Research Article
Phylogenetics of *Serjania* (Sapindaceae-Paullinieae), with emphasis on fruit evolution and the description of a new species from Michoacán, Mexico

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*Serjania* is among the largest Neotropical genera of Sapindaceae and comprises ~240 species. Traditionally, the genus has been defined by its schizocarpic fruits separating into three distally winged mericarps. However, recent phylogenetic studies have revealed that fruit type is not consistent within the genus and that it also includes a few species having capsular fruits that were previously placed in other genera. A phylogenetic analysis is presented based on nuclear ITS and chloroplast *trnL-F* sequences. The ingroup consisted of 48 species broadly sampled from across the geographic range and taxonomic spectrum of *Serjania* and focusing on species with atypical fruits. An ancestral character state reconstruction of fruit type was performed and demonstrated that the ancestral fruit type of the genus is strongly supported to be a schizocarp, but there are at least five independent derivations to capsular fruits and at least one transition back from capsules to schizocarps. Also, transitions from winged to wingless mericarps have occurred at least twice. Infrafamilial classification is problematic and all of the sections that were represented by more than one species come out as poly- or paraphyletic. Our limited sample of taxa precludes the possibility of a new classification at present and a broader phylogenetic sample of the genus will be needed to understand relationships and determine which lineages warrant formal recognition. In addition to the phylogenetic study, *Serjania frutescens*, a new capsular-fruited species from Michoacán, Mexico, is described, illustrated, and compared with its putative closest relatives. A key is provided to differentiate this species from other Mexican *Serjania* with capsular fruits, and new synonymies and lectotypifications associated with capsular-fruited *Serjania tortuosa* and *S. sonorensis* are established. Phylogenetic results suggest that these two are cryptic species and at least superficially indistinguishable by morphology.

**Key words:** Balsas depression, capsular fruit, cryptic species, ITS, Mexican vascular flora, molecular phylogeny, *trnL-F*

Introduction

*Serjania* Mill. is one of the largest Neotropical genera of the family Sapindaceae, and like many other taxa of angiosperms, its circumscription has changed considerably during the past decade due to a better understanding of the relationships among its species and those of closely related genera. It comprises ~240 species (Ferrucci & Steinmann, 2019) and belongs to the tribe Paullinieae, which includes climbers or climber-derived shrubs with stipulate, compound leaves and a pair of tendrils at the base of the inflorescence rachis (Acevedo-Rodríguez et al., 2017). Recently, these authors confirmed the position of *Serjania* in the tribe and placed it in the supertribe Paullinioidae. Most species of this genus are woody vines that form dense masses on their supporting vegetation, although a rare few are erect shrubs or subshrubs, which may be low climbers, such as *Serjania rosalindae* Ferrucci & V. W. Steinm., *S. bitemnata* (Weath.), *S. erecta* Radlk., *S. tortuosa* (Benth.) Ferrucci & V. W. Steinm., *Serjania sonorensis* (S. Watson) Ferrucci & V. W. Steinm., *S. dissecta* (S. Watson) Ferrucci & V. W. Steinm., and *S. cristobaliae* (Ferrucci & Urdampilleta) Ferrucci & V. W. Steinm. Vegetative, floral, and fruit diversity is shown in Figs 1–17. The two main centres of diversity are Brazil (± 120 spp.) followed by Mexico (± 60 spp.) (Acevedo-Rodríguez et al., 2017; Ferrucci & Medina Lemos, 2013; Ferrucci & Steinmann, 2016),
Fig. 1–8. Flowers, inflorescences and leaves of Serjania species. (1, 3, 6) Serjania tortuosa; (2, 5) Serjania mexicana; (4) Serjania palmeri; (7) Serjania sp.; (8) Serjania rosalindae.
and both diversity of species (Acevedo-Rodríguez, 1993) and relative abundance (Goodland, 1969) decreases from wetter to drier tropical areas. The majority of Serjania are frequent in thickets or open environments, such as rock fields and tropical scrub, but also along the margins of gallery or tropical deciduous forests. In the tribe, they share these preferences for habitats with species of Urvillea H.B.K. and Cardiospermum L., whereas most species of Paullinia L. inhabit dense humid forests, especially in the Amazon area.

Miller (1754) first proposed Serjania as independent of Paullinia, and his approach was further sustained by Schumacher (1794), who recognized fruit morphology as an essential feature. Since its conception the genus has been defined by its schizocarpic fruits (Figs 10, 12, 16, 17) separating into three distally winged mericarps. Plants with divergent fruit types were placed into other genera of Paullinieae, e.g., Cardiospermum L., Urvillea, Paullinia, Houssayanthus Hunz., Balsas J. Jiménez Ram. & K. Vega, Chimborazoa H. T. Beck, and Thinouia Triana & Planch. This circumscription was followed until

Fig. 9–17. Fruits of Serjania species. (9) Serjania guerrerensis; (10) Serjania mexicana; (11) Serjania tortuosa; (12) Serjania brachylopha; (13) Serjania incana; (14) Serjania rosalindae; (15) Serjania frutescens; (16) Serjania sp.; (17) Serjania sp.
a broad phylogenetic study of Paullinieae, including 20 species of *Serjania*, revealed that fruit type was not consistent for the identification of this genus, and the segregate genera *Houssayanthus*, *Balsas*, and *Chimboraaza* were all nested within a paraphyletic *Serjania* (Acevedo-Rodríguez et al., 2017). Two species previously placed in *Cardiospermum*, *C. urvilleoides* (Radlk.) Ferrucci and *C. integerrimum* Radlk., form a grade basal to *Serjania*. They may also belong to the genus, but were not included in our phylogenetic analysis.

So far, only one study in Paullinieae has tested the evolutionary dynamics of fruit morphology evolution in a phylogenetic context. Chery et al. (2019) presented the results of a molecular phylogeny of *Paullinia* including 11 molecular markers and 64 species. They found that the fruit type of the genus is generally a septifragal capsule, with the exception of a few species in sect. *Castanella* (Spruce ex Hook.f) Radlk. that have indehiscent fruits dispersed by water. However, the pericarp is highly variable with regard to the presence of wings and spines, and there have been repeated evolutionary transitions and reversals.

The purpose of the current study is to expand the phylogenetic sampling of *Serjania*, focusing on species with unusual fruits in order to better understand relationships within the genus and the evolution of fruit types and their morphology. Specifically, the fruit types – schizocarps and capsules – are here hypothesized to be dispersion-related adaptations. Among the morphological traits, the position of the locule (apical vs. central or basal) and the presence or absence of wings were considered. Fruit type is mapped on a molecular phylogeny to observe the patterns of fruit evolution within the genus. In addition, a new species of capsular-fruited *Serjania* from Michoacán, Mexico is described and illustrated, and taxonomic information is provided for two other species closely related to the new one.

**Materials and methods**

**Phylogenetic analysis**

**Taxon sampling and outgroup selection.** We sampled a broad representation of *Serjania* from across its distributional range and taxonomic spectrum. All species with capsular fruits were included, as too were the species initially placed in segregate genera now considered within *Serjania* by Acevedo-Rodríguez et al. (2017). The outgroup was composed of 11 species from closely related genera of tribe Paullinieae: *Cardiospermum* (3 spp.), *Lophostigma* Radlk. (1 sp.), *Paullinia* (4 spp.), *Thinouia* Tr. & Planch. (1 sp.), and *Urvillea* (2 spp.). The ingroup consisted of 29 previously sampled species (from Acevedo-Rodríguez et al., 2017 and Chery et al., 2019) and 19 newly sequenced species. All but one accession were determined to species. In total, the ingroup contained 48 species, and 13 of these were represented by multiple accessions for a total of 69 OTUs or 80 when also considering the outgroup. We included all of the 12 sections recognized by Radlk. (1931–1934), and most of these were represented by more than one taxon. Sectional names are found in Fig. 18, as too are the names of the genera for species previously recognized outside *Serjania*. Material of the newly sequenced species came from either field-collected material or specimens housed in the herbaria ARIZ, IEB, MEXU, and RSA. All newly sequenced representatives included in the phylogenetic reconstruction are associated with an herbarium voucher number and a GenBank code, and information from the previously sequenced representatives is also included (see Appendix 1).

**DNA extraction, amplification and sequencing.** For the newly included species, total genomic DNA was extracted following the protocols of Doyle and Doyle (1987) and Cullings (1992) for DNA isolation from dried leaves or herbarium specimens. Two regions were selected for this study: ITS for nuclear and the *trnL* intron for chloroplast. Both of these are non-coding regions and were chosen because they have been used successfully in previous studies of Sapindaceae (e.g., Acevedo-Rodríguez et al., 2017). Genomic DNA was diluted to a concentration of 5–10 ng per µl in order to reduce inhibition of enzymes during the polymerase chain reactions (PCR), but some samples that did not amplify at these concentrations were successfully amplified at considerably higher concentrations using stock DNA.

Molecular work was conducted at the laboratory of California Botanic Garden in Claremont, CA, USA. PCR reactions were carried out using GoTaq Flexi DNA Polymerase (Promega, Madison, WI, USA) in a T100 Thermal Cycler (Bio-Rad, Hercules, CA, USA). A negative control was used in each reaction run, replacing DNA with nuclease-free water to test for contamination. The PCR mixture included 16.38 µl of nuclease-free water, 2.5 µl of 5× colourless GoTaq flexi buffer, 1.25 µl of dNTP (250 µM), 1.25 µl of MgCl₂ (25 mM), 0.125 µl of 5 µl Taq polymerase, 1.25 µl of each primer (10 µmol/l) and 1 µl of template DNA.

The ITS region was amplified using the primers ITS4 and ITS5 from White et al. (1990), and the *trnL* intron was amplified with the primers C and F from Taberlet et al. (1991); for those samples with degraded DNA, we used internal primers E and D from Taberlet et al.
Fig. 18. Cladogram of *Serjania* obtained from the concatenated ITS and trnL intron analysis. Numbers above the branches are SH-aLRT values and below the branches are UFBoot values. CA, Central America; MX, Mexico; SA, South America; US, United States; A, Antilles (see Materials and Methods); †, wingless mericarps.
 Phylogenetic and character state reconstruction. Both the ITS region and the trnL intron were concatenated using SequenceMatrix v.1.8 (Vaidya et al., 2011), and they were aligned with MUSCLE v.3.8.31 (Edgar, 2004) using default parameters and subsequently manually adjusted in PhyDE v.0.9971 (Müller et al., 2006). Maximum likelihood phylogenetic analysis was conducted using IQ-TREE multicore v.2.0.3 (Minh et al., 2020). The best evolutionary model was determined using the ModelFinder (Kalyaanamoorthy et al., 2017) built-in option in IQ-TREE. TIMe + R3 was the best-fit model according to Bayesian Information Criterion. Support was determined by the Shimodaira–Hasegawa approximate likelihood ratio test (SH–aLRT) with 1000 replicates (Guindon et al., 2010) and ultrafast bootstrap (UFBoot) (Minh et al., 2013). The Bayesian analyses were conducted under the GTR model using MrBayes v.3.2.6 (Ronquist et al., 2012) in CIPRES (Miller et al., 2010) with two simultaneous runs, each with four Markov chains (three cold and one heated) for 5,000,000 generations. Trees were sampled every 1000 generations, and for the summarization, the first 25% of generated trees were discarded, followed by reconstruction of the majority consensus tree. A simple ancestral character state reconstruction of fruit type (capsule vs. schizocarp) was performed with Mesquite v.3.61 (Maddison & Maddison, 2019) using likelihood as the estimation method under the Mk1 model, assuming an equal probability of character states at the root node. Fruit type was determined by examining the voucher specimens or for instances in which the specimen lacked fruit, by reviewing other material of the species or pertinent literature. Ancestral states were mapped in the main phylogeny tree.

Biogeography

To understand biogeographic patterns, the 48 species included here are broadly classified by distribution, and this feature is mapped on the phylogeny. The following categories are used: South America (SA), Mexico (MX), Central America (CA), United States (US), and the Antilles (A).

Taxonomic treatment

A detailed review of the published literature of Serjania was conducted, including the consultation of the protologues of all capsular-fruit species as well as the only monograph of the genus (Radlkofer, 1931–1934). Herbarium material from A, BCMEX, BM, CTES, F, G, GH, K, M, MEXU, MO, NY, QMEX, UC, US, and WU was examined. Additional high-resolution images of type specimens on JSTOR Global Plants (2020) were viewed for material at C, M, and NDG. The acronyms of the cited herbaria follow Index Herbariorum (Thiers, 2020). For species delimitation, we adopt the Unified Species Concept of De Queiroz (2005), which defines species as separately evolving metapopulations of lineages. Leaf samples were fixed in FAA (formalin/70%/alcohol/acetic acid), immersed in CO2 for critical-point drying, and sputter coated with gold-palladium for scanning electron microscope (SEM) studies. Pollen grains were obtained from anthers of one collection. Samples for light microscopy (LM) were acetylated according to the procedure of Erdtman (1966) and mounted in glycerin jelly, a mixture of gelatin and glycerine (Johansen, 1940). Permanent slides were deposited at the Palynological Laboratory of the National University of the Northeast, Corrientes, Argentina (PAL-CTES). Polar axis and equatorial diameter were measured on 20 grains using a Leica DM LB2 microscope. The terminology used to describe the grains follows Erdtman (1966) and Punt et al. (2007). Scanning electron images (SEM) were taken from leaves and acetylated pollen grains. The equipment used was a JEOL 5800 LV operating at 20 KV. The conservation status assessment of Serjania frutescens was based on IUCN Standards and Petitions Subcommittee (2017) Red List criteria recommendations. Extent of occurrence (EOO) and area of occupancy (AOO) were estimated utilizing GeoCAT (Bachman et al., 2011), for the latter utilizing grid cells of 4 km², as recommended by the IUCN Standards and Petitions Subcommittee (2017), since it relates to thresholds of criterion B.

Results

Phylogenetic analysis

DNA sequencing. The entire ITS region was obtained and analysed for all species and all accessions, whereas the trnL intron was analysed for all but six species and eight
accessions (see Appendix 1). The ITS sequences ranged from 577 to 652 bp. The aligned matrix was 761 bp, with 241 (31.7\%) parsimoniously informative sites. Approximately 40\% of the trnL intron sequences were partial. They varied from 537 to 990 bp, with the shorter length representing a partial sequence. The aligned matrix was 1098 bp, with 46 (4.2\%) parsimoniously informative sites. The alignment and resulting trees are archived on Zenodo (https://doi.org/10.5281/zenodo.5593388).

Phylogenetic and character state reconstruction. The Maximum likelihood tree (Fig. 18) is well resolved and moderately well supported with many nodes having greater than 90\% SH-aLRT and UFBoot values. Results from the Bayesian analysis are shown in Supplemental Fig. S1, and the 50\% majority-rule consensus tree is similarly well resolved with many supported nodes. Cardiospermum urvilleoides is sister to Serjania, but not closely related to the other species of Cardiospermum included here. The reconstruction retrieves Serjania as monophyletic, but only with the inclusion of the taxa mentioned below that were transferred by Acevedo-Rodríguez et al. (2017). We designate nine well-supported clades (SH-aLRT = 85–100, six of them also well-supported by UFBoot = 90–100, see Fig. 18), that correspond to the primary lineages recovered in the analysis. Clade 1 contains S. amelopsis, S. cardiophyllum, and S. communis (SH-aLRT = 98, UFBoot = 90) and is sister to the remainder of the genus (SH-aLRT = 84, UFBoot = 65). All of these species were previously placed in sect. Platycoccus, but the section is here supported to be polyphyletic with S. cuspidata of Clade 2 being more closely related to S. caracasana (sect. Eucoccus) than to the other members of sect. Platycoccus. In fact, all of the sections that were represented by more than one species come out as poly- or paraphyletic. As proposed by Acevedo-Rodríguez et al. (2017), the segregate genera Balsas, Houssayanthus, and Chimboraaza are nested within Serjania, as too are the following previously unsampled species that had been placed in Cardiospermum or Paullinia but recently transferred to Serjania based on morphology: Serjania sonorensis (Paullinia), S. cristobalvae (Cardiospermum), S. dissecta (Cardiospermum), and S. tortuosa (Cardiospermum).

Biogeography
Concerning distribution, the earliest two diverging clades (1 and 2) contain species that occur mostly in South America as well as Central America and Mexico. The next clade (3) has only South American species. Of the remaining lineages, some are composed entirely of Mexican and Central American species (clade 7), others entirely of South American species (clades 6 and 8), but most have Mexican, Central American, and South American species (clades 4, 5, and 9).

The ancestral fruit type of the genus is strongly supported to be a schizocarp (Figs 10, 12, 16, 17). However, there are at least five reversals to capsular fruits, one represented by the South American S. cristobalvae, and the other occurring in Mexican lineages: (1) S. biternata/S. rosalindae (Fig. 14), (2) S. tortuosa (Fig. 11), (3) S. dissecta, and (4) the grade including S. guerrerensis (Fig. 9), S. frutescens (Fig. 15), S. crucensis, and S. sonorensis. It is further suggested that there is at least one transition from capsules to schizocarps within Serjania, this occurring in clade 9, with the schizocarpic S. schiedeana being nested within a clade that contains capsular-fruited species.

Discussion
Phylogenetic analysis
There is considerably less variation in the trnL-F region (4.2\%) than in the ITS region (31.7\%). When analysed separately, trnL-F provides little resolution, thus our decision to present only the results from a combined analysis. Twelve species are represented by more than one accession. In all instances, the species form a single monophyletic lineage with the exception of S. paucidenata being nested within S. pyramidalata (clade 5).

One unsuspected and enigmatic result is the distant relationship between Serjania tortuosa and S. sonorensis. Both of these species occur in arid north-western Mexico, with the former endemic to Baja California and the latter restricted to the states of Sonora and Sinaloa. Although they were traditionally placed in separate genera (Cardiospermum and Paullinia, respectively), they are remarkably similar in morphology. In fact, we are unable to ascertain characters that consistently differentiate the two. However, mainland plants and peninsular plants, both represented by more than one accession, belong to distinct lineages with vastly different evolutionary histories. They are not even closely related with S. tortuosa forming part of clade 7 (SH-aLRT = 99, UFBoot = 92) and S. sonorensis being a member of clade 9 (SH-aLRT = 96, UFBoot = 99). More study of the two would be beneficial to determine any potential differences that would support their placement in different clades of Serjania, and S. tortuosa in itself would benefit from research on its variability to determine if one or more species might be involved.

Fruit evolution. No other character has played a more important role in the classification of the tribe
Paullineae than fruit type. Since its conception, *Serjania* has been defined by the possession of schizocarps that separate into three winged mericarps. This is certainly an adaptation to wind dispersal, but Acevedo-Rodríguez (1993) mentions that the mericarps also can be secondarily dispersed by water.

The ancestral fruit of *Serjania* is strongly supported to be a schizocarp, and the lineages just outside the genus possess capsules. Within the tribe *Paullineae* schizocarps are otherwise only found in the distantly related *Lophostigma* and *Thinouia*, which have a basal position in the tribe, showing that this trait is homoplasious in *Paullineae*. More than 95% of the species of *Serjania* possess schizocarps, but there are at least five reversals to capsules: (1) *S. cristobalai* of clade 3; (2) *S. biternata* and *S. rosalindae* of clade 4; (3) *S. tortuosa* of clade 7; (4) *S. dissecta* of clade 7; and (5) the grade including *S. sonorensis*, *S. frutescens*, *S. crucensis*, and *S. guerrerensis* of clade 9. Interestingly, there is also evidence of one transition back to a schizocarp from a capsular fruit, this supported by the schizocarpic *S. schiedeana* being nested within a clade that contains capsular-fruited species.

Although there have been many independent derivations of capsular fruit from the typical fruit of *Serjania*, in all instances, there has been no subsequent radiation of species. Four times there is but a single species resulting from the reversal. The most diverse group of capsular *Serjania* is represented by the grade of *S. sonorensis*, *S. frutescens*, *S. crucensis*, and *S. guerrerensis* in clade 9. Still though, there are only four species involved. The lack of subsequent diversification despite various derivation capsular fruits suggests that transitions are all either very recent and/or that this change results in an evolutionary dead end due to the loss of the highly adaptive wind dispersal mechanism.

The capsules of some *Serjania* are winged, e.g., the longitudinal locular wings of *S. rosalindae* (Fig. 14) or the atale stipe of *S. frutescens* (Fig. 15). In *S. tortuosa*, there is a reduction to exhibiting wingless capsules, or exceptionally only a carina or rarely a reduced wing is observed in the proximal half, at the dorsal vein level of each carpel (Fig. 11). However, in all these species the wings are insignificant and unlikely to aid in dispersal. In fact, the capsular fruited species appear to be atelechorous, and further research is needed to understand their mechanisms of dispersal. Atelechory is generally associated with arid regions and deserts in particular (Fillner & Shmida, 1981), and traits constraining seed dispersal are common in arid and semiarid floras (Van Rheede van Oudtshoorn & van Rooyen, 1999). The occurrence of capsular fruits having especially large seeds has been documented in some species of *Serjania* (e.g., Ferrucci & Steinmann, 2019; Ferrucci & Urdampilleta, 2011), and there appears to be a correlation between these two traits. However, a statistical analysis of more species will be necessary for confirmation. The larger size of the seed would be a mechanism to avoid being transported over long distances but also give rise to larger seedlings and these better withstand environmental hazards like deep shade and drought (Bruun & Ten Brink, 2008). This character is observed not only in species of *Serjania* native to arid lands, but also in some occupying the interior of deciduous tropical forests, e.g., *S. biternata*.

The only two species that are found in true deserts both possess capsular fruits, *S. tortuosa* of the Sonoran Desert and *S. dissecta* of the Chihuahuan Desert. As mentioned above, these taxa represent independent transitions from the typical schizocarpic fruit. The capsular fruited *Serjania frutescens* and *S. crucensis* occur in the Infiermillo region of Michoacán, Mexico, which is the most arid portion of the Balsas Depression. Similarly, *S. cristobalai* is restricted to rocky outcrops in a semiarid portion of Minas Gerais, Brazil.

There are some other interesting fruit trends in *Serjania*. Independent transitions from winged to wingless mericarps have occurred at least twice, once in *S. lachnocrapa* (clade 6) and again in *Serjania rzedowskiana* (clade 9). This feature was used to justify the segregate genus *Chimborazoa* to accommodate the latter species. However, Acevedo-Rodríguez (1998) relegated *Chimborazoa* to synonymy under *Serjania* based on fruit morphology, and his decision was supported by Acevedo-Rodríguez et al. (2017) and is further reinforced here. The other species possessing short winged or wingless mericarps at maturity are *S. cissoides* Radlk., *S. herteri* Ferrucci, and *S. macrocoeca* Radlk. However, none of these were assessed in our study. The mericarps of *Serjania incana* Radlk. are noteworthy in having a central locus and a circumferential wing that extends longitudinally (Fig. 13). That trait was used to define the segregate genus *Houssyanthus*, but molecular evidence supports that *Houssyanthus* is nested within *Serjania*, and the change represents a relatively minor modification from the typical fruits of *Serjania* with their distal locus and proximal wings.

**Biogeography**

Our sample represents fairly well the geographic distribution of *Serjania*, which ranges from Texas in the USA to northern Argentina and the Caribbean. Twenty species included here are restricted to South America, and 14 are endemic to Mexico. Of the remainder, five are shared between Mexico and Central America, one
occurs in Texas and northern Mexico, one is endemic to Central America, and an additional seven range from South America to Central America, Mexico and/or the Antilles. No endemic Antillean species were included in our analysis. Acevedo-Rodriguez (1993) suggests a South American origin of *Serjania*, and our results support his proposal in that the earliest diverging lineages are primarily South American. Clades 1, 2, 4, 5, and 9 contain species from both South America and Mexico. Clades 3, 6, and 8 are strictly South American, whereas only clade 7 is comprised of entirely Mexican and Central American species. In the clades with species from Mexico/Central America and South America, complex patterns of distribution occur. For example, all the species of clades 2 and 5 occur in South America, but there is at least one widespread member that extends as far north as Mexico. Within clade 9, the lineage containing the South American species *S. inflata*, *S. deltoidea*, and *S. rhombea* is nested in a group of Mexican and Central American species. Of the four species in clade 4, *S. marginata* is restricted to Brazil, Bolivia, and Argentina, *S. mexicana* is widespread from Brazil to Mexico and the Antilles, and *S. rosalindae* is widespread from northern South America to Mexico and the Antilles, and *S. biter-nata* and *S. rosalindae* are narrow endemic species known from small areas in the Balsas Depression of central Mexico. As more species are included in the phylogeny, more complex patterns will certainly emerge and a more complete picture of the biogeography of *Serjania* will be revealed. For now, we explain the existence of widely distributed clades by the fact that the fruits of most *Serjania* are wind dispersed and presumably able to travel long distances.

Infrageneric classification

Our study further supports the conclusion of Acevedo-Rodriguez et al. (2017) that *Serjania*, as traditionally defined by schizocarpic fruits with winged mericarps, is highly paraphyletic. Monophyly is achieved only after the inclusion of some capsular fruited species that were previously placed in closely related genera (*Cardiospermum crisblalae*, *C. dissectum*, *C. tortuosum*, and *Paulinia sonorensis*), as well the synonymization of *Houssayanthus* and *Balsas*. As a result, *Serjania* loses much of its taxonomic predictability and becomes more difficult to define.

The last complete treatment of *Serjania* is Radlkofer's (1931–1934) monograph for *Engler's Das Pflazenreich*, in which he recognized 12 sections and 208 species. Since then, numerous additional species have been proposed, and the most significant post-Radlkofer treatment is Acevedo-Rodríguez's 1993 revision of *Serjania* sect. *Platyoccus*. In addition to his account of the section, Acevedo-Rodríguez provides a detailed synopsis of the genus and proposes substantial modifications to Radlkofer's infrageneric classification, which he describes as 'untenable' and 'difficult to use'. Acevedo-Rodriguez, in contrast to Radlkofer, recognizes only six sections, describing a new one (sect. *Confertiflora*), correctly applying the name sect. *Serjania* (= sect. *Dictyococcus* sensu Radlkofer), and reducing seven of Radlkofer's sections to synonymy under sect. *Serjania* (sects. *Eucoccus*, *Pachyecoccus*, *Holcococcus*, *Simococcus*, *Oococcus*, *Phacococcus*, and *Syncoccus*). Both Radlkofer and Acevedo-Rodriguez emphasized fruit characters as defining features of their sections. Furthermore, Radlkofer used numbers of sepals, cambial variants, and presence of mucilaginous idioblasts in the epidermis of the leaflets, whereas Acevedo-Rodríguez placed importance on seed shape.

Coulier et al. (2012) applied a cytogenetic approach to evaluate infrageneric classification of *Serjania*. The authors also considered some important reproductive and vegetative morphological traits. Their results did not support either of the two classifications and demonstrated a lack of diagnostic characters specific to each section in Radlkofer's proposal and, on the other hand, the reduced number of traits under consideration, only carpological, in Acevedo-Rodriguez's classification.

Our sample contains ~20% of the genus, and all of the 12 sections proposed by Radlkofer (1931–1934) are represented. However, we were unable to include Acevedo-Rodriguez's monotypic sect. *Confertiflora*. Our results clearly demonstrate that most of the previously defined supraspecific taxa recognized by Radlkofer (1931–1934) or Acevedo-Rodriguez (1993) are not monophyletic. In fact, the classification of *Serjania* can be summarized in two words … *a mess!* For example, three members of sect. *Platyoccus* (*S. communis*, *S. cardiospermoideis*, and *S. ampeolopsis*) form the earliest diverging lineage within the genus, clade 1 (SH-aLRT = 98, UFBoot = 91). However, a fourth species assigned to the section is strongly supported (SH-aLRT = 100, UFBoot = 95) to belong in clade 2 with *S. caracasana* of sect. *Eucoccus* (following Radlkofer) or sect. *Serjania* (following Acevedo-Rodriguez). To further complicate matters, an additional species assigned to sect. *Eucoccus* by Radlkofer, *S. pyramidata*, is not closely related to *S. caracasana* but instead forms part of clade 5. Other examples of polyphyletic assemblages of Radlkofer's sections that were later reduced to synonmys of sect. *Serjania* by Acevedo-Rodriguez (1993) include sects. *Oococcus* (clades 5, 6 and 8), *Syncoccus* (clades 5 and 9), *Pachyecoccus* (clades 4), and *Holcococcus* (clade 5). Section *Eucoccus* is among the sections circumscribed similarly by both Radlkofer and
Acevedo-Rodríguez. However, our results show that it is monophyletic only after the inclusion of *S. cristobalii*, which was initially described as a species of *Cardiospermum*. *Physococcus* is another section recognized by both Radlkofier and Acevedo-Rodríguez that is clearly polyphyletic with its species coming out in three independent portions of clades 7 and 9. With regard to Acevedo-Rodríguez’s expanded sect. *Serjania*, it too is highly paraphyletic, not only as a result of containing many species previously placed in other genera, but also because members of sects *Ceratococcus* and *Physococcus* are nested within it.

Fruit characteristics have been of monumental importance in the classification of the tribe Paulinieae, but in the case of *Serjania*, they are not good indicators of relationship, and previous attempts to construct a natural infrageneric classification based on them have been unsuccessful. The recent inclusion of a small group of *Serjania* with capsular fruits makes the infra-generic classification even more difficult, and our limited sample of taxa precludes the possibility of a new system at present. A considerably broader phylogenetic sample of the genus will be needed to understand relationships and determine which lineages warrant formal recognition. Also, much more research is needed on the individual species to determine morphological, anatomical, cytological, and/or palynological features that could define future infrageneric taxa because little is gained by simply recognizing infrageneric taxa that are not predictable and supported by other evidence.

**Taxonomic treatment**

**Serjania frutescens** V.W. Steinm. & Ferrucci, sp. nov.

_Type._ MEXICO. Michoacán. Mpio. La Huacana, sobre MEX 37 (libre), 5.2 km al sureste de Cupuancillo, arriba de la carretera, cara suroeste de la Mesa La Lima, approx. 18°48′00″ N, 102°05′00″ W, 350 m, arbusto de 1.5 m de alto, flores blancas y frutos verdes, bosque tropical caducifolio, 16 Aug 2007 (fl, fr. immat.), Y. Ramírez-Amezúa & V. W. Steinmann 1075 (holotype, QMEX!; isotype, CTES!).

**Diagnosis.** Species morphologically similar to the polymorphic *Serjania tortuosa* and *S. sonorensis* but distinguished by a completely shrubby habit; 3-foliolate leaves, subchartaceous, laticifers absent from lower epidermis; tendrils absent; the two posterior nectary lobes ovoid, obtuse at the apex and the anterior ones circular in outline; pistillode and gynoecium glabrous; and capsule globose stipitate, stipe narrowly winged, ± 7 mm long, glabrous.

**Description.** Duodichogamous, drought-deciduous shrubs 1–3 m tall, erect, glabrous; tendrils absent. Young branched axes covered with short, curved and whitish hairs, and few reddish glandular ones on the leaf axis and blade base; young leaflets densely glandular on both faces. Flowering branchlets slightly genculate, greenish brown, adult stems grey to dark brown, tiny rust-coloured lenticels; stem cross section with a single vascular cylinder, pith solid. Sepals triangular, caducous, 0.25–1 × 0.2–0.5 mm, glabrous or pubescent, simple and glandular hairs on margins. Leaves 3-foliolate; petiole semiterete, bicanaliculate along adaxial surface, 8.5–30 mm long, pubescent on the midrib; petiolules 6–14 mm long on the distal leaflet, pubescent along the midrib, 0.5–1.5 mm long on lateral ones, narrowly margined; leaflets subchartaceous, concolorous, green opaque, glabrous, ovate, 2–3.5 × 1.2–2.8 cm, lateral leaflets asymmetric with a narrower acroscopic side; apex obtuse or rounded, glandular; truncated or truncated-rounded base; margins with reddish cartilaginous line, with 4–6 obtuse glandular teeth; venation mixed craspedodromous; hypophyllastic, upper surface glabrous, midrib and basal lateral veins slightly marked, pubescent, with short, curved or curly hairs; lower surface with venation slightly marked, primary vein somewhat prominent on lower surface, domatia in tuft of hairs in basal veins axils. Thryse axillary, simple, axis puberulent to glabrous, primary peduncle quadrangular, 1.5–5 mm long, rachis very short, up to 2 mm long; cincinni 1 to 4, 2–5-flowered, on a peduncle 1–2 mm long; floral pedicel 1.5–2.5 mm long, fruiting pedicel 4 mm long, articulated slightly above the base or up to the middle, glabrous; bracts ovate-triangular, persistent, ~0.5–1 mm long, simple and glandular short hairs on the margin, bracteoles similar but smaller, 0.5 mm long. Flowers whitish, 5 mm long; sepals 5, free, the outer two cucullate, oblong, 2–2.5 × 1–1.8 mm, glabrous, the inner obovate, 3–4 × 1.2–2.5 mm, tomentose, all ciliate; petals 4, obovate, clawed, 3.25–4 × 1.9–2.3 mm, margin erose, densely glandular on both faces, appendages of posterior petals with bipartite crest, villous; nectary lobes 4, glabrous, the posterior ovoid, apex obtuse, ~1 mm high, the anterior 2 circular in outline, smaller than the posterior ones; androgynophore glabrous. Stamens connivent at the base; staminate flowers with stamens 2.5–5 mm long; the filaments sparsely pilose in the basal half; pistillode 0.8 mm long, glabrous. Pistillate flowers with staminodia 1.85–2.5 mm long, filaments puberulent at base, anthers indehiscent; gynoecium 3.85 mm long, the ovary trigonous obovate, glabrous, the style curved or straight, 1–2 mm long, longer than stigma branches, glabrous. Capsule globose stipitate, hard when dry, pendulous,
septifragal, green tinged with red to light brown, dehiscing from the top, 19–20 × 14.5 mm, including the stipe, apex rounded, semiferous distal portion globose, stipe narrowly winged, ± 7 × 3.7 mm; epicarp glabrous, venation not visible, endocarp pubescent, short and curly hairs, the seed fills the locule, double subchartaceous sepal walls glabrous. Seeds brown, hemispherical, flat side facing the septum, 9.4–10.5 mm in diameter, dry aril crescent shaped, ~4 × 2 m; attached at the base of locule. Embryo with abaxial cotyledon curved and adaxial cotyledon bipplicate. Pollen grains heteropolar, hemisyncolporate, oblate, rarely peroblate, polar axis 21.25 (30.81) 37.5 μm, equatorial diameter 50 (51) 62.5 μm; sexine perforate-rugulate in the distal polar side to perforate-microreticulate in the proximal polar side. (Figs 19–40.)

**Distribution, ecology and phenology.** Endemic to the state of Michoacán (Fig. 41), where it is known from the municipalities of Múgica and La Huacana. It occurs on hillsides in thornscrub and tropical deciduous forest; 300–500 m. Flowering is in July and August, with fruiting in August and September.

**Etymology.** The specific epithet refers to the shrubby habit.

**IUCN conservation status.** *Serjania frutescens* is known from six collections, representing four locations. Although two of these are inside the Zicuirán-Infiernillo Biosphere Reserve, there are still threats of deforestation and extensive cattle raising. The northern-most population along the Río Marqués was lost in 2011 when the area was flooded after the construction of a dam. The initial extent of occurrence (EOO) was calculated to be ~186.6 km², but is now less with the loss of the northern-most population. The area of occupancy (AOO) is estimated at 16 km². Therefore, following the IUCN criteria (IUCN Standards & Petitions Subcommittee, 2017), and if a formal analysis were performed this species would probably be considered as endangered B1ab(ii,iii,iv)+2ab(ii,iii,iv).

**Paratypes.** MEXICO. Michoacán: Mpio. de Múgica, Río Marqués, 5.8 km al nor-noreste de la salida a Nueva Italia sobre la Autopista Morelia-Lázaro Cárdenas y unos 350 m al este de la carretera, 19°01′59″N, 102°02′55″W, 300 m, 11 Jul 2009 (fl), Y. Ramírez-Amezcua & V. W. Steinmann 1731 (CTES, QMEX); Mpio. La Huacana, sobre MEX 37 (libre), 5.2 km SE de Cupuancillo, ladera arriba de la carretera, cara SW de la Mesa La Lima, 18°48′07″N, 102°05′08″W, 300 m, 11 Oct 2012 (sterile), M. S. Ferrucci et al. 3118 (CTES);

~1.5 km (by air) east-northeast of Los Ranchos, southwestern side of Cerro El Barril, 18°42′30″N, 102°00′10″W, 500 m, uncommon on hillside in thorn forest, 30 Aug 2003 (fr immat.), V. W. Steinmann 3447 (CTES, QMEX); ~3.5 km south-west of Los Ranchos, along the trail to Cañada Las Cruces, 18°41′20″N, 102°03′W, 350 m, common on a gently sloping and relatively open hillside in thorn forest, 12 Jul 2003 (fl), V. W. Steinmann 3381 (CTES, QMEX); sobre MEX 37 (libre), 5.2 km al sureste de Cupuancillo, ladera arriba de la carretera, cara suroeste de la Mesa La Lima, La Lima, 18°48′07″N, 102°05′08.1″W, 300 m, 4 Sep 2011 (fr. immat.), V. W. Steinmann & Y. Ramírez-Amezcua 7348 (CTES, QMEX).

**Notes.** The leaves of *S. frutescens* are characterized by the presence of stomata on the lower surface and few stomata near the midrib on the upper surface, a condition called hypoamphistomatic (Martínez Quesada, 2009). Approximately 35% of the species of *Serjania* are narrow endemics known from few collections (Acevedo-Rodríguez, 1993), and *S. frutescens* is another one of these.

*Serjania frutescens* is characterized by its shrubby habit, apterous capsules with winged stipe, 3-foliolate leaves lacking laticifers on the lower epidermis, deciduous stipules, and the absence of tendrils. Among its congeners, the most similar taxa are two cryptic species, *S. tortuosa* and *S. sonorensis*, and the differences are listed in Table 1. Both *S. tortuosa* and *S. sonorensis* were previously treated in *Cardiospermum* or *Paullinia*, and their placement in *Serjania* is the result of the molecular phylogenetic analysis conducted by Acevedo-Rodríguez et al. (2017). A synopsis of these two species is presented below, including a description of the fruit, as well as data on distribution, ecology, phenology, and list of specimens examined. Lectotypifications for both species and new synonyms for *S. tortuosa* are also included. Finally, a key to identify this small group of Mexican *Serjania* species with capsular fruit is presented.

**Serjania tortuosa** (Benth.) Ferrucci & V. W. Steinm., Syst. Bot. 42(1): 111. 2017. = *Cardiospermum tortuosum* Benth., Bot. Voy. Sulphur 1: 9. pl. 6. 1844. = *Paullinia tortuosa* (Benth.) Brandegee, Zoë 2: 74. 1891. TYPE: [MEXICO]. Lower California [Baja California Sur], Bay of Magdalena Bay, *Hinds s.n.* (lectotype here designated, K 000037463!; islectotype K 000074509!).

= *Serjania californica* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8: 222. 1878. TYPE: ‘In California inferiore ad promontorium S. Lucas: Xantus n. 19’. MEXICO. South Lower California [Baja California Sur]: Cape St. Lucas, & C.,
Fig. 19–28. Illustration of *Serjania frutescens*. (19) Flowering branch; (20) Staminate flower; (21) Pistillate flower; (22) Posterior petal with adnate appendage; (23) Anterior petal with adnate appendage; (24) Stamen from staminate flower; (25) Pistillate flower devoid of petals, showing the two posterior nectary lobes; (26) Mature fruit shortly before natural dehiscence; (27) Seed, lateral view; (28) Longitudinal section of seed showing embryo (19, Steinmann 3381, CTES; 20–25, Ramírez-Amezcua & Steinmann 1075, CTES; 26–28, Steinmann & Ramírez-Amezcua 7348 CTES).
Fig. 29–35. Photos of *Serjania frutescens*. (29) Branch with immature fruit; (30) Flowering branch; (31) Mature fruit in the process of dehiscence; (32) Inflorescence detail; (33) Leaf detail; (34) Flower detail, the yellow crests of posterior petals appendages are highlighted; (35) Different views of immature fruits, mature ones, and seeds (29, 31, 33, 35, Steinmann & Ramírez-Amezcue 7348; 30, 32, 34, Ramírez-Amezcue & Steinmann 1731).
Aug 1859–Jan 1860, L. J. Xantus 19 (lectotype here designated, K 000037461!; isolecotypes, GH!, NY 00008345!). Syn. nov. = Paullinia californica (Radlk.) I. M. Johnst., Proc. Calif. Acad. Sci. 4(12): 1084. 1924.

Syn. nov. = Cardiospermum spinosum Radlk., Contr. U.S. Natl. Herb. 1(9): 368. 1895. TYPE: MEXICO. South Lower California [Baja California Sur]: La Paz, 20 Jan–5 Feb 1890 (fl), E. J. Palmer 2 (lectotype here designated GH!; isolecotypes K 000037460!, UC!, US 00095194!).

Syn. nov. = Paullinia spinosa (Radlk.) I. M. Johnst., Proc. Calif. Acad. Sci. 4(12): 1083. 1924. = Serjania spinosa (Radlk.) Ferrucci & Steinmann, Syst. Bot. 42(1): 111. 2017. Syn. nov.

= Serjania albida Radlk., Contr. U. S. Natl. Herb. 1 (9): 367. 1895. ‘In California inferiore ad Santa Agueda: Palmer No. 263!’. TYPE: MEXICO. South Lower California: Santa Agueda, Mar 1890 (fl), E. J. Palmer 263 (lectotype here designated M 0212268!; isolecotypes MEXU 00018883!, NY!). Syn. nov.

Only the collection site of Cardiospermum tortuosum is provided in the protologue, but two syntypes with duplicates were located. These correspond to the collections of R.B. Hinds s. n. and G.W. Barclay 3078. The duplicates detected coincide with those detailed by Raven (1964) in his very useful paper about George Barclay and his collecting in California. The sheet on which K 000037463 is mounted also contains material from the Barclay collection which was given to Bentham by Hooker in 1842 and is separately barcoded. The specimen here selected as lectotype is a branch in good condition and with a fruit.

Fig. 36–37. Scanning electron micrographs of foliar epidermis of Serjania frutescens. (36) Adaxial surface, stomata only on both sides of the middle vein, epidermal cells smooth or with fine cuticular striae, anomocytic stomata and trichomes; (37) Abaxial surface, epidermal cells with fine cuticular striations or smooth, anomocytic stomata and bent glandular trichomes (Ferrucci et al. 3118, CTES).

Fig. 38–40. Scanning electron micrographs of pollen grains of Serjania frutescens. (38) Distal view; (39) Proximal view, note colpi reduce to colpoids; (40) Subequatorial view (Steinmann 3381, CTES).
Table 1. Morphological comparison of *Serjania frutescens* with its closest relatives *S. sonorensis* and *S. tortuosa*.

| Characters            | *Serjania frutescens*                                                                 | *S. tortuosa*/*S. sonorensis*                                                                 |
|-----------------------|---------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|
| Habit                 | Shrub 1–3 m tall                                                                      | Shrub, subshrub or climber reaching to 2 m high                                               |
| Leaves                | 3-foliolate                                                                           | 3- or 5-foliolate or biternate                                                                 |
|                       | Subchartaceous                                                                        | Chartaceous, often little fleshy                                                                |
|                       | Laticifers absent in lower epidermis                                                   | Conspicuous laticifers present in lower epidermis                                              |
| Thyrsis               | Tendrils absent                                                                        | Base with 2 short tendrils, spinning and uncinate, or delicate or absent                        |
| Rachis                | To 2 mm long                                                                           | To 15 mm long                                                                                  |
| Flower                | The two posterior ovoid, obtuse at the apex, the anterior two circular                 | The two posterior ovoid-oblong, the anterior two ovoid, obtuse at the apex                      |
| Nectary lobes         | in outline                                                                            |                                                                                                 |
| Pistillode            | Glabrous                                                                              | Pubescent rarely glabrous                                                                      |
| Gynoecium             | Glabrous                                                                              | Pubescent rarely glabrous                                                                      |
| Capsule               | Globose, stipe ± 7 mm long, narrowly winged                                            | Trigonous tubinate, stipe 2.6–6 mm long, wingless, only one dorsal carina or rarely a reduced wing is observed in the proximal half at the dorsal vein level of each carpel |
| Geographic distribution| Michoacán                                                                              | Southern Baja California Sur/Sinaloa and Sonora                                               |
The pencil annotations on the sheet indicate that Bentham had both specimens available when describing the species and preparing the excellent figure that accompanies it.

In the protologue of *Serjania californica*, the author does not indicate in which herbarium the material studied by him is deposited, and we were unable to find a specimen in M. Among the three duplicates of the type collection located, we choose as lectotype the specimen deposited in K that was identified by Radlkofner in his handwriting in October 1885.

The protologue of *Cardiospermum spinosum* (Radlkofner, 1895) states ‘Affinis Cardiospermo tortuoso’ and mentions a collection made by Palmer in La Paz, Lower California. We have located specimens in GH, K, UC, and US that coincide with the collector and morphology. Among these specimens, we designate the one at GH as lectotype because it is a very well-preserved specimen.

The protologue of *Serjania albida* states ‘Affinis videtur Serjaniae (?) californicae’ and cites a collection made in California inferiori ad Santa Agueda’. Three duplicates were found that match perfectly with the protologue in locality, collector, and collection number (M 0212268, MEXU 00018883, NY). The lectotype at M that we here designated is the best preserved, although it is still very poor. Also, it is identified by Radlkofner in his own handwriting.

The following carpological and seminal characters are described for the first time. *Serjania tortuosa* shares these traits with *S. sonorensis*, a very close species that cannot be distinguished by morphological characters.

Capsules chartaceous, trigonous turbinate, brown reddish, generally wingless, only one carina or rarely a reduced wing is observed in the proximal half at the dorsal vein level of each carpel; locules inflated, totally occupied by the seeds; apiculate, persistent style, dorsal vein level of each carpel; locules inflated, totally reduced wing is observed in the proximal half at the dish, generally wingless, only one carina or rarely a.

Distribution, ecology, and phenology. Mexican endemic of Baja California Sur, where it occurs along volcanic rocks and forms part of the thornscrub vegetation, at elevations of 0 to 1200 m. Flowers from August to April and fruits from September to March.
Phylogenetics of *Serjania* (Sapindaceae)

Mason 1942 (GH, US); S end of San José Island, B. C.; 12 Apr 1962, *R. Moran* 9440 (MEXU, UC); Near N end of Isla Partida, Espiritu Santo Island, 20 Apr 1962, *R. Moran* 9617 (MEXU); Magdalena Island, Man of War Cove, 24 Apr 1963, *R. Moran* 10820 (UC); Sierra de La Giganta, Cerro Mechudo and vicinity, Cerro Mechudo between Portezuelo de San Antonio and La Sabanilla, 4 Nov. 1971, *R. Moran* 16355

According to the protologue of *P. sonorensis*, the author precisely indicates the locality, collector and number, and five duplicates were found. However, none are at GH, where Sereno Watson was the curator. The duplicate housed at US (US 00095174) is in the best condition and chosen as the lectotype of the name.

Distribution, ecology and phenology. Endemic to the Mexican states of Sinaloa and Sonora. Flowers from August to April and fruits from September to March.

Specimens examined. MEXICO. Sinaloa: Cerro Llano Redondo, W of Caymanero, 8 Oct 1944, *H. S. Gentry* 7101 (ARIZ, UC); Cerros del Fuerte, 18–24 miles north of Los Mochis, 25 Sep 1954, *H. S. Gentry* 14294 (MEXU, US); Cerros de Navachiste about Bahia Topolobampo, 26–30 Sep 1954, *H. S. Gentry* 14342 (MEXU, US). Sonora: Cerro El Verde, San Javier Son., 1 km al N del molino metalúrgico 'El Verde', 16 Feb 1996, *Bárcenas et al.* 96-072 (MEXU); Foothills at south end of Sierra Libre, 12.3 miles south of La Palma on Mex Hwy 15 (at km marker 190), then 0.8 miles east of Hwy on road to Microondas Avispas, 8 Oct 1985, *R. S. Felger & F. W. Reichenbacher* 85-1086 (ARIZ, MEXU); Sierra Bojihuacame south-east of Cd. Obregon, 17–25 Oct 1954, *H. S. Gentry* 14491 (US); Guaymas, *E. Palmer* 239 (GH); ~2 km north of Teachive, south-east end of Cerro Terucuchi, Municipio de Navojoa, 28 Sep 1996, *A. L. Reina et al.* 96-574 (ARIZ, MEXU); 15 miles south of La Palma between Hermosillo and Guaymas, 2 Sep 1941, *I. L. Wiggins & R. C. Rollins* 224 (NY, US).

Notes. *Serjania tortuosa* and *S. sonorensis* are cryptic species and at least superficially indistinguishable by morphology, although more study would be beneficial. They are mainly recognized by having leaves that are 3- or 5-foliolate or biternate. The leaflets are obovate or ovate, incise-dentate or dentate-serrate, less often pinnatisect, and abaxially they have conspicuous laticifers. Their fruits are with inconspicuous venation or little marked. The abundant material reviewed indicates that it is a fairly polymorphic species with xeromorphic adaptive characters such as: development of spinescent tendrils, the abundance of stomata in the adaxial leaf surface, and the degree of division of the blade.

Key to the Mexican species of *Serjania* with capsular fruits

1. Cross section of flowering or fruiting branch with a single vascular cylinder.............................2
2. Cross section of flowering or fruiting branch with 3 or 5 peripheral vascular cylinders........................6
2. Leaves lacking laticifers in lower epidermis. Tendrils absent. Stipules caducous or persistent..........3
2. Leaves having laticifers in lower epidermis, 3- or 5-foliolate pinnately compound, or bipinnate 2-5-jugate. Stipules caducous.........................4
3. Leaves 3-foliolate, leaflets ovate, 2–3.5 × 1.2–2.8 cm. Stipules caducous. Capsule globose stipitate, stipe narrowly winged. Michoacán..................S. tortuosa (Benth.) Ferrucci & V. W. Steinm.
3. Leaves 3-jugate, lower pair of juga 3- or 5-pinnate foliolate, the middle pair 3-pinnate foliolute and the distal one 1-foliolate, leaflets narrow ovoid, 6.5–7.5 × 1–3.5 cm. Stipules persistent. Capsule trigonous obovate, shortly stipitate. Michoacán........S. rosalindae Ferrucci & V. W. Steinm.
4. Leaves 3- or 5-foliolate or biternate. Capsule semi-woody, epicarp with inconspicuous or little marked venation. Seeds attached near the base of the locules.................................................................5
4. Leaves supradecompound, 3–5-jugate, the basal juga 5-foliolate or biternate. Capsule chartaceous, epicarp with marked venation. Seeds attached little below the middle of locules. Texas (USA) and, Chihuahua and Coahuila..............................................................................5
5. Species distributed in the Baja California Peninsula. ..........S. dissecta (S. Watson) Ferrucci & V. W. Steinm.
5. Species distributed in Sinaloa and Sonora. ..................S. sonorensis (S. Watson) Ferrucci & V. W. Steinm.
6. Semi-woody vines, pubescent. Cross section with 3 peripheral vascular cylinders. Leaves 5-foliolate.7
6. Erect shrubs or subshrubs, almost glabrous. Cross section with 5 peripheral vascular cylinders. Leaves biternate. Guerrero. .................................................................S. biternata (Weath.) Acev.-Rodr.
7. Flowering branch with 6 ribs. Stipules caducous. Leaflets sessile. Petals densely glandular on both faces. Pericarp almost woody. Michoacán. ...............S. crucensis Ferrucci & V. W. Steinm.
7. Flowering branch with 3 ribs. Stipules persistent. Leaflets petiolulate. Petals glandular on the adaxial surface. Pericarp immature fleshy, leathery when drying. Guerrero.................................S. guerrerensis (Cruz Durán & K. Vega) Acev.-Rodr.

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Disclosure statement
There are no potential conflicts of interest.

Supplemental material
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Appendix 1. Voucher and GenBank information for taxa included in the phylogenetic analyses. The order is as follows: taxon, collection, herbarium, place of origin, and GenBank accession numbers (ITS, trnL intron). Herbarium acronyms follow Index Herbariorum (Thiers, continuously updated). An em-dash (—) indicates missing data for one of the regions.

Cardiospernum corindum L., Harder & Bringham 3495 (MO), Zambia, KX584912, KX585007. Cardiospernum grandiflorum Sw., ATBP 603 (MO), Uganda, KX584915, KX585009. Cardiospernum urvilleoides (Radlk.) Ferrucci, Urdampilleta 425 (US), Brazil, KX584922, KX585013. Lophostigma plumosum Radlk., Aceredo-Rodriguez 6554 (US), Bolivia, KX584929, KX585020. Paullinia clathrata Radlk., Aceredo-Rodriguez 14305 (US), Peru, KX584930, KX585021. Paullinia hystric Radlk., Aceredo-Rodriguez 14417 (US), Peru, KX584934, KX585025. Paullinia olivacea Radlk., Schunke Vigo 16002 (US), Peru, KX584936, KX585027. Paullinia pinnata L., Aceredo-Rodriguez 11088 (US), French Guiana, KX584937, KX585028. Serjania alissima (Poepp.) Radlk., Aceredo-Rodriguez 14953 (US), Brazil, KX584945, KX585036. Serjania amplexopsis Planch. & Lind., Aceredo-Rodriguez 11181 (US), Bolivia, KX584946, KX585037. Serjania bibernata (Weath.) Acev.-Rodr., Ferrucci et al. 3107 (CTES), Mexico, OK423685, OK423721. Serjania brachylopha Radlk., Steinmann 4529 (QMEX), Mexico, OK423686, OK423722. Serjania caracasana (Jacq.) Wild., Aceredo-Rodriguez 15107 (US), Mexico, KX584947, KX585038. Serjania cardiospermoides Schltdl. & Cham. (1), Garcia 7236 (IEB), Mexico, OK423688, OK423724. Serjania cardiospermoideis Schltdl. & Cham. (2), Steinmann 5860 (IEB), Mexico, OK423689, OK423725. Serjania clematidifolia Cambess., Sommer 1078 (RBR), Brazil, KX584949, KX585040. Serjania communis Cambess. (1), Sommer 1334 (US), Brazil, KX584950, KX585041. Serjania communis Cambess. (2), Ferrucci et al 2910 (CTES), Brazil, OK423690, OK423726. Serjania cornigera Turecz., Chery 36 (US), unknown, MZ892369.— Serjania cristobalae (Ferrucci & Urdampilleta) Ferrucci & V.W. Steinn., Urdampilleta 421 (UEC), Brazil, KX584913.— Serjania cruncensis Ferrucci & V.W. Steinn., Steinnmann 3051 (QMEX), Mexico, OK423691, OK423727. Serjania cuspidata Cambess., Sommer 1400 (US), Brazil, KX584951, KX585042. Serjania deltoidea Radlk., Aceredo-Rodriguez 15725 (US), unknown, MZ892370.— Serjania dissecta (S. Watson) Ferrucci & V.W. Steinn., Carr 29022 (TEX), United States, OK423692, OK423728. Serjania elongata J.F. Macbr., Aceredo-Rodriguez 13547 (US), Brazil, KX584953.— Serjania emarginata H.B.K. (1), Ramírez & Steinnmann 977 (QMEX), Mexico, OK423693, OK423729. Serjania emarginata H.B.K. (2), Steinnmann 4185 (QMEX), Mexico, OK423694, OK423730. Serjania emarginata H.B.K. (3), Aceredo-Rodriguez 15135 (US), Mexico, KX584954, KX585043. Serjania erythrocaulis Acev.-Rodr. & Sommer, Aceredo-Rodriguez 3729 (US), Brazil, KX584955, KX585044. Serjania eucardia Radlk., Sommer 1072 (RBR), Brazil, KX584956, KX585045. Serjania frutescens V.W. Steinn. & Ferrucci, Steinnmann 7348 (QMEX), OK423696, OK423732. Serjania fusculifolia Radlk. (1), Sommer 1455 (RBR), Brazil, KX584957, KX585046. Serjania fusculifolia Radlk. (2), Coulleri & Ferrucci 305 (CTES), Argentina, OK423697, OK423733. Serjania goniocarpa Radlk., Aguilar 5379 (IEB), Mexico, OK423698.— Serjania grandiceps Radlk., Aceredo-Rodriguez 13704 (US), Brazil, KX584958, KX585047. Serjania guerrerensis (Cruz Duran & K. Vega) Acev.-Rodr., Vega & Jiménez 1318 (FCME), Mexico, OK423699, OK423734. Serjania ichthyocotona Radlk., Sommer 1081 (RBR), Brazil, KX584960, KX585048. Serjania incana Radlk., Coulleri & Ferrucci 271 (CTES), Argentina, OK423700, OK423735. Serjania inflata Poepp., Nee 52811 (MEXU), Bolivia, OK423701.— Serjania lachnocarpa (Radlk.) Acev.-Rodr., Wiggens 11060 (US), Ecuador, KX584923, KX585014. Serjania lethalis St. Hil. (1), Roque 1860.
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Serjania lethalis St. Hil. (2), Sommer 1381 (RBR), Brazil, KX584962, KX585050. Serjania marginata Casar. (1), Acevedo-Rodriguez 11131 (US), Bolivia, KX584963, KX585051. Serjania marginata Casar. (2), Coulleri & Ferrucci 310 (CTES), Argentina, OK423702, OK423736. Serjania membranacea Splig. (1), Acevedo-Rodriguez 12329 (US), French Guiana, KX584964, — Serjania membranacea Splig. (2), Acevedo-Rodriguez 15227 (US), unknown, MZ892371, — Serjania mexicana (L.) Willd. (1): Acevedo-Rodriguez 12014 (US), Jamaica, KX584965, KX585052. Serjania mexicana (L.) Willd. (2): Acevedo-Rodriguez 15080 (US), Mexico, KX584966, KX585053. Serjania mexicana (L.) Willd. (3): Ramirez & Steinmann 624 (QMEX), Mexico, OK423704, OK423738. Serjania mexicana (L.) Willd. (4): Chery 45 (US), unknown, MZ892373, — Serjania multiflora Cambess., Ferrucci et al. 2881 (CTES), Brazil, OK423705, — Serjania paniculata H.B.K., Acevedo-Rodriguez 15143 (US), Mexico, KX584967, KX585054. Serjania pachydermata DC., Chery 34 (US), unknown, MZ892374, — Serjania perulacea Radl., Acevedo-Rodriguez 11134 (US), Bolivia, KX584968, KX585055. Serjania pygmaea (Radl.) Ferrucci & Medina, Ferrucci et al. 3109 (CTES), Mexico, OK423706, OK423739. Serjania pyramidal Radl. (1), Acevedo-Rodriguez 15243 (US), unknown, MZ892375, — Serjania pyramidal Radl. (2), Chery 29 (US), unknown, MZ892376, — Serjania cf. racemosa Schumach., Porter & Steinmann 14742 (RSA), Mexico, OK423703, OK423737. Serjania rhombea Radl., Acevedo-Rodriguez 15213 (US), unknown, MZ892378, — Serjania rosalindae Ferrucci & V.W. Steinm., Steinmann 7359 (QMEX), Mexico, OK423695, OK423731. Serjania rzedowskiana Ferrucci & V.W. Steinm. (1), Steinmann 3514 (MEXU), Mexico, OK423707, OK423740. Serjania rzedowskiana Ferrucci & V.W. Steinm. (2), Steinmann 3939 (MEXU), Mexico, OK423708, OK423742. Serjania schiedeana Schldl. (1): Steinmann 5282 (QMEX), Mexico, OK423709, OK423742. Serjania schiedeana Schldl. (2): Steinmann 5579 (QMEX), Mexico, OK423710, OK423743. Serjania schiedeana Schldl. (3): Ferrucci et al. 3099 (CTES), Mexico, OK423711, OK423744. Serjania sonorense (S. Watson) Ferrucci & V.W. Steinm. (1), A.L. Reina 96-574 (RSA), Mexico, OK423712, OK423745. Serjania sonorense (S. Watson) Ferrucci & V.W. Steinm. (2), Jenkins 91-134 (ARIZ), Mexico, OK423717, — Serjania tortuosa (Benth.) Ferrucci & V.W. Steinm. (1), Rocha 116 (IEB), Mexico, OK423719, OK423750. Serjania tortuosa (Benth.) Ferrucci & V.W. Steinm. (2), Hodges 9509 (SD), Mexico, OK423713, OK423746. Serjania tortuosa (Benth.) Ferrucci & V.W. Steinm. (3), Penez-Navarro 964 (SD), Mexico, OK423714, OK423747. Serjania tortuosa (Benth.) Ferrucci & V.W. Steinm. (4), Dominguez 4793 (HCIB), Mexico, OK423715, — Serjania tortuosa (Benth.) Ferrucci & V.W. Steinm. (5), Leon de la Luz 8163 (SD), Mexico, OK423716, OK423748. Serjania tortuosa (Benth.) Ferrucci & V.W. Steinm. (6), Rebnman 7728 (SD), Mexico, OK423718, OK423749. Serjania triquetra Radl., Ferrucci et al. 3110 (CTES), Mexico, OK423720, OK423751. Serjania uguiculata Radl., Acevedo-Rodriguez 15081 (US), Mexico, KX584969, KX585056. Serjania yucatanensis Standl., Acevedo-Rodriguez 12183 (US), Mexico, KX584970, KX585057. Serjania sp., Hernández 5394 (IEB), Mexico, OK423687, OK423723. Thinouia mucronata Radl., Keller 6919 (US), Argentina, KX584971, KX585058. Urvillea cuchuyaguensis (Ferrucci & Acev.-Rodr.) Acev.-Rodr. & Ferrucci, Van Devender 92-1012 (ARIZ), Mexico, KX584914, KX585008. Urvillea ulmacea H.B.K., Acevedo-Rodriguez 15145 (US), Mexico, KX584979, KX585066.