Title

Phylogenetic systematics of Vigna sensu stricto in the context of Physostigma and allies

Journal

American Journal of Botany, 111(9)

ISSN

0002-9122

Authors

Horton, Dasha M
Feleke, Yonas
Pasquet, Remy S
et al.

Publication Date

2024-09-01

DOI

10.1002/ajb2.16381

Peer reviewed

American Journal of Botany

Phylogenetic systematics of Vigna sensu stricto in the context of Physostigma and allies (Leguminosae).

--Manuscript Draft--

Manuscript Number:	
Full Title:	Phylogenetic systematics of Vigna sensu stricto in the context of Physostigma and allies (Leguminosae).
Short Title:	Phylogeny of Vigna s.s.
Article Type:	Research Article
Section/Category:	Systematics & Phytogeography
Corresponding Author:	Ashley N. Egan Utah Valley University Aarhus, DENMARK
Corresponding Author E-Mail:	ashegan2@gmail.com
First Author:	Ashley N. Egan, PhD
Abstract:	• Premise of study: Vigna includes economic crop and wild species that sustain much of the world. The evolutionary relationships estimated between the diverse Vigna species across both the Old and New Worlds have resulted in many taxonomic revisions, with much of the New World species segregated to other genera. Limited sampling with the Old World (OW) Vigna has left questions regarding their inter- and intraspecific relationships. • Methods: African species, including the putative sister genus Physostigma, were comprehensively sampled within the context of New World (NW) relatives and genera within Phaseolinae. Maximum likelihood and Bayesian phylogenetic analyses using the chloroplast matK-trnK region and the nuclear ribosomal ITS/5.8S (ITS) DNA region were undertaken to resolve long-standing OW Vigna taxonomic questions. Divergence dates were estimated using BEAST to date key nodes in the phylogeny. • Key results: The matK and ITS data analyses concurred in resolving five well-supported clades of Vigna s.s.: subg. Lasiospron, a reduced subg. Vigna, subg. Haydonia, subg. Ceratotropis, an enlarged subg. Plectrotropis, and a clade including V. kirkii and V. stenophylla that could be considered as new subgenus or section. • Conclusions: Former subg. Vigna is reduced to yellow and blue flowered species and subg. Plectrotropis is enlarged to mostly all white-pink-purple flowered species. Vigna s.s. in the Americas now includes subg. Lasiospron and a few pantropical species. The age of the split between American and its Old World sister clade is approximately 6 – 7 million yr ago.
Keywords:	bayesian inference; biogeography; Fabaceae; Leguminosae; phylogenetic systematics; Physostigma; taxonomy; Vigna
Suggested Reviewers:	Suman Lakhanpaul Delhi University
	Matt Lavin Montana State University mlavin@montana.edu
	SK Malik National Bureau of Plant Genetic Resources, India
	Annah Moteetee University of Johannesburg
	Cristiane Snak Universidade do Estado de Santa Catarina

Opposed Reviewers:	
Funding Information:	
Order of Authors (with Contributor Roles):	Ashley N. Egan, PhD (Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing – original draft; Writing – review & editing)
	Dasha M Horton (Data curation; Formal analysis; Methodology; Writing – original draft; Writing – review & editing)
	Yonas Feleke (Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Writing – original draft)
	Remy S. Pasquet (Conceptualization; Data curation; Funding acquisition; Investigation; Project administration; Resources; Writing – original draft; Writing – review & editing)
	Firouzeh Javadi (Investigation; Resources; Supervision; Visualization; Writing – original draft; Writing – review & editing)
	Kaycie A. Melville (Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Validation; Writing – review & editing)
	Alfonso Delgado-Salinas (Investigation; Resources; Validation; Writing – review & editing)
	Mats Thulin (Investigation; Resources; Writing – review & editing)
	Richard Mithen (Resources; Writing – review & editing)
	Paul Gepts (Conceptualization; Funding acquisition; Investigation; Supervision; Validation; Writing – review & editing)

Dr. Pamela Diggle 1 Dec 2023
Editor, American Journal of Botany

Dear Dr. Diggle,

I am writing in submission of a manuscript entitled "Phylogenetic systematics of *Vigna* sensu stricto in the context of *Physostigma* and allies (Leguminosae)" to *American Journal of Botany*. The economically important plant genus *Vigna* – from which several crop species including mung bean, bombara ground nut, and other vital protein pulse crops arise, has historically included species in both the new and old worlds, including Asia and Africa. In 2011, *Delgado-Salinas* et al published an important work regarding *Vigna* taxonomy that focused on exploring the taxonomic relationships among *Vigna* species of the New World, resulting in a number of segregate genera being named to improve taxonomy and reflect phylogenetic history. However, this work was limited in taxonomic sampling from the Old World. This work addresses some of the last remaining questions regarding overall taxonomy of the genus *Vigna* by building on the work of *Delgado-Salinas* et al through comprehensive Old World and Asian sampling within *Vigna*. Further, this work tests an unusual association discovered previously between the African genus *Physostigma* and *Vigna* s.s.

Here, we utilized both chloroplast and nuclear DNA markers to reconstruct evolutionary history via bifurcating phylogenetic trees and network analyses to test the relationship among *Physostigma* and *Vigna* s.s., investigate infrageneric relationships and improve infrageneric taxonomy within the group, with an emphasis on Old World taxa. We also estimate the genome sizes of two species, *V. kirkii* and *V. stenophylla*, two species with unusual but not unprecedented placements within the phylogeny and present a summary of genome sizes with *Vigna* s.s. as a means of exploring their placement.

Ultimately, we revise infrageneric relationships at subgeneric and sectional rankings and discuss further needs to definitively elucidate the unique relationships within *Vigna*. We present a key to *Physostigma* and *Vigna* and present a full taxonomic overview of *Vigna* s.s. This work adds to body of work to elucidate the evolutionary history of this important economic genus, placing cultivated species within the context of wild species. We comment on the importance of floral morphology and evolution to taxonomy. This collection of knowledge will be useful to field workers, plant breeders, and other scientists who work with *Vigna* species.

We feel that *AJB* is the perfect place for publication of this work, as this represents a sort of followup to that of Delgado-Salinas et al 2011. I thank you for consideration of this manuscript for publication in *American Journal of Botany*.

Sincerely,
Dr. Ashley N. Egan

Utah Valley University
Dept of Biology
800 W University Pkwy
Orem, UT 84058
aegan@uvu.edu

American Journal of Botany Author Agreement Form

Corresponding Author's Name: Ashley N Egan

Date: 1/2/24

Respond to all the statements below by either typing your initials or checking the appropriate box. After you have completed this form, save it as a PDF and upload it with your manuscript submission in Editorial Manager (https://www.editorialmanager.com/ajb/).

1. All Authors know of and concur with the submission of this manuscript to *AJB*. [Single authors, please also initial.]
   Initials: ANE

2. All Authors of this research paper have directly contributed [https://casrai.org/credit/]
   AND
   All authors of this paper have read and approved the final version submitted.
   Initials: ANE

3. The contents of this manuscript have not been copyrighted or published previously and are not now under consideration for publication elsewhere. The contents of this manuscript will not be copyrighted, submitted, or published elsewhere while acceptance by *AJB* is under consideration.
   Initials: ANE

4. Authors are responsible for recognizing and disclosing any duality of interest that could be perceived to bias their work, acknowledging all financial support and any other personal connections.

   ☑ No, there is no duality of interest that I should disclose, having read the above statement.

   ☐ Yes, having read the above statement, there is potential duality of interest. This has been fully detailed in my cover letter.

5. Have the results/data/figures in this manuscript been published, or are they under consideration for publication elsewhere?

   ☑ No, the results/data/figures in this manuscript have not been published elsewhere, nor are they under consideration (from any of the Authors) by another publisher.

☐ Yes, some portion of the results/data/figures in this manuscript has been published or is under consideration for publication elsewhere.

If Yes is selected, please identify results/data/figures taken from other published/pending manuscripts in the textbox below and explain why this does not constitute dual publication. [Note: The existence of pending or previously published articles that use or have used any of the same results presented in the submitted manuscript does not generally prejudice review and acceptance.]

6. To take advantage of the free page charges policy, at least one author must be a member of the Botanical Society of America when the manuscript is submitted for review and also during the year of publication (except for Special Invited Papers). Authors who are not members of the BSA may also submit manuscripts for consideration. A fee of US$1,000 per article, regardless of length, will be charged to the corresponding author.

   [To become a member of the BSA, please go to https://crm.botany.org/. NOTE: If you are contributing to a Special Issue by invitation, the BSA membership requirement is waived.]

   ☐ No, no authors of this manuscript are members of the BSA.

   ☑ Yes, I confirm that at least one author is a BSA member.

7. *AJB* authors have the option to make their accepted paper Open Access. The Article Processing Charges are available here: https://cms.botany.org/home/membership/member-benefits.html

   ☑ No, I do not choose Open Access.

   ☐ Yes, I choose Open Access and have funds available for the Article Processing Charges.

Contact the Editorial Office at ajb@botany.org for more information.

[Last revised 27 October 2020.]

Phylogenetic systematics of *Vigna* sensu stricto in the context of *Physostigma* and allies (Leguminosae).

Dasha M. Horton[1*], Yonas Feleke[2*], Remy S. Pasquet[3], Firouzeh Javadi[4,5], Kaycie A. Melville[1], Alfonso Delgado-Salinas[6], Mats Thulin[7], Richard Mithen[8], Paul Gepts[2], Ashley N. Egan[1~]

1 Department of Biology, Utah Valley University, Orem, Utah, 84058, USA
2 Department of Plant Sciences, Section of Crop and Ecosystem Sciences, University of California, Davis, California, USA
3 DIADE, IRD, Univ Montpellier, Montpellier, France
4 Institute of Decision Science for a Sustainable Society, Kyushu University, Fukuoka, Japan
5 Kyushu University Museum, Kyushu University, Fukuoka, Japan
6 Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado postal 70-233, 04510, CDMX, México
7 Department of Systematic Biology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-75236, Uppsala, Sweden.
8 Liggins Institute, University of Auckland, New Zealand

[*] equal authorship.   ~ corresponding author
Corresponding e-mail address: aegan@uvu.edu; orcid ID 0000-0001-7803-4444

Manuscript received _______; revision accepted _______.

Vigna s.s. systematics

ABSTRACT

• *Premise of study*: *Vigna* includes economic crop and wild species that sustain much of the world. The evolutionary relationships estimated between the diverse *Vigna* species across both the Old and New Worlds have resulted in many taxonomic revisions, with much of the New World species segregated to other genera. Limited sampling with the Old World (OW) *Vigna* has left questions regarding their inter- and intraspecific relationships.

• *Methods:* African species, including the putative sister genus *Physostigma*, were comprehensively sampled within the context of New World (NW) relatives and genera within Phaseolinae. Maximum likelihood and Bayesian phylogenetic analyses using the chloroplast *matK-trnK* region and the nuclear ribosomal ITS/5.8S (ITS) DNA region were undertaken to resolve long-standing OW *Vigna* taxonomic questions. Divergence dates were estimated using BEAST to date key nodes in the phylogeny.

• *Key results:* The *matK* and ITS data analyses concurred in resolving five well-supported clades of *Vigna* s.s.: subg. *Lasiospron*, a reduced subg. *Vigna*, subg. *Haydonia*, subg. *Ceratotropis*, an enlarged subg. *Plectrotropis*, and a clade including *V. kirkii* and *V. stenophylla* that could be considered as new subgenus or section.

• *Conclusions*: Former subg. *Vigna* is reduced to yellow and blue flowered species and subg. *Plectrotropis* is enlarged to mostly all white-pink-purple flowered species. *Vigna* s.s. in the Americas now includes subg. *Lasiospron* and a few pantropical species. The age of the split between American and its Old World sister clade is approximately 6 – 7 million yr ago.

Key words: bayesian inference; biogeography; Fabaceae; Leguminosae; phylogenetic systematics; *Physostigma*; taxonomy; *Vigna*.

INTRODUCTION

The genus *Vigna* Savi (Fabaceae, tribe Phaseoleae, subtribe Phaseolinae) includes several important tropical food crops, such as cowpea, *Vigna unguiculata*, and mung bean, *Vigna radiata*, as well as a number of other more geographically restricted crop species, including Bambara groundnut, *Vigna subterranea*, moth bean, *Vigna aconitifolia,* black gram, *Vigna mungo*, adzuki beans, *Vigna angularis*, and the ricebean, *Vigna umbellata*, among others. Historically, numerous species were initially described within *Dolichos* L. or *Phaseolus* L. in the first edition of Species Plantarum (Linnaeus, 1753). *Vigna* was created by Savi in 1824, after which the boundaries between the three genera changed frequently (Fig. 1). Consequently, the characterization of *Vigna* was also a matter of almost continuous change.

Initially, *Vigna* was separated from *Dolichos* by two inaccurate characters (standard callosities convergent versus divergent, pod curved versus terete). A few years later, Bentham (1837) gave an improved *Vigna* diagnosis (keel not spiralized, stigma lateral, and pod terete) leading to a clear separation of *Vigna* from *Dolichos* (stigma lateral versus terminal) and *Phaseolus* (keel not spiralized versus spiralized). Bentham's concept of *Phaseolus* included Asian species of present subg. *Ceratotropis* (Piper) Verdc. (included in Bentham's sect. *Strophostyles* Benth.), and sect. *Lasiospron* Benth., while *Vigna* was almost reduced to African and pantropical species. Surprisingly, Bentham (1859) included *V. vexillata* in *Vigna* even though its flower shape is very close to that of species from his *Phaseolus* subg. *Ceratotropis* (Fig. 2). Similarly, Harms (1915) kept *Ceratotropis* species within *Phaseolus* while he placed *V. vexillata* in *Vigna*. He was followed by Baker (1929) who added *P. kirkii* Baker to *Phaseolus*.

This *Phaseolus*-*Vigna* boundary was accepted for nearly a century, until Wilczek (1954a) challenged it while characterizing *Vigna* by three new characters (stipules extended below the point of insertion, keel erect-incurved, rarely making almost one complete spiral turn, and style ending beyond the stigma in a more or less distinct beak). This concept grouped Old World *Vigna* species and led to the transfer of *Phaseolus* subg. *Ceratotropis* to *Vigna* (Verdcourt, 1970) (Fig. 1). However, while restricting *Phaseolus* to the American species with hooked hairs, tightly coiled style and exine devoid of wide reticulation, Verdcourt (1970) and Maréchal et al. (1978) moved *Phaseolus* sects. *Lasiospron*, *Sigmoidotropis* Piper, *Condylostyles* Piper, and *Leptospron* Benth., also to *Vigna*, leading to the largest genus *Vigna* ever circumscribed (the 'rag bag' *Vigna* genus as Verdcourt qualified it), with 7 subgenera, 19 sections, and 87 species (Maréchal et al., 1978) (Fig. 1). In order to fit all these groups, Maréchal et al. (1978) provided a complex *Vigna* diagnosis: no hooked hairs, non-persistent floral bracts, 1-2-flowered thickened and glandulous rachis nodes, pedicel shorter or equal to calyx tube, all petals ± as long, non-persistent style, pod linear and non-septate, and a blend of the following characters: appendaged stipule, contracted inflorescence rachis, style with a beak beyond the stigma, triporate pollen, coarsely reticulated exine. Recent molecular systematic work resulted in the raising of most former *Phaseolus* sections to generic rank and *Vigna* was reduced to Maréchal et al.'s subgenera *Vigna*, *Haydonia* (R.Wilczek) Verdc., *Plectrotropis* (Schumach.) Baker, *Ceratotropis* and *Lasiospron* (Benth. ex Piper) Maréchal, Mascherpa & Stainier (Thulin et al., 2004; Delgado-Salinas et al., 2011) (Fig. 1). Inasmuch as the delimitation of this monophyletic *Vigna* sensu stricto was improved, its internal organization is still far from clear.

Although De Candolle's (1825) Prodrome can be considered as a first attempt, Harms (1915) is the one who provided the first serious *Vigna* infrageneric classification. While Harms maintained subg. *Ceratotropis* species within *Phaseolus*, his four *Vigna* sections were not so far from Verdcourt's (1970) classification. *Vigna* sect. *Microdontae* Harms included Verdcourt's subg. *Vigna* and *Haydonia*. Sect. *Appendiculatae* Harms, with both *V. unguiculata* and *V. schlechteri*, equated to Verdcourt's sect. *Catiang* (DC.) Verdc. Sect.

Macrodontae Harms included Verdcourt's sects. *Macrodontae*, *Liebrechtsia* (De Wild.) Baker f., and *Reticulatae* Verdc., which effectively pooled all African taxa with purple flower color and a chromosome number of 2n=20. Sect. *Vexillatae* Harms equated to Verdcourt's subg. *Plectrotropis*. Baker (1929) added to this classification a sect. *Liebrechtsia* Baker f. for pyrophytic plants and a sect. *Procerae* Baker f. for *V. procera* alone.

In the context of Delgado-Salinas' et al. (2011) new delimitation of genus *Vigna s.s*, comprising mostly Old World and Asian *Vigna* species, Verdcourt’s (1970) classification is reduced to four subgenera and 13 sections, while Maréchal et al. (1978) would comprise five subgenera, raising *Lasiospron* to subgenus status. However, recent molecular systematic studies (i.e. Delgado-Salinas et al., 2011) focused on New World taxon sampling, leaving sparse sampling to infer infraspecific groups within *Vigna* s.s. Here, we expand Old World sampling within *Vigna* s.s. in the context of previous works and sampling efforts to provide a more comprehensive view of the evolutionary and taxonomic relationships within *Vigna* s.l. and s.s. Our intent is to expand taxonomic sampling of Old World *Vigna* to taxonomically formalize the clades of *Vigna* species, provide a more natural infrageneric classification scheme, and improve the diagnosis of genus *Vigna*.

MATERIALS AND METHODS

***Taxon sampling* —** In our study, *Vigna* is examined with expanded sampling of the Old World (OW), in addition to available sequences in GenBank. Ingroup sampling included New World (NW) and OW *Vigna* as described by Verdcourt (1970) and Maréchal et al. (1978). Herein, names and determination criteria are reflective of definitions and findings in contemporary works such as Tomooka et al. (2002a), Pasquet (2001), Van der Maesen and Pasquet (2006), and Delgado-Salinas et al. (2011, 2022). This was done so that the species names were up-to-date with the accepted scientific names (World Flora Online). In total, our study utilizes 229 samples from vouchers and living specimens and includes 67 species of *Vigna* s.s. with 61 of these being OW *Vigna*. Multiple samples of these species and their varieties resulted in 128 individual *Vigna* s.s. samples included, representing subgenera *Ceratotropis, Haydonia, Vigna, Plectrotropis,* and *Lasiospron* (Supplementary file 1). Newly sequenced accessions (Supplementary File 1) were added to those from previous studies available on GenBank (National Center for Biotechnology), including from Thulin et al. (2004) and Delgado-Salinas et al. (2011), resulting in a total of 146 taxa for ITS and 200 for *matK* sampled broadly for *Vigna* and 35 other genera from Phaseoloid legumes (see Supplementary Table 1 for a breakdown of sampling across taxonomic groups). All sections once proposed are included in this study except *Procerae* and *Pseudoliebrechtsia*. The combined dataset was shrunk down to maximize accessions that were paired from the same plant. The ultimate outgroups included *Butea monosperma* and *Platycyamus regnellii* along with thirteen other species within subtribe Phaseolinae (Supplementary File 1). For ITS analyses alone, the outgroup was *Dipogon lignosus. Physostigma* Balf. is an OW genus in the Phaseolinae subtribe and represents the sister group to *Vigna s.s*. (Delgado-Salinas et al. 2011).

Molecular sampling — The nuclear ribosomal 5.8S and flanking internal transcribed spacers (ITS) region were sequenced in addition to the chloroplast *trnK* intron and *matK* locus. The entire region containing both ITS1 & 2 and the 5.8S of the rDNA repeat unit was amplified with primers described in Delgado-Salinas et al. (1999) and for *matK* in Riley-Hulting et al. (2004) and Wojciechowski et al. (2004) (Table 1). Amplification of the *trnK/matK* region of the chloroplast genome was achieved using primers trnKIL and trnK2R (Hu et al., 2000). Each 50 µl reaction mixture contained 100 ng of genomic DNA with 1 µM of each primer, 0.25 unit of DNA polymerase, 1X Thermopol buffer (20 mM Tris-HCl, 10 mM $(NH_4)SO_4$, 10 mM KCl, 2 mM $MgSO_4$, 0.1% Triton X-100 pH 8.8 @ 25°C), 200 µM of each dNTPs and 0.5 µl BSA (100 ug/ml). Due to its high fidelity, VentR polymerase (NE Biolabs, MA, USA) was used in most reactions; however, when recalcitrant samples were encountered, *Taq* DNA polymerase (Promega Crop, WI, USA) was then used to increase the product yield. Following an initial denaturation step of 4 min at 94°C, the PCR mixture underwent 25 cycles of 30 s at 94°C (denaturation), 30 s at 55°C (annealing) and 2 min at 72°C (extension), followed by a final extension at 72°C for 10 min. The PCR reactions were performed in MJ Research™ PTC-220 (Bio-Rad Laboratories Inc., MA, USA) thermal cyclers. ITS PCR process replicated the same conditions as *trnK/matK* except the annealing temperature was kept at 50°C and time of extension was reduced to 1 min. The PCR amplification produced multiple bands in agarose gel electrophoresis for ITSF and ITSR in a few *V. unguiculata* accessions. Multiple of these bands were cloned into the pGEMT vector (Promega) and sequenced in both directions using SP6 and T7 sequencing primers. Two clones from each accession were sequenced, however only one of these sequences was used in the phylogenetic analysis because the preliminary analysis revealed identical topology between cloned sequences. Reverse and forward reads were assembled with Sequencer 4.1 (Gene Codes, Ann Arbor, Michigan). Cleaning of PCR products was done through QIAquick PCR purification Kit (Qiagen Inc., Almeda, CA, USA). Both *trnK/matK* and ITS loci were compiled from GenBank for samples incorporated from outside of this study, referenced in the Supplementary File 1. These loci were chosen because they present the most phylogenetically informative data enabling incorporation of and building upon previous work to expand taxonomic sampling and knowledge across molecular loci (Thulin et al., 2004; Lavin et al., 2005; Delgado-Salinas et al., 2011).

Phylogenetic & Network Analyses **—** Phylogenies were reconstructed for the ITS and *matK* regions independently and as a combined dataset. MUSCLE (Edgar, 2004) was employed within AliView (Larsson, 2014) to align each gene region separately using default parameters. The combined data set was cut down such that major lineages were still represented but multiple accessions with non-overlapping gene sets were culled to include mostly matching sequences from the same sample while still maintaining taxonomic breadth of sampling.

Models of evolution for maximum likelihood were determined using the automodel selection tool in PAUP* v4.0a (Swofford, 2003). These models were determined as TVM+I+G (*matK*) and GTR+G+I (ITS). The model for the combined data set was selected as GTR+I+G based on a third model selection test in PAUP, treating the combined sequences as total evidence. The output tree was used as a starting tree in the CIPRES portal (Miller et al., 2010 where a RAxML-NG (Kozlov et al., 2019) analysis was initiated. This was done for *matK*, ITS, and a combined *matK* and ITS (total evidence) data set (Supplementary Table 1). Rapid bootstrapping was accessed using the auto convergence criteria called as –autoMRE. RAxML parameters for both data sets and the combined dataset were set at default, although inputs such as the number of patterns and evolutionary model were updated independently for each dataset. Pattern numbers were 2012, 606, and 2618 for *matK*, ITS, and combined datasets respectively.

Using the ITS and *matK* alignments independently, BEAUTi was used within the BEAST2 (Bouckaert et al., 2014) package to format the input xml file. BEAST2 implemented Bayesian Markov chain Monte Carlo (MCMC) algorithms to infer a phylogeny. Node ages were calibrated using secondary dates estimated based on numerous fossils shown in Table 2 by Lavin et al. (2005). BEAST analyses were run using unlinked parameters, calibrated yule birth model, relaxed log normal clock, and for 30 million generations. Results were analyzed to ensure adequate mixing and convergence in Tracer v1.4.1 (Rambaut and Drummond, 2007) after 20% burin-in was removed.

Phylogenetic networks were produced within SplitsTree v.4 (Huson and Bryant, 2006) under default parameters for the ITS and *matK/trnK* alignments separately. The alignments used for the network analyses were trimmed of all outgroups except *Physostigma*.

Genome size estimation — Seeds from *V. kirkii* and *V. stenophylla* were germinated in sterile water and petri dishes, then planted in a soil mixture of 80/20 peat moss and perlite. Seedlings were initially grown in a growth chamber with a 10/14 day/night schedule. After seedlings outgrew the chamber, two plants per species were transplanted to larger pots in a greenhouse where they were allowed to climb twine held between the bench and the ceiling rafters. Genome sizes were estimated using a Beckman Coulter CytoFLEX Flow Cytometer (Beckman Coulter, Hialeah, Fl, USA) following the Galbraith protocol (Loureiro et al. 2023). Briefly, 50-100 mg of young, fresh leaf tissue was harvested from each species (two from each plant). Each sample was co-chopped with 40-60 mg of fresh iceberg lettuce (used as a known genome size standard size of 2.56 Mb) on ice into a fine purée in 1 mL of Galbraith buffer. Chopped samples were filter-sterilized using a 30 um filter to remove particulates. 80 uL of 1 mg/mL of Propidium Iodide and RNase A was added to the eluted, filtered sample and left to stain on ice, in the dark, for approximately 20 minutes each. The 2C-value was calculated using the formula: ((mean of sample peaks)/(mean of standard peaks)) × 2 CDNA amount (pg) of the standard. Each plant was assessed for genome size estimation twice, each by two of the authors, for a maximum of eight replicates of genome size estimation per species. *Vigna unguiculata* was also grown and assessed as a control with its known genome size estimated to be between 588 (Parida et al. 1990) and 641 mb (Lonardi et al 2019) by flow cytometry.

RESULTS

Phylogenetic analyses using both maximum likelihood (ML) and Bayesian inference (BI) resolved *Vigna* s.s. as a maximally supported monophyletic clade across all datasets (ITS, *matK*, and combined analyses). Results from phylogenetic analyses are summarized in Table 3. *Physostigma* was resolved as sister to *Vigna* s.s. with maximum support in all analyses, with an estimated divergence time of ~7.5 - 7.8 mya (Figs. 3 & 4). *Vigna* s.s. is estimated to have begun diversifying ~6.3 - 6.73 mya (Table 4).

Some of the previously delineated subgenera were resolved as monophyletic groups in both ML and BI analyses, providing support for their taxonomic recognition. Subg. *Ceratotropis* is resolved as monophyletic with maximum support in all analyses and is estimated to have begun radiating as a lineage at least ~2.89 - 3.57 mya (Table 4; Figs. 3 & 4). Subg. *Lasiospron* is likewise resolved as monophyletic and estimated to have begun diversifying as a lineage at least 2.4 mya (Table 4). Subg. *Haydonia* is determined to be monophyletic with maximum support in BI and high support (bp = 96 - 98) in ML analyses (Fig. 4, Supp. Figs 1 & 2), representing a lineage at least 3.19 - 4.68 my old (Table 4; Figs 3& 4) that diverged from its sister lineages (variously defined) between 4.75 - 5.71 mya (Figs 3 & 4). Subg. *Plectrotropis* is determined as paraphyletic in both ML and BI analyses, with sect. *Plectrotropis* resolved as a monophyletic group and estimated to have diverged from subg. *Vigna* sect. *Reticulatae* ca. 2.76 mya (ITS; Fig. 4) or from subg. *Vigna* sect. *Catiang* ca. 3 mya (*matK*; Fig. 3). A clade comprised of *V. kirkii* and *V. stenophylla* is maximally supported in all analyses and is estimated to have diverged from subg. *Vigna* sect. *Macrodontae* ca. 4 mya (*matK*; Fig. 3) or as far back as ca. 5.63 mya (ITS; Fig. 4) as a lineage sister to a large clade comprising *Haydonia*, *Plectrotropis* sect. *Plectrotropis*, and *Vigna* sects. *Catiang, Macrodontae,* and *Reticulatae*. Subg. *Vigna* sensu Verdc. is polyphyletic, with four strongly supported monophyletic clades evident across the various phylogenies, comprising sects. *Catiang*, *Macrodontae, Reticulatae,* and *Vigna*. *Vigna* sect. *Comosae* is nested within *Vigna* sect. *Vigna* in all analyses with strong support. Relationships among the subgenera and these four major *Vigna* sectional clades differ between analyses, largely due to shallow and poorly supported resolutions along the backbone. However, both ML and BI ITS analyses (Supp. Figs 1 & 2), as well as the combined ML phylogeny (Fig. 5), resolved a clade comprising sects. *Plectrotropis, Catiang, Macrodontae,* and *Reticulatae* with high support (PP=0.97, BP=89, 99). Resolutions differing from this in other analyses all involved poorly supported backbone resolutions, providing support for this grouping based on phylogenetic robustness.

Varying hypotheses are supported regarding the first diverging lineage or clade within *Vigna* s.s. due to lack of strongly supported resolution along the backbone: ITS analyses resolve subg. *Ceratotropis* as the earliest branching lineage within *Vigna* s.s. (Fig. 4; Supp. Fig. 2 & 3) diverging ca 6.73 mya, with subg. *Lasiospron* as the second diverging lineage breaking off ca. 6.41 mya. In contrast, *matK* BI suggests subg. *Lasiospron* as the earliest branching lineage diverging ca. 6.3 mya (Fig. 3), whereas *matK* ML analyses suggests a clade comprising subg. *Vigna* sects. *Vigna* plus *Comosae* as basally branching (Supp. Fig. 1); both of these hypotheses are visualized in the *matK* network (Supp. Fig. 3). The combined ML analyses suggest a poorly supported grouping of *Lasiospron* + *Vigna* sects. *Vigna* and *Comosae* as the earliest branching clade (Fig. 5), a result that is seemingly less supported by network analyses (Supp. Fig. 3). With all that said, support for the determination of the earliest branching lineage within *Vigna* s.s. is lacking to nonexistent, suggesting a complicated evolutionary history during the early evolution among lineages within *Vigna* s.s., a conclusion supported by network analyses (Supp. Fig. 3).

As a follow up on the unexpected finding of clade *kirkii/stenophylla*, with varying placement in nuclear vs. chloroplast datasets, genome size estimates were conducted to further investigate evidence of hybridization or polyploidy. The genome size of *Vigna unguiculata* was estimated as 659 mb over a total of 5 replicates (Supp. Table 2), slightly larger than previous estimates. Genome size estimates of 601 mb for *V. kirkii* and 810 mb for *V. stenophylla*, with eight and six replicates respectively, were found (Supp. Table 2). Efforts to gather estimates of genome size for other *Vigna* species from the literature for context and comparative purposes yielded 28 estimates within 20 *Vigna* taxa, ranging from 370 mb (*V. aconitifolia*; Suranjika et al 2023) to 1372 mb (*V. luteola*; Parida et al. 1990) with a mean of 625.64 mb and median of 565 mb (Supp. Table 3).

DISCUSSION

This study reassesses evolutionary relationships and taxonomy of the genus *Vigna* in a wholistic manner through comprehensive phylogenetic sampling of Old World taxa newly added within the context of New World sampling using *matK* and ITS data in maximum likelihood and Bayesian analyses. We present taxonomic revisions and expanded knowledge within a comprehensive discussion of previous taxonomic and molecular systematic works. We also discuss the placement of *Vigna* within the context of related legume genera.

Delimitation of *Physostigma* and *Vigna* —The african genus *Physostigma* includes 4-5 species circumscribed into two subgenera (Gillett, 1966), with our sampling inclusive of *P. mesoponticum* (subg. *Taubertiophyton* Gillett) and *P. venenosum* (subg. *Physostigma*). *Physostigma* is determined as the sister group to a monophyletic *Vigna* s.s., an association noted previously (Thulin et al., 2004; Delgado-Salinas et al., 2011), but, then, through the inclusion of only *P. venenosum*. Delgado-Salinas et al. (2011) noted the sister relationship between *Physostigma* and *Vigna* s.s. as “unexpected” and recognized that further insight into this relationship required comprehensive phylogenetic sampling of Old World *Vigna*. Our extensive sampling of OW *Vigna* yielded the same placement, with *Vigna* s.s. diverged from a monophyletic *Physostigma* ca. 7.48 - 7.8 mya (Figs. 3 & 4).

The association of *Physostigma* is important to the circumscription of Old and New World *Vigna* clades (i.e. *Vigna* s.l. *vs. Vigna* s.s.) from both a phylogenetic and morphological standpoint. The phylogenetic placement of *Physostigma* separates all OW *Vigna* plus the NW subg. *Lasiospron* (*Vigna* s.s.*)* from all other NW Phaseolinae and NW *Vigna* s.l., now recognized as the segregate genera (i.e. NWSG) *Ancistrotropis* A. Delgado, *Cochliasanthus* Trew, *Condylostylis* Piper, *Leptospron* (Benth.) A. Delgado, *Sigmoidotropis* (Piper) A. Delgado, *Helicotropis* A. Delgado (Delgado-Salinas et al., 2011) and *Delgadoa* F.S.Santos, Snak, & L.P.Queiroz (Santos et al., 2023). Our molecular phylogenetic results strongly support a monophyletic *Physostigma* as sister to *Vigna* s.s.

Phylogenetically, and morphologically, *Physostigma* lies in an intermediate position between NWSG and *Vigna* s.s., with certain traits uniting *Physostigma* with NWSG taxa and others with *Vigna* s.s. *Physostigma* exhibits several typical *Vigna* s.s. traits, i.e. style with a beak beyond the stigma, and pollen triporate and coarsely reticulated, and several typical NWSG traits, i.e. stipule not appendanged, flower with a right-handed floral asymmetry (from a face-view perspective), and keel distinctly beaked and loosely coiled to 270-360°. Ultimately, it is the vegetative character of medifixed or peltate (unilobed or bilobed at the base) stipules that separates *Vigna* s.s., inclusive of most OW *Vigna* and the NW subg. *Lasiospron*, from *Physostigma* and the rest of NW Phaseolinae. Medifixed or peltate, appendaged stipules is thus an apomorphy of *Vigna* s.s., although they are lacking in some species of subg. *Haydonia*, in *V. comosa* and *V. haumaniana*.

It should be noted that the right-handed floral asymmetry makes *Physostigma* closer to subg. *Lasiospron* than to the rest of *Vigna s.s*., thus uniting morphology with some phylogenetic and network-based conclusions. For some important morphological characters separating *Vigna* s.s. from NWSG, *Physostigma* is split in the middle: *Physostigma* subg. *Taubertiophyton* is very distinct from *Vigna* s.s. (lax inflorescence rachis without extrafloral nectaries) whereas subg. *Physostigma* shows an inflorescence rachis with extrafloral nectaries (although zig-zag shaped and not linear) closer to those of most *Vigna s.s*. A zig-zag rachis is also encountered in *Cochliasanthus caracalla*, a NWSG species. In addition, subg. *Physostigma* pods are cylindrical (although with a size and ovule number unusual in *Vigna* s.s.) while subg. *Taubertiophyton* pods and seeds are flat (with a size and an ovule number of *Vigna* s.s.) like most NWSG species.

In the end, the keel shape of *Physostigma* has no equivalent within *Vigna* s.s. or NWSG: the spur is on the right side of the flower but the upper junction of the two sides of the keel is across this spur which indeed stands on the axis of the flower in a central position. Further, *Physostigma* produces a style beak beyond the stigma, very different from the *Vigna*-style beak (Figs 2 & 6). Baker (1929) described it as a "blunt stigma, covered by a hood which extends along the upper part of the convexity of the style". These two morphological traits are *Physostigma* apomorphies. The style of *Physostigma* is strikingly similar to that of *Vatovaea* pseudolablab (Gillett, 1966), and the reversed beak has apparently evolved in parallel in these two genera.

Vigna s.s. **infrageneric classification —** Prior to this work, Maréchal et al. (1978) organized *Vigna* s.s. into 5 subgenera: 1) Subg. *Vigna* has seven sections: *Vigna*, *Comosae, Macrodontae* Harms, *Reticulatae* Verdc., *Liebrechtsia* (de Wild.) Baker f., and *Catiang* (DC.) Verdc.; sect. *Condylostylus* Verdc. was not maintained in this subgenus and was lumped under sect. *Vigna*; 2) Subg. *Haydonia* with sects. *Haydonia*, *Microspermae* Maréchal, Mascherpa & Stainier and *Glossostylus* Verdc.; 3) Subg. *Plectrotropis* with sects. *Plectrotropis* and *Pseudoliebrechtsia* Verdc., the latter not represented in this study.; 4) Subg. *Ceratotropis* with sects. *Ceratotropis*, *Angulares* Tomooka & Maxted, and *Aconitifoliae* Tomooka & Maxted (Tomooka et al., 2002b); and 5) Subg. *Lasiospron,* which is not circumscribed into sections. Our phylogenetic results strongly support the resolution of five or six main clades, largely equivalent to Maréchal et al. 1978's subgenera *Lasiospron, Ceratotropis*, *Haydonia, Plectrotropis,* and *Vigna*, with a sixth grouping *V. kirkii* and *V. stenophylla* (Figs. 3 & 4, Supp. Figs 1 & 2). However, sectional rearrangements are required to maintain natural groupings. The lack of resolution and conflicting placement of groups between the nuclear ITS and chloroplast *matK* regions is most prominent between subgenera.

Relationships among the subgenera within *Vigna* s.s. differ between genomes and analyses. The definitive placement of subg. *Lasiospron* is elusive due to lowly supported or lack of resolution along the backbone of *Vigna* s.s. ITS analyses suggest *Vigna* subg. *Ceratotropis* as the first branching lineage within *Vigna* s.s. (Fig. 4 and Supp. Fig 2), whereas *matK* analyses suggesting subg. *Vigna* (ML; Supp. Fig. 1), subg. *Lasiospron* (BI; Fig. 3), similar to a recent ITS-based study (Delgado-Salinas et al., 2022), or a clade of subg. *Lasiospron* and subg. *Vigna* as sisters (ML combined; Fig. 5), but again, all with low support. The lack of resolution along the backbone may indicate rapid radiation or ancient hybridization among early branching lineages, or both. Indeed, the *matK* network shows a close association between *Physostigma* and subg. *Lasiospron* (Supp. Fig. 3). In the end, while, morphologically, subg. *Lasiospron* is clearly at the margin of *Vigna* s.s., both ITS and *matK* data do not clearly separate subg. *Lasiospron* from the rest of old world *Vigna*. That said, strongly support defining clades within *Vigna* s.s. exists.

Lasiospron — *Vigna* subg. *Lasiospron* is the only group recognized in *Vigna* s.s. found in the Americas. Subg. *Lasiospron* includes yellow flowered species and is unequivocably nested within *Vigna* s.s., however, its relationship to other subgenera is unresolved, with some analyses supporting *Lasiospron* as the 1st or 2nd most basally branching lineage within *Vigna* s.s. with varying support. The basally branching position of subg. *Lasiospron* provides some context within which to explore the evolution of floral morphology and its connection to historical classifications, as mentioned previously. NWSG exhibit a prominent keel beak like that found in subg. *Lasiospron*. Additionally, *V. lasiocarpa* has a long-recurved style beak while *V. jurana* has a terminal stigma, and the other species have sub-apical stigma or a short style beak (Delgado-Salinas et al., 2022). The twisting of the pod pedicels is not encountered in any OW *Vigna* nor NWSG species. Taken together, these morphological observations support the hypothetical position of subg. *Lasiospron* as basally branching in *Vigna s.s*, due to shared features with NWSG. However, the placement of *Lasiospron* within *Vigna* s.s. is supported by its having appendaged stipules, contracted inflorescence with extrafloral nectaries, triporate pollen with coarsely reticulated exine, and cylindrical pods, all of which are typical of *Vigna* s.s.

Haydonia — Wilczek (1954b) segregated those *Vigna* species from Africa having glands on the anthers into genus *Haydonia* R.Wilczek. Verdcourt (1970) later reclassified genus *Haydonia* as *Vigna* subg. *Haydonia* based on the fact the included species also had many characteristics of *Vigna*, but lacked pollen reticulated exine, having instead smooth to finely reticulated pollen exine. Then, Maréchal et al. (1978) pooled into subg. *Haydonia* all *Vigna* species with smooth pollen exine, adding to the subgenus *V. schimperi* and sect. *Glossostylus*. Our phylogenetic results confirm Maréchal et al.’s (1978) subg. *Haydonia* as nested within *Vigna* s.s. and represent a strongly monophyletic clade in all analyses.

Vigna subg. *Haydonia* is mostly presented as an evolved subgenus with the loss of the widely reticulate pollen exine, and, in some species, the loss of prolonged stipules below their insertion point (stipules basifixed), the loss of the prolongation of the style above the stigma, and the evolution of unique anther glands (Maréchal et al., 1978). All these characters are present in sect. *Haydonia*, partially present in sect. *Microspermae,* and limited to the loss of the reticulated exine in sect. *Glossostylus*. Our results would suggest that subg. *Haydonia* sits as a hinge subgenus within the context of others. Not considering subg. *Ceratotropis*, subg. *Haydonia* is between the yellow-blue flowered clades and the pink-white flowered clades and it includes yellow flowered species (especially *V. schimperi*) as well as pink-flowered species (sect. *Glossostylus*). In addition, it stands between the right-handed asymmetric flower species (subg. *Lasiospron*) and the left-handed asymmetric flower species (most of sect. *Plectrotropis* and subg. *Ceratotropis*), having a species (*V. juncea*) with a slight right-handed asymmetry (Fig. 6).

Within subg. *Haydonia*, sect. *Glossostylus* is confirmed and monophyletic in all analyses. In our sampling, sect. *Microspermae* is represented by two of its five species: *V. microsperma* and *V. schimperi*. Sect. *Haydonia* is resolved in all analyses as a monophyletic clade, but with our single accession of *V. microsperma*, the type species of sect. *Microspermae,* nested therein, a finding that would suggest sect. *Microspermae* be combined with sect. *Haydonia*. However, *V. schimperi*, represented by multiple accessions, is found as sister to either sect. *Haydonia* in ITS analyses (Fig. 4, Suppl. Fig. 2) or sect. *Glossostylus* in *matK* and combined analyses (Figs. 3, 5 and Suppl. Fig. 1). More sampling is thus required to truly test these sectional hypotheses, and revisions within the three sections require further research.

Ceratotropis — *Vigna* subg. *Ceratotropis* is found mainly from South Asia to Southeast Asia (Tomooka et al. 2002a) and characterized by yellow flowers, left-handed asymmetry (from a face-view perspective), medifixed stipule that is bilobed or mostly unilobed below point of insertion, pocket on the left keel petal, style extending beyond the stigma as a beak, and keel curled to the left between 160° and 360° (Maréchal et al., 1978; Tateishi 1985). Subg. *Ceratotropis* is resolved as a monophyletic sister to all other *Vigna* s.s. subgenera in ITS analyses (Fig. 4, Supp. Fig. 2), diverging about 6.73 Mya (Table 2), placing it as the earliest branching lineage of *Vigna* s.s., a placement observed previously (Goel et al., 2002; Takahashi et al., 2016). However, other analyses present a more complex picture regarding *Ceratotropis'* position, suggesting various clades as sister, including the *V. kirkii/stenophylla* clade (Fig. 5). *MatK*/*trnK* analyses (Fig. 3) resolves subg. *Ceratotropis* in an evolved position close to subg. *Plectrotropis,* as in Delgado-Salinas et al. (2011) or (Takahashi et al., 2016), an association that makes sense in light of morphology, considering the similar twisted keel shape found in both subg. *Ceratotropis* and sect. *Plectrotropis* (Fig. 1; Maréchal et al. 1978; Tateishi, 1985). The conflicting data sets indicate that the ITS and *mat*K genes have not evolved in the same way between the subgenera and may indicate potential ancient hybridization or chloroplast capture.

In subg. *Ceratotropis,* three groups were initially identified by Tateishi (1996) using seedling and morphological characteristics. These groups were later revised and ranked as three sections by Tomooka et al. (2002a,b), based on traits such as floral size, seedling germination type, pod pubescence, and growth habit: sect. *Angulares* (azuki bean group), sect. *Aconitifoliae* (intermediate group), and sect. *Ceratotropis* (mung bean group). The three sections are not highly resolved in our study, a finding also reported previously (Tun and Yamaguchi, 2007; Takahashi et al., 2016). The *matK* and combined analyses resolved two main clades (Supp. Fig. 1, Fig. 5), with crown node ages of 2.13 and 1.98 mya (Fig. 3), which almost fit the morphological sections: sect. *Angulares* on the one side, sect. *Ceratotropis* and *Aconitifoliae* on the other side. As in previous works, two *Angulares* species do not stand with the rest of the section: *Vigna reflexopilosa* (2n = 4x= 44; Swindell et al., 1973) and *V. trinervia* (2n=22). *Vigna trinervia* exhibits an intermediate morphology, characterized by the sect. *Angulares* germination types, a *Ceratotropis*-type dull seed coat, and brown, bristle-like hairs on mature pods (Tomooka et al., 2002a). The two species are linked in terms of their relationship, with *V. trinervia* being considered a possible donor of the chloroplast genome to the only tetraploid species within subg. *Ceratotropis* (Egawa et al., 1996 a, b; Konarev et al., 2002; Yano et al., 2004; Tun & Yamaguchi 2007).

The second major clade includes all species from sects. *Ceratotropis* and *Aconitifoliae*, as well as the aforementioned *V. reflexopilosa* clade. Recent research by Takahashi and Tomooka (2020) found that *V. stipulacea*, previously thought to be the only hypogeal germination species of sect. *Aconitifoliae*, also exhibits epigeal germination. This shared trait supports the phylogenetic placement of sect. *Aconitifoliae* within sect. *Ceratotropis.* Sect. *Aconitifoliae* is paraphyletic due to *V. stipulacea* and *V. trilobata* which group with members of sect. *Ceratotropis*. Javadi et al. (2011) demonstrated this relationship based on their evaluation of several cpDNA gene regions of subg. *Ceratotropis*, which revealed a correlation between clades and geographic regions, including tropical, subtropical, and temperate groups.

In summary, our current *matK* and combined phylogenetic trees do not support Tomooka’s classification (2002 a,b) nor the transferring of *V. subramaniana* to sect. *Aconitifoliae* (Takahashi et al. 2018). While our ITS analyses resolved two clades and a grade with a crown node age of 2.89 mya (Fig. 4) and resolved sect. *Angulares* (*V. umbellata*, *V. angularis*, and *V. reflexopilosa* var. *glabra*) as a monophyletic clade (Fig. 4, Suppl. Fig 2), this result is only partly reflective of previous phylogenies based on nuclear DNA (Doi et al., 2002, Goel et al., 2002, Saini and Jawali 2009; Takahashi et al., 2016). Thus, all phylogenetic analyses, past and present, find discord between nuclear and chloroplast-based markers within this group, indicative of intermediate lineage sorting (Maddison 1997), hybridization or chloroplast capture (Rieseberg and Soltis, 1991) or potentially the creation of ITS variants due to heteroduplex formation during PCR (Saini et al. 2008). Chloroplast captures were demonstrated in the recent evolution of *V. unguiculata* (Pasquet et al., 2021; Quenum et al., 2023). Taxonomic revision is likely needed, but more sampling from each section and species is recommended to enable determination of the diagnostic characters that should be used for infrageneric classification of subg. *Ceratotropis.* Thus, at this time, due to conflicting phylogenetic and inconclusive morphological evidence, we do not recognize sections with subg. *Ceratotropis*.

Plectrotropis — Based on past taxonomy, our phylogenetic analyses suggest a great mixing of taxa once ascribed to subgenera *Vigna* and *Plectrotropis*, resolving subg. *Plectrotropis* nested within sections of former subg. *Vigna*. This study supports an enlarged circumscription of subg. *Plectrotropis* that also includes Verdcourt's subg. *Vigna* sects. *Macrodontae* Harms, *Reticulatae* Verdc., and *Catiang* (DC.) Verdc., and perhaps sect. *Procerae* Baker f., a section unsampled herein. Others have also noted the close genetic relationship of these sections to subg. *Plectrotropis* (Vaillancourt et al., 1993; Jaaska, 1999; Goel et al., 2002, Vijaykumar et al., 2010). Morphologically, our expanded concept revises subg. *Plectrotropis* to include most pink- or purple-flowered species, leaving only blue- and yellow-flowered species in subg. *Vigna*.

Within the enlarged subg. *Plectrotropis*, all analyses are showing clades corresponding to sects. *Macrodontae*, *Reticulatae*, *Catiang*, and *Plectrotropis*. De Candolle (1825) created *Dolichos* sect. *Catiang* and Harms (1915) created *Vigna* sect. *Macrodontae*;

Verdcourt (1970) moved both sections to subg. *Vigna*. Verdcourt (1970) created sect. *Reticulatae* within subg. *Vigna*. Based on isozyme data, Pasquet and Vanderborght (2000) merged sect. *Liebrechtsia* (De Wild.) Baker fil. into sect. *Macrodontae*, a revision supported in this work with *V. frutescens* A.Rich nested within sect. *Macrodontae* in all analyses.

Vigna subg. *Plectrotropis* (Shumach.) Bak. was conceptualized by Verdcourt (1970) to include two sections: sect. *Plectrotropis* (Schumach.) Bak. which included three species that flowered when in full leaf, and sect. *Pseudoliebrechtsia* Verdc. which included three species that flowered when leafless or in leaf bud, including *V. lobatifolia* (now reduced to *V. vexillata* var. *lobatifolia*). However, clear groups based on these divisions are not supported by our analyses and we therefore merge sect. *Pseudoliebrechtsia* with sect. *Plectrotropis*.

Within sect. *Plectrotropis*, a surprise comes from the close relationship between *V. vexillata* and *V. angivensis* within both *matK* and ITS data, suggesting the transfer of *V. angivensis* to sect. *Plectrotropis,* as previously suggested by allozymes (Jaaska, 1999). Verdcourt (1970) suggested that *V. angivensis* formed a link between subgenera *Plectrotropis* and *Vigna*. Although both species share a special kind of pubescence (Verdcourt, 1970), a straight pod beak and the presence of para-amino-phenylalanine in the seeds (Birch et al., 1986), they have flowers completely different: *V. angivensis* flowers are almost symmetric, leading to its placement in subg. *Vigna* sect. *Vigna* by Verdcourt (1970) and Maréchal et al. (1978), whereas *V. vexillata* is characterized by a strongly asymmetric flower, with the keel bearing a long beak and a pocket on its left side, the tip of the pocket facing the tip of the style. This pocket allows the left wing to be horizontal and act as a landing platform for pollinators (Hedstrom and Thulin, 1986). An infraspecific phylogeny of the *V. vexillata* species complex is needed, especially since *V. angivensis* seems to be part of this complex. Ultimately, subg. *Plectrotropis* is herein revised to include five sections: sects. *Plectrotropis, Macrodontae, Catiang, Reticulatae,* and *Procerae*.

Vigna — *Vigna* subg. *Vigna* was formerly classified into six sections by Maréchal et al. (1978), including sects. *Vigna, Catiang, Macrodontae, Reticulatae, Liebrechtsia,* and *Comosae*. Verdcourt (1970) also included sect. *Procerae*. As mentioned above, sects. *Macrodontae, Reticulatae, Procerae* and *Catiang* are herein transferred to subg. *Plectrotropis*, with sect. *Liebrectsia* merged with *Macrodontae*. This leaves sects. *Vigna* and *Comosae* only.

Verdcourt's (1970) subg. *Vigna* is now reduced to yellow and blue flowered species only. Although this reduced subg. *Vigna* is made of two main clades that are largely separated by flower color, identifying sections according to flower color (yellow versus blue) is not possible, with analyses showing majority color-based clades inclusive of one or two oppositely colored species (Figs. 3-5), notably the 'aberrant' placement of *V. hosei*, *V. heterophylla*, and *V. comosa*.

Maréchal et al. (1978) created sect. *Comosae* to accommodate *V. comosa* and *V. haumaniana*. Like *V. procera, V. haumaniana* was unfortunately not included in this study and is very different from other *Vigna* s.s. species, being an erect, non-twining, subshrubby plant, characteristics that may place the species outside of *Vigna* s.s. (Verdcourt 1970). In all phylogenetic tree reconstructions, *V. comosa*, the type species of sect. *Comosae,* is nested within sect. *Vigna* (Figs. 3-5) and allied to *V. gazensis*. However, the position of these taxa, along with *V. verdcourtii,* are all basally branching within their respective clades and their position differs slightly among chloroplast and nuclear based trees (Figs. 3-5; Suppl. Figs. 1, 2). All three taxa are also basally branching in the network analyses (Suppl. Fig. 3), with *V. comosa* basally branching within subg. *Vigna* and *V. gazensis* branching slightly internal to it, along the network trunk. *Vigna verdcourtii* branches basally and peripherally within subg. *Vigna* in the *matK* network but falls outside subg. *Vigna* and between the trunks of subg.

Ceratotropis and clade *V. kirkii/stenophylla* for ITS, suggesting a potential chloroplast capture or hybrid original for this species. Taken alone, the phylogenetic tree results would suggest sect. *Comosae* as obsolete and to be merged with sect. *Vigna*, however, the sampling of *V. haumaniana* could potentially clarify and solidify the placement of *Comosae* as a separate clade. It is therefore difficult to consider sections within subg. *Vigna* and we do not do so at this time, but further research may bring sectional relevance forward with further taxonomic sampling and expanded marker selection.

Vigna kirkii/stenophylla clade — Lastly, all analyses agree on the resolution of the unique clade and sister relationship of *V. kirkii* and *V. stenophylla*. This phylogenetic result is not without morphological or molecular precedent. Although both species show different keel shapes, Verdcourt (1970) included both in subg. *Vigna* sect. *Vigna*. However, he later wrote "Despite the twisted keel with a distinct pocket [*V. kirkii*] does not seem to be related to other species with these characters, e.g. *V. vexillata* (L.) A.Rich. Its nearest relative is I believe the W. African *V. stenophylla* with which it shares the capitate style-apex and standard devoid of appendages" (Verdcourt 1971 p. 638). Maréchal et al. (1978) included *V. stenophylla* in their subg. *Vigna* and *V. kirkii* in subg. *Plectrotropis* due to keel shape while recognizing that *V. stenophylla* (and *V. angivensis*) were intermediate between their subg. *Plectrotropis* and subg. *Vigna*.

In our analyses, *matK* shows the *V. kirkii/stenophylla* clade nested within the enlarged subg. *Plectrotropis* and loosely associated with sect. *Macrodontae* species (Fig. 2; Supp. Fig 1), ITS analyses show them sister to *Haydonia*+*Plectrotropis*, but with low support (Fig. 3; Supp. Fig. 2), whereas the combined analysis places the *V. kirkii/stenophylla* clade as sister to subg. *Ceratotropis* (Fig. 5). Interestingly, the *matK* network places the *V. kirkii/stenophylla* as a clade nested within *Plectrotropis* but that clearly splits two major groups therein (Supp.

Fig. 3) whereas the ITS network places the group between *Ceratotropis* and *Haydonia+Plectrotropis* (Supp. Fig. 3). Taxonomically, these hypotheses for the evolutionary placement of the *V. kirkii/stenophylla* clade could be interpreted variously as support to raise this clade to the subgenus (Figs. 4, 5) or section (Fig. 3) levels.

Few former molecular studies have incorporated *V. kirkii,* but those that did noted odd placements or associations. For example, an early chloroplast restriction digest-based analysis suggested *V. kirkii* be placed outside subg. *Plectrotropis* and sister to a larger group of species from multiple subgenera (Vaillancourt et al., 1993). Similarly, an RFLP-based study noted the association of *V. kirkii* with *V. reticulata* (Fatokun et al., 1993), a taxon now included in our expanded subg. *Plectrotropis*. Goel et al. (2002) noted that the position of *V. kirkii* changed between analyses but was also associated to species of our expanded subg. *Plectrotropis*. In the end, *V. kirkii* and *V. stenophylla* appear intermediate between subg. *Ceratotropis* and sect. *Macrodontae*, the discrepancy of which may suggest a chloroplast capture event through admixture, hybridization, or potentially polyploidization.

To further investigate evidence for the former processes, genome size estimates of *V. kirkii* and *V. stenophylla* were determined using flow cytometry. In the context of other genome sizes gathered from previous works, *V. kirkii* has an estimated genome size of 601 mb, a size not unusual to most other *Vigna* species with estimates thus far (Supp. Table 3; Supp. Fig. 4). The estimate of 810 for *V. stenophylla* is on the larger side, and closer to those of *V. nakashimae* (756 mb), *V. vexillata* (715 mb) or *V. subterranea* (882 mb, as estimated by flow cytometry). This backs up other hypotheses regarding relationships among these taxa based on morphology discussed above. It is possible that the most recent common ancestor of *V. kirkii* and *V. stenophylla* may have been a hybrid included instances of admixture or introgression (chloroplast capture) involving one or more members of the *vexillata* clade. A more in depth, multi-gene or whole genome analysis will be required to elucidate the potential hybrid nature of *V. kirkii* and *V. stenophylla*.

Implications for Taxonomy — Although the backbone resolving relationships between major clades and subgenera is sometimes unresolved or poorly supported, our expanded sampling across OW *Vigna* has provided critical insight into strongly supported clades, and evolutionary and taxonomic relationships among species and we suggest taxonomic revisions to *Vigna s.s*. based on our results. *Vigna* s.s. subgenera *Lasiospron*, *Haydonia*, and *Ceratotropis* are unchanged since 1978. Our results provide evidence to back the movement of whole sections from subg. *Vigna* to subg. *Plectrotropis,* with subg. *Vigna* now reduced to yellow and blue flowered species only and subg. *Plectrotropis* enlarged to include all pink-flowered species previously included in subg. *Vigna*. Our results also support the unique clade *V. kirkii/stenophylla*. In the end, sects. *Liebrechtsia* (*V. frutescens* vs. the rest of sect. *Macrodontae*) and *Pseudoliebrechtsia* (*V. antunesii*, *V. lobatifolia* and *V. longissima* versus the rest of sect. *Plectrotropis*) based on pyrophytic habit are not justified. In the same way, our results do not justify sect. *Comosae* within subg. *Vigna* nor sections *Aconitifoliae* and *Angulares* within subg. *Ceratotropis.*

Key to *Physostigma* subgenera and *Vigna* subgenera and sections

1 - Keel with an almost spirally twisted beak, with a marked central spur on the upper side; style with a marked reversed beak beyond stigma. ***Physostigma* - 2**
  2 - Inflorescence rachis zig-zag shaped with nectariferous nodes; seed large (length > 3 cm), with linear hilum as long as the seed. ***P.* subg. *Physostigma***
  2 - Inflorescence rachis almost straight with nodes not nectariferous; seed medium sized (length = 5 mm), with short hilum (1 mm long). ***P.* subg. *Taubertiophyton***
1 - Keel truncate or beaked, the beak incurved through up to 360° (*V. lasiocarpa*) but not spiralized, without a marked central spur on the upper side; style with a short beak or a long straight beak (sect. *Glossostylus*). ***Vigna* - 3**

3 - Flower with a right-handed floral asymmetry, yellow; pod held erect or patent by twisting of the pedicel. **subg. *Lasiospron***

3 - Flower symmetric or with a left-handed floral asymmetry, or if with a right-handed asymmetry, then flower purple to white; pedicel straight, never twisted. **4**

4 - Pollen exine not coarsely reticulate. **subg. *Haydonia* - 5**

5 - Flower pink to purple; style with a long, straight and fleshy beak beyond stigma; seed with an eccentric aril. **sect. *Glossostylus***

5 - Flower yellow or purple; style with short beak or almost without beak; seed without aril, or with a very slight rim-aril. **sect. *Haydonia***

4 - Pollen exine coarsely reticulate. **6**

6 - Flower yellow or blue. **7**

7 - Flower with a left-handed asymmetry, yellow; keel with a curved beak (up to 270°) with a pocket on the left-hand side. **subg. *Ceratotropis***

7 - Flower symmetric, yellow or blue; keel not beaked and without a pocket on the left-hand side. **subg. Vigna**

6 - Flower purple to white or pink. **subg. *Plectrotropis* - 8**

8 - Leaflets with tertiary nerves parallel and perpendicular to primary nerve.**9**

9 - Petiole reduced to pulvinus. **sect. *Procerae***

9 - Petiole with three parts. **sect. *Reticulatae***

8 - Leaflets with reticulate venation. **10**

10 - Stipules unilobed at base; pod beak curved. **sect. *Catiang***

10 - Stipules bilobed at base or, if unilobed, then with a straight pod beak. **11**

11 - Pod beak straight; seed containing para-aminophenylalanine.**sect. *Plectrotropis***

11 - Pod beak curved; seed without para-aminophenylalanine. 12

12 - Standard petal with appendages; seed with a small central hilum and without aril. **sect. *Macrodontae***

12 - Standard petal without appendages; seed with an eccentric hilum and eccentric aril. **clade *V. kirkii/stenophylla***

Physostigma Balf., Trans. Roy. Soc. Edinburgh 22: 310 (1861). Type: *Physostigma venenosum* Balf.

Diagnosis—Stipules not produced below the point of insertion; leaf venation reticulate; inflorescence rachis not contracted; bracts and bracteoles deciduous; flower pink to white with a right-handed floral asymmetry (from a face-view perspective); keel with an almost spirally twisted beak with a marked central spur on the upper side; style with a marked reversed beak beyond stigma; pollen triporate, exine widely reticulate; seed without aril, containing alkaloids.

Physostigma subg. ***Physostigma***

Diagnosis— Inflorescence rachis zig-zag shaped with nectariferous nodes; ovary with 2-3 ovules; seed large (length > 3 cm), with linear hilum as long as the seed.

The subgenus includes 2 species: *Physostigma cylindrospermum* (Welw. ex Baker) Holmes and *P. venenosum* Balf.

Physostigma subg. ***Taubertiophyton*** Gillett, Kew Bull. 20: 108 (1966). Type: *Physostigma mesoponticum* Taub.

Diagnosis— Inflorescence rachis almost straight with nodes not nectariferous; seed medium sized (length = 5 mm), with short hilum (1 mm long).

The subgenus includes a single species: *Physostigma mesoponticum* Taub. (=*P. coriaceum* Merxm. syn. nov., =*P. laxius* Merxm. syn. nov.)

Vigna Savi. Pisa Nuov. Giorn. Lett 8: 113 (1824), nom. cons. Type: *Vigna glabra* Savi, nom. illeg. (≡ *Dolichos luteolus* Jacq., ≡ *Vigna luteola* (Jacq.) Benth.)

Diagnosis—Vigna can be diagnosed by the combination of the following characters: swollen inflorescence rachis nodes with extrafloral nectaries; bracts and bracteoles deciduous, keel truncate or beaked, the beak incurved through up to 360° (*V. lasiocarpa*) but not spiralized, without a central appendage; pollen triporate; pod cylindrical or if compressed (*V. comosa*) without raised sutures. In addition, most of the species present the following characters: stipules appendaged, inflorescence rachis contracted, style extended in a beak beyond stigma, pollen exine coarsely reticulate.

Vigna* subg. *Vigna *Callicysthus* Endl., Prodr. Fl. Norfolk.: 90 (1833). Type: *Callicysthus volubilis* Endl. (= *Vigna luteola* (Jacq.) Benth.).

Scytalis sect. *Helicopus* E. Mey., Comm. Pl. Afr. Austr.: 146 (1836). Lectotype (designated here): *Scytalis helicopus* E. Mey. (= *Vigna luteola* (Jacq.) Benth.).

Vigna [unranked] *Microdontae* Harms in Engl., Pflanzenw. Afr. 3: 685 (1915). Lectotype (designated here): *Vigna luteola* (Jacq.) Benth.

Vigna sect. *Microdontae* (Harms) Baker f., Leg. Trop. Afr. 2: 392 (1929).

Vigna sect. *Condylostylus* Verdc., Kew Bull. 24: 533 (1970). Type: *Vigna multinervis* Hutch. & Dalziel.

Vigna sect. *Comosae* Maréchal et al., Taxon 27: 200 (1978). Type: *Vigna comosa* Baker.

Diagnosis— Leaf venation reticulate (with exception of *V. multinervis* where secondary nerves are parallel and perpendicular to primary nerve); inflorescence rachis contracted; flower yellow or blue, almost symmetric; keel obtuse or shortly beaked; style extended in a short beak beyond stigma; pod beak curved; pollen exine coarsely reticulate.

The subgenus includes 23 species: *Vigna bequaertii* R. Wilczek, *V. comosa* Baker, *V. filicaulis* Hepper, *V. gazensis* Baker f., *V. gracilis* (Guill. & Perr.) Hook. f., *V. haumaniana* R. Wilczek, *V. heterophylla* A. Rich, *V. hosei* (Craib) Backer, *V. lanceolata* Benth. (= *V. suberecta* Benth., = *V. triodiophila* A.E. Holland & R. Butcher, syn. nov.), *V. laurentii* De Wild., *V. luteola* (Jacq.) Benth., *V. marina* (Burm. f.) Merr., *V. mendesii* Torre, *V. multinervis* Hutch. & Dalziel, *V. oblongifolia* A. Rich., *V. owahuensis* Vogel, *V. parkeri* Baker, *V.*

parviflora Welw. ex Baker (≡ *V. oblongifolia* var. *parviflora* (Welw. ex Baker) Verdc.), *V. pseudovenulosa* (Maréchal et al.) Pasquet & Maesen, *V. pubigera* Baker (≡ *V. ambacensis* var. *pubigera* (Baker) Maréchal et al.), *V. racemosa* (G. Don) Hutch. & Dalziel, *V. subterranea* (L.) Verdc., and *V. verdcourtii* Pasquet.

The status of *V. bequaertii* (close to *V. luteola*) and *V. mendesii* (which could belong to a different genus) would need to be confirmed by molecular systematic evidence. According to Vu et al. (2012), Lawn et al. (2016), and Lawn and Cottrell (2018), *V. lanceolata* should be considered as a single complex species (like *V. unguiculata* or *V. vexillata*) and the seven morphotypes should deserve varietal or subspecies rank.

Vigna* subg. *Ceratotropis (Piper) Verdc., Kew Bull. 24: 550 (1970).

Phaseolus subg. *Ceratotropis* Piper, U.S. Dep. Agric. Bull. 119: 2 (1914). Lectotype (designated by Verdcourt, 1970): *Vigna radiata* (L.) R. Wilczek.

Phaseolus sect. *Ceratotropis* (Piper) Piper, Contrib. U.S. Nat. Herb. 22: 682 (1926).

Cadelium Medik., Vorles. Churpfälz. Phys.- Ökon. Ges. 2: 352 (1787), nom. rej. Lectotype (designated by Pasquet 2002): *Cadelium nigrum* Medik. (= *Vigna radiata* (L.) R. Wilczek).

Azukia Takah. ex Ohwi, Fl. Japan: 690 (1953). Type: *Azukia angularis* (Willd.) Ohwi (≡ *Dolichos angularis* Willd., ≡ *Vigna angularis* (Willd.) Ohwi & Ohashi).

Rudua F. Maek., Jap. J. Bot. 15: 114 (1955). Type: *Rudua aurea* (Roxb.) F. Maek. (≡ *Phaseolus aureus* Roxb., = *Vigna radiata* (L.) R. Wilczek).

Vigna sect. *Aconitifoliae* N. Tomooka & Maxted, Kew Bull. 57: 623 (2002). Type: *Vigna aconitifolia* (Jacq.) Maréchal.

Vigna sect. *Angulares* N. Tomooka & Maxted, Kew Bull. 57: 623 (2002). Type: *Vigna angularis* (Willd.) Ohwi & Ohashi

Diagnosis—Stipules medifixed; leaf venation reticulate; inflorescence rachis contracted; flower yellow with left-handed asymmetry (from a face-view perspective); keel with a beak incurved through 160-360° (Tateishi, 1985) and with a pocket on the left keel petal; style extending beyond the stigma in a beak; pollen exine coarsely reticulate; pod beak curved.

The subgenus includes 27 species: *V. aconitifolia* (Jacq.) Maréchal, *V. angularis* (Willd.) Owhi & H.Ohashi, *V. aridicola* N. Tomooka & Maxted, *V. dalzelliana* (Kuntze) Verdc., *V. exilis* Tateishi & Maxted, *V. grandiflora* (Prain) Tateishi & Maxted, *V. hirtella* Ridley, *V. indica* T.M. Dixit et al., *V. khandalensis* (Santapau) Raghavan & Wadhwa, *V. konkanensis* Latha et al., *V. minima* (Roxb.) Ohwi & Ohashi, *V. mungo* (L.) Hepper, *V. nakashimae* (Ohwi) Ohwi & Ohashi, *V. nepalensis* Tateishi & Maxted, *V. pandeyana* Gore et al., *V. radiata* (L.) R. Wilczek, *V. reflexopilosa* Hayata, *V. riukiuensis* (Ohwi) Ohwi & H. Ohashi, *V. sahyadriana* Aitawade et al., *V. sathishiana* Balan & Pradepp, *V. stipulacea* (Lam.) Kuntze, *V. subramaniana* (Babu ex Raizada) Raizada, *V. tenuicaulis* N. Tomooka & Maxted, *V. trilobata* (L.) Verdc., *V. trinervia* (Heyne ex Wight & Arn.) Tateishi & Maxted, *V. umbellata* (Thunb.) Ohwi & Ohashi, and *V. yadavii* Gaikwad et al.

According to results of Umdale et al. (2023), *V. konkanensis* could be considered as a variety of *V. radiata*. The status of *V. pandeyana* (close to *V. dalzelliana*), *V. sathishiana* close to *V. mungo*), and *V. yadavii* (close to *V. dalzelliana*) would need to be confirmed by molecular systematic evidence.

Vigna* subg. *Lasiospron (Benth.) Maréchal et al., Taxon 27: 201 (1978).

Phaseolus sect. *Lasiospron* Benth., Comm. Leg. Gen.: 76 (1837). Lectotype (designated by Verdcourt, 1970): *Phaseolus lasiocarpus* Mart. ex Benth. (≡ *Vigna lasiocarpa* (Mart. ex Benth.) Verdc.).

Vigna sect. *Lasiospron* (Benth.) Verdc., Kew Bull. 24: 539 (1970)

Diagnosis---Stipules medifixed; leaf venation reticulate; inflorescence rachis contracted; flower yellow with a right-handed floral asymmetry (from a face-view perspective), keel distinctly beaked and loosely coiled to 270-360°; pod erect by post-pollination twisting of the pedicel; pod beak curved; seed with an eccentric hilum and aril; pollen exine coarsely reticulate (Delgado-Salinas et al., 2022).

This subgenus includes six species: *Vigna diffusa* (Scott-Elliot) A. Delgado & Verdc., *V. juruana* (Harms) Verdc., *V. lasiocarpa* (Mart. ex Benth.) Verdc., *V. longifolia* (Benth.) Verdc., *V. schottii* (Benth.) A. Delgado & Verdc., and *V. trichocarpa* (C. Wright) A. Delgado.

Vigna* subg. *Haydonia (R. Wilczek) Verdc., Kew Bull. 24: 565 (1970). *Haydonia* R. Wilczek, Bull. Jard. Bot. Brux. 24: 405 (1954). Type: *Vigna monophylla* Taub.

Diagnosis—Leaf venation reticulate; pod beak curved, pollen exine smooth and not coarsely reticulate.

Vigna* subg. *Haydonia* sect. *Haydonia Maréchal et al., Taxon 27: 197 (1978). *Haydonia* R. Wilczek, Bull. Jard. Bot. Etat 24: 405 (1954). Type: *Haydonia monophylla* (Taub.) R. Wilczek (≡ *Vigna monophylla* Taub.).

Vigna sect. *Microspermae* Maréchal et al., Taxon 27: 199 (1978). Type: *Vigna microsperma* R. Vig.

Diagnosis—Stipules slightly bilobed at base or not produced below the point of attachment; style oblique and terminal or extended into a short beak; seed without aril or with a very slight rim-aril (in *V. schimperi*).

The section includes seven species: *Vigna juncea* Milne-Redh., *V. microsperma* R. Vig., *V. monophyla* Taub., *V. nyangensis* Mithen, *V. richardsiae* Verdc., *V. schimperi* Baker, and *V. triphylla* (R.Wilczek) Verdc.

Sect. *Haydonia* and sect. *Microspermae* have equal priority and when here uniting them, we prefer the former name.

Vigna* subg. *Haydonia* sect. *Glossostylus Verdc., Kew Bull. 24: 551 (1970). Type: *Vigna nigritia* Hook. f.

Diagnosis— Stipules bilobed below point of insertion; inflorescence rachis contracted, flower pink, almost symmetric; keel with a short beak; style extended beyond stigma into a long straight beak; seed with an eccentric aril.

The section includes two species: *Vigna nigritia* Hook f. and *V. venulosa* Baker.

Verdcourt (1970) described the section within subg. *Vigna*; Maréchal et al. (1978) moved it to subg. *Haydonia*.

Vigna* subg. *Plectrotropis (Schumach. & Thonn.) Baker, Fl. Brit. India 2: 206 (1876).

Diagnosis— Stipules medifixed; inflorescence rachis contracted; flower purple to white; style extended into a short beak beyond stigma; pollen exine coarsely reticulate.

Vigna* subg. *Plectrotropis sect. ***Plectrotropis*** (Schumach. & Thonn.) Taub. in Engl. & Prantl, Nat. Pflanzenfam. 3(3): 382 (1894). *Plectrotropis* Schumach. & Thonn., Beskriv. Guin. Pl.: 338 (1827). Lectotype (designated by Verdcourt, 1970): *Plectrotropis angustifolia* Schumach. & Thonn. (≡ *Vigna vexillata* (L.) A. Rich. var. *angustifolia* (Schumach. & Thonn.) Baker).

Vigna [unranked] *Vexillatae* Harms in Engl., Pflanzenw. Afr. 3: 689 (1915). Type: *Vigna vexillata* (L.) A. Rich.

Vigna sect. *Vexillatae* (Harms) Baker f., Leg. Trop. Afr. 2: 396 (1929).

Vigna sect. *Pseudoliebrechtsia* Verdc., Kew Bull. 24: 555 (1970). Type: *Vigna nuda* N. E. Br. (= *V. antunesii* Harms).

Diagnosis— Stipules bilobed at base, rarely unilobed; leaf venation reticulate, flower almost symmetric (*V. angivensis*) or with a left-handed asymmetry; the left-handed asymmetric flowers have a keel beak incurved through 180° with a pocket on the left petal; pod beak straight; seed with aril reduced or absent. All species tested so far have para-aminophenylalanine (PAPA) in their seeds.

The section includes four species: *Vigna angivensis* Baker (= *V. keraudrenii* Du Puy & Labat, syn. nov.), *V. antunesii* (= *V. nuda*), *V. longissima* Hutch., and *V. vexillata*.

Vigna vexillata includes several infraspecific taxa, including var. *lobatifolia* (Baker) Pasquet, formerly from sect. *Pseudoliebrechtsia*.

Vigna* subg. *Plectrotropis* sect. *Catiang (DC.) Verdc., Kew Bull. 24: 542 (1970). *Dolichos* sect. *Catiang* DC., Prodr. 2: 398 (1825). Type: *Dolichos catjang* Burm. f. (= *Vigna unguiculata* (L.) Walp.).

Dolichos sect. *Unguicularia* DC., Prodr. 2: 400 (1825). Type: *Dolichos unguiculatus* L. (≡ *Vigna unguiculata* (L.) Walp.).

Scytalis E. Mey., Comm. Pl. Afr. Austr.: 144 (1836). Type: *Scytalis catjang* (Burm. f.) E. Mey. (≡ *Dolichos catjang* Burm. f., = *Vigna unguiculata* (L.) Walp.).

Scytalis sect. *Catiang* (DC.) E. Mey., Comm. Pl. Afr. Austr.: 145 (1836),

Vigna [unranked] *Appendiculatae* Harms in Engl., Pflanzenw. Afr. 3: 686 (1915). Lectotype (designated here): *Vigna sinensis* (L.) Endl. ex Hassk. (= *V. unguiculata* (L.) Walp.).

Vigna sect. *Appendiculatae* (Harms) Baker f., Leg. Trop. Afr. 2: 395 (1929).

Vigna subg. *Catiang* (DC.) Jaaska & Jaaska, Pl. Syst. Evol. 159: 157 (1988).

Diagnosis— Stipules unilobed at base; leaf venation reticulate; flower almost symmetric; keel obtuse or shortly beaked; pod beak curved.

The section includes three species: *Vigna monantha* Thulin, *V. schlechteri* Harms (= *V. nervosa* Markötter), and the cowpea *V. unguiculata* (L.) Walp. *V. unguiculata* includes numerous infraspecific taxa.

Vigna* subg. *Plectrotropis* sect. *Macrodontae (Harms) Baker f., Leg. Trop. Afr. 2: 396 (1929).

Vigna [unranked] *Macrodontae* Harms in Engl., Pflanzenw. Afr. 3: 688 (1915). Lectotype (designated by Verdcourt, 1970): *Vigna membranacea* A. Rich.

Liebrechtsia De Wild., Ann. Mus. Congo, sér. 4, 1: 70 (1902). Lectotype (designated by Verdcourt, 1970): *Liebrechtsia esculenta* De Wild. (= *Vigna frutescens* A. Rich.)

Vigna sect. *Liebrechtsia* (De Wild.) Baker f., Leg. Trop. Afr. 2: 397 (1929).

Diagnosis— Stipules bilobed at base; leaf venation reticulate; flower almost symmetric; standard with two parallel appendages; keel obtuse or shortly beaked; pod beak curved; seed with a small central hilum without aril.

The section includes six species: *Vigna caesia* Chiov. (≡ *V. membranacea* subsp. *caesia* (Chiov.) Verdc.), *V. friesiorum* Harms (= *V. kokii* Pienaar, syn. nov., = *V. mudenia* Pienaar, syn. nov.), *V. frutescens* A. Rich., *V. hapalantha* Harms (≡ *V. membranacea* subsp. *hapalantha* (Harms) Verdc.), *V. membranacea* A. Rich., and *V. somaliensis* Baker f.

The status of *Vigna somaliensis* (close to *V. caesia*) would need to be confirmed by molecular evidence.

Vigna* subg. *Plectrotropis* sect. *Procerae Baker f., Leg. Trop. Afr. 2: 397 (1929). Type: *Vigna procera* Welw. ex Hiern.

Diagnosis—Stipules bilobed at base; leaflets with tertiary nerves parallel, perpendicular to primary nerve; leaf petiole reduced to pulvinus; flower almost symmetric; standard with two parallel appendages; keel obtuse or shortly beaked; pod beak curved.

The section includes one species: *Vigna procera* Welw. Ex Hiern.

Vigna* subg. *Plectrotropis* sect. *Reticulatae Verdc., Kew Bull. 24: 550 (1970). Type: *Vigna reticulata* Hook. f.

Diagnosis—Stipules bilobed at base; leaflets with tertiary nerves parallel and perpendicular to primary nerve; leaf petiole made of three parts; flower almost symmetric; standard with two parallel appendages; keel obtuse or shortly beaked; pod beak curved.

The section includes seven species: *Vigna dolomitica* R. Wilczek, *V. phoenix* Brummitt, *V. platyloba* Welw. ex Hiern, *V. pygmaea* R.E. Fr., *V. radicans* Welw. ex Baker, *V. reticulata* Hook f., and *V. tisserantiana* Pellegr.

The status of *V. tisserantiana* (close to *V. pygmaea*) would need to be confirmed by molecular systematic evidence. Sections *Procerae* and *Reticulatae* could be united on a morphological basis, both sections having leaflets with parallel tertiary nerves, but this would also need to be confirmed by molecular evidence.

Vigna* clade *V. kirkii-V. stenophylla

Diagnosis—Stipules medifixed, bilobed at base; leaf venation reticulate; flower almost symmetric; standard without appendages; seed with an eccentric aril.

The clade includes two species: *Vigna kirkii* (Baker) J.B. Gillett and *V. stenophylla* Harms. The *matK* phylogeny and morphology suggest sectional rank, whereas ITS suggests rank as subgenus. Pending further data, we prefer not to decide at this stage.

Note—*Vigna bosseri* Du Puy & Labat, never assigned to any subgenus or section, may be close to or synonymous with *Wajira grahamiana* (Wight & Arn.) Thulin & Lavin, but this would need to be confirmed by molecular systematic evidence. *Vigna clarkei* Prain, which could belong to *Dysolobium* (Benth.) Prain, and *V. mukerjeanus* (Babu ex Raizada) Raizada, would also need further study. *Vigna ramanniana* Rossberg, only known through a destroyed specimen, is also difficult to attribute to a section or subgenus.

ACKNOWLEDGMENTS. The authors thank Thierry Vanderborght formerly of Meise Botanic Garden, Belgium for continuous supply of living accessions, Matt Lavin for input into initial project design, Robert J. Lawn for sharing important plant material and helpful comments on the manuscript, and Steven Kelty, Lark Andrus, Jonah Weight, and Alisa Baadsgaard and students of Utah Valley University’s 2020 BOT 4200 Plant Systematics class for input on initial phylogenetic analyses through their course-based undergraduate research experience (CURE) classroom work.

AUTHOR CONTRIBUTIONS. Y.F., R.S.P., and P.G. designed the initial research. Y.F. did the molecular work and the first phylogenetic analyses in P.G.'s lab. A.D.S, M.T., and R.M. provided important material. K.M. and A.N.E. did genome size work. D.M.H. and A.N.E. did the final phylogenetic analyses. A.N.E, R.S.P., D.M.H., and F.J. wrote the paper. All authors contributed to the final version of the paper.

DATA AVAILABILITY. DNA sequences are deposited in…

SUPPORTING INFORMATION. Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary file 1. Taxon sampling with accession numbers, herbarium voucher information, etc for all taxa.

Supplementary Table 1. Taxon sampling in maximum likelihood datasets.

Supplementary Table 2. Raw genome size estimates from flow cytometry for *V. unguiculata* (control), *V. kirkii* and *V. stenophylla* with iceberg lettuce as the size standard.

Supplementary Table 3. Genome size estimates for various *Vigna* species gathered from the literature.

Supplementary figure 1. Best tree from Maximum likelihood phylogram of *matK* estimated using RAxML. Node numbers are bootstrap support values. Alphanumerics after taxon name are accession numbers as in Supplementary File 1.

Supplementary figure 2. Best tree from Maximum likelihood phylogram of ITS estimated using RAxML. Node numbers are bootstrap support values. Alphanumerics after taxon name are accession numbers as in Supplementary File 1.

Supplementary figure 3. Splitstree analyses of ITS and *matK* alignments.

Supplementary figure 4. Genome size estimates mapped onto the *matK* and ITS phylogenies. The size of the circle is relative to genome size. Estimates newly determined in this study in blue circles.

LITERATURE CITED

Baker, E.G. 1929. The Leguminosae of tropical Africa, part II. Erasmus Press, Ghent, Belgium.

Bentham, G. 1837. Commentationes de leguminosarum generibus. J.P. Sollinger, Wien, Austria.

Bentham, G. 1859. Papilionaceae. *In* C.F.P. Martius, Flora Brasiliensis 15: 1–215. Fleischer, Leipzig, Germany.

Birch, A. N. E., L. E. Fellows, S. V. Evans, and K. Doharty. 1986. Para-aminophenylalanine in *Vigna*: possible taxonomic and ecological significance as a seed defense against burchids. *Phytochemistry* 25: 2745–2749.

Bouckaert, R., J. Heled, D. Kühnert, T. Vaughan, C. H. Wu, D. Xie, M. A. Suchard, et al. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 10: e1003537.

De Candolle, A. P. 1825. Prodromus systematis naturalis regni vegetabilis, vol. 2. Treuttel et Würtz, Paris, France.

Delgado-Salinas, A., T. Turley, A. Richman, and M. Lavin.1999. Phylogenetic analysis of the cultivated and wild species of *Phaseolus* (Fabaceae). *Systematic Botany* 24: 438–460.

Delgado-Salinas, A., M. Thulin, R. Pasquet, M. Weeden, and M. Lavin. 2011. *Vigna* (Leguminosae) sensu lato: the names and identities of the American segregate genera. *American Journal Botany* 98:1694–1715.

Delgado-Salinas, A., M. Lavin, C. Snak, and G. P. Lewis. 2022. Systematics of *Vigna* subgenus *Lasiospron* (Leguminosae: Papilionoideae: Phaseolinae). *Systematic Botany* 47: 97–124.

Doi, K., A. Kaga, N. Tomooka, and D. A. Vaughan. 2002. Molecular phylogeny of genus *Vigna* subgenus *Ceratotropis* based on rDNA ITS and *atpB-rbcL* intergenic spacer of cpDNA sequences. *Genetica* 114: 129–145.

Edgar, R. C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.

Egawa, Y., I. B. Bujang, S. Chotechuen, N. Tomooka, and Y. Tateishi.1996a. Phylogenetic differentiation of tetraploid *Vigna* species, *V. glabra* and *V. reflexopilosa. JIRCAS Journal* 3: 49–58.

Egawa, Y., S. Chotechuen, N. Tomooka, C. Thavarasook, and C. Kitbamroong. 1996b. Cross-compatability among the subgenus *Ceratotropis* of the genus *Vigna. In* Y. Egawa and S. Chotechuen [eds.] Phylogenetic differentiation of mungbean germplasm (subgenus *Ceratotropis* of the genus *Vigna*) and evaluation for breeding program, pp. 19–30. Japan International Research Center for Agricultural Science, Tsukuba, Japan.

Fatokun, C. A., D. Danesh, N. D. Young, and E. L. Stewart. 1993. Molecular taxonomic relationships in the genus *Vigna* based on RFLP analysis. *Theoretical and Applied Genetics* 86: 97–104.

Gillett, J. B. 1966. Notes on Leguminosae (Phaseoleae). *Kew Bulletin* 20: 103–111.

Goel, S., S. N. Raina, and Y. Ogihara. 2002. Molecular evolution and phylogenetic implications of internal transcribed spacer sequences of nuclear ribosomal DNA in the *Phaseolus-Vigna* complex. *Molecular Phylogenetics and Evolution* 22: 1–19.

Harms, H. 1915. Leguminosae, *In* A. Engler and O. Drude [eds.] Die Pflanzenwelt Afrikas (Die Vegetation der Erde 9): 327–698. Wilhelm Engelmann, Leipzig, Germany.

Hedstrom, I., and M. Thulin. 1986. Pollination by a hugging mechanism in *Vigna vexillata* (Leguminosae-Papilionoideae). *Plant Systematics and Evolution*. 154: 275–283.

Hu, J. M., M. Lavin, M. F. Wojciechowski, and M. J. Sanderson. 2000. Phylogenetic systematics of the tribe Millettieae (Leguminosae) based on *matK* sequences, and implications for evolutionary patterns in Papilionoideae. *American Journal of Botany* 87: 418– 430.

Huson, D.H., and D. Bryant. 2006. Applications of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* 23: 254–267.

Jaaska, V. 1999. Isoenzyme diversity and phylogenetic affinities among the African beans of the genus *Vigna* Savi (Fabaceae). *Biochemical Systematics and Ecology* 27(6): 569–589.

Javadi, F., Y. T. Tun, M. Kawase, K.Y. Guan, and H. Yamaguchi. 2011. Molecular phylogeny of the subgenus *Ceratotropis* (genus *Vigna*, Leguminosae) reveals three eco-geographical groups and Late Pliocene-Pleistocene diversification: evidence from four plastid DNA region sequences. *Annals of Botany* 108: 367–380.

Kang, Y. J., S. K. Kim, M. Y. Kim, P. Lestari, K. H. Kim, B. K. Ha, T. H. Jun, W. J. Hwang, T. Lee, J. Lee, S. Shim, M. Y. Yoon, et al. 2014. Genome sequence of mungbean and insights into evolution within *Vigna* species. *Nature Communications* 5: 5443. doi:10.1038/ncomms6443

Kang, Y. J., D. Satyawan, S. Shim, T. Lee, J. Lee, W. J. Hwang, S. K. Kim, P. Lestari, K. Laosatit, K. H. Kim, T. J. Ha, A. Chitikineni, et al. 2015. Draft genome sequence of adzuki bean, *Vigna angularis*. *Scientific Reports* 5: 8069. doi:10.1038/srep08069

Konarev, A.V., N. Tomooka, and D.A. Vaughan. 2002. Proteinase inhibitor polymorphism in the genus *Vigna* subgenus *Ceratotropis* and its biosystematic implications. *Euphytica* 123: 165–177.

Kozlov, A. M., D. Darriba, T. Flouri, B. Morel, and A. Stamatakis. 2019. RAxML- NG: a fast, scalable and user- friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* 35: 4453–4455.

Lakhanpaul, S., and C. R. Babu. 1991. Genome size and evolution in asiatic *Vigna* Savi. In: Symposium on Grain Legumes, New Delhi. pp 47-57.

Larsson, A. 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 30: 3276–3278.

Lavin, M., P. S. Herendeen, and M. F. Wojciechowski. 2005. Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the tertiary. *Systematic Biology* 54: 575–594.

Lawn, R.J., H.T.T. Vu, L.M. Bielig, and A. Kilian. 2016. Genetic compatibility among morphotypes of *Vigna lanceolata* and implications for breeding improved cultivars. *Crop & Pasture Science* 67: 739–750.

Lawn, R. J. and A. Cottrell. 2018. Distribution, habitat, morphological diversity and genetic interrelations of native *Vigna* in the Pilbara, Western Australia. *Crop and Pasture Science* 69(10): 985–998.

Lestari, P., Y. J. Kang, K. S. Han, J. G. Gwag, J. K. Moon, Y. H. Kim, Y. H. Lee, and S. H. Lee. 2014. Genome-wide single nucleotide polymorphism discovery and validation in adzuki bean. *Molecular Breeding* 33: 497–501. doi:10.1007/s11032-013-9962-5

Linnaeus, C. 1753. Species Plantarum, edition 1, vol. 2, Laurent Salvii, Stockholm, Sweden.

Lonardi S., M. Muñoz-Amatriaín, Q. Liang, S. Shu, S. I. Wanamaker, S. Lo, J. Tanskanen, A. H. Schulman, T. Zhu, M. C. Luo, and H. Alhakami. 2019. The genome of cowpea (*Vigna unguiculata* [L.] Walp.). *The Plant Journal* 98: 767–782. doi:10.1111/tpj.14349

Loureiro, J., M. Čertner, M. Lučanová, E. Sliwinska, F. Kolář, J. Doležel, S. Garcia, S. Castro, and D.W. Galbraith. 2023. The use of flow cytometry for estimating genome sizes and DNA ploidy levels in plants. *In Plant Cytogenetics and Cytogenomics: Methods and Protocols* (pp. 25-64). New York, NY: Springer US.

Maddison, W.P. 1997. Gene trees in species trees. *Systematic biology* 46(3): 523–536.

Maréchal, R., J.M. Mascherpa, and F. Stainier. 1978. Etude taxonomique d'un groupe complexe d'espèces des genres *Phaseolus* et *Vigna* (Papilionaceae) sur la base de données morphologiques et polliniques, traitées par l'analyse informatique. *Boissiera* 28: 1–273.

Miller, M. A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. 2010 Gateway Computing Environments Workshop (GCE), 1–8, New Orleans, LA, USA.

Naito, K., T. Wakatake, T. F. Shibata, K. Iseki, S. Shigenobu, Y. Takahashi, E. Ogiso-Tanaka et al. 2022. "Genome sequence of 12 *Vigna* species as a knowledge base of stress tolerance and resistance." *bioRxiv* (2022): 2022-03.

Parida A., S. N. Raina, and R. K. J. Narayan. 1990. Quantitative DNA variation between and within chromosome complements of *Vigna* species (Fabaceae). *Genetica* 82: 125-133.

Pasquet, R. S. 2001. *Vigna* Savi. *In* Mackinder, B., R. S. Pasquet, R. Polhill, B. Verdcourt, eds. *Flora Zambesiaca* vol. 3 part 5 pp. 121–156. Royal Botanic Gardens, Kew, United Kingdom.

Pasquet, R. S., and T. Vanderborght. 2000. Isozyme polymorphism in the *Vigna frutescens* - *V. membranacea* complex (Tribe Phaseoleae, Fabaceae). *Biochemical Systematics and Ecology* 28: 29–43.

Pasquet, R. S., Y. Feleke, and P. Gepts. 2021. Cowpea [*Vigna unguiculata* (L.) Walp.] maternal lineages, chloroplast captures, and wild cowpea evolution. *Genetic Resources and Crop Evolution*, 68(7): 2799–2812.

Pulse Crop Database. *Vigna subterranea* https://www.pulsedb.org/organism/983374 accessed 16 Nov 2023.

Quenum, A.J.C., R.S. Pasquet, A. Bodian, D. Fonceka, Y.R. Djiboune, N. Cisse, M.S. Mbaye and D. Diouf. 2023. Molecular characterization of cowpea [*Vigna unguiculata* (L.)

Walp.] subspecies with SSR markers. *Genetic Resources and Crop Evolution* 70 https://doi.org/10.1007/s10722-023-01738-x

Rambaut, A., and A. J. Drummond. 2007. Tracer v1.4. Available from http://beast.bio.ed.ac.uk/Tracer.

Rieseberg, L.H. and D.E. Soltis. 1991. Phylogenetic consequences of cytoplasmic gene flow in plants. *Evolutionary Trends in Plants* 5(1): 65–84.

Riley-Hulting, E. T., A. Delgado-Salinas, and M. Lavin. 2004. Phylogenetic systematics of *Strophostyles* (Fabaceae): A North American temperate genus within a neotropical diversification. *Systematic Botany* 29: 627–653.

Saini, A., K. S. Reddy, and N. Jawali. 2008. Intra-individual and intra-species heterogeneity in nuclear rDNA ITS region of *Vigna* species from subgenus *Ceratotropis*. *Genetics Research* 90: 299–316.

Saini, A., and N. Jawali. 2009. Molecular evolution of 5S rDNA region in *Vigna* subgenus *Ceratotropis* and its phylogenetic implications. *Plant Systematics and Evolution* 280: 187–206.

Santos, F. D., C. Snak, C. L. Ribeiro, C. Silva, and L. P. de Queiroz. 2023. Phylogenetic analyses of Phaseolinae (Leguminosae) reveal a new genus endemic to limestone outcrops in seasonally dry forests of Bahia, Brazil. *Taxon* 72(1): 64–77.

Savi, G. 1824. Osservazioni sopra i generi *Phaseolus* et *Dolichos*. *Pisa Nuova Giornale dei Letterati* 8: 106–123.

Suranjika, S., S. Pradhan, R. K. Kalia, and N. Dey. 2023. De novo assembly of the whole genome of Moth bean (*Vigna aconitifolia*), an underutilized *Vigna* species of India. bioRxiv. 2023:2023-05.

Swindell, R. E., E. E. Watt, and G. M. Evans.1973. A natural tetraploid mung bean of suspected amphidiploid origin. *Journal of Heredity* 64:107.

Swofford, D. L. 2003. *PAUP*: phylogenetic analysis using parsimony (* and other methods) Version 4*. Sinauer Associates, Sunderland (MA), USA.

Takahashi, Y., P. Somta, C. Muto, K. Iseki, K. Naito, M. Pandiyan, S. Natesan, and N. Tomooka. 2016. Novel genetic resources in the genus *Vigna* unveiled from gene bank accessions. *PLoS One* 11: e0147568.

Takahashi, Y., C. Muto, K. Iseki, K. Naito, P. Somta, M. Pandiyan, N. Senthil, N. Tomooka. 2018. A new taxonomic treatment for some wild relatives of mungbean (*Vigna radiata* (L.) Wilcz.) based on their molecular phylogenetic relationships and morphological variations. *Genetic Resources and Crop Evolution* 65: 1109–1121.

Takahashi, Y., and N. Tomooka. 2020. Taxonomy of Mungbean and its relatives. *In* R. Nair, R. Schafleitner, and S. H. Lee [eds.] The Mungbean Genome, Compendium of Plant Genomes, 27–41. Springer, Cham.

Tateishi, Y. 1985. A revision of the Azuki bean group, the subgenus *Ceratotropis* of the genus *Vigna*. PhD dissertation, Tohoku University, Sendai, Japan.

Tateishi, Y. 1996. Systematics of the species *Vigna* subgenus *Ceratotropis*. *In* P. Srineves, C. Kitbamroong, and S. Miyazaki [eds.], Mungbean germplasm: Collection, evaluation and utilization for breeding programs, 9–24. Japan International Research Center for Agricultural Sciences, Tsukuba, Japan.

Thulin, M., M. Lavin, R. Pasquet, and A. Delgado-Salinas. 2004. Phylogeny and biogeography of *Wajira* (Leguminosae): A monophyletic segregate of *Vigna* centered in the Horn of Africa region. *Systematic Botany* 29: 903–920.

Tomooka, N., N. Maxted, C. Thavarasook, and A. H. M. Jayasuriya. 2002a. Two new species, sectional designations and new combinations in *Vigna* subgenus *Ceratotropis* (Piper) Verdc. (Leguminosae, Phaseoleae). *Kew Bulletin* 57: 613–624.

Tomooka, N., D. A.Vaughan, H. Moss, and N. Maxted. 2002b. The Asian *Vigna*: genus *Vigna* subgenus *Ceratotropis* genetic resources. Kluwer Academic Publishers, Dordrecht, Netherlands.

Tun, Y.T. and H. Yamaguchi. 2007. Phylogenetic relationship of wild and cultivated *Vigna* (Subgenus *Ceratotropis*, Fabaceae) from Myanmar based on sequence variations in non-coding regions of trnT-F. *Breeding Science* 57(4): 271–280.

Umdale, S. D., N. B. Gaikwad, S. Kadam, M. L. Ahire, P. S. Mundada, and K. V. Bhat. 2023. Genetic diversity of Asian *Vigna* species (Subgenus *Ceratotropis*; Genus *Vigna*) in India based on ITS2 sequences data. *Plant Molecular Biology Reporter* 41: 454-469.

Vaillancourt, R. E., N. F. Weeden, A. Bruneau, and J. J. Doyle. 1993. Chloroplast DNA phylogeny of old world *Vigna* (Leguminosae). *Systematic Botany* 18: 642–651.

Van der Maesen, L. J. G., and R. Pasquet. 2006. *Vigna* Savi. *In* A. Akoegninou, W. J. Van der Burg, and L. J. G. Van der Maesen [eds.] Flore Analytique du Benin: 734–747. Backhuis Publishers, Wageningen, Netherlands.

Verdcourt, B. 1970. Studies in the Leguminosae-Papilionoideae for the Flora of Tropical East Africa. IV. *Kew Bulletin* 24: 507–569.

Verdcourt, B. 1971. Phaseoleae. *In* Milne-Redhead, E. & R.M. Polhill [eds] Flora of Tropical East Africa, Leguminosae (part 4), Papilionoideae (2): 1–807. Crown agents for oversea governments and administrations, London.

Vijaykumar, A., A. Saini, and N. Jawali. 2010. Phylogenetic analysis of subgenus *Vigna* species using nuclear ribosomal RNA ITS: Evidence of hybridization among *Vigna unguiculata* subspecies. *Journal of Heredity* 101: 177–188.

Vu, T.T.H., R.J. Lawn, L.M. Bielig, S.J. Molnar, L. Xia, and A. Kilian. 2012. Development and initial evaluation of Diversity Array Technology for soybean and mungbean. *Euphytica* 186: 741–754.

Wilczek, R. 1954a. Phaseolinae. *In* W. Robyns et al. [eds.] Flore du Congo belge et du Ruanda-Urundi 6: 260–409. Institut national pour l'étude agronomique du Congo belge, Brussells, Belgium.

Wilczek, R. 1954b. Groupes nouveaux des Phaseoleae-Phaseolinae du Congo belge et du Ruanda-Urundi. *Bulletin du Jardin botanique de l'État à Bruxelles* 24: 405–450.

Wojciechowski, M. F., M. Lavin, and M. J. Sanderson. 2004. A phylogeny of legumes (Leguminosae) based on analyses of the plastid *matK* gene resolves many well-supported subclades within the family. *American Journal of Botany* 9: 1846–1862.

Yano, A., K. Yasuda, and H. Yamaguchi. 2004. A test for molecular identification of Japanese archaeological beans and phylogenetic relationship of wild and cultivated species of subgenus *Ceratotropis* (Genus *Vigna*, Papilionaceae) using sequence variation in two non-coding regions of the *trnL* and *trnF* genes. *Economic Botany* 58: S135–S146.

Tables

Table 1. Primers used for PCR amplification and sequencing. F = forward primer, R - reverse primer.

Primer name	**Sequence 5' to 3'**	**Direction**	**Source**
trnKIL	CTC AAT GGT AGA GTA CTC G	F	Hu et al., 2000
trnK685F	GTA TCG CAC TAT GTA TCA TTT G	F	Hu et al., 2000
matK1362F	GTA TGG GAA TAT GAA TCT ATC TT	F	This study
matK1932F	CCT ATT AGT AAG CCG GTT TG	F	This study, Modified from *matK* 1932R; Hu et al., 2000
matK708R	TCA AAT GAT ACA TAG TGC GAT A	R	Hu et al., 2000
matK4R	CAT CTT TTA TCC AAT ATC GAA GG	R	This study
matK1777R	CAT TTG ACT HCG TAC CAC TGA A	R	Hu et al., 2000
trnK2R	AAC TAG TCG GAT GGA GTA G	R	Hu et al., 2000
ITS 1&2	GTC CAC TGA ACC TTA TCA TTT AGA GG	F	Delgado-Salinas et al., 1999
ITS 1&2	GCC GTT ACT AAG GGA ATC CTT GTT AG	R	Delgado-Salinas et al., 1999

Table 2. Secondary calibration dates used for calibration of the BEAST time tree across the most recent common ancestor of indicated species. Mya = million years ago, SD = standard deviation, My = Million years. (Lavin et al., 2005).

Node defined		**Mean age (Mya)**	**SD (age My)**	**Minimum (Mya)**	**Maximum (Mya)**	**Mean rate (s/s/Mya)**	**SD (rate)**
Wajira albescens – Phaseolus vulgaris	*WP*	10.7	0.9	8.7	13.2	0.00216	0.00013
Phaseolus vulgaris – Vigna subterranea	*PV*	8	0.8	6.4	10.4	0.00246	0.00014

Table 3. Summary of the molecular phylogenetic analyses results across different datasets.

DNA region or dataset	**ITS**	***MatK***	**Combined**
OTUs (BEAST/ RAxML)	146/137	200	224
# patterns (BEAST/ RAxML)	611/610	2005/1994	2618
% gaps et al. (RAxML)	31.15%	22.05%	33.44%
Evolutionary Model	GTR+I+G	TVM+I+G	GTR+I+G
Aligned length (BEAST/ RAxML)	895/863	3014	3770
Parsimony informative	87	887	1356
Likelihood (RAxML)	-16717.02	-25271.33	-43420.543
Posterior mean (BEAST)	-17136.38	-27444.307	na
Likelihood (BEAST)	-16903.59	-25475.398	na
Burnin (BEAST)	20%	20%	na
Generations (BEAST/ RAxML)	30 million	30 million	30 million

Table 4. Summary of divergence dates (node ages) and posterior probabilities estimated for defined clades using BEAST.

Node	MatK		ITS	
	Node Age	Posterior	Node Age	Posterior
Subgenus *Plectrotropis*	4.87	0.78	3.75	1
Sect. *Catiang*	1.91	1	1.98	1
Sect. *Macrodontae*	2.73	1	2.18	1
Sect. *Reticulatae*	0.82	1	0.7	1
Sect. *Plectrotropis*	1.04	1	1.53	1

Clade *V. kirkii/stenophylla*	2.16	1	2.18	1
Subg. *Ceratotropis*	2.89	0.28	3.57	1
Subg. *Haydonia*	4.68	1	3.19	1
Sect. *Haydonia*	1.72	1	0.57	1
Sect. *Glossostylus*	3.26	1	0.86	1
Subg. *Vigna*	4.89	0.26	4.91	1
Vigna unguiculata	0.72	1	0.74	1
Vigna radiata	0.22	1	2.89	0.84
Subg. *Lasiospron*	2.4	1	2.45	1
Genus *Physostigma*	2.83	1	7.8	1
Genus *Vigna* s.s.	6.3	1	6.73	1

Figure Legends

Figure 1. Diagram of taxonomic and classification schemes regarding *Vigna* over time.

Figure 2. Floral diversity within *Vigna* s.s. Subg. *Lasiospron*: A) *V. trichocarpa*, B) *V. lasiocarpa*. Subg. *Vigna:* C) *V. pubigera*; D) *V. parkeri* subsp. *maranguensis*. Subg. *Haydonia* sect. *Glossostylus*: E) *V. nigritia*. Subg. *Haydonia* sect. Haydonia: F) *V. juncea*. Subg. *Ceratotropis:* G) *V. radiata*. Clade *V. kirkii/stenophylla*: H) *V. kirkii*. Subg. *Plectrotropis* sect. *Macrodontae*: I) *V. caesia*. Subg. *Plectrotropis* sect. *Reticulatae*: J) *V. reticulata*. Subg. *Plectrotropis* sect. *Catiang*: K) *V. unguiculata* subsp. *baoulensis*. Subg. *Plectrotropis* sect. *Plectrotropis*: L) *V. vexillata* var. *ovata*.

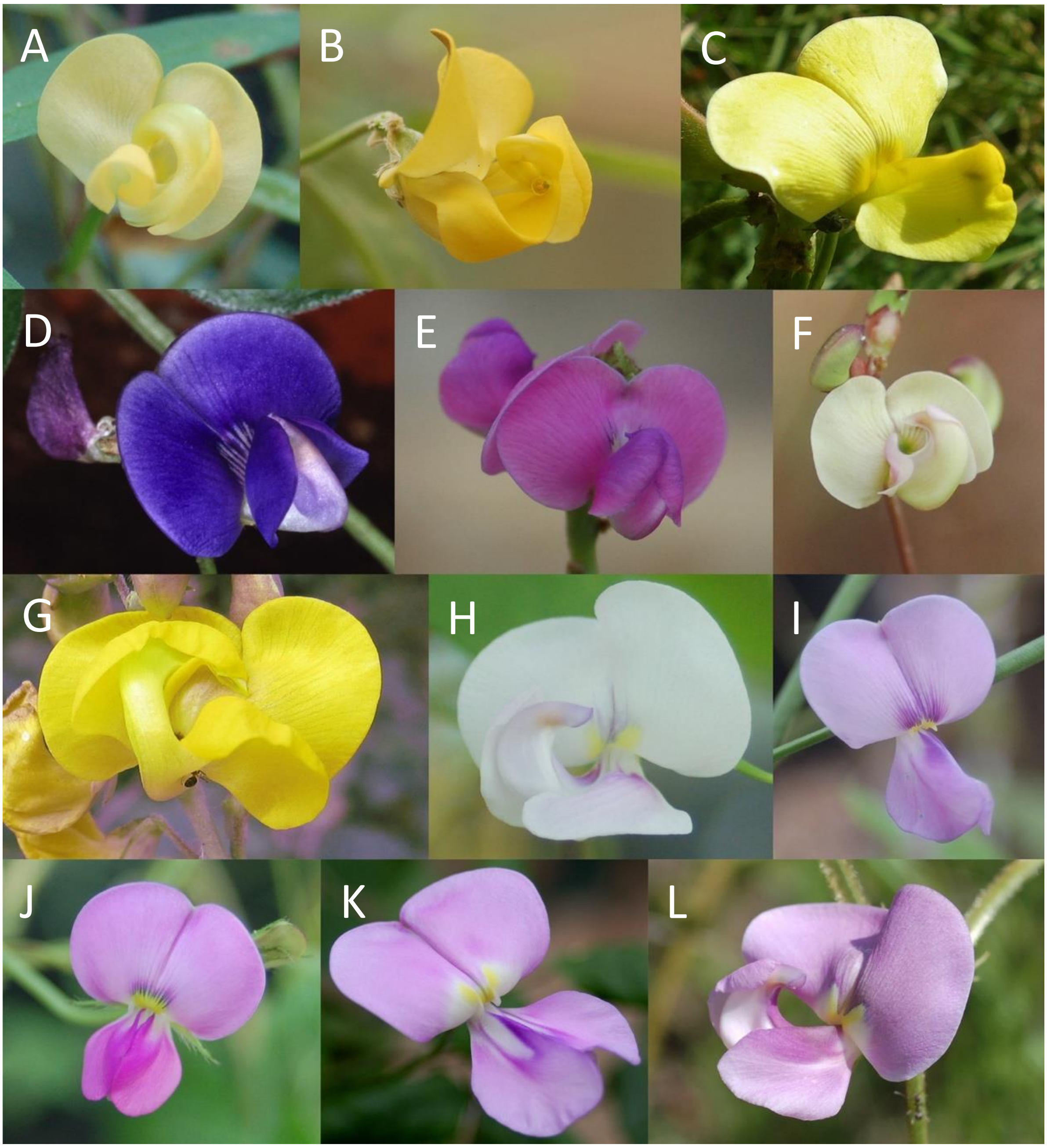


Figure 3. Bayesian inference maximum clade credibility *matK* chronogram. Subgenera and clades of interest are colored by group. Node values represent node age estimate / posterior probability. Alphanumerics following taxon name are accessions numbers according to Supplementary File 1.

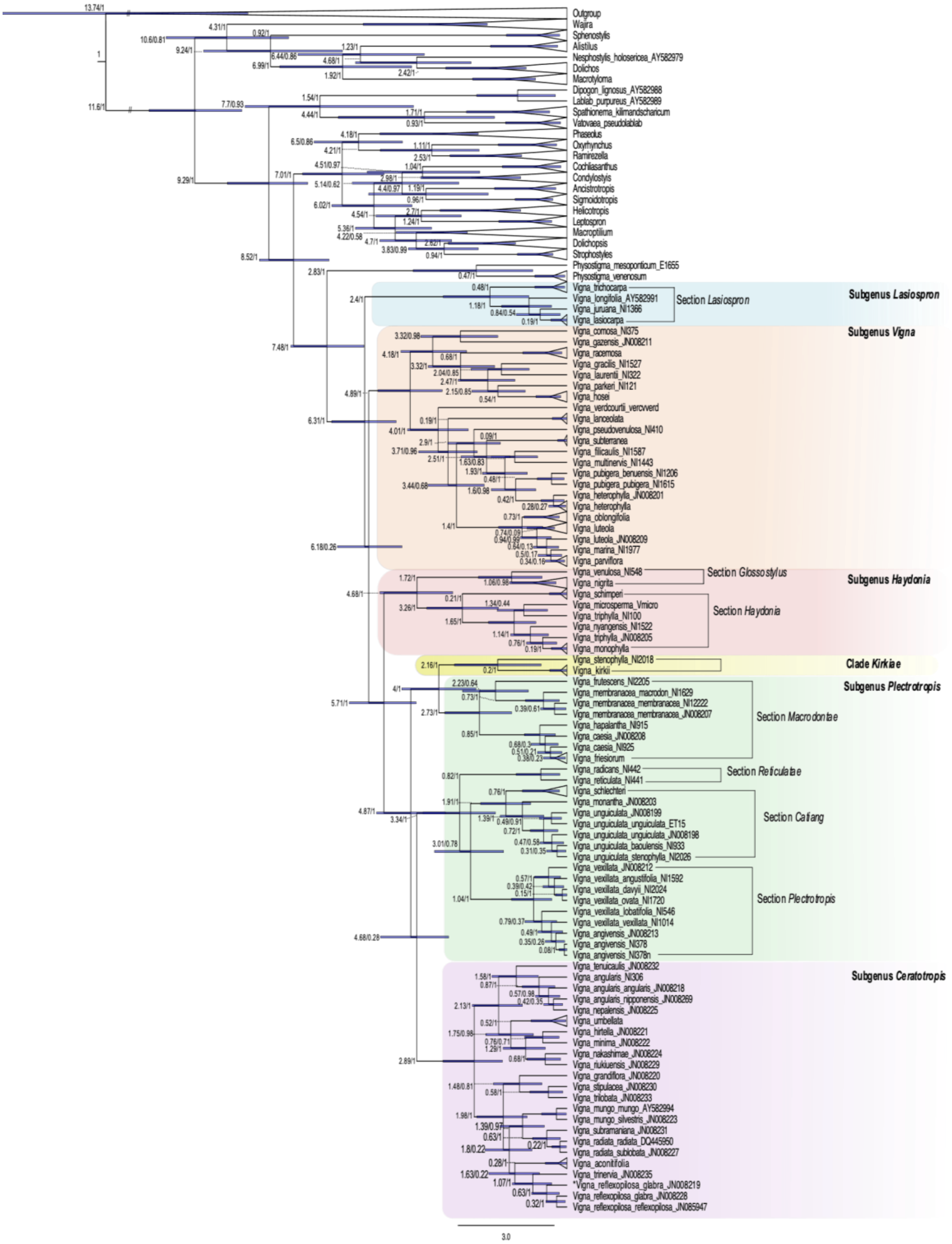


Figure 4. Bayesian inference maximum clade credibility ITS chronogram. Subgenera and clades of interest are colored by group. Node values represent node age estimate / posterior probability. Alphanumerics following taxon name are accessions numbers according to Supplementary File 1.

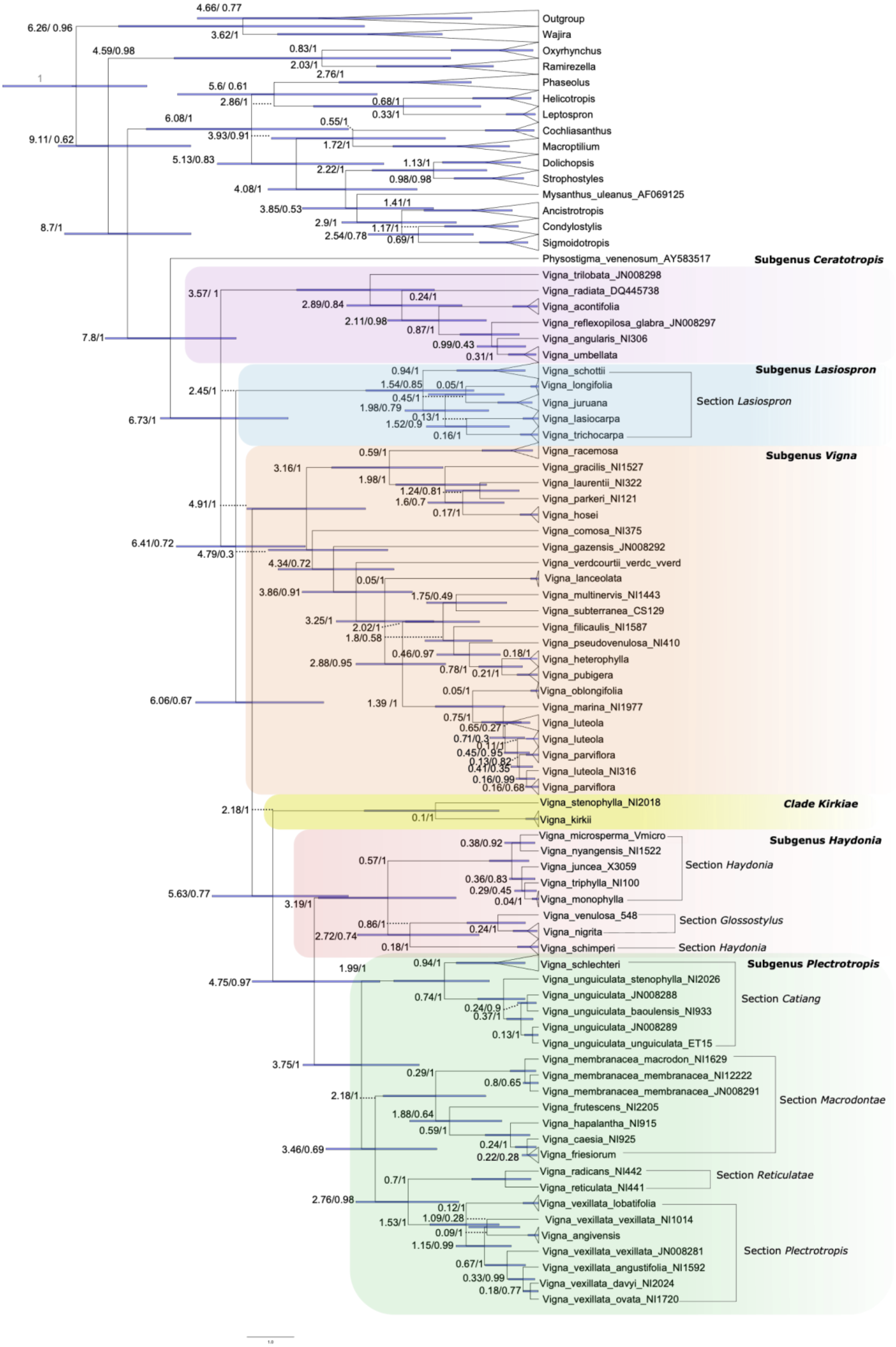


Figure 5. Maximum likelihood RAxML phylogram based on combined data. Node values are bootstrap support values. Alphanumerics following taxon name are accession or GenBank numbers for *matK* and ITS, respectively, with information as in Supplementary File 1.

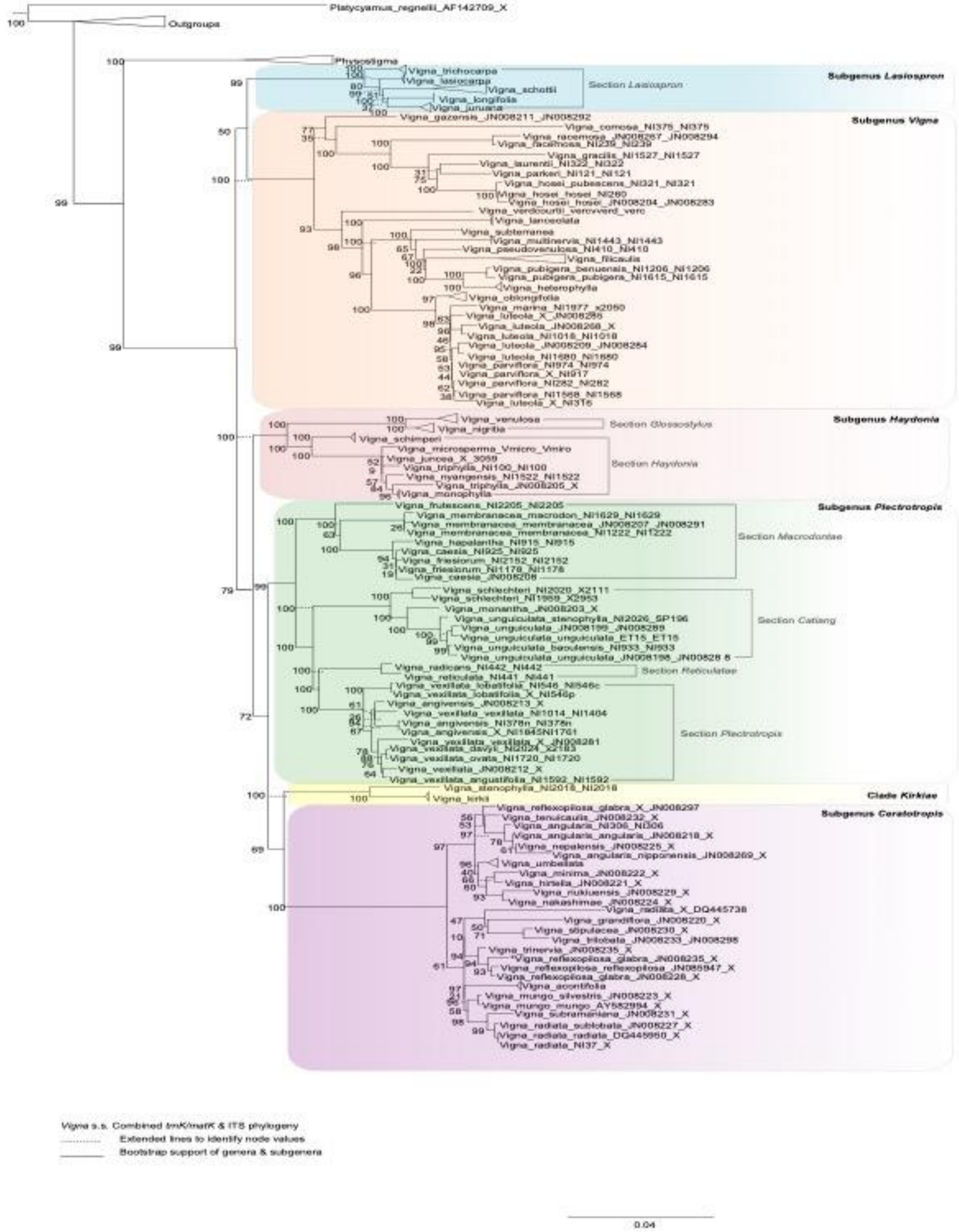


Figure 6. *Physostigma mesoponticum* Taub.: A) flower, B) keel with its appendage, C) style.

Supplementary File 1. Taxon sampling with accession numbers, herbarium voucher information, etc for all taxa (see excel file).

Supplementary Table 1. A breakdown of taxonomic sampling within maximum likelihood datasets. OTUs = operational taxonomic units; number under heading '# genera/sections' represents the number of monophyletic clades that equate to recognized sections, with that in parentheses being the number of historically recognized sections that may be lumped into a clade.

	*mat*K			ITS			combined		
Group	# sp.	# OTUs	# gen./ sect.	# sp.	# OTUs	# gen./ sect.	# sp.	# OTUs	# gen./ sect.
Outgroups	38	42	25				15	15	15
NW Phaseolinae	38	46	13	41	46	16	62	79	23
Physostigma	2	3	1	1	1	1	2	3	1
Vigna s.s.	66	109	1	51	99	1	66	133	1
subg. *Vigna*	22	34	1	19	33	1	19	44	1
subg. *Lasiospron*	4	7	1	5	14	1	5	14	1
subg. *Haydonia*	7	11	2(3)	8	12	2(3)	9	13	3(4)
subg. *Ceratotropis*	18	26	3	6	9	3	19	29	3
subg. *Plectrotropis*	13	28	4	11	28	4	12	30	4
clade *Kirkiae*	2	3	1	2	3	1	2	3	1
Total	144	200	40	93	146	18	145	230	40

Supplemental Table 2: Genome size estimates across *Vigna kirkii, V. stenophylla,* and *V. unguiculata* (control). Iceberg lettuce was used as reference with a known genome size of 2.59 Mb. Run code has plant 1 or 2 preceded by first two letters of species epithet, KM = Kaycie Melville or ANE = Ashley N Egan who performed estimate, last designation is for replicate number.

Species	*Vigna kirkii*								**average**
Plant	Plant 1				Plant 2				
run code	Ki1-KM-1	Ki1-KM-2	Ki1-ANE-1	Ki2-ANE-2	Ki2-KM-1	Ki2-KM-2	Ki2-ANE-1	Ki2-ANE-2	
Lettuce FC size	361815.6	304630.8	256383	344255.4	337509	343976.4	338765.9	322436.7	326221.6
Vigna FC size (peak 1)	82931.7	72182.3	59303.5	78894.5	77477	79519.2	84226.1	74636.6	76146.36
Peak 2	165876.1	142527.3	118175.8	155822.3	152518.5	155538.9	165210.3	149020.1	150586.2
Vigna Genome size (Mb)	593.65352	613.70077	599.08834	593.56151	594.54838	598.74668	643.94202	599.52479	**604.5958**

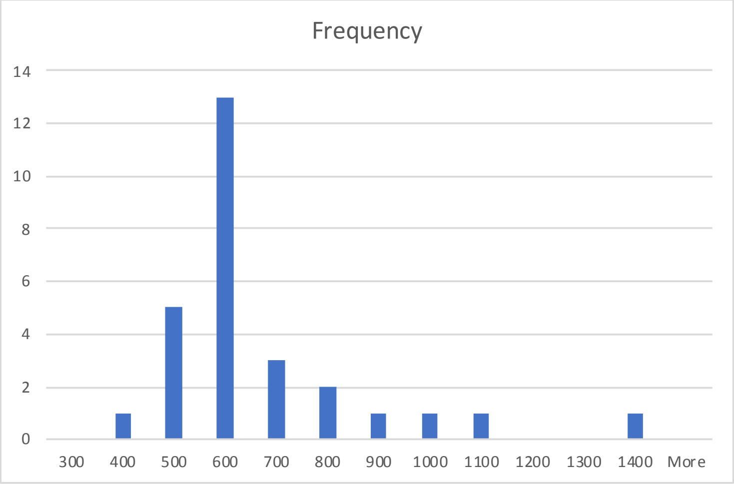
Species	*Vigna stenophylla*								**average**
Plant	Plant 1				Plant 2				
run code	St1-KM-1	St1-KM-2	St1-ANE-1	St2-ANE-2	St2-KM-1	St2-KM-2	St2-ANE-1	St2-ANE-2	
Lettuce FC size			342785.1	350548.2	330117.9	304999.6	329788.6	315325.5	328927.5
Vigna FC size (peak 1)			106819.9	112587.5	104364.6	96986.6	102745.5	98335.2	103639.9
Peak 2			213765.8	223129.7	205895.4	191294.9	205503.5	195805.6	205899.2
Vigna Genome size (Mb)			797.75622	822.20933	809.32714	814.05253	797.56693	798.34365	**806.5426**

Species	*Vigna unguiculata*								**average**
Plant	Plant 1				Plant 4				
run code	Un1-KM-1	Un1-KM-2	Un1-ANE-1	Un2-ANE-2	Un2-KM-1	Un2-KM-2	Un2-ANE-1	Un2-ANE-2	
Lettuce FC size		361000.7	408184.2	334812.3			375036.7	343151	364437
Vigna FC size (peak 1)		89188.3	96819.4	87322.6			99166.1	94265.4	93352.36
Peak 2		171586.9	n/a	171437			n/a	185479.4	176167.8
Vigna Genome size (Mb)		639.88158	614.33599	675.49948			684.84017	711.48674	**665.2088**

Supplementary Table 3. Genome size estimates for various *Vigna* species gathered from the literature.

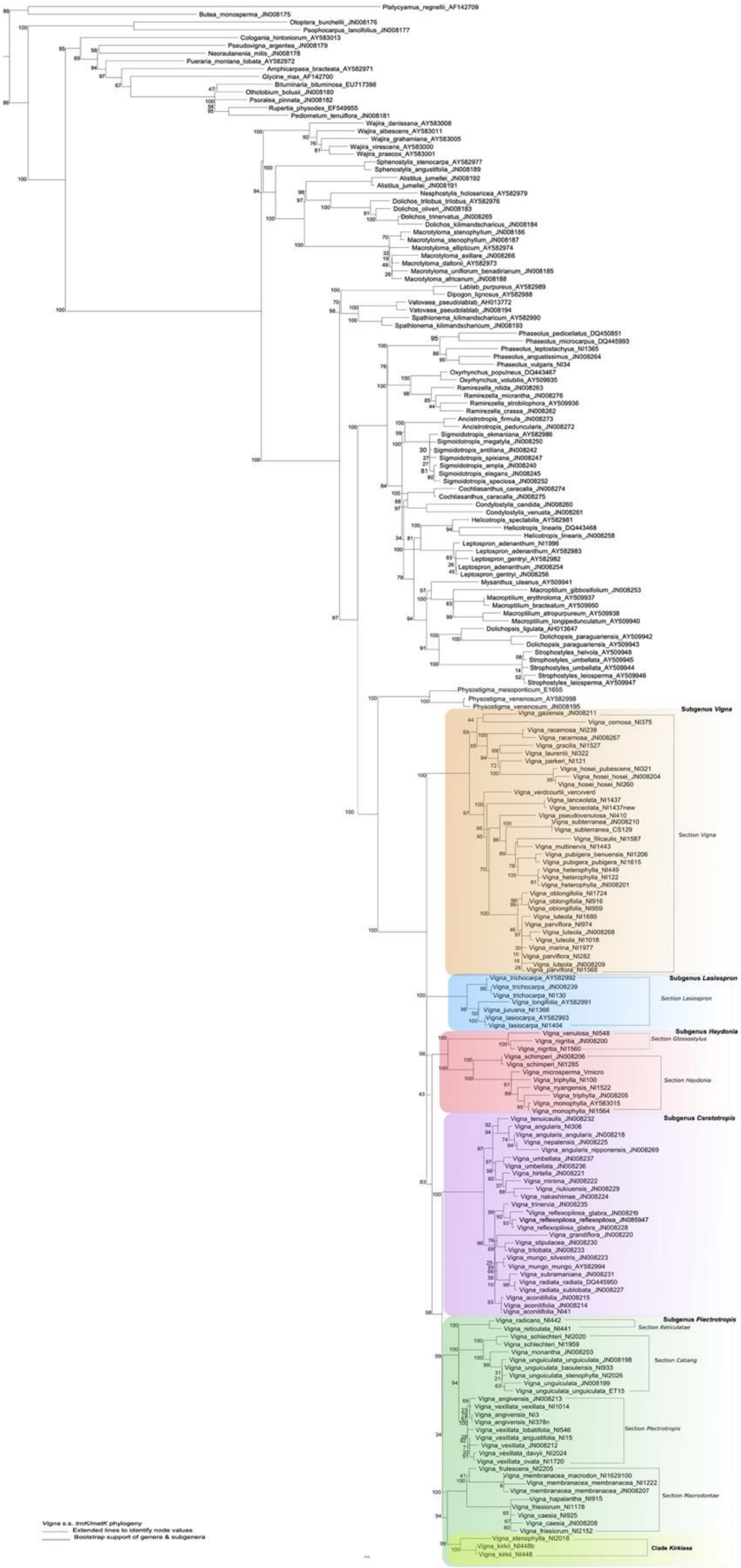
	species	**gs (mb)**	**method**	**reference**
Vigna	*aconitifolia*	370	k-mer distribution	Suranjika et al 2023
Vigna	*aconitifolia*	1078	flow cytometry	Lakhanpaul & Babu 1991
Vigna	*angularis*	490	flow cytometry	Parida et al 1990
Vigna	*angularis*	533	k-mer distribution	Naito et al 2022
Vigna	*angularis*	538	k-mer distribution	Kang et al 2015
Vigna	*angularis*	612	k-mer distribution	Kang et al 2015
Vigna	*luteola*	1372	flow cytometry	Parida et al 1990
Vigna	*marina*	570	k-mer distribution	Naito et al 2022
Vinga	*minima*	521	k-mer distribution	Naito et al 2022
Vigna	*mungo*	584	k-mer distribution	Naito et al 2022
Vigna	*nakashimae*	756	k-mer distribution	Lestari et al 2014
Vigna	*oblongifolia*	490	flow cytometry	Parida et al 1990
Vigna	*parviflora*	588	flow cytometry	Parida et al 1990
Vigna	*radiata radiata*	579	k-mer distribution	Kang et al 2014
Vigna	*radiata var. sublobata*	501	k-mer distribution	Kang et al 2014
Vigna	*reflexopilosa glabra*	968	k-mer distribution	Kang et al 2014
Vigna	*riukiuensis*	512	k-mer distribution	Naito et al 2022
Vigna	*stipulacea*	442	k-mer distribution	Naito et al 2022
Vigna	*subterranea*	528	unknown	www.pulsedb.org
Vigna	*subterranea*	535	k-mer distribution	Kang et al 2014
Vigna	*subterranea*	882	flow cytometry	Lakhanpaul & Babu 1991
Vigna	*trilobata*	490	flow cytometry	Parida et al 1990
Vigna	*trilobata*	560	k-mer distribution	Naito et al 2022
Vigna	*umbellata*	455	k-mer distribution	Kang et al 2014
Vigna	*unguiculata*	620	k-mer distribution	Lonardi et al 2019
Vigna	*unguiculata*	641	flow cytometry	Lonardi et al 2019
Vigna	*vexillata*	588	flow cytometry	Parida et al 1990
Vigna	*vexillata*	715	k-mer distribution	Naito et al 2022

gs (mb)	
Mean	625.64
Standard Error	40.516
Median	565
Mode	490
Standard Deviation	214.39
Sample Variance	45963
Kurtosis	4.9297
Skewness	2.1228
Range	1002
Minimum	370
Maximum	1372
Sum	17518
Count	28
Confidence Level(95.0%)	83.131

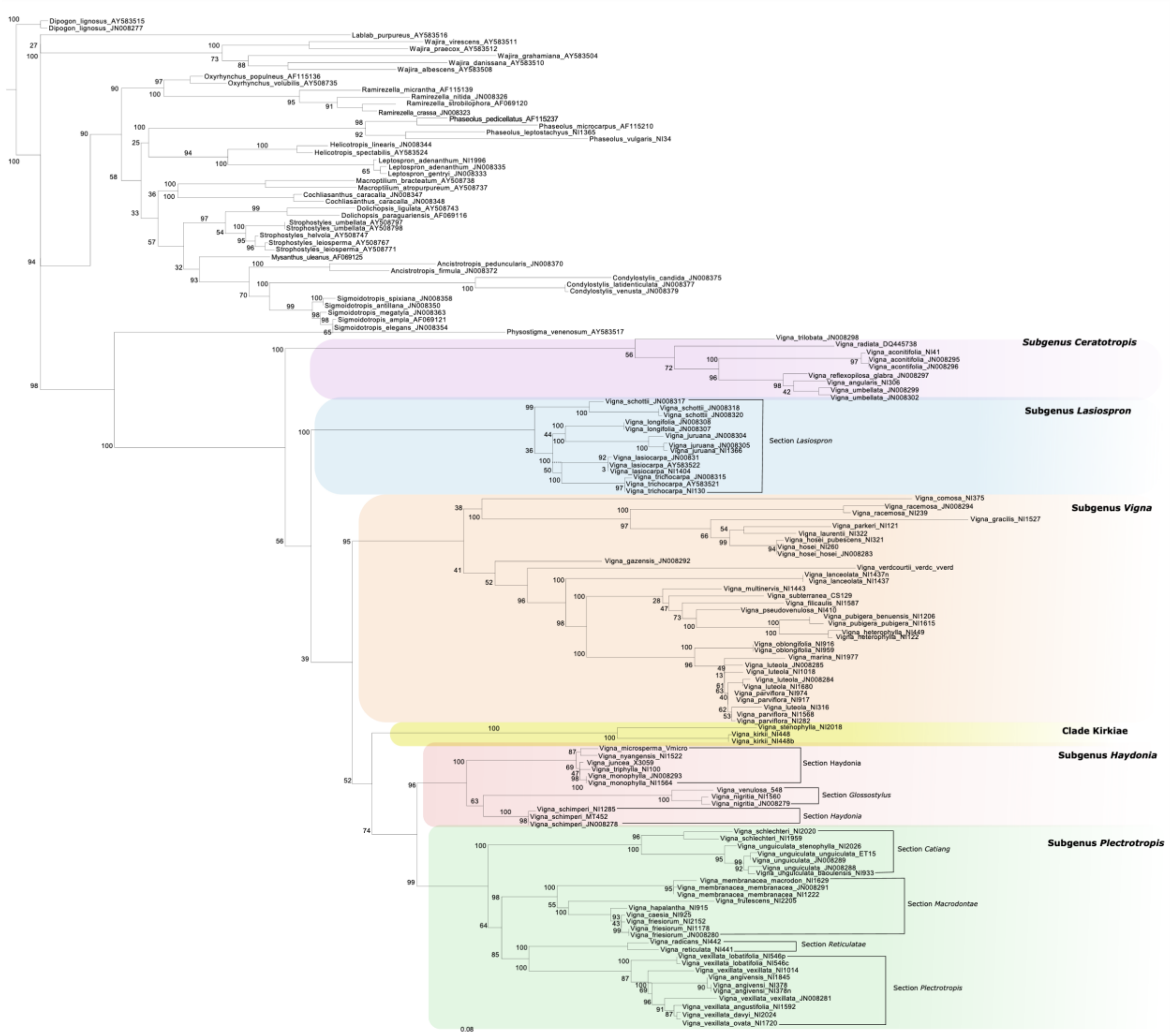


Bins in increments of 100

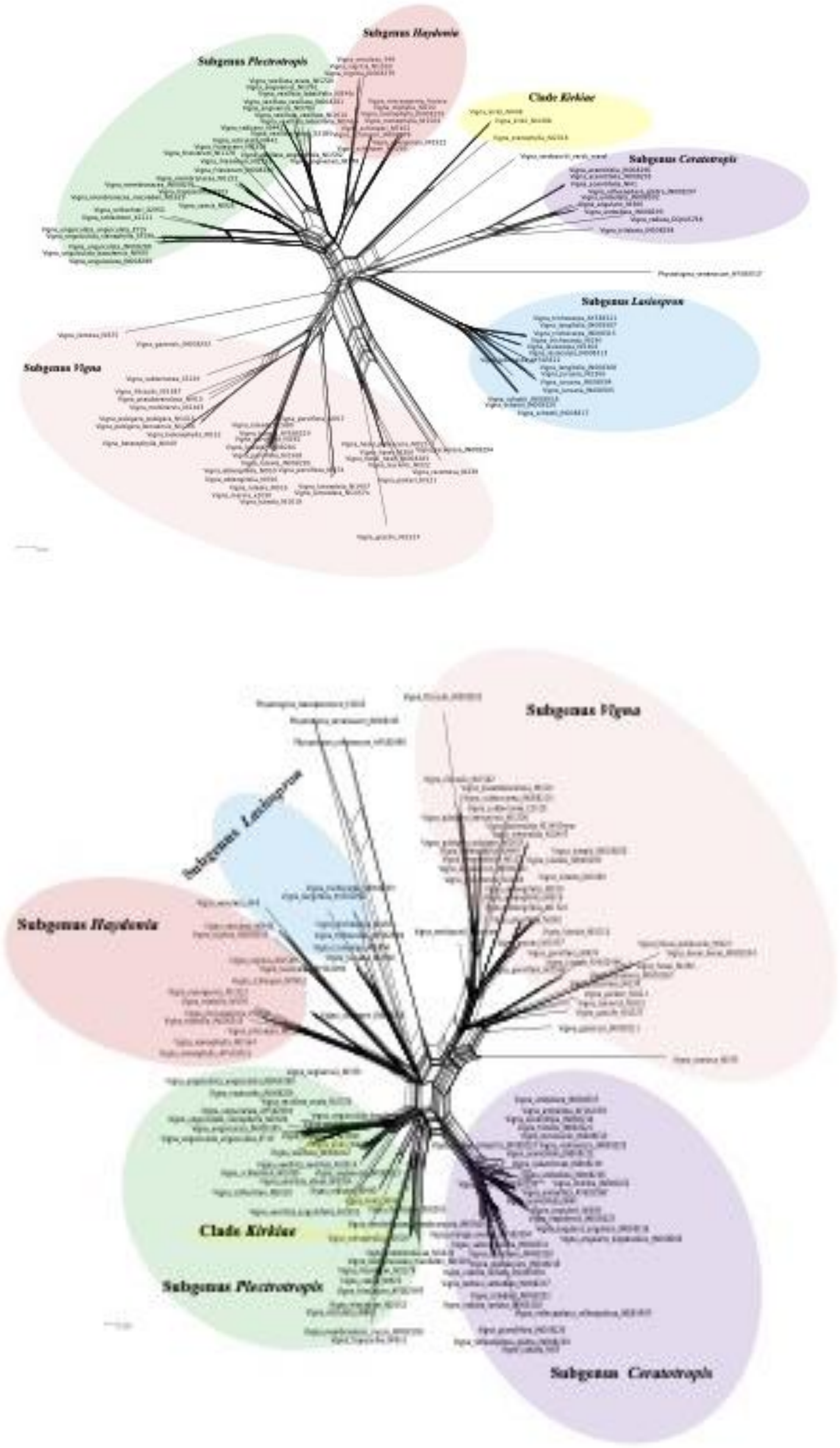
Supplementary figure 1. Best tree from Maximum likelihood phylogram of *matK* estimated using RAxML. Node numbers are bootstrap support values. Alphanumerics after taxon name are accession numbers as in Supplementary File 1.



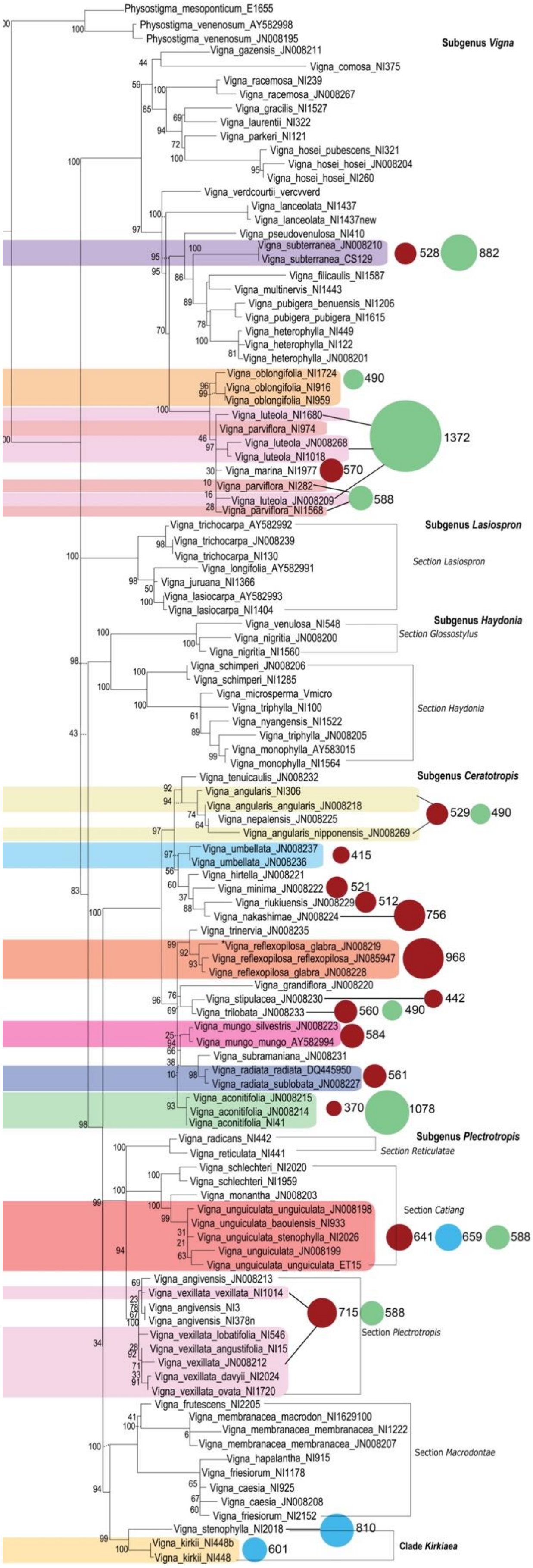
Supplementary figure 2. Best tree from Maximum likelihood phylogram of ITS estimated using RAxML. Node numbers are bootstrap support values. Alphanumerics after taxon name are accession numbers as in Supplementary File 1.



Supplementary figure 3. Splitstree analyses of ITS and *MatK* alignments. Top: ITS; Bottom: *matK*



Supplementary figure 4. Genome size estimates from this study and others, collated from the literature, mapped on the *matK* ML (left) and BI ITS (right) trees cropped to *Vigna* s.s. The size of the circle is proportional to the genome size (GS) estimate. Colors designate GS estimated in this study (blue), 1C values in megabases (mb) (green) and undesignated C values (mb) from literature. See also supplementary table 3.



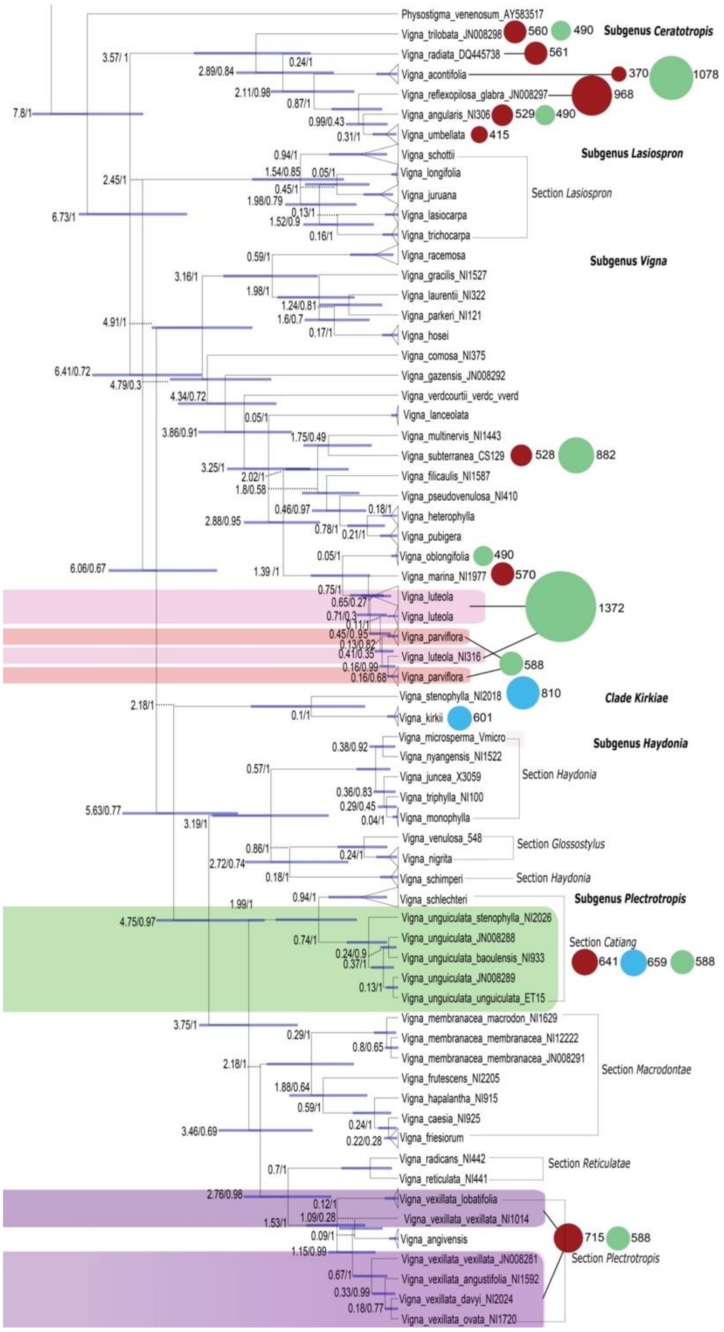


Figure 1

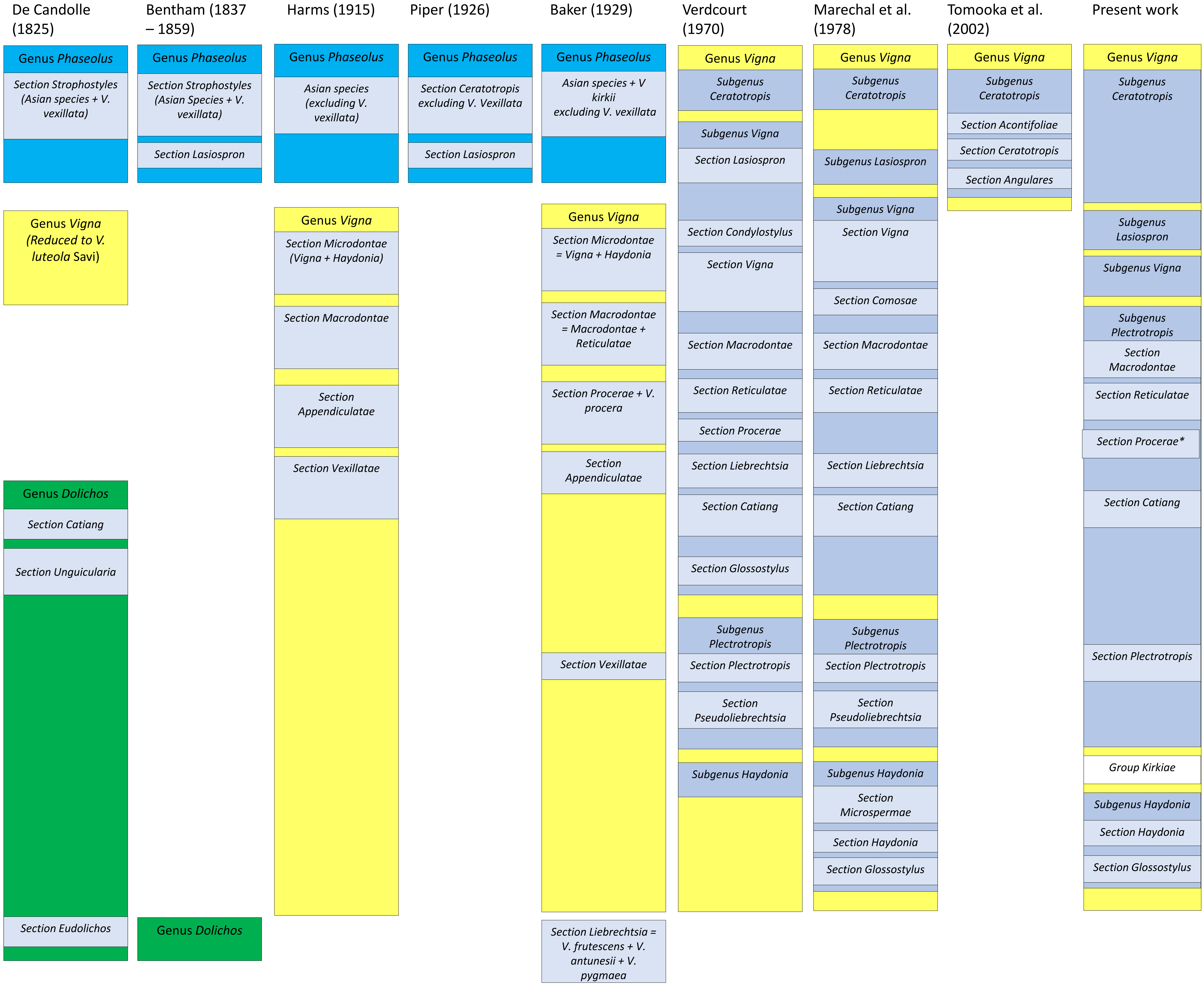

De Candolle (1825)
Genus *Phaseolus*
Section Strophostyles (Asian species + V. vexillata)
Genus *Vigna* (Reduced to V. luteola Savi)
Genus *Dolichos*
Section Catiang
Section Unguicularia
Section Eudolichos
Bentham (1837 – 1859)
Genus *Phaseolus*
Section Strophostyles (Asian Species + V. vexillata)
Section Lasiospron
Genus *Dolichos*
Harms (1915)
Genus *Phaseolus*
Asian species (excluding V. vexillata)
Genus *Vigna*
Section Microdontae (Vigna + Haydonia)
Section Macrodontae
Section Appendiculatae
Section Vexillatae
Piper (1926)
Genus *Phaseolus*
Section Ceratotropis excluding V. Vexillata
Section Lasiospron
Baker (1929)
Genus *Phaseolus*
Asian species + V kirkii excluding V. vexillata
Genus *Vigna*
Section Microdontae = Vigna + Haydonia
Section Macrodontae = Macrodontae + Reticulatae
Section Procerae + V. procera
Section Appendiculatae
Section Vexillatae
Section Liebrechtsia = V. frutescens + V. antunesii + V. pygmaea
Verdcourt (1970)
Genus *Vigna*
Subgenus Ceratotropis
Subgenus Vigna
Section Lasiospron
Section Condylostylus
Section Vigna
Section Macrodontae
Section Reticulatae
Section Procerae
Section Liebrechtsia
Section Catiang
Section Glossostylus
Subgenus Plectrotropis
Section Plectrotropis
Section Pseudoliebrechtsia
Subgenus Haydonia
Marechal et al. (1978)
Genus *Vigna*
Subgenus Ceratotropis
Subgenus Lasiospron
Subgenus Vigna
Section Vigna
Section Comosae
Section Macrodontae
Section Reticulatae
Section Liebrechtsia
Section Catiang
Subgenus Plectrotropis
Section Plectrotropis
Section Pseudoliebrechtsia
Subgenus Haydonia
Section Microspermae
Section Haydonia
Section Glossostylus
Tomooka et al. (2002)
Genus *Vigna*
Subgenus Ceratotropis
Section Acontifoliae
Section Ceratotropis
Section Angulares
Present work
Genus *Vigna*
Subgenus Ceratotropis
Subgenus Lasiospron
Subgenus Vigna
Subgenus Plectrotropis
Section Macrodontae
Section Reticulatae
Section Procerae*
Section Catiang
Section Plectrotropis
Group Kirkiae
Subgenus Haydonia
Section Haydonia
Section Glossostylus

Figure 2

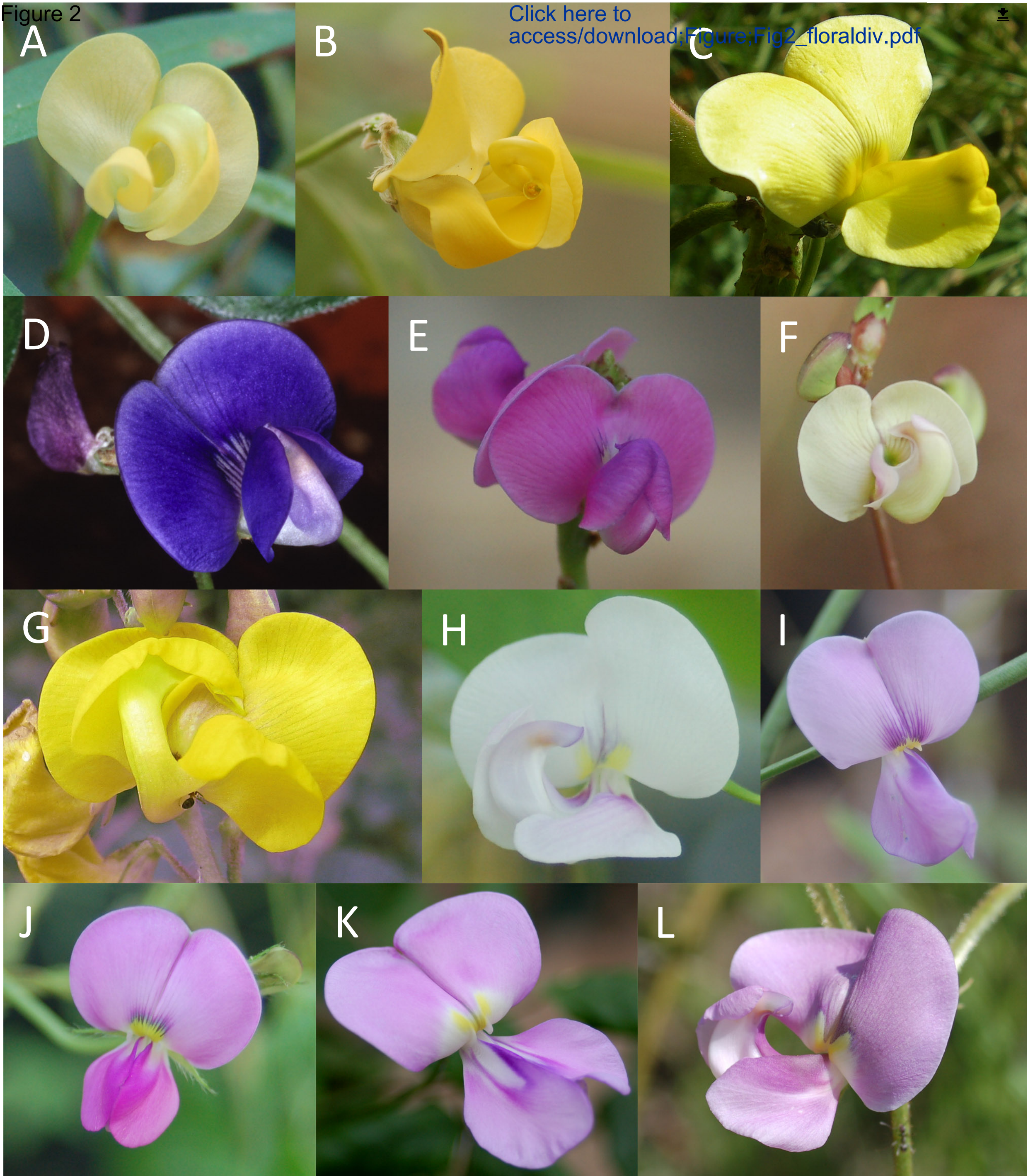
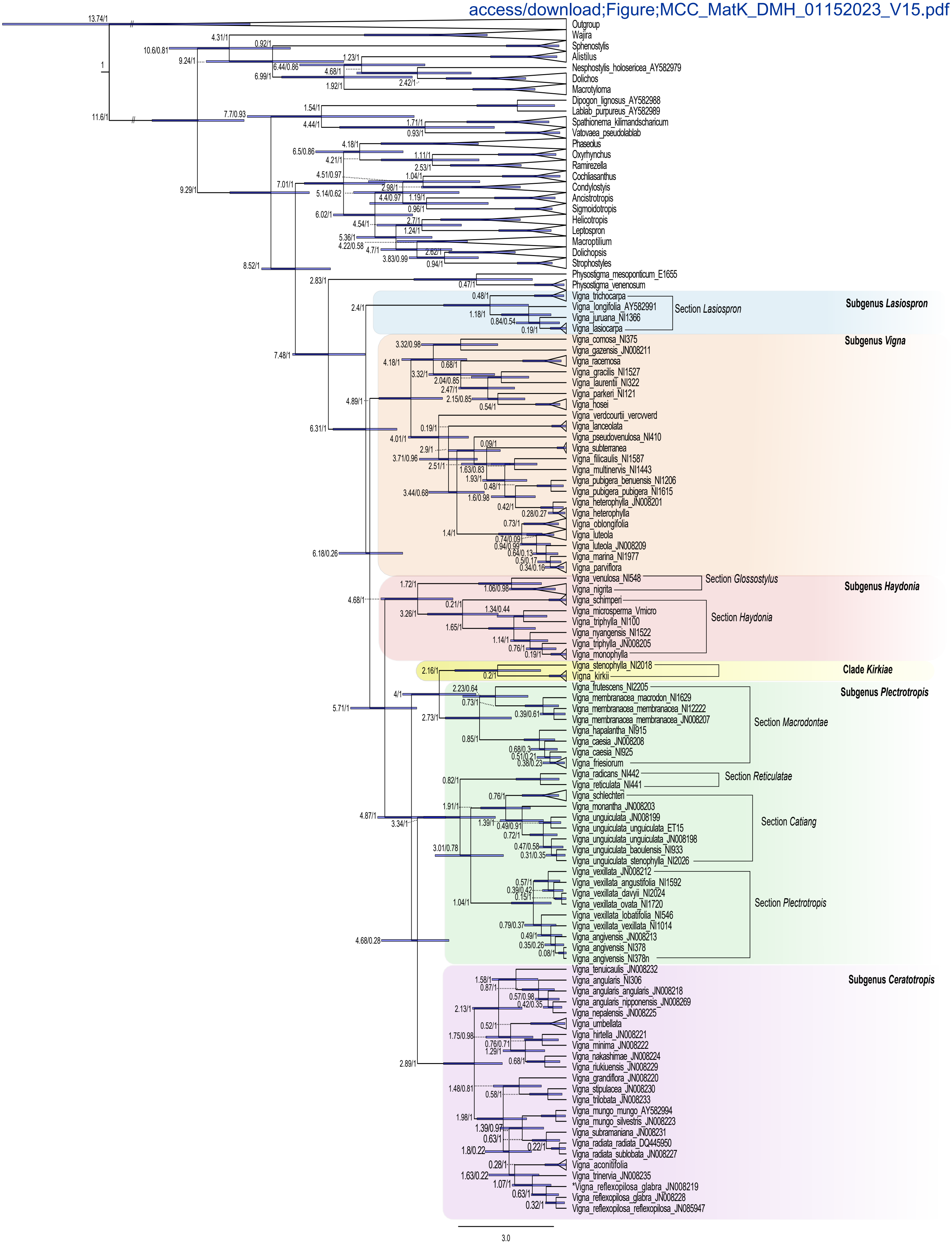


Figure 3


13.74/1
1
10.6/0.81
4.31/1
0.92/1
9.24/1
1.23/1
6.44/0.86
4.68/1
6.99/1
2.42/1
1.92/1
11.6/1
7.7/0.93
1.54/1
4.44/1
1.71/1
0.93/1
4.18/1
6.5/0.86
1.11/1
4.21/1
2.53/1
4.51/0.97
1.04/1
7.01/1
2.98/1
9.29/1
5.14/0.62
4.4/0.97
1.19/1
0.96/1
6.02/1
2.7/1
4.54/1
1.24/1
5.36/1
4.22/0.58
4.7/1
2.62/1
3.83/0.99
0.94/1
8.52/1
2.83/1
0.47/1
0.48/1
2.4/1
1.18/1
0.84/0.54
0.19/1
3.32/0.98
7.48/1
4.18/1
0.68/1
3.32/1
2.04/0.85
2.47/1
4.89/1
2.15/0.85
0.54/1
0.19/1
6.31/1
4.01/1
0.09/1
2.9/1
3.71/0.96
2.51/1
1.63/0.83
1.93/1
0.48/1
3.44/0.68
1.6/0.98
0.42/1
0.28/0.27
0.73/1
1.4/1
0.74/0.09
0.94/0.99
0.64/0.13
6.18/0.26
0.5/0.17
0.34/0.16
1.72/1
1.06/0.98
4.68/1
0.21/1
3.26/1
1.34/0.44
1.65/1
1.14/1
0.76/1
0.19/1
2.16/1
0.2/1
2.23/0.64
4/1
0.73/1
5.71/1
2.73/1
0.39/0.61
0.85/1
0.68/0.3
0.51/0.21
0.38/0.23
0.82/1
0.76/1
1.91/1
4.87/1
3.34/1
1.39/1
0.49/0.91
0.72/1
3.01/0.78
0.47/0.58
0.31/0.35
0.57/1
0.39/0.42
0.15/1
1.04/1
0.79/0.37
0.49/1
4.68/0.28
0.35/0.26
0.08/1
1.58/1
0.87/1
0.57/0.98
0.42/0.35
2.13/1
0.52/1
1.75/0.98
0.76/0.71
1.29/1
0.68/1
2.89/1
1.48/0.81
0.58/1
1.98/1
1.39/0.97
0.63/1
0.22/1
1.8/0.22
0.28/1
1.63/0.22
1.07/1
0.63/1
0.32/1
Outgroup
Wajira
Sphenostylis
Alistilus
Nesphostylis_holosericea_AY582979
Dolichos
Macrotyloma
Dipogon_lignosus_AY582988
Lablab_purpureus_AY582989
Spathionema_kilimandscharicum
Vatovaea_pseudolablab
Phaseolus
Oxyrhynchus
Ramirezella
Cochliasanthus
Condylostylis
Ancistrotropis
Sigmoidotropis
Helicotropis
Leptospron
Macroptilium
Dolichopsis
Strophostyles
Physostigma_mesoponticum_E1655
Physostigma_venenosum
Vigna_trichocarpa
Vigna_longifolia_AY582991
Vigna_juruana_NI1366
Vigna_lasiocarpa
Section *Lasiospron*
Subgenus *Lasiospron*
Vigna_comosa_NI375
Vigna_gazensis_JN008211
Vigna_racemosa
Vigna_gracilis_NI1527
Vigna_laurentii_NI322
Vigna_parkeri_NI121
Vigna_hosei
Vigna_verdcourtii_vercvverd
Vigna_lanceolata
Vigna_pseudovenulosa_NI410
Vigna_subterranea
Vigna_filicaulis_NI1587
Vigna_multinervis_NI1443
Vigna_pubigera_benuensis_NI1206
Vigna_pubigera_pubigera_NI1615
Vigna_heterophylla_JN008201
Vigna_heterophylla
Vigna_oblongifolia
Vigna_luteola
Vigna_luteola_JN008209
Vigna_marina_NI1977
Vigna_parviflora
Subgenus *Vigna*
Vigna_venulosa_NI548
Vigna_nigrita
Section *Glossostylus*
Vigna_schimperi
Vigna_microsperma_Vmicro
Vigna_triphylla_NI100
Vigna_nyangensis_NI1522
Vigna_triphylla_JN008205
Vigna_monophylla
Section *Haydonia*
Subgenus *Haydonia*
Vigna_stenophylla_NI2018
Vigna_kirkii
Clade *Kirkiae*
Vigna_frutescens_NI2205
Vigna_membranacea_macrodon_NI1629
Vigna_membranacea_membranacea_NI12222
Vigna_membranacea_membranacea_JN008207
Vigna_hapalantha_NI915
Vigna_caesia_JN008208
Vigna_caesia_NI925
Vigna_friesiorum
Section *Macrodontae*
Subgenus *Plectrotropis*
Vigna_radicans_NI442
Vigna_reticulata_NI441
Section *Reticulatae*
Vigna_schlechteri
Vigna_monantha_JN008203
Vigna_unguiculata_JN008199
Vigna_unguiculata_unguiculata_ET15
Vigna_unguiculata_unguiculata_JN008198
Vigna_unguiculata_baoulensis_NI933
Vigna_unguiculata_stenophylla_NI2026
Section *Catiang*
Vigna_vexillata_JN008212
Vigna_vexillata_angustifolia_NI1592
Vigna_vexillata_davyii_NI2024
Vigna_vexillata_ovata_NI1720
Vigna_vexillata_lobatifolia_NI546
Vigna_vexillata_vexillata_NI1014
Vigna_angivensis_JN008213
Vigna_angivensis_NI378
Vigna_angivensis_NI378n
Section *Plectrotropis*
Vigna_tenuicaulis_JN008232
Vigna_angularis_NI306
Vigna_angularis_angularis_JN008218
Vigna_angularis_nipponensis_JN008269
Vigna_nepalensis_JN008225
Vigna_umbellata
Vigna_hirtella_JN008221
Vigna_minima_JN008222
Vigna_nakashimae_JN008224
Vigna_riukiuensis_JN008229
Vigna_grandiflora_JN008220
Vigna_stipulacea_JN008230
Vigna_trilobata_JN008233
Vigna_mungo_mungo_AY582994
Vigna_mungo_silvestris_JN008223
Vigna_subramaniana_JN008231
Vigna_radiata_radiata_DQ445950
Vigna_radiata_sublobata_JN008227
Vigna_aconitifolia
Vigna_trinervia_JN008235
*Vigna_reflexopilosa_glabra_JN008219
Vigna_reflexopilosa_glabra_JN008228
Vigna_reflexopilosa_reflexopilosa_JN085947
Subgenus *Ceratotropis*
3.0


4.66/ 0.77
6.26/ 0.96
3.62/1
4.59/0.98
0.83/1
2.03/1
1
2.76/1
5.6/ 0.61
2.86/1
0.68/1
0.33/1
6.08/1
0.55/1
3.93/0.91
9.11/ 0.62
1.72/1
5.13/0.83
2.22/1
1.13/1
0.98/0.98
4.08/1
1.41/1
3.85/0.53
2.9/1
8.7/1
1.17/1
2.54/0.78
0.69/1
Outgroup
Wajira
Oxyrhynchus
Ramirezella
Phaseolus
Helicotropis
Leptospron
Cochliasanthus
Macroptilium
Dolichopsis
Strophostyles
Mysanthus_uleanus_AF069125
Ancistrotropis
Condylostylis
Sigmoidotropis
Physostigma_venenosum_AY583517
Subgenus Ceratotropis
3.57/ 1
2.89/0.84
0.24/1
2.11/0.98
0.87/1
7.8/1
0.99/0.43
0.31/1
Vigna_trilobata_JN008298
Vigna_radiata_DQ445738
Vigna_acontifolia
Vigna_reflexopilosa_glabra_JN008297
Vigna_angularis_NI306
Vigna_umbellata
Subgenus Lasiospron
0.94/1
1.54/0.85
0.05/1
2.45/1
0.45/1
1.98/0.79
0.13/1
6.73/1
1.52/0.9
0.16/1
Vigna_schottii
Vigna_longifolia
Vigna_juruana
Vigna_lasiocarpa
Vigna_trichocarpa
Section Lasiospron
Subgenus Vigna
0.59/1
3.16/1
1.98/1
1.24/0.81
1.6/0.7
4.91/1
0.17/1
6.41/0.72
4.79/0.3
4.34/0.72
0.05/1
3.86/0.91
1.75/0.49
3.25/1
2.02/1
1.8/0.58
0.46/0.97
0.18/1
2.88/0.95
0.78/1
0.21/1
0.05/1
6.06/0.67
1.39 /1
0.75/1
0.65/0.27
0.71/0.3
0.11/1
0.45/0.95
0.13/0.82
0.41/0.35
0.16/0.99
0.16/0.68
Vigna_racemosa
Vigna_gracilis_NI1527
Vigna_laurentii_NI322
Vigna_parkeri_NI121
Vigna_hosei
Vigna_comosa_NI375
Vigna_gazensis_JN008292
Vigna_verdcourtii_verdc_vverd
Vigna_lanceolata
Vigna_multinervis_NI1443
Vigna_subterranea_CS129
Vigna_filicaulis_NI1587
Vigna_pseudovenulosa_NI410
Vigna_heterophylla
Vigna_pubigera
Vigna_oblongifolia
Vigna_marina_NI1977
Vigna_luteola
Vigna_luteola
Vigna_parviflora
Vigna_luteola_NI316
Vigna_parviflora
Clade Kirkiae
2.18/1
0.1/1
Vigna_stenophylla_NI2018
Vigna_kirkii
Subgenus Haydonia
0.38/0.92
0.57/1
0.36/0.83
0.29/0.45
5.63/0.77
0.04/1
3.19/1
0.86/1
0.24/1
2.72/0.74
0.18/1
Vigna_microsperma_Vmicro
Vigna_nyangensis_NI1522
Vigna_juncea_X3059
Vigna_triphylla_NI100
Vigna_monophylla
Section Haydonia
Vigna_venulosa_548
Vigna_nigrita
Vigna_schimperi
Section Glossostylus
Section Haydonia
Subgenus Plectrotropis
0.94/1
1.99/1
4.75/0.97
0.74/1
0.24/0.9
0.37/1
0.13/1
3.75/1
0.29/1
0.8/0.65
2.18/1
1.88/0.64
0.59/1
3.46/0.69
0.24/1
0.22/0.28
0.7/1
2.76/0.98
0.12/1
1.09/0.28
1.53/1
0.09/1
1.15/0.99
0.67/1
0.33/0.99
0.18/0.77
Vigna_schlechteri
Vigna_unguiculata_stenophylla_NI2026
Vigna_unguiculata_JN008288
Vigna_unguiculata_baoulensis_NI933
Vigna_unguiculata_JN008289
Vigna_unguiculata_unguiculata_ET15
Section Catiang
Vigna_membranacea_macrodon_NI1629
Vigna_membranacea_membranacea_NI12222
Vigna_membranacea_membranacea_JN008291
Vigna_frutescens_NI2205
Vigna_hapalantha_NI915
Vigna_caesia_NI925
Vigna_friesiorum
Section Macrodontae
Vigna_radicans_NI442
Vigna_reticulata_NI441
Section Reticulatae
Vigna_vexillata_lobatifolia
Vigna_vexillata_vexillata_NI1014
Vigna_angivensis
Vigna_vexillata_vexillata_JN008281
Vigna_vexillata_angustifolia_NI1592
Vigna_vexillata_davyi_NI2024
Vigna_vexillata_ovata_NI1720
Section Plectrotropis
1.0

Figure 5


Platycyamus_regnellii_AF142709_X
Butea_monosperma_JN008175_X
Otoptera_burchellii_JN008176_X
Psophocarpus_lancifolius_JN008177_X
Cologania_hintoniorum_AY583013_X
Neorautanenia_mitis_JN008178_X
Pseudovigna_argentea_JN008179_X
Pueraria_montana_lobata_AY582972_X
Amphicarpaea_bracteata_AY582971_X
Glycine_max_AF142700_X
Otholobium_bolusii_JN008180_X
Bituminaria_bituminosa_EU717398_X
Psoralea_pinnata_JN008182_X
Psoralea_tenuiflora_JN008181_X
Rupertia_physodes_EF549955_X
Wajira_danissana_AY583008_AY583510
Wajira_albescens_AY583011_AY583508
Wajira_grahamiana_AY583005_AY583504
Wajira_virescens_AY583000_AY583511
Wajira_praecox_AY583001_AY583512
Sphenostylis_stenocarpa_AY582977_X
Sphenostylis_angustifolia_JN008189_X
Alistilus_jumellei_JN008192_X
Alistilus_jumellei_JN008191_X
Nesphostylis_holosericea_AY582979_X
Dolichos_trilobus_trilobus_AY582976_X
Dolichos_oliveri_JN008183_X
Dolichos_kilimandscharicus_JN008184_X
Dolichos_trinervatus_JN008265_X
Macrotyloma_ellipticum_AY582974_X
Macrotyloma_stenophyllum_JN008186_X
Macrotyloma_stenophyllum_JN008187_X
Macrotyloma_daltonii_AY582973_X
Macrotyloma_uniflorum_benadirianum_JN008185_X
Macrotyloma_africanum_JN008188_X
Macrotyloma_axillare_JN008266_X
Lablab_purpureus_AY582989_AY583516
Dipogon_lignosus_X_JN008277
Dipogon_lignosus_AY582988_AY583515
Vatovaea_pseudolablab_JN008194_X
Vatovaea_pseudolablab_AH013772_X
Spathionema_kilimandscharicum_AY582990_X
Spathionema_kilimandscharicum_JN008193_X
Oxyrhynchus_volubilis_X_AY508735
Oxyrhynchus_populneus_DQ443467_AF115136
Oxyrhynchus_volubilis_AY509935_X
Ramirezella_micrantha_JN008276_AF115139
Ramirezella_nitida_JN008263_JN008326
Ramirezella_strobilophora_AY509936_XAF069120
Ramirezella_crassa_JN008262_JN008323
Phaseolus_leptostachyus_NI1365_NI1365
Phaseolus_angustissimus_JN008264_X
Phaseolus_pedicellatus_DQ450
Phaseolus_vulgaris_NI34_851_X
Phaseolus_pedicellatus_X_AF115237
Phaseolus_microcarpus_DQ445993_AF115210
Helicotropis_spectabilis_AY582981_AY583524
Helicotropis_linearis_DQ445468_X
Helicotropis_linearis_JN008258_JN008344
Leptospron_adenanthum_NI1996_X
Leptospron_adenanthum_X_NI1996
Leptospron_adenanthum_JN008254_JN008335
Leptospron_adenanthum_AY582983_X
Leptospron_gentryi_JN008256_JN008333
Leptospron_gentryi_AY582982_X
Cochliasanthus_caracalla_JN008275_X
Cochliasanthus_caracalla_JN008274_JN008348
Cochliasanthus_caracalla_X_JN008347
Condylostylis_candida_JN008260_JN008375
Condylostylis_venusta_JN008261_JN008379
Condylostylis_latidenticulata_X_JN008377
Ancistrotropis_peduncularis_JN008272_JN008370
Ancistrotropis_firmula_JN008273_JN008372
Sigmoidotropis_ekmaniana_AY582986_X
Sigmoidotropis_spixiana_JN008247_JN008358
Sigmoidotropis_antillana_JN008242_JN008350
Sigmoidotropis_megatyla_JN008250_JN008363
Sigmoidotropis_speciosa_JN008252_JN008367
Sigmoidotropis_elegans_JN008245_JN008354
Sigmoidotropis_ampla_JN008240_AF069121
Mysanthus_uleanus_AY509941_AF069125
Macroptilium_longipedunculatum_AY509940_X
Macroptilium_atropurpureum_AY509938_AY508737
Macroptilium_gibbosifolium_JN008253_X
Macroptilium_erythroloma_AY509937_X
Macroptilium_bracteatum_AY509950_AY508738
Dolichopsis_ligulata_AH013647_AY508743
Dolichopsis_paraguariensis_AY509942_AF069116
Dolichopsis_paraguariensis_AY509943_X
Strophostyles_umbellata_AY509944_AY508798
Strophostyles_umbellata_AY509945_AY508797
Strophostyles_helvola_AY509948_AY508747
Strophostyles_leiosperma_AY509947_AY508767
Strophostyles_leiosperma_AY509946_AY508771
Physostigma_mesoponticum_E1655_X
Physostigma_venenosum_AY582998_X
Physostigma_venenosum_JN008195_AY583517
Subgenus Lasiospron
Vigna_trichocarpa_AY582992_AY583521
Vigna_trichocarpa_NI130_NI130
Vigna_trichocarpa_JN008239_JN008315
Vigna_lasiocarpa_X_JN008313
Vigna_lasiocarpa_NI1404_NI1404
Vigna_lasiocarpa_AY582993_AY583522
Vigna_schottii_X_JN008317
Vigna_schottii_X_JN008318
Vigna_schottii_X_JN008320
Vigna_longifolia_AY582991_JN008307
Vigna_longifolia_X_JN008308
Vigna_juruana_X_JN008304
Vigna_juruana_X_JN008305
Vigna_juruana_NI1366_NI1366
Section Lasiospron
Subgenus Vigna
Vigna_gazensis_JN008211_JN008292
Vigna_comosa_NI375_NI375
Vigna_racemosa_JN008267_JN008294
Vigna_racemosa_NI239_NI239
Vigna_gracilis_NI1527_NI1527
Vigna_laurentii_NI322_NI322
Vigna_parkeri_NI121_NI121
Vigna_hosei_pubescens_NI321_NI321
Vigna_hosei_hosei_NI260
Vigna_hosei_hosei_JN008204_JN008283
Vigna_verdcourtii_vercverd_verc
Vigna_lanceolata_NI1437_NI1437
Vigna_lanceolata_NI1437new_NI1437n
Vigna_pseudovenulosa_NI410_NI410
Vigna_subterranea_JN008210_X
Vigna_subterranea_CS129_CS129
Vigna_multinervis_NI1443_NI1443
Vigna_filicaulis_NI1587_NI1587
Vigna_filicaulis_JN008202_X
Vigna_pubigera_benuensis_NI1206_NI1206
Vigna_pubigera_pubigera_NI1615_NI1615
Vigna_heterophylla_NI449_NI449
Vigna_heterophylla_NI122_NI122
Vigna_heterophylla_JN008201
Vigna_oblongifolia_NI1724_X
Vigna_oblongifolia_NI959_NI959
Vigna_oblongifolia_NI916_NI1916
Vigna_marina_NI1977_X2050
Vigna_luteola_X_JN008285
Vigna_luteola_JN008268_X
Vigna_luteola_NI1018_NI1018
Vigna_luteola_JN008209_JN008284
Vigna_luteola_NI1680_NI1680
Vigna_parviflora_NI974_NI974
Vigna_parviflora_X_NI917
Vigna_parviflora_NI282_NI282
Vigna_parviflora_NI1568_NI1568
Vigna_luteola_X_NI316
Subgenus Haydonia
Vigna_venulosa_548_548
Vigna_venulosa_NI548_X
Vigna_nigritia_JN008200_JN008279
Vigna_nigritia_NI1560_NI1560
Section Glossostylus
Vigna_schimperi_NI1285_NI1285
Vigna_schimperi_JN008206_JN008278
Section Microspermae
Vigna_microsperma_Vmicro_Vmicro
Vigna_juncea_X3059
Vigna_triphylla_NI100_NI100
Vigna_nyangensis_NI1522_NI1522
Vigna_triphylla_JN008205_X
Vigna_monophylla_AY583015_JN008293
Vigna_monophylla_NI1564_NI1564
Section Haydonia +
V. Microseperma
Subgenus Plectrotropis
Vigna_frutescens_NI2205_NI2205
Vigna_membranacea_macrodon_NI1629_NI1629
Vigna_membranacea_JN008207_JN008291
Vigna_membranacea_membranacea_NI1222_NI1222
Vigna_hapalantha_NI915_NI915
Vigna_caesia_NI925_NI925
Vigna_friesiorum_NI2152_NI2152
Vigna_friesiorum_NI1178_NI1178
Vigna_caesia_JN008208
Section Macrodontae
Vigna_schlechteri_NI2020_X2111
Vigna_schlechteri_NI1959_X2953
Vigna_monantha_JN008203_X
Vigna_unguiculata_stenophylla_NI2026_SP196
Vigna_unguiculata_JN008199_JN008289
Vigna_unguiculata_unguiculata_ET15_ET15
Vigna_unguiculata_baoulensis_NI933_NI933
Vigna_ung_ung_JN008198_JN008288
Section Catiang
Vigna_radicans_NI442_NI442
Vigna_reticulata_NI441_NI441
Section Reticulatae
Vigna_vexillata_lobatifolia_NI546_NI546c
Vigna_vexillata_lobatifolia_X_NI546p
Vigna_angivensis_JN008213_X
Vigna_vexillata_vexillata_NI1014_NI1404
Vigna_angivensis_NI378n_NI378n
Vigna_angivensis_X_NI1845NI1761
Vigna_vexillata_vexillata_X_JN008281
Vigna_vexillata_davyii_NI2024_X2183
Vigna_vexillata_ovata_NI1720_NI1720
Vigna_vexillata_JN008212_X
Vigna_vexillata_angustifolia_NI1592_NI1592
Section Plectrotropis
Clade Kirkiae
Vigna_stenophylla_NI2018_NI2018
Vigna_kirkii_NI448_NI448
Vigna_kirkii_NI448b_NI448b
Subgenus Ceratotropis
Vigna_reflexopilosa_glabra_X_JN008297
Vigna_tenuicaulis_JN008232_X
Vigna_angularis_NI306_NI306
Vigna_angularis_angularis_JN008218_X
Vigna_nepalensis_JN008225_X
Vigna_angularis_nipponensis_JN008269_X
Vigna_umbellata_JN008236_JN008299
Vigna_umbellata_JN008237_JN008302
Vigna_minima_JN008222_X
Vigna_hirtella_JN008221_X
Vigna_riukiuensis_JN008229_X
Vigna_nakashimae_JN008224_X
Vigna_radiata_X_DQ445738
Vigna_grandiflora_JN008220_X
Vigna_stipulacea_JN008230_X
Vigna_trilobata_JN008233_JN008298
Vigna_trinervia_JN008235_X
Vigna_reflexopilosa_glabra_JN008219
Vigna_reflexopilosa_reflexopilosa_JN085947_X
Vigna_reflexopilosa_glabra_JN008228_X
Vigna_aconitifolia_NI41_NI41
Vigna_aconitifolia_JN008215_JN008296
Vigna_aconitifolia_JN008214_JN008295
Vigna_mungo_silvestris_JN008223_X
Vigna_mungo_mungo_AY582994_X
Vigna_subramaniana_JN008231_X
Vigna_radiata_sublobata_JN008227_X
Vigna_radiata_radiata_DQ445950_X
Vigna_radiata_NI37_X
0.04

Figure 6

Online Supplemental File 1 Appendix

Click here to access/download

Online Supplemental (not built into PDF)

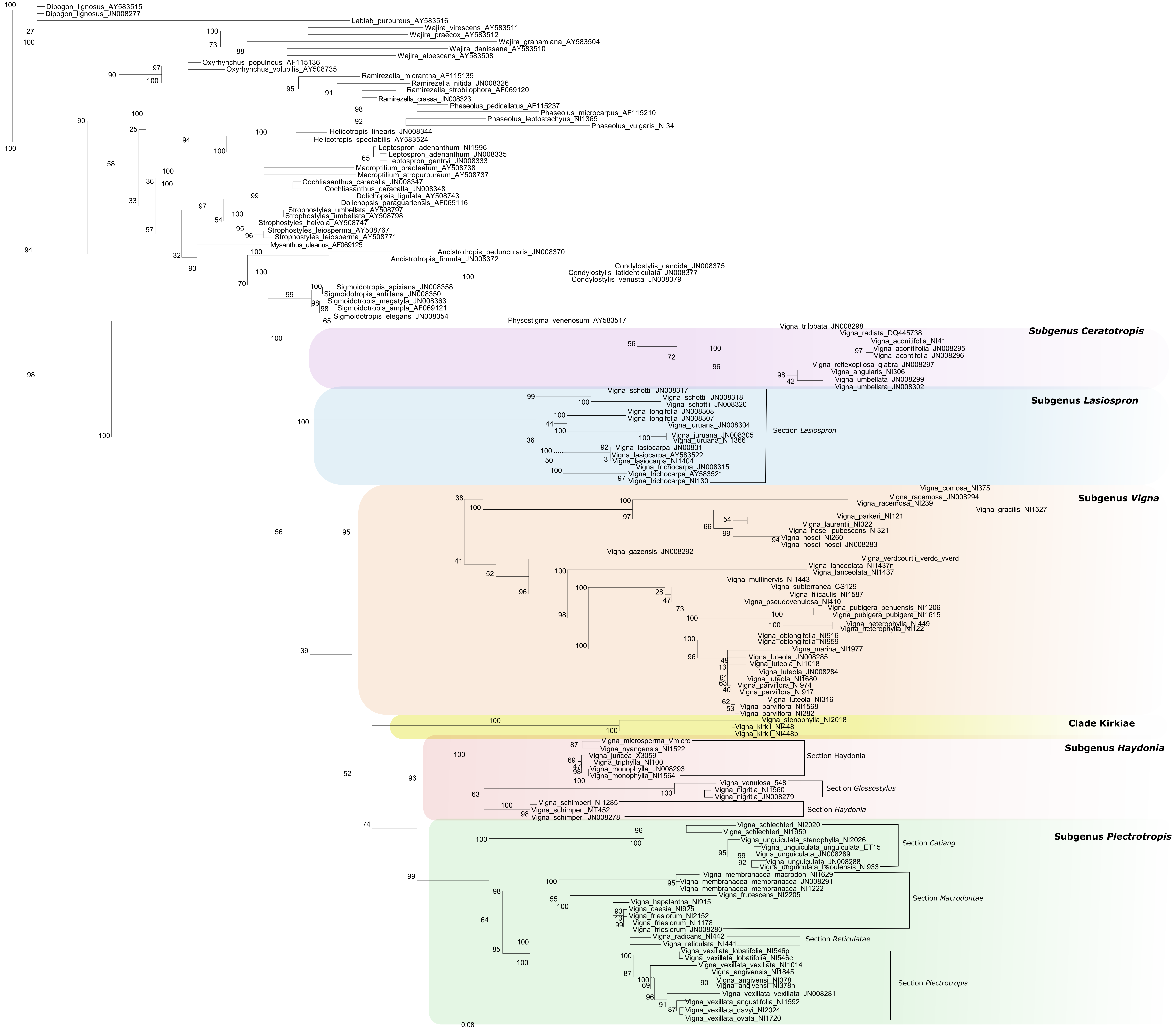
Appendix_OldWorldVigna_RP_FJ_Dec282023.xlsx

Supplemental Table 2 in Excel format

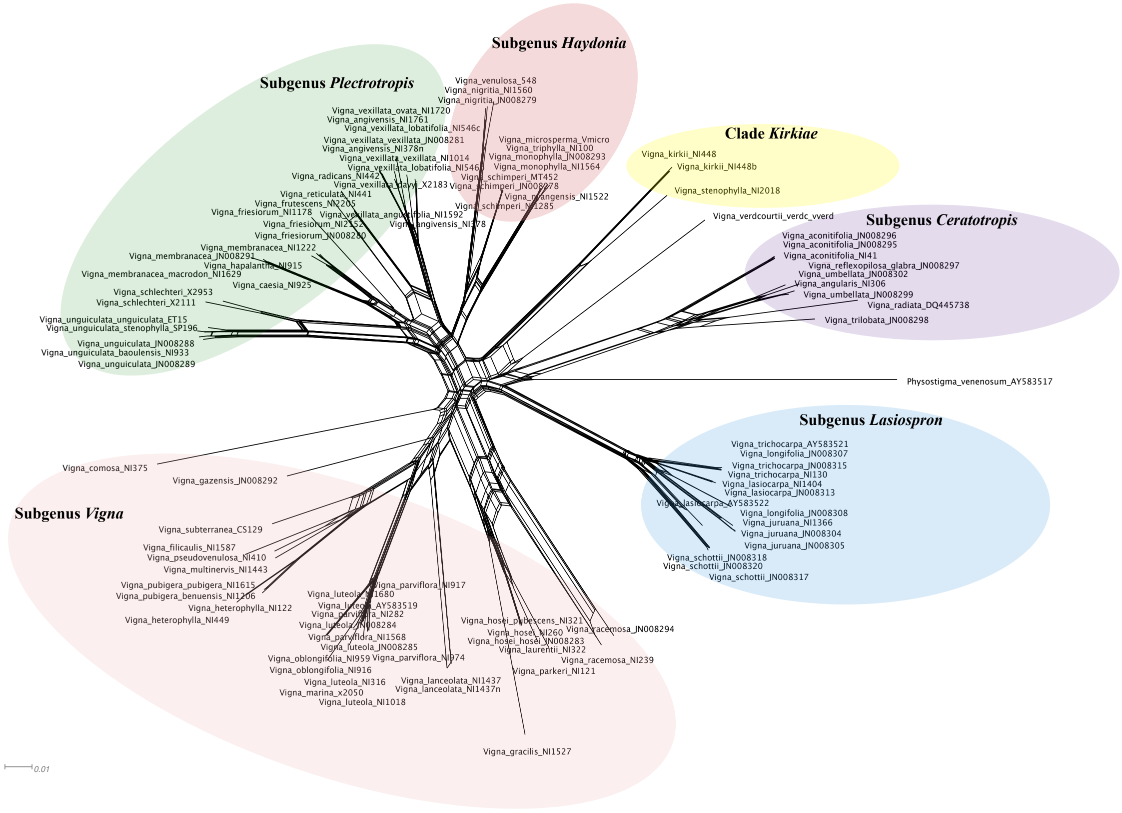
Supplemental Table 3 in Excel format


Platycyamus_regnellii_AF142709
Butea_monosperma_JN008175
Otoptera_burchellii_JN008176
Psophocarpus_lancifolius_JN008177
Cologania_hintoniorum_AY583013
Pseudovigna_argentea_JN008179
Neorautanenia_mitis_JN008178
Pueraria_montana_lobata_AY582972
Amphicarpaea_bracteata_AY582971
Glycine_max_AF142700
Bituminaria_bituminosa_EU717398
Otholobium_bolusii_JN008180
Psoralea_pinnata_JN008182
Rupertia_physodes_EF549955
Pediomelum_tenuiflora_JN008181
Wajira_danissana_AY583008
Wajira_albescens_AY583011
Wajira_grahamiana_AY583005
Wajira_virescens_AY583000
Wajira_praecox_AY583001
Sphenostylis_stenocarpa_AY582977
Sphenostylis_angustifolia_JN008189
Alistilus_jumellei_JN008192
Alistilus_jumellei_JN008191
Nesphostylis_holosericea_AY582979
Dolichos_trilobus_trilobus_AY582976
Dolichos_oliveri_JN008183
Dolichos_trinervatus_JN008265
Dolichos_kilimandscharicus_JN008184
Macrotyloma_stenophyllum_JN008186
Macrotyloma_stenophyllum_JN008187
Macrotyloma_ellipticum_AY582974
Macrotyloma_axillare_JN008266
Macrotyloma_daltonii_AY582973
Macrotyloma_uniflorum_benadirianum_JN008185
Macrotyloma_africanum_JN008188
Lablab_purpureus_AY582989
Dipogon_lignosus_AY582988
Vatovaea_pseudolablab_AH013772
Vatovaea_pseudolablab_JN008194
Spathionema_kilimandscharicum_AY582990
Spathionema_kilimandscharicum_JN008193
Phaseolus_pedicellatus_DQ450851
Phaseolus_microcarpus_DQ445993
Phaseolus_leptostachyus_NI1365
Phaseolus_angustissimus_JN008264
Phaseolus_vulgaris_NI34
Oxyrhynchus_populneus_DQ443467
Oxyrhynchus_volubilis_AY509935
Ramirezella_nitida_JN008263
Ramirezella_micrantha_JN008276
Ramirezella_strobilophora_AY509936
Ramirezella_crassa_JN008262
Ancistrotropis_firmula_JN008273
Ancistrotropis_peduncularis_JN008272
Sigmoidotropis_ekmaniana_AY582986
Sigmoidotropis_megatyla_JN008250
Sigmoidotropis_antillana_JN008242
Sigmoidotropis_spixiana_JN008247
Sigmoidotropis_ampla_JN008240
Sigmoidotropis_elegans_JN008245
Sigmoidotropis_speciosa_JN008252
Cochliasanthus_caracalla_JN008274
Cochliasanthus_caracalla_JN008275
Condylostylis_candida_JN008260
Condylostylis_venusta_JN008261
Helicotropis_spectabilis_AY582981
Helicotropis_linearis_DQ443468
Helicotropis_linearis_JN008258
Leptospron_adenanthum_NI1996
Leptospron_adenanthum_AY582983
Leptospron_gentryi_AY582982
Leptospron_adenanthum_JN008254
Leptospron_gentryi_JN008256
Mysanthus_uleanus_AY509941
Macroptilium_gibbosifolium_JN008253
Macroptilium_erythroloma_AY509937
Macroptilium_bracteatum_AY509950
Macroptilium_atropurpureum_AY509938
Macroptilium_longipedunculatum_AY509940
Dolichopsis_ligulata_AH013647
Dolichopsis_paraguariensis_AY509942
Dolichopsis_paraguariensis_AY509943
Strophostyles_helvola_AY509948
Strophostyles_umbellata_AY509945
Strophostyles_umbellata_AY509944
Strophostyles_leiosperma_AY509946
Strophostyles_leiosperma_AY509947
Physostigma_mesoponticum_E1655
Physostigma_venenosum_AY582998
Physostigma_venenosum_JN008195
Subgenus *Vigna*
Vigna_gazensis_JN008211
Vigna_comosa_NI375
Vigna_racemosa_NI239
Vigna_racemosa_JN008267
Vigna_gracilis_NI1527
Vigna_laurentii_NI322
Vigna_parkeri_NI121
Vigna_hosei_pubescens_NI321
Vigna_hosei_hosei_JN008204
Vigna_hosei_hosei_NI260
Vigna_verdcourtii_vercvverd
Vigna_lanceolata_NI1437
Vigna_lanceolata_NI1437new
Vigna_pseudovenulosa_NI410
Vigna_subterranea_JN008210
Vigna_subterranea_CS129
Vigna_filicaulis_NI1587
Vigna_multinervis_NI1443
Vigna_pubigera_benuensis_NI1206
Vigna_pubigera_pubigera_NI1615
Vigna_heterophylla_NI449
Vigna_heterophylla_NI122
Vigna_heterophylla_JN008201
Vigna_oblongifolia_NI1724
Vigna_oblongifolia_NI916
Vigna_oblongifolia_NI959
Vigna_luteola_NI1680
Vigna_parviflora_NI974
Vigna_luteola_JN008268
Vigna_luteola_NI1018
Vigna_marina_NI1977
Vigna_parviflora_NI282
Vigna_luteola_JN008209
Vigna_parviflora_NI1568
Subgenus *Lasiospron*
Vigna_trichocarpa_AY582992
Vigna_trichocarpa_JN008239
Vigna_trichocarpa_NI130
Vigna_longifolia_AY582991
Vigna_juruana_NI1366
Vigna_lasiocarpa_AY582993
Vigna_lasiocarpa_NI1404
Section Lasiospron
Subgenus *Haydonia*
Vigna_venulosa_NI548
Vigna_nigritia_JN008200
Vigna_nigritia_NI1560
Section Glossostylus
Vigna_schimperi_JN008206
Vigna_schimperi_NI1285
Vigna_microsperma_Vmicro
Vigna_triphylla_NI100
Vigna_nyangensis_NI1522
Vigna_triphylla_JN008205
Vigna_monophylla_AY583015
Vigna_monophylla_NI1564
Section Haydonia
Subgenus *Ceratotropis*
Vigna_tenuicaulis_JN008232
Vigna_angularis_NI306
Vigna_angularis_angularis_JN008218
Vigna_nepalensis_JN008225
Vigna_angularis_nipponensis_JN008269
Vigna_umbellata_JN008237
Vigna_umbellata_JN008236
Vigna_hirtella_JN008221
Vigna_minima_JN008222
Vigna_riukiuensis_JN008229
Vigna_nakashimae_JN008224
Vigna_trinervia_JN008235
*Vigna_reflexopilosa_glabra_JN008219
Vigna_reflexopilosa_reflexopilosa_JN085947
Vigna_reflexopilosa_glabra_JN008228
Vigna_grandiflora_JN008220
Vigna_stipulacea_JN008230
Vigna_trilobata_JN008233
Vigna_mungo_silvestris_JN008223
Vigna_mungo_mungo_AY582994
Vigna_subramaniana_JN008231
Vigna_radiata_radiata_DQ445950
Vigna_radiata_sublobata_JN008227
Vigna_aconitifolia_JN008215
Vigna_aconitifolia_JN008214
Vigna_aconitifolia_NI41
Subgenus *Plectrotropis*
Vigna_radicans_NI442
Vigna_reticulata_NI441
Section *Reticulatae*
Vigna_schlechteri_NI2020
Vigna_schlechteri_NI1959
Vigna_monantha_JN008203
Vigna_unguiculata_unguiculata_JN008198
Vigna_unguiculata_baoulensis_NI933
Vigna_unguiculata_stenophylla_NI2026
Vigna_unguiculata_JN008199
Vigna_unguiculata_unguiculata_ET15
Section *Catiang*
Vigna_angivensis_JN008213
Vigna_vexillata_vexillata_NI1014
Vigna_angivensis_NI3
Vigna_angivensis_NI378n
Vigna_vexillata_lobatifolia_NI546
Vigna_vexillata_angustifolia_NI15
Vigna_vexillata_JN008212
Vigna_vexillata_davyii_NI2024
Vigna_vexillata_ovata_NI1720
Section *Plectrotropis*
Vigna_frutescens_NI2205
Vigna_membranacea_macrodon_NI1629100
Vigna_membranacea_membranacea_NI1222
Vigna_membranacea_membranacea_JN008207
Vigna_hapalantha_NI915
Vigna_friesiorum_NI1178
Vigna_caesia_NI925
Vigna_caesia_JN008208
Vigna_friesiorum_NI2152
Section *Macrodontae*
Vigna_stenophylla_NI2018
Vigna_kirkii_NI448b
Vigna_kirkii_NI448
Clade *Kirkiaea*
0.02

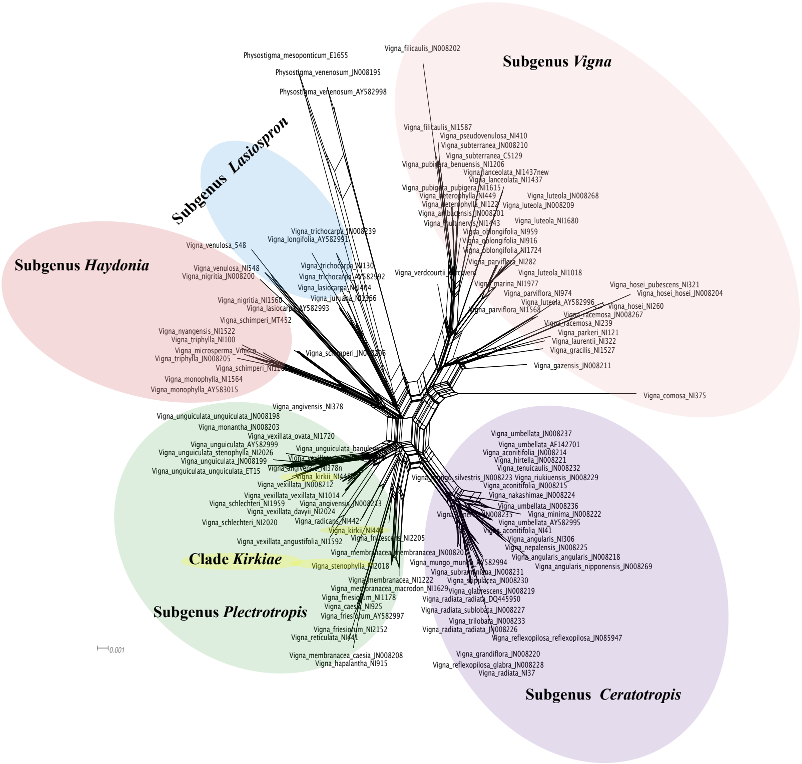
Online Supplemental Figure 2



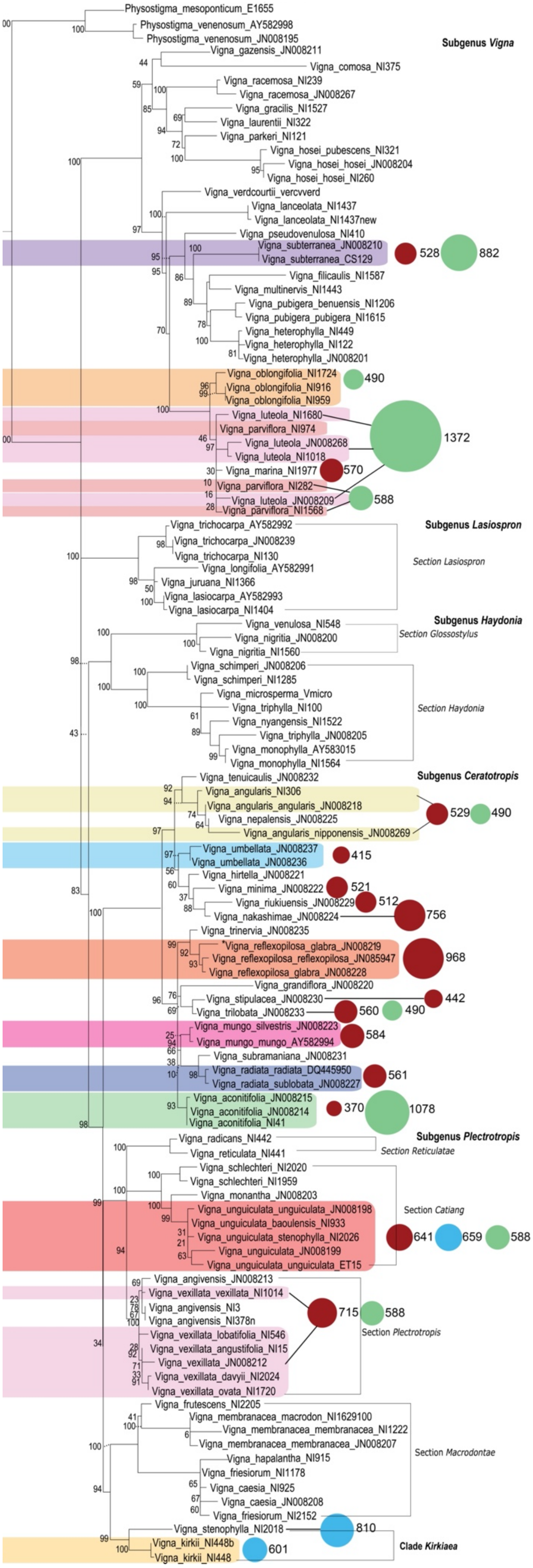
Online Supplemental Figure 3 top



Online Supplemental Figure 3 bottom



Vigna s.s. systematics



Supplementary figure 4. Genome size estimates from this study and others, collated from the literature, mapped on the *matK* ML (left) and BI ITS (right) trees cropped to *Vigna* s.s. The size of the circle is proportional to the genome size (GS) estimate. Colors designate GS estimated in this study (blue), 1C values in megabases (mb) (green) and undesignated C values (mb) from literature. See also supplementary table 3.