

VIGNA (LEGUMINOSAE) SENSU LATO: THE NAMES AND IDENTITIES OF THE AMERICAN SEGREGATE GENERA¹

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- *Premise of study:* The legume genus *Vigna* and close relatives have highly elaborated floral morphologies that involve the coiling, bending, and intricate connection of flower parts. Banners, levers, platforms, and pumps have evolved that attract pollinators and then manipulate their movement. Given this three-dimensional floral complexity, the taxonomy of *Vigna* and relatives has been confounded by the study of mostly two-dimensional museum specimens. A molecular phylogenetic analysis was undertaken in the effort to resolve long-standing taxonomic questions centered on floral morphology.
- *Methods:* The phylogenetic analysis included cpDNA *trnK* and nuclear ribosomal ITS/5.8S (ITS) sequence variation. The American species were comprehensively sampled and outgroups included Old World relatives.
- *Key results:* The *trnK* and ITS data analyses concurred in resolving six well-supported clades of American *Vigna* that are most closely related to other American genera: *Dolichopsis*, *Macropodium*, *Mysanthus*, *Oryxis*, *Oxyrhynchus*, *Phaseolus*, *Ramirezella*, and *Strophostyles*. These 14 American clades ranked here as genera are resolved as sister to a clade comprising the mainly Old World species of *Vigna*.
- *Conclusions:* American *Vigna* clades were reassigned to the genera *Ancistrotropis*, *Cochliasanthus*, *Condylostylis*, *Leptospron*, *Sigmoidotropis*, and the newly described *Helicotropis*. *Vigna* sensu stricto in the Americas now includes relatively few and mostly pantropical species. Elaborate floral asymmetries are readily used to apomorphically diagnose nearly all of the American genera. The age estimates of the extant diversification of the American and its Old World sister clade are approximately coeval at ca. 6–7 million yr, which belies much greater floral variation in the Americas.

Key words: biogeography; floral evolution; geographic phylogenetic structure; *Phaseolus*; phylogenetic systematics; rates analysis.

The pantropical genus *Vigna* Savi includes over 100 species (Schrire, 2005), some of which are economically important crop species from Africa and Asia including the cowpea, *Vigna unguiculata*, and mung bean, *Vigna radiata*. Historically, *Vigna*

has included many more species because of taxonomic confusion with *Phaseolus* (tribe Phaseoleae subtribe Phaseolinae), summarized in Maréchal et al. (1978b) and Delgado-Salinas et al. (1993). As circumscribed, *Vigna* potentially comprises disparate New and Old World groups (e.g., Maréchal et al., 1978b; Lackey, 1981, 1983). Chloroplast DNA restriction site studies of Old World (Vaillancourt et al., 1993) and New World *Vigna* (Delgado-Salinas et al., 1993; Bruneau et al., 1995) resolved a monophyletic *Phaseolus* and a paraphyletic *Vigna*. New World *Vigna* were more closely related to other New World genera of Phaseolinae (e.g., *Phaseolus*) than to the Old World *Vigna*. Regardless, Maréchal's (1982) comprehensive circumscription of *Vigna*, which was derived from a morphometric analysis of the *Phaseolus*–*Vigna* complex (Maréchal et al., 1978b) and a seminal taxonomic study of *Vigna* (Verdcourt, 1970), has remained intact. Maréchal's (1982) phylogenetic arguments resting on phenetic similarity (Maréchal et al., 1978b) and interspecific crossing ability among “gene pools” (Smartt, 1980) continue to influence the acceptance of the current *Vigna* circumscription.

Molecular phylogenetic studies of Phaseolinae (Riley-Hulting et al., 2004; Thulin et al., 2004; Delgado-Salinas et al., 2006; Feleke, 2006) unequivocally reveal that the majority of New World *Vigna* species are more closely related to other New World genera of Phaseolinae than to *Vigna* sensu stricto. Our intent is to expand taxonomic sampling of *Vigna* and close relatives to circumscribe and taxonomically formalize the clades of *Vigna* species endemic to the Americas.

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MATERIALS AND METHODS

Taxon sampling—The genera and species of subtribe Phaseolinae Bronn of the tribe Phaseoleae (Bronn) DC. were as comprehensively sampled as possible, especially in regard to American species. Multiple accessions of individual species were sampled when available to confirm DNA sequence integrity. The extensive sampling performed during this study (Appendix 1) builds on that of Delgado-Salinas et al. (1999, 2006), Riley-Hulting et al. (2004), and Thulin et al. (2004).

Outgroup sampling was guided by the phylogenetic studies of Wojciechowski et al. (2004), Lavin et al. (2005), and Schrire (2005) and included tribes Psoraleae Lowe and Phaseoleae subtribe Glycininae Benth., as well as miscellaneous millettoid and phaseoloid genera (Appendix 1). Selection of outgroups was made to detect the root of the crown clade containing all species traditionally assigned to *Vigna*. Ingroup sampling focused on the New World Phaseolinae, including the genera *Phaseolus* L., *Dolichopsis* Hassl., *Macroptilium* (Benth.) Urb., *Mysanthus* G. P. Lewis & A. Delgado, *Oxyrhynchus* Brandege, *Ramirezella* Rose, *Strophostyles* Elliott, and *Vigna* Savi subg. *Lasiospron* (Benth.) Maréchal et al., and subg. *Sigmoidotropis* (Piper) Verdc., and all of its constituent sections, *Caracallae* (DC.) Maréchal et al., *Condylostylis* (Piper) Maréchal et al., *Leptospron* (Benth.) Maréchal et al., *Pedunculares* Maréchal et al., and *Sigmoidotropis* Piper (Maréchal et al., 1978a, b). Only the genus *Oryxis* A. Delgado & G. P. Lewis of New World Phaseolinae did not yield amplifiable DNA, and its phylogenetic position within the New World *Vigna* clade is resolved only with morphological data (Riley-Hulting et al., 2004). Old World Phaseolinae samples included as many genera for which we could obtain PCR-amplifiable tissue, and these included *Alistilus* N. E. Br., *Dipogon* Liebm., *Dolichos* L., *Lablab* Adans., *Macrotyloma* (Wight & Arn.) Verdc., *Nesphostylis* Verdc., *Otoptera* DC., *Physostigma* Balf., *Psophocarpus* Neck. ex DC., *Spathionema* Taub., *Sphenostylis* E. Mey., *Wajira* Thulin, and *Vigna* subg. *Vigna*, subg. *Plectrotropis* (Schumach.) Baker, subg. *Ceratotropis* (Piper) Verdc., and subg. *Haydonia* (R. Wilczek) Verdc. (Schrire, 2005). In addition to *Oryxis*, three genera of Old World Phaseolinae, *Austrodolichos* Verdc., *Decorsea* R. Vig., and *Dysolobium* (Benth.) Prain, did not yield amplifiable DNA and thus could not be included in this study. From the taxonomic enumeration of subtribe Phaseolinae by Schrire (2005), all but four genera and 135 of ca. 320 species were analyzed.

Phylogenetic 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 Clara, California, USA). DNA sequencing was performed at Northwoods DNA (Solway, MN).

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* locus) were analyzed because they have been the most phylogenetically informative (Delgado-Salinas et al., 1999, 2006; Riley-Hulting et al., 2004; Thulin et al., 2004; Lavin et al., 2005). PCR primers for the ITS region were described in Delgado-Salinas et al. (1999) and those for the *trnK* locus in Riley-Hulting et al. (2004) and Wojciechowski et al. (2004). Sequences from the ITS region in papilionoid legumes often show little evidence of paralogous evolution. Where paralogous ITS products are commonly amplified in legumes, such as in many mimosoids, they are readily identified as pseudogenes by the numerous small insertion-deletion regions that occur even in the 5.8S region and by not being GC-rich (e.g., Bailey et al., 2003; Hughes et al., 2003, 2006). With the exception of certain species of *Macroptilium* (Espert et al., 2007), we did not detect paralogs in this study, pseudogenes or otherwise. In the case of *Macroptilium*, we limited sampling to just a few of the common species for which putative ITS orthologs sequenced cleanly and directly from PCR templates (i.e., without polymorphisms or the hallmarks of pseudogenes).

The ITS and *trnK* data were not combined because sampling was performed differently between these two genetic loci. Sequencing of the *trnK* locus was broadly focused on all of the traditionally recognized Old and New World tribes, subtribes, genera, and subgenera. Sequencing of the ITS region was more narrowly focused on the American species, in part because such sequences could be more readily aligned. The ITS region was in general more readily amplified and sequenced across many species so it could be used to validate the broader membership of the *trnK*-resolved American clades.

Phylogenetic analysis—Reverse and forward reads were assembled with the program Sequencher 4.1 (Gene Codes, Ann Arbor, Michigan, USA) and aligned with Clustal X version 2.0.10 using the default parameters (Larkin et al., 2007) or the similarity criterion of Simmons (2004). Parsimony and boot-

strap analyses used the heuristic search strategies implemented in the program PAUP* 4.0b10 (Swofford 2002). These strategies included SIMPLE and CLOSEST addition sequences with tree-bisection-reconnection (TBR) branch swapping, and retention of all most parsimonious trees. All characters were unweighted and unordered and maxtrees was set to 10000. Clade support was estimated with nonparametric bootstrap resampling (Felsenstein 1985) as implemented in PAUP* 4.0b10, where 10000 bootstrap replicates were each analyzed using the heuristic search parameters mentioned but with only one tree retained per replicate. Insertions and deletions were not coded for the phylogenetic analysis because none were detected as phylogenetically informative among more than a few species. Missing entries amounted to 8.5% for the *trnK* and 0.05% for the ITS data set. Most of these missing sites involved leading and trailing gaps. Data were deposited with the database TreeBase (<http://www.treebase.org>; submission ID 11214). Voucher specimens are reported for DNA sequences generated during this analysis (Appendix 1) as well as in Riley-Hulting et al. (2004), Thulin et al. (2004), and Delgado-Salinas et al. (2006).

Evolutionary rates analysis—A Bayesian analysis generated a set of phylogenetic trees that were subjected to an evolutionary rates analysis. MrBayes (Huelsenbeck and Ronquist, 2001) was used to search tree and nucleotide substitution parameter space. Two separate runs of a Metropolis-coupled Markov chain Monte Carlo permutation of parameters were initiated each with a random tree and four chains set at default temperatures (Huelsenbeck et al., 2001). The nucleotide substitution model was selected via the Akaike information criterion (AIC) implemented in the program ModelTest (Posada and Crandall, 1998) for nested models, or manually for nonnested models (Burnham and Anderson, 2002; Johnson and Omland, 2004); $AIC = [-2 \cdot \ln L + 2K]$, where K is the number of parameters in the model). A model having the lowest AIC value by over 2 units was considered the best fit (Burnham and Anderson, 2002). Markov chains were run for at least 5×10^6 permutations of tree parameters, and sampled no less than every 5×10^4 permutations such that sampling yielded 100 Bayesian trees at stationarity that were not autocorrelated.

The program r8s (Sanderson, 2004) was used to estimate nucleotide substitution rates and ages of crown clades for the *trnK* data, as described in Lavin et al. (2005). Rate and age estimates were obtained by constraining the age of the root of the Phaseolinae-Glycininae crown clade to 22 million years (Myr) or to the maximum age estimate for node 65 in Lavin et al. (2005). The maximum age constraint was used because it biases all other age estimates toward older ages and to emphasize that relatively young age estimates are still obtained even after biasing in favor of older ages (cf., Lavin et al., 2004). Age estimates were derived via penalized likelihood (PL) rate smoothing (Sanderson, 2002), which were then compared to the estimates derived from rate constant (LF; Langley and Fitch, 1974) and the rate variable nonparametric rate smoothing (NPRS) methods (Sanderson, 1997). An ITS rates analysis was not presented because of alignment difficulties among species of the Phaseolinae and Glycininae, so only the *trnK* results are reported. Regardless, attempts at ITS rates analysis yielded younger ages than those derived from the *trnK* data (data not shown), so the *trnK* results are taken as maximum age estimates.

RESULTS

Analysis of *trnK* data—The *trnK* phylogeny resolves the African Phaseolinae genera *Wajira*, *Sphenostylis*, *Alistilus*, *Nesphostylis*, *Dolichos*, *Macrotyloma*, *Lablab*, *Dipogon*, *Spathionema*, and *Vatovaea* as a grade in which the *Vigna*-containing clades are nested (*Vigna* s.l. in Fig. 1). The African genus *Physostigma* with four species in two subgenera is represented by only *P. venosum* of subg. *Physostigma*, which is resolved as sister to *Vigna* sensu stricto (Fig. 2). *Vigna* sensu stricto includes African species in which the Asian *Ceratotropis* subclade is nested (Fig. 2). *Vigna* subg. *Lasiospron* (represented by *Vigna lasiocarpa*, *V. longifolia*, and *V. trichocarpa*; “American *Vigna*” in Fig. 2) is also nested among African subclades. The mostly New World clade (Fig. 3) comprises species that have been traditionally designated as *Vigna*. They are resolved into six primary clades (indicated by asterisks in Fig. 3) that are nested among the American Phaseolinae genera *Phaseolus*,

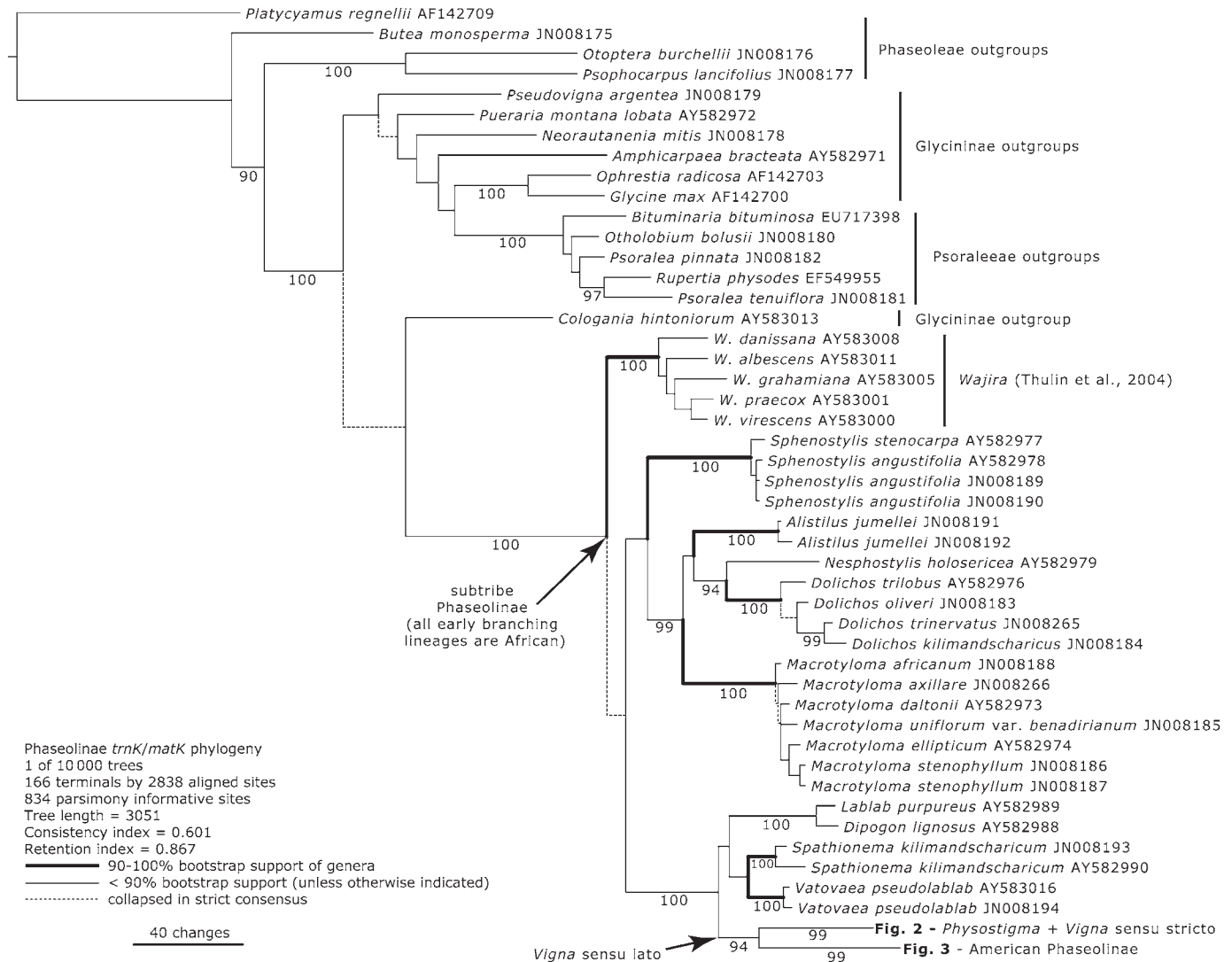


Fig. 1. One of the most parsimonious trees derived from analysis of *trnK* and showing the relationships among representatives of the legume tribe Phaseoleae subtribe Phaseolines and outgroups. Labels indicate where the clade is geographically concentrated. Bootstrap values (90–100%) are reported below the associated branch. Voucher specimens for GenBank accessions beginning with AF were reported by Delgado-Salinas et al. (1999), those beginning with AY by Riley-Hulting et al. (2004) and Thulin et al. (2004), those with DQ were reported by Delgado-Salinas et al. (2006), and those with JN are reported in Appendix 1.

Ramirezella, *Oxyrhynchus*, *Mysanthus*, *Macrotylimum*, *Dolichopsis*, and *Strophostyles*.

Analysis of ITS data—The ITS parsimony analysis resolves the representative Old World *Vigna* samples as paraphyletic with respect to the mostly American Phaseolines (Figs. 4, 5). The American Phaseolines, *Vigna* subg. *Lasiospron*, and *Vigna* subg. *Ceratotropis* are the well-supported primary clades in this analysis (Fig. 4). Most of the traditionally recognized American genera and infrageneric taxa of Phaseolines are resolved with very strong support (Fig. 5). These include *Phaseolus*, *Oxyrhynchus*, *Ramirezella*, *Macrotylimum*, *Mysanthus*, and *Dolichopsis*, as well as clades formerly classified as infrageneric taxa of American *Vigna* (those marked with an asterisk in Fig. 5). Only *Strophostyles* is weakly supported. The ITS results strongly support the monophyly of each of the primary New World clades identified in the *trnK* analysis (the labeled clades in Figs. 3 and 5).

Relationships among these primary New World clades are all weakly supported in both the ITS and the *trnK* analyses.

Evolutionary rates analysis of *trnK* sequence data—A molecular clock was rejected for the *trnK* data set (LR = 251.61, df = 243, $p < 0.00001$). In addition, the nucleotide substitution model selected using AIC for the *trnK* data set was the general time reversible with a gamma distribution for variable sites and a proportion for invariant sites (GTR+G+I). A mixed model invoking the general time reversible model with site-specific substitution rates (GTR+SS) applied to the *matK*-coding region was over 200 AIC units higher than the GTR+G+I model applied to the entire *trnK* sequence. The PL mean rate estimates derived from 100 *trnK* Bayesian trees sampled at likelihood stationarity ranged 0.0043–0.0074 substitutions per site per million years (Myr) (Table 1). The PL estimated ages for Phaseolines crown clades ranged approximately 1–14 Myr

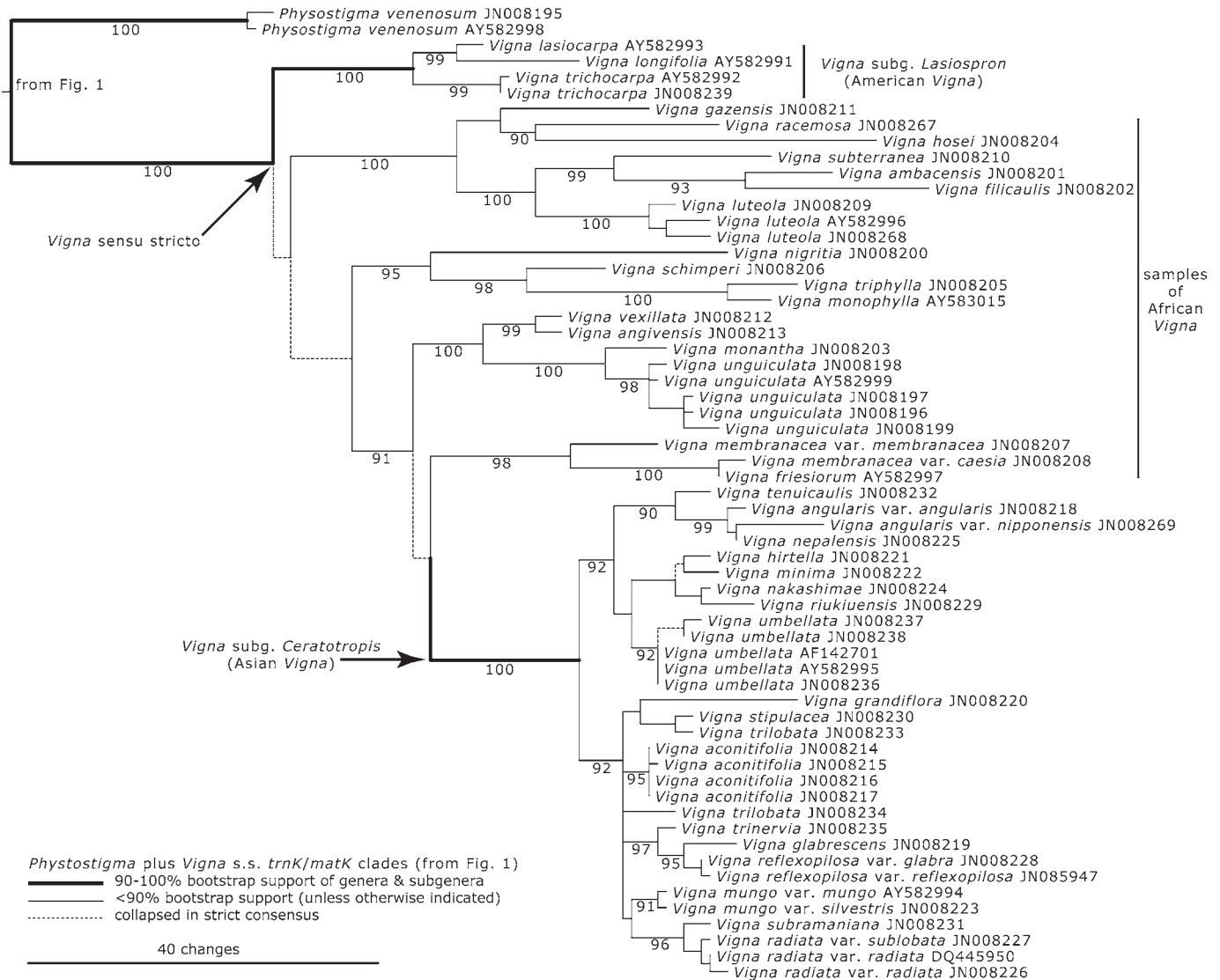


Fig. 2. Continuation of the *trnK* phylogeny (from Fig. 1) depicting relationships among the representatives of *Physostigma* and *Vigna* s.s. Labels indicate where the clade is geographically concentrated. Bootstrap values (90–100%) are below the associated branch. See Fig. 1 legend for references detailing voucher-specimen information for each of the GenBank accessions.

(Table 1). The diversification of the extant worldwide Phaseolinae has an age of at least 14 Myr. The age of the *Vigna sensu lato* crown clade (i.e., comprising both the predominantly Old and New World clades) is ca. 9 Myr. The Old and New World *Vigna*–containing crown clades are approximately coeval with estimated ages ranging about 6–7 Myr. All constituent American crown clades that are ranked here as genera (those labeled in Fig. 3) are distinctly young, with *Phaseolus* having the oldest point age estimate at about 5 Myr. The ages of the stem and crown clades confined to Africa are generally over 5 Myr (Table 1; ages of all African *Vigna* subclades not shown).

DISCUSSION

The monophyletic clades resolved here with molecular data were generally congruent with traditionally recognized taxa

ranked at the genus and infrageneric levels. The six clades of American species formerly assigned to *Vigna* (indicated by asterisks in Figs. 3, 5) are well marked by floral morphologies traditionally considered taxonomically diagnostic (Figs. 6–10; Maréchal et al., 1978a, b). The unexpected finding pertaining to *Physostigma* (at least subg. *Physostigma* with its sole constituent, *P. venenosum*) and its sister relationship with *Vigna sensu stricto* is beyond the scope of this analysis and can be dealt with only when African *Vigna* are subjected to exhaustive sampling and phylogenetic analysis.

Morphology that poorly predicts phylogenetic relatedness is sometimes the case, as illustrated in the dalbergioid legumes (Lavin et al., 2001). That it predicts relationships so well among the Phaseolinae finds precedence in the study of *Wajira*, formerly *Vigna* subg. *Macrorhynchus* Verdc. (Thulin et al., 2004). *Wajira* was well supported in a molecular phylogeny and was additionally well marked by its woody habit and a style bearing

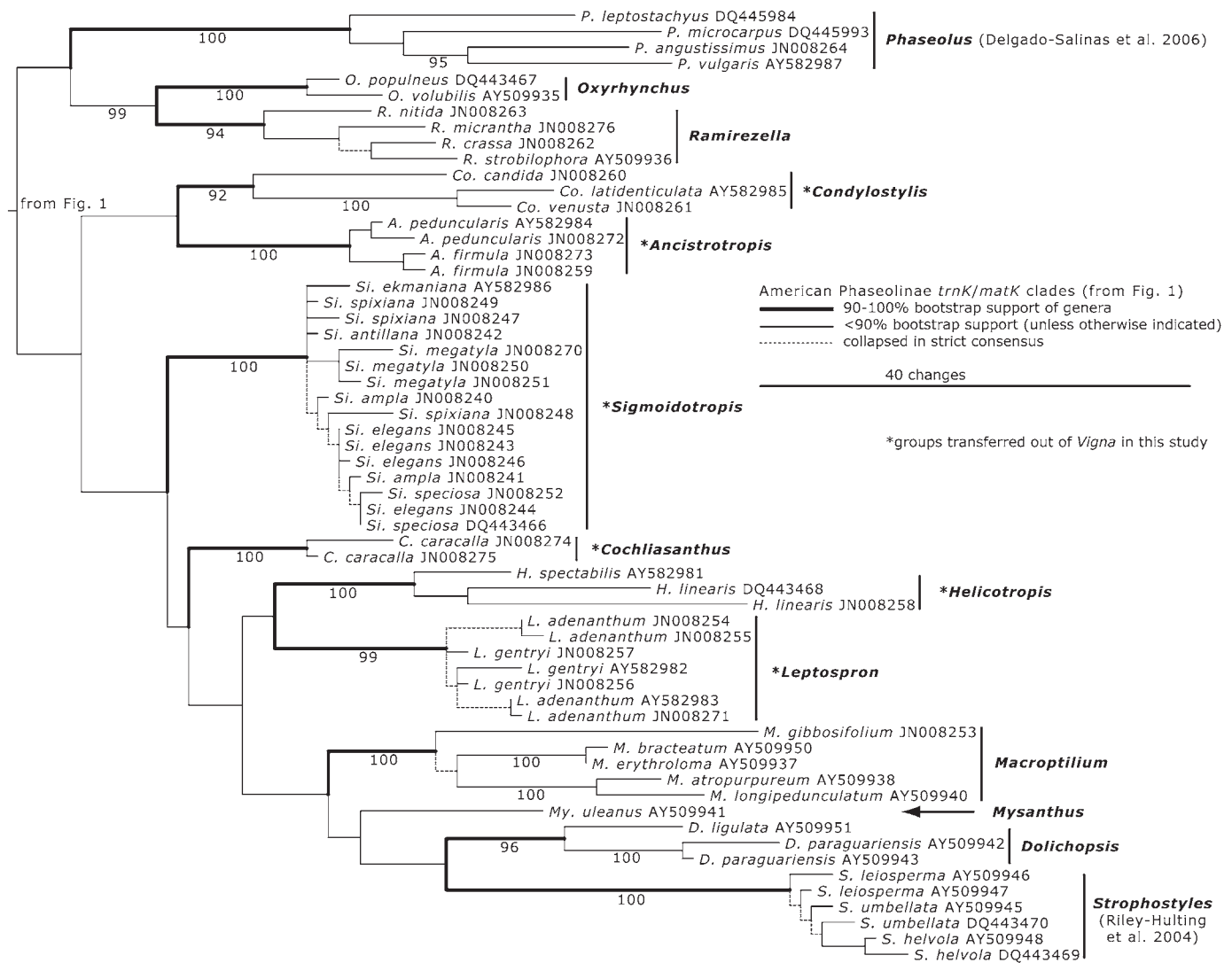


Fig. 3. Continuation of the *trnK* phylogeny (from Fig. 1) depicting relationships among representatives of the 13 genera of American Phaseolinae (the 14th genus, *Oryxis* is not represented; see Riley-Hulting et al., 2004). Bootstrap values (90–100%) are below the associated branch. Labels indicate where the clade is geographically concentrated. See Fig. 1 legend for references detailing voucher-specimen information for each of the GenBank accessions.

an introrse pollen brush of linear arrayed, unicellular, and often branched hairs. Floral morphology predicting phylogenetic relatedness suggests that, as new floral syndromes have evolved, they have remained fixed over evolutionary time so as to encompass multiple speciation events.

Geographic structure of the principal clades of Phaseolinae—In addition to morphology predicting phylogenetic relatedness, geography does also. All of the early-branching clades resolved in the Phaseolinae *trnK* analysis are highly concentrated in Africa and Madagascar, including *Alistilus*, *Dipogon*, *Dolichos*, *Lablab*, *Macrotyloma*, *Nesphostylis*, *Physostigma*, *Spathionema*, *Sphenostylis*, *Vatovaea*, and *Wajira*, as well as many subclades of *Vigna* s.s. (Figs. 1, 2), and the unsampled Old World genera *Decorsea* and *Dysolobium* (*Austrodolichos* is Australasian; Schrire, 2005). The Phaseolinae clade shows further geographic structure in that *Vigna* subg. *Ceratotropis*

is concentrated in Asia and subg. *Lasiospron* in the Americas. Both are nested among the primarily African *Vigna* subclades (Fig. 2), in agreement with the broader sampling of African *Vigna* by Feleke (2006). The nesting of the primarily American and Asian Phaseolinae subclades (Figs. 2, 4) within the larger world wide Phaseolinae clade suggests a more recent occurrence of extant Phaseolinae in Asia and the Americas relative to Africa.

The ages of the various crown clades within the Phaseolinae phylogeny were biased old by fixing the root node (i.e., the Phaseolinae stem clade) at the maximum age estimated in the analysis of Lavin et al. (2005). This distributes the number of nucleotide substitutions over a longer time frame, thus biasing for slower substitution rates that in turn bias for older age estimates along all branches. This approach was taken by Lavin et al. (2004) to demonstrate that after biasing for older ages, the estimated ages of crown clades distributed on more than one

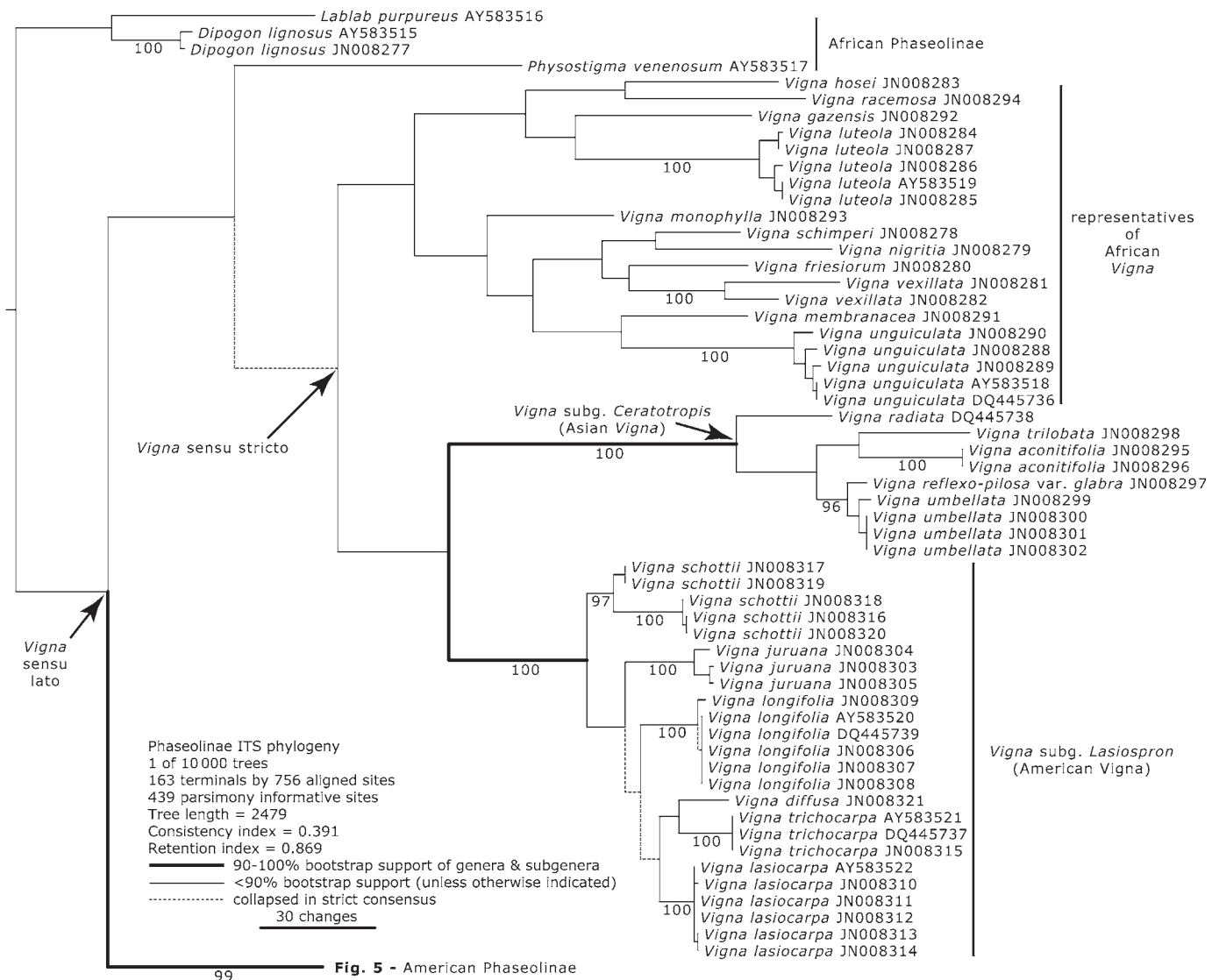


Fig. 4. One of the most parsimonious trees derived from analysis of ITS region and showing the relationships of the primarily Old World *Vigna* clade and outgroups (*Lablab* and *Dipogon*). Labels indicate where the clade is geographically concentrated. Bootstrap values (90–100%) are below the associated branch. See Fig. 1 legend for references detailing voucher-specimen information for each of the GenBank accessions.

continent (transoceanic crown clades) were still much less than 20 Myr. This finding precluded unique historical explanations (e.g., plate tectonics, land bridges) because such geological events putatively structuring extant biodiversity patterns were all older than 30 Myr (summarized in Lavin and Beyra-Matos, 2008). Likewise, transoceanic and transcontinental subclades of Phaseolinae are far too young to be explained by plant tectonic or landbridge hypotheses (Table 1).

Ecological structure of the Phaseolinae phylogeny—The ecological predilection of Phaseolinae commonly includes forest and savanna vegetation with an abundance of grass species, a pronounced dry season, and an intermittent fire regime (e.g., the Brazilian cerrado). Exceptions to this include some species of *Vigna* s.s. and species of *Vigna* subgenus *Laiospron*, which inhabit tropical wet forests. The genus *Wajira* is distributed mostly in the bush thicket in the Horn of Africa region and

Mysanthus is confined to the caatinga and Chiquitano, two regions of South American seasonally dry tropical woodlands (e.g., SDTFs of Pennington et al., 2004, 2009). These last three regions are notably poor in grass but rich in succulent plants (the succulent biome; Schrire et al., 2005). *Strophostyles* (North America) and its sister *Dolichopsis* (Chaco) inhabit temperate forest or savanna settings with a regular frost period. Regardless, Phaseolinae subclades contrast to other tropical legume groups (e.g., Robinieae Hutch.; Lavin et al., 2003; Lavin, 2006) in transgressing different types of woodlands and forests.

Legume phylogenies are often structured more by ecology and geography. Ecologies marking legume clades commonly include temperate vs. tropical vegetation (i.e., annual frost vs. frost-free) and seasonally dry tropical woodlands rich in succulent plants (i.e., the succulent biome) vs. seasonal vegetation rich in grass cover and thus impacted by episodic fire or drought

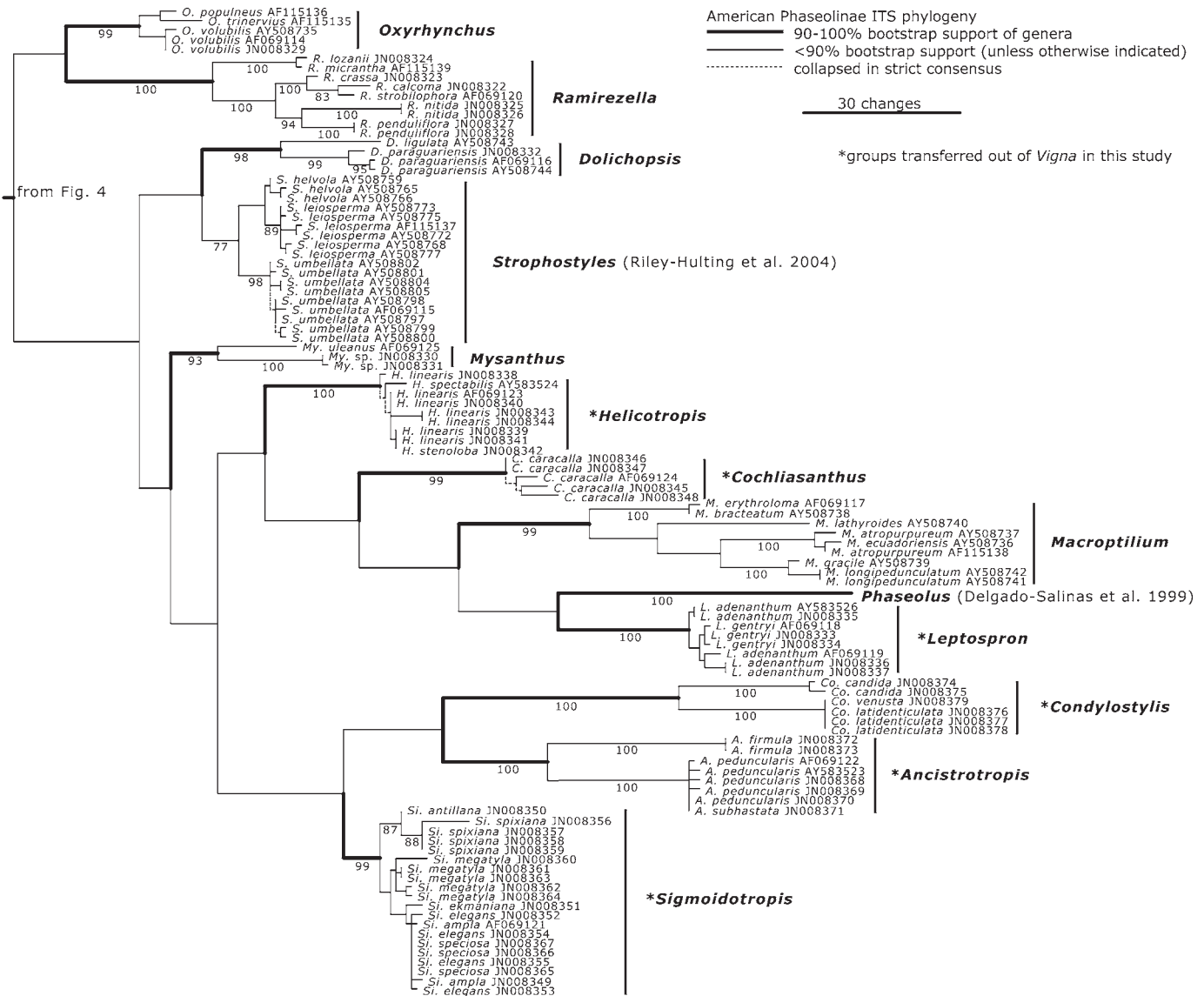


Fig. 5. Continuation of ITS phylogeny (from Fig. 4) depicting relationships among the primarily New World *Vigna* clade. Labels indicate where the clade is geographically concentrated. Bootstrap values (90–100%) are reported below the associated branch (the low support value for the *Strophostyles* clade is also reported). See Fig. 1 legend for references detailing voucher-specimen information for each of the GenBank accessions.

(e.g., savanna woodlands; Schrire et al., 2005). The broad ecological amplitudes of the clades of legume vines resolved in this analysis suggest that the phylogenetic history of Phaseolinae has not been so constrained by the different aforementioned woody vegetation types. The ecological setting for Phaseolinae vines encompasses all kinds of vegetation types with a woody physiognomy, generally without regard to the degree of frost, drought, or fire.

The relatively few Phaseolinae species with a pantropical distribution often inhabit wet forest settings. The pantropical species of *Vigna* s.s., *Vigna vexillata*, and *V. luteola* and its segregate species such as *V. marina* (Burm.) Merr. are distributed among many tropical islands of the world (Pasquet, 2001). The occurrence of *V. luteola*, *V. marina*, and *V. vexillata* in Asia and the New World is relatively recent compared to presence of these pantropical species in Africa (Hedström and

Thulin, 1986; T. Kajita et al., Chiba University, unpublished manuscript). Among the New World species, the *Lasiospron* clade is confined to tropical wet forests and includes three ampho-Atlantic species, *Vigna juruana*, *V. diffusa*, and *V. trichocarpa*. The concentration of species and populations of the *Lasiospron* clade in the neotropics suggests that the occurrence of these species in Africa and Madagascar (Verdcourt, 1970; Maxted et al., 2004; Delgado-Salinas et al., UNAM, unpublished manuscript) is relatively recent. Other pantropical species nested in the American Phaseolinae clade and that have broad ecological tolerances involving wet forests include *Leptospron adenanthum*, *Macroptilium lathyroides*, and *Phaseolus lunatus*, but these are likely human dispersed. *Oxyrhynchus papuanus* (Pulle) Verdc., endemic to New Guinea (Verdcourt, 1979) is most closely related to *Oxyrhynchus* species from Mexico, Cuba and the Bahamas, Central America, and western Colombia

TABLE 1. Crown clades and their native distribution, with penalized likelihood (PL) rate-smoothed estimated ages and substitution rates (subs/site/million years) derived from the *trnK* locus.

Crown clade	Native geographical distribution	PL age (Myr)	PL rate (subs/site/Myr)
Phaseolinae	Pantropical	13.3 ± 0.9	0.0052 ± 0.0005
<i>Wajira</i>	Mostly Horn of Africa, one extending into Asia	7.2 ± 1.3	0.0043 ± 0.0006
<i>Vigna sensu lato</i>	Pantropical	9.1 ± 1.0	0.0058 ± 0.0007
<i>Vigna sensu lato</i> + <i>Physostigma</i>	Mostly African or Asian, some pantropical, <i>Vigna lanceolata</i> endemic to Australia	6.0 ± 0.7	0.0067 ± 0.0009
<i>Vigna</i> subg. <i>Lasiospron</i>	Mostly neotropical, three extending to Africa	2.3 ± 0.5	0.0065 ± 0.0009
<i>Vigna sensu stricto</i>	Mostly African or Asian, some pantropical	4.5 ± 0.6	0.0074 ± 0.0009
<i>Vigna</i> subg. <i>Ceratotropis</i>	Mostly Asian, some pantropical	2.6 ± 0.4	0.0069 ± 0.0010
American Phaseolinae	Mostly New World, some pantropical	7.4 ± 1.0	0.0058 ± 0.0008
<i>Cochliasanthus</i>	New World, cultivated worldwide	1.5 ± 0.5	0.0045 ± 0.0009
<i>Condylostylis</i>	New World but not West Indies	4.3 ± 0.7	0.0051 ± 0.0009
<i>Ancistrotropis</i>	New World	1.3 ± 0.3	0.0053 ± 0.0010
<i>Sigmoidotropis</i>	New World	1.6 ± 0.6	0.0046 ± 0.0011
<i>Helicotropis</i>	New World but not West Indies except Trinidad and Tobago	3.2 ± 0.6	0.0059 ± 0.0010
<i>Leptospron</i>	New World but <i>L. adenanthum</i> pantropical	1.4 ± 0.4	0.0055 ± 0.0010
<i>Macroptilium</i>	New World but <i>M. lathyroides</i> pantropical and other species cultivated worldwide	3.3 ± 0.5	0.0066 ± 0.0010
<i>Dolichopsis</i>	South American	2.5 ± 0.5	0.0064 ± 0.0010
<i>Strophostyles</i>	North American	0.8 ± 0.2	0.0068 ± 0.0010
<i>Phaseolus</i>	New World, <i>P. lunatus</i> in West Indies and other New World islands and also cultivated in Africa, other species cultivated worldwide	5.1 ± 0.7	0.0062 ± 0.0008

Note: Ages and rates pertain to crown clades in Figs. 1–3. Point estimates and standard deviations were derived from the analysis of 100 non-autocorrelated Bayesian trees sampled broadly at likelihood stationarity. The optimal rate smoothing parameter for the *trnK* sequence data ranged from 10^0 to $10^{0.5}$, which results in rates that are on average intermediate between those of rate constancy and nonparametric rate smoothing. These estimates are derived from a fixed root age of 22 Myr for the Phaseolinae stem clade (Lavin et al., 2005).

(Rudd, 1967; A. Delgado-Salinas et al., UNAM, unpublished manuscript). PCR-amplifiable DNA has yet to be obtained to validate this relationship. *Oxyrhynchus papuanus*, like the aforementioned species with a pantropical distribution, is known from at least tropical wet forests. No transoceanic species come from seasonally dry tropical woodlands rich in succulent taxa.

A phylogenetic classification of the American Phaseolinae—Phaseolinae is a taxonomically distinct subtribe of papilionoid vines that bear leaves each with three leaflets and with the two laterals having a characteristic basispic outline. In this context, Phaseolinae includes all descendants from the most recent common ancestor of *Wajira* and *Phaseolus* and is apomorphically diagnosed by a 78-kb inversion within the large single-copy region of the chloroplast genome, seeds bearing an epihilum (Bruneau et al., 1990), the lack of accumulation of the nonprotein amino acid canavanine (Lackey, 1981), and a style bearing a pollen brush (Lavin and Delgado-Salinas, 1990). The pollen brush is secondarily lost in the clade comprising *Alistilus*, *Dolichos*, *Nesphostylis*, and *Macrotyloma* (Fig. 1). The *trnK* analysis suggests that *Otoptera* and *Psophocarpus* should be excluded from Phaseolinae because they are part of the early-branching grade of the Phaseoloid clade, as delimited in Wojciechowski et al. (2004). The pollen brush of *Otoptera* is lacking, and that of *Psophocarpus* comprises sparse, multicellular, crisped hairs (Lavin and Delgado-Salinas, 1990). In addition, *Psophocarpus* is known to lack the 78-kb inversion of the chloroplast genome that is otherwise known from only the genera of Phaseolinae as delimited in this analysis (Bruneau et al., 1990).

The variable floral morphologies among the subclades of the primarily New World Phaseolinae are used to formally circumscribe genera. Throughout this manuscript, floral asymmetries refer to a particular wing that takes over the function of the standard (e.g., as in *Macroptilium*) or that serves as the main landing platform, or to the location of a supporting structure such as boss-and-socket joints or spurs, or to the direction in

which the keel tip or distal keel coils are directed. The expression of floral asymmetries at anthesis renders a unique floral presentation and presumably a unique functionality to each of the American genera herein delimited. As such, a “right-handed” asymmetry is with reference to a human observing the flower from the back of the blade of the standard petal, as if the face of the standard petal (i.e., the face bearing the nectar guide) had two wing petals as its right and left hands.

The right-handed floral asymmetries consistently mark all of the American genera of Phaseolinae (Figs. 6–10) and deviate only in *Condylostylis candida* (Figs. 8E, 8F), where the keel beak slightly twists to the left side and the left-hand wing serves as a landing platform. The right-handed floral asymmetry of the primarily American *Vigna* subg. *Lasiospron* clade sets it apart from the rest of the primarily Old World *Vigna* s.s., which has floral morphologies that are either bilaterally symmetric or with left-handed asymmetries. The *Vigna* s.s. subgenera *Plectrotropis* and *Ceratotropis* have the left-hand keel petal bearing a conspicuous pocket or a distinctive spur that supports the adjacent wing petal, which serves as a landing platform for the visiting pollinator (Hedström and Thulin, 1986; Tomooka et al., 2002).

In contrast to floral morphology, vegetative morphology is relatively uniform among the genera and higher taxa of Phaseolinae. *Vigna* s.s. (including the primarily New World *Lasiospron* clade) is apomorphically diagnosed by having medifixed stipules (i.e., peltate or appendiculate, however slight the downward projection; Maréchal et al., 1978b). All other Phaseolinae, including *Physostigma* and the New World clades, possess basifixed stipules, the most ubiquitous form among legumes. The only other notable instance of a distinctive vegetative morphology marking a large subclade of Phaseolinae involves the uncinata hairs on the foliage of *Phaseolus* (Delgado-Salinas et al., 1999).

The following enumeration of the 14 American Phaseolinae genera plus *Vigna* subg. *Lasiospron* underscores the great apomorphic floral and inflorescence variation in this group.

Key and descriptions to the genera of the American Phaseolinae—

1. Stipules produced below the zone of attachment (medifixed) or sometimes shortly auriculate; corolla yellow; legume resupinate by twisting of the pedicel and held patent or erect on the infructescence; seeds mostly with a white aril *Vigna* subg. *Lasiospron*
1. Stipules not produced below the zone of attachment (basifixed); corolla various in color, rarely yellow; legume not resupinate, held in different positions on the infructescence; seeds without an aril **2**
2. Plant always with uncinata or minutely hooked hairs (at least on pulvini in glabrous species); nodes of pseudoraceme neither swollen nor nectariferous; pedicels equal to or longer than length of calyx tube; floral bracts mostly persistent; keel petals beaked, apex laterally and tightly coiled..... *Phaseolus*
2. Plants with straight, loosely tangled, and glandular hairs, never with uncinata or hooked hairs; nodes of pseudoraceme swollen (or not in *Ramirezella*), always nectariferous; pedicels of various lengths, mostly shorter than calyx tube; floral bracts variably persistent, mostly caducous; keel beak with different shapes and coils but not laterally so (the downward projected keel coils of *Leptospron* species may appear laterally positioned after drying in a plant press) **3**
3. Pseudoraceme nodes not noticeably swollen although nectariferous; pedicels mostly longer than calyx tube; flowers 2.0–3.0 cm long (sometimes resupinate by a twist of the pedicel); keel beak recurved and twisted, often sigmoid (similar to *Sigmoidotropis*) *Ramirezella*
3. Pseudoraceme nodes usually conspicuously swollen and nectariferous; pedicels mostly shorter than calyx tube (not in *Cochlianthus*); flower length and keel shape various **4**
4. Blade of wing petals narrowly elliptical and not projected beyond distal bend (upward curvature) of keel (wings scarcely longer in *Dolichopsis*)..... **5**
5. Keel petals fused along upper margin where a gibbosity or hump forms proximal to the beak; standard petal without appendages on inner face in region of nectar guide or elsewhere **6**
6. Stipules divergent from the main axis; calyx with four acute to attenuate teeth; secondary floral bracts (subtending the pedicel) persistent; style terete the full length; legume cylindrical to subcylindrical with longitudinally arranged seeds *Strophostyles*
6. Stipules antrorse and closely appressed to main axis; calyx with five blunt teeth; secondary floral bracts (subtending pedicel) caducous; style distally flattened and furrowed; legume broad and laterally flat, with transversely arranged seeds *Dolichopsis*
5. Keel petals fused along upper margin without forming a gibbosity or hump proximal to the beak; standard petal with two prominent appendages on inner face above region of nectar guide..... **7**
7. Leaflets cordate to subcordate; legume subcylindrical, chartaceous, 5–7 cm long, ca. 0.5 cm wide; mature seeds unknown; seasonally dry forest; Brazil..... *Oryxis*
7. Leaflets not cordate to subcordate; legume cylindrical, coriaceous, 3–11 cm long, (1.3) 2–4 cm wide; seeds 2–6, spheroidal to oblong-thick, hilum 50–98% of seed length; tropical wet, seasonally dry, and montane forests; Mexico, Central America, northwest South America, and New Guinea *Oxyrhynchus*
4. Blade of wing petals broadly elliptical and projected conspicuously beyond distal bend (upward curvature) of keel **8**
8. Beak of keel distinctly sigmoid or hooked, in the case of *Macroptilium* the left-hand wing petal adopts the standard location within the flower..... **9**
9. Beak of keel narrowly hooked or tightly curved, tip of keel beak usually hidden from visual inspection (Fig. 9C, 9E)..... **10**
10. Plants usually climbing, herbaceous to woody; corolla lilac-purple, fading to yellowish, right-hand wing petal functioning as a landing platform, left wing held vertically and apparently not engaged with standard or keel petals; legume 0.8–1.0(–1.4) cm wide..... *Mysanthus*
10. Plants trailing or climbing, herbaceous; corolla red, pink, purple, or yellow, but in any case usually fading to purple; left-hand wing petal directed upward to adopt the function of the standard petal (the standard is reduced in size, coloration, and becomes a supporting structure of the wing petal that takes its place); legume 0.2–0.3 cm wide..... *Macroptilium*
9. Beak of keel widely curved, openly hooked, or sigmoid-curved, tip of keel beak usually readily opens to visual inspection (Figs. 8A, 8B, 10E)..... **11**
11. Beak of keel gradually curved upward into a hook-shape, with the upper overlapping margins (located to the inside or introrse) bordered with long trichomes (0.2–0.5 mm long), the distalmost portion of keel beak folded back on itself; legume short-rostrate at apex, mostly erect in the infructescence..... *Ancistrotropis*
11. Beak of keel distinctly sigmoid-curved with the upper overlapping margins (located to the inside or introrse) bordered with minute trichomes, distal portion of keel beak not folded back; legume sometimes long-rostrate at apex, spreading in the infructescence *Sigmoidotropis*
8. Beak of keel straight, erect, or tightly to loosely coiled, but never sigmoid or hooked and not necessarily projected upward in a plane parallel to that of the standard blade **12**
12. Lateral and lower calyx lobes, like the upper two lobes, obtusely rounded and shorter than calyx tube; herbage with whitish or grayish hairs; legume without strongly thickened sutures, valves neither strongly laterally compressed nor covered with minute antrorse barbs..... **13**
13. Standard petal coiled; keel beak with numerous coils; style not swollen especially at or near the base; stigma not surpassed by a projection of the style; legumes pendent on the infructescence *Cochlianthus*
13. Standard petal not coiled; keel beak mostly erect or with a slight twist to left side; style with globose thickening near base; stigma surpassed by a distal projection of the style; legumes erect to slightly spreading on the infructescence *Condylostylis*
12. Lateral and lower calyx lobes, unlike the shorter upper two lobes, acute and equal to or longer than calyx tube; herbage with stiff reddish brown hairs; legume with strongly thickened sutures, valves both strongly laterally compressed and covered with minute antrorse barbs **14**
14. Distal portion of keel very tightly coiled (ca. 4 mm diam.) like that of *Phaseolus* but projected downward rather than laterally; lateral calyx teeth shorter than calyx tube and falcate, 1–2 mm long; legume falcate, with 10–18 seeds *Leptospron*
14. Distal portion of the keel loosely coiled (ca. 8 mm diam.) in a forward direction (i.e., directly away from the calyx and inner face of the standard petal); lateral and abaxial calyx teeth longer than calyx tube, narrowly triangular-attenuate, 5–8 mm long; legume straight, with 18–20 seeds..... *Helicotropis*

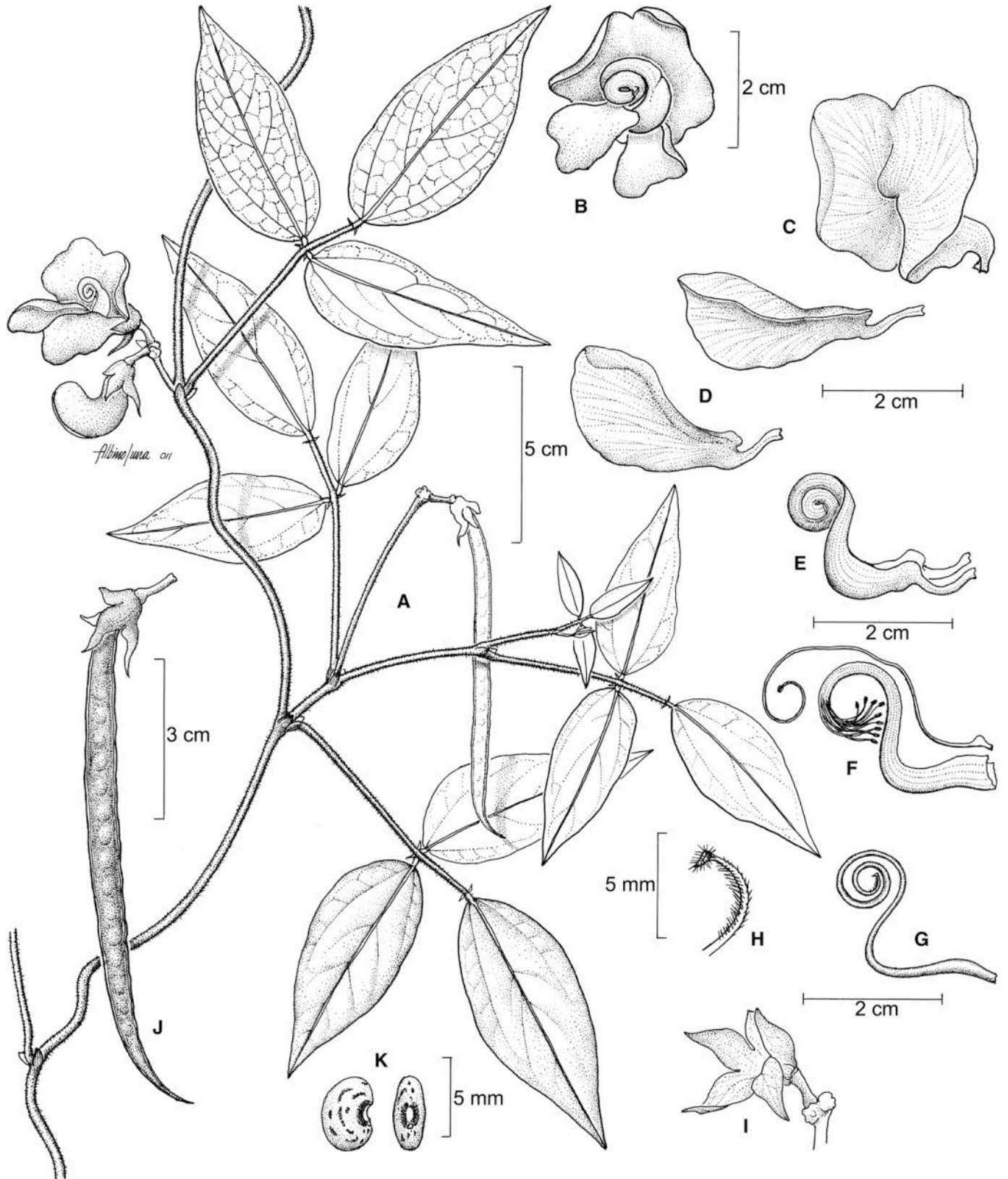


Fig. 6. The genus *Helicotropis* exemplified by *H. spectabilis* (M. Sousa 12815, MEXU). (A) Twining branch with axillary pseudoracemes each with one swollen node where one bears a flower at anthesis and in bud and the other an immature fruit. (B) Front view of flower showing the coiled keel beak in a forward position (D.E. Breedlove 29563, MEXU). (C) Side view of standard petal. (D) Wing petals. (E) Keel petals. (F) Androecium comprising a staminal tube and a free vexillary stamen with a swollen base. (G) Gynoecium with the style coiled distally into two loops. (H) Distal portion of style with pollen brush and penicillate stigma. (I) Calyx with lanceolate lateral and lower lobes, which are longer than the two upper lobes. (J) Legume with persistent calyx (D.E. Breedlove 29563, MEXU). (K) Front and side views of the seed (A. Valera s.n., MEXU). Drawn by Albino Luna (IBUNAM).

Ancistrotropis A. Delgado, nom. & stat. nov., *Phaseolus* ser. *Pedunculares* Hassl., *Candollea* 1: 433–434, 1923. *Vigna* sect. *Pedunculares* Maréchal et al., *Taxon* 27: 201, 1978. Type: *Ancistrotropis peduncularis* (Fawcett & Rendle) A. Delgado (= *Phaseolus peduncularis* Fawcett & Rendle).

Diagnosis—This genus is characterized by small to medium-size flowers (less than 2 cm) with a pleated calyx tube, a standard petal forming a hood, wing petals much longer than keel, and a hooked keel beak similar to that of *Sigmoidotropis* but with the distalmost portion splayed open. The inner margins of the keel beak are not fused but closed by conspicuous interlocking marginal hairs. The style thickens distally and extends as a small beak beyond the stigma. The stigma is laterally extrorse due to torsion of the style (i.e., laterally positioned initially but ultimately turned to the outside face in an extrorse position). The pollen is tricolporate, widely reticulate, with a columellar exine ultrastructure (Maréchal et al., 1978b). The legume is linear to slightly curved and is maintained erect in the infructescence. This latter character is shared with *Condylostylis*. Drawings of flowers of *Ancistrotropis peduncularis* and *A. firmula* are found in Lackey (1979, pp. 179, 180) and sketches of their general habit in Aymard (1999, p. 429). Chromosome counts of *A. peduncularis* include an aneuploid number $2n = 18$ (Vanderborgh et al., 1989), which differs from $2n = 22$ recorded for most other species of American Phaseolinae (e.g., Mercado-Ruaro and Delgado-Salinas, 1996; Vanderborgh et al., 1989). *Ancistrotropis* is distributed throughout much of the neotropics mainly in secondary and primary forests with or without a dry season (0–1200 m a.s.l.). *Ancistrotropis* from the Greek, *ancistrōn*: fish-hook, and *tropis*: keel of a ship, referring to the hooked distal portion of the keel petals of the flower. Figures 8A, 8B.

As a guide to the eventual comprehensive list of constituent species, the following six species embody all of the diagnostic traits of *Ancistrotropis* and capture much of its species diversity (this study sampled the first three of these):

Ancistrotropis firmula (Bentham) A. Delgado comb. nov., based on *Phaseolus firmulus* Martius ex Bentham in *Comm. Legum. Gen.* 74. 1837. (= *Vigna firmula* (Mart. ex Benth.) Maréchal et al. in *Taxon* 27(2–3): 201. 1978). Type: Brazil, in sepibus et in campis provinciae ae Minas Geraes. *Martius* s.n. (lectotype here designated M!).

Ancistrotropis peduncularis (Fawcett & Rendle) A. Delgado comb. nov. *Phaseolus peduncularis* Fawcett & Rendle nom. nov. in *Verdc., Kew Bull.* 56: 229–232. 2001, based on *Phaseolus peduncularis* Kunth in *Humb. & Bonpl., nov. gen. sp. (folio ed.)* 6: 350. 1824. nom. illegit. (= *Vigna peduncularis* (Kunth) Fawcett & Rendle in *Fl. Jam.* 4: 68. 1920), non *Phaseolus peduncularis* (Muhl.) W.P.C. Barton in *Comp. Fl. Philadelph.* 2: 81. 1818. Type: Colombia, Central Cordilleras, Mariquita to Santa Ana, Jun 1801, *Humboldt & Bonpland* s.n. (holotype P!) Illustration: *Boisseria* 28: 225. fig. 47. 1978.

Ancistrotropis subhastata (Verdc.) A. Delgado comb. nov., based on *Vigna subhastata* Verdc. in *Kew Bull.* 56: 229–232. figs. 1a–h; 2a–d. 2001. Type: Bolivia, Santa Cruz, Velasco, Reserva Forestal Bajo Paraguá, 12 May 1994, *Killeen & Wellens* 6305 (holotype K!; isotype MO). Illustration: *Kew Bull.* 56: 229–232. fig. 1. 2001.

Ancistrotropis arrabidae (Steud.) A. Delgado comb. nov. *Phaseolus arrabidae* Steudal nom. nov. in *Nomencl. Bot. Ed.* 2(10): 316. 1841, based on *Phaseolus dolichooides* Vellozo in *Fl. Flumin.* 7: 312; t. 127. 1825. nom. illegit., non *Phaseolus*

dolichooides Roxburgh in *Hort. Bengal.* 54. 1814 (= *Vigna dolichooides* Baker in Hooker f., *Fl. Brit. India* 2(4): 206. 1876). Type: Brazil, “Habitat ad ripas fluvii Parat’y prope Pharmacopolim” (lectotype designated here, illustration t. 127 in Vellozo, *Fl. Flumin.* 7: 312. 1825).

Ancistrotropis clitorioides (Bentham) A. Delgado comb. nov., based on *Phaseolus clitorioides* Martius ex Bentham in *Comm. Legum. Gen.* 73–74. 1837. Type: Brazil, in campis provinciae Minas Geraes, *Martius* s.n. (holotype M!).

Ancistrotropis robusta (Piper) A. Delgado comb. nov., based on *Phaseolus robustus* Piper in *Contr. U. S. Natl. Herb.* 22(9): 676. 1926. Type: Brazil, San Antonio, near Petropolis, in the vicinity of Rio de Janeiro, Nov 1879, *M. Glaziou* 10566 (holotype K!).

Cochlianthus Trew, *Pl. Rar.* 41, t. 10. 1763. *Vigna* subg. *Cochlianthus* (Trew) Verdc., *Kew Bull.* 24: 552, 1970. *Phaseolus* sect. *Caracallae* DC., *Prodr.* 2: 390. 1825. *Vigna* sect. *Caracallae* (DC.) Maréchal et al., *Taxon* 27: 201, 1978. Type: *Cochlianthus caracalla* (L.) Trew (= *Phaseolus caracalla* L.).

Diagnosis—A monotypic genus characterized by flowers born on pedicels that are longer than the calyx, which results in a very open or diffuse pseudoraceme. The flowers are characteristically large (e.g., the total calyx length measures ca. 1 cm on average) and very showy in that the standard and wing petals are twisted (spiraled) in a right-handed fashion, and the keel is distally twisted with up to five loose right-handed coils. Pollination studies and field observations in northern Argentina (Etcheverry et al., 2008) have reported *Xylocopa* bees as pollinators. Male and female *Eufriesea* bees are reported as visitors and copious nectar is consumed by humans in northern Argentina (C. Skov, Rungsted Gymnasium, Denmark, personal communication). *Cochlianthus* is distributed in secondary and primary wet forests, mostly without a dry season, from southern Mexico to northern Argentina and Uruguay. *Cochlianthus caracalla* has long been cultivated worldwide for its spectacular flowers. Figures 8C, 8D.

The monotypic *Cochlianthus* includes the following species (multiple accessions of each were sampled during this analysis):

Cochlianthus caracalla (L.) Trew, based on *Phaseolus caracalla* L. in *Sp. Pl.* 2: 725. 1753. Type: “Habitat in India” (lectotype “*Phaseolus Indicus cochleato flore*” in Trionfetti, *Obs. Ortu Veg. Pl.*: 93, unnumbered plate. 1685). Epitype: Brasil, S. of Rio Ivaí, N. of Boa Esperanca, ca. 30 km E of Cianorte, 29 Mar 1966, *Lindeman & de Haas* 823 (K!). [= *Vigna caracalla* (L.) Verdc. in *Kew Bull.* 24(3): 552. 1970]. Illustration: *Pl. Rar.* 41, t. 10. 1763. *Fl. Fluminense* 312. t. 126. 1825.

Maréchal et al. (1978b) classified *Vigna hookeri* Verdc. and *V. vignoides* (Rusby) Maréchal et al., which were not sampled for molecular data in this study, and *V. linearis* as members of sect. *Caracallae*. These three are here readily classified using floral morphology into *Sigmoidotropis*, *Condylostylis*, and *Helicotropis*, respectively.

Condylostylis Piper, *Contr. U. S. Natl. Herb.* 22: 667. pl. 64. 1926. *Vigna* sect. *Condylostylis* (Piper) Maréchal et al., *Taxon* 27: 201, 1978, non *Vigna* sect. *Condylostylis* Verdc., *Kew Bull.* 24: 533–534, 1970. Type: *Condylostylis venusta* Piper.

Diagnosis—This genus is apomorphically diagnosed by a style that bears a globose thickening near its base and by seeds that are covered with a caducous waxy layer. The thick style base gives structural support to the tubular or bottle-shaped

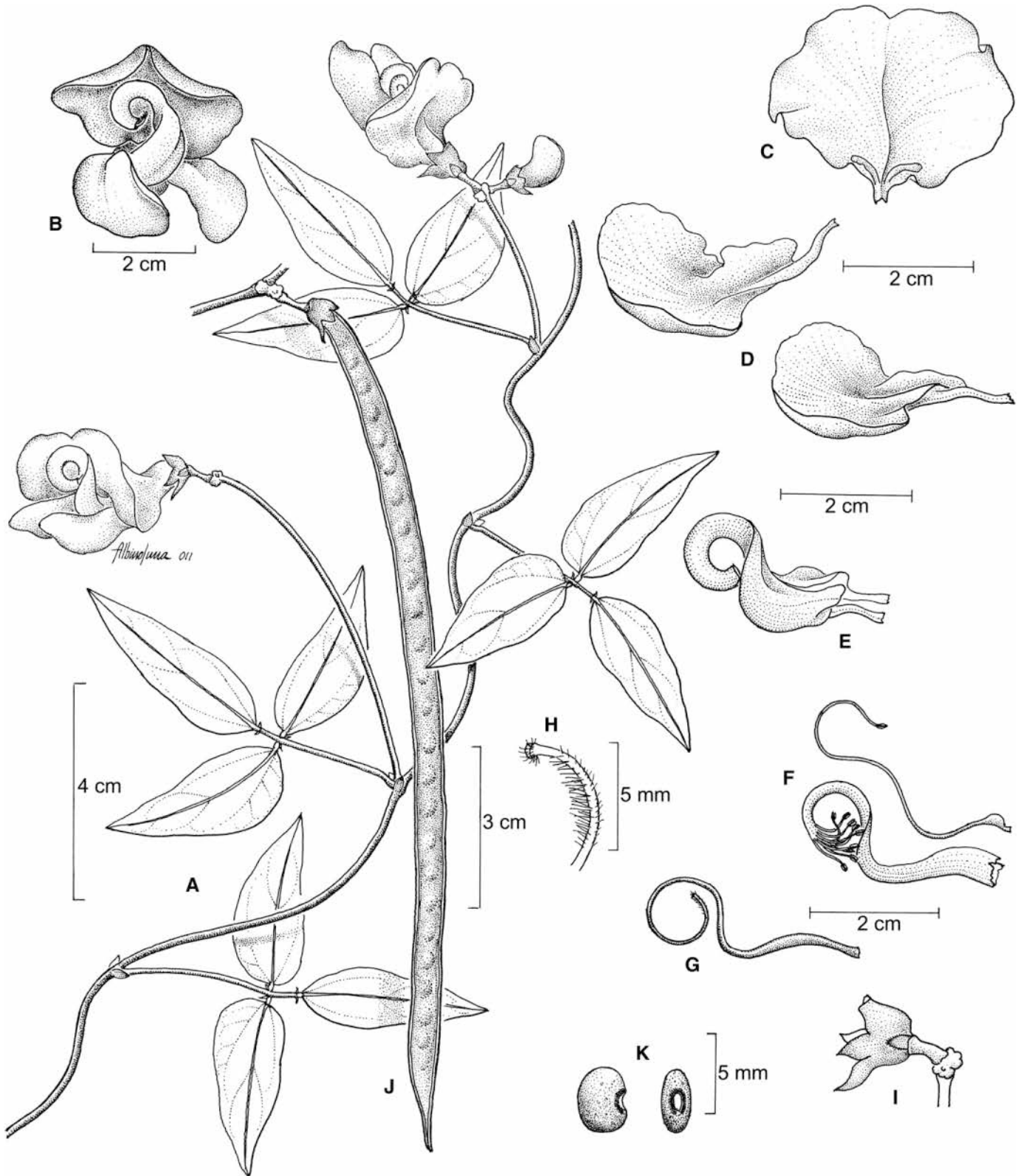


Fig. 7. The genus *Sigmoidotropis* exemplified by *S. speciosa* (F. Ventura 7632, MEXU). (A) Twining branch with axillary pseudoracemes each with one swollen node where one bears a flower at anthesis and in bud and the other one flower at anthesis. (B) Front view of flower showing the S-shaped keel beak. (C) Front view of standard petal. (D) Wing petals. (E) Keel petals. (F) Androecium comprising a staminal tube and a free vexillary stamen with a swollen base. (G) Gynoecium with style coiled distally into a single loop. (H) Distal portion of style with pollen brush and penicillate stigma. (I) Calyx showing one of the pair of minute bracteoles at base and the triangular lateral and lower lobes. (J) Legume with persistent calyx (C. Gutiérrez 3883, MEXU). (K) Front and side views of the seed (M. Elorsa 6439, MEXU). Drawn by Albino Luna (IBUNAM).

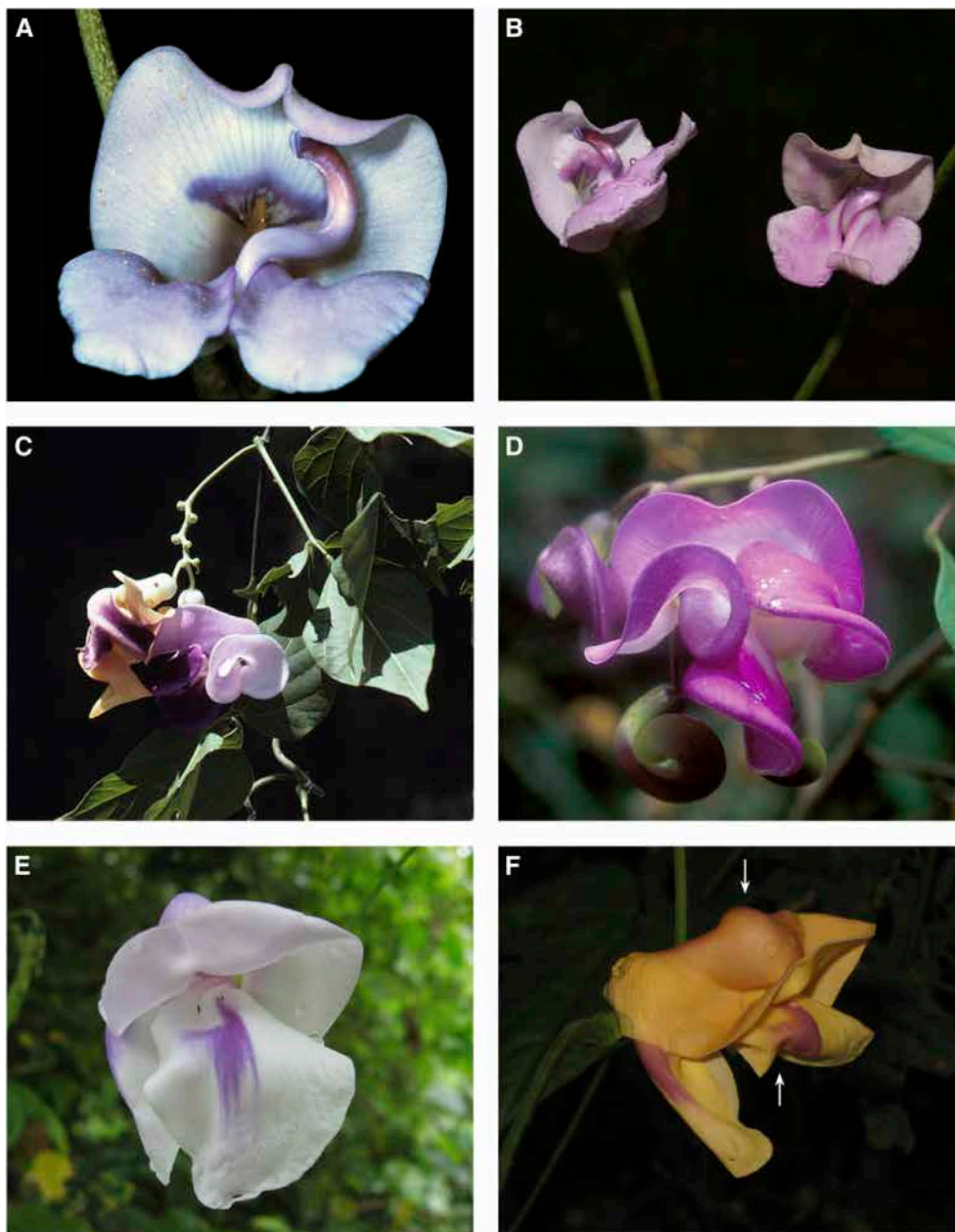


Fig. 8. Representative flowers of American Phaseolinae. (A, B) *Ancistrotropis peduncularis*. The keel beak is hook-shaped, and margins at tip of beak are splayed outward or folded back (photos: C. Westerkamp and Domingos Cardoso, respectively). (C, D) *Cochlianthus caracalla*. (C) Inflorescence with a zigzag axis and glandular nodes, one of which bears a pair of large, coiled flowers (photo: M. Lavin). (D) The standard petal (uppermost) is coiled, and the wing petals mostly cover the coiled keel petals (photo: C. Hughes). (E, F) *Condyllostylis candida*. (E) The distally incurved keel is tucked into the whitish standard petal, and the left wing with lavender stripes serves as the landing platform. The visual cue for the pollinator located on this wing petal is an exceptional feature among the New World Phaseolinae (photo: Domingos Cardoso). (F) Flower, faded yellow by end of the day, with the standard petal slumped over the keel such that the prominent hump (upper arrow) is formed by the rigidity of the keel. The distal end of the platform formed by the left wing petal is folded back (lower arrow; photo: Domingos Cardoso).

keel, which curves to the left as a prospective insect pollinator lands on the flower. In *Condyllostylis candida*, the weight of the prospective insect pollinator causes the stigma to protrude from the distal tip of the keel beak in the direction of the left-hand wing. Such left-handed asymmetry is unique among New World Phaseolinae. Franco (1995) reports that flowers of this species are visited by bees of the genus *Centris*. *Condyllostylis* inhabits secondary and primary wet to semideciduous forests from

southern Mexico south to Argentina and Uruguay (0–1500 m a.s.l.). It is absent from the West Indies. Figures 8E, 8F.

As a guide to the eventual comprehensive list of constituent species, the following four species embody all of the diagnostic traits of *Condyllostylis* and reflect most of the species diversity (this study sampled three of these):

Condyllostylis candida (Vellozo) A. Delgado comb. nov., based on *Phaseolus candidus* Vellozo in Fl. Flumin. 7: 311–312;

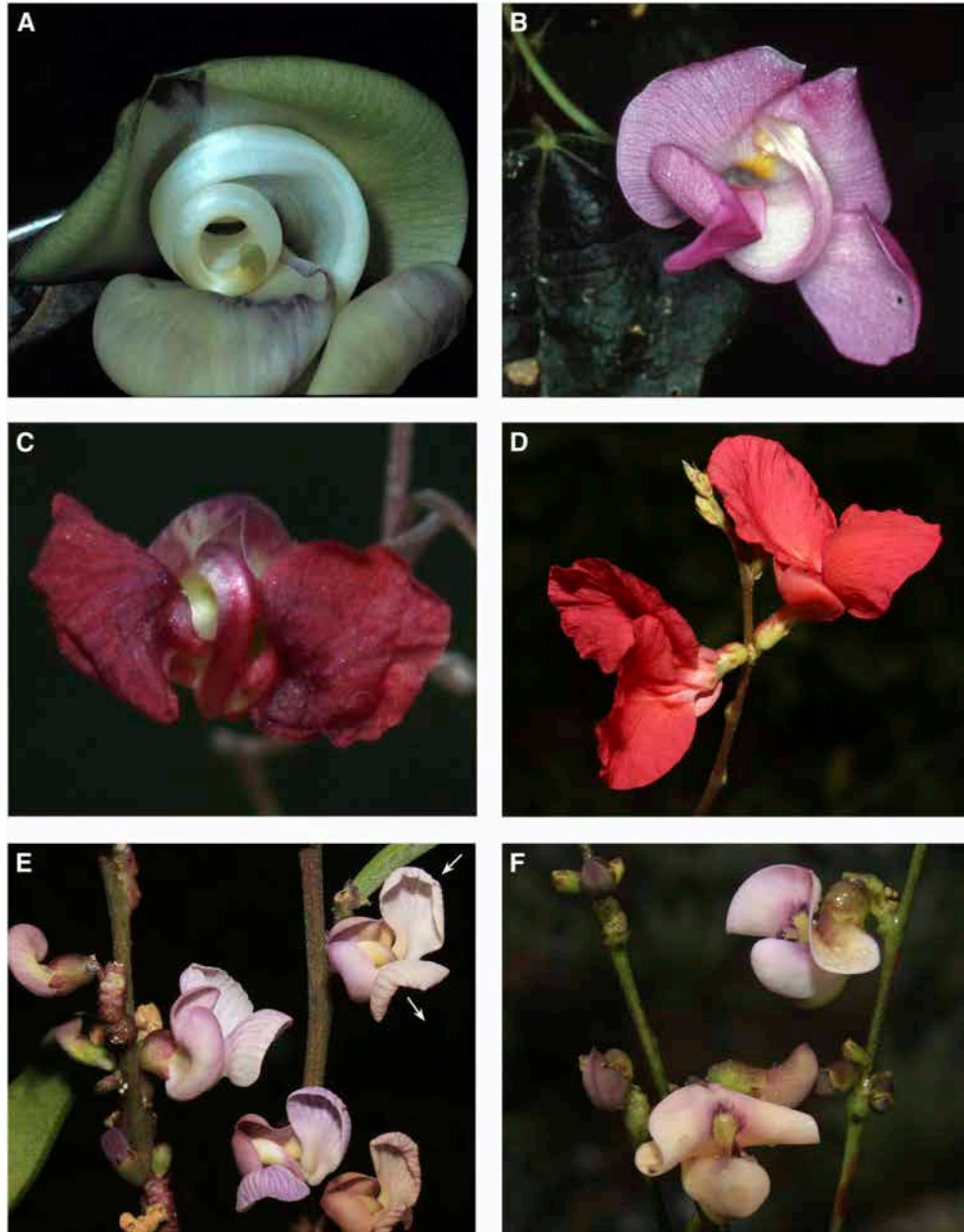


Fig. 9. Representative flowers of American Phaseolinae. (A) *Helicotropis linearis*. The keel beak is loosely coiled in a forward direction (photo: C. Westerkamp). (B) *Leptospron adenanthum*. The keel beak is very tightly coiled like the keel coil in *Phaseolus*, but with the axis of the coil oriented downward rather than laterally (photo: R. Bye). (C) *Macroptilium cochleatum*. The left-hand wing petal is slightly elevated and thereby adopts the standard position, whereas the standard (central upper petal) is reduced in size and coloration and the coiled keel takes a central position. This exceptional Brazilian species is the only *Macroptilium* to coil its keel beak (Delgado-Salinas and Lewis, 2008; photo: Domingos Cardoso). (D) *Macroptilium lathyroides*. The inflorescence has noticeable swollen floral nodes where one bears a pair of red flowers. The wing petals are large and prominent, and left-hand one adopts the standard position. The keel beak is covered by the standard petal (photo: Domingos Cardoso). (E) *Misanthus uleanus*. The wing petals are held at right angles to each other; one faces down, and the other is across the axis of the flower (indicated by arrows). The standard is slightly excentric and covers the beak of the keel, which is hooked and twisted to the right. The inflorescence has prominent floral nodes (photo: Domingos Cardoso). (F) *Oyxis monticola*. Flowers with upper central portion of standard reflexed. The maculae or visual cue for pollinator in the central position is large and outlined in dark purple. The wing petals fully embrace the keel (photo: Domingos Cardoso).

t. 125. 1825. (= *Vigna candida* (Vell.) Maréchal et al. auct. non, in *Taxon* 27(2–3): 201. 1978). Type: Brazil, “Habitat ad ripas fluvii Parat’y prope Pharmacopolim. Floret mensibus calidis” (lectotype here designated, illustration t. 125, in Vellozo, *Fl. Flumin.* 7: 311–312. 1825). Maréchal et al. (1978a, b) misclas-

sified *Condylostylis candida* in sect. *Sigmoidotropis*. Illustration: *Catálogo Ilustrado de las Plantas de Cundinamarca* 3, figure 32. 1968.

Condylostylis latidenticulata (Harms) A. Delgado comb. nov., based on *Phaseolus latidenticulatus* Harms in Notizbl.



Fig. 10. Representative flowers of American Phaseolinae. (A) *Oxyrhynchus trinervius*. The keel is incurved, blunt, and slightly laterally twisted at the apex. The wing petals distally embrace the main body of the keel (photo: A. Campos Villanueva). (B) *Phaseolus leptostachyus*. The keel beak is tightly coiled and laterally projected to the right (photo by A. Wong León). (C, D) *Ramirezella strobilophora*. (C) The keel beak is sigmoid and twisted to the right (similar to *Sigmoidotropis*). The wing petals distally embrace the keel (photo: E. González Soriano). (D) The inflorescence rachis has inconspicuous albeit nectariferous floral nodes. The cone-like structure in the upper center is the result of very broad floral bracts covering the buds in an imbricate fashion. The legumes are cylindrical and have very lignescent valves (photo: E. González Soriano). (E) *Sigmoidotropis ampla*. The keel beak is distinctly sigmoid-curved and appressed to the face of the keel petal (photo: M. Thulin). (F) *Strophostyles helvola*. The tubular portion of the keel rostrum is curved to the right (photo: M. Lavin). *Strophostyles* is the only genus of American Phaseolinae to be distinguished by other than floral traits (Riley-Hulting et al., 2004).

Bot. Gart. Berlin-Dahlem 7: 504–505. 1921. (= *Vigna latidenticulata* (Harms) A. Delgado in Monogr. Syst. Bot. Gard. 45: 1254. 1993). Type: Perú, “Dep. Piura, Prov. Ayavaca, 800–900 m, 5° südl. Br., Westhänge der Anden unter Frias”, May 1912, A. Weberbauer 6427 (holotype B, photo MEXU!).

Condylostylis venusta Piper in Contr. U. S. Natl. Herb. 22: 667–668; fig. 64. 1926. [= *Vigna venusta* (Piper) Maréchal et al. in Taxon 27: 202. 1978]. Type: Costa Rica, Prov. Alajuela, Su-

rubres near San Mateo, P. Biolley 7034 (holotype BR!). Illustration: Contr. U. S. Natl. Herb. 22: 667. pl. 64. 1926.

Condylostylis vignoides (Rusby) A. Delgado comb. nov., based on *Phaseolus vignoides* Rusby in Bull. N. Y. Bot. Gard. 4: 395. 1907. [= *Vigna vignoides* (Rusby) Maréchal et al. in Taxon 27: 202. 1978]. Type: Bolivia, Coroico, “Climbing 10 to 15 ft., the flowers yellow and violet; abundant in wet mold near the roadside”, 8 Jul 1894, M. Bang 2328 (holotype NY!; isotypes NY!, MO!).

Dolichopsis Hassler. A genus with two species, *Dolichopsis paraguariensis* Hassl. and *D. ligulata* (Piper) A. Delgado, known from the Chaco vegetation of Paraguay and adjacent Argentina (ca. 300 m a.s.l.). *Dolichopsis* is diagnosed by a long-beaked keel, a distally flattened and furrowed style, and broad and flat pods housing transversely arranged seeds. The hilum extends for about 50–60% of the length of the seed (Riley-Hulting et al., 2004; Delgado-Salinas and Torres-Colín, 2004).

Helicotropis A. Delgado, gen. nov.

Herbae perennes; caulis subvolubilis vel volubilis; folia foliolis brevipetiolatis, firme membranaceis vel subcoriaceis, reticulatis; stipulae lanceolato-ovatae, rigidae, antrorsae; pseudoracemi pedunculis foliis longioribus, nodis 3–9, tumidis, glanduliferis, floribus per anthesin brevipedicellatis, magnis; calyx campanulato, labio superiore latissimo, obtuso, emarginato, brevi, inferiore 3-partito; laciniis lanceolato-linearibus, elongatis, acutis, calycis tubus duplo superantibus; vexillum quam alae brevius; carinae rostrum in 2–3 spiris laxis contortum; pollinis grana tri-vel biporata, exinio reticulato ultrastructura granulati-columellari; stylus superne incrassatus, interne infra apicem villosus-barbatus; stigma globosum, apicaliter obliquum, ciliis cinctum; legumina linearia, compressa, rostrata, patentia, dehiscentia, marginibus incrassatis, scabris; semina 20–25, suborbicularia vel quadrata, compressa.

Type: *Helicotropis linearis* (Kunth) A. Delgado (= *Phaseolus linearis* Kunth).

Perennial twining vines, from a thick taproot up to 30 cm deep. Stems hollow, striate, with adventitious roots at nodes. Leaves trifoliolate, leaflets entire or lobed, linear-ovate to lanceolate-ovate, commonly thick in texture, reticulate, mucronate at apex. Stipules triangular to lanceolate, rigid, striate, persistent. Inflorescences with long peduncles, thicker than the stems that support them, with up to nine swollen and nectariferous floral nodes; secondary bracts semipersistent; pedicel at anthesis shorter than calyx tube; bracteoles ovate-lanceolate, about as long as calyx tube, basifixed (not auriculate), caducous. Flowers violet-purple, sometimes lavender-blue; calyx campanulate, upper lip broad, emarginate, median and lower teeth triangular-lanceolate, as long as or longer than the tube, (7)10–13 mm long; 2–4 mm wide; corolla with standard obovate to widely ovate, with blotches of purple along the upper margin, hooded, flap-like auricles at either side of distal portion of claw; right-handed wing forming a landing platform; left-handed wing spoon-like, curled; keel beak fused with short, closely interlocking hairs, beak with 2–3 loose coils, with distal portion extended, forming an obtuse, short and flat opening; androecium diadelphous, with free vexillary stamen; pollen triporate or biporate, semioblate to subprolate-spheroidal, exine reticulate, heterobrochate, operculi smooth to verrugate, exine ultrastructure granular-columellar; ovary elongate, with thick margins; style thickened at base, slender above the base to tip, style beak not extended beyond the stigma; stigma at anthesis apical to slightly lateral, introrse or extrorse, with a ring of hairs, not penicillate. Legume linear, 7–17.5 cm long, 5–8 mm wide, nearly flat (rectangular in section), valves with strongly thickened margins, sometimes covered with scabrous trichomes, elongated beak, ca. 1.5 cm long, glabrous, patent. Seeds 18–25, reniform to quadrate, compressed, testa smooth, the encircling halo of the hilum slightly darker than testa, hilum short, eccentric, rim-aril narrow, lens slightly prominent, divided. Seedlings with epigeal germination, eophylls with well-developed petioles. Chromosome number, $2n = 22$. Drawings of flowers of

Helicotropis linearis are found in Lackey (1979, p. 182) and sketches of its general habit in Aymard (1999, p. 428).

Diagnosis—*Helicotropis* has flowers with the lower calyx teeth much longer than the tube, wing petals extended well beyond the keel, the left wing petal embracing the keel, and the keel beak loosely coiled. *Helicotropis* comprises three species formerly classified in *Vigna* sect. *Caracallae* (pro parte). The keel petals of *Helicotropis* are diagnostic in having a beak that is loosely coiled in a forward direction (i.e., directly away from the calyx) for about two and half coils. *Helicotropis* is distributed in diverse savanna communities, in grassy openings of wet and seasonally dry, cloud, evergreen gallery, pine-oak, and pine forests, on floodplains (alluvial soils) or on rocky hillsides. From Mexico (Nayarit and Tamaulipas to Chiapas, excluding the Yucatán Peninsula), Central America, Lesser Antilles (only in Trinidad and Tobago), and in all of South America (except in Argentina, Chile, Ecuador, French Guiana, and Uruguay); 0–2100 m a.s.l. *Helicotropis* derives from the Greek, *helicoide*: helicoidal, and *tropis*: keel of a ship, referring to the helicoidal distal portion of the keel petals of the flower. Figures 6, 9A.

As a guide to the eventual comprehensive list of constituent species, the following four species exemplify the diagnostic traits of and reflect most of the species diversity within *Helicotropis* (this study sampled three of these):

Helicotropis linearis (Kunth) A. Delgado comb. nov., based on *Phaseolus linearis* Kunth in Humb. & Bonpl., nov. gen. & sp. (folio ed.) 6: 349. 1824. [= *Vigna linearis* (Kunth) Maréchal et al. in Taxon 27(2–3): 202. 1978]. Type: Venezuela, “crescit in ripa Orinoco”, *Humboldt & Bonpland s.n.* (lectotype here designated P!).

Helicotropis spectabilis (Standl.) A. Delgado comb. nov., based on *Phaseolus stenolobus* Standley in Contr. U. S. Natl. Herb. 17: 430; pl. 25. 1914. [= *Vigna spectabilis* (Standl.) A. Delgado, Novon 8: 352. 1998]. Type: Guatemala, Department of Alta Verapaz, vicinity of Secanquím, 550 m a.s.l., 7 May 1905, *H. Pittier 280* (holotype US!).

Helicotropis stenoloba (Standley) A. Delgado comb. nov., based on *Phaseolus stenolobus* Standley in Contr. U. S. Natl. Herb. 17: 431. 1914. Type: Guatemala, Department of Santa Rosa, Cerro Redondo, 1500 m a.s.l., *J.D. Smith 6135* (holotype US!; isotypes GH!, K!).

Helicotropis hookeri (Verdc.) A. Delgado comb. nov. *Vigna hookeri* Verdc. nom. nov. in Kew Bull. 24(3): 552. 1970, based on *Phaseolus lobatus* Hooker in Bot. Mag. 70, pl. 4076. 1844. nom. illegit., non *Phaseolus lobatus* Roxburgh in Wight & Arn., Prod. Fl. Ind. 1: 427. 1834 [= *Vigna lobata* (Willd.) Endl. in Bijdragen tot de flora van Nederlandsch Indië 1(1): 188. 1855]. Type: Argentina, *J. Tweedie s.n.* (lectotype here designated, K!).

Leptospron (Benth.) A. Delgado, comb. nov., *Phaseolus* sect. *Leptospron* Benth., in Benth. & Hook., Gen. Pl. 1: 538. 1865. *Vigna* sect. *Leptospron* (Benth.) Maréchal et al., Taxon 27: 202, 1978. Type: *Phaseolus rostratus* Wall. [*Leptospron adenanthum* (G. Mey.) A. Delgado].

Diagnosis—This clade is apomorphically diagnosed by the very tightly coiled distal portion of the keel that is projected downward, similar to the keel coil in *Phaseolus*, which has a tight coil projected laterally. A relationship of *Leptospron* with *Helicotropis* is supported by the *trnK* and ITS analyses and by a shared vestiture comprising stiff reddish brown hairs and a legume with sutures beset with minute antrorse barbs. A putative broader relationship of these two genera with *Condylostylis*

is suggested by only a shared pollen morphology involving a columellar structure of the infratectum (Maréchal, 1982). The species in this group include *L. adenanthum* and *L. gentryi*, which inhabit secondary and primary forests, with or without a dry season, and also coastal vegetation or temperate forests (mainly *L. gentryi*). *Leptospron* is distributed throughout Mexico, Central America, the West Indies, and in South America south to Argentina and Uruguay (0–2000 m a.s.l.). Human-mediated dispersal has naturalized *Leptospron adenanthum* in limited areas of the paleotropics including Africa and Asia. Flower drawings are found in Lackey (1979, p. 181) and sketches of general habit in Aymard (1999, p. 429). Figure 9B.

As a guide to the comprehensive list of constituent species, the following two species show the diagnostic traits of *Leptospron* and capture probably all of the species diversity (this study sampled both species):

Leptospron adenanthum (G. Meyer) A. Delgado comb. nov., based on *Phaseolus adenanthus* G. Meyer, Prim. Fl. Esseq.: 239–240. 1818 (= *Vigna adenantha* (G. Mey.) Maréchal et al., Taxon 27(–3): 202. 1978). Type: Guyana, Essequibo, *Rodschied s.n.* (holotype GOET, not seen). Illustration: Manual de Plantas de Costa Rica 5: 757. 2010.

Leptospron gentryi (Standley) A. Delgado comb. nov. *Phaseolus gentryi* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22(1): 28–29. 1940 [= *Vigna gentryi* (Standl.) Stainier & F. Horvat, Pollen et Spores 25: 31. 1983]. Type: Mexico, Chihuahua, Rio Mayo, Batopilillas, in oak and grass savanna, 8 Sep 1936, H.S. Gentry 2615 (holotype F!).

Macroptilium (Benth.) Urb. A genus of ca. 20 species distributed throughout the neotropics (Delgado-Salinas and Lewis, 2008; Espert et al., 2007) in mainly savanna-type vegetation, although several species inhabit temperate woodlands (0–2800 m a.s.l.). *Macroptilium* is diagnosed by flowers in which the right-hand wing petal twists upward to assume the function of the standard petal, whereas the standard is reduced in size and coloration and positions itself as a support structure of the very wing petal that takes its place (Fig. 9C, 9D). The keel beak assumes a distinctive hook-like configuration. Although *Macroptilium cochleatum* A. Delgado & G. P. Lewis has a keel beak coiled in a manner similar to *Phaseolus* (Delgado-Salinas and Lewis, 2008), the genus remains diagnosed by the standard-wing reconfiguration and the distinctive distally hooked keel beak. Pollen morphology supports a proposed infrageneric classification of *Macroptilium* (Torres-Colín, 2006; Torres-Colín et al., 2010). Section *Macroptilium* has pollen with long colpi (longicolpate), margo nonthickened, apex of the ectoaperture acute, membrane granular, pollen outline circular to semiangular, exine tectate or semitectate, apocolpium punctuate to foveolate, and mesocolpium microreticulate to foveolate, and section *Microcochle* has pollen with small colpi (brevicolpate), margo thickened, apex of the ectoaperture round, membrane granular, polar outline convex angular, exine tectate or semitectate, apocolpium punctate or rugulate, and mesocolpium microreticulate or rugulate.

Mysanthus G. P. Lewis & A. Delgado. This genus comprises *Mysanthus uleanus* (Harms) G. P. Lewis & A. Delgado with two varieties, the typical from the Caatinga in east central Brazil (Bahia) and *M. uleanus* var. *dolichopsoides* (Hoehne) G. P. Lewis & A. Delgado from Ytú, São Paulo. An undescribed species resides in the Chiquitano of eastern Bolivia. *Mysanthus* is diagnosed by its long inflorescences with numerous floral nodes, flowers with wing petals surpassing the distal keel curvature, the right wing serving as a prominent landing platform

and the left one upwardly projected (Fig. 9E), a keel with a hooked distal beak, and a laterally compressed legume that is nearly as broad as long (Lewis and Delgado-Salinas, 1994). The undescribed *Mysanthus* from the Chiquitano inhabits seasonally dry woodlands very similar to that of the Caatinga with low grass abundance due to a pronounced dry season.

Oryxis A. Delgado & G. P. Lewis. This monotypic genus of the “campos rupestres” and cerrados in east central Brazil (Minas Gerais) is diagnosed by leaflets that are basally subcordate to cordate, standard petal with two prominent appendages on its inner face, wings as long as the keel, and keel with a distinctive narrow beak that is fully embraced by the keel petals (Fig. 9F; Delgado-Salinas and Lewis, 1997). Phylogenetic analysis of combined morphology and ITS sequence data suggested that *Oryxis monticola* (Mart. ex Benth.) A. Delgado & G. P. Lewis, the sole species in the genus and represented in this study only by its morphology, was sister to *Mysanthus* (Riley-Hulting et al., 2004).

Oxyrhynchus Brandege. This genus of four species is endemic to Mexico and New Guinea and inhabits seasonally dry to wet tropical and subtropical forests, but also occurs in montane forests or coastal thickets (Rudd, 1967; Verdcourt, 1979; Delgado-Salinas and Estrada-Castillón, 2010). *Oxyrhynchus* (Fig. 10A) is diagnosed by spheroidal to oblong and rounded seeds with long hila extending 50–98% of the seed length and by cylindrical coriaceous pods. DNA isolations from old material of *Oxyrhynchus papuanus* (Pulle) Verdc. did not yield PCR amplifications. Thus, the phylogenetic position of this species remains uncertain. The morphology of the inflorescence and flowers, however, suggests that the New Guinean species could be part of the otherwise Mexican *Oxyrhynchus*. A trans-Pacific distribution is perhaps unsurprising given the broad ecological amplitude of *Oxyrhynchus* that encompasses lowland wet forest.

Phaseolus L. This genus of over 70 species is concentrated in Mexico with a secondary diversification in the central Andes (Delgado-Salinas et al., 1999, 2006; Freytag and Debouck, 2002). *Phaseolus* most commonly inhabits upper elevation pine or oak forests but with some notable exceptions, such as *P. viridis* Piper from tropical wet forests and *P. microcarpus* Mart. from seasonally dry tropical forests. *Phaseolus* represents one of the oldest New World lineages of the Phaseolinae (Table 1) and is readily diagnosed by its tightly coiled and laterally projected keel rostrum (Fig. 10B) and vegetative parts variously bearing uncinata hairs.

Ramirezella Rose. This genus comprises woody vines bearing stipules with a distinctive, broad base, thick inflorescences usually with numerous unswollen yet nectariferous nodes, thick and broadly ovate floral bracts that are deciduous or subpersistent at anthesis, persistent ovate bracteoles, pedicels longer than the calyx tube, keel mostly sigmoid (Fig. 10C; similar to the one in *Sigmoidotropis*), and pods that are inflated to nearly cylindrical (Fig. 10D). A relationship of *Ramirezella* with *Oxyrhynchus* is supported by both *trnK* and ITS analyses, as well as by the presence of sterile floral nodes toward the base of the inflorescence (i.e., the proximal nodes regularly do not produce flowers; Ochoterena-Booth, 1991; Ochoterena-Booth and Delgado-Salinas, 1994). *Ramirezella* includes seven species, all of which are endemic to Mexico except *R. penduliflora* and *R. strobilophora* that extend into adjacent Central America. These species inhabit mainly montane temperate forests and seasonally dry tropical forests (0–1900 m a.s.l.).

Sigmoidotropis (Piper) A. Delgado, comb. nov., *Phaseolus* sect. *Sigmoidotropis* Piper, Contr. U. S. Natl. Herb. 22: 674,

1926. This section of *Phaseolus* was transferred to *Vigna* as subg. *Sigmoidotropis* (Piper) Verdc. (Kew Bull. 24: 551, 1970) and later on subdivided by Maréchal et al. (1978a) to distinguish sect. *Sigmoidotropis* (Piper) Maréchal et al. (Taxon 27: 201, 1978) to include a wide diversity of New World *Vigna* species. Type: *Sigmoidotropis speciosa* (Kunth) A. Delgado (= *Phaseolus speciosus* Kunth).

Diagnosis—The clade is apomorphically diagnosed by its distinctly sigmoid-curved keel that lacks the distal fold of *Ancistrotropis*. The inner margins of the keel beak are not fused but closed by short interlocking marginal hairs. The distalmost portion of the keel is flat and extended. In addition, the stigma is penicillate, and the linear laterally compressed pods are maintained in a spreading position in the infructescence. *Sigmoidotropis* inhabits secondary and primary forests, with or without a dry season, as well as coastal thickets and riparian forests throughout much of the neotropics (0–2250 m a.s.l.). *Sigmoidotropis speciosa* is cultivated as an ornamental. Drawings of flowers of the species mentioned above are found in Lackey (1979: 178–181). Figures 7, 10E.

As a guide to the eventual comprehensive list of constituent species, the following nine species embody the diagnostic traits of and represent most of the species diversity within *Sigmoidotropis* (this study sampled seven of these):

Sigmoidotropis ampla (Benth.) R. Ram. & A. Delgado comb. nov., based on *Phaseolus amplus* Benth. in Bot. Voy. Sulphur 85–86. 1844. Type: “Central América”, *D. Sinclair s.n.* (holotype K!).

Sigmoidotropis antillana (Urban) A. Delgado comb. nov., based on *Phaseolus antillanus* Urban in Symb. Antill. 4(2): 309. 1905. [= *Vigna antillana* (Urban) Fawcett & Rendle in Fl. Jam. 4: 69. 1920]. Type: Cuba, *C. Wright 1594* (lectotype GH!; isolectotypes K!, MO!, P!).

Sigmoidotropis ekmaniana (Urban) A. Delgado comb. nov., based on *Macroptilium ekmanianum* Urban in Ark. Bot. 22A(8): 52–53. 1928. Type: Haiti, “Massif du Nord prope Dondon ad Citadelle La Ferriere cr. 800 m a.s.l., m. Majo flor.”. [May 1926], *E.L. Ekman 8262* (lectotype here designated S!).

Sigmoidotropis elegans (Piper) A. Delgado comb. nov., based on *Phaseolus elegans* Piper in Contr. U. S. Nat. Herb. 22(9): 674. 1926. [= *Vigna elegans* (Piper) Maréchal et al. in Taxon 27(2–3): 201. 1978]. Type: Jamaica, near Kingston, in the vicinity of Mona Mountain, 29 Apr 1903, *Maxon 1666* (holotype US!).

Sigmoidotropis grandiflora (Stoldal) A. Delgado comb. nov. *Phaseolus grandiflorus* Stoldal nom. nov. in Nom. Bot. ed. 2. 2: 817. 1841, based on *Phaseolus violaceus* Vellozo in Fl. Flumin. 7: 311; t. 124. 1825. nom. illegit. non *Phaseolus violaceus* Moench. in *Methodus* 141. 1794. Type: Brazil, “Habitat ad litus quadam insula amphractu Pharmacopolitano, Floret Jul” (lectotype here designated, illustration t. 124, in Vellozo, Fl. Flumin. 7: 311. 1825).

Sigmoidotropis megatyta (Piper) A. Delgado comb. nov., based on *Phaseolus megatylus* Piper in Contr. U. S. Nat. Herb. 22(9): 675. 1926. [= *Vigna megatyta* (Piper) A. Delgado in Monog. Syst. Bot. 45: 1254. 1993]. Type: Peru, [Cuzco], Santa Ana, 900 m a.s.l., 4 Jul 1915, *Cook & Gilbert 1634* (holotype US!).

Sigmoidotropis polytyla (Harms) A. Delgado comb. nov., based on *Phaseolus polytylus* Harms in Notizbl. Bot. Gart. Berlin 7: 505. 1921. [= *Vigna polytyla* (Harms) A. Delgado in Monog. Syst. Bot. 45: 525. 1993]. Type: Peru, “Gebiet des Rio

Acre, Seringal Auriestella, Jul 1911, *E. Ule 9464* (holotype B not seen; isotype K!).

Sigmoidotropis speciosa (Kunth) A. Delgado comb. nov., based on *Phaseolus speciosus* Kunth, in Humb. & Bonpl., Nov. Gen. Sp. (folio ed.) 6: 354. 1824. [= *Vigna speciosa* (Kunth) Verdc. in Kew Bull. 24(3): 552. 1970] Type: Venezuela, “Crescit ad flumen Orinoco, May 1800, *Humboldt & Bonpland s.n.* (holotype P!).

Sigmoidotropis spixiana (Martius ex Benth.) A. Delgado comb. nov. *Phaseolus spixianus* Mart. ex Benth. in Comm. Legum. Gen.: 73. 1837. Type: Brazil, “Inter virgulta prope Brejo, praedium provinciae Piaui, [May], *Martius s.n.* (lectotype here designated M!, of four sheets, the selected one is that has Martius description; isolectotypes M!).

These species of *Sigmoidotropis* were formerly classified in *Vigna* subg. *Sigmoidotropis*, except for *S. ampla*, which was placed in *Phaseolus*, and *S. ekmaniana*, which was described as a *Macroptilium*.

Strophostyles Elliott. This genus includes three species from temperate forests and woodlands and adjacent grasslands in eastern North America. *Strophostyles* (Fig. 10F) is apomorphically diagnosed by divergent stipules, persistent secondary floral bracts, calyces with four acute to sometimes attenuate lobes, and seed testa often with a caducous cellular coat (Riley-Hulting et al., 2004). A relationship with *Dolichopsis* is supported in part by a shared keel petal morphology involving a gibbous ventral margin proximal to the beak. A broader relationship of these two with *Macroptilium* and *Mysanthus* is supported in the *trnK* analysis (Fig. 3) and apomorphically supported by pollen with medium-sized colpi and stipules firmly appressed (antrorse) to the main stem, the latter reversed in *Strophostyles* (Riley-Hulting et al., 2004). These last character states are variously transformed to the ancestral state (i.e., small colpi, divergent stipules) in certain of the species in these genera.

Vigna Savi. The circumscription of *Vigna* s.s. now includes five subgenera, *Ceratotropis*, *Haydonia*, *Lasiospron*, *Plectrotropis*, and *Vigna*, of the seven recognized by Maréchal (1982). *Vigna* subg. *Macrorhynchus* is now included in *Wajira* (Thulin et al., 2004), and *Vigna* subg. *Sigmoidotropis* is now divided into the American genera formally proposed in this study. *Vigna* subg. *Ceratotropis* and *Vigna* subg. *Lasiospron* are here established as monophyletic subgenera with distinctive geographical centers. Issues related to the other subgenera of *Vigna* s.s. will be addressed in a more comprehensive study of this genus (Y. Feleke and R. Pasquet, International Centre of Insect Physiology and Ecology, Kenya, unpublished manuscript). Only three species of *Vigna* s.s. have a pantropical distribution and have been naturally established in the Americas, *Vigna luteola* (Jacq.) Benth., *V. marina* (Burm.) Merr., and *V. vexillata* (L.) A. Rich.

Vigna subg. *Lasiospron* (Benth.) Maréchal et al. Although primarily diversified in the New World, this group is clearly part of the otherwise Old World radiation (Figs. 2, 4). Two new combinations are needed in this subgenus for the species included in this study:

Vigna diffusa (Scott-Elliott) A. Delgado & Verdc. comb. nov. *Phaseolus diffusus* Scott-Elliott, J. Linn. Soc. 29: 12. 1891. Type: Madagascar, sandy dunes near Fort Dauphin, Sep 1890, *G.F. Scott Elliot 2366* (lectotype K!; isolectotypes BM!, P!).

Vigna schottii (Benth.) A. Delgado & Verdc. comb. nov. *Phaseolus schottii* Benth. in Comm. Legum. Gen.: 75. 1837. Type: Brazil, ad Tejuco. *Schott s.n.* (holotype W!; isotype NY).

Four additional species traditionally belonging to this subgenus are *Vigna juruana* (Harms) Verdc., *V. lasiocarpa* (Mart. ex

Benth.) Verdc., *V. longifolia* (Benth.) Verdc., and *V. trichocarpa* (C. Wright ex Sauvalle) A. Delgado. All six of the species just discussed were sampled during this study, and these reflect most of the species diversity within subgen. *Lasiospron*. These six thus should serve as a guide to the eventual comprehensive list of constituent species (A. Delgado-Salinas, et al., UNAM, unpublished manuscript).

Diagnosis—Although part of *Vigna* s.s., this clade is included here because of its mostly neotropical distribution. The *Lasiospron* clade is clearly part of an otherwise mostly Old World clade, as revealed by the molecular data and by its petate (medifixed) stipules, yellow flowers, and granular interstium of the pollen exine. Like other New World Phaseolinae and unlike *Vigna* s.s., any floral asymmetry in *Lasiospron* is right-handed (Hoc et al., 1993). *Lasiospron* is distributed in secondary and primary riparian forests throughout much of the neotropics. Populations of *V. juruana* and *V. trichocarpa* have extended their distribution to include west-central Africa and *V. ovata* to the east coast of Madagascar. This subgenus is diagnosed by inflorescences with short pedicels that twist during fruit maturation and predominantly golden or greenish-yellow corollas that are otherwise not common among New World Phaseolinae genera (the latter perhaps a plesiomorphic trait). The right wing petal serves as the landing platform for pollinators, whereas the left wing clasps the left side of the keel, which effectively blocks a nonpollinating access to the nectaries. The style distinctly projects beyond the stigma to produce a small beak, hook, or gland. The seeds of *Lasiospron* are subglobose and surrounded in fruit by a whitish membranous layer. The seeds also have a distinctly raised rim-aril around the excentric hilum or have conspicuous white arils situated toward one end, as in some Old World *Vigna* species.

Conclusions—As a result of this study, subtribe Phaseolinae now comprises 27 genera and a minimum of 340 species. These are *Vigna* (a minimum of 90 species), *Phaseolus* (75), *Dolichos* (60), *Macrotyloma* (24), *Macroptilium* (20), *Sigmoidotropis* (9), *Ramirezella* (7), *Sphenostylis* (7), *Wajira* (5), *Nesphostylis* (4), *Oxyrhynchus* (4), *Physostigma* (4), *Alistilus* (3), *Ancistrotropis* (6), *Condyllostylis* (4), *Helicotropis* (3), *Strophostyles* (3), *Dolichopsis* (2), *Leptospron* (2), *Mysanthus* (2), *Cochliasanthus* (1), *Dipogon* (1), *Lablab* (1), *Oryxis* (1), *Austrodolichos* (1), *Spathionema* (1), and *Vatovaea* (1). These species are all vines and concentrated in tropical savanna woodlands (e.g., Maxted et al., 2004), but some subgroups have diversified in tropical montane woodlands (e.g., *Phaseolus*; Delgado-Salinas et al., 2006). An ecological predilection to specific types of tropical woodlands and forests suggests phylogenetic niche conservatism (e.g., Wiens and Graham, 2005) as an explanation for why this group has a relatively poor representation within temperate woodlands or seasonally dry tropical forests (sensu Pennington et al., 2009).

The highly elaborated floral morphologies of the American Phaseolinae embody the essence of sexually selected traits. Traits involved with reproductive advertisement carry an attendant cost, but here the cost is also incurred by the pollinator. The beautiful visual cues used by the flowers of American Phaseolinae to attract pollinators belie the potential difficulty that a prospective pollinator has in gaining access to nectar via a hurdle of levers, platforms, and pumps. The unique floral presentations in each genus restrict the directionality of approach and movement of pollinators within and between flowers

(Hedström and Thulin, 1986; Sousa-Peña et al., 1996; Etcheverry et al., 2008). The distinctive asymmetries are associated with the presence of secondary pollen presentation via a pollen brush (e.g., Lavin and Delgado-Salinas, 1990) on mechanically reinforced styles and stigmatic surfaces, which ensure that pollen and nectar are doled out in a conservative manner so that more than one pollinator visit is required to expend these much sought-after resources. This architecture has rendered a great diversity of pollination systems among the American Phaseolinae that involve pollen deposition on either the dorsal side of the pollinator (i.e., nototribic; e.g., *Cochliasanthus caracalla*, Etcheverry et al., 2008), the lateral side (i.e., pleurotribic; e.g., *Phaseolus coccineus*, Sousa-Peña et al., 1996), or the ventral side (i.e., sternotribic; e.g., *Macroptilium atropurpureum* and *M. longipedunculatum*, Torres-Colín, 2006). An increase in more specialized plant–pollinator interactions has perhaps enhanced reproductive isolation and thus the floral diversification of this group of legumes (Lavin and Delgado-Salinas, 1990; Neal et al., 1998). Bilateral symmetry with surprise and predictability yet with novelty are carried to the extreme in the flowers of American Phaseolinae all to manipulate pollinators. Each of the 14 New World genera has its own distinctive floral novelty, yet the right-handed floral asymmetry renders all of these genera to be florally of the American Phaseolinae.

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APPENDIX 1. Voucher information for DNA sequences generated during this study. Herbarium abbreviations are as defined by Thiers, (2011). Superscripts before GenBank accession numbers indicate sequence: ¹ITS or ²*trnK*.

TAXON: Collection locale, Voucher specimen (Herbarium), GenBank accession.

Outgroups

Butea monosperma (Lam.) Taub.: Indonesia. *Ridder-Neuman s.n.* (L), ²JN008175. *Neorautanenia mitis* (A. Rich.) Verdc.: Ethiopia. Gojjam Region, *Thulin & Hunde 3997* (UPS), ²JN008178. *Otoptera burchellii* DC.: Botswana. *Skarpe S-134* (UPS), ²JN008176. *Otholobium bolusii* (H. M. L. Forbes) C. H. Stirton: Wales National Botanic Garden. *Stirton 10052*, ²JN008180. *Pseudovigna argentea* (Willd.) Verdc.: Kenya. Coastal. *Pasquet s.n.*, ²JN008179. *Psophocarpus lancifolius* Harms: Tanzania. *Hedrén, Kibuwa & Pettersson 566* (UPS), ²JN008177. *Psoralea pinnata* L.: Wales National Botanic Garden. *Stirton 1999-1318*, ²JN008182. *Psoralea tenuiflora* L.: USA. *Lavin 6140* (BH), ²JN008181.

Old World Phaseolinae excluding *Vigna*. *Alistilus jumellei* (R. Vig.) Verdc.: Madagascar, 34 km SW of Ambalavao, *Thulin & Razafindraibe 11787* (UPS), ²JN008192. Madagascar, Tsimilaha, *Thulin & Razafindraibe 11823* (UPS), ²JN008191. *Dipogon lignosus* (L.) Verdc.: USA. California, cultivated, *Dean SAF-960031* (UCD), ¹JN008277. *Dolichos kilimandscharicus* Taub.: Ethiopia. Gojjam Region, *Thulin & Hunde 3998* (UPS), ²JN008184. *Dolichos oliveri* Schweinf.: Ethiopia. Gamu-Gofa Region, *Gilbert & Thulin 244* (UPS), ²JN008183. *Dolichos trinervatus* Baker: Tanzania. *Hedrén, Kibuwa & Pettersson 405* (UPS), ²JN008265. *Macrotyloma africanum* (Brenan ex R. Wilczek) Verdc.: Cameroon. *NI 1209* (BR), ²JN008188. *Macrotyloma axillare* (E. Mey.) Verdc.: Democratic Republic of Congo. *NI 219* (BR), ²JN008266. *Macrotyloma stenophyllum* (Harms) Verdc.: Ethiopia. Wollega Region. *Gilbert & Thulin 643* (UPS), ²JN008186, ²JN008187. *Macrotyloma uniflorum*

(Lam.) Verdc. var. *benadirianum* (Chiov.) Verdc.: Somalia. Mogadishu. *Thulin 4748* (UPS), ²JN008185. *Physostigma venenosum* Balf.: Ghana. Atewa Range, *Jongkind 1792* (MEXU), ²JN008195. *Spathionema kilimandscharicum* Taub.: Kenya. *Pasquet V330* (K), ²JN008193. *Sphenostylis angustifolia* Sonder: South Africa. Johannesburg, *Van Wyk 2604* (BH), ²JN008189, ²JN008190. *Vatovaea pseudolablab* (Harms) J.B. Gillett: Kenya. *Pasquet V331* (K), ²JN008194.

New World Phaseolinae excluding *Vigna*. *Ancistrotropis firmula* (Benth.) A. Delgado. Brazil. *B. Machado et al. 2590* (NY), ¹JN008372, ¹JN008373, ²JN008273, ²JN008259. *Ancistrotropis peduncularis* (Fawcett & Rendle) A. Delgado: Argentina. Corrientes, *Arbo 6519* (MEXU), ¹JN008368. Brazil. Minas Gerais, *Gottsberger 127-3386* (NY), ¹JN008369. México. Oaxaca, *Salas 4259* (MEXU), ¹JN008370. ²JN008272. *Ancistrotropis subhastata* (Verdc.) A. Delgado: Bolivia. Santa Cruz, *Seidel 172* (MEXU), ¹JN008371. *Cochlianthus caracalla* (L.) Trew: Bolivia. Santa Cruz, *Nee 40602* (MEXU), ¹JN008345. Bolivia. Santa Cruz, *Nee et al. 48608* (MEXU), ¹JN008346. Argentina. General San Martín, *Vanni et al. 4144* (MEXU), ¹JN008347. Bolivia. Cochabamba, *Caballero-Pardo 50* (MEXU), ¹JN008348, ²JN008274. French Guiana. St. Elie, *Poncy 1435* (MEXU), ²JN008275. *Condylostylis candida* (Vell.) A. Delgado: Paraguay. Cordillera, *Zardini 13905* (MEXU), ¹JN008374. Argentina. Ituzzaingó, *Krapovickas et al. 41117* (MEXU), ¹JN008375, ²JN008260. *Condylostylis latidenticulata* (Harms) A. Delgado: Colombia. Huila, *Debouck 2910* (MEXU), ¹JN008376. Perú. Jaén, *Delgado-Salinas 2053* (MEXU), ¹JN008377. México. Chiapas. *Martínez 32337* (MEXU),

- ¹JN008378. *Condylostylis venusta* Piper, Colombia. *CIAT 2468* (MONT), ¹JN008379, ²JN008261. *Dolichopsis paraguariensis* Hassl.: Bolivia. Beni, *Orellana 383* (MEXU), ¹JN008332. *Helicotropis linearis* (Kunth) A. Delgado: Colombia. Vichada, *CIAT 4623* (MONT), ¹JN008338. México. Oaxaca, *Delgado-Salinas 1359* (MEXU), ¹JN008339. Mexico. Chiapas, *CIAT 24064* (MONT), ¹JN008340. NI 0654 (BR), ¹JN008341. Honduras. San Antonio de Oriente, *Linares 5296* (MEXU), ¹JN008343. Bolivia. La Paz, *Beck 24136* (MEXU), ¹JN008344, ²JN008258. *Helicotropis stenoloba* (Standl.) A. Delgado: México. Oaxaca, *Salas et al. 4149* (MEXU), ¹JN008342. *Leptospron adenanthum* (G. F. Mey.) A. Delgado.: Colombia. *CIAT 4022*, ²JN008271. México, *Delgado-Salinas 2200* (MONT), ¹JN008335, ²JN008254. TVNU-228 (MEXU), ²JN008255. Perú. Contumazá, *Delgado-Salinas 2102* (MEXU), ¹JN008336, ¹JN008337. *Leptospron gentryi* (Standl.) A. Delgado: México. *Delgado-Salinas 1713* (MEXU), ¹JN008333, ²JN008256. México. Oaxaca, *Campos 735* (MEXU), ¹JN008334. México. Chiapas, *Valera s.n.* (MEXU), ²JN008257. *Macroptilium gibbosifolium* (Ortega) A. Delgado. México. Distrito Federal, *Delgado-Salinas s.n.* (MEXU), ²JN008253. *Mysanthus* sp.: Bolivia. Santa Cruz, *Abbott 16932* (MEXU, MO), ¹JN008330, ¹JN008331. *Oxyrhynchus volubilis*: México. Veracruz, *Di Constanzo 289* (MEXU), ¹JN008329. *Phaseolus angustissimus* A. Gray: USA. Arizona, *T. J. Ayers 1741* (ASC), ²JN008264. *Ramirezella calcoma* Ocho.-Booth & A. Delgado: México. E. de México, *Téllez et al. 13054* (MEXU), ¹JN008322. *Ramirezella crassa* (McVaugh) Ocho.-Booth & A. Delgado: México. Sinaloa, *Bartholomew 2513* (MEXU), ¹JN008323, ²JN008262. *Ramirezella lozani* (Rose) Piper: México. Guerrero, *Calónico-Soto 13204* (MEXU), ¹JN008324. *Ramirezella micrantha* A. Delgado & Ocho.-Booth: México. Jalisco, *Ochoterena-Booth 86* (MEXU), ²JN008276. *Ramirezella nitida* Piper: México. Tamaulipas, *Hernández 2339* (MEXU), ¹JN008325. México. Tamaulipas, *Ochoterena-Booth 63* (MEXU), ¹JN008326, ²JN008263. *Ramirezella penduliflora* A. Delgado & Ocho.-Booth: México. Chiapas, *Martínez 20746* (MEXU), ¹JN008327, ¹JN008328. *Sigmoidotropis ampla* (Benth.) R. Ramírez & A. Delgado: México. Quintana Roo, *CIAT 4070*, ¹AF069121, ²JN008240. México. Quintana Roo, *Ramírez-Delgadillo 3476* (MEXU), ¹JN008349, ²JN008241. *Sigmoidotropis antillana* (Urb.) A. Delgado: Dominican Republic. La Romana, *Delgado-Salinas 1986* (MEXU), ¹JN008350, ²JN008242. *Sigmoidotropis ekmaniana* (Urb.) A. Delgado: Dominican Republic. La Vega, *Delgado-Salinas 1990* (MEXU), ¹JN008351. *Sigmoidotropis elegans* (Piper) A. Delgado: México. Quintana Roo, *Ramírez-Delgadillo 3467* (MEXU), ¹JN008352, ²JN008243. México. Quintana Roo, *Ramírez-Delgadillo 3472* (MEXU), ¹JN008353, ²JN008244. México. Yucatán, *Ramírez-Delgadillo 3464* (MEXU), ¹JN008354, ²JN008245. México. Quintana Roo, *Ramírez-Delgadillo 3722* (MEXU), ¹JN008355, ²JN008246. *Sigmoidotropis spixiana* (Martius ex Benth.) A. Delgado. Perú. Lambayeque, *Llatas Quiroz 3113* (MEXU), ¹JN008356, ¹JN008357, ¹JN008358, ²JN008247, ²JN008248. Perú. Amazonas, *Delgado-Salinas 2050* (MEXU), ¹JN008359, ²JN008249. *Sigmoidotropis megatyla* (Piper) A. Delgado: Ecuador. Chimborazo, *Debouck 2862* (MEXU), ¹JN008360. Perú. Chachapoyas, *Delgado-Salinas 2026* (MEXU), ¹JN008361, ¹JN008364, ²JN008251. Perú. Chachapoyas, *Delgado-Salinas 2066* (MEXU), ¹JN008362, ¹JN008363, ²JN008250. Ecuador. Loja, *Lewis 2378* (MEXU), ²JN008270. *Sigmoidotropis speciosa* (Kunth) A. Delgado: México. Jalisco, *Ramírez-Delgadillo 3450* (MEXU), ¹JN008365. México. Jalisco, *Ramírez-Delgadillo 3733* (MEXU), ¹JN008366. México. Jalisco, *Ramírez-Delgadillo 3440* (MEXU), ¹JN008367, ²JN008252.
- Vigna* subg. *Lasiospron*. *Vigna juruana* (Harms) Verdc.: Ecuador. *Neill 650* (MEXU), ¹JN008303. México. Tabasco, *Novelo 1938* (MEXU), ¹JN008304. Bolivia. Pando, *Beck et al., 19433* (MEXU), ¹JN008305. *Vigna lasiocarpa* (Mart. ex Benth.) Verdc.: CIAT 4193 (MONT), ¹JN008310. México. Tabasco, *Delgado-Salinas 995* (MEXU), ¹JN008311. NI 0633 (BR, MONT), ¹JN008312. Bolivia. La Paz, *Beck 10122* (MEXU), ¹JN008313, ¹JN008314. *Vigna longifolia* (Benth.) Verdc.: México. Tabasco, *Tenorio 19602* (MEXU), ¹JN008306. México. Tabasco, *Novelo 3298* (MEXU), ¹JN008307, ²AY582991. México. Tabasco, *Novelo 2938* (MONT), ¹JN008308, ¹AY583520. México. Tabasco, *Novelo 2894* (MEXU), ¹JN008309. *Vigna diffusa* (Scott-Elliot) A. Delgado & Verdc.: Brazil. Espírito Santo, *Folli 2427* (RB), ¹JN008321. *Vigna schottii* (Benth.) A. Delgado & Verdc.: Paraguay. Paraguari, *Zardini 8650* (MEXU), ¹JN008316. Bolivia. El Beni, *Beck 24295* (MEXU), ¹JN008317. Paraguay. Paraguari, *Zardini 25163* (MEXU), ¹JN008318. Bolivia. El Beni, *Beck 18854* (MEXU), ¹JN008319. Paraguay. *Hassler 8470* (US), ¹JN008320. *Vigna trichocarpa* (C. Wright ex. Sauv.) A. Delgado: *CIAT 4122* (MONT), ¹JN008315, ²JN008239.
- African *Vigna* s.s.**
- Vigna* subg. *Haydonia*. *Vigna monophylla* Taub. 1284: Tanzania. NI413, *Richards 8484* (BR, K, MONT), ¹JN008293. *Vigna nigrifolia* Hook. f.: TVNu 612 (MONT), ¹JN008279, ²JN008200. *Vigna schimperii* Baker: University of California Davis, *Vg 102* (GH 88102-1), ¹JN008278, ²JN008206. *Vigna triphylla* (R. Wilczek) Verdc.: Ethiopia. Arussi Region, *Thulin 1617* (UPS), ²JN008205. *VIGNA* SUBG. *PLECTROTROPIS*. *Vigna vexillata* (L.) A. Rich. Mexico. Veracruz. *M. Sousa 13399* (MEXU), ¹JN008281. Namibia. National Botanic Garden Belgium, *NI0546* (BR), ¹JN008282. Ethiopia. Arussi Region, *Thulin 1451* (UPS), ²JN008212.
- Vigna* subg. *Vigna*. *Vigna ambacensis* Welw. ex Bak.: TVNu 166 (MONT), ²JN008201. *Vigna angivensis* Baker: Madagascar, Andringitra, *Thulin & Razafindraibe 11778* (UPS), ²JN008213. *Vigna filicaulis* Hepper: University of California Davis, *Vg 818* (MONT), ²JN008202. *Vigna friesiorum* Harms: National Botanic Garden, Belgium, *NI1178* (MONT), ¹JN008280. *Vigna gazensis* Baker f.: University of California Davis, *Vg 98* (MONT), ¹JN008292, ²JN008211. *Vigna hosei* (Craib) Backer: TVNu, 20 (MONT), ¹JN008283, ²JN008204. *Vigna luteola* (Jacq.) Benth.: Argentina. *CIAT 4424* (MONT), ¹JN008284, ²JN008209. Mexico. Tabasco, *A. Novelo R. 3139* (MEXU), ¹JN008285. Mexico. Oaxaca, *Delgado-Salinas 2090* (MEXU), ¹JN008286. Argentina. La Plata, *A. M. Arambarri s.n.* (MEXU), ¹JN008287. Puerto Rico. *A. Salywon 1235* (AZ), ²JN008268. *Vigna membranacea* A. Rich. subsp. *membranacea*: India. *PI 292867* (MONT), ¹JN008291, ²JN008207. *Vigna membranacea* subsp. *caesia* (Chiov.) Verdc.: Ethiopia. Shoa Region, *Gilbert & Thulin 195* (UPS), ²JN008208. *Vigna monantha* Thulin: Somalia. Bari Region, *Thulin et al. 10617* (UPS), ²JN008203. *Vigna racemosa* (G. Don) Hutch. & Dalziel: *CIAT 4574* (MONT), ¹JN008294, ²JN008267. *Vigna subterranea* (L.) Verdc.: Zimbabwe. *PI 2419993* (MONT), ¹JN008210. *Vigna unguiculata* (L.) Walp. 243: Yuri Cahui, *V14* (MEXU), ²JN008196. Thailand. *PI 487500* (MONT), ²JN008197. Colombia. Cali. *Baudoin s.n. CIAT 1167* (MONT), ¹JN008288, ²JN008198. Botswana. Ngwapa, *PI 491449* (MONT), ¹JN008289, ²JN008199. University of Florida. *IRFI 6678* (MONT), ¹JN008290.
- Vigna* subg. *Ceratotropis*. *Vigna aconitifolia* (Jacq.) Maréchal: Yemen. Taíma, *PI 372355* (MONT), ¹JN008295, ²JN008214. Pakistan. *PI 365427* (MONT), ¹JN008296, ²JN008215, ²JN008216. Pakistan. *Maréchal 104332* (BR), ²JN008217. *Vigna angularis* (Willd.) Ohwi & H. Ohashi var. *angularis*: Japan. *JP No. 72985* (MONT), ²JN008218. *Vigna angularis* var. *nipponensis* (Ohwi) Ohwi & H. Ohashi: Japan. *JP No. 107861* (MONT), ²JN008269. *Vigna glabrescens* Maréchal et al.: University of California Davis, *Vg 129* (MONT), ²JN008219. *Vigna grandiflora* (Prain) Tateishi & Macted: Thailand. *JP No. 107862* (MONT), ²JN008220. *Vigna hirtella* Ridley: Thailand. *JP No. 109681* (MONT), ²JN008221. *Vigna minima* (Roxb.) Ohwi & H. Ohashi: Thailand. *JP No. 107869* (MONT), ²JN008222. *Vigna mungo* (L.) Hepper var. *silvestris* Lukoki, Maréchal & Otoul: India. Lukoki, *JP No. 107874* (MONT), ²JN008223. *Vigna nakashimae* (Ohwi) Ohwi & H. Ohashi: Japan. *JP No. 107879* (MONT), ²JN008224. *Vigna nepalensis* Tateishi & Macted: Nepal. *JP No. 107881* (MONT), ²JN008225. *Vigna radiata* (L.) Wilczek var. *radiata*: Nigeria. *PI 425754* (MONT), ²JN008226. *Vigna radiata* var. *sublobata* (Roxb.) Verdc.: Australia. *PI 107876* (MONT), ²JN008227. *Vigna reflexopilosa* Hayata var. *reflexopilosa*: Japan. *JP No. 108815* (MONT), ²JN085947. *Vigna reflexopilosa* var. *glabra* Tomooka & Macted: Philippines. *JP No. 109684* (MONT), ²JN008228. Cultivated. University of California Davis, *Vg 129* (MONT), ¹JN008297. *Vigna riukiensis* (Ohwi) Ohwi & H. Ohashi: Japan. *JP No. 108810* (MONT), ²JN008229. *Vigna stipulacea* Kuntze: India. National Botanic Garden Belgium, *NI 1030* (MONT), ²JN008230. *Vigna subramaniana* (Babu ex Raizada) M. Sharma: India. National Botanic Gardens Belgium, *NI 1135* (BR), ²JN008231. *Vigna tenuicaulis* N. Tomooka & Macted: Thailand. *Maréchal et al. 109682* (MONT), ²JN008232. *Vigna trilobata* (L.) Verdc.: Ivory Coast. *PI 286306* (MONT), ¹JN008298, ²JN008233. India. National Botanic Garden Belgium, *NI958* (MONT), ²JN008234. *Vigna trinervia* (Heyne ex Wall.) Tateishi & Macted: Malaysia. *JP No. 108840* (MONT), ²JN008235. *Vigna umbellata* (Thunb.) Ohwi & H. Ohashi: *CIAT 4279* (MONT), ¹JN008299, ²JN008236. Cultivated. *D. Charlet s.n.* (MONT), ¹JN008300, ¹JN008301. Myanmar. Kachin, *PI 200841* (MONT), ¹JN008302, ²JN008237. Japan. *JP No. 99485* (MONT), ²JN008238.