Poisonia eriantha (Leguminosae) From Cuzco, Peru: An Overlooked Species Underscores a Pattern of Narrow Endemism Common to Seasonally Dry Neotropical Vegetation

R. Toby Pennington,1 Aniceto Daza,2 Carlos Reyner,3 and Matt Lavin1,4

1Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, Scotland, EH3 5LR, U. K.
2Departamento de Manejo Forestal, Facultad de Ciencias Forestales, Universidad Nacional Agraria La Molina, Apartado 456, La Molina, Lima, Peru
3Plant Sciences and Plant Pathology, Montana State University, Bozeman Montana 59717, U. S. A.
4Author for correspondence (mlavin@montana.edu)

Communicating Editor: Mark P. Simmons

Abstract—The Peruvian Poisonia eriantha is segregated from peripatric Poisonia orbicularis and reinstated as the third unifoliolate species of Poisonia and the second from the Apurimac River basin in Peru. Poisonia eriantha is distinguished phenotypically and by DNA sequence from the ITS and cpDNA trnD–T region and morphology. This overlooked species is known from the type specimen and a recent collection from north of the Apurimac River in west-central Cuzco where seasonally dry tropical forest vegetation predominates that is rich in succulent taxa (e.g. Cactaceae). Poisonia orbicularis is known from downstream along the Apurimac River and is disjunct further north along the Mantaro River, all within the same kind of seasonally dry vegetation. This seemingly small geographic distinction belies large genetic and phylogenetic differences, a finding that may be most common to species groups confined to seasonally dry Neotropical forest vegetation. The case of Poisonia eriantha exemplifies the potentially high degree of niche conservatism and dispersal limitation that seasonally dry succulent-rich woodlands can impose on its constituent lineages.

Keywords—coalescence, dispersal limitation, geographic phylogenetic structure, phylogenetic niche conservatism, seasonally dry tropical woodlands.

The genera of the papilionoid tribe Robinieae (Lavin and Sousa 1995; Lavin et al. 2003) are representative of the many legume lineages that show a strong affinity to seasonally dry Neotropical woodlands characterized by an abundance of succulent plants (seasonally dry tropical forest sensu Prado and Gibbs 1993; Pennington et al. 2000). This analysis was prompted by the general finding of geographically structured ITS and 5.8S sequence variation, including the coalescence of genetic loci sampled from geographically localized conspecific individuals. These findings have revealed undescribed or improperly circumscribed species (e.g. Duno de Stefano et al. 2010; Queiroz and Lavin 2011). Such patterns of strong geographic phylogenetic structure may well be common to species such as those of Robinieae, which show a strong affinity for seasonally dry tropical woodlands that are often rich in succulent plants (e.g. Schrire et al. 2003).

Four morphologically disparate species of the genus Coursetia DC. (Lavin 1988) were removed and placed into Poisonia Baillon because phylogenetic analysis of nuclear and cpDNA sequence resolved them as monophyletic and not necessarily most closely related to Coursetia (Lavin et al. 2003). The morphological incoherence of these four species contrasted to a strong ecological and geographic integrity in loose gravelly or sandy soils of steep hillsides and adjacent river beds in the southern Andes. Two of the Poisonia species were distinguished by a habit of trees and large shrubs, unifoliolate leaves, and a predilection to seasonally dry tropical forests. Of these two, Poisonia orbicularis was diagnosed in part by its flowers with a predominantly whitish standard petal and a geographic distribution encompassing the Apurimac and Mantaro River basins of southern Peru. The other unifoliolate species, Poisonia hypoleuca, was distinguished by its larger flowers with a lavender standard petal and a geographic distribution from northern Argentina and adjacent Bolivia in the seasonally deciduous piedmont forests (Lavin 1988; Lavin et al. 2003).

Although Poisonia eriantha had been distinguished by Hauman (1925) and Macbride (1943; as Coursetia eriantha), Lavin (1988) synonymized it with P. orbicularis in part because of the putative weak phenotypic distinction (e.g. cordate leaflets in Poisonia eriantha versus orbiculate leaves in Poisonia orbicularis). Poisonia eriantha also was known from essentially the same area of Peru and only from the type collection. Other morphological distinctions of the type collection of P. eriantha (e.g. relatively large leaflets, style with a distally confined latrorse pollen brush, and stem nodes projected and confluent with the leaf petiole) were considered aberrant (Lavin 1988). With additional collections from a newly discovered site, we show that Poisonia eriantha is geographically, phylogenetically, and phenotypically distinct from Poisonia orbicularis and represents the third species of unifoliolate Poisonia and the fifth species in the genus.

Materials and Methods

Taxon Sampling—Sampling for morphological and intraspecific geographic DNA sequence variation focused on the species of Poisonia as delineated in Lavin et al. (2003). Other Robinieae samples, including those of Coursetia reported in Lavin et al. (2003) and Duno de Stefano et al. (2010), were designated as outgroups. In addition to herbarium collections studied by Lavin (1988) and Lavin and Sousa (1995), additional specimens of Poisonia at E, FHO, and MONT were analyzed during this study. Geographic distributions of all samples were mapped using DIVA-GIS (Hijmans 2009).

DNA Sequence Data and Analysis—Total genomic DNA was sampled from leaf tissue using the Qiagen DNeasy plant mini kit (Valencia, California). The ITS region (Bailey et al. 1995) was subjected to exhaustive sampling within and among species of Poisonia because this locus shows high levels of intra and interspecific geographic variation in legumes (e.g. Lavin et al. 2003; Riley-Hulting et al. 2004) and is readily amplified from specimens stored under greatly variable conditions. Chloroplast DNA sequences from the phylogenetically informative trnD–T region (Shaw et al. 2005) were also sampled to validate findings from the analysis of the ITS region. Amplification and sequencing primers and reaction conditions for the ITS region were described in Lavin et al. (2003) and those for the trnD–T region were described in Shaw et al. (2005).

Preliminary results suggested that no paralogous ITS sequences that were not homogenized by concerted evolution were generated (e.g. Bailey et al. 2003). The entire ITS region was PCR-amplified using a low annealing temperature of 50°C and sequenced directly. Forward and reverse reads were readily assembled and the aligned ITS region revealed no divergent
5.8S sequences. This was confirmed by subjecting the ITS sequences to Bayesian MCMC phylogenetic analysis, which revealed the homogeneity of base frequencies and among-site substitution rates, which were estimated separately for the ITS1, 5.8S, and ITS2 regions. Reverse and forward reads were assembled with Sequencher 4.1 (Gene Codes, Ann Arbor, Michigan) and aligned with Clustal X version 2.0.10 using the default parameters (Larkin et al. 2007) or the similarity criterion of Simmons (2004). Parsimony and bootstrap analyses used the heuristic search strategies implemented in PAUP* 4.0b10 Swofford (2002). These strategies included SIMPLE and CLOSEST addition sequences with tree-bisection-reconnection (TBR) branch swapping, and retention of all most parsimonious trees. All characters were unweighted and unordered. Maximum trees were set to 10,000, the consensus of which captured all branches well supported (≥90%) by bootstrap analysis. Clade support was estimated with nonparametric bootstrap resampling (Felsenstein 1985) as implemented in PAUP* 4.0b10, where 10,000 bootstrap replicates were each analyzed using the heuristic search parameters mentioned above but with only one tree retained per replicate. Simple gap coding followed Simmons and Ochoterena (2000).

The ITS data set of 52 terminal taxa by 673 aligned nucleotide sites plus 24 insertion/deletion characters (indels) and the trnD–T data set of 45 terminals by 1,662 aligned sites plus 21 indels are both accessioned with TreeBASE (study number S10435). The ITS data set contained 0.7% missing entries and this largely from a single accession of Poissonia orbicularis (the 5′ and 3′ sections of these sequences have separate GenBank numbers, AF542499 and AF542500). The trnD–T data set contained about 2.9% missing entries and this mostly from leading and trailing ends. GenBank accession numbers and associated voucher details are reported in Lavin et al. (2003) and Duno de Stefano et al. (2010) for Robinieae species used as outgroups and in Representative Specimens Examined (Taxonomic Treatment) and Appendix 1 for data generated during this study. Voucher specimens are housed at E, F, FHO, HUH, K, MEXU, MICH, MO, MONT, NY, and US (acronyms follow Thiers 2009).

**Evolutionary Rates Analysis**—A Bayesian analysis (Yang and Rannala 1997) was used to generate a set of phylogenetic trees that were subjected to an evolutionary rates analysis. MrBayes 3.1 (Husonbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) was used to search tree and nucleotide substitution parameter space. Substitution parameters were estimated separately for the ITS1, 5.8S, and ITS2 regions for a large scale Robinieae ITS data set (Lavin et al. unpublished). The program run for 5,000,000 generations with nonparametric bootstrap resampling (Felsenstein 1985) as implemented in PAUP* 4.0b10, where 10,000 bootstrap replicates were each analyzed using the heuristic search parameters mentioned above but with only one tree retained per replicate. Simple gap coding followed Simmons and Ochoterena (2000). The program r8s version 1.71 (Sanderson 2004) was used to estimate nucleotide substitution rates and ages of specified clades, as described in Lavin et al. (2003, 2005). Absolute rates and ages were obtained by constraining the age of the root of the Robinieae crown clad to 31 Ma, or the minimum age estimate for a deep node within the Robinieae phylogeny (node 74 in Lavin et al. 2005). This minimum root age constraint was used because it biases all other age estimates toward younger ages. This was done to emphasize that relatively old age estimates are still obtained even after biasing in favor of younger ages (cf., Lavin et al. 2005). Age estimates were derived via penalized likelihood (PL) rate smoothing (Sanderson 2002). These were compared to the estimates derived from the rate constant (LF; Langley and Fitch 1974) and the rate variable nonparametric rate smoothing (NPRS) methods (Sanderson 1999). Only rates analyses of ITS sequences were performed. The few trnD–T sequences with relatively limited nucleotide sequence variation yielded a broad range of smoothing values and rate and age estimates with broad confidence intervals and these results are not reported.

**Discussion**

***Poisonia eriantha*** is phenotypically and phylogenetically distinct from the two other *Poisonia* species with unifoliolate leaves, *P. hypoleuca* and *P. orbicularis*. *Poisonia eriantha* thus combines features of the two *Poisonia* species with unifoliolate leaves. The details of these and unique morphological distinctions are reported in the Taxonomic Treatment (below).

**Nuclear ITS Analysis**—Parsimony analysis of the data set of 52 accessions by 673 aligned nucleotide sites plus 24 indels resolved many well supported clades that include the *Poisonia* accessions (Fig. 1). The monophyly of *Poisonia* and two primary subclades are well resolved. The species of trees and large shrubs with unifoliolate leaves from seasonally dry tropical forests (*Poisonia eriantha, P. orbicularis, and P. hypoleuca*) were resolved as sister to the herbaceous to small shrubby species with pinnate leaves from short-statured arid vegetation (*Poisonia heterantha* and *P. weberbaueri*). Although from only a single site, the five widely separated *P. eriantha* individuals were marked in part by a uniquely derived eight base pair (bp) deletion towards the 3′ end of the ITS 2 region. *Poisonia eriantha, P. orbicularis,* and *P. hypoleuca* were resolved in essentially a polytomy (Fig. 1).

**Chloroplast trnD–T Analysis**—Parsimony analysis of the cpDNA trnD–T data set of 45 accessions by 1,662 aligned nucleotide sites plus 21 indels resolved essentially the same relationships to those of the ITS analysis with respect to *Poisonia*. The monophyly of *Poisonia* and its two primary subclades were well resolved (Fig. 2). The three trnD–T accessions of *Poisonia eriantha*, albeit from a single locality, were marked by two indel characters (a six bp insert toward the 5′ end and a 17 bp insert towards the 3′ end of this cpDNA region) and weakly resolved as sister to the other two species with unifoliolate leaves.

**Evolutionary Rates Analysis**—The great antiquity of *Poisonia* in the arid regions of southern Peru, southern Bolivia, and northern Argentina is demonstrated by old age estimates for the *Poisonia* crown node (approximately 18 Ma), the *P. heterantha* and *P. weberbaueri* crown node (14 Ma), and the unifoliolate species crown (six Ma, equivalent to the stem clade of *P. eriantha*; Table 1). These age estimates contrast greatly to the relatively recent age estimates for the crown clades of individual *Poisonia* species, which are typically around one Ma or less in age (Table 1). The fastest substitution rate, approximately 3.4 × 10⁻⁹ substitution per site per year, was estimated for the *Poisonia* stem clade, whereas the slowest, approximately 1.0 × 10⁻⁹ substitution per site per year, was estimated for the herbaceous *Poisonia heterantha* crown clade. In general, the fastest substitution rates were estimated for the deepest nodes in the *Poisonia* phylogeny (Table 1).
Fig. 1. One of the most parsimonious trees derived from analysis of nuclear ribosomal ITS sequence data and showing relationships among Poissonia species. GenBank accession numbers follow the terminal taxon labels. The associated voucher information for GenBank accessions beginning with “AF” are reported in Lavin et al. (2003), for those beginning with “GQ” in Duno de Stefano et al. (2010), and those HQ are reported in the Taxonomic Treatment (see Representative Specimens Examined) and Appendix 1.
per year (Table 1), which are in the range of ITS substitution rates reported by Kay et al. (2006) for woody plant species. The slight geographic distinction of *Poissonia eriantha*, lying east of the Apurimac River and of the distribution of *Poissonia orbicularis*, belies the much larger phenotypic and phyloge-netic distinctions and divergence time estimate. *Poissonia eriantha* is ranked as a distinct species because it likely represents a separately evolving metapopulation (cf. de Queiroz 2007)

![Diagram of *Poissonia* species showing their relationships and geographic distribution.](Image)

**Fig. 2.** One of the most parsimonious trees derived from the analysis of chloroplast trnD-T sequence data and showing relationships among the species of the *Poissonia*. GenBank accession numbers follow the terminal taxon labels and associated voucher information is provided in the Taxonomic Treatment (see Representative Specimens Examined) and Appendix 1.
as evinced by the coalescence of its constituent genes and its diagnosability using qualitative or fixed character states (e.g., Nixon and Wheeler 1990).

Ecological Significance—Most species of tribe Robinieae have a predilection for arid succulent-rich woodlands, suggesting that they are phylogenetically niche conserved (sensu Harvey and Pagel 1991; Donoghue 2008). The allopatric and peripatric distributions of sister lineages within seasonally dry tropical woodlands suggests that divergence within Poissonia and many other Robinieae was determined as much by geography as by ecology.

The clade of Poissonia species with unifoliolate leaves is restricted to seasonally dry tropical forests (sensu Schrire et al. 2005; Pennington et al. 2006, 2009). The other two species in the genus, Poissonia heterantha (Monte Desert in northern Argentina and Bolivia) and P. weberbaueri (Arequipa Desert in Peru), are also known from similar seasonal arid woodland vegetation that harbors a diversity of succulent species, most notably Cactaceae and Bromeliaceae (e.g. Rundel et al. 1991). Mares et al. (1985), for example, suggests that monte vegetation is similar in physiognomy and diversity to the Sonoran Desert. Tall cacti and terrestrial bromeliads are common, as are woody plant families such as legumes. While the Sonoran Desert is likely the northern extension of seasonally dry tropical forests (e.g. Schrire et al. 2005), monte vegetation could likewise be the southern higher elevation extension.

Phylogenies of woody-plant lineages that have an ecological affinity to such seasonally dry tropical woodlands commonly show strong geographic structuring, in contrast to woody-plant lineages with affinities to tropical wet forests or savannas (e.g. Lavin 2006; Pennington et al. 2006). An explanation for this involves seasonally dry tropical vegetation being more dispersal limited than other Neotropical vegetation types. The high degree of dispersal limitation could well be a function of the patchy geographic distribution combined with the evolutionary persistence of resident communities, even when geographically localized (Pennington et al. 2006, 2009). Seasonally dry tropical plant lineages are able to withstand erratic moisture availability or long periods of drought. The lack of abundant grasses renders this forest type not prone to fire-disturbance (Schrire et al. 2005; Pennington et al. 2009). Coalescence of multiple accessions of DNA sequences of such local endemics, especially for nuclear loci, is evidence for the evolutionary persistence of geographically restricted populations (e.g., Spering et al. 2007). The recent crown age estimates contrasting to much older stem age estimates for individual species could be a signature of populations of small effective sizes that are persistent over evolutionary timescales (e.g. Barraclough 2010). Such a genetic signature, exemplified by the conspecific samples of Poissonia (Figs. 1–2), may be more common to woody lineages with affinities to seasonally dry tropical vegetation than to woody lineages showing a predilection to other Neotropical vegetation types (Pennington et al. 2009).

Suggesting seasonal dry tropical woodlands are highly dispersal limited does not imply that constituent lineages are unable to disperse but rather that immigration rates are low into localized patches of seasonally dry woodlands (cf., Hubbell 2001). For example, the dispersal potential of the inhabitants of seasonally dry woodlands is exemplified by Poissonia heterantha. The disjunct population of Poissonia heterantha in southern Peru in the Department of Moquegua (Schwarzer et al. 2010) is identical to conspecific accessions from northern Argentina with respect to ITS sequences (accession HQ283426 of Poissonia heterantha; Fig. 1). This is taken as evidence of its recent origin in southern Peru. A recent northern disjunction can be explained by the Huaynaputina eruption in 1600 AD, which denuded the vegetation in a large region in this area of Peru (Schwarzer et al. 2010). Resident plant communities adapted to the arid conditions there and that formerly limited immigration into this site were eradicated, thus opening up the opportunity for increased immigration rates.

Taxonomic Treatment

The two main lineages of Poissonia, one marked by a synapomorphy of unifoliolate leaves and the other by pinnate leaves and an herbaceous to small shrubby habit, are each geographically concentrated to the central Andes of southern Peru and northern Argentina (Fig. 3). The analysis presented here changes the circumscription of Poissonia in Lavin et al. (2003) only by taking Poissonia heterantha out of synonymy with Poissonia orbicularis. In the following key to Poissonia species, couplets 2–3 pertaining to species with unifoliolate leaves would replace couplet 11 on page 45 of Lavin (1988), where Poissonia was placed in the genus Coursetia.

### Key to the Species of Poissonia

1. Leaves unifoliolate; shrubs and treelets over 1 m tall and typically 2–3 m tall, basal trunks usually well over 2 cm in diameter .......................... 2
2. Floral pedicels 8–18 mm long, conspicuously articulated with the calyx; banner 14–20 mm long, lavender or purplish blue at anthesis; pollen brush confined to a small subapical lateral patch near the distal end of the style; legume 3–9.5 cm long, 5–10 mm wide, 3–19 seeds; leaflets (3–) 4–9 cm long, upper leaflet surfaces glabrate, greenish; branches, inflorescence rachises, and calyces glabrate to sericeous, or densely whitish lanate; inter-Andean seasonal forests of southern Peru in Cuzco (east of the Apurimac River) and northern Argentina and southern Bolivia .......................... 3
3. Petals purplish blue at anthesis; legume 5–7 cm long, 8.5–10 mm wide, with straight to sinuous margins and 3–6(–7) seeds; branches, inflorescence rachises, and calyces densely whitish lanate but this is caducous and some of these structures are then glabrate; stem nodes projected such that the stipules sit on a pseudopetiode; inter-Andean seasonal forests of southern Peru in Cuzco just to the east of the Apurimac River. 

Poissonia eriantha

Poissonia eriantha (Bentham) Hauman, Kew Bull. 1925: 279. 1925

Shrubs to small trees 1–4 m tall, trunk to 10 cm diameter at base. Bark brown, fissuring vertically. Branches densely whitish lanate beneath. Inflorescence rachises 3–6 cm long, with straight margins and 3–8 seeds; leaflets 1–3(–4) cm long, upper leaflet surfaces lanate, although this indumentum is caducous on older branches. Bark brown, fissuring vertically. Branches densely whitish lanate beneath. Inflorescence rachises 3–6 cm long, with 3–8 nodes; pedicels 9–12 mm at anthesis, articulated with the calyx; calyx tube 4–7 cm long, densely whitish lanate, teeth 4–7 mm long. Petals with a predominantly purplish blue pigment; standard petal 16–17 mm long, with a yellow-green nectar guide; ovary with less than 10 ovules, style with a distinctly laterally tufted pollen brush concentrated at the distal tip. Mature legume 50–70 mm long, 8.5–10 mm wide, with straight to slightly sinuose margins, with 3–6(–7) seeds (Figs. 4A–C).

Phenology—Flowering and fruiting specimens are known from November and January.

Distribution and Habitat—Poissonia eriantha is currently known from only one site in west central Cuzco just to the east of the Apurimac river. The locality of the type remains uncertain. The nearest populations of Poissonia orbicularis occur 30 km to the southwest along the Apurimac River. The vegetation in this entire region comprises seasonally dry tropical forest; elev. 2,250–ca. 2,700 m.

Diagnosis—Poissonia eriantha combines features of the peripatric P. orbicularis and the geographically more distant P. hypoleuca. Like P. orbicularis, P. eriantha (Figs. 4D–E) produces a whitish lanate vestiture on the inflorescence rachises and pedicels even though this vestiture may be caducous on some branches. Also like P. orbicularis, P. eriantha produces distinctly wide pods with straight to slightly sinuose margins and eight or fewer seeds. These pod margins are effectively intermediary between the straight-margined pods of Poissonia orbicularis and the sinuose-margined pods of P. hypoleuca. Like P. hypoleuca, P. eriantha produces large flowers with predominantly lavender pigments and a distinctly lateral pollen brush that is concentrated at the distal tip of the style. The orbiculate terminal leaflet of P. eriantha is mostly about 4–7 cm long and that of P. hypoleuca encompasses this range but extends up to 9.5 cm long (Fig. 4F). The orbiculate leaflet of P. orbicularis is mostly less than 4 cm long. The distinctions used by Macbride (1943), the cordate leaflet on a petiole longer than 10 mm in Poissonia eriantha contrasting to an orbiculate leaflet on a petiole shorter than 10 mm in P. orbicularis, do not consistently hold. The pseudopetiode shared by Poissonia eriantha and P. heterantha renders the stipules and pulvinus seemingly arising from above the base of the petiole. This pseudopetiode morphology is otherwise noted for the dalbergioid genera Adesmia, Arachis, and Stylosanthes, which are also generally from the southern Andean region (Lavin et al. 2001).

Representative Specimens Examined—(GenBank accession numbers are reported as: ‘ITS, trnD–T). PERU. Cuzco: Road to Mollepata ca 0.5 km from junction of main Cuzco to Abancay road, 2,250 m, -13.52, -72.51, R. T. Pennington 1801, 1802, 1803, 1804, 1805 (E, MOL), 1HQ283430, 1HQ283430, 1HQ283430, 1HQ283430, 1HQ283430, 1HQ283430, 1HQ283430, 1HQ158058, 1HQ158059, 1HQ158060.

Hauman (1925) has been vindicated in this analysis with his recognition of two unifoliolate species of Poissonia from southern Peru. Whether populations from the Mantaro River Valley, referred to as P. orbicularis var. mantaroana (Harms) Hauman, are distinct from populations from the Apurimac Valley remains to be validated by molecular phylogenetic analysis. The putative phenotypic distinction between these two valley populations pertains to leaflet vestiture and is weak at best. Poissonia orbicularis var. mantaroana remains to be further sampled and is yet known from only the type collections in spite of three separate field trips by the first two authors attempting to relocate this variety. Of note, Pennington et al. (2010) found that populations of Cytalthostegia matthewsi (Benth.) Schery (Leguminosae- Swartzieae) disjunct between the seasonally dry tropical forests of the Mantaro and Apurimac River valleys were weakly differentiated on an ITS phylogeny of 29 conspecific accessions of this monotypic genus (e.g., the Mantaro River valley samples were weakly nested within a clade of samples from the Apurimac River valley).
With *Poissonia eriantha* distinguished as a species of *Poissonia*, the nomenclature of the remaining unifoliolate species of *Poissonia* is as follows:


**Poissonia solanacea** Baillon, Adansonia 9: 296. (Apr) 1870.—TYPE: PERU, Prov. Huancavelica, Pampas, *Pearce s. n.* (holotype: K!).


Representative Specimens Examined—(GenBank accession numbers are reported as: 1 ITS, 2 *trnD–T*). PERU. Apurimac: Abancay, Km 84 E of Abancay, 2,100 m, -13.68, -72.34, *Hutchinson 1747* (F), 1 AF542499, 1 AF542500; Abancay, Quebrada Honda, 1,700 m, -13.65, -72.95, *Vargas 9808* (F), 1 AF988835; Rio Abancay, 10 km NW Puente Yurac, 2,020 m, -13.55, -72.66, *Hughes 2384* (FHO), 1 HQ283438, 1 HQ158066; km 121 road Abancay to Cuzco below Curahuasi, 2,150 m, -13.63, -72.68, *Pennington 1202* (E, MOL), 1 HQ283435, 1 HQ158063; below Curahuasi, 2,150 m, -13.63, -72.68, *Pennington 1203* (E, MOL), 1 HQ283436, 1 HQ158064; Cuzco: road Abancay to Cuzco by Puente Cunyac along bank of Rio Apurimac, 1,900 m, -13.56, -72.57, *Pennington 1157* (E, MOL), 1 HQ283437, 1 HQ158065.

![Distribution map of Poissonia species](image)

**Fig. 3.** Distribution of *Poissonia*. Representative collections of *Poissonia heterantha* are indicated by bullets (from San Juan, Argentina, north to Omate, Peru), *Poissonia weberbaueri* by black squares (in Arequipa, Peru), *Poissonia hypoleuca* by gray squares (in Salta and Jujuy, Argentina, and Santa Cruz, Bolivia), *Poissonia orbicularis* by crosses (Huancavelica, Apurimac, and Cuzco, Peru), and *Poissonia eriantha* by the closed circle (west-central Cuzco, Peru). Scale bar = 400 km, crosshairs = -30.00 latitude and -74.00 longitude.
Fig. 4. Species of *Poissonia* with unifoliolate leaves. A-C. *Poissonia eriantha* (Peru: Cuzco. Mollepata, 5 Nov 2002, Pennington 1801); A. Flower; B. Pod; C. Habitat on steep slope with cover of seasonally dry tropical forest. D-E. *Poissonia orbicularis* (Peru: Cuzco. Rio Apurimac, 1 Nov 2002, Pennington 1157); D. Flower; E. Flowering and fruiting branch. F. Flowering and fruiting branch of *Poissonia hypoleuca* (Argentina. Salta: Parque Calilegua, 1 Feb 1986, Lavin 5814). Scale bar: A = 0.5 cm, B = 1.0 cm, C = 0.5 m, D = 0.5 cm, E = 2.0 cm, F = 1.0 cm.

Representative Specimens Examined—(GenBank accession numbers are reported as: "ITS", "trnD–T"). ARGENTINA. Jujuy: Parque Nacional Calilegua, 600 m, -23.76, -64.85, Lavin 5814 (MONT: 231089); AF989834, HQ158061 (TEX); AF542485, HQ158061. S of Alemania, 1,190 m, -25.63, -65.62, Lavin 5787 (TEX); AF542485, HQ158061. S of Alemania, 1,190 m, -25.63, -65.62, Lavin 5787 (MONT: 121088); AF542486. BOLIVIA. Santa Cruz: Charagua, 800 m, -19.80, -63.20, Cárdenas 2174 (F).

Katinas et al. (2000) and Gutiérrez et al. (2002) have clarified the uncertainties pertaining to the legume type collections of Carlos Spegazzini, including LPS as the main repository.

Acknowledgements. Colin Hughes, Tiina Särkinen, and Max Weigend kindly provided seed or leaf material for certain collections of Poisonia. Alex Monro and Barbara MacKinder assisted in fieldwork. We thank two anonymous reviewers and Mark Simmons for constructive comments. We also thank the Peruvian authorities for research permission and divergence times: a penalized likelihood approach. Molecular Biology and Evolution 19: 101 – 109.


Sanderson, M. J. 2004. r8s, version 1.7 (beta), User’s manual (December 2004). Distributed by the author (http://ginger.ucdavis.edu/r8s/). Davis: University of California.


Sanderson, M. J. 2004. r8s, version 1.7 (beta), User’s manual (December 2004). Distributed by the author (http://ginger.ucdavis.edu/r8s/). Davis: University of California.


Sanderson, M. J. 2004. r8s, version 1.7 (beta), User’s manual (December 2004). Distributed by the author (http://ginger.ucdavis.edu/r8s/). Davis: University of California.


Sanderson, M. J. 2004. r8s, version 1.7 (beta), User’s manual (December 2004). Distributed by the author (http://ginger.ucdavis.edu/r8s/). Davis: University of California.
