

# Ancient speciation of the papilionoid legume *Luetzelburgia jacana*, a newly discovered species in an inter-Andean seasonally dry valley of Colombia

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**Abstract** Ecology, geography, morphology, and a combined phylogenetic analysis of DNA sequence variation support the recognition of the new species *Luetzelburgia jacana* (Leguminosae, Papilionoideae, vataireoid clade). This species is found in the inter-Andean Rio Cauca Valley in Colombia. Phylogenetic analyses of nine plastid and nuclear DNA sequences from 44 accessions representing all known *Luetzelburgia* species show that *L. jacana* is sister to the rest of the genus and has a mean estimated stem age of ca. 4 Ma, much older than other *Luetzelburgia* species. *Luetzelburgia jacana* is distinguished by a combination of mostly 7–9-foliolate, glabrous leaves with leaflets obtuse to shortly acute at the apex, flowers up to 9.6 mm long, and samaras bearing two small lateral wings on the seed chamber. *Luetzelburgia jacana*, along with two other earliest-branching species in the genus, *L. guaissara* and *L. trialata*, are geographical outliers in the genus, with *L. jacana* having the northernmost distribution and *L. guaissara* and *L. trialata* having the southernmost distributions. These three earliest-branching species are also ecological outliers within *Luetzelburgia* by occurring in wetter and less seasonal settings than other species. The discovery of *L. jacana* resolves these three earliest-branching species in *Luetzelburgia* as ecologically transitional between most species of the vataireoid clade that inhabit wet forests and most species of *Luetzelburgia* that inhabit highly seasonal dry forests and woodlands.

**Keywords** Andes; Leguminosae; Papilionoideae; phylogeny; taxonomy

**Supplementary Material** The Electronic Supplement (Table S1; Figs. S1–S9) and DNA sequence alignment is available from <https://doi.org/10.12705/675.6.S1> and <https://doi.org/10.12705/675.6.S2>, respectively.

## ■ INTRODUCTION

Molecular phylogenies of legumes that are densely sampled at the intra-specific level have often revealed overlooked species (Govindarajulu & al., 2011; Pennington & al., 2011; Queiroz & Lavin, 2011; Särkinen & al., 2011a; Gagnon & al., 2015; Lavin & al., 2018) especially for populations confined to island-like patches of the seasonally dry tropical forest and woodland (SDTFW) biome (Pennington & al., 2009, 2010; Särkinen & al., 2012; Pennington & Lavin, 2016; Queiroz & al., 2017). The general finding of closely related species showing endemism to separate patches of SDTFW suggests that phylogenetic niche

conservatism (e.g., Wiens, 2004; Donoghue, 2008) together with dispersal limitation (e.g., Hubbell, 2001) have strongly shaped legume biodiversity in the SDTFW biome (Lavin, 2006; Lavin & al., 2004; Pennington & al., 2009, 2010; Särkinen & al., 2012; Pennington & Lavin, 2016).

The focus of this study is *Luetzelburgia* Harms, which includes 14 species and is closely related to the genera *Sweetia* Spreng., *Vatairea* Aubl., and *Vataireopsis* Ducke (Cardoso & al., 2012a, 2013a). Together these four genera compose the early branching vataireoid clade of the papilionoid legumes (Cardoso & al., 2012a, 2013b; LPWG, 2013, 2017). The vataireoid genera include ~27 tree species that share a samaroid fruit with a

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transversely veined apical wing arising from a basal seed chamber, which usually bears a small lateral wing on each side of the chamber. Other unequivocal vataireoid synapomorphies include congested or fascicled leaves at the distal ends of branches and free keel petals with overlapping distal margins. *Luetzelburgia* is marked by the combination of: (i) externally sericeous and crimped petals each with a bi-auriculate and symmetrical base; (ii) the lateral (wing-like) and abaxial (keel-like) petals free and undifferentiated with respect to the distinct wing and keel shape of most papilionoid legumes; (iii) the usually oblong to obovate blade of the standard petal (not emarginate at the apex); (iv) basally connate staminal filaments; and (v) the samara with an indistinct endocarp and usually bearing a small wing on each side of the seed chamber (Cardoso & al., 2013a, 2014). The vataireoid clade can be ecologically dominant in savanna and rain forest biomes (*Vatairea* and *Vataireopsis* species; e.g., *Vatairea macrocarpa* (Benth.) Ducke in the cerrado: Bridgewater & al., 2004), but *Luetzelburgia* species and the monospecific genus *Sweetia* are concentrated in the SDTFW biome, particularly in the Brazilian Caatinga (Queiroz & al., 2017). Additionally, these genera are known to extend geographically into seasonally dry forest enclaves in northern and western Amazonia as well as the Bolivian inter-Andean dry valleys and Chiquitania region (Cardoso & al., 2014). *Luetzelburgia trialata* (Ducke) Ducke of the Atlantic forest is the only rain forest inhabiting species in the genus, although it sometimes occurs in more seasonally dry settings. *Luetzelburgia praecox* (Harms ex Kuntze) Harms is savanna-inhabiting (e.g., the Cerrado of eastern Brazil), though generally in areas of more fertile, SDTFW-like soils, and *Luetzelburgia auriculata* (Allemão) Ducke, although most common and abundant in the SDTFW biome, is occasionally found in savanna.

The basis for this paper is a previously unidentified leafless fruiting specimen collected in 1979 in Colombia. The specimen had the diagnostic samara features of *Luetzelburgia*, yet its geographic distribution occurred outside the known range of the genus (Cardoso & al., 2014). The specimen was collected by Alwyn Howard Gentry in a localized patch of seasonally dry tropical forest along the Rio Cauca Valley in the Department of Antioquia. We have used an integrative taxonomic approach to show that *Luetzelburgia* specimens from Colombia represent populations of a phylogenetically distinct lineage marked by a unique phenotype and that occupies an ecologically and geographically distinct setting, and thus warrants recognition as a separate species (Freudenstein & al., 2017).

## ■ MATERIALS AND METHODS

**Morphological studies.** — Morphological measurements were taken from more than 1597 herbarium collections of the vataireoid clade from herbaria ALCB, ASE, BHCN, BRIT, CEN, CEPEC, CESJ, CTES, E, EAC, ESA, F, FLOR, FURB, GUA, HBR, HRB, HST, HUA, HUEFS, HUESB, HUNEB, HVASF, IAC, IAN, INPA, IPA, JAUM, JOI, JPB, K, LPB, MBM, MBML, MG, MIRR, MO, MOSS, MONT, NY, PEUFR, R, RB, SI, SP, SPF, SPSF, TEPB, UB, UEC, UESC, UFMT,

UFP, UFRN, USZ, VIC, W and XAL. Measurements from floral organs come from rehydrated tissue by boiling and dissection. Vegetative measurements were captured with digital images analyzed with the software ImageJ v.1.52g (Rasband, 2016).

**Taxon sampling, acquiring molecular data, alignment, and phylogenetic analyses.** — To place the putatively new Colombian species in the context of the *Luetzelburgia* phylogeny, we have sampled all species described for the genus (Cardoso & al., 2014), including multiple conspecific accessions that capture as much as possible the species' morphological and geographical variation. Such sampling included only one DNA-amplifiable accession (*Banda 386*) of the putatively new Colombian species (Appendix 1). *Vatairea* and *Vataireopsis* species were chosen as outgroups following the comprehensive study of Cardoso & al. (2013b) on the vataireoid clade.

Our molecular datasets include nine markers: the nuclear ribosomal ETS and ITS/5.8S and the plastid regions *matK/3'trnK*, *psbA-trnH*, *trnL* intron, *rps16* intron, *trnD-T*, and *trnQ-5'rps16*. Of the total 346 DNA sequences representing 44 terminals, 115 were newly generated (Appendix 1) and the remaining 231 sequences derive from Cardoso & al. (2013b).

DNA isolation, polymerase chain reaction (PCR) amplifications, and template purifications were performed as described by Cardoso & al. (2013b), except for the reaction conditions of the nuclear ETS which consisted of an initial denaturation at 94°C for 4 min followed by 30 cycles of denaturation at 94°C for 40 s, annealing at 56°C for 45 s, and extension at 72°C for 1 min, and a final extension step at 72°C for 7 min; and for the plastid *trnQ-5'rps16* which was amplified using an initial denaturation at 80°C for 5 min followed by 32 cycles of denaturation at 95°C for 1 min, annealing at 51°C for 1 min, and extension at 65°C for 2 min, and a final extension step at 65°C for 5 min. Amplification and sequencing primers are described in Table S1 (Electr. Suppl.). Forward and reverse reads were assembled and base-calling verified with the Staden package v.2.0.0b11 (Staden & al., 2003). Sequences were aligned manually in AliView v.1.17.1 (Larsson, 2014), in order to avoid inconsistencies derived from automated multiple alignment. The alignment of the protein-coding *matK* gene involved the nucleotide and amino acid sequences because of the high number of indels (Wojciechowski & al., 2004).

Combinability of DNA markers was assessed by comparing clade support amongst individual-gene-derived phylogenetic trees (Wiens, 1998). To identify possible conflict between the molecular markers, we used the more conservative parsimony bootstrap supports as generated in PAUP v.4.0b10 (Swofford, 2002), because Bayesian posterior probability values are often biased high (e.g., Suzuki & al., 2002; Alfaro & al., 2003; Erixon & al., 2003). Heuristic parsimony search options included stepwise addition with a random sequence addition and holding 10 trees at each step, random addition replicates set to 100, use of non-minimum trees during TBR branch swapping, invoking steepest descent, and retention of multiple most parsimonious trees. Nonparametric bootstrap resampling (Felsenstein, 1985) included 1000 replicates each subjected to the same heuristic search options but with no retention of multiple trees per

bootstrap replicate. We considered incongruence as conflicting clades each with bootstrap support >80%. We did not observe significant incongruence using this criterion and further evidence for compatibility of data from separate regions comes from increased resolution after combining molecular datasets in this study. Hence, we will present only the more robustly resolved tree derived from the combined analyses of the two nuclear and seven plastid DNA markers.

**Evolutionary rates analysis.** — Phylogenetic analysis involved BEAST v.2.5 (Bouckaert & al., 2014; <http://www.beast2.org/>), which integrated the choice of nucleotide substitution models, molecular clock models, and tree (speciation) models. Aligned nexus files defining interleaved data partitions were imported into BEAUti v.2.5. Clock and tree models were then linked for all data partitions. The site model was set to the following for all data partitions: reversible jump substitution model (involving six models ranging in complexity from F81 to GTR), gamma category count set to a prior of 4, gamma shape parameter set to a prior of 1.0, proportion of invariant sites set to a prior of 0.2. Estimates were then requested by ticking the checkbox for substitution rate, gamma shape parameter, and proportion of invariant sites.

For the clock model, separate analyses were set up to run the relaxed log normal and relaxed exponential molecular clock (Drummond & al., 2006), as well as the strict molecular clock (the random clock model included excessive run times and was thus not amenable to multiple runs and analysis exploration).

For the tree model, the birth-death and fossilized birth-death models were run in separate analyses (the calibrated Yule and the various coalescent models produced results that resolved the main clades as having very old stem ages and very young crown ages and these were then not further explored). For the birth-death tree models, MRCA (most recent common ancestor) priors were added. These included the entire dataset (outgroup and ingroup). An exponential (and a log normal, in a separate analysis) density calibration was offset at 17 Ma for this MRCA prior involving the entire dataset. This 17 Ma age estimate is the average age of the vataireoid crown clade derived from a reanalysis of Lavin & al. (2005). MRCA priors included also the outgroup, the genus *Luetzelburgia*, and each of the 14 *Luetzelburgia* species. Ages were then estimated for the outgroup and the genus *Luetzelburgia* by setting a prior age of each of these clades to 5 Ma (but this prior was also set to ages from 1 and 10 Ma in separate analyses in order to determine the influence of the prior on the final mean age estimates). Estimated ages were set to a normal distribution. The MRCA priors for each of the 14 species of *Luetzelburgia* were simply set to a single age estimate of the stem clade per sampled tree by ticking the “use originate” checkbox and not invoking an estimated age distribution. All MRCA priors were set to monophyletic.

The Markov Chain Monte Carlo (MCMC) length was set to 25 million generations. Parameters were sampled every 25,000 generations. Log files of parameter and tree samples were named to specify the combination of clock and tree models of each analysis. Tracer v.1.6 (Rambaut & Drummond, 2013) facilitated the identification of the burn-in as well as the output of

desired parameter estimates at likelihood stationarity from each of the separate BEAST2 analyses. The data-wrangled output in a tab-delimited text file was analyzed graphically in R ([http://www.montana.edu/mlavin/594/Analysis\\_of\\_Luetzelburgia\\_output.html](http://www.montana.edu/mlavin/594/Analysis_of_Luetzelburgia_output.html)). TreeAnnotator v.2.5, part of the BEAST2 package, output the Bayesian maximum clade credibility (MCC) tree with median ages and 95% highest posterior density (HPD) intervals of node ages from each BEAST2 analysis using a specified burn-in.

**Ecological analyses of climatic variables.** — A total of 509 herbarium collections of *Luetzelburgia* species was georeferenced. From the latitude and longitude of each collection, monthly precipitation, minimum and maximum temperatures were extracted from the WorldClim v.2.0 model layers (WGS84 projection; Fick & Hijmans, 2017) using the R library raster (Hijmans & al., 2017). Bioclimatic variables (O’Donnell & Ignizio, 2012) were derived from these climate models using the *biovars* function in the raster library. A principal components analysis and generation of biplots were performed on all climate data in order to detect the two orthogonal climate variables that showed the greatest amount of variation among the *Luetzelburgia* sample sites. Climate variables showing the most variation were also downloaded from CHELSA (Climatologies at high resolution for the earth’s land surface areas; <http://chelsa-climate.org/>; Karger & al., 2017a, b), 30 arcsec resolution climate models, which were compared with the WorldClim models with respect to the 509 *Luetzelburgia* collection sites.

## ■ RESULTS

**Phylogenetic relationships and divergence times in *Luetzelburgia*.** — The final aligned dataset of 44 terminals and nine DNA markers had a length of 7721 sites. Parsimony analysis of 446 informative sites yielded 253 most parsimonious trees each with a consistency index of 0.821 and a retention index of 0.882. The high retention index reflected high levels of phylogenetic resolution of mainly monophyletic groups of conspecific *Luetzelburgia* accessions. The strict consensus tree resolved a monophyletic *Luetzelburgia* (bootstrap support of 100%). One of the few other well supported relationships was the Colombian accession (*Banda 386*), resolved as sister to all other accessions of *Luetzelburgia* species with a bootstrap support of 92% (Electr. Suppl.: Fig. S1).

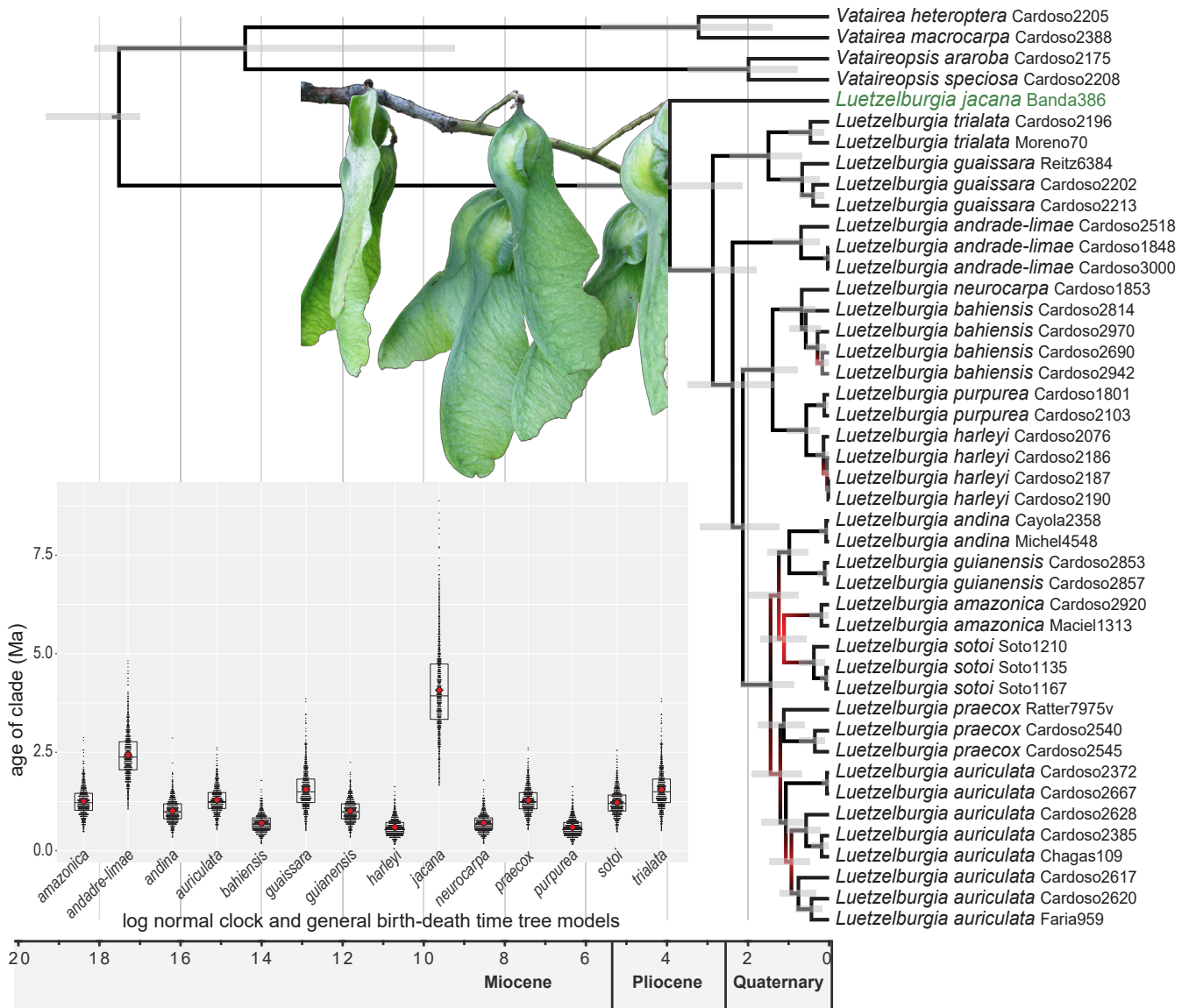
Results from the poorly-resolved single-gene Bayesian phylogenetic trees are available in the Electronic Supplement (Electr. Suppl.: Figs. S2–S9). The Bayesian phylogenetic analysis of the combined nine molecular markers resolved a monophyletic *Luetzelburgia* with the Colombian accession (*Banda 386*) as sister to the rest of the genus, relationships supported with posterior probabilities of 1.00 and 0.99, respectively (Fig. 1). The estimated stem age of the Colombian accession centers on 4 Ma in the mid Pliocene (Fig. 1) regardless of the clock and tree model combination implemented during each BEAST2 analysis. The estimated overall rate of substitution depends on the clock and tree model combination but ranges mostly between  $1.3 \times 10^{-9}$  and  $1.9 \times 10^{-9}$  substitutions per site per year for the



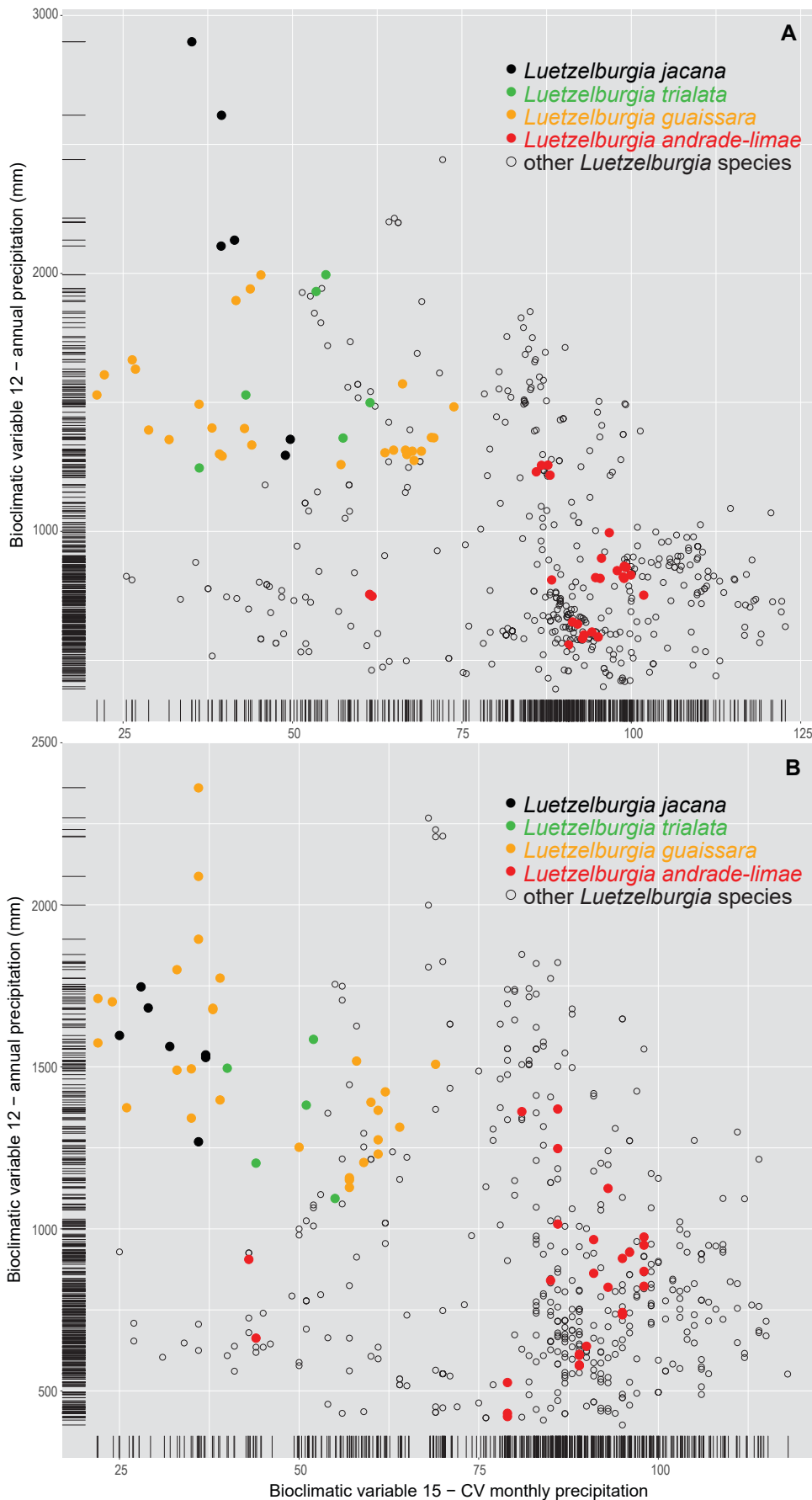
combined nrDNA and cpDNA dataset ([http://www.montana.edu/mlavin/594/Analysis\\_of\\_Luetzelburgia\\_output.html](http://www.montana.edu/mlavin/594/Analysis_of_Luetzelburgia_output.html)).

**Ecological distinctiveness.** — The 509 herbarium collections of *Luetzelburgia* were arrayed in two dimensions by the most variable and orthogonal climate variables, annual precipitation (mm) and the coefficient of variation (CV) of monthly precipitation, bioclimatic variables 12 and 15 (Fig. 2). *Luetzelburgia* collections were collected at sites mostly with less than 1500 mm annual precipitation and with high precipitation

seasonality, or a CV of greater than 80%. These high values represent sites where the variance (standard deviation) of the precipitation throughout the year (the numerator) equaled or exceeded the average precipitation (the denominator), which reflect drought periods that varied greatly both intra- and inter-annually. Collection sites of the Colombian specimens of *Luetzelburgia* differ from most other *Luetzelburgia* species by having a widely disjunct northern distribution (Fig. 3) and a distinctly greater annual precipitation (over 1500 mm) and



**Fig. 1.** Chronogram of *Luetzelburgia* derived from the BEAST2 analysis of nuclear ribosomal ETS and ITS/5.8S and plastid *matK*, 3'*trnK* intron, *psbA-trnH*, *trnL* intron, *rps16* intron, *trnD-T*, and *trnQ-5'rps16* DNA sequences and showing a Pliocene divergence of the newly discovered Colombian species *L. jacana* (Banda 386). Bars on the nodes represent 95% of high posterior density of divergence times. Posterior probabilities from 0.5 to 1.0 are shown as color gradient on the branches, where black branches have the highest support. The photograph of the Colombian species by Álvaro Idárraga shows the samaroid fruits with small lateral wings on the seed chamber that are typical of the genus *Luetzelburgia*. The inset figure shows an age distribution for the stem clades of each of the 14 *Luetzelburgia* species derived from the BEAST2 analysis, which derives from 901 age estimates per specified branch sampled at likelihood stationarity. Similar age estimates were obtained with different combinations of clock models (e.g., relaxed exponential or strict) and MRCA prior density calibrations (e.g., log normal; see [http://www.montana.edu/mlavin/594/Analysis\\_of\\_Luetzelburgia\\_output.html](http://www.montana.edu/mlavin/594/Analysis_of_Luetzelburgia_output.html)).



**Fig. 2.** Climate distribution of 509 vouchered (herbarium) collections of the genus *Luetzelburgia* with the collection sites highlighted for those of the new Colombian species *L. jacana* and the three other early branching *Luetzelburgia* species (*L. andrade-limae* is ecologically representative of the other *Luetzelburgia* species). These herbarium collections were part of the taxonomic revision of the genus *Luetzelburgia* (Cardoso & al., 2014). **A**, *Luetzelburgia* herbarium collections plotted using the WorldClim climate models (Fick & Hijmans, 2017); **B**, *Luetzelburgia* herbarium collections plotted using the CHELSA climate models (Karger & al., 2017a, b).

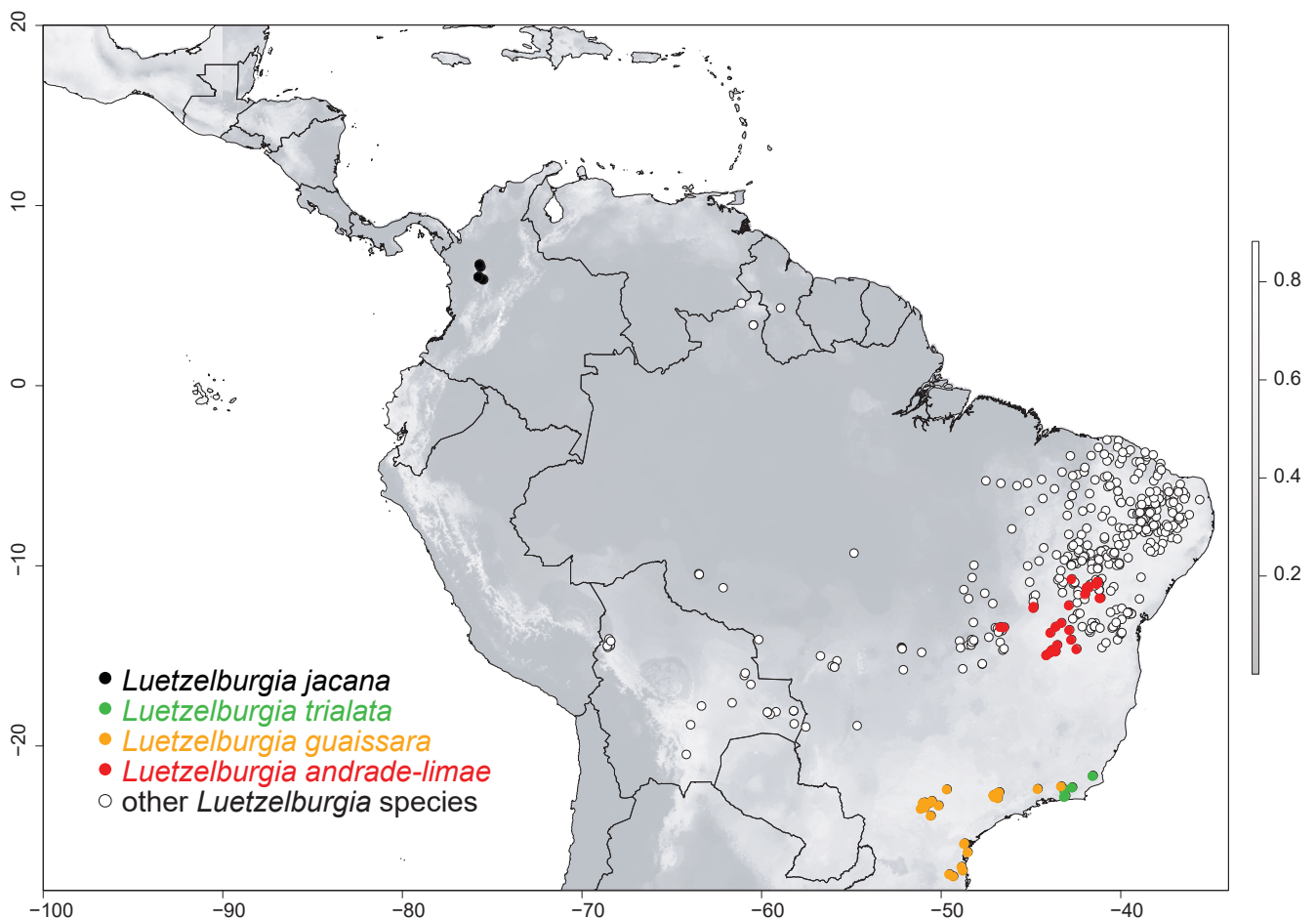
less seasonality (CV less than 50%) (Fig. 2). This finding was true for collection sites of the three earliest-branching species (Fig. 1; Electr. Suppl.: Fig. S1), *Luetzelburgia jacana*, *L. guais-sara* Toledo, and *L. trialata* for both WorldClim and CHELSA climate models. *Luetzelburgia andrade-limae* H.C.Lima, the next most early-branching *Luetzelburgia* species (Fig. 1; Electr. Suppl.: Fig. S1), occupies seasonally dry forests of the Caatinga domain in northeastern Brazil (Fig. 3) and is representative of most other *Luetzelburgia* species by inhabiting sites with an annual precipitation of generally less than 1500 mm and a precipitation seasonality or CV of greater than 50%; (Fig. 2).

## DISCUSSION

This study added considerably to resolving relationships among *Luetzelburgia* species. A previous phylogenetic analysis involving seven genes was comprehensive at sampling almost all vataireoid species and demonstrating the monophyly of the four constituent genera in the clade, *Luetzelburgia*, *Sweetia*, *Vatairea*, and *Vataireopsis* (Cardoso & al., 2013b). Species-level

relationships, however, were still poorly supported particularly at the deep nodes of the *Luetzelburgia* phylogeny. In contrast, almost all of the deep branches in the *Luetzelburgia* clade were well resolved here with the combined data that included the additional nuclear ETS and plastid *trnQ-5'rps16* genes (i.e., well supported with posterior probabilities >0.95; Fig. 1). This result confirms that adding more characters can enhance phylogenetic resolution (e.g., Wortley & al., 2005; Parks & al., 2009).

Adding more taxa, however, equally enhanced phylogenetic resolution. Of the deeply branching *Luetzelburgia* clades, we also provide strong molecular evidence for the Colombian sample of *Luetzelburgia* as a new and distinct lineage that merits ranking at the species level. The phylogenetic position of the newly added Colombian accession (*Banda 386*) as sister to all remaining *Luetzelburgia* species is suggestive of a separately evolving geographically isolated species lineage. If our samples are representative, this Colombian *Luetzelburgia* species has been geographically isolated for perhaps 4 Ma (Fig. 1). This age estimate falls within the range of ages estimated for other dry-adapted Andean legume species, 3.0–18.8 Ma, by Särkinen & al. (2011a).



**Fig. 3.** Geographical distribution of 509 collections of the genus *Luetzelburgia* with the collection sites highlighted for those of the new Colombian species *L. jacana* and the three other early branching *Luetzelburgia* species (*L. andrade-limae* is geographically representative of the other *Luetzelburgia* species). The gray shading on the map refers to the probability of the SDFW (succulent) biome (from Särkinen & al., 2011b).

The limited geographic distribution of the Colombian *Luetzelburgia* species, and indeed most *Luetzelburgia* species, to isolated small patches of SDTFW mirrors other legume clades largely endemic to this biome (e.g., Pennington & al., 2009, 2011; Duno-de-Stefano & al., 2010; Queiroz & Lavin, 2011; Särkinen & al., 2011a; Gagnon & al., 2015; Pennington & Lavin, 2016). The widely disjunct distribution of the new *Luetzelburgia* species in the dry forests of the Rio Cauca Valley represents the first record of the genus in Colombia (Fig. 3). This Colombian *Luetzelburgia* species is also ecologically distinctive. Despite its ancient evolutionary conservatism in the SDTFW biome since the Pliocene, which no doubt involves abiotic variables other than climate including substrate variables (e.g., well-drained, rocky, and fertile soils), the ecological distinction of this Colombian species involves a climatic niche marked by distinctly greater annual precipitation and less seasonality, which is otherwise shared with *L. guaissara* and *L. trialata* (Fig. 2). Of the next two earliest-branching species, *L. guaissara* occurs in semi-deciduous dry forests of the Atlantic Forest domain in southeastern Brazil, ranging from Rio de Janeiro southwards to Santa Catarina (Fig. 3). *Luetzelburgia trialata* resides in mostly wetter settings of the Atlantic Forest domain in southeastern Brazil, yet it can border SDTFW enclaves (Fig. 3). Notably, the newly discovered Colombian *Luetzelburgia* species shares with *L. guaissara*, *L. trialata*, and *L. andrade-limae* (the next earliest-branching *Luetzelburgia* species) the morphologically distinctive combination of small flowers (<12 mm long) with predominantly dark red petals. *Luetzelburgia andrade-limae*, however, is ecologically (Fig. 2) and geographically (Fig. 3) representative of the rest of the *Luetzelburgia* species. The ecologically transitional nature of *L. guaissara* and *L. trialata* and the Colombian *Luetzelburgia* species will be the subject of a companion paper (Cardoso & al., unpub. data).

The myriad of new legume species that have been recently described from SDTFW patches and enclaves (e.g., Hughes & al., 2004; Cardoso & Queiroz, 2008; Cardoso & al., 2008, 2012b, c, 2014; Queiroz & Cardoso, 2008, in press; Lewis & al., 2010; Queiroz & al., 2010; Govindarajulu & al., 2011; Queiroz & Lavin, 2011; Pennington & al., 2011; Särkinen & al., 2011a; Gagnon & al., 2015; Sotuyo & al., 2017; São-Mateus & al., 2018; Lavin & al., 2018) highlights the remarkable diversity and endemism in this largely threatened biome (Pennington & al., 2006; DRYFLOR, 2016). New insights from fossil calibrated phylogenies of SDTFW legume genera suggest that such extraordinary endemism has resulted, in part, from an ancient diversification history with limited dispersal in the SDTFW biome (Pennington & al., 2009, 2010; Oliveira-Filho & al., 2013; Pennington & Lavin, 2016). Evidence for the long-term evolutionary persistence of the SDTFW biome particularly in the Andes is derived from estimates of legume species divergence spanning 3.0–18.8 Ma (Fig. 1; Pennington & al., 2010; Särkinen & al., 2011a), well-preserved Miocene plant macrofossils that resemble extant SDTFW genera (Burnham, 1995; Burnham & Carranco, 2004), and geological and palaeoclimatic data (Hartley & al., 2005). Furthermore, palaeodistribution modelling and palynological evidence that report the stability and antiquity of the Colombian seasonally dry forests, especially

in the Rio Cauca Valley, over the last 21 kyr BP during the Last Glacial Maximum (Berrío & al., 2002; Werneck & al., 2011) could be viewed as underestimates of the potential ages of SDTFW nuclei, according to the phylogenetic evidence reported here and in the above references. The phylogenetic evidence suggests that species endemic to a SDTFW enclave or nucleus potentially can persist through millions of years of drought-prone climate regimes. Such species are not likely to be replaced through immigration of plant species not as well drought-adapted to these SDTFW settings where water availability is erratic. The often shallow crown clades of these endemics to SDTFW nuclei reveal generally low levels of genetic variation, which suggests, within a given SDTFW enclave, extinction of many within-species lineages and survival of just a few, even in well adapted endemic species.

The phenotypic, geographic, ecological, and phylogenetic distinction of the widely disjunct *Luetzelburgia* population from Colombia suggests that it represents a separately evolving lineage (De Queiroz, 2007) that warrants recognition at the species rank. This is also in line with the “phenophyletic” view of biodiversity (Freudenstein & al., 2017), where species are defined as historically connected populations with unique ecological role and phenotypic and evolutionary distinctiveness.

## ■ TAXONOMY

*Luetzelburgia jacana* D.B.O.S.Cardoso, **sp. nov.** – Holotype: COLOMBIA. Antioquia: Municipio de Sopetrán, predio corralito de la Universidad Nacional, lado izquierdo de la vía que conduce de Medellín a Santa Fé de Antioquia, Cañón del Río Cauca, 06°27'45.72"N, 75°45'56.29"W, 537 m, 8 Oct 2012 (fl), *Diego A. Zapata C. 27* (JAUM barcode JAUM0000583).

Tree 4–16 m high, trunk 9–25 cm dbh, external bark greyish, easily exfoliating in irregular, soft and flaky sheets, the superficial internal wood greenish, branchlets erect or slightly curved, arising in fascicles of 2–4 per node, glabrous to very sparsely sericeous, with dark brown trichomes, flowering and fruiting almost completely leafless. Stipules 1–2 mm long, conical, early caducous. Leaves 20–34.5 cm long, imparipinnately compound, (5)7–9-foliolate, spirally alternate at branch apex; petiole 3.3–7.2 cm long, pulvinus 3–5 mm long, glabrous; leaf rachis 4–10(20) cm long, slightly channeled above, glabrous, interfoliolar segments 1.5–6 cm long; pulvinules 2–4.6 mm long, greenish, terete, glabrous; leaflets 5.5–13 × 3.5–7 cm, the basalmost usually smaller, oval to broadly elliptic, chartaceous, opposite to subopposite, rarely alternate, apex acute to obtuse, base rounded to obtuse, symmetrical, margin entire or slightly to conspicuously denticulate, bearing a minute, globular gland-like dot on each crenation, glabrous on both surfaces, mid-vein abaxially prominent. Inflorescences terminal on shoot apices, composed of ca. 4 pyramidal panicles, the central one always larger and erect, the main axis ca. 14 cm long, each panicle formed by several densely flowered racemose shoots, these becoming progressively shorter towards the panicle apex, the panicle ending in terminal flowers; axes, pedicels, and bracts



sericeous with dense, short, appressed dark brown trichomes; pedicels 2.8–4.2 mm long; bracteoles 2, ca. 2.5 mm long, placed submedially at the pedicel, early caducous, deltoid, apex acuminate; flower buds ellipsoid. Flowers 7.8–9.6 mm long, zygomorphic, nearly papilionate; calyx 3.7–4.8 × 3.4–4.6 mm, including a short, ca. 1 mm long hypanthium, almost as wide as long, campanulate, densely dark brown sericeous externally, with short, appressed trichomes, lobes 0.7–1.1 mm long, inflexed against the petals, triangular, the two upper lobes partially united; petals dark red, crimped, auriculate at the base, dark brown sericeous submedially on outer surface; standard petal 8–8.3 × 3.5–4.2 mm, pandurate to suboblong, apex as wide as the base, median portion thick and succulent, claw 1.8–2.1 × 0.8–1.3 mm, thick; lateral (wing-like) and abaxial (keel-like) petals 7.5–8 × 3.4–3.6 mm, undifferentiated in shape but slightly differentiated in size, free, overlapping, widely obovate, apex 1.5–1.8 × wider than the base, symmetrical, apex rounded, lamellate sculpturing present externally only on the wing-like petals, long clawed, the claw 2.4–3 mm long; stamens 10, unequal, filaments 4.5–6.2 mm long, basally connate to 0.5–1 mm, glabrous, flattened towards the base, anthers 0.4–0.5 × 0.3–0.5 mm, oblong, apex rounded; gynoeceum 6.7–7.2 mm long, the ovary 3.2–3.8 × 1.2–1.4 mm long, densely dark brown sericeous, laterally compressed, subfalcate, with a crest-like vein on each side, borne on a stipe 0.5–0.7 mm long, ovule 1, style 2.4–2.8 mm long, glabrous, upwardly curved, stigma punctiform. Samaras 7.3–8.8 cm long, subfalcate, stipe ca. 4 mm long, seed chamber 2.2–2.7 × 1.3–1.6 cm, lateral wings 21–23 × 4–5 mm, apical wing 4.5–6 × 2.3–2.5 cm, oval to elliptical, apex rounded. Figure 4.

*Additional material examined.* – COLOMBIA. Antioquia: 26 km NE of Bolivar on road to Bolombolo, Rio Cauca Valley, dry forest remnants, 580 m, 16 Jan 1979 (fr), *A. Gentry & E. Renteria A. 24248* (HUA, MO); Mun. La Pintada, 700 m, Aug 2009 (st), *C. Sánchez & L.E. Vera 262* (HUA); Mun. Salgar, Margen derecha de la quebrada El Guineo, 05°54'44"N, 75°53'11"W, 622 m, 22 May 2014 (st), *A. Idárraga & al. 5675* (HUA); *ibid.*, 22 May 2014 (st), *K. Banda & al. 386* (E, HUA); Mun. Santa Fé de Antioquia, vereda el tunal, sector la mariscal 06°36'34.3"N; 75°49'46.4"W, 617 m, 22 May 2014 (st), *A. Idárraga & al. 5631* (HUA); *ibid.*, finca El Rodeo, 06°36'20.8"N, 75°49'36.7"W, 601 m, 4 Feb 2018 (fr), *A. Idárraga & al. 6602* (COL, FMB, HUA, ICESI, JAUM); *ibid.*, 5 Feb 2018 (fr), *J. Jiménez & al. 2168* (HUA, HUCO); Mun. Támesis, vereda La Mina, finca La Guamo, 05°47'42"N, 75°40'11"W, 550 m, 9 May 2009 (st), *P. Morales & al. 67* (HUA).

*Distribution and habitat.* – *Luetzelburgia jacana* has been collected only in the inter-Andean seasonally dry forests of the Rio Cauca Valley in the Department of Antioquia, Colombia (Fig. 3), between 537 and 700 m altitude where annual precipitation averages about 2000 mm and CV of monthly temperature averages about 40%. The Rio Cauca Valley dry vegetation is perhaps the most species-rich among the Colombian SDTFWs (Pizano & al., 2014), probably due in part to the large geographical area that the valley covers, which includes a mixture of environments influenced by montane and humid floristic elements (Vargas, 2012). The region floristically comprises

typical SDTFW species (Pizano & al., 2014). *Luetzelburgia jacana* grows in dry settings where the understory is less diverse, yet highly covered by terrestrial bromeliads (*Bromelia karatas* L.) and some cacti (*Opuntia* sp., *Cereus* sp.). Among the commonest associate woody species there are *Achatocarpus nigricans* Triana (Achatocarpaceae), *Bursera simaruba* Sarg. (Burseraceae), *Brosimum alicastrum* Sw. (Moraceae), *Astronium graveolens* Jacq., *Spondias mombin* L. (Anacardiaceae), *Aralia excelsa* (Griseb.) J.Wen (Araliaceae), *Casearia praecox* Griseb. (Salicaceae), *Cecropia peltata* L. (Cecropiaceae), *Platymiscium pinnatum* (Jacq.) Dugand (Leguminosae), *Zanthoxylum fagara* Sarg., *Zanthoxylum schreberi* (J.F.Gmel.) Reynel (Rutaceae), *Gyrocarpus americanus* Jacq. (Hernandiaceae).

*Conservation.* – *Luetzelburgia jacana* should be classified in IUCN's conservation status as CR (critically endangered), based on criteria B1abiii (IUCN, 2012). The few known records of *L. jacana* come from virtually the same locality. Additionally, the lower slopes of the Andes in the Rio Cauca Valley are woefully deforested. Forero-Medina & Joppa (2010) consider the “Zonobioma alternohigrico y/o subxerofítico tropical del Valle del Cauca” among the six priority vegetation types for conservation in Colombia largely because of natural land cover conversion and high numbers of threatened species. Dense population and high road densities are also concentrated in the seasonally dry forest landscape of the upper Rio Cauca Valley. Less than 10% of the natural vegetation remains, but less than 3% of this remaining area is protected by national reserves (Forero-Medina & Joppa, 2010).

*Phenology.* – Flowers of the new species have been collected in October and fruits in January and February.

*Etymology.* – The specific epithet “jacana” derives from the Colombian environmental education group Jacana Jacana (<http://jacanajacana.com>), a collaboration between the biologist Juanita Aldana and the musicians Andrés Álvarez and Janni Ben. Together with Fundación Mágica Música, they have contributed greatly to conservation education, especially for children, by highlighting the importance of preserving the spectacular Colombian tropical forests and biodiversity. This is beautifully exemplified in their musical production “Canción del bosque seco” that features seasonally dry tropical forests and the associated rich biodiversity.

*Taxonomic comments.* – *Luetzelburgia jacana* has some morphological similarities with the Caatinga-inhabiting *L. andrade-limae*, and *L. guaissara* and *L. trialata* from southeastern Brazil, all of which represent the earliest-branching clades in the *Luetzelburgia* phylogeny. They all have small flowers, up to 12 mm long, with predominantly dark red petals. However, the new species, *L. jacana* (Fig. 4; Electr. Suppl.: Fig. S1) is readily distinguished by the mostly 7–9-foliolate, glabrous leaves (vs. leaves mostly 11–19-foliolate, densely pubescent or tomentose in *L. andrade-limae* and *L. guaissara*), the leaflets with obtuse to shortly acute apex (vs. leaflets acute to strongly acuminate at the apex in *L. guaissara* and *L. trialata*), flowers up to 9.6 mm long (vs. 9–11 mm long in *L. trialata*), samaras with two small lateral wings on the seed chamber (vs. samaras with a smooth seed chamber in *L. andrade-limae* and *L. guaissara*).





**Fig. 4.** *Luetzelburgia jacana*. **A**, Leafy branch; **B**, Flowering shoot; **C**, Bracteole; **D**, Flower; **E**, Detail of the sericeous indumentum on the calyx; **F**, Detail of sericeous indumentum on the external face of the standard petal; **G**, Calyx opened out; **H**, Petals: the adaxial standard petal, lateral wing-like petals, and abaxial keel-like petals; **I**, Stamens; **J**, Gynoecium; **K**, Samara. — Drawn by Klei Sousa from *Zapata 27* (A–J) and *Gentry 24248* (K).

The recently described *L. andina* D.B.O.S. Cardoso & al. was heretofore the sole species in the genus known to occur in inter-Andean dry valleys, yet it has been collected thus far only in Bolivia (Cardoso & al., 2012c). This species and *L. jacana* are morphologically similar in having small flowers, less than 12 mm long, with predominantly dark red petals, leaves with up to nine glabrous leaflets, and samaras bearing two small lateral wings. Nevertheless, in addition to being phylogenetically unrelated (Fig. 1), *L. jacana* also differs from *L. andina* by having flowers up to 9.6 mm long (vs. 10–11 mm long in *L. andina*); the standard petal pandurate to suboblong, the apex as wide as the base (vs. standard petal oblong in *L. andina*); and the lateral (wing-like) and abaxial (keel-like) petals 3.4–3.6 mm long wide, widely obovate, the apex 1.5–1.8× wider than the base (vs. 3.5–4 mm wide, subovate, the apex narrower than the base in *L. andina*). The disparate phylogenetic positions of the Colombian *Luettelburgia* and the Bolivian *L. andina* underscore these morphological differences.

## ■ AUTHOR CONTRIBUTIONS

Research conception and design: DBOSC, DTC; field study and sampling: AI, AC, KB; acquisition of molecular data: DBOSC, DTC; acquisition of morphological data: DBOSC, DTC, AI; herbarium database for mapping and ecological analysis: DBOSC; analysis and interpretation of molecular and ecological data: DBOSC, DTC, ML; drafting of the manuscript: DBOSC, DTC, ML; final critical revisions: AI, CVDB, DBOSC, DTC, KB, LPQ, ML, RTP. —AI, alvaro.idarraga@gmail.com; AC, Alvaro.cogollo@jbotanico.org; CVDB, <https://orcid.org/0000-0001-5028-0686>, vcassio@gmail.com; DBOSC, <https://orcid.org/0000-0001-7072-2656>; DTC, daianetrabuco@yahoo.com.br; KB, kbandar@gmail.com; LPQ, <https://orcid.org/0000-0001-7436-0939>, luciano.paganucci@gmail.com; ML, mlavin@montana.edu; RTP, t.pennington@exeter.ac.uk

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#### Appendix 1. Species and DNA sequences analyzed in this study, with associated GenBank accession numbers.

Voucher details follow the format: taxon name, country, collector and collector number, herbarium code, nrETS, nrITS/5.8S, *matK*/3psbA-trnH, *trnL* intron, *rps16* intron, *trnD-T*, and *trnQ-5'rps16* GenBank accession numbers. –, missing data; \*, newly generated sequences.

**Outgroup:** *Vatairea heteroptera* (Allemão) Ducke, Brazil, D. Cardoso & E. Mitch 2205 (HUEFS), MH367100\*, JX152677, JX152603, JX187775, JX187655, JX187864, JX187935, MH367142\*; *Vatairea macrocarpa* (Benth.) Ducke, Brazil, D. Cardoso & al. 2388 (HUEFS), MH367101\*, JX152683, JX152609, JX187781, JX187661, JX187870, JX187941, MH367143\*; *Vataireopsis araroba* (Aguiar) Ducke, Brazil, D. Cardoso & al. 2175 (HUEFS), –, JX152688, JX152614, JX187786, JX187666, JX187875, JX187946, MH367140\*; *Vataireopsis speciosa* (Aguiar) Ducke, Brazil, D. Cardoso & E. Mitch 2208 (HUEFS), MH367099\*, JX152689, JX152615, JX187787, JX187667, JX187876, JX187947, MH367141\*.

**Ingroup:** *Luetzelburgia amazonica* D.B.O.S. Cardoso, L.P. Queiroz & H.C. Lima, Brazil, D. Cardoso & al. 2920 (HUEFS), MH367102\*, JX152696, JX152622, JX187794, JX187674, JX187883, JX187954, MH367144\*; Brazil, U.N. Maciel & al. 1313 (RB), MH367103\*, JX152697, JX152623, JX187795, JX187675, JX187884, JX187955, MH367145\*; *Luetzelburgia andina* D.B.O.S. Cardoso, L.P. Queiroz & H.C. Lima, Bolivia, R. Michel & E. Mayta 4548 (HUEFS), MH367105\*, JX152699, JX152625, JX187797, JX187677, JX187886, JX187957, MH367147\*; Bolivia, L. Cayola & al. 2358 (LPB), MH367104\*, JX152698, JX152624, JX187796, JX187676, JX187885, JX187956, MH367146\*; *Luetzelburgia andrade-limae* H.C. Lima, Brazil, D. Cardoso & R.M. Santos 1848 (HUEFS), MH367106\*, JX152700, JX152626, –, JX187678, JX187887, MH367204\*, MH367148\*; Brazil, D. Cardoso & al. 2518 (HUEFS), MH367107\*, MH367097\*, MH367210\*, JX187800, JX187680, JX187889, JX187960, MH367149\*; Brazil, D. Cardoso & al. 3000 (HUEFS), MH367108\*, JX152701, JX152656, MH367184\*, JX187679, JX187888, JX187959, MH367150\*; *Luetzelburgia auriculata* (Allemão) Ducke, Brazil, D.B. Chagas 109 (HUEFS), MH367115\*, MH367096\*, MH367208\*, MH367186\*, MH367194\*, MH367199\*, MH367203\*, MH367158\*; Brazil, D. Cardoso & al. 2372 (HUEFS), MH367109\*, JX152705, JX152630, JX187803, JX187683, JX187892, JX187963, MH367151\*; Brazil, D. Cardoso & al. 2385 (HUEFS), MH367110\*, JX152704,

**Appendix 1.** Continued.

JX152629, JX187802, JX187682, JX187891, JX187962, MH367152\*; Brazil, *D. Cardoso & al. 2617* (HUEFS), MH367111\*, JX152708, JX152633, JX187806, JX187686, JX187895, JX187966, MH367153\*; Brazil, *D. Cardoso & al. 2620* (HUEFS), –, JX152703, MH367209\*, JX187801, JX187681, JX187890, JX187961, MH367154\*; Brazil, *D. Cardoso & al. 2628* (HUEFS), MH367114\*, KC595436, JX152628, MH367185, MH367193, MH367198\*, MH367202\*, MH367157\*; Brazil, *D. Cardoso & al. 2667* (HUEFS), MH367112\*, JX152706, JX152631, JX187804, JX187684, JX187893, JX187964, MH367155\*; Brazil, *S.M. Faria 959* (RB), MH367113\*, JX152724, JX152647, JX187822, JX187702, JX187911, JX187982, MH367156\*; *Luettelburgia bahiensis* Yakovlev, Brazil, *D. Cardoso & al. 2690* (HUEFS), MH367116\*, JX152712, JX152635, MH367187\*, JX187690, JX187899, MH367205\*, MH367159\*; Brazil, *D. Cardoso & al. 2814* (HUEFS), MH367117\*, JX152709, JX152634, JX187807, JX187687, JX187896, JX187967, MH367160\*; Brazil, *D. Cardoso & al. 2942* (HUEFS), –, JX152710, JX152658/59, JX187808, JX187688, JX187897, JX187968, MH367161\*; Brazil, *D. Cardoso & al. 2970* (HUEFS), MH367118\*, JX152711, JX152661, MH367188\*, JX187689, JX187898, JX187969, MH367162\*; *Luettelburgia gnaissara* Toledo, Brazil, *D. Cardoso & E. Mitch 2202* (HUEFS), MH367119\*, JX152713, JX152636, JX187811, JX187691, JX187900, JX187971, MH367163\*; Brazil, *D. Cardoso & E. Mitch 2213* (HUEFS), MH367120\*, JX152714, JX152637, JX187812, JX187692, JX187901, JX187972, MH367164\*; Brazil, *R. Reitz 6384* (SI), MH367121\*, JX152715, –, JX187813, JX187693, MH367200\*, JX187973, MH367165\*; *Luettelburgia guianensis* D.B.O.S.Cardoso, L.P.Queiroz & H.C.Lima, Brazil, *D. Cardoso & al. 2853* (HUEFS), MH367122\*, JX152717, JX152640, JX187815, JX187695, JX187904, JX187975, MH367166\*; Brazil, *D. Cardoso & al. 2857* (HUEFS), MH367123\*, JX152716, JX152639, JX187814, JX187694, JX187903, JX187974, MH367167\*; *Luettelburgia harleyi* D.B.O.S.Cardoso, L.P.Queiroz & H.C.Lima, Brazil, *D. Cardoso 2076* (HUEFS), MH367124\*, JX152719, JX152642, JX187817, JX187697, JX187906, JX187977, MH367168\*; Brazil, *D. Cardoso 2186* (HUEFS), MH367125\*, JX152718, MH367211\*, JX187816, JX187696, JX187905, JX187976, MH367169\*; Brazil, *D. Cardoso & A.M. Bastos 2187* (HUEFS), MH367126\*, JX152720, JX152643, JX187818, JX187698, JX187907, JX187978, MH367170\*; Brazil, *D. Cardoso & A.M. Bastos 2190* (HUEFS), MH367127\*, JX152721, JX152644, MH367189\*, JX187699, JX187908, JX187979, MH367171\*; *Luettelburgia jacana* D.B.O.S.Cardoso, Colombia, *K. Banda 386* (E), MH367128\*, MH367098\*, MH367212\*, MH367190\*, MH367195\*, MH367201\*, MH367206\*, MH367172\*; *Luettelburgia neurocarpa* D.B.O.S.Cardoso, L.P.Queiroz & H.C.Lima, Brazil, *D. Cardoso & R.M. Santos 1853* (HUEFS), MH367129\*, JX152722, JX152645, JX187820, JX187700, JX187909, JX187980, MH367173\*; *Luettelburgia praecox* (Harms ex Kuntze) Harms, Brazil, *D. Cardoso & al. 2540* (HUEFS), MH367130\*, JX152707, JX152632, JX187805, JX187685, JX187894, JX187965, MH367174\*; Brazil, *D. Cardoso & al. 2545* (HUEFS), MH367131\*, JX152723, JX152646, JX187821, JX187701, JX187910, JX187981, MH367175\*; Brazil, *J.A. Ratter & al. 7975v* (UB), MH367132\*, JX152725, MH367213\*, JX187823, JX187703, JX187912, JX187983, MH367176\*; *Luettelburgia purpurea* D.B.O.S.Cardoso, L.P.Queiroz & H.C.Lima, Brazil, *D. Cardoso & al. 1801* (HUEFS), MH367133\*, JX152727, JX152649, –, MH367196\*, JX187914, JX187985, MH367177\*; Brazil, *D. Cardoso & al. 2103* (HUEFS), MH367134\*, JX152726, JX152648, JX187824, JX187704, JX187913, JX187984, MH367178\*; *Luettelburgia sotoi* D.B.O.S.Cardoso, L.P.Queiroz & H.C.Lima, Bolivia, *D. Soto & al. 1135* (HUEFS), MH367135\*, JX152729, JX152652, JX187827, JX187707, JX187916, JX187987, MH367179\*; Bolivia, *D. Soto & al. 1167* (HUEFS), MH367136\*, JX152730, JX152653, MH367191\*, JX187708, JX187917, JX187988, MH367180\*; Bolivia, *D. Soto & al. 1210* (HUEFS), MH367137\*, JX152728, JX152650, MH367192\*, MH367197\*, JX187915, MH367207\*, MH367181\*; *Luettelburgia trialata* (Ducke) Ducke, Brazil, *D. Cardoso & E. Mitch 2196* (HUEFS), MH367138\*, JX152731, JX152617, JX187829, JX187709, JX187918, JX187989, MH367182\*; Brazil, *M.R. Moreno 70* (RB), MH367139\*, JX152732, JX152596, JX187830, JX187710, JX187919, JX187990, MH367183\*.