



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

MAIRA S. VITALI¹ & JESSICA N. VIERA BARRETO¹

¹División Plantas Vasculares, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

E-mail: vitali@fcnym.unlp.edu.ar (corresponding author).

E-mail: jvierabarreto@fcnym.unlp.edu.ar

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 monofilía 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,

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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