



Phylogenetic studies in *Smallanthus* (Millerieae, Asteraceae): a contribution from morphology

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Abstract

We present a cladistic analysis of all the species of *Smallanthus*. Six taxa within *Rumfordia*, *Ichthyothere*, *Acanthospermum* and *Tridax* served as outgroups. We evaluated the monophyly and the relationships between the species of *Smallanthus* through a maximum parsimony study based on morphological data. The matrix included 31 qualitative characters from floral and vegetative parts of the specimens. We also explored the phylogenetic significance of treating quantitative characters as continuous. Only one most parsimonious tree was obtained. In agreement with previous phylogenetic studies based on molecular data, we recovered a monophyletic *Smallanthus*. The presence of ray corollas, densely pubescent at the base, was the synapomorphy that defined *Smallanthus*. *Smallanthus microcephalus* and two other major clades were recovered. The first clade included *S. glabratus*, *S. fruticosus*, *S. jelskii* and *S. pyramidalis*, while the second one contained the remaining species of *Smallanthus*. The analysis recovered one species of *Rumfordia* as sister to *Smallanthus*. We present a new combination, *Smallanthus cocuyensis*, based on morphological analysis of the type specimen.

Keywords: Cladistic analysis, Compositae, quantitative characters, *Rumfordia*

Resumen

En este trabajo se presenta un análisis cladístico de todas las especies del género *Smallanthus*. Se utilizaron como grupos externos seis especies potencialmente relacionadas incluidas en los géneros *Rumfordia*, *Ichthyothere*, *Acanthospermum* y *Tridax*. Se evaluó la monofilia y relaciones entre las especies de *Smallanthus* a través de un estudio de máxima parsimonia basado en caracteres morfológicos. La matriz incluyó treinta y un caracteres cualitativos, tanto florales como vegetativos. También se analizó la importancia filogenética de los caracteres cuantitativos tratados como continuos. Se obtuvo como resultado un único árbol más parsimonioso. Como resultado se obtuvo al género *Smallanthus* como monofilético, apoyando estudios previos basados en datos moleculares. La presencia de una densa concentración de pelos en la base de las corolas de las flores del radio fue la sinapomorfía que soportó a *Smallanthus*. Dentro de *Smallanthus* se obtuvieron dos grandes clados y un linaje independiente, *Smallanthus microcephalus*. El primer clado incluyó a *S. glabratus*, *S. fruticosus*, *S. jelskii* y *S. pyramidalis*, y el segundo se encontró formado por las restantes especies de *Smallanthus*. El análisis mostró a una especie de *Rumfordia* como hermana del género *Smallanthus*. Se propone una nueva combinación, *Smallanthus cocuyensis*, en base a observaciones basadas en la morfología del material tipo.

Introduction

Smallanthus Mackenzie (Asteraceae, Millerieae) includes 24 species distributed from the southern United States to Central-East Argentina. Many species of *Smallanthus* occur in Mexico (seven species) and Peru (eight species). The remaining species are distributed in North America (United States), Central America (Costa Rica, El Salvador, Honduras, Nicaragua and Panama) and South America (Argentina, Bolivia, Brazil, Colombia, Ecuador, Paraguay,

Uruguay and Venezuela). The species of *Smallanthus* are perennial herbs (Fig. 1A, D), shrubs or trees, with opposite leaves (Fig. 1B, E), capitula solitary or arranged in panicles or corymbs (Fig. 1C, F); the inner phyllaries embrace the cypselae (Fig. 2A); the ray florets (Fig. 2B) are female with yellow, reddish-orange or white corollas; the disc florets (Fig. 2C) are functionally staminate with yellow or purple corollas, and lacking pappus (Fig. 2D). *Smallanthus* includes some important medicinal species and others with various uses such as in food and cosmetics. The example most recognized worldwide is the medicinal plant *S. sonchifolius* (Poeppig) Robinson, “yacón” (Sanchez & Genta 2007, Aybar *et al.* 2001). Furthermore, there is an evidence that other species of *Smallanthus* have medicinal properties similar to “yacón”, such as *S. macroscyphus* (Baker) A. Grau (Fig. 1D–F) (Coll Aráoz *et al.* 2008) and *S. connatus* (Sprengel) Robinson (Fig. 1A–C) (Bach *et al.* 2007). The ecological importance of *S. pyramidalis* (Triana) Robinson for the recovery and maintenance of Bogota’s wetlands has also been reported, as it participates in the regulation of soil water, acts as wind barrier and provides shade support to slow-growing plant species. Additionally, the secondary metabolites of *S. pyramidalis* play a distinctive role in the ecosystem, acting as pollinator attractants, producing repellent agents, etc. (Guzmán Avendaño & Barrera Adame 2011).

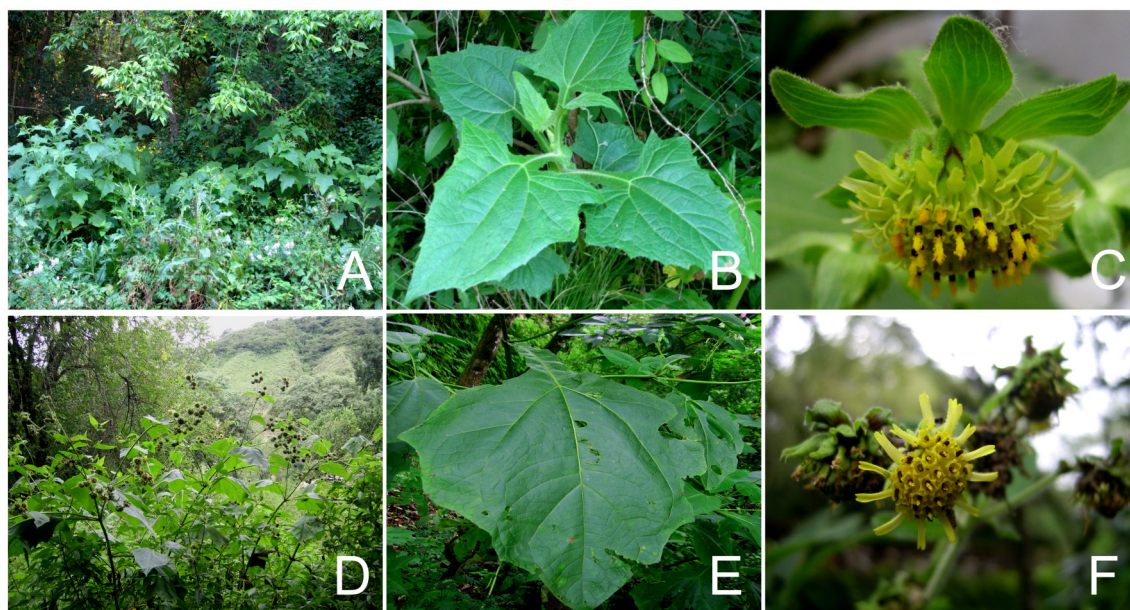


FIGURE 1. Selected morphological aspects of *Smallanthus connatus* and *S. macroscyphus*. **A–C.** *S. connatus*: **A.** Habit. **B.** Leaves. (Buenos Aires, Punta Lara, photo by Diego G. Gutiérrez). **C.** Capitulum. (Buenos Aires, Magdalena, photo by Maira Vitali). **D–F.** *S. macroscyphus*: **D.** Habit. **E.** Leaf. **F.** Capitula. (Salta, Chicoana, photo by Diego G. Gutiérrez).

The genus *Smallanthus* was described by Mackenzie (1933) based on *Osteospermum uvedalia* Linnaeus. Wells (1965) transferred the species *S. uvedalius* (L.) Mackenzie to the genus *Polymnia* Linnaeus. In 1978, Robinson restored the genus *Smallanthus* and recognized 19 species. Later, four new species were described in *Smallanthus*: *S. obscurus* B.L. Turner (Turner 1988), *S. riograndensis* Mondin, *S. araucariophilus* Mondin (Mondin 2004) and *S. putlanus* B.L. Turner (Turner 2010). Also, a new combination was made, *S. macroscyphus* (Baker) Grau (Grau & Rea 1997), for a total of 24 species.

Traditionally, *Smallanthus* was placed in the subtribe Melampodiinae Less., based on the presence of functionally staminate disc florets, an expanded outer series of phyllaries, and its fruit wall anatomy (Robinson *et al.* 1981, Karis 1993, Karis & Ryding 1994). However, subsequent molecular studies relocated *Smallanthus* in the subtribe Milleriinae Benth. & Hook. f. (Panero *et al.* 2001, Panero & Funk 2002, Panero 2007).

Results from phylogenetic studies of Heliantheae based on a large set of morphological characters (Karis 1993, Karis & Ryding 1994) showed that *Smallanthus* is sister to *Rumfordia* Candolle. This relationship was also observed in studies based on molecular characters (Panero *et al.* 1999). A more recent molecular phylogenetic study based on nrDNAITS sequences of the *Espeletia* Mutis ex Bonpland “complex” (Rauscher 2002) included 13 species of *Smallanthus*. In that analysis, *Smallanthus* was recovered as monophyletic and as part of a trichotomy

including *R. guatemalensis* (J.M. Coulter) S.F. Blake and a clade with *Ichthyothere* Martius and the *Espeletia* “complex”.

Although other phylogenetic analyses at the tribe and subtribe level that included some species of *Smallanthus* have been undertaken (Panero *et al.* 1999, Baldwin *et al.* 2002), none has considered all the 24 species of the genus. A comprehensive phylogenetic analysis of *Smallanthus* based on morphology would help to elucidate the relationships among its species.

Most morphological phylogenetic studies in plants have been based on information provided by qualitative characters, and continuous quantitative characters has been seldom used (De Gennaro & Scataglini 2012, Grossi & Katinas 2013). Continuous characters treated as such, rather than distorted through discretization, seem to carry useful phylogenetic information (Goloboff *et al.* 2006). In the present study, we propose to explore the value of treating quantitative characters as continuous to test the hypothesis that they may provide relevant phylogenetic information of *Smallanthus*.

The main aims of this work were to test the monophyly of *Smallanthus* based on its morphological characters, to establish the phylogenetic relationships among its species and with other putative related genera (*Ichthyothere*, *Acanthospermum* Schrank, *Rumfordia*), and to study the phylogenetic value and evolution of some morphological characters that have been used in the classification of the group. Finally, we aim to explore the utility of quantitative characters in defining the relationships of *Smallanthus*.

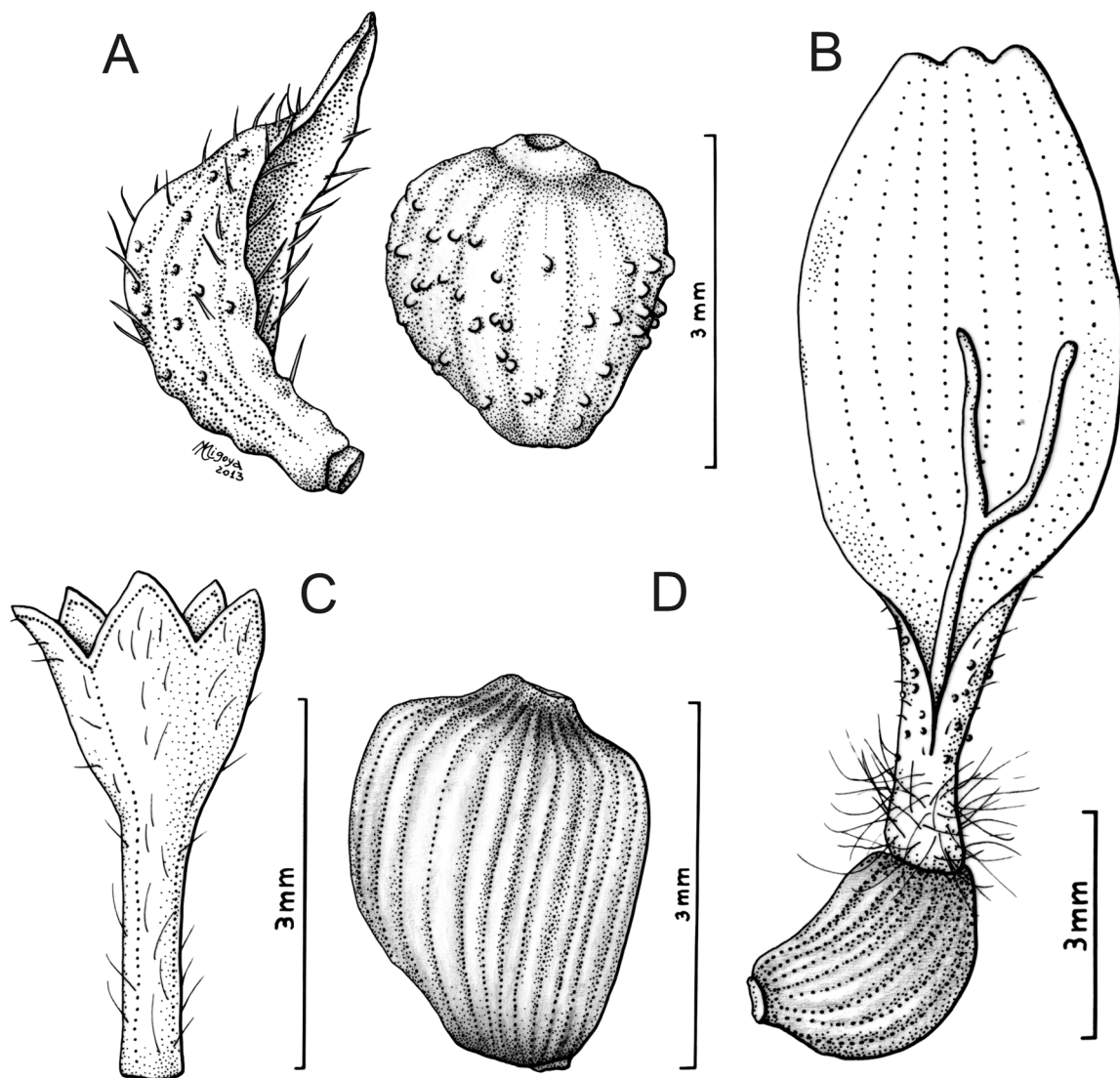


FIGURE 2. Selected reproductive structures of *Smallanthus*. **A.** *S. oaxacanus*: cypselum with inner phyllary (Molina 10854, F). **B.** *S. obscurus*: ray floret (Breedlove 41387, TEX). **C.** *S. pyramidalis*: disc floret (Cuatrecasas 20886, F). **D.** *S. siegesbeckius*: detail of cypselum (Dusén 9503, GH). Drawings by Alejandra Migoya.

Materials & Methods

Taxon sampling. Thirty one species of five genera were included in the analyses (Appendix 1). The sampling included 24 species of *Smallanthus* as ingroup. Taxa of *Smallanthus* at the level of variety were not included because of the absence of substantial differences among them. To test previous observations of the authors (Vitali in prep.) that suggest *Polymnia cocuyensis* Cuatrecasas and *Smallanthus meridensis* Steyermark (so far considered synonyms) as not morphologically related, we coded these two species as different entities based on the type and other material (Appendix 1). To test the monophyly of *Smallanthus* we used six species from four potentially related genera within Millerieae according to Rauscher (2002): *Tridax* Linnaeus (we sampled one species of 30; subtribe Dyscritothamninae), *Acanthospermum* (2/6; subtribe Melampodiinae), *Ichthyothere* (1/20) and *Rumfordia* (2/6), both within subtribe Milleriinae (subtribes from Panero 2007). From *Rumfordia*, *R. guatemalensis* was chosen because it was regarded by previous authors (Sanders 1977) as closely related to *Smallanthus*. *Tridax trilobata* served as outgroup.

Characters. This study is based on herbarium specimens of the following herbaria: B, BAF, CAS, F, G, GH, HASU, ICN, K, LL, LP, M, MICH, MO, NY, P, QCNE, S, SI, TEX, US and W (acronyms from Thiers 2013). When no material was available, data were taken from digital images, photographs and literature. For light microscopic examination, vegetative and reproductive parts were rehydrated, treated with a clearing process using sodium hypochlorite 5%, stained with 2% safranin, washed in water, and mounted on microscope slides. Observations of morphological features were performed using a Nikon Eclipse E200 light microscope equipped with a camera lucida and a binocular microscope. General terminology for morphological structures follows Ramayya (1962), Metcalfe & Chalk (1979) and Harris & Harris (1994). For each terminal, 38 morphological characters from floral and vegetative parts of the specimens were coded (Appendix 2). Of the total of 38 characters, 31 were coded as qualitative, 22 as binary and 9 as multistate (3–5 states). Character 20 (number of inner phyllary series), although quantitative, was coded as qualitative because of the presence of evident gaps along the variation of the character. All characters were treated as non-additive and of equal weight. In the case of species with two traits, the characters were coded as polymorphic. The remaining seven characters were quantitative (three discrete and four continuous). First, we conducted the analysis regarding these characters as discretized, but the lack of evident gaps throughout the character ranges yield confusing results and a weak phylogenetic signal. So we treated these characters as continuous quantitative variables. Then, we proceeded to analyze these characters with standardized values, a practice that ensures equal character contribution to the analysis. Moreover, it prevents characters with extremely large numbers from exerting more influence than those with smaller values (Donato 2011). The standard score of an observation is the number of standard deviation units; it is above or below the mean and is calculated by subtracting the mean from the observation, then dividing by the standard deviation (Sokal 1961). Because of the standardization process, some characters (those below the mean) acquire negative values and therefore cannot be analyzed. To prevent this problem, the standardized matrix was transformed through the addition of a constant value of 3 to ensure positive values for all characters (Donato 2011). Discrete characters were coded as non-additive, and quantitative continuous characters were analyzed as additive. Inapplicable characters were coded as missing data.

Phylogenetic analysis. The maximum parsimony analysis was conducted in TNT v. 1.1 (Goloboff *et al.* 2008). Cladograms were generated through an heuristic search using 1000 Random Addition Sequences (RAS) submitted to tree bisection-reconnection (TBR) algorithm, holding 10 trees on each repetition; and using a random seed=0. Consistency and retention indices (CI and RI, respectively) were calculated using scripts in TNT. Support values for each clade were obtained by Jackknife analysis (Farris *et al.* 1996). They were estimated using 1000 replicates. A tree search of 10 random addition sequences plus TBR, saving 10 trees per replicate, were applied. Bremer support or “decay-index” values were also obtained (Bremer 1988). In the data matrices (doi:10.5061/dryad.67r03, Matrix 1 and 2), both unknown and inapplicable character states were indicated with “?”. The option “Character mapping” of TNT was used to observe character evolution.

Results

The cladistic analysis resulted in one most parsimonious cladogram (Fig. 3) 172.213 steps long, a consistency index (CI)=0.39 and a retention index (RI)=0.51. *Ichthyothere* and *Acanthospermum* were recovered as sister

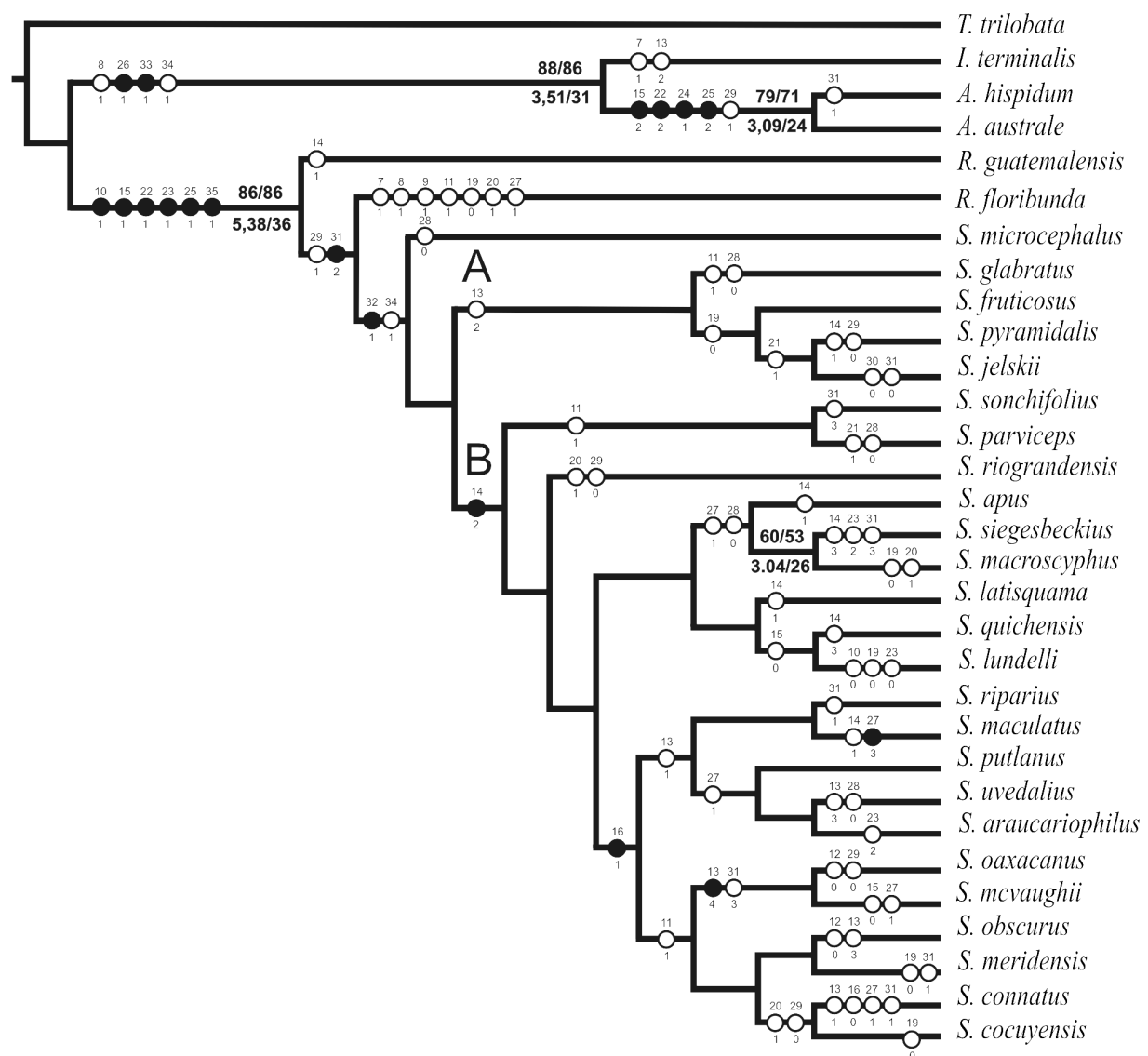


FIGURE 3. The single most parsimonious cladogram showing the qualitative characters. Numbers above branches are Jackknife support values (absolute/GC). Numbers below branches are Bremer support values (absolute/relative). A and B are the two main clades of *Smallanthus*. Black circles are synapomorphies and white circles are homoplasies. Numbers above circles indicate character number and numbers below circles indicate character state according to Appendix 2. Abbreviations: *T.*: *Tridax*, *I.*: *Ichthyothere*, *A.*: *Acanthospermum*, *R.*: *Rumfordia*, *S.*: *Smallanthus*.

genera in a clade with a Jackknife absolute value of 88 (JK=88), a Jackknife GC value of 86 [JK (GC)=86], a Bremer support absolute value of 3,51 (BS=3,51) and a Bremer support relative of 31 [BS(relative)=31]; whereas the group *A. hispidum* Candolle and *A. australe* (Loefling) Kuntze obtained a support value of JK=79, JK (GC)=71, BS=3,09 and BS (relative)=24. *Rumfordia* and *Smallanthus* are sister genera in a well supported monophyletic group with JK=86, JK (GC)=86, BS=5,38 and BS (relative)=36. From the two species of *Rumfordia* included in the analysis, *R. floribunda* was retrieved sister to *Smallanthus*. The species of *Smallanthus* were recovered monophyletic in the unique cladogram obtained, but this clade obtained a weak support (JK<50 and BS=1). The *Smallanthus* clade was supported by ray corollas densely pubescent at the base (Fig. 2B) and functionally staminate disc florets (characters 32 and 34 respectively). Within *Smallanthus*, two major clades (A and B) and one independent lineage, *S. microcephalus* (Hieronymus) Robinson, are recovered. Clade A is integrated by *S. glabratus* (Candolle) Robinson, *S. fruticosus* (Bentham) Robinson, *S. pyramidalis* (Triana) Robinson and *S. jelskii* (Hieronymus) Robinson, and supported by characters 6/20 (20 ray florets) and character 13/2 (entire blade margin). Within clade A, *S. pyramidalis* and *S. jelskii* were monophyletic, supported by character 21/1 (inner phyllaries papyraceous). The *S. pyramidalis*, *S. jelskii* and *S. fruticosus* clade was defined by character 19/0 (apices of outer phyllaries obtuse).

Clade B was defined by character 14/2 (blade base truncate to hastate), and composed of *S. sonchifolius*, *S. parviceps* (S.F. Blake) Robinson, *S. riograndensis*, *S. apus* (S.F. Blake) Robinson, *S. siegesbeckius* (Candolle) Robinson, *S. macroscyphus*, *S. latisquamus* (S.F. Blake) Robinson, *S. quichensis* (J.M. Coulter) Robinson, *S. lundelli* Robinson, *S. riparius* (Kunth) Robinson, *S. maculatus* (Cavanilles) Robinson, *S. putlanus*, *S. uvedalius*, *S. araucariophilus*, *S. oaxacanus* (Schultz Bipontinus ex Klatt) Robinson, *S. mcvaughii* (J.R. Wells) Robinson, *S. obscurus*, *S. meridensis*, *S. connatus* and *Polymnia cocuyensis*. Within clade B, *S. macroscyphus* and *S. siegesbeckius* form a monophyletic group, with JK=60, JK(GC)=53, BS=3,04 and BS (relative)=26, supported by all quantitative characters 1/0,45–0,6 (ligule length ranging from 0,45 to 0,6 cm), 4/15 (15 capitula) and 6/25 (25 ray florets). The species considered so far as synonyms, *Smallanthus meridensis* and *Polymnia cocuyensis* were not recovered as sisters in the cladogram, although *P. cocuyensis* was nested within *Smallanthus*. Most clades within *Smallanthus* received JK<50 and lower Bremer support values.

Discussion

Circumscription of *Smallanthus*.

Our study recovered a single most parsimonious tree that showed a monophyletic *Smallanthus*, although with a low support. These results agree with those obtained by molecular studies (Rauscher 2002). *Smallanthus* is defined by ray corollas densely pubescent at the base, a character indicated by Robinson (1978) to distinguish *Smallanthus* from *Polymnia*.

The results obtained in our study also show close relationships between *Smallanthus* and *Rumfordia*, in agreement with previous studies (Karis & Ryding 1994, Panero *et al.* 1999). According to Sanders (1977), *Rumfordia*, and particularly *R. guatemalensis*, resembles certain species of *Polymnia*, although the author did not specify which species of *Polymnia* he was referring to. Sander's treatment of *Rumfordia* was prior to the current circumscription of *Smallanthus* (Robinson 1978), which nowadays includes many species formerly placed in *Polymnia*. Therefore, it could be possible that some of the species which Sanders found similar to *Rumfordia* are now placed in *Smallanthus*. In Rauscher's study (2002), *Smallanthus* was recovered in a trichotomy with *R. guatemalensis* and the *Ichthyothere*-"*Espeletia* complex" clade. Our work, however, partially resolved the trichotomy obtained by Rauscher (2002) by recovering *Ichthyothere* as distantly related to *Smallanthus*, and *Rumfordia* as sister to *Smallanthus*.

The two species of *Rumfordia* analyzed here were not recovered as a monophyletic group. Our results differ from those of Rauscher who found that species of *Rumfordia* are more closely related to *Smallanthus* (i.e. *R. floribunda* in our work vs. *R. guatemalensis* in Rauscher's study). This could be due to the limited sampling of *Rumfordia*. Evidently, the relationships between certain species of *Rumfordia* and *Smallanthus* appear to be closer than expected. However, further studies including all species of *Rumfordia* are needed to solve and define the monophyly of this genus, the relationships among its species and those with *Smallanthus*.

Relationships between the species of *Smallanthus*.

The most informative clades recovered in the single most parsimonious tree will be discussed below, although some of them obtained a weak support.

According to our results, the "Glabrata complex" of species defined by Wells (1965) would be not monophyletic. The "Glabrata complex" was described to include *S. glabratus*, *S. fruticosus*, *S. parviceps* and *S. microcephalus* because they share a similar habit (shrub or tree) and geographical distribution (South America, specifically southwestern Venezuela, Ecuador, Peru, and Colombia). In Rauscher's molecular study (2002) two of the species of this complex, *S. fruticosus* and *S. microcephalus*, were recovered distantly related. Our study shows some of the species of the "Glabrata complex", *S. glabratus* and *S. fruticosus*, are included in the clade A, although the remaining species appeared in other relatively distantly related clades. The molecular and our own results based on morphology agree in regarding the "Glabrata complex" as an artificial entity. The species of clade A have morphological characters in common, such as the habit (shrubs or trees), winged petioles, usually isomorphic ovate leaves with acute apices and entire margins, and small and numerous capitula. All of these characters give a distinctive appearance to the species of clade A, making them look different from the other species of *Smallanthus*. On the other hand, the species of *Smallanthus* included in clade A resemble *Rumfordia* in the blade shape and the

size and number of capitula. The low support obtained for clade A would suggest the shared morphological characters as potentially homoplasious.

Within the clade A, *S. jelskii* and *S. pyramidalis* were recovered as sister species, although with a low support. These two species have papyraceous inner phyllaries and they are also the only two species of *Smallanthus* with a tree habit. Other authors, such as Robinson (1978), proposed that *S. jelskii* is closely related to *S. pyramidalis* because they share short ray corolla limbs and dense fine hairs on the peduncles and paleae. Rauscher's analysis (2002), for its part, found that both species formed a monophyletic group, in agreement with Robinson (1978) and our results.

In clade B, *S. siegesbeckius* and *S. macroscyphus* formed the only relatively well supported monophyletic group. Both were included in the "Yacon group" (Grau & Rea 1997) defined on the basis of habit, morphology of the aerial parts and a common geographical distribution. The "Yacon group", as circumscribed by Grau & Rea (1997), included *S. sonchifolius*, *S. connatus*, *S. riparius*, *S. meridensis*, *S. siegesbeckius* and *S. macroscyphus*. The results of Rauscher (2002) recovered these species in distantly related clades. Our results, however, partially agree with the "Yacon group" by recovering *S. siegesbeckius* and *S. macroscyphus* as sisters.

Certain deeply nested clades obtained in our study had been analyzed previously by other authors. This is the case of the *S. maculatus*-*S. riparius* clade, here defined by 15 ray florets. Wells (1965) (in agreement with our results) suggested that these species are closely related. Molecular studies, however, did not support these relationships (Rauscher 2002). Wells (1965) and Robinson (1978) considered *S. maculatus* and *S. uvedalius* as different species. Wells (1965) indicated that differences in cypsela size were enough to keep them separate, but Turner (1988) considered that cypsela size is a very inconsistent and variable character. Our results show that both species are not closely related, in agreement with Rauscher's results, evidencing that *S. maculatus* and *S. uvedalius* could be different entities.

In our analysis, the *Smallanthus oaxacanus*-*S. mcvaughii* clade was defined by 10 ray florets, pinnatifid blade margins and obovate ray limbs. These results agree with Wells (1967) who suggested that *S. mcvaughii* is very similar to *S. oaxacanus*. Despite this, both species differ in several features, such as plant size, shape of blade base, capitulum size, shape and size of phyllaries and paleae, ray floret size and colour, and cypsela shape and size.

Wells (1965) regarded *Polymnia cocuyensis* and *Polymnia meridensis* as synonyms. Robinson (1978), when restoring the genus *Smallanthus*, transferred *Polymnia meridensis* to this genus, among other species. In agreement with Wells, Robinson considered *Polymnia cocuyensis* as a synonym of *Smallanthus meridensis*. In our study, we coded these species as two separate entities based on considerable differences in morphology (Vitali, in prep.). Neither species were recovered as sisters in the cladogram. Indeed, according to our own observations of type and other specimens (Vitali, in prep.), the two species differ in habit, number of inner phyllary series, palea pubescence and ray limb shape. Based on our results, *Polymnia cocuyensis* and *S. meridensis* are not regarded as synonyms. Since in this study *Polymnia cocuyensis* was recovered nested within *Smallanthus*, we propose a new combination for this species:

***Smallanthus cocuyensis* (Cuatrec.) Vitali comb. nov.**

Basionym: *Polymnia cocuyensis* Cuatrecasas (1954: 247).

Type:—COLOMBIA. Boyacá: 14 September 1938, J. Cuatrecasas & H. García Barriga 1700 (holotype F!, isotype COL).

Evolution and value of quantitative characters.

Quantitative characters were not discretized in this analysis because of the lack of manifest gaps throughout the range values. Wiens (2001) raises three additional problems when cutoffs or ranges are implemented. First, considerable variation within character state ranges may be ignored. Second, differences within intervals may be larger than between intervals. Third, the use of cutoffs and ranges may not reflect the differences in the amount of change between character states. Several authors have suggested that these problems can be solved by replacing cutoffs with characters coded as continuous variables (Poe & Wiens 2000, Wiens 2001, Goloboff *et al.* 2006).

From the analysis of quantitative characters, different patterns were obtained (Fig. 4). The species of *Smallanthus* that presented shorter corolla rays and shorter inner phyllaries had also a higher total number of capitula. By contrast, the species that showed higher values of ray corolla length and inner phyllary length had also a lower total number of capitula. This corresponds to the idea that longer rays favor pollinator attraction when the units are individual heads rather than clusters of small heads in large compound inflorescences (Andersson 1996,

2008). It is possible that the aggregation of capitula into larger units enhances the plant's visual display, relaxing selection for more conspicuous florets (Andersson 1991) (i.e., with longer ray limbs). Indirect evidence for such synergy is provided by the occasional reduction (or loss) of attractive structures in Asteraceae, with many heads assembled into compound inflorescences (Burt 1977, Leppik 1977, Andersson 1991, Andersson & Widen 1993).

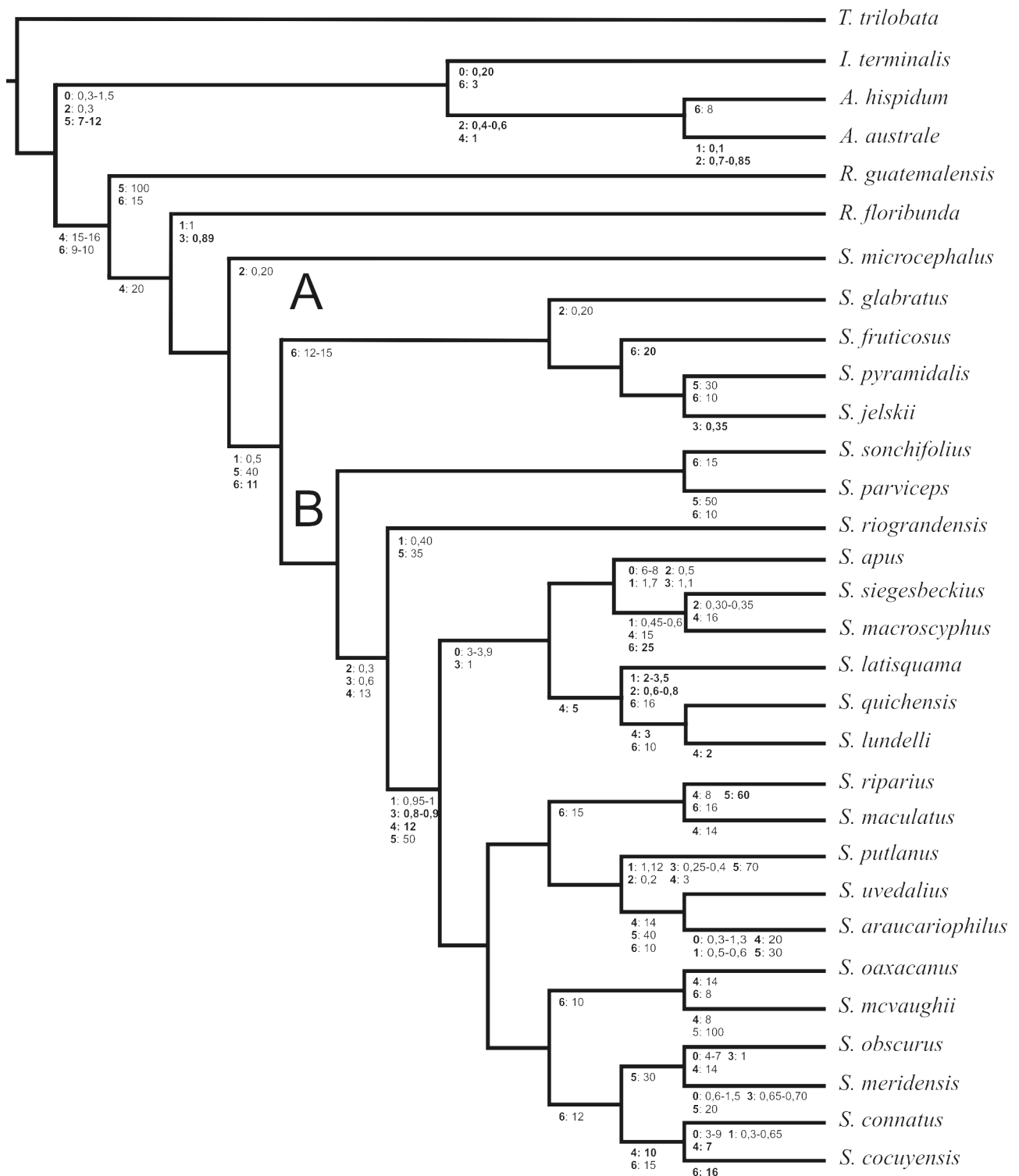


FIGURE 4. The single most parsimonious cladogram showing the quantitative characters. Below branches the characters and their optimized states are shown, synapomorphies in bold. Quantitative characters were transformed from the standardized to raw data for a better understanding (Appendix 2). Abbreviations as in Fig. 3.

The number of disc and ray florets has helped to define clades within *Smallanthus*. For instance, clade A (including *S. glabratus*, *S. fruticosus*, *S. pyramidalis* and *S. jelskii*) was defined here by the presence of 20 ray florets (Fig. 4). In addition, two deeply nested species, *S. obscurus* and *S. meridensis*, were supported as sisters by 30 disc florets. We observed that the number of disc florets among the species of *Smallanthus* is highly variable (from 30 to 100 florets) with respect to the number of ray florets (8 to 25). This pattern was previously noticed by Dos Santos & Stubblebine (1987) in *Acanthospermum hispidum* Candolle. These authors suggested a greater commitment of the plants to maintaining a smaller variation in the number of female ray florets than in the number of male disc florets, probably due to the importance of the first in the control of the number of seeds.

The quantitative characters used in this work provided phylogenetic information that allowed distinguishing some patterns in the number and measurements of selected floral structures of *Smallanthus*. More specific studies of this genus are required to establish whether plant-pollinator interactions, and the consequent dispersal mechanisms of the genus, are related with these patterns.

Evolution of qualitative characters.

The presence of functionally staminate disc florets has been used to define groups within Heliantheae (sensu lato) such as, for instance, Melampodiinae. All the species of *Smallanthus* and those of the clade *Ichthyothere-Acanthospermum* shared functionally staminate disc florets. However, this character provided no information on the taxa analyzed in our work. This agrees with Rauscher (2002), who considered that the presence of functionally male florets might be an evolutionarily labile character in these taxa and other Heliantheae. As evidenced by the occurrence of sterility of the disc florets in several different tribes of the family (Bentham 1873, Panero 2007), grouping genera by this character might seem artificial because such a feature has evolved independently in several instances of Asteraceae (Gray 1884, Turner & Johnston 1956, Stuessy 1973, Turner 1978). Frequent changes in disc floret function could be a result of a simple underlying genetic system (Turner 1978). The presence of functionally staminate disc florets within the tribe Millerieae would not be informative either, since these florets seem to have arisen independently in distantly related taxa within the tribe (e.g., within the subtribes Desmanthodiinae, Espeletiinae, and rarely in Galinsoginae and Guadiolinae) (Panero 2007).

Another particular character was the bilabiate-like marginal corollas of *Smallanthus jelskii*, which are similar to those present in *Tridax*. These are not found in any other species of *Smallanthus* nor in other genera of Milleriinae (Panero 2007). Karis (1993) states that *Smallanthus* and *Tridax* sometimes have a smaller adaxial lobe in marginal corollas. Wells (1965) called the adaxial lobe outer “ligule” and suggested that it was an extension of the pericarp. In this study, we consider that the corollas of *S. jelskii* are bilabiate-like, with one or two very minute inner lobes, smaller than a 2–3-lobed external lip, similar to those present not only in *Tridax* but in many other subtribes of Millerieae (Panero 2007). This character seems to have arisen independently in different groups of this tribe, so we question its value for defining groups within the tribe.

Phylogenetic analyses and chemical compounds.

Some authors have proposed relationships between the species of *Smallanthus* based on chemical constituents. *S. connatus* and *S. macrocyphus* have been regarded as synonyms by Wells (1965) and Robinson (1978), based on morphological data. Bach *et al.* (2007), however, proposed that these species are distinct taxa, based on differences in the sesquiterpene lactone chemistry of florets and leaves. The same result was obtained by Coll Aráoz *et al.* (2010) in a study on diterpenes of the root cortex. In the present study, we considered that they are different species, in agreement with Cabrera (1978) and Grau & Rea (1997). In our phylogenetic analysis, both species were recovered as distantly related, supporting the results from chemical data. All this evidence allows us to conclude that they are different species.

Moreover, Bach *et al.* (2007) state in their study that *S. connatus* is more chemically similar to *S. sonchifolius* than to *S. macrocyphus*. In our study and in the molecular analysis of Rauscher (2002), *S. connatus* and *S. sonchifolius* were also phylogenetically distant. Thus, in this case, the phylogenetic results do not support the chemical evidence.

On the other hand, melampolides, kaurenoic acid derivatives and geranylnerol derivatives, similar to those reported in *Smallanthus*, have been found in other members of Milleriinae, e.g. *Ichthyothere* spp. (Coll Aráoz *et al.* 2010). As stated above, the presence of shared chemical constituents could have a phylogenetic value. Additional chemical studies on other genera related to *Smallanthus* (e.g., *Rumfordia*) could help answering phylogenetic and taxonomic questions.

TABLE 1. Distribution of the species of *Smallanthus* by country. ARG: Argentina, URY: Uruguay, PRY: Paraguay, BRA: Brazil, BOL: Bolivia, PER: Peru, ECU: Ecuador, COL: Colombia, VEN: Venezuela, PAN: Panama, CRI: Costa Rica, NIC: Nicaragua, HND: Honduras, SLV: El Salvador, GTM: Guatemala, BLZ: Belice, MEX: Mexico, USA: United States.

	ARG	URY	PRY	BRA	BOL	PER	ECU	COL	VEN	PAN	CRI	NIC	HND	SLV	GTM	BLZ	MEX	USA
<i>S. microcephalus</i>																		
<i>S. glabratus</i>																		
<i>S. fruticosus</i>																		
<i>S. pyramidalis</i>																		
<i>S. jelskii</i>																		
<i>S. sonchifolius</i>																		
<i>S. parviceps</i>																		
<i>S. riograndensis</i>																		
<i>S. apus</i>																		
<i>S. siegesbeckius</i>																		
<i>S. macroscyphus</i>																		
<i>S. latisquamis</i>																		
<i>S. quichensis</i>																		
<i>S. lundelli</i>																		
<i>S. riparius</i>																		
<i>S. maculatus</i>																		
<i>S. putlanus</i>																		
<i>S. ivedaluis</i>																		
<i>S. araucariophilus</i>																		
<i>S. oaxacanus</i>																		
<i>S. mcvaughii</i>																		
<i>S. obscurus</i>																		
<i>S. meridensis</i>																		
<i>S. connatus</i>																		
<i>S. cocuyensis</i>																		

CLADE A

CLADE B

Distribution of *Smallanthus*.

The genus *Smallanthus* is distributed throughout most of the American continent, covering the southernmost portion of the Holarctic Region and the northern and central portions of the Neotropical Region, except the Caatinga Province (Cabrera 1973). *S. microcephalus* and all species of clade A live in the Moist North-Central Andes system (Josse *et al.* 2003). Within clade A, only *S. jelskii* is restricted to the Peruvian Andes (2200–3350 m elev.), whereas the other species have wider distributional ranges. Most species of clade B are found in Dry Meso-America Systems and Meso-American Seasonal Highlands Systems (Josse *et al.* 2003). A large number of endemics are found within this clade. There are two species endemic to south-eastern Brazil: *S. araucariophilus* lives in wet areas of the Araucaria Forest (1000 m elev.) and *S. riograndensis* lives in the Atlantic and Subtropical Rain Forests of north-eastern Rio Grande do Sul (300–500 m elev.). Other species are found exclusively in forests of south-central Mexico, such as *S. putlanus* (1000 m elev.), *S. obscurus* (2300 m elev.) and *S. mcvaughii* (1500–2200 m elev.). Finally, *S. cocuyensis* is endemic to the Andes of Colombia (1700–2750 m elev.), and *S. meridensis* to the Andes of Venezuela (2500–3045 m elev.).

In the molecular analysis of Rauscher (2002), the major clades recovered for *Smallanthus* contained both South American and Central or North American species, suggesting that dispersal across the Isthmus of Panama has occurred multiple times in the history of the genus. Our results, based on morphology, showed a similar pattern to that of Rauscher, with mixed distributional patterns involving South American and Central or North American species.

Conclusion

Based on the results of our single most parsimonious tree we could consider *Smallanthus* as monophyletic, in agreement with previous molecular analyses. *Smallanthus* is defined here by ray corollas densely pubescent at the base. We could recognize two clades in *Smallanthus*, the first including *S. glabratus*, *S. fruticosus*, *S. jelskii* and *S. pyramidalis*, and the second including *S. siegesbeckius*, *S. macroscyphus*, *S. maculatus*, *S. riparius*, *S. uvedalius*, *S. cocuyensis*, *S. meridensis*, *S. oaxacanus*, *S. mcvaughii*, *S. sonchifolius*, *S. parviceps*, *S. riograndensis*, *S. apus*, *S. latisquamus*, *S. quichensis*, *S. lundelli*, *S. obscurus*, *S. putlanus* and *S. araucariophilus*. These clades, however, had a weak support. The species of the first clade share several morphological characters with *Rumfordia*.

Furthermore, as a contribution to the understanding of the relationships between subtribes of Millerieae, *Ichthyothere* was recovered as phylogenetically more distantly related to *Smallanthus* than to *Rumfordia*.

Based on our results, *Polymnia cocuyensis* and *Smallanthus meridensis* were regarded as distinct entities. Regarding the characters used for this study, we could conclude that: 1) quantitative characters were found to be informative when treated as continuous variables, 2) the presence of functionally staminate disc florets provided no information on the groups analyzed in our work, and neither did the bilabiate-like marginal corollas. The evidence from chemical studies on species of *Smallanthus* with medicinal uses partially support some of the clades obtained in our analyses.

The major clades of *Smallanthus* contained both South American and Central or North American species, suggesting that dispersal across the Isthmus of Panama has occurred multiple times in the history of the genus, as stated by other studies on this tribe.

Further studies at the level of subtribe, based on both molecular and morphological characters, would be necessary to resolve questions about the relationship of *Smallanthus* with other genera of the subtribe Millerieae, particularly with the potentially closely related genus *Rumfordia*.

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APPENDIX 1. Additional specimens examined.

- Tridax trilobata* (Cavanilles) Hemsley: MEXICO. *Berlandier* 922 (LP). México: 28 August 1890, *C. G. Pringle* 3148 (LP); 2 km. al O de Tlalnepantla, 2300 m orilla de camino, 18 August 1962, *G. C. Rzedowski* 15870 (LP); Cuautitlán, 2250 m orilla de canal cercano a la carretera, 1 August 1965, *C. Rzedowski* 20315 (LP); 12 September 1865. Michoacán, 12 October 1892, *C. G. Pringle* 4271 (LP).
- Acanthospermum australe* (Loefling) Kuntze: ARGENTINA. Buenos Aires: Isla Martín García, April 1935, *A. Pastore* 225 (LP, SI); April 1997, *J. Hurrell et al.* 2402 (LP). Entre Ríos: Gualeguaychú, August 1932, *A. Burkart* 4252 (LP); December 1936, *A. Cabrera* 4001 (LP).
- URUGUAY. Colonia: Carmelo, November 1934, *A. Cabrera* 2337 (LP). Rio Negro: San Javier, January 1936, *J. Chebataroff* 2310 (LP). Montevideo: February 1876, *Gibert s. n.* (LP).
- Acanthospermum hispidum* Candolle: ARGENTINA. Buenos Aires: *J. F. Molfino* 595 (BAF). Salta: La Caldera, en cause de arroyo seco, 16 April 1942, *A. T. Hunziker* 1633 (LP); Capital: Ciudad de Salta, 10 November 1939, *M. Scott de Birabén & M. Birabén* 1305 (LP).
- PARAGUAY. San Pedro: Colonia Primavera, 3 April 1956, *A. Woolston* 669 (LP). Asunción: Mercado Pettirossi, 4 September 1971, *A. Krapovickas* 19675 (LP).
- Ichthyothere terminalis* (Sprengel) Blake: BRASIL. Amazonas: San Gabriel, Rio Negro, Alto Caiari, en terrenos abandonados, 27 December 1945, *R. Froes* 21553 (LP); Manaus, Taramá, 27 January 1963, *E. Santos et al. s. n.* 25548 (LP).
- COLOMBIA. Boyacá: Casanare, about 70 km. south, about 150 m, 65° east of Orocué, open llanos, 22 April 1939, *O. Haught* 2780 (LP).
- VENEZUELA. Bolívar: Bajo Caura, común en la sabana, 100 m 11 April 1939, *W. Llewellyn* 11740 (LP).
- Rumfordia guatemalensis* (J.M. Coulter) S.F. Blake: GUATEMALA. Alta Verapaz: Senahú, 3500 feet, April 1889, *D. Smith* 1592 (K).
- Rumfordia floribunda* Candolle: MEXICO. *Karwinski von Karwin s/n.* (M). Oaxaca: Cerro San Felipe, 29 November 1895, *C. Conzatti* 30 (GH). Guerrero: at and just below Summit of Cerro Alquitrán, 17–18 km. by road west of Méx. highway 95 and Mazatlán, 2600–2650 m, 6 December 1966, *W. Anderson & C. M. Laskowski* 4410 (MICH). Jalisco: camino de Atenquique al Nevado de Colima, 10 January 1965, *G. C. Rzedowski* 19370 (LP); Steep mountains 20–22 km. south of Talpa de Allende, in the headwaters of a west branch of Río de Talpa, 1200–1450 m, 28–30 March 1965, *R. McVaugh* 23286 (LL).
- Polymnia cocuyensis* Cuatrecasas: COLOMBIA. Boyacá: a los alrededores de Cocuy, 2750 m, 14 September 1938, *J. Cuatrecasas* 1700 (F). Cundinamarca: valle del rio Guavio, 4 km. al N de Ubalá, 1725 m, en carretera de bosque templado, 19 May 1944, *M. L. Grant & F. R. Fosberg* 9375 (F).
- Smallanthus putlanus* B.L. Turner: MEXICO. Oaxaca: Putla, Santa Cruz, Itundujia, a 5 km. en LR (W) de la Agencia de la Victoria, 191 m, 16°44'7'' N, 97°45'36'' W, 2 August 2008, *K. V. Gutierrez* 3099 (TEX).
- Smallanthus apus* (S.F. Blake) Robinson: MEXICO. Nayarit: Sierra Madre, between Santa Gertrudis and Santa Teresa, 8 August 1897, *J. N. Rose* 2077 (NY); 2079 (US).
- Smallanthus obscurus* B.L. Turner: MEXICO. Chiapas: San Cristobal, along road to Chanal a 16–20 km. east of Chilil, 2380 m, 10 November 1976, *D. E. Breedlove* 41387 (TEX, MO).
- Smallanthus meridensis* (Steyermark) H. Robinson: VENEZUELA. Mérida: rocky tickets on slopes below Chachopo, 3045 m, 22 July 1944, *J. A. Steyermark* 57519 (F); La Carbonera, 2500 m, September 1956, *L. Aristegieta* 2484 (F).
- Smallanthus araucariophilus* Mondin: BRASIL. Rio Grande do Sul: Cambará do Sul, na estrada para São José dos Ausentes, 13 November 2002, *C. Mondin & A. Iob* 2553 (HASU); Ouro Verde, ca. 2 km. da celulosa Cambará, 31 January 2003, *C. Mondin & A. Iob* 2920 (HASU); Cacapava do Sul, beira da estrada, 9 December 2005, *V. F. Kinupp* 3131 (ICN).
- Smallanthus lundelli* Robinson: GUATEMALA. Baja Verapaz: Unión Barrios, on the Salama-Coban Road, south of km. 147, in high on hill, 5 February 1975, *C. L. Lundell & E. Contreras* 18916 (F, LL, US); 27 February 1972, *E. Contreras* 11065 (S).

- Smallanthus microcephalus* (Hieronymus) Robinson: ECUADOR. Cañar: 2–6 km. NE of Pindilig to Rivera, hillside road, 3000 m, 2°36' S, 78°49' W, 19 January 1985, *J. L. Luteyn & E. Cotton 11133* (F). Chimborazo: Valle Pallatanga, *A. Sodiro 24/2* (B); Chimborazo, 13,8 km. North of the entrance to the Soffhuigra more near the Panamerican highway, road to Riobamba, 2340 m, 3 July 1992, *J. L. Panero & B. Clark 2906* (TEX). PERU. Cajamarca: Contumazá, El Molino (Cascas-Contumazá), 2200 m, 31 May 1990, *A. A. Sagástegui et al. 14271* (TEX).
- Smallanthus maculatus* (Cavanilles) Robinson: BELICE. Cayo, Smokey Branch Camp. Camp. Environs, path side ticket, 450 m, 13 May 1995, *C. Whitefoord 9306* (F). COSTA RICA. Alajuela: Zarcero, 1650 m, 1 October 1937, *A. Smith 462* (F). EL SALVADOR. San Salvador: in forest El Picacho, NE of El Boquerón, Volcán San Salvador, 1950 m, 1 March 1968, *A. R. Molina & E. Montalvo 21838* (F). GUATEMALA. Baja Verapaz: 17 miles from Salamá on road to Cobán, Patal, 1600 m, July–December 1958, *J. G. Hawkes, J. P. Hjerting & R. N. Lester 1936* (F, K). HONDURAS. Comayagua: along trail about 6 km. N of Siguatepeque, 1200 m, 8 April 1936, *T. G. Yuncker, R. F. Dawson & H. R. Youse 6311* (G, K, S). MEXICO. San Luis de Potosí: 15 km. NE de ciudad del Maíz, ladera caliza, 1300 m, 30 June 1959, *J. C. Rzedowski 11146* (LP). NICARAGUA. Jinotega: camino entre Wiwili y El Carmen, sobre los márgenes del Río Coco, 300 m aproximadamente, 13°37' N a 13°42' N y 85°50' W, 2 March 1980, *M. Araquistain & P. P. Moreno 1582* (F). PANAMA. Chiriquí: Distrito Boquete: Volcán de Chiriquí, 2550 m, 15 July 1938, *M. E. Davidson 978* (F).
- Smallanthus connatus* (Sprengel) Robinson: ARGENTINA. Buenos Aires: Isla Martín García, cantera, 22 January 1996, *J. Hurrell et al. 2817* (LP); La Plata, Punta Lara, 2 January 1939, *A. Cabrera 4906* (LP). Corrientes: San Martín, Yapeyú, 18 December 1946, *A. M. R. Huidobro 3726* (F, S). Misiones: Apóstoles, Ruta 203 entre Ruta 14 y Ruta 1, 13 November 1978, *A. Cabrera & A. A. Sáenz 29177* (LP). BRASIL. Paraná: Ponta Grossa, 9 December 1903, *P. Dusén 2494* (S). Rio Grande do Sul: Porto Alegre, Triunfo, Barretos, 6 April 2002, *C. Mondin 2643* (HASU). PARAGUAY. Misiones: Estancia La Soledad, Santiago, 13 December 1969, *T. M. Pedersen 9551* (S). URUGUAY. Maldonado: La Barra, cerca del Rio Santa Lucia, February 1936, *J. Chebataroff 969* (LP). Rocha: Palmares de Castillos, región de colinas al N de Castillos, 22 January 1944, *H. H. Barlett 21385* (LP).
- Smallanthus sonchifolius* (Poeppig) Robinson: BOLIVIA. Santa Cruz: Vallegrande, Santa Cruz, Huasacañada, 5 km. al S de Vallegrande, 18°31'05'' S, 64°05'08'' W, 2050 m, 15 June 1991, *G. Israel & C. Vargas 1012* (F). Cochabamba: 1891, *M. Bang 1229* (G). La Paz: Larecaja, vicinus Sorata, *Andium Boliviensium*, 2700 m, April 1859, *G. Mandon 28* (G, S). ECUADOR. Pichincha: Quito, in hortulo, 29 December 1919, *I. Holmgren 130* (S). Chimborazo: Riobamba, Altiplano Interandino, 2800 m, April *A. Rimbach 727* (S). PERU. Cajamarca: Celendín, Choctapampa cerca de Celendín, campos de cultivo, 2780 m, 3 July 1975, *Sanchez Vega 1648* (F); Cajabamba, Caserío Campana, carretera a Lluchubamba, 3800 m, 11 April 1991, *Sanchez Vega 5550* (F).
- Smallanthus macroscyphus* (Baker) Grau: ARGENTINA. Salta: Orán, Cordillera Oriental de Zenta Trancas, 2200 m, 23°07'0,73''S, 64°54'59,7''W, *A. Schinini, C. T. Saravia & R. Neuman 34710* (F, GH); Rosario de Lerma, Quebrada del Toro, frente al Rio Blanco, en quebrada húmeda con selva en galería, 1700 m, 7 April 1987, *L. J. Novara 6484* (G, S); El Pacara, Ruta 23, 4 km. al NE de R. de Lerma, en banquinas y alambrados próximos a cultivos, 1330 m, 15 March 1987, *L. J. Novara 6288* (G, S); La Caldera, Alto La Sierra, Ruta 68 km., pasando Vialidad Nacional, yungas, bosque montano, templado húmedo, 1500–1600 m, 12 February, *L. J. Novara 8575* (G, S); Chicoana, La Viña a 6–7 km. al Sur de Rosario de Lerma. Ambiente con modificación antrópica, 1250–1300 m, 20 March 1988, *L. J. Novara 7846* (G, S). BRASIL. Rio de Janeiro: Itatiaia, 1200 m, December 1992, *O. Kuntze s. n.* (G).
- Smallanthus riograndensis* Mondin: BRASIL. Rio Grande do Sul, São Francisco de Paula, Tainhas, Serra do Pintos, 27 April 2002, *C. Mondin & A. Iob 2653* (HASU, ICN); *C. Mondin & A. Iob 2654* (HASU, ICN); Tainhas, Aratinga, a 8 km. da vila em direcao a Terra de Areia, 31 January 2003, *C. Mondin 2922* (HASU, ICN); Tres Coroas, al borde de la carretera de tierra que conecta el RS 020 a Tres Coroas, justo debajo de la entrada del Centro Budista, 24 February 2006, *V. F. Kinupp 3149 & H. Lorenzi* (ICN); *Matzenbacher 53449* (ICN).
- Smallanthus siegesbeckius* (Candolle) Robinson: BOLIVIA. La Paz: Sud Yungas, 1890, *M. Bang 466* (G). BRASIL. Paraná, Ponta Grossa, 6 March 1910, *P. Dusén 9503* (GH, LP). Minas Geraes, 1845, *Widgren s. n.* (GH). PARAGUAY. Guairá: Colonia Independencia, orilla de arroyo selvático, March 1924, *T. Rojas 4833* (LP). PERU. Cusco: La Convención, potrero, cerro San Pedro, laderas, borde del camino, 1300–1600 m, 8 March 1942, *C.*

Vargas 2583 (LP). Cajamarca: Jaén, Ruta Huahuaya-Tabaconas, riachuelo, 870 m, 2 August 1994, *S. G. Leiva, P. Chuna & J. Cadle 1267* (F).

Smallanthus riparius (Kunth) Robinson: COLOMBIA. Cauca: plateau of Popayan, 1700–2500 m, *F. C. Lehmann 5528* (F); Cordillera central, vertiente occidental, Hoya del Río Palo, márgenes del río entre Tacueyó y La Tolda, 1780–1900 m, 19 December 1944, *J. Cuatrecasas 19511* (F).

ECUADOR. Pichincha: Chiriboga, 1900 m, 26 April 1955, *E. Asplund 16066* (S). Tungurahua, Río Verde, along the road Baños-Puyo, 1300–1400 m, 17 July 1967, *B. Sparre 17685* (S).

PERU. Piura: Huancabamba, San Antonio, 1000–1200 m, March 1912, *A. Weberbauer 6016* (GH).

VENEZUELA. Miranda: Petare and vicinity near Caracas, 800 m, 11 September 1921, *H. Pittier 9787* (GH); Los Teques, in German plantations, Parque de los Bárbaros, 1400–1500 m, 19 October 1917, *H. Pittier 7510* (GH).

Smallanthus fruticosus (Benth) Robinson: BOLIVIA. La Paz: Larecaja, vicinus Sorata, 18 September 1818, *G. Mandon 30* (GH).

COLOMBIA. Cauca: Nariño, Samaniego, road 5 km. from Tuquerres, headwaters of Río Pasqual, ca. 3000 m, 7 February 1945, *A. J. Ewan 16893* (F).

ECUADOR. *K. T. Hartweg 1158* (K). Bolívar: Pucará de Telimbela, descenso de Cordillera Occidental, 2600–3000 m, 18 November 1943, *M. Acosta Solís 6814* (F). Cañar: along the Pan-American Highway (route 1) ca. 1 km. SE of Cañar, ca. 10200 feet, 30 January 1974, *R. M. King 6621* (F). Azuay: Cochapata, parroquia Cochapata, bosque húmedo montano bajo, 2720 m, 03°23' S, 79°05' W, 8 August 1991, *C. E. Cerón 16048* (QCNE).

PERU. La Libertad: Otuzco, arriba de piedra gorda (ruta Salpo-Samne), borde de carretera, ladera de arbustos. 2840 m, 16 June 1994, *S. G. Leiva, Paredes & M. Rodríguez 1196* (F); debajo de Shitahuara (camino a San Andrés de Cárcel), ladera de arbustos, 2000 m, 16 May 1991, *S. Leiva & P. Leiva 314* (F).

Smallanthus quichensis (J.M. Coulter) Robinson: GUATEMALA. Quiché: 8000 feet, April 1982, *E. T. Heyde & A. Lux 3, 375* (F, G); within edge of heavy forest, 8500 feet, 17 November 1934, *A. F. Skutch 1704* (GH). San Marcos: barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta, an upper part of the barranco between Finca La Lucha and Buena Vista, damp ticket, 2500–2700 m, 6 February 1941, *C. P. Standley 86278* (G); *C. P. Standley 86278* (F); along road above Barranco Eminencia, 2700 m, 14 March 1939, *C. P. Standley 68575* (F); between San Sebastian and Todos Santos, upper slopes of Volcán Tajumulco, 3000–3800 m, 1 March 1940, *J. A. Steyermark 36952* (F); montane cloud forest on outer slopes of Tajumulco Volcano, Sierra Madre Mountains, about 10 km west of San Marcos, 2400–2700 m, 3 January 1965, *L. O. Williams et al. 27187* (F).

Smallanthus oaxacanus (Schultz Bipontinus ex Klatt) Robinson: GUATEMALA. Huehuetenango: trail between Democracia and Santa Ana Huista, Sierra de los Cuchumatanes, 800–1000 m, 25 August 1942, *J. A. Steyermark 51306* (F, G, GH). Alta Verapaz: Coban, 1350 m, December 1907, *H. von Türckheim II 1494* (F, G, GH, S). Chiquimula: in forest of Quebrada Resimiento, 4 km. north of Esquipulas, 1100 m, 27 September 1971, *A. R. Molina & A. R. Molina 26794* (F). Quiché: 1942, *J. I. Aguilar 1193* (F).

HONDURAS. Comayagua: Barranco de Trincheras, 1300 m, 29 August 1955, *A. R. Molina 5815* (F).

MEXICO. Chiapas: Hacienda Monserrate, September 1923, *C. A. Purpus 9102* (GH).

Smallanthus pyramidalis (Triana) Robinson: COLOMBIA. Boyacá: south side of valley of Río Gomeza (Río Arobispo), 6 km E. of Socha, 3050–3070 m, 72°57' W, 6° N, 11 November 1944, *F. R. Fosberg 22308* (F). Cundinamarca: Cordillera oriental, sabana de Bogotá, 2600 m, 8 January 1942, *J. Cuatrecasas 13548* (F, LP); Canyon at N.E. edge of Bogotá, (E. of calle 72), in dwarf forest at canyon bottom, 9000 feet, 19 March 1945, *E. L. Little & R. R. Little 9792* (F, LP). Santander: vicinity of La Baja, 2700–3500 m, 14–31 January 1927, *E. P. Killip & A. C. Smith 18043* (GH).

VENEZUELA. Mérida: Santo Domingo-Apartaderos, 2600 m, September 1956, *L. Aristeguieta 2421* (F); Santo Domingo, La Honda, alrededores El Medio, 2500 m, 2 May 1969, *C. E. Benítez de Rojas 664* (F); Rangel, alrededores de Mucuruba, 2300 m, 23 October 1972, *V. M. Badillo 5320* (F).

Smallanthus jelskii (Hieronymus) Robinson: PERU. Cajamarca: Cajamarca, La Encañada-Jalca de Kumulca, ladera, 3300 m, 17 June 1975, *A. A. Sagástegui, J. S. Cabanillas & O. C. Dios 8090* (F); entre La Encañada y Kumullca, quebrada con arbustos, 3300 m, 17 June 1975, *I. Sanchez Vega & J. Sanchez Vega 1589* (F); Chota, Chota-Bambamarca, en ladera de arbustos 2740 m, 27 May 1965, *A. Lopez & A. A. Sagástegui 5471* (LP); near villaje de El Campamento, ca. 21 km. W.N.W. of Huambos, fragmented montane forest, 2430 m, 6°24'23" S, 79°01'19" W, 20 April 1993, *M. O. Dillon, V. I. Sanchez & M. M. Sanchez 6422* (F); Cutervo, Madre Mía entre el Suro y la Flor, al Noroeste del Parque, bosque de neblina perennifolio, 2400 m, 25 June 1992, *I. Sanchez Vega & A. Miranda 6331* (F); Celendín: Guañambra-Sendemal, quebrada, 2800 m, 19 August 1984, *A. A. Sagástegui, J. Mostacero & S. Leiva 12197* (F); km. 61 carretera Celendín hacia Cajamarca, a 21 km. de la Pampa del Toro hacia Cajamarca, 3350 m, 10 November 1984, *C. P. Cowan & C. V. Torrel 4422* (F). Amazonas: Chachapoyas, 5 km. de Quebrada Molino, below Chachapoyas, 2200 m, 30 May 1962, *J. J. Wurdack 618* (GH, LP).

- Smallanthus latisquamus* (S.F. Blake) Robinson: COSTA RICA. Cartago: hickets along Rio Birris, Volcán Irazú, 9000 feet, 9°57'5N, 83°51' W, 30 July 1977, *G. L. Webster 22131* (F); east of Volcán Irazú, along streams in forest, 9000 feet, 17 May 1928, *H. E. Stork 2071* (GH); Cartago, Río Birris, southern slope of Volcán de Irazú, wet thicket, 23 February 1924, *P. C. Standley 35412* (GH); Cartago, road to Volcán Irazú, 23 August 1940, *M. A. Chrisles 5544* (F). GUATEMALA. Huehuetenango: San Mateo Ixtatan, sierra de los Cuchumatanes, cloud forest 4 miles east San Mateo Ixtatan on road to Barillas, 2800 m, 7 February 1965, *D. E. Breedlove 8724* (F); rich moist cool foresta round Cruz de Limón, 3 ½ miles east of San Mateo Ixtatán, Sierra de los Cuchumatanes, 2900 m, 10 July 1942, *J. A. Steyermark 49833* (F). Jalapa: vicinity of Soledad, montaña Marimundo, between Jalapa and Mataquesuintla, 2000–2500 m, 4 December 1939, *J. A. Steyermark 32621* (F).
- Smallanthus glabratus* (Candolle) Robinson: BOLIVIA. La Paz: Larecaja, Sorata, 8000 feet, September 1888, *H. H. Rusby & N. L. Britton 1669* (K).
- PERU. Lima: Huarochiri, San Mateo, 3200 m, 28 May 1940, *E. Asplund 11186* (S); Rio Blanco, open hillside, 3000–3500 m, 15–17 April 1929, *E. P. Killip & A. C. Smith 21647* (F). Cajamarca: Celendin carretera Celendín-Balsas, cerca de Jelig, 2800 m, 14 April 1982, *I. Sanchez Vega 2781* (F); 41 km. NE of Cajamarca along the road to Celendín, 10,4000 feet, 9 January 1983, *L. R. Merrill King & L. E. Bishop 9138* (G, K). Huancavelica: Castrovirreyna, open quebrada, in sun, good drainage, 3050–3300 m, 27–28 March 1942, *R. D. Metcalf 30279* (G, GH).
- Smallanthus parviceps* (S.F. Blake) Robinson: BOLIVIA. La paz: Larecaja, 21 April 1920, *E. W. D. & M. M. Holway 558* (GH).
- PERU. Cajamarca: Contumazá, El Túnel (Cascas-Contumazá), quebrada 2700 m, 6 April 1985, *A. A. Sagástegui et al. 12634* (F). Cusco: Quispicanchi Hda. Tio, laderas. 2000 m, 1 January 1943, *C. C. Vargas 3065* (LP); Calca, Vilcabamba, laderas arbustivas, 2700 m, 7 January 1944, *C. C. Vargas 3972* (LP). Ancash: Bologsi, cerca de Chiquián, cerca de una acequia de aguas permanentes. 3350–3400 m, 15 March 1950, *R. Ferreyra 7456* (LP). Huancavelica: Tayacaja, Ampurco, 3000–3100 m, 19 April 1962, *O. Tovar 3789* (LP). Puno: Sandía, Cuyo-cuyo, growing along river. Bank of river on plane of valley, 3600 m, Long. 69°35', Lat. 14°25', 18 July 1981, *T. Johns 81–54* (F).
- Smallanthus mcvaughii* (J.R. Wells) Robinson: MEXICO. Jalisco: Sierra de Manantlán, 30–35 km. southeast of Autlán, precipitous seaward-facing slopes 1–4 km. below the Summit called "La Cumbre", near the lumber-road between El Chante and Cuzalapa, and above the abandoned site of Durazno, 1500–1900 m, 104°14' W, 19°32' N, 22–23 March 1964, *R. McVaugh 23189* (CAS, LL, MICH, MO); headwaters of Rio Mascota, 20–25 km, airline, southeast of Talpa de Allende, narrow valley of steep mountain stream ascending to the west from a point 12–13 km above (south of) El Rincón, on the road to Aserradero La Cumbre, humid forest, 1700–1900 m, 3–4 April 1965, *McVaugh R. 23456* (LL, TEX); Estación de Biología Las Joyas, en la sierra de Manantlán, entrando por El Chante, carretera Autlan-El Gruyo, 19°34' N, 104°14' W, 9 March 1992, *A. V. Campos 4363* (GH); *A. V. Campos, L. Panero & L. I. Cabrera 4563* (GH); at Las Joyas field station, on edge of cloud forest on top of Sierra de Manantlan occidental, 1900 m, 19°35' N, 104°15' W, *H. H. Iltis, B. F. Benz, A. G. Vázquez & M. B. Cházaro 29436* (F); Ca 2.5 km. (air) SE de Estación Biológica Las Joyas, 13 km. (air) SSE de Ahuacapán, big gate on main lumber road at very head of Arroyo San Campus, below crest of the NE slope of Sierra de Manantlán, bosque mesófilo de montaña, 2120 m, 19°34'31'' N, 104°15'12'' W, 19 March 1989, *M. A. Wetter, T. S. Cochrane & F. J. Santana 2034* (TEX).
- Smallanthus uvedalius* (Linnaeus) Mackenzie: COSTA RICA. San José: Aserrí, Cuenca del Tárcoles, carretera a Tarbaca, 500 mts. después de la entrada a Barrio Lourdes, a orilla de la calle, 1800 m, 9°50'25" N, 84°06'28.0007" W, 9 August 2001, *L. Acosta & V. Ramirez 3136* (S).
- EL SALVADOR. San Salvador: In forest El Picacho NE of El Boquerón, Volcán San Salvador, 1950 m, 1 March 1968, *A. R. Molina & E. Montalvo 21838* (F).
- ESTADOS UNIDOS. Pensilvania: Kettle Creek, forestal long Kettle Creek 6 1/2 miles S. W. of Washington., 135 m, 24 April 1907, *H. Wilbur & L. Duncan 11409* (LP). Virginia: Virginia, Scotland Wharf, James River, Surrey Co., 1 September 1930, *E. H. Walker 1314* (LP). Kentucky: County of Harlan Southeastern, August 1893, *T. H. Kearney s. n.* (G, S).
- GUATEMALA. Retalhuleu: San Felipe, 650 m, April 1892, *J. D. Smith 2863* (GH).
- HONDURAS. Atlántida: Cordillera Nombre de Dios, near Summit of pass on mountain road from Olanchite to La ceiba, roadside through patches of montane broad lead forest, 22 May 1987, *S. Blackmore & M. Chorley 4084* (F).
- MEXICO. Chiapas: Roadside weed in coffee plantation región at south base of Volcán Tacana, 2 km. south of Cacahuatan to the northeast of Tapachula, 400 m, 4 November 1970, *A. Cronquist 10874* (F, S).
- NICARAGUA. Jinotega: Santa Lastenia, between Matagalpa and Jinotega cloud forest remnants, 1450 m, 13°02' N, 85°57' W, 22 August 1984, *W. D. Stevens 23003* (F).
- PANAMA. Chiriquí: Boquete District, Volcán of Chiriquí, 2550 m, 15 July 1938, *M. E. Davidson 978* (F).

APPENDIX 2. Characters and character states used in the phylogenetic analysis.

Quantitatives:

0. Peduncle length.
1. Ray limb length.
2. Ray floret cypsela length.
3. Internal phyllary length.
4. Capitulum number.
5. Disc floret number.
6. Ray floret number.

Qualitatives:

7. Stem surface: (0) striated (1) smooth.
8. Stem structure: (0) hollow (1) massive.
9. Inferior leaf petiole: (0) present (1) absent.
10. Petiole shape: (0) unwinged (1) winged.
11. Auricule at petiole base: (0) absent (1) present.
12. Auricule disposition at petiole base: (0) not completely surrounding the stem (1) completely surrounding the stem.
13. Blade margin: (0) erose (1) cleft (2) entire (3) tripartite (4) pinnatifid.
14. Blade base form: (0) obtuse (1) cordate to rounded (2) truncate to hastate (3) attenuate to acute.
15. Blade apex: (0) attenuate (1) acute (2) obtuse.
16. Blade venation: (0) acrodromus (1) actinodromus.
17. Capitulum arrangement: (0) terminal (1) axillary.
18. Outer phyllary consistency: (0) coriaceous (1) foliaceous.
19. Outer phyllary apex: (0) obtuse (1) acute.
20. Number of inner phyllary series: (0) 4 (1) 2 (2) 1.
21. Inner phyllary consistency: (0) coriaceous (1) papyraceous (2) foliaceous.
22. Inner phyllary shape: (0) flat (1) concave (2) closed.
23. Inner phyllary apex: (0) obtuse (1) attenuate to acute (2) caudate.
24. Inner phyllary surface echinate to spinose: (0) absent (1) present.
25. Inner phyllary-cypsela relationship: (0) separated (1) embracing (2) fused.
26. Receptacle: (0) convex (1) flat.
27. Paleae shape: (0) elliptic (1) ovate-lanceolate (2) oblanceolate to rhombic (3) oblong.
28. Conical trichomes on paleae: (0) absent (1) present.
29. Glandular trichomes on paleae: (0) absent (1) present.
30. Ray floret type: (0) bilabiate-like (1) not bilabiate-like.
31. Ray limb shape: (0) orbicular (1) ovate to elliptic (2) oblong (3) obovate.
32. Ray corollas densely pubescent at the base: (0) absent (1) present.
33. Ray corolla-cypsela relationship: (0) corolla longer than cypsela (1) corolla shorter than cypsela.
34. Disc floret sexuality: (0) hermaphrodite (1) functionally staminate.
35. Cypsela surface: (0) smooth (1) striated.
36. Cypsela pubescence: (0) pubescent (1) glabrous.
37. Pappus: (0) present (1) absent.