Botanical Journal of the Linnean Society, 2020, **194**, 439–459. With 6 figures.

Molecular phylogenetic insights into the evolution of *Eriosema* (Fabaceae): a recent tropical savanna-adapted genus

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Received 4 February 2020; revised 30 April 2020; accepted for publication 17 June 2020

Eriosema comprises *c*. 150 species and has a pantropical distribution and two centres of diversity, Africa and America. The species occur in tropical savannas and grasslands, including the cerrado in Brazil. They have adapted to these environments by developing specialized underground organs, and an abundance of trichomes. Here we present the first comprehensive molecular phylogenetic analysis of *Eriosema*, including species from its entire distribution range and generating 391 new DNA sequences. We sampled 140 species from nine genera of Cajaninae, of which 94 (60% of the genus) were *Eriosema*. Our analyses were based on the nuclear ITS and plastid *rpl32* and *trnQ* regions, and used maximum likelihood and Bayesian phylogenetic analyses of individual and combined data sets. In all analyses, *Eriosema* was resolved as monophyletic, but its interspecific relationships are not well resolved. *Rhynchosia* is not monophyletic, and some African *Rhynchosia* spp. emerged together as sister to *Eriosema*. Our study supports the monophyly of *Adenodolichos*, *Dunbaria*, *Flemingia* and *Cajanus*, but *Chrysoscias* and *Bolusafra* formed a clade that is sister to a group of *Rhynchosia* spp. *Paracalyx* was resolved as paraphyletic and nested among African *Rhynchosia* spp. Divergence time analysis suggested that the *Eriosema* lineages diverged 6.5–10.7 Mya. Two major lineages have diversified in *Eriosema*, one including most of the African species (4.41–6.68 Mya), the other mainly composed of

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the South American cerrado species (3.56–5.78 Mya). These results revealed that *Eriosema* is a recent and tropical savanna-adapted group, and its diversification occurred in the late Miocene in parallel with the expansion of C_4 grasslands.

ADDITIONAL KEYWORDS: Cajaninae – cerrado – divergence time – grassland – Leguminosae – recent diversification – *Rhynchosia* – systematics.

INTRODUCTION

Eriosema (DC.) Desv. comprises *c.* 150 species and is the second-largest genus of subtribe Cajaninae (tribe Phaseoleae), Fabaceae (Grear, 1970; LPWG, 2017). It has two centres of diversification, one in Africa (including Madagascar) with *c.* 110 species and the other in the New World (from Mexico to northern Argentina, except for Chile) with *c.* 40 species. In addition, one species, *E. chinense* Vogel, occurs in Southeast Asia and northern Australia (Grear, 1970; van der Maesen, 2003; Schrire, 2005). The genus is used throughout its distribution range for traditional medicine and food. For instance, in South Africa, 'Zulu' people use the roots as a medicine for the treatment of erectile dysfunction and/or impotence (Ojewole, 2007). In the Neotropics, Brazilian traditional communities use some species as laxatives or as an anti-inflammatory medicine (Hirschmann & De Arias 1990; Rodrigues & Carvalho, 2001; Santos *et al.*, 2016) and in the Northern Territory of Australia, root tubers of *E. chinense* have been used as human food (Smith, 1991).

Previous molecular phylogenetic studies, although including a limited number of sampled taxa, have demonstrated that subtribe Cajaninae and *Eriosema* are monophyletic (Bruneau, Doyle & Doyle, 1995; Kajita *et al.*, 2001; Egan, Vatanparast & Cagle, 2016; LPWG, 2017). Cajaninae, as traditionally recognized, comprise ten genera: *Adenodolichos* Harms (20 species), *Bolusafra* Kuntze Harms (one species); *Cajanus* DC. (34 species), *Carrissoa* Baker f. (one species), *Chrysoscias* E.Mey. (three or four species), *Dunbaria* Wight & Arn. (20 species), *Eriosema* (150 species), *Flemingia* Roxb. ex W.T.Aiton (30–35 species), *Paracalyx* S.I.Ali (six species) and *Rhynchosia* Lour. (230 species) (Grear, 1970, 1978; Schrire, 2005). *Eriosema* is morphologically similar and phylogenetically closely related to *Rhynchosia* (Grear, 1970; Doyle & Doyle, 1993; Bruneau *et al.*, 1995; Kajita *et al.*, 2001; Egan *et al.*, 2016; LPWG, 2017). These two genera are the largest and the only pantropical members of Cajaninae, all other genera of the subtribe occurring exclusively in the Palaeotropics, including Oceania (Grear, 1970, 1978). To date, there is no comprehensive molecular phylogenetic study focused on *Eriosema* or on any other genus of Cajaninae. There are, however, some studies focused on population genetics of *Cajanus* (Nadimpalli *et al.*, 1993; Kassa *et al.*, 2012; Saxena *et al.*, 2014; Kaila *et al.*, 2016).

Eriosema spp. are mainly distributed in tropical savannas, grasslands and mountainous areas of Africa and in Brazilian cerrado (Fig. 1; Grear, 1970; Cândido *et al.*, 2019). The main life form and morphological characteristics of *Eriosema* spp. that have adapted to these environments are their herbaceous, sub-shrubby or shrubby habit (Fig. 2A, C, G), frequently with a specialized underground root system such as a woody rootstock (Fig. 2A–C), the apex of which has a bud-generating portion often called a xylopodium, and an abundance of trichomes throughout the plant (Fig. 2D–H). In addition, secretory structures that are peculiar to Cajaninae are usually present, such as bulbous-based trichomes, vesicular glands and secretory-based trichomes (Grear, 1970; Lackey, 1978; Cândido *et al.*, 2016; Vargas *et al.*, 2018; Cândido *et al.*, 2019).

Savannas evolved in close association with frequent fires and native megafaunal herbivory (Buisson *et al.*, 2019, Dwyer *et al.*, 2000). As a result, these environments have become resilient and often dependent on these disturbances, and the plants that occur in these adverse environments have evolved peculiar adaptive morphologies (Coutinho, 1990; Bond & Keeley, 2005; Beerling & Osborne, 2006; Simon *et al.*, 2009; Ratnam *et al.*, 2011; Parr *et al.*, 2014; Veldman *et al.*, 2015; Bond & Zaloumis 2016; Buisson *et al.*, 2019). This type of vegetation began to evolve *c.* 30 Mya, with the emergence of C_4 photosynthetic grasslands (Scholes & Archer, 1997; Edwards *et al.*, 2010; Van der Werf *et al.*, 2010; Parr *et al.*, 2014). Fossil records of pollen and phytoliths show an expansion of C_4 grasses between 6 and 8 Mya (Cerling *et al.*, 1997; Parr *et al.*, 2014).

Tropical savanna and grassland environments cover *c.* 20% of the global land surface (Parr *et al.*, 2014; Buisson *et al.*, 2019). In Brazil, cerrado is a tropical moist savanna and is the most diverse tropical savanna in the world; it is considered a biodiversity hotspot with a high number of endemic species, the existence of which is extremely threatened by habitat loss (Myers *et al.*, 2000; Hoekstra *et al.*, 2005; Simon *et al.*, 2009; Sano *et al.*, 2010) (Fig. 1).

In the savannas, there is a diverse array of habitats, including woodland, wooded-grassland,

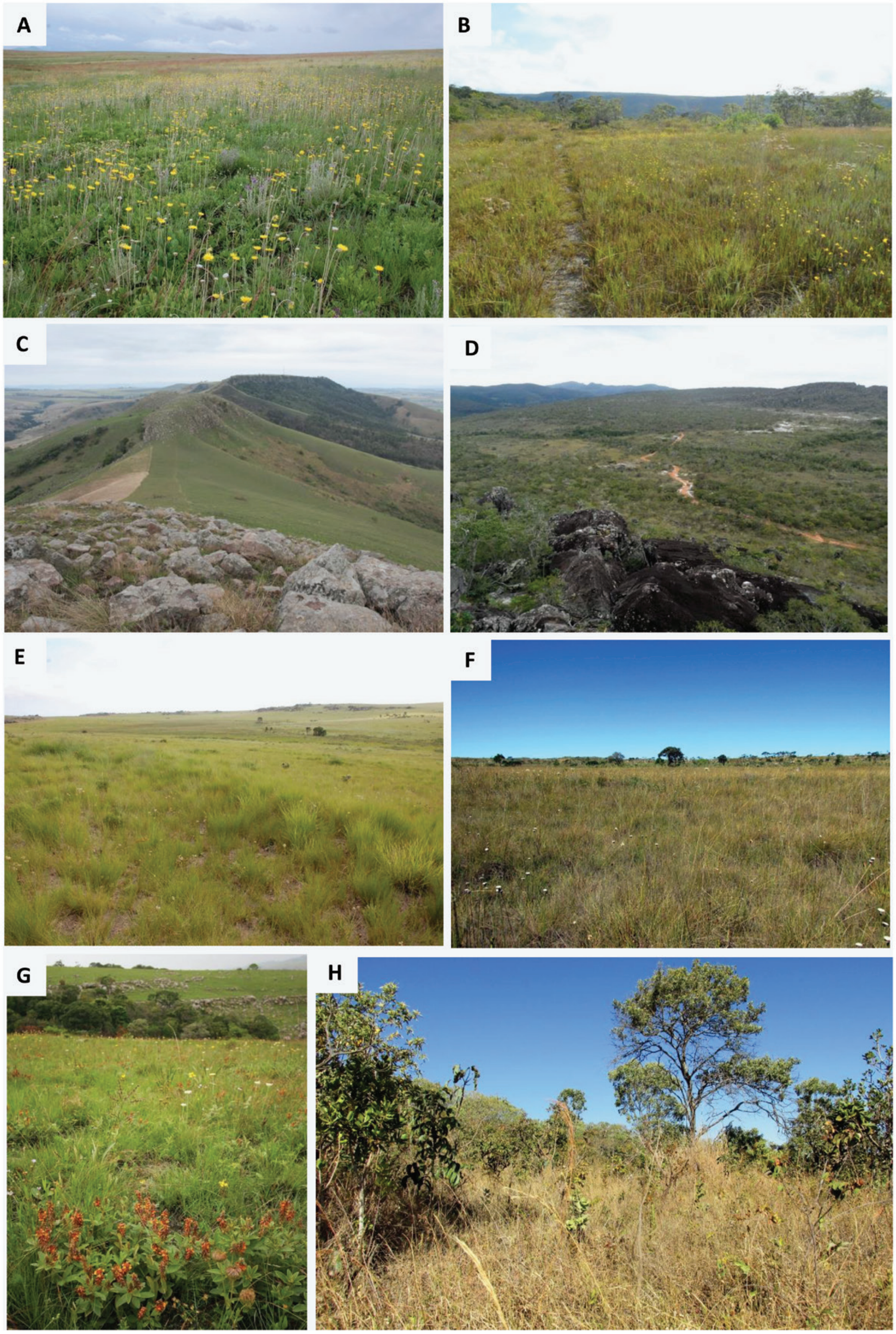

Figure 1. Tropical savannas and grassland environments in Africa and South America, the natural habitat of *Eriosema*. A, Bergville (KwaZulu-Natal), South Africa. B, D, Rio Preto State Park (Minas Gerais), Brazil. C, Ingomankulu (KwaZulu-Natal), South Africa. E, G, Umtamvuna Nature Reserve (KwaZulu-Natal), South Africa. F, Chapada dos Veadeiros National Park (Goiás), Brazil. H, Cerrado of São João da Aliança (Goiás), Brazil. Photographs: A, C, E, David Styles; B, D, Luísa M.P.A. Bezerra; F, H, Elisa Cândido; G, Braam Van Wyk.

Figure 2. *Eriosema* morphology adapted to the savanna. A–C, *E. crinitum* showing the morphology of the underground root system. D, *E. defoliatum* showing trichomes on the inflorescence and flowers. E, *E. floribundum* showing trichomes throughout the plant. F, *E. irwinii* showing trichomes on mature fruits. G, The small subshrub habit of *E. macrostipulatum*. H, *E. rufum* var. *macrostachyum* showing trichomes on fruits. Photographs: A–C, E, Ambar Soldevila; D, F, Elisa Cândido; G, Marcelo Simon; H, Isa L. Morais.

bushy-grassland and grassland (Lock, 2006), in which *Eriosema* spp. grow. These habitats form a gradient of woody vegetation ranging from a canopy cover of up to 40%, to open grassland with a limited occurrence of shrubs (White, 1983; Pennington, Prado & Pendry, 2000; Lock, 2006; Cândido *et al.*, 2019). The characteristics of these habitats include a single dry season lasting more than four months, tussock-forming and xeromorphic narrow-leaved grasses, a single shrub or grass layer, often the occurrence of regular fires, natural grasslands in sites with seasonal waterlogging, shallow soils and a high metallic ion concentration (Lock, 2006). At higher elevations in the savanna biome, a vegetational mosaic of mountain-top 'islands' dominated by seasonal drought and rocky or sandy soils of low fertility occurs. In the Neotropics, these rocky 'islands' are referred to as 'campos rupestres' (literally rocky fields), and the Espinhaço Range in eastern Brazil is one of the main areas for this habitat. Many *Eriosema* spp. occur in campo rupestre vegetation (Grear, 1970; Fortuna-Perez *et al.*, 2013b, 2017, 2018; Cândido *et al.*, 2014a, b, 2019) (Fig. 1D). In tropical Africa, similar vegetation to the Espinhaço Range is found in the Chimanimani mountains on the Zimbabwe–Mozambique border (Lock, 2006) where one of the most abundant shrubs is *Eriosema montanum* Baker f. (Phipps & Goodier, 1962).

Given the lack of a comprehensive phylogenetic evaluation of *Eriosema*, its intrinsic ecological relationship with savanna and grassland environments and its pantropical distribution, we decided to construct a molecular phylogenetic tree for the genus, examining its infra- and intergeneric relationships. Also, we estimated the timing of diversification of the genus in tropical savannas. We addressed the following questions. (1) Can we confirm that *Eriosema* is a monophyletic group? (2) What are the relationships of *Eriosema* with other genera in Cajaninae? (3) How can the transatlantic disjunct distribution of *Eriosema* be explained? (4) Where and when did major diversification events occur in the tropical savanna-adapted genus *Eriosema*?

MATERIAL AND METHODS

Taxon sampling

Ninety-three species (98 accessions) of *Eriosema* were included in this study, of which 58 species are from Africa, 34 are from America and *E. chinense* is from Asia. The sampling covers the entire distribution range of the genus and represents 62% of the species (Appendix S1). To assess relationships among genera in Cajaninae, we also sampled one *Chrysoscias* sp., the monospecific genus *Bolusafra*, two species each of *Adenodolichos* and *Paracalyx*, three species each of *Cajanus*, *Dunbaria* and *Flemingia*, and 32 species of *Rhynchosia* (Appendix S1). *Galactia striata* (Jacq.) Urb. and *Camptosema grandiflorum* Benth. from subtribe Diocleinae were included as outgroups (Queiroz *et al.*, 2015). The monospecific genus *Carrissoa* (*C. angolense* Baker f.), was not included in this study as we were unable to access material for DNA analysis. This species was known only from a type specimen housed in the herbarium of the University of Coimbra (COI), Portugal. Recently, this species has been collected in Angola by David Goyder (Royal Botanic Gardens, Kew) and we have received this material. It will be included in our next manuscript on the phylogenetics of Cajaninae.

DNA extraction, amplification and sequencing

Most samples for DNA extraction were obtained from herbarium collections (Appendix S1). Samples of some species that occur in Brazil and a few from Africa were collected in the field and stored in silica gel. Total genomic DNA was isolated using the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany), based mainly on the manufacturer's protocols, but with a modification at the beginning of the procedure, i.e. adding 4 μL of RNase A stock solution, and for herbarium samples we left the heater on for *c*. 3 h. About 1 cm^2 of dried leaf material of each sample was ground with a pestle and mortar using liquid nitrogen or in a Geno Grinder 2010 machine (SPEX Sample Prep LLC, Metuchen, NJ, USA) for 2 min at 2 rpm. Before the final selection of plastid DNA markers for phylogenetic analyses, we evaluated various markers to examine their phylogenetic informativeness among selected closely related *Eriosema* spp. (data not shown). After an initial screening step, we selected *rpl32-trnL* and *trnQ*-5'*rps16* intergenic spacers for subsequent steps. These were amplified using trnL (UAG)/rpL32-F and trnQ (UUG)/rpS16x1 primers, respectively (Shaw *et al.*, 2007). To amplify the ITS region (including ITS1 and ITS2 spacer regions and the 5.8S ribosomal subunit) of nuclear ribosomal DNA (nrDNA), primer pairs 17SE and 26SE were used (Sun *et al.*, 1994) (Appendix S2).

The PCR reactions were prepared in 25 μL solution containing 2 μL 10× PCR buffer, 1.5 μL 50 mM $MgCl_2$, 1 μL 2.5 mM dNTPs, 1 μL KB Extender (Invitrogen), 1 μL 5%DMSO, 0.5 μL bovine serum albumin, 0.5 μL betaine, 2 μL each primer (5 pM), 0.2 μL Platinum Taq DNA polymerase (Invitrogen) and 1.5 μL DNA template, adjusted with deionized water. The amplification program for the plastid regions consisted of 35 cycles of 95 °C for 1 min, 55 °C for 1 min and 72 °C for 1 min and a final extension 72 °C for 7 min and 10 °C constant at the end of the reaction. The ITS region was amplified with 11 cycles using the touchdown strategy: 94 °C for 3 min, 94 °C for 1 min; −1 °C per cycle from 65 °C; 72 °C for 1 min; 15 cycles back to step 2, 94 °C for 1 min; 50 °C for 1 min; 72 °C for 4 min; 21 cycles back to step 2; 72 °C for 1 min and 15 °C constant at the end of the reaction (Appendix S2). After the PCR, 2 μL of the PCR solution was run on 1% agarose gel to detect successful amplification. The amplified PCR products were purified using the NucleoSpin Gel and PCR clean-up kit (Macherey-Nagel, Düren, Germany) and sent for sequencing with the same primers used for the amplification. DNA sequencing reactions were performed in an automatic sequencer ABI 3730xl (Macrogen Inc., Seoul, South Korea).

ALIGNMENT AND PHYLOGENETIC ANALYSIS

Forward and reverse sequences were assembled and aligned into contigs with Geneious v.8.1.9 (Kearse *et al.*, 2012). All sequences generated in this study were deposited in GenBank (Appendix S1). A BLAST search (Altschul *et al.*, 1990) was conducted for all sequences to check for possible contamination. DNA regions were aligned using MAFFT v.7.369b (Katoh & Standley, 2013) using the L-INS-i method with '--localpair' and '--maxiterate 1000' and `--adjustdirection` options. Alignments were corrected and edited by eye in AliView v.1.23 (Larsson, 2014).

Our phylogenetic analyses are based on maximum likelihood (ML) and Bayesian inference (BI) approaches. We inferred the maximum-likelihood tree using IQ-TREE v.1.6.12 (Nguyen *et al.*, 2015). ModelFinder (Kalyaanamoorthy *et al.*, 2017) tested 286 DNA models for accurate phylogenetic estimates. We obtained branch supports with the ultrafast bootstrap feature, '-bb 10000' (Hoang *et al.*, 2018), and performed the SH-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al.*, 2010) by using the '-alrt 1000' option to assess branch supports. We ran IQ-TREE on each marker independently, concatenated plastid regions and concatenated plastid regions plus ITS (four data matrices in total). BI was performed using a Markov chain Monte Carlo (MCMC) method, as implemented in MrBayes, v.3.2.6 (Ronquist, Huelsenbeck & Teslenko, 2012) using parallel version (mb-mpi). We used MrModeltest v.2.3 (Nylander, 2004) to find the best substitution model for each region separately. For *rpl32-trnL* and ITS SYM+G and for the *trnQ*-5'*rps16* HKY+G were selected based on the Akaike information criterion (AIC) (Akaike, 1974). Two independent runs were performed on four data matrices as mentioned above. For each BI run, we set the number of generations to 20 million, sampling every 2000 generations, discarding 20% of the trees as burn-in. All runs were inspected to check that the average standard deviation of split frequencies was < 0.1 (Ronquist *et al.*, 2011). Convergence of MCMC inference was evaluated using Tracer v.1.7.1 (Rambaut *et al.*, 2018). The phylogenetic analyses were completed on the Smithsonian Institution High-Performance Cluster (https://doi.org/10.25572/SIHPC).

DIVERGENCE TIME ANALYSIS

Estimates of divergence time of lineages in Cajaninae were obtained using BEAST v.1.8.2 (Drummond *et al.*, 2012) using the ITS matrix. A literature search revealed no fossil records of Cajaninae for use as a calibration point, and calibration of the root of the tree was implemented based on the estimation from Lavin, Herendeen & Wojciechowski (2005). A normal distribution was applied with the mean of 27.8 Mya and a standard deviation of 1.6 according to Lavin *et al.* (2005). An uncorrelated relaxed molecular clock with a lognormal distribution of rates and a Yule speciation model was used. Two independent runs, each with 50 million generations were performed sampling every 5000 generations. A maximum clade-credibility (MCC) tree was retrieved using TreeAnnotator v.1.8.2 (Drummond *et al.*, 2012) after discarding the first 20% of trees as burn-in. We used Tracer v.1.7.1 (Rambaut *et al.*, 2018) to assess Effective Sample Size (ESS) and convergence.

RESULTS

DATA MATRICES AND PHYLOGENETIC ANALYSIS

Our dataset includes 140 species from nine genera of Cajaninae and *Galactia striata* and *Camptosema grandiflorum* from Diocleinae as outgroups. In this study, we produced 391 new DNA sequences (123, 141 and 127 for ITS, *rpl32-trnL* and *trnQ*-5'*rps16*, respectively; Appendix S1). The alignment lengths of ITS, *rpl32-trnL* and *trnQ*-5'*rps16* were 818, 832 and 789 bp, respectively, of which 460, 154 and 187 bp were potentially parsimony informative (Appendix S3).

The ML and BI analyses of the combined dataset (ITS + plastid regions) revealed that Cajaninae and *Adenodolichos, Dunbaria*, *Flemingia* and *Cajanus* are monophyletic (BP = 100, PP = 1.00, Fig. 3A, Appendix S4). *Rhynchosia* was recovered as polyphyletic and emerged as three separate lineages. *Rhynchosia volubilis* Lour. (clade I), the type species of the genus, alone is sister to the *Cajanus* clade, although the bootstrap support for their ancestral node is only moderate (BP = 95, Fig. 3A). The second lineage of *Rhynchosia*, clade II (*Rhynchosia* Old World + (*Rhynchosia* Old World +*Paracalyx*) + *Rhynchosia* AM), in which most of the sampled species are placed,

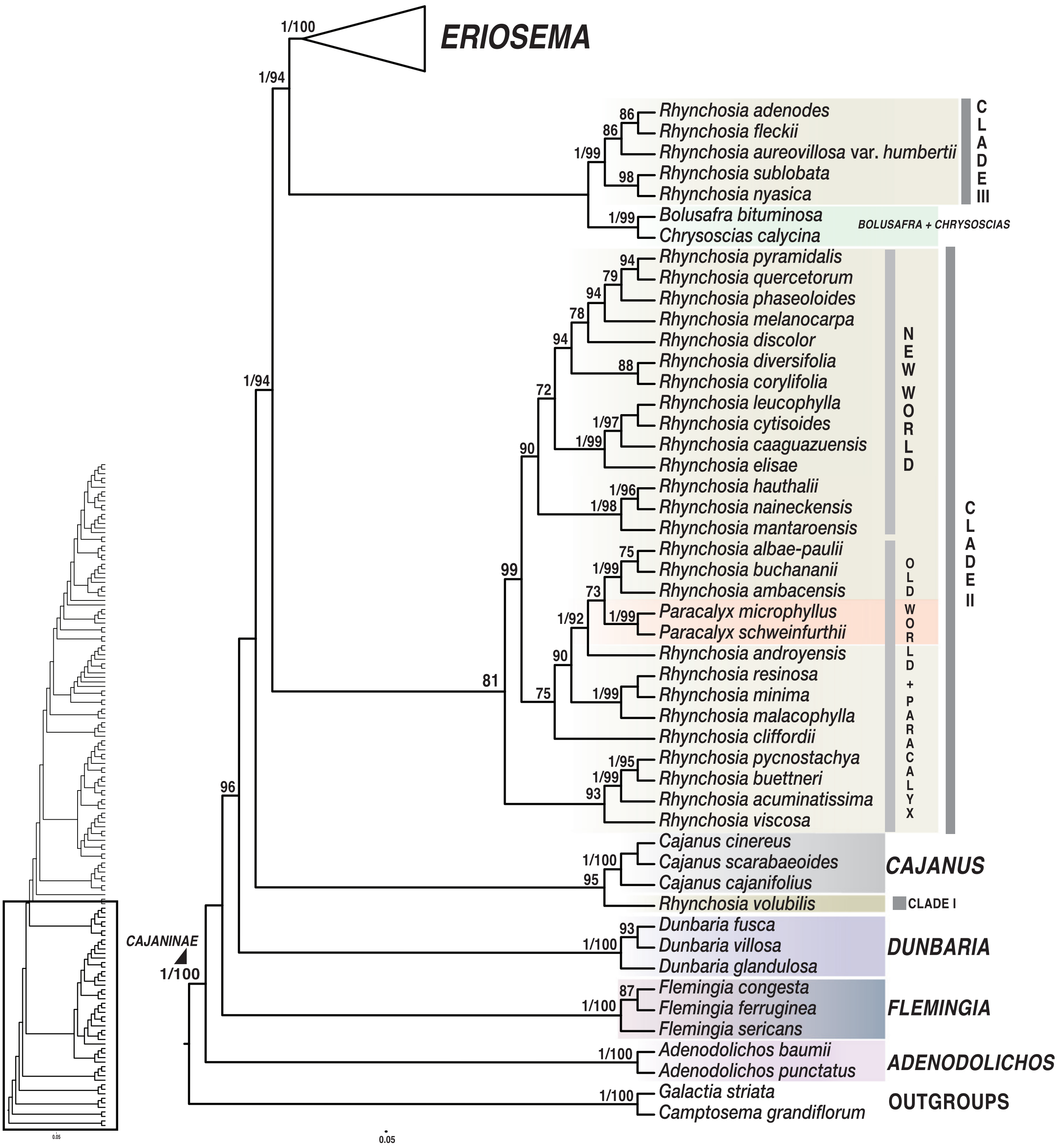

Figure 3. A scheme of the phylogenetic tree for *Eriosema* from maximum likelihood analysis of the ITS/5.8S and plast DNA dataset (*rpl32-trnL* and *trnQ*-5'*rps16*). A, Detail of the other genera of Cajaninae. B, Detail of *Eriosema*. Numbers along branches are bootstrap values and posterior probabilities.

also includes *Paracalyx* with moderate support (BP = 81; Fig. 3A), and a clade of American species (*Rhynchosia* AM) (BP = 90; Fig. 3A).

Chrysoscias and *Bolusafra* form a clade (BP = 99, PP = 1.00, Fig. 3A; Appendix S4) that is sister to the third lineage of *Rhynchosia* [*Rhynchosia* AF (Africa)],

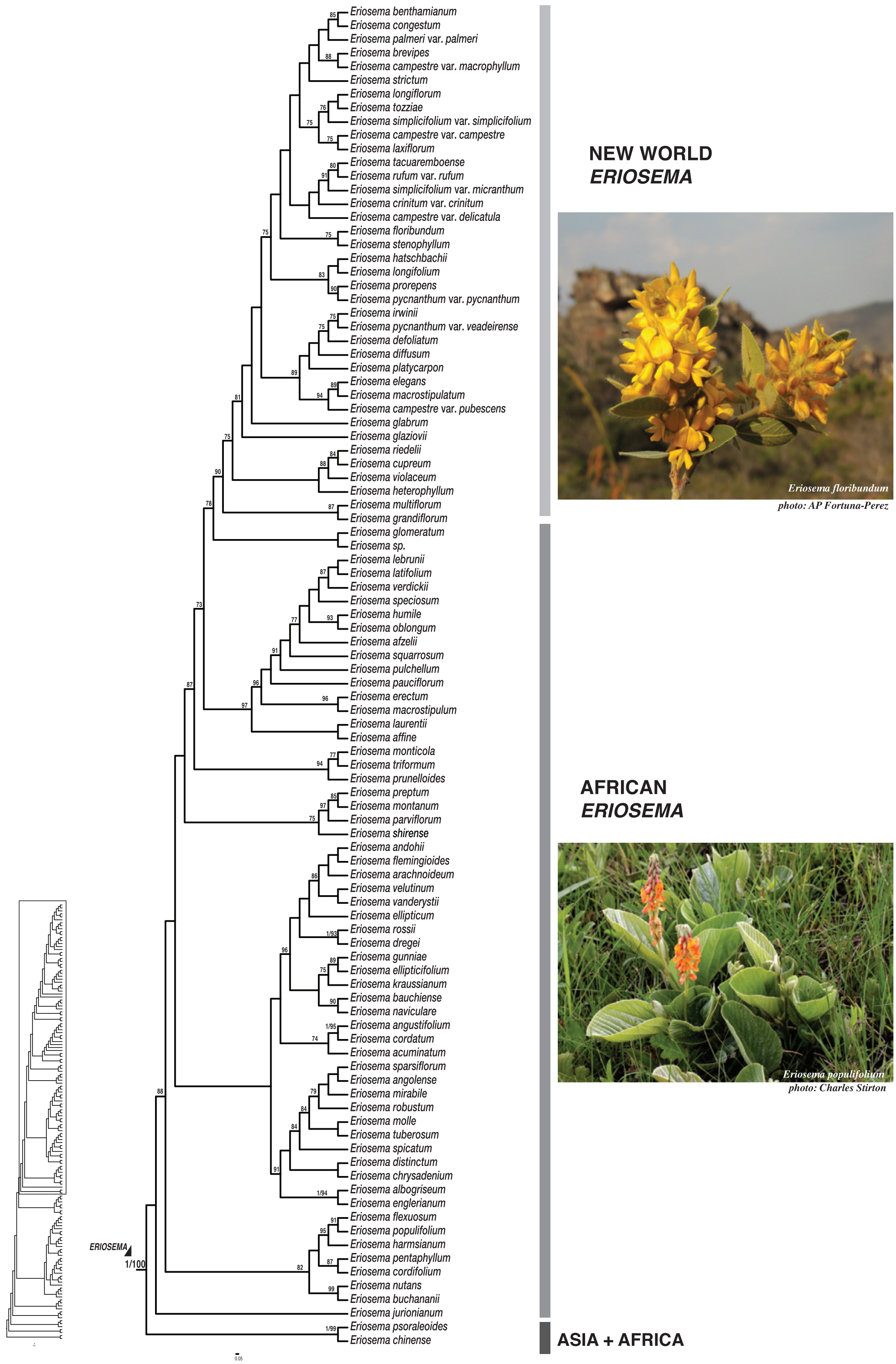

Figure 3. Continued.

clade III (Fig. 3A; BP = 99, PP = 1.00). This clade includes the African species *Rhynchosia adenodes* Eckl. & Zeyh., *R. fleckii* Schinck, *R. aureovillosa* Hauman var. *humbertii* Hauman, *R. sublobata* (Schumach.) Meikle and *R. nyasica* Baker (Appendix S4). Together, clades III and *Chrysoscias* + *Bolusafra* are sister to the *Eriosema* clade (Fig. 3A). In all analyses, *Eriosema* was resolved as monophyletic with maximum support (BS = 100, PP = 1.00, Fig. 3A, B, Appendix S4). However, interspecific relationships in *Eriosema* so far have not been fully resolved. Inside the *Eriosema* clade, one group comprising only American species (subclade IV) has moderate bootstrap support (BP = 78; Fig. 3B) and there is no good resolution of species relationships inside this American group. Likewise, there is no intra-cladal support within the groupings of African species. The only Asian species, *Eriosema chinense* [*Eriosema* AS (Asian)], formed part of clade V with African *E. psoraleoides* (Lam.) G.Don (BP = 99, PP = 1.00, Fig. 3B), and this clade is the sister group of the rest of *Eriosema*.

DIVERGENCE TIME ANALYSIS

Age estimates are presented for relevant crown nodes (mean and 95% credibility intervals). Cajaninae were estimated to have diversified 24.29–30.64 Mya (Fig. 4A, Appendix S5). The *Adenodolichos* clade diverged first (3.25–6.78 Mya) in Cajaninae (Fig. 4A, Appendix S5). *Flemingia* and *Dunbaria* diverged *c.* 2.09–4.45 and 4.09–7.21 Mya, respectively. The diversification time of *Cajanus* + *Rhynchosia volubilis* is estimated at 11.53–17.70 Mya (Fig. 4A, Appendix S5). *Cajanus* itself diversified 3.61–6.61 Mya (Fig. 4A, Appendix S5). The clade that includes most *Rhynchosia* spp. + *Paracalyx* is estimated to date from 11.18–16.91 Mya (Fig. 4A, Appendix S5). The African clade of *Rhynchosia fleckii*, *R. adenodes*, *R. nyasica*, *R. aureovillosa* var. *humbertii* and *R. sublolata* plus *Bolusafra bituminosa* (L.) Kuntze and *Chrysoscias calycina* E.Mey. diversified 10.59–16.44 Mya (Fig. 4A, Appendix S5). Stem and crown group ages of *Eriosema* were estimated as 12.25–18.11 and 6.50–10.79 Myr, respectively (Fig. 4B, Appendix S5). Group 1 of *Eriosema* comprises species that occur in Africa and has an estimated crown group age of 4.41–6.68 Myr (Fig. 4B, Appendix S5). The group that includes American *Eriosema* spp. (Group 2) diverged from African species *c.* 3.56–5.78 Mya (Fig. 4B, Appendix S5). Species in this group occur mainly in the cerrado and campos rupestres vegetation types in Brazil, especially in the states of Goiás and Minas Gerais. The age of the crown clade formed by the only Asian species, *E. chinense*, and the African species *E. psoraleoides* (Group 3) was estimated at 1.73–4.64 Myr (Fig. 4B, Appendix S5).

DISCUSSION

MONOPHYLY OF *ERIOSEMA*

Our phylogenetic study confirms the monophyly of *Eriosema* (Fig. 3B, Appendix S4). Previous phylogenetic studies focusing on Phaseoleae or the entire Fabaceae (e.g. Doyle & Doyle, 1993; Bruneau *et al.*, 1995; Kajita *et al.*, 2001; Egan *et al.*, 2016; LPWG, 2017), albeit including a limited number of *Eriosema* spp., also supported the monophyly of the genus. Among these studies, the most recent and well sampled so far, based on the plastid *matK* gene (LPWG, 2017), included only 12 *Eriosema* spp. (8% of the genus). In our initial screening of loci for this project, the *matK* gene was sequenced for 13 accessions of *Eriosema* spp., but we found the genetic diversity and parsimony informativeness of *matK* to be lower than the two plastid markers that we used in this study.

Interspecific relationships in *Eriosema* have not yet been resolved (Fig. 3B, Appendix S4), even using some selective plastid DNA markers in combination with nrITS. In all our analyses, there is a tendency for species to cluster in geographical groups, although not always with strong support, with the American species (BP 78%, Fig. 3B) and the African species forming two large groups (Fig. 3B, Appendix S4). In some analyses, the African species are the first diverging group in the *Eriosema* clade, possibly suggesting an African origin of the genus, but our results are not able to fully confirm this hypothesis. One possible explanation for this may be related to the recent and rapid diversification of *Eriosema* (10.79–6.50 Mya) (Fig. 4B, Appendix S5). Future studies that focus on the evolution of *Eriosema* should incorporate phylogenomic techniques that would obtain high resolution phylogenetic trees, which should better explain the morphological and biogeographical relationships in the genus.

Morphologically, *Eriosema* shares with other genera of Cajaninae the papilionaceous flowers (yellow or red), unifoliolate or trifoliolate leaves, fruits elastically dehiscent, peculiar secretory structures, absence of canavanine (except in *Adenodolichos*) and absence of bracteoles (except in *Adenodolichos*) (Grear, 1970; Lackey, 1978; Lewis *et al.*, 2005; Cândido *et al.*, 2016; Vargas *et al.*, 2018). Clade III, which is the sister group of *Eriosema*, comprises African species of *Rhynchosia*, *Bolusafra* and *Chrysoscias* (Fig. 3A) and morphologically these three genera are similar. This similarity was also observed by Lackey (1981), who described *Bolusafra* as a 'viscid *Rhynchosia*-like vine'. The representatives of clade III are usually trifoliolate, have a climbing habit, flowers yellow and red and calyx lobes exceeding the corolla (Vargas, 2019).

Of the *Eriosema* spp. occurring in the Americas, those belonging to the *Eriosema campestre* Benth. complex need nomenclatural attention. Taxa of

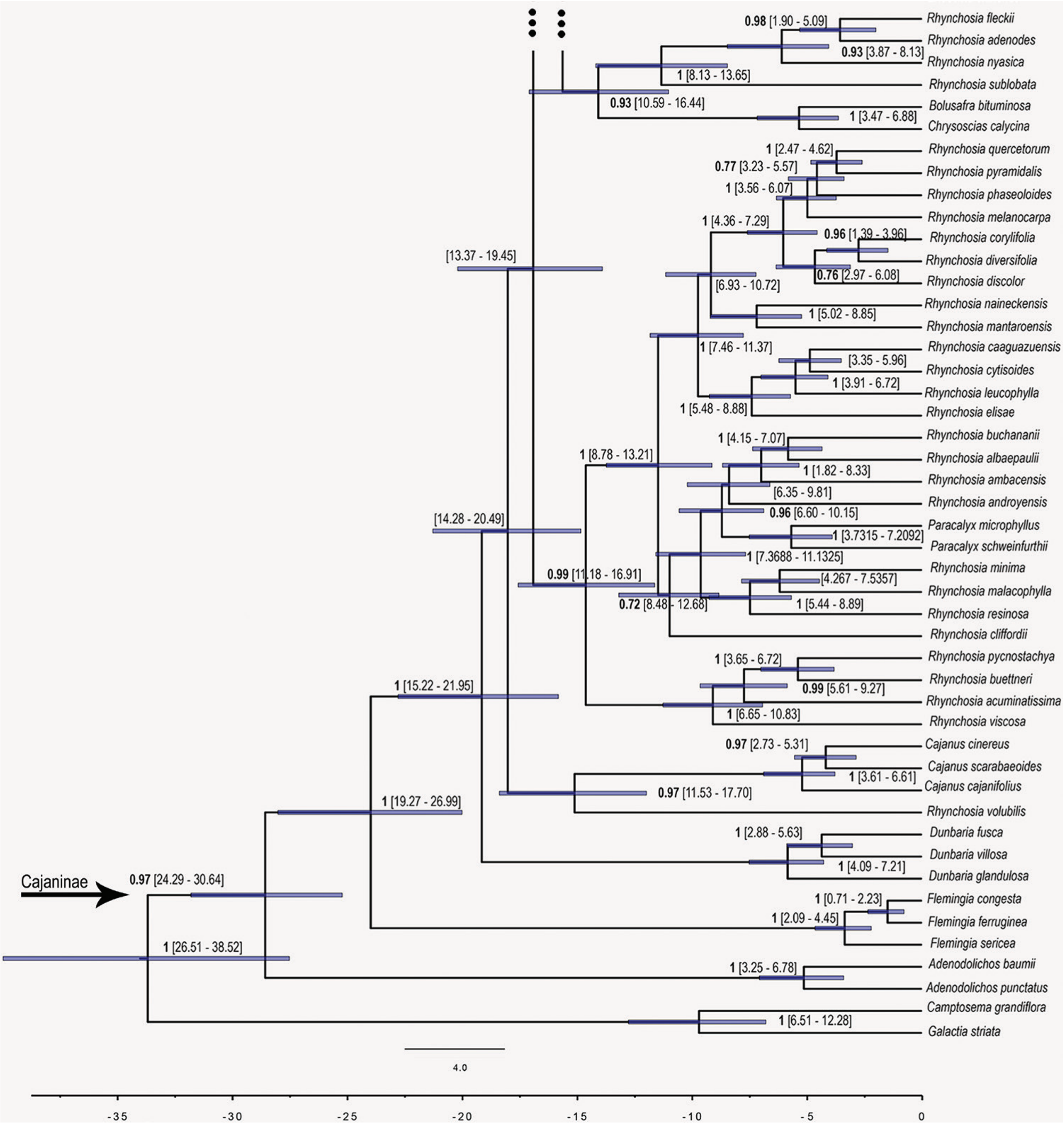

Figure 4. Analysis performed on the maximum clade credibility tree from divergence dating analysis (BEAST) using lognormal uncorrelated relaxed clock models for the combined data (ITS/5.8S, *rpl32-trnL* and *trnQ*-5'*rps16*). A, Detail of the genera of Cajaninae (except *Eriosema*). B, Detail of *Eriosema*. Blue bars represent 95% confidence intervals (CI) for the estimated mean dates. Posterior probabilities are indicated at nodes.

this complex [E. *campestre* Benth. var. *campestre*, *E. campestre* var. *macrophyllum* (Grear) Fortunato, *E. campestre* var. *pubescens* (Chodat & Hassl.) Grear and *E. campestre* var. *delicatula* Fortunato] do not form a group in our analyses (Fig. 3B) and the varieties would be better recognized as distinct species, as also supported by the anatomical studies of Seixas, Fortuna-Perez & Rodrigues (2019). Another

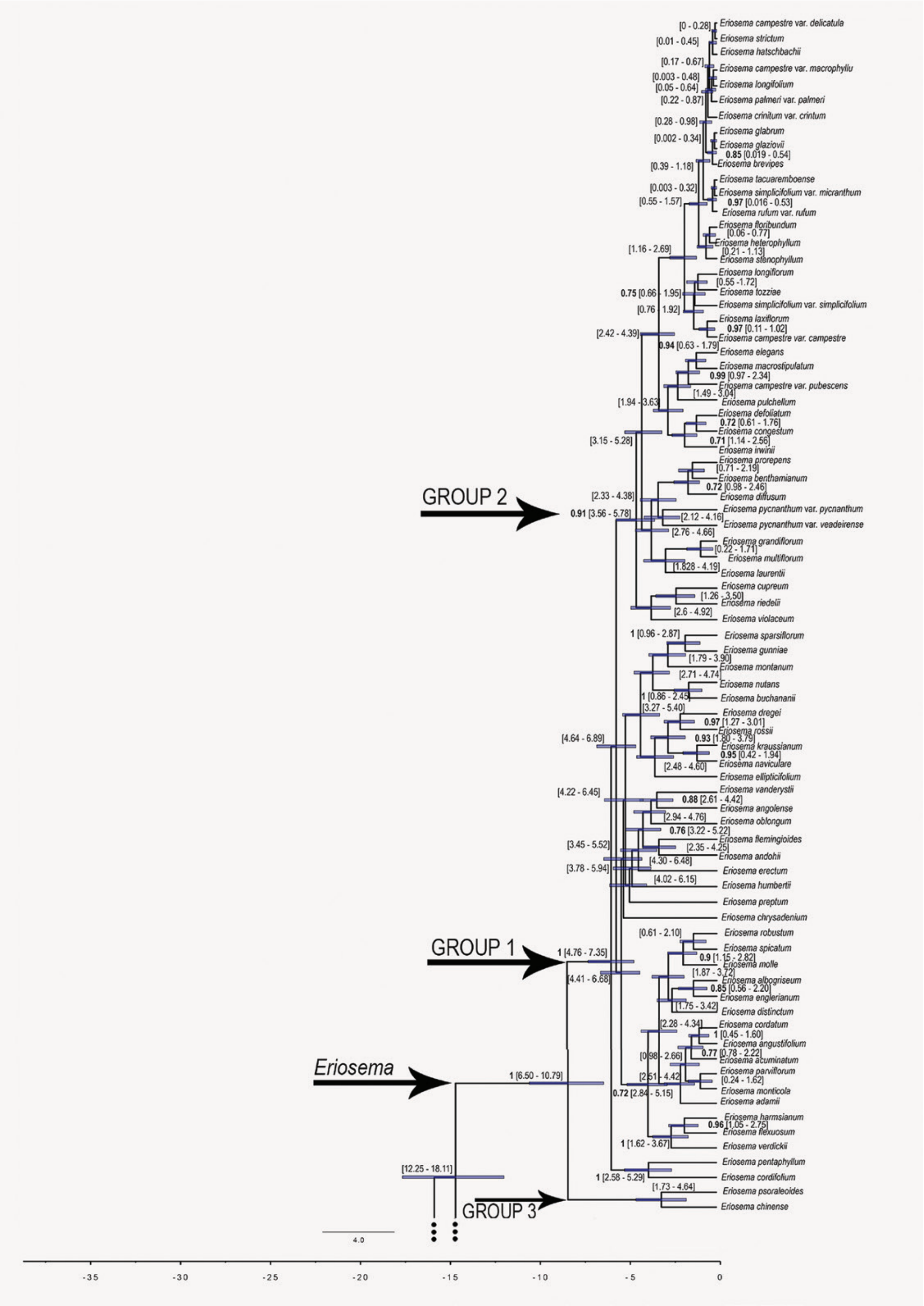

Figure 4. Continued.

complex that requires attention is *E. simplicifolium* (DC.) G.Don with two varieties: var. *simplicifolium* and var. *micranthum* Grear, because these appeared in different lineages in our analyses (Fig. 3B). *Eriosema simplicifolium* var. *micranthum* has an erect habit (prostrate in var. *simplicifolium*), smaller flowers and longer inflorescences than the typical variety (Cândido *et al.*, 2019). Fortunato (1993) synonymized *E. simplicifolium* var. *micranthum* under the typical variety, but our study clearly shows that *E. simplicifolium* var. *micranthum* should be elevated to species rank. Also, *E. pycnanthum* Benth. var. *pycnanthum* and *E. pycnanthum* var. *veadeirense* Grear appeared in different lineages in the phylogenetic tree (Fig. 3B). Cândido *et al.* (2019) stated that the varieties of *E. pycnanthum* are distinguished morphologically mainly by the length of the inflorescence (3.5–6.5-cm long in *E. pycnanthum* var. *pycnanthum* vs. 1.5–3.0-cm long in *E. pycnanthum* var. *veadeirense*) and leaflet texture (membranaceous to chartaceous in *E. pycnanthum* var. *pycnanthum* vs. thin-coriaceous to coriaceous in *E. pycnanthum* var. *veadeirense*) (Cândido *et al.*, 2019). Our analyses suggest that *E. pycnanthum* var. *veadeirense* would be better recognized at the rank of species.

HISTORICAL BIOGEOGRAPHY OF *ERIOSEMA*

Eriosema has a pantropical, intercontinental disjunct distribution, a common pattern in plants in general (Thorne, 1972; Givnish & Renner, 2004; Bartish *et al.*, 2011) and in Fabaceae (e.g. Fortuna-Perez *et al.*, 2013a; Vatanparast *et al.*, 2013; Moura *et al.*, 2016). According to molecular dating analyses, *Eriosema* originated in the Miocene, with an estimated crown-group age of 10.79–6.50 Myr and a stem group age of 18.11–12.25 Myr (Fig. 4B, Appendix S5). There are two major groups of species in *Eriosema*. Group 1 includes species that occur in Africa and has an estimated crown group age of 6.68–4.41 Myr (Fig. 4B, Appendix S5). This lineage comprises the greatest species diversity in the genus and is morphologically characterized by having racemose inflorescences, flowers occurring along the inflorescence rachis and, generally, inflorescences longer than the leaves (Fig. 5). A xylopodium, a specialized underground root system, is a synapomorphic character for species of this group. Group 2, which encompasses the majority of the New World species, has a divergence time of *c*. 5.78–3.56 Mya in the late Miocene (Fig. 4B, Appendix S5). It comprises species that occur mainly in the cerrado and campos rupestres vegetation in Brazil (Fig. 1B, D, F, H), including *E. brevipes* Grear (Fig. 6B), *E. defoliatum* Benth. (Fig. 6F), *E. elegans* Fort.-Perez & M.J.Silva (Fig. 6G), *E. floribundum* Benth. (Fig. 6H), *E. hatschbachii* Fort.-Perez & G.P.Lewis (Fig. 6K) and *E. irwinii* Grear (Fig. 6L), and a few species occurring in open areas of Mexico, Central and South America. The species in this clade have a racemose inflorescence and flowers crowded at the apex of the inflorescence, generally not surpassing the leaves in length (Fig. 6). Characters shared between species of the 'Old World' and 'New World' include the uni- to trifoliolate leaves, the abundant, long trichomes and glands throughout the plant and the presence of a specialized underground root system (Fig. 2A–C).

According to a previous study (Li *et al.*, 2013), as observed in this study for Cajaninae, during the late Oligocene some lineages of phaseoloid members of Fabaceae (mainly woody plants) underwent a rapid adaptive radiation, probably in response to the warming and increased aridity during this geological period; taxa rapidly evolved to exploit new niche opportunities in Africa, Asia and Australia. According to our results, *Eriosema* probably first appeared in Africa or Asia, during the late Miocene, (Fig. 3B, Appendix S4) and the great diversification in Africa and America was subsequently driven by rapid adaptation to these new ecological opportunities and the range expansion of C_4 grasses.

Our results strongly support the Old World as being the centre of origin of *Eriosema*. The chronogram resulting from the dating analysis indicates that the unique shifting event of *Eriosema* from the Old World to America occurred *c*. 6.89–4.64 Mya (Fig. 4B, Appendix S5). Considering the age of this migratory event and the estimates of the young age of the African-Neotropical disjunctions in *Eriosema*, continental drift or boreotropical migration can be discarded as explanations for this amphi-Atlantic migration. Some studies have reported local ants or beetles as the dispersal agents of *Eriosema* spp. (van der Pijl, 1982; Kergoat *et al.*, 2011). Transoceanic long-distance dispersal from Africa/Asia to the Neotropics is the most likely explanation. Several molecular dating studies report that the current distribution of taxa has occurred after these transoceanic long-distance dispersal events; these include studies in Fabaceae (e.g. Herendeen, Crepet & Dilcher, 1992; Lavin *et al.*, 2004; Lavin, Herendeen & Wojciechowski, 2005; Schrire *et al.*, 2005; Pennington, Richardson & Lavin, 2006; Simon *et al.*, 2011; Fortuna-Perez *et al.*, 2013a; Snak *et al.*, 2016; Cardoso *et al.*, 2017; Tosso *et al.*, 2018; Vasconcelos *et al.*, 2020). Future studies of *Eriosema* should explore in more depth the biogeographical hypotheses outlined here, and discuss in more detail the ancestral areas and geoclimatic events coexisting at the time of *Eriosema* speciation.

DIVERSIFICATION AND SAVANNA-ADAPTED MORPHOLOGY OF *ERIOSEMA*

Tropical savanna and grassland environments evolved *c*. 30 Myr and expanded worldwide in the late Miocene. Their evolution was simultaneous in Africa and America, and coincided with the substantial increase in C_4 grasses, which currently account for 25% of all terrestrial photosynthesis (Scholes & Archer, 1997; Cerling *et al.*, 1997; Keeley & Rundel, 2005; Beerling & Osborne, 2006; Edwards *et al.*, 2010; Van der Werf *et al.*, 2010; Parr *et al.*, 2014; Maurin *et al.*, 2014; Pennington & Hughes, 2014). In accordance with

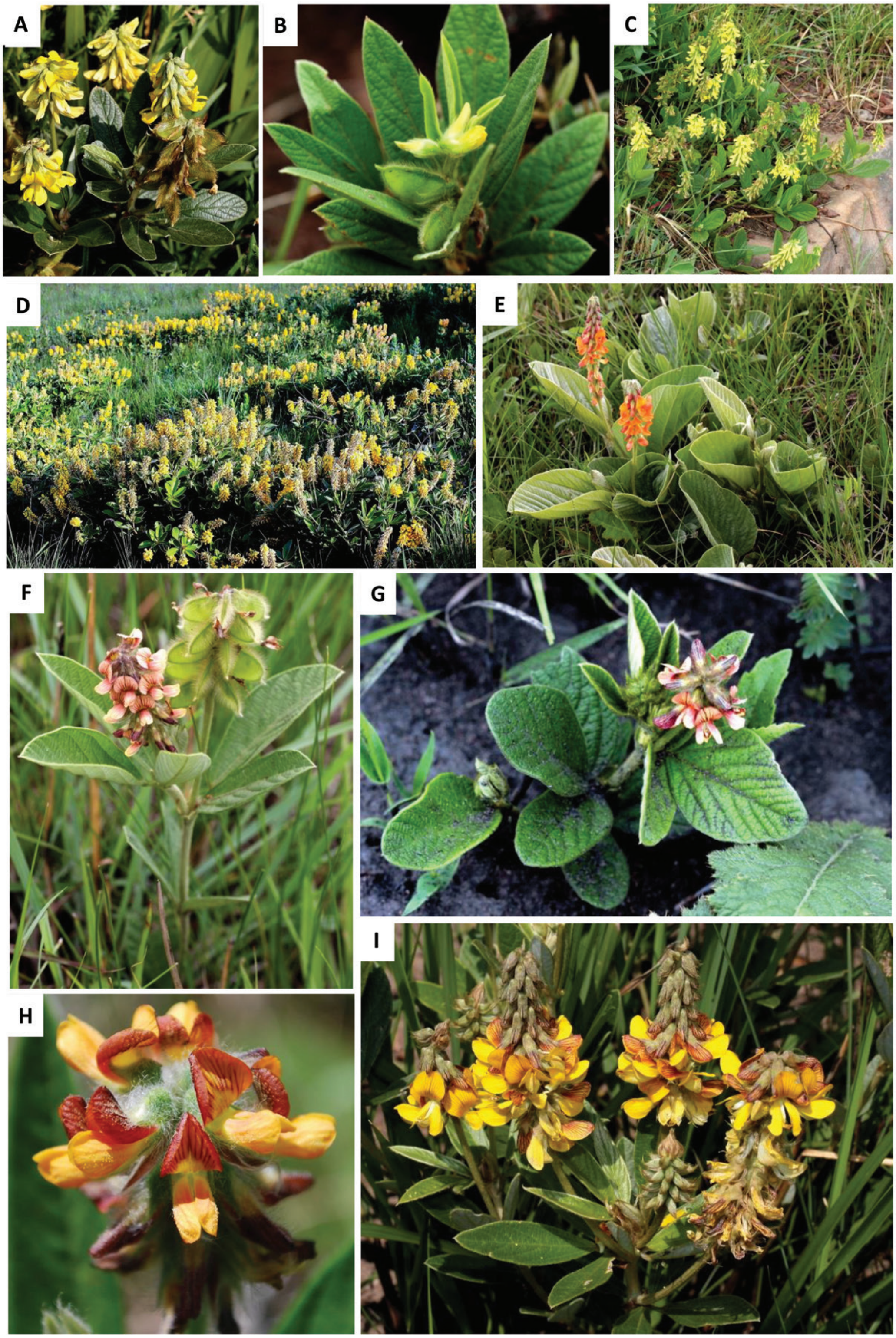

Figure 5. African *Eriosema* species. A, *E. dregei*. B, *E. ellipticifolium*. C, *E. guenzii*. D, *E. luteopetalum*. E, *E. populifolium*. F, *E. preptum*. G, *E. rossii*. H, *E. salignum*. I, *E. umtamvunense*. Photographs: David Styles.

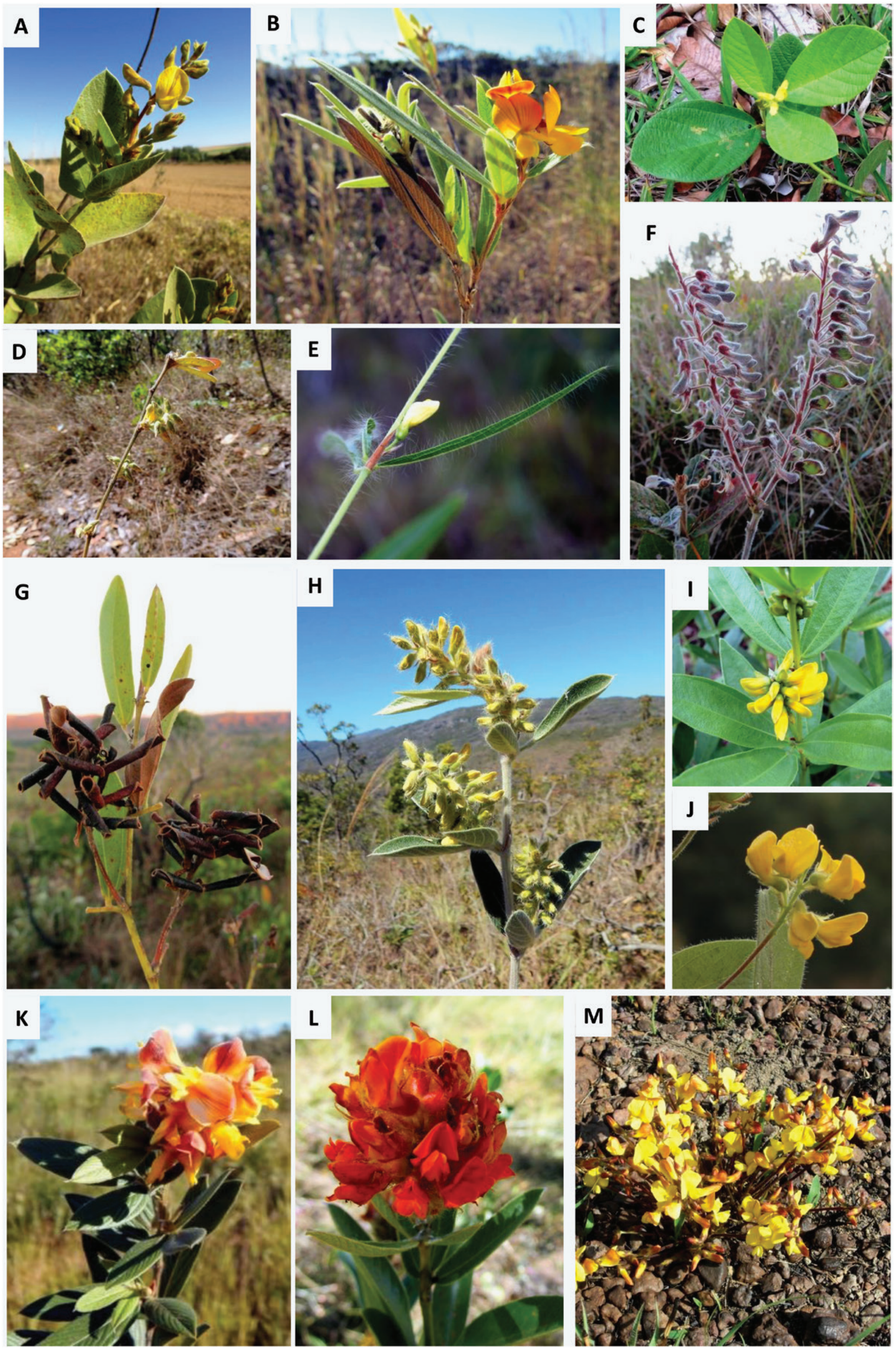

Figure 6. American *Eriosema* species. A, *E. benthamianum*. B, *E. brevipes*. C, *E. campestre* var. *campestre*. D, *E. congestum*. E, *E. crinitum* var. *crinitum*. F, *E. defoliatum*. G, *E. elegans*. H, *E. floribundum*. I, *E. glabrum*. J, *E. heterophyllum*. K, E. *hatschbachii*. L, *E. irwinii*. M, *E. laxiflorum*. Photographs: A–C, F, G, L, Elisa Cãndido; D, E, I, Ana Paula Fortuna-Perez; H, Ambar Soldevila; J, Gustavo H. Shimizu; M, Marcos Silva.

the age estimate of *Eriosema* (10.7–6.5 Myr; Fig. 4B, Appendix S5) the diversification of the genus occurred in parallel with the savanna biome expansion. Time-calibrated phylogenetic trees of other plant taxa also suggest that savanna lineages started to diversify < 10 Mya and that the rapid diversification of these lineages coincided with the increase and dominance of C_4 grasses in tropical savannas around the world (e.g. Simon *et al.*, 2009, 2011; Simon & Pennington, 2012; Souza *et al.*, 2013; Trovó *et al.*, 2013; Maurin *et al.*, 2014; Souza-Neto, Cianciaruso & Collevatti, 2015; Rando *et al.*, 2016).

Eriosema is a recent, tropical savanna-adapted subshrub/shrub group and the current distribution of its representatives occurs, essentially, in the tropical savannas and grasslands of the African continent and the Brazilian cerrado (Grear, 1970; Cândido *et al.*, 2019) (Fig. 1). *Eriosema*, like other genera that evolved and occur in these environments, displays specialized morphological, physiological and ecological survival strategies. Morphologically, we highlight the underground root system and the presence of trichomes throughout the plant (Fig. 2), including secretory structures (bulbous-based trichomes, vesicular glands and secretory-based trichomes) (Grear, 1970; Lackey, 1978; Cândido *et al.*, 2016; Vargas *et al.*, 2018; Cândido *et al.*, 2019). Grear (1970) named the underground specialized root system a xylopodium, and this terminology has been followed by subsequent studies (e.g. Stirton, 1975, 1981, 1986; Stirton & Gordon-Gray, 1978; Grear, 1978; Miotto, 1988; Fortunato, 1993, 1999; Fortuna-Perez *et al.*, 2013, 2017, 2018; Cândido *et al.*, 2014a, b, 2016; Oliveira, Fortuna-Perez & Silva, 2018). However, only now are detailed anatomical studies being conducted to investigate the variation in the thickened underground root system found in *Eriosema* spp. A preliminary survey has found that in some species this root system can take the form of a xylopodium, a tuberous or non-tuberous root (often daucate and with or without smaller side appendages) or a rhizome (Piva *et al.,* 2020; Stirton, C, unpubl. data). Future investigations should focus on the ecological functions of this underground system. Root systems in African savannas are often different from those in coastal and upland grassland systems (Stirton, C, unpubl. data).

Regarding the trichome types encountered in *Eriosema*, Vargas *et al.* (2018) carried out the most comprehensive anatomical and micromorphological study of representatives of Cajaninae, confirming that only vesicular glands are a unifying character of the subtribe. Another recent study analysed the ultrastructure and histochemistry of glandular trichomes in the leaflets of species of Cajaninae, including *E. rufum* (Kunth) G.Don and *E. simplicifolium*, two species widely distributed in the American continent. The authors suggested that glandular trichomes and their exudates (lipids and phenolic compounds) act as a defence against herbivory and also help to prevent damage by ultraviolet radiation. This is especially important for the survival of *Eriosema* spp. that have diversified in environments with high light intensity and high temperatures (Vargas *et al.*, 2019).

Although there exists no published reproductive phenological study of *Eriosema* spp., there are some examples reporting the intrinsic ecological relationship between *Eriosema* spp. and savanna environments. *Eriosema laxiflorum* Harms (Fig. 6M), a small subshrub (10–26-cm tall) with an erect habit and a tufted (caespitose) appearance, is endemic to the cerrado of central Brazil and only blooms directly after fire. All flowering individuals of this species collected by us were encountered in recently burnt vegetation (Cândido *et al.*, 2019). *Eriosema kraussianum* Meisn. is a small hysteranthous pyrophyte from the grasslands of Kwa-Zulu Natal in South Africa that only flowers after fire. This post-fire flowering phenomenon has also been reported for other angiosperm species in similar environments (Coutinho, 1976; Conceição & Orr, 2012; Conceição *et al.*, 2013; Fidelis & Blanco, 2014). Two species which are endemic to the Brazilian cerrado, *Eriosema defoliatum* Benth. (Fig. 6F) and *Eriosema congestum* Benth. (Fig. 6D), only flower and fruit in the dry season when they are leafless, so that leaves and flowers are rarely collected together (Cândido *et al.*, 2019). This reproductive trait needs to be better investigated.

MORPHOLOGICAL AND PHYLOGENETIC RELATIONSHIPS BETWEEN *ERIOSEMA* AND *RHYNCHOSIA*: THE TWO MOST SPECIES-RICH GENERA OF CAJANINAE

Rhynchosia, the largest genus of Cajaninae, comprises *c.* 230 species (Schrire, 2005). The genus is not, however, monophyletic, and one clade of African species is the sister group of *Eriosema*. Egan *et al.* (2016) also demonstrated *Rhynchosia* to be paraphyletic, although they only sampled two species in their study of *Pueraria* DC. (subtribe Glycininae, tribe Phaseoleae). The close morphological and phylogenetic relationship between *Eriosema* and *Rhynchosia* has also been demonstrated in other previous studies, albeit with lower sampling of the two genera (Doyle & Doyle, 1993; Bruneau *et al.*, 1995; Kajita *et al.*, 2001; LPWG, 2017). Our phylogenetic analyses support the two genera as distinct evolutionary lineages (Fig. 3, Appendix S4).

Eriosema and *Rhynchosia* together comprise *c.* 380 species, representing the large majority of species in Cajaninae; they are the only genera in the subtribe that have species in the New World. The two genera share several morphological characteristics, including typically papilionaceous and mostly yellow flowers; two-seeded dehiscent fruits; uni- or trifoliolate leaves and stipules usually lanceolate to triangular (Oliveira *et al.*, 2018; Bezerra *et al.*, 2019a, b, c; Cândido *et al.*, 2019). Traditionally, the two genera have been separated in morphological studies mainly by the apparent differing insertion point of the funicle in relation to the hilum of the seed (Baker, 1895; Grear, 1970; 1978; Miotto, 1988; Cândido *et al.*, 2014a). The distinction between these genera based only on this character is not, however, consistent or reliable. A suite of characters is needed to reliably separate *Rhynchosia* from *Eriosema*, including habit, stipules (free or connate), presence or absence of stipels, inflorescence type, seed colour, hilum shape, extension of the strophiole and fruit constriction between the seeds (Cândido *et al.*, 2019).

In southern Africa, the two genera are easily identified by the shape of the fruits (box-like rectangular and shaggy-haired in *Eriosema* versus attenuate at both ends and less prominently hairy in *Rhynchosia*), the seedlings (epicotyls shaggy-haired in *Eriosem*a and finely pubescent in *Rhynchosia*); the presence of dense glands on the keel petals and back of the standard petal (ubiquitous in *Eriosema*, rare in *Rhynchosia*) and the patterns formed on leaflets by species of Agromyzidae (leaf-miners) and species of Bruchidae (seed weevils) that attack the fruits (Stirton, C, unpubl. data). These traits might provide useful diagnostic characters if surveyed across the geographical distribution of the two genera. In addition, although the two genera have an essentially pantropical distribution, some *Rhynchosia* spp. extend to temperate regions and forest environments, whereas *Eriosema* spp. are restricted to savanna, savanna-like environments or grasslands (Fig. 1) (Grear, 1978; Bezerra *et al.*, 2019a, b; Cândido *et al.*, 2019).

INTERGENERIC RELATIONSHIPS IN CAJANINAE

Cajaninae, with *c.* 500 species, are the largest subtribe of Phaseoleae (Fig. 3, Appendix S4). They are included in core Phaseoleae *sensu* Schrire (2005) with Psoraleeae, Glycininae, Erythrininae and the genus *Butea* Roxb. ex Willd. (Egan *et al.*, 2016). In our study we sampled nine out of the ten genera traditionally placed in Cajaninae (Appendix S1). Material of the monospecific *Carrissoa* Baker f. (*C. angolense* Baker f.) will be include in future studies of the subtribe. *Adenodolichos* is strongly supported as monophyletic (Fig. 3A, Appendix S4). Bruneau *et al.* (1995) resolved *Adenodolichos* as sister to all other representatives of Cajaninae, but in our study its position is not fully resolved. *Adenodolichos* is the only genus in the subtribe that possesses bracteoles on its flowers and the chemical compound canavanine, and Lackey (1977, 1981) considered it as anomalous in Cajaninae. Egan *et al.* (2016) found that canavanine production is the ancestral condition in Phaseoleae although its presence has been lost and regained more than once in lineages of the tribe. *Adenodolichos* shares vesicular glands with other members of Cajaninae, and these glands are considered as a unifying character of the subtribe (Vargas *et al.*, 2018). The other genera of Cajaninae that have been recovered as monophyletic are *Cajanus*, *Dunbaria* and *Flemingia* (Fig. 3A, Appendix S4). *Rhynchosia* is separated into two distinct lineages; here we included *R. volubilis* (the type species, native to Asia and sister to the *Cajanus* clade) and *C. cinereus* (F.Muell. ex Benth.) F.Muell., *C. cajanifolius* (Haines) Maesen and *C. scarabaeoides* (L.) Thouars, all native to Asia and northern Australia (Fig. 3A, Appendix S4). *Paracalyx* emerged nested in a group of *Rhynchosia* spp. Egan *et al.* (2016) identified *Paracalyx* as sister to *Rhynchosia*. The species belonging to *Paracalyx* were originally included in *Cylista* Aiton and the type species of that genus is included in *Rhynchosia* (Egan *et al.*, 2016). Our study included the largest, to date, sampling of *Rhynchosia* spp. across its geographical range. Further work including a broader sample of *Cajanus*, *Paracalyx* and *Rhynchosia* and multiple accessions of *R. volubilis* is needed to completely unravel the relationships between these taxa.

CONCLUSIONS

Our study presents the first comprehensive molecular phylogenetic analysis of *Eriosema* and allied genera of Cajaninae. Our results support the monophyly of the subtribe and of *Adenodolichos*, *Eriosema*, *Dunbaria*, *Flemingia* and *Cajanus*. *Eriosema* originated in the Miocene (10.7–6.5 Mya), and its great diversification in Africa and the New World was driven by the opportunities generated by the appearance of new ecological niches and the range expansion of C_4 grasses, in parallel with the expansion of the savanna biome around the world. Future studies should focus on phylogenomic approaches to further elucidate evolutionary relationships in *Eriosema*. *Rhynchosia* is polyphyletic and should be reclassified based on its distinct evolutionary lineages. The close relationship between the evolution and diversification of *Eriosema* with the emergence of the savanna biome is clear from our analyses, and the conservation of *Eriosema* spp. is intimately connected to the conservation of this under-protected biome. Additional taxonomic, morphological, anatomical and biogeographical studies are necessary to better understand the evolution of and relationships between lineages of *Eriosema*.

ACKNOWLEDGEMENTS

This work is one of the results from the project 'Estudos taxonômicos, filogenéticos e biogeográficos no gênero *Eriosema* (DC.) Desv. (Leguminosae, Papilionoideae, Phaseoleae)', which is funded by FAPESP/Brazil - Fundação de Amparo a Pesquisa do Estado de São Paulo (process 2015/13386-0; 09/53002-5); CNPq/Brazil - Conselho Nacional de Desenvolvimento Científico e Tecnológico (process 400567/2016-4), both granted to A.P. Fortuna-Perez. The authors also thank Fundação de Amparo à Pesquisa do Estado de Minas Gerais/Brazil (process APQ-02323-12), and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) Print/UNESP (process 88887.373155/2019-00), for financial support granted to A.P. Fortuna-Perez; Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro/Brazil (process 203.007/2017) and CNPq (process 312766/2009-2) for financial support granted to V.F.Mansano; CNPq - REFLORA Project (process 563550/2010-4) for financial support granted to A. Tozzi; CAPES/Brazil and CNPq/Brazil (process 141628/2016-2) for a PhD scholarship to E.S. Cândido; the Rupert Barneby Award of The New York Botanical Garden awarded to E.S. Cândido. We thank the Biologia Vegetal post-graduate program at UNICAMP, the UNESP-Botucatu, the Instituto de Pesquisas JBRJ, the UFOP for the support to E.S. Cândido; the UFG for all the support in the field in the state of Goiás. We thank the curators and staff of all herbaria visited for providing access to specimens and photographs in their collections, and all the people who helped us in the field in Brazil. The majority of the analyses were conducted at the Smithsonian Institution (USA) High-Performance Cluster (https://doi.org/10.25572/SIHPC).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Nucleotide sequence database accession numbers of taxa used in the phylogenetic analysis.
Appendix S2. List of molecular markers and primers used in this study.
Appendix S3. Information relating to the separate DNA datasets.
Appendix S4. Phylogenetic tree for *Eriosema* from maximum likelihood analysis of the ITS/5.8S and plastid DNA dataset (*rpl32-trnL* and *trnQ*-5'*rps16*). Numbers along branches are bootstrap values and posterior probabilities.
Appendix S5. BEAST chronogram based on combined dataset (ITS/5.8S, *rpl32-trnL* and *trnQ*-5'*rps16*). Numbers at nodes refer to mean age of the nodes (My). Blue bars represent 95% confidence intervals (CI) for the estimated mean dates. Posterior probabilities are indicated at nodes.