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Phylogenetic Systematics and Biogeography of the Pantropical Genus *Sesbania* (Leguminosae)

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Abstract—The pantropical genus *Sesbania* (Leguminosae) comprises approximately 85 species and 34 infraspecific taxa. This genus is unusual ecologically in its predilection for wetlands, and morphologically distinctive among legumes, yet has never been comprehensively investigated for the phylogenetic integrity of its subgeneric classification. We subjected a broad sampling of *Sesbania* species to phylogenetic analysis using both nuclear and plastid DNA sequence data. The resulting phylogenies support the monophyly of *Sesbania* and two constituent subclades, one represented by the New World endemic *Sesbania* sections *Daubentonia*, *Daubentoniopsis* and *Glottidium*, and the second comprising the pantropically distributed *S.* section *Sesbania* and former *S.* subgenera *Pterosesbania* and *Agati*. The species-rich *S.* section *Sesbania* is paraphyletic with respect to *S.* subg. *Agati* and *Pterosesbania,* while *S.* sect. *Daubentonia* is paraphyletic with respect to *S.* sect. *Daubentoniopsis*. Based on these results we revise the sectional classification of *Sesbania*. The genus is consistently though weakly supported as sister to tribe Loteae. Rate and age estimates suggest that the *Sesbania* crown clade has an estimated mean age of approximately 18.9 Ma. This implicates long-distance dispersal as causing the pantropical distribution of the genus. Regardless, the New World is optimized as the ancestral area for *Sesbania*. The prevalence of *Sesbania* in riparian, wetland, and coastal systems combined with low levels of geographic phylogenetic structure suggested that hydrochory and local extinction potentially explain present-day distributions.

Keywords—Dispersal, hydrochory, legume morphology, riparian, Robinieae, taxonomy.

The genus *Sesbania* Adanson (Papilionoideae, Leguminosae) includes approximately 85 species of trees, shrubs, and perennial or annual herbs, which are widely distributed in tropical and subtropical regions of the world. Africa and Madagascar harbor about 30 species, Asia, Australia, and Pacific islands about 16, and the Neotropics (southern USA to northern Argentina, especially North and Central America) with nine species. About five species are pantropical in distribution (Evans 1990; Lavin and Schrire 2005). Species of *Sesbania* are widely used and cultivated in agroforestry for soil improvement as green manures and other products (Evans 1990; Giller 2001; Bruning et al. 2015). The broad economic importance of *Sesbania*, especially in Africa and Asia, includes their use as shade plants, windbreaks, cover crops, ornamentals, fish poisons (e.g. source of isoflavones), fiber sources, construction materials, and food for both humans and livestock (Gillett 1963). *Sesbania* flowers and seeds also contain compounds that reduce anti-tumor activity (e.g. Powell et al. 1976; Laladhas et al. 2010). Several species have been shown to be very effective at bioremediation of lead, zinc, and copper from industrial waste sites and other contaminated soils (Barlow et al. 2000; Qureshi et al. 2002; Yang et al. 2003; Branzini et al. 2012).

Sesbania possesses several features that are distinctive among legumes, and combines morphologies that individually or in combination are atypical among papilionoids. For example, cytogenetically the genus is unique among tropical papilionoids in having a base chromosome number of six (Gillett 1963). The most unusual morphology of *Sesbania* is the even-pinnate (paripinnate) leaf, in which the strictly opposite leaflets fold forward during the night, a nyctinastic movement more like that found in dalbergioid and many non-papilionoid legumes, especially the "mimosoid" legumes (= Mimosoid clade of subfamily Caesalpinioideae; LPWG 2017). Although studies have revealed a diversity of nyctinastic movements within and among legume genera (e.g. Satter et al. 1988; Roblin et al. 1989; Luckow 1993; Hughes 1998), variation in nyctinasty is highly taxonomically correlated (e.g. Lavin 1988).

There is considerable variation among the fruits of *Sesbania* (Fig. 1), which has served as the basis for the subgeneric classification of *Sesbania* (Table 1; Rydberg 1923; Gillett 1963; Hutchinson 1964; Lavin and Sousa S. 1995). The fruits take on four forms: 1) tardily dehiscent, linear, and many-seeded (e.g. *S.* sect. *Sesbania*, Fig. 1E–H, L); 2) tardily dehiscent, torulose, and few- to several-seeded (*S.* sect. *Daubentoniopsis* (Rydb.) Lavin, Fig. 1B); 3) tardily dehiscent, bladdery-inflated, and 2-seeded (*S.* sect. *Glottidium* (Desv.) Lavin, Fig. 1A); and 4) sometimes indehiscent, quadrangular to 4-winged, and several-seeded (*S.* sect. *Daubentonia* (DC.) Benth., Fig. 1C–D, I–K).

Also in contrast to most legumes, at least one species of *Sesbania* forms nodules for symbiotic nitrogen fixation on both belowground roots and laterally on aboveground stems (e.g. Goormachtig et al. 1998). In *Sesbania rostrata* Bremek. & Oberm., these "stem nodules" are associated with junctions at the bases of lateral roots or adventitious roots, and the rhizobia enter the host plant shoot via cracks in the epidermis that arise from protrusion of lateral and adventitious roots (James et al. 1992; Goormachtig et al. 1998, 2004b; Bomfeti et al. 2013). Stem nodulation in *S. rostrata* is facultative and differs from the more typical form of root nodulation and occurs in plants with non-submerged or well-aerated roots (Goormachtig et al. 2004b). That this facultative form of nodulation is also found in aquatic species of the distantly related genera *Aeschynomene* L. (Loureiro et al. 1995; Chaintreuil et al. 2013) and *Neptunia* Lour. (James et al. 1992), both wetlands-inhabiting legumes, suggests that the underlying processes could be more widespread in legumes (Goormachtig et al. 2004a).

The ecological predilection of most *Sesbania* species for either riparian or wetland habitats (Evans 1990) is quite unusual compared to the mostly dry-site inhabiting members of the legume family (Schrire et al. 2005a, b), and especially compared to its closest relatives (tribes Loteae and Robinieae). Many *Sesbania* are well adapted to fluctuations in soil moisture

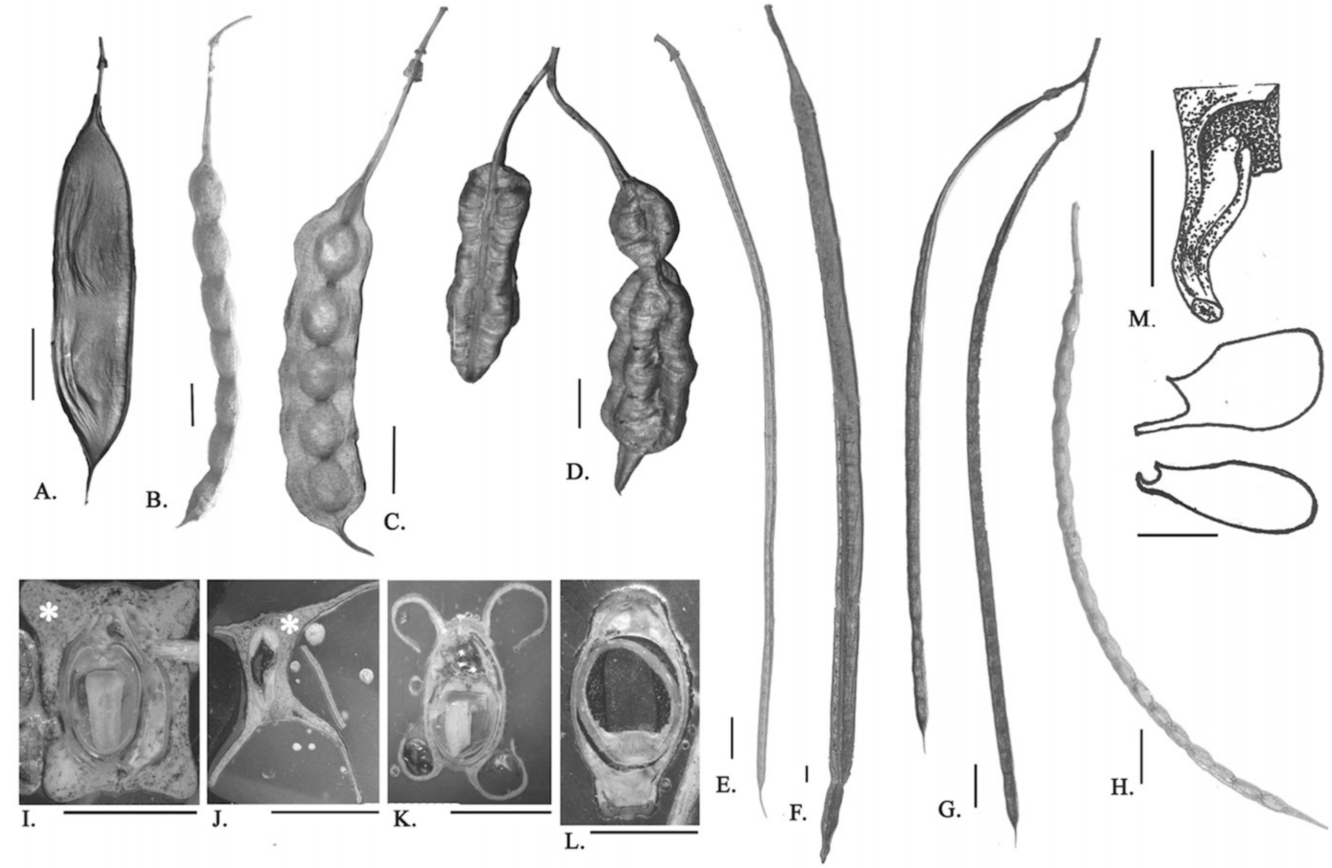

FIG. 1. Legume diversity within *Sesbania*. A. *Sesbania vesicaria*. B. *S. cavanillesii*. C. *S. drummondii*. D. *S. macroptera*. E. *S. herbacea*. F. *S. grandiflora*. G. *S. exasperata*. H. *S. bispinosa*. I–L. Cross-sections of *Sesbania* fruits. I. *S. virgata* fruit showing thickened mesocarp layer (*). J. *S. punicea* fruit showing prominent four wings, and thickened mesocarp. K. *S. macroptera* fruit showing prominent and contorted four wings. L. *S. herbacea* fruit showing typical morphology of sect. *Sesbania* taxa. Note lack of thickened mesocarp and lack of wings. M. *S. herbacea* calli on base of banner petal, and auricle on upper margin of keel and wing petals. Scale bars: A–H = 1 cm; I–M = 0.5 cm.

and are tolerant of both drought and waterlogged conditions. Under flooded conditions, most species form floating roots and produce a surrounding thick layer of spongy aerenchyma to protect stems, roots, and root nodules. This tissue ensures the support and survival of nodulating rhizobial symbionts even when roots are temporarily submerged (Evans 1990).

Perhaps because of this preference for wet habitats, *Sesbania* includes some species with pantropical or transoceanic distributions. Such species distributions are never observed in legume groups like Loteae and Robinieae, which typically inhabit semi-arid vegetation and commonly show highly localized species distributions (Allan and Porter 2000; Duno de Stefano et al. 2010; Pennington et al. 2011; Queiroz and Lavin 2011). Few if any species of Loteae and Robinieae are widespread, and no individual species naturally occurs on different continents separated by open water, excepting islands adjacent to a mainland (e.g. Canary Islands), while species selected at random from Loteae or Robinieae are very likely to find their sister species in the same region, much more than would be predicted for *Sesbania*. This preference of *Sesbania* for seasonally flooded riverine and waterlogged sites suggests that transoceanic clades would have an average age that is younger than transcontinental crown clades of Loteae and Robinieae and that the *Sesbania* phylogeny should show less geographic phylogenetic structure compared to the phylogenies of Loteae and Robinieae (Lavin et al. 2004; Pennington et al. 2009; Pennington and Lavin 2016).

This study represents the first attempt to comprehensively sample the diversity of *Sesbania* worldwide to resolve its phylogenetic relationships in the context of its closest relatives (Lavin and Schrire 2005). This analysis is intended to improve our understanding of phylogenetic relationships within the genus, and to provide a phylogenetic framework for the subgeneric classification and subsequent revision of the New World species of *Sesbania* (Farruggia et al. in prep.). In addition, molecular phylogenetic analyses are used to estimate the ages of major subclades of the genus and infer a biogeographical history that can be compared to the patterns found in Loteae and Robinieae.

MATERIALS AND METHODS

Taxonomic Sampling—Molecular sequence data were sampled from 48 species of *Sesbania*, as well as a broad representation of species from the Robinieae, Loteae, and the Inverted Repeat Lacking Clade (“IRLC”; Wojciechowski et al. 2004). *Sesbania* specimens from the following herbaria (A, ASU, B, BM, CTES, E, F, FLAS, G, GH, HAO, K, L, LL, MA, MEXU, MO, MU, NY, P, QCA, QCNE, RB, SI, TEX, UNR, US, USM, W, and WAG; Thiers 2017) represented the main source of data for this study (see Farruggia 2009). New voucher specimens and genomic DNAs are deposited primarily at ASU and the principal herbarium in the country of origin if other than USA (e.g. K). Species taxonomy follows that of Lavin and Sousa S. (1995) and Farruggia (2009).

DNA Sequence Data—Previous molecular phylogenetic studies that have included representatives of *Sesbania* and closely related taxa (i.e. Loteae, Robinieae, and genera of the IRLC; Lavin et al. 2003; Wojciechowski et al. 2004) have shown that high quality DNA is easily extracted from

TABLE 1. List of *Sesbania* species used in this study, showing membership in traditional classification sensu Rydberg (1923), Gillett (1963), Burbidge (1965), Sachet (1987), and current sectional classification as revised here in brackets. Native geographic distributions indicated.

Sectional classification	Species	Geographic Classification
S. subg. *Agati* [S. = sect. *Sesbania*]	*Sesbania coccinea* (L.f.) Poir. (two subspecies, six varieties)	Pacific
	Sesbania formosa (F.Muell.) N.T.Burb.	Australia
	Sesbania grandiflora (L.) Pers.	Pacific
S. sect. *Daubentonia*	*Sesbania drummondii* (Rydb.) Cory	North America
	Sesbania macroptera Micheli	South America
	Sesbania punicea (Cav.) Benth.	South America & North America
	Sesbania virgata (Cav.) Poir.	South America & North America
S. sect. *Daubentoniopsis* [S. = sect. *Daubentonia*]	*Sesbania cavanillesii* S.Watson	North America
S. sect. *Glottidium*	*Sesbania vesicaria* (Jacq.) Elliott	North America
S. subg. *Pterosesbania* [S. = sect. *Sesbania*]	*Sesbania tetraptera* Hochst. ex Baker (two subspecies)	Africa
S. sect. *Sesbania*	*Sesbania benthamiana* Domin	Australia
	Sesbania bispinosa (Jacq.) W.F.Wight (three varieties)	Pantropical
	Sesbania brachycarpa F.Muell.	Australia
	Sesbania brevipeduncula J.B.Gillett	Africa
	Sesbania campylocarpa (Domin) N.T.Burb.	Australia
	Sesbania cannabina (Retz.) Pers. (two varieties)	Africa & Australasia
	Sesbania chippendalei N.T.Burb.	Australia
	Sesbania cinerascens Welw. ex Baker	Africa
	Sesbania coerulescens Harms	Africa
	Sesbania concolor J.B.Gillett	Africa
	Sesbania dalzielii Phillips & Hutch.	Africa
	Sesbania dummeri Phillips & Hutch.	Africa
	Sesbania erubescens (Benth.) N.T.Burb.	Australia
	Sesbania exasperata Kunth	Mexico to South America
	Sesbania goetzei Harms (two subspecies)	Africa
	Sesbania greenwayi J.B.Gillett	Africa
	Sesbania hepperi J.B.Gillett	Africa
	Sesbania herbacea (Mill.) McVaugh	Americas
	Sesbania hirtistyla J.B.Gillett (two varieties)	Africa
	Sesbania hobdyi O.Deg. & I.Deg.	Pacific
	Sesbania javanica Miq.	Australia
	Sesbania keniensis J.B.Gillett	Africa
	Sesbania leptocarpa DC. (two varieties)	Africa
	Sesbania macowaniana Schinz	Africa
	Sesbania macrantha Welw. ex Phillips & Hutch (two varieties)	Africa
	Sesbania madagascariensis Du Puy & Labat	Madagascar
	Sesbania mannii Sachet	Pacific
	Sesbania melanocaulis Bidgood & Friis	Africa
	Sesbania microphylla Harms	Africa
	Sesbania mossambicensis Klotzsch (two subspecies)	Africa
	Sesbania notialis J.B.Gillett	Africa
	Sesbania oligosperma Taub.	South America
	Sesbania pachycarpa DC. (two varieties)	Africa
	Sesbania paucisemina J.B.Gillett	Africa
	Sesbania procumbens Wright & Arn.	Africa
	Sesbania quadrata J.B.Gillett	Africa
	Sesbania rostrata Bremek. & Oberm.	Africa
	Sesbania sericea (Willd.) Link (three varieties)	Africa & Americas
	Sesbania sesban (L.) Merr. (two subspecies, five varieties)	Africa
	Sesbania simpliciuscula F. Muell ex. Benth. (two varieties).	Australia
	Sesbania somaliensis J.B. Gillett	Africa
	Sesbania speciosa Taubert	Australasia & Pacific
	Sesbania sphaerosperma Welw.	Africa
	Sesbania subalata J.B.Gillett	Africa
	Sesbania sudanica J.B.Gillett (two subspecies)	Africa
	Sesbania tomentosa Hook.& Arn.	Pacific
	Sesbania transvaalensis J.B.Gillett	Africa

herbarium specimens and amenable to PCR amplification for the markers used in this study. In addition to sampling herbarium specimens (e.g. DNA samples from Old World taxa were all obtained from herbarium sheets), field collections targeting the principal diversity of *Sesbania* in the New World were made in the southeastern USA (North Carolina, South Carolina, Georgia, Florida) and northeastern Argentina. Genomic DNAs were extracted using Qiagen DNeasy kits (Valencia, California) as per the manufacturer's instructions.

DNA sequence analyses included the plastid *trnK* intron-*matK* gene (Hu et al. 2000) and the *trnG-trnS* (Shaw et al. 2005) regions, and the nuclear ribosomal DNA ITS/5.8S region (nrDNA ITS; Baldwin et al. 1995), the triosphosphate translocator gene, TRPT (Farruggia and Howard 2011), and the phosphogluconate dehydrogenase gene (Choi et al. 2006). These loci have been shown to provide excellent phylogenetic resolution compared to other plastid loci (e.g. Hu et al. 2000, 2002; Lavin et al. 2003; Luckow et al. 2003; McMahon and Hufford 2004; Wojciechowski et al. 2004; Farruggia and Howard 2011). Amplification of the TRPT locus using the Choi et al. (2006) primers involved subsequent cloning of PCR products to detect potential paralogs, which sequence analysis failed to reveal.

The nrDNA ITS region has been used extensively for phylogenetic reconstruction in flowering plants (Baldwin et al. 1995; Hershkovitz et al. 1999), especially in legumes (Amorpheae, McMahon and Hufford 2004; *Astragalus* L., Wojciechowski et al. 1999; Indigofereae, Schrire et al. 2009; *Leucaena* Benth., Hughes et al. 2003; and *Wajira* Thulin, Thulin et al. 2004), including the taxa that are the focus of this study, Loteae (Allan and Porter 2000; Allan et al. 2003), Robinieae (Lavin et al. 2003), and other close relatives (Sanderson and Wojciechowski 1996; Hu et al. 2002). Furthermore, nrDNA ITS sequences are effective for exhaustive taxon sampling because they are readily PCR amplified, straightforward to align for the groups of interest in this study, and contain high levels of informative variation at and below the species level (e.g. Lavin et al. 2003).

The PCR products were amplified using an annealing temperature of 55°C and sequenced directly in both the forward and reverse directions for 100% overlap. Sequence reads (and alignments) were directly examined to detect any sequence polymorphism. PCR results suggested that cloning of TRPT sequences was required for only *S. drummondii* (Rydb.) Cory, *S. punicea* (Cav.) Benth., *S. macroptera* Micheli, and *S. virgata* (Cav.) Poir. The PCR amplified products (and cloned copies of PCR products) from all molecular regions used in this study were sequenced on ABI capillary sequencers at the DNA Laboratory at Arizona State University. Primary sequence data was assembled into contigs and edited using Sequencher v. 4.0 (GeneCodes). Initial alignments were made using ClustalX (Thompson et al. 1997), then manually edited in MacClade v. 4.06 (Maddison and Maddison 2003). All new sequences have been deposited in GenBank (see Appendix 1) and final data matrices have been deposited in TreeBASE (study number S20641) and Dryad (Farruggia et al. 2018).

Phylogenetic Analyses—Relationships among the species of *Sesbania* and among potential sister groups were explored using phylogenetic analyses, which included accessions of all the New World taxa plus representative Old World species of *Sesbania* (Table 1). To account for sequence variation at the infraspecific level and to verify the monophyly of geographically disjunct species, and the pantropical distribution of many species, multiple accessions were sampled for several widespread taxa (e.g. *Sesbania sesban*).

Representatives of two monophyletic groups, Loteae s. l. (Allan et al. 2003), and Robinieae (Lavin et al. 2003), as well as two early branching genera of the IRLC, *Caragana* Fabr. and *Wisteria* Nutt., were designated outgroups in this study. This outgroup sampling is sufficient to test the monophyly and resolve the root of *Sesbania*, as well as assess its sister group relationships (e.g. Wojciechowski et al. 2004; LPWG 2017).

Maximum parsimony (MP) and Bayesian inference methods, implemented in PAUP* (Swofford 2002) and MrBayes 3.04 (Ronquist and Huelsenbeck 2003) respectively, were used for phylogeny reconstruction. Modeltest 3.06 (Posada and Crandall 1998) was used to choose among nucleotide substitution models for each of the data sets using the AIC criterion. The MP analyses were conducted using heuristic searches with random addition sequence and TBR branch swapping options in PAUP*, saving a maximum of 10,000 trees per analysis. Clade support was estimated by non-parametric bootstrapping (Felsenstein 1985) and from Bayesian posterior probabilities (Huelsenbeck et al. 2002). Bootstrap values were derived from 1000 replicates using similar branch swapping options and one random addition per replicate. We derived posterior probabilities by running Bayesian analyses for 5,000,000 to 20,000,000 generations and sampling every 1000 to 200,000 generations and using the default 25% burn-in. This large number of generations and burn-in were consistently identified as achieving likelihood stationarity by using the convergence diagnostics implemented in the MrBayes sump function. Gene trees derived from analyses of each locus and search method were evaluated for congruence.

We have taken a relatively conservative conditional combination approach (Huelsenbeck et al. 1996) for evaluating phylogenetic congruence, which was assessed in three ways: 1) parsimony bootstrap proportions and Bayesian posterior probabilities were compared among corresponding clades on trees derived from separate analyses; 2) the parsimony-based "partition homogeneity" or "ILD" test (Farris et al. 1995), implemented in PAUP*, was used to assess heterogeneity among data sets using a $p < 0.05$ threshold of significance; and 3) Matrix Representation using Parsimony (MRP) was used to compare topologies obtained from traditional consensus methods (Bininda-Emonds and Bryant 1998; Baum and Ragan 2004). For the MRP analysis, the strict consensus tree of 200 Bayesian trees sampled at stationarity for each data analysis was converted to a data matrix representing taxon membership in resolved nodes (scored as 0 = not a member, 1 = member) using Mesquite v. 2.6 (Maddison and Maddison 2009). The matrices for each molecular sequence region were concatenated into a single data set. This required the addition of unknown positional relationships, coded as a "?", when taxa were not included in the original data sets. This data set was then analyzed using the parsimony and Bayesian methods described above.

Biogeographic Analysis—To investigate the geographic structure within *Sesbania*, ages for each of the subclades of *Sesbania* were estimated as described below. Continental occurrences of the taxa were traced on 100 randomized trees generated in MacClade. Areas defined and taxa scored as present or absent in each area used native ranges (Table 2). Distribution of tree lengths reflected only geographic characters, which were mapped onto the phylogeny of *Sesbania*. The resulting randomized tree length distribution was compared with the actual tree length for the given biogeographical characters using the trace option in MacClade.

To determine the ages of transoceanic clades, penalized likelihood rate analyses (r8s; Sanderson 2002, 2003) were conducted on 200 Bayesian trees sampled at stationarity. Means and standard errors were estimated for both ages and rates of substitution for selected nodes for each of the three gene data sets, and were calculated from three independent analyses (Lavin et al. 2005). Relative substitution rates and ages were converted to absolute rates and ages using fossil calibrations from a previous study: a minimum age constraint derived from the *Robinia* L. wood fossil record (discussed in Lavin et al. 2003, 2005) was imposed on the Robinieae clade (34 Ma), and the age of the Robinioid crown clade (i.e. defined by most recent common ancestor of Robinieae, Loteae and *Sesbania*) was fixed at 48 MYA, as estimated by Lavin et al. (2005). A test of a clock-like rate of sequence evolution for each of the molecular sequence regions was determined using a likelihood ratio test of Felsenstein (1981) and the χ^2 test of the difference in likelihood scores (at the 0.05 level).

RESULTS

Plastid trnK-matK Phylogenetic Analyses—The final *trnK-matK* data set contained 24 terminal *Sesbania* taxa, and seven outgroup taxa by 2662 total aligned characters, of which 403 were potentially parsimony-informative. All trees derived from the analyses of *trnK-matK* sequences resolved two principal *Sesbania* clades corresponding to a "New World clade" that included traditional sections *Glottidium, Daubentonia,* and *Daubentoniopsis*, and a "Pantropical clade" comprising a more broadly defined sect. *Sesbania* with linear fruits that includes the formerly recognized Pacific subg. *Agati* (Adans.) Baker and the African subg. *Pterosesbania* Gillett with 4-winged fruits (see revised sectional taxonomy below).

Relationships within the New World clade are mostly poorly resolved apart from the bladdery-fruited sect. *Glottidium*, which is the well-supported sister to the rest of the New World species. Relationships among the species of the 4-winged-fruited sect. *Daubentonia*, are poorly resolved and the monotypic sect. *Daubentoniopsis* (*S. cavanillesii* S. Watson (= *S. longifolia* (Cavanilles) DC.) with its torulose fruits is nested

TABLE 2. Taxon coverage and phylogenetic utility of complete bi-directional sequences for each DNA sequence locus. [1]Total does not include subspecies or varietal level taxa. MP = Maximum Parsimony.

DNA locus	Number of sampled *Sesbania* species[1]	Number of characters (# Parsimony Informative)	MP tree length	Number of MP trees	Bayesian average -lnL score	CI	RI
nuclear rDNA ITS	48	635 (326)	1457	10,000	9634.3	0.48	0.80
nuclear TRPT	37	345 (75)	185	22	1622.6	0.78	0.86
plastid *trnK-matK*	24	2662 (403)	908	10,000	8917.8	0.87	0.92

within it. Despite their close relationship, species of the sects. *Daubentoniopsis* and *Daubentonia*, which are very similar in regard to floral and seed morphology, habit and habitat, and geographic distribution, are very distinct in legume morphology.

The Pantropical clade comprises species with linear fruits and corresponds closely to sect. *Sesbania* and includes the Pacific subg. *Agati*, also with linear fruits, and the African subg. *Pterosesbania* with 4-winged fruits. A few well-resolved and well-supported subclades include a subclade containing *Sesbania herbacea* (Mill.) McVaugh and *Sesbania sericea* (Willd.) Link, two species often mistaken for each other in herbarium specimens. Another subclade is primarily Austral-Pacific in distribution and includes the widely cultivated, large-flowered tree species *Sesbania grandiflora* (L.) Poir., along with *Sesbania brachycarpa* F.Muell., *Sesbania campylocarpa* (Domin) N.T.Burb., and *Sesbania chippendalei* N.T.Burb. A third well-supported subclade includes the southeastern African *Sesbania dummeri* Phillips & Hutch., *Sesbania goetzii* Harms, *Sesbania greenwayii* J.B. Gillett, and the widely distributed *Sesbania sesban* (L.) Merr. complex (Fig. 2).

Nuclear rDNA ITS Phylogenetic Analyses—The final nrDNA ITS data set contained 48 *Sesbania* and 20 outgroup taxa by 703 total aligned characters, of which 326 were potentially parsimony-informative characters (Table 2). Because the nrDNA ITS sequences had the highest percentage of

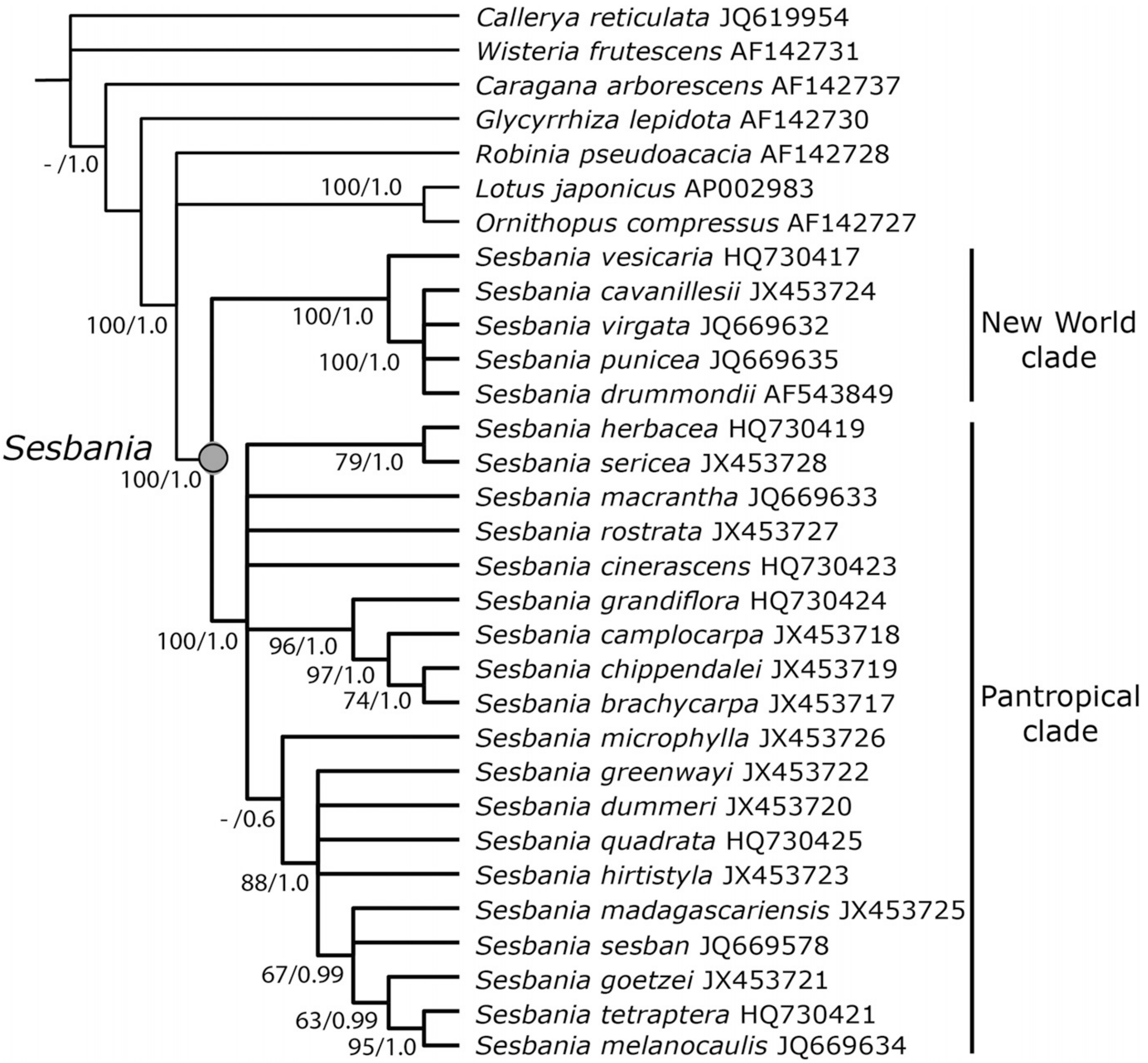

FIG. 2. Phylogeny of *Sesbania* based on a Bayesian analysis of plastid *trnK-matK* sequences (2662 included characters), with designated outgroups. Tree shown is majority-rule consensus of final 200 trees sampled post-stationarity in a minimum 5 million generation analysis, assuming TVM + Γ model of sequence evolution, with trees saved every 1000 generations. Average -ln L = 8917.8; base frequencies: A = 0.3368, C = 0.1380, G = 0.1576, T = 0.3676; rate matrix: A-C = 1.2634, A-G = 2.1365, A-T = 0.4894, C-G = 1.3339, C-T = 2.1365, G-T = 1.0000; proportion of invariant sites = 0; rates = gamma, with shape parameter = 0.8720. Non-parametric bootstrap proportions (from maximum parsimony analyses) and Bayesian posterior probabilities greater than 50% and 0.5, respectively, are indicated below each supported node.

informative characters of any of the DNA sequence loci used in this study (Table 2), this region was extensively sampled across *Sesbania*.

The phylogenies derived from maximum parsimony and Bayesian analyses of the nrDNA ITS data (Fig. 3) resolved several well-supported clades. The posterior probabilities show broad, robust support (0.9–1.0 posterior probability) throughout *Sesbania*. These results show weak support for Loteae as sister to *Sesbania* by maximum parsimony analysis, consistent with previous studies based on nrDNA ITS (e.g. Lavin et al. 2003) and *matK* (Wojciechowski et al. 2004) sequence analyses, but the relationship is strongly supported by Bayesian inference.

Within *Sesbania*, relationships based on analysis of nrDNA ITS sequence are largely congruent with those of the *trnK-matK* phylogenies. Notably, the New World clade is sister to the Pantropical clade and the former subgenera *Pterosesbania* (*S. tetraptera* Hochst. ex Baker) and *Agati* (*S. formosa* (F.Muell.) N.T.Burb., *S. grandiflora*) are nested within sect. *Sesbania*. Many subclades within the Pantropical clade also are resolved and well-supported. The New World species *S. exasperata* Kunth and *S. oligosperma* Taub. are sister to each other and nested within a pantropically distributed clade that is largely dominated by African taxa.

Three accessions of the polyploid *S. bispinosa* (Jacq.) W. Wight are scattered throughout the Pantropical clade (Fig. 3), rendering this species polyphyletic on the nrDNA ITS tree. Interestingly, each of these accessions groups with accessions of other taxa collected from geographically adjacent localities. For example, the specimen *S. bispinosa* FTF38 (JX453669; Fig. 3), collected in Australia, is sister to *S. campylocarpa*, an endemic Australian species. Accession FTF38 morphologically matches *S. bispinosa* var. *bispinosa*, and it is indistinguishable from the other *S. bispinosa* accessions from worldwide collections.

Nuclear TRPT Gene Phylogenetic Analyses—The final TRPT gene data set consisted of 37 terminal *Sesbania* taxa, plus five outgroup taxa, and 345 total aligned characters, of which 75 were potentially parsimony-informative characters. Analyses of TRPT sequences using parsimony and Bayesian searches (e.g. Fig. 4) generally support the relationships resolved in both the nrDNA ITS and *trnK-matK* analyses.

Combined Molecular Data Analysis—Results of the partition homogeneity test, conducted on all combinations of the sequence data sets, were significant at the 0.01 level, suggesting that the data are providing information supporting different evolutionary histories, i.e. evidence of incongruence among the data sets. Next, the topologies of trees derived from each data set were compared for bootstrap/posterior probability support and using MRP. The resulting MRP supertree (Fig. 5) shows low support for the previously suggested outgroup relationships of *Sesbania*; Loteae and *Sesbania* form a clade, albeit with weak support, that is sister to Robinieae, while each of these three groups individually are strongly supported as monophyletic.

Age and Biogeographic Analyses—Age estimates for specific clades varied slightly among trees derived from analyses of the nrDNA ITS and plastid *trnK-matK* data sets, but age estimates derived from analyses of the nuclear TRPT region were older than those obtained from the other loci (Table 3). However, the age estimates are mostly within a standard deviation of each other. The average of the *Sesbania* crown clade is estimated at 19.4 ± 2.4 Ma, whereas the age of the Loteae crown clade from nrDNA ITS sequences is estimated at 21.5 ± 2.5 Ma, which is older than the *matK* sequence estimate of 14.4 ± 1.3 Ma (Lavin et al. 2005). These relatively young age estimates are for the older clades that are well distributed globally.

Continental distributions scored for each of the terminal taxa (Tables 1, 4) showed a pattern of aggregation or phylogenetic structure (Fig. 5). Parsimony optimization of geographic characters resulted in a tree length distinctly shorter than a distribution of tree lengths derived from the optimization of those same characters on 100 random trees (data not shown). The alternative, which was not supported by our results, is the finding that the length of the supertree was within the random distribution of tree lengths. This then would have suggested that geography had imposed little if any constraint on the phylogeny of *Sesbania*.

Discussion

Phylogenetic Relationships within Sesbania—Loteae remains poorly supported as the sister group to the genus *Sesbania*. *Sesbania* comprises two principal, strongly-supported groups corresponding to the New World and Pantropical clades according to the molecular phylogeny (Fig. 5), a division consistent with morphology. The New World clade is marked by a stipitate legume bearing few reniform seeds (typically much fewer than 12), the claw of the banner petal lacking calli at distal end, and keel and wing petals with ventral margins lacking an auricle ("tooth"). The molecular phylogeny resolves the annual *Sesbania vesicaria* (Jacq.) Elliott, which sometimes has an inconspicuous auricle along the ventral margin of the keel petal, as sister to the rest of the New World clade, which comprises shrubs and trees. This early branching position of *Sesbania vesicaria* mirrors its presumed pleisiomorphic traits, such as the annual habit and the sometimes-toothed ventral margin of keel, that are shared with species of the Pantropical clade.

The Pantropical clade includes all members of the section *Sesbania* (incl. former subgenera *Agati* and *Pterosesbania*). This clade has a few potential morphological synapomorphies, the most distinguishing of which are the many-seeded legume (usually well over 20 seeds per legume; Fig. 1E–H) with a short stipe and columnar seeds (except for *S. grandiflora* and *S. formosa* which have reniform seeds), well-developed calli along the banner claw, and the presence of a pronounced auricle along the ventral margin of the keel and wing petals (e.g. Fig. 1M). Of all the species in this clade, only *S. oligosperma*, *S. tetraptera,* and a few Australian species, all of which are nested well within the Pantropical clade, appear to have reverted back somewhat to the ancestral condition by producing legumes with occasionally fewer seeds (less than 20). The nested position of *Pterosesbania* within the sect. *Sesbania* clade supports Gillett's (1963) description of *Pterosesbania* as being closely related to sect. *Sesbania*.

The New World species *S. herbacea*, the Hawaiian *S. tomentosa* Hook. & Arn. complex (circumscribed by Char 1983; Cole 2015), and the pantropical *S. sericea* and *S. cannabina* (Retz.) Poir. form a well-supported clade that is sister to the rest of the Pantropical clade. This placement of the *S. tomentosa* complex is unexpected given the morphological similarity of its members to the South Pacific species *S. coccinea* (L. f.) Poir., *S. grandiflora*, and *S. formosa* (Char 1983; Sachet 1987).

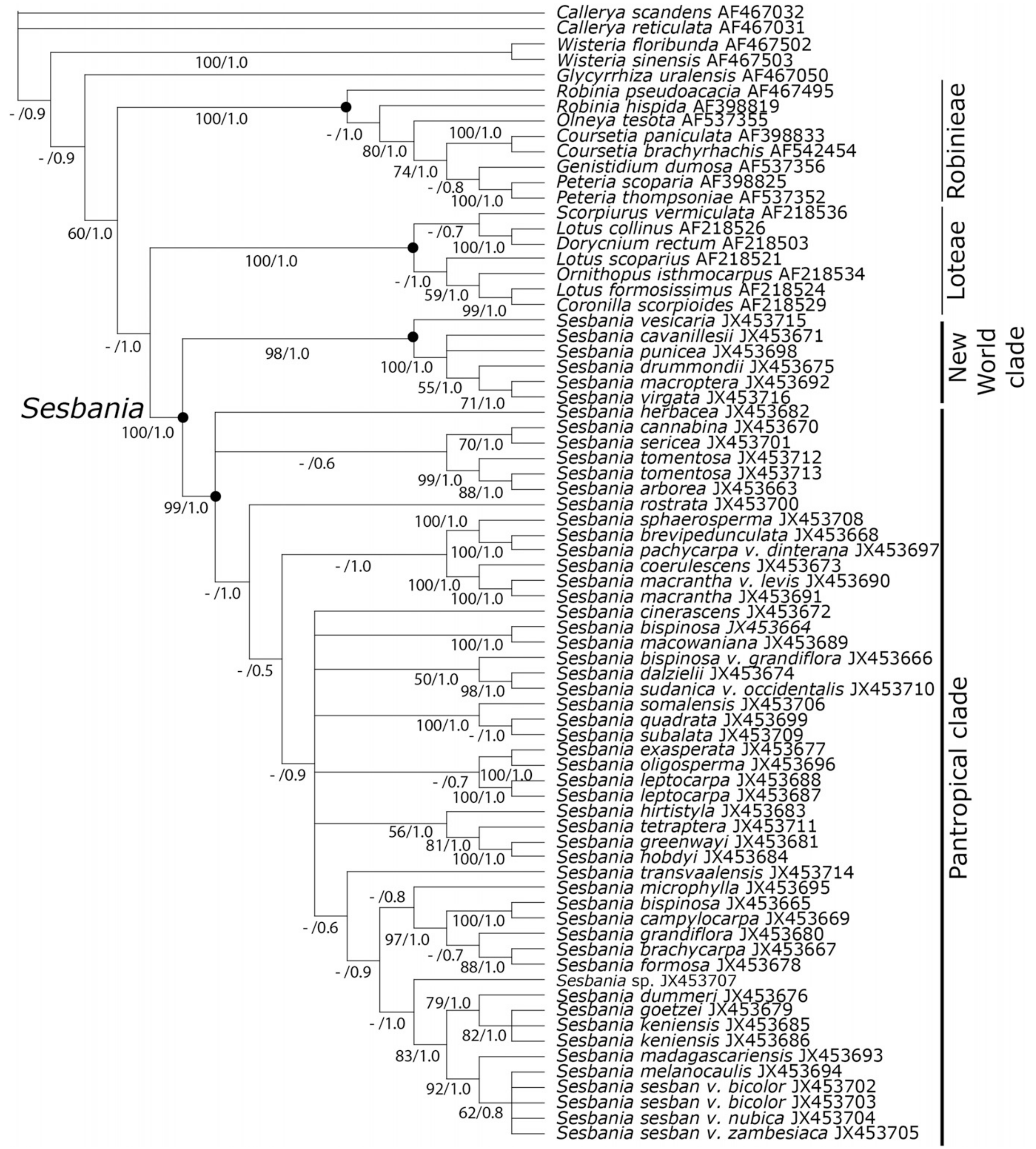

FIG. 3. Phylogeny of *Sesbania* based on a Bayesian analysis of nrDNA ITS sequences (703 included characters), with designated outgroups. Tree shown is majority-rule consensus of final 200 trees sampled post-stationarity in a minimum 5 million generation analysis, assuming GTR + Γ + I model of sequence evolution, with trees saved every 1000 generations. Average -ln L = 9634.266; base frequencies: A = 0.2331, C = 0.2782, G = 0.2646, T = 0.2241; rate matrix: A-C = 0.8683, A-G = 2.0524, A-T = 1.2007, C-G = 0.5965, C-T = 4.5447, G-T = 1.0000; proportion of invariant sites = 0.3005; rates = gamma, with shape parameter = 1.4505. Non-parametric bootstrap proportions (from maximum parsimony analyses) and Bayesian posterior probabilities greater than 50% and 0.5, respectively, are indicated below each supported node.

The Pantropical clade is dominated by African taxa that in some instances are poorly resolved. Such instances of low resolution may be the result of interspecific hybridization among closely related species. For example, within the *S. sesban*-*S. dummeri* clade (node J; Fig. 5), morphological, geographic, and molecular evidence suggests that *S. sesban*, *S. goetzii*, and *S. keniensis* J.B. Gillett are distinct species but successful hybrids can be produced between them (Heering and Hanson 1993). Similarly, there are various possible explanations for the apparent polyphyly of *S. bispinosa* in the

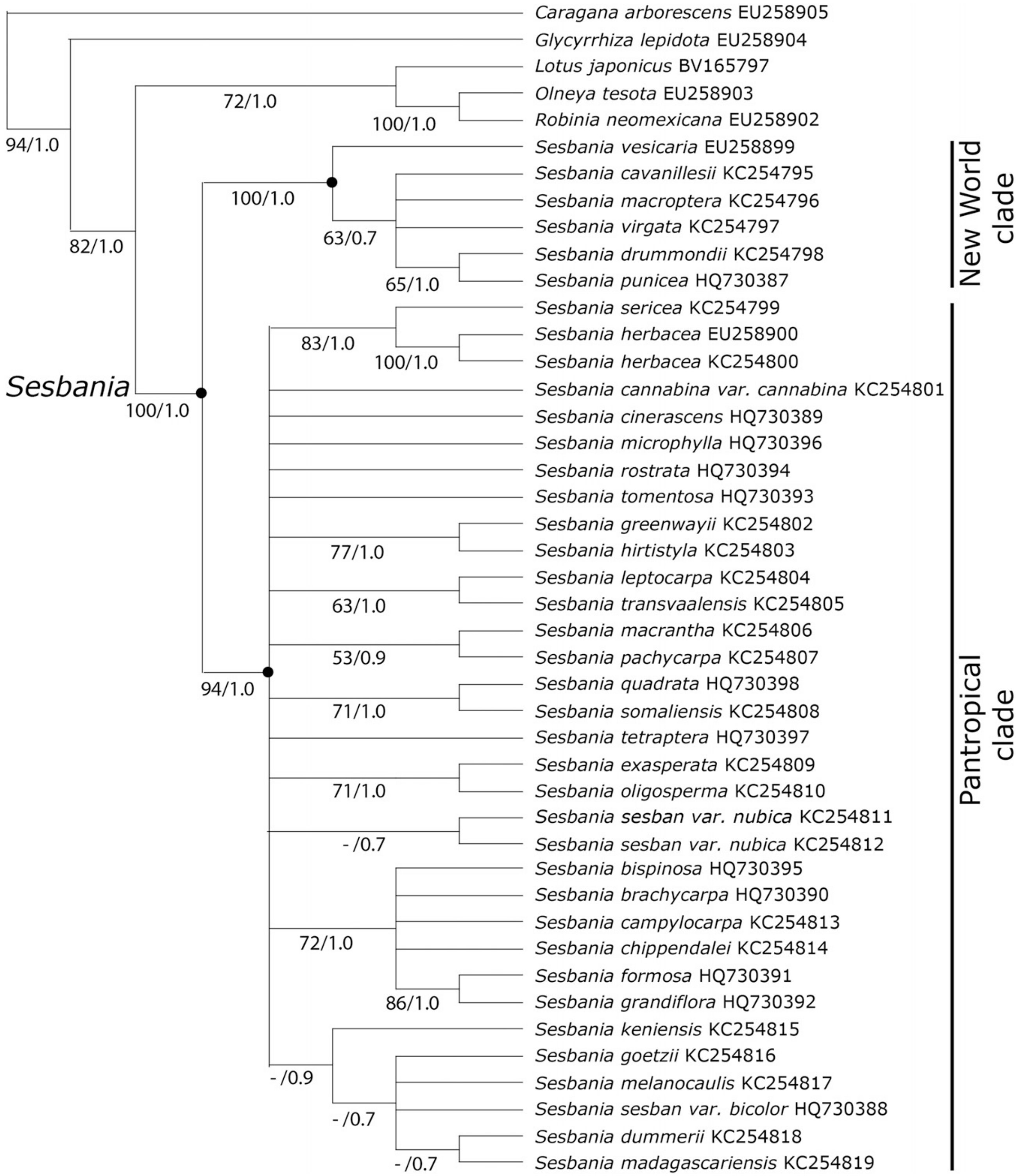

FIG. 4. Phylogeny of *Sesbania* based on a Bayesian analysis of nuclear TRPT sequences (345 included characters), with designated outgroups. Tree shown is majority-rule consensus of final 200 trees sampled post-stationarity in a minimum 5 million generation analysis, assuming TVM + Γ model of sequence evolution, with trees saved every 1000 generations. Average -ln *L* = 1622.6; base frequencies: A = 0.2742, C = 0.1703, G = 0.2630, T = 0.2925; rate matrix: A-C = 0.6304, A-G = 3.0282, A-T = 0.9540, C-G = 1.8234, C-T = 3.0282, G-T = 1.0000; proportion of invariable sites = 0.0; rates = gamma, with shape parameter = 0.9118. Non-parametric bootstrap proportions (from maximum parsimony analyses) and Bayesian posterior probabilities greater than 50% and 0.5, respectively, are indicated below each supported node.

nrDNA ITS tree. The African and Madagascan accessions of *S. bispinosa* (JX453664 from Africa and JX453666 from Madagascar) group with other African *Sesbania* species whereas an Australian accession (JX453665) groups with Austral-Pacific species (Figs. 2, 5, S1). *Sesbania bispinosa*, a polyploid taxon, may have multiple hybrid origins given the findings of wide hybridization in the genus (Heering 1994; Jamnadass et al. 2005). Of course, other explanations are equally plausible, such

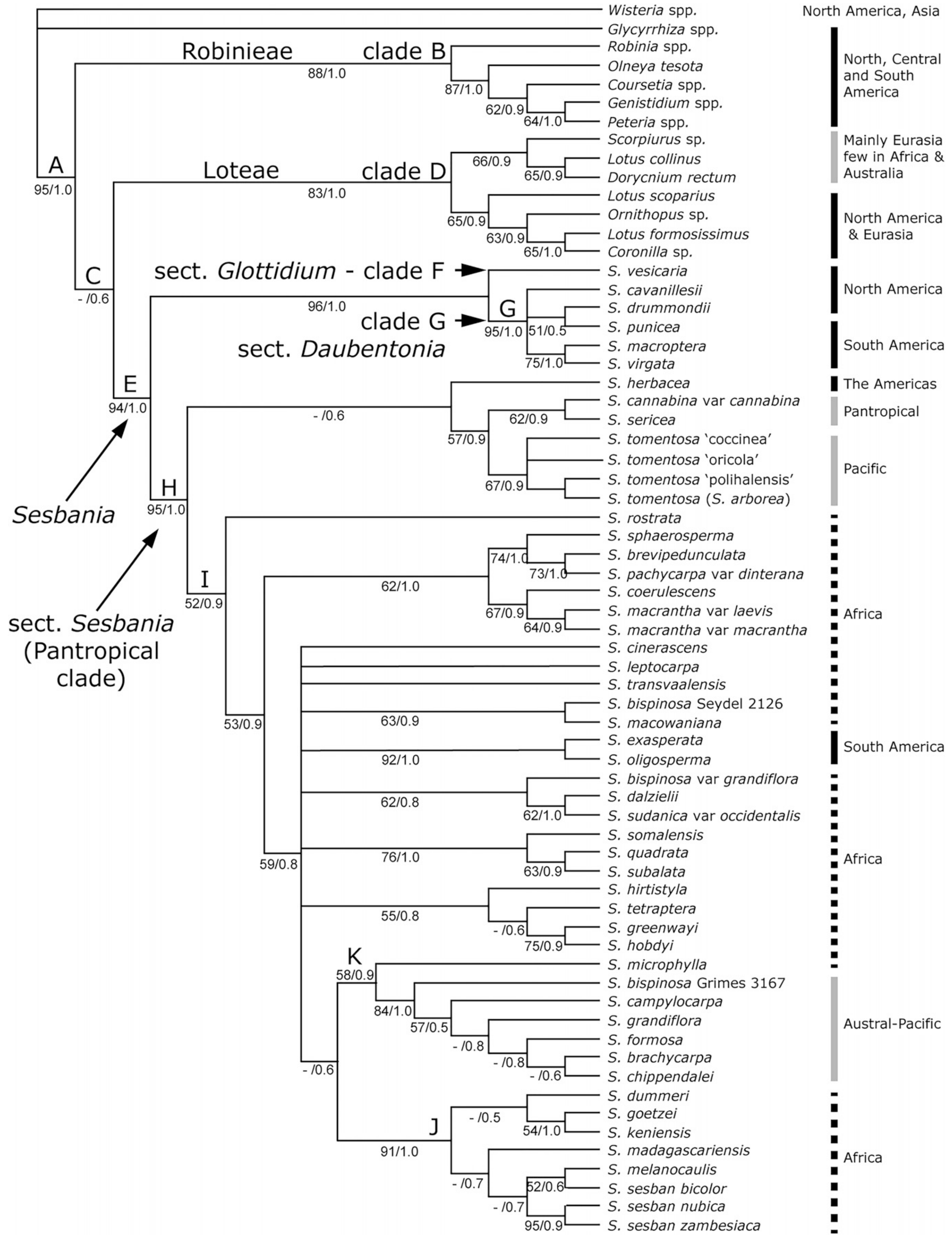

FIG. 5. Supertree of *Sesbania* and designated outgroups. Tree shown is majority-rule consensus of final 100 trees derived from the MRP analysis of a supermatrix generated from a combination of nrDNA ITS, nuclear TRPT, and plastid *trnK-matK* strict consensus trees (104 included characters). Non-parametric bootstrap proportions (from maximum parsimony analyses) and Bayesian posterior probabilities greater than 50% and 0.5, respectively, are indicated below each supported node. Letters indicate selected nodes in Table 3. Taxon distributions are indicated to right of phylogeny.

TABLE 3. Estimates of ages for specific crown clades of Robinioid legumes (nodes labeled as in Fig. 5). Absolute ages were estimated using the program r8s (Sanderson 2003) on 200 trees derived from Bayesian analyses of three data sets. Numbers in parentheses are standard deviations. Age estimates are missing (-) for unresolved nodes in the trees derived from analyses of *trnK-matK* and TRPT sequences. Repeated analyses of TRPT region sequences failed to return an age estimate (*) for the New World clade despite its presence across all trees. The age of Robinieae and Robinioids were fixed based on ages reported in Lavin et al. (2005).

Node	Label	plastid *trnK-matK*	nuclear TRPT	nrDNA ITS	Average (s.d.)
Robinioids	A	48	48	48	48
Robinieae	B	33.7	33.7	33.7	33.7
Loteae-*Sesbania*	C	-	-	36.7 (1.8)	36.7 (1.8)
Loteae	D	-	-	21.5 (2.3)	21.5 (2.3)
Sesbania	E	17.9 (2.1)	24.7 (2.8)	15.8 (2.3)	19.4 (2.4)
New World clade	F	6.7 (1.2)	*	5.4 (1.1)	6.1 (1.2)
Sect. *Daubentonia*	G	1.9 (0.9)	8.6 (3.6)	1.2 (0.7)	3.9 (2.0)
Pantropical clade	H	5.2 (2.0)	14.4 (4.9)	11.0 (2.5)	10.2 (3.3)
African clade	I	-	-	7.8 (2.0)	7.8 (2.0)
East African clade	J	1.7 (1.1)	4.1 (2.2)	1.1 (0.9)	2.3 (1.4)
Austral-Pacific clade	K	3.3 (1.3)	7.0 (3.0)	2.9 (1.0)	4.4 (1.9)

as: specimen misidentification; the taxon *S. bispinosa* comprises more than one distinct species; and/or the polyploid is hybridizing with other species in different areas. This widespread taxon needs to be investigated further.

Biogeography—An analysis of area relationships suggest a hypothetical ancestral geographic area centered in the New World for the Loteae-*Sesbania* clade, supported by the early-diverging New World clades and the predominantly tropical North American distribution of Robinieae. The recent origins of most of the geographic phylogenetic structure (Table 3) suggest that long-distance dispersal events have led to the pantropical distribution of *Sesbania* (Fig. 6). This is the case also with the intercontinental distributions of some individual *Sesbania* species (e.g. *S. cannabina*). This is consistent with the findings of Lavin et al. (2004) who suggested that legumes inhabiting wet forests or wetlands generally have a higher incidence of transoceanic clades compared to legumes inhabiting seasonally dry settings. Also, Les et al. (2003) suggested a general angiosperm pattern of a high incidence of transoceanic dispersal associated mostly with clades confined to wetlands habitats.

In contrast to the biogeography of *Sesbania*, Loteae and Robinieae have few if any naturally occurring transcontinental and transoceanic species or subclades. In the case of Loteae, with 22 constituent genera and about 280 species, only one or possibly two dispersal events are suggested between the Old and New World and no Loteae species is known to have a transcontinental distribution (Allan et al. 2003). Robinieae, with 12 constituent genera and about 77 species (Lavin and Sousa S. 1995; Lavin et al. 2003), is naturally confined to the New World.

Sesbania subclades with recently evolved transoceanic distributions (Table 3) include the American *S. exasperata* and *S. oligosperma* within what is otherwise a paleotropical clade. *Sesbania exasperata* is found throughout South America and northward into Mexico, Cuba, and southern Florida, whereas *S. oligosperma* is restricted to southeast Brazil. Also included here is the South Pacific and Australian clade comprising *S. grandiflora, S. formosa, S. campylocarpa, S. chippendalei*, and *S. brachycarpa*, which is nested among mainly African clades (Fig. 5). These species share similar geographic distributions and have larger flowers than most other *Sesbania* species. Also, the American *S. herbacea* is sister to the clade comprising the paleotropical species *S. tomentosa*, *S. cannabina*, and *S. sericea*. Long distance dispersal also might explain the pantropical distributions of each of *S. sericea, S. cannabina*, and *S. bispinosa*, but it is uncertain whether this is due to natural or human-mediated dispersal (Gillett 1963; Burbidge 1965).

Phylogenetic patterns suggest a directionality of dispersal in *Sesbania* with a New World to Old World trend. Early-diverging lineages of the Pantropical clade (sect. *Sesbania*) are from the New World and western Africa whereas the more distally-branching clades show an east Africa clade (node J, Fig. 5) sister to an Austral-Pacific clade (node K, Fig. 5). These are hypothesized dispersal events because the associated age estimates are about 10 Ma or less (Fig. 6). We elaborate on the main dispersal events using the vector labels (Fig. 6), below.

IA—The sister group to the rest of *Sesbania* is the New World clade (clade F, Fig. 5), which has early-diverging branches that are North American. Of the species occurring in South America, only *Sesbania macroptera* is endemic to the continent in Paraguay and adjacent Argentina and Brazil. Haffer (2008) explains such patterns by dispersal to the subtropical dry region of northern Argentina or isolation due to the shifting ecological conditions over the last 4 to 6 million years during the Miocene and Pliocene.

IB—The estimated time of divergence of the Pantropical clade (=sect. *Sesbania*; clade H, Fig. 5) from New World *Sesbania* is far too young to invoke vicariance to explain its distribution between the New World and West Africa (Table 3; Fig. 6). The New World *Sesbania herbacea* is notably the earliest-branching species in an otherwise pantropically distributed clade that is sister to clade I (Figs. 5, 6), which contains most of the Old World *Sesbania* species. West Africa harbors all of the early-branching species in this predominantly African clade (clade I; Figs. 5, 6). The estimated age of clade I (Figs. 5, 6), 7.8 ± 2.0 Ma, is similar to the age estimate of the legume genus *Vigna* s. s., 6.0 ± 0.7 Ma, which has a comparable geographic distribution centered in Africa (Delgado-Salinas et al. 2011). The ability of species in the Pantropical clade to disperse may be related to *Sesbania* seeds as a potential food resource for birds. Flunker et al. (1991) cite reports from wildlife enthusiasts and seed providers suggesting that the species of sect. *Sesbania* are not poisonous to birds and serves as food sources for waterfowl. In contrast, Flory and Hebert (1984) report that the seeds of *S. drummondii*, in addition to *S. punicea*, are toxic to chickens and other birds and suggest that this toxicity may explain why the distribution of these species is naturally restricted to the New World.

IIA—The sister group relationship between the American *S. herbacea* and the Hawaiian *S. tomentosa* complex is reminiscent

Table 4. Geographic area character matrix used in the cladistic analysis of *Sesbania* biogeography. Eight areas are defined: A. North America, B. Central America and Caribbean, C. South America, D. Europe and Middle East, E. Africa and Madagascar, F. Asia, G. Pacific Islands, H. Australia. Presence in ("1") or absence from ("0") a geographic area was determined only on the native ranges for each taxon.

Biogeographic Region	A	B	C	D	E	F	G	H
IRLC								
Glycyrrhiza	1	1	1	0	0	0	0	0
Wisteria	1	0	0	0	0	1	0	0
Loteae s.l.								
Coronilla	0	0	0	1	1	0	0	0
Dorycnium	0	0	0	0	1	0	0	0
Hosackia	1	1	0	0	0	0	0	0
Lotus	0	0	0	1	1	1	0	1
Ornithopus	0	0	1	0	1	0	0	0
Scorpiurus	0	0	0	1	1	1	0	0
Syrmatium	1	0	0	0	0	0	0	0
Robinieae								
Robinia	1	0	0	0	0	0	0	0
Genistidium	1	0	0	0	0	0	0	0
Olneya	1	0	0	0	0	0	0	0
Coursetia	1	1	1	0	0	0	0	0
Peteria	1	0	0	0	0	0	0	0
Sesbanieae								
Sesbania bispinosa	1	1	1	1	1	1	1	0
Sesbania bispinosa var. *grandiflora*	0	0	0	1	0	0	0	0
Sesbania brachycarpa	0	0	0	0	0	0	0	1
Sesbania brevipedunculata	0	0	0	1	0	0	0	0
Sesbania campylocarpa	0	0	0	0	0	0	0	1
Sesbania cannabina	0	0	0	1	0	1	1	1
Sesbania cinerascens	0	0	0	1	0	0	0	0
Sesbania coerulescens	0	0	0	1	0	0	0	0
Sesbania dalzielii	0	0	0	1	0	0	0	0
Sesbania dummeri	0	0	0	1	0	0	0	0
Sesbania exasperata	1	1	1	0	0	0	0	0
Sesbania formosa	0	0	0	0	0	0	1	1
Sesbania goetzei	0	0	0	1	0	0	0	0
Sesbania grandiflora	0	0	0	0	0	0	1	0
Sesbania greenwayi	0	0	0	1	0	0	0	0
Sesbania hepperi	0	0	0	1	0	0	0	0
Sesbania herbacea	1	1	1	0	0	0	0	0
Sesbania hirtistyla	0	0	0	1	0	0	0	0
Sesbania hobdyi	0	0	0	1	0	0	0	0
Sesbania keniensis	0	0	0	1	0	0	0	0
Sesbania leptocarpa	0	0	0	1	0	0	0	0
Sesbania macowaniana	0	0	0	1	0	0	0	0
Sesbania macrantha	0	0	0	1	0	0	0	0
Sesbania madagascarensis	0	0	0	1	0	0	0	0
Sesbania melanocaulis	0	0	0	1	0	0	0	0
Sesbania microphylla	0	0	0	1	0	0	0	0
Sesbania mossambicensis	0	0	0	1	0	0	0	0
Sesbania oligosperma	0	0	1	0	0	0	0	0
Sesbania pachycarpa	0	0	0	1	0	0	0	0
Sesbania quadrata	0	0	0	1	0	0	0	0
Sesbania rostrata	0	0	0	1	0	0	0	0
Sesbania sericea	1	1	1	1	0	1	0	0
Sesbania sesban	0	0	1	1	0	1	0	1
Sesbania simpliscula	0	0	0	0	0	0	0	1
Sesbania somalensis	0	0	0	1	0	0	0	0
Sesbania sphaerosperma	0	0	0	1	0	0	0	0
Sesbania subalata	0	0	0	1	0	0	0	0
Sesbania sudanica	0	0	0	1	0	0	0	0
Sesbania tetraptera	0	0	0	1	0	0	0	0
Sesbania tomentosa	0	0	0	0	0	0	1	0
Sesbania arborea	0	0	0	0	0	0	1	0
Sesbania transvaalensis	0	0	0	1	0	0	0	0
Sesbania drummondii	1	0	0	0	0	0	0	0
Sesbania cavanillesii	1	0	0	0	0	0	0	0
Sesbania punicea	1	0	1	0	0	0	0	0
Sesbania macroptera	0	0	1	0	0	0	0	0
Sesbania virgata	0	0	1	0	0	0	0	0
Sesbania vesicaria	1	0	0	0	0	0	0	0

of patterns seen in other vascular plants (e.g. Hawaiian Silverswords, Asteraceae, Baldwin et al. 1991; *Sanicula* L., Apiaceae, Vargas et al. 1998). Although such long-distance dispersal may be rare, successful dispersal does occur (Carlquist 1967). The pattern of diversification in the *S. tomentosa* complex mirrors that of other recent island radiations (e.g. Hawaiian Silverswords, Baldwin et al. 1991; MacArthur and Wilson 1967) in terms of many morphological, ecological, and isozyme differences contrasting to low levels of DNA sequence variation.

IIb—The hypothesized dispersal of a clade containing *S. exasperata* and *S. oligosperma* from western Africa to possibly the subtropical regions of Brazil, Argentina, and Uruguay represents a pattern exhibited by other plant groups (e.g. *Annona* L., Annonaceae, and *Menodora* Bonpl., Oleaceae; Renner 2004a).

IIc—The dispersal of *S. sericea* and *S. bispinosa* from Africa to the Caribbean has been postulated by Gillett (1963) and Burbidge (1965) to be due to human-mediated dispersal, despite having somewhat narrow native African distributions. Renner (2004a) suggests potential routes for floating plant "islands" across the Atlantic Ocean, which include the North Equatorial Counter-Current and the South Equatorial Current. Rates of surface transport along these two currents could deliver a rafting plant from South America to West Africa in approximately two weeks (Renner 2004a). These currents could readily disperse species like those of *Sesbania* that are abundant in disturbed riparian habitats, coastlines, and the major river deltas of the large rivers like the Amazon, the Congo, and the Senegal Rivers.

IIIa and IIIb—The close relationship between the eastern African (clade J, Figs. 5, 6) and the Austral-Pacific taxa (clade K, Figs. 5, 6) may be explained by dispersal over land (i.e. via East Africa and southern Asia, IIIa) or by sea (i.e. via the Indian Ocean, IIIb). The floristic similarities between East Africa, Madagascar, Southeast Asia, and Australasia because of dispersal from Africa is well documented (e.g. Malcomber 2002; Renner 2004b, 2005; Yuan et al. 2005) with notable examples in legumes (e.g. *Ormocarpum* P. Beauv.; Thulin and Lavin 2001; *Vigna* Savi, s. s.; Delgado-Salinas et al. 2011; *Wajira*; Thulin et al. 2004).

IV—The strong relationship between the Australian and the Pacific groups of *Sesbania* was originally proposed by Burbidge (1965), who postulated this relationship based upon the morphological similarity of Pacific taxa, such as *S. coccinea* and *S. grandiflora*, and the Australian *S. formosa*. Our results support the taxonomic relationships proposed by Burbidge and suggest that dispersal and local isolation of *Sesbania* populations throughout the South Pacific has led to the evolution of species complexes, as exemplified by *Sesbania coccinea* (Sachet 1987) and *S. tomentosa* (Cole 2015).

Phylogenetic analyses, evolutionary age estimates, and current geographic distributions all suggest that the *Sesbania* crown clade has at most a Miocene origin and a history that involved transoceanic long-distance dispersals. As is the case

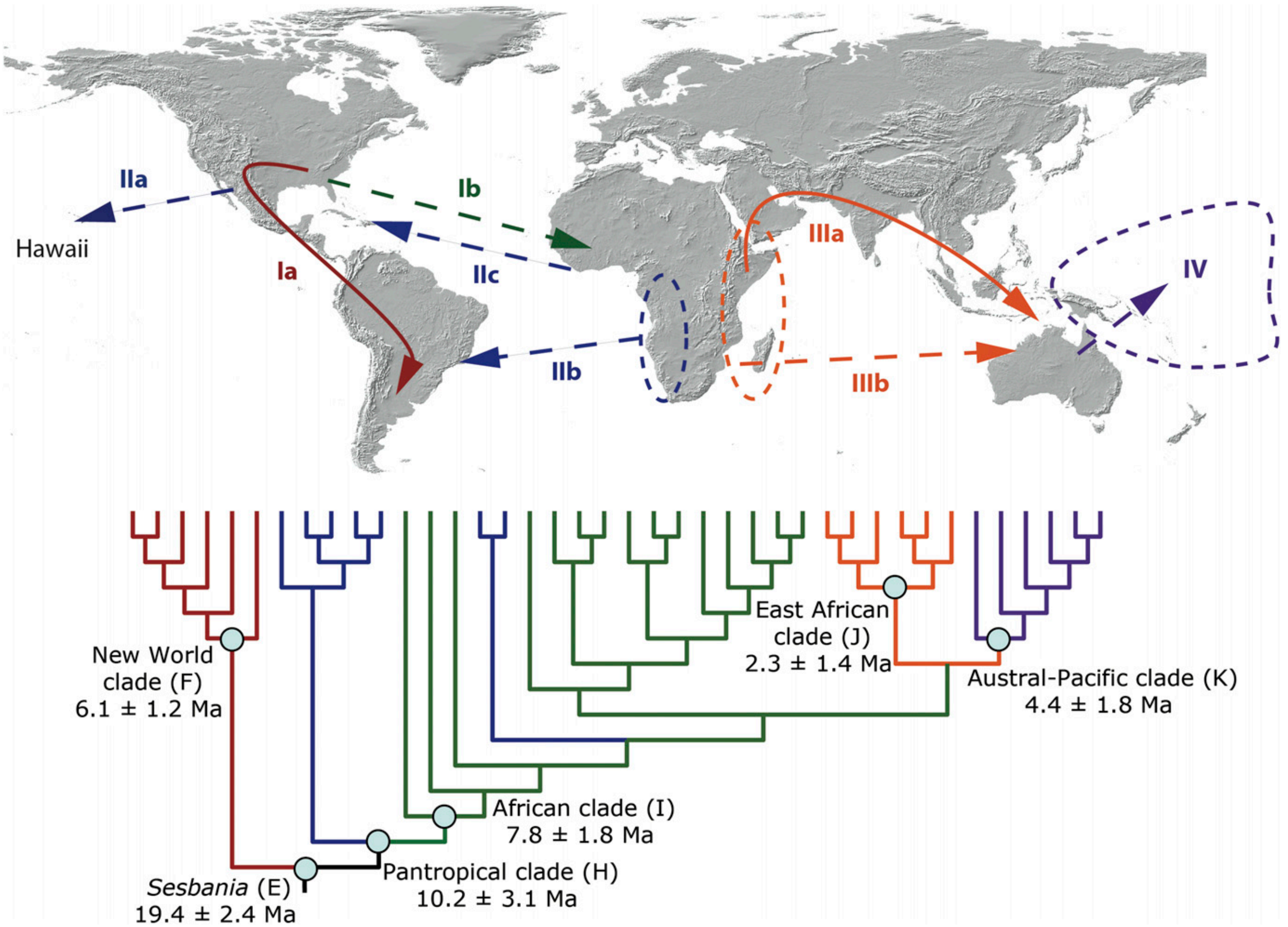

FIG. 6. Phylogenetic relationships of *Sesbania* species and hypotheses of dispersal history using current distributions of subclades. Estimated ages (average ± s.d.) are reported for some of the principal subclades (Table 3; Fig. 5). Hypothesized dispersal corridors depicted alphanumerically follow the Discussion section. Dashed vectors suggest hypothesized long-distance transoceanic dispersal.

for all the many recent origins of transcontinental crown clades in legumes (Lavin et al. 2004), these young age estimates of *Sesbania* are much younger than the proposed Cretaceous opening of the southern Atlantic (Parrish 1993), the latest Mid-Tertiary North Atlantic land bridge (Tiffney 1985), and the Mid-Tertiary connection between North and South America, including the proto-Antilles (Coates et al. 1992; Iturralde-Vinent and MacPhee 1999; O'Dea et al. 2016). *Sesbania* populations commonly inhabit coastal and riparian areas on most continents, which have the potential for recurrent episodes of high-energy flooding (e.g. the Amazon, Paraná, and Mississippi Rivers of the Americas), and this increases the chance for dispersal especially of the shallow-rooted annual species that are common in the Pantropical clade. Off-shore ocean currents could disperse coastal and riparian *Sesbania* species across the Atlantic Ocean, Indian Ocean, and throughout the Pacific Ocean in a relatively short time, perhaps on the order of only a couple of weeks (e.g. Renner 2004a, b). *Sesbania* populations can establish rapidly (e.g. Hoffmann and Moran 1997; Hrusa et al. 2002), have a potential for selfing (Heering and Hanson 1993), and produce high annual seed yields (~1000–10,000 seeds/plant/yr). These features would facilitate transoceanic dispersal and subsequent establishment (e.g. Jamnadass et al. 2005).

Other features may promote dispersal ability via hydrochory (e.g. Nilsson et al. 2010). For example, we have noted elsewhere the structural differences in fruit anatomy/morphology among *Sesbania* species (Fig. 1), differences that may be related to or promote differential buoyancy and survival under waterlogged or flooded conditions. We tested both fruit buoyancy and seed survival, as measured by imbibition, under both fresh and simulated salt water conditions for six species representing *S.* sects. *Daubentonia* and *Sesbania*. Our results (Farruggia 2009; data not shown) show no significant differences in mean fruit buoyancy or seed survival between *Sesbania* species and across treatments although the species in *S.* sect. *Daubentonia* (*S. macroptera* and *S. virgata*) exhibited longer periods of fruit buoyancy. Cross-sections of the fruits of *Sesbania* species reveal the structural differences that likely promote buoyancy in *S.* sect. *Daubentonia* (Fig. 1I–K). Such features include a thickened mesocarp in *S. virgata* and *S. punicea*, and air pockets created by the convoluted wings of *S. macroptera* (Fig. 1K). The lack of these structures in *S. herbacea* (Fig. 1L), as well as most of *S.* sect. *Sesbania* taxa may relate to their potentially more limited fruit buoyancy.

Survival and dispersal in fresh water is also potentially enhanced by a newly observed feature of *Sesbania* species from both the New World and Pantropical clades (Farruggia 2009; data not shown). *Sesbania* seeds in the fresh water buoyancy treatments ultimately imbibed water while those in the salt-water treatment remained dormant. In the fresh water treatments, seedlings developed while submerged but soon became buoyant and ultimately produced second, third, and fourth sets of true leaves while floating. These seedlings remained buoyant until the termination of those experiments.

That the pantropical distribution of *Sesbania* may have been facilitated by certain distinctive morphological features involving the entire plant prompted our initial investigation of hydrochory. Additional studies could focus on the abilities of *Sesbania* species to either readily uproot or dislodge such that the above-ground plant laden with fruit is a potential dispersal unit, perhaps facilitated by chambered or spongy pith occupying significant portions of the stem. In essence, *Sesbania* may be distinct in its ability to disperse in the form of seeds, fruits, seedlings, or entire plants. These life history traits can confer an advantage in environments with seasonal waterlogging or flooding, thus contributing to the pantropical distribution of the genus, its subclades, and some of its constituent species.

Taxonomic Treatment

Sesbania Adanson, Fam. pl. 2: 327. 1763, nomen conserv. (as *Sesban*, but corrected to *Sesbania* by Scopoli, Intr. hist. nat. 308. 1777; see Gillett 1963). Type: *Sesbania sesban* (L.) Merrill.

A sectional classification of the genus *Sesbania* is adapted from Lavin and Sousa S. (1995) and revised and updated using information produced since that study. We arrive at a classification of all species of *Sesbania* into just three sections (Fig. 5).

Sesbania sect. *Glottidium* (Desvaux) Lavin, Syst. Bot. Monogr. 45: 44. 1995. *Glottidium* Desvaux, J. Bot. Agric. 1: 119. 1813. Type: *Sesbania vesicaria* (Jacquin) Elliott.

Although strongly resolved as New World sister clades, sect. *Glottidium* is maintained as distinct from sect. *Daubentonia* (DC.) Bentham because of the large genetic (Fig. 5) and morphological differences that separate *Glottidium* from *Daubentonia*. The morphological differences include an annual growth habit and auricle along the upper margin of the keel petals, albeit inconspicuous, which are pleisomorphic traits shared by *Glottidium* and the Pantropical clade. Differences also pertain mostly to the inflated pod of *Glottidium*, which contains two seeds that are together enclosed inside an endodermal sac that has abscised from the other dermal layers of the fruit wall, compared to the typical 4-winged, several-seeded sect. *Daubentonia*. Whereas *Daubentonia* is mostly neotropical in distribution, *Glottidium* occurs in temperate southeastern U.S.A.

Sesbania sect. *Daubentonia* (DC.) Bentham in Bentham & Hooker, Gen. pl. 1: 502. 1865. *Daubentonia* DC., Mém. Légum. 285. 1823. *Sesbania* subg. *Daubentonia* (DC.) Baker in Oliver, Fl. trop. Afr. 2: 133. 1871. Type: *Sesbania punicea* (Cavanilles) Bentham.

Sesbania sect. *Daubentoniopsis* Lavin, Syst. Bot. Monog. 45: 43. 1995. *Daubentoniopsis* Rydberg, Amer. J. Bot. 10: 497. 1923. Type: *Sesbania longifolia* (Cavanilles) DC.

As now circumscribed, sect. *Daubentonia* comprises only New World species, although *Sesbania punicea* is an escaped ornamental in Africa and elsewhere (Lewis 1988). *Daubentonia* now includes sect. *Daubentoniopsis*, which has long, linear, but torulose pods that are quite different from the short, quadrate-bodied, often-winged pods of the traditionally circumscribed *Daubentonia*. Given the distribution of *Daubentoniopsis* is centered in Jalisco and Michoacan, Mexico (McVaugh 1987), geographic proximity predicts the degree of phylogenetic relatedness more than similarities in pod morphology, at least for species of *Sesbania*. McVaugh (1987; pp. 697–698) details the complicated nomenclature of the sole species of *Daubentoniopsis*, *Sesbania cavanillesii* S. Watson (= *S. longifolia* DC.).

Sesbania sect. *Sesbania*.

Agati Adanson, Fam. pl. 2: 326. 1763. *Sesbania* subg. *Agati* (Adanson) Baker in J. D. Hooker, Fl. Brit. Ind. 2: 115. 1876. Type: *Agati grandiflora* (L.) Desvaux [=*Sesbania grandiflora* (L.) Poiret].

Resupinaria Rafinesque, Sylva tell. 115. 1838. Type: *Resupinaria* (L.) Rafinesque [=*Sesbania grandiflora* (L.) Poiret].

Darwinia Rafinesque, Fl. ludov. 106. 1817, non *Darwinia* Rudge, 1815 [Myrtaceae]. *Monoplectra* Rafinesque, Fl. ludov. 106. 1817, pro. syn. Type: *Darwinia exaltata* Rafinesque [=*Sesbania herbacea* (Mill.) McVaugh].

Sesbania subgenus *Pterosesbania* Gillett, Kew Bull. 17: 149. 1963. Type: *Sesbania tetraptera* Hochst. ex Baker.

We recircumscribe the pantropical *S.* sect. *Sesbania* to include former *S.* subg. *Agati* and *S.* subg. *Pterosesbania*, which comprises two species mainly from southern Africa, *S. tetraptera* and *S. rogersii* Phill. & Hutch., the latter of which is now considered a subspecies of *S. tetraptera* (Lewis 1988). These two species (or subspecies) produce mature legumes that are very similar to those of *S.* sect. *Daubentonia* (DC.) Benth. in that they have legumes with four longitudinal wings along the legume body. This shared similarity in legume morphology prompted Lavin and Sousa S. (1995) to synonymize *S.* subg. *Pterosesbania* under *S.* sect. *Daubentonia*. Results of our phylogenetic analysis strongly suggest that the four-winged legume was independently evolved in the New World sect. *Daubentonia* and the African *S. tetraptera* (including *S. rogersii*). However, *S.* subg. *Pterosesbania* have generally long, many-seeded linear fruits, which are characteristic of the species of *S.* sect. *Sesbania*.

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Appendix 1. Accessions included in this study. Species, Voucher, Country, Herbarium Acronym, GenBank Numbers (nrDNA-ITS, plastid *trnK-matK*, nuclear TRPT).

Sesbania arborea (= ***S. tomentosa*** **Hook. & Arn**.), *W. Wagner et al. 4912*, USA (F) (JX453663, -, -); ***Sesbania bispinosa*** **(Jacq.) W.F.Wight**, *J. Grimes 3167*, Australia (MO) (JX453665, -, HQ730395); *R. Seydel 2126, Africa* (MO) (JX453664, -, -); *M. Peltier 5045*, Madagascar (MO) (JX453666, -, -); ***Sesbania brachycarpa*** **F.Muell.**, *G. Chippendale 5574*, Australia (K) (JX453667, JX453717, HQ730390); ***Sesbania brevipedunculata*** **J.B.Gillett**, *P. A. Smith 4246*, Botswana (MO) (JX453668, -, -); ***Sesbania campylocarpa*** **(Domin) N. T.Burb.**, *N. T. Burbridge 5353*, Australia (K) (JX453669, JX453718, KC254813); ***Sesbania cannabina*** **(Retz.) Pers.**, *Hu & But 22498D*, Hong Kong (MO) (JX453670, -, KC254801); ***Sesbania cavanillesii*** **S.Watson**, *T. Gonzalez Guizer 3*, Mexico (MU) (JX453671, JX453724, KC254795); ***Sesbania chippendalei*** **N.T.Burb.**, *Pedley 2021*, Australia (K) (-, JX453719, KC254814); ***Sesbania cinerascens*** **Welw. ex Baker**, *P. A. Smith 4127*, Botswana (K) (JX453672, HQ730423, HQ730389); ***Sesbania coerulescens*** **Harms**, *R. D. A. Bayliss 10185*, Zimbabwe (MO) (JX453673, -, -); ***Sesbania dalzielii*** **Phillips & Hutch.**, *J. M. Fay 5779*, Central African Republic (MO) (JX453674, -, -); ***Sesbania drummondii*** **(Rydb.) Cory**, *E. Lehto L23318*, USA (ASU) (JX453675, -, KC254798); *R. K. Godfrey 80742*, USA (MU) (-, AF543849, -); ***Sesbania dummeri*** **Phil. & Hutch.**, *Friis et al. 1746*, Ethiopia (K) (JX453676, JX453720, KC254818); ***Sesbania exasperata*** **Kunth**, *Coradin et al. 5865*, Brazil (K) (JX453677, -, KC254809); ***Sesbania formosa*** **(F. Muell.) N.T. Burb.**, *Lepschi 4729*, Australia (MU) (JX453678, -, HQ730391); ***Sesbania goetzei*** **Harms**, *D. A. Kamundi et al. 23*, Africa (MO) (-, -, KC254816); *R. Mithen 373*, Malawi (K) (JX453679, JX453721, -); ***Sesbania grandiflora*** **(L.) Persoon**, *D. H. Lorence 8823*, USA (MO) (JX453680, HQ730424, HQ730392); ***Sesbania greenwayi*** **J.B.Gillett**, *C. J. Kayombo et al. 4307*, Tanzania (MO) (JX453681, JX453722, KC254802); ***Sesbania herbacea*** **(Mill.) McVaugh**, *F. T. Farruggia 1115*, USA (ASU) (-, HQ730419, KC254800); *F. T. Farruggia 1138*, USA (ASU) (JX453682, -, -); ***Sesbania hirtistyla*** **J.B.Gillett**, *M. A. Mwangoka & G. M. Kufya 1344*, Tanzania (MO) (JX453683, JX453723, KC254803); ***Sesbania hobdyi*** **O.Deg. & I.Deg**., *E. Desha & The Degeners 24187*, USA (MO (JX453681, -, -); ***Sesbania keniensis*** **J.B.Gillett**, (JX453686, -, -); *J. M. Lock 83/100 Kenya* (K) (JX453685, -, KC254815); ***Sesbania leptocarpa*** **DC.**, *I. Friis et al. 9578*, Ethiopia (K) (JX453688, -, KC254804); *F. T. Farruggia 144*, (JX453687, -, -); ***Sesbania macowaniana*** **Schinz**, *W. Giess 8582*, South West Africa (MO) (JX453689, -, -); ***Sesbania macrantha*** **Welw. ex Phillips & Hutch.**, *D. Philcox & R. B. Drummond 9074*, Zimbabwe (MO) (JX453690, -, -); *L. Festo 1188*, Tanzania (MO) (JX453691, -, KC254806); *S. Bidgood et al. 3840*, Tanzania (K) (-, JQ669633, -); ***Sesbania macroptera*** **Micheli**, *F. Mereles 003898*, Paraguay (NY) (JX453692, -, KC254796); ***Sesbania madagascariensis*** **Du Puy & Labat**, *L. Sussman 175*, Madagascar (MO) (-, JX453725, KC254819); *Du Puy et al. M993*, Madagascar (K) (JX453693, -, -); ***Sesbania melanocaulis*** **Bidgood & Friis**, *Friis et al. 8207*, Ethiopia (K) (JX453694, JQ669634, KC254817); ***Sesbania microphylla*** **Phil. & Hutch**., *S. Bidgood & K. Vollesen 3173*, Tanzania (K) (JX453695, -, HQ730396); *Binghavr 10043*, Zambia (K) (-, JX453726, -); ***Sesbania oligosperma*** **Taub**., *R. C. Mendonca et al. 3692*, Brazil (NY) (JX453696, -, KC254810); ***Sesbania pachycarpa*** **DC.**, *H. Merxmuller & W. Giess 32468*, Southwest Africa (MO) (JX453697, -, KC254807); ***Sesbania punicea*** **(Cav.) Benth.**, *F. T. Farruggia 1133*, USA (K) (JX453698, -, HQ730387); *R. Kral 88361* (MU) (-, JQ669635, -); ***Sesbania quadrata*** **J.B.Gillett**, *P. Metele 154*, Tanzania (MO) (JX453699, HQ730425, HQ730398); ***Sesbania rostrata*** **Bremek. & Oberm**., *Bjornstad AB749*, Tanzania (K) (JX453700, JX453727, HQ730394); ***Sesbania sericea*** **(Willd.) Link,** *Wittahn 4809*, Guyana (NY) (JX453701, JX453728, KC254799); ***Sesbania sesban*** **(L.) Merrill**, *UC 1520206*, Iraq (cult.) (UC) (-, JQ669578, -); ***Sesbania sesban*** **(L.) Merrill subsp. *sesban* var. *bicolor* (Wight & Arnott) F. W.Andrews**, *Fr. M. Arnoldo 2292*, Dutch West Indies (NY) (JX453703, -, -); *D. H. Lorence 6778*, USA (MO) (JX453702, -, HQ730388); ***Sesbania sesban*** **(L.) Merrill ssp. *sesban* var. *nubica* Chiov.**, *I. Friis et al. 9302*, Ethiopia (K) (JX453704, -, KC254812); *Brummitt 11414*, Malawi, (K) (-, -, KC254811); ***Sesbania sesban*** **(L.) Merrill ssp. *sesban* var. *zambesiaca* J.B.Gillett**, *H. Kolberg et al. 632*, Namibia (K) (JX453705, -, -); ***Sesbania somalensis*** **J.B. Gillett**, *M. Thulin 10735*, Somalia (K) (JX453706, -, KC254808); ***Sesbania*** **sp.,** *S. Bidgood et al. 2711*, Tanzania (K) (JX453707, -, -); ***Sesbania sphaerosperma*** **Welw**., *D. S. Hardy 6517*, South Africa (MO) (JX453708, -, -); ***Sesbania subalata*** **J.B.Gillett**, *R. Abdallah & K. Vollesen 95/197*, Tanzania (K) (JX453709, -, -); ***Sesbania sudanica*** **J.B.Gillett**, *D. B. L. Gautier-Beguim 516*; Ivory Coast (MO) (JX453710, -, -); ***Sesbania tetraptera*** **Hochst. ex Baker**, *Salubeni & Tamakali 5768*, Malawi (MO) (-, -, HQ730397); *Richards 19230* (K) (JX453711, HQ730421, -); ***Sesbania transvaalensis*** **J.B.Gillett**, *I. Friis et al. 6871*, Ethiopia (K) (-, -, KC254805); *A. Nicolas & B. Bishop 2180*; South Africa (MO) (JX453714, -, -); ***Sesbania vesicaria*** **(Jacq.) Elliott**, *F. T. Farruggia 1109*, USA (ASU) (JX453715, -, EU258899); *F. T. Farruggia 1113*, USA (ASU) (-, HQ730417, -); ***Sesbania virgata*** **(Cav.) Poir.**, *H. J. A. Hurre 5005*, Argentina (MU) (JX453716, JQ669632, -); *C. H. Ramos 854*, Mexico (MU) (-, -, KC254797).