

An update of the Verbenaceae genera and species numbers

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Background and aims – The last comprehensive study that estimated the number of Verbenaceae genera and species was published in 2004, and included 34 genera and around 1200 species. Since then, several publications based on morphology and/or molecular data have proposed important changes within the family. Due to the lack of updated literature to cite when referring to the number of Verbenaceae taxa, a review of these estimates is necessary.

Key results and conclusion – We present a detailed list of genera currently accepted in Verbenaceae with the number of species contained in each and compare our numbers with the previous estimate. In addition, we indicate the geographic distribution and the most recent important taxonomic or phylogenetic works for each genus. Our compilation shows that Verbenaceae have 32 genera and 800 species currently accepted. This work provides up-to-date numbers and brings a holistic view of the family.

Keywords – Diversity; Lamiales; New World; taxonomy; Verbenaceae.

INTRODUCTION

Tropical regions of the Americas are some of the most species-rich ecoregions in the world and several studies have investigated its plant diversity (Antonelli & Sanmartín 2011; Ulloa et al. 2017). Yet, some lineages are challenging and still need further investigation, such as the taxonomically complex and diverse family Verbenaceae. This group is a particularly important component of arid to semi-arid communities in the New World (Frost et al. 2017), but is also well represented in wet and dry tropical forests, high Andean grasslands, and cloud forests (Olmstead 2013).

First described by Saint-Hilaire (1805), the vervain family has been variously circumscribed (e.g. Schauer 1847; Briquet 1895; Troncoso 1974; Atkins 2004). The composition

and close allies of Verbenaceae have been controversial, and relationships among genera ascribed to the family have been poorly understood. In this context, much of that diversity was recognized to be more closely related to Lamiaceae by Junell (1934). Later, this was confirmed by phylogenetic studies (Cantino 1992; Wagstaff & Olmstead 1997), with 10 tribes and about 50 genera previously belonging to the Verbenaceae being transferred to the Lamiaceae (Cantino et al. 1992).

One of the most active researchers on Verbenaceae was Harold N. Moldenke, who described several genera and hundreds of species and infraspecific taxa within the family. These descriptions are dispersed in numerous publications between 1930 and 1980. Nérida Troncoso also made important contributions to the taxonomy of the

family (Troncoso 1974). Atkins (2004) presented a historical overview on the classification of Verbenaceae, including a compilation of several studies based on different sources of evidence, such as morphology, anatomy, inflorescence structure, palynology, and karyology. In this treatment, 34 genera and around 1200 species were estimated for the family, organized into six tribes (Atkins 2004).

With the widespread adoption of DNA sequencing, molecular systematics began to revolutionize the understanding of relationships within Verbenaceae. The most comprehensive molecular phylogeny for the family to date was proposed by Marx et al. (2010), who recognized eight tribes (Casseliae, Citharexyleae, Duranteae, Lantaneae, Neospartoneae, Petreeae, Priveae, Verbenae) and 35 genera. A subsequent study (O’Leary et al. 2012a) found morphological traits that support most of the tribes of Marx et al. (2010). The classification proposed by Marx et al. (2010) has formed the basis for the regional treatment of the family as a whole for floristic and systematic projects, including the Flora Argentina (Múlgura et al. 2012) and Flora of Brazil (2020).

Since the work of Marx et al. (2010), many publications based on morphology and/or molecular data have proposed important changes within the family, including several generic realignments. In tribe Duranteae, *Verbenoxylum* has been included within *Recordia* (Thode et al. 2013); in tribe Citharexyleae, *Baillonia* has been included within *Citharexylum* (Christenhusz et al. 2018); in tribe Lantaneae *Acantholippia* and *Xeroaloyisia* were included in *Aloysia* (Lu-Irving et al. 2014); while *Diphyllocalyx* and *Isidroa* were described as new genera (Greuter & Rodríguez 2016), and in tribe Petreeae, *Xolocotzia* has been included within *Petrea* (Christenhusz et al. 2018). The inclusion of *Diostea* in *Dipyrena* by Ravenna (2008) is contradicted by phylogenetic evidence and has not been accepted. *Diostea* belongs to tribe Neospartoneae, while *Dipyrena* remains unassigned to a tribe (Marx et al. 2010).

Numerous nomenclatural changes have occurred in the tribe Verbenae since Atkins (2004) and before Marx et al. (2010), including recognition of the genus *Mulguraea* (e.g. O’Leary et al. 2007, 2009, 2010; Yuan & Olmstead 2008). In addition, Frost et al. (2017), while investigating the role of a putative Andean dispersal corridor connecting North and South America in Verbenae, identified a distinct and as yet unnamed clade in this tribe comprising species currently assigned to *Junellia* and *Verbena*. Later, after Marx et al. (2010), substantial changes were proposed within tribe Lantaneae, which has been the subject of several phylogenetic studies and taxonomic revisions (O’Leary & Múlgura 2012; Lu-Irving & Olmstead 2013; Lu-Irving et al. 2014, in press; Greuter & Rodríguez 2016). These studies suggest the need for redefining the generic boundaries within Lantaneae. As mentioned above, *Aloysia* and related genera have already been recircumscribed (Lu-Irving et al. 2014; O’Leary et al. 2016), with *Aloysia* now including taxa previously recognized as *Acantholippia* and *Xeroaloyisia*. The remainder of Lantaneae forms a large clade comprising seven genera in which five from among them are embedded within the two large genera, *Lantana* and *Lippia*, neither of which is monophyletic (Lu-Irving et al. in press).

These results also show that the African/Malagasy genus, *Coelocarpum*, which was assigned to Lantaneae by Marx et al. (2010), despite being morphologically discordant, is sister to all other Lantaneae, raising the question whether to include it in the tribe at all (Lu-Irving et al. in press).

In light of above, the need for a review of the estimates of genus and species numbers in the Verbenaceae becomes evident. Thus, based on a compilation of the past 16 years of taxonomic and phylogenetic studies on the family, we here provide a list of the currently accepted Verbenaceae genera with the number of species they include compared to the numbers reported by Atkins (2004) and with an indication of the tribe to which they are assigned sensu Marx et al. (2010). In addition, information about their geographical distribution is also provided, along with references to most recent monographic or other systematic study carried out for each genus.

RESULTS

Our compilation shows that Verbenaceae has 32 genera and 800 species currently recognized (table 1). Despite the publication of many new species since 2004 (e.g. Thulin 2005; O’Leary et al. 2009; Salimena 2010; Silva et al. 2017; O’Leary & Frost 2018; Cardoso et al. 2019a, 2019b, 2019c, 2019d, 2019e, 2019f, 2019g, 2020; Harley et al. 2019; Moroni et al. 2019; Thode & Bordignon 2019), this estimate of the number of species is a reduction of approximately one-third from that of Atkins (2004), which continues to be used to represent the diversity in Verbenaceae due to the lack of an updated estimate for the species number in this family. Since the publication of Marx et al. (2010), five genera were placed in synonymy, while two others were described (see above and table 1). Although ongoing work on tribe Lantaneae is likely to change the number of genera recognized in that tribe in the future, the update for the family proposed here is important for current taxonomic and floristic projects involving Verbenaceae. Finally, this compilation is a first step for continuing updates, as new taxonomic changes within the family are necessary.

Ongoing research on the taxonomy and phylogeny of specific groups within Verbenaceae is active (e.g. tribe Citharexyleae – L.A. Frost, R. Olmstead, University of Washington & N. O’Leary, Instituto de Botânica Darwinion, unpubl. res.; tribe Lantaneae – Lu-Irving et al. in press; tribe Duranteae – Moroni & O’Leary 2019, 2020; P. Moroni & N. O’Leary, Instituto de Botânica Darwinion, unpubl. res.; *Stachytarpheta* – P.H. Cardoso et al., Universidade Federal do Rio de Janeiro, unpubl. res.).

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Table 1 – Verbenaceae tribes, genera, species numbers, and distribution. The classification follows Marx et al. (2010). The last comprehensive species estimates by Atkins (2004) are updated based on the most recent monographs and other systematic studies. ¹ synonym under *Citharexylum*; ² synonym under *Recordia*; ³ synonym under *Aloysia*; ⁴ genera described after Marx et al. (2010); ⁵ synonym under *Petrea*; ⁶ synonym under *Junellia*; * genera for which circumscription is likely to change based on Lu-Irving et al. (in press).

Tribes and genera (following Marx et al. 2010)	Number of species recognized by Atkins (2004)	Updated number of species (based on studies in the last column)	Distribution	Important taxonomic or phylogenetic studies on the genus
Casselleae (Schauer) Tronc.				Martínez & Múlgura (2003)
<i>Casselia</i> Nees & Mart.	11	6	South America (Bolivia, Brazil, and Paraguay)	O’Leary & Múlgura (2010)
<i>Parodianthus</i> Tronc.	2	2	South America (Argentina)	Troncoso (1941, 1973)
<i>Tamonea</i> Aubl.	6 or 7	6	Americas (Mexico and Caribbean to Bolivia and Brazil)	O’Leary et al. (2008)
Citharexyleae Briq.				Frost et al. (unpubl. res.)
<i>Baillonia</i> Bocq. ¹	1	–		Christenhusz et al. (2018)
<i>Citharexylum</i> L.	130	60	Americas (Mexico and Caribbean to northern Argentina)	Frost et al. (unpubl. res.), O’Leary et al. (unpubl. res.)
<i>Rehdera</i> Moldenke	3	3	Central America	
<i>Verbenoxylum</i> Tronc. ²	1	–		Thode et al. (2013)
Duranteae Bent.				Thode et al. (2013), Moroni & O’Leary (2019)
<i>Bouchea</i> Cham.	9	13	Americas (SW USA to northern Argentina)	Moroni & O’Leary (2019)
<i>Chascanum</i> E.Mey.	27	27	Africa, Arabian Peninsula, and India	Gillett (1955)
<i>Duranta</i> L.	20	31	Americas	Moroni & O’Leary (2020)
<i>Recordia</i> Moldenke	1	2	South America (Bolivia and Brazil)	Thode et al. (2013)
<i>Stachytarpheta</i> Vahl	90	120	Tropical and subtropical Americas (and as circumtropical weeds)	Atkins (2005), Pedro H. Cardoso (pers. comm.)
Lantaneae Endl.				Lu-Irving & Olmstead (2013), Lu-Irving et al. (in press)
<i>Acantholippia</i> Griseb. ³	6	–		Lu-Irving et al. (2014)
<i>Aloysia</i> Juss.	30	36	Americas	Lu-Irving et al. (2014), O’Leary et al. (2016)
<i>Burroughsia</i> Moldenke*	–	2	North America	Moldenke (1940), Lu-Irving & Olmstead (2013)
<i>Coelocarpum</i> Balf.f.	5	5	Africa (Socotra, Somalia) and Madagascar	
<i>Diphyllocalyx</i> (Griseb.) Greuter & R.Rankin ^{4*}	–	6	Caribbean (Cuba)	Greuter & Rodríguez (2016)

Table 1 (continued) – Verbenaceae tribes, genera, species numbers, and distribution. The classification follows Marx et al. (2010). The last comprehensive species estimates by Atkins (2004) are updated based on the most recent monographs and other systematic studies. ¹ synonym under *Citharexylum*; ² synonym under *Recordia*; ³ synonym under *Aloysia*; ⁴ genera described after Marx et al. (2010); ⁵ synonym under *Petrea*; ⁶ synonym under *Junellia*; * genera for which circumscription is likely to change based on Lu-Irving et al. (in press).

Tribes and genera (following Marx et al. 2010)	Number of species recognized by Atkins (2004)	Updated number of species (based on studies in the last column)	Distribution	Important taxonomic or phylogenetic studies on the genus
<i>Isidroa</i> Greuter & R. Rankin ^{4*}	–	1	Caribbean (Cuba)	Greuter & Rodríguez (2016)
<i>Lantana</i> L.*	150	100	Americas and Africa (and as circumtropical weeds)	Sanders (2006, 2012) Rotman (2009), Silva (1999), Mendez Santos (2002)
<i>Lippia</i> L.*	200	140	Americas and Africa	Múlgura (2000), Salimena (2000), O’Leary et al. (2012b)
<i>Nashia</i> Millsp.*	7	1	Caribbean (Puerto Rico, Bahamas, and Virgin Islands)	Greuter & Rodríguez (2016)
<i>Phyla</i> Lour.	15	5	Americas (and as cosmopolitan weeds)	O’Leary & Múlgura (2012)
<i>Xeroaloyisia</i> Tronc. ³	1	–		Lu-Irving et al. (2014)
Neospartoneae Olmstead & N.O’Leary				Lu et al. (2019)
<i>Diostea</i> Miers	1	1	South America (Argentina and Chile)	
<i>Lampayo</i> Phil. ex Murillo	2 or 3	3	South America (Argentina, Bolivia, and Chile)	Múlgura et al. (2012)
<i>Neosparton</i> Griseb.	4	3	South America (Argentina)	Múlgura et al. (2012)
Petreeae Briq.				
<i>Petrea</i> L.	11	12	Americas	Rueda (1994)
<i>Xolocotzia</i> Miranda ⁵	1	–		Christenhusz et al. (2018)
Priveae Briq.				
<i>Pitraea</i> Turcz.	1	1	South America (Argentina and Chile to southern Peru)	
<i>Priva</i> Adans.	20	20	Africa, Americas and Asia	Moldenke (1936)
Verbeneae Dumort.				Yuan & Olmstead (2008), O’Leary et al. (2009), O’Leary & Múlgura (2014), Frost et al. (2017)
<i>Glandularia</i> J.F.Gmel.	100	88	North and South America	Peralta & Múlgura (2011), O’Leary & Thode (2016), O’Leary et al. (2013)

Table 1 (continued) – Verbenaceae tribes, genera, species numbers, and distribution. The classification follows Marx et al. (2010). The last comprehensive species estimates by Atkins (2004) are updated based on the most recent monographs and other systematic studies. ¹ synonym under *Citharexylum*; ² synonym under *Recordia*; ³ synonym under *Aloysia*; ⁴ genera described after Marx et al. (2010); ⁵ synonym under *Petrea*; ⁶ synonym under *Junellia*; * genera for which circumscription is likely to change based on Lu-Irving et al. (in press).

Tribes and genera (following Marx et al. 2010)	Number of species recognized by Atkins (2004)	Updated number of species (based on studies in the last column)	Distribution	Important taxonomic or phylogenetic studies on the genus
<i>Hierobotana</i> Briq.	1	1	Andean South America (Colombia, Ecuador, and Peru)	O’Leary & Moroni (2014)
<i>Junellia</i> Moldenke	47	38	Andean South America (Argentina, Chile, and Peru)	Peralta et al. (2008), O’Leary et al. (2009), O’Leary et al. (2011)
<i>Mulguraea</i> N.O’Leary & P.Peralta	–	11	Andean South America (Argentina, Chile, and Peru)	O’Leary et al. (2009)
<i>Urbania</i> Phil. ⁶	1	–		O’Leary et al. (2009)
<i>Verbena</i> L.	200–250	57	North and South America (and as cosmopolitan weeds)	O’Leary et al. (2007, 2010)
Unassigned				
<i>Dipyrena</i> Hook.	1	1	South America (Argentina)	Troncoso (1974)
<i>Rhaphithamnus</i> Miers	2	2	South America (Argentina and Chile)	Moldenke (1937)

REFERENCES

- Antonelli A. & Sanmartín I. 2011. Why are there so many plant species in the Neotropics? *Taxon* 60(2): 403–414. <https://doi.org/10.1002/tax.602010>
- Atkins S. 2004. Verbenaceae. In: Kubitzki K. & Kadereit J.W. (eds) The families and genera of vascular plants: 449–468. Springer-Verlag, Berlin.
- Atkins S. 2005. The genus *Stachytarpheta* (Verbenaceae) in Brazil. *Kew Bulletin* 60(2): 161–272.
- Briquet J. 1895. Verbenaceae. In: Engler A. & Prantl K. (eds) Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten, insbesondere den Nutzpflanzen, unter Mitwirkung zahlreicher hervorragender Fachgelehrten begründet IV: 132–182. Wilhelm Engelmann, Leipzig.
- Cantino P.D. 1992. Evidence for a polyphyletic origin of the Labiateae. *Annals of the Missouri Botanical Garden* 79(2): 361–379. <https://doi.org/10.2307/2399774>
- Cantino P.D., Harley R.M. & Wagstaff S.J. 1992. Genera of Labiateae: status and classification. In: Harley R.M. & Reynolds T. (eds) Advances in Labiate science: 511–522. Royal Botanic Gardens, Kew.
- Cardoso P.H., Alves R.J.V., Menini Neto L. & Salimena F.R.G. 2019a. *Stachytarpheta sobraliana* (Verbenaceae), a new species from the Serra de São José, Minas Gerais, Brazil. *Phytotaxa* 415(5): 286–292. <https://doi.org/10.11646/phytotaxa.415.5.5>
- Cardoso P.H., Menini Neto L., Cabral A. & Salimena F.R.G. 2019b. *Lantana caudata* (Verbenaceae), a new species from the Brazilian Atlantic Forest. *Phytotaxa* 424(3): 191–196. <https://doi.org/10.11646/phytotaxa.424.3.7>
- Cardoso P.H., Menini Neto L., Salimena F.R.G. 2019c. A new species of *Lippia* (Verbenaceae) from the inselbergs of Brazilian Atlantic Forest. *Phytotaxa* 406(4): 243–249. <https://doi.org/10.11646/phytotaxa.406.4.3>
- Cardoso P.H., Menini Neto L. & Salimena F.R.G. 2019d. A new species of *Stachytarpheta* (Verbenaceae) from an inselberg of Espírito Santo state, Brazil. *Phytotaxa* 400(5): 273–278. <https://doi.org/10.11646/phytotaxa.400.5.3>
- Cardoso P.H., Menini Neto L. & Salimena F.R.G. 2019e. *Lippia mantiqueirae* (Verbenaceae), a new species from Minas Gerais, Brazil. *Phytotaxa* 420(3): 249–254. <https://doi.org/10.11646/phytotaxa.420.3.5>
- Cardoso P.H., Menini Neto L. & Salimena F.R.G. 2019f. *Stachytarpheta grandiflora*, a new species of Verbenaceae from the Parque Nacional da Serra da Canastra, Minas Gerais, Brazil. *Phytotaxa* 413(1): 61–66. <https://doi.org/10.11646/phytotaxa.413.1.7>
- Cardoso P.H., Menini Neto L., Bernacci L.C. & Salimena F.R.G. 2019g. *Stachytarpheta kriegeiriana* (Verbenaceae), a new species from São Paulo State, Brazil. *Phytotaxa* 422(3): 248–254. <https://doi.org/10.11646/phytotaxa.422.3.5>
- Cardoso P.H., Valério V.I.R., Menini Neto L., Trovó M. & Salimena F.R.G. 2020. Novelty in *Lippia* (Verbenaceae) from Minas Gerais State, Brazil. *Phytotaxa* 455(1): 47–52. <https://doi.org/10.11646/phytotaxa.455.1.6>
- Christenhusz M.J.M., Fay M.F. & Byng J.W. 2018. The Global Flora. Vol. 4: special Edition, GLOVAP Nomenclature Part 1. Plant Gateway Ltd, Bradford.
- Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Available from <http://floradobrasil.jbrj.gov.br/> [accessed 14 Sep. 2020].
- Frost L.A., McAdams Tyson S., Lu-Irving P., O’Leary N. & Olmstead R.G. 2017. Origins of North American arid-land

- Verbenaceae: more than one way to skin a cat. *American Journal of Botany* 104(11): 1708–1716. <https://doi.org/10.3732/ajb.1700292>
- Gillett J.B. 1955. *Svensonia* and *Chascanum* in East and North-East Tropical Africa and Arabia. *Kew Bulletin* 10(1): 131–145. <https://doi.org/10.2307/4113930>
- Greuter W. & Rodríguez R.R. 2016. Revision of the Caribbean endemics currently placed in *Nashia* (Verbenaceae). *Willdenowia* 46: 5–23. <https://doi.org/10.3372/wi.46.46101>
- Harley R.M., Antar G.M. & Giulietti A.M. 2019. *Stachytarpheta atkinsiae*, a new species of Verbenaceae endemic to the Chapada Diamantina, Bahia, Brazil. *Phytotaxa* 401(2): 127–132. <https://doi.org/10.11646/phytotaxa.401.2.4>
- Junell S. 1934. Zur Gynäceummorphologie und Systematik der Verbenaceen und Labiaten. *Symbolae Botanicae Upsaliensis* 4: 1–219.
- Lu M., Frost L.A., O’Leary N. & Olmstead R.G. 2019. Phylogenetic relationships of the tribe Neospartoneae (Verbenaceae) based on molecular data. *Darwiniana* 7(2): 305–324. <https://doi.org/10.14522/darwiniana.2019.72.841>
- Lu-Irving P. & Olmstead R.G. 2013. Investigating the evolution of Lantaneae (Verbenaceae) using multiple loci. *Botanical Journal of the Linnean Society* 171(1): 103–119. <https://doi.org/10.1111/j.1095-8339.2012.01305.x>
- Lu-Irving P., O’Leary N., O’Brien A. & Olmstead R.G. 2014. Resolving the genera *Aloysia* and *Acantholippia* within tribe Lantaneae (Verbenaceae), using chloroplast and nuclear sequences. *Systematic Botany* 39(2): 644–655. <https://doi.org/10.1600/036364414X680816>
- Lu-Irving P., Bedoya A.M., Salimena F.R.G., et al. in press. Phylogeny of *Lantana*, *Lippia*, and related genera (Lantaneae: Verbenaceae). *American Journal of Botany*.
- Martínez S. & Múlgura M.E. 2003. The taxonomic position of *Parodianthus* (Verbenaceae): a morphological survey of the gynoeceum and inflorescence. *Kew Bulletin* 58(4): 929–938.
- Marx H., O’Leary N., Yuan Y., et al. 2010. A molecular phylogeny and classification of Verbenaceae. *American Journal of Botany* 97(10): 1647–1663. <https://doi.org/10.3732/ajb.1000144>
- Mendez Santos I.E. 2002. A taxonomic revision of *Lantana* sect. *Lantana* (Verbenaceae) in the Greater Antilles. *Willdenowia* 32(2): 285–301. <https://doi.org/10.3372/wi.32.32210>
- Moldenke H.N. 1936. A monograph of the genus *Priva*. *Repertorium novarum specierum regni vegetabilis* 41: 1–76. <https://doi.org/10.1002/fedr.19360410103>
- Moldenke H.N. 1937. A monograph of the genus *Rhaphithamnus*. *Repertorium novarum specierum regni vegetabilis* 42: 62–82. <https://doi.org/10.1002/fedr.19370420111>
- Moldenke H.N. 1940. Novelty in the Avicenniaceae and Verbenaceae. *Phytologia* 1: 409–432.
- Moroni P. & O’Leary N. 2019. Insights into the systematics of Tribe Duranteae (Verbenaceae): a taxonomic revision of the New World genus *Bouchea*. *Annals of the Missouri Botanical Garden* 104(3): 355–399. <https://doi.org/10.3417/2019383>
- Moroni P. & O’Leary N. 2020. Insights into the systematics of Tribe Duranteae (Verbenaceae) II: a taxonomic revision of the New World Genus *Duranta* L. *Annals of the Missouri Botanical Garden* 105(4): 502–577. <https://doi.org/10.3417/2020581>
- Múlgura M.E. 2000. The species of *Lippia* L. sect. *Dioicolippia* Tronc. (Verbenaceae). *Candollea* 55(2): 227–254.
- Múlgura M.E., O’Leary N. & Rotman A. 2012. Dicotyledonae. Verbenaceae. In: Anton A.M. & Zuloaga F.O. (eds) *Flora Argentina* 14: 1–220. Estudio Sigma, Buenos Aires.
- O’Leary N. & Frost L. 2018. A new species of *Citharexylum* (Verbenaceae) from the Andean foothills of Peru. *Systematic Botany* 43(4): 1046–1050. <https://doi.org/10.1600/036364418X697733>
- O’Leary N. & Moroni P. 2014. *Hierobotana* Briq., an intriguing monotypic genus of tribe Verbeneae (Verbenaceae). *Phytotaxa* 164(4): 286–290. <https://doi.org/10.11646/phytotaxa.164.4.8>
- O’Leary N. & Múlgura M.E. 2010. A taxonomic revision of *Casselia* (Verbenaceae), a genus endemic to the South American Cerrado and Mata Atlántica biogeographic provinces. *The Journal of the Torrey Botanical Society* 137(2): 166–180. <https://doi.org/10.3159/09-RA-029R.1>
- O’Leary N. & Múlgura M.E. 2012. A taxonomic revision of the genus *Phyla* (Verbenaceae). *Annals of the Missouri Botanical Garden* 98(4): 578–597. <https://doi.org/10.3417/2009120>
- O’Leary N. & Múlgura M.E. 2014. Synopsis of tribe Verbeneae Dumortier (Verbenaceae) in Peru. *Phytotaxa* 163(3): 121–148. <https://doi.org/10.11646/phytotaxa.163.3.1>
- O’Leary N. & Thode V. 2016. The genus *Glandularia* (Verbenaceae) in Brazil. *Annals of the Missouri Botanical Garden* 101(4): 699–749. <https://doi.org/10.3417/2014008>
- O’Leary N., Múlgura M.E. & Morrone O. 2007. Revisión taxonómica de las especies del género *Verbena* (Verbenaceae): serie *Pachystachyae*. *Annals of the Missouri Botanical Garden* 94(3): 571–621. [https://doi.org/10.3417/0026-6493\(2007\)94\[571:RTDLED\]2.0.CO;2](https://doi.org/10.3417/0026-6493(2007)94[571:RTDLED]2.0.CO;2)
- O’Leary N., Peralta P. & Múlgura M.E. 2008. A taxonomic revision of the genus *Tamonea* (Verbenaceae). *Botanical Journal of the Linnean Society* 157: 357–371. <https://doi.org/10.1111/j.1095-8339.2008.00783.x>
- O’Leary N., Yuan Y.W., Chemisquy A. & Olmstead R.G. 2009. Reassignment of species of paraphyletic *Junellia* s.l. to the new genus *Mulguraea* (Verbenaceae) and new circumscription of genus *Junellia*: molecular and morphological congruence. *Systematic Botany* 34(4): 777–786. <https://doi.org/10.1600/036364409790139691>
- O’Leary N., Múlgura M.E. & Morrone O. 2010. Revisión Taxonómica de las especies del género *Verbena* (Verbenaceae). II: serie *Verbena*. *Annals of the Missouri Botanical Garden* 97: 365–424. <https://doi.org/10.3417/2007070>
- O’Leary N., Peralta P. & Múlgura M.E. 2011. Sinopsis del género *Junellia* (Verbenaceae). *Darwiniana* 49(1): 47–75. <https://doi.org/10.14522/darwiniana.2014.491.270>
- O’Leary N., Calviño C.I., Martínez S., Lu-Irving P., Olmstead R.G. & Múlgura M.E. 2012a. Evolution of morphological traits in Verbenaceae. *American Journal of Botany* 99(11): 1778–1792. <https://doi.org/10.3732/ajb.1200123>
- O’Leary N., Denham S.S., Salimena F. & Múlgura M.E. 2012b. Species delimitation in *Lippia* section *Goniostachyum* (Verbenaceae) using the phylogenetic species concept. *Botanical Journal of the Linnean Society* 170: 197–219. <https://doi.org/10.1111/j.1095-8339.2012.01291.x>
- O’Leary N., Peralta P. & Múlgura M. 2013. El género *Glandularia* (Verbenaceae) en Chile. *Darwiniana, Nueva Serie* 1(2): 253–278. <https://doi.org/10.14522/darwiniana.2014.12.527>
- O’Leary N., Lu-Irving P., Moroni P. & Siedo S. 2016. Taxonomic revision of *Aloysia* (Verbenaceae, Lantaneae) in South America. *Annals of the Missouri Botanical Garden* 101(3): 568–609. <https://doi.org/10.3417/2013015>

- Olmstead R.G. 2013. Phylogeny and biogeography in Solanaceae, Verbenaceae and Bignoniaceae: a comparison of continental and intercontinental diversification patterns. *Botanical Journal of the Linnean Society* 171(1): 80–102. <https://doi.org/10.1111/j.1095-8339.2012.01306.x>
- Peralta P. & Múlgura M.E. 2011. El género *Glandularia* (Verbenaceae) en Argentina. *Annals of the Missouri Botanical Garden* 98(3): 358–412. <https://doi.org/10.3417/2007185>
- Peralta P., Múlgura M.E., Denham S.S. & Botta S.M. 2008. Revisión del género *Junellia* (Verbenaceae). *Annals of the Missouri Botanical Garden* 95(2): 338–390. <https://doi.org/10.3417/2004167>
- Ravenna P.F. 2008. Studies in Verbenaceae V. *Dipyrena* Hook., a valid genus antedating *Diostea* Miers, including a new species and transfers. *Onira* 11(15): 40–44.
- Rotman A.D. 2009. El género *Lantana* L. (Verbenaceae-Verbenoideae) en Paraguay: sinopsis y novedades. *Candollea* 64(2): 297–301.
- Rueda R.M. 1994. Systematics and evolution of the genus *Petrea* (Verbenaceae). *Annals of the Missouri Botanical Garden* 81: 610–652. <https://doi.org/10.2307/2399914>
- Saint-Hilaire J.J.H. 1805. Exposition des familles naturelles et de la germination des plantes vol. 1. Treuttel et Würtz, Paris.
- Salimena F.R.G. 2000. Revisão taxonômica de *Lippia* sect. *Rhodolippia* Schauer (Verbenaceae). PhD thesis, Universidade de São Paulo, Brazil.
- Salimena F.R.G. 2010. A new species of *Lippia* L. (Verbenaceae) from Brazilian Cerrado. *Acta Botanica Brasílica* 24(1): 232–234. <https://doi.org/10.1590/S0102-33062010000100024>
- Sanders R.W. 2006. Taxonomy of *Lantana* sect. *Lantana* (Verbenaceae): correct application of *Lantana camara* and associated names. *SIDA, Contributions to Botany* 22: 381–421.
- Sanders R.W. 2012. Taxonomy of *Lantana* sect. *Lantana* (Verbenaceae): taxonomic revision. *Journal of the Botanical Research Institute of Texas* 6: 403–441.
- Schauer J.C. 1847. Verbenaceae. In: de Candolle A.L.P.P. (ed.) *Prodromus systematis naturalis regni vegetabilis*: 561–700. Victor Masson, Paris.
- Silva T.R.S. 1999. Redelimitação e revisão do gênero *Lantana* L. (Verbenaceae) no Brasil. PhD thesis, Universidade de São Paulo, Brazil.
- Silva T.R.S., Salimena F.R.G. & Lima C.T. 2017. Two new species of *Lantana* (Verbenaceae) from Brazil. *Phytotaxa* 299(1): 125–131. <https://doi.org/10.11646/phytotaxa.299.1.11>
- Thode V.A., O’Leary N., Olmstead R.G. & Freitas L.B. 2013. Phylogenetic position of the monotypic genus *Verbenoxylum* (Verbenaceae) and new combination under *Recordia*. *Systematic Botany* 38(3): 805–817. <https://doi.org/10.1600/036364413X670386>
- Thode V.A. & Bordignon S.A.L. 2019. Two new species of *Glandularia* (Verbenaceae) from Rio Grande do Sul and an updated key to the species occurring in Brazil. *Phytotaxa* 441: 39–48. <https://doi.org/10.11646/phytotaxa.411.1.3>
- Thulin M. 2005. Three new species of *Chascanum* (Verbenaceae) and notes on the genus in the Horn of Africa region. *Nordic Journal of Botany* 23: 513–517. <https://doi.org/10.1111/j.1756-1051.2003.tb00425.x>
- Troncoso N.S. 1941. Un nuevo género de Verbenáceas de la Argentina: *Parodianthus*, nov. gen. *Darwiniana* 5: 31–40.
- Troncoso N.S. 1973. Una nueva especie de *Parodianthus* (Verbenaceae): *P. capillaris* nov. spec. *Darwiniana* 18: 19–26.
- Troncoso N.S. 1974. Los géneros de Verbenáceas de Sudamérica extratropical. *Darwiniana* 18: 295–412.
- Ulloa C., Acevedo-Rodríguez P., Beck S., et al. 2017. An integrated assessment of the vascular plant species of the Americas. *Science* 358(6370): 1614–1617. <https://doi.org/10.1126/science.aao0398>
- Wagstaff S.J. & Olmstead R.G. 1997. Phylogeny of the Labiatae and Verbenaceae inferred from *rbcL* sequences. *Systematic Botany* 22(1): 165–179. <https://doi.org/10.2307/2419684>
- Yuan Y.W. & Olmstead R.G. 2008. Evolution and phylogenetic utility of the PHOT gene duplicates in a recently diversified group: dramatic intron size variation and footprint of ancestral recombination. *American Journal of Botany* 95: 1166–117. <https://doi.org/10.3732/ajb.0800133>

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