



Phylogenetic systematics of *Strophostyles* (Fabaceae)
by Erin Thais Riley-Hulting

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Plant Sciences

Montana State University

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Abstract:

The genus *Strophostyles* comprises three species centered in southeastern USA. *Strophostyles umbellata* is the most genetically variable at the nrDNA ITS locus with allelic variation concentrated in southern Appalachia. The geographically most widespread *S. helvolus* shows the least amount of intraspecific genetic variation at this locus, suggesting recent and rapid range expansion throughout the eastern half of the USA. Allelic variation of *Strophostyles leiosperma* is intermediate and centered in eastern Texas. The genus *Strophostyles* is apomorphically diagnosed by divergent stipules, persistent secondary floral bracts, a calyx with four acute lobes, and seeds often producing a waxy testa. In contrast, the closely related New World genera, *Dolichopsis*, *Macroptilium*, *Mysanthus*, *Oryxis*, *Oxyrhynchus*, *Phaseolus*, and *Vigna* subgenus *Sigmoidotropis* (the New World Phaseolinae), have mostly appressed stipules (except *Macroptilium*), deciduous secondary floral bracts, a calyx with 4-5 blunt lobes, and seeds with a consistently smooth testa. In contrast to the usual perception of geographic relationships of the flora of the southeastern USA, *Strophostyles* appears to be sister to South American *Dolichopsis*. This is supported by the shared apomorphy of a gibbous upper margin of the keel petals and phylogenetic analyses of sequences from the nrDNA ITS region and CpDNA trnK locus. A rate-smoothed Bayesian likelihood analysis was performed on Old and New World Phaseolinae sequences with an imposed time constraint of 33.7 Ma for the closure of the tropical North Atlantic land bridge. As such, the estimates of $3.3\text{-}7.1 \times 10^{-9}$ and $4.7\text{-}6.9 \times 10^{-10}$ substitutions per site per year are made for the ITS region and the matK locus, respectively, which are similar for other legume groups. This corresponds to an estimated divergence time between *Strophostyles* and *Dolichopsis* of 18-19 Ma.

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APPROVAL

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is read for submission to the College of Graduate Studies.

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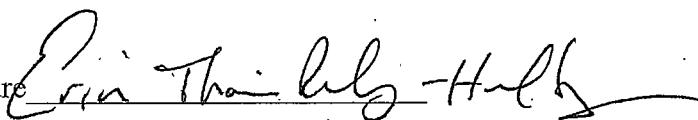
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ABSTRACT

The genus *Strophostyles* comprises three species centered in southeastern USA. *Strophostyles umbellata* is the most genetically variable at the nrDNA ITS locus with allelic variation concentrated in southern Appalachia. The geographically most widespread *S. helvolus* shows the least amount of intraspecific genetic variation at this locus, suggesting recent and rapid range expansion throughout the eastern half of the USA. Allelic variation of *Strophostyles leiosperma* is intermediate and centered in eastern Texas. The genus *Strophostyles* is apomorphically diagnosed by divergent stipules, persistent secondary floral bracts, a calyx with four acute lobes, and seeds often producing a waxy testa. In contrast, the closely related New World genera, *Dolichopsis*, *Macroptilium*, *Mysanthus*, *Oryxis*, *Oxyrhynchus*, *Phaseolus*, and *Vigna* subgenus *Sigmoidotropis* (the New World Phaseolinae), have mostly appressed stipules (except *Macroptilium*), deciduous secondary floral bracts, a calyx with 4-5 blunt lobes, and seeds with a consistently smooth testa. In contrast to the usual perception of geographic relationships of the flora of the southeastern USA, *Strophostyles* appears to be sister to South American *Dolichopsis*. This is supported by the shared apomorphy of a gibbous upper margin of the keel petals and phylogenetic analyses of sequences from the nrDNA ITS region and cpDNA *trnK* locus. A rate-smoothed Bayesian likelihood analysis was performed on Old and New World Phaseolinae sequences with an imposed time constraint of 33.7 Ma for the closure of the tropical North Atlantic land bridge. As such, the estimates of $3.3-7.1 \times 10^{-9}$ and $4.7-6.9 \times 10^{-10}$ substitutions per site per year are made for the ITS region and the *matK* locus, respectively, which are similar for other legume groups. This corresponds to an estimated divergence time between *Strophostyles* and *Dolichopsis* of 18-19 Ma.

LITERATURE REVIEW

*Strophostyles*An Introduction to *Strophostyles*

The genus *Strophostyles* is a member of the legume family and classified within the tribe Phaseoleae of the subfamily Papilionoideae because of its papilionoid flower, liana habit, and trifoliolate leaves. The viney habit characteristic of *Strophostyles* is fairly common among papilionoid legumes, but most generally of tropical forest genera. The asymmetric floral morphology of *Strophostyles*, whereby the keel petals curve slightly or prominently to the right-side of the flower, is characteristic of a New World group of trifoliolate-leaved vines comprising such well known genera such as *Phaseolus* and *Vigna*. Indeed, the most recent higher level taxonomic treatment of Phaseoleae (Lackey 1983), in addition to phylogenetic analyses of nuclear ribosomal 5.8S and flanking internal transcribed spacers (the ITS region) and the chloroplast *trnK/matK* locus (Delgado et al. 1999, and unpublished data), suggest that the closest relatives of the temperate *Strophostyles* are primarily neotropical *Vigna* subgenus *Sigmoidotropis*, *Phaseolus*, *Ramirezella*, *Oxyrhynchus*, *Macroptilium*, *Mysanthus*, *Oryxis*, and *Dolichopsis*. These form a strongly supported monophyletic clade and are referred to as the New World Phaseolinae.

The genus *Strophostyles* was subjected to intensive phylogenetic and systematic study because of its distinctive morphology and biogeography, and the lack of attention given to the delimitation of constituent species. The flowers of *Strophostyles* lack the morphological complexity of its close relatives. The banner, wing, and keel petals all have a general bilateral symmetry typical of most papilionoid legumes. The keel petals deviate only slightly from the typical papilionoid symmetry by having a rostrum that is curved to the right side of the flower. All putative relatives of *Strophostyles* have flower petals that strongly deviate from bilateral symmetry, at least with respect to the keel rostrum which is coiled at least one-half turn to the right side of the flower. In addition to floral morphology, *Strophostyles* has a distinctive cool temperate distribution compared with its tropical relatives. Finally, traditional floristic treatments dealing with *Strophostyles* (e.g., Radford 1968; Correll and Johnston 1970) have recognized at least three species that are most common to temperate forest and grassland habitats in the southeastern quadrant of the USA. However, misidentification is common especially with specimens collected from the very southeastern USA. This difficulty arises because either the key morphologies are inadequate for diagnosing species identity, or species delimitations have been incorrectly drawn.

This study was designed in part to discover the closest relatives of *Strophostyles* in order to interpret the degree of morphological and biogeographic change that took place during the evolution of this genus. 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 the constituent taxa within the genus, as well as the relationships of the genus to neotropical relatives. Using rate-smoothing methods for estimating nucleotide substitution rates, we estimate an absolute time frame during which the *Strophostyles* lineage (stem clade) and diversification (crown clade) evolved.

MATERIALS AND METHODS

Taxon sampling

Three sampling strategies were employed during this study. The first involves exhaustive sampling at the population level within and among the traditionally recognized species of *Strophostyles*. As was found in the closely related genus *Phaseolus* (Delgado et al. 1999), the ITS region in *Strophostyles* is phylogenetically very informative at and below the species level. Thus, sampling of this genetic locus was as exhaustive as possible among populations, including latitudinal and longitudinal extremes for each of the traditionally recognized species. Such information was used to delimit the constituent species of *Strophostyles*. The second strategy involves exhaustive sampling of molecular sequence data (ITS and *matK* sequences) at the genus level among the traditionally recognized genera of New World Phaseolinae. Included in this group are *Dolichopsis*, *Mysanthus*, *Oryxis*, *Oxyrhynchus*, *Phaseolus*, *Ramirezella*, and *Vigna* subgenus *Sigmoidotropis* (e.g., Lackey 1981; Delgado et al. 1999). This sampling was performed in order to best determine the sister group relationships of *Strophostyles*. The third strategy involved the sampling of morphological data from among the genera *Macroptilium*, *Mysanthus*, *Oryxis*, *Dolichopsis*, and *Strophostyles*. These genera were targeted for such sampling because broad scale sampling of the *matK* locus of New and Old World Phaseolinae (Lavin et al. unpublished data) revealed that these five genera form a well supported monophyletic clade. Such sampling permitted a

phylogenetic evaluation of the characters that have been traditionally or recently used in the classification of *Strophostyles* and closely related genera.

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).

DNA sequences from the nuclear ribosomal 5.8S and flanking internal transcribed spacers (the ITS region) and the chloroplast *trnK* intron including *matK* (the *trnK/matK* locus) were analyzed. PCR and sequencing primers for the ITS region are described in Beyra-M. and Lavin (1999) and Delgado-Salinas et al. (1999). They include the PCR primer sequences from the small subunit forward 5'-

GTCCACTGAACCTTATCATTAGAGG-3' and from the large subunit reverse 5'-

GCCGTTACTAAGGGAATCCTTGTTAG-3'. Sequencing primers nested within the

region delimited by the above two primers are from the small subunit forward, 5'-

AAGTCGTAACAAGGTTCCGTAG-3', and from the large subunit reverse, 5'-

GTTAGTTTCTTTTCCTCC-3'. Primers for *matK* and flanking *trnK* intron sequences

are as follows: from the 5' *trnK* intron forward, TK1F: 5'-

GGGTTGCTAACTCAATGGTAG-3'; middle of the *matK* coding region reverse, M4PF:

5'-CCTTCGATATTGGATAAAAGATG-3'; near 3' end of *matK* coding region reverse,

M7MR: 5'-CGGCTTACTAATAGGATGAC-3'; middle of *matK* coding region forward,

M4PR: 5'-CTTTTATCCAATATCGAAGG-3'; and 3' trnK intron reverse, TK2R: 5'-CCCGGAACTAGTCGGATGG-3'. DNA sequencing was performed on an automated sequencer at Northwoods DNA (Becida, Minnesota).

DNA sequences were aligned manually and unambiguously with Se-AI (Rambaut 1996). Maximum parsimony analyses were performed with PAUP* (Swofford, 2001). Heuristic search options included 100 random addition replicates, tree-bisection-reconnection branch swapping, and retention of multiple parsimonious trees. A maximum of 10,000 trees was allowed to accumulate, which is sufficient to capture all topological variation (cf. Sanderson and Doyle 1993). Clade stability tests involved bootstrap resampling (Felsenstein 1985; Sanderson 1995), where each of 10,000 bootstrap replicates was subjected to heuristic search options that included one random addition sequence per replicate, swapping with tree-bisection-reconnection, and invoking neither steepest descent nor mulpars.

Morphometric analysis

Vegetative, floral, and fruiting traits were identified for a multivariate statistical analysis in an effort to delimit species and determine which traits would be most taxonomically informative. A preliminary list of traits was derived from characters that have been traditionally used in taxonomic and floristic treatments of the genus *Strophostyles*. In addition, we refined and added to this list by observation of those traits

on herbarium specimens that varied within and among species of *Strophostyles*. Quantitative character analysis was performed using the multivariate approaches available in the computer program NTSYSpc (Rohlf 2000), including cluster and ordination analyses.

A total of 436 herbarium specimens was analyzed for morphological variation. These specimens were selected from among over 1,000 herbarium specimens on loan to the Montana State University Herbarium (MONT). These 436 specimens possessed the greatest array of mature and healthy vegetative, floral, and fruiting characters. For each of these herbarium specimens, floral, fruiting, and vegetative traits were selected for measurement. Seven vegetative traits were ultimately 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. Five flowering traits were measured, including lengths of banner petal, calyx tube, bracteole, and inflorescence rachis, and number of nodes per inflorescence. The remaining five were fruiting traits, including length and width of pod, number of ovules per ovary, hair density on the surface of the fruit, and the presence of a cellular covering on the ovules. All traits were quantitative, with the exception of the presence of the cellular covering, which was qualitative. Because not all specimens displayed both floral and fruiting characters, subsets of the data that minimized missing floral or fruiting measurements were analyzed.

Evolutionary Rates Analysis

The program r8s (Sanderson 2001) was used to assess variance in evolutionary substitution rates for nucleotide sequences from the ITS region and the *matK* locus, and incorporate such variance into the estimation of ages of lineages (Sanderson 1997, 1998, 2001, 2002). This program uses a rate smoothing approach, penalized likelihood (PL), to identify an optimal rate smoothing parameter that renders evolutionary substitution rates and ages for each of the branches in a phylogeny. The optimal smoothing parameter is determined by a cross validation approach whereby the value chosen best predicts the overall terminal branch lengths in a saturated rate model. This predictive ability is then compared with that of an autocorrelated rate smoothing approach (nonparametric rate smoothing; Sanderson 1997) and rate constant model (Langley and Fitch 1974), which potentially define the extremes of the continuum from the saturated to the clock-like rates model. These latter two approaches are also implemented in r8s.

For the ITS and *matK* data sets, branch lengths were estimated during a maximum likelihood analysis that involved a search of tree parameter space using a Bayesian approach. This involves a Metropolis-coupled Markov Chain Monte Carlo permutation of tree parameters, an initial random tree, 2,000,000 permutations of tree parameters, and four chains (Huelsenbeck and Ronquist, 2001; Huelsenbeck et al. 2001). Parsimony searches in PAUP* (Swofford 2001) were used to validate the branching order parameter estimated with MrBayes, whereas the AIC model selection approach was used to validate the estimated nucleotide substitution parameters (Posada and Crandall 1998). All

estimated parameters (branching order, branch lengths, and nucleotide substitution) were then used to generate parametric bootstrap replicates using Seq-Gen (Rambaut and Grassley 2001), each of which were subjected to analyses with r8s to obtain mean and standard deviations of evolutionary substitution rates and ages of specified clades.

Relative substitution rates and ages estimated with r8s were converted to absolute rates and ages by enforcing an age constraints at the separation of the Old and New World Phaseolinae. Molecular phylogenetic analyses reveal that New World Phaseolinae for a well supported monophyletic clade that is sister to an essentially Old World clade of *Vigna* species (Lavin et al., unpublished data). The divergence of these two sister clades is assumed to be the results of the closure of the North Atlantic land bridge to tropical migration, possibly around the end of the Eocene or very early Oligocene (summarized in Lavin et al. 2000), which is estimated at ca. 33.7 Ma (Berggren et al. 1995). This age estimate is corroborated by a large scale analysis of legume *matK* sequences (Wojciechowski, in press; Wojciechowski et al., in mss.), which suggests the age of the Phaseolinae is around 30-40 Ma. This large-scale analysis uses an age constraint for the legume crown clade of 59.9 Ma, which represents the age of the oldest unequivocal legume fossil (Herendeen et al. 1992 and personal communication).

The genus *Dolichopsis* is sister to *Strophostyles*, as suggested by molecular data and the shared apomorphies of a gibbous upper margin of the keel petals just behind the rostrum (#9), arched ovaries (#11), and the lateral placement of the stigma (although this last trait has been hypothetically lost in *Dolichopsis paraguariensis*). The monotypic *Oryxis* is sister to the *Dolichopsis-Strophostyles* clade, as suggested by the morphological apomorphies of a curved (not hooked or coiled) keel rostrum (#10), subterete fruits (#13; independently evolved in some *Macroptilium* species), and an oblanceolate hilum (#16). No molecular data were obtained for *Oryxis*, and morphology provides the only clues for the relationships of this monotypic South American genus. Finally, the *Mysanthus-Macroptilium* clade is sister to that formed by *Oryxis*, *Dolichops*, and *Strophostyles* (Fig. 1), a relationship well supported in a global *trnK/matK* analysis of world wide Phaseolinae (Lavin et al. unpublished data; see below).

Intragenetic Phylogenetic Relationships

An exhaustive sampling of ITS sequences from 68 *Strophostyles* accession yielded an unequivocal alignment with a total length of 658 sites. A parsimony analysis reveals very few instances of homoplasy, as indicated by the high values of the consistency and retention index (Fig. 2). Furthermore, two principle monophyletic clades are resolved, and these correspond to *S. umbellata* in one, and *S. helvolus* and *S. leiosperma* in the other (Fig. 2). *Strophostyles helvolus* is resolved as paraphyletic with respect to *S. leiosperma*.

Table 2. Parsimony scores for each of the 17 morphological characters used in the combined phylogenetic analysis (Table 1). The length, consistency index (ci), and retention index (ri) are reported for each character. Overall, these morphological characters added a length of 21 steps to the most parsimonious trees (Fig. 1) and had a combined consistency index of 0.810 and a retention index of 0.913. Both of these values are higher than the average consistency and retention index for all of the combined characters on the combined maximum parsimony trees (0.845 and 0.856, respectively).

Character (from Table 1)	length	ci	ri
1	1	1.00	1.00
2	2	0.50	0.67
3	1	1.00	1.00
4	2	0.50	0.00
5	1	1.00	1.00
6	1	1.00	1.00
7	1	1.00	1.00
8	1	1.00	1.00
9	1	1.00	1.00
10	1	1.00	1.00
11	1	1.00	1.00
12	2	0.50	0.67
13	2	0.50	0.50
14	1	1.00	1.00
15	1	1.00	1.00
16	1	1.00	1.00
17	1	1.00	1.00

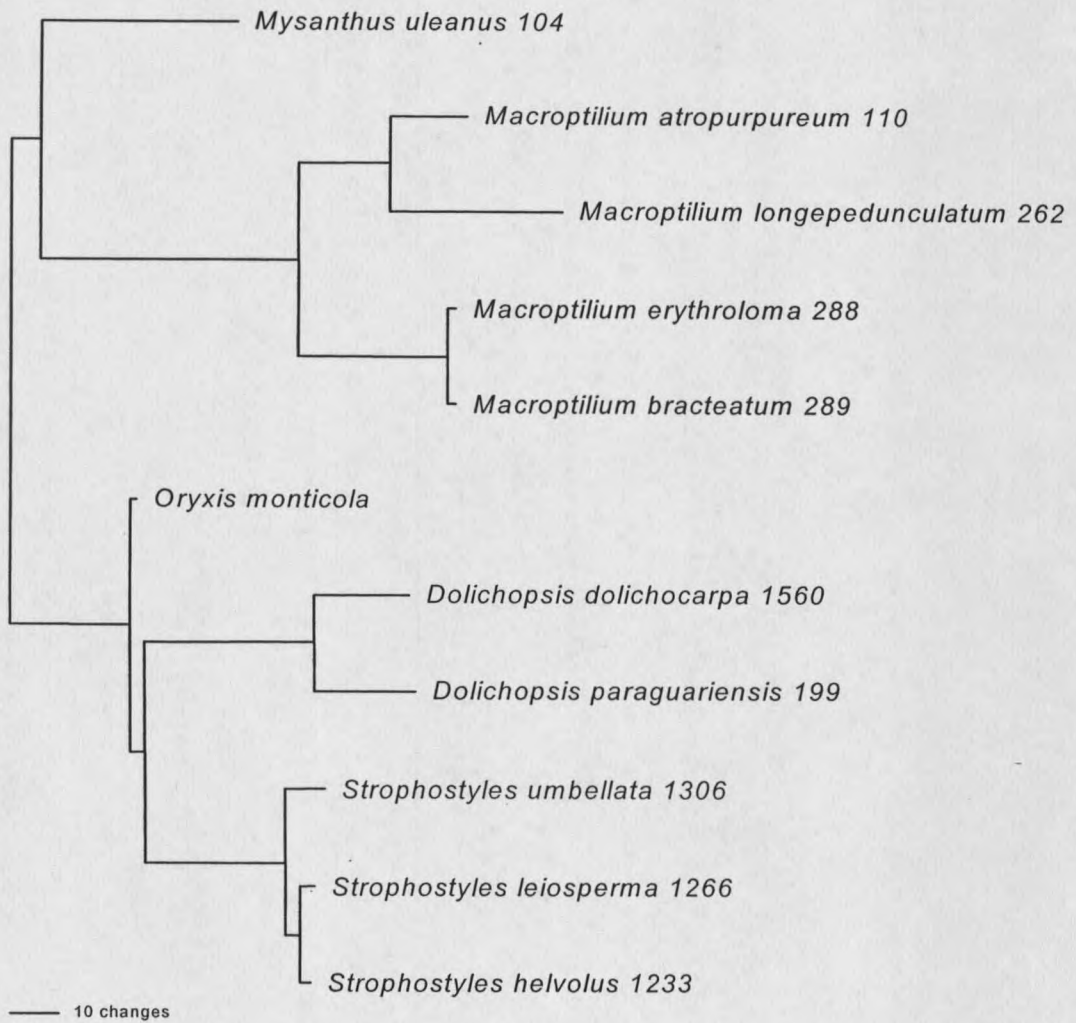
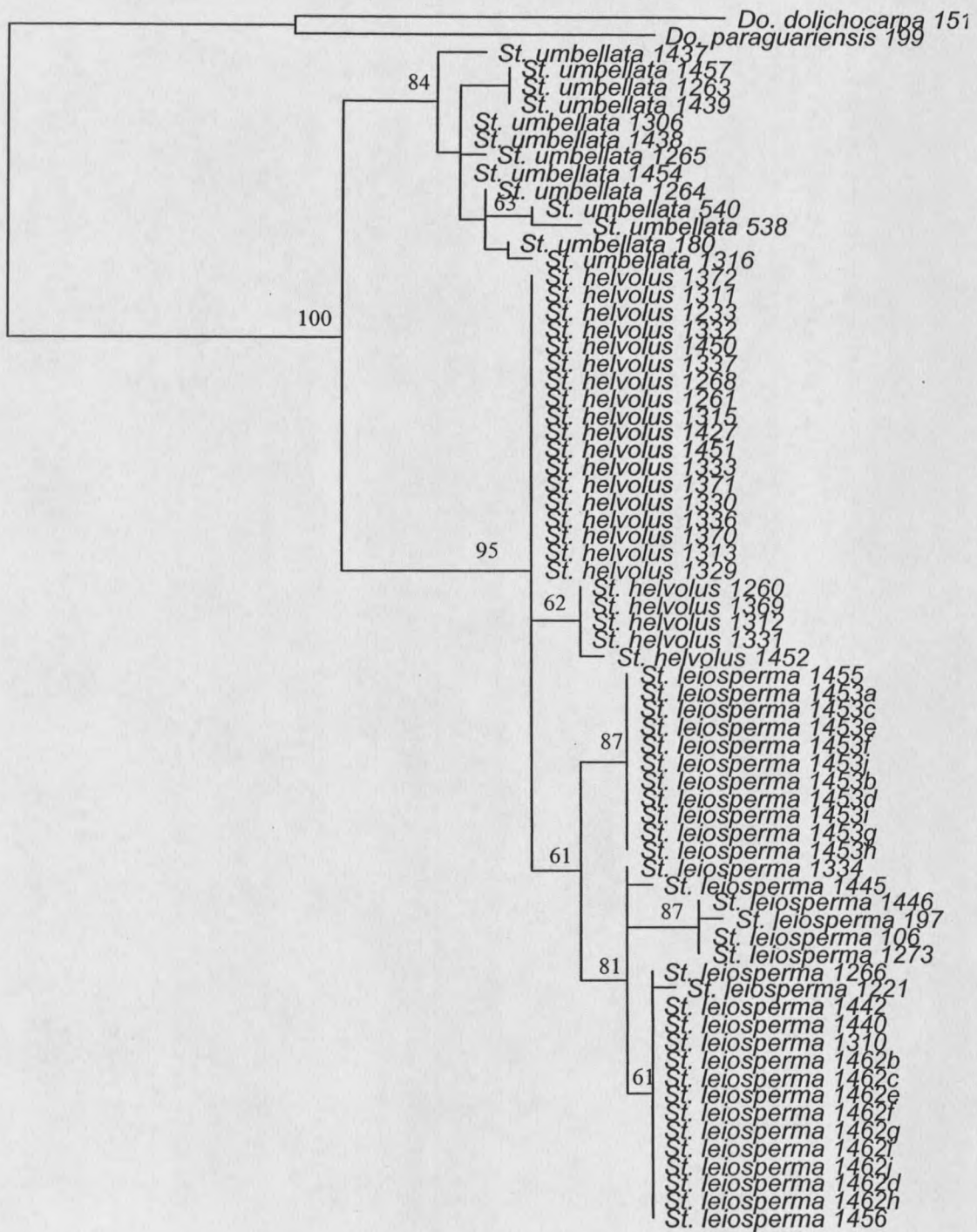


Fig. 1. Combined analysis of morphological, ITS/5.8S, and *matK* sequence data for *Strophostyles* and close relatives (a partition homogeneity test suggests little data set conflict at $p=0.206$)

Of the four substitutions derived and fixed among all accessions of *S. umbellata*, one of them is a transversion (Table 3). The derived substitutions fixed among *S. helvolus* and *S. leiosperma* accessions include three transversions (Table 3). In contrast to this pattern of reciprocal monophyly, *S. leiosperma* ITS alleles are derived from a paraphyletic assemblage of alleles within *S. helvolus*. The *S. leiosperma* accessions are distinguished from those of *S. helvolus* the nucleotide A (from an ancestral T in all accessions of *Dolichopsis* and *S. leiosperma*) at site 579 from the ITS2 region, and by the nucleotide A (from an ancestral G in all the rest of the accessions) at site 34 from the ITS1 region. With the exception of the two main subclades within *Strophostyles*, all other clades are only weakly to moderately supported by bootstrap values. However, the very high consistency and retention indices reveals that there very few ways to map character state changes onto the population-level allelic phylogeny (Fig. 1).

Table 3. Substitutions mapped to the two principle subclades of *Strophostyles* (Fig. 2). These represent 12 of the 49 phylogenetically informative sites for the total data set (*Dolichopsis* accession included), or 11 of the 41 variable sites among the *Strophostyles* accessions (*Dolichopsis* excluded).

clade (Fig. 2)	position	length	ci	change
<i>Strophostyles umbellata</i>	51	1	1.00	C ==> G
	91	1	0.5	A ==> G
	436	1	1.00	A ==> G
	476	1	1.00	T ==> C
<i>Strophostyles helvolus</i> and <i>S. leiosperma</i>	112	1	1.00	C ==> T
	218	1	1.00	G ==> A
	428	1	1.00	A ==> C
	434	1	1.00	C ==> T
	509	1	1.00	C ==> T
	579	1	0.67	C ==> A
	582	1	0.50	C ==> G
	630	1	1.00	C ==> T



— 1 change

Fig. 2 Phylogram of 68 *Strophostyles* accessions derived from an analysis of the sequences from the ITS region with *Dolichopsis* species as the designated outgroups.

Intraspecific Phylogenetic Relationships

Unrooted networks for each of the three species of *Strophostyles* reveals geographical patterns of the allelic variation. The allelic variation in *Strophostyles umbellata* was the greatest of the three species, with 10 alleles obtained from 13 sampled sequences from throughout the range of this species, which is principally from southeastern USA (Fig. 3). Remarkably, eight of the 13 substitutions distinguishing these 10 alleles are transversions (Table 4). Furthermore, the alleles are distinguished from each other commonly by more than one base substitution. The alleles most centrally located in the network are all taken from south Appalachia, whereas some of those at the tips are from geographical extremes of the species. For example, U1263 (Mississippi), 1439 (Louisiana), 1457 (Texas) represent a single terminally positioned allele sampled from the eastern margin of the range of *S. umbellata* (Fig. 3 and Appendix A).

In contrast, the ITS alleles of *Strophostyles helvolus* sampled from throughout its range in the eastern USA (and adjacent southeastern Canada) show the least amount of nucleotide variation. Only three alleles were detected from a sample of 23 sequences and these differ from each other by mostly one or two nucleotide substitutions (Fig. 4). The principal allelic subdivision within the accessions of *S. helvolus* (internode L in Fig. 4) shows no geographic patterning because alleles from both sublineages are distributed across the eastern half of the USA.

Table 4. Intraspecific substitutions from the ITS/5.8S region mapped onto the unrooted networks derived from figure 2 for each of the constituent species of *Strophostyles* (Figs. 3-4). These represent both phylogenetically informative and uninformative substitutions.

	Site	Steps	CI	Substitution
<i>Strophostyles umbellata</i>				
(Fig. 3)				
Node A	59	1	1.00	G ↔ C
Node B	619	1	1.00	C ↔ A
	642	1	1.00	C ↔ A
Node C	647	1	1.00	G ↔ A
Node D	528	1	1.00	C ↔ G
Node E	549	1	1.00	G ↔ A
Node F	435	1	1.00	A ↔ C
Node G	587	1	1.00	A ↔ G
Node H	128	1	1.00	T ↔ C
Node I	74	1	1.00	T ↔ C
	433	1	1.00	C ↔ G
Node J	434	1	1.00	C ↔ A
Node K	199	1	1.00	G ↔ T
<i>Strophostyles helvolus</i>				
(Fig. 4)				
Node L	253	1	0.50	T ↔ C
	484	1	1.00	C ↔ A
Node M	418	1	1.00	A ↔ C
<i>Strophostyles leiosperma</i>				
(Fig. 4)				
Node N	37	1	1.00	G ↔ A
	590	1	1.00	A ↔ T
Node O	70	1	1.00	T ↔ C
	115	1	1.00	T ↔ C
Node P	592	1	1.00	T ↔ C
Node Q	412	1	1.00	T ↔ C
Node R	253	1	0.50	T ↔ C
	494	1	1.00	T ↔ C
	636	1	1.00	T ↔ C
Node S	636	1	1.00	C ↔ G
Node T	499	1	1.00	G ↔ T
Note U	162	1	1.00	C ↔ G
	168	1	1.00	T ↔ C

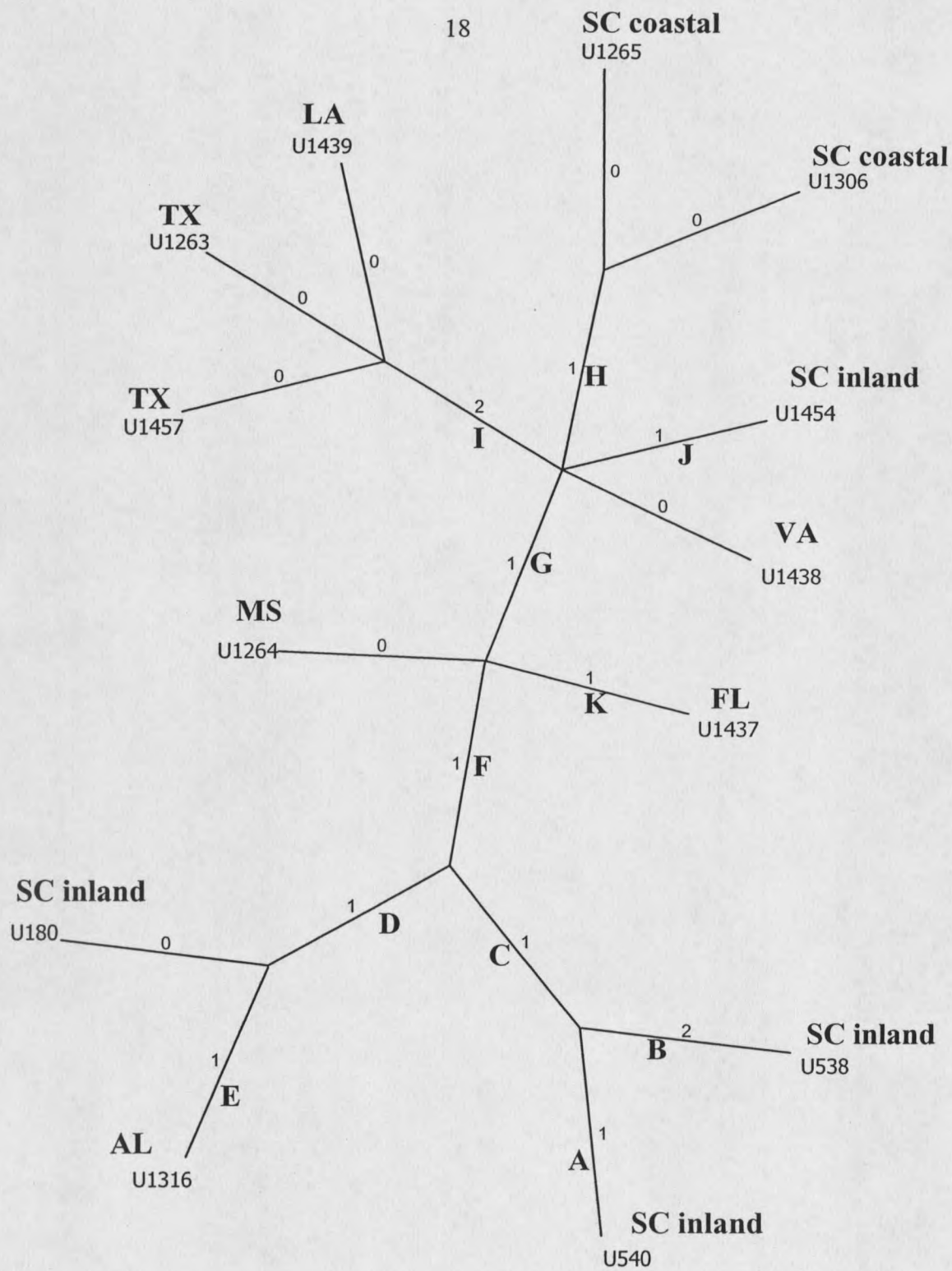


Fig. 3 Unrooted network of the *Strophostyles umbellata* accessions derived from parsimony analysis of the ITS region.

The unrooted network of ITS alleles taken from *S. leiosperma* reveals an intermediate amount of genetic variation, with seven alleles detected from a sample of 32 ITS sequences taken from across the geographic range of this species (Fig. 4). Notably, alleles from central to eastern Texas occupy central and peripheral positions in this unrooted network, suggesting an area of greatest allelic diversity in this species. In contrast to the other two species, the main allelic lineages sampled from *S. leiosperma* are separated from each other by multiple nucleotide substitutions (i.e., combined internodes O and U; Fig. 4). The terminally positioned alleles L1446 (Oklahoma), 197 (central Texas), 106 (New Mexico), and 1273 (Kansas) represent two alleles found in the western periphery of the range of *S. leiosperma*.

In contrast to the generally high intraspecific allelic diversity in *Strophostyles*, no heterozygous individuals were detected in this analysis (as inferred from double peaks on the sequence chromatograms). This result suggests that little allelic variation occurs within populations and that the great majority of variation is among populations. Certainly this result is expected for *S. helvolus* with only a total of four alleles detected from throughout its range in eastern North America. Little within population variation is expected for *S. leiosperma* given that self-pollination is commonly observed in this species and indeed this species was the only one to set flower and fruit in our greenhouse studies. Indeed, two nearby populations of *S. leiosperma* sampled from coastal Texas (L1453 and 1462; Fig. 4; Appendix A) revealed no within population allelic variation even though the two alleles detected were distinguished from each other by five

nucleotide substitutions. That no heterozygous *S. umbellata* individuals were detected is surprising given the high number of alleles found in a relatively small sample. Further sampling of this species is needed to verify if this indeed representative of a pattern of little within population allelic diversity.

Morphometric analysis

A total of 17 characters was determined to vary most among the species of *Strophostyles* and thus have greatest discriminating power for delimiting species. All but one of these varies quantitatively, and these are summarized in Table 5. The single qualitative trait, presence/absence of a cellular or waxy covering on the seed testa, was not used in the morphometric analysis. However, this trait was absent mostly in *S. leiosperma*. For example, 14 specimens of *S. umbellata* were observed with mature seed, and 13 of these possessed the cellular coating on the testa. Of the 38 specimens of *S. helvolus* observed with mature seed, 31 possessed the cellular coating. In contrast, 25 specimens of *S. leiosperma* were observed with mature seed, and only 8 of these possessed the cellular coating. Otherwise, such a seed trait has not been observed on any other New World Phaseolinae.

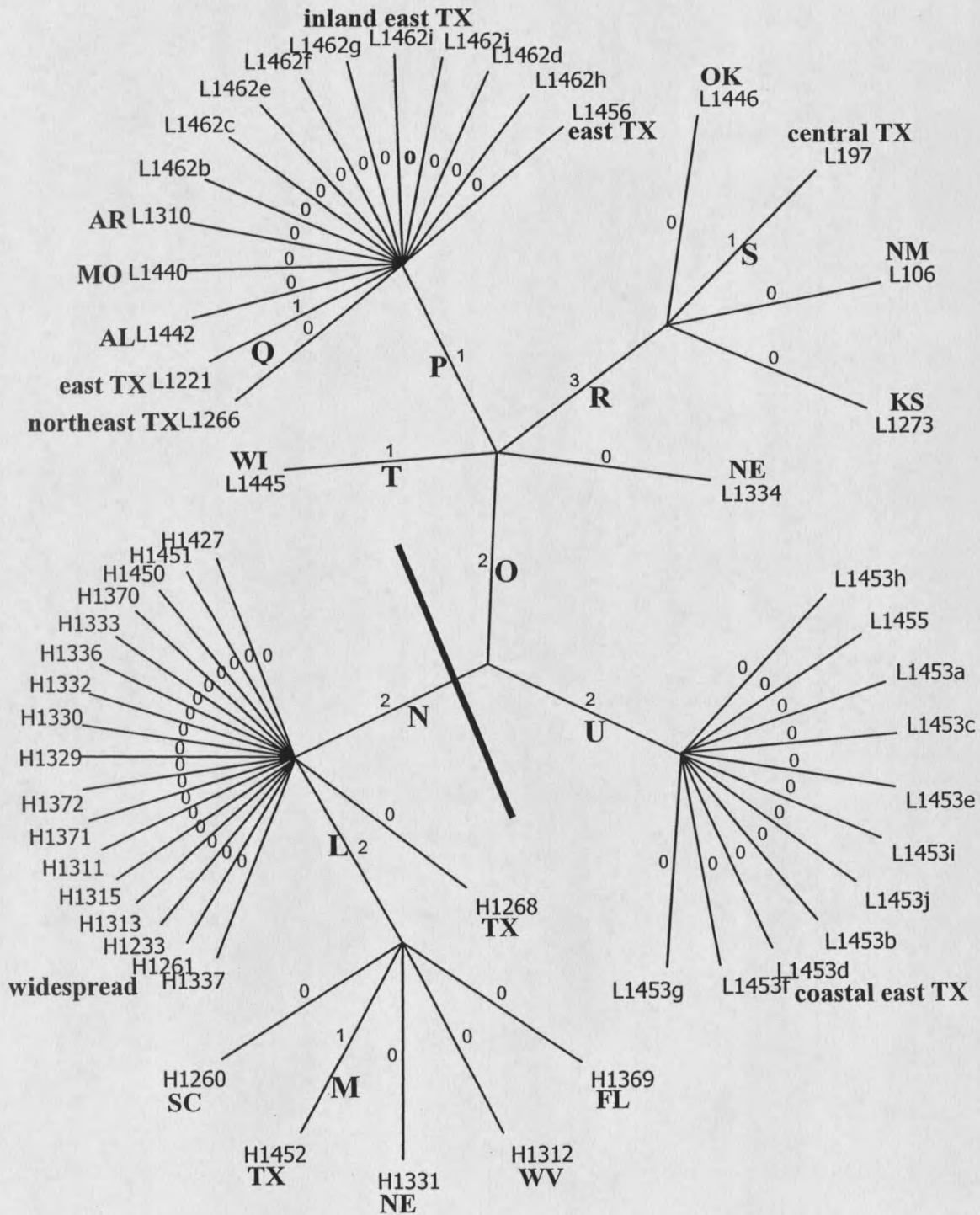


Fig. 4 Unrooted network of the *Strophostyles helvolus* and *S. leiosperma* accessions derived from parsimony analysis of the ITS region.

Table 5. Summary statistics for each of the 16 quantitative characters used in the morphometric analysis. 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=number of flowers per inflorescence, 10=calyx tube length, 11=bracteole length, 12=petal length, 13=number of ovules per ovary, 14=pod length, 15=pod width, 16=density of hairs on pod valve.

		character															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>S. umbellata</i>	n	146	146	146	146	146	145	144	138	138	130	129	114	41	44	38	45
	mean	29.0	10.4	24.9	10.0	0.4	2.7	2.7	133.2	3.2	2.5	1.5	10.2	8.9	42.5	2.9	4.7
	std	7.5	4.7	5.8	3.8	0.5	2.3	1.6	49.5	1.0	0.4	0.3	1.6	1.3	8.2	0.7	2.8
	max	70.0	21.8	40.4	27.0	1.0	13.0	10.0	300.0	6.0	4.0	2.1	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	1.0	1.6	0.8	7.3	6.0	26.0	2.0	0.0
<i>S. helvolus</i>	n	159	159	160	160	158	160	160	145	148	131	130	133	121	126	99	127
	mean	36.6	24.2	30.6	19.7	4.3	1.2	1.5	91.3	3.0	2.2	2.6	9.6	6.3	60.6	5.3	1.5
	std	11.0	8.3	9.5	6.9	4.1	1.0	1.4	37.3	0.9	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	215.0	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	1.0	1.3	1.1	6.7	5.0	30.2	3.0	0.0
<i>S. leiosperma</i>	n	120	120	120	120	120	120	120	111	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	1.3	1.6	1.3	5.6	5.3	26.4	3.7	10.0
	std	9.2	4.1	8.0	3.7	0.4	4.5	4.9	24.7	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	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	1.0	0.8	0.8	3.6	4.0	12.2	2.2	1.0

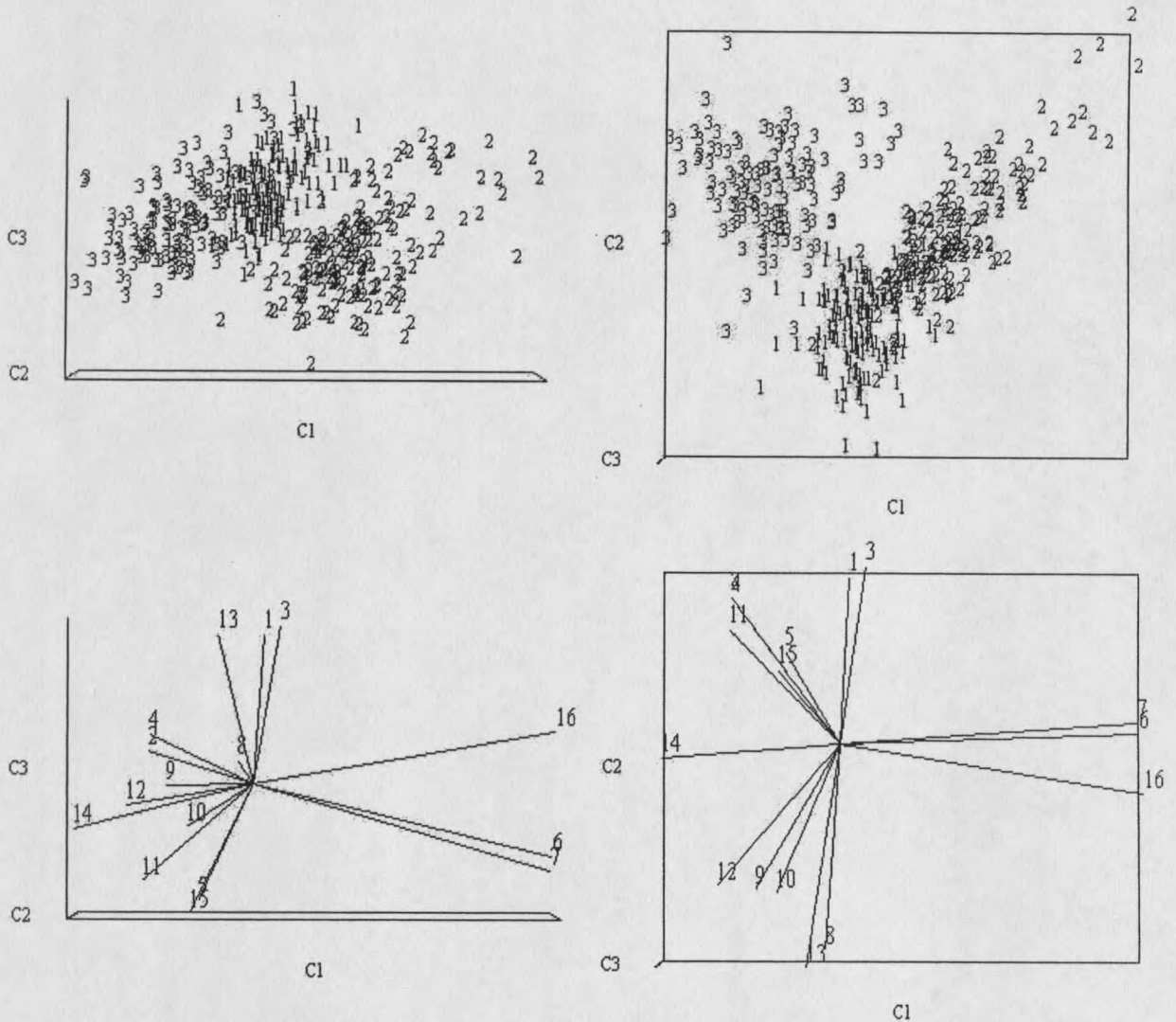


Fig. 5-8. Ordination of 426 herbarium specimens of *Strophostyles* along the three dominant eigenvectors, which captured 75% of variation for the total data set, 73% for the floral data subset, and 74% for the fruiting data subset. Figure is also located on disk.

Of the 16 traits that varied quantitatively (Table 5), the trends are as follows.

Leaflet length (characters 1 and 3) was generally the greatest in *S. helvolus*, whereas width (characters 2 and 4) was the narrowest in *S. leiosperma* (occasional Texas individuals of *S. umbellata* could have leaflets at the smallest end of the width scale). Lobed leaflets (character 5) was most pronounced only in *S. helvolus* (although some individuals entirely or in part possessed entire leaflets). Trichome density on the leaves

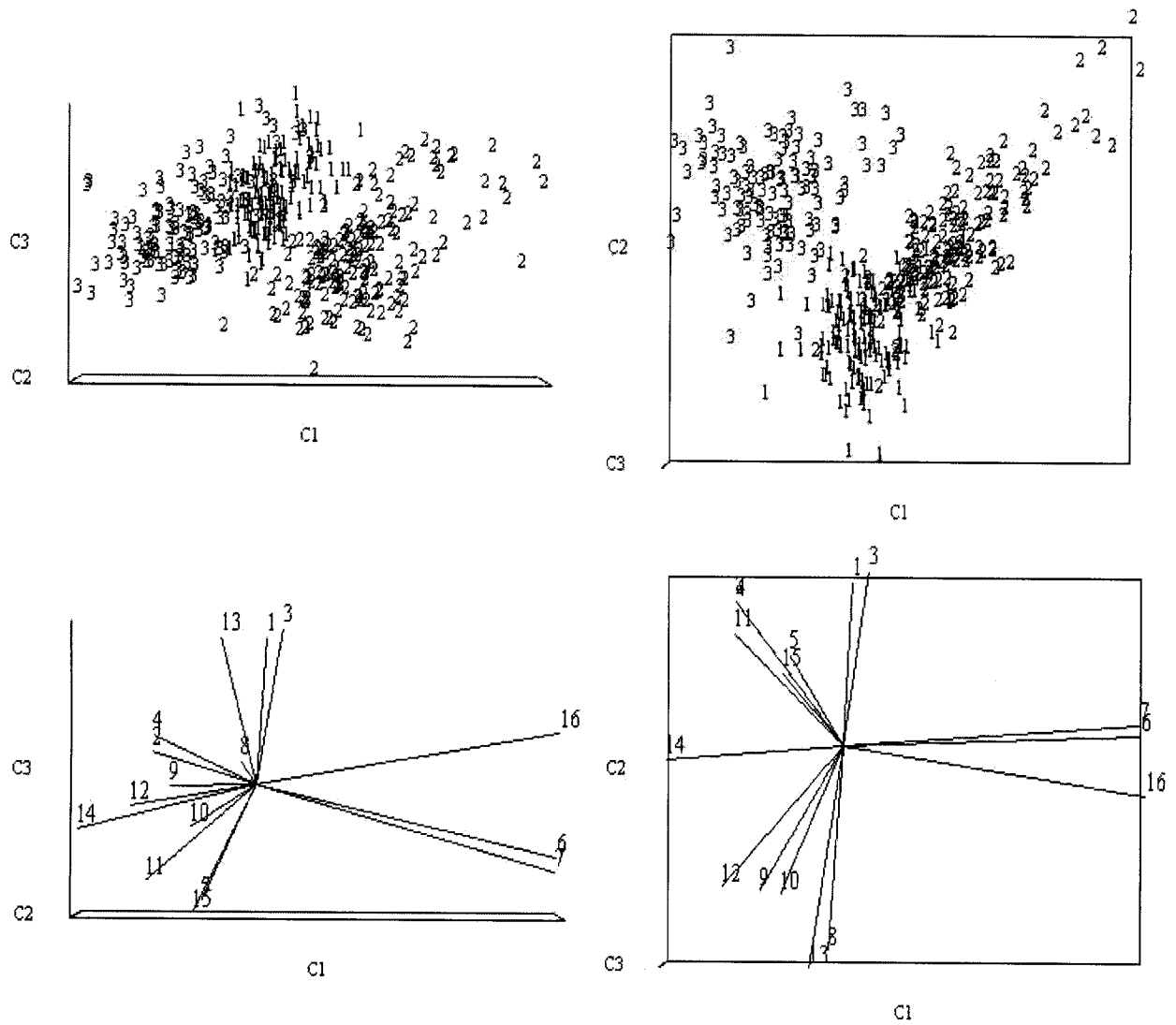


Fig. 5-8. Ordination of 426 herbarium specimens of *Strophostyles* along the three dominant eigenvectors, which captured 75% of variation for the total data set, 73% for the floral data subset, and 74% for the fruiting data subset. Figure is also located on disk.

(characters 6 and 7) was consistently highest among the accessions of *S. leiosperma*. The length of the inflorescence peduncle (character 8) was consistently the shortest (and narrowest in diameter) in *S. leiosperma*, as was the fewest number of flowers per inflorescence rachis (character 9). *Strophostyles umbellata* typically has a calyx tube surpassing the length of the subtending bracteole (characters 10 and 11), where as the other two species tend to have bracteoles equal to or longer than the calyx tube. The smallest flowers, including lengths of petals (character 12) are generally found in *S. leiosperma*. The number of ovules per ovary (character 13) tends to be greatest in *S. umbellata*. Pod length and width (characters 14 and 15) tend to be largest in *S. helvolus*. Although *S. leiosperma* tends to have the shortest pods, they also tend to be wider than those of *S. umbellata*. Finally, trichome density on pod valves (character 16) tend to be greatest in *S. leiosperma*, although some individuals of *S. umbellata* come close these high densities.

Ordination analysis of the above 16 quantitative traits reveals that the three species traditionally recognized in *Strophostyles* are phenotypically distinct. The first eigenvector (C1 in Fig. 5) arranges specimens with short hairy pods and hairy leaflets (see characters 6, 7, 14, and 16; Fig. 6) at one end (#3, *S. leiosperma*) and specimens with long glabrous pods and glabrous leaves at the other (#2, *S. helvolus*). The second eigenvector (C2 in Fig. 7) arranges specimens with generally short leaflets, few ovules per ovary, and long inflorescences (see characters 1, 3, 8, and 13; Fig. 8) from the base (#1, *S. umbellata*). The third eigenvector (Fig. 5) has somewhat less discriminating power, but still ordines specimens with lobed leaflets, short bracteoles, and wider pods (see character 5, 11, and 15; Fig. 9) from the base (Fig. 5; #2, *S. helvolus*).

Evolutionary rates analysis

The estimated rate of substitution for the sequences from the ITS region range from $3.3\text{--}8.5 \times 10^{-9}$ substitution per site per year using the penalized likelihood rate smoothing approach (Table 6). The rate constant estimate (LF; Table 6) suggests a rate at the higher end of this range, or 7.2×10^{-9} substitution per site per year. Indeed, the cross-validation approach implemented in the r8s program suggests a rate smoothing value (10^1) for the penalized likelihood approach that is much closer to rate constant than highly rate variable (e.g., as allowed by NPRS; Table 6).

The estimated rate of substitution for the sequences from the *matK* locus range from $4.7\text{--}6.9 \times 10^{-10}$ substitution per site per year using the penalized likelihood rate smoothing approach (Table 7), which is an order of magnitude slower than that estimated for the ITS sequences. The rate constant estimate (LF; Table 7) suggests a rate at the higher end of this range, or 6.6×10^{-10} substitution per site per year. The cross-validation approach suggests a rate smoothing value ($10^{1.5}$) for the penalized likelihood approach that is much closer to rate constant than highly rate variable, which is allowed by the NPRS approach (Table 7).

The age estimates derived from the rates analyses of these two sequences yield very similar results (compare Tables 6 and 7, Figs. 9 and 10). This is particularly true for the age of the *Strophostyles* stem clade, where an age of 18-19 Ma is estimated since this genus diverged from its sister South American genus *Dolichopsis*. The age of the diversification of the modern species of *Strophostyles* (i.e., the crown clade) is estimated

at pre-Pleistocene with ITS sequences (e.g., 5.4 Ma PL estimate) and post-Pleistocene (e.g., 2.3 Ma PL estimate) with *matK* sequences. Regardless of which sequence or what method of rate smoothing, the *Strophostyles* crown clade is significantly more recent in age compared to the stem clade. Indeed, the ages of the *Strophostyles* stem and crown clades are consistently much younger than the other major lineages within the New World Phaseolinae suggesting its cool temperate tolerance is a recent derivation in this otherwise predominantly neotropical legume clade.

Table 6. Rates analysis of ITS/5.8S sequences of New World Phaseolinae rooted against *Vigna* subgenus *Lasiospron*. Codes for the crown clades are those referred to in Fig. 10. PL = penalized likelihood rate smoothing, LF = rate constant rate smoothing, and NPRS – non-parametric rate smoothing. The first number in each box is the estimated age in Ma. The second number is the estimated substitution per site per Ma. Error estimates were made using a parametric bootstrap approach (Lavin et al. In press).

Crown clade	PL (10.0)	LF	NPRS
LASI	7.14 ± 0.85 0.00855 ± 0.00096	8.30 ± 0.90 0.00723 ± 0.00095	13.84 ± 2.05 0.01460 ± 0.00389
RAOX	26.53 ± 3.39 0.00449 ± 0.00076	19.58 ± 5.04 0.00723 ± 0.00095	28.97 ± 2.18 0.00640 ± 0.00181
PHVI	27.22 ± 2.50 0.00542 ± 0.00082	22.65 ± 3.96 0.00723 ± 0.00095	27.34 ± 2.43 0.00870 ± 0.00147
SPEC	26.56 ± 2.58 0.00501 ± 0.00057	20.14 ± 3.55 0.00723 ± 0.00095	26.83 ± 2.28 0.00796 ± 0.00102
STRO	5.44 ± 2.41 0.00332 ± 0.00067	2.47 ± 0.80 0.00723 ± 0.00095	11.91 ± 3.34 0.00278 ± 0.00069
STDO	19.41 ± 3.25 0.00386 ± 0.00055	11.87 ± 2.84 0.00723 ± 0.00095	22.14 ± 2.87 0.00466 ± 0.00095

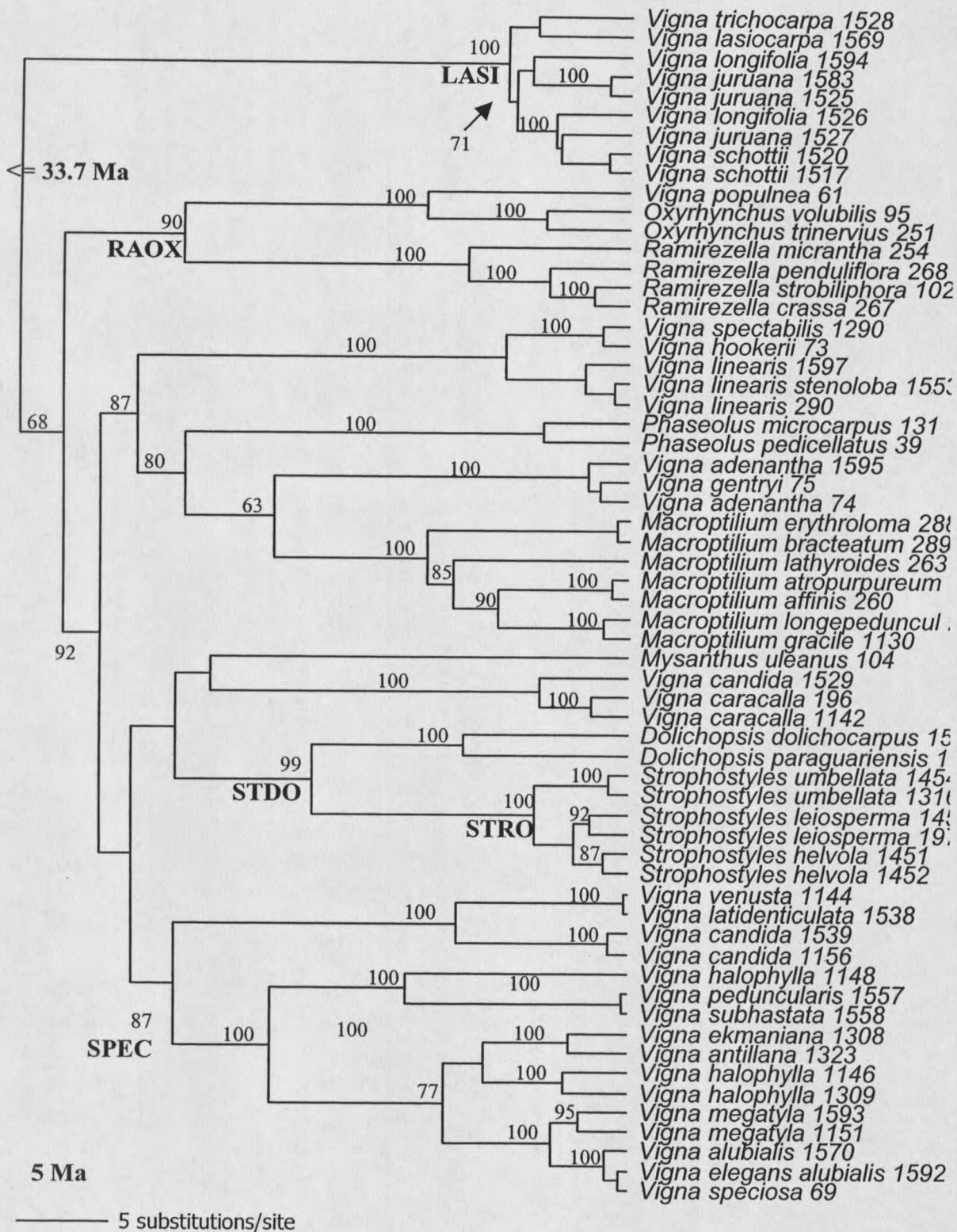


Fig. 9 Chorogram for New World Phaseolinae derived from penalized likelihood rate smoothing of a Bayesian likelihood tree, which was estimated with sequences from the ITS region.

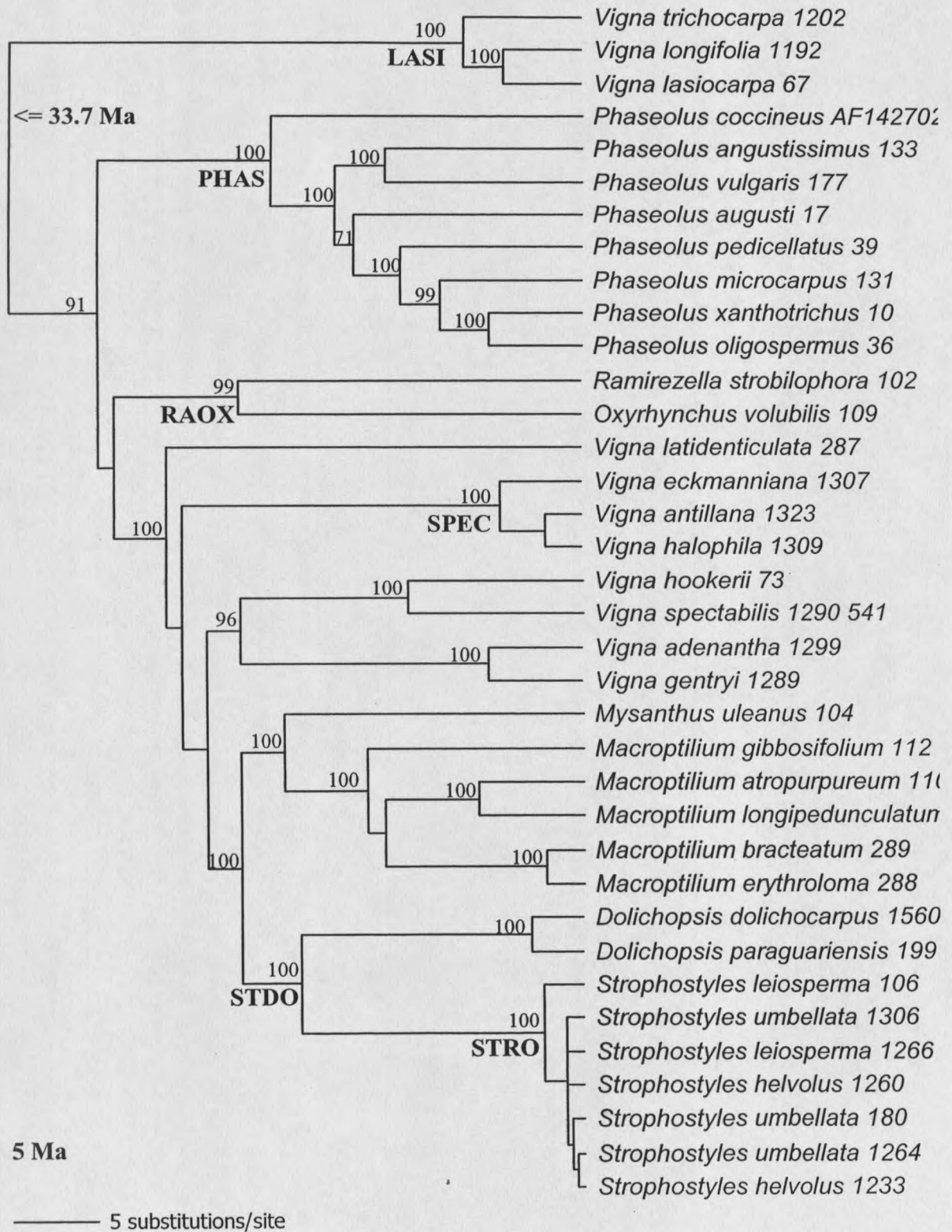


Fig. 10 Chronogram for all major clades of New World Phaseolinae derived from penalized likelihood rate smoothing of a Bayesian likelihood tree, which was estimated with sequences from the *matK* locus.

Table 7. Rates analysis of the cpDNA *matK* locus of New World Phaseolinae rooted against *Vigna* subgenus *Lasiospron*. Codes for the crown clades are those referred to in Fig. 11. PL = penalized likelihood rate smoothing, LF = rate constant rate smoothing, and NPRS = non-parametric rate smoothing. The first number in each box is the estimated age in Ma. The second number is the estimated substitution per site per Ma. Error estimates were made using a parametric bootstrap approach (Lavin et al. In press).

Crown clad e	PL (31.623)	LF	NPRS
LASI	7.19 ± 1.48 0.000687 ± 0.000089	7.37 ± 1.50 0.000658 ± 0.000060	10.41 ± 1.95 0.000900 ± 0.000165
PHAS	18.74 ± 2.01 0.000563 ± 0.000068	17.59 ± 2.16 0.000658 ± 0.000060	19.99 ± 2.03 0.000673 ± 0.000086
RAOX	20.79 ± 3.17 0.000528 ± 0.000092	18.44 ± 3.13 0.000658 ± 0.000060	22.42 ± 3.02 0.000576 ± 0.000104
PHVI	28.80 ± 2.25 0.000509 ± 0.000162	26.75 ± 2.88 0.000658 ± 0.000060	29.54 ± 1.78 0.000836 ± 0.000282
SPEC	25.10 ± 2.92 0.000474 ± 0.000082	22.36 ± 2.85 0.000658 ± 0.000060	26.26 ± 2.28 0.000684 ± 0.000140
STRO	2.32 ± 1.04 0.000693 ± 0.000105	2.33 ± 1.00 0.000658 ± 0.000060	5.15 ± 2.15 0.000818 ± 0.000182
STDO	17.96 ± 2.76 0.000682 ± 0.000098	16.98 ± 2.09 0.000658 ± 0.000060	19.38 ± 2.43 0.000946 ± 0.000168

DISCUSSION

Taxonomy.*Strophostyles*

Strophostyles Elliott, Sketch bot. S. Carolina 2(3): 229. 1823. Lectotype (Britton and Brown 1913): *S. angulosa* (Muhl. ex Willd.) Ell. [= *S. helvolus* [L.] Ell.].

Phaseolus Medik., Vorles. Churpfälz, Phys. Ökon. Ges. 2: 352. 1787. nom. rej. prop. Type: *P. roseus* Medik., nom. illeg. [= *Phaseolus farinosus* L. or *Strophostyles helvolus* (L.) Ell.]. *Strophostyles* was conserved over *Phaseolus* by the General Committee of the ICBN (Taxon 48: 377. 1999). See Verdcourt's (1997) original proposal 1299.

Phaseolus section *scandentes* L., Sp. pl. 723. 1753. Lectotype (here designated): *Phaseolus helvulus* L. [= *Strophostyles helvolus* (L.) Ell.]

Phaseolus section *Strophostyles* (Ell.) DC., Prodr. 2:394. 1825. *Phaseolus* section *Strophostyles* (Ell.) DC. subsection *Lobatifolii* DC., Prodr. 2:394. (1825). Type: *Phaseolus angulosa* Ortega [= *Strophostyles helvolus* (L.) Ell.]

Phaseolus section *Strophostyles* (Ell.) DC. subsection *Integrifolii* DC., Prodr. 2:394. 1825. Type: *Phaseolus helvolus* L. [= *Strophostyles helvolus* (L.) Ell.]

Phaseolus section *Strophostyles* (Ell.) DC. *emmend* Benth. Comm. Legum. Gen. 75. 1837. Type: *Phaseolus helvolus* L. [= *Strophostyles helvolus* (L.) Ell.]

Perennial and annual, slender flexible or wiry vines, trailing or climbing occasionally up to 2 m long on shrubs and trees, stems herbaceous, not woody, often

branching at lower nodes; plants variously pubescent (hairs not uncinata), sparse to densely short-pilose, the hairs retrorse in stems and flowering axis, except in 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 basisropic, 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 buds, 0-2 of which flower; pedicels short, thicken at fruit; bracts at base of peduncle present, often only in 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, striate, persistent through anthesis, often at fruit. Calyx campanulate, the hypanthium discrete; 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, banner often with yellowish maculae, the keel tip darkest, fading pale brownish yellow when dry; blade of the banner 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; 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 prow of the keel; keel-petals basally broad with a prominent bulge or lobe along the upper margin, usually with a longitudinal fold where adherent to the wing, gradually narrowed above this, the tubular apical portion, twisted. Stamens 10, vexillar stamen free bearing a fleshy callus about 1 mm from base, the others basally connate and distally free, length of filaments dimorphic; anthers uniform, sub-basifixed; pollen tricolporate, with micro-reticulate exine sculpture, endoapertures (pori) covered with pseudo-operculi. 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, distal portion introrsely bearded; stigma terminal and introrse; fruit 2-valved, mostly linear, straight or slightly curved, subterete to slightly laterally compressed (in *S. umbellata*), the valves separating along both sutures and twisting at maturity, 3-10-seeded, seeds longitudinally orientated; seeds spherical-plumpy or subquadrate, truncate at both ends, commonly covered with a cellular (waxy) layer; hilum oblongate covered with an epihilum, lens discernible. Seedlings with epigeal germination. Chromosome number, $n=11$ (Roy, Bera, and Sarkar, 1992).

Nomenclature

DeCandolle (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).

Diagnosis

DNA sequence data corroborates morphological evidence in revealing that the temperate *Strophostyles* is a monophyletic clade of three species that are collectively well distinguished from their closest relatives in the Neotropics. In a global context, *Strophostyles* is distinctive because of its confinement to temperate eastern North America in combination with its viney habit, trifoliate leaves, and flowers that deviate from bilateral symmetry because of a right-hand curvature of the keel rostrum. Such phenotypic traits are otherwise found in the Neotropics among the closest relatives of *Strophostyles* (*Vigna* subgenus *Sigmoidotropis*, *Phaseolus*, etc.). In the context of its closest relatives (i.e., *Dolichopsis*, *Macroptilium*, *Mysanthus*, and *Oryxis*), *Strophostyles* is apomorphically diagnosed by divergent stipules, persistent secondary floral bracts, a calyx with four acute to attenuate lobes, and seeds often with a waxy testa. These closest 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. The waxy or cellular coat on the seed testa is distinctive of most populations of *Strophostyles* and is otherwise found among New World relatives only in *Vigna latidenticulata*. This trait may be in part ecologically dependent. Individuals of *Strophostyles leiosperma* sometimes do not produce with waxy covering, at least more often than the other species do not. *Strophostyles leiosperma* also tends to inhabit drier and more open sites than the other two species of *Strophostyles*, which are more often located near water compared to *S. leiosperma*. This association suggests a possible role of the waxy coating in seed dispersal.

That *Strophostyles* is the sister genus of the South American *Dolichopsis* is not surprising in terms of morphology. Both genera have similar flowers in that the keel rostrum is only slightly curved to the right of the flower, and in the fused and gibbous (spurred) upper margins of the keel petals, just less than midway to the tip of the rostrum. The function of this spur is unknown. That the wing petals are adnate to the keel petals in this region suggests physical support perhaps during visitation by insect visitors that land on the wings. *Strophostyles* and *Dolichopsis* share with *Oryxis*, another South American genus but with a single species, a thickened distal end of the style that is jointed to the basal section, as well as a keel rostrum that is curved upward and to the right side of the flower, rather than hooked or coiled as in all other New World Phaseolinae. All three species of *Strophostyles* produce isorhamnetin glycosides, which are also found in some *Macroptilium* and *Vigna* subgenus *Sigmoidotropis*, but not *Dolichopsis paraguariensis*, one of two species in the genus analyzed for constitutive chemistry (Williams et al. 1995; Zalocchi et al. 1995; Pelotto and del Pero Martínez 1998). The production of isorhamnetin glycosides could be an apomorphy of *Strophostyles*, but this phytochemical trait is too inadequately surveyed among the New World *Vigna*, *Phaseolus*, and close relatives, in particular *Oryxis monticola* and *Dolichopsis dolichocarpa*, to state this definitively.

Biogeographical origins 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 traditionally perceived Holarctic relationships of the

Appalachian flora, namely one with tropical South American floras. The sister clade of *Strophostyles* is *Dolichopsis*, a genus confined to a relatively narrow region comprising the Chaco of Paraguay, Bolivia, Brazil (here called pantanal), and northeastern Argentina. *Oryxis*, endemic to Minas Gerais, Brazil (Delgado-Salinas and Lewis 1997), is sister to the *Dolichopsis-Strophostyles* clade (yet inferred from morphological evidence only). Of the remaining two genera closely allied to *Strophostyles*, *Mysanthus* is confined to Bahia and Sao Paulo, Brazil (Lewis and Delgado-Salinas 1994), and *Macroptilium* is widespread throughout the Neotropics. Thus, *Strophostyles* is nested within a clade that is predominantly tropical South American.

The evolutionary rates analysis of sequences from both the ITS and *matK* regions suggest that the age of the *Strophostyles* stem clade is on the order of 19 Ma. In contrast, the reports summarized by Wen (1999) show most northern hemisphere disjunctions involving closely related congeneric species with divergence ages estimated generally younger than 10 Ma. An exception to these young age estimates is that involving another legume genus, or the divergence of *Gymnocladus chinensis* and *G. dioica* at about 18 Ma (Schnabel and Wendel 1998). The 19 Ma estimate for the age of the *Strophostyles* stem clade might be common to legume groups showing temperate-tropical disjunction in the New World. Two species of *Sesbania* endemic to the southeastern portion of the USA (*S. drummondii*, *S. vesicaria*) each diverged from their tropical sister species perhaps at about the same time, as did *Strophostyles* (Lavin unpublished data). The stem clade that includes the four species of *Robinia*, a genus confined to temperate regions of the USA and mostly in Appalachia, could be as old as Late Eocene (33.7 Ma) according to fossil and evolutionary rates analysis (Lavin et al. 2003). Notably, the sister clade of *Robinia*,

the genus *Poissonia*, is also in tropical South America. In contrast, however, *Amorpha* with about a dozen species confined to the USA is very closely related to other temperate North American legume genera (Wojciechowski et al. unpublished data) and thus appears to be of recent origin. Similarly, the many other native legume species common to temperate eastern USA, such as species of *Acacia*, *Aeschynomene*, *Centrosema*, *Chamaecrista*, *Clitoria*, *Dalea*, *Desmanthus*, *Desmodium*, *Dioclea*, *Erythrina*, *Galactia*, *Indigofera*, *Mimosa*, *Phaseolus*, *Rhynchosia*, *Senna*, *Styphnolobium*, and *Tephrosia* (Isely 1990), have a tropical ancestry that is very likely post Pleistocene. This is inferred from the location of these genera primarily in the tropics and with only one to a relatively few species in each of genus being confined to eastern USA. In sum, the old disjunct pattern exemplified by *Strophostyles* could be exceptional for the flora of the eastern USA, although this needs to be verified with additional molecular phylogenetic studies.

The rates estimates from which was derived the 19 Ma age estimate of the *Strophostyles* stem clade are $3.3\text{-}8.5 \times 10^{-9}$ substitution per site per year for the ITS/5.8S region and 6.9×10^{-10} substitution per site per year for the *matK* locus. These rates are similar to estimates made for other angiosperms, including legumes (e.g., Richardson et al. 2001; Lavin et al. 2003), thus supporting the validity of the age estimates.

Constituent taxa

Several varieties have been formally recognized in the taxonomic and floristic literature of *Strophostyles* (see taxonomic synonymy, below). Morphometric and genetic analysis, however, revealed no distinctive infraspecific taxon. Thus, all previous infraspecific nomenclature and taxonomy is not used in this treatment.

The three species that have been most commonly recognized in the floristic and taxonomic literature, *Strophostyles umbellata*, *S. helvolus*, and *S. leiosperma* (e.g., Isely 1990), are also recognized in this study as distinct from each other and ranked at the species level. According to field observations and herbarium label data, *Strophostyles leiosperma* and *S. helvolus* are found together in certain localities, particularly in Texas. Similarly, *Strophostyles helvolus* and *S. umbellata* occur sympatrically in at least three states, Texas, Tennessee, and Virginia. No record exists of all three species at a single locality, or of sympatry between *Strophostyles leiosperma* and *S. umbellata*. Birds are reported to swallow the seeds of *Strophostyles* (Ridley 1990; D. S. Wiseman 1997; Bird and Bird 1931) and could thus serve as dispersal agents. Human activity, however, has been a major cause of sympatry, as inferred from label data and personal observations. Roadsides, pastures and lots, and railroad tracks or railroad stations are the most commonly reported or observed habitats. During the mid and late 1800's construction of railroads, seeds of *Strophostyles* were likely moved with ballast used as fill between the roadbed and the bottoms of crossties and sleepers. That railways crossed streams, rivers, and lakes, further influenced the spread of *Strophostyles*. In contrast to the usual perception of human influence on distributions of native species, all three species of *Strophostyles* have prospered with human activity.

The seeds of *Strophostyles* species are commonly covered with a waxy layer derived from the inner epidermis of the pod valve. No doubt this has some relationship to water dispersal because the waxy layer does provide buoyancy in laboratory tests, at least temporarily. Water is often associated with the habitat of all three species of *Strophostyles*, whether as inland fresh water (e.g., seasonally flooded basins or flats,

swamps, bogs), saline water areas (e.g., inland saline marshes, coastal and salty meadows), or human-made water 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; Ercikson and Young 1995). Notably, such habitat preference is the case also for *Dolichopsis*, the sister genus of *Strophostyles*.

Each of the three species of *Strophostyles* could have had an original allopatric distribution, as is implied by the intraspecific ITS networks: *Strophostyles umbellata* in the southern Appalachian region, *S. helvolus* in the eastern Great Plains, and *S. leiosperma* in the southcentral USA. Regardless, herbarium label data suggests that human-influenced habitat is common throughout the range of each species. That is, there is no pattern of populations within a region of genetic diversity being more likely to come from a habitat uninfluenced by humans. It is thus difficult to discern with habitat and geographical distribution data whether speciation initially occurred allopatrically.

In spite of sympatric distributions, there is very little evidence of gene flow among the three species. Remarkably, all three species bloom during the same season, and insects commonly visit the flowers and extrafloral nectaries for nectar (Foerste 1885; Robertson 1890; Krombein et al. 1979; Delgado-Salinas, personal observation). Floral visitors include wild bees of the genera *Bombus*, *Calliopsis*, *Chalicodoma*, *Heteranthidium*, *Megachile*, *Melissoides*, and *Nomia*. Visitors of extrafloral nectaries include wasps, bees, ants, flies, and beetles. Although it is uncertain if reproductive isolation mechanisms exist in this genus, putative hybrids are essentially unknown. Only

Isely (1990) mentions that two specimens were observed to have the lobed leaflets of *Strophostyles helvolus* and the short bracteoles of *S. umbellata*. Such specimens were not observed in this study possibly because more than these two characters were used to diagnose each of these two species (although these traits are two of the more informative). Regardless of whether reproductive isolation exists, the genetic and morphological evidence obtained in this study point to a long history of genealogical isolation of each of the three species. Recognizing three species under the phylogenetic species concept would not be insulted by the possible finding that a small amount of present day gene flow exists among certain populations from different species of *Strophostyles*.

The only potentially problematic species with respect to applying the phylogenetic species concept is *Strophostyles helvolus*. This is because this species is not distinguished by any DNA sequence apomorphies with respect to *S. leiosperma*. Regardless, *Strophostyles helvolus* is morphologically and chemically very distinct from *S. leiosperma*, and is distinguished in part by derived traits such as having the longest pods, lobed leaflets, and bracteoles longer than the length of the calyx tube. Such traits are not found in the other species of *Strophostyles* nor in the genera most closely related, *Dolichopsis* and *Oryxis* (Fig. 1), which have very short pods. In contrast to the findings in this study, *S. umbellata*, rather than *S. leiosperma*, has been thought to be the closest relative of *S. helvolus*, as determined by a combined analysis of morphology and phytochemical data (Pelotto and del Pero Martínez 1998). Given the derived characters shared by all populations of *Strophostyles helvolus*, and the conflicting data where combined morphology and phytochemistry point to a relationship different from that

suggested by ITS sequence data, the populations of *Strophostyles hevolus* are treated together as a single lineage and ranked at the species level.

Key to the Species of *Strophostyles*

1. Leaves and fruits with 0-13 hairs per mm²; banner petal 6.7-15.0 mm long at anthesis; keel petal with a prominently curved rostrum that protrudes upward just below to above the upper margin of the banner; pod (26.0) 30.0-96.1; inflorescence with a peduncle (23.5) 50.0-300.0 mm long, with (1) 2-6 flower-bearing nodes, upon fruit growth becoming stout, lignescent, and usually 1.0 mm in diameter or thicker; leaflets variably ovate to lanceolate to sometimes narrowly lanceolate, entire to deeply lobed.

2. Leaflets ovate-lanceolate to sometimes narrowly lanceolate, entire to rarely shallowly lobed, the sinus 0.0-1.0 mm deep, terminal leaflets (15.4) 20.0-40.0 (70.0) mm long by 2.0-21.8 mm wide; calyx tube (1.6) 2.0-4.0 mm long, bracteoles 0.8-2.1 mm long, generally shorter than the calyx

tube.....*Strophostyles umbellata*

2. Leaflets ovate to lanceolate, deeply lobed to entire, the sinus 0.0-18.2 mm deep, terminal leaflets 17.5-71.5 mm long by 8.5-46.2 mm wide; calyx tube 1.3-3.6 mm long, bracteoles 1.1-4.2 mm long, generally as long or longer than the calyx tube*Strophostyles hevolus*

1. Leaves and fruit with (1) 5-24 hairs per mm²; banner petal 3.6-7.0 (8.3) mm long at anthesis; keel petal with a slightly curved rostrum that protrudes upward but well below the upper margin of the banner; pod 12.2-40.7 mm long; inflorescence with a peduncle 11.5-110 (123) mm long, with 1-2 (4) flower-bearing nodes, upon fruit

growth remaining slender, herbaceous, and usually less than 1.0 mm in diameter;
 leaflets lanceolate, never deeply lobed, terminal leaflets 16.8-54.2 mm long by 2.2-
 22.6 mm wide..... *Strophostyles leiosperma*

Strophostyles umbellata

Strophostyles umbellata (Muhl. ex Willd.) Britton, in Britton & Brown, Ill. Fl. 2: 339.

1897. *Glycine umbellata* Muhl. ex Willd., Sp. Pl. 3: 1058. 1802. *Phaseolus umbellatus* (Muhl. ex Willd.) Britton, Trans. N.Y. Acad. 9: 10. 1889. TYPE - USA. Pennsylvania. Habitat in Am. boreali, *Muhlenberg s.n.* (holotype: B-Willd., photo!).

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: PHIL, 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!; isotype: GH!, PHIL, photo!, PHIL, photo!).

Glycine peduncularis Muhl. ex Elliott, Cat. Pl. Amer. Sept. ed. 1: 64. 1813.

Strophostyles peduncularis (Muhl. ex Elliott) Elliott., Sketch bot. S. Carolina 2(3): 230. 1823. *Phaseolus helvolus* sensu Torrey & A. Gray, Fl. N. Amer. 1(2): 280. 1838. *Phaseolus helvolus* sensu A. Gray, Manual, ed. 5: 140. 1867. TYPE - USA. Locality unknown. Muhlenberg Herbarium (holotype: not located). According

Weatherby (1942) the descriptions in Muhlenberg's *Catalogue* were prepared by Elliott.

Perennial from a slender taproot. Stems about 1-1.5 mm in diameter. Leaflets ovate-lanceolate to sometimes narrowly lanceolate, entire to rarely shallowly lobed, the sinus 0.0-1.0 mm deep, terminal leaflets (15.4) 20.0-40.0 (70.0) mm long by 2.0-21.8 mm wide, laterals, 15-40.4 mm wide by 3.0-27 mm wide; strigose, hairs 1-5 (13) per mm² on upper surface, 1-5 (10) per mm² on lower surface. Inflorescence with a peduncle (44) 60-300 mm, with (1) 2-6 flower-bearing nodes, upon fruit growth becoming stout, lignescent, and usually at least 1.0 mm in diameter. Calyx tube (1.6) 2.0-4.0 mm long, bracteoles 0.8-2.1 mm long, generally shorter than the calyx tube. Banner 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 a dark pink to purple tip. Ovary with 6-12 ovules. Pod cylindrical to slightly laterally compressed, (26.0) 30.0-63.9 mm long, 2.0-5.6 mm wide, with 5-10 seeds, valves glabrate to strigose, hairs (0) 3-13 per mm². Seeds sometimes faintly mottled at most, with or without a cellular covering. Chromosome number $x=11$ (Roy, Bera, and Sarkar, 1992).

Phenology

Throughout the range of this species, flowering specimens come from July, August, and September, rarely in June; fruiting specimens mostly from September and October.

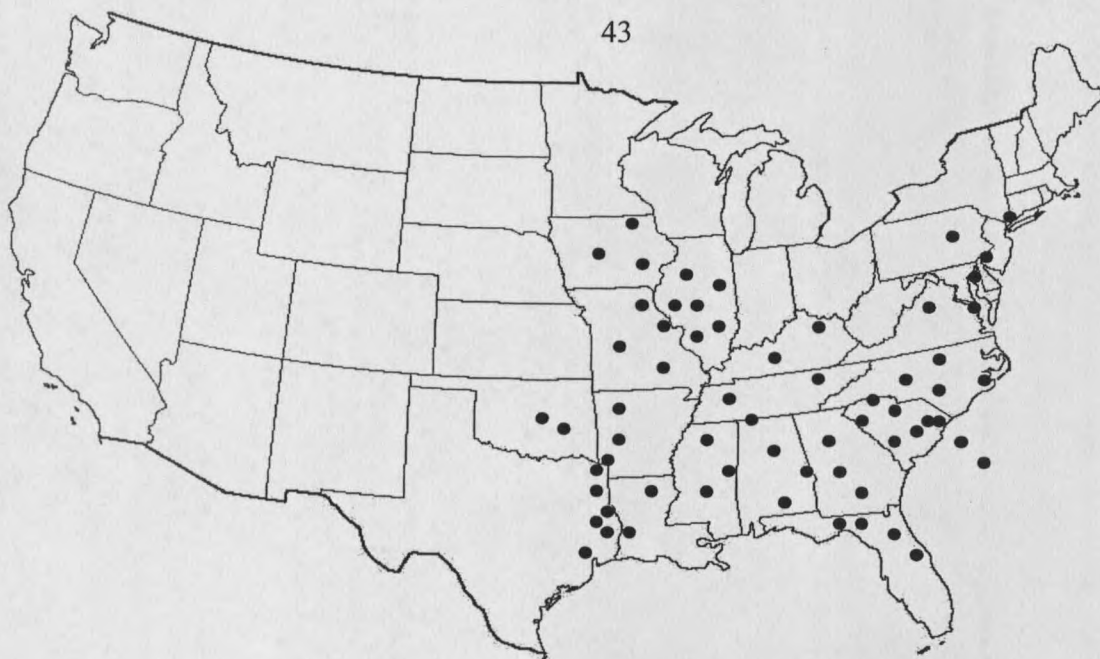


Fig. 12. Distribution of *Strophostyles umbellata*.

Distribution.

From southeastern Texas northwest to Nebraska and eastward from Pennsylvania south to Florida (Fig. 11); elev. 0-1500m.

Additional Specimens Examined

U.S.A. Alabama. Autauga Co.: between Swift and Whitewater, R. M. Harper 4465 (MO). Lamar Co.: 5.5 mi N Sulligent, R. Kral 33044 (MO). Conecuh Co.: 6.8 mi N Brooklyn, R. Kral 40981 (MO). Crenshaw Co.: E. of Georgiana, Patsulga Creek, R. Kral 88958 (USCH). Dozier, C. T. Reed 2027 (TEX). Lee Co.: "Sept. 12, 1948," S. P. Snow s.n. (TEX), "Sept. 19, 1948," S. P. Snow s.n. (TEX). 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); Fulton, B. F. Buch (MO), D. Demaree 21504 (MO), J. H. Kellogg s.n. (MO), E. J. Palmer 12655 (MO). Howard Co.: Baker Spring, J. H. Kellogg s.n. (MO). Lonoke Co.: Grand Prairie, D. Demaree 22447 (MO). Miller Co.: Texarkana, A. A. Heller 4155 (MO). Monroe Co.: Wheatley, D. Demaree 10907 (MO). Pairie Co.: Hazen, D. Demaree 15481 (MO); Devalls Bluff, D. Demaree 15538 (MO). Pope Co.: Nogo, G. M. Merrill 665 (MO). Pulaski Co.: Little Rock, D. Demaree 8168 (MO), D. Demaree 18280 (MO). Saline Co.: Benton, D. Demaree 23991 (MO), and J. M. Greenman 4309 (MO). Sevier Co.: Neal Springs, E. Brinkley 6 (MO). Union Co.: El Dorado, H. J. Ploch s.n. (MO). Washington Co.: no locality, J. H. Kimmons 6404 (MONT). Delaware. Rehoboth Beach, U. Fitchy 14 (MO). Rehoboth, pine woods, J. R. Churchill s.n. (MO). District of Columbia. Near Avalon Heights, F. Blanchard s.n. (MO), "11 Sept. 1891," F. Blanchard s.n. (MO). Dry banks, E. S. Steele s.n. (MO). Tacoma Park, Mell and Knopf s.n. (MO). Florida. "Hab. Florida," S. B. Buckley s.n. (MO). "1897," A. W. Chapman s.n. (MO). Gulf Coast, A. W. Chapman s.n. (MO). Leon Co.: N shore of Lake Iamonia, L. C. Anderson 12191 (MO); sandy pine woods at Silver Lake, N. C. Henderson 63-1245 (TEX); Bellair, G. V. Nash 2548 (MO); NE of Tallahassee, McCracklin Road, J. B. Nelson 1190 (USCH). Near Jacksonville, A. H. Curtiss 5788 (MO). Georgia. Thomas Co.: Wade Tract, R. R. Clinebell II 1334 (MO). Dougherty Co.: Flint River below Albany, R. M. Harper 1953 (MO). Oglethorpe Co.: 2 mi SE of Winterville, W. H. Duncan 11610 (MO). Bartow Co.: Allatoona Dam, W of Rowland Springs Church, W. H. Duncan 8708 (MO). Illinois. Lawrence Co., 1859, J. Q. A. Fritchey 229 (MO). Iowa. Sioux City, L. H. Pammel 19 (MO). Kentucky. Fulton Co.: Fulton, roadsides and dry fields, F. J. McFarland 172 (MO). Lincoln Co.: 2 mi N of

Ottenheim, M. E. Wharton 4878 (MO). Madison Co.: Berea outskirts, end of Harrison Rd., D. A. Johnson 283 (USCH). Louisiana. Calcasieu Parish: Lack Charles, S. M. Tracy 3476 (MO); vicinity of Lake Charles, K. K. Mackenzie 408 (MO). Caldwell Parish: just south 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). Maryland. Calvert Co. Chesapeake Beach, S. F. Blake 5342 (TEX), S. F. Blake 7059 (TEX), S. F. Blake 7165 (TEX); Scientists' Cliff, F. C. Seymour 24680 (MO). Salisbury, J. W. Chickering Jr. s.n. (MO). Cecil Co., B. M. Everhart s.n. (MO). Ocean City, U. Fitchy 1 (MO). 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), J. F. Joor 16-09-1891 (MO); Gulf Port, S. M. Tracy 170 (MO). Jackson Co.: Ocean Springs, J. Kershaw 195 (MO). Unknown Co.: Bond's Point, S. M. Tracy 4841 (MO). Unknown Parish: Louisiana, J. Gregg 1847 (MO). Missouri. Butler Co.: Poplar Bluff, Dewart 14-08-1892 (MO); old fields near Poplar Bluff, J. H. Kellogg 11-10-1937 (MO); 12 mi N of Poplar Bluff, N of Rombauer, J. A. Steyermark 11612 (MO). Camden Co.: E. of Ellis Ford, 2 mi S of Barnumton, J. A. Steyermark 6997 (MO). Carter Co.: 7 mi SE of Ellsinore, J. A. Steyermark 11726 (MO). Christian Co.: 2 mi S of Saunders, J. A. 23196 (MO). Crawford Co.: 5 mi W of Steelville, Mrs. J. A. Steyermark 02-10-1931 (MO). Between Davisville and Cherryville, J. A. Steyermark 19782 (MO). Dent Co.: Rhyse, old fields, J. H. Kellogg 994 (MO), J. H. Kellogg 14-08-1929 (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); 3.5 mi N of Brandsville, B. Summers 6388 (MO). Iron Co.: Pilot Knob, G. Englemann 20293 (MO); sandy ground, H. Eggert 15-08-1894 (MO); "N.E.," W. Trelease 209 (MO); eastern Iron Co., W. Trelease 210 (MO). Jasper Co.: Yalesburg, E. J. Palmer 3876 (MO). Jefferson Co.: sandy ground, H. Eggert 09-10-1896 (MO). Laclede Co.: Pine Creek Hollow, SW of Nebo, J. A. Steyermark 25172 (MO); tributary to Mill Creek, J. A. Steyermark 25190 (MO); 5 mi E of Lebenon, J. A. Steyermark 25217 (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). Phelps Co.: Jerome, J. Kellogg 200 (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); 5 mi E of Bonne Terre, F. Mazanec 17 (MO). Saint Louis City: St. Louis, G. Englemann 20262 (MO), G. Englemann 20296 (MO), G. Englemann 20297 (MO), G. Englemann 20342 (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); no locality, B. F. Bush 22-07-1891 (MO). Taney Co.: S of Hercules, J. A. Steyermark 22928 (MO). Texas Co.: near Roubidoux Cr., near Plato, J. A. Steyermark 25027 (MO). Unknown Co.: Spring Park, F. W. Dewart 94 (MO). New Jersey. Atlantic Co.: Atlantic City, J. H. Redfield 1631 (MO). Cape May Co.: 1935, J. A. Druskel 8120 (MO); sandy road, back of beach, E. H. Ludwig 456 (MO); Avalon, Seven Mile Beach, W. J. Langenheim 37 (MO). Ocean Co.: Barnegat Bay, J. R. Churchill 14-08-1892 (MO). Unknown Co.: "Aug," R. Perry s.n. (MO); Squan, W. Trelease s.n. (MO). North Carolina. Wake Co.: Sycamore Creek, G. P. Sawyer Jr. 1445 (USCH); Turkey Creek, G.

P. Sawyer Jr. 1513 (USCH). Durham, W. V. Brown s.n. (TEX). Rowan Co.: vicinity of Salisbury, A. A. Heller 37 (MO); Dunn's Mountain, J. K. Small s.n. (MO). 5 mi E of Chapel Hill, W. V. Brown s.n. (TEX). Wilson Co.: Little River, A. Patten 123 (TEX). Oklahoma. Le Flore Co.: near Page, at grassy edge of field, O. W. Blakely 3411 (MO); Talihina, pine and oak woods, F. W. Pennell 19389 (TEX). McCurtain Co.: 4 mi SW of Broken Bow, R. Stratton 584 (MO); 1 mi W of Tom, U. T. Waterfall 8048 (TEX). Pennsylvania. Lancaster Co.: Peach Bottom, 1887, A. F. Eby s.n. (MO); Peach Bottom, 1890, A. F. Eby s.n. (MO); Pleasant Grove, J. K. Small s.n. (MO). Hestonville, Philadelphia, J. H. Redfield 1632 (MO). South Carolina. Barnwell Co.: Savannah River Operation, 2.8 mi SW of Station No. 22, Batson & Kelley 499 (USCH); Bwl. State Park, C. L. Porter 101 (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, SW Edgefield, J. B. Nelson 17763 (MONT, USCH). Fairfield Co.: N of Ridgeway, T. Hulting 3040 (MONT). Georgetown Co.: Cat Island, Main Rd, J. B. Nelson 9724 (USCH); Sandy Island, J. B. Nelson 8489 (USCH); 12 mi S of Georgetown, J. B. Nelson 16,133 (MONT); N of Georgetown, G. W. Seckinger Jr. 346 (USCH); Waccamaw River, G. W. Seckinger 406 (USCH). Jasper Co.: Cypress Creek, WNW of Grays, C. A. Aulbach-Smith 2740 (USCH). McCormick Co.: McCormick, J. Davis s.n. (MO). Bradley, J. Davis s.n. (MO). Richland Co., Fort Jackson Army Installation: Combat 2 area, J. B. Nelson 11347 (USCH); Yankee Division Rd, J. B. Nelson 13426 (MONT, USCH); Fort Jackson Army Installation, A. B. Pittman 08089606 (MONT, USCH). Tennessee. Carroll Co.: Hollow Rock, H. Eggert 05-08-1897

(MO); Bruceton, R. E. Woodson Jr. 856 (MO). Knox Co.: sandy ground, Knoxville, A. Ruth 07-1896 (MO, TEX). Lewis Co.: Meriweather Lewis National Monument, old entrance, C. B. King 220 (TEX). Sumner Co.: Mitchelville, J. Eggert 17-08-1897 (MO). Texas. Angelina Co.: in open pinelands near Bouton Lake, D. S. Correll and I. M. Johnston 19653 (TEX - very narrow leaflets). Bowie Co.: near Texarkana, A. A. Heller 4284 (MONT); Texarkana, B. C. Tharp 2709 (TEX). Hardin Co.: S of bridge over Village Creek, SE of McNeely bridge road, W. R. Carr 10820 (TEX); in field, Silsbee, D. S. Correll 34945 (TEX); Kountze-Silsbee Rd., R. L. Crockett 1142 (TEX); 6 mi SW of Kountze on rd to Saratoga, B. C. Tharp 54931 (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), B. C. Tharp 2327 (TEX), and M. S. Young 1908 (TEX). Matagorda Co.: Bay City, banks of Peytons Creek, E. J. Palmer 9677 (TEX). Montgomery Co.: Willis, S. R. Warner s.n. (TEX). 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.: 1.5 mi E of Vidor, D. S. Correll 34240 (TEX); 6 mi SW of Vidor, D. S. Correll 36501 (TEX); 50 mi W of Galveston, T. Hulting 3004 (MONT). Polk Co.: 6.7 mi E of Corrigan, B. C. Tharp 54691 (TEX). San Augustine Co.: near Boykin Spring Camp, Angelina National Forest, 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.: 4 mi E of Mineola, J. A. Mears 860 (TEX). Virginia. Vinson Station, S. F. Blake 6999 (TEX). Clarendon, grassy fields, S. F. Blake 10659 (TEX). Gordonsville, F. Blanchard s.n. (MO). Fairfax Co.: W of Fairfax City, Braddock Rd., T. Bradley 21598 (USCH); Falls Church, Great Falls St., F. J.

Hermann 9603 (MO). Amherst, A. H. Curtiss s.n. (MO). New Kent Co.: SE of Windsor Shades, Shady Rest, M. L. Fernald & B. Long 12689 (MO). Isle of Wight Co.: Bailey's Beach, Burwell's Bay, M. L. Fernald & B. Long 13964 (MO). Arlington, W. Trelease s.n. (MO). Unknown state. G. Englemann 20341 (MO).

Strophostyles umbellata is consistently well resolved as the earliest branch within the *Strophostyles* clade. This clade is diagnosed apomorphically by ovate leaflets (rarely lanceolate) that are never deeply lobed, inflorescence with a stout long peduncle that bears 3-4 flower-bearing nodes at the distal end, pods generally cylindrical but occasionally laterally compressed, and bracteoles that usually extend the full length of the calyx tube or more in length.

Strophostyles helvulus (L.)

Strophostyles helvulus (L.) Elliott, Sketch bot. S. Carolina 2(3): 230 (1823). *Phaseolus helvulus* L., Sp. Pl.: 724. 1753. *Phaseolus helvulus* L. sensu Pursh, Fl. Amer. sept. 2: 470. 1813. *Dolichos helvulus* (L.) Nuttall, Gen. N. Amer. Pl. 2: 112. 1818. *Glycine helvula* (L.) Elliott, J. Acad. Nat. Sci. Philadelphia 1: 326. 1818. *Cajanus helvulus* (L.) Spreng., Syst. ed. 16, 3: 248. 1826. Non *Phaseolus helvulus* L. sensu Sessé & Mociño, *Plantae Novae Hispaniae* ed. 1. 117. 1888. ed. 2. 109. 1893. *Strophostyles helvola* (L.) Britton in Britton & Brown, Ill. fl. n. U. S. 2:338 1897. TYPE - USA. North Carolina, Biltmore, sandy flats, 19 Aug 1896, Biltmore Herbarium No. 1302 (holotype: US No. 966089 - see Verdcourt [1997] and Report of the General Committee: 8 [Taxon 48: 377. 1999]).

Phaseolus farinosus L., Sp. Pl.:724. 1753. TYPE.- India, collector unknown

(holotype: not located).

Phaseolus vexillatus Walters, Fl. Carol. 182 .1788. TYPE - USA. South Carolina.

Walters (holotype: BM, but not located).

Phaseolus angulosus Ortega, Nov. pl. descr. Dec. 2: 24.1797. TYPE - USA. [?], Bute,

D. Marchionissam s.n. (holotype possibly MA - there may be no authentic

herbarium specimen because this species was described from a living plant grown in the Royal Botanic Gardens of Madrid).

Glycine angulosa Muhl. ex Willd., Sp. Pl. 3: 1056. 1802. *Strophostyles angulosa*

(Muhl. ex Willd.) Ell., Sketch bot. S. Carolina 2(3): 230. 1823. *Strophostyles*

angulosa (Muhl. ex Willd.) A. Gray, Manual, ed. 6: 145. 1890. TYPE - USA.

"Habitat in Pennsylvania," *Muhlenberg s.n.* (lectotype: B, photo! - of the three specimens at Willdenow Herbarium, the one with two flowers at anthesis, sheet #1, is selected as lectotype).

Phaseolus trilobus Michaux, Fl. bor.-amer. 2: 60. 1803. Non *Phaseolus trilobus* Roth.

TYPE - USA. Carolina, *A. 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.

Strophostyles angulosa (Muhl.ex Willd.) A. Gray var. *missouriensis* S. Watson in A.

Gray, Manual, ed. 6, 145. 1890. *Strophostyles helvola* var. *missouriensis* (S. Wats.)

Britton, in Britton & Brown, Ill. fl. n. U.S. 2: 338. 1897. *Strophostyles*

missouriensis (S. Wats.) Small, Fl. S. E. U.S., 1st ed., 653. 1903. TYPE - USA.

Missouri. Jackson Co. "riverbottoms near Independence", *F. Bush* "Sept. 21"
(lectotype, designated by Ruff): GH!).

Phaseolus vexillatus Pursh, Fl. Amer. sept. 2: 470. 1813. Non *P. vexillatus* L., nec *P. vexillatus* Walter, nec *P. vexillatus* Michaux. TYPE – Locality and collector unknown (holotype: not located).

Perennial from a thick taproot. Stems about 1.0-1.5 mm in diameter. Leaflets ovate to lanceolate, deeply lobed to entire, the sinus 0.0-18.2 mm deep, terminal leaflets 17.5-71.5 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 mm² on upper surface, 0-5 (12) per mm² on lower surface. Inflorescence with a peduncle (23.5) 50.0-215.0 mm long, with (1) 2-5 flower-bearing nodes, upon fruit growth becoming stout, lignescent, and usually at least 1.0 mm in diameter. Calyx tube 1.3-3.6 mm long, teeth 1.0-2.5 mm long, bracteoles 1.1-4.2 mm long, generally as long or longer than the calyx tube. Banner petal 6.7-13.3 mm long, pinkish at anthesis; wing petals 7-9 mm long, light pink; keel petal 8-13 mm long with prominent dark purple tip. Ovary with 5-10 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, hairs 0-4 (7) mm². Seeds faintly mottled, generally with a cellular or waxy covering. Chromosome number $n=11$ (Roy, Bera, and Sarkar, 1992).



Fig. 14 Distribution of *Strophostyles helvolus*

Phenology

Flowering specimens come from July, August, September, and October; fruiting specimens mostly from July, August, September and October.

Distribution

From Quebec, Canada south to Florida, west to south Texas (and perhaps adjacent Tamaulipas, Mexico) and north to North Dakota (Fig.12); generally dense or extensive populations in fields and open understory; 0-1500 m.

Additional Specimens Examined

Canada. Quebec. *P. H. Hawkins* 34952 (MONT); Lonueuil, comté de Chambly, sur les

ravages du fleuve (Saint Laurent section alluviale), *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). U.S.A. Alabama. Baldwin Co.: next to salt marsh at Fort Morgan, *R. Kral 51301* (MO). Mobile Co.: Chaumont near Octavius, *R. Deramus D656* (MO); area just N of boundary of Old Air Force Base, *R. Kral 51376* (MO); sandy edge of salt marsh, W side of Dauphin Island, *R. Kral 47099* (MO).

Arkansas. Benton Co.: no locality, *J. H. Kimmons 6405* (MONT). Craighead Co.: ditch banks, *D. Demaree 25800* (TEX). Crittenden Co.: between Leuce and Mississippi River, W Memphis, *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 at Ark 69 bypass N of Batesville, *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.: sand bars, Arkansas River below Little Rock, *D. Demaree 8454, 8686* (MO). Searcy Co.: Maumee, *W. H. Emig 44* (MO). Sebastian Co.: Arkansas River, frequently flooded banks, *T. A. Thompson c0177* (MO). St. Francis Co.: Crowleys Ridge, *D. Demaree 21564* (MO). Stone Co.: rocky ridges, *D. Demaree 61018* (MO). Washington Co.: no locality, *D. Demaree 661* (MO). Connecticut. Hartford Co.: Southington, *C. H. Bissell 622* (MO). Middlesex Co.: salt marsh, Madison, *F. C. Seymour 29626* (MO); roadside not near salt water, *F. C. Seymour 23008* (MO). New London Co.: Groton, *K. P. Jansson s.n.* (TEX). Delaware. Sussex Co.: sand dunes on beach Rehoboth, *E. L. Larsen 437* (MO). District of Columbia: Washington, *F. Blanchard s.n.* (MO); Eckington rd, *F. Blanchard s.n.* (MO); Terra Cotta swamp, *T.*

Holm 171g (MO); river marsh, E branch of Potomac, *E. S. Steele s.n.* (MO); Chesapeake Beach, *A. Truth 47* (MO). Florida.: Bay Co.: adjacent to Reba Motel off US 98, E of Panama City in Parker, *J. B. Nelson 990* (USCH). Duval Co.: banks of St. John's River, *A. H. Curtiss 15552* (MO); low beach area near mouth of river E of East Mayport, *J. W. Hardin 326* (TEX). Escambia Co.: *S. Orzell 12423* (USCH). Okaloosa Co.: Eglin Air Force Base, 0.6 mi E of rte 85 on rte 232 at Turkey Creek, *J. S. Miller 9091* (MO). St. Johns Co.: between Matanzas and Marineland, *R. K. Godfrey 70655* (TEX); St. Augustine Beach, *J. B. Nelson 695* (USCH); Jacksonville, *A. H. Curtiss 4251* (MO); Rivershore near Jacksonville, *A. H. Curtiss 5764* (MO). Walton Co.: along rte 20 ca. 2 mi E of Cilla Tesso along Choctaw Beach, *J. S. Miller 9159* (MO). Unknown Co.: no locality, *S. B. Buckley s.n.* (MO). Georgia. Bartow Co.: about 4.5 mi SE of Adairsville on Cassville Mountain, *P. Greear 64283* (TEX). Cherokee Co.: on south side of Etowah River, *W. H. Duncan 8782A* (MO). Floyd Co.: Rome, *A. W. Chapman s.n.* (MO). McIntosh Co.: near S end of Sapelo Island, *W. H. Duncan 20593* (TEX). Illinois. Adams Co.: along railroad near Coatsburg, *R. A. Evers 591* (MO); Mill Creek, 4 mi SE of Quincy, *R. Brinker 1265* (TEX). Bureau Co.: sand beaches, Dover Bay, *L. D. Stain s.n.* (MO). Jackson Co.: on Illinois Central railroad near Carbondale, *J. McMree Jr. 1142* (MO). Kankakee Co.: Altorf Island in Kankakee, *O. E. Lansing 4* (MO); near Kankakee, *J. M. G. 3545* (MO). Knox Co.: Galesburg, *J. Solomon 1115* (MO). Lake Co.: Lake Forest, *M. C. Jensen s.n.* (MO). LaSalle Co.: Starved Rock, *F.H.Thone 159* (MO). Macon Co. Decatur, *O. S. Knight 25* (MO). Madison Co.: Mississippi in Venice, *H. Eggert s.n.* (MO). Madison Co.: *H. Eggert s.n.* (MO). Mason Co.: Bath, *V. H. Chase I0008* (TEX). Peoria Co.: sandy bottom bank of Illinois river, Peoria, *F. E.*

McDonald s.n. (UC). St. Clair Co.: bottomland NE, *H. Eggert s.n.* (MO); Cahokia, *F. Wisligeuus 92, 93* (MO); Cahokia, *E. Daughua s.n.* (MO); Cahokia, *A. S. Hitchcock s.n.* (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). Unknown Co.: no locality, *C. A. Geyer 20288* (MO). Indian fossil, *G. Engelmann 20275* (MO). Fish Lake, *A. S. Hitchcock s.n.* (MO); Fish Lake, *L. H. Pammel s.n.* (MO); Graceland, *L. H. Pammel s.n.* (MO). Indiana. Cass Co.: sandy ridge about ¼ mile S of Lake Cicott, *R. C. Friesner 10118* (UC). Clark Co.: no locality, *L. M. Umbach 28070* (MONT). Porter Co.: dunes of Lake Michigan, Chesterton, *J. R. Churchill s.n.* (MO). Unknown Co.: margin of Cabinet River, *H. H. Smith 5769* (MO); Millers, *A. Sandig s.n.* (MEXU). Iowa. Davis Co.: Salt Creek Township, *A. Hayden 11313* (MO). Decatur Co.: sandy soil, *L. P. Anderson s.n.* (MO). Dickenson Co.: in sand shore of Spirit Lake, *R. I. Cratty s.n.* (MO). Mahaska Co.: on a sand ridge 2.5 mi NW of Eddyville, *D. W. Augustine 433b* (TEX). Story Co.: 1 mi W of Hickory Grove Lake along bank of small stream, *G. Davidse 1989* (MO); sandy ground, *A. S. Hitchcock s.n.* (MO). no locality, *P. Barker s.n.* (TEX). Henry Co.: Mt. Pleasant, *J. H. Mills 530* (MO). Story Co.: Ames, *L. H. Pammel 18* (MO). Johnson Co.: sandy prairie along railroad W of rivers of Iowa City, *B. Shimek s.n.* (TEX). Unknown Co.: hills of Iowa, *B. Hwarnoch 20652* (TEX). Kansas. Riley Co.: Manhattan, *W. A. Kellerman s.n.* (MO); sandy soil, *J. B. Norton 119* (MO); no locality, *Waugh s.n.* (MO). Wyandotte Co.: common in the bottoms of the big rivers, *K. K. Mackenzie 2968* (MO). Unknown Co.: waste ground, *R. Hoffman s.n.* (MO). Kentucky. McCracken Co.: banks of Ohio River, *D. Demaree 31507* (TEX). Trigg Co.:

dry gravel creek terraces at Hematite Lake in the Land Between the Lakes, *R. Athey 1489* (MO). Warren Co.: near Barren River, roadside, *S. F. Price s.n.* (MO). Louisiana. Ascension Parish: along US 61, 0.2 miles N of its junction with I-10, at the intersection of US 61 and LA 3140, *A. W. Lievens 3263* (MEXU). Caldwell Parish: Corps of Engineers picnic area and boat launch area, *R. D. Thomas 107475* (MO). Cameron Parish: no locality, *W. Q. C. Holmes 4723* (TEX). Franklin Parish: along west bank of Boeruf River, S of La. 4 at Caldwell Parish line, *R. Dale Thomas 77524 & 1483* (MEXU). East Baton Rouge Parish: along edge of woods beside Perkins rd at Quail Dr., along first 0.3 mi of Quail, *R. D. Thomas 138602* (MO). Orleans Parish: Orleans, vacant lot on S side of Claiborne St. just W of Napoleon St. in New Orleans, *R. D. Thomas 123551* (MO). no locality, *J. Pruski 2116* (TEX). Red River Parish. along west bank of Red River S of US 84 Bridge at Coushatta, *R. D. Thomas 114908* (USCH). St. John The Baptist Parish: no locality, *A. Lievens 4489* (MO). Unknown Parish: Morehouse, along E bank of Ouachita River about 2 mi N of the mouth of Bayou Bartholomew, *R. D. Thomas 132384* (MO); Isle a Pitre, *Tracy and Lloyd 199* (MO); Breton, *Tracy and Lloyd 197* (MO). Maryland. Calvert Co.: Scientists' Cliffs, *F. C. Seymour 17505, 24679* (MO). Prince Georges Co.: dry sandy soil, 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); 1/4 mi W of Havre de Grace, *G. H. Shull 174* (MO). Worcester Co.: plants of Assateague Island North Beach National Seashore, *S. R. Hill 15519* (MO). Unknown Co.: along the upper Marlboro, *E. T. Wherry 12407* (MO). Massachusetts. Dorchester Co.: The 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. Unknown Co.: 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.: Long Beach, *J. F. Joor s.n.* (MO); Biloxi, *Persoon 4842* (MO); Biloxi, *S. M. Tracy s.n.* (MO). Jackson Co.: Oceansprings, *D. Demaree 31304* (MO). Unknown Co.: Big Lake, *D. Demaree 7085* (TEX). Missouri. Adair Co.: Kirksville, *G. S. S. s.n.* (MO). Boone Co.: abundant in field NW of Round Pools, Columbia, *F. Drouet 72* (MO). Butler Co.: Poplar Bluff, *Dewart s.n.* (MO). Cass Co.: woods and roadside, *H. Eggert s.n.* (MO); bottoms of Janes Creek, *no collector* (MO); woods beside Polk Bayou at Ark 69 bypass N of Batesville, *s.n.* (MO). Clark Co.: 0.5 mi SE of Wayland, Upper Mississippi River section of Big Rivers Natural Division, *T. E. Smith 3125* (MO); 0.5 mi S of Wayland, *T. E. Smith 3129* (MO). Clay Co.: in low woods along Missouri River, *K. K. Mackenzie s.n.* (MO). Dade Co.: Bona Glade Natural Area, 1 mi W of Bona, *R. D. Collett 370* (MO). Dallas Co.: along Nisngus River, 2 mi SW of Windyville, *J. A. Steyermark 13736* (MO). Daviess Co.: 7 mi SE of Pattonburg, *T. E. Smith 3230* (MO). DeKalb Co.: dried lake bed along CRI and PRR between Clarksdale and Bayfield, *J. A. Steyermark 14939* (MO). Dent Co.: dry sand bed of Little Pine Creek just W of confluence, *J. A. Steyermark 25462a* (MO). Dunklin Co.: Campbell, *B. F. Bush s.n.* (MO). Franklin Co.: Meramec State Park, *D. V. Darigo 988* (MO). Franklin Co.: Gray Summit, *J. H. Kellogg 992* (MO); Engelmann woods NW side of road 0.5 mi S of St. Albens, *M. S. Taylor 5535* (MO). Gasconade Co.: low ground along Gasconade river near Gasconade, *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). Jackson Co.: common here, *B. F. Bush* 43 (MO). Jasper Co.: along railway, Duenweg, *E. J. Palmer* 778 (MO); Galesburg, *E. J. Palmer* 3876 (MO); Joplin, *E. J. Palmer* 789, 892, 4362 (MO). Jefferson Co.: in Walden, *H. Eggert s.n.* (MO); The Cedars, Barnhart, *J. M. Greenman* 4471 (MO). Johnson Co.: base of ravine in Cave Hollow between old and new cemetery near Warrensburg, *J. A. Steyermark* 24576 (MO). Lewis Co.: bordering wooded area 3 mi E of La Belle, *J. A. Steyermark* 25688 (MO); slopes along Middle Fabine river 4 mi NE of La Belle, *J. A. Steyermark* 25747 (MO). Lincoln Co.: King's Lake, *J. H. Kellogg s.n.* (MO); alluvial ground at N end of King's Lake near Apex, *J. A. Steyermark* 8937 (MO). Marion Co.: W Hannibal, *J. Davis* 6240 (MO); Hannibal, *J. Davis* 9060 (MO); abandoned field 1 mi SW of Hannibal, *J. A. Steyermark s.n.* (MO). McDonald Co.: dry ground, *B. F. Bush* 15761 (MO); 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.: 6.5 mi S of Versailles on rd B at Gravois Creek, edge of sandbars, *D. Castaner* 4277 (MO); 1.7 mi S of Florence on rd BB, *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); no locality, *J. Davis* 6194 (MO). Pike Co.: Eolia, *J. Davis* 3175, 6282 (MO). Ralls Co.: sandy flats near Oakwood, *J. Davis* 9185 (MO); Oakwood, *J. Davis* 668, 7304 (MO); Hannibal, *J. Davis* 6398 (MO); W of Hannibal, *J. Davis* 1347 (MO). Randolph Co.: Mt. Airy, *G. Engelmann s.n.* (MO). Reynolds Co.: North Fork of Webb Creek, along gravel bars at edge of creek, *R. Jensen s.n.* (MO). Schuyler Co.: Trebel's Cove Conservation Area, *C. E. Darigo s.n.* (MO). St.

Charles Co.: SE edge of trail near old railroad, *C. E. Darigo s.n.* (MO); Near Old Monroe, *J. Davis 3176* (MO); Spur dike access rd, rte 67 by New Lock and Dam 26 on Mississippi, *L. J. Raechal 47* (MO); 6 mi NW of St. Charles, *J. A. Steyermark 9245* (MO); low alluvial meadow between St. Peters and St. Charles, *J. A. Steyermark 7123* (MO); along Mississippi river, directly across from Alton, *G. H. Zhu 1401* (MO); Riverlands Environmental Demonstration Area, *G. H. Zhu 1217* (MO); E side of Osage River, *J. A. Steyermark 24345* (MO). St. Francois Co.: near creek crossing Silver Springs rd about 2 mi W of old hwy 67, *J. Saunders 1042* (MO). St. Genevieve Co.: St. Genevieve, *W. Trelease 1008* (MO). St. Louis Co.: Fern Glen, *A. Christ 128* (MO); no locality, *H. Eggert s.n.* (MO); railroad near Valley Park, *H. Eggert s.n.* (MO); Hazelwood, *no collector 804* (MO); Fenton, *F. S. Wolpert 636* (MO); Creve Couer Lake, *F. S. Wolpert 152* (MO); vicinity of St. Louis, *H. Eggert s.n.* (MO); Cliff Cave, *H. Eggert s.n.* (MO); no locality, *G. Engelmann 20286* (MO); St. Louis, *G. Engelmann 20284* (MO); Hills S of St. Louis, *G. Engelmann 20263* (MO); Forest Park, St. Louis, *G. H. M. Goehring s.n.* (MO); no locality, *W. Webster & J. M. Greenman 3793, 3795* (MO); S of St. Louis, *J. H. Kellogg s.n.* (MO); Meremac Highlands, *J. H. Kellogg s.n.* (MO); Allenton, *M. C. Lodewyks 39* (MO); Allenton, *J. H. Kellogg s.n.* (MO); railroad sites city of St. Louis, *V. Muehlenbach 363* (MO); W of Kings hwy, *V. Muehlenbach 715* (MO); E of right of way of Missouri Pacific railroad, *V. Muehlenbach 363* (MO); E of right of way of the manufacturers railway, *V. Muehlenbach 381* (MO); large open area between the right of way on the Missouri Pacific and Frisco railroad, *V. Muehlenbach 394* (MO); Fairlawn, *O. S. Redman 8* (MO); woods on Pseudo Island at junction of Missouri and Mississippi, *J. A. Steyermark 19710* (MO); alluvial banks of S channel of

Missouri river, *J. A. Steyermark 8993* (MO); sand dunes near mud cracks on Pseudo island, *J. A. Steyermark 19715* (MO); Creer Cover Lake, *R. E. Vaughn s.n.* (MO); railroad track banks, in SW St. Louis, *J. A. Steyermark 8248* (MO). Taney Co.: 3.5 mi NNE of Forsyth, *T. E. Smith 2977* (MO); Osage Prairie, *Y. Chang 648* (MO). Wood Co., no locality, *C. G. Broadwater s.n.* (MO). Taney Co.: Swan, *B. F. Bush 767* (MO); Jackson Co.: Courtney, *B. F. Bush 7786a* (MO); no locality, *B. F. Bush 30, 1857, 7743, 7791* (MO); Meremac highlands, *A. Chandler 2816* (MO); Skinkers Moon, *H. Eggert s.n.* (MO); Beach Island, *G. Engelmann 20274* (MO); Webster, *J. M. Grossman 4008* (MO); Jefferson Barracks, *L. H. Pammel s.n.* (MO); Jeefer, Mayne, *W. Trelease 8120* (MO); Little Rock, *without collector* (MO); river bottom, *without collector* (MO).

Nebraska. Cass Co.: Lower Cornish Island, *J. L. Morrison 1355* (MO). Cuming Co.: 3 mi S of West Point on hwy 275 and 1/4 mi E, *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, meadows 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.: sea beaches, *K. K. Mackenzie 1150* (MO); New Brunswick, *J. A. Drushel 9570* (MO). Ocean Co.: Chadwick, *K. K. Mackenzie 2392* (MO); no locality, *A. L. Moldenke 26110* (TEX); Toms River, *A. L. Moldenke 29117* (MO); sand dunes, Lavallette, *A. L. Moldenke 28086* (TEX); Bay Head, *L. H. L. s.n.* (TEX). no locality, *H. V. Anaz s.n.* (MO). Union Co.: Garwood, *J. A. Drushel 6900* (MO). Monmouth Co.: Spring Lake, *J. A. Drushel 7753* (MO). Unknown Co.: Seashore Avore, *L. H. L. s.n.* (TEX). North

Carolina. Brunswick Co.: marshy roadside on Long Beach, *J. Stevenson 3399* (USCH).
 Burke Co.: meadow on rte 1913 ca. 1 mi E of Pleasant Grove, *H. E. Ahles 58775*
 (USCH). Dare Co., on sandy beach near sound of Lost Colony, Roanoke I., Radford &
 Stewart 819 (UC). Ohio. Hamilton Co.: Sandy bank, *B. C. Stephenson s.n.* (MO).
 Lorain Co.: edge of sand dune, Lake Erie beach, Oak Point, Black River Township, *G. T.*
Jones 73-9-9-1223 (MONT). Clermont Co.: Cincinnati, *C. G. Lloyd s.n.* (MO).
 Oklahoma. Attawa Co.: no locality, *B. F. Bush 15771* (MO); no locality, *B. F. Bush*
15776 (MO). Cleveland Co.: shaded ravine 5 mi E of Norman, *G. J. Goodman 2032*
 (MO). Comanche Co.: moist silty soil, Medicine Park, *R. Stratton 27* (TEX); vicinity of
 Fort Sill, *J. Clemens 11644* (MO). Grady Co.: South Canadian River Floodplain, 6 mi E
 and 2.7 mi N of Tuttle, *R. Pearce 971* (TEX). Lincoln Co.: 5 mi NE of Harrah, roadside,
P. DeLozier 1636 (MO); sandy bank 5 mi S of Chandler, *R. Stratton 544* (MO). Major
 Co.: Samduspo 14 mi NE Seiling, *R. Shatton 473* (MO). Marshall Co.: along strand of
 Lake Texoma, *J. Williams 462* (MEXU, TEX). Osage Co.: sandy bank of Coon Creek,
G. W. Stevens 2159 (MO). Payne Co.: 4 mi SE of Stillwater, *L. Dorr 86* (TEX);
 Stillwater, *J. P. Hollis 39* (TEX); 2 mi N of Stillwater, *T. H. King 83* (TEX); 4 mi SE of
 Stillwater, *M. Ladd 14* (MONT); Stillwater, *R. Stratton 196* (MO); Stillwater, *Waugh*
s.n. (MO). Pottawatomie Co.: no locality, *F. A. Barkley 1429* (MO). Stephens Co.:
 sandy soil along Dry creek, 7 mi SW of Comanche, *W. F. Mhaler 1278* (TEX). Tulsa
 Co.: roadside, Tulsa, *G. E. Tenney s.n.* (TEX). Pennsylvania. Bedford Co.: railroad
 bank 1/8 mi E of Bedford Station, *D. Berkheimer 5401* (UC). Forest Co.: Tionesta
 Township, along Allegheny River, gravel bar along edge of river, *B. L. Isaac 5396*
 (MEXU). Rhode Island. New Port Co.: Tiverton, *J. M. G. 1705* (MO). South Carolina.

Anderson Co.: road between Pendleton Place Apts. and landfill entrance, *S. R. Hill* 18790 (USCH). Beaufort Co.: St. Helena Island 1 km W of Harbor River on rte 21, *D. E. Boufford* 23097 (MO); along dead end road, N of US 21 on west side of Hunting Island, *J.W. Leonard & A. E. Radford* 1958 (MEXU). Charleston Co.: KOA campsite, Mt. Pleasant, *E. T. Riley-Hulting* 3024 (MONT); vacant lot on Omni Blvd, Mt. Pleasant, *D. Cothran* 7 (MONT); S side of Sec 94 about 3 mi E of jct with hwy 171, *J. B. Nelson* 6126 (USCH); Isle of Palms, *J. N. Pinson* 230 (USCH). Fairfield Co.: W side of S-35 just E of Broad River and S of Sec 213, *J. B. Nelson* 8388 (USCH). Georgetown Co.: edge of marsh on oceanside of Beach rd about 1 mi N of its terminus on S Island, *J. B. Nelson* 11140 (MONT); docks at Sampit Rivers side of Georgetown, *J. B. Nelson* 14641 (MONT); SE edge of Georgetown at Winyah Bay near Municipal Recreation Complex, *J. B. Nelson* 19556 (USCH). Horry Co.: dunes near Waiter Island, *J. N. Pinson* 401 (USCH). Jasper Co.: sand dunes, *R. Stalter s.n.* (USCH). Newberry Co.: hwy 176 at Duncan's Creek, *C. N. Horn* 1342 (USCH). Pickens Co.: East Toe Bottoms, *C. L. Rodgers* 69959 (MO). Richland Co.: -Saluda River, Columbia river front park, *M. R. Polkowsky* 67 (USCH); Rose Island, SE Island going W to E, *A. B. Pittman* 9140015 (USCH); no locality, *J. Nelson* 22202 (USCH). York Co.: Extension of rte 73 at Kirkpatrick Branch 1.3 mi S of Sec 97, *C. N. Horn* 6107 (USCH). Sumter Co.: Ft. Sumter, *R. Stalter s.n.* (USCH). South Dakota. Grant Co.: 3 mi S of Vermillion near Bigstone Lake, *P. Johnson* 81 (MO). Unknown Co.: Dakota, *N. M. Glatfelter* T.4 (MO). Tennessee. Wilson Co.: sandy gravelly quarry by US 231 just N of entrance of Cedars of Lebanon Park, S of Lebanon, *R. Kral* 56479 (MO). Knox Co.: Knoxville, *A. Ruth s.n.* (MO). Texas. Anderson Co.: Palestine, *B. C. Tharp s.n.* (TEX); along rte 256 E of

Palestine between rte 79 and 48 in wet meadow, *D. S. Correll 31758* (TEX). Aransas Co.: Rockport, *V. L. Cory 45350* (TEX); slope between high bank and water of E Bay, Aransas Wildlife Refuge, *R. J. Fleetwood 9328* (TEX). Bastrop Co.: Bastrop State Park, *D. S. Correll 17419* (TEX); Collected on Piney Creek, *H. H. Duval. 476* (MEXU, TEX); Piney Creek growing near water, *H. Duval s.n.* (TEX); 30 mi W of Austin along hwy 290 turn off on hwy 71 along Old Potato rd, *E. T. Riley-Hulting 3010* (MONT); railway below Butler, *B. C. Tharp s.n.* (TEX); Elgin, *E. Whitehouse 128d* (TEX); west-facing hillside along old road from Wilbarger Creek to brick kiln, ca. 1 mile upstream from Colorado River NW of Bastrop, *B. Ertter 4866* (TEX, MEXU). Bell Co.: sandy terrace of Leon R. W of old site of Tennessee Valley Church, Lake Benton, *C. G. York 55135* (TEX). Brazoria Co.: Brazoria Refuge, *R. J. Fleetwood 9564* (TEX); parking lot behind bldg on Velascost Angleton, *R. J. Fleetwood 9352* (TEX); W shore of San Luis pass, *H. Hildebrand 24* (TEX). Brazos Co.: along the Navasota River near Democrat Bridge, *D. S. Correll 36384* (TEX); College Station, *R. W. Strandman 662F* (TEX). Burnet Co.: moist granitic gravel at edge of lake, Inks Lake State Park, *J. R. Crutchfield 2305* (TEX). Crawford Co.: Colony, 35 (MO). 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.: 1.75 mi 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.: sandy soil, Tehuacana Creek, *B. L. Turner 3145* (TEX); no locality?, *W. Cholmes 187* (TEX). Galveston Co.: Galveston Island State Park, *R. J. Fleetwood 10504* (TEX); Galveston, *J. Reverchon s.n.* (MO); no locality?, *E. T. Riley-Hulting 3012* (MONT); Patton, *B. C.*

Tharp s.n. (TEX); Galveston ID., *S. M. Tracy 7784* (TEX); 5 mi W of Galveston at air base, *B. L. Turner 3151* (TEX); N of Texas City Dike ca 7 mi ESE of Texas City, *F. R. Waller 3026* (MO). Gonzales Co.: Ottine, *E. Whitehouse s.n.* (TEX). Grayson Co.: edge of Lake Texoma, *D. S. Correll 33629* (TEX); hwy 75, 5 mi N of Denison and 1/6 mi S of Red River, *V. L. Cory 54803* (TEX); sandy field SE of Perrin Air Base Recreational Area, *H. Gentry 511343* (TEX); gravel of spillway channel of Lake Texoma, *M. Nee 44062* (TEX). Harris Co.: Sims Bayou, *E. Boon 283* (TEX). Hemphill Co.: Gageby creek 10 mile E, 1 mi N of hwy 83 on farm market 277, *R. DeArment 3* (TEX). Henderson Co.: 2.5 mi SE of Athens on Farm rd, *D. S. Correll 32054* (TEX). Jackson Co.: Lavaea River, *B. C. Tharp s.n.* (TEX). Jefferson Co.: Beaumont, *Hooks s.n.* (TEX); Beaumont, *B. C. Tharp s.n.* (TEX); Sabine Pass, *R. W. Strandman s.n.* (TEX); no locality, *B. C. Tharp 3143* (TEX). Karnes Co.: banks of San Antonio River, between Conquista Crossing and Farm-to-Market Rd., *M. C. Johnson 1612* (TEX). Kaufman Co.: sandy post oak woods near Mabank, *C. L. Lundell 9583* (TEX); disturbed prairie beside Terrell outlet Mall, *R. D. Thomas 146127* (MO). Lamar Co.: seepage and sandy stream on east edge of Direct, *D. S. Correll 37936* (TEX); 1/3 mi E of Chicotah, *V. L. Cory 54669* (TEX). Laredo Co.: Laredo, Rio Grande river, *E. Palmer 263* (K). Lee Co.: *M. Knobloch s.n.* (TEX). Llano Co.: lower S slope of Enchanted Rock, *M. Butterwick 3052* (TEX); Enchanted Rock, *M. Butterwick 3377* (TEX); along the Llano river 7 mi E of Llano, *D. S. Correll 17307* (TEX); gravel hills, *G. Engelmann 20287* (MO); Enchanted Rock, *B. C. Tharp s.n.* (TEX). Mason Co.: Flat Rock, *V. L. Cory 43043* (TEX). McLennan Co.: East Waco, *L. D. Smith 666* (TEX); old field north of Childress Creek clay, *L. D. Smith 969* (TEX); Gaphead rd, *L. D. Smith 75* (TEX).

Montgomery Co.: Houston, *F. Lindeheimer s.n.* (MO); Willis, *S. R. Warner 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.: 300 ft N of Glen Oak Dr. from a point W of
 Laguna Shores rd, *W. R. Carr 16869* (TEX); Mustang Island, far south end, *T. Gillespie*
277 (TEX). Parker Co.: Mineral Wells State Park, *B. L. Lipscomb 2409* (TEX). Polk
 Co.: 1.6 mi W of Sandy Creek on hwy 190, *B. Ertter 5204* (TEX). Presidio Co.: Marfa,
W. P. Taylor s.n. (TEX). Rusk Co.: no locality?, *D. Correll 33978* (USCH). Smith Co.:
 hwy 271 near Sabine River SE of Gladewater, *D. L. Wilkinson 393* (MO). Tarrant Co.:
 Lake Worth, *D. Timmons s.n.* (TEX). Travis Co.: Austin, E Quadrangle, *W. R. Carr*
4536 (TEX); along N bank of Colorado river 100-500 ft W of rte 183 bridges, Austin, *W.*
R. Carr 3434 (TEX); 1st knoll E of Garfield on hwy 71, *J. A. Mears 1014* (TEX).
 Walker Co.: Harmon Creek, 7 mi NW of Huntsville on rte 19, *D. S. Correll 31967*
 (MO); 7 mi NW of Huntsville on rte 19, *D. S. Correll 31967* (TEX). Washington Co.:
 Brenham, *C. C. A. s.n.* (TEX); no locality, *E. Brackett s.n.* (TEX). Woods Co.: pine
 land, Lake Ellis 5 mi. NE of Crow, *C. L. Lundell 11739* (TEX); Golden, *E. McMullen*
s.n. (TEX); no locality, sandy banks, *J. Reverchon 258* (MO); Timbalier, *B. C. Tharp*
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.: base of seeping argillaceous and calcareous bluffs along Burwells Bay, James
 River, *M. L. Fernald & Long 13965* (MO). Kurn Co.: sandy soil, *A. Ruth 334* (MO).
 Lancaster Co.: on beach, windmill point, *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.: Roland Park, *F. A. Gilbert 365* (MO);

roadside near Depot Milton, *L. Williams* 533 (MO). Monongulia Co.: *W. Grafton* s.n. (USCH). Wisconsin. Crawford Co.: dry sand plain, *N. C. Fassett* 4399 (MO). Grant Co.: wooded bluff near summit, *N. C. Fassett* 17901 (MO). Pepin Co.: Maiden Rock, *N. C. Fassett* 17902 (MO); lower sand terrace, *N. C. Fassett* 4400 (MO); Lake Pepin; *T. J. Hale* s.n. (MO). Lacrosse Co.: Lacrosse, *S. D. Swanson* 2177 (MO).

Strophostyles helvolus is very closely related to *S. leiosperma*, as suggested by the analysis of ITS sequence data only. This phylogenetic analysis suggests that *S. leiosperma* was derived from within a *S. helvolus* gene pool. *Strophostyles helvolus* is, however, apomorphically diagnosed by its leaflets that tend to be wider than those of the other two species and often with a lateral lobe, a keel rostrum with a prominent right-hand curve, and long cylindrical pods. Furthermore, the morphometric analysis and a combined analysis of secondary chemistry and morphology (Pelloto and del Pero Martínez 1988) both suggest that *Strophostyles helvolus* is very distinct from the *S. leiosperma*.

The paraphyletic assemblage of ITS sequences representing *Strophostyles helvolus* suggests that *S. helvolus* could have given rise to *S. leiosperma*. Such a putative finding has long precedence in the biosystematic literature (e.g., Gottlieb 1973 and 1974). Viewing *Strophostyles helvolus* as the founding species for *S. leiosperma*, however, is problematic because of the limited genetic diversity detected in this species that contrast to the much greater amount detected in *S. leiosperma*. Indeed, a broad range across eastern North America combined with little genetic variation is indicative of a recent and rapid range expansion of *Strophostyles helvolus* rather than it being a relictual species.

harboring ancestral genetic polymorphisms. That no ITS heterozygotes were detected in *Strophostyles helvolus* (as evidence by double peaks in sequence chromatograms) is not surprising given that only four alleles were detected from throughout its range in eastern North America.

Strophostyles leiosperma

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, *Dr. Leavenworth s.n.* (lectotype, designated by W. F. Ruff in herb., NY! - in Torrey Herbarium).

Phaseolus pauciflorus Benth., Comm. Legum. Gen. 76. 1837; non Don (1832); nec Dalzell (1851). *Strophostyles pauciflora* (Benth.) S. Watson in A. Gray, Manual, ed. 6: 146. 1890. TYPE - USA. Texas. 1835. *Drummond s.n.* (holotype: K!, isotypes: K!, K!).

Strophostyles pauciflorus (Benth.) 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).

Annual from a slender taproot. Stems about 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 mm² on upper surface, (1) 4-24 per mm² on lower surface. Inflorescence with a peduncle 11.5-110.0 (123.0) mm long, with 1-2 (4) flower-

bearing nodes, upon fruit growth remaining slender, herbaceous, and usually less than 1.0 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. Banner 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 except for the dark purple tip. Ovary with 4-9 ovules. Pod cylindrical, 12.2-40.7 mm long, 2.2-4.5 (5.2) mm wide, with 3-8 seeds, valves usually sericeous, hairs (1) 5-24 per mm^2 . Seeds often distinctly mottled, commonly without a cellular or waxy covering.

Chromosome number uncertain.

Phenology

Flowering specimens come from July, August, and September; fruiting specimens mostly from September.



Fig 16. Distribution of *Strophostyles leiosperma*

Distribution

From Louisiana westward through Texas, northward to Kansas and Illinois, and sporadically west to New Mexico and Colorado [where in northern Mexico, Alfonso???] (Fig. 13); scattered to dense populations in dry open areas or open understory; 100-1500 m.

Additional Specimens Examined

U.S.A. Alabama. Baldwin Co.: Ft. Morgan, *R. Kral* 51304 (MO). Bullock Co.: edge of farm pond by US 29 2 mi S Union Springs, *R. Kral* 33124 (MO). Arkansas. Bradley Co.: Banks, *D. Demaree* 23875 (MO). Craighead Co.: dry banks on Crowleys Ridge, *D. Demaree* 26564 (TEX); Jonesboro, *D. Demaree* 3716 (MO). Poinsett Co.: edge of dry woods, *T. Heineke* 3231 (MO). Sebastian Co.: Snakepit Lake, Sec 12 T7N R31W, *R. D. Thomas* C0733 (MO). Union Co.: between road and Ouachita River just N of Felsenthal Dam, *R. D. Thomas* 102675 (MO, USCH). Unknown Co.: most grassy places at thickets, valley of the Little Marnelle, *Torrey & Gray* 1025 (MO); near Fort Man, *A. Fendler* 133 (MO). Colorado. Baca Co.: south banks of Cimarron River SE corner of county, *W. Weber* 5168 (TEX, UC). Yuma Co.: bluffs of Arikaree River, 8 mi NE of Idalia, *W. Weber* 12963 (TEX). Florida. Franklin Co.: Apalachicola, *A. Chapman* s.n. (MO). Unknown Co.: no locality, *S. B. Buckley* s.n. (MO). Illinois. Hancock Co.: Augusta, *J. B. Mead* s.n. (MO). Johnson Co.: Parker, *H. C. Benke* 5230 (UC). Madison Co.: Madison W of State Street, *V. Muehlenbach* 4268 (MO); Oldenburg, *F. E. McDonald* s.n. (UC). Menard Co.: Athens *I. W. Clokey* 45 (MO; UC); St. Clair Co.: Mississippi, *H. Eggert* s.n. (MO); on moist bank of terrace between the line of limestone

bluffs and bluff lake near Palling springs, *J. A. Steyermark 611* (MO). Washington Co.: Ashley, *F. Beckwith 30* (MO). Unknown Co.: *J. B. Mead 1078* (MO); *G. Vasey 1633* (MO). Iowa. Black Hawk Co.: sandy soil, high prairie, *M. Burk 903* (MO). Boone Co.: ledges, *L. H. Pammel 1807* (MO). Davis Co.: 1 mi W of Floris on the Hill Culture Experimental Farm, sandy banks of Lick Creek, *A. Hayden 9946* (MO). Dickenson Co.: along a sandy pit bordering Miller's Bay, Lake Okoboji, *A. Hayden 4060* (MO). Louisa Co.: Muscatine Island, *B. Shimck s.n.* (TEX). Johnson Co.: Iowa City, *A. S. H. 18* (MO); plants of Iowa state gallery of agriculture, *J. H. Pammel 1804* (MO). Kansas. Barber Co.: vicinity of Kiowa along road 9 mi NW of town, *P. A. Rydberg 642* (MO). Edwards Co.: sandy ground, *A. Finch 90* (MO). Reno Co.: 9.5 mi N, 0.5 mi W of Sylvia, property of Esther Smith on E side of Sylvia Rd., *C. A. Morse 4057* (USCH). Riley Co.: sandy soil, *J. B. S. Norton s.n.* (MO); Manhattan, *W. A. Kellerman s.n.* (MO); Manhattan, *J. B. S. Norton s.n.* (MO). Kentucky. Unknown Co.: Mickliffe, *F. T. McFarland 190* (MO); Louisiana. Ouachita Parish: Monroe, E of saline bayou N of LA 156 at Natchitoches Parish line, E of Goldonna, *R. D. Thomas 102898* (MO). Red River Parish: *Dr. Hale s. n.* (NY). St. Tammany Parish: S of jct of rte 11 and 41 off hwy 11, *K. Rogers 1511* (MO). Minnesota. Anoka Co.: sand dunes west side of 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). Unknown Co.: Cat Island, *S. M. Tracy 7783* (TEX). Missouri. Adair Co.: Kirksville, *C. S. Sheldon 2019* (MO, UC). Boone Co.: prairie pasture 3 mi E of Stephens Sta., *F. Drouet 795* (MO). Butler Co.: Poplar Bluff, *G. W. Dewart 39* (MO); on hwy 158, just W of Harviell, *S. Hudson 139* (MO). Callaway Co.: upper slopes along

Stinson Creek SE of Fulton, *J. A. Steyermark* 26/39 (MO). Camden Co.: near Bagnall Dam, open woods, *J. H. Kellogg s.n.* (MO). Clark Co.: 0.5 mi SE of Wayland, upper Mississippi, *T. E. Smith* 3134 (MO). Clay Co.: Oakwood, *J. Davis* 428 (MO). Cole Co.: NW of Jefferson City, *R. Thom s.n.* (MO); Soluman, *W. Trelease* 211 (MO). Dent Co.: Little Pine Creek, 3 mi NE of Edgar springs, *J. A. Steyermark* 25462 (MO); Old fields, *J. H. Kellogg s.n.* (MO). Franklin Co.: 600 m NE of Trail House at Missouri Botanical Garden Arboretum, *B. Davit* 113 (MO); Gray Summit, *J. H. Kellogg* 993 (MO); near Pacific, *E. E. Sherff* 999 (MO). Gasconade Co.: 3.5 mi W of Hermann off hwy 100, *B. Summers* 4515 (MO); South side of Ben Church rd, 2.1 mi W of intersection with hwy 19, *R. E. Gereau* 2288 (MO). Greene Co.: Willard, *J. W. Blankship s.n.* (MO). Henry Co.: 1 mi W of hwy F and 2 mi S of Hwy. 52, Chapel View prairie, *B. Summers* 3066 (MO). Howell Co.: 3.5 mi N of Brandsville, *B. Summers* 5525 (MO); rocky open woods bordering rattlesnake draft, *B. Summers* 262 (MO). Iron Co.: Patterson Mountain area, NE of hwy, *C. Anderson* M0166 (MO); eastern Iron, *W. Trelease* 212 (MO). Jackson Co.: Sheffield, *B. F. Bush* 159 (MO); no locality, *B. F. Bush s.n.* (MO). Jasper Co.: along railway grade, gravelly soil, *E. J. Palmer* 31420 (MO); common on dry prairies, Webb City, *E. J. Palmer* 3070 (MO); Webb City, *E. J. Palmer* 2522 (MO); Webb City, *E. J. Palmer* 817 (MO); no locality, *B. F. Bush s.n.* (MO). Jefferson Co.: Harine, *H. Eggert s.n.* (MO); near Festus, *M. M.* 753 (MO); in field, *A. Christ* 128 (MO); Kimmswick, *F. Wisligeuus s.n.* (MO); sand N of Florine, *H. Eggert s.n.* (MO); Victoria, *C.S.H. s.n.* (MO); no locality, *H. Eggert s.n.* (MO). Montgomery Co.: sandstone glade in Graham Cave Glades Natural area, *B. Schuette* 2068 (MO). Morgan Co.: Avky Banks, *B. F. Bush* 14362 (MO). Oregon Co.: along state highway 19 ca. 1/2

mi N of Treer, *G. & K. Yatskievych 93-320* (MO). Perry Co.: 1.5 mi N of Wittenburg, *J. A. Steyermark 14058* (MO). Phelps Co.: banks of railroad, Jerome, *J. H. Kellogg 200* (MO). Ralls Co.: cherty upper slopes along salt river W of Center, *J. A. Steyermark 25848* (MO); near creek bottom, *J. Davis 3178* (MO). Ripley Co.: sand ponds natural area, *S. Hudson 59* (MO). Scott Co.: 3 mi NE of Blodgett on W side of dirt county rd 1.5 mi from junction with State hwy 77, *S. Holmes 93269* (MO). St. Clair Co.: prairie on upland 2 mi N of Iconium, *J. A. Steyermark 24275* (MO). St. Francois Co.: Bismarck, *B. F. Bush s.n.* (MO). Ste. Genevieve Co.: tributary of Jonca creek S of Wingarten, *J. A. Steyermark 20956* (MO). St. Louis City: City of St. Louis, *V. Muehlenbach 281, 323, 236* (MO). St. Louis Co.: Washington University, *J. Drushell 4147* (MO); Washington University, *R. E. W. 762* (MO); Des Peres, *A. Chandler 2818* (MO); Fairlawn, *O. S. Ledinan 6* (MO); Forest park, *G. H. M Goehring s.n.* (MO); Kirkwood flora of MO project 826 (MO); Kirkwood, *M. Greenman 3700* (MO); Merau, *L. H. Pammel s.n.* (MO); near 4200 Flora Ave., St. Louis, *M. C. Jensen s.n.* (MO); near Grand and Magnolia, *J. Drushell 4100* (MO); Osage Hills, *A. Christ 128* (MO); sandy woods on the eastern bank of the Mississippi, *G. Engelmann 20307* (MO); SW St. Louis, *J. A. Steyermark 8825* (MO); St. Louis, *G. Engelmann s.n.* (MO); St. Louis, *G. Engelmann 20302* (MO); St. Louis, *G. Engelmann 20304* (MO); St. Louis, *G. Engelmann 280* (TEX); St. Louis environs, *G. Engelmann 1025* (MO); St. Louis environs, *E. C. Epling s.n.* (MO); W of Webster, *L. M. Greenman 3794* (MO); Clayton, *B. Hubert s.n.* (MO); Courtney, *B. F. Bush 2146* (MO); no locality, *C. A. Geyer s.n.* (MO); no locality, *Cherokee s.n.* (MO); no locality, *F. Comto 826* (MO). Unknown Co.: Station Greene Leo, *J. W. Blankship s.n.* (MO). near Jefferson Barracks, *E. E. Sherff 1045* (MO); Swan,

B. F. Bush 622 (MO); Willow bar, *A. Fendler* 134 (MO); no locality, *B. F. Bush s.n.* (MO); no locality, *N. M. Glatfelter s.n.* (MO); no locality, *J. F. Joor* 18 (MO); no locality, *J. H. K. s.n.* (MO). Nebraska. Antelope Co.: 2.5 mi W of Oakdale, sandhill pasture, *L. M. Rohrbough* 131 (TEX). Cass Co.: sandy soil *T. J. Fitzpatrick* 38 (MO); common at 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); along railroad Lincoln, 65 (MO). Nuckolls Co.: sandy soil, along streams, *G. G. Fledrick* 2887 (MO). Unknown Co.: Expedition of Capt. J. H. Simpson, *G. Engelmann* 20255 (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); no locality, *M. Meissner* 440 (MO). Oklahoma. Caddo Co.: N of Apache, *G. J. Goodman* 2343 (MO). Creek Co.: Sapulpa, *B. F. Bush* 119 (MO). Garfield Co.: no locality, *M. White* 99 (MO). Grady Co.: 4.5 mi S and 3 mi W of Rush Springs, *R. Pearce* 924 (TEX). Harper Co.: open ground along creek, plains near Laverne, *E. J. Palmer* 41907 (MO, UC). Kay Co.: sand pit 1 mi 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.: on upper sandy bank of Coon Creek near Copan, *G. W. Stevens* 2166 (MO). Payne Co.: 3 mi from Ripley, *W. Henson* 272 (UC); 4.5 mi W of Boomer Lake Dam, *W. F. Mahler* 960 (TEX); 6 mi N of Stillwater, *L. Hubbard* 82 (TEX); loam soil 1 mi N of Stillwater, *D. G. Clarke* 52 (TEX); loam soil 3 mi N of Stillwater, *R. Stratton* 70 (TEX); sandy clay soil, *R. Stratton* 187 (MO); Stillwater, *Waugh s.n.* (MO). Pottawatomie Co.: SE of Shawnee, *F. A. Barkley s.n.*

(MO). Tillman Co.: Frederick, *J. T. Duncan 65* (MO). Woods Co.: in waste place, hard soil near Alva, *G. W. Stevens 2824* (MO). Unknown Co.: near Oklahoma City, *S. S. White 1163 & 1179* (MEXU). South Dakota. Beadle Co. Iroquois, *J.J. Thornber s.n.*

(UC). Brookings Co.: Brookings Co.: *S. S. Visher 3034* (MO). Fall River Co.: Cheyenne River, East of Hot Springs, *W. H. Over 16080* (UC). Spink Co.: vicinity of Redfield, *A. E. Ricksecker 64* (UC). Unknown Co.: Sand Lake, *D. Griffiths 11* (NY). Texas.

Angelina Co.: Diboll, *C. A. Mcleod 4* (TEX). Aransas Co.: Headquarters of Aransas Wildlife Refuge, *R. J. Fleetwood 9349* (TEX); sand in Goose Island State park, *M. C. Johnston 541254* (TEX). Bastrop Co.: 30 mi W of Austin along hwy 290 turn off on hwy 71, *E. T. Riley-Hulting 3001* (MONT). Bell Co.: sandy soil of old Tennessee Valley river Terrace W of old site of Tennessee Valley Church, *G. York 54443* (TEX). Brazoria Co.: Angleton, *R. J. Fleetwood 10615* (TEX); Brazoria Refuge, *R. J. Fleetwood 92780* (TEX); Brazoria Refuge, *R. J. Fleetwood 9280* (TEX); off hwy 288 in Angleton, *E. T. Riley-Hulting 3005* (MONT); S of Galveston on San Luis pass, *E. T. Riley-Hulting 3006* (MONT); Angleton. *E. T. Riley-Hulting s.n.* (MONT). Brazos Co.: College Station, *H. B. Parks s.n.* (TEX); College Station, *Shaw s.n.* (TEX); Fish Lake behind Easterwood Airport, *J. R. Massey 379* (TEX). Cass Co.: 0.5 mi E of McLeod, *D. S. Correll 30085* (TEX). Chauburn Co.: coastal prairie, *B. C. Tharp 3139* (TEX). Dallas Co.: light soil, *J. Reverchon 257* (MO). De Witt Co.: no locality, *M. Riedel s.n.* (TEX). Erath Co.: behind science building, campus, Stephenville, *P. Hoisington 198* (TEX). Falls Co.: dry sand woodland, on county rd along Southern Pacific railroad, *S. L. Orzell 10492* (TEX). Fayette Co.: sandy loam upland oak woodland, *F. A. Barkley 46359* (TEX). Galveston Co.: 0.5 mi W of Galveston, at air base, *B. L. Turner 3150* (TEX); field in which old

house is located, *R. J. Fleetwood 10556* (TEX); Galveston Island State Park, *R. J. Fleetwood 10556* (TEX). Garza Co.: clacareous clay loam, eroded pasture 2.7 air mi W of Post, *B. Hutchins 1269* (TEX). Grayson Co.: 0.5 mi on dirt road by transformer station E of farm rd 901 2 mi S of Gordonville, *D. S. Correll 33625* (TEX). Gregg Co.: along Sabine river, 7 mi S of Longview, *D. S. Correll 33980* (TEX); sandy ground N of Longview, *H. Eggert s.n.* (MO); no locality, *C. L. York s.n.* (TEX). Grimes Co.: 5 mi E of Navasota, *B. L. Turner 3074* (TEX). Hardeman Co.: Chillicothe, *C. R. Ball 1159* (TEX). Harrison Co.: 7 mi SE of Marshall, *B. L. Turner 3090* (TEX); along Cypress creek 8 mi E of Cypress, *D. S. Correll 31921* (TEX). Hemphill Co.: Canadian Valley, *E. L. Reed 4022* (TEX). Houston Co.: E of road to Halls Field Cemetery 0.5 mi 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.: Hechos river marsh, Beaumont, *B. C. Tharp s.n.* (TEX). Johnson Co.: Joshua, *E. Whitehouse s.n.* (TEX). Kenedy Co.: El Toro Island mud flats of the Laguna Madre, *B. C. Tharp 49137* (TEX); Laguna Madre El Toro Island, *B. C. Tharp 4832* (TEX). Lamar Co.: 1/3 mi E of Chicotah, *V. L. Cory 54668* (TEX); 2 mi N of Powderly, along rte 271, *D. S. Correll 37931* (TEX). Leon Co.: dune area at hilltop lakes, *D. S. Correll 36422* (TEX). Limestone Co.: gravel rd NE of Morgan Hill, *S. L. Orzell 10512* (TEX). Liberty Co.: edge of woods along rte 146, 2.5 mi N of Moss Hill, *D. S. Correll 33999* (TEX). Live Oak Co.: Santa Fe Ranch, *B. C. Tharp s.n.* (TEX). Llano Co.: creek 7-8 mi E of Llano tributary of Llano river, *D. S. Correll s.n.* (TEX). Mason Co.: 15.5 mi E of Mason, *V. L. Cory 37829* (TEX). Medina Co.: deep sandy soil, Carizo outcrop 2 mi SW of Devine, *M. C. Johnston 3421* (TEX); sandy upland near Devine, *R. Wagoner 13911* (TEX).

Montgomery Co.: Conroe, in city limits, *B. L. Turner 3914* (TEX); Willis, *S. R. Warner s.n.* (MO). Nolan Co.: Sweetwater, *E. J. Palmer 12473* (MO). Nueces Co.: Mustang Island, *D. S. Correll 17666* (TEX). Oldham Co.: West Alamosa Creek bank, Mansfield Ranch S of Canadian River, *J. Smith 132* (TEX). Parker Co.: Mineral Wells State Park, *B. L. Lipscomb 2423* (TEX); Peaster, *Z. Wiggins 34* (TEX). Polk Co.: Jackson hwy cut N of Corrigan, *B. C. Tharp 51-1507* (TEX). Randall Co.: Palo Duflo Canyon, *E. L. Reed 3981* (TEX). Red River Co.: 3 mi E of Detroit, *B. L. Turner 3115* (TEX); Clarksville, *R. Reese s.n.* (TEX); post oak savannah 4 mi S of Bogata, *D. S. Correll 36589* (TEX). Robertson Co.: no locality, *L. Morris 46* (TEX). San Patricio Co.: loose sand prairie 1 mi N of Nueces River on hwy 77, *M. C. Johnston 541333* (TEX); Naval Station Ingleside, *W. R. Carr 16877* (TEX). Smith Co.: Amigo, *H. E. Moore 995* (MEXU, TEX, UC); neglected sandy field, *H. E. Moore 1360* (MONT); Tyler, *E. Whitehouse s.n.* (TEX). Tarrant Co.: along GTP railroad, Fort Worth, *A. Ruth 135* (TEX); along J railroad, *A. Ruth 205* (MO). Travis Co.: NE bank of Lake Austin at S end of Lake Austin, *W. R. Carr 10057* (TEX); 26th Street, City of Austin, *A. Delgado Salinas s.n.* (MEXU). Upshur Co.: sandy soil in pine oak woods along rte 80, *R. Merrill 2184* (TEX). Walker Co.: 7 mi NW Huntsville on rte 19, *D. S. Correll 31944* (MO); Huntsville, *H. B. Parkes s.n.* (UC). Washington Co.: Brenham, *E. Whitehouse s.n.* (TEX). Wichita Co.: Red River above Burkburnett, *B. C. Tharp 563* (TEX). Wilbarger Co.: near Pease River, 3 mi W of Vernon, *G. J. Goodman 2268* (MO). Wilbarger Co.: Red River above Vernon, *B. C. Tharp 4400* (TEX). Woods Co.: 4 mi E of Mineola, *J. A. Mears 883* (TEX). Unknown Co.: common in valley, *E. Stearns s.n.* (MO); no locality, *E. Hall 106* (MO); Patton, *B. C. Tharp s.n.* (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 near Pierce Co., *N. C. Fassett 17395* (MO). Unknown Co.: Lake Pepin, *T. J. Hale 1861* (MO).

Strophostyles leiosperma, thought to be largely a self-pollinator, has the smallest flowers of the species of *Strophostyles*. Furthermore the keel rostrum is only very slightly curved to the right side of the flower. In contrast, the generally larger flowers of each of *S. helvolus* and *S. umbellata* have a distinctly long keel rostrum that is more prominently curved to the right. The leaflets of *S. leiosperma* are consistently the narrowest and hairiest, but some specimens of *S. umbellata*, especially from Texas and Florida (i.e., the south end of the range of *S. umbellata*), have narrow leaflets like those of *S. leiosperma*. In this case, *S. leiosperma* is distinguished by its slender inflorescence peduncles, and small flowers or pods (see key for size differences).

The seeds of *Strophostyles leiosperma* tend to be as commonly glabrous as they are covered in the cellular or waxy coating. If the waxy coating is related to seed dispersal via water, then this observation is consistent with *Strophostyles leiosperma* being found more often in open drier sites than the other two species of the genus.

Strophostyles leiosperma is indeed the more westerly distributed species in the genus (Fig. 16) and ITS allelic diversity occurs to the west of that of the other two species (Fig. 4).

Although a moderate amount of intraspecific allelic diversity was detected in *Strophostyles leiosperma*, no heterozygous individuals were detected in this analysis. Little within population variation is expected for *S. leiosperma* given that self-pollination

is commonly observed in this species from both field and greenhouse observations.

Indeed, two nearby population of *S. leiosperma* sampled from coastal Texas (L1453 and 1462; Fig. 4; Appendix A) revealed no within population allelic variation even though the two alleles detected 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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APPENDICES

APPENDIX A

DNA VOUCHERS AND GENBANK ACCESSION NUMBERS

Appendix A. DNA vouchers and GenBank accession numbers for *Strophostyles* and *Dolichopsis*. ¹Sequence from the ITS region; ²Sequence from the *trnK/matK* locus. (XXXXXXXX signifies GenBank accession to be obtained upon acceptance for publication).

Dolichopsis paraguariensis. Argentina: DNA 199, *Krapovickas 46512* (MEXU), ¹AF069116. DNA 1138, *Ahumada 1741* (MEXU), ¹XXXXXXXX. *Dolichopsis dolichocarpus*. Paraguay: DNA 1516, *Beck 24296* (MEXU), ¹XXXXXXXX. *Strophostyles umbellata*. USA. Alabama: DNA 1316, Crenshaw Co. *R. Kral 88958* (USCH), ¹XXXXXXXX. Florida: DNA 1437, Leon Co. *J. B. Nelson 1190* (USCH), ¹XXXXXXXX. Louisiana: DNA 1439, Jefferson Davis Co. *C. M. Allen 15589* (MO), ¹XXXXXXXX. Mississippi: DNA 1264, Clarke Co. *S. B. Jones 14586* (TEX), ¹XXXXXXXX. South Carolina: DNA 180, Columbia. *J. B. Nelson s.n.* (MONT), ¹XXXXXXXX. DNA 538, Richland Co. *A. B. Pittman 8089606* (MONT), ¹XXXXXXXX. DNA 540, Edgefield Co. *J. B. Nelson 17763* (MONT); ¹AF069115. DNA 1265, Georgetown Co. *J. B. Nelson 9724* (TEX), ¹XXXXXXXX. DNA 1306, Georgetown Co. *J. B. Nelson 9724* (USCH), ¹XXXXXXXX. DNA 1454, Fairfield Co. *E. T. Riley 3040* (MONT), ¹XXXXXXXX. Texas: DNA 1457, Orange Co. *E. T. Riley 3004* (MONT), ¹XXXXXXXX. DNA 1263, Hardin Co. *W. R. Carr 10820* (TEX), ¹XXXXXXXX. Virginia: DNA 1438, Fairfax Co. *T. Bradley 21598* (USCH), ¹XXXXXXXX. *Strophostyles helvola*. Canada: DNA 1450, Quebec, *P. H. Hawkins 34952* (MONT). México. Nayarit: DNA 1332, *O. Norvell PI603808* (USDA accession), ¹XXXXXXXX. DNA 1330, *O. Norvell PI603809*, (USDA accession), ¹XXXXXXXX. USA. California: DNA 1333, *O. Norvell PI 60197* (USDA accession), ¹XXXXXXXX. DNA 1329, *O. Norvell PI 601970*, (USDA accession), ¹XXXXXXXX. Delaware: DNA 1371, *T. Hymowitz cu-175* (private seed accession), ¹XXXXXXXX. Florida: DNA 1313, Escambia Co., *S. Orzell 12423* (USCH), ¹XXXXXXXX. Illinois: DNA 1369, Morrito, *T. Hymowitz cu-177* (private seed accession), ¹XXXXXXXX. DNA 1315, Tazwell Co., *V. Chase 13521* (TEX), ¹XXXXXXXX. Maryland: DNA 1372, Worcester Co., *T. Hymowitz cu-176* (private seed accession), ¹XXXXXXXX. Missouri: DNA 1336, *O. Norvell PI599666* (USDA accession), ¹XXXXXXXX. DNA 1370, Elsberry, *T. Hymowitz cu-439*, (private seed

accession), ¹XXXXXXXX. Nebraska: DNA 1331, *C. McMillian PI215296*, (USDA accession). Florida ¹XXXXXXXX. DNA 1337, Leon Co. *C. Mcmillian PI215295*, (USDA accession), ¹XXXXXXXX. South Carolina: DNA 1260, Beaufort Co. *A. R. Darr 525* (MONT), ¹XXXXXXXX. DNA 1427, Richland Co., *J. Nelson 22202* (USCH), XXXXXXXX. Virginia: DNA 1311, Richmond Co. *T. Bradley 24735* (USCH), ¹XXXXXXXX. West Virginia: DNA 1312, Monongulia Co., *W. Grafton* (USCH), ¹XXXXXXXX. Texas. Bastrop Co.: DNA 1451, *E. T. Riley* (MONT), ¹XXXXXXXX. DNA 1268, *E. Barbuero 4866* (TEX), XXXXXXXX), Galveston Co.: DNA 1452, *E. T. Riley 3012* (MONT), ¹XXXXXXXX. Rusk Co.: DNA 1233, *Correll 33978* (USCH), ¹XXXXXXXX. Freestone Co.: DNA 1261, *W. Cholmes 187* (TEX), ¹XXXXXXXX.

Strophostyles leiosperma. USA. Arkansas: DNA 297 & 1310, Union Co., *R. D. Thomas 102675* (USCH), ¹XXXXXXXX. Alabama: DNA 1442, Baldwin Co., *R. Kral 51304* (MO), ¹XXXXXXXX. Kansas: DNA 1273, Reno Co., *C. A. Morse 4057* (USCH), ¹XXXXXXXX. Missouri: DNA 1440, St. Louis Co., *F. Comto 826* (MO), ¹XXXXXXXX.

Nebraska: DNA 1334, *McMillian PI215298* (USDA accession), ¹XXXXXXXX. New Mexico: DNA 106, *McIntosh 3115* (MEXU), ¹XXXXXXXX. Oklahoma: DNA 1446, Rady Co., *R. Pearce 924* (TEX), ¹XXXXXXXX. Texas. Bastrop Co.: DNA 1456, *E. T. Riley 3001* (MONT), ¹XXXXXXXX. Brazoria Co.: DNA 1453 a-j, N. W. Refuge. *E. T. Riley 3005* (MONT), ¹XXXXXXXX. DNA 1455, *E. T. Riley 3006* (MONT), ¹XXXXXXXX. DNA 1462b-j, Angleton, *E. T. Riley s.n.* (MONT), ¹XXXXXXXX. Falls Co.: DNA 1221, *Orzell 10492* (TEX), ¹XXXXXXXX. Lamar Co.: DNA 1266, *D. S. Correll 37931* (TEX), ¹XXXXXXXX. Travis Co.: DNA 197, *A. Delgado s.n.* (TEX), ¹AF115137 (reported as *S. helvula* in Delgado et al. 1999). Wisconsin: DNA 1445, St. Croix Co., *N. C. Fassett 17395* (MO), ¹XXXXXXXX.

APPENDIX B

LIST AND EXPLANATION OF FIGURES

Fig. 1. Combined analysis of morphological, ITS/5.8S, and *matK* sequence data for *Strophostyles* and close relatives (a partition homogeneity test suggests little data set conflict at $p=0.206$). This is one of three most parsimonious phylograms derived from 182 phylogenetically informative characters. Each of the three maximum parsimony trees has a length of 355, a consistency index of 0.845, and a retention index of 0.856. Bootstrap values are associated only with those clades that were resolved in the strict consensus.

Fig. 2. Phylogram of 68 *Strophostyles* accessions derived from an analysis of the sequences from the ITS region with *Dolichopsis* species as the designated outgroups. This is one of 10,000 most parsimonious phylograms derived from 49 phylogenetically informative sites (out of 658 aligned sites). Each of the maximum parsimony trees has a length of 100, a consistency index of 0.930, and a retention index of 0.977. Bootstrap values are associated only with those clades that were resolved in the strict consensus.

Fig. 3. Unrooted network of the *Strophostyles umbellata* accessions derived from parsimony analysis of the ITS region. This tree has both a consistency and retention index of 1.00. Of the 13 variable sites, six are phylogenetically informative (see Table 4).

Fig. 4. Unrooted network of the *Strophostyles helvolus* AND *S. leiosperma* accessions derived from parsimony analysis of the ITS region. This tree has both a consistency index of 0.94 and retention index of 0.99. Of the 16 variable sites, 11 are phylogenetically informative.

Fig. 5-8. Ordination of 426 herbarium specimens of *Strophostyles* along the three dominant eigenvectors, which captured 75% of variation for the total data set, 73% for the floral data subset, and 74% for the fruiting data subset. Fig. 6. Plot contrasting the first (C1) and second (C2) eigenvectors. 1=*Strophostyles umbellata*, 2 = *S. helvolus*, and 3=*S. leiosperma*. This ordination was derived from all herbarium specimens, including those with missing fruiting or floral characters. Very similar results were obtained with subsets of this data set representing only herbarium specimens with complete floral or fruiting data. Fig. 7. Plot of the ordination of the 16 morphological characters used in the morphometric analyses and contrasting the first and second eigenvectors. 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=number of flowers per inflorescence, 10=calyx tube length, 11=bracteole length, 12=petal length, 13=number of ovules per ovary, 14=pod length, 15=pod width, 16=density of hairs on pod valve. Fig. 8. Plot of the ordination of specimens and contrasting the first (C1) and third (C3) eigenvectors. 9. Plot of the ordination of traits and contrasting the first (C1) and third (C3) eigenvectors. For the ordination of traits, 69.01% of variation was

captured for the total data set, 68.82% for the floral data set, and 68.76% for the fruiting data set.

Fig. 9. Chronogram for New World Phaseolinae derived from penalized likelihood rate smoothing of a Bayesian likelihood tree, which was estimated with sequences from the ITS region. Codes for crown clades (e.g., LASI, RAOX, SPEC, STDO, and STRO) are those used in Table 4 and the text. Numerical codes in brackets after terminal taxa labels are the DNA accessions (Appendix A). Average nucleotide substitution parameters estimated for 1,000 likelihood trees that were uniformly sampled from over 1,700,000 at stationarity are $r(\text{GT})=1.000$, $r(\text{CT})=5.063676$, $r(\text{CG})=1.066733$, $r(\text{AT})=0.946619$, $r(\text{AG})=2.208306$, $r(\text{AC})=0.812540$, $p(\text{A})=0.223907$, $p(\text{C})=0.275692$, $p(\text{G})=0.287723$, $p(\text{T})=0.212678$, $\alpha=1.477198$, $iP=0.285052$. See Table 4 for the estimated ages and rates of substitution. Numbers above branches are Bayesian posterior probabilities.

Fig. 10. Chronogram for the major clades of New World Phaseolinae derived from penalized likelihood rate smoothing of a Bayesian likelihood tree, which was estimated with sequences from the *matK* locus. Codes for crown clades (e.g., LASI, PHAS, RAOX, SPEC, STDO, and STRO) are those used in Table 4 and the text. Numerical codes in brackets after terminal taxa labels are the DNA accessions (Appendix A). Average nucleotide substitution parameters estimated for 1,000 likelihood trees that were uniformly sampled from over 1,000,000 at stationarity are $r(\text{GT})=1.000$,

$r(CT)=0.679103$, $r(CG)=0.577224$, $r(AT)=0.128302$, $r(AG)=0.689330$, $r(AC)=1.254482$,
 $p(A)=0.316808$, $p(C)=0.147822$, $p(G)=0.138046$, $p(T)=0.397324$, $SS1=1.023661$,
 $SS2=0.766846$, $SS3=1.209493$. See Table 6 for the estimated ages and rates of
substitution. Numbers above branches are Bayesian posterior probabilities.

APPENDIX C

DRAWINGS OF STROPHOSTYLES

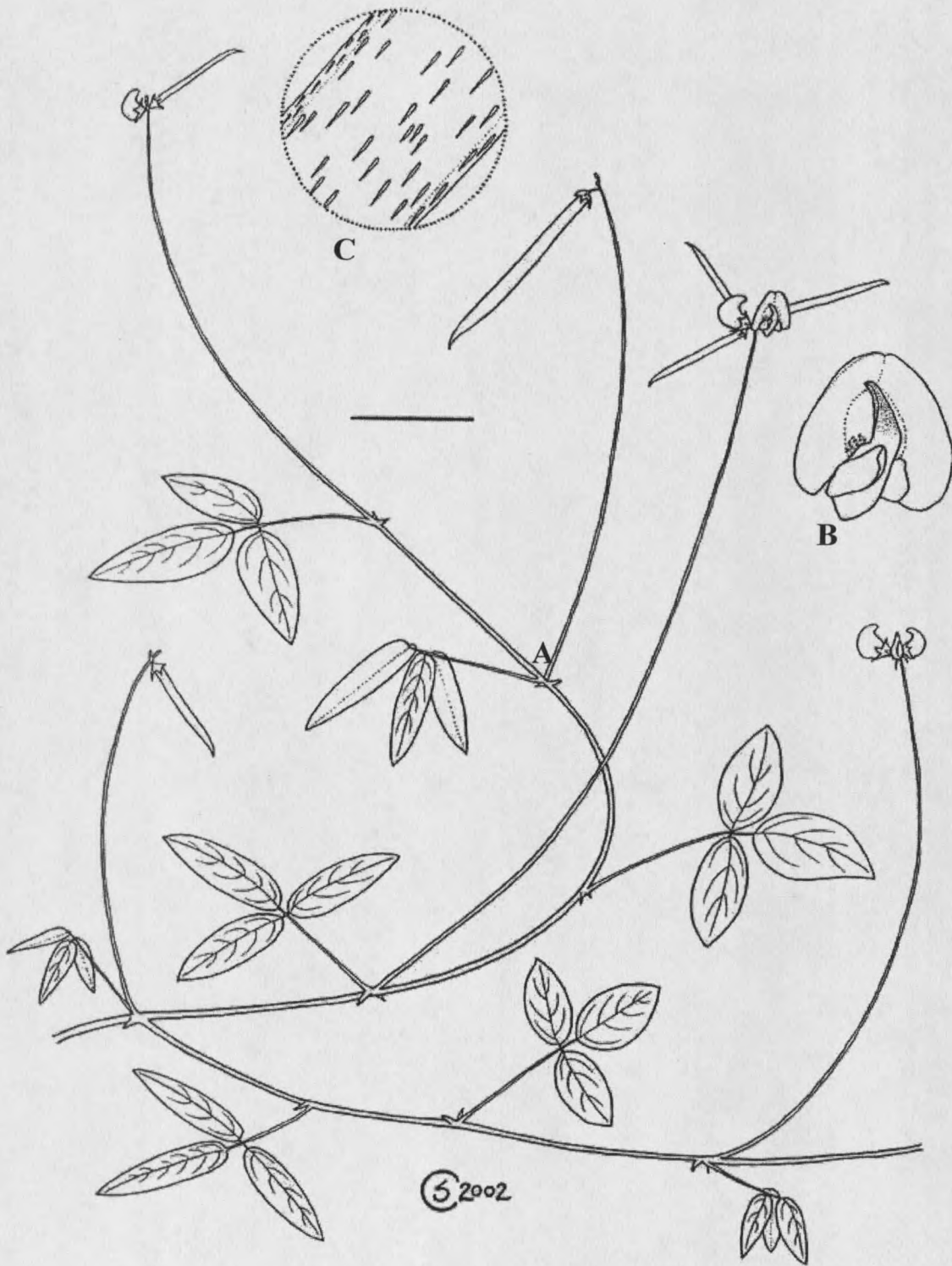


Fig. 11 – *Strophostyles umbellata*. A. Habit. B. Flower. C. Close-up of fruit

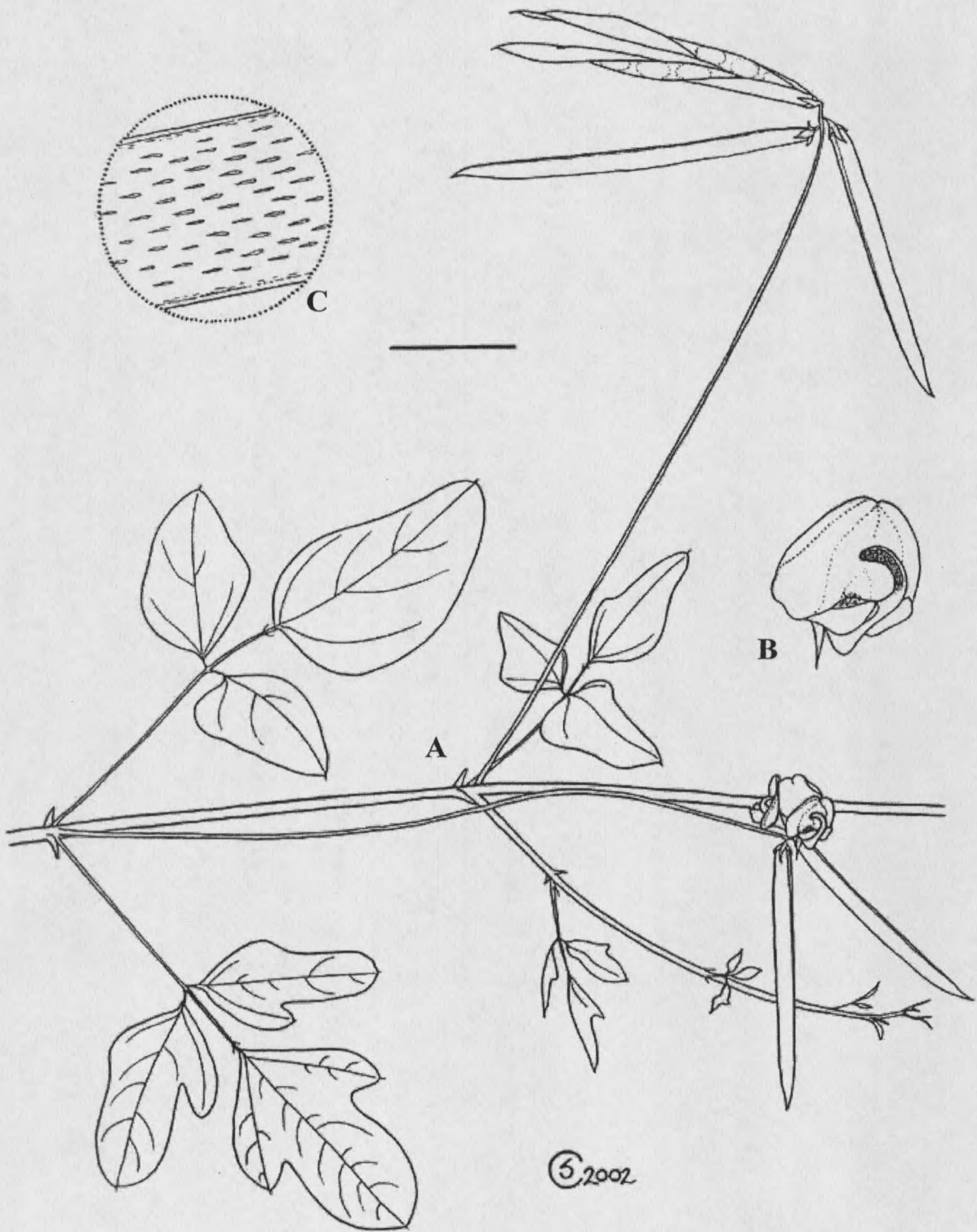


Fig. 13 – *Strophostyles helvolus*. A. Habit. B. Flower. C. Close-up of fruit.

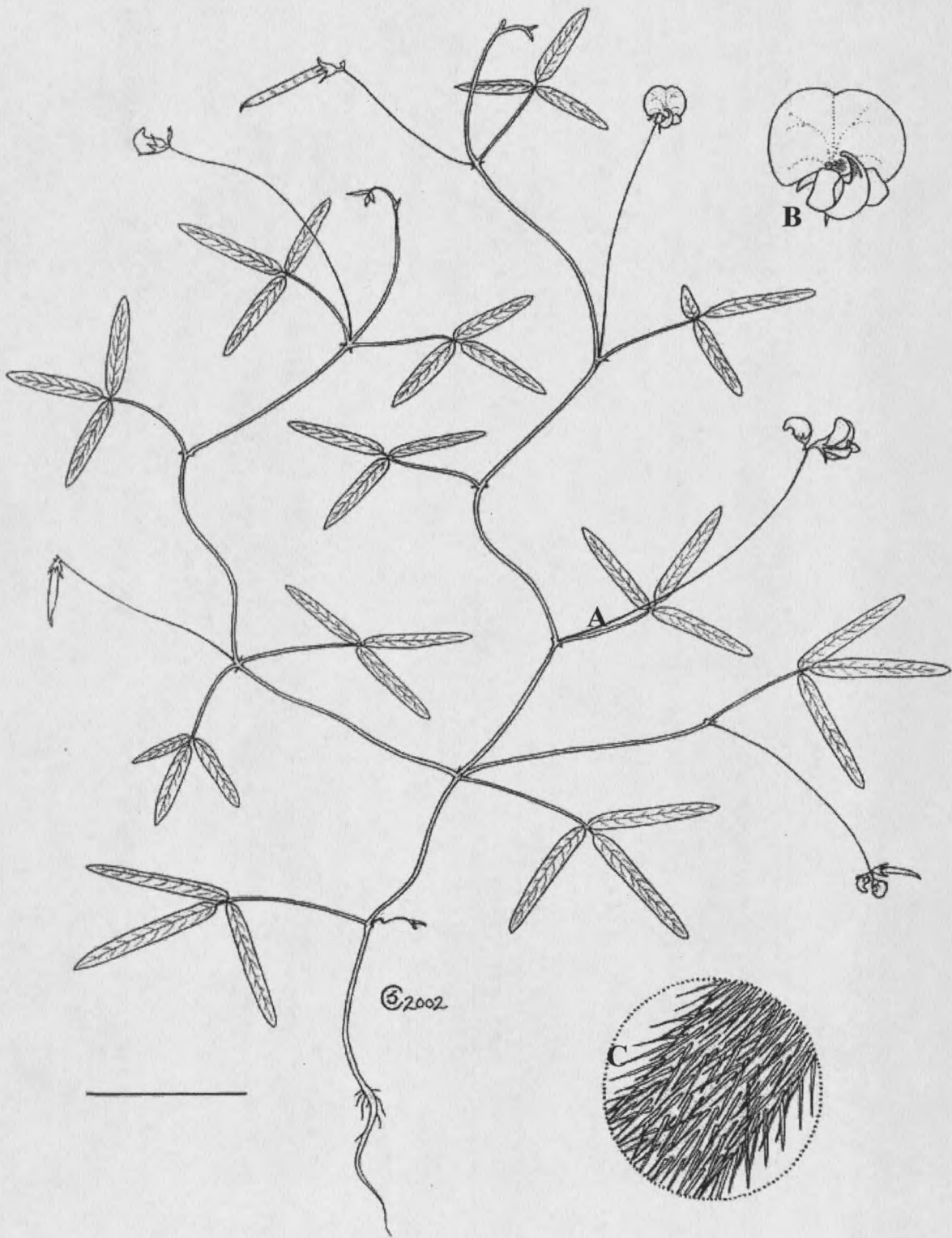


Fig. 15 – *Strophostyles leiosperma*. A. Habit. B. Flower C. Fruit.

APPENDIX D

MORPHOMETRIC MEASUREMENTS

		m	n	o	p	q	c	d	j	l	i	h	k	e	f	r	b	g
Strophostyles helvola																		
Indiana																		
H. H. Smith MO 5769	2	1	46.8	27.6	44.0	26.3	10.1	2	1		2	2.5	2.5	12.5		4.2	1	
C. S. Sheldon MO 246	2	2	56.3	38.2	36.4	22.3	4.3	1	1									
J.R. Churchill MO (1059839)	2	3	50.7	37.4	43.5	28.0	0.8	1	1	109.6	2	1.8	2.2	11.2	48.3			
Ohio																		
Bernice C. Stephenson MO (989310)	2	4	71.5	46.2	63.4	39.1	11.4	1	2	56.3	3	2.4	3.3	10.1		6.3		
C.G.Lloyd MO (1812837)	2	5	32.9	21.0	29.6	18.1	15.2	1	2	123.5	4	2.3	3.1	12.5	7.0	64.7	7.9	2
G. T. Jones MONT79-9-9-1223	2	6	32.2	20.4	30.7	19.7	0.5	2	1	44.0	2	2.3	2.8	12.4	5.0	65.7	6.3	2
Steven D. Swanson MO 2177	2	7	65.0	43.4	50.0	31.6	0.5	1	1	130.8	2	2.1	2.7	11.8	5.0	61.6		1
Wisconsin																		
N.C. Fassett MO 17901	2	8	38.0	24.0	33.5	19.6	0.5	1	2	74.2	2	1.9	1.6	10.0	37.6			3
N.C.Fassett MO 4400	2	9	32.3	20.2	22.6	15.5	1.0	1	2	87.1	3	1.9	2.0	9.8				
N.C.Fassett MO 17902	2	10	30.6	18.4	29.5	16.4	11.3	1	1	91.9	3				6.0	67.8	1	1
Minnesota																		
J.B.Mayle MO 2304	2	11	32.8	22.9	27.2	16.2	1.0	3	2	117.3	3	1.7	2.4	6.8	5.0	66.1		2
Iowa																		
J.H.Mills MO 530	2	12		32.4	21.6			1	1	97.5	2				5.0	51.4	4.7	2
L.H.Pammell MO 18	2	13	19.5	14.0	23.9	17.2		2	1	91.8	3	1.9	2.1	11.3		3.3		
R.I.Cratty MO (1812839)	2	14	36.0	20.8	21.8	13.0	4.0	1	0	136.8	3	1.3	2.1	9.2	7.0	49.9	3.1	3
Gerrit Davidse MO (2259631)	2	15	44.2	17.1	36.0	21.4	5.1	1	0	104.1	3	3.5	3.1	10.0		6.8		7
Ada Hayden.MO 11313	2	16	33.6	17.1	24.4	12.7	13.4	1	1	153.4	3				5.0	67.4	3.1	1
A.S.Hitchcock MO (1731211)	2	17	29.9	18.6	25.6	14.7	5.1	0	3	125.8	3	1.6	2.5	7.4	6.0	56.9	3.6	1
Paul Barker TEX (80186)	2	18	34.7	24.7	28.9	17.6	5.3	1	1	45.8	3	1.7	3.5	8.3	6.0	52.6		
D.W.Augustine TEX 433b	2	19	57.0	41.5	40.1	27.5	1.0	0	1	138.3	4	2.0	2.6	7.4				2
South Dakota																		
Philip Johnson MO 81	2	20	54.1	37.0	44.8	28.3	0.0	0	1	50.8	2	2.3	2.4	10.5		5.2		
T.4. MO (1812843)	2	21	37.4	23.2	30.8	21.9	5.1	1	1	112.7	3	2.6	2.6	9.1	7.0	59.5		0
Illinois																		
Frederick Wisli MO 93	2	22	65.2	45.0	57.4	37.5	17.5	1	1	120.6	5	1.5	2.6	8.7				
L.H.Pammel MO (1812833)	2	23	35.5	26.4	35.6	21.3	9.1	1	1		2				6.0	68.8	1	1
A.S.Hitchcock MO(208460)	2	24	33.3	31.9	37.8	23.6	10.8	3	4	152.1	3				5.0	40.6		2

L. Barnard MO (1812834)	2	25	30.5	17.0	31.7	16.4	1.0	0	1	54.8	3					50.8	1	1	
Leg H. Eggert MO(208464)	2	26	30.1	13.8	24.3	14.4	5.7	3	2	79.4	5	2.4	3.2	9.4	5.0				
Leg.H. Eggert MO(208463)	2	27	37.4	23.9	28.0	17.7	2.0	0	1	85.8	3	3.3	2.9	7.7	5.0	50.1	1		
Leg.H.Eggert MO(208510)	2	28	64.5	41.2	56.8	35.3	4.2	0	0	73.9	2			10.6	7.0	65.2	0		
Leg H. Eggert MO(208468)	2	29	28.8	20.0	26.4	17.1	0.0	0	0	135.6	5	2.8	2.8	10.1	6.0	54.7	0		
Virginius H. Chase MO 732	2	30	34.5	19.9	29.5	19.4	13.2	1	1		4				6.0	71.6	1		
Chas A. Geyer MO 20288	2	31	51.5	24.6	42.0	23.4	1.0	0	2	103.0	2	2.3	2.6	9.7	5.0	47.8	6.1	0	
T.Lindhuman MO 20283	2	32	22.5	13.3	13.4	5.8	3.2	2	11						8.0	58.6	5.0	4	
Virginius H. Chase TEX 13521	2	33	21.8	11.9	17.9	9.2	3.3	1	2	153.4	4	1.6	2.0	10.6	7.0	63.9	0		
Virginius H. Chase TEX I0008	2	34	22.8	15.8	22.1	15.4	9.5	1	2	84.5	3	1.9	2.3	11.3	7.0	50.7	2		
New Jersey																			
AlmaL.Moldenke MO 29117	2	35	31.0	23.5	28.5	18.5	6.8	0	1	73.5	3				7.0	52.6	1		
J.A. Prushel MO 6900	2	36	26.9	15.8	22.3	11.6	8.4	0	0	40.1	2				5.0	53.9	1	1	
KennethK. Mackenzie MO 2392	2	37	22.1	12.7	16.1	9.7	3.5	1	1	72.3	3	1.9	2.0	9.9	5.0	55.0	3	1	
J.A.Prushel MO 9570	2	38	33.5	24.2	29.2	20.6	5.5	1	1	102.0	3	1.4	1.9	9.2	6.0	57.5	0		
L.H.L. TEX 80190	2	39	37.3	24.7	24.0	14.1	6.7	0	1	61.6	2	2.5	2.7	10.3	6.0	73.5	1		
Alma L. Molkenke TEX 26110	2	40	20.0	16.2	17.8	13.3	3.6	0	1	90.1	2	2.0	2.5	6.8	5.0	66.8	2	1	
Virginia																			
Albert Ruth MO 334	2	41	37.3	21.4	35.9	17.2	11.7	2	1	215.0	3	1.8	1.4	9.8	6.0	55.2	5.3	1	
M.L.Fernald MO 13965	2	42	50.4	40.0	37.8	27.8	0.0	0	0		2				6.0	69.7	7.4	1	
C.J.Wheeler MO (825681)	2	43	24.5	15.8	24.2	14.5	4.7	1	1	84.1	3	1.9	3.0	10.7	5.0	53.6	3.1	1	
Gabriel Edwin TEX 393	2	44	20.1	14.5	28.1	16.5	3.2	0	1	130.6	4	1.8	1.7	6.7	7.0	53.1	4.4	1	
Massachusetts																			
J.R.C. MO (1059836)	2	45	30.4	21.1	28.1	21.9	6.5	0	0	98.1	2			6.9	8.0	64.0	5.8	0	
J.R.C. MO (1059835)	2	46	32.4	23.8	30.1	23.0	2.0	0	0	69.1	3	1.7	2.3	10.0	6.0	62.4	7.5	0	
J.R.Churchill MO(1059837)	2	47	30.6	20.2	27.8	19.5	2.7	0	1	79.2	3	2.4	2.6	8.3	6.0	59.8	5.1	1	
C.W.Swan MO (1812807)	2	48	33.7	27.0	22.8	17.7	6.0	0	1	83.4	5	2.6	2.4	8.8		5.8			
R.G.Leavitt TEX Sept.8 1902	2	49	36.7	23.7	31.8	23.3	11.6	0	1	86.2	3	2.0	2.8	8.7	6.0	66.6		1	
Washington D.C.																			
E.S.Steele MO (1812825)	2	50	50.2	35.3	29.3	21.0	5.2	0	0	91.4	3	2.4	3.6	8.8	5.0	63.3		1	
Th.Holm MO (779539)	2	51	27.6	18.5	21.3	14.3	7.0	1	1	42.2	2	2.4	2.7	9.7					
Albert Ruth MO 47	2	52	31.6	19.6	28.5	18.0	5.0	1	1	83.7	3				6.0	59.1		1	
Ferdinand Blanchard MO(749859)	2	53	26.9	16.6	25.1	14.5	0.0	2	1	59.9	3	2.3	2.0	8.8					
Ferdinand Blanchard	2	54	42.5	32.0	30.9	22.4	0.0	1	1	56.9	3				49.3			1	

MO(749857)

New York

E.S.Steele MO(1812945)

2 55 29.7 15.7 25.8 11.4 0.0 1 1 75.1 3 2.3 2.2 10.1 5.0 39.5 3

Florida

R.K. Godfrey 70655

2 56 40.4 33.1 25.3 16.8 5.1 3 2 6.0 70.4 6.5 1

James W. Hardin 326

2 57 27.8 22.1 22.1 14.9 5.0 1 2 6.0 60.7 6.3 3 1

J.B.Nelson 990

2 58 50.1 37.2 46.2 31.7 1.0 2 2 153.4 3 2.9 11.4 6.0 68.4 5.3 1

A.H. Curtiss 15552

2 59 53.9 41.7 50.0 35.4 18.2 1 1 187.0 4 3.1 2.6 13.3 5.0 61.6 7.5 2 1

James S. Miller 9091

2 60 31.4 19.9 25.2 17.5 2.0 0 1 70.5 2 1.9 2.9 9.7 6.0

J.B.Nelson 695

2 61 31.7 21.6 29.3 15.7 5.9 2 2 6.0 49.4 3.8 1

A.H.Curtiss 5764

2 62 40.7 30.5 34.6 25.7 8.3 1 1 119.2 2 2.0 2.8 10.5 5.0 58.4 7.1 1

Louisiana

John Pruski 2116

2 63 32.0 22.2 32.4 22.3 5.2 1 1 23.5 3 1.9 2.5 9.1 7.0 65.3 5.9 1

W.C. Holmes 4723

2 64 30.8 22.4 26.3 18.9 1.0 1 2 118.0 3 2.3 3.1 9.6

Alan W. Lievens 4489

2 65 32.7 19.2 30.5 19.3 6.9 2 3 71.2 3 2.1 1.8 9.5 6.0 43.0 3.3 5

Kentucky

Engelmann 20273

2 66 28.8 22.2 28.0 20.5 4.0 1 2 89.2 3 1.3 2.1 9.3 5.0 58.0 1 1

C.W.Short 01-104

2 67 62.8 38.4 52.6 32.6 9.9 1 1 135.6 3 2.2 2.8 10.2

F.T.McFarland 209

2 68 24.8 17.1 21.1 14.3 2.6 1 3 75.4 2 1.7 3.1 10.9

Alabama

R.Kral 51301

2 69 45.7 23.4 42.8 24.9 8.8 2 2 170.0 4 2.0 2.8 10.4 8.0 67.6 4.2 4

R.Kral 47099

2 70 29.4 20.8 40.7 27.4 4.8 2 1 110.6

R.Kral 51376

2 71 43.1 26.2 29.5 20.0 4.7 1 1 36.4 3 1.8 2.7 7.2

Rebecca Deramus 656

2 72 36.1 35.0 35.3 25.4 2.0 2 2 190.0 3 1.8 2.3 10.8

Georgia

Wilbur H. Duncan 8782A

2 73 28.8 17.4 14.9 23.8 8.9 1 2 90.4 3 2.7 2.7 9.5 1

Philip Greear 64283

2 74 18.6 9.6 19.9 10.1 6.6 3 3 145.0 5 2.5 1.1 10.7

Wilbur H. Duncan 20593

2 75 34.5 34.0 28.1 22.1 2.0 2 1 81.4 2 1.7 1.6 9.6 7.0 51.2

North Carolina

Biltmore, N.C. 1302

2 76 33.5 20.8 30.2 20.2 6.0 1 1 115.1 4 2.4 1.8 10.2 8.0 46.9 1

James Solomon 3957

2 77 48.8 26.0 36.1 21.4 8.8 1 1 69.5 3 2.3 3.1 10.4 5.0 49.5 3

Ted Bradley 3399

2 78 34.0 25.8 26.1 21.0 3.9 1 0 99.1 2 1.8 2.7 9.2 9.0 59.0 3

West Virginia

Louis Williams 533

2 79 28.8 16.2 26.2 17.3 0.0 1 1 69.2 3 1.9 3.4 9.1 7.0 66.8 6.2 0

W.C. Muenschler 3747	2	80	32.9	25.2	29.2	21.5	0.0	1	1	54.7	3	1.9	2.9	8.0	7.0	38.1	3.5	2	
Maryland																			
Frank C. Seymour 17505	2	81	28.1	19.6	27.7	15.4	0.0	1	1	110.6	3	2.7	3.8	10.0	6.0	81.2	7.2	1	1
Steven R. Hill 15519	2	82	30.2	17.5	23.9	13.6	6.5	1	1	120.3	3	2.4	3.1	9.0	6.0				
George H. Shull 174	2	83	46.8	33.6	42.4	31.2	1.4	1	1	153.4	4	2.2	3.1	9.3					
Conn																			
C.H. Bissell 622	2	84	44.5	29.1	30.8	16.0	2.0	1	1	74.9	3	1.8	2.4	10.7	6.0	51.7	5.1	2	
Frank C. Seymour 23008	2	85	42.1	29.7	38.3	24.1	6.7	0	1	74.2	4	1.5	2.3	8.6					
Frank C. Seymour 29626	2	86	43.0	26.5	35.6	20.1	0.0	1	1	55.5	3				6.0	60.5	4.2	1	1
South Carolina																			
John B. Nelson 11140	2	87	29.2	22.2	24.6	18.0	7.1	1	1	72.6	2			9.8					
C.Leland Rodgers 69959	2	88	36.4	24.8	23.8	16.9	5.6	3	1	31.8	1	2.5	2.7	8.7	8.0	66.2	5.1	1	0
Charles N. Horn 6107	2	89	30.4	20.5	23.2	16.7	1.3	3	2	64.5	3	2.6	3.6	8.6	6.0	46.2	3.5	3	
Steven R. Hill 18790	2	90	27.3	16.9	34.0	21.2	3.0	0	1	24.3	4	3.1	3.1	7.5	7.0	65.2	5.1	1	
John B. Nelson 8388	2	91	26.3	18.3	23.2	15.4	4.4	1	2	127.7	3	1.9	2.7	11.9		51.1	3.9	1	
John B. Nelson 6126	2	92	29.4	18.6	25.8	16.9	1.0	2	1	136.0	2	1.6	1.7	9.8	6.0	61.5	6.4	1	1
John B. Nelson 14641	2	93	29.6	19.9	17.9	10.6	1.0	4	5	103.7	3	2.2	2.4	10.4	6.0	78.3	7.5	2	
Delaware																			
Wm. Trelease 14	2	94	44.1	30.4	37.9	23.8	1.0	2	1	85.7	4	2.3	2.0	10.6		30.2	3.9	1	
Esther L. Larson 437	2	95	24.1	19.6	20.7	15.2	0.0	0	1						6.0	63.6	4.8	1	1
R.I.																			
J.M.G. 1705	2	96	26.6	16.6	22.3	15.2	1.0	1	1	73.1	2	2.2	1.9	8.4	6.0	70.8	6.7	0	
Arkansas																			
J.H. Kimmons 6405	2	97	32.3	20.0	29.2	13.8	10.0	0	1	66.5	3	2.5	3.0	9.6	6.0	73.7	5.1	3	
Delzie Demaree 61018	2	98	57.0	31.2	49.0	27.4	11.8	1	1	52.1	4	2.7	3.1	10.3	6.0				
D. Demaree 661	2	99	24.8	15.7	24.8	15.1	7.8	0	1	97.1	2	2.4	3.3	9.0	10.0	71.8	6.1	1	0
Delzie Demaree 31354	2	100	38.9	24.5	24.5	16.7	9.6	2	4	86.0	4	1.8	3.1	11.4					
D. Demaree 16245	2	101	38.4	29.2	31.0	19.8	0.7	0	1	59.7	3				6.0	72.2	7.2	2	
Delzie Demaree 11062	2	102	42.1	30.4	37.6	27.5	0.0	0	1	26.3	2	2.3	2.5	7.7	6.0	54.7	3.3	1	1
Nebraska																			
Geo G. Hedgcock (1812845)	2	103	39.8	33.7	35.2	20.6	0.0	1	1	60.2	3	2.0	2.7	8.7			6.2	1	
John L. Morrison 1355	2	104	38.9	29.7	30.8	16.4	1.0	1	1	142.9	2	2.3	2.2	11.2					
Geo G. Hedgcock (1812844)	2	105	45.6	32.3	31.4	17.2	3.4	1	1	80.3	3	1.6	2.5	6.8	6.0	70.9			
Kansas																			

W.A. Kellerman (1812848)	2	106	33.1	23.8	24.7	19.1	4.0	1	1	79.9	3	2.5	2.2	10.6	39.3	1
R. Hoffman (857997)	2	107	46.8	32.5	34.2	23.6	12.9	1	1	77.0	3	1.9	2.5	8.8	6.0 45.3 3.0	1
Kenneth K. Mackenzie (208513)	2	108	46.5	30.2	41.8	20.1	0.0	2	1	47.5		1.4	2.4	8.6		
Oklahoma																
John P. Hollis 39	2	109	32.9	21.3	25.1	17.7	1.0	1	1						7.0 82.7 5.6	1 0
Lavis Derr 86	2	110	17.9	10.9	20.6	9.6	3.7	1	2	69.9	2	1.6	2.1	8.3	7.0 65.4 5.1	3
John Williams 462	2	111	31.0	19.1	15.8	10.3	9.6	3	2	160.0	2				6.0 59.1 3.3	2
T.H. King 83	2	112	20.7	10.8	18.5	9.1	1.0	1	2	72.9	2	2.7	2.9	6.9	44.6 4.3	2 0
Robert Stratton (972680)	2	113	46.7	36.4	41.4	30.0	1.0	1	1	69.9	3	3.2	4.2	10.5	6.0 69.9 5.8	1
Waugh (1812852)	2	114	24.7	14.3	20.8	10.3	3.2	0	1	49.3	3	1.8	2.4	11.4	5.0 56.9 4.1	2
Eastern Texas																
D.S. Correll 32054	2	115	48.7	26.4	20.6	10.2	2.0	1	2	122.9	3	1.7	2.2	10.8	7.0 64.5 5.1	1
Logan D. Smith 969	2	116	25.5	18.4	22.5	12.3	6.1	1	3						5.0 56.8 4.7	2 1
Logan D. Smith 666	2	117	42.3	27.8	33.9	21.5	1.0	1	1			1.9	3.4			
D.S. Correll 31967	2	118	45.3	24.8	34.3	20.2	1.7	2	3	55.8	2	1.9	2.2	8.7	10.0 79.2 7.3	0 1
D.S. Correll 36384	2	119	41.8	20.0	33.7	19.3	3.3	2	1	54.6	4	2.0	2.0	10.7	7.0 81.4 5.9	3
D.S. Correll 33629	2	120	43.4	26.3	37.3	19.8	1.0	0	0	95.7	3	2.5	3.2	10.0	6.0 63.2 4.9	1
V.L. Cory 54702	2	121	35.0	14.9	27.7	13.9	2.0	1	1	124.2	3	1.7	2.7	9.2	6.0 58.2 4.9	3
Engelmann 20287	2	122	32.1	18.7	26.3	13.8	10.0	1	2	98.1	5	2.7	3.3	8.4	6.0 74.9 5.8	2
J. Bauml 3026	2	123	29.4	19.8	26.1	17.0	3.0	2	2	73.6	3	2.4	2.4	9.6	6.0 60.1 8.1	1 1
Danny L. Wilkinson 393	2	124	30.6	19.2	18.6	13.4	3.0	3	2	102.5	4	2.1	2.7	13.1	7.0 61.1 3.3	2
R.W. Strandtmann TEX p.5	2	125	34.3	22.9	31.1	25.9	2.5	1	2	153.4	3	2.2	2.6	10.6	5.0 54.3 3.4	4
Henry Hildebrand 24	2	126	18.6	14.1	19.7	10.4	3.9	0	2	43.6	5	2.5	2.7	7.4	6.0 40.2 4.4	2
B.L. Turner 3151	2	127	52.5	42.4	53.0	36.4	10.4	1	1	132.8	4	2.2	2.6	8.8	8.0 68.6 5.8	1
Raymond J. Fleetwood 9352	2	128	25.5	37.6	29.8	29.8	0.0	2	1	43.4	3	3.6	3.6	10.8	7.0 69.5 3.8	1
Southern Texas																
W.R. Carr 16869	2	129	41.5	28.0	36.3	23.9	2.4	2	1	131.6	4	2.9	2.9	7.6	7.0 77.8 7.1	2 1
Terry Gillespie 277	2	130	32.7	23.5	27.4	18.6	9.0	1	1	98.1	3	2.1	2.4	11.3	7.0 64.9 5.9	1
Richard De Arment 3	2	131	29.6	20.6	18.8	14.6	0.6	1	2	83.2	3	1.9	2.9	9.8	7.0 61.0 3.9	3 0
Middle Texas																
D.S. Correll 17307	2	132	33.9	24.4	26.9	17.4	9.8	3	3	132.0	2	2.9	3.8	11.1	7.0 77.6 5.3	2 0
John R. Crutchfield 2305	2	133	43.5	23.4	34.0	20.1	14.1	1	2	153.4	1	2.1	3.2	7.4	8.0 85.3 6.1	2
H.H.D. 476	2	134	44.2	33.8	38.9	28.0	9.6	2	1	86.3	4	2.3	2.4	10.3	7.0 79.5 5.7	2 1
V.L. Cory 45350	2	135	25.1	17.6	30.2	22.5	1.0	3	2	153.4	4	2.7	2.6	8.6	7.0 61.6 4.6	0

