



THE UNPREDICTABLE EXPLOSIVE DISPERSAL MECHANISM OF A PRICKLY NEOTROPICAL *Solanum* (SOLANACEAE)

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Abstract: The mechanism of explosive dehiscence is rare in fruits in *Solanum* (Solanaceae), being reported for *Solanum* sect. *Gonatotrichum*, a small non-aculeate group belonging to the Brevantherum clade. We tested empirically the presence of this strategy in populations of the closely related *S. mellobarretoii* and *S. leptostachys*, species belonging to the Leptostemonum clade, a group that comprises most aculeate species of the genus. Our results showed the occurrence of the explosive dehiscence in berries of *S. mellobarretoii*, but not in *S. leptostachys*, besides their phylogenetic and morphological similarities. We confirmed the homoplastic nature of the mechanism within the genus and highlight the importance of conducting empirical studies, contributing to reduce knowledge gaps on seed dispersal in the Neotropics.

Keywords: Autochory; berry; dispersal syndromes; explosive mechanism; seed dispersal.

Seed dispersal is a fundamental process of the life cycle of any plant species and influences competition, reproduction and colonization, as well as genetic structure within and among populations (Ouborg *et al.* 1999, Nathan & Muller-Landau 2000). Despite its importance, there are still knowledge gaps and poor-quality data regarding seed dispersal among flowering plants (Driscoll *et al.* 2014). In Brazil, Ribeiro *et al.* (2016) reported geographic, phylogenetic and functional biases in the available data on seed dispersal, with trees with fleshy fruits dispersed by vertebrates being studied disproportionately more than herbaceous plants with abiotic seed dispersal. Many studies infer dispersal agents by syndrome observation, considering certain fruit characteristics such as colour, size, and accessibility (Pijl 1972, Zama *et al.* 2012). In some cases, however, complex or unusual dispersion strategies may not be presumed without

experimental studies and accurate observations (Deminics *et al.* 2009, Vasconcellos-Neto *et al.* 2009). Empirical studies that gather field data take comparatively longer, represent isolated and local efforts and clearly fail to compete with current demands that give more importance to fast, complex and global studies (Ríos-Saldaña *et al.* 2018).

Solanum L. (Solanaceae) is considered one of the richest genera among angiosperms and the largest in Solanaceae, with about 1500 species (Frodin 2004, Weese & Bohs 2007) that occur on all continents except Antarctica (Vorontsova *et al.* 2013). The genus contains many species of economic interest, such as eggplant (*Solanum melongena* L.), tomato (*Solanum lycopersicum* Mill.) and potato (*Solanum tuberosum* L.). In addition, some species of the genus are known to have ecological importance in tropical forests, such as providing food for the fauna (Hernández-

Conrique *et al.* 1997) and playing a fundamental role in succession by behaving as pioneers (Guariguata & Ostertag 2001, Catterall 2016).

Fruits of Neotropical *Solanum* are typically berries that usually carry several seeds. They vary in size and colour, traits associated mostly with dispersal mediated by animals, such as bats and birds (Knapp 2002). Autochory is described to the Leptostemonum clade (Androceras and Elaeagnifolium subclades), where some species have the censer type, in which ripe berries become dry and their epicarp opens exposing seeds that are carried by wind or rain (Whalen, 1979, Stern *et al.* 2010, Knapp *et al.* 2017). Explosive dehiscence, an unusual dispersal mechanism, was only reported for species of *Solanum* sect. *Gonatotrimum* Bitter, a small non-aculeate group belonging to the Brevantherum clade (Stern & Bohs 2012, Stern *et al.* 2013). This mechanism ejects seeds, along with the watery mesocarp, after the rupture of the thin pericarp (Stern *et al.* 2013). A similar mechanism seems to occur in *Solanum mellobarretoi* Agra & Stehmann, a species belonging to Leptostemonum clade, the group that encompasses almost all aculeate species of the genus (Agra & Stehmann 2016). When describing the species, it was reported the mechanism but no empirical data about the occurrence of the explosive mechanism was provided. The species is morphologically and phylogenetically related to *S. leptostachys* Dunal (Bragioni *et al.*, unpublished data), which also inhabits the montane forests of Espinhaço Range and shares similar fleshy fruits.

We experimentally investigated the dispersal mechanism of these two aculeate species, *S. mellobarretoi* and *S. leptostachys*. Our aim was to confirm the occurrence of the explosive mechanism in *S. mellobarretoi*, and to check if it is also present in *S. leptostachys*.

Solanum mellobarretoi (Figure 1a) is an erect shrub reaching up to 4 m. It bears green, globose berries of 1.5–2.0 cm in diameter, with a glabrous, leathery, and viscous epicarp. Each fruit produces about 20 flattened, ovoid to subreniform seeds, measuring 2.9–3.5 mm in length and 2.3–2.5 mm in width. The species inhabits *capões de altitude* (Figure 1b) between 1000 and 1400 m, with a distribution restricted to the southern Espinhaço Range in Minas Gerais, Brazil (Agra & Stehmann 2016). *Capões de altitude* are characterized by

being forest islands near the rounded tops or slopes of mountains (Meguro *et al.* 1996). *Solanum leptostachys* (Figure 1c) shares the same habit and similar fruit morphology, but its fruits are smaller (0.9–1.2 cm in diameter) and have 15–22 flattened-reniform seeds, measuring 3.7–4.0 mm in length and 2.7–3.0 mm in width. The species occurs in a larger range of montane forests associated with remnants of the Atlantic Forest and disturbed forests from northeastern São Paulo to southern Bahia States. The fruits of both species are sticky, smell like chiropterochoric fruits (Pijl 1972) and have seeds surrounded by a mucilaginous substance.

We studied one population of each species in the southern region of the Espinhaço Range, both in montane forests with histories of fire disturbance. The population of *S. mellobarretoi* corresponds to that from which the type specimen of the species was originally gathered, which is located in a *capão de altitude* at Serra do Cipó, municipality of Santana do Riacho, Minas Gerais (19°15'36.3" S, 43°32'32.0" W; 1364 m a.s.l.). The population of *S. leptostachys* studied is located at Serra do Gandarela, about 100 km from that of *S. mellobarretoi*, on the edge of a montane forest remnant in the municipality of Rio Acima, Minas Gerais (20°05'50" S, 43°37'52" W; 1396 m a.s.l.). Vouchers were deposited in the BHCN herbarium of Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, under the accession numbers BHCN 178204 (*S. mellobarretoi*) and BHCN 181899 (*S. leptostachys*).

Testing for the explosive mechanism employed organza bags (ca. 10 x 5 cm) with the capacity to enclose the fruits (Figure 1d). During fieldwork the bags were checked for damage by external agents, in which case they were excluded from data analysis. A total of 45 immature fruits belonging to 29 individuals were bagged in the population of *S. mellobarretoi*, which were visited twice in December 2015 to collect data. A total of 750 immature fruits belonging to 15 individuals were bagged in *S. leptostachys* population, which were visited monthly between November 2016 and April 2017. Ejected and non-ejected seeds were counted for each intact bag. In addition, dehiscent fruits were inspected to determine whether the crack that opened during explosive dehiscence was partial or complete in relation to

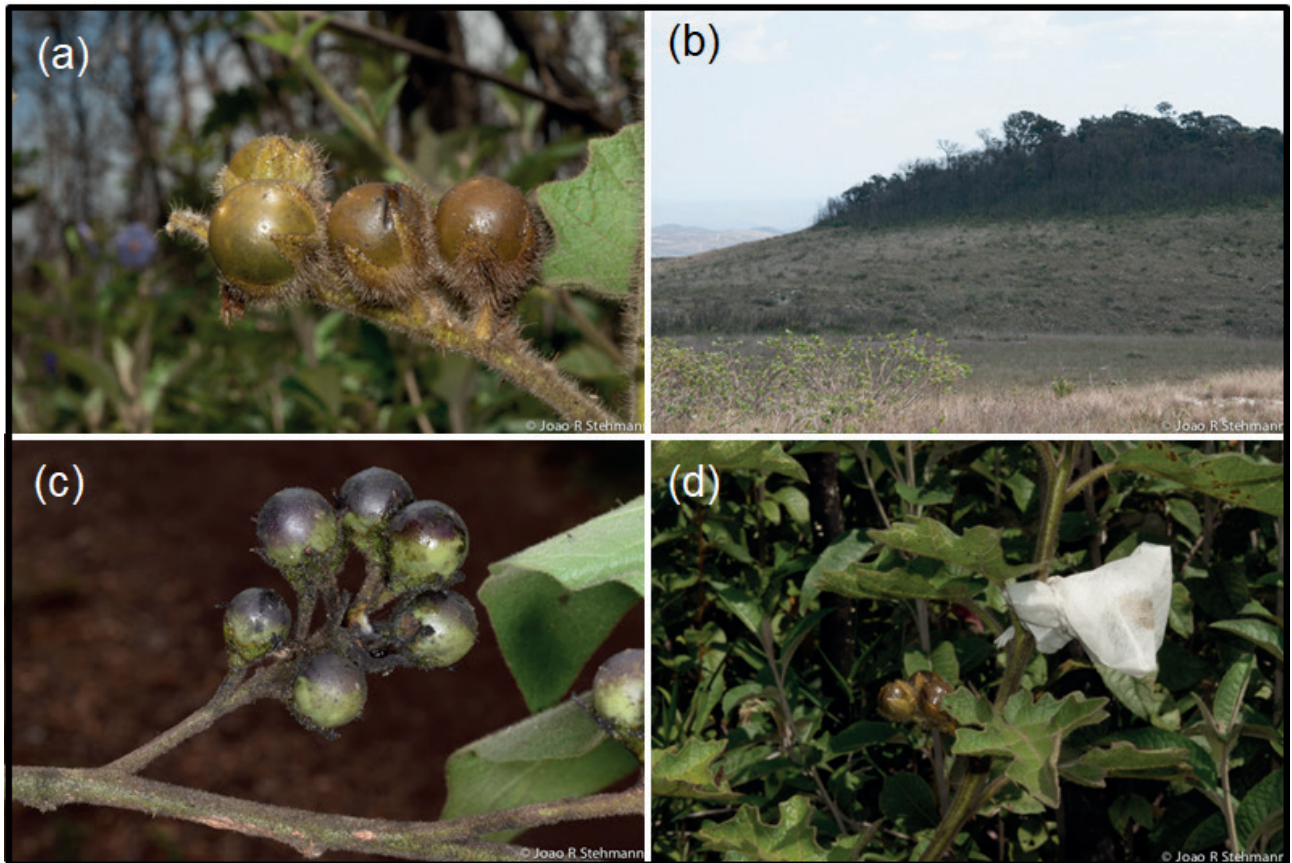


Figure 1. a) Mature fruits of *Solanum mellobarretoii* Agra & Stehmann. b) View of a *capão de altitude*, an island of montane forest (1000 to 1400 m) surrounded by rocky grasslands in the southern Espinhaço Range, where *S. mellobarretoii* occurs. c) Mature fruits of *Solanum leptostachys* Dunal. d) Bagged fruits for testing the explosive mechanism.

fruit diameter.

The species were found not share the same strategy of seed dispersal. Most seeds of *S. mellobarretoii* were ejected, while no seeds of *S. leptostachys* were released. Of the 45 bagged fruits of *S. mellobarretoii*, 4 (8.9 %) suffered damage and were discarded from analysis, thus reducing the sample size to 41 fruits from 27 individuals. Seeds were ejected in 93 % of the 41 fruits, while no explosive mechanism occurred in the remaining 7 %, with the left seeds intact inside the fruit. A total of 470 (78 %) of the 604 seeds involved in the experiment were ejected. In 34 (83 %) of the fruits, seeds were ejected through a partial opening of a crack (less than the diameter of the fruit), while in 7 (17 %) the opening was complete and tore open the fruit. Crack size (partial or complete), however, could not be associated with the amount of ejected seeds because 54 % of the seeds were ejected from fruits with a complete opening and 77 % from fruits a partial opening. The comparison of ejected and retained seeds is showed in Figure 2, where the average of seeds produced was 21 (± 7), the

ejected 15 (± 8) and retained 6 (± 6). The fruits of *S. leptostachys* remained indehiscent throughout the experiment, without spontaneous ejection of seeds being recorded.

The results of the present study show that *S. mellobarretoii* and *S. leptostachys* do not share the same seed dispersal strategy, despite being phylogenetically and morphologically related. Although herbaria analyses or even superficial field observations suggest that *S. mellobarretoii* fruits are typically chiropterochoric, the results presented here indicates that they primarily feature the explosive dispersal mechanism of fleshy berries as predicted by Agra & Stehmann (2016). Contrary to expectations, however, the fruits of *S. leptostachys* do not share the same seed dispersal mechanism with fruits of *S. mellobarretoii*.

The present work also indicates that the mechanism of explosive dehiscence may have appeared more than once in the evolutionary history of the genus, occurring at least in two distinct lineages, the *Brevantherum* and

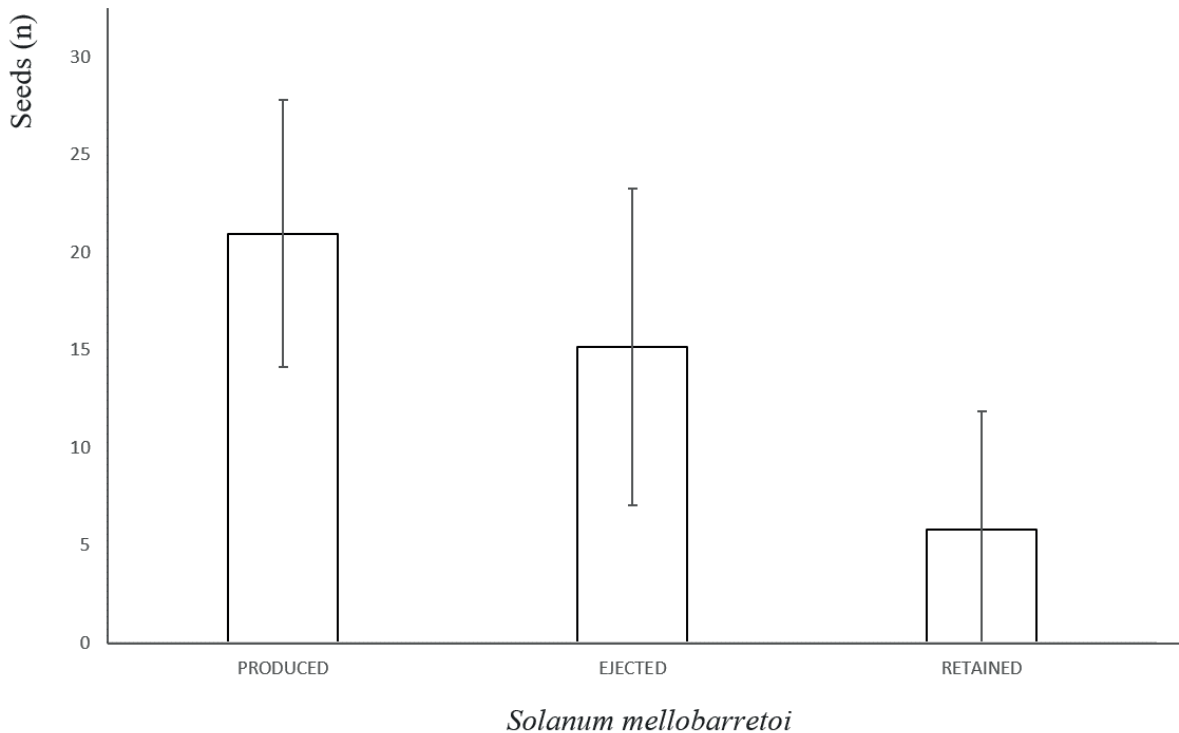


Figure 2. Comparison between the produced, ejected and retained seeds in the bagged fruits of *S. mellobarretoii* Agra & Stehmann.

Leptostemonum clades (Särkinen et al. 2013). As described for species of *Solanum* sect. *Gonatotrichum* (Stern & Bohs 2012), the epicarp of *S. mellobarretoii* becomes translucent at maturity and, due to high internal pressure, breaks up and explosively ejects seeds. Only ontogenetic and anatomical studies can elucidate if the mechanism is homologous in both clades.

Despite the apparent berries uniformity (Knapp, 2002), different seed dispersal strategies have been reported for *Solanum*. Symon (1979) attributed six probable zoochoric dispersal syndromes in Australia, the most common being ornithochory. Albuquerque (2001) concluded that, in *Solanum*, chiropterochory is the most frequent syndrome in Brazil, and that ornithochory prevails over other dispersion syndromes in Mexico, but pointed out that although both represent trends, more studies are needed to have a better scope of the diversity of evolved dispersion strategies within the genus. Deminics *et al.* (2009) drew attention to the fact that most classification systems based on fruit morphology simply designate species as having a single dispersal agent, and thus overlook alternative modes of dispersal or polychory. Vasconcellos-Neto *et al.*

(2009), for example, demonstrated that birds, mammals, lizards and ants are involved in seed dispersal of *S. thomasiifolium* Sendtn.

It is noteworthy that the distribution of *S. mellobarretoii* is restricted to *capões de altitude*, often disturbed by fire (Agra & Stehmann 2016). This vegetation is connected to grasslands, with abundance of Poaceae and Cyperaceae, which are combustible during the dry and windy season (Ribeiro & Figueira 2011). The explosive dispersion strategy may then be related to fire pressure, since dehiscence helps seed dispersal under specific environmental conditions (Cronk, 2009). Temporal series of data following the studied population are necessary to test this hypothesis.

Our experimental investigation demonstrated autochory for *S. mellobarretoii*, indicating that explosive dehiscence of fleshy berries may have emerged independently in at least two distinct clades of *Solanum*. We also highlight the relevance of conducting observational or empirical experimental studies.

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REFERENCES

- Agra, M. F., & Stehmann, J. R. 2016. A new species of *Solanum* subg. *Leptostemonum* (Solanaceae) from the Southern Espinhaço range, Minas Gerais, Brazil. *Phytotaxa*, 288(3), 258–264. DOI: 10.11646/phytotaxa.288.3.6
- Albuquerque, L. B. 2001. Polinização e dispersão de sementes em solanáceas neotropicais. Doctoral thesis, Instituto de Biologia da Universidade Estadual de Campinas (Unicamp), p. 183.
- Bragioni, T. L. S. 2018. Diversidade morfológica dos frutos e síndromes de dispersão em espécies de *Solanum* L. clado *Leptostemonum* (Solanaceae) neotropicais e anatomia de bagas explosivas. Master thesis. Departamento de Botânica da Universidade Federal de Minas Gerais. p. 98.
- Catterall, C. P. 2016. Dynamics of preemergent herbicides in production systems with straw. *Biotropica*, 48(6), 809–824. DOI: 10.1111/btp.12384
- Cronk, Q. 2009. The molecular organography of plants. Oxford University Press, New York: p. 288.
- Deminics, B., Vieira, H. D., Araújo, S. A. C., Jardim, J. G., Pádua, F. T., & Neto, A. C. 2009. Dispersão Natural de Sementes: Importância, Classificação e sua Dinâmica nas Pastagens Tropicais. *Archivos de Zootecnia*, 58, 35–58.
- Driscoll, D. A., Banks, S. C., Barton, P. S., Ikin, K., Lentini, P., Lindenmayer, D. B., Smith, A. L., Berry, L. E., Burns, E. L., Edworthy, A., Evans, M. J., Gibson, R., Heinsohn, R., Howland, B., Kay, G., Munro, N., Scheele, B. C., Stirnemann, I., Stojanovic, D., Sweaney, N., Villaseñor, N. R., & Westgate, M. J. 2014. The trajectory of dispersal research in conservation biology. Systematic review. *PLoS ONE*, 9(4), 1–18. DOI: 10.1371/journal.pone.0095053
- Frodin, D. G. 2004. History and Concepts of Big Plant Genera. *Taxon*, 53(3), 753–776.
- Guariguata, M. R., & Ostertag, R. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management*, 148(1–3), 185–206. DOI: 10.1016/S0378-1127(00)00535-1
- Hernandez-Conrique, D., Iniguez-Divalos, L. I., & Storz, J. F. 1997. Selective feeding by phyllostomid fruit bats in a subtropical montane cloud forest. *Biotropica*, 29(3), 376–379. DOI: 10.1111/j.1744-7429.1997.tb00441.x
- Knapp, S. 2002. Tobacco to tomatoes: a phylogenetic perspective on fruit diversity in the Solanaceae. *Journal of Experimental Botany*, 53(377), 2001–2022. DOI: 10.1093/jxb/erf068
- Knapp, S., Sagona, E., Carbonell, A. K. Z., & Chiarini, F. 2017. A revision of the *Solanum elaeagnifolium* clade (Elaeagnifolium clade; subgenus *Leptostemonum*, Solanaceae). *PhytoKeys*, 2017(84), 1–104. DOI: 10.3897/phytokeys.84.12695
- Meguro, M., Pirani, J. R., Mello-Silva, R. de, & Giulietti, A. M. 1996. Caracterização florística e estrutural de matas ripárias e capões de altitude da Serra do Cipó, Minas Gerais. *Boletim de Botânica Da Universidade de São Paulo*, 15, 13–29.
- Nathan, R., & Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15(7), 278–285. DOI: 10.1016/S0169-5347(00)01874-7
- Oliveira, A. B., Silva, A. M., Lopes, C. A., Ribeiro, C. S. C., Lopes, D., Cruz, D. M. R., Marques, D. M. C., França, F. H., Reifschneider, F. J. B., Buso, G. S. C., Bianchetti, L. de B., Ferreira, M. E., Pozzobon, M. T., Resende, R. de O., Carvalho, S. I. C. de, Pinheiro, V. L., & Casali, V. W. D. 2000. *Capsicum*: pimenta e pimentões no Brasil. Brasília, DF: Embrapa Informação Tecnológica: p. 113.
- Ouborg, N. J., Piquot, Y., & Van Groenendael, J. M. 1999. Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology*, 87(4), 551–568. DOI: 10.1046/j.1365-2745.1999.00389.x
- Pijl, L. Van Der 1972. Principles of dispersal in higher plants. Editora Springer-Verlag, New York. p. 170.
- Ribeiro, G. V. T., Teixeira, A. L., Barbosa, N. P. U., & Silveira, F. A. O. 2016. Assessing bias and

- knowledge gaps on seed ecology research: implications for conservation agenda and policy. *Ecological Applications*, 26(7), 2033–2043. DOI: 10.1890/15-1852.1
- Ribeiro, M. C., & Figueira, J. E. C. 2011. Uma abordagem histórica do fogo no Parque Nacional da Serra do Cipó, Minas Gerais – Brasil. *Biodiversidade Brasileira*, 2, 212–227.
- Ríos-Saldaña, C. A., Delibes-Mateos, M., & Ferreira, C. C. 2018. Are fieldwork studies being relegated to second place in conservation science? *Global Ecology and Conservation*, 14, e00389. DOI: 10.1016/j.gecco.2018.e00389
- Särkinen, T., Olmstead, R. G., Bohs, L., & Knapp, S. 2013. A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. *BMC Evolutionary Biology*, 13, 214. DOI:10.1186/1471-2148-13-214
- Stern, S., & Bohs, L. 2012. An explosive innovation: Phylogenetic relationships of *Solanum* section *Gonatotrimum* (Solanaceae). *PhytoKeys*, 98(8), 89–98. DOI: 10.3897/phytokeys.8.2199
- Stern, S., Bohs, L., Giacomini, L., Stehmann, J., & Knapp, S. 2013. A Revision of *Solanum* Section *Gonatotrimum*. *Systematic Botany*, 38(2), 471–496. DOI: 10.1600/036364413x666624
- Stern, S. R., Weese, T., & Bohs, L. A. 2010. Phylogenetic Relationships in *Solanum* Section *Androceras* (Solanaceae). *Systematic Botany*, 35(4), 885–893. DOI: 10.1600/036364410x539934
- Symon, D. E. 1979. Fruit diversity and dispersal in *Solanum* in Australia. *Journal of the Adelaide Botanic Garden*, 1(6), 321–331.
- Vasconcellos-neto, J., Albuquerque, L. B. De, & Silva, W. R. 2009. Seed dispersal of *Solanum thomasiifolium* Sendtner (Solanaceae) in the Linhares Forest, Espírito Santo state, Brazil. *Acta Botanica Brasilica*, 23(4), 1171–1179.
- Vorontsova, M. S., Stern, S., Bohs, L., & Knapp, S. 2013. African spiny *Solanum* (subgenus *Leptostemonum*, Solanaceae): A thorny phylogenetic tangle. *Botanical Journal of the Linnean Society*, 173(2), 176–193. DOI: 10.1111/boj.12053
- Weese, T. L., & Bohs, L. 2007. A Three-Gene Phylogeny of the Genus *Solanum* (Solanaceae). *Systematic Botany*, 32(2), 445–463. DOI: 10.1017/CBO9781107415324.004
- Whalen, M. D. 1979. Taxonomy of *Solanum* section *Androceras*. *Gentes Herbarum* (11) 1–67.
- Zama, M. Y., Bovolenta, Y. R., Carvalho, E. S., Rodrigues, D. R., Araújo, C. G., Sorace, M. A. F., & Luz, D. G. 2012. Florística e síndromes de dispersão de espécies arbustivo-arbóreas no Parque Estadual Mata São Francisco, PR, Brasil. *Hoehnea*, 39(3), 369–378.

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