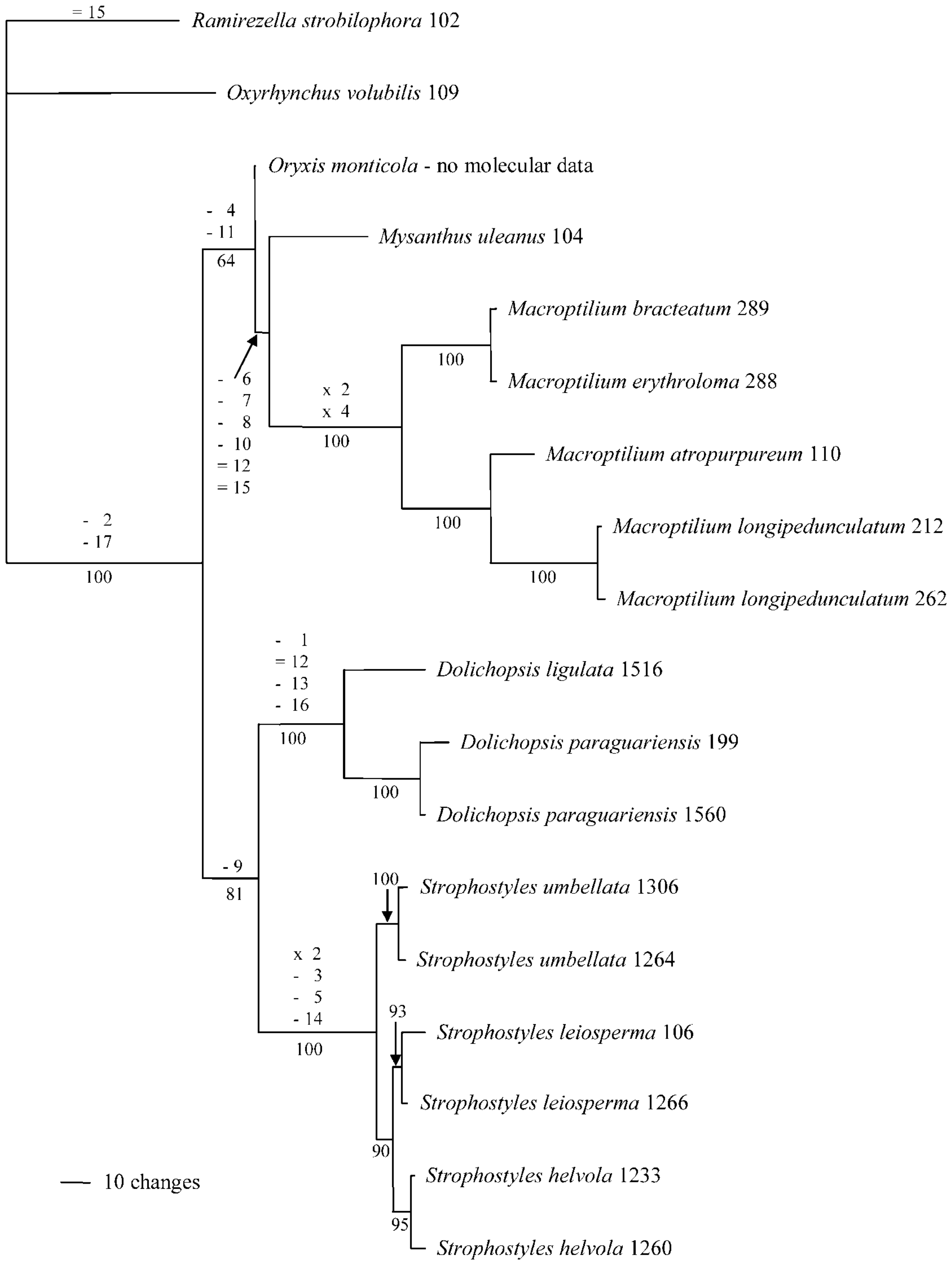

FIG. 4. The single most parsimonious phylogram generated during a maximum parsimony analysis of combined morphology, cpDNA *trnK,* and nrDNA ITS/5.8S sequences (a partition homogeneity test suggests no data conflict, p=0.7405). The data set contains 18 terminals and 3172 characters, of which 276 are parsimony informative. Of the 3172 characters, 17 are morphological, 2484 are aligned *trnK* nucleotide sequences, and 671 are aligned ITS/5.8S nucleotide sequences. This maximum parsimony phylogram has a length of 615, a consistency index of 0.798 (0.725 with autapomorphies excluded), and a retention index of 0.853. Bootstrap values greater than 50% are given below the branch. Numbers after the species name refer to DNA accession numbers listed in Appendix B (*Oryxis monticola* was represented in this analysis with only morphological data). The numbers above the branches refer to morphological apomorphies listed in Table 1 and Appendix A, where a single origin is indicated by a dash (-), independent gains by an =, and a reversal by an x.

TABLE 2. Summarized statistics for each of the 17 quantitative characters measured from 424 herbarium specimens. 1 = terminal leaflet length, 2 = terminal leaflet width, 3 = lateral leaflet length, 4 = lateral leaflet width, 5 = depth of sinus on lateral leaflet, 6 = density of hairs on upper leaflet surface, 7 = density of hairs on lower leaflet surface, 8 = length of inflorescence peduncle, 9 = width of inflorescence peduncle, 10 = number of flowers per inflorescence, 11 = calyx tube length, 12 = bracteole length, 13 = petal length, 14 = number of ovules per ovary, 15 = pod length, 16 = pod width, 17 = density of hairs on pod valve. Abbreviations: n = number of herbarium specimens sampled, sd = standard deviation, max = maximum value, min = minimum value.

		Quantitative characters																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
S. umbellata	n	148	148	148	148	148	147	146	140	148	139	133	132	117	41	44	37	45
	mean	29.0	10.7	24.9	10.1	0.5	2.6	2.6	133.2	1.1	3.2	2.5	1.5	10.2	8.8	42.9	2.9	4.4
	sd	7.6	5.0	5.9	3.9	0.7	2.3	1.5	49.9	0.1	1.0	0.5	0.3	1.6	1.3	8.0	0.8	2.6
	max	70.0	30.2	41.8	27.0	6.0	13.0	10.0	300.0	1.3	6.0	4.0	2.4	15.0	12.0	63.9	5.6	13.0
	min	15.4	2.0	15.0	3.0	0.0	0.0	0.0	44.0	0.8	1.0	1.4	0.8	7.3	6.0	26.0	2.0	0.0
S. helvola	n	155	155	156	156	154	156	156	141	156	145	127	126	129	119	124	98	125
	mean	36.6	24.3	30.5	19.8	4.2	1.2	1.5	90.2	1.1	3.0	2.2	2.6	9.6	6.3	60.8	5.3	1.5
	sd	11.0	8.3	9.5	7.0	4.0	1.0	1.4	35.8	0.1	0.8	0.4	0.5	1.4	1.0	11.8	1.3	1.1
	max	71.5	46.2	63.4	42.7	18.2	5.0	12.0	190.0	1.3	5.0	3.6	4.2	13.3	10.0	96.1	8.1	7.0
	min	17.9	8.5	13.4	5.8	0.0	0.0	0.0	23.5	0.8	1.0	1.3	1.5	6.7	5.0	30.2	3.0	0.0
S. leiosperma	n	120	120	120	120	120	120	120	111	120	111	91	90	93	85	92	60	92
	mean	31.9	8.0	28.6	7.8	0.3	9.3	10.0	59.9	0.4	1.3	1.6	1.3	5.6	5.3	26.4	3.7	10.0
	sd	9.2	4.1	8.0	3.7	0.4	4.5	4.9	24.7	0.1	0.6	0.3	0.3	0.8	1.1	5.0	0.7	3.7
	max	54.2	22.6	55.6	20.6	1.0	24.0	24.0	123.0	0.7	4.0	2.4	2.3	8.3	9.0	40.7	5.2	24.0
	min	16.8	2.2	14.8	2.2	0.0	1.0	1.0	11.5	0.2	1.0	0.8	0.8	3.6	4.0	12.2	2.2	1.0

6 and 7) and pod valves (#17), short and slender inflorescence peduncles (#'s 8 and 9) that bear the fewest number of nodes (#10), and small flowers (#13). *Strophostyles umbellata* is marginally distinct from *S. helvola* with respect to this morphometric analysis of herbarium specimens. This is the only species commonly to have bracteoles shorter than the adjacent calyx tube (compare characters 11 and 12 in Table 2), and an ovary with the greatest number of ovules (#14). *Strophostyles helvola* tends to have the largest leaflets (character #'s 1 and 3) and pods (#'s 15 and 16), and usually deeply lobed leaflets (#5).

The first eigenvector (C1 in Figs. 5, 6) arranges specimens with short hairy pods and hairy leaflets (see characters 6, 7, 15, and 17) at one end (*S. leiosperma*) and specimens with long glabrous pods and glabrous leaves at the other (*S. helvola*). The second eigenvector (C2 in Fig. 5) arranges specimens with generally short leaflets, few ovules per ovary, and long inflorescences (see characters 1, 3, 8, and 14) from the base (*S. umbellata*). The third eigenvector (C3 in Fig. 6) ordinates specimens having lobed leaflets, long bracteoles, and wider pods (character 5, 12, and 16) from the top (*S. helvola*). In spite of not being able to measure some traditionally used diagnostic traits from herbarium specimens (e.g., growth habit, the shape of the keel beak, and the compression of the pod valves) the above 17 quantitative traits resolve fairly well three phenotypic groups with marginal overlap, and these correspond to the traditionally recognized species of *Strophostyles*.

DISCUSSION

The analysis presented here unequivocally shows that the genus *Strophostyles* is monophyletic, sister to *Dolichopsis*, and comprises three species with no detectable infraspecific taxa. The monophyly of the genus has never been tested before, at least with explicit phylogenetic analysis of combined data. The well-established sister group relationship of *Strophostyles* and *Dolichopsis* vindicates Maréchal et al. (1978) and Pelotto and del Pero Martínez (1998), who detected this relationship from less comprehensive data or taxon sampling. Furthermore, the recognition of just three species in the genus does not differ from the recent floristic research on the genus (e.g., Radford 1968; Correll and Johnston 1970; Isely 1998).

Diagnosis. With respect to close relatives *Dolichopsis*, *Macroptilium*, *Mysanthus*, and *Oryxis*, the genus *Strophostyles* is apomorphically diagnosed by divergent stipules, persistent secondary floral bracts, a calyx with four acute to attenuate lobes, and seeds often with a testa covered by a cellular coat that is derived from the inner epidermis of the pod valve. The close relatives have appressed stipules (except where independently evolved in *Macroptilium*), deciduous secondary floral bracts, a calyx with four to five blunt lobes, and seeds with a smooth testa. All three species of *Strophostyles* produce isorhamnetin glycosides, which are also found in some species of *Macroptilium* and *Vigna* subgenus *Sigmoidotropis*, but not for example, in *Dolichopsis paraguariensis* Hassler (Williams et al. 1995; Zallocchi et al. 1995; Pelotto and del Pero Martínez 1998). The production of isorhamnetin glycosides might be a shared derived apomorphy of *Strophostyles*, but this phytochemical trait is too inadequately surveyed among the New World Phaseolinae.

The north temperate *Strophostyles* and the South American *Dolichopsis* share a similar floral morpholo-

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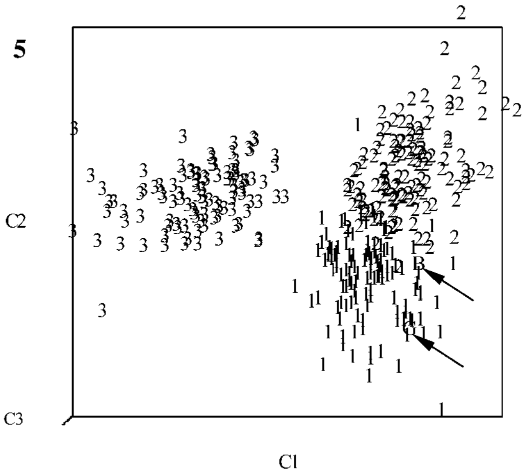

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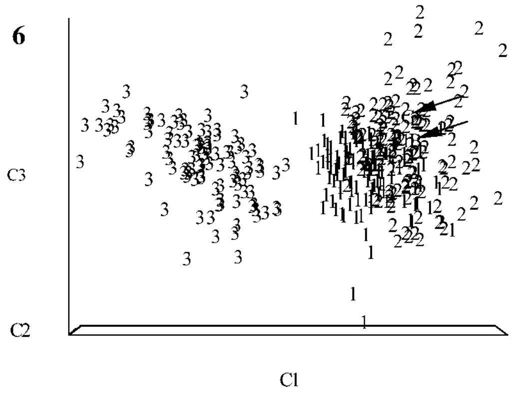


FIGS. 5, 6. Multidimensional scaling of 362 herbarium specimens of *Strophostyles* using 17 continuous morphological variables that were readily available for measurement from pressed herbarium specimens. Certain diagnostic floral and fruiting morphologies and growth habit are thus not included. These first three axes captured about 73% of variation during the initial computation of eigenvectors. Fig. 5. Ordination of specimens contrasting the C1 and C2 axes. Fig. 6. Plot contrasting the C1 and C3 axes. 1=*Strophostyles umbellata* specimens, 2=*S. helvola* specimens, and 3=*S. leiosperma* specimens. The arrows point to the *Strophostyles umbellata* specimens with lobed leaflets: G=*Greear 64283* (TEX) and B=*Biltmore 1302* (MO).

gy, where the keel beak curves rather than coils to the right of the flower, and a fused upper margin of the keel petals forms a gibbosity or hump proximal to the beak. The exact function of this hump is unknown but no doubt provides structural support during pollinator visitation (Lackey 1981). The wing petals are adnate to the keel petals in this region, suggesting physical support for insect visitors that land on the wings.

Habitat. All three species of *Strophostyles* usually inhabit inland fresh water sites (e.g., seasonally flooded basins or flats, swamps, and bogs), saline water areas (e.g., inland saline marshes, coastal sands and meadows), or human-made mesic environments (e.g., stock ponds, roadside ditches). Moreover, when *Strophostyles* is reported from drier environments, plants are commonly found next to ditches or mud holes (inferred from herbarium label data, personal observations, and literature; Yanful and Maun 1996a and 1996b; Erickson and Young 1995). The cellular covering common to *Strophostyles* seeds have been shown to provide at least temporary buoyancy in laboratory tests (Riley-Hulting unpublished data). Individuals of *Strophostyles leiosperma* produce smooth seeds more often than individuals of the other species, and *S. leiosperma* tends to inhabit drier and more open sites than the other two species. This association further suggests a role of the cellular coating in seed buoyancy (Hutton and Porter 1937) and thus water dispersal. Outside of *Strophostyles* this association breaks down. For example, both species of the tropical South American sister genus *Dolichopsis* produce only smooth seeds while inhabiting seasonally inundated sites or other settings associated with water.

***Biogeography of* Strophostyles.** Relationships of plant species from the southeastern USA have been sought commonly among the floristic elements of the southeastern Asia flora (e.g., Wen 1999). This study suggests an alternative to the putative vicariant Holarctic relationships of the Appalachian flora. The sister genus of *Strophostyles*, *Dolichopsis*, is confined to a relatively narrow region comprising the Chaco of Paraguay, Bolivia, Brazil (Pantanal), and northeastern Argentina. The Chaco is distinguished from other seasonal forests in South America by having a frost period (e.g., Prado and Gibbs 1993; Pennington et al. 2000), and thus may not be so different ecologically from the seasonally deciduous temperate forests in North America. The closely related *Oryxis* is restricted to the campos rupestres and cerrado forests of Minas Gerais, Brazil (Delgado-Salinas and Lewis 1997). *Mysanthus* is confined to seasonally dry forest and caatinga (thorn scrub) communities of Bahia and Sao Paulo, Brazil (Lewis and Delgado-Salinas 1994), and *Macroptilium* is widespread throughout the neotropics frequently in seasonally dry forests. The ecological similarity shared by the disjunct species of *Strophostyles* and *Dolichopsis* is matched to some degree by other legume examples. *Gleditsia amorphoides* (Griseb.) Taub., an endemic of seasonally dry forests bordering the Chaco (Darien Prado personal communication), is sister to a north temperate clade of two species, *G. rolfei* Vidal from Taiwan and *G. sinensis* Lam. from eastern China (Schnabel et al. 2003). Similarly, the North American temperate genus *Robinia* L. is sister to the South American *Poissonia* Baill., a genus of four species confined to deserts (Monte and Arequipa) and higher elevations in seasonally dry scrub of the southern Andes of Peru, Bolivia, and Northern Argentina (Lavin et al. 2003). Perhaps the eastern North American temperate forests should be viewed as part of a global metacommunity, sensu Hubbell (2001), involving other seasonal forests in temperate or montane tropical settings.

Constituent Taxa. The taxonomic and floristic literature is rich in names pertaining to infraspecific taxa of *Strophostyles*, and indeed these are not recognized in this treatment. For example, Torrey and Gray (1838) described five unnamed forms under *Phaseolus helvolus* L. and mentioned that some of these may not even belong to this species. Their descriptions are impossible to relate to names because they are vague and no types were designated, and the morphometric and genetic analysis performed here yield no evidence of infraspecific taxa within *Strophostyles helvola*.

The three species recognized in this study, *Strophostyles umbellata*, *S. helvola*, and *S. leiosperma*, are phenotypically distinct. The morphometric analysis did not illustrate this unequivocally because of the lack of preservation on herbarium specimens of certain diagnostic characters. For example, *Strophostyles umbellata* is the only species in the genus to produce a perennial branched caudex and its keel beak is stout and held in close approximation to the face of the standard petal (Figs. 8, 9). *Strophostyles helvola* is the only species in the genus to produce cylindrical pods and a long slender keel beak that curves upwards and away from the face of the standard (Figs. 10, 11). *Strophostyles leiosperma* is the only annual species in the genus and its keel beak is only marginally extended above the wing petals (Figs. 12, 13). Even with these most diagnostic characters omitted from analysis, the morphometric analysis still resolved three clusters albeit with some overlap especially between *Strophostyles umbellata* and *S. helvola* (Figs. 5–6). The morphometric analysis does demonstrate that flowerless herbarium specimens of *Strophostyles leiosperma* can be correctly identified. Difficulty will come when distinguishing between certain specimens of *Strophostyles umbellata* and *S. helvola*.

Despite the phenotypic distinctions of the three species of *Strophostyles*, their geographic distributions overlap greatly and it is uncertain whether they are originally allopatric. Field observations and herbarium label data reveal that *Strophostyles leiosperma* and *S. helvola* are commonly sympatric in Texas. *Strophostyles helvola* and *S. umbellata* occur sympatrically in at least Texas, Tennessee, and Virginia. No record exists of all three species at a single locality, or of sympatry between *Strophostyles leiosperma* and *S. umbellata*. If *Strophostyles* species are of allopatric origin, then dispersal since divergence has been rampant (compare distributions in Figs. 14–16).

Whatever the inherent dispersal capability of *Strophostyles* species, humans may have been a predominant factor in their population expansion during the last few centuries. Although birds swallow the seeds of *Strophostyles* (Bird and Bird 1931; Ridley 1990; Wiseman 1997) and thus could serve as dispersal agents, the common habitats of *Strophostyles* species implicate humans as primary dispersers. Roadsides, pastures and lots, and railroad tracks or railroad stations are by far the most common habitats cited on herbarium specimens. Railroad construction during 19th century would have facilitated *Strophostyles* seed dispersal with ballast used as fill. In contrast to the usual perception of human influence on distributions of native species, all three species of *Strophostyles* have prospered with human activity.

Along with sympatry, all three species of *Strophostyles* bloom during the same season and generalist insects commonly visit their flowers and extrafloral nectaries (Foerste 1885; Robertson 1890; Krombein et al. 1979; Delgado-Salinas, personal observation). Floral visitors include wild bees of the genera *Bombus*, *Calliosis*, *Chalicodoma*, *Heteranthidium*, *Megachile*, *Melissoides*, and *Nomia*. Visitors of extrafloral nectaries include wasps, bees, ants, flies, and beetles.

It is uncertain if reproductive isolation mechanisms exist among the species of *Strophostyles*, yet putative hybrids are essentially unknown. Isely (1990, 1998) mentioned that two specimens were observed to have the lobed leaflets of *Strophostyles helvola* and the short bracteoles of *S. umbellata*. In this study, we observed two collections mixing traits otherwise diagnostic of species. *Biltmore 1302* (MO, US) from North Carolina and *Greear 64283* (TEX) from Georgia combine the lobed leaflets of *Strophostyles helvola* and the flower with a large keel beak of *S. umbellata* (Fig. 5). It is unknown if these specimens are the same ones referred to by Isely. Regardless, the genetic and morphological distinctions revealed in this study suggest a long history of genealogical isolation for each of the three species. Recognizing three species under the phylogenetic species concept (sensu Donoghue 1985) is not inconsistent with the potential findings that a small amount of recent gene flow exists among populations of different species of *Strophostyles*.

TAXONOMY

Strophostyles Elliott, nom. cons. Sketch Bot. S. Carolina 2(3): 229. 1823. Lectotype (Britton and Brown, Ill. Fl. N. U. S., ed. 2. 2: 423. 1913): *S. angulosa* (Muhl. ex Willd.) Elliott [= *S. helvola* [L.] Elliott].

Phasellus Medik., Vorles. Churpfälz, Phys. Ökon. Ges. 2: 352. 1787. nom. rej. Type: *P. roseus* Medik., nom. illeg. [based on *Phaseolus farinosus* L. (1753)].

Phaseolus sect. *Strophostyles* (Elliott) DC., Prodr. 2: 394. 1825.

Phaseolus sect. *Strophostyles* (Elliott) DC. subsect. *Lobatifolii* DC., Prodr. 2:394. 1825.

Phaseolus sect. *Strophostyles* (Elliott) DC. subsect. *Integrifolii* DC., Prodr. 2:394. 1825.

Phaseolus sect. *Strophostyles* (Elliott) DC. *emend.* Benth. Comm. Legum. Gen.75. 1837.

Perennial and annual, slender flexible or wiry lianas, trailing or climbing occasionally up to 2 m long on shrubs and trees, with root systems bearing abundant conspicuous nodules, stems herbaceous, not woody, often branching at lower nodes; plants variously pubescent (trichomes not uncinate), sparse to densely short-pilose, the hairs retrorse on stems and flowering axis, except on petioles with a mix of retrorse and antrorse hairs. Leaves pinnately trifoliolate, pulvinate, long-petiolate, the petiole and rachis canaliculate; leaflets ovate to lanceolate, the lateral ones oblique or basiscopic, often panduriform or rhombic, sometimes basally lobed, membranous to chartaceous; stipules sessile, not produced below the point of insertion into retrorse auricles, striate, triangular-ovate, divergent from the stem; stipels linear, often curved, striate (multi-nerved), persistent. Inflorescences pseudoracemose, axillary, the peduncles angulated, often canaliculate, flowering rachis much contracted (rendering the appearance of an umbellate inflorescence) and obscurely angulate, with 1–6-flowering nodes, clustered distally, the nodes often swollen, functioning as extrafloral nectaries; each bearing at most 2 flowers; pedicels short, thickened at fruit; bracts at base of peduncle present, often only on one side; primary floral bracts early deciduous or wanting; secondary floral bracts (subtending the pedicels), ovate to lanceolate, persistent; bracteoles lanceolate, on distal portion of pedicels, rigid and striate, persistent through anthesis, often at fruit. Calyx campanulate, hypanthium essentially lacking; adaxial two lobes united into an acute tooth; lateral teeth triangular; abaxial tooth more narrowly triangular and often the longest and surpassing the calyx tube in length, 1.5–4.0 mm long. Flowers papilionaceous, corolla generally pinkish at anthesis, standard often with yellowish maculae, the keel tip darkest, fading pale brownish yellow when dry; blade of the standard reflexed about 90 degrees at anthesis, suborbicular, mostly auriculate at base adjacent to the broad claw, with submarginal lamellae or folds in this region, as well as callus appendages ringing the sides and upper margin of the nectar guide (area above the claw); nectar guide with micropapillae; wing-petals lightly adherent to the keel, and orientated (in fresh condition) more or less oblique to the plane of the keel, the blades oblong, asymmetric, protruding as long as or longer than the beak of the keel; keel-petals basally broad with a prominent gibbosity along the upper margin proximal to the rostrum, usually with a longitudinal fold where adherent to the wing, gradually narrowed above this, the tubular apical portion curved to the right-side of the flower. Stamens 10, vexillar stamen free bearing a fleshy callus about 1 mm from base, the others basally connate and distally free, length of filaments dissimilar, the staminal sheath with prominent auricles embracing the swollen base of the vexillary stamen; anthers uniform, sub-basifixed. Pollen subprolate to oblate-spheroidal due to harmomegathic changes (Fig. 17), tricolporate, with micro-reticulate exine sculpture, ectoapertures (colpi) medium-sized, endoapertures (pori) covered with pseudo-operculi having a granular surface (deciduous by acetolysis techniques). Ovary sessile, arched, sparsely to densely strigose, at base surrounded by a nectariferous sheath; style incurved like the keel, often becoming twisted, jointed at the first (proximal) curve, distinctly incrassate and flattened, distal portion introrsely bearded; stigma terminal and introrse. Pods 2-valved, mostly linear, straight or slightly curved, cylindrical to slightly laterally compressed in *S. umbellata* and *S. leiosperma*, the valves separating along both thickened sutures and twisting at maturity, 3–10-seeded; seeds longitudinally orientated, spherical to subquadrate, truncate at both ends, commonly covered with an endocarpic cellular layer; hilum ca. half the length of the seed, oblanceolate, covered with an epihilum, rim-aril and hylar tongue much reduced, lens distinct and divided. Seedlings with epigeal germination; eophylls unifoliolate and opposite with stipules entire and lanceolate; petiole with well-developed pulvini at the base and at the apex; stipels lacking.

Nomenclature. De Candolle (1825) and Bentham (1837) once ranked *Strophostyles* as a section of the genus *Phaseolus*. Both authors included miscellaneous species in this section, but all such species are now placed in other genera such as *Macroptilium* and *Vigna* subgenus *Sigmoidotropis* (Delgado-Salinas 1985). *Strophostyles* was conserved over *Phasellus* by the General Committee of the ICBN (Taxon 48: 377. 1999). See Verdcourt's (1997) original proposal 1299.

***Key to the Species of* Strophostyles.** Measurements provided in the key are derived from pressed and dried herbarium specimens. Flower length was measured at anthesis from the base of the calyx to the tip of the fully expanded standard petal. Such measures essentially correspond to petal length because *Strophostyles* and related genera lack a hypanthium.

1. Keel petal with a prominently curved beak that protrudes well above the wing petals (keel beak asymmetry is readily detectable in pressed specimens); inflorescence peduncle stout, lignescent, 0.8–1.3 mm in diameter, (23.5) 50–300 mm long; leaves and fruits glabrate to sparsely strigose (rarely sericeous); flowers commonly 6.7–15 mm long; pod (26) 30–96.1 mm long; leaflets variably ovate to lanceolate to sometimes narrowly lanceolate, entire to deeply lobed.
    2. Flowers with a stout erect and slightly curved keel beak measuring 1.5–2.0 mm in diameter at the base and remaining closely associated with the face of the standard petal; bracteoles 0.8–2.4 mm long, generally shorter than the calyx tube; pods

subcylindrical, with a distinct lateral compression; leaflets entire to shallowly lobed, rarely deeply lobed, the sinus 0.0–1.0 (6.0) mm deep, terminal leaflets (15.4) 20–40 (70) mm long, 2.0–21.8 (30.2) mm wide . . . . *Strophostyles umbellata*

2. Flowers with a slender curved keel beak measuring about 1 mm in diameter at the base and projected outward from the face of the standard petal; bracteoles 1.5–4.2 mm long, generally as long or longer than the calyx tube; pods cylindrical; leaflets deeply lobed to entire, the sinus 0.0–18.2 mm deep, terminal leaflets 17.9–71.5 mm long, 8.5–46.2 mm wide . . . . *Strophostyles helvola*

1. Keel petal with a slightly curved beak that is largely enveloped by the wing petals (keel beak asymmetry is not detectable in pressed specimens); inflorescence peduncle slender, herbaceous, 0.2–0.7 mm in diameter, 11.5–110 (123) mm long; leaves and fruit distinctly sericeous; flowers 3.6–7.0 (8.3) mm long; pod 12.2–40.7 mm long; leaflets lanceolate, never deeply lobed . . . . *Strophostyles leiosperma*

1. *STROPHOSTYLES UMBELLATA* (Muhl. ex Willd.) Britton, in Britton & Brown, Ill. Fl. 2: 339. 1897. *Glycine umbellata* Muhl. ex Willd., Sp. Pl. 3: 1058. 1802. *nom. cons. prop. Phaseolus umbellatus* (Muhl. ex Willd.) Britton, Trans. N.Y. Acad. 9: 10. 1889. TYPE: USA. South Carolina. Georgetown County. E side of Waccamaw River, 7 mi NE of Georgetown, 12 Sept 1996, *B. Seckinger 406* (holotype *cons. prop.*: USCH!; isotypes: MEXU!, MONT!). This proposed type replaces the following specimen, which is now classified as a non-type specimen under *Strophostyles helvola* (Delgado-Salinas and Lavin in press): TYPE—USA. Pennsylvania. ''Habitat in Am. Boreali'', *Muhlenberg s.n.* (holotype: B-Willd.).

Strophostyles umbellata (Muhl. ex Willd.) Britton forma *ochroleuca* Fernald, Rhodora 42: 458. 1940.—TYPE: USA. Virginia. Greenville Co., open thickets, clearings and borders of woods east of Emporia, August 18, 1939. *Fernald & Long 11065* (holotype: GH!; isotype: PH, photo!).

Strophostyles umbellata (Muhl. ex Willd.) Britton var. *paludigena* Fernald, Rhodora 44: 420. 1942.—TYPE: USA. Virginia: New Kent Co., fresh tidal marsh by Lacey Creek, west of Walker, September 9, 1941, *Fernald & Long 13663* (holotype: GH!; isotypes: GH!, PH (2 sheets), photos!).

Perennial from a slender taproot. Stems terete, often lignescent at base, coming from a subterranean branched caudex, sometimes with adventitious roots bearing nodules at buried nodes, lower stems 1–1.5 mm in diameter. Leaflets ovate-lanceolate to sometimes narrowly lanceolate, entire to shallowly (rarely deeply) lobed, the sinus 0.0–1.0 (6.0) mm deep, terminal leaflets (15.4) 20–40 (70) mm long, 2.0–21.8 (30.2) mm wide, laterals, 15–41.8 mm long, 3.0–27 mm wide; strigose, hairs 0–5 (13) per mm^2 on upper surface, 0–5 (10) per mm^2 on lower surface. Inflorescence with a peduncle (44) 60–300 mm, angulate, with (1) 2–6 (–11 in *C. L. Lundell 11739*) flower-bearing nodes, upon fruit growth becoming stout, lignescent, and 0.8–1.3 mm in diameter. Calyx tube (1.4) 2.0–4.0 mm long, teeth 1.0–2.5 (3.0) mm long, bracteoles 0.8–2.4 mm long, generally shorter than the calyx tube. Standard petal 7.3–15.0 mm long, pink at anthesis; wing petals 7.0–12.0 mm long, pinkish; keel petal 8.0–13.0 mm long, pinkish with dark purple beak, which is prominent, erect, 1.5–2.0 mm in diameter, slightly curved, and closely positioned to the face of the standard petal. Ovary with 6–12 ovules. Pod subcylindrical, with a distinct lateral compression, (26) 30–63.9 (70) mm long, 2.0–5.6 mm wide, with 5–10 seeds, valves glabrate to strigose, trichome density (0) 3–13 per mm^2. Seeds sometimes faintly mottled at most, generally with a cellular or waxy covering. Chromosome number $n=11$ (Turner 1956). Figs. 7–9.

Phenology. Throughout the range of this species, flowering July to September, rarely in June; fruits mostly from September and October.

Distribution. From southeastern Texas north to eastern Kansas and eastward from Pennsylvania south to Florida (Fig. 14); generally scattered individuals and populations in open sites to forest understory; elev. 0–1500 m. *Strophostyles umbellata* has been reported from Long Island, New York (Jellife 1899), and Rhode Island and Connecticut (Magee and Ahles 1999).

Representative Specimens. U.S.A. Alabama. Autauga Co.: between Swift and Whitewater, *R. M. Harper 4465* (MO). Baldwin Co.: NW of Gulf shores, *R. M. Harper 4128* (MO). Crenshaw Co.: Patsulga Creek, *R. Kral 88958* (USCH). Lamar Co.: 5.5 mi N Sullighent, *R. Kral 33044* (MO). Conecuh Co.: 6.8 mi N Brooklyn, *R. Kral 40981* (MO). **Arkansas.** Bradley Co.: Jersey, *D. Demaree 18232* (MO). Cleburne Co.: Heber Springs, *D. Demaree 10942* (MO). Craighead Co.: Joneboro, *D. Demaree 3716* (MO). Drew Co.: Monticello, *D. Demaree 13655* (MO). Greene Co.: Paragould-Buch Grove, *D. Demaree 4012* (MO). Hempstead Co.: Ozan, *D. Demaree 15962* (MO). Howard Co.: Baker Spring, *J. H. Kellogg s.n.* (MO). Lonoke Co.: Grand Prarie, *D. Demaree 22447* (MO). Miller Co.: Texarkana, *A. A. Heller 4155* (MO). Monroe Co.: Wheatley, *D. Demaree 10907* (MO). Prairie Co.: Hazen, *D. Demaree 15481* (MO). Pope Co.: Nogo, *G. M. Merrill 665* (MO). Pulaski Co.: Little Rock, *D. Demaree 8168* (MO). Saline Co.: Benton, *D. Demaree 23991* (MO). Sevier Co.: Neal Springs, *E. Brinkley 6* (MO). Union Co.: El Dorado, *H. J. Ploch s.n.* (MO). **Delaware.** Rehoboth Beach, *U. Fitchy 14* (MO). **District of Columbia.** Avalon Heights, *F. Blanchard s.n.* (MO). **Florida.** Leon Co.: Lake Iamonia, *L. C. Anderson 12191* (MO). Walton Co.: Bay Grove Loop, *H. A. Davis 15403.A* (MEXU). **Georgia.** Bartow Co.: Allatoona

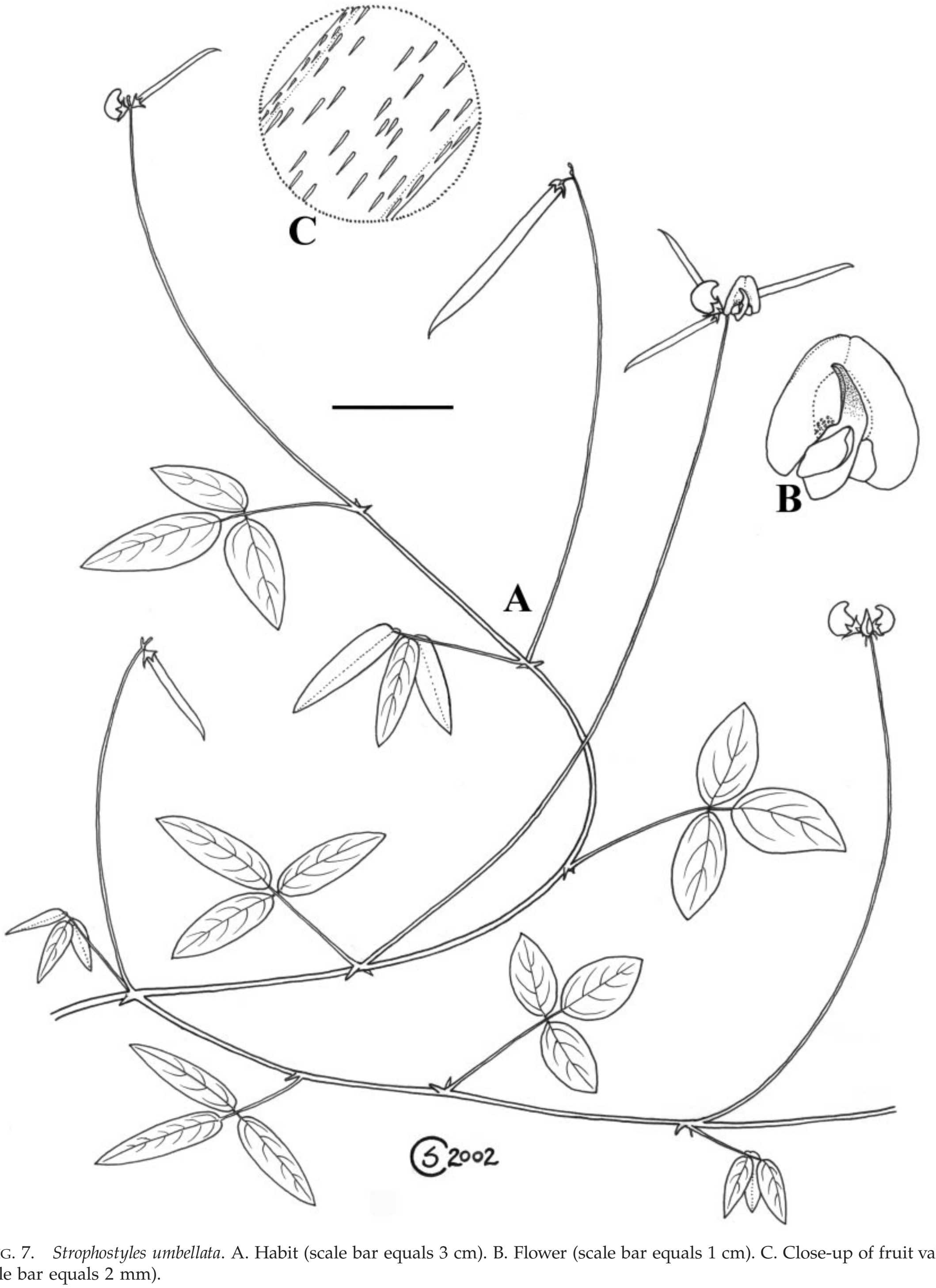
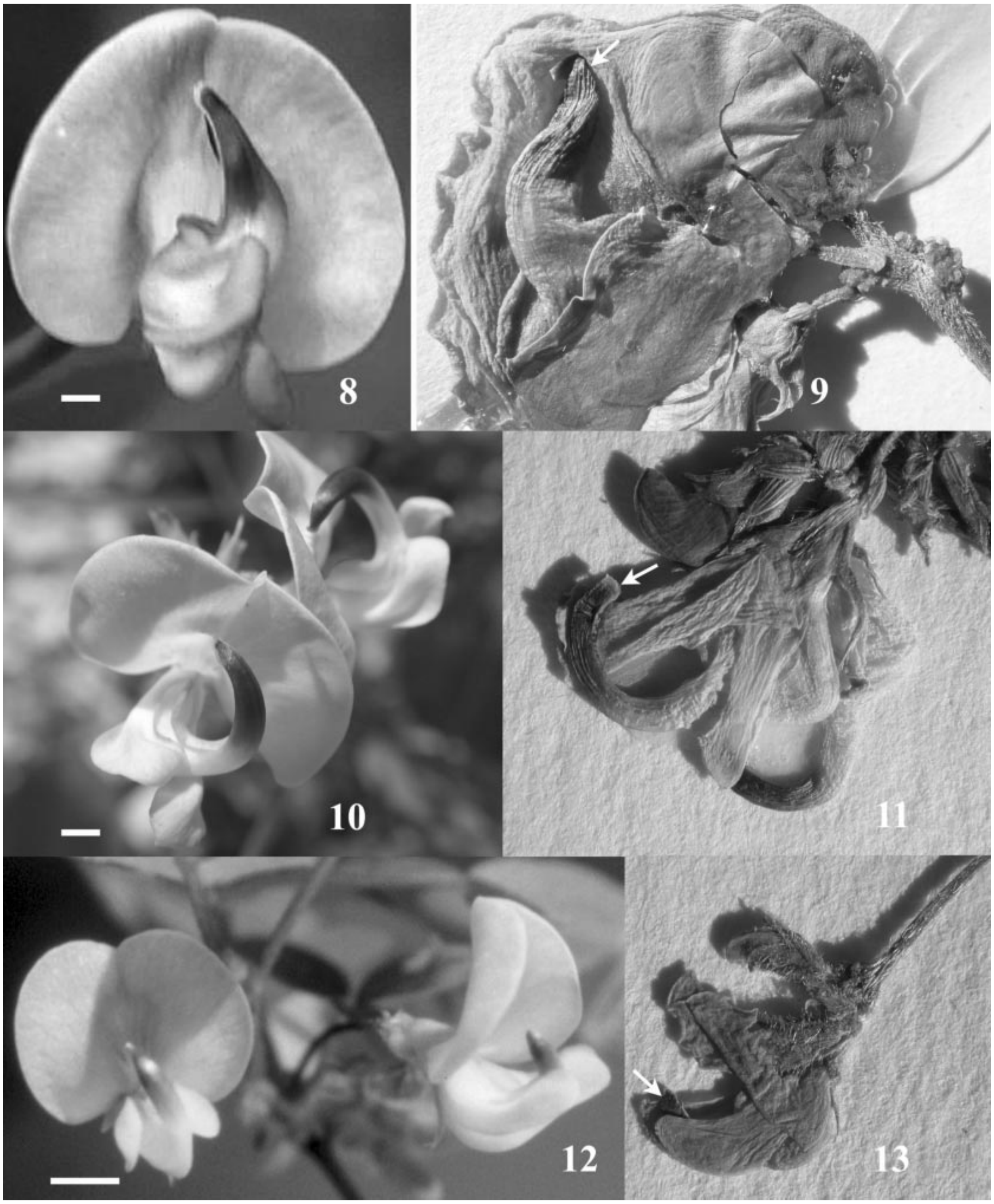


FIG. 7. *Strophostyles umbellata*. A. Habit (scale bar equals 3 cm). B. Flower (scale bar equals 1 cm). C. Close-up of fruit valve (scale bar equals 2 mm).

Dam, W of Rowland, *W. H. Duncan 8708* (MO). Dougherty Co.: Flint River below Albany, *R. M. Harper 1953* (MO). Oglethorpe Co.: 2 mi SE of Winterville, *W. H. Duncan 11610* (MO). Thomas Co.: Wade Tract, *R. R Clinebell II 1334* (MO). **Illinois.** Lawrence Co.: 1859, *J. Q. A. Fritchey 229* (MO). **Indiana.** Clay Co.: *R. C. Friesner s.n.* (UC). Harrison Co.: *C. C. Deam 59817* (UC). **Iowa.** Sioux City, *L. H. Pammel 19* (MO). **Kentucky.** Fulton Co.: Fulton, *F. J. McFarland 172* (MO). Lincoln Co.: 2 mi N of Ottenheim, *M. E. Wharton 4878* (MO). Madison

Co.: Berea outskirts, *D. A. Johnson 283* (USCH). **Louisiana.** Calcasieu Parish: Lack Charles, *S. M. Tracy 3476* (MO). Caldwell Parish: just S of Columbia, *R. D. Thomas 107658* (MO). East Feliciana Parish: Jackson, *W. H. P. s.n.* (MO). Jackson Parish: near Cartwright, *W. I. Rockett 31* (MO). Jefferson Davis Parish: 1 mi S of Fenton, *C. M. Allen 15589* (MO). St. Tammany Parish: Slidell, *B. C. Sharp 1928* (TEX). Sabine Parish: along La 475, 6 miles N of La. 6, *N. Carroll and R. Hutchinson 166* (MEXU). **Kansas.** Wyandotte Co.: common in the bottoms of the big rivers, *K. K. Mackenzie 2968* (MO). **Maryland.** Calvert Co.: Chesapeake Beach, *S. F. Blake 5342* (TEX). **Mississippi.** Clarke Co.: 2.3 mi NNE of Pachuta, *S. B. Jones 14586* (TEX). Harrison Co.: Long Beach, *J. F. Joor 04-09-1891* (MO). Jackson Co.: Ocean Springs, *J. Kershaw 195* (MO). **Missouri.** Butler Co.: Poplar Bluff, *Dewart 14-08-1892* (MO). Camden Co.: 2 mi S of Barnumton, *J. A. Steyermark 6997* (MO,UC). Carter Co.: 7 mi SE of Ellsinore, *J. A. Steyermark 11726* (MO). Crawford Co.: 5 mi W of Steelville, *Mrs. J. A. Steyermark 02-10-1931* (MO). Dent Co.: Rhyse, *J. H. Kellogg 994* (MO). Dunklin Co.: Campbell, *B. F. Bush 191* (MO). Hickory Co.: 3 mi NE of Elkland, *J. A. Steyermark 24478* (MO). Howell Co.: NW of Willow Springs, *J. A. Steyermark 23437* (MO). Iron Co.: Pilot Knob, *G. Englemann 20293* (MO). Jefferson Co.: sandy ground, *H. Eggert 09-10-1896* (MO). Laclede Co.: SW of Nebo, *J. A. Steyermark 25172* (MO). Lincoln Co.: 3 mi NE of Silex, *J. A. Steyermark 26005* (MO). Ozark Co.: Blue Springs Game Refuge, *J. A. Steyermark 20044* (MO). Perry Co.: ''VIII. 86,'' *G. H. M. Goehring 316* (MO). Pike Co.: 5 mi W of Louisiana, *J. A. Steyermark 25902* (MO). Saint Francois Co.: slopes of Iron Mountain, *A. E. Brant 2620* (MO). Saint Louis City: St. Louis, *G. Englemann 20262* (MO). Saint Louis Co.: Cliff Cave, *H. Eggert 12-08-1892* (MO). Sainte Genevieve Co.: N of Sainte Genevieve, *W. Trelease 1008* (MO). Scott Co.: Morley, *H. Eggert 31-08-1894* (MO). Shannon Co.: Montier, *B. F. Bush 8693* (MO). Taney Co.: S of Hercules, *J. A. Steyermark 22928* (MO). Texas Co.: near Roubidoux Cr., *J. A. Steyermark 25027* (MO). **New Jersey.** Atlantic Co.: Atlantic City, *J. H. Redfield 1631* (MO). Cape May Co.: 1935, *J. A. Druskel 8120* (MO). Ocean Co.: Barnegat Bay, *J. R. Churchill 14-08-1892* (MO). **North Carolina.** Wake Co.: Sycamore Creek, *G. P. Sawyer Jr. 1445* (USCH). Rowan Co.: vicinity of Salisbury, *A. A. Heller 37* (MO). Wilson Co.: Little River, *A. Patten 123* (TEX). **Oklahoma.** Le Flore Co.: near Page, *O. W. Blakely 3411* (MO). McCurtain Co.: 4 mi SW of Broken Bow, *R. Stratton 584* (MO). **Pennsylvania.** Lancaster Co.: Pleasant Grove, *J. K. Small s.n.* (MO). **South Carolina.** Barnwell Co.: 2.8 mi SW of Station No. 22, *Batson & Kelley 499* (USCH). Charleston Co.: Santee Coastal Reserve, *S. R. Hill 24269* (USCH). Sumter Co.: Shaw Air Force Base, *J. B. Nelson 16546* (USCH). Dorchester Co.: Four Hole Swamp, Bird Lake, *A. B. Pittman 09049707* (MONT, USCH). Edgefield Co.: Horn Creek, *J. B. Nelson 17763* (MONT, USCH). Fairfield Co.: N of Ridgeway, *E. T. Riley-Hulting 3040* (MONT). Georgetown Co.: Cat Island, *J. B. Nelson 9724* (USCH). Jasper Co.: Cypress Creek, *C. A. Aulbach-Smith 2740* (USCH). McCormick Co.: McCormick, *J. Davis s.n.* (MO). Richland Co.: Fort Jackson Army Installation, *J. B. Nelson 11347* (USCH). Saluda Co.: 8 mi N of Saluda, *C. N. Horn 9725* (USCH). Williamsburg Co.: 3 mi S of Lane, *J. B. Nelson 8123* (USCH). **Tennessee.** Carroll Co.: Hollow Rock, *H. Eggert 05-08-1897* (MO). Knox Co.: Knoxville, *A. Ruth 07-1896* (MO, TEX). Lewis Co.: Meriweather Lewis National Monument, *C. B. King 220* (TEX). Morgan Co. exposed roadside along Rt. 299, *V. E. McNeihus 99-812* (MEXU). Sumner Co.: Mitchelville, *H. Eggert 17-08-1897* (MO). **Texas.** Angelina Co.: near Bouton Lake, *D. S. Correll and I. M. Johnston 19653* (TEX). Bowie Co.: near Texarkana, *A. A. Heller 4284* (MONT). Hardin Co.: S of bridge over Village Creek, *W. R. Carr 10820* (TEX). Harrison Co.: 6 mi WNW of Karnack, *D. S. Correll 30165* (TEX). Henderson Co.: 4 mi SE of Athens, *D. S. Correll 28517* (TEX). Jefferson Co.: Beaumont, *B. C. Tharp 10-09-1937* (TEX). Liberty Co.: 2.5 mi N of Moss Hill, *D. S. Correll 33999* (TEX). Matagorda Co.: Peytons Creek, *E. J. Palmer 9677* (TEX). Montgomery Co.: Houston, *G. L. Fisher s. n.* (UC). Morris Co.: Daingerfield State Park, *D. S. Correll 24656* (TEX). Newton Co.: 6 mi E of Buna, *W. W. Lay 27-08-1947* (TEX). Orange Co.: 50 mi W of Galveston, *E. T. Riley-Hulting* 3004 (MONT). Polk Co.: 6.7 mi E of Corrigan, *B. C. Tharp 54691* (TEX). San Augustine Co.: near Boykin Spring Camp, *F. W. Gould 6543* (TEX). Shelby Co.: 12 mi NW of Center, *A. Lee 114* (TEX). Tyler Co.: 7.5 mi E of Hillister, *B. C. Tharp 54854* (TEX). Wood Co.: Lake Ellis, *C. L. Lundell 11739* (TEX). **Virginia.** Fairfax Co.: W of Fairfax City, *T. Bradley 21598* (USCH). New Kent Co.: SE of Windsor Shades, *M. L. Fernald & B. Long 12689* (MO). Isle of Wight Co.: Bailey's Beach, *M. L. Fernald & B. Long* 13964 (MO). **West Virginia.** Roane Co.: *C. E. Wood Jr. 6677* (UC).

Discussion. *Strophostyles umbellata* is diagnosed primarily by its flower with a prominent keel beak, which has a thick base, a curved tip, and is held in close approximation to the standard face. Even in pressed condition, this beak is so thick that its close position to the standard is retained (compare Figs. 8, 9). Otherwise, *Strophostyles umbellata* is morphologically highly variable especially with regard to its leaves that range from narrowly lanceolate like those of *S. leiosperma* to ovate-lanceolate like those of *S. helvola*. Two collections of *Strophostyles umbellata*, *Greear 64283* (TEX) from Adairsville, Georgia, and *Biltmore 1302* (MO, US) from Buncombe County, North Carolina, have deeply lobed leaflets otherwise found only in *S. helvola*. Indeed, an ordination analysis places these two specimens at or near the interface of the *S. umbellata* and *S. helvola* clusters (Figs. 5–6). Generally, *Strophostyles umbellata* com-



FIGS. 8–13. Flowers of the *Strophostyles* species. 8. Flower of *S. umbellata* showing a thick and slightly curved keel rostrum (from Barnes and Francis 2004; USDA-NRCS 2003). 9. Pressed flower of *S. umbellata* showing keel rostrum (indicated by white arrow) retaining close approximation to standard petal. 10. Flower of *S. helvola* showing a slender and highly curved keel rostrum. 11. Pressed flower of *S. helvola* showing keel rostrum (indicated by white arrow) projected away from standard petal. 12. Flower of *S. leiosperma* that shows a slender and slightly curved keel rostrum. 13. Pressed flower of *S. leiosperma* showing little evidence of asymmetry of the keel beak (indicated by white arrow). Scale bars equal 1 mm.

bines traits of *S. helvola* (e.g., larger flowers borne from long stout inflorescence rachises) and *S. leiosperma* (the usually entire leaflets that at times can be sericeous or narrowly lanceolate). This is confirmed by the morphometric analysis where *Strophostyles umbellata* accessions (#1 in Figs. 5, 6) are positioned intermediate between those of *S. helvola* (#2) and *S. leiosperma* (#3) in a three-dimensional array of herbarium specimens.

Flowerless specimens of *Strophostyles umbellata* will be difficult to distinguish from *S. helvola*. *Strophostyles* *umbellata* specimens rarely possess mature fruit (possibly due to self-incompatible individuals occurring at low population densities), whereas *S. helvola* specimens commonly have mature fruit (possibly due to self-compatibility or high population densities that result in a high rate of fruit production per flower). If the pressed nature of the herbarium specimen has not distorted fruit morphology, cylindrical pods would be diagnostic of *Strophostyles helvola* whereas pods with a slight but distinct lateral compression would distinguish *S. umbellata*. A branching caudex would distinguish *Strophostyles umbellata* from *S. helvola*, which has an unbranched one. Because bracteoles are so persistent, an old persistent calyx with bracteoles shorter than the tube would distinguish *Strophostyles umbellata* from *S. helvola*. Other diagnostic traits become less certain. For example, deeply lobed leaflets are most common in *Strophostyles helvola*, but *S. umbellata* apparently produces such leaflets even if rarely. As with the other genera of Phaseolinae, the best diagnostic traits of *Strophostyles* at all taxonomic levels from the genus to the varietal level will involve the flower, and thus flowers should be sought if possible for positive identification.

The intraspecific ITS sequence variation detected in this analysis is most diverse in *Strophostyles umbellata*, despite limited sampling. Five ITS sequences distinguished from each other by up to six nucleotide substitutions came from South Carolina (Fig. 2). This contrasts to *Strophostyles helvola* for which only three ITS sequences were detected over its entire geographic range in eastern North America. The large nucleotide diversity of *Strophostyles umbellata* is possibly indicative of long population persistence in Appalachia.

Despite the generally high intraspecific sequence diversity among populations of *Strophostyles umbellata*, no heterozygous individuals were detected in this analysis (as inferred from double peaks on the sequence chromatograms). Fixed ITS sequence variation within populations of *S. umbellata* could be explained by the highly scattered populations of low density, which are characteristic of this species.

2. STROPHOSTYLES HELVOLA (L.) Elliott, Sketch Bot. S. Carolina 2(3): 230 (1823). *Phaseolus helvolus* L., Sp. PI.: 724. 1753, nom. & orth. cons. *Dolichos helvolus* (L.) Nutt., Gen. N. Amer. Pl. 2: 112. 1818. *Glycine helvola* (L.) Elliott, J. Acad. Nat. Sci. Philadelphia 1: 326. 1818. *Cajanus helvulus* (L.) Spreng., Syst. ed. 16, 3: 248. 1826.—TYPE: USA., South Carolina, Georgetown Co. edge of marsh on ocean side of Beach Rd., about 1 mile N of its terminus on South Island, 22 Aug 1991, *J. B. Nelson 11140* (holotype *cons. prop.*: USCH!; isotype: MEXU!). This proposed type replaces the following specimen, which is now classified as a non-type specimen under *Strophostyles umbellata* (Delgado-Salinas and Lavin in press): USA. North Carolina, Buncombe Co., sandy flats, 19 Aug 1896, *Biltmore 1302* (holotype: US No. 966089!; isotype: MO!—see Verdcourt [1997] and Report of the General Committee: 8 [Taxon 48: 377. 1999]).

Phaseolus farinosus L., Sp. Pl.:724. 1753.—TYPE: [USA?] ''*Habitat in* India''[?], collector unknown (lectotype is a line drawing designated by Verdcourt in Taxon 46: 358. 1997: [icon] ''*Phaseolus peregrinus, flore roseo, semine tomentoso*'' in Nissole, Mém. Acad. R. Soc. Paris 1730: 577–580, t. 24. 1732). non *Phasellus roseus* Medik, Vorles. Churpfälz, Phys. Ökon. Ges. 2: 352. 1787, nom. illeg. Linnaeus's statement of provenance was from India, whereas according to Nissole, the plant described and drawn in 1732 was grown in Montpellier Botanical Garden from a mixture of seeds that he received from Holland. According to Miller's Gard. Dict. (1768, ed. 8) those seeds were brought from ''America''.

Phaseolus vexillatus Walter, Fl. Carol. 182 .1788; non Linnaeus (1753).—TYPE: USA. South Carolina. *Walter s.n.* (holotype: BM! Herb. Walter).

Phaseolus angulosus Ortega, Nov. pl. descr. Dec. 2: 24.1797; non Schuebler & Martens (1860).—TYPE: USA. ''In America Septentrionali'', *Gómez Ortega s. n.* (holotype: MA!). Plant grown from seeds in the Royal Botanic Gardens at Madrid; given to C. Gómez Ortega by the Marchioness of Bute, wife to the ambassador of England in Spain.

Glycine angulosa Muhl. ex Willd., Sp. Pl. 3: 1056. 1802. *Strophostyles angulosa* (Muhl. ex Willd.) Elliott, Sketch bot. S. Carolina 2(3): 230. 1823.—TYPE: USA. ''Habitat in Pennsylvania,'' *Muhlenberg s.n.* (lectotype: B, photos!—of the three specimens at Willdenow Herbarium, the one comprising a single leafy stem with two flower buds showing short bracteoles, sheet #3, is designated here as lectotype).

Phaseolus trilobus Michaux ex Rich., in Michaux, Fl. bor.-amer. 2:60. 1803, nom. illeg.; non Aiton (1789); nec Wallich (1831–1832)—TYPE: USA. Carolina [herbarium label states Virginia], *Michaux s. n.* (holotype: P!). According to Stafleu & Cowan (1981), this species was described by L. C. Richard because Michaux's name was not expressly indicated after the epithet.

Phaseolus diversifolius Persoon, Syn. pl. 2(2): 296. 1807; non Pittier (1944).—TYPE: USA. ''Carolina''. *Persoon s.n.* (holotype: P).

Glycine peduncularis Muhl., Cat. Pl. Amer. Sept. ed. 1: 64. 1813.—TYPE: USA. Carolina. *Muhlenberg s.n.* (lectotype: P, Michaux herbarium!, IDC microfiche 6211!; isotypes: PH!). The validation and lectotypification of *G. peduncularis* with a Michaux collection follows Art. 32 and others of the ICBN (Greuter et al. 2000) and is explained in Delgado-Salinas and Lavin (in press).

Glycine peduncularis var. *parabolicus* Muhl. ex Barton, Fl. Philadelph. Prodr. 71. 1815.—*Phaseolus parabolicus* Nuttall, Gen. N. Amer. Pl. 2: 112. 1818, nom. nud. *Phaseolus peduncularis* (Muhl. Ex Barton) W. Barton, Comp. Fl. Philadelph. 2: 81: 1818.—TYPE: USA. [Philadelphia]. No extant type exists at the PH-Barton herbarium. *Strophostyles peduncularis* (Muhl. ex Elliott) Elliott, Sketch Bot. S. Carolina 2(3): 230. 1823.

Strophostyles angulosa (Muhl. ex Willd.) A. Gray var. *missouriensis* S. Watson in A. Gray, Manual, ed. 6, 145. 1890. *Strophostyles helvola* var. *missouriensis* (S. Watson) Britton, in Britton & Brown, Ill. fl. n. U.S. 2: 338. 1897. *Strophostyles missouriensis* (S. Watson) Small, Fl. s. e. U.S., 1st ed., 653. 1903.—TYPE: USA. Missouri. Jackson Co. ''riverbottoms near Independence'', Sept. 21, *F. Bush s.n.* (lectotype, designated by Ruff in herb.: GH!).

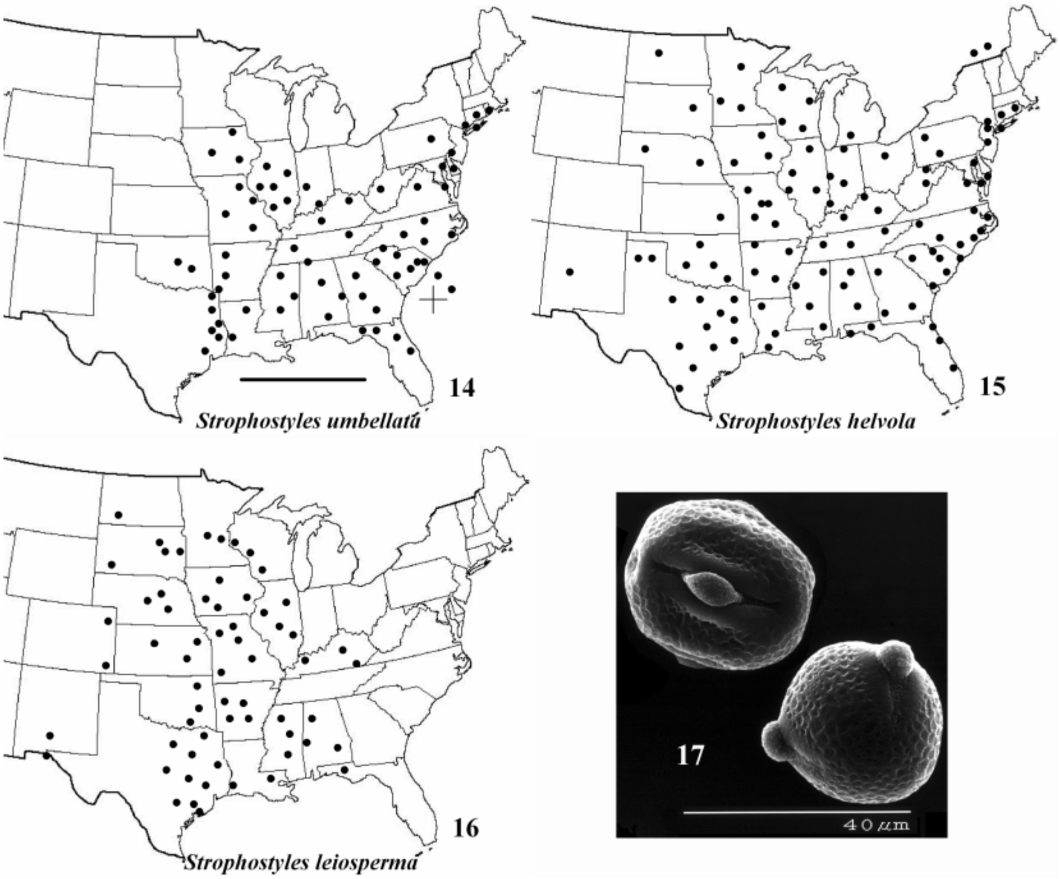
Perennial from a thick taproot. Stems angulate, occasionally lignescent at base, not coming from a subterranean branched caudex, lower stems 1.0–1.5 mm in diameter. Leaflets ovate (rarely orbicular) to lanceolate, panduriform, deeply lobed to entire, the sinus 0.0–18.2 mm deep, terminal leaflets 17.9–71.5 mm long by 8.5–46.2 mm wide, lateral leaflets 13.4–63.4 mm long, 5.8–42.7 mm wide; strigose, hairs 0–5 per mm^2 on upper surface, 0–5 (12) per mm^2 on lower surface. Inflorescence with a peduncle (23.5) 50–215 mm long, angulate, with (1) 2–5 flower-bearing nodes, upon fruit growth becoming stout, lignescent, and 0.8–1.3 mm in diameter. Calyx tube 1.3–3.6 mm long, teeth 1.0–2.5 mm long, bracteoles 1.5–4.2 mm long, generally as long or longer than the calyx tube. Standard petal 6.7–13.3 mm long, pinkish at anthesis; wing petals 7–9 mm long, light pink; keel petal 8–13 mm long, pinkish with a dark purple beak, which is slender, distinctly curved, about 1 mm in diameter, and projected away from the face of the standard petal. Ovary with 5–7 (10) ovules. Pod cylindrical, 30.2–96.1 mm long, (3.0) 4.0–8.1 mm wide, with 5–10 seeds, valves glabrous to lightly strigose, trichome density 0–4 (7) mm^2. Seeds faintly mottled, generally with a cellular or waxy covering. Chromosome number $n=11$ (Roy et al. 1992). Figs. 10, 11, 18.

Phenology. Flowering and fruiting mostly from July to October.

Distribution. From Quebec, Canada south to Florida, west to south Texas, and northwest to North Dakota (Fig. 15); often comprising extensive populations in fields and open understory; 0–1500 m.

Representative Specimens. **Canada. Québec.** *P. H. Hawkins 34952* (MONT); Lonueuil, comté de Chambly, *Fr. Rolland-Germain 43 483* (UC); Ile St.-Ignace: (cté Berthier), *P. Louis-Marie s. n.* (MEXU); Du fleuve, vers Yamachiche, *L. Cinq-Mars 63-1097* (MEXU,UC).

U.S.A. Alabama. Baldwin Co.: salt marsh at Fort Morgan, *R. Kral 51301* (MO). Mobile Co.: Chaumont near Octavius, *R. Deramus D656* (MO). **Arkansas.** Craighead Co.: ditch banks, *D. Demaree 25800* (TEX). Crittenden Co.: between Leuce and Mississippi River, *D. Demaree 11062* (MO). Hempstead Co.: Fulton, *B. F. Bush 1039* (MO). Hot Springs Co.: wooded bottoms, *D. Demaree 16281* (MO). Independence Co.: woods beside Polk Bayou, *R. D. Thomas 125928* (MO). Jefferson Co.: Arkansas river bottom, *D. Demaree 16245* (MO). Jefferson Co. Valley land, *D. Demaree 24005* (MO). Lawrence Co.: bottoms of Janes Creek, *D. Demaree 31354* (TEX). Pulaski Co.: Arkansas River below Little Rock, *D. Demaree 8454, 8686* (MO). Searcy Co.: Maumee, *W. H. Emig 44* (MO). Sebastian Co.: Arkansas River, *T. A. Thompson c0177* (MO). St. Francis Co.: Crowleys Ridge, *D. Demaree 21564* (MO). Stone Co.: rocky ridges, *D. Demaree 61018* (MO). **Connecticut.** Hartford Co.: Southington, *C. H. Bissell 622* (MO). Middlesex Co.: salt marsh, Madison, *F. C. Seymour 29626* (MO). New London Co.: Groton, *K. P. Jansson s.n.* (TEX). **Delaware.** Sussex Co.: beach, Rehoboth, *E. L. Larsen 437* (MO). **District of Columbia**: Chesapeake Beach, *A. Truth 47* (MO). **Florida.** Bay Co.: E of Panama City, *J. B. Nelson 990* (USCH). Duval Co.: banks of St. John's River, *A. H. Curtiss 15552* (MO). Okaloosa Co.: Eglin Air Force Base, Turkey Creek, *J. S. Miller 9091* (MO). St. Johns Co.: between Matanzas and Marineland, *R. K. Godfrey 70655* (TEX). Walton Co.: along Choctaw Beach, *J. S. Miller 9159* (MO). **Georgia.** Cherokee Co.: Etowah River, *W. H. Duncan 8782A* (MO). Floyd Co.: Rome, *A. W. Chapman s.n.* (MO). McIntosh Co.: S end of Sapelo Island, *W. H. Duncan 20593* (TEX). **Illinois.** Adams Co.: along railroad near Coatsburg, *R. A. Evers 591* (MO). Bureau Co.: sand beaches, Dover Bay, *L. D. Stain s.n.* (MO). Jackson Co.: Illinois Central railroad near Carbondale, *J. McMree Jr. 1142* (MO). Kankakee Co.: Altorf Island in Kankakee, *O. E. Lansing 4* (MO). Knox Co.: Galesburg, *J. Solomon 1115* (MO). Lake Co.: Lake Forest, *M. C. Jensen s.n.* (MO). Lasalle Co.: Starved Rock, *F. H. Thorne 159* (MO). Macon Co. Decatur, *O. S. Knight 25* (MO). Madison Co.: Venice, *H. Eggert s.n.* (MO). Mason Co.: Bath, *V. H. Chase I0008* (TEX). Peoria Co.: sandy bottom, Peoria, *F. E. McDonald s.n.* (UC). St. Clair Co.: Cahokia, *F. Wisligeuus 93* (MO). Stark Co.: E of Wady Petra, *V. H. Chase 732* (MO). Tazewell Co.: Pekin, *V. H. Chase 13521* (TEX). Vermillion Co.: along the Middle Fork of the Vermillion River, *G. N. Jones 16229* (MO). Will Co.: sandy soil, *W. S. Moffatt 180* (MO). **Indiana.** Cass Co.: S of Lake Cicott, *R. C. Friesner 10118* (UC). Porter Co.: dunes of Lake Michigan, Chesterton, *J. R. Churchill s.n.* (MO). **Iowa.** Davis Co.: Salt Creek Township, *A. Hayden 11313* (MO). Decatur Co.: sandy soil, *L. P. Anderson s.n.* (MO). Dickenson Co.: sand shore of



FIGS. 14–17. Geographical distribution and pollen morphology of *Strophostyles* species. 14. Distribution of *Strophostyles umbellata* (scale bar equals 500 miles, longitude-latitude mark equals 32° 0′ N and 78° 0′ W). 15. Distribution of *Strophostyles helvola*. 16. Distribution of *Strophostyles leiosperma*. 17. Pollen morphology of *Strophostyles helvola* showing harmomegathic change in shape (left-hand grain) from the normally spheroidal grain (right-hand). This pollen morphology, from reticulate exine and three colpores to harmomegathy, is found in all three species of *Strophostyles*.

Spirit Lake, *R. I. Cratty s.n.* (MO). Mahaska Co.: 2.5 mi NW of Eddyville, *D. W. Augustine 433b* (TEX). Story Co.: 1 mi W of Hickory Grove Lake, *G. Davidse 1989* (MO). Henry Co.: Mt. Pleasant, *J. H. Mills 530* (MO). Story Co.: Ames, *L. H. Pammel 18* (MO). Johnson Co.: sandy prairie along railroad, Iowa City, *B. Shimek s.n.* (TEX). **Kansas.** Riley Co.: Manhattan, *W. A. Kellerman s.n.* (MO). **Kentucky.** McCracken Co.: banks of Ohio River, *D. Demaree 31507* (TEX). Trigg Co.: dry gravel creek terraces at Hematite Lake, *R. Athey 1489* (MO). Warren Co.: near Barren River, *S. F. Price s.n.* (MO). **Louisiana.** Ascension Parish: along US 61, *A. W. Lievans 3263* (MEXU). Caldwell Parish: boat launch area, *R. D. Thomas 107475* (MO). Franklin Parish: along west bank of Boeruf River, *R. Dale Thomas 77524* (MEXU). East Baton Rouge Parish: along edge of woods beside Perkins rd, *R. D. Thomas 138602* (MO). Orleans Parish: Orleans, vacant lot, *R. D. Thomas 123551* (MO). Red River Parish: S of US 84 Bridge at Coushatta, *R. D. Thomas 114908* (USCH). **Maryland.** Calvert Co.: Scientists' Cliffs, *F. C. Seymour 17505, 24679* (MO). Prince Georges Co.: old farm near Fellsta, *T. H. Truth 552* (MO). Hartford Co.: In small bog 1/2 mi SSW of Havre de Grace, *G. H. Shull 401* (MO). Worcester Co.: Assateague Island North Beach National Seashore, *S. R. Hill 15519* (MO). **Massachusetts.** Dorchester Co.: railroad at Cedar Grove, *J. R. C. 528* (MO). Essex Co.: Swampscott, *C. W. Swan s.n.* (MO). Norfolk Co.: sandy railroad bank, Weymouth, *R. G. Leavitt s.n.* (TEX). Plymouth Co.: Furnace Pond, Pembroke *J. R. Churchill s.n.* (MO). **Michigan.** Gaugatuck, bank of Kalamazoo River, *N. V. Hayne 3429* (MEXU). **Minnesota.** Park Co.: Island in Lacqui Park, *J. B. Mayle 2304* (MO). **Mississippi.** Harrison Co.: Biloxi, *Persoon 4842* (MO). Jackson Co.: Oceansprings, *D. Demaree 31304* (MO). **Missouri.** Adair Co.: Kirksville, *G. S. S. s.n.* (MO). Boone Co.: Columbia, *F. Drouet 72* (MO). Butler Co.: Poplar Bluff, *Dewart s.n.* (MO). Cass Co.: woods and roadside, *H. Eggert s.n.* (MO). Clark Co.: Big Rivers Natural Division, *T. E. Smith 3125* (MO). Clay Co.: along Missouri River, *K. K.*

Mackenzie s.n. (MO). Dade Co.: Bona Glade Natural Area, *R. D. Collett 370* (MO). Dallas Co.: along Nisngus River, *J. A. Steyermark 13736* (MO). Daviess Co.: 7 mi SE of Pattonburg, *T. E. Smith 3230* (MO). DeKalb Co.: dried lake bed between Clarksdale and Bayfield, *J. A. Steyermark 14939* (MO). Dent Co.: dry sand bed of Little Pine Creek, *J. A. Steyermark 25462a* (MO). Dunklin Co.: Campbell, *B. F. Bush s.n.* (MO). Franklin Co.: Meramec State Park, *D. V. Darigo 988* (MO). Gasconade Co.: along Gasconade river, *J. A. Steyermark 8451* (MO). Greene Co.: Sac River Ford, *W. Trelease 208* (MO). Henry Co.: Bear Creek, *J. Davis 3937* (MO). Hickory Co.: wet margins and shallow water of Pomme De Terre, *B. Summers 2829* (MO). Howell Co.: 3.5 mi N of Brandsville, *B. Summers 5524* (MO). Jasper Co.: along railway, Duenweg, *E. J. Palmer 778* (MO). Jefferson Co.: The Cedars, Barnhart, *J. M. Greenman 4471* (MO). Johnson Co.: Cave Hollow near Warrensburg, *J. A. Steyermark 24576* (MO). Lewis Co.: bordering wooded area 3 mi E of La Belle, *J. A. Steyermark 25688* (MO). Lincoln Co.: alluvial ground at N end of King's Lake, *J. A. Steyermark 8937* (MO). Marion Co.: W Hannibal, *J. Davis 6240* (MO). McDonald Co.: Elk River Noel, *E. J. Palmer 4189* (MO). Mississippi Co.: Charleston, *J. H. Kellogg s.n.* (MO). Monroe Co.: Salt River basin, *B. Hinterthuer 1047* (MO). Morgan Co.: 1.7 mi S of Florence, *D. Castaner 4262* (MO). Newton Co.: Nash, *W. C. Prince s.n.* (MO). Pemiscot Co.: 7 mi S of Portageville, *J. A. Steyermark 8300* (MO). Phelps Co.: Jerome, *J. H. Kellogg 185* (MO). Pike Co.: Eolia, *J. Davis 6282* (MO). Ralls Co.: sandy flats near Oakwood, *J. Davis 9185* (MO). Randolph Co.: Mt. Airy, *G. Engelmann s.n.* (MO). Reynolds Co.: North Fork of Webb Creek, *R. Jensen s.n.* (MO). Schuyler Co.: Trebel's Cove Conservation Area, *C. E. Darigo s.n.* (MO). St. Charles Co.: Near Old Monroe, *J. Davis 3176* (MO). St. Francois Co.: Silver Springs rd, *J. Saunders 1042* (MO). St. Genevieve Co.: St. Genevieve, *W. Trelease 1008* (MO). St. Louis Co.: Fern Glen, *A. Christ 128* (MO). Taney Co.: 3.5 mi NNE of Forsyth, *T. E. Smith 2977* (MO). **Nebraska.** Cass Co.: Lower Cornish Island, *J. L. Morrison 1355* (MO). Cuming Co.: 3 mi S of West Point, *S. P. Churchill 2020* (MO). Nuckalls Co.: Rudeval, *G. G. Hedgcock s.n.* (MO). Otoe Co.: Nebraska City, *G. G. Hedgcock s.n.* (MO). **New Mexico.** Socorro Co.: Socorro, *T. H. Snow s.n.* (UC). **New Jersey.** Atlantic Co.: Atlantic City, *J. H. Redfield 1630* (MO). Bergen Co.: Hackensack, along railroad, *K. K. Mackenzie 617* (MO). Camden Co.: Kaighus Point, Camden, *B. Meredith s.n.* (MO). Cape May Co.: Sea Isle City, *J. M. G. 977* (MO). Middlesex Co.: New Brunswick, *J. A. Drushel 9570* (MO). Monmouth Co.: Spring Lake, *J. A. Drushel 7753* (MO). Ocean Co.: Chadwick, *K. K. Mackenzie 2392* (MO). Union Co.: Garwood, *J. A. Drushel 6900* (MO). **New York.** Vicinity of New York City, Bedford Park, *S. H. Burnham 589* (BH). North Carolina. Brunswick Co.: marshy roadside on Long Beach, *J. Stevenson 3399* (USCH). Burke Co.: 1 mi E of Pleasant Grove, *H. E. Ahles 58775* (USCH). Dare Co., Roanoke I., *Radford & Stewart 819* (UC). **Ohio.** Hamilton Co.: sandy bank, *B. C. Stephenson s.n.* (MO). Lorain Co.: Lake Erie beach, Oak Point, *G. T. Jones 73-9-9-1223* (MONT). Clermont Co.: Cincinnati, *C. G. Lloyd s.n.* (MO). **Oklahoma.** Cleveland Co.: 5 mi E of Norman, *G. J. Goodman 2032* (MO). Comanche Co.: vicinity of Fort Sill, *J. Clemens 11644* (MO). Grady Co.: N of Tuttle, *R. Pearce 971* (TEX). Lincoln Co.: 5 mi S of Chandler, *R. Stratton 544* (MO). Major Co.: 14 mi NE Seiling, *R. Shatton 473* (MO). Marshall Co.: along strand of Lake Texoma, *J. Williams 462* (MEXU, TEX). Osage Co.: Coon Creek, *G. W. Stevens 2159* (MO). Payne Co.: 2 mi N of Stillwater, *T. H. King 83* (TEX). Stephens Co.: 7 mi SW of Comanche, *W. F. Mhaler 1278* (TEX). Tulsa Co.: Tulsa, *G. E. Tenney s.n.* (TEX). **Pennsylvania.** Bedford Co.: railroad bank E of Bedford Station, *D. Berkheimer 5401* (UC). Forest Co.: along Allegheny River, *B. L. Isaac 5396* (MEXU). **Rhode Island.** New Port Co.: Tiverton, *J. M. G. 1705* (MO). **South Carolina.** Anderson Co.: landfill entrance, *S. R. Hill 18790* (USCH). Beaufort Co.: St. Helena Island, *D. E. Boufford 23097* (MO). Charleston Co.: KOA campsite, Mt. Pleasant, *E. T. Riley-Hulting 3024* (MONT). Fairfield Co.: W side of S-35 just E of Broad River, *J. B. Nelson 8388* (USCH). Georgetown Co.: docks at Sampit River, *J. B. Nelson 14641* (MONT). Horry Co.: dunes near Waiter Island, *J. N. Pinson 401* (USCH). Jasper Co.: sand dunes, *R. Stalter s.n.* (USCH). Newberry Co.: Duncan's Creek, *C. N. Horn 1342* (USCH). Pickens Co.: East Toe Bottoms, *C. L. Rodgers 69959* (MO). Richland Co.: Saluda River, *M. R. Polkowsky 67* (USCH). York Co.: rte 73 at Kirkpatrick Branch, *C. N. Horn 6107* (USCH). Sumter Co.: Ft. Sumter, *R. Stalter s.n.* (USCH). **South Dakota.** Grant Co.: near Bigstone Lake, *P. Johnson 81* (MO). **Tennessee.** Knox Co.: Knoxville, *A. Ruth s.n.* (MO). Wilson Co.: Cedars of Lebanon Park, *R. Kral 56479* (MO). **Texas.** Anderson Co.: E of Palestine, *D. S. Correll 31758* (TEX). Aransas Co.: Rockport, *V. L. Cory 45350* (TEX). Bastrop Co.: 30 mi W of Austin, *E. T. Riley-Hulting 3010* (MONT). Bell Co.: Lake Benton, *C. G. York 55135* (TEX). Brazoria Co.: Brazoria Refuge, *R. J. Fleetwood 9564* (TEX). Brazos Co.: College Station, *R. W. Strandman 662F* (TEX). Burnet Co.: Inks Lake State Park, *J. R. Crutchfield 2305* (TEX). Eastland Co.: 2 mi E of Cisco, *B. H. Warnock 46391* (TEX, UC). Ellis Co.: 5 mi NE of Ennis, *V. L. Cory 5230* (NY). Fannin Co.: S of Sowell's Bluff, *V. L. Cory 54702* (TEX). Fayette Co.: Muldoon, *A. L. Ripple 51730* (TEX). Fort Bend Co.: near Richmond 50 yds from river, *A. Traverse 228* (TEX). Franklin Co.: Mt. Vernon, *B. C. Tharp 2331* (TEX). Freestone Co.: Tehuacana Creek, *B. L. Turner 3145* (TEX). Galveston Co.: Galveston Island State Park, *R. J. Fleetwood 10504* (TEX). Gonzales Co.: Ottine, *E. Whitehouse s.n.* (TEX). Grayson Co.: gravel of spillway channel of Lake Texoma, *M. Nee 44062* (TEX). Harris Co.: Sims Bayou, *E. Boon 283* (TEX). Hemphill Co.: Gageby

Creek, *R.DeArment 3* (TEX). Henderson Co.: 2.5 mi SE of Athens, *D. S. Correll 32054* (TEX). Jackson Co.: Lavaea River, *B. C. Tharp s.n.* (TEX). Jefferson Co.: Beaumont, *B. C. Tharp s.n.* (TEX). Karnes Co.: banks of San Antonio River, *M. C. Johnston 1612* (TEX). Kaufman Co.: disturbed prairie, *R. D. Thomas 146127* (MO). Lamar Co.: 1/3 mi E of Chicotah, *V. L. Cory 54669* (TEX). Laredo Co.: Rio Grande river, *E. Palmer 263* (K). Llano Co.: lower S slope of Enchanted Rock, *M. Butterwick 3052* (TEX). Mason Co.: Flat Rock, *V. L. Cory 43043* (TEX). McLennan Co.: Gaphead rd, *L. D. Smith 75* (TEX). Montgomery Co.: Houston, *F. Lindeheimer s.n.* (MO). Nacogdoches Co.: Cushing, *B. C. Tharp 53–122* (MEXU, TEX). Newton Co.: 6 mi E of Buna, *D. W. Lay s.n.* (TEX). Nueces Co.: Mustang Island, *T. Gillespie 277* (TEX). Parker Co.: Mineral Wells State Park, *B. L. Lipscomb 2409* (TEX). Polk Co.: 1.6 mi W of Sandy Creek, *B. Ertter 5204* (TEX). Presidio Co.: Marfa, *W. P. Taylor s.n.* (TEX). Smith Co.: near Sabine River SE of Gladewater, *D. L. Wilkinson 393* (MO). Tarrant Co.: Lake Worth, *D. Timmons s.n.* (TEX). Travis Co.: E of Garfield, *J. A. Mears 1014* (TEX). Walker Co.: 7 mi NW of Huntsville, *D. S. Correll 31967* (TEX). Wood Co.: Golden, *E. McMullen s.n.* (TEX). **Virginia.** Bath Co.: vicinity of Millboro, *E. S. Steele 450* (MO). Fairfax Co.: along railroad tracks, New Alexandria, *W. C. Muenscher 3747* (MO). Isle of Wight Co.: bluffs along Burwells Bay, *M. L. Fernald & Long 13965* (MO). Lancaster Co.: on beach, *G. Edwin 393* (TEX). Princess Anne Co.: low woods, *K. K. Mackenzie 1809* (MO). North Hampton Co.: Cape Charles, *T. Tidestrom 4287* (MO, UC). **West Virginia.** Cabell Co.: roadside near Depot Milton, *L. Williams 533* (MO). **Wisconsin.** Crawford Co.: dry sand plain, *N. C. Fassett 4399* (MO). Grant Co.: wooded bluff, *N. C. Fassett 17901* (MO). Pepin Co.: Maiden Rock, *N. C. Fassett 17902* (MO). Lacrosse Co.: Lacrosse, *S. D. Swanson 2177* (MO).

Discussion. *Strophostyles helvola* is diagnosed primarily by its flower with a prominently curved slender keel beak that projects upward from the keel lamina and outward away from the face of the standard petal. With pressed specimens, this keel beak often projects away from the other petals (compare Figs. 10, 11). The cylindrical pods are also diagnostic because *Strophostyles umbellata* and *S. leiosperma* have subcylindrical pods with a distinct lateral compression. Pelloto and del Pero Martínez (1988) performed a combined analysis of secondary chemistry and morphology to show that *Strophostyles helvola* is distinct from *S. umbellata* and *S. leiosperma*. Regardless, distinguishing *Strophostyles helvola* from *S. umbellata* will be difficult with flowerless specimens (see discussion of *S. umbellata*).

The sister relationship of *Strophostyles helvola* and *S. leiosperma* is suggested by only the ITS and *trnK* sequence data in the phylogenetic analyses (Figs. 1–4). There are no shared morphological apomorphies suggesting this relationship. The limited ITS sequence diversity detected in *Strophostyles helvola* contrasts to a greater amount found in *S. leiosperma*. The sister relationship of these two species axiomatically indicates that they have an equivalent stem-clade age. The limited genetic diversity in *Strophostyles helvola* could thus indicate a recent range expansion across eastern North America (i.e., a young crown clade), possibly due to human activity, which is inferred from numerous herbarium labels. Despite high population densities, direct PCR sequencing of the ITS region was straightforward in *Strophostyles helvola* most likely because the paucity of ITS sequence variation harbored in this species has resulted in fixation within most populations.

3. *STROPHOSTYLES LEIOSPERMA* (Torrey & A. Gray) Piper, Contr. U.S. Natl. Herb. 22: 668. 1926. *Phaseolus leiospermus* Torrey & A. Gray, Fl. N. Amer. 1(2): 280. 1838.—TYPE: USA. Arkansas. *Leavenworth s.n.* (lectotype, designated by W. F. Ruff in herb., NY!—in Torrey Herbarium).

Phaseolus pauciflorus Bentham, Comm. legum. gen. 76. 1837; non Don (1832); nec Dalzell (1851). *Strophostyles pauciflora* (Bentham) S. Watson, in A. Gray, Manual, ed. 6: 146. 1890.—TYPE: USA. Texas. 1835. *Drummond s.n.* (lectotype, here designated: K!, sheet labeled ''Texas II''; isotypes: K!, sheets labeled ''Texas III'').

Strophostyles pauciflorus (Bentham) S. Watson var. *canescens* R.W. S. Cocks, Legum. Louisiana: 20. 1910.—TYPE: USA. Louisiana. Cameron Parish: beach at Cameron, Sept. 1906, *Cocks s.n.* (holotype: NO, photo!).

Annual or rarely a short-lived perennial from a long and slender taproot. Stems terete, strictly herbaceous at base, not coming from a subterranean branched caudex, lower stems around 1 mm in diameter. Leaflets lanceolate, entire to rarely shallowly lobed, the sinus 0.0–1.0 mm deep, terminal leaflets 16.8–54.2 mm long by 2.2–22.6 mm wide, lateral leaflets 14.8–55.6 mm long by 2.2–20.6 mm wide; sericeous, hairs (1) 4–24 per mm^2 on upper surface, (1) 4–24 per mm^2 on lower surface. Inflorescence with a peduncle 11.5–110 (123) mm long, with 1–2 (4) flower-bearing nodes, upon fruit growth remaining slender, herbaceous, and 0.2–0.7 mm in diameter. Calyx tube 0.8–2.4 mm long, teeth 0.5–1.5 mm long, bracteoles 0.8–2.3 mm long, nearly as long as the calyx tube. Standard petal 3.6–7.0 (8.3) mm long, light pink at anthesis; wing petals 3.5–6.5 mm long, light pink; keel petal 3.5–6.0 mm long, pinkish, with a dark purple beak that is slightly curved and mostly concealed by the wing petals, and which is 1 mm or less in diameter. Ovary with 4–9 ovules. Pod subcylindrical, with a distinct lateral compression, 12.2–40.7 mm long, 2.2–4.5 (5.2) mm wide, with 3–8 seeds, valves usually sericeous, trichome density (1) 5–

24 per mm^2. Seeds often distinctly mottled, commonly without a cellular or waxy covering. Chromosome number $2n=22$ (Mercado-Ruaro and Delgado-Salinas unpublished data). Figs. 12–13, 19.

Phenology. Flowering from July to September; fruiting mostly September.

Distribution. From Louisiana westward through Texas, northward to Kansas and Illinois, and sporadically west to Colorado, New Mexico, and Chihuahua, Mexico (Fig. 16); scattered to dense populations in dry open areas or open understory; 100–1500 m.

Representative Specimens. **Mexico. Chihuahua.** Ciudad Juárez, *Elmer Stearns 398* (US).

U.S.A. Alabama. Baldwin Co.: Ft. Morgan, *R. Kral 51304* (MO). Bullock Co.: edge of farm pond S of Union Springs, *R. Kral 33124* (MO). **Arkansas.** Craighead Co.: dry banks on Crowleys Ridge, *D. Demaree 26564* (TEX). Poinsett Co.: edge of dry woods, *T. Heineke 3231* (MO). Sebastian Co.: Snakepit Lake, *R. D. Thomas C0733* (MO). Union Co.: N of Felsenthal Dam, *R. D. Thomas 102675* (MO, USCH). **Colorado.** Baca Co.: south banks of Cimarron River, *W. Weber 5168* (TEX, UC). Yuma Co.: bluffs of Arikaree River, *W. Weber 12963* (TEX, UC). **Florida.** Franklin Co.: Apalachicola, *A. Chapman s.n.* (MO). **Illinois.** Hancock Co.: Augusta, *J. B. Mead s.n.* (MO). Johnson Co.: Parker, *H. C. Benke 5230* (UC). Madison Co.: Madison, *V. Muehlenbach 4268* (MO). Menard Co.: Athens, *I. W. Clokey 45* (MO, UC). St. Clair Co.: near Palling Springs, *J. A. Steyermark 611* (MO). **Iowa.** Black Hawk Co.: high prairie, *M. Burk 903* (MO). Boone Co.: ledges, *L. H. Pammel 1807* (MO). Davis Co.: Lick Creek, *A. Hayden 9946* (MO). Dickenson Co.: Lake Okoboji, *A. Hayden 4060* (MO). Johnson Co.: Iowa State Gallery of Agriculture, *J. H. Pammel 1804* (MO). Louisa Co.: Muscatine Island, *B. Shimick s.n.* (TEX). **Kansas.** Barber Co.: vicinity of Kiowa, *P. A. Rydberg 642* (MO). Edwards Co.: sandy ground, *A. Finch 90* (MO). Reno Co.: Sylvia, *C. A. Morse 4057* (USCH). Riley Co.: Manhattan, *J. B. S. Norton s.n.* (MO). **Kentucky.** Mickliffe, *F. T. McFarland 190* (MO). **Louisiana.** Ouachita Parish: Monroe, saline bayou, *R. D. Thomas 102898* (MO). St. Tammany Parish: off hwy 11, *K. Rogers 1511* (MO). **Minnesota.** Anoka Co.: Moore Lake, *J. W. Moore 10269* (UC). Stearns Co.: St. Cloud, *F. W. Dewart s.n.* (MO). **Mississippi.** Harrison Co.: Long Beach, *J. F. Joor s.n.* (MO). Jackson Co.: Ocean Springs, *A. B. Seymour 9199.*22 (MO). **Missouri.** Adair Co.: Kirksville, *C. S. Sheldon 2019* (MO, UC). Boone Co.: prairie pasture E of Stephens Sta., *F. Drouet 795* (MO). Butler Co.: Poplar Bluff, *G. W. Dewart 39* (MO). Callaway Co.: along Stinson Creek, *J. A. Steyermark 26/39* (MO). Camden Co.: near Bagnall Dam, *J. H. Kellogg s.n.* (MO). Clark Co.: Wayland, upper Mississippi, *T. E. Smith 3134* (MO). Clay Co.: Oakwood, *J. Davis 428* (MO). Cole Co.: Soluman, *W. Trelease 211* (MO). Dent Co.: Little Pine Creek, *J. A. Steyermark 25462* (MO). Franklin Co.: Missouri Botanical Garden Arboretum, *B. Davit 113* (MO). Gasconade Co.: 3.5 mi W of Hermann, *B. Summers 4515* (MO). Greene Co.: Willard, *J. W. Blankenship s.n.* (MO). Henry Co.: Chapel View prairie, *B. Summers 3066* (MO). Howell Co.: 3.5 mi N of Brandsville, *B. Summers 5525* (MO). Iron Co.: Patterson Mountain area, *C. Anderson M0166* (MO). Jackson Co.: Sheffield, *B. F. Bush 159* (MO). Jasper Co.: along railway grade, *E. J. Palmer 31420* (MO). Jefferson Co.: in field, *A. Christ 128* (MO). Montgomery Co.: Graham Cave Glades Natural Area, *B. Schuette 2068* (MO). Morgan Co.: Avky Banks, *B. F. Bush 14362* (MO). Oregon Co.: N of Treer, *G. & K. Yatskievych 93-320* (MO). Perry Co.: N of Wittenburg, *J. A. Steyermark 14058* (MO). Phelps Co.: banks of railroad, Jerome, *J. H. Kellogg 200* (MO). Ralls Co.: along Salt River W of Center, *J. A. Steyermark 25848* (MO). Ripley Co.: Sand Ponds Natural Area, *S. Hudson 59* (MO). Scott Co.: NE of Blodgett, *S. Holmes 93269* (MO). St. Clair Co.: N of Iconium, *J. A. Steyermark 24275* (MO). St. Francois Co.: Bismarck, *B. F. Bush s.n.* (MO). Ste. Genevieve Co.: Jonca Creek S of Wingarten, *J. A. Steyermark 20956* (MO). St. Louis City: City of St. Louis, *V. Muehlenbach 281* (MO). St. Louis Co.: Washington University, *J. Drushell 4147* (MO). **Nebraska.** Antelope Co.: W of Oakdale, *L. M. Rohrbough 131* (TEX). Cass Co.: bad lands, *F. V. Hayden 20305* (MO). Cedar Co.: St. Helena, *T. A. Bruhin 20252* (MO). Kearney Co.: Minden, *Dr. H. Hapeman s.n.* (UC). Lancaster Co.: Lincoln, *H. J. Webber s.n.* (MO). Nuckolls Co.: along streams, *G. G. Fledrick 2887* (MO). **New Mexico.** Dona Ana Co.: 2 mi N of San Miguel, *F. R. Fosberg S35644* (MEXU); Las Cruces, on bank of irrigation canal, L. *McIntosh 3115* (MEXU). **North Dakota.** Hettinger Co.: *M. Meissner 37856* (MONT). **Oklahoma.** Caddo Co.: N of Apache, *G. J. Goodman 2343* (MO). Creek Co.: Sapulpa, *B. F. Bush 119* (MO). Grady Co.: Rush Springs, *R. Pearce 924* (TEX). Harper Co.: Laverne, *E. J. Palmer 41907* (MO, UC). Kay Co.: E of Ponca City, *R. H. Davy 19* (MO). Kingfisher Co.: Huntsville, *L. A. Blankinship s.n.* (MO). McClain Co.: Johnson's pasture, *F. A. Barkley 1500* (MO, UC). Osage Co.: sandy bank of Coon Creek near Copan, *G. W. Stevens 2166* (MO). Payne Co.: W of Boomer Lake Dam, *W. F. Mahler 960* (TEX). Pottawatomie Co.: SE of Shawnee, *F. A. Barkley s.n.* (MO). Tillman Co.: Frederick, *J. T. Duncan 65* (MO). Woods Co.: Alva, *G. W. Stevens 2824* (MO). **South Dakota.** Beadle Co.: Iroquois, *J. J. Thornber s.n.* (UC). Fall River Co.: Cheyenne River, E of Hot Springs, *W. H. Over 16080* (UC). Spink Co.: vicinity of Redfield, *A. E. Ricksecker 64* (UC). **Texas.** Angelina Co.: Diboll, *C. A. McCleod 4* (TEX). Aransas Co.: Headquarters of Refuge, *R. J. Fleetwood 9349* (TEX). Bastrop Co.: 30 mi W of Austin, *E. T. Riley-Hulting 3001* (MONT). Bell Co.: Tennessee Valley Church, *G. York 54443* (TEX). Brazoria Co.: S of Galveston, *E. T. Riley-Hulting 3006* (MONT). Brazos Co.: Fish Lake, *J. R. Massey 379* (TEX). Cass Co.: E of McLeod, *D. S. Correll*

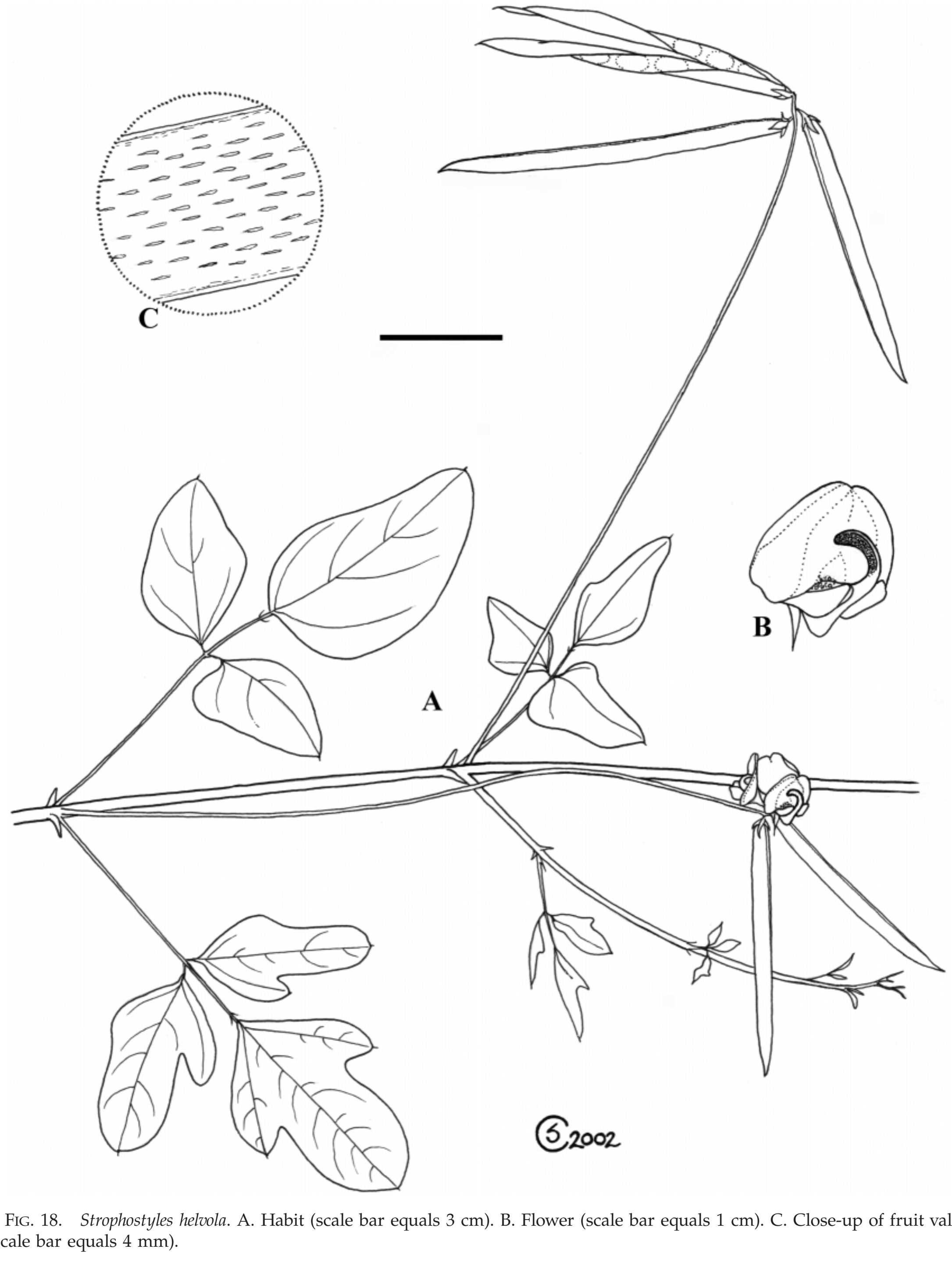


FIG. 18. *Strophostyles helvola*. A. Habit (scale bar equals 3 cm). B. Flower (scale bar equals 1 cm). C. Close-up of fruit valve (scale bar equals 4 mm).

30085 (TEX). Dallas Co.: light soil, *J. Reverchon 257* (MO). Erath Co.: campus, Stephenville, *P. Hoisington 198* (TEX). Falls Co.: along Southern Pacific railroad, *S. L. Orzell 10492* (TEX). Fayette Co.: oak woodland, *F. A. Barkley 46359* (TEX). Galveston Co.: W of Galveston, *B. L. Turner 3150* (TEX). Garza Co.: eroded pasture W of Post, *B. Hutchins 1269* (TEX). Grayson Co.: S of Gordonville, *D. S. Correll 33625* (TEX). Gregg Co.: Sabine River, *D. S. Correll 33980* (TEX). Grimes Co.: E of Navasota, *B. L. Turner 3074* (TEX). Hardeman Co.: Chillicothe, *C. R. Ball 1159* (TEX). Harrison Co.: SE of Marshall, *B. L. Turner 3090* (TEX). Hemphill Co.: Canadian

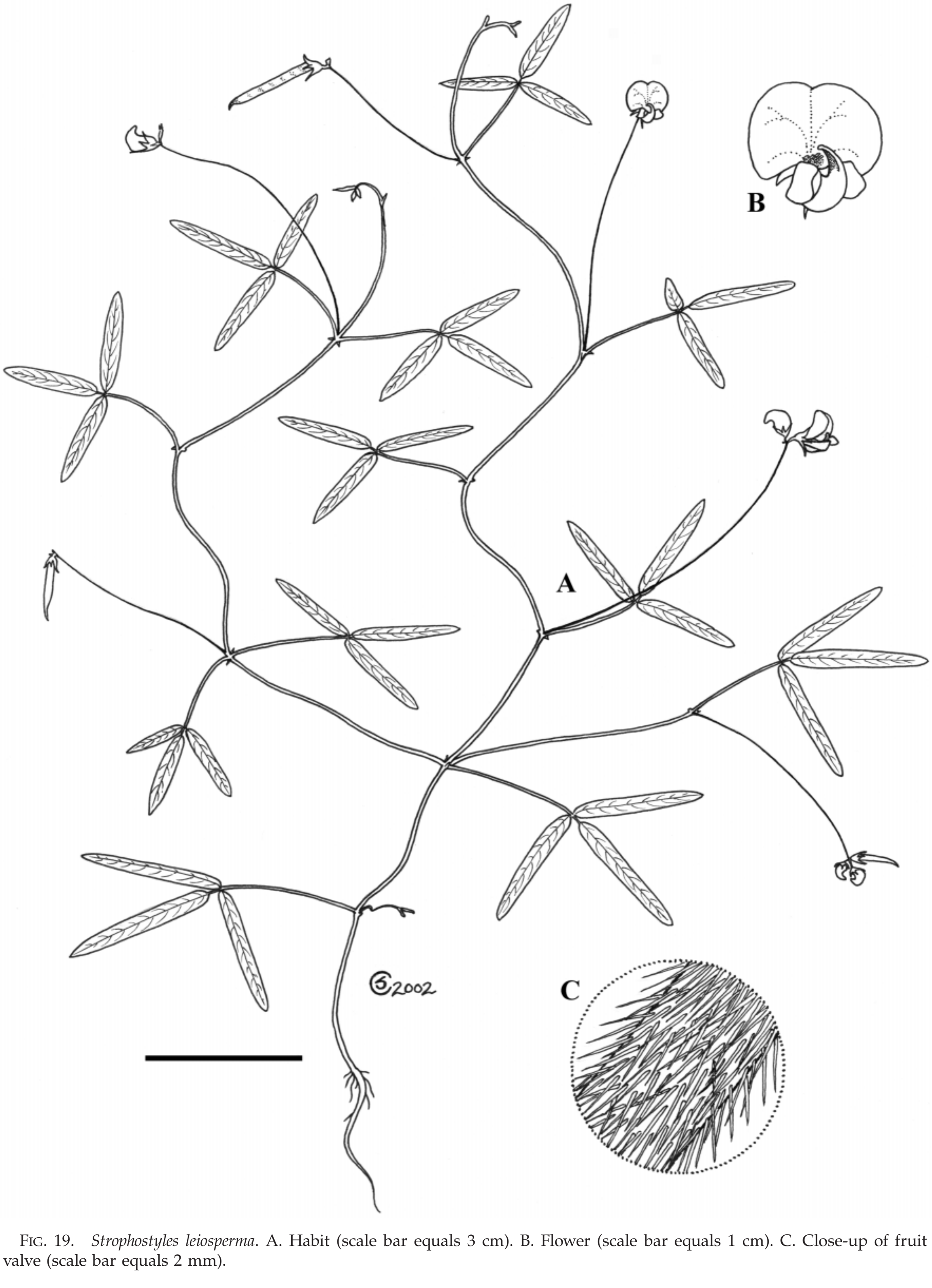


FIG. 19. *Strophostyles leiosperma*. A. Habit (scale bar equals 3 cm). B. Flower (scale bar equals 1 cm). C. Close-up of fruit valve (scale bar equals 2 mm).

Valley, *E. L. Reed 4022* (TEX). Houston Co.: SE of dam of Houston County Lake, *S. L. Orzell 11234* (TEX). Hutchinson Co.: Canadian River breaks, N of Phillips, *C. Drake 172* (TEX). Jefferson Co.: river marsh, Beaumont, *B. C. Tharp s.n.* (TEX). Johnson Co.: Joshua, *E. Whitehouse s.n.* (TEX). Kenedy Co.: El Toro Island, B. C. *Tharp 4832* (TEX). Lamar Co.: E of Chicotah, *V. L. Cory 54668* (TEX). Leon Co.: dune area, *D. S. Correll 36422* (TEX). Limestone Co.: NE of Morgan Hill, *S. L. Orzell 10512* (TEX). Live Oak Co.: Santa Fe Ranch, *B. C. Tharp s.n.* (TEX). Llano Co.: Llano River, *D. S. Correll s.n.* (TEX). Mason Co.: E of Mason, *V. L. Cory 37829* (TEX). Medina Co.: SW of Devine, *M. C. Johnston 3421* (TEX). Montgomery Co.: Conroe, *B. L. Turner 3914* (TEX). Nolan Co.: Sweetwater, *E. J. Palmer 12473* (MO). Nueces Co.: Mustang Island, *D. S. Correll 17666* (TEX). Oldham Co.: Mansfield Ranch, *J. Smith 132* (TEX). Parker Co.: Mineral Wells State Park, *B. L. Lipscomb 2423* (TEX). Polk Co.: N of Corrigan, *B. C. Tharp 51-1507* (TEX). Randall Co.: Palo Dufo Canyon, *E. L. Reed 3981* (TEX). Red River Co.: E of Detroit, *B. L. Turner 3115* (TEX). San Patricio Co.: 1 mi N of Nueces River, *M. C. Johnston 541333* (TEX). Smith Co.: Amigo, *H. E. Moore 995* (MEXU, TEX, UC). Tarrant Co.: along GTP railroad, Fort Worth, *A. Ruth 135* (TEX). Travis Co.: City of Austin, *A. Delgado-Salinas s.n.* (MEXU). Upshur Co.: along rte 80, *R. Merrill 2184* (TEX). Walker Co.: NW Huntsville, *D. S. Correll 31944* (MO). Washington Co.: Brenham, *E. Whitehouse s.n.* (TEX). Wichita Co.: Red River above Burkburnett, *B. C. Tharp 563* (TEX). Wilbarger Co.: W of Vernon, *G. J. Goodman 2268* (MO). Woods Co.: E of Mineola, *J. A. Mears 883* (TEX). **Wisconsin.** Buffalo Co.: Fountain City, *N. C. Fassett 4393* (MO). Iowa Co.: *M. Nee 4330* (MEXU). St. Croix Co.: sandy shore of St. Croix, *N. C. Fassett 17395* (MO).

Discussion. *Strophostyles leiosperma* is the most westerly distributed species and is diagnosed by its small flowers that measure usually less than 8 mm long and have a keel beak only slightly laterally curved and largely enveloped by the wing petals. Pressed flowers often show a strict bilaterally symmetric keel because the slight curve of the beak readily flattens and becomes undetectable (compare Figs. 12, 13). The conspicuous sericeous leaflets and pods of *Strophostyles leiosperma* are also very diagnostic, as is the annual habit of this species. Even seedlings flower after the production of a few leaves (Riley-Hulting unpublished data). Flowers of *Strophostyles leiosperma* evidently self-pollinate because fruits bearing viable seed are produced at least occasionally by flowers in which the fully expanded standard petal never unfolds.

The leaflets of *S. leiosperma* are consistently the narrowest, measuring 2.2–22.6 mm wide. However, southern ranging specimens of *S. umbellata* in Texas and Florida have such narrow leaflets. In this case, *S. leiosperma* is readily distinguished by its slender inflorescence peduncles that measure 0.2–0.7 mm in diameter, small flowers less than 8 mm long, and sericeous leaves, stems, and pods. The seeds of *Strophostyles leiosperma* are commonly glabrous and the cellular seed coat occurs in much less than 50% of specimens bearing seed. If this cellular seed coat is related to dispersal via water, this observation is consistent with *Strophostyles leiosperma* being found more often in open drier sites than the other two species of the genus.

Although a moderate amount of intraspecific ITS sequence variation was detected in *Strophostyles leiosperma*, direct PCR sequencing did not detect putative heterozygotes. Little within population variation might be the expectation in this species if self-pollination is the predominant mode of reproduction. Indeed, two nearby populations of *S. leiosperma* sampled from coastal Texas (accessions of 1453 and 1462 in Fig. 3; Appendix B) revealed no within population sequence variation even though a different ITS sequence was harbored in each of these two populations, and these were distinguished from each other by five nucleotide substitutions.

EXCLUDED TAXA

Strophostyles capensis E. Meyer, and *Strophostyles capensis* var. *lanceolata* E. Meyer, Comm. Pl. Afr. Austr. 147. 1836. This species and its variety are taxonomic synonyms of *Vigna vexillata* (L.) A. Rich.

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Appendix A

Characters that were scored for discrete characters states in Table 1 are: 1) Stems solid = 0, hollow = 1. The hollow stems of *Dolichopsis paraguariensis* and *D. ligulata* might provide buoyancy because these two species uniquely inhabit periodically inundated sites. 2) Stipules primarily perpendicular or retrorse to the stem = 0, primarily appressed or antrorse to the stem = 1. *Mysanthus*, *Oryxis*, and *Dolichopsis* share this distinctive positioning of the stipules. 3) Secondary floral bracts early deciduous = 0, persistent = 1. Secondary bracts arise directly from the swollen node of the pseudoraceme and do not subtend the floral pedicel. They persist through anthesis only on *Strophostyles*. Primary floral bracts subtending the pedicels are generally early deciduous or wanting in Phaseolinae. 4) Bracteoles persistent through anthesis = 0, early deciduous = 1. *Mysanthus* and *Oryxis* have early deciduous bracteoles. 5) Upper teeth of calyx united to varying degrees but always free at the tip (i.e., upper calyx lobe with a bifid tip) = 0, fused into one tooth = 1. The latter condition occurs only in *Strophostyles*, where all calyx lobes have acuminate apices that contrast to the blunt ones of related New World genera. 6) Standard position at anthesis central to plane of bilateral symmetry of the flower = 0, oblique to the plane of symmetry=1. In the latter condition, the left wing essentially assumes the position of the standard, a state shared by *Macroptilium* and *Mysanthus*. 7) Wing petals oblique to the plane of the keel petals = 0, perpendicular to the plane of the keel = 1. Wing petals with the latter condition occur in *Macroptilium* and *Mysanthus*, where the right wing petal serves as a well-developed landing platform for visiting insects. 8) Claw of keel petal short, stout, and abruptly contracted from the blade = 0, long, slender, and gradually tapering from the blade = 1. Long slender claws from the keel petals are distinctive of *Macroptilium* and *Mysanthus*. 9) Upper margin of the keel petal just behind the beak: flat or straight = 0, gibbous = 1. In *Strophostyles* and *Dolichopsis*, the fused upper margin of the keel petals has a hump or gibbosity proximal to the beak, a condition much more pronounced in *Strophostyles* than *Dolichopsis*. 10) The distal portion of the keel beak gradually curved = 0, abruptly hooked or coiled = 1. *Dolichopsis*, *Oryxis*, *Strophostyles*, *Ramirezella*, and *Oxyrhynchus* have a keel beak that is gradually curved out of the plane of floral symmetry. The tip of the keel beak in *Macroptilium* and *Mysanthus*, in contrast, is tightly hooked to coiled. 11) Longitudinal axis of the ovary arched or curved = 0, straight = 1. A curved ovary is found in *Dolichopsis*, *Strophostyles*, *Ramirezella*, and *Oxyrhynchus*, whereas a straight one is found in *Macroptilium*, *Mysanthus*, and *Oryxis*. 12) Fruits terete to subterete = 0, strongly laterally compressed = 1. Terete to subterete pods occur in *Oryxis*, *Strophostyles*, *Ramirezella*, and *Oxyrhynchus*, and strongly laterally compressed ones in *Dolichopsis* and *Mysanthus*. The species of *Macroptilium* collectively show both states, and the ''L'' designates a multistate taxon for this character. 13) Seed borne in a longitudinal position with respect to the long axis of the fruit = 0, transversally placed (perpendicular to the suture) = 1. The latter trait is present only in the two species of *Dolichopsis*. 14) Seed testa smooth = 0, covered with a cellular layer (giving a woolly appearance) = 1. The latter characterizes the seeds of *Strophostyles*, even if this covering is deciduous. 15) Seed hilum circular-ovate in outline = 0, oblanceolate = 1. In the former, the length of the hilum is much less than one-half the length of the seed. For the latter, the hilum length is one-half or more the length of the seed. 16) Seed epihilum persistent = 0, caducous = 1. The latter condition occurs only in *Dolichopsis*. The remaining New World Phaseolinae genera have seeds with a persistent epihilum. 17) Pollen with small-sized colpi = 0, medium-sized colpi = 1. Small colpi have a length about half that of the polar axis, as found in *Ramirezella*, *Oxyrhynchus*, and variously in *Macroptilium*. Medium-sized colpi have a length about equal to that of the length of polar axis, as in *Dolichopsis*, *Mysanthus*, *Oryxis*, and *Strophostyles*.

Appendix B

DNA vouchers and GenBank accession numbers for ^{1}nrDNA ITS/5.8S and the ^{2}*trnK*/*matK* sequences. The DNA accession numbers correspond to those in Figs. 1–4.

Oxyrhynchus volubilis Brandegee. DNA 95: México, Veracruz, *Cedillo 3006* (MEXU), ^{1}AY508735. DNA 109: México, Veracruz, *Cortéz & Vázquez 195* (MEXU), ^{2}AY509935. DNA 251: México, Querétero, *Carranza 1069* (MEXU), ^{1}AF115135. *Ramirezella strobilophora* (B. L. Rob.) Rose. DNA 102: México, Jalisco, *Pérez J. s.n.* (MEXU), ^{1}AF069120, ^{2}AY509936. *Macroptilium ecuadoriensis* (Hassler) L. Torres Colín & A. Delgado. DNA 260: Ecuador, Pichincha, *Blasco 1778* (MEXU),^{1}AY508736. *Macroptilium atropurpureum* (Sessé & Moc. ex DC.) Urb. DNA 110: México, Jalisco, *Torres C. et al. 1070* (MEXU), ^{1}AF115138, ^{2}AY509938. DNA 1131: Mexico, Jalisco, *L. Torres C. 1070* (MEXU),^{1}AY508737. *Macroptilium bracteatum* (Nees & C. Mart.) Maréchal & Baudet. DNA 289: Bolivia, CIAT 4080, ^{1}AY508738, ^{2}AY509950. *Macroptilium erythroloma* (Mart. ex Benth.) Urb. DNA 288: Colombia, Cauca, CIAT 24403, ^{1}AF069117, ^{2}AY509937. *Macroptilium gracile* (Poepp. ex Benth.) Urb. DNA 1130: México, Chiapas, *A. Delgado-Salinas 2501* (MEXU), ^{1}AY508739. *Macroptilium lathyroides* (L.) Urb. DNA 263: México, Tabasco, *R. Torres C. 14445* (MEXU), ^{1}AY508740. *Macroptilium longipedunculatum* (Mart. ex Benth.) Urb. DNA 212: México, Jalisco, *L. Torres C. 1071* (MEXU),^{1}AY508741, ^{2}AY509939. DNA 262: Mexico, Jalisco, *L. Torres C. 1072* (MEXU), ^{1}AY508742, ^{2}AY509940. *Mysanthus uleanus* (Harms) G.P. Lewis & A. Delgado. DNA 104: Brazil, Bahia, *G. P. Lewis 1923* (MEXU), ^{1}AF069125, ^{2}AY509941. *Dolichopsis paraguariensis* Hassl. DNA 199: Argentina, Corrientes, *Krapovickas 46512* (MEXU), ^{1}AF069116, ^{2}AY509942. DNA 1138: Argentina, Corrientes, *Ahumada 1741* (MEXU), ^{1}AY508744. DNA 1560: Bolivia, Beni, *Orellana 383* (MEXU), ^{2}AY509943. *Dolichopsis ligulata* (Piper) A. Delgado. DNA 1516: Bolivia, Beni, *Beck 24296* (MEXU), ^{1}AY508743, ^{2}AY509951–AY509952. *Strophostyles umbellata*. DNA 1316: USA, Alabama, Crenshaw Co., *R. Kral 88958* (USCH), ^{1}AY508799. DNA 1437: Florida, Leon Co., *J. B. Nelson 1190* (USCH), ^{1}AY508800. DNA 1439: Louisiana, Jefferson Davis Co., *C. M. Allen 15589* (MO), ^{1}AY508805. DNA 1264: Mississippi, Clarke Co., *S. B. Jones 14586*

(TEX), ^{1}AY508797, ^{2}AY509945. DNA 180: South Carolina, Columbia, *J. B. Nelson s.n.* (MONT), ^{1}AY508810. DNA 538: South Carolina, Richland Co., *A. B. Pittman 8089606* (MONT), ^{1}AY508808. DNA 540: South Carolina, Edgefield Co., *J. B. Nelson 17763* (MONT); ^{1}AF069115. DNA 1265: South Carolina, Georgetown Co., *J. B. Nelson 9724* (TEX), ^{1}AY508801. DNA 1306: South Carolina, Georgetown Co., *J. B. Nelson 9724* (USCH), ^{1}AY508798, ^{2}AY509944. DNA 1454: South Carolina, Fairfield Co., *E. T. Riley-Hulting 3040* (MONT), ^{1}AY508802. DNA 1457: Texas, Orange Co., *E. T. Riley-Hulting 3004* (MONT), ^{1}AY508809. DNA 1263: Texas, Hardin Co., *W. R. Carr 10820* (TEX), ^{1}AY508804. DNA 1438: Virginia, Fairfax Co., *T. Bradley 21598* (USCH), ^{1}AY508803. *Strophostyles helvola*. Canada. DNA 1450: Quebec, *P. H. Hawkins 34952* (MONT), ^{1}AY508807. USA. DNA 1332: Missouri, Dent Co., *O. Norvell 760* (PI603808), ^{1}AY508755; DNA 1330: Missouri, between Anitt and Edgar Springs, *O. Norvell* 756 (PI603809), ^{1}AY508754. DNA 1333: Missouri, Shannon Co., road to Barren Fork of Burking Creek, *O. Norvell 76l* (PI601971), ^{1}AY508757; DNA 1329, Missouri, between Anitt and Edgar Springs, *O. Norvell 755* (PI601970), ^{1}AY508753. DNA 1371: Delaware, *T. Hymowitz cu-175* (private seed accession), ^{1}AY508751. DNA 1313: Florida, Escambia Co., *S. Orzell 12423* (USCH), ^{1}AY508748. DNA 1369: Florida, Morrito, *T. Hymowitz cu-177* (private seed accession), ^{1}AY508762. DNA 1315: Illinois, Tazwell Co., *V. Chase 13521* (TEX), ^{1}AY508749. DNA 1372: Maryland, Worcester Co., *T. Hymowitz cu-176* (private seed accession), ^{1}AY508752. DNA 1336, Missouri, *O. Norvell PI599666* (USDA accession), ^{1}AY508756. DNA 1370: Missouri, Elsberry, T. H*ymowitz cu-439* (private seed accession), ^{1}AY508758. DNA 1331: Nebraska, *C. McMillan PI215296,* (USDA accession), ^{1}AY508764. DNA 1337: Nebraska, Jefferson Co., *C. McMillan PI215295,* (USDA accession), ^{1}AY508745. DNA 1260: South Carolina, Beaufort Co., *A. R. Darr 525* (MONT), ^{1}AY508766, ^{2}AY509949. DNA 1427: South Carolina, Richland Co., *J. B. Nelson 22202* (USCH), ^{1}AY508760. DNA 1451: Texas, Bastrop Co., *E. T. Riley-Hulting 3010* (MONT), ^{1}AY508759. DNA 1268: Texas, Bastrop Co., *B. Ertter 4866* (TEX), ^{1}AY508761. DNA 1261: Texas, Freestone Co., *W. Cholmes 187* (TEX), ^{1}AY508746. DNA 1452: Texas, Galveston Co., *E. T. Riley-Hulting 3012* (MONT), ^{1}AY508765. DNA 1233: Texas, Rusk Co., *Correll 33978* (USCH), ^{1}AY508747, ^{2}AY509948. DNA 1311: Virginia, Richmond Co., *T. Bradley 24735* (USCH), ^{1}AY508750. DNA 1312: West Virginia, Monongalia Co., *W. Grafton s.n.* (USCH), ^{1}AY508763. *Strophostyles leiosperma*. USA. DNA 1310: Arkansas, Union Co., *R. D. Thomas 102675* (USCH), ^{1}AY508776. DNA 1442, Alabama, Baldwin Co., *R. Kral 51304* (MO), ^{1}AY508774. DNA 1273: Kansas, Reno Co., *C. A. Morse 4057* (USCH), ^{1}AY508772. DNA 1440: Missouri, St. Louis Co., *F. Comto 826* (MO), ^{1}AY508806. DNA 1334: Nebraska, *C. McMillan PI215298* (USDA accession), ^{1}AY508773. DNA 106: New Mexico, Dona Ana Co., *McIntosh 3115* (MEXU), ^{1}AY508771, ^{2}AY509946. DNA 1446: Oklahoma, Grady Co., *R. Pearce 924* (TEX), ^{1}AY508770. DNA 1456: Texas, Bastrop Co., *E. T. Riley-Hulting 3001* (MONT), ^{1}AY508796. DNA 1453 (a-j): Texas, Brazoria Co., Brazoria National Wildlife Refuge. *E. T. Riley-Hulting 3005* (MONT), ^{1}AY508786–AY508795. DNA 1455: Texas, Brazoria Co., S of Galveston, *E. T. Riley-Hulting 3006* (MONT), ^{1}AY508769. DNA 1462 (b-j): Texas, Brazoria Co., Angleton, *E. T. Riley-Hulting s.n.* (MONT), ^{1}AY508777–AY508785. DNA 1221: Texas, Falls Co., *S. Orzell 10492* (TEX), ^{1}AY508768. DNA 1266: Texas, Lamar Co., *D. S. Correll 37931* (TEX), ^{1}AY508767, ^{2}AY509947. DNA 197: Texas, Travis Co., *A. Delgado-Salinas s.n.* (TEX), ^{1}AF115137 (reported as ''*S. helvula*'' in Delgado-Salinas et al. 1999). DNA 1445: Wisconsin, St. Croix Co., *N. C. Fassett 17395* (MO), ^{1}AY508775.