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RESEARCH ARTICLE

Towards a new classification of *Rhynchosia* (Leguminosae, Phaseoleae) and allied genera: A comprehensive phylogeny of Cajaninae

The Cajaninae Phylogeny Working Group (CPWG)[†]

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Abstract Cajaninae is the most speciose subtribe of the traditionally recognized legume tribe Phaseoleae, comprising 10 genera and close to 500 species, with an overall pantropical distribution. This subtribe is perhaps the most easily diagnosed within Phaseoleae because of its peculiar secretory structures, including bulbous-based trichomes and vesicular glands. Some previous taxonomic studies indicated that the genera *Bolusafra*, *Carrissoa*, and *Chrysoscias* should be recognized as synonyms of *Rhynchosia*, but those studies failed to fully elucidate the relationship between the two largest genera, *Eriosema* (150 spp.) and *Rhynchosia* (250 spp.). To test the monophyly of Cajaninae and clarify the phylogenetic relationships among the genera within the subtribe, new comprehensive phylogenetic analyses using nuclear ITS and chloroplast *rpl32-trnL* (UAG) and *trnQ* (UUG)-*5′rps16* DNA sequences were performed. The analyses support the monophyly of Cajaninae and indicate that *Eriosema* is embedded within *Rhynchosia*. Our results also confirm the polyphyly of *Rhynchosia*, demonstrating that it additionally encompasses *Bolusafra*, *Carrissoa*, *Chrysoscias*, and *Paracalyx* in addition to the previously recognized inclusion of *Eriosema*. Moreover, the type of the genus, *R. volubilis*, forms a distinct clade, along with *R. dielsii*, separated from the rest of the genus and close to *Dunbaria*. The analyses also resolve the infrageneric relationships in *Rhynchosia* s.l. as well as the relationships among the genera of the subtribe. These results suggest that a new classification is needed to circumscribe a monophyletic *Rhynchosia* and to recircumscribe other taxa of the subtribe.

Keywords Fabaceae; Papilionoideae; phylogenetics; systematics; taxonomy

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Pantropical Cajaninae Benth. is the most speciose subtribe of Phaseoleae (Leguminosae) and comprises approximately 500 species, distributed in 10 genera: *Adenodolichos* Harms, *Bolusafra* Kuntze, *Cajanus* DC., *Carrissoa* Baker f., *Chrysoscias* E.Mey., *Dunbaria* Wight & Arn., *Paracalyx* Ali, *Flemingia* W.T.Aiton, *Eriosema* (DC.) Desv., and *Rhynchosia* Lour. (Schrire, 2005). A number of taxonomic studies indicated that the genera *Carrissoa* and *Chrysoscias* should be recognized as synonyms of *Rhynchosia* (Germishuizen, 2000; Schrire, 2005), and that the species of *Paracalyx* which were originally described in the genus *Cylista* Aiton, should also be recognized as belonging to *Rhynchosia* (Ali, 1968; Schrire, 2005). However, previous studies failed to fully elucidate the relationship between the two largest genera, *Eriosema* and *Rhynchosia*, partly due to limited taxon sampling.

Cajaninae genera are mainly distributed in the tropical and subtropical regions of the Old World (Africa, Asia) and Oceania, except the two most speciose genera, *Eriosema* and *Rhynchosia* (comprising about 150 and 250 species, respectively), which are both pantropical (Schrire, 2005; Bezerra & al., 2019, 2024; Cândido & al., 2019). The taxa occur mainly in seasonally dry tropical forests and in grasslands, where they often have a woody rootstock that allows them to survive in fire-prone environments. They also occur along watercourses in rocky areas, and in Mediterranean montane sclerophyllous shrubland in South Africa (fynbos) (Schrire, 2005). Moreover, some genera occur in seasonally drought-prone environments, growing in rocky or sandy shallow soils of low fertility (Cândido & al., 2020). These environments in the Neotropics (especially in Brazil) are referred to as “campos rupestres”; in Africa, a very similar vegetation is found in the Chimanimani Mountains on the border between Zimbabwe and Mozambique (Lock, 2006), where one of the abundant genera is *Eriosema* (Timberlake & al., 2016). These types of vegetation are among the world’s most threatened ecosystems, due to mining activities, climate change, and agricultural and urban expansion (Martinelli, 2007; Timberlake & al., 2016).

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The Cajaninae includes many important species used for human food, e.g., *Cajanus cajan* (L.) Huth: pigeon pea or gungo pea; *Flemingia*: for edible underground tubers; species of *Eriosema* and *Rhynchosia*: as famine foods; *Dunbaria*: related to *Cajanus* and useful in breeding programs of pigeon pea (Van der Maesen, 1998; Schrire, 2005). Some species are also used for medicine, for erectile dysfunction, coughs, bacterial infections, infertility treatment, menopause, dysentery, rheumatism treatment and menstrual pain (e.g., *Eriosema kraussianum* Meisn, *E. laurentii* De Wild., *E. robustum* Baker, *Rhynchosia adenodes* Eckl. & Zeyh.) (Burkill, 1995; Ojewole, 2007; Awouafack & al., 2008, 2013; Kokwaro, 2009; Ajao & al., 2025). A detailed assessment of the pharmacognosy of *Eriosema* and *Rhynchosia* was provided by Ateba & al. (2021) and Rammohan & al. (2019), respectively. Some species of Cajaninae are also useful as green manure (most genera), for handicrafts, including jewellery (*Rhynchosia* with bicoloured seeds; Bezerra & al., 2024) and as cover crops (Schrire, 2005). However, despite the importance of the taxa of this subtribe, the relationships among the infratribal groups remain poorly understood.

Cajaninae taxa include herbs, climbing vines, shrubs, and subshrubs, with mainly trifoliolate leaves (occasionally unifoliolate or 5-foliolate), flowers arranged in racemose inflorescences (the flowers lax or crowded), frequently yellow or red petals, and a legume fruit commonly with two seeds (rarely three or more); they mostly lack bracteoles and canavanine (except in *Adenodolichos*) (Fig. 1) (Lackey, 1977, 1981). The group is characterized by special secretory structures, including bulbous-based trichomes, secretory-based trichomes and vesicular glands (Debold, 1892; Solereder, 1908; Lackey, 1977, 1981; Cândido & al., 2016; Vargas & al., 2018). Indeed, secretory structures are such an important diagnostic feature of Cajaninae that Lackey (1981) cited the bulbous-based trichomes and vesicular glands of *Adenodolichos* as a reason for maintaining it in the subtribe, despite it being morphologically anomalous in other features, such as possessing bracteoles, a bearded style, and canavanine.

In agreement with the morphological distinctiveness of Cajaninae (Lackey, 1977, 1981; Baudet & Marechal, 1976), molecular phylogenetic analyses have consistently supported the monophyly of the subtribe (Egan & al., 2016; LPWG, 2017; Cândido & al., 2020; Zhao & al., 2021; Choi & al., 2022; Kates & al., 2024; Cai & al., 2025). The chloroplast DNA results of Bruneau & al. (1995) suggested that the subtribe originated as part of a major radiation of Phaseoleae (including Desmodieae), separate from Clitoriinae, Diocleinae, *Neorudolphia* (Willd.) Britton (now a synonym of *Rhodopis* Urb.), Ophrestiinae, and *Rhodopis*. Doyle & al. (2000) and Kajita & al. (2001) resolved the subtribe Cajaninae as a basal polytomy with Phaseolinae, Glycininae and the tribe Psoraleeae. More recently, Egan & al. (2016) showed that Cajaninae plus the subtribes Glycininae, Erythrininae, and the genus *Butea* Roxb. ex Willd. comprise the core Phaseoleae (sensu Schrire, 2005). Their study also supported Cajaninae as monophyletic in the molecular analysis of chloroplast markers, although in analyses of the AS2 nuclear marker, the subtribe was recovered as monophyletic only when expanded to also include the genus *Apios* Fabr.

Prior to the current study, the analysis of Cândido & al. (2020) contained the most complete sampling of representatives of Cajaninae. In that study, *Rhynchosia* emerged as paraphyletic, but the sampling was focused on members of *Eriosema*, and the inclusion of other genera in Cajaninae was limited. To date, no phylogenetic studies have sampled comprehensively across *Rhynchosia*, and a precise circumscription of the genus. The relationships among the genera of Cajaninae remain unclear.

With these shortcomings in mind, we aim here to provide a robust phylogeny for the subtribe Cajaninae, based on an expanded taxon sampling. We address the following questions: (1) Is *Rhynchosia* paraphyletic as suggested by previous studies? (2) What are the relationships of *Rhynchosia* with respect to other Cajaninae genera? (3) Is a new classification for Cajaninae warranted?

■ MATERIALS AND METHODS

Taxon sampling. — In this study, we included representatives of all 10 of the traditionally recognized genera of subtribe Cajaninae. The taxonomic sample spans the geographic and ecological range of the subtribe (300 accessions) and includes the following number of accessions per genus/total number of species currently in the genus: *Adenodolichos* (4/22), *Bolusafra* (4/1), *Cajanus* (10/34), *Carrissoa* (1/1), *Chrysoscias* (3/8), *Dunbaria* (5/19), *Eriosema* (106/165), *Flemingia* (9/45), *Paracalyx* (7/5) and *Rhynchosia* (151/257). For rooting purposes, we also included one species each of the more distantly related phaseoloid genera *Centrosema* (1), *Camptosema* (1), and *Galactia* (1).

DNA extraction, amplification and sequencing. — Total DNA was obtained from fresh leaves collected in the field and stored in silica gel, as well as from herbarium specimens housed in Brazilian, South African, and other international herbaria. For the African taxa, total DNA was obtained from herbarium specimens housed in JRAU, NBG, NH, NU, and PRE, and amplified at the African Centre for DNA Barcoding (ACDB), University of Johannesburg, South Africa. For *Cajanus*, sequences produced by Kassa (2011) were used.

Approximately 1 cm^2 of dried leaflet of each sample was ground with a mortar and pestle using liquid nitrogen, or in a Geno/Grinder 2010 machine (SPEX SamplePrep LLC for 2 minutes on speed 2). For DNA extraction, we used the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany) following the manufacturer's protocol, but with 4 µl RNAse A added to the stock solution at the beginning of the procedure and extension of the heating period for material from herbarium specimens to about three hours.

The chloroplast regions *rpl32* and *trnQ* were sequenced for 274 and 215 accessions, respectively, while nrITS was sequenced for 202 accessions. *rpl32* was amplified using the primers trnL(UAG)/rpl32-F, *trnQ* using the primers

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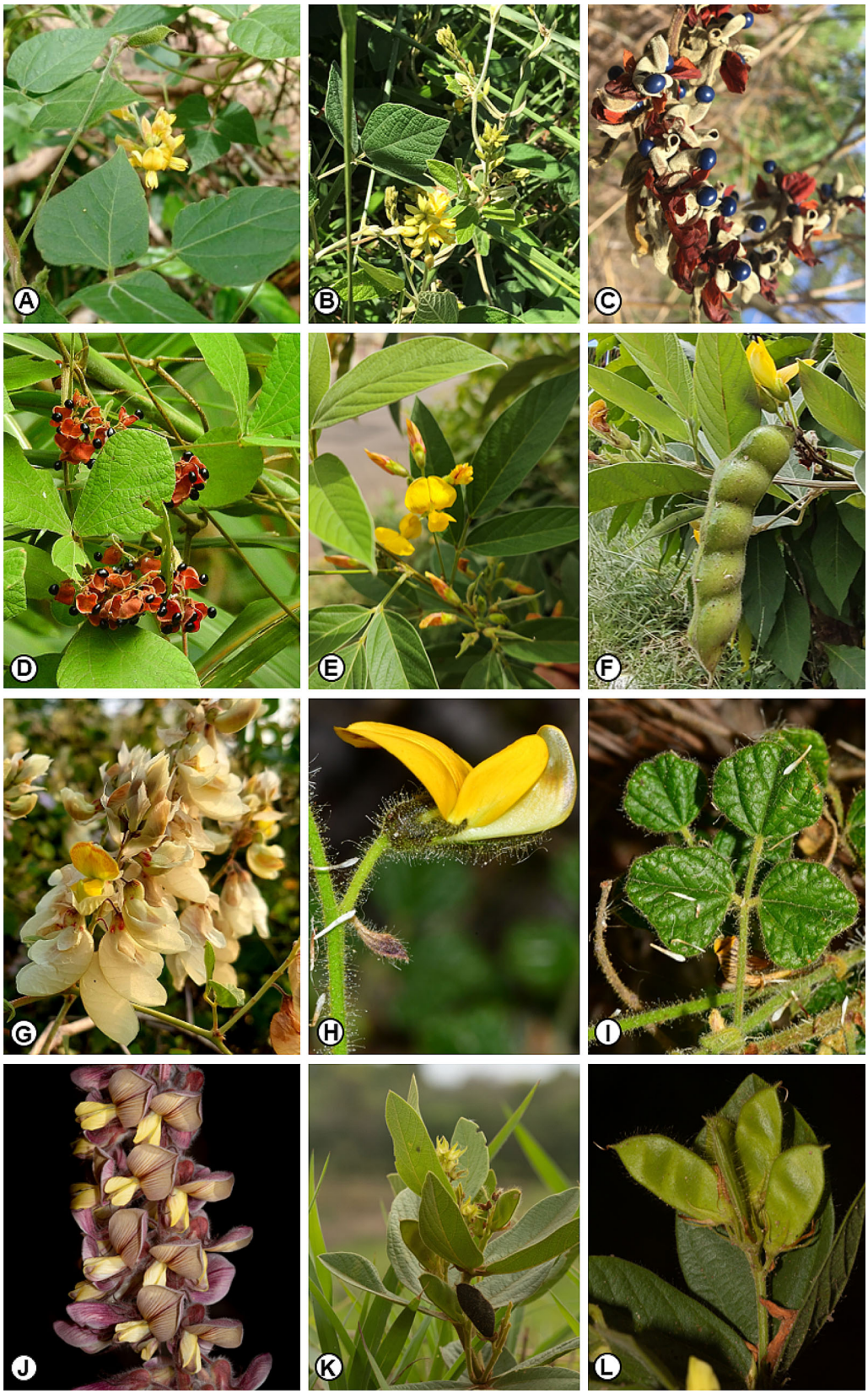


Fig. 1. Morphological diversity in the subtribe Cajaninae. **A**, *Rhynchosia edulis*; **B**, *R. reticulata*; **C**, *R. hirta*; **D**, *R. volubilis*; **E** & **F**, *Cajanus cajan*; **G**, *Paracalyx scariosus*; **H** & **I**, *Bolusafra bituminosa*; **J**, *Eriosema defoliatum*; **K** & **L**, *E. campestre*. — A by D.S. Gissi; B by L.M.P.A. Bezerra; C by Len deBeer; D by Kinmatsu Lin; E & F by E.S. Cândido; G by Pravin Kawale; H & I by Joey Santore; J–L by T.C. Monteiro.

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trnQ(UUG)/rpS16x1 (Shaw & al., 2007) and nrITS (including ITS1 and ITS2 spacer regions and the 5.8S ribosomal subunit) of nuclear ribosomal DNA (nrDNA), using the primer pairs 17SE and 26SE (Sun & al., 1994) (suppl. Table S1). Amplifications followed the protocol described by Cândido & al. (2020); products were checked by agarose gel electrophoresis using 0.8% agarose gels and purified using the NucleoSpin gel and PCR clean-up kit (Macherey-Nagel). DNA sequencing reactions were carried out on purified PCR products using the same primers on an ABI 3730xl sequencer (Macrogen, Seoul, South Korea).

Alignment and phylogenetic analysis. — The software Geneious v.8.1.9 (http://www.geneious.com, Kearse & al., 2012) was used to edit and assemble sequences. To exclude the possibility of contaminant DNA a BLAST search (http://blast.ncbi.nlm.nih.gov/) was performed for all sequences. DNA sequences of each region were aligned using MAFFT v.7.369b (Katoh & Standley, 2014) under the default settings. The alignments were manually revised in AliView v.1.26 (Larsson, 2014). Large indels and gaps were excluded using trimAL v.1.5.0 (Capella-Gutiérrez & al., 2009) with option -gt = 0.65 for all analyses. Maximum likelihood (ML) and Bayesian inference (BI) were used to build a phylogeny as these out-perform other methods in terms of tree reconstruction accuracy (Ogden & Rosenberg, 2006). For the ML method, we used IQ-TREE v.1.6.12 (Nguyen & al., 2015). ModelFinder (Kalyaanamoorthy & al., 2017) selected SYM + Γ as the best-fit model according to the Bayesian information criterion. We obtained branch support using 1000 ultra-fast bootstraps (Hoang & al., 2018). The BI analysis was performed using the MPI version of Phylobayes v.1.8b (Lartillot & al., 2013) with two independent runs using the CAT-GTR model. We let the chains run for more than 20,000 cycles and evaluated the discrepancy of bipartition frequencies between two runs using "bpcomp" v.1.8b with a burn-in of 5000 and sub-sampling every 10 trees. We calculated "maxdiff" and "meandiff" as criteria for the convergence of Markov chain Monte Carlo (MCMC) estimates which were 0.088 and 0.006, respectively. The majority-rule consensus tree with posterior probability (PP) values was obtained with the "readpb" v.1.8b. The sequence alignment in FASTA format generated and analyzed during this study is provided in suppl. Data S1.

■ RESULTS

New sequences were obtained for 300 accessions for Cajaninae, with the following number of sequences per DNA region: 274 of *rpl32* and 215 of *trnQ*, and 202 of ITS. Voucher information and GenBank accession numbers for all sequences, including newly generated sequences, are provided in Appendix 1.

In both ML analyses of fully combined nuclear and plastid data (ITS, *rpl32*, *trnQ*) and combined plastid markers (*rpl32*, *trnQ*), the subtribe Cajaninae was recovered as monophyletic with high support (Figs. 2, 3; suppl. Fig. S1). In addition, the genera *Adenodolichos*, *Cajanus*, *Dunbaria*, *Eriosema*, *Flemingia* and *Paracalyx* also emerged as monophyletic, each with high support (almost all with BS = 100; Figs. 2, 3, suppl. Fig. S1). The analyses were uninformative regarding the monophyly of *Chrysoscias* and *Bolusafra* but clearly revealed the polyphyletic nature of *Rhynchosia*.

The deepest relationships within Cajaninae were well resolved and robustly supported. A monophyletic *Adenodolichos* was placed as sister to a well supported clade (BS = 99%; Fig. 2) containing all other members of the subtribe. Within the latter clade, *Flemingia* was placed as sister to another strongly supported clade containing all the sampled species of *Rhynchosia*, as well as the species of the remaining genera of Cajaninae. Within the last group, the species of *Rhynchosia* were placed in two distantly related major clades, referred to here as the "Dunbaria clade" and the "Rhynchosia clade".

The Dunbaria clade was moderately supported (BS 92%; Fig. 2) and formed the sister group to the genus *Cajanus*. It was comprised entirely of Asian species, namely *Rhynchosia volubilis* Lour.—the type of its genus—and *R. dielsii* Harms, along with the sampled species of *Dunbaria*. Within the Dunbaria clade, the two *Rhynchosia* species formed a well-supported subclade (Figs. 2, 3; suppl. Fig. S1).

The Rhynchosia clade was also highly supported (BS 99%, PP 1.00, Fig. 2, suppl. Fig. S1). It contained all the other species of *Rhynchosia*, along with the sampled species of *Bolusafra*, *Carrissoa*, *Chrysoscias*, *Eriosema*, and *Paracalyx*, which, in general, were placed in nested positions relative to *Rhynchosia*. Within the Rhynchosia clade, species were distributed among five major constituent subclades, which we call clades 1–5.

In clade 1, the speciose and well-supported circumtropical genus *Eriosema* (BS 100%, PP 1.00, Figs. 2, 3; suppl. Fig. S1) is subtended by a grade formed by several species of African *Rhynchosia* and the monospecific genus *Carrissoa*. Within that grade, a small clade groups together *R. thorncroftii* and *R. versicolor*, while another, forming the sister group to *Eriosema*, comprises *Carrissoa angolensis* and *Rhynchosia insignis*.

Clade 3 (BS 91%; Fig. 2, suppl. Fig. S1) comprises several other Old World species of *Rhynchosia* plus species of the small genera *Bolusafra* and *Chrysoscias*. While the monophyly of the latter two genera were poorly resolved, the analysis did recover a well-supported subclade grouping their members along with the species *Rhynchosia chrysoscias* (BS 98%, suppl. Fig. S1). The other species of *Rhynchosia* that were placed in clade 3 are mainly African.

In contrast to clades 1 and 3, which each combined species of different genera, clades 2 (BS 95%; Fig. 2, suppl. Fig. S1) and 4 (BS 99%; Fig. 2, suppl. Fig. S1) were composed entirely of Old World species of *Rhynchosia*. Most of these species are also from Africa, with notable exceptions in clade 4, such as *R. hirta* (Andrews) Meikle & Verdc., which also occurs in India and Sri Lanka, and *R. acuminatissima* Miq., which is restricted to parts of Asia and Oceania.

Finally, clade 5 (BS 83%; Fig. 2, suppl. Fig. S1) included all the sampled New World species of *Rhynchosia*, as well as a

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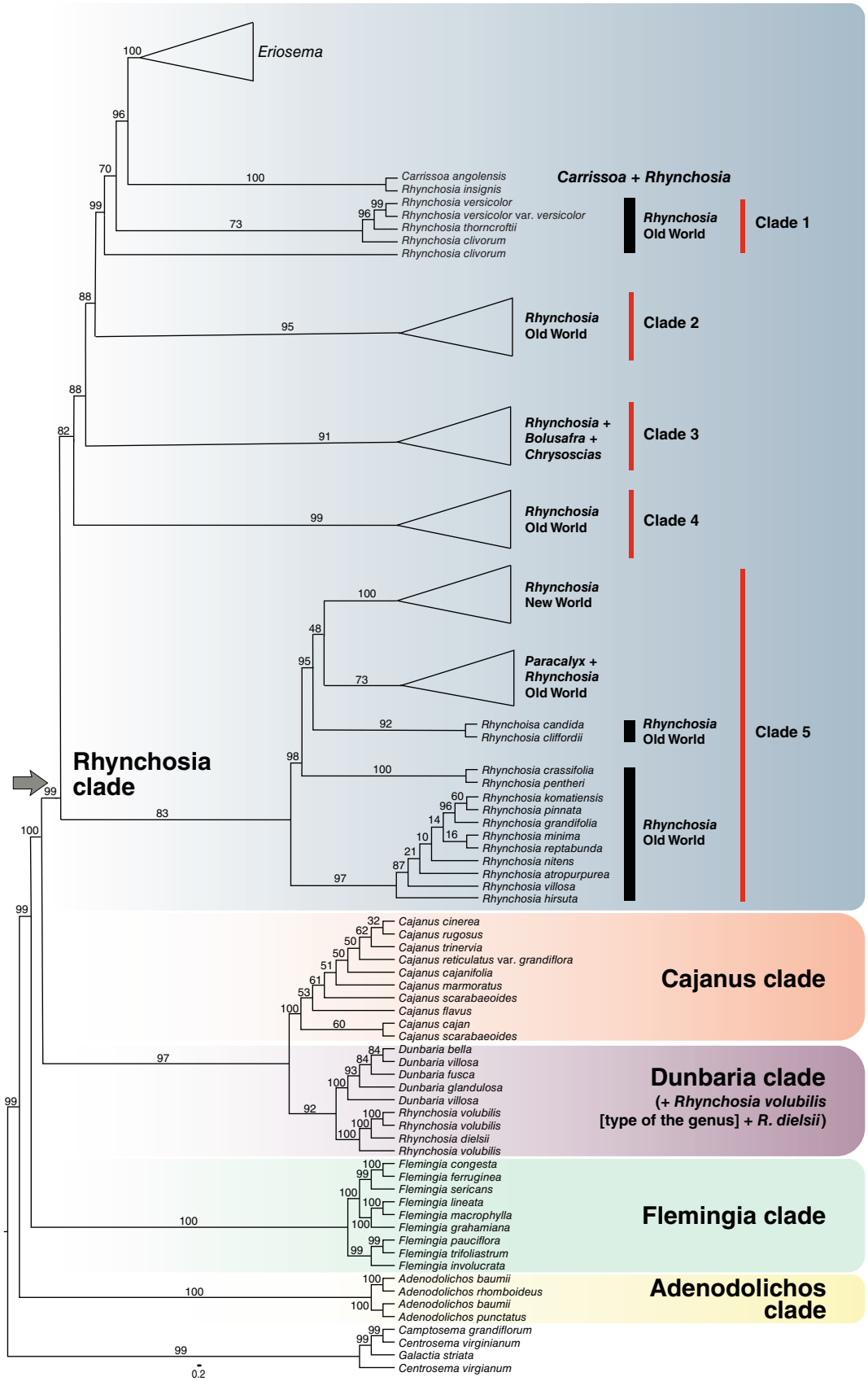


Fig. 2. Maximum likelihood phylogenetic tree of the subtribe Cajaninae based on the combined dataset (ITS, *rpl32-trnL*, and *trnQ-5'rps16*). Numbers above branches are bootstrap support (BS) values. The arrow indicates the Rhynchosia clade.

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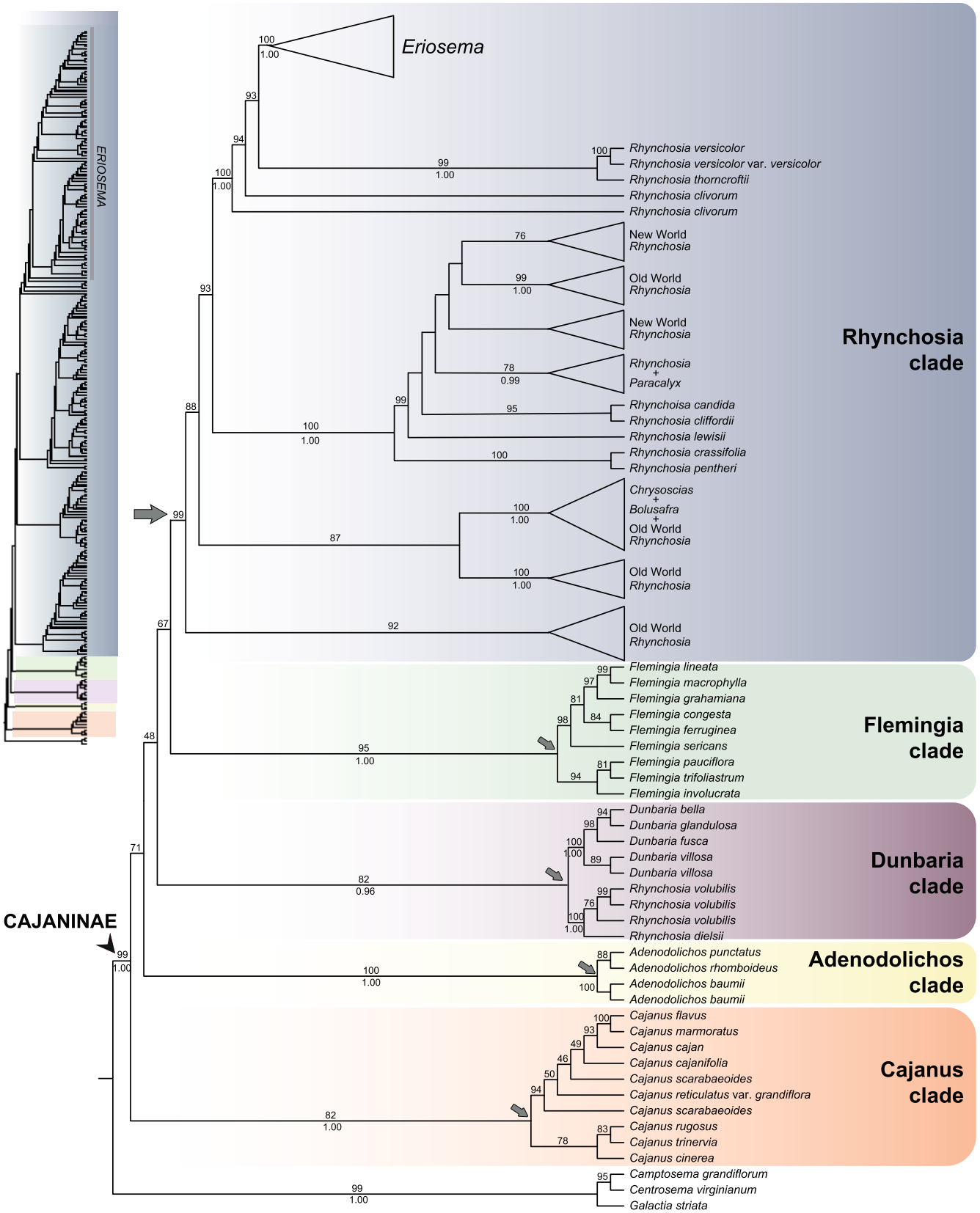


Fig. 3. Maximum likelihood phylogenetic tree of the subtribe Cajaninae based on the chloroplast DNA dataset (*rpl32-trnL* and *trnQ-5'rps16*). Numbers above branches are bootstrap support (BS) values and numbers below branches are Bayesian posterior probabilities (PP). One arrow indicates the Cajaninae clade, while the upper arrow indicates the Rhynchosia clade.

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sizeable number of Old World species, plus the small genus *Paracalyx*. Distributed in NE Tropical Africa, the Indian subcontinent, and Indo-China, *Paracalyx* was embedded within a moderately supported clade (BS 73%; Fig. 2, suppl. Fig. S1) of mostly Old World *Rhynchosia* representatives (suppl. Fig. S1).

■ DISCUSSION

The recovery of a monophyletic Cajaninae by our analyses (Figs. 2, 3, suppl. Fig. S1) corroborates previous phylogenetic studies of the Leguminosae and tribe Phaseoleae (Egan & al., 2016; LPWG, 2017; Cândido & al., 2020; Zhao & al., 2021; Kates & al., 2024; Choi & al., 2022; Cai & al., 2025). However, our study was based on a more comprehensive taxonomic and geographical sampling of the Cajaninae members and provides new insights into the monophyly of the currently recognized genera (see also Egan & al., 2016 and Cândido & al., 2020) and the relationships among them.

The resolution of a monophyletic *Adenodolichos* as sister to all other Cajaninae genera (Figs. 2, 3, suppl. Fig. S1) agrees with the findings of Bruneau & al. (1995) and Cândido & al. (2020). The monophyly of this genus is further supported by its unifying morphological characteristics, including a herbaceous, subshrubby or shrubby, erect or prostrate habit, plants often glandular, leaves usually 3–5-foliolate; leaflets glandular beneath; and fruit a legume, generally with two seeds (see Lackey, 1977, 1978, 1981). Lackey (1978) initially considered *Adenodolichos* to be a doubtful member of Cajaninae because of its possession of canavanine and bracteolate flowers, characteristics absent in the other representatives of the subtribe. However, in a later publication (Lackey, 1981), he reversed that position, stating that *Adenodolichos* best sits within Cajaninae, based on its possession of bulbous-based trichomes and vesicular glands, characters considered to be diagnostic for the subtribe (Vargas & al., 2018).

The placement of *Flemingia* as a relatively divergent clade within Cajaninae (sister to the rest of the tribe excluding *Adenodolichos*) and the well-supported monophyly of the genus (Figs. 2, 3, suppl. Fig. S1) are also in agreement with our previous study (Cândido & al., 2020). *Flemingia* species occur mainly in Asia (Lackey, 1977; Schrire, 2005) and are morphologically distinct from species of *Rhynchosia* in having larger leaflets and inflorescences, but are similar to species of *Cajanus* and *Dunbaria* in number of seeds per fruit (3+) and a herbaceous or shrubby habit (Lackey, 1977).

With respect to the largest genus, *Rhynchosia*, its polyphyly (Figs. 2, 3, suppl. Fig. S1) is also in agreement with previous studies (Egan & al., 2016; LPWG, 2017; and Cândido & al., 2020). The placement of *R. volubilis*, the type of *Rhynchosia*, together with *R. dielsii* and members of the genus *Dunbaria* in the Dunbaria clade (Fig. 2), phylogenetically distant from the majority of *Rhynchosia* species, presents future challenges for achieving a new generic classification of Cajaninae based on monophyly, while at the same time minimizing necessary nomenclatural changes.

We are unaware of any morphological synapomorphy supporting the Dunbaria clade. *Rhynchosia volubilis* and *R. dielsii* are restricted to Asia and share with *Dunbaria* a climbing habit, pinnately trifoliolate leaves, inflorescences that can exceed the subtending leaf in length, and laterally compressed, oblong legumes that are slightly constricted between the seeds. *Rhynchosia volubilis* and *R. dielsii* also have bluish-black seeds that remain attached to one of the dehisced valves, forming an exposed cluster on the infructescence. *Dunbaria* comprises about 20 species and has a predominantly Asian distribution. The genus can also be characterized by yellow flowers with twisted or recurved keels, arranged in axillary, pedunculate or almost sessile pseudoracemes, and elongated fruits (Van der Maesen, 1998). Most of these vegetative and reproductive features are shared between *Dunbaria* and the Asian *Rhynchosia* species occurring in this clade, rather than representing morphological synapomorphies of the Dunbaria clade. The preferred habitats of these taxa are also broadly similar, including seasonally dry tropical forests, thickets, scrubland, and grasslands.

The close relationship between *Dunbaria* and the two *Rhynchosia* species included in the Dunbaria clade is noteworthy because several characters traditionally used to distinguish these genera overlap among them. The most evident morphological distinction concerns seed number: *Dunbaria* species generally have 3–10 seeds per fruit, whereas *Rhynchosia* species typically have one or two, and only rarely three seeds per fruit (Grear, 1978; Van der Maesen, 1998). Thus, seed number may help distinguish *Dunbaria* from most *Rhynchosia* species, but it should not be interpreted as a synapomorphy of the Dunbaria clade.

The species-rich genus *Eriosema* was recovered as monophyletic and nested within a large clade containing *Rhynchosia* species, together with the genera *Carrissoa*, *Paracalyx*, *Bolusafra*, and *Chrysoscias*, here named the Rhynchosia clade (Fig. 2). The inclusion of these genera in *Rhynchosia* is also supported by morphology. All are erect, prostrate, or climbing herbs, subshrubs, or shrubs, with 2-seeded fruits (except in *Bolusafra* with three or more seeds) and trifoliolate leaves (but some species of *Eriosema* and *Rhynchosia* are unifoliolate). *Eriosema* was first established as a section of *Rhynchosia* by Candolle (1825: 388). The two sections were differentiated mainly by the location of the insertion point of the funicle in relation to the hilum, which is subcentral to terminal in *Rhynchosia* and always terminal in *Eriosema*. However, this character was subsequently found to display substantial overlap between the two genera (Bezerra & al., 2019; Cândido & al., 2019).

Carrissoa is a monospecific genus endemic to Angola that was first described by Baker (1933). *Carrissoa angolensis*, together with *Rhynchosia insignis*, appears in the current phylogeny as sister to *Eriosema* (Fig. 2, suppl. Fig. S1). *Carrissoa* is morphologically very similar to species of *Eriosema* and *Rhynchosia* (Baker, 1933; Fort.-Perez, pers. obs.) in their mostly 2-seeded fruits. Baker (1933) commented

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that the only difference between *Carrissoa* and *Rhynchosia* is that the ovules in the ovary of *Carrissoa* are attached to their funiculi about 1/3 of the ovule length from their distal ends, not centrally as in *Rhynchosia*. However, Grear (1970) and Bezerra & al. (2024) clarified that the insertion point of the funicle in *Rhynchosia* can be central, subcentral, or terminal.

Paracalyx comprises six species that were originally described in the genus *Cylista* Aiton. *Paracalyx* emerged embedded within a well-supported clade of mostly Old World *Rhynchosia* species (Fig. 2, suppl. Fig. S1). Species of *Paracalyx* occur in Africa and Asia and morphologically resemble *Rhynchosia*, having a twining herbaceous or erect shrubby habit, with leaves pinnately 3-foliolate and leaflets with yellowish gland-dots on their lower surface, flowers in axillary racemes and pods laterally compressed and 1–2-seeded (Thulin, 1993). However, *Paracalyx* differs in having distinct calyx lobes, which are greatly expanded, papery, and persistent after flowering (Moteetee & Van Wyk, 2006).

Chrysoscias E.Mey. is placed together with some African *Rhynchosia* species and with the monospecific genus *Bolusafra* Kuntze also embedded in this clade (Figs. 2, 3, suppl. Fig. S1). Some authors already had treated *Chrysoscias* as a synonym of *Rhynchosia* (e.g., Grear, 1978; Germishuizen, 2000; Govaerts, 1999), but it has also been treated as a distinct genus (Schrire, 2005) or as a section of *Rhynchosia* (Baker, 1923; Moteetee & al., 2012; Jaca & al., 2017).

The phylogenetic relationships recovered in this study provide additional evidence that species currently recognized as *Chrysoscias* are nested among African species of *Rhynchosia*. This topology is consistent with the results obtained by Cândido & al. (2020) and supports the conclusions of the unpublished phylogenetic study conducted by Manyelo (2014), reinforcing the non-monophyly of *Chrysoscias* as traditionally circumscribed.

A recent study by Jaca & al. (2018) clarified the taxonomy of the species placed in *Rhynchosia* sect. *Chrysoscias* E.Mey. and circumscribed it to comprise four species: *Rhynchosia angustifolia* (Jacq.) DC., *R. chrysoscias* Benth. ex Harv., *R. leucoscias* Benth. ex Harv. and *R. microscias* Benth. ex Harv. The species in *R.* sect. *Chrysoscias* are restricted to the Core Cape Subregion of the Greater Cape Region of South Africa and are characterized mainly by having golden coloured glands and bulbous-based trichomes distributed throughout the plant (Jaca & al., 2018). These species are also distinctive in their twining stems, pinnately trifoliolate leaflets with slightly to strongly revolute margins, yellow-petaled flowers arranged in axillary umbels or solitary, and by the pods compressed to slightly turgid, mucronate and partially dehiscent (Jaca & al., 2018).

Like *Rhynchosia* sect. *Chrysoscias*, the monospecific genus *Bolusafra* is also restricted to the Cape Province of South Africa (Moteetee & Van Wyk, 2006). This genus is characterized mainly by its twining habit and viscid branches (Moteetee & Van Wyk, 2006). It resembles *Rhynchosia* in having a similar twining growth habit, pinnately trifoliolate leaves with conspicuous veins, leaflets generally covered with glands on their lower surface, and yellow flowers (Moteetee & Van Wyk, 2006; Jaca & al., 2018). Nevertheless, *Bolusafra* is distinguished by its turgid 5–7-seeded fruits with prominent seed arils (vs. seed arils almost absent and fruits 2-seeded in *Rhynchosia*) (Schrire, 2005; Jaca & al., 2018). Due to the morphological similarity of the genera, some authors have considered *Bolusafra* to be a "viscid *Rhynchosia*-like vine" (Lackey, 1981; Moteetee & Van Wyk, 2006).

A recent study by Kates & al. (2024) presents the most extensive phylogenomic analysis to reconstruct the evolutionary history of the representatives of the nitrogen-fixing clade (NFC) in Angiosperms. In their analysis, a large sample of subtribe Cajaninae was included, comprising 74 accessions of *Eriosema*, 54 of *Rhynchosia*, 14 of *Cajanus*, 10 of *Flemingia*, 7 of *Dunbaria*, and 6 of *Adenodolichos*. As the phylogenetic tree presented by Kates & al. (2024) was designed to address relationships at the family level among nitrogen-fixing plants and includes genomic data from more than 12,000 herbarium samples, the study was not specifically focused on Cajaninae, despite sampling numerous species of this subtribe. Nevertheless, the phylogenetic placements of Cajaninae representatives recovered by Kates & al. (2024) are largely congruent with the results presented here.

Flemingia and *Adenodolichos* are resolved as monophyletic. *Eriosema* is also recovered as monophyletic but is nested within *Rhynchosia*, with *Eriosema* and *Rhynchosia clivorum* forming closely related lineages. In contrast, the Asian species *R. volubilis* (the type of *Rhynchosia*) and *R. dielsii*, together with *R. acuminatifolia* Makino (not sampled in this study), belong to a distinct clade that is sister to *Dunbaria* and *Cajanus*.

Within the remaining *Rhynchosia* lineages, species of *R.* sect. *Arcyphyllum* (Elliott) Torr. & A.Gray from South America form a closely related species group. Likewise, several Neotropical species currently assigned to *R.* sect. *Copisma* (E.Mey.) Endl. are recovered together, particularly those characterized by bicoloured seeds (i.e., series 2 of Grear, 1978). Although there are few published studies discussing the relationships among representatives of Cajaninae, many previous studies have mentioned that they are indeed closely related genera (Lackey, 1981; Schrire, 2005; Moteetee & Van Wyk, 2006; Manyelo, 2014; Jaca & al., 2018; Cândido & al., 2020). Our study represents the most complete and comprehensive phylogenetic study of subtribe Cajaninae and the genus *Rhynchosia* to date. Our results confirm the polyphyly of *Rhynchosia* with respect to *Eriosema*, *Paracalyx*, *Bolusafra*, *Carrissoa* and *Chrysoscias*. *Rhynchosia volubilis*, the type of *Rhynchosia*, emerged with *R. dielsii* in a separate clade that has taxonomic and nomenclatural implications. Furthermore, our study helps to elucidate the infrageneric relationships within *Rhynchosia* sensu lato, as well as the generic relationships between the genera of the subtribe.

Implications for the circumscription of *Rhynchosia*. — Our results show that the circumscription of *Rhynchosia* should be modified to include all species of *Bolusafra*, *Chrysoscias*, *Eriosema*, and *Paracalyx*, and to exclude *R. volubilis* (type of the genus), *R. dielsii*, and *R. acuminatifolia*. In our

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phylogenetic tree, this revised concept of the genus would correspond to the Rhynchosia clade.

The newly circumscribed *Rhynchosia* would then contain over 400 species. *Dunbaria* could be expanded to include three species of *Rhynchosia* (*R. volubilis*, *R. dielsii*, *R. acuminatifolia*). *Adenodolichos*, *Cajanus*, and *Flemingia* would remain unchanged in circumscription.

Morphological evidence is congruent with the phylogenetic placement of *Bolusafra*, *Carrissoa*, *Chrysoscias*, *Eriosema*, and *Paracalyx* within *Rhynchosia*. These genera share a suite of characters, notably trifoliolate leaves and fruits that are typically 2-seeded, although *Bolusafra* usually bears fruits with three or more seeds. Unifoliolate leaves occur in some species currently assigned to *Eriosema* and *Rhynchosia*.

Nevertheless, these characters are not exclusive to the Rhynchosia clade. Trifoliolate leaves, for example, are also found in related genera such as *Adenodolichos*, *Cajanus*, *Dunbaria*, and *Flemingia*, among others. Consequently, although morphology provides support for the broader circumscription suggested here, the strongest argument in favor of this classification comes from the molecular phylogenetic results, which consistently recover these genera as a well-supported evolutionary lineage.

According to Vargas (2019), in a thesis addressing character evolution in Cajaninae, the hypothetical ancestor of the subtribe was inferred to most likely possess vesicular glands and capitate trichomes as secretory structures. These secretory structures were also proposed as probable synapomorphies of the subtribe Cajaninae. This hypothesis will be further investigated in future studies using more comprehensive and refined approaches.

Considering that most species of *Rhynchosia* as currently circumscribed (ca. 150 of 257) are African, whereas the type of the genus is Asian (occurring in Southeast China, Hainan, Japan, Korea, Nansei-shoto, Taiwan, and Vietnam), and that only two species, including the type species, are resolved outside the remainder of *Rhynchosia* in the current phylogeny, the more nomenclaturally practical solution is to adopt a new type for *Rhynchosia*. This species would likely be African, thereby minimizing the nomenclatural impact of our results. The CPWG is currently working on two forthcoming papers: one that will formally present the taxonomic treatment of these changes, along with all necessary new combinations, and another presenting a proposal to adopt a replacement type.

■ FINAL CONSIDERATIONS

This study is part of a large project developed by a network of researchers under the collaborative title of the Cajaninae Phylogeny Working Group (CPWG). The results presented here, as well as biogeographic, phylogenomic, and character evolution analyses that are being carried out by the CPWG, will support the proposal of a new generic classification of Cajaninae. Future studies will also include divergence time analyses to determine the timing of diversification within the subtribe and to help explain its biogeographical history.

■ AUTHOR CONTRIBUTIONS

Design of the research: APFP, JSB, WV, LMPAB, ESC, ANM, AAA, MV; performance of the research: APFP, JSB, ANM, AAA, WV, LMPAB, ESC; data analysis: MV, APFP, FP; data collection: APFP, WV, LMPAB, ESC, JSB, ANM, AAA, NPB, MTK; writing the manuscript: APFP, WV, LMPAB, ESC, JSB, ANM, AAA, GPL, MV, BMT, CS, NPB. All authors revised the manuscript and approved the final version.

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Appendix 1. Voucher information for the sequences used in this study.

Taxon name, country and/or locality, collector(s), collection number and herbarium, and GenBank accession numbers available (ITS, *rpl32* and *trnQ*, respectively). Newly generated sequences are indicated by an asterisk (*); missing sequences are indicated by an n-dash (–).

Adenodolichos baumii Harms, Africa, Zambia, *M.G. Bingham 14158* (K); PZ865204*; –; PZ872950*. ***Adenodolichos baumii*** Harms, Africa, South Africa, *J.P. Laveridge 403* (PRE); MT376874; MT547492; MT577460. ***Adenodolichos punctatus*** (Micheli) Harms, Africa, Malawi, *J. Pawek 9896* (PRE); MT376875; MT547493; MT577461. ***Adenodolichos rhomboideus*** Harms, Africa, *E.A. Robinson 3794* (PRE); PZ865203*; PZ862415*; PZ872951*. ***Bolusafra bituminosa*** (L.) Kuntze, Africa, South Africa, *Adolf Hafström s.n.* (S13-6630); MT376865; MT547491; MT577442. ***Bolusafra bituminosa*** (L.) Kuntze, Africa, South Africa, *Adolf Hafström & Gösta Lindeberg s.n.* (S13-6627); PZ865202*; PZ862426*; PZ872959*. ***Bolusafra bituminosa*** (L.) Kuntze, Africa, South Africa, *B.-E. Van Wyk 2739* (JRAU); –; PZ862425*; –. ***Bolusafra bituminosa*** (L.) Kuntze, Africa, South Africa, *Cowell, C. 1174* (K); –; PZ862427*; –. ***Cajanus cajan*** (L.) Huth, South America, Venezuela, *O.O. Miller & J.R. Johnston 139* (P02921261); PZ865207*; PZ862417*; PZ872954*. ***Cajanus cajanifolius*** (Haines) Maesen, Asia, India, *L.J.G. van der Maesen 2739* (K); MT376908; MT547497; MT577495. ***Cajanus cinereus*** (F.Muell. ex Benth.) F.Muell., Oceania, Australia, *Martin J.S. Sands 4590* (K); MT376909; MT547498; –. ***Cajanus flavus*** DC. (= *C. cajan*), Africa, Ethiopia, *C.G.T. Kotschy 266* (P06892742); PZ865205*; –; PZ872955*. ***Cajanus marmoratus*** (R.Br. ex Benth.) F.Muell., Oceania, Australia, *Anzancot de Menezes 1100* (P); PZ865208*; PZ862418*; PZ872952*. ***Cajanus reticulatus*** var. ***grandifolius*** (F.Muell.) Maesen, Oceania, Australia, *Verdcourt, Huxley & White 4870* (K); PZ865209*; PZ862419*; –. ***Cajanus rugosus*** (Wight & Arn.) Maesen, Asia, Sri Lanka, *L.J.G. van der Maesen 4033* (K); –; PZ862420*; –. ***Cajanus scarabaeoides*** (L.) Thouars, Africa, Tanzania, *H. Faulkner 3202* (P02723639); PZ865206*; PZ862416*; PZ872953*. ***Cajanus scarabaeoides*** (L.) Thouars, Asia, Thailand, *A.N. Egan 13-0733* (K); MT376910; MT547499; MT577496. ***Cajanus trinervius*** (DC.) Maesen, Asia, Sri Lanka, *L.J.G. van der Maesen 4159* (K); –; PZ862421*; –. ***Camptosema grandiflorum*** Benth. (= *Cratylia spectabilis* Tul.); South America, Brazil, *L.B. Santos & F.L.S. Ferreira 199* (BOTU); MT376938; MT547526; –. ***Carrissoa angolensis*** Baker f.; Africa, Angola, *Goyder, Darbyshire, Godinho & Kodo 7153* (K); PZ865137*; –; –. ***Centrosema virginianum*** (L.) Benth., South America, Brazil, *A. Amaral Jr. & al. 306* (BOTU); PZ865217*; PZ862438*; –. ***Chrysoscias calycina*** E.Mey., Africa, South Africa, *S.L. Williams 841* (K); MT376914; MT547503; MT577500. ***Chrysoscias grandiflora*** E.Mey., Africa, South Africa, *H.T. Scharf 1433* (K); –; PZ862424*; –. ***Chrysoscias parviflora*** E.Mey., Africa, South Africa, *E. Esterhuysen 13330* (K); –; –; PZ872958*. ***Dunbaria bella*** Prain, Asia, Thailand, *Chantaronothai & al. 854* (K); –; PZ862422*; PZ872956*. ***Dunbaria fusca*** (Wall.) Kurz, Asia, Thailand, *A.N. Egan 13-0808* (K); MT376911; MT547500; MT577497. ***Dunbaria glandulosa*** Prain, Asia, Thailand, *K. Larsen & & S.S. Larsen* (K003822665); MT376912; MT547501; MT577498. ***Dunbaria villosa*** (Thunb.) Makino,

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Appendix 1. Continued.

Asia, South Korea, *B.R. Yinger & al. 2634* (K); MT376913; MT547502; MT577499. ***Dunbaria villosa*** (Thunb.) Makino, Africa, Laos, *J. Klackenberg 1123* (S04-2090); –; PZ862423*; PZ872957*. ***Eriosema acuminatum*** (Eckl. & Zeyh.) C.H.Stirt., Africa, South Africa, *K. Grieve 967* (PRE); MT376854; MT547414; MT577432. ***Eriosema affine*** De Wild., Africa, Republic of Malawi, *L.J. Brass 17426* (NY); –; MT547474; MT577505. ***Eriosema afzelii*** Baker, Africa, Guinea, *N. Diarra 1391* (S); –; MT547409; MT577423. ***Eriosema albo-griseum*** Baker f., Africa, Angola, *Anzancot de Menezes 1100* (P); MT376844; MT547408; MT577422. ***Eriosema andohii*** Milne-Redh., Africa, Mali, *R. Demange 2670* (P); MT376864; MT547420; MT577440. ***Eriosema angolense*** Baker f., Africa, Burundi, *M. Reekmans 6308* (K); MT376898; MT547460; MT577484. ***Eriosema angustifolium*** Burtt Davy, Africa, South Africa, *K.W. Grieve 990* (PRE); MT376855; MT547415; MT577433. ***Eriosema arachnoideum*** Verdc., Africa, Tanzania, *S. Bidgood & I. Darbyshire 5279* (P); –; MT547421; MT577441. ***Eriosema bauchiense*** Hutch. & Dalziel, Africa, Democratic Republic of the Congo, *H.M. Richards 20643* (S); –; MT547444; MT577467. ***Eriosema benthamianum*** Mart. ex Benth., South America, Brazil, *E.S. Cândido 1101* (BOTU); MT376887; MT547451; MT577473. ***Eriosema brevipes*** Grear, South America, Brazil, *A.P. Fortuna-Perez 2101* (BOTU); MT376822; MT461281; MT547529. ***Eriosema buchananii*** Baker f., Africa, Rwanda, *H.G. Troupin 7480* (NY); MT376920; MT547475; MT577506. ***Eriosema campestre*** Benth. var. ***campestre***, South America, Brazil, *E.S. Cândido & al. 1098* (BOTU); MT376876; MT547439; MT577462. ***Eriosema campestre*** var. ***delicatula*** Fortunato, South America, Brazil, *W. Vargas 6* (CGMS); MT376838; MT547402; MT577416. ***Eriosema campestre*** var. ***macrophyllum*** (Grear) Fortunato, South America, Brazil, *A.P. Fortuna-Perez 1436* (OUPR); MT376828; MT461287; MT547535. ***Eriosema campestre*** var. ***pubescens*** (Chodat & Hassl.) Grear, South America, Brazil, *A. Flores & R.S. Rodrigues 711* (UEC); MT376837; MT547401; MT577415. ***Eriosema chinense*** Vogel, Asia, Philippines, *E.D. Merrill 878* (S); MT376944; –; –. ***Eriosema chrysadenium*** Taub., Africa, Tanzania, *F.J. Breteler 11638* (S); MT376892; MT547455; MT577478. ***Eriosema congestum*** Benth., South America, Brazil, *M.J. Silva 7396* (UFG); MT376888; MT547452; MT577474. ***Eriosema cordatum*** E.Mey., Africa, South Africa, *K.W. Grieve 987* (PRE); MT376856; MT547416; MT577434. ***Eriosema cordatum*** E.Mey., Africa, South Africa, *Style 5004* (NH); –; PZ862411*; PZ872943*. ***Eriosema cordifolium*** Hochst. ex A.Rich., Africa, South Sudan, *I. Friis & K. Vollesen 433* (K); MT376904; MT547470; MT577492. ***Eriosema crinitum*** (Kunth) G.Don var. ***crinitum***, South America, Brazil, *E.S. Cândido & al. 1075* (OUPR); MT376823; MT461282; MT547530. ***Eriosema cupreum*** Harms, South America, Brazil, *A. Glaziou 20888* (S); MT376882; –; –. ***Eriosema defoliatum*** Benth., South America, Brazil, *E.S. Cândido 1109* (BOTU); MT376889; MT547453; MT577475. ***Eriosema diffusum*** (Kunth) G.Don, Central America, Costa Rica, *J. Bustamante 202* (S); MT376893; MT547456; MT577479. ***Eriosema distinctum*** N.E.Br., Africa, South Africa *K.W. Grieve 1039* (PRE); MT376859; MT547419; –. ***Eriosema distinctum*** N.E.Br. Africa, South Africa, *Style 4531* (NH); –; PZ862408*; –. ***Eriosema dregei*** E.Mey., Africa, South Africa, *Style 4443* (NH); –; PZ862412*; PZ872945*. ***Eriosema dregei*** E.Mey., Africa, South Africa, *A. Abbott 9272* (K); MT376905; MT547471; MT577493. ***Eriosema elegans*** Fort.-Perez & M.J.Silva, South America, Brazil, *M.J. Silva 7228* (UFG); MT376885; MT547449; MT577472. ***Eriosema ellipticifolium*** Schinz, Africa, South Africa, *C.H. Stirton 1441* (K); MT376906; MT547472; –. ***Eriosema ellipticum*** Welw. ex Baker, Africa, Mozambique, *A.R. Torre 265* (S); –; MT547422; MT577443. ***Eriosema englerianum*** Harms, Africa, Zimbabwe, *R.D. Bayliss 10499* (S); MT376866; MT547423; MT577444. ***Eriosema erectum*** Baker f., Africa, Democratic Republic of the Congo, *H.M. Richards 15782* (S); MT376867; MT547424; MT577445. ***Eriosema flemingioides*** Baker, Africa, Cote d'Ivoire, *A. Fournier 145* (NY); MT376921; MT547476; MT577507. ***Eriosema flexuosum*** Staner, Africa, Democratic Republic of the Congo, *E. Milne-Redhead & P. Taylor 8920* (S); MT376868; MT547425; MT577446. ***Eriosema floribundum*** Benth., South America, Brazil, *E.S. Cândido & al. 1090* (OUPR); MT376824; MT461283; MT547531. ***Eriosema glabrum*** Mart. ex Benth., South America, Brazil, *E.S. Cândido & al. 1067* (OUPR); MT376832; MT547398; MT577411. ***Eriosema glaziovii*** Harms, South America, Brazil, *A.P. Fortuna-Perez & al. 1457* (OUPR); MT376825; MT461284; MT547532. ***Eriosema glomeratum*** (Guill. & Perr.) Hook.f., Africa, Tanzania, *O. Flock 356* (S); –; MT547445; MT577468. ***Eriosema grandiflorum*** (Schltdl. & Cham.) G.Don, North America, Mexico, *H.S. Gentry 1837* (S); MT376869; MT547426; MT577447. ***Eriosema gunniae*** C.H.Stirt., Africa, South Africa, *C.H. Stirton & Germishuizen 6938* (K); MT376899; MT547461; MT577485. ***Eriosema harmsianum*** Dinter, Africa, South Africa, *K. Dinter 5750* (S); MT376870; MT547427; MT577448. ***Eriosema hatschbachii*** Fort.-Perez & G.P.Lewis, South America, Brazil, *A.P. Fortuna-Perez & al. 1401* (OUPR); MT376827; MT461286; MT547534. ***Eriosema heterophyllum*** Benth., South America, Brazil, *E.S. Cândido & al. 1068* (OUPR); MT376826; MT461285; MT547533. ***Eriosema humile*** Hauman, Africa, Angola, *D.J. Goyder 6273* (K); –; MT547462; MT577486. ***Eriosema irwinii*** Grear, South America, Brazil, *E.S. Cândido 1106* (BOTU); MT376890; MT547454; MT577476. ***Eriosema jurionianum*** Staner & De Craene, Africa, Ethiopia, *I. Ambjörn 372* (S); –; MT547428; MT577449. ***Eriosema kraussianum*** Meisn., Africa, South Africa, *K.W. Grieve 942* (PRE); MT376857; MT547417; MT577435. ***Eriosema kraussianum*** Meisn., Africa, South Africa, *Style 5419* (NU); –; PZ862410*; PZ872947*. ***Eriosema latifolium*** (Benth. ex Harv.) C.H.Stirt., Africa, South Africa, *C.H. Stirton 5599* (K); –; MT547463; –. ***Eriosema laurentii*** De Wild., Africa, Uganda, *Kare Arnstein Lye s.n.* (K); MT376907; MT547473; MT577494. ***Eriosema laxiflorum*** Harms, South America, Brazil, *M.J. Silva 4407* (UFG); MT376879; MT547441; MT577464. ***Eriosema lebrunii*** Staner & De Craene, Africa, Burundi, *M. Reekmans 8784* (S); –; MT547429; MT577450. ***Eriosema longiflorum*** Benth., South America, Brazil, *M. Silva 4025* (UFG); MT376880; MT547442; MT577465. ***Eriosema longifolium*** Benth., South America, Brazil, *A.P. Fortuna-Perez & al. 1442* (OUPR); MT376829; MT461288; MT547536. ***Eriosema macrostipulatum*** Fort.-Perez, Cândido & M.J.Silva, South America, Brazil, *M.J. Silva 4696* (UFG); MT376886; MT547450; MT586133. ***Eriosema macrostipulum*** Baker f., Africa, Burundi, *M. Reekmans 4134* (K); –; MT547464; –. ***Eriosema mirabile*** R.E.Fr., Africa, Angola, *R.G.N. Young 1107* (NY); –; MT547477; MT577508. ***Eriosema molle*** Hutch. ex Milne-Redh., Africa, Togo, *H. Ern & al. 119* (S); MT376845; MT547410; MT577424. ***Eriosema montanum*** Baker f., Africa, Mozambique, *A. Stolz 222* (S); MT376883; MT547446; MT577469. ***Eriosema monticola*** Taub., Africa, Togo, *J.M. Lock 84/94* (S); MT376843; MT547407; MT577421. ***Eriosema multiflorum*** B.L.Rob. ex Pringle, North America, Mexico, *M. Hahn 386* (P); MT376840; MT547404; MT577418. ***Eriosema naviculare*** C.H.Stirt., Africa, South Africa, *C.H. Stirton 9839* (K); MT376900; MT547465; MT577487. ***Eriosema nutans*** Schinz, Africa, South Africa, *B.D. Schrire 2422* (K); MT376901; MT547466; MT577488. ***Eriosema oblongum*** Benth. ex Harv., Africa, South Africa, *R.F. Rand 590* (NY); MT376922; MT547478; MT577509. ***Eriosema palmeri*** S.Watson var. ***palmeri***, North America, Mexico, *H.S. Gentry 2536* (S); MT376848; MT547413; MT577427. ***Eriosema parviflorum*** E.Mey., Africa, Liberia, *J.G. Adam 20593* (P); MT376841; MT547405; MT577419. ***Eriosema pauciflorum*** Klotzsch, Africa, South Africa, *A. Hafström & J.P.H. Acock 579* (S); –; MT547430; MT577451. ***Eriosema pentaphyllum*** Harms, Africa, Zambia, *H.M. Richards 8193* (K); MT376902; MT547467; MT577489. ***Eriosema platycarpon*** Micheli, South America, Paraguay, *T.M. Pedersen 4372* (S); –; MT547431; MT577452. ***Eriosema populifolium*** Benth. ex Harv., Africa, South Africa, *C.H. Stirton 1200* (S); –; MT547433; MT577454. ***Eriosema populifolium*** Benth. ex Harv. & Sond., Africa, South Africa, *Style 5415* (NU); –; PZ862407*; PZ872948*. ***Eriosema psoraleoides*** (Lam.) G.Don, Africa, South Africa, *Style 4674* (NH); –; PZ862409*; PZ872946*. ***Eriosema preptum*** C.H.Stirt., Africa, South Africa, *H.J. Venter & A. Venter 10237* (S); MT376871; MT547432; MT577453. ***Eriosema prorepens*** Benth., South America, Brazil, *R. Romero & al. 4653* (VIC); MT376894; MT547457; MT577480. ***Eriosema prunelloides*** Welw. ex Baker f., Africa, Zambia, *D.B. Fanshawe 8910* (K); –; MT547468; MT577490. ***Eriosema psoraleoides*** (Lam.) G.Don, Africa, South Africa, *A. Burkart 24522* (S); MT376943; –; –. ***Eriosema pulchellum*** (Kunth) G.Don, North America, Mexico, *C.G. Pringle 9748* (S); MT376884; MT547447; MT577470. ***Eriosema pycnanthum*** Benth. var. ***pycnanthum***, South America, Brazil, *S.G. Rezende & M.S. Medens 2088* (BHCB); MT376895; MT547458; MT577481. ***Eriosema pycnanthum*** var. ***veadeirense*** Grear, South America, Brazil, *H.S. Irwin & al. 12885* (NY); MT376896; MT547459; MT577482. ***Eriosema robustum*** Baker, Africa, Ethiopia, *J.B. Gillett 14595* (S); MT376872; MT547434; MT577455. ***Eriosema rossii*** C.H.Stirt., Africa, South Africa, *K.W. Grieve 946* (PRE); MT376858; MT547418; –. ***Eriosema rossii*** C.H.Stirt., Africa, South Africa, *Style 5416* (NU); –; PZ862413*; PZ872944*. ***Eriosema rufum*** (Kunth) G.Don var. ***rufum***, South America, Brazil, *W. Vargas 12* (CGMS); MT376833; MT547399; MT577412. ***Eriosema shirense*** Baker f., Africa, Guinea, *Adam 14687* (S); MT376846; MT547411; MT577425. ***Eriosema simplicifolium*** var. ***micranthum*** Grear, South America, Brazil, *R.S. Rodrigues & al. 1386* (UEC); MT376835; MT547400; MT577414. ***Eriosema simplicifolium*** (DC.) G.Don var. ***simplicifolium***, South America, Brazil, *E.S. Cândido & al. 1099* (BOTU); MT376877; MT547440; MT577463. ***Eriosema simplicifolium*** (DC.) G.Don var. ***simplicifolium***, South America, Brazil, *A.P. Fortuna-Perez s.n.* (BOTU); PZ865139*; PZ862414*; PZ872949*. ***Eriosema simplicifolium*** (DC.) G.Don var. ***simplicifolium***, South America, Brazil, *A.P. Fortuna-Perez & al. 2012* (BOTU); PZ865138*; –; –. ***Eriosema sparsiflorum*** Baker f., Africa, Tanzania, *A. Borgdan 3680* (S); MT376873; MT547435; MT577456. ***Eriosema speciosum*** Welw. ex Baker, Africa,

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Appendix 1. Continued.

Angola, *B. Fritzsche 101* (S); –; MT547436; MT577457. ***Eriosema spicatum*** Hook.f., Africa, Togo, *J.M. Lock 84/49* (K); MT376842; MT547406; MT577420. ***Eriosema squarrosum*** (Thunb.) Walp., Africa South, Africa, *A. Hafstrom & J.P.H. Acock 616* (S); –; MT547448; MT577471. ***Eriosema stenophyllum*** Harms, South America, Brazil, *L.P. Queiroz 15074* (HUEFS); MT376839; MT547403; MT577417. ***Eriosema strictum*** Benth., South America, Brazil, *G. Hatschbach 8643* (HB); MT376941; –; –. ***Eriosema tacuaremboense*** Arechav., South America, Brazil, *A.P. Fortuna-Perez & al. 1443* (OUPR); MT376830; MT461289; MT547537. ***Eriosema tozziae*** Cândido & Fort.-Perez, South America, Brazil, *L.S. Kinoshita & al. 02/158* (UEC); MT376881; MT547443; MT577466. ***Eriosema triformum*** Burgt, Africa, Guinea, *X.M. van der Burgt & al. 1240* (NY); –; MT547480; MT577511. ***Eriosema tuberosum*** A.Rich., Africa, Ethiopia, *Schimper 1202* (S); –; MT547437; MT577458. ***Eriosema vanderystii*** (De Wild.) Hauman, Africa, Zambia, *S.M. Chisumpa S.M.C3* (K); MT376903; MT547469; MT577491. ***Eriosema velutinum*** Baker f. & Haydon, Africa, Democratic Republic of the Congo, *A.A. Bullock 2844* (S); –; MT547438; MT577459. ***Eriosema verdickii*** De Wild., Africa, Niger, *J. Louve 2699* (K); MT376847; MT547412; MT577426. ***Eriosema violaceum*** (Aubl.) G.Don, South America, Brazil, *E. Ule 8160* (K); MT376942; –; –. ***Eriosema umtamvunense*** C.H.Stirt., Africa, South Africa, *Style 4473* (NH); –; PZ862406*; –. ***Flemingia congesta*** Roxb. ex W.T. Aiton, Asia, India, *P. Remanandan 4698* (K); MT376915; MT547504; MT577501. ***Flemingia ferruginea*** Wall., Asia, India, *K. Larsen 9152* (K); MT376916; MT547505; MT577502. ***Flemingia grahamiana*** Wight & Arn., African, South Africa, *W.J. Hanekom 2315* (P); PZ865210*; PZ862428*; PZ872960*. ***Flemingia involucrata*** Benth., Oceania, Australia, *B.R. Maslin 5115* (K); –; PZ862430*; –. ***Flemingia lineata*** (L.) Roxb. ex W.T.Aiton, Asian, India, *H.F. Mooney 3166* (K); –; –; PZ872962*. ***Flemingia macrophylla*** (Willd.) Kuntze ex Merr., African, Cameroon, *P. Mezeli 258* (P); PZ865211*; PZ862429*; PZ872961*. ***Flemingia pauciflora*** Benth., Oceania, Australia, *J.R. Clarkson & V.J. Nelder 7998* (K); PZ865212*; PZ862431*; PZ872963*. ***Flemingia sericans*** Kurz, Oceania, Australia, *J. Cowie & K.G. Brennan 9083* (K); MT376917; MT547506; –. ***Flemingia trifoliastrum*** Domin, Oceania, Australia, *Evans M. 3012* (K); PZ865213*; PZ862432*; –. ***Galactia striata*** (Jacq.) Urb., South America, Brazil, *W. Vargas & E.S. Cândido 72* (BOTU); MT376923; MT547509; –. ***Paracalyx balfourii*** (Vierh.) Ali, Asia, Yemen, *A.G. Miller & al. 8654* (K); –; PZ862433*; –. ***Paracalyx microphyllus*** Ali, Africa, Somalia, *M. Thulin & al. 10558* (K); MT376918; MT547507; MT577503. ***Paracalyx nogalensis*** (Chiov.) Ali, Africa, Somalia, *M. Thulin & A.M. Warfa 5425* (K); PZ865214*; PZ862434*; PZ872967*. ***Paracalyx scariosus*** (Roxb.) Ali, Asia, India, *L.J.G. van der Maesen 1973* (K); –; PZ862435*; PZ872964*. ***Paracalyx scariosus*** (Roxb.) Ali, Asia, India, *N. Kameswara Rao 12* (K); PZ865216*; PZ862436*; PZ872965*. ***Paracalyx schweinfurthii*** Ali, Oceania, Australia *O. Cronk 3* (K); MT376919; MT547508; MT577504. ***Paracalyx somalorum*** (Vierh.) Ali, Africa, Ethiopia, *I. Friis 9993* (K); PZ865215*; PZ862437*; PZ872966*. ***Rhynchosia acuminatissima*** Miq., Africa, Papua New Guinea, *W. Takeuchi 9284* (NY); MT376937; MT547525; MT577524. ***Rhynchosia adenodes*** Eckl. & Zeyh., Africa, South Africa, *R.D.A. Bayliss 6409* (NY); MT376932; MT547519; MT577519. ***Rhynchosia albae-paulii*** Berhaut, Africa, Senegal, *Berhaut 7495* (P); MT376860; MT547487; MT577436. ***Rhynchosia albissima*** Gand., Africa, South Africa, *Germishuizen 8686* (PRE); –; PZ862310*; PZ872883*. ***Rhynchosia ambacensis*** (Hiern) K.Schum., Africa Cameroon, *J. Raynal 12914* (P); MT376861; MT547488; MT577437. ***Rhynchosia americana*** (Mill.) Metz, s. loc., *Fredholm 5399* (SI); PZ865173*; –; –. ***Rhynchosia androyensis*** Du Puy & Labat, Africa, Madagascar, *L. Alorge 2295* (P); MT376850; MT547483; MT577429. ***Rhynchosia arida*** C.H.Stirt., Africa, South Africa, *Van Wyk 3029* (JRAU); –; PZ862337*; –. ***Rhynchosia arenicola*** Hassl., South America, Brazil, *G. Hatschbach 2577* (SI); PZ865199*; –; –. ***Rhynchosia atropurpurea*** Germish., Africa, South Africa, *Hankey, Turner, Aubrey 1064* (PRE); –; PZ862340*; –. ***Rhynchosia aureovillosa*** var. ***humbertii*** Hauman, Africa, Rwanda, *H.G. Troupin 5686* (NY); –; MT547520; MT577520. ***Rhynchosia avensis*** Benth. ex Baker f., Asia, Thailand, *D. Kerr 4642* (P); PZ865141*; –; PZ872910*. ***Rhynchosia balansae*** Micheli, South America, Argentina, *M. Micken 235* (SI); PZ865171*; –; –. ***Rhynchosia balansae*** Micheli, South America, Brazil, *G. Hatschbach & al. 74908* (K); PZ865182*; PZ862379*; –. ***Rhynchosia balansae*** Micheli var. ***balansae***, South America, Brazil, *A.L.B. Sartori & al. 709* (BOTU); PZ865196*; PZ862404*; PZ872929*. ***Rhynchosia baukea*** Du Puy & Labat, Africa, Madagascar, *M. Peltier 1102* (P); PZ865143*; PZ862360*; –. ***Rhynchosia breviracemosa*** Hauman, Africa, Angola, *Azancot de Menezes 732* (P); –; PZ862364*; –. ***Rhynchosia brunnea*** Baker f., Africa, Gana, *R.A.A. Oldeman 803* (P); –; PZ862365*; PZ872919*. ***Rhynchosia buchananii*** Harms, Africa, Malawi, *K. Kaunda & R.B. Kwatha 632* (NY); MT376933; MT547521; –. ***Rhynchosia buettneri*** Harms, Africa, Cote d'Ivoire, *P. de Fabrègues 3473* (P); MT376862; MT547489; MT577438. ***Rhynchosia caaguazuensis*** Hassl., South America, Paraguay, *E. Hassler 11067* (NY); MT376929; MT547515; MT577515. ***Rhynchosia calycosa*** Hemsl., South America, Ecuador, *L. Holm-Nielsen & S. Ieppensen 83* (SI); PZ865172*; –; –. ***Rhynchosia calvescens*** Meikle, Africa, South Africa, *Smith 5933* (PRE); –; PZ862309*; PZ872882*. ***Rhynchosia candida*** (Welw. ex Hiern) Torre, Africa, South Africa, *Giess 8077* (PRE); –; PZ862331*; –. ***Rhynchosia capensis*** Schinz, Africa, South Africa, *Boatwright & al. 667* (NBG); –; PZ862307*; PZ872881*. ***Rhynchosia capensis*** Schinz, Africa, South Africa, *N.S. Pillans 10165* (NY); PZ865155*; PZ862308*; –. ***Rhynchosia caribaea*** (Jacq.) DC., Africa, South Africa, *Acock 20303* (PRE); PZ865145*; PZ862343*; –. ***Rhynchosia chapelieri*** Baill., Africa, Madagascar, *P. Ranirison 699* (P); PZ865144*; PZ862361*; –. ***Rhynchosia chrysoscias*** Benth. ex Harv., Africa, South Africa, *Boatwright & al. 597* (NBG); –; PZ862316*; –. ***Rhynchosia chrysoscias*** Benth. ex Harv., Africa, South Africa, *Schuh, Cassis, Weirauch PBI_SA03_H191* (NY); PZ865156*; PZ862317*; PZ872898*. ***Rhynchosia ciliata*** (Thunb.) Druce, Africa, South Africa, *Van Wyk 3307* (JRAU); –; PZ862339*; –. ***Rhynchosia claussenii*** Benth., South America, Brazil, *C.R. Martins 252* (UEC); PZ865174*; PZ862376*; PZ872927*. ***Rhynchosia claussenii*** Benth., South America, Brazil, *E.P. Heringer s.n*. (UB); –; PZ862377*; –. ***Rhynchosia clivorum*** S.Moore, Africa, South Africa, *Esterhuysen 21485* (PRE); –; PZ862313*; PZ872887*. ***Rhynchosia clivorum*** S.Moore, Africa, South Africa, *W.J. Hanekom s.n*. (P); PZ865152*; PZ862314*; PZ872890*. ***Rhynchosia cliffordii*** Hutch. & E.A.Bruce, Africa, Somalia, *J.B. Gillett 4864* (P); MT376863; MT547490; MT577439. ***Rhynchosia coddii*** Germish., Africa, South Africa, *Germishuizen 399* (PRE); –; PZ862342*; –. ***Rhynchosia cooperi*** (Baker f.) Harv. ex Burtt, Africa, South Africa, *Davy Van Wyk & Van Wyk 374* (JRAU); –; PZ862323*; PZ872904*. ***Rhynchosia crassifolia*** Benth. ex Harv., Africa, South Africa, *Bester 7285* (PRE); –; PZ862318*; PZ872899*. ***Rhynchosia corylifolia*** Mart. ex Benth., South America, Brazil, *A.P. Fortuna-Perez 1531* (UEC); MT376940; MT547528; MT577526. ***Rhynchosia craibiana*** Rehder, Asia, China, *D.E. Boufford & al. 3114* (P); PZ865140*; PZ862355*; PZ872909*. ***Rhynchosia cytisoides*** (Bertol.) Wilbur, North America, U.S.A., *R.K. Godfrey 84172* (NY); MT376925; MT547511; MT577513. ***Rhynchosia debilis*** G.Don, Africa, Ghana, *J.M. Robertson 50* (NY); PZ865157*; PZ862366*; –. ***Rhynchosia densiflora*** subsp. ***chrysadenia*** (Taub.) Verdc., Africa, South Africa, *Zambatis 2420* (PRE); –; PZ862332*; –. ***Rhynchosia dielsii*** Harms, Asia, Japan, *K. Yao 9152* (NY); PZ865167*; –; PZ872895*. ***Rhynchosia difformis*** (Elliott) DC., North America, U.S.A., *S. McDaniel 29983* (NY); PZ865183*; PZ862388*; PZ872923*. ***Rhynchosia discolor*** M.Martens & Galeotti, Central America, Guatemala, *J.J. Castillo & J.M. Vargas 2741* (NY); MT376926; MT547512; MT577514. ***Rhynchosia diversifolia*** Micheli, South America, Uruguay, *M. Bonifacino & al. 1803* (S); MT376939; MT547527; MT577525. ***Rhynchosia diversifolia*** var. ***diversifolia*** Micheli, South America, Argentina, *A. Krapovickas & al. 21474* (P); PZ865176*; –; PZ872940*. ***Rhynchosia edulis*** Griseb., South America, Brazil, *F. França & al. 2164* (HUEFS); PZ865200*; PZ862385*; –. ***Rhynchosia elisae*** O.Téllez, North America, Mexico, *O. Tellez 12583* (NY); MT376897; MT547496; MT577483. ***Rhynchosia emarginata*** Germish., Africa, South Africa, *Smook 7965* (PRE); –; PZ862305*; –. ***Rhynchosia emarginata*** Germish., Africa, South Africa, *Boatwright 572* (NBG); –; –; PZ872879*. ***Rhynchosia ferulifolia*** (C.Presl) Benth. ex Harv., Africa, South Africa, *H. Bolus 3775* (NY); –; PZ862367*; –. ***Rhynchosia ferulifolia*** (C.Presl) Benth. ex Harv., Africa, South Africa, *F.M. Leighton 1889* (NY); PZ865158*; PZ862368*; PZ872913*. ***Rhynchosia fleckii*** Schinz, Africa, Namibia, *R. Seydel 1806* (NY); MT376934; MT547522; MT577521. ***Rhynchosia ferulifolia*** (C.Presl) Benth. ex Harv., Africa, South Africa, *Jaca & al. 462* (NBG); –; PZ862306*; PZ872914*. ***Rhynchosia fleckii*** Schinz, Africa, South Africa, *Ajao & Moteetee 005* (JRAU); –; PZ862330*; PZ872897*. ***Rhynchosia galpinii*** Baker f., Africa, South Africa, *Ajao & Moteetee 001* (JRAU); –; PZ862322*; PZ872903*. ***Rhynchosia grandifolia*** (E.Mey.) Steud., Africa, South Africa, *Von Staden 19* (PRE); –; PZ862338*; –. ***Rhynchosia harveyi*** Baker f., Africa, South Africa, *Acock 17959* (PRE); –; PZ862329*; PZ872908*. ***Rhynchosia hauthalii*** (Kuntze) Grear, South America, Argentina, *T.M. Pedersen 2982* (P); –; PZ862383*; PZ872941*. ***Rhynchosia hauthalii*** (Kuntze) Grear, South America, Argentina, *T.M. Pedersen 2982* (NY); –; MT547516; MT577516. ***Rhynchosia himalensis*** Benth. ex Baker, Asia, India, *R.R. Stewart 21264* (NY); –; PZ862375*; PZ872917*. ***Rhynchosia hirsuta*** Eckl. & Zeyh., Africa, South Africa, *R.D.A. Bayliss 8297* (NY); –; PZ862321*; PZ872902*. ***Rhynchosia hirsuta*** Eckl. & Zeyh., Africa, South Africa, *Van Wyk 3373* (JRAU); –; PZ862320*; PZ872901*. ***Rhynchosia hirta*** (Andrews) Meikle & Verdc., Africa, South Africa, *Jaca, Mkkhize & Mashele s.n*. (PRE); –; PZ862334*; –. ***Rhynchosia hirta*** (Andrews) Meikle & Verdc., Africa, Malawi, *E.J. Tawakali & A.C. Chikuni 1672* (NY); PZ865159*; PZ862335*; PZ872920*. ***Rhynchosia hockii*** De Wild., Africa, Rwanda, *H.G. Troupin 3664* (NY); –; PZ862369*;

Appendix 1. Continued.

PZ872915*. ***Rhynchosia holosericea*** Schinz, Africa, South Africa, *Smith 3201* (PRE); –; PZ862341*; –. ***Rhynchosia insignis*** (O.Hoffm.) R.E.Fr., Africa, Zimbabwe Bayliss *10169A* (NY); PZ865160*; –; –. ***Rhynchosia komatiensis*** Harms, Africa, South Africa, *Deall 1040*, *1434* (PRE); –; PZ862349*; –. ***Rhynchosia lineata*** Benth., South America, Uruguay, *Cabrera A.L. & Zuloaga F 32380* (SI); PZ865201*; –; –. ***Rhynchosia lateritia*** Burkart, South America, Argentina, *E.L. Ekman 1679* (NY); PZ865169*; PZ862381*; PZ872942*. ***Rhynchosia lateritia*** Burkart, South America, Argentina, *H.A. Keller, J. Pirelli, L. Ritter 4566* (UEC); PZ865194*; PZ862402*; –. ***Rhynchosia latifolia*** Nutt. ex Torr. & A.Gray, North America, U.S.A., *D. Atha 12874* (NY); PZ865184*; PZ862389*; PZ872937*. ***Rhynchosia leucophylla*** (Benth.) Benth., South America, Brazil, *W. Vargas 10* (CGMS); MT376834; MT547481; MT577413. ***Rhynchosia leucoscias*** Benth. ex Harv., Africa, South Africa, *Boatwright 668* (NBG); –; PZ862336*; –. ***Rhynchosia lewisii*** L.M.P.Bezerra & Fort.-Perez, South America, Brazil, *M.L. Guedes & al. 20795* (UB); PZ865170*; PZ862401*; PZ872934*. ***Rhynchosia longeracemosa*** M.Martens & Galeotti, North America, Mexico, *M. Souza 7851* (SI); PZ865175*; –; –. ***Rhynchosia longeracemosa*** M.Martens & Galeotti, Central America, Guatemala, *J.J. Castillo & A. Castillo 2718* (NY); PZ865189*; PZ862393*; –. ***Rhynchosia luteola*** (Hiern) K.Schum. var. ***luteola***, Africa, Malawi, *E.J. Tawakali & J.L. Balaka 1513* (NY); PZ865161*; PZ862370*; PZ872911*. ***Rhynchosia macrocarpa*** Benth., North America, Mexico, *P. Tenorio L. & al. 10290* (NY); PZ865190*; PZ862394*; –. ***Rhynchosia madagascariensis*** R.Vig., Africa, Madagascar, *M. Bardot-Vaucoulon 743* (P); PZ865142*; PZ862356*; –. ***Rhynchosia malacophylla*** (Spreng.) Bojer, Asia, Yemen, *R. Spellenberg 7535* (NY); MT376936; MT547524; MT577523. ***Rhynchosia mantaroensis*** J.F.Macbr., South America, Peru, *A. Sagástegui & al. 15255* (NY); MT376930; MT547517; MT577517. ***Rhynchosia mantaroensis*** J.F.Macbr., South America, Peru, *Reichlen 100* (P); PZ865177*; PZ862384*; PZ872936*. ***Rhynchosia melanocarpa*** Grear, South America, Brazil, *A.P. Fortuna-Perez s.n*. (BOTU); MT376878; MT547494; –. ***Rhynchosia minima*** (L.) DC., South America, Brazil, *V.C. Lima 46* (IPA); MT376891; MT547495; MT577477. ***Rhynchosia minima*** (L.) DC., Africa, South Africa, *Winter 5728* (PRE); –; –; PZ872886*. ***Rhynchosia micrantha*** Harms, Africa, Tanzania, *M.E. Archbold 1069* (NY); –; PZ862371*; PZ872916*. ***Rhynchosia naineckensis*** Fortunato; *M. Nee 50484* (NY); MT376931; MT547518; MT577518. ***Rhynchosia nipensis*** Urb., Central America, Cuba, *J.P. Carabia 3719* (NY); –; PZ862399*; –. ***Rhynchosia nervosa*** Benth. ex Harv., Africa, South Africa, *Hartley, Balkwill & Moodley 919* (JRAU); –; PZ862328*; PZ872907*. ***Rhynchosia ngwenyii*** Ajao, Jaca & Moteetee, Africa, South Africa, *Germishuizen 5669 8016* (PRE); –; PZ862346*; –. ***Rhynchosia nitens*** Benth. ex Harv., Africa, South Africa, *Ghver 1* (JRAU); –; PZ862347*; –. ***Rhynchosia nyasica*** Baker, Africa, Zimbabwe, *R.D.A. Bayliss 10129* (NY); MT376935; MT547523; MT577522. ***Rhynchosia nyikensis*** Baker, Africa, Malawi, W Nachamba, *I.H. Patel & E.J. Tawakali 78* (NY); PZ865162*; PZ862372*; PZ872912*. ***Rhynchosia ovata*** J.M.Wood & M.S.Evans, Africa, South Africa, *Codd 1886* (PRE); –; PZ862345*; –. ***Rhynchosia pallida*** var. ***boliviana*** Grear, South America, Bolivia, *M. Nee 36388* (NY); PZ865195*; PZ862400*; PZ872928*. ***Rhynchosia parvifolia*** DC., North America, U.S.A., *W.C. Brumbach 9455* (NY); PZ865185*; PZ862390*; PZ872938*. ***Rhynchosia pedunculata*** M.M.le Roux & Moteetee, Africa, South Africa, *Kroon 12060* (PRE); –; PZ862344; –. ***Rhynchosia pentheri*** Schltr. ex Zahlbr., Africa, South Africa, *Hartley, Balkwill & Moodley 926* (JRAU); –; PZ862319*; PZ872900*. ***Rhynchosia pycnostachya*** (DC.) Meikle, Africa, Togo, *H. Ern 2562* (P); PZ865148*; –; –. ***Rhynchosia pinnata*** (Eckl. & Zeyh.) Harv., Africa, South Africa, *Acock 23124* (PRE); –; PZ862348*; –. ***Rhynchosia phaseoloides*** (Sw.) DC., South America, Brazil, *R.B. Pinto 500* (UEC); MT376831; MT461290; MT547538. ***Rhynchosia platyphylla*** Benth., South America, Brazil, *J. Raveratti & al. 640* (UB); PZ865180*; PZ862378*; PZ872930*. ***Rhynchosia precatoria*** DC., North America, Mexico, *A. Reyes-Garcia & al. 6211* (NY); PZ865191*; PZ862395*; –. ***Rhynchosia pringlei*** Rose, North America, Mexico, *H.D. Ripley & R.C. Barneby 14,675* (NY); –; PZ862396*; PZ872924*. ***Rhynchosia prostrata*** Brandegee, North America, Mexico, *C.A. Purpus 3205* (NY); PZ865192*; PZ862397*; PZ872926*. ***Rhynchosia puberula*** Steud., Africa, South Africa, *R.D.A. Bayliss 4114* (NY); PZ865163*; PZ862373*; PZ872892*. ***Rhynchosia pycnostachya*** (DC.) Meikle, Africa, Togo, *H. Ern 2562* (P); MT376852; MT547485; MT577431. ***Rhynchosia pyramidalis*** (Lam.) Urb., Central America, Honduras, *S. Palma 346* (NY); MT376927; MT547513; –. ***Rhynchosia quercetorum*** Standl., Central America, Costa Rica, *W.A. Haber 3674* (NY); MT376928; MT547514; –. ***Rhynchosia reniformis*** DC., North America, U.S.A., *S.W. Leonard & A.E. Radford 1547* (P); PZ865178*; PZ862387*; PZ872922*. ***Rhynchosia resinosa*** Hochst. ex Baker, Africa, Guinea, *C.C.H. Jongkind 8035* (P); MT376851; MT547484; MT577430. ***Rhynchosia resinosa*** (Hochst. ex A.Rich.) Baker, Africa, South Africa, *Van der Sciff 5413* (PRE); PZ865146*; –; –. ***Rhynchosia resinosa*** (Hochst. ex A.Rich.) Baker, Africa, Burundi, *J. Lewalle I643* (NY); PZ865197*; PZ862333*; PZ872918*. ***Rhynchosia reticulata*** (Sw.) DC., South America, Brazil, *L.P. Queiroz & al. 1314* (HUEFS); –; PZ862405*; PZ872933*. ***Rhynchosia reticulata*** var. ***kuntzei*** (Kuntze) Grear, South America, Brazil, *F. França 3175* (UB); PZ865181*; PZ862380*; PZ872932*. ***Rhynchosia reptabunda*** N.E.Br., Africa, South Africa, *Story 691* (PRE); –; PZ862352*; –. ***Rhynchosia rojasii*** Hassl., South America, Brazil, *M. Groppo Jr. 414* (HUEFS); PZ865198*; –; –. ***Rhynchosia rojasii*** Hassl., South America, Paraguay, *E.M. Zardini & M. Vera 45368* (P); PZ865179*; PZ862382*; PZ872935*. ***Rhynchosia schomburgkii*** Benth., South America, Guyana, *J. Ollerton & al. 201* (K); –; PZ862403*; PZ872931*. ***Rhynchosia senna*** Gillies ex Hook. & Arn., North America, U.S.A., *K.C. Rice 1428* (NY); PZ865186*; PZ862386*; PZ872939*. ***Rhynchosia smithiana*** Moteetee & Boatwr., Africa, South Africa, *Van Wyk 3155* (JRAU); –; PZ862304*; PZ872880*. ***Rhynchosia sordida*** (E.Mey.) Schinz, Africa, South Africa, *Schutte 461* (JRAU); –; PZ862324*; PZ872905*. ***Rhynchosia spectabilis*** Schinz, Africa, South Africa, *Bester 11418* (PRE); –; PZ862312*; PZ872885*. ***Rhynchosia stenodon*** Baker f., Africa, South Africa, *H.J. Venter & A. Venter 10216* (NY); PZ865164*; PZ862374*; PZ872896*. ***Rhynchosia sublobata*** (Schumach.) Meikle, Africa, South Africa, *Boatwright 251* (NBG); –; PZ862311*; PZ872884*. ***Rhynchosia sublobata*** (Schumach. & Thonn.) Meikle, Africa, s. loc., *R. Seydel 459* (NY); PZ865165*; –; –. ***Rhynchosia sublobata*** (Schumach. & Thonn.) Meikle, Africa, Tanzania, *S. Bidgood & al. 6418* (P); MT376853; MT547486; –. ***Rhynchosia swartzii*** (Vail) Urb., North America, U.S.A., *D.S. & H.B. Correll & J. Popenoe 48124* (NY 2626961); PZ865187*; PZ862391*; –. ***Rhynchosia tarphantha*** Standl., North America, Mexico, TS Cochrane, *M.A. Wetter & M. Rosales C 11,782* (NY); PZ865193*; PZ862398*; –. ***Rhynchosia thorncroftii*** (Baker f.) Burtt Davy, Africa, South Africa, *Ajao & Moteetee 008* (JRAU); –; PZ862315*; PZ872888*. ***Rhynchosia tomentosa*** (L.) Hook. & Arn., North America, U.S.A., *R. Dale Thomas & A. Dunn 157,685* (NY); PZ865188*; PZ862392*; PZ872925*. ***Rhynchosia totta*** (Thunb.) DC., Africa, South Africa, *C.H. Stirton 14089* (PRE); PZ865151*; PZ862327*; PZ872891*. ***Rhynchosia totta*** var. ***rigidula*** (DC.) Moteetee & M.M.le Roux, Africa, South Africa, *Ellery 327* (PRE); –; PZ862325*; PZ872906*. ***Rhynchosia totta*** var. ***venulosa*** (Hiern) Verdc., Africa, South Africa, *Mogg & Cunliff 36524* (JRAU); PZ865149*; PZ862326*; –. ***Rhynchosia totta*** var. ***venulosa*** (Hiern) Verdc., Africa, Namibia, *O.H. Volk 6268* (P); –; PZ862362*; –. ***Rhynchosia vendae*** C.H.Stirt., Africa, South Africa, *Grobbelaar 02336* (PRE); –; PZ862351*; –. ***Rhynchosia verdcourtii*** Thulin, Africa, Tanzania, *R. Abdallah & K. Vollesen 96/220* (P); –; PZ862359*; PZ872921*. ***Rhynchosia verdcourtii*** Thulin, Africa, Madagascar. *D.J. & B.P. Du Puy M322* (NY); PZ865150*; –; –. ***Rhynchosia versicolor*** Baker, Africa, Madagascar, *Y. Veyret 1329* (P); –; PZ862357*; –. ***Rhynchosia versicolor*** Baker subsp. ***versicolor***, Africa, Madagascar, *D.J. & B.P. Du Puy M322* (NY); PZ865166*; PZ862358*; PZ872889*. ***Rhynchosia villosa*** (Meisn.) Druce, Africa, South Africa, *Stirton 8110* (PRE); –; PZ862350*; –. ***Rhynchosia viscosa*** (Roth) DC., Africa, Madagascar, *J. Bosser 21902* (P); MT376849; MT547482; MT577428. ***Rhynchosia volubilis*** Lour., Asia, Japan, *F. Konta 35508* (P); PZ865154*; PZ862353*; PZ872893*. ***Rhynchosia volubilis*** Lour., Asia, Japan, *G. Murata 13831* (NY); MT376924; MT547510; MT577512. ***Rhynchosia volubilis*** Lour., Asia, Japan, *Y.N. Xiong & K. Yao 122* (NY); PZ865153*; PZ862354*; PZ872894*. ***Rhynchosia woodii*** Schinz, Africa, South Africa, *F. Willms s.n*. (K); PZ865147*; –; –.

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Appendix 2. Authors and affiliations.

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