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Phylogeny of Robinioid Legumes (Fabaceae) Revisited: *Coursetia* and *Gliricidia* Recircumscribed, and a Biogeographical Appraisal of the Caribbean Endemics

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Abstract. Morphological data and sequences from the nuclear ribosomal ITS region, and the chloroplast *trnL* intron and *matK* locus were sampled from robinioid legumes to infer phylogenetic relationships. The monophyletic robinioid clade includes 11 genetically and often morphologically distinct subclades ranked as genera with the following well supported higher level relationships: ((*Hebestigma*, *Lennea*), ((*Gliricidia*, *Poitea*), (*Olneya*, *Robinia*, *Poissonia*, *Coursetia*, *Peteria*, *Genistidium*, and *Sphinctospermum*))). In order to render all 11 robinioid genera monophyletic, the genus *Hybosema* is synonymized with *Gliricidia*, and the genus *Poissonia* is resurrected to accommodate four morphologically disparate species previously classified in *Coursetia*. Three new combinations are required to accommodate these two generic recircumscriptions: ***Gliricidia robustum*, *Poissonia heterantha*,** and ***Poissonia weberbaueri*.** Ages of clades and evolutionary substitution rates are derived from a rate-smoothed Bayesian likelihood approach on sequences from the ITS region and the *matK* locus. Time constraints are derived from the Tertiary fossil wood species *Robinia zirkelii*, which shares apomorphic wood characters with the *Robinia* stem clade. The Cuban endemic *Hebestigma* is estimated to have diverged at least 38 Ma from its Mesoamerican sister genus *Lennea*, whereas the Greater Antillean *Poitea* is estimated to have diverged at least 16 Ma from its continental sister *Gliricidia*. This study reveals that sequences from the ITS region are amenable to exhaustive taxon sampling because of the high levels of variation at and below the species level. The evolutionary substitution rate for the ITS region is estimated at 3.1–3.5 x 10^{-9} substitutions/site/year, approximately an order of magnitude faster than that estimated for the *matK* locus.

The tribe Robinieae comprises 12 genera concentrated in the deserts and seasonally dry tropical forests of North America (Lavin and Sousa 1995). In this study, we distinguish the robinioid legumes from the tribe Robinieae so as to exclude the genus *Sesbania*. Phylogenetic evidence from chloroplast *matK* sequences firmly place the robinioids in a monophyletic clade along with *Sesbania* and the genera of the tribes Loteae and Coronilleae. Collectively this trichotomous clade is sister to the very large legume clade marked by the loss of the chloroplast DNA inverted repeat, or the inverted-repeat-lacking clade (IRLC; Wojciechowski, in press; Wojciechowski et al. 2000).

Although three monographs detailing the relationships and circumscriptions of robinioid genera have been produced (Lavin 1988; Lavin 1993; Lavin and Sousa 1995), accumulating DNA sequence and morphological data suggest that some of these genera and their relationships are in need of reinvestigation. Although the problematic taxonomies are confined to two robinioid genera, *Coursetia* and *Gliricidia*, a comprehensive reanalysis has been undertaken for the first time at the species level for all robinioid legumes. Such exhaustive sampling enabled the detection of a root for the robinioid phylogeny, a reevaluation of all generic circumscriptions and relationships, and a biogeographic analysis that included an evolutionary rates analysis. Robinioids are represented in the fossil record throughout North America, and to some extent Europe, by Late Eocene to Pliocene wood and leaf samples (Matten et al. 1977; Wheeler and Landon 1992; Page 1993; Wheeler 2001). The early continental distribution of these well characterized fossils, as well as recent advances in Bayesian likelihood and evolutionary rates analysis, provides an opportunity to confidently estimate the ages of insular and continental robinioid diversifications. In particular, these include two Greater Antillean robinioid genera, *Hebestigma* and *Poitea*, the ages of which were estimated previously (Lavin et al. 2001b) but with parsimony methods and nominal consideration of apomorphic traits shared between the fossil and extant taxa.

Materials and Methods

Taxon Sampling. All 12 genera and all constituent species traditionally classified in the tribe Robinieae, excepting those of *Sesbania*, have been sampled for morphological data (Appendix A and B). Such data have been derived in large part from a monographic treatment of the tribe (Lavin and Sousa 1995) and two of the larger constituent genera, *Coursetia* (Lavin 1988) and *Poitea* (Lavin 1993). All robinioid genera and most constituent species have been sampled for nuclear ribosomal internal transcribed spacers and intervening 5.8S sequences (the ITS region; Appendix C). This includes *Lennea* (all three species sampled), *Gliricidia* (all three), *Hybosema* (all two), *Poitea* (12 of 13 taxa), *Coursetia* (35 of 40 species), *Peteria* (three of four), *Robinia* (all four), and the following monotypic genera: *Hebestigma*, *Olneya*, *Genistidium*, and *Sphinctospermum*. The ITS region was sampled exhaustively because this provides a means of identifying potentially problematic paralogs (e.g., Buckler et al. 1997) even though such have never been detected among robinioid legumes and close relatives. Also, these sequences contain much informative variation among genera and species, and they are readily amplified and are not problematic to align for robinioid legumes and close relatives (e.g., Lavin et al. 2001a; Lavin et al. 2001b; Wojciechowski et al. 1993). In addition, exhaustive sampling increases overall phylogenetic accuracy (Zwickl and Hillis 2002). The single exception to the sampling of the morphological data and the ITS sequences is the genus *Sesbania*. Because this genus has been shown to be a distinct lineage from the robinioid legumes (Wojciechowski, in press; Wojciechowski et al. 2000), *Sesbania* has been sampled as one of the designated outgroups in this analysis.

The chloroplast *trnL* intron and the *matK* loci were more discriminately sampled for selected species to verify certain of the findings derived from the analysis of the morphological data and ITS region. The *matK* locus was sampled to verify findings at higher levels, particularly the root of the robinioid phylogeny. For these chloroplast loci, sampling was performed for at least one species from each of the robinioid genera (*Hebestigma*, *Lennea*, *Gliricidia*, *Hybosema*, *Poitea*, *Coursetia*, *Genistidium*, *Olneya*, *Peteria*, *Robinia*, and *Sphinctospermum*) and designated outgroups (*Sesbania*, *Anthyllis*, *Lotus*, *Ornithopus*, and *Securigera*).

The designated outgroups in this study include representatives of two monophyletic clades that are the closest relatives of the robinioid clade, the genus *Sesbania* and the Loteae-Coronilleae tribal alliance. Five species of the Loteae-Coronilleae alliance for which at least *matK* sequences were available have been incorporated into this analysis. These include *Anthyllis vulneraria*, *Securigera varia*, *Lotus unifoliolatus*, *Lotus japonicus*, and *Ornithopus compressus*. According to the phylogeny of Allan and Porter (2000), *Anthyllis* and *Securigera* represent the basal-most branching lineage of the Loteae-Coronilleae clade, whereas *Ornithopus* represents a more distally branching clade very closely related to species traditionally placed in the genus *Lotus*. Five species were selected that represent the major subgenera of *Sesbania* (Lavin and Sousa 1995): the most speciose subgenus *Sesbania* (Old World *S. cannabina* and *S. tomentosa*, and New World *S. emerus*), subgenus *Daubentonia* (*S. drummondii*), subgenus *Agati* (*S. grandiflora*), and subgenus *Glottidium* (*S. vesicaria*). These outgroup species were sampled especially for sequences from the ITS region and the *matK* locus, but more discriminately for morphological and *trnL* intron variation because these last two sources of data were used mostly for addressing questions at phylogenetic levels within the robinioid legumes (Appendix C).

Sequence Data and Analysis. DNA isolations, PCR amplifications, and template purifications were performed with Qiagen Kits (i.e., DNeasy Plant Mini Kit, Taq PCR Core Kit, QIAquick PCR Purification Kit; Qiagen, Santa Clarita CA). PCR primers and amplification conditions for the ITS region, the *trnL* intron, and the *matK* locus are described in Beyra-M. and Lavin (1999), Lavin et al. (2000), and Lavin et al. (2001a and 2001b). Sequencing products were run on an ABI 377 and 3700 automated sequencer at Northwoods DNA (Becida, Minnesota), Davis Sequencing (Davis, California), DNA Sequencing and Synthesis Facility (Ames, Iowa), and The ASU-DNA Laboratory (Tempe, Arizona).

DNA sequences were aligned manually with the aid of Se-Al (Rambaut 1996). Multiple manual alignments were continuously analyzed during the development of the various data sets to identify those clades consistently resolved regardless of taxon composition or sequence alignment of the data set. Individual data sets were developed for sequence data from the ITS region, the *trnL* intron, and the *matK* locus, morphological characters. Combined data sets were developed for all possible combinations of these four individual data sets. Maximum likelihood and parsimony analyses were performed with MrBayes (Huelsenbeck and Ronquist 2001) and PAUP* (Swofford 2001). For nucleotide sequence data, multiple Bayesian analyses each began with a random tree and the most general nucleotide substitution model, a general time reversible model plus a shape parameter for a gamma distribution and invariant sites parameter. Parsimony heuristic searches on all data sets included 100 random addition replicates, tree bisection reconnection branch swapping, and retention of multiple parsimonious trees. Clade stability tests involved Bayesian posterior probabilities (Huelsenbeck et al. 2001) and parsimony bootstrap resampling (Felsenstein 1985). For the latter, each of 10,000 non-parametric bootstrap replicates was subjected to a heuristic search as above, but with one random addition sequence and only one tree saved per replicate. For the various data sets, the percentage of data matrix cells scored as missing data are reported in Table 1.

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

For the ITS and *matK* data sets, branch lengths were estimated during a maximum likelihood analysis that involved a search of tree parameter space using a Bayesian approach. This involves a Metropolis-coupled Markov Chain Monte Carlo permutation of tree parameters, an initial random tree, 1,000,000 permutations of tree parameters, and four chains (Huelsenbeck and Ronquist, 2001; Huelsenbeck et al. 2001). Parsimony searches in PAUP* (Swofford 2001) were used to validate the branching order parameter estimated with MrBayes, whereas the AIC model selection approach was used to validate the estimated nucleotide substitution parameters (Posada and Crandall 1998). All estimated parameters (branching order, branch lengths, and nucleotide substitution) were then used to generate parametric bootstrap replicates using Seq-Gen (Rambaut and Grassley 2001), each of which were subjected to analyses with r8s to obtain mean and standard deviations of evolutionary substitution rates and ages of specified clades.

Relative substitution rates and ages estimated with r8s were converted to absolute rates and ages by enforcing two time constraints. One time constraint was derived from an evolutionary rates analysis of *matK* sequences for all Fabaceae (Wojciechowski, in press; Wojciechowski et al., in mss.). This large-scale analysis uses an age constraint for the legume crown clade of 59.9 Ma, which represents the age of the oldest unequivocal legume fossil (Herendeen et al. 1992 and personal communication). From this, the maximum age estimate for the robinioid crown clade (i.e., the most recent common ancestor of *Hebestigma* and *Robinia*) is 45 Ma. A second constraint was derived from the robinioid fossil record, where Tertiary North American fossil wood samples of *Robinia zirkellii* (Platen) Matten, Gastaldo, and Lee range in age from Late Eocene to Pliocene (Matten et al. 1977; Wheeler and Landon 1992; Page 1993; Wheeler 2001). The apomorphic traits displayed by these fossils place it clearly on the *Robinia* stem clade, which therefore must have a minimum age of Late Eocene, or 33.7 Ma following Berggren et al. (1995). These wood characters are detailed in the discussion.

Results

ITS Data Set. The parsimony analysis of sequences from the ITS region yielded 10,000 trees (Table 1). The strict consensus resolves clades that are well support-

TABLE 1. Data set and tree statistics for the separate and combined analyses. PI = parsimony informative, CI = consistency index, RI = retention index, and PHT = partition homogeneity test. The p values for the PHT were derived from 1000 random partitions, each analyzed with only informative characters (actual partitions are indicated in the most left-hand column; NA = not applicable). Bootstrap values are given in parentheses in last four columns. In all analyses, the maximum number of trees was set at 10,000.

Data set	Taxa	Total characters (% missing)	PI characters	Trees	Length	PHT (p)	CI	RI	*Hebestigma-Lennea* clade	*Gliricidia-Hybosema* clade	*Poitea-Gliricidia* clade	*Poissonia* clade
nrDNA ITS1, 5.8S, ITS2	178	737 (0.6)	435	10,000	2003	0.209	0.447	0.901	basalmost clade (88%)	monophyletic (86%)	monophyletic (100%)	monophyletic (94%)
cpDNA *trnL* intron & indels	53	682 (1.0)	111	10,000	247	0.474	0.791	0.916	not resolved	monophyletic (73%)	not resolved	monophyletic (60%)
cpDNA *matK*	37	1557 (2.8)	291	180	660	NA	0.811	0.898	not resolved	not resolved	monophyletic (100%)	monophyletic (71%)
morphology	82	40 (6.7)	40	10,000	104	NA	0.452	0.907	not resolved	not resolved	monophyletic (62%)	not resolved
morphology and ITS region	82	777 (0.4)	400	3,360	1639	0.039	0.481	0.829	basalmost clade (88%)	monophyletic (79%)	monophyletic (100%)	monophyletic (100%)
all data sets	26	3017 (0.7)	554	2	1743	0.288	0.690	0.752	basalmost clade (94%)	monophyletic (97%)	monophyletic (100%)	monophyletic (100%)

ed by bootstrap analysis (Figs. 1–3). Unambiguous and phylogenetically informative indels were few in the ITS region and the few that were detected corresponded with already well supported clades derived from nucleotide substitutions (e.g., the genus *Lennea*, or subclades within *Poitea*). The clade including *Hebestigma* and *Lennea* is sister to the rest of the robinioids, and *Gliricidia* and *Hybosema*, the latter depicted as *G. robustum* and *G. ehrenbergii* in Fig. 1, form the well-supported sister clade of *Poitea*. The robinioid genera bearing a style with a pollen brush, *Olneya*, *Robinia*, *Peteria*, *Genistidium*, *Sphinctospermum*, and *Coursetia*, form a fairly well supported monophyletic clade (Fig. 2). Only *Coursetia* in this group of six genera is not resolved as monophyletic (Figs. 2–3). The *Coursetia* clade containing most species of the genus (Fig. 3) is weakly resolved as sister to a clade comprising *Peteria*, *Sphinctospermum*, and *Genistidium* (Figs. 2–3). The other *Coursetia* clade comprises four species, *Coursetia hypoleuca*, *C. orbicularis*, *C. heterantha*, and *C. weberbaueri*, depicted as *Poissonia* in Fig. 2, that form the moderately supported sister clade of *Robinia*.

trnL *Data Set.* Analysis of the *trnL* locus did not show much variation among robinioid legumes and was thus not sampled as thoroughly as the ITS region. Parsimony analysis of the *trnL* data set (670 aligned sites plus 12 shared indel characters) yielded 10,000 equally minimal length trees (Table 1). Branch support for the relatively few resolved clades was generally low. Exceptions included the clade comprising *Robinia*, *Olneya*, *Peteria*, *Genistidium*, *Sphinctospermum*, and *Coursetia*, which was resolved at 94% support. The *Gliricidia* clade (including *Hybosema*) was resolved with 73% bootstrap support, and the *Poissonia* clade comprising *Coursetia hypoleuca*, *C. orbicularis*, *C. heterantha*, and *C. weberbaueri* was resolved as monophyletic with 60% bootstrap support. Notably, there was no conflict among any of the clades supported at 60% or more and those that were detected during the analysis of sequences from the ITS region.

matK *Data Set.* Parsimony analysis of the *matK* locus yielded 180 equally minimal length trees (Table 1). The *Poitea-Gliricidia* clade and that comprising *Robinia*, *Olneya*, *Poissonia*, *Peteria*, *Genistidium*, *Sphinctospermum*, and *Coursetia* were very well supported by high bootstrap values of over 96% (Fig. 4). *Hebestigma* and *Lennea* were resolved as a clade and as sister to the rest of robinioids in most of the minimal length trees, but the strict consensus placed these two in an unresolved position at the base of the robinioid clade. Relationships resolved during the analysis of *matK* sequences did not conflict with any of those hypothesized by the ITS region or the *trnL* intron sequence data.

Morphological Data Set. Analysis of 40 morphological traits did not resolve many well supported relationships among the robinioid legumes (Table 1). The

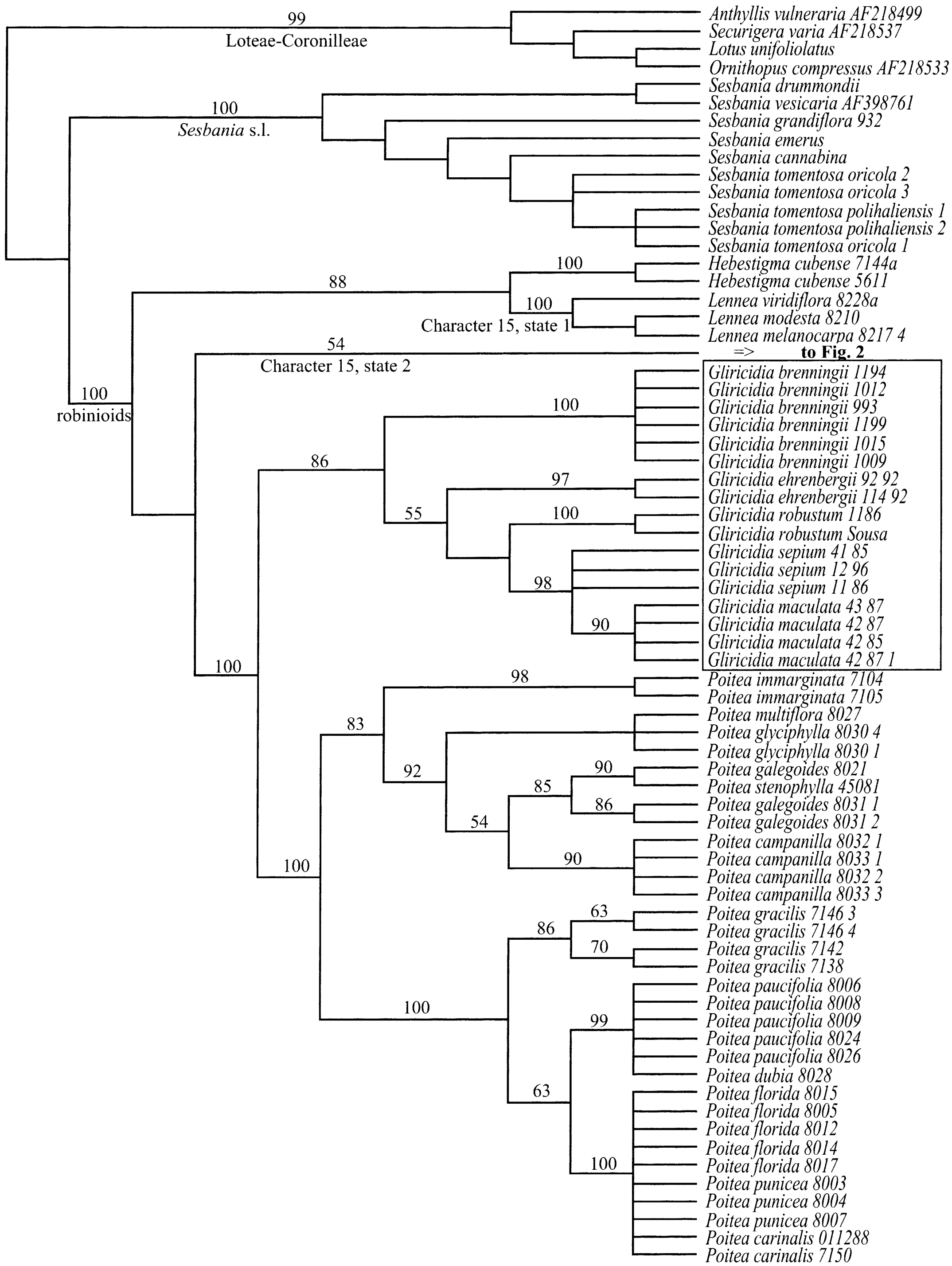

FIG. 1. Strict consensus of 10,000 (=maxtrees) equally most parsimonious trees derived from the analysis of the ITS region. The 178 sequences comprise 737 aligned sites, 435 of which are parsimony informative. The maximum parsimony trees have a length of 2003, a consistency index of 0.447, and a retention index of 0.901 (Table 1). Values above the nodes are parsimony bootstrap values. The species classified as the genus *Gliricidia* in this study are shown inside the box. The genus *Lennea* and the genera depicted in Figs. 2–3 are shown marked by states of character 15, which are described in Appendix A.

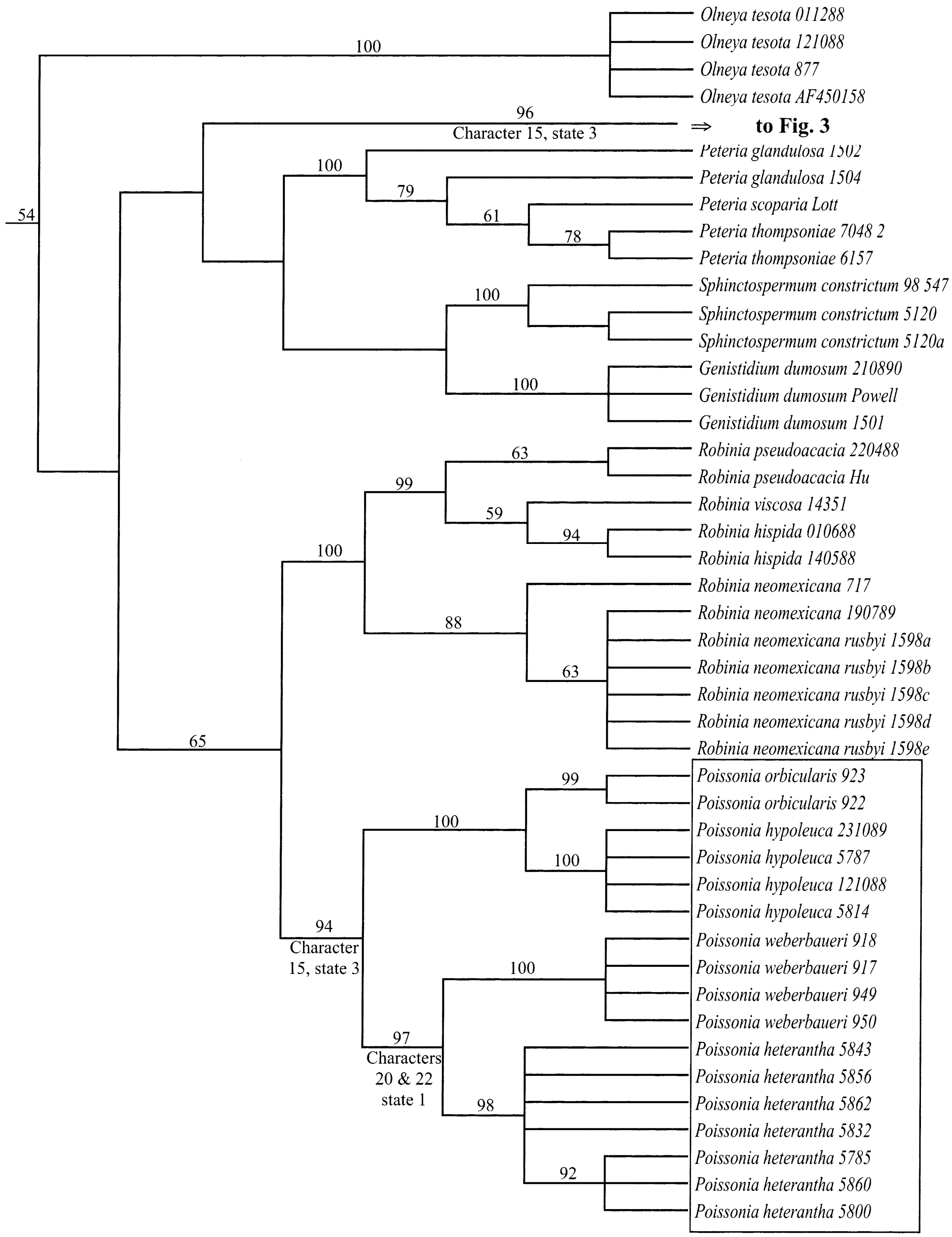

FIG. 2. Continuation of Fig. 1 showing the clade comprising the genera *Olneya*, *Robinia*, *Poissonia*, *Peteria*, *Genistidium*, *Sphinctospermum*, and *Coursetia*, genera traditionally grouped as the barbistyled genera because of the shared pollen brush on the style. Values above the nodes are parsimony bootstrap values. The species classified as the genus *Poissonia* in this study are shown inside the box. A subgroup of *Poissonia* is marked by a post-pollination floral resupination syndrome and a long pedunculate inflorescence (character #'s 20 and 22 in Appendix A).

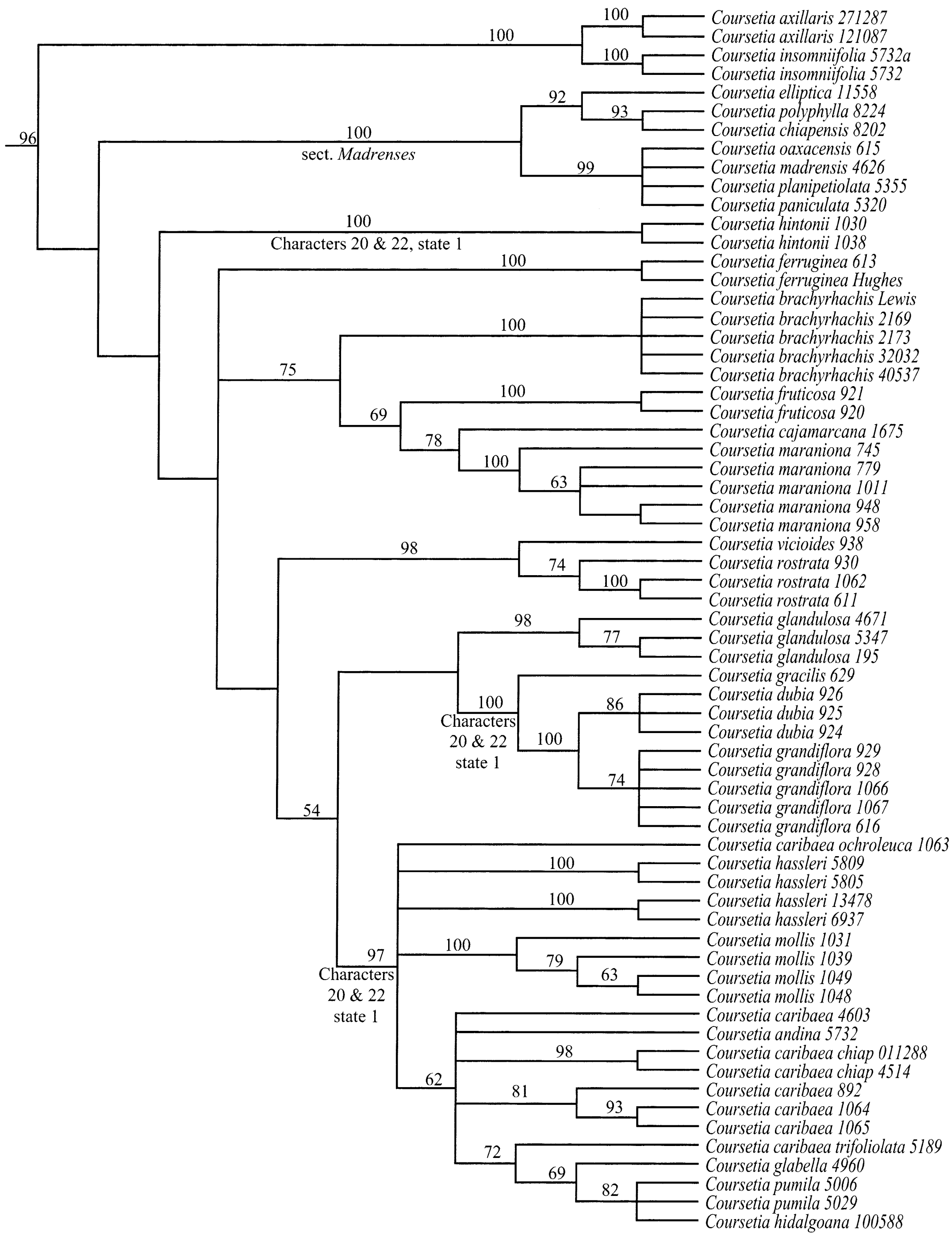

FIG. 3. Continuation of Figs. 1 and 2 showing the clade comprising the species of the genus *Coursetia* (sensu stricto—as defined in this study). Values above the nodes are parsimony bootstrap values. *Coursetia* subclades possessing a post-pollination floral resupination syndrome and a long pedunculate inflorescence are indicated (character #'s 20 and 22 in Appendix A).

robinioids are moderately supported as a monophyletic clade (76% bootstrap support) comprising four major subclades. The genera *Hebestigma* and *Lennea* each represent a basal branching clade. *Gliricidia*, *Hybosema*, and *Poitea* comprise a third clade (62% bootstrap support), and *Robinia*, *Olneya*, *Peteria*, *Genistidium*, *Sphinctospermum*, and *Coursetia* a fourth (73% bootstrap support). These are the same four groups that were resolved in all analyses of the individual molecular data sets. The bulk of the missing entries for this particular

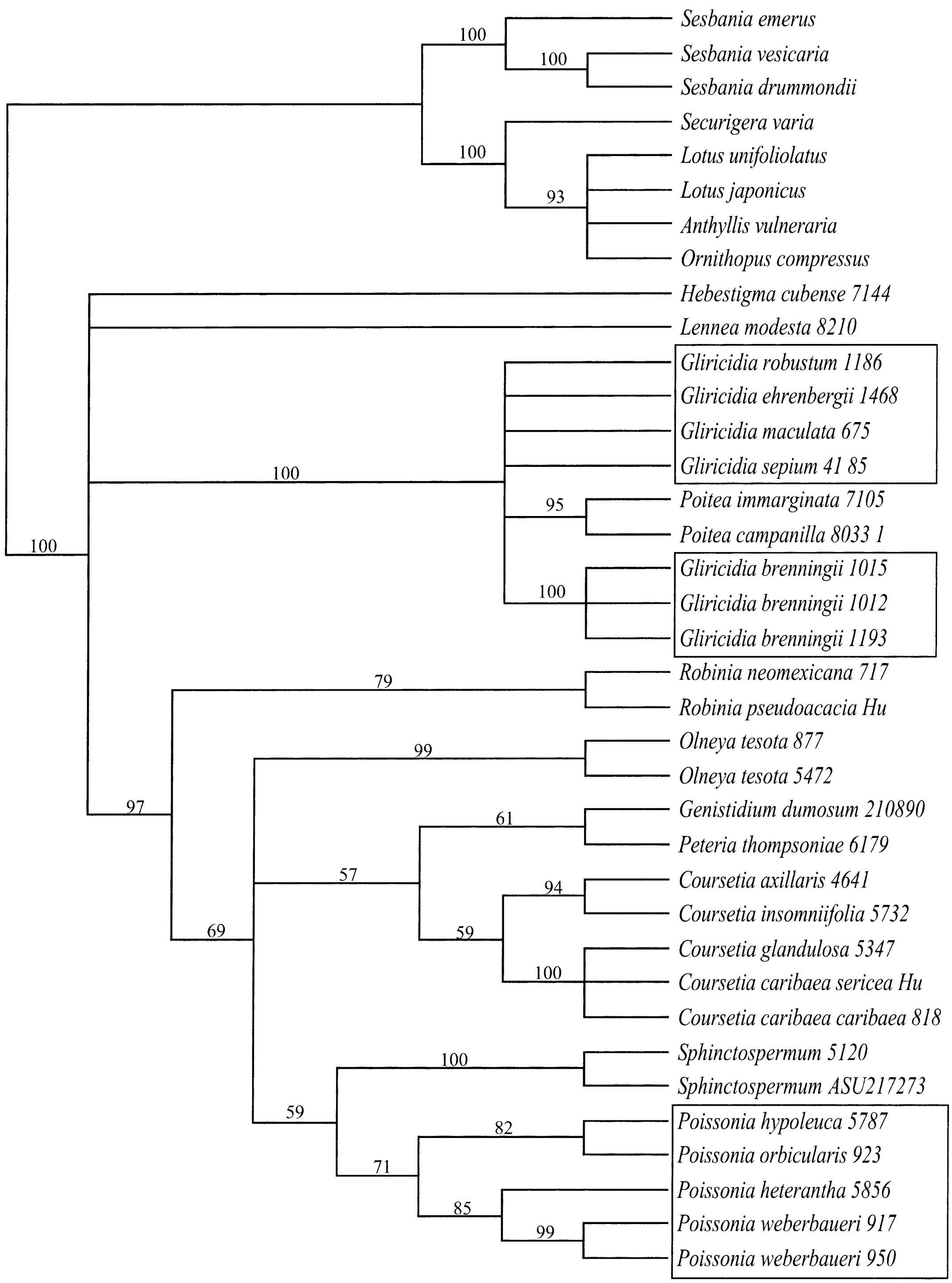

FIG. 4. Strict consensus of 180 equally most parsimonious trees derived from the analysis of the *matK* locus. The 37 sequences comprise 1557 aligned sites, 291 of which are parsimony informative. This tree has a length of 660, a consistency index of 0.811, and a retention index of 0.898. Values above the nodes are parsimony bootstrap values. The species classified as the genera *Gliricidia* and *Poissonia* in this study are shown inside the boxes.

data set came from the wood anatomical characters, because many species have yet to be studied for wood traits.

Combined Data Sets. A partition homogeneity test revealed no significant conflict among any of the possible data partitions, except between the sequences from the ITS region and the morphological data set (Table 1). Other than the *Hebestigma-Lennea* clade, no conflict was detected among the these two data sets during individual data set analyses, if only because all the well supported nodes detected in one analysis with bootstrap values well over 60% were also resolved with the other data set. Apparent conflict detected in the combined morphology and ITS data set was the result of the many missing entries in the wood characters. Omitting wood characters during this test suggested no conflict between the morphological and ITS data sets.

Just two of the combined data sets will be presented here because they capture the essence of results for all possible data combinations. The first is the combined morphological (40 characters) and ITS region (737 aligned sites) data set. Because of the exhaustive sampling of these two data sets at the species level, a combined analysis allows for the most comprehensive comparisons. Analysis of the combined ITS-morphological data set yielded 3,360 equally parsimonious trees (Table 1). Only the *Sesbania* species were used as outgroups because of the difficulty of scoring homologous morphological characters among the robinioids and species of the Loteae-Coronilleae alliance.

The only substantive differences between the analysis of this combined data set and that of the ITS region alone was that branch support increased significantly in a few clades. Most notably, the genus *Coursetia* (sensu stricto) showed an increase from 92% in the ITS analysis to 98% in the combined analysis. Although, the combined analysis of the ITS region and the morphological data sets yielded very similar results to the individual analyses of constituent data sets, combined data allowed for mapping the evolution of the morphological characters that have most heavily influenced previous taxonomies of the robinioid genera (see discussion).

The second combined analysis involved all of the molecular data sets in combination with the morphological one. Because of limited sampling of the *matK* locus, this analysis included only 23 ingroup terminal taxa (Table 1; Fig. 5). One significant finding was that *Hebestigma* and *Lennea* form a well supported clade that is resolved as one of three basal branches in the robinioid diversification. A second major subclade in the robinioid diversification is the clade comprising *Poitea*, *Gliricidia*, and *Hybosema*, and a third includes *Robinia*, *Poissonia*, *Olneya*, *Peteria*, *Genistidium*, *Sphinctospermum*, and *Coursetia*. In both of the combined analyses, samples of the two hybosemas (depicted as *Gliricidia robustum* and *G. ehrenbergii* in Figs. 4 and 5) are nested within *Gliricidia*, and *Coursetia* includes two major sublineages (*Coursetia* sensu stricto and *Poissonia*). *Coursetia* is resolved with weak support as a close relative of *Genistidium*, *Peteria*, and *Sphinctospermum*, whereas *Poissonia* is weakly resolved as the sister to *Robinia*. This latter clade comprises *Coursetia hypoleuca*, *C. orbicularis*, *C. weberbaueri*, and *C. heterantha* (depicted as *Poissonia* in Fig. 5), four South American species confined to the Andes in southern Peru, Bolivia, and northern Argentina.

Evolutionary Rates Analysis. A likelihood ratio test rejected models with a uniform rate across all branches for both the ITS and *matK* phylogenies (ITS region: LR=182.87, df=77, p=0.000000; *matK*: LR=345.56, df=27, p=0.000000). With the root of each of the ITS and *matK* robinioid phylogenies constrained to a maximum of 45 Ma, and that of the *Robinia* stem clade set to 33.7 Ma, the penalized likelihood (PL) and rate constant (LF) methods of rate smoothing yielded very similar age and rate estimates (Tables 2–3). Autocorrelated rate smoothing (NPRS) generally produced faster rates or older age estimates than PL and LF for sequences from both the ITS region and *matK* locus. Sequences from the *matK* locus yielded slightly older age estimates than sequences from the ITS region (compare clades A–D in Tables 2–3; Figs. 6–7). Regardless, the estimated substitution rates using PL fall within a very close range, suggesting a high degree of constancy in substitution rate. The PL estimates are uniformly 3.9×10^{-10} substitution/site/year for *matK* and $3.1–3.5 \times 10^{-9}$ substitutions/site/year for the ITS region (Tables 2–3).

The two vicariant Caribbean clades, *Hebestigma-Lennea* (crown clade A in Fig. 6, Table 2) and *Poitea-Gliricidia* (crown clade B in Figs. 6–7, Tables 2–3) are estimated to be at least 38 and 16 Ma in age, respectively. The *Poitea* diversification (crown clade B2, Table 2, Fig. 6), estimated at least 9 Ma in age, is at least as old as its mainland sister diversification, *Gliricidia* (crown clade B1, Table 2, Fig. 6). Andean South American clades occur within the robinioid diversification, and involve only the species of *Poissonia* (crown clade C in Fig. 6), *Gliricidia brenningii* (crown clade B1), and subclades within *Coursetia* (all within crown clade D1). The crown clade *Poissonia* (clade C in Figs. 6–7, Tables 2–3) is at least 18 Ma in age, which is at least as old or older than the other South American diversifications (crown clade D1 in Fig. 6, Table 2). The youngest clade within the robinioid diversification that contains both North and South American species is that of involving *Coursetia caribaea* and close relatives (crown clade D2 in Fig. 6, Table 2), which is estimated at around 5 Ma in age.

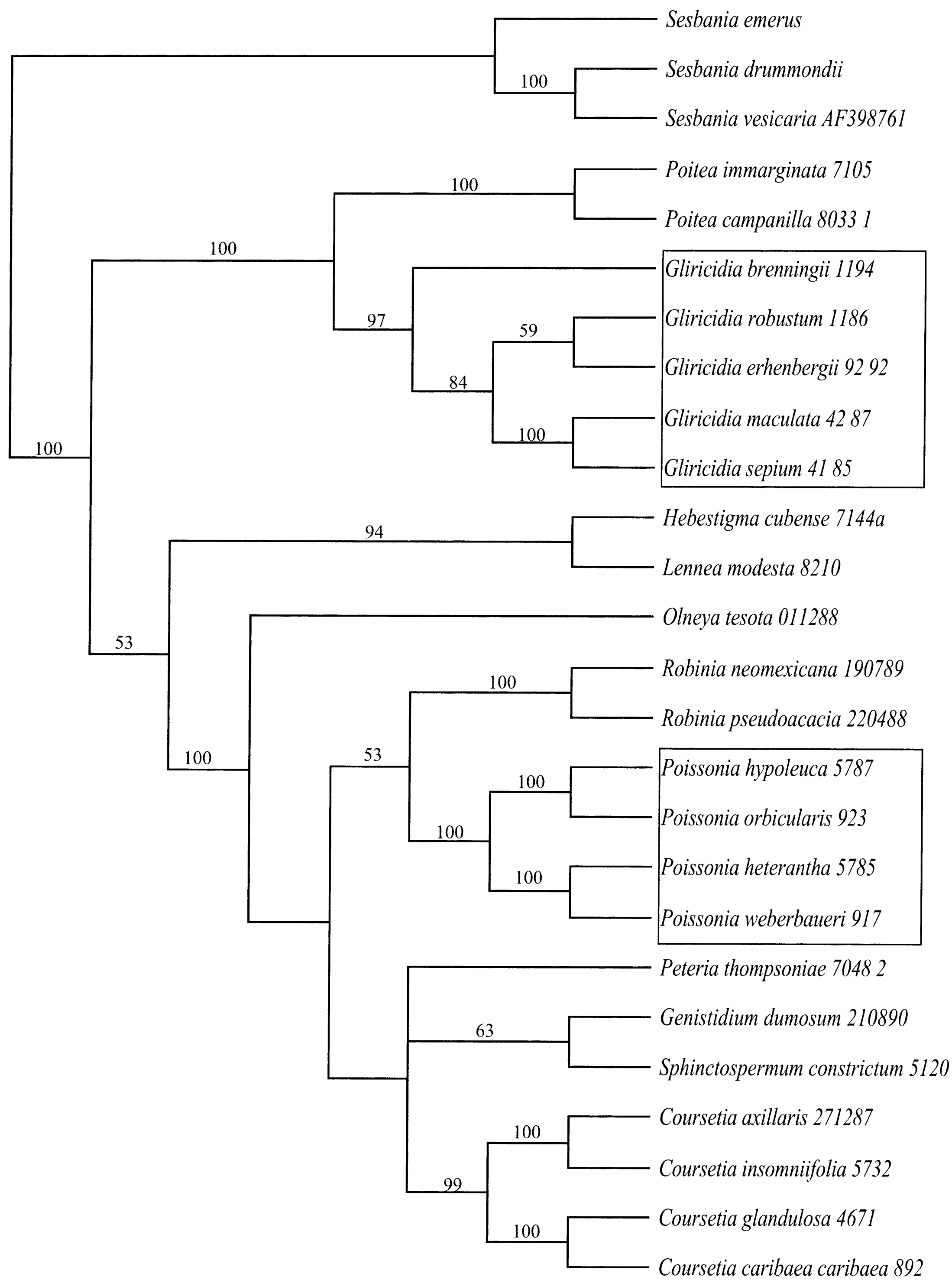

FIG. 5. The strict consensus of two equally most parsimonious trees derived from the combined data set comprising 26 species represented by sequences from the combined ITS region (737 aligned sites), the *trnL* intron (670 aligned sites plus 12 indel characters), and the *matK* locus (1557 aligned sites plus one indel character), as well as 40 morphological characters. Of these 3017 characters, 554 were parsimony informative. This tree has a length of 1743, a consistency index of 0.690, and a retention index of 0.752 (Table 1). Values above the nodes are parsimony bootstrap values. Species classified in the genera *Gliricidia* and *Poissonia* in this study are shown inside the boxes.

TABLE 2. Estimated ages (Ma) and rates (per site per Ma—below the age estimate) of selected clades from the rate smoothed Bayesian likelihood trees derived from sequences from the ITS region. The root of the robinioid crown clade was calibrated at a maximum of 45 Ma and the *Robinia* stem clade calibrated at 33.7 Ma (Fig. 6). The rate smoothing methods are PL = penalized likelihood, LF = rate constant, and NPRS = nonparametric rate smoothing. Means and standard deviations were estimated with a rate smoothing analysis of 100 Bayesian likelihood trees, each of which was derived from a parametric bootstrapped data set.

Crown clade	PL (45)	LF (45)	NPRS (45)
A	38.3 ± 3.8	38.4 ± 3.8	37.9 ± 4.1
	0.0031 ± 0.0012	0.0035 ± 0.0002	0.0055 ± 0.0022
B	16.3 ± 4.3	16.3 ± 4.3	26.4 ± 3.9
	0.0034 ± 0.0004	0.0035 ± 0.0002	0.0060 ± 0.0011
B1	8.2 ± 1.6	8.2 ± 1.6	20.8 ± 4.1
	0.0035 ± 0.0002	0.0035 ± 0.0002	0.0029 ± 0.0007
B2	9.3 ± 1.2	9.3 ± 1.2	18.4 ± 2.8
	0.0035 ± 0.0002	0.0035 ± 0.0002	0.0044 ± 0.0006
C	18.1 ± 2.1	17.7 ± 2.1	25.8 ± 2.2
	0.0034 ± 0.0002	0.0035 ± 0.0002	0.0036 ± 0.0007
D	19.8 ± 2.5	19.6 ± 2.4	28.2 ± 3.0
	0.0034 ± 0.0002	0.0035 ± 0.0002	0.0046 ± 0.0008
D1	15.7 ± 1.8	15.6 ± 1.8	23.8 ± 2.9
	0.0034 ± 0.0002	0.0035 ± 0.0002	0.0037 ± 0.0006
D2	4.8 ± 0.9	4.8 ± 0.9	8.1 ± 1.9
	0.0035 ± 0.0002	0.0035 ± 0.0002	0.0026 ± 0.0006

DISCUSSION

The results of this analysis bear on two general areas. The first involves the taxonomies of the genera *Gliricidia* and *Coursetia*. The evolution of certain distinctive morphological traits that have been used to diagnose these genera (e.g., Lavin 1988; Lavin and Sousa 1995) are now at odds with the findings derived from molecular data. The second involves the Caribbean endemic genera, *Hebestigma* and *Poitea*. With the root of the robinioid phylogeny firmly established for the first time with multiple data sets, it is clear that this primarily North American tropical radiation includes two independent cases of Caribbean and continental vicariant sister clades: *Hebestigma* (Cuba) and *Lennea* (Mesoamerica), and *Poitea* (Greater Antilles and Dominica) and *Gliricidia* (Mesoamerica but with one species from Ecuador and adjacent Peru).

***The Genus* Gliricidia.** The *Gliricidia* and *Poitea* phylogenies derived from the sequence analysis of the ITS region are highly congruent with previously published phylogenies of these genera, which were derived from cpDNA restriction site data (e.g., Lavin et al. 1991; Lavin 1993). As such, the genus *Gliricidia* is herein circumscribed to include five species: *Gliricidia brenningii*, *G. ehrenbergii*, *G. maculata*, *G. robustum*, and *G. sepium*. The genus is not diagnosed by morphological characters, but the taxonomic keys to genera and species provided by Lavin and Sousa (1995) remain valid as long as *Hybosema* species are placed within *Gliricidia*. That *Hybosema* is nested within a paraphyletic *Gliricidia* sensu stricto is revealed not only by molecular data, but also by wood anatomy. For example, wood with septate fibers (#35; Table 4, Appendix A and B) and storied rays (character #36) is derived at the base of the clade containing *Gliricidia robustum*, *G. ehrenbergii*, *G. maculata*, and *G. sepium* (storied rays are secondarily lost in *G. ehrenbergii*). Wood and molecular data are concordant in resolving the South American *Gliricidia brenningii* as sister to the rest of the species of *Gliricidia*. As now circumscribed, *Gliricidia* is confined to Mexico and ad-

TABLE 3. Estimated ages (Ma) and rates (per site per Ma—below the age estimate) of selected clades from the rate smoothed Bayesian likelihood trees derived from sequences from the *matK* locus. The root of the robinioid crown clade was calibrated at a maximum of 45 Ma and the *Robinia* stem clade calibrated at 33.7 Ma (Fig. 7). The rate smoothing methods are PL = penalized likelihood, LF = rate constant, and NPRS = nonparametric rate smoothing. The estimated age of the crown clade A (the *Hebestigma-Lennea* clade; Fig. 6) did not differ significantly from the fixed age of the robinioid crown clade (45 Ma). Means and standard deviations were estimated with a rate smoothing of 100 Bayesian likelihood trees, each of which was derived from a parametric bootstrapped data set.

Crown clade	PL	LF	NPRS
B	18.0 ± 2.4	17.9 ± 2.4	17.0 ± 3.2
	0.00039 ± 0.00003	0.00039 ± 0.00003	0.00059 ± 0.00011
C	22.3 ± 3.1	22.3 ± 3.0	22.1 ± 3.5
	0.00039 ± 0.00003	0.00039 ± 0.00003	0.00048 ± 0.00008
D	23.2 ± 3.3	23.2 ± 3.3	25.2 ± 3.1
	0.00039 ± 0.00003	0.00039 ± 0.00003	0.00042 ± 0.00007

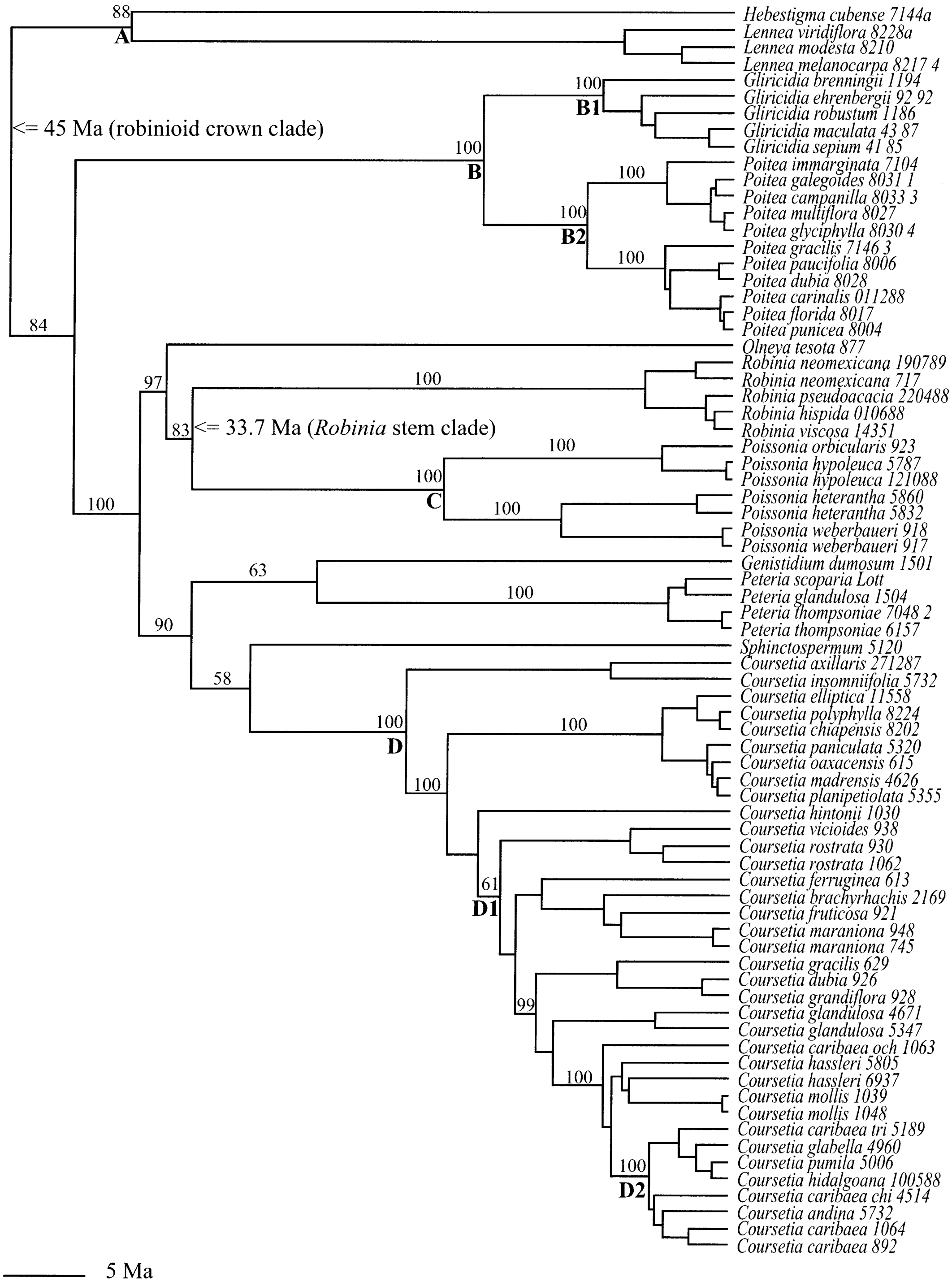

FIG. 6. Chronogram derived from penalized likelihood rate smoothing of a consensus Bayesian likelihood tree, which was estimated with sequences from the ITS region. The 45 Ma maximum age constraint at the basal node is derived from a large scale rates analysis of all legumes (Wojciechowski, in press; Wojciechowski et al., in mss.). The 33.7 Ma minimum age constraint is derived from the fossil wood record (see methods and material, and discussion). The average nucleotide substitution parameters for 10,000 Bayesian trees at stationarity are r(GT) = 1.00, r(CT) = 6.379, r(CG) = 0.980, r(AT) = 1.758, R(AG) = 3.018, r(AC) = 1.155, pi(A) = 0.204, pi(C) 0.271=, pi(G) = 0.293, pi(T) = 0.233, alpha = 1.418, iP = 0.216. See Table 2 for the estimated ages and rates of substitution for the clades marked A, B, C, and D. Values above nodes are Bayesian posterior probabilities for selected clades.

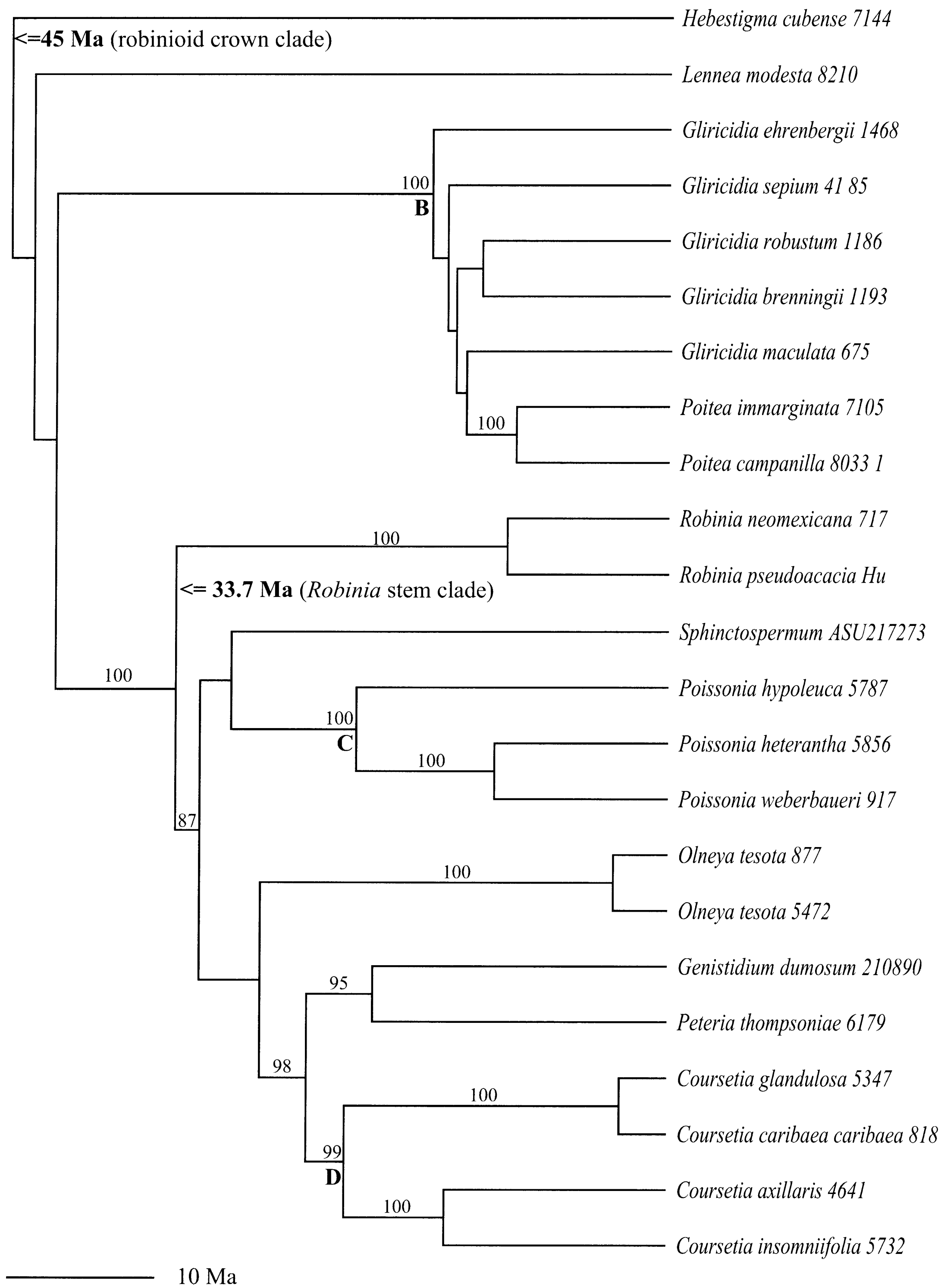

FIG. 7. Chronogram derived from penalized likelihood rate smoothing of a consensus Bayesian likelihood tree, which was estimated with sequences from the *matK* locus. The 45 Ma maximum age constraint at the basal node is derived from a large scale rates analysis of all legumes (Wojciechowski, in press; Wojciechowski et al., in mss.). The 33.7 Ma minimum age constraint is derived from the fossil wood record (see methods and material, as well as discussion). The average nucleotide substitution parameters for 10,000 Bayesian likelihood trees at stationarity are r(GT) = 1.00, r(CT) = 2.201, r(CG) = 2.059, r(AT) = 0.274, R(AG) = 1.925, r(AC) = 1.508, pi(A) = 0.324, pi(C) = 0.145, pi(G) = 0.147, pi(T) = 0.384, SS(1) = 0.849, SS(2) = 0.705, SS(3) = 1.446. See Table 3 for the estimated ages and rates of substitution for the clades marked B, C, and D (which correspond with those marked in Fig. 6). Values above nodes are Bayesian posterior probabilities.

TABLE 4. Parsimony tree scores for the 40 morphological characters listed in Appendix A and taken from the analysis of the combined morphological and nrDNA ITS/5.8S data set. The range of the length, consistency index, and retention index is over the 3,360 minimal length trees. These morphological characters added a length of 120 to the total 1639 (Table 1). The CI for all 40 morphological characters is 0.392, and the RI is 0.882, suggesting that the morphological traits are comparable to ITS in resolving relationships (compare to values in Table 1).

	Length		Consistency index		Retention index	
Character	Minimum	Maximum	Best	Worst	Best	Worst
1	7	8	0.143	0.125	0.769	0.731
2	3	3	0.333	0.333	0.895	0.895
3	6	6	0.333	0.333	0.636	0.636
4	1	1	1.000	1.000	1.000	1.000
5	2	2	1.000	1.000	1.000	1.000
6	2	2	0.500	0.500	0.889	0.889
7	1	1	1.000	1.000	1.000	1.000
8	1	1	1.000	1.000	1.000	1.000
9	3	3	0.333	0.333	0.944	0.944
0	4	4	0.500	0.500	0.923	0.923
11	2	2	0.500	0.500	0.500	0.500
12	1	1	1.000	1.000	1.000	1.000
13	2	2	0.500	0.500	0.750	0.750
14	1	1	1.000	1.000	1.000	1.000
15	4	4	0.750	0.750	0.971	0.971
16	1	1	1.000	1.000	1.000	1.000
17	1	1	1.000	1.000	1.000	1.000
18	2	2	0.500	0.500	0.955	0.955
19	3	3	0.333	0.333	0.929	0.929
20	4	4	0.250	0.250	0.864	0.864
21	3	3	0.333	0.333	0.926	0.926
22	4	4	0.250	0.250	0.864	0.864
23	8	8	0.125	0.125	0.806	0.806
24	5	5	0.200	0.200	0.600	0.600
25	2	2	0.500	0.500	0.941	0.941
26	3	4	0.667	0.500	0.969	0.938
27	3	3	0.333	0.333	0.946	0.946
28	6	6	0.167	0.167	0.808	0.808
29	6	6	0.167	0.167	0.722	0.722
30	1	1	1.000	1.000	1.000	1.000
31	1	1	1.000	1.000	1.000	1.000
32	1	1	1.000	1.000	1.000	1.000
33	2	2	1.000	1.000	1.000	1.000
34	3	3	0.333	0.333	0.857	0.857
35	3	3	0.333	0.333	0.667	0.667
36	3	3	0.333	0.333	0.500	0.500
37	1	1	1.000	1.000	1.000	1.000
38	3	3	0.333	0.333	0.500	0.500
39	8	8	0.125	0.125	0.500	0.500
40	2	2	0.500	0.500	0.667	0.667

jacent parts of Central America, with the exception of *G. brenningii*, which is from Ecuador and Peru (Lavin and Sousa 1995). The following nomenclature is modified from Lavin and Sousa (1995) to adjust for this recircumscription.

Gliricidia H. B. K., Nov. gen. Sp. 6: 393. 1823.—Type: *Gliricidia sepium* (Jacq.) Steud.

Yucaratonia Burkart, Darwiniana 15: 523. 1969.—Type: *Yucaratonia brenningii* (Harms) Burkart [= *Gliricidia brenningii* (Harms) Lavin].

Hybosema Harms, Repert. Spec. Nov. Regni Veg. 19: 66. 1923.—Type: *Hybosema ehrenbergii* (Schltdl.) Harms [=*Gliricidia ehrenbergii* (Schltdl.) Rydb.].

1. *Gliricidia robustum* (M. Sousa & Lavin) Lavin, comb. nov. *Hybosema robustum* M. Sousa & Lavin, Anales Inst. Biol. Univ. Nac. Mexico, Ser. Bot. 63: 143. 1992.—Type: MÉXICO. Chiapas: Cañón del Sumidero, *Martínez S. & Reyes G. 22047* (holotype: MEXU; isotypes: BM, MEXU, MO).

2. *Gliricidia ehrenbergii* (Schltdl.) Rydb., N. Amer. Fl. 24: 239. 1924. *Robinia ehrenbergii* Schltdl., Linnaea 12: 303. 1838. *Hybosema ehrenbergii* (Schltdl.) Harms, Repert. Spec. Nov. Regni Veg. 19: 66. 1923.—Type: MÉXICO. In solo calcareo boream versus ab aquis calidis pr. Grande, *Ehrenberg 645* (holotype: HAL, photo: MONT; isotypes: B, destroyed, HAL, fragment of B isotype: F, photos of B isotype: F, G,

GH, MEXU, MICH, MO, NY, TEX). See Lavin and Sousa (1995) for taxonomic synonyms.

3. *Gliricidia brenningii* (Harms) Lavin, Syst. Bot. Monogr. 45: 83. 1995. *Sesbania brenningii* Harms, Repert. Spec. Nov. Regni Veg. 19: 68. 1923. *Yucaratonia brenningii* (Harms) Burkart, Darwiniana 15: 526. 1969.—Type: ECUADOR. Guayaquil, an Wegrändern in der Nähe des Río Salado, *Brenning 238* (holotype: B, destroyed, fragment: F, photos: F, NY).
4. *Gliricidia maculata* (H. B. K.) Steud., Nom. Bot., ed. 2, 1: 688. 1840. *Robinia maculata* H. B. K., Nov. gen. Sp. 6: 393. 1823. *Lonchocarpus maculatus* (H. B. K.) DC., Prodr. 2: 260. 1825.—Type: MÉXICO. Campeche: crecit prope Campeche, *Humboldt & Bonpland s.n.* (holotype: P-HBK, microfiche IDC 6209. 161:II.7).
5. *Gliricidia sepium* (Jacq.) Steud., Nom. Bot., ed. 2, 1: 688. 1840. *Robinia sepium* Jacq., Enum. Syst. Pl. 28. 1760 [Select. stirp. amer. hist. 211, t. 179, f. 101. 1763]. *Lonchocarpus sepium* (Jacq.) DC., Prodr. 2: 260. 1825.—Type: COLOMBIA. Cartegena, *N. J. Jacquin s.n.* (holotype: not located). See Lavin and Sousa (1995) for taxonomic synonyms.

The present circumscription of *Gliricidia* represents only a minor modification from previous taxonomies. Indeed, *Hybosema ehrenbergii* was formally treated as a species of *Gliricidia* until Lavin and Sousa (1995) determined that no apomorphic characters diagnosed *Gliricidia* unless *G. ehrenbergii* (and the then newly described *H. robustum*) were removed to the genus *Hybosema*. Phylogenetic analysis of morphological data suggested that *Gliricidia*, *Hybosema*, and *Poitea* formed a distinct clade but with a trichotomous or unresolved relationship (Lavin and Sousa 1995). Indeed, the two hybosemas (*Gliricidia ehrenbergii* and *G. robustum*) shared certain morphological apomorphies with other robinioid genera. For example, the pseudomonadelphous staminal column (character 13 in Table 4 and Appendix A and B) was derived among robinioids only in *Lennea* and *Hybosema*, and the bilabiate calyx was determined to be derived only in *Lennea*, *Hybosema*, and *Poitea* (character 10; Table 4, Appendix A and B). Clearly, molecular data reveal that the hybosemas are derived from within the *Gliricidia* radiation. It is notable that in spite of the high degree of floral similarity, including the unique banner callus that is centrally located on the nectar guide (character 4; Table 4, Appendix A and B), the two hybosemas are separated from each other by long terminal branches and are only occasionally suggested to be sister species but then with weak support (compare Figs. 1, 4–7).

***The Genus* Poissonia.** The circumscription of *Poissonia* is revised such that the genus includes four species, *Coursetia hypoleuca*, *C. orbicularis*, *C. heterantha*, and *C. weberbaueri*. Two of these species, *Coursetia heterantha* and *C. weberbaueri*, share a very unusual post-pollination floral resupination syndrome, which results in a mature resupinate pod, with certain subclades of *Coursetia* sensu stricto (character 20; Figs. 2–3, Table 4, Appendix A and B). Indeed, Lavin (1988) and Lavin and Sousa (1995) considered such a trait to be a synapomorphy of the clade containing *Coursetia* sections *Neocracca* (monotypic, including just *Coursetia heterantha*) and section *Craccoides*. Co-occurring precisely with resupinate pods is an inflorescence with a long peduncle (character 22; Figs. 2–3, Table 4, Appendix A and B). Both of these traits, previously thought to have evolved once at the base of a clade containing sections *Neocracca* and *Craccoides*, are now considered to have independently evolved four separate times (Table 4, Figs. 2–3).

Another remarkable parallelism occurs with the latrorse pollen brush (state 3 of character 15; see Figs. 1–3, Table 4, Appendix A and B). Previously thought to have evolved once at the base of the clade containing all the species of *Coursetia* (Lavin 1988), this character state must now be hypothesized to have evolved twice, once each at the bases of the *Poissonia* and *Coursetia* clades. In spite of these extraordinary shared morphological similarities, *Coursetia* and *Poissonia* are never resolved as even weakly supported sister clades in any other individual or combined analyses.

As now characterized, *Poissonia* is apomorphically diagnosed by leaves bearing orbicular leaflets (character 31; Table 4, Appendix A and B) and seedlings that bear two eophylls (character 4; Table 4, Appendix A and B), although the latter has been observed from only two of the four species, *Poissonia hypoleuca* and *P. heterantha*. Also, petal pigments that are bluish at anthesis are unique (in the context of robinioids, *Sesbania*, and Loteae-Coronilleae) to *Poissonia hypoleuca*, *P. orbicularis*, and *P. heterantha*. The brick-red petals of *Poissonia weberbaueri* could represent an evolutionary transformation away from an originally blue-color state. Although these shared vegetative and floral similarities were noted for *Poissonia hypoleuca*, *P. orbicularis*, and *P. heterantha* by Lavin (1988) and Lavin and Sousa (1995), blue petal pigments and orbicular leaflets were considered too trivial to be scored as cladistic characters, and their occurrence in *P. heterantha* was thought to be due to a hybrid origin of this species. With both nuclear and chloroplast sequences showing a close relationship of these species, such interpretations are no longer considered valid. Regarding *Poissonia weberbaueri* from Arequipa, Peru, no one had previously suspected a close relationship of this species with the Argentine-Bolivian *P. heterantha*. Lavin (1988) and Lavin and Sousa (1995) had suggested this species to be closely related to *Coursetia dubia*, *C. grandiflora*, and *C. tumbezensis*. All four of these species have a similar distribution including southern Ecuador and Peru.

The following nomenclature is modified from Lavin and Sousa (1995) to adjust for the new circumscription of *Poissonia*.

Poissonia Baill., Adansonia 9: 295. 1870. *Coursetia* sect. *Poissonia* (Baill.) Lavin, Advances legume syst. 3: 58: 1987.—Type: *Poissonia solanacea* Baill. [=*Poissonia orbicularis* (Benth.) Hauman].

Coursetia section *Neocracca* (Kuntze) Lavin, Advances legume syst. 3:59. 1987.—Type: *Coursetia heterantha* (Griseb.) Lavin [= *Poissonia heterantha* (Griseb.) Lavin].

1. *Poissonia orbicularis* (Benth.) Hauman, Kew Bull. 1925: 278. 1925. *Coursetia orbicularis* Benth., Hooker's Ic. Pl. 11: 52, pl. 1065. 1870.—Type: PERU. Huancavelica: Pampas, *Pearce s.n.* (holotype: K). See Lavin (1988) for taxonomic synonyms.
2. *Poissonia hypoleuca* (Speg.) Lillo, Boletín del Museo de Ciencias Naturales de la Universidad Nacional de Tucumán 6: 8. 1925. *Chiovendaea hypoleuca* Speg., Anales Soc. Ci. Argent. 82: 220. 1917. *Poissonia hypoleuca* (Speg.) Hauman, Kew Bull. 1925: 279. 1925. *Coursetia hypoleuca* (Speg.) Lavin, Advances legume syst. 3: 63: 1987. Hooker's Ic. Pl. 11: 52, pl. 1065. 1870.—Type: ARGENTINA. Salta: En las barrancas del Río Guachipas, cerca de las Tres Cruces, *Spegazzini s.n.* (holotype: LPS; isotype: LPS—Gutiérrez et al., in press).
3. *Poissonia heterantha* (Griseb.) Lavin, comb. nov., *Tephrosia heterantha* Griseb., Symbolae ad fl. argent. 101. 1878. *Neocracca heterantha* (Griseb.) Speg., Physis 8: 119. 1925. *Coursetia heterantha* (Griseb.) Lavin, Advances legume syst. 3: 64. 1987.—Type: ARGENTINA. Catamarca: Río de los Nacimientos, *Schickendantz 101* (holotype: B, destroyed, fragment: F, photos: F, GH, MO, NY). See Lavin (1988) for taxonomic synonyms.
4. *Poissonia weberbaueri* (Harms) Lavin, comb. nov., *Coursetia weberbaueri* Harms, Bot. Jahrb. Syst. 42: 95. 1908—Type: PERU. Arequipa: Tambo prope Mollendo, in arenosis, *Weberbauer 1568* (holotype: B, destroyed, fragment: F, photos: F, GH, MO, NY, TEX).

The genus *Poissonia* comprises two well-supported clades, one with *P. hypoleuca* and *P. orbicularis*, and the other with *P. heterantha* and *P. weberbaueri*. Notably, a similar geographic pattern occurs within each of these two clades: an Argentine-Bolivian species (*P. hypoleuca* or *P. heterantha*) as sister to a southern Peruvian species (*P. orbicularis* or *P. weberbaueri*). The difference between the two clades is that *P. hypoleuca* and *P. orbicularis* occur in seasonally dry tropical forests, whereas *P. heterantha* and *P. weberbaueri* occur in the deserts (Monte in northern Argentina and Arequipa in Peru). The evolutionary rates analysis (see below and Fig. 6) suggests that the potential vicariant event involving the two desert species is about three times older (i.e., 3 Ma) than that involving the two species from the seasonally dry forest.

Other Taxonomic Implications. The other potential taxonomic implications of this analysis mainly involve species of *Coursetia* (sensu stricto), which were classified into sections by Lavin (1988) and Lavin and Sousa (1995). The ITS and combined morphological and ITS data suggest that of the species retained in *Coursetia*, only sect. *Madrenses* is monophyletic (e.g., Fig. 3). In contrast, species of *Coursetia* sections *Coursetia* and *Craccoides* form disparate groups of small clades. For example, the species in the clade including the most recent common ancestor of *C. brachyrhachis* and *C. maraniona* (Fig. 3) were classified into sect. *Coursetia*, as were the distantly related *C. ferruginea*, *C. rostrata*, and *C. glandulosa*. Similarly, the species in the clade delimited by the most recent common ancestor of *C. hassleri* and *C. pumila*, and that by the most recent common ancestor of *C. gracilis* and *C. grandiflora*, as well as the distantly related *C. hintonii* were classified into sect. Craccoides (Lavin 1988). Generally, the species of both of these sections are interdigitated on the ITS and combined phylogeny (Fig. 3). Because of this, the formal sectional classification of *Coursetia* (Lavin 1988) is abandoned.

The abandonment of the sectional classification of *Coursetia* is motivated by the realization that morphological traits that formed the basis of this classification are prone to a higher level of independent evolution than previously considered. This is exemplified by the resupinate pod and long pedunculate inflorescence (state 1 for each of characters 20 and 22 in Appendix A). These two traits, in part, readily distinguished sect. *Craccoides* from sect. *Coursetia* (Lavin 1988). The combined morphology and ITS data set suggests that each of these traits has evolved independently four separate times among robinioid legumes (Figs. 2–3; Table 4). The high retention indexes of most of the 40 morphological traits used in this analysis suggest that morphological data are phylogenetic informative (compare values in Tables 1 and 4). However, the consistency indexes are low enough to suggest that morphology should be used in combination with molecular data for phylogenetic inference.

Evolutionary Rates Analysis. The best evidence for the age of robinioid legumes (i.e., without *Sesbania*) comes from Tertiary fossil wood samples. In contrast to wood, the fossil leaves and fruits reported for *Robinia* are doubtful (Herendeen et al. 1992). For example, *Robinia californica* Axelrod (Axelrod 1987) is described from fossil leaves that are definitively not those of *Robinia* (Wolfe and Schorn 1990; personal observation of published photos) and fruits that have been determined to be fossilized crane-fly larvae (Jack Wolfe, in litt.).

From thorough comparisons of extant and Tertiary fossil woods, Matten et al. (1977), Wheeler and Landon (1992), Page (1993), and Wheeler (2001) have recognized all fossil *Robinia* woods as *Robinia zirkelii* (Platen) Matten, Gastaldo, and Lee. As a fossil wood species, *Robinia zirkelii* existed from the Late Eocene through the Pliocene and was widespread across North America, as well as in western Europe. Although spanning a great range in time and geography, these wood samples have been assigned to this single fossil species because they display very uniform qualitatively diagnostic traits found only in the modern genus *Robinia*. A set of diagnostic wood traits displayed by *Robinia zirkelii* that is found as a combination otherwise only in extant robinioid legumes are 1) vestured intervessel pits, 2) storied axial parenchyma and vessel elements, and 3) numerous thin-walled tyloses. In particular, the thin-walled tyloses are very uncommon in wood of papilionoid legumes and definitely have never been observed in numerous wood samples of *Sesbania* or (when wood is produced) the Loteae-Coronilleae tribal alliance. More importantly, extant species of *Robinia* and *Robinia zirkelii* share apomorphic wood characters, including 1) ring-porous wood (approached otherwise to some extent only in *Sesbania punicea*—character #37 in Appendix A), 2) homocellular rays (otherwise observed only in some samples of *Lennea*, *Hybosema*, *Gliricidia*, and *Coursetia*—character #38 in Appendix A), and 3) spiral sculpturing in narrow vessels (otherwise observed only in *Genistidium*—character #40 in Appendix A). The three apomorphies listed immediately above map to the *Robinia* stem clade in the robinioid phylogeny using the character reconstruction option in PAUP on the combined data sets. Although ring porosity (#37) may be ecologically determined (Wheeler and Landon 1992), the other two apomorphies (#'s 38 and 40), and the unique combination of the three additional wood traits shared between extant *Robinia* and *R. zirkellii* compel us to date the *Robinia* stem clade from the Late Eocene, or 33.7 Ma in accordance with Berggren et al. (1995).

The analysis of rates of evolution in sequences from the ITS region and the *matK* locus revealed similar estimates of ages of clades within the robinioid phylogeny. The ITS region gave better resolution among closely related species, as is typical for this locus in legumes (e.g., Lavin et al. 2001a; Lavin et al. 2001b). The substitution rate of 3.1–3.4 x 10^{-9} substitutions/site/year (Table 2) is typical for the ITS region of legumes (e.g., Lavin et al. 2001b; Richardson et al. 2001; Wojciechowski et al. 1999). The substitution rate for the *matK* locus, estimated in this study to be 3.9 x 10^{-10} substitutions/site/year (Table 3), is an order of magnitude slower, and this is in conformity with the use of this locus for resolving higher level relationships that can be achieved with sequences from the ITS region (e.g., Hu et al. 2000; Lavin et al. 2001a).

The three main robinioid lineages, *Hebestigma-Lennea*, *Poitea-Gliricidia*, and *Robinia* and close relatives, all diverged from each other sometime between the Middle and Late Eocene (Figs. 6–7). That the Cuban *Hebestigma* diverged from the Mesoamerican *Lennea* during this same time frame strongly implicates a Caribbean vicariance event in explaining the distribution of *Hebestigma* on the island of Cuba (e.g., Rosen 1976; Iturralde-Vinent and MacPhee 1999). The other Greater Antillean endemic, *Poitea*, diverged from its sister mainland clade, *Gliricidia*, much later (Figs. 6–7), at about 16 Ma. This suggests a different historical event as causing the island distribution of this clade. However, *Poitea* and *Gliricidia* show the pattern of reciprocal monophyly (Cunningham and Collins 1998; Riddle 1996). Notably, the pattern of reciprocal monophyly is rare if non-existent among studies of oceanic island radiations (Lavin, in mss.). The significance of reciprocal monophyly is that any attempt at ancestral area estimation at the base of lineages such as that containing *Gliricidia* and *Poitea* would render equivocal ancestral states. That is, both a continental and island distribution would be optimized at the base of the lineage especially because of the relatively long branches leading to each sister clade. This implies that the island lineage could just as well serve as the source for the continental lineage, rather than reverse. The pattern of reciprocal monophyly is not associated with an endemic diversification following chance dispersal, but rather with a historical vicariant event (Cunningham and Collins 1998; Lavin et al. 2000). With the Greater Antilles represented in two of the three basal robinioid clades, the pattern of reciprocal monophyly involved in one of these (i.e., *Poitea-Gliricidia*), and an estimated range of Caribbean lineages all well into the Tertiary, a Greater Antillean representation in the ancestral area of robinioids is strongly suggested.

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APPENDIX A

Enumeration of the morphological characters derived from the monographs of *Coursetia* (Lavin 1988), *Poitea* (Lavin 1993), and the tribe Robinieae (Lavin and Sousa 1995).

1. Floral pedicles articulated with calyx=0 (as in *Gliricidia*), confluent with the calyx=1 (as in *Hebestigma*).

2. Standard claw gradually tapered from the blade of petal=0 (as in *Poitea* and *Sphinctospermum*), abruptly contracted from the blade=1 (most robinioids).

3. Petal pigments with reddish to yellowish pigments=0, predominantly whitish=1 (as in *Coursetia brachyrhachis*), predominantly bluish=2 (*Coursetia heterantha*, *C. hypoleuca*, *C. orbicularis*). Bluish petal pigments are confined to three of the four species of the newly circumscribed *Poissonia*.

4. Callus of the nectar guide on standard petal: as a pair, one on either side of the midrib=0 (nearly all robinioids), single, centered along the midrib=1 (*Hybosema*). The single central nectar guide is unique to the two hybosemas, which are nested within the *Gliricidia* clade.

5. Wing petals lateral to the keel petals=0 (most robinioids), assuming the position of the standard=1 (as in *Poitea galegoides*), highly reduced and covered by the base of standard=2 (*P. glyciphylla* and *P. multiflora*).

6. Keel petals fused along the abaxial side to near the distal tip=0 (most robinioids), fused for a short distance along the abaxial side equidistant between basal and distal ends=1 (as in *Poitea galegoides*).

7. Keel petals markedly shorter than wing and standard petals=0 (most robinioids), keel petals longer than the other petals=1 (*Poitea*).

8. Wing and keel petals free from each other=0 (most robinioids), wing and keel connate via a boss and socket joint=1 (as in *Poitea florida*).

9. Keel petals blunt=0 (most robinioids), distal keel tip curved upward to a sharp point, rostrate=1 (*Coursetia* and *Poissonia*). The rostrate keel tip has evolved several times, including independently in the newly circumscribed genera *Poissonia* and *Coursetia*.

10. Calyx lobes much shorter than and evenly spaced around calyx tube=0 (*Hebestigma* and *Gliricidia*), lobes as long or longer than the tube=1 (as in *Coursetia*), calyx lobes short and unevenly spaced to render a bilabiate calyx=2 (*Lennea*, *Hybosema*, and *Poitea*). The last character condition was used by Lavin and Sousa (1995) as evidence for the segregation of *Hybosema* from *Gliricidia*.

11. Margins of calyx lobes without long whitish hairs=0 (nearly all robinioids), with long whitish hairs=1 (*Coursetia ferruginea*, *Poissonia hypoleuca*, and *P. orbicularis*).

12. Calyx tube not persisting with maturing fruit=0 (most robinioids), persisting with mature fruit=1 (*Hybosema*, *Poitea*, and *Gliricidia*).

13. Staminal tube diadelphous=0 (most robinioids), pseudomonodelphous=1 (as in *Lennea* and *Hybosema*). The narrow distribution of the pseudomonadelphous staminal tube among robinioid legumes was used as evidence for distinguishing *Hybosema* from *Gliricidia* by Lavin and Sousa (1995).

14. Stamens enveloped by keel tip at anthesis=0 (most robinioids), protruding beyond the tip of keep petals=1 (as in *Poitea galegoides*).

15. Style brush absent=0 (as in *Hebestigma*), comprising loose wavy hairs=1 (*Lennea*), comprising bunched straight hairs surrounding the distal end of the style=2 (as in *Robinia* and *Olneya*), comprising bunched straight hairs along the side of the style=3 (*Coursetia* and *Poissonia*). The pollen brush confined to the side of the style (latrorse) has arisen independently in *Poissonia* and *Coursetia*, according to the molecular data.

16. Style base not differentiated from the rest of the style=0 (as in *Hebestigma* and *Gliricidia*), bulbous or inflated=1 (all genera with a pollen brush; as in *Coursetia* and *Robinia*).

17. Stigma apical=0 (most robinioids), introrse=1 (*Poitea paucifolia* and *P. dubia*).

18. Ovary stipe shorter than calyx tube=0 (most robinioids), as long or longer than calyx tube and remaining distinct in the mature fruit=1 (*Hybosema*, *Gliricidia*, and *Poitea*).

19. Mature pods with a continuous chamber housing the seeds=0 (as in *Hebestigma* and *Robinia*), forming individual seed chambers=1 (as in *Coursetia*, *Peteria*, and *Sphinctospermum*).

20. Orientation of the mature legume such that the placenta runs along the upper margin=0 (most robinioids), such that the placenta runs along the lower margin=1 (*Coursetia* sections *Neocracca* and *Craccoides* sensu Lavin and Sousa 1995). Resupinate legumes are rare among papilionoid legumes and surprisingly have independently evolved several times among robinioids. This includes once in the two species of the newly circumscribed *Poissonia* (*P. heterantha* and *P. weberbaueri*) and three times in a large subclade nested within *Coursetia* (i.e., that defined by the most recent common ancestor of *C. pumila* and *C. dubia*). Post-pollination resupination of flower and fruit have been reported for other legumes, including *Astragalus tortipes* (Anderson and Porter 1994) and *A. miser* (M. Lavin, personal observation). However, in these *Astragalus* species, resupination results from hyperflexion of the floral pedicel and not from the twisting action characteristic of the certain species of *Coursetia* and *Poissonia*.

21. Testa of seed uniform in color=0 (as in *Hebestigma* and *Sphinctospermum*), mottled with purple patches=1 (as in *Robinia* and *Coursetia*).

22. Inflorescence with a peduncle no longer than the basal internode length=0 (most robinioids), with a very long peduncle much longer than lower internode length=1 (*Coursetia* sections *Neocracca* and *Craccoides*).

23. Stipitate glands lacking especially on reproductive organs=0 (as in *Hebestigma* and *Gliricidia*), present on at least the reproductive organs, especially the ovary=1 (as in *Robinia* and *Peteria*).

24. Spinescent stipules lacking=0 (as in *Hebestigma* and *Gliricidia*), present=1 (as in *Robinia*, *Olneya*, and *Peteria*).

25. Stipule pairs free=0 (as in *Hebestigma* and *Robinia*), adnate along inner surface=1 (*Sesbania* and *Poitea*).

26. Leaflet nyctinasty with a downward movement=0 (most robinioids), with a backward movement=1 (as in *Coursetia* section *Coursetia*), with a forward movement=2 (*Sesbania*).

27. Dried leaflets lacking tanniniferous patches=0 (most robinioids), with patches of tannins forming distinct patterns=1 (*Hybosema*, *Gliricidia*, *Poitea*, and various species of *Coursetia*).

28. Leaflets imparipinnate=0 (most robinioids), paripinnate=1 (*Sesbania* and various species of *Poitea* and *Coursetia*).

29. Leaflets uniform in size from base to distal tip=0 (most robinioids), distally accresent=1 (as in various species of *Poitea* and *Coursetia*).

30. Leaflets with a thin texture such that secondary veins are readily visible=0 (most robinioids), with a thick texture that generally obscures the secondary venation=1 (*Poitea gracilis*, *P. paucifolia*, and *P. dubia*).

31. Leaflets generally elliptical, at least longer than wide=0 (most robinioids), orbiculate, as wide as long=1 (the newly circumscribe *Poissonia*: *P. hypoleuca*, *P. orbicularis*, *P. heterantha*, and *P. weberbaueri*). Leaflets as wide as long are uniquely characteristic of the newly circumscribed *Poissonia*.

32. Short shoots occasionally produced but not covered by distichous persistent stipules=0 (most robinioids), commonly produced and densely covered by persistent distichous stipules=1 (*Poitea*).

33. Seedlings producing only one eophyll=0 (most robinioids), producing two eophylls=1 (as in *Poissonia hypoleuca* and *P. heterantha*), producing no eophylls=2 (*Olneya*). Seedlings with two eophylls might be a distinction of the newly circumscribed *Poissonia*, although this condition is unknown for *P. orbicularis* and *P. weberbaueri*.

34. Secondary roots slender and branching from a central taproot=0 (most robinioids), fusiform and fascicled=1 (as in *Coursetia caribaea*).

35. Wood with non-septate fibers=0 (most robinioids), with septate fibers=1 (*Gliricidia robustum*, *G. ehrenbergii*, *G. maculata*, *G. sepium*, *Olneya*, and *Genistidium*). Septate fibers occur in the two hybosemas (*G. ehrenbergii* and *G. robustum*) and two species traditionally recognized as *Gliricidia* (*G. maculata* and *G. sepium*). Notably, they are absent in *G. brenningii*, which is the basal branching species in the *Gliricidia* clade. Although wood characteristics have been well sampled from the tribe Robinieae, only 14 of about 75 species of *Sesbania* and four of about 180 species of Coronilleae-Loteae have been studied for wood anatomical variation (most Coronilleae-Loteae are herbaceous, however). Regardless, wood traits have been sampled for all the major subgroups for each of *Coursetia*, *Poitea*, and *Sesbania*, including *Poissonia*, the new segregate of *Coursetia*. This character and the two other wood traits listed below generally follow the suggestions provided by Herendeen and Miller (2000).

36. Wood with unstoried rays=0 (most robinioids), with all rays storied=1 (*Hebestigma*, *Hybosema robustum*, *Gliricidia maculata*, and *G. sepium*). Wood with storied rays is notably concentrated among the robinioid legumes in the species of the newly circumscribed *Gliricidia*.

37. Wood diffuse porous=0 (most robinioids), ring porous=1 (*Robinia* and *Sesbania punicea*). Ring porosity, one of the critical wood characters used in the assignment of fossil wood to the genus *Robinia*, may be more ecologically than phylogenetically determined because it is often used as an indicator of temperate climates, paleo or extant (e.g., Wheeler and Landon 1992; Herendeen and Miller 2000).

38. Cellular composition of rays heterocellular=0 (*Sesbania*, *Hebestigma* and most other robinioids), homocellular=1 (*Lennea viridiflora*, *Hybosema robusta*, *Gliricidia sepium*, *Robinia*, *Coursetia glandulosa*, and *C. rostrata*).

39. Tyloses absent=0 (Loteae-Coronilleae, *Sesbania*), present =1 (most robinioids). The tyloses in robinioid wood, when present, are always distinctively thin-walled and commonly contain crystals. Although tyloses are abundant in fossil and extant *Robinia* wood, crystals in tyloses have yet to be observed for this genus.

40. Spiral sculpturing in vessel elements absent=0 (most robinioids), present=1 (*Robinia* and *Genistidium*). Page (1993) suggests this could be an adaptation to xeric conditions, which could well be the case for *Genistidium*, an inhabitant of the Chihuahuan Desert.

APPENDIX B. Data matrix representing the 40 morphological characters scored for 82 terminal taxa. L = multistate taxon (01); J = uncertain state taxon {01}. This morphological data set combined with the sequence data from the ITS data set is deposited with TreeBase study accession number S813 (http://www.treebase.org/treebase/index.html) and from http://gemini.oscs.montana.edu/~mlavin/data/robin.htm.

Sesbania emerus	00000 00000 00000 00000 00000 00000 00000 00000
Sesbania drummondii	00000 00000 00000 00000 00000 00000 00000 00000
Sesbania vesicaria	00000 00000 00000 00000 00000 00000 00000 00000
Hebestigma cubense 7144a	11000 00000 00000 00000 00000 00000 00000 10010
Lennea modesta 8210	11000 00002 00101 00000 00000 00010 00000 00000
Lennea viridiflora 8228a	11000 00002 00101 00000 00000 000L0 00000 00110
Lennea melanocarpa 8217-4	11000 00002 00101 00000 00000 00000 00000 00000
Poitea immarginata 7105	00001 11002 01000 00100 00001 01010 01000 00000
Poitea galegoides 8021	00001 11002 01010 00100 00001 01000 01000 00000
Poitea galegoides 8031-1	00001 11002 01010 00100 00001 01000 01000 00000
Poitea stenophylla 45081	00001 11002 01010 00100 00001 01000 01000 000?0
Poitea campanilla 8033-1	00001 11002 01010 00100 00001 01010 0100? ?????
Poitea multiflora 8027	00002 11002 01010 00100 00001 01010 0100? ?????
Poitea glyciphylla 8030-4	00002 11002 01010 00100 00001 01010 01000 000?0
Poitea florida 8017	00000 11102 01000 00100 00001 01100 01000 000L0
Poitea punicea 8004	00000 11102 01000 00100 00001 01100 0100? ?????
Poitea carinalis 7150	00000 11102 01000 00100 00001 01100 01000 00010
Poitea gracilis 7146 3	10000 01102 01000 00100 00001 01101 01000 00010
Poitea gracilis 7138	10000 01102 01000 00100 00001 01101 01000 00010
Poitea paucifolia 8006	10000 01102 01000 01100 00001 01101 01000 00000
Poitea paucifolia 8026	10000 01102 01000 01100 00001 01101 01000 00000
Poitea dubia 8028	10000 01112 01000 01100 00001 01101 01000 00010
Gliricidia robustum 1186	01010 00002 01100 00100 00000 01000 00001 10L10
Gliricidia ehrenbergii 92/92	01010 00002 01100 00100 00000 01000 00001 000L0
Gliricidia brenningii 1194	01000 00000 01000 00100 00000 01000 00000 00010
Gliricidia maculata 42 87	01000 00000 01000 00100 00000 01000 00001 10010
Gliricidia sepium 12 96	01000 00000 01000 00100 00000 01000 00001 10L10
Gliricidia sepium 41 85	01000 00000 01000 00100 00000 01000 00001 10L10
Coursetia elliptica 11558	01000 00011 00003 10010 10000 01010 0000? ?????
Coursetia polyphylla 8224	01000 00011 00003 10010 10000 01010 0000? ?????
Coursetia oaxacensis 615	01000 00011 00003 10010 10100 01010 0000? ?????
Coursetia chiapensis 8202	01000 00011 00003 10010 10100 01010 0000? ?????
Coursetia madrensis 4626	11000 00011 00003 10010 10100 01010 00000 00010
Coursetia planipetiolata 5355	01000 00011 00003 10010 10100 01010 00000 00000
Coursetia paniculata 5320	01000 00011 00003 10010 10100 01010 00000 00000
Coursetia ferruginea 613	01100 00011 10003 10010 10000 10100 0000? ?????
Coursetia brachyrhachis 2173	11100 00011 00003 10010 10000 10100 0000? ?????
Coursetia fruticosa 920	11000 00011 00003 10010 10000 10100 00?0? ?????
Coursetia glandulosa 4671	11100 00011 00003 10010 10100 101L0 00000 00L10
Coursetia glandulosa 195	11100 00011 00003 10010 10100 100L0 00000 00L10
Coursetia axillaris 271287	11000 00011 00003 10010 10100 10100 0000? ?????
Coursetia insomniifolia 5732	11000 00011 00003 10010 10100 00100 0000? ?????
Coursetia pumila 5006	11000 00011 00003 10011 11000 11000 0001J JJJJJ
Coursetia hidalgoana 100588	11000 00011 00003 10011 11000 11000 0001J JJJJJ
Coursetia glabella 4960	11000 00011 00003 10011 11000 11000 0001J JJJJJ
Coursetia caribaea trifoliolata 5189	11000 00011 00003 10011 11100 11010 0001J JJJJJ
Coursetia caribaea 4603	11000 00011 00003 10011 11100 11010 0001? ?????
Coursetia caribaea ochroleuca 1063	11000 00011 00003 10011 11100 11010 0001? ?????
Coursetia caribaea 1064	11000 00011 00003 10011 11100 11010 0001? ?????
Coursetia caribaea 892	11000 00011 00003 10011 11100 11010 0001? ?????
Coursetia caribaea chiapensis 011288	11000 00011 00003 10011 11100 11010 0001? ?????
Coursetia caribaea chiapensis 4514	11000 00011 00003 10011 11100 11010 0001? ?????
Coursetia andina 5732	11000 00011 00003 10011 11100 10000 0000? ?????
Coursetia vicioides 938	01000 00011 00003 10011 11100 10100 00??? ?????
Coursetia hassleri 5805	11000 00011 00003 10011 11100 10100 0001? ?????
Coursetia hassleri 6937	11000 00011 00003 10011 11100 10100 0001? ?????
Coursetia dubia 926	11000 00011 00003 10011 11100 10000 0000? ?????
Coursetia grandiflora 929	11000 00011 00003 10011 11100 10000 00?00 00010
Coursetia gracilis 629	11000 00011 00003 10011 11000 10000 00?0? ?????
Coursetia hintonii 1030	01000 00011 00003 10011 11110 10000 00?0? ?????
Coursetia mollis 1039	11000 00011 00003 10011 11110 10000 0000? ?????
Coursetia mollis 1049	11000 00011 00003 10011 11110 10000 0000? ?????

APPENDIX B. Continued.

Coursetia maraniona 948	11100 00011 00003 10010 10000 10100 00?0? ?????
Coursetia maraniona 745	11100 00011 00003 10010 10000 10100 00?0? ?????
Coursetia maraniona 779	11100 00011 00003 10010 10000 10100 00?0? ?????
Coursetia cajamarcana 1675	11100 00011 00003 10010 ?0000 10100 00??? ?????
Coursetia rostrata 1062	11000 00011 00003 10010 10100 10100 00000 00100
Poissonia hypoleuca 5787	01200 00011 10003 10010 10000 000J0 1010? ?????
Poissonia orbicularis 923	01200 00011 10003 10010 10000 000J0 10?0? ?????
Poissonia heterantha 5785	11200 00011 00003 10011 11100 00000 1010J JJJJJ
Poissonia heterantha 5843	11200 00011 00003 10011 11100 00000 1010J JJJJJ
Poissonia weberbaueri 950	11000 00011 00003 10011 11100 ?0000 10?00 00000
Robinia neomexicana 190789	11000 00001 00002 10000 10110 00000 0000? ?????
Robinia hispida 010668	11000 00001 00002 10000 10110 00000 00000 01111
Robinia viscosa 14351	11000 00001 00002 10000 10110 00000 00000 01111
Robinia pseudoacacia 220488	11100 00001 00002 10000 10110 00000 00000 01111
Olneya tesota 011288	11000 00001 00002 10010 10010 00100 00201 000L0
Peteria scoparia Lott	11000 00001 00002 10010 10110 00000 0001J JJJJJ
Peteria thompsoniae 7048 2	11000 00001 00002 10010 10110 00000 0001J JJJJJ
Peteria glandulosa 1504	11000 00001 00002 10010 10110 00000 0001J JJJJJ
Genistidium dumosum 210890	10000 00001 00002 10010 10000 00000 00001 00001
Sphinctospermum constrictum 5120	10000 00001 00002 10010 00100 000J0 0000J JJJJJ

APPENDIX C

Species, locality, voucher specimen, and GenBank accession number ([1]ITS/5.8S, [2]*trnL*, [3]*matK*) are provided. Data sets and consensus tree descriptions in nexus format are available from TreeBase study accession number S813 (http://www.treebase.org/treebase/index.html) and from http://gemini.oscs.montana.edu/~mlavin/data/robin.htm.

Loteae: *Anthyllis vulneraria* L.; Allan and Porter (2000); [1]AF218499. *Anthyllis vulneraria* spp. *lapponica* (Hylander) Jalas; Sweden. Vasterbotten. *R. Lampinen 10057* (UC 1586976); [3]AF543845. *Securigera varia* L., Allan and Porter (2000); [1]AF218537; USA. Arizona. Huachuca Mtns. *McLaughlin 6823* (ARIZ); [3]AF543846. *Lotus unifoliolatus* (Hook.) Benth. USA. California. *Wojciechowski 707* (DAV); [1]AF467067. Hu et al. (2000); [3]AF142729 [reported as *Lotus purshianus* (Benth.) F. Clements & E. Clements]. *Ornithopus compressus* L.; Old World; Allan and Porter (2000); [1]AF218533; USDA seed source: Spain. *Hu 1074*; [3]AF142727.

Sesbania (subgenus in parentheses): *Sesbania* (*Agate*) *grandiflora* (L.) Pers.; USA: Hawaii; *Flynn & Hume 1627* (UC: 932); [1]AF536354. *Sesbania* (*Sesbania*) *cannabina* (Retz.) Poir.; China: Jiangsu (USDA PI458759); *Hu 1111* (DAV); [1]AF536351. *Sesbania* (*Sesbania*) *emerus* (Aubl.) Urb.; USA: Texas; *Lavin s.n.* (TEX); [1]AF536352; [3]AF543848. *Sesbania* (*Daubentonia*) *drummondii* (Rydb.) Cory; USA: Texas; *Lavin s.n.* (TEX); [1]AF536353; [3]AF543849. *Sesbania* (*Sesbania*) *tomentosa* Hook. & Arn. Hawaii, Nihoa, West landing, ''polihaliensis'' *Char 905370* (HAW); [1]AF536355; [1]AF536356. Hawaii, Oahu, Mokuleia,. ''oricola'' *Char WFP74s2096* (HAW); [1]AF536357. Hawaii, Oahu, Kaena Point, ''oricola'' *Char 905568* (HAW); [1]AF536358; [1]AF536359. *Sesbania* (*Glottidium*) *vesicaria* (Jacq.) Elliott; USA: Texas; *Lavin 6194* (BH); [1]AF398761; [3]AF543847.

Robinioid legumes: *Coursetia andina* Lavin; Venezuela: Mérida; *Lavin 5732a* (TEX); [1]AF398848; [2]AF529403. *Coursetia axillaris* Coulter & Rose; USA: Texas; *Lavin 4641* (TEX: 271287); [1]AF398840; [3]AF543854. USA: Texas; nursery specimen; *Lavin s.n.* (MONT: 121087); [1]AF542498. *Coursetia brachyrhachis* Harms; Argentina: Jujuy; *Lewis 2169* (MONT); [1]AF398837. Argentina: Jujuy; *Lewis s.n.* (MONT); [1]AF542454. Argentina: Jujuy; *Lewis 2173* (MONT); [1]AF542455. Bolivia: La Paz; *Nee 32032* (MONT); [1]AF542456. Bolivia: La Paz; *M. Lewis 40537* (MONT); [1]AF542457. *Coursetia cajamarcana* Lavin; Peru. Cajamarca. Hughes 2208 (MONT); [1]AF547187. *Coursetia caribaea* (Jacq.) Lavin; Mexico: Oaxaca; *Lavin 4603* (TEX); [1]AF398846. Ecuador: El Oro; *Klitgaard 524* (MONT: 1064); [1]AF542464. Guatemala; *Martinez 23760* (MO: 818); AF529405; [3]AF543853. Ecuador: Loja; *Klitgaard 155* (MONT: 1065); [1]AF542465. Mexico; *Pendry 892* (E); [1]AF542466. *Coursetia caribaea* var. *chiapensis* (Rydb.) Lavin; Mexico: Chiapas; *Lavin 4514* (TEX); [1]AF542468; [2]AF529404. Mexico: Chiapas; *Lavin 4514A* (MONT: 011288); [1]AF542468. *Coursetia caribaea* var. *ochroleuca* (Jacq.) Lavin; Ecuador: Manabi; *Klitgaard 564* (MONT: 1063); [1]AF398847. *Coursetia caribaea* var. *sericea* (A. Gray) Lavin; Mexico: cultivated from seed; *Hu 1112* (DAV); [3]AF155814. *Coursetia caribaea* var. *trifoliolata* (Rydb.) Lavin; Mexico: Puebla; *Lavin 5189* (TEX); [1]AF542463. *Coursetia chiapensis* Lavin & M. Sousa; Mexico: Chiapas; *Lavin 8202* (MEXU); [1]AF398830. *Coursetia dubia* (H.B.K.) DC.; Ecuador: Pichincha; *Humbles 6170* (F: 926); [1]AF398851. Ecuador: Chimborazo; *Franquemont 161* (F: 925); [1]AF542472. Ecuador: Baños; *Asplund* (F: 924); [1]AF542473. *Coursetia elliptica* M. Sousa & V. Rudd; Costa Rica: Guanacaste; *Janzen 11558* (MO); [1]AF398828; [2]AF529400. *Coursetia ferruginea* (H.B.K.) Lavin; Venezuela; *Hughes s.n.* (MONT: 613); [1]AF398836. Venezuela: Trujillo. *Hughes 771* (FHO); [1]AF542453. *Coursetia fruticosa* (Cavanilles) MacBride; Peru: Huanuco; *Ferreyra 6640* (F: 921); [1]AF398838. Peru: Huanuco; *Stork 9393* (F: 920); [1]AF542458. *Coursetia glabella* (A. Gray) Lavin; Mexico: Chihuahua; *Lavin 4960* (TEX); [1]AF398845. *Coursetia glandulosa* A. Gray; USA: Arizona; *Lavin 4671* (TEX); [1]AF398839. Mexico: Guerrero; *Lavin 5347* (TEX); [1]AF542459; [2]AF529399; [3]AF543852. Mexico: Guerrero; *Lavin 5347* (MONT: 195); [1]AF542460. *Coursetia gracilis* Lavin; Ecuador: Pichincha; *Gentry 70194* (MONT: 629); [1]AF398854. *Coursetia grandiflora* Benth.; Peru: Cajamarca; *Sagastegui 15495* (F: 929); [1]AF398853. Peru: Yalén; *Alayo-B. 023* (F: 928); [1]AF542474. Ecuador: Loja; *Klitgaard 141* (MONT: 1066); [1]AF542475. Ecuador: Loja; *Klitgaard 396* (MONT: 1067); [1]AF542476. Ecuador: Costa; *E. R. 2988* (MONT: 616); [1]AF542495. *Coursetia hassleri* Chodat; Argentina: Salta; *Lavin 5807* (TEX); [1]AF398850; this voucher was mistakenly reported in Lavin et al. (2001b) as *Lavin 5809* from Tucuman, Argentina. Argentina: Tucuman; *Lavin 5805* (TEX); [1]AF542471. Paraguay: Amanbay; *Solomon 6937* (MONT); [1]AF542470. Bolivia: Santa Cruz; *Solomon 13478* (MONT); [1]AF542469. *Coursetia hidalgoana* Lavin; Mexico: Hidalgo; *Lavin 5901* (TEX: 100588); [1]AF398844. *Coursetia hintonii* V. Rudd; Mexico: Tejupilco; *Guizar 261* (TEX: 1030); [1]AF398855:

[2]AF529398. Mexico: Tejupilco; *Guizar 261* (TEX: 1038); [1]AF542477. *Coursetia insomniifolia* Lavin; Mexico: Coahuila; *Lavin 5732* (TEX); [1]AF398841; [2]AF529397; [3]AF543855. Mexico: Coahuila; *Lavin 5732a* (MONT); [1]AF542461. *Coursetia madrensis* Micheli; Mexico: Puebla; *Lavin 4626* (TEX); [1]AF398831; [2]AF529401. *Coursetia maraniona* Lavin; Peru: San Martin; *Gentry 37672* (MONT: 948); [1]AF398857. Peru. *Pennington 745* (MONT); [1]AF542480. Peru: *Pennington 779* (MONT); [1]AF542481. Peru: Amazonas; *Pennington 958* (E); [1]AF542482. Peru: Río Marañon; *Pennington 1011* (E); [1]AF542483. *Coursetia mollis* Robinson & Greenman; Mexico: Michoacan; *Lavin 5360* (TEX: 1039); [1]AF398856. Mexico: Michoacan; *Lavin 5360* (TEX: 1031); [1]AF542501 and [1]AF542502. Mexico: El Ranchito; *Soto-N. 2825* (TEX: 1049); [1]AF542478. Mexico: Nyarit; *Tenorio 15557* (TEX: 1048); [1]AF542479. *Coursetia oaxacensis* M. Sousa & V. Rudd; Mexico: Guerrero; *MacQueen 444* (MONT: 615); [1]AF398829. *Coursetia paniculata* M. Sousa & Lavin; Mexico: Oaxaca; *Lavin 5320* (TEX); [1]AF398833: [2]AF529402. *Coursetia planipetiolata* Micheli; Mexico: Guerrero; *Lavin 5355* (TEX); [1]AF398832. *Coursetia polyphylla* Brandegee; Mexico: Veracruz; *Lavin 8224* (MEXU); [1]AF398859. *Coursetia pumila* (Rose) Lavin; Mexico: Durango; *Lavin 5006* (TEX); [1]AF398843. Mexico: Durango; *Lavin 5029* (TEX); [1]AF542462. *Coursetia rostrata* Benth.; Brazil: Bahia; *Anderson 36955* (F: 930); [1]AF398858. Brazil: Bahia; *Klitgaard 78* (MONT: 1062); [1]AF398860. Brazil: Bahia; *Lewis 1863* (MONT: 611); [1]AF398861. *Coursetia vicioides* (Nees & Martius) Benth.; Brazil: Bahia; *Silva 177* (TEX: 938); [1]AF398849.

Genistidium dumosum I. M. Johnston; USA: Texas; *Lavin 210890* (MONT); [1]AF398826; [3]AF543858. USA: Texas; *Powell s.n.* (MONT); [1]AF537356; [2]AF529394. Mexico; Coahuila, *Wendt et al. 1951* (MEXU - 1501); [1]AF537357.

Gliricidia brenningii (Harms) Lavin; Ecuador: Chone; *Hughes 993* (FHO); [1]AF398806. Ecuador: San Pablo; *Hughes 1193* (FHO); [2]AF529411; [3]AF547199. Ecuador: Montalvo; *Hughes 1194* (FHO); [1]AF398804. Ecuador: Palestina; *Hughes 1009* (FHO); [1]AF398809. Ecuador: Palmales; *Hughes 1012* (FHO); [1]AF398805, [2]AF400140; [3]AF547202 and [3]AF547203. Ecuador: Portovelo; *Hughes 1015* (FHO); [1]AF398808; [2]AF529412; [3]AF547200 and [3]AF547201. Ecuador: San Pablo; *Hughes 1199* (FHO); [1]AF398807. *Gliricidia ehrenbergii* (Schltdl.) Rydb.; Guatemala: Ixtahuacan; *Hughes 1468* (FHO); [1]AF398770, [2]AF400136; [3]AF547195. Guatemala: La Ruda; *Hughes 1458* (FHO); [1]AF398769. *Gliricidia robustum* (M. Sousa & Lavin) Lavin; Mexico: Chiapas; *Hughes 1186* (FHO); [1]AF398767; [3]AF547194. Mexico: Chiapas; *Sousa 13212* (MEXU); [1]AF398768, [2]AF400137. *Gliricidia maculata* (H.B.K.) Steud.; Mexico: Campeche; *Hughes 678* (FHO: 42-87); [1]AF398812. Mexico: Campeche; *Hughes 678* (FHO: 42-87-1); [1]AF398813. Mexico: Quintana Roo; *Hughes 675* (FHO: 42-85); [1]AF398811; [3]AF547196. Mexico: Yucatan; *Hughes 939* (FHO: 43-87); [1]AF398810, [2]AF400139. *Gliricidia sepium* (Jacq.) Steud.; Guatemala: Cuyotenango; *Hughes 430* (FHO); [2]AF400138. Costa Rica: Nicoya; *Hughes 11-86* (FHO); [1]AF398816. Mexico: Jalisco; *Hughes 622* (FHO: 41-85); [1]AF398814; [3]AF547197. Costa Rica: Santa Cruz; *Hughes 799* (FHO: 12-86); [1]AF398815.

Hebestigma cubense (H.B.K.) Urban; Cuba: Habana; *Lavin 5611* (TEX); [1]AF398763, [2]AF400134. Cuba: Guardalavaca; *Lavin 7144a* (MONT); [1]AF398762; [3]AF543850.

Lennea melanocarpa (Schltdl.) Vatke ex Harms; Mexico: Veracruz; *Lavin 8217-4* (MEXU); [1]AF398766. *Lennea modesta* (Standley & Steyermark) Standley & Steyermark; Mexico: Chiapas; *Lavin 8210* (MEXU); [1]AF398764, [2]AF400135; [3]AF543851. *Lennea viridiflora* Seemann; Mexico: Veracruz; *Lavin 822a* (MEXU); [1]AF398765.

Olneya tesota A. Gray; USA: Arizona; *Lavin 4654* (MONT: 011288); [1]AF398823. USA: Arizona; *Lavin 5472* (TEX: 121088); [1]AF398822; [2]AF529393; [3]AF543859. USA: California; *Wojciechowski 877* (ASU); [1]AF537355; [3]AF543857.

Peteria glandulosa (S. Watson) Rydb.; Mexico. Nuevo Leon. Zaragoza, Hinton et al. 23109 (MEXU - 1502); [1]AF537353. Mexico. San Luis Potosí. Salinas, García M. s. n. (MEXU - 1504); [1]AF537354. *Peteria scoparia* A. Gray; USA: Texas; *Lott s.n.* (TEX); [1]AF398825; [2]AF529396. *Peteria thompsoniae* S. Watson; USA: Utah. *Lavin & Hedrick 6157* (BH); [1]AF537352; [2]AF529395. USA: Arizona; *Lavin 6179* (MONT); [3]AF547190. USA: Idaho; *Lavin 7048-2* (MONT); [1]AF398824.

Poissonia heterantha (Griseb.) Lavin; Argentina: Salta; *Lavin 5785* (TEX); [1]AF398842. Argentina: Jujuy; *Lavin 5843* (TEX); [1]AF542487. Argentina: Molinos; *Lavin 5856* (TEX); [1]AF542488; [3]AF547192. Argentina: Cafayate; *Lavin 5860* (TEX); [1]AF542489. Argentina: Catamarca; *Lavin 5862* (TEX); [1]AF542490; [2]AF529407. Argentina: Tilcara; *Lavin 5832* (TEX); [1]AF542491; [2]AF529408. Argentina: Río Juramento; *Lavin 5800* (TEX); [1]AF542496. *Poissonia hypoleuca* (Speg.) Lillo; Argentina: Jujuy; *Lavin 5814* (MONT: 231089); [1]AF398834; [2]AF529409. Argentina: Jujuy; *Lavin 5814* (TEX); [1]AF542497. Argentina: Salta; *Lavin 5787* (TEX); [1]AF542485; [2]AF529410; [3]AF547193. Argentina: Salta; *Lavin 5787* (MONT: 121088); [1]AF542486. *Poissonia orbicularis* (Benth.) Hauman; Peru: Abancay; *Vargas 9808* (F: 923); [1]AF398835; [3]AF547208. Peru: Abancay; *Hutchinson 1747* (F: 922); [1]AF542499 and [1]AF542500. *Poissonia weberbaueri* (Harms) Lavin; Peru: Arequipa; *Hutchinson 7259* (F: 918); [1]AF398852. Peru: Arequipa; *Hutchinson 7259* (F: 917); [1]AF542492; [2]AF529406; [3]AF547188. Peru: Jahuay; *Dillon 3251* (TEX: 949); [1]AF542493. Peru: Ocoña; *Dillon 3857* (TEX: 950); [1]AF542494; [3]AF547189.

Poitea campanilla DC.; Dominican Republic: Piedra Blanca; *Lavin 8032–1* (MONT); [1]AF398777. Dominican Republic: Piedra Blanca; *Lavin 8032-2* (MONT); [1]AF398778. Dominican Republic: Jarabacoa; *Lavin 8033-1* (MONT); [1]AF398779, [2]AF400145; [3]AF547206 and [3]AF547207. Dominican Republic: Jarabacoa; *Lavin 8033-3* (MONT); [1]AF398780. *Poitea carinalis* (Griseb.) Lavin; Dominica; *Lavin 7150* (MONT); [1]AF398793, [2]AF400148. Dominica; *Lavin 011288* (MONT); [1]AF398792. *Poitea dubia* (Poiret) Lavin; Dominica Republic: Las Matas de Farfan; *Lavin 8028* (MONT); 1AF398803, [2]AF400151. *Poitea florida* (Vahl) Lavin; Puerto Rico: Yauco; *Lavin 8005* (MONT); [1]AF398785. Puerto Rico: Susua; *Lavin 8012* (MONT); [1]AF398786. Puerto Rico: Ponce; *Lavin 8014* (MONT); [1]AF398787, [2]AF400146. Puerto Rico: Coamo; *Lavin 8015* (MONT); [1]AF398784. Puerto Rico: El Verde; *Lavin 8017* (MONT); [1]AF398788. *Poitea galegoides* Ventenat; Dominican Republic: Hato Damas; *Lavin 8021* (MONT); [1]AF398773, [2]AF400142. Dominican Republic: Aceitillar; *Lavin 8031-1* (MONT); [1]AF398774. Dominican Republic: Aceitillar; *Lavin 8031-2* (MONT); [1]AF398775. *Poitea galegoides* var. *stenophylla* Ekman ex Lavin; Dominican Republic: Rancho Arriba; *Zanoni 45081* (NY); [1]AF398776. *Poitea glyciphylla* (Poiret) Lavin; Dominican Republic: Pedernales; *Lavin 8030-1* (MONT); [1]AF398783. Dominican Republic: Pedernales; *Lavin 8030-2* (MONT); [2]AF400144. Dominican Republic: Pedernales; *Lavin 8030-4* (MONT); [1]AF398782. *Poitea gracilis* (Griseb.) Lavin; Cuba: Levisa; *Lavin 7138* (MONT); [1]AF398797, [2]AF400149. Cuba: Cananova; *Lavin 7142* (MONT); [1]AF398796. Cuba: Santa Lucia; *Lavin 7146-3* (MONT); [1]AF398794. Cuba: Santa Lucia; *Lavin 7146-4* (MONT); [1]AF398795. *Poitea immarginata* (C. Wright) Lavin; Cuba: Pinar del Rio; *Lavin 7104* (MONT); [1]AF398772, [2]AF400141. Cuba: Pinar del Rio; *Lavin 7105* (MONT); [1]AF398771; [3]AF547198. *Poitea multiflora* (Swartz) Urban; Dominican Republic: Las Matas de Farfan; *Lavin 8027* (MONT); [1]AF398781, [2]AF400143. *Poitea paucifolia* (DC.) Lavin; Puerto Rico: Yauco; *Lavin 8006* (MONT); [1]AF398798. Puerto Rico: Sabana Grande; *Lavin 8008* (MONT); [1]AF398799. Puerto Rico: Susua; *Lavin 8009* (MONT); [1]AF398800. Dominican Republic: Rio Nigua; *Lavin 8024* (MONT); [1]AF398801. Dominican Republic: Boca Nigua; *Lavin 8026* (MONT); [1]AF398802,

[2]AF400150. *Poitea punicea* (Urban) Lavin; Puerto Rico: Sabana Grande; *Lavin 8003* (MONT); [1]AF398789. Puerto Rico: N of Sabana Grande; *Lavin 8004* (MONT); [1]AF398790. Puerto Rico: Yauco; *Lavin 8007* (MONT); [1]AF398791, [2]AF400147.

Robinia hispida L.; USA: New York; *Lavin 010688* (MONT); [1]AF398819. USA: New York; *Lavin 140588* (MONT); [1]AF537360; [2]AF529390. *Robinia neomexicana* A. Gray; USA: Arizona; *Lavin 190789* (MONT); [1]AF398817. USA: Arizona; *Wojciechowski 717* (DAV); [1]AF398818; [3]AF543856. *Robinia neomexicana* var. *rusbyi* (Wooton & Standl.) Peabody; USA: Arizona; Mogollon Rim; *Lavin & Wojciechowski s.n.* (no specimen); [1]AF537347; [1]AF537348; [1]AF537349; [1]AF537350; [1]AF537351. *Robinia pseudoacacia* L.; USA: New York; *Lavin 6200* (BH: 220488); [1]AF398820; AF529391. USA: California (cultivated); *Hu 1067* (DAV); [1]AF467495; [3]AF142728. *Robinia viscosa* Ventenat; USA: South Carolina; *Nelson 14351* (MONT); [1]AF398821.

Sphinctospermum constrictum (S. Watson) Rose; Mexico: Michoacan; *Lavin 5120* (TEX); [1]AF398827; [2]AF529392. Mexico: Michoacan; *Lavin 5120-a* (MONT); [1]AF537358; [3]AF547204 and [3]AF547205. Mexico: Sonora. Tonichi; *Reina et al. 98-547* (ASU); [1]AF537359; [3]AF547191.