RESEARCH ARTICLE

Phylogeny of *Lantana, Lippia*, and related genera (Lantaneae: Verbenaceae)

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Abstract

Premise: *Lantana* and *Lippia* (Verbenaceae) are two large Linnean genera whose classification has been based on associated fruit traits: fleshy vs. dry fruits and one vs. two seed-bearing units. We reconstruct evolutionary relationships and the evolution of the two fruit traits to test the validity of these traits for classification.

Methods: Previous studies of plastid DNA sequences provided limited resolution for this group. Consequently, seven nuclear loci, including ITS, ETS, and five PPR loci, were sequenced for 88 accessions of the *Lantana/Lippia* clade and three outgroups.

Results: Neither *Lantana* nor *Lippia* is monophyletic. *Burroughsia, Nashia, Phyla*, and several *Aloysia* species are included within the clade comprising *Lantana* and *Lippia*. We provide a hypothesis for fruit evolution and biogeographic history in the group and their relevance for classification.

Conclusions: Fleshy fruits evolved multiple times in the *Lantana/Lippia* clade and thus are not suitable taxonomic characters. Several sections of *Lantana* and *Lippia* and the small genera are monophyletic, but *Lippia* section *Zappania* is broadly paraphyletic, making circumscription of genera difficult. *Lippia* sect. *Rhodolippia* is a polyphyletic group characterized by convergence in showy bracts. Species of *Lantana* sect. *Sarcolippia*, previously transferred to *Lippia*, are not monophyletic. The clade originated and diversified in South America, with at least four expansions into both Central America and the Caribbean and two to Africa. The types species of *Lantana* and *Lippia* occur in small sister clades, rendering any taxonomy that retains either genus similar to its current circumscription impossible.

Ovary structure and fruit anatomy often were used in traditional angiosperm classifications to distinguish taxa at levels above the species. For example, in the clade recognized today as Lamiales, the number of carpels typically is fixed at two per flower, but the number of ovules per carpel varies from one or two to many, and the latter often was used as a primary family-defining trait, or even to assign families to orders (e.g., Takhtajan, 1980; Cronquist, 1981). Molecular phylogenetic studies have shown that the reliance on such gynoecial traits in Lamiales often was misplaced and that ovule number, locule number, and fruit type (dry vs. fleshy) are much more labile characters than implied by traditional classifications (Wagstaff and Olmstead, 1997).

In Verbenaceae, fruit characters often were used to define tribes (Schauer, 1847; Troncoso, 1974; Atkins, 2004) and, similar to the examples cited for Lamiales, have been shown to be unreliable indicators of relationship at that level (Marx et al., 2010; O'Leary et al., 2012a). Molecular phylogenetic studies have identified several clades in which genera characterized by both fleshy and dry fruits occur (fleshy-fruited taxa listed first): *Parodianthus* Tronc. with

Casselia Nees & Mart. and *Tamonea* Aublet in Casselieae (Schauer) Troncoso (O'Leary et al., 2008; Marx et al., 2010; O'Leary and Múlgura, 2010), *Citharexylum* L. with *Rehdera* Moldenke in Citharexyleae Briq. (Marx et al., 2010; O'Leary et al., 2021; L. Frost, unpublished data), *Duranta* L. with *Recordia* Moldenke in Durantaee Benth. (Thode et al., 2013; Moroni and O'Leary, 2020), *Neosparton* Gris. with *Diostea* Miers and *Lampayo* Phil. in Neospartoneae Olmstead and O'Leary (Lu et al., 2019), *Lantana* L. and *Nashia* Millsp. with *Lippia* L. in Lantaneae Endl., and *Xeroaloysia* Tronc. with *Aloysia* Paláu also in Lantaneae (Marx et al., 2010; Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014). In all of these examples the fleshy- and dry-fruited taxa are sister groups, except in tribe Lantaneae, where the monotypic *Xeroaloysia* is now included in *Aloysia* (Lu-Irving et al., 2014), and in the *Lantana/Lippia* clade, where the evidence to date suggests complicated relationships among dry- and fleshy-fruited species in which neither *Lantana* nor *Lippia* appears to be monophyletic (Marx et al., 2010; Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014).

Lantaneae are the most species-rich tribe of Verbenaceae and form a strongly supported clade (Yuan et al., 2009b; Marx et al., 2010). *Lantana* and *Lippia*, along with a handful of taxa variously recognized either as genera (*Nashia, Burroughsia* Moldenke, *Phyla* Lour.) or isolated species from other genera (*Acantholippia seriphioides* (A. Gray) Moldenke and five North American species of *Aloysia*), form a clade comprising the core of tribe Lantaneae, hereafter referred to as the *Lantana/Lippia* clade (Marx et al., 2010; Lu-Irving and Olmstead, 2013). Phylogenetic studies have identified an expanded *Aloysia*, including *Acantholippia* Gris. and the monotypic *Xeroaloysia* (but excluding *Acantholippia seriphioides* and the five species of *Aloysia* mentioned above) as sister to the *Lantana/Lippia* clade (Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014; O'Leary et al., 2016). Within the *Lantana/Lippia* clade, *Acantholippia seriphioides* (basionym: *Lippia seriphioides* A. Gray) was inferred to be sister to the rest of the clade. *Coelocarpum* Balf., native to Madagascar, Socotra, and Somalia, also belongs to the clade with other Lantaneae, and was included in this tribe on the basis of cpDNA (Marx et al., 2010), despite differing in many morphological traits, because there was not a clear case for monophyly of Lantaneae without this genus. Subsequent studies, with better sampling and a mix of plastid and nuclear DNA, have obtained strong support for *Coelocarpum* as sister to all other Lantaneae (Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014).

Recently, studies of groups within Lantaneae have been published, including a taxonomic revision of *Phyla* (O'Leary and Múlgura, 2011), resolution of *Acantholippia* and *Aloysia* (Lu- Irving et al., 2014; O'Leary et al., 2016), and splitting of *Nashia* into three genera (Greuter and Rodriguez, 2016). Neither *Lippia* nor *Lantana* have been treated comprehensively, but revisions of *Lantana* sect. *Lantana* (Sanders, 2006, 2012), *Lippia* sect. *Dioicolippia* Tronc. (Múlgura, 2000), *Lippia* sect. *Goniostachyum* Schauer (O'Leary et al., 2012b), and several works in which species are transferred from *Lippia* to *Lantana*

or vice versa (Salimena, 2002a; Silva and Salimena, 2002; Salimena and Múlgura, 2015; Salimena et al., 2017) have been published. Numerous regional studies, such as *Lantana* in Brazil (Silva, 1999), Paraguay (Rotman, 2009), and Argentina (Rotman, 2012), *Lantana* sect. *Lantana* in the Greater Antilles (Mendes Santos, 2002), *Lippia* in Argentina (Múlgura, 2014), and works describing new taxa or new distributional ranges (e.g., Silva, 2001; Salimena, 2002b, 2010; Silva et al., 2017; Cardoso and Salimena, 2019; Cardoso et al., 2019a, 2019b, 2019c, 2020) have added to the nomenclatural and taxonomic complexity of the clade.

Lantana and *Lippia* (ca. 100 species and ca. 120–150 species, respectively; Cardoso et al., 2021) comprise the majority of species of Lantaneae and, along with the few smaller genera below, share characteristics that distinguish them from other Lantaneae, including a bilobed calyx and an axillary, condensed inflorescence rachis with spirally arranged flowers at the end of a long peduncle, creating a head-like floral display. *Acantholippia seriphioides* differs from other species previously assigned to *Acantholippia* in sharing these traits. *Aloysia*, sister to the *Lantana/Lippia* clade, is characterized by elongate inflorescences and four-lobed calyces. *Lantana* and *Lippia* traditionally are distinguished from each other by fleshy, drupaceous fruits and dry, schizocarpous fruits, respectively (Endlicher, 1838; Bentham, 1839; Schauer, 1847). The small related genera typically share the above traits, but are distinguished by additional traits: *Phyla* (five species distributed throughout North and South America) has dry fruits, a trailing herbaceous habit, and malpighiaceous hairs (O'Leary and Múlgura, 2011), *Burroughsia* (two species of arid habitats in Mexico) has dry fruits and a glandular appendage extending from the anther connective in the ventral stamens (Moldenke, 1940), and *Nashia* (seven species of arid habitats in the Greater Antilles) is a spinescent shrub with reduced axillary inflorescences and fruits with varying degrees of fleshiness and separation into one or two dispersal units (Greuter and Rodriguez, 2016). The seven species of *Nashia* have recently been segregated into three genera, *Diphyllocalyx* Greuter & R. Rankin (six species from Cuba, including one reduced to synonymy and two newly described), *Isidroa* Greuter & R. Rankin (one species from Hispaniola), and *Nashia* (one species from Puerto Rico) (Greuter and Rodriguez, 2016).

The sectional classifications of *Lantana* and *Lippia* have been much revised, due to complex morphological patterns involving intermediate character combinations and suspected parallel trait evolution (Figure 1). Two sections are currently recognized in *Lantana* (Rotman, 2012), sect. *Lantana* (sensu Sanders, 2006; equivalent to sect. *Camara* (Cham.) Schauer in Chamisso, 1832) and sect. *Callioreas* (Cham.) Schauer (Chamisso, 1832, including sect. *Rhytidocamara* Briq., Briquet, 1904). All species of a third section, *Lantana* sect. *Sarcolippia* Schauer, were transferred to *Lippia* (Silva and Salimena, 2002). Troncoso (1974) recognized seven sections in *Lippia*, including sects. *Dioicolippia, Dipterocalyx* (Cham.) Schauer, *Goniostachyum, Lippia, Pseudoaloysia* Tronc., *Rhodolippia* Schauer, and *Zappania* (Scop.) Schauer. However,
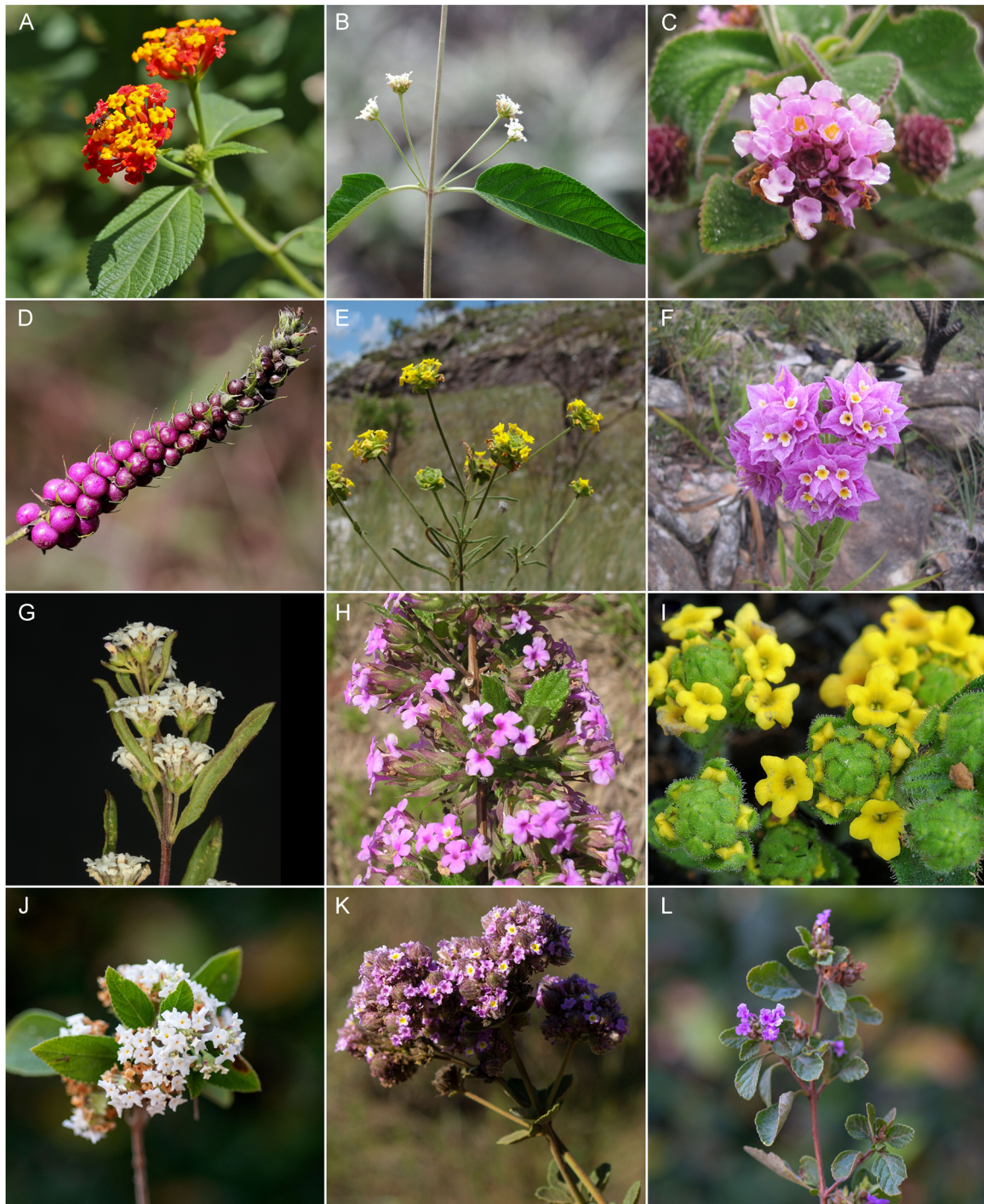
FIGURE 1 Floral diversity in *Lantana* and *Lippia*. Traditional taxonomic assignments are given with each species. (A) *Lantana camara* (*Lantana* sect. *Lantana*), (B) *Lantana canescens* (*Lantana* sect. *Callioreas*), (C) *Lantana speciosa* (*Lantana* sect. *Callioreas*), (D) *Lantana trifolia* (*Lantana* sect. *Callioreas*), (E) *Lippia filifolia* (*Lippia* sect. *Zappania*), (F) *Lippia florida* (*Lippia* sect. *Rhodolippia*), (G) *Lippia integrifolia* (*Lippia* sect. *Zappania*), (H) *Lippia lasiocalycina* (*Lippia* sect. *Zappania*), (I) *Lippia nana* (*Lippia* sect. *Dioicolippia*), (J) *Lippia origanoides* (*Lippia* sect. *Goniostachyum*), (K) *Lippia rotundifolia* (*Lippia* sect. *Zappania*), and (L) *Lippia rubela* (*Lippia* sect. *Dipterocalyx*). Photo credits: A, D, and I by M. Mercadante; B and J by R. Stehmann; C by V. Dittrich; E by L. M. Neto; F, H, J, K, and L by F. Salimena; G by F. Zuloaga

the type of sect. *Pseudoaloysia*, *L. phryxocalyx* Briq., is now considered a synonym of *L. lasiocalycina* Cham. (sect. *Zappania*), so sect. *Pseudoaloysia* is no longer recognized, leaving the number of sections in *Lippia* at six. Despite the transfer of the species in *Lantana* sect. *Sarcolippia* to *Lippia*, no section "Sarcolippia" has ever been validated in *Lippia* (hereafter this group will be referred to as "Sarcolippia").

The *Lantana/Lippia* clade includes many aromatic species of ethnobotanical and economic significance, as well as several species widely planted as ornamentals. *Lantana*

camara L. is both prized as an ornamental and despised as a pantropical weed. The *Lantana/Lippia* clade is distributed (excluding ornamental and invasive plants) widely from ~45°N to ~50°S latitude in the New World (Olmstead, 2013) and also occurs in Africa. The greatest diversity in this clade is found in arid and semiarid habitats, with fewer species occurring in wet tropical environments. Species in this clade frequently colonize open and disturbed habitats. *Lantana* and *Lippia* have very similar distributions throughout the Neotropics, rarely occurring beyond 30° latitude north or south (Lu-Irving and Olmstead, 2013; Olmstead, 2013), and each having one dispersal event to Africa leading to a handful of species there. The herbaceous habit of *Phyla* has permitted extension of its distribution into temperate zones in North and South America (O'Leary and Múlgura, 2011), a trend seen in other woody/herbaceous plant groups (Zanne et al., 2014). *Acantholippia seriphioides* extends the southern distribution of Lantaneae to southern Argentina (Olmstead, 2013).

Previous phylogenetic studies of Lantaneae included limited sampling of the *Lantana/Lippia* clade (Marx et al., 2010; Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014) and provided limited resolution of relationships, but the results of those studies strongly suggest that neither *Lantana* nor *Lippia* is monophyletic and that the smaller genera aligned with them are all nested within a phylogenetic matrix of *Lantana* and *Lippia* species. The present study addresses relationships within the *Lantana/Lippia* clade and uses this as the backbone to reconstruct the evolution of fruit type and seed units, as well as to propose a biogeographic hypothesis for this group.

MATERIALS AND METHODS

Seventy-four species belonging to the *Lantana/Lippia* clade were chosen to represent the taxonomic and geographic diversity of the group (following Lu-Irving and Olmstead, 2013). A total of 88 accessions formed the ingroup, with several widespread, variable species represented by two or three accessions, to provide indicators of intraspecific sequence variation and to test monophyly of these species. Based on prior analyses (Marx et al., 2010; Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014), three species of *Aloysia* were used as the outgroup (Appendix 1).

Leaf tissue was collected from herbarium specimens or from field or garden-collected plants. DNA was extracted following a standard modified CTAB protocol (Doyle and Doyle, 1987) and purified by isopropanol precipitation. All PCR and sequencing reactions were carried out according to standard protocols as described by Lu-Irving and Olmstead (2013).

Ten nuclear loci and one plastid genome spacer region were screened for variability among *Lantana* and *Lippia* species (ETS, ITS, PPR11, PPR24, PPR47, PPR81, PPR90, PPR97, PPR123, PHOTII, *trnL/rpl32*). Each locus was amplified and sequenced in four representatives of the

Lantana/Lippia clade (*Lantana trifolia*, *Lantana depressa*, *Lantana ferreyrae*, *Lippia dulcis*) and pairwise distances between each representative species were calculated.

Primers used to amplify and sequence ITS were universal primers ITS 4 and ITS 5 (White et al., 1990). A custom forward primer was substituted in a few cases in which universal primers amplified fungal ITS sequences. The ETS primers used were those described by Lu-Irving and Olmstead (2013). The PPR loci were amplified and sequenced using previously published primers (Yuan et al., 2009a, 2009b; Lu-Irving and Olmstead, 2013) and primers developed to target additional loci following the general procedure outlined by Yuan et al. (2009b). Sequences of primers used are listed in Table 1.

Sequence data from each locus were aligned using MAFFT version 7 (Katoh and Standley, 2013) with minor manual adjustments, and assembled into individual data sets. Model testing for alignments representing the seven sequenced individual loci was conducted using 24 models of nucleotide evolution, as implemented in jModeltest version 2.31 (Darriba et al., 2012), and the best-fit model for each data set was determined under the BIC criterion. Phylogenetic trees were estimated for each of the seven data sets that represent individual loci and for the concatenated alignment using maximum likelihood (ML) and Bayesian inference (BI). RAxML-HPC on BlackBox and MrBayes version 3.2.1 on XSEDE, both via the CIPRES Science Gateway (Ronquist and Huelsenbeck, 2003; Miller et al., 2010), were used for phylogenetic reconstruction. The concatenated data were partitioned into individual loci with substitution models specified respectively. For each ML analysis, RAxML was set to halt bootstrapping automatically to estimate support for branches. Bayesian analyses consisted of two independent runs of four chains and 10 million generations each, and convergence was assessed by examining the standard deviations of split frequencies between runs. A burn-in fraction of 25% was discarded when summarizing trees.

A species tree from the combined data was inferred using *BEAST (Heled and Drummond, 2010) as implemented in BEAST version 2.5.1 (Bouckaert et al., 2019). The seven loci were treated as six separate partitions (ETS and ITS are linked on the rDNA repeat) with unlinked substitution, clock and tree model estimates. The species tree inference was performed under a coalescent model with piecewise constant population sizes, and an uncorrelated relaxed clock model with a lognormal prior, and a birth-death species tree prior. The substitution models found previously with jModeltest version 2.3.1 for each loci were specified. The multiple accessions of individual species were defined as the same species or taxon set for a total of 77 species in the species tree analysis. Markov chain Monte Carlo was run twice for 300 million generations and convergence was assessed by examining logged states using Tracer version 1.7.1 (Rambaut et al., 2018). A burn-in fraction of 25% was discarded when summarizing trees for each run. The resulting trees from the two independent runs were combined using LogCombiner version 2.5.1 (Bouckaert et al., 2019).

TABLE 1 Sequences of PCR and sequencing primers used in this study

Locus	Primer	Use	Sequence (5′–3′)	Reference/Description
ETS	ETSB	PCR/Sequencing	ATAGAGCGCGTGAGTGGTG	Lu-Irving and Olmstead (2013)
	18SIGS	PCR/Sequencing	GAGACAAGCATATGACTACTGGCAGGATCAACCAG	Baldwin and Markos (1998)
ITS	ITS4	PCR/Sequencing	TCCTCCGCTTATTGATATGC	White et al. (1990)
	ITS5	PCR/Sequencing	GGAAGGAGAAGTCGTAACAAGG	New; optimized for Lamiales
	ITS.LL.F	PCR/Sequencing	ATCCCGCCTGACCTGGGGTCG	New; optimized for *Lantana/Lippia*
PPR 11	320 F	PCR/Sequencing	TCTTCTCTTTCTTCACATGGCT	Yuan et al. (2009b)
	1110 F	Sequencing	GATTTGGCWATGGARATTTA	Y-W. Yuan, unpublished data
	1300 R	Sequencing	TCCARATCTCCYTCCTTACAA	Yuan et al. (2009b)
	1590 R	PCR/Sequencing	TAACCGTTCATAAGCACATTGTA	Yuan et al. (2009b)
PPR 81	81.LL.F	PCR/Sequencing	GCAAAGTGCAGAARAGTTGA	New; optimized for *Lantana/Lippia*
	81.LL.R	PCR/Sequencing	CCAATGTGRCTACATGCAGT	New; optimized for *Lantana/Lippia*
PPR 90	313 F	PCR/Sequencing	TCTGTTRTTAAACTCGGCTATGATTC	New; optimized for Lamiales
	613 F	Sequencing	GGRAAGSAAGTTCATGGSTATA	New; optimized for Lamiales
	1073 R	Sequencing	TATAACCAGYRAGCATRGCATTCCA	New; optimized for Lamiales
	1346 R	PCR/Sequencing	TATCTTTRCTCTCCATRKTGTGAAA	New; optimized for Lamiales
PPR 97	781 F	PCR/Sequencing	CTTGTRGATTTGGGTGCWARGTGGTT	New; optimized for Lamiales
	1585 R	PCR/Sequencing	TTTTTCACATAAGCWGTYACAAGAAT	New; optimized for Lamiales
PPR 123	123.LL.F	PCR/Sequencing	GTGCCTGGGGATTTGGTTCTGTA	New; optimized for *Lantana/Lippia*
	LL.825 F	Sequencing	GTGTTTGGAAAGGCTAAGC	New; optimized for *Lantana/Lippia*
	1030 R	Sequencing	GCCCATAMACATCKATCATTAT	Yuan et al. (2009b)
	1890R	PCR/Sequencing	AGACTCAGCATCTGRAAATGAAC	Yuan et al. (2009b)

Ancestral character state reconstruction was conducted for fruit characters historically used to distinguish *Lantana* and *Lippia*. Evolution of both fruit type (i.e., dry vs. fleshy) and seed dispersal units (i.e., one vs. two units) was assessed using the R package Phytools (Revell, 2012). We fit the equal rates (ER), all rates different (ARD), and symmetric rates (SYM) models to the species tree obtained with *BEAST and selected the best model by Akaike information criterion (AIC) ranking. We then performed character mapping by summarizing a distribution of 1000 character maps under the selected model.

To delimit the geographic distribution for each taxon, the localities of the studied taxa were compiled from our own fieldwork and databases and from the literature. Four operational biogeographic areas (South America, Central/North America, Caribbean, Africa) were defined on the basis of major distribution patterns of the extant taxa. Terminals were coded as present or absent for each of the four selected areas. We inferred ancestral geographic range shifts in the species tree generated in *BEAST using the dispersal-extinction-cladogenesis model (DEC; Ree et al., 2005) with the maximum number of ancestral areas set to two in the software Lagrange-CPP (C++ version) (Ree and Smith, 2008).

RESULTS

Based on the pairwise sequence comparisons for the four taxa (Appendix S1), seven loci were selected for sequencing for all taxa (ETS, ITS, PPR loci 11, 81, 90, 97, 123). The PHOTII intronic region, though highly variable (Yuan and Olmstead, 2008), was not selected because it could not be directly sequenced, due to allelic length variation. Sequence data were collected for 92.3% of cells in the data matrix (91 terminal accessions by seven loci). Approximately 11% of states in the final (combined) analyses were scored as missing (including gaps). Voucher information and GenBank accession numbers are in Appendix 1.

Alignment lengths and details of models inferred for each alignment are summarized in Table 2. Phylogenetic analyses conducted using MrBayes resulted in gene trees for individual loci that were well resolved at the level of major clades; these loci were sufficiently informative to infer phylogenetic history at this level in Lantaneae (Appendix S2). There were some well-supported differences between individual gene trees, indicating that one or more gene trees differ from the species tree (Maddison, 1997).

TABLE 2 Summary of sequence data collected as part of this study: alignment dimensions for each of seven loci, assembled into individual data sets, and best-fit models for each data set

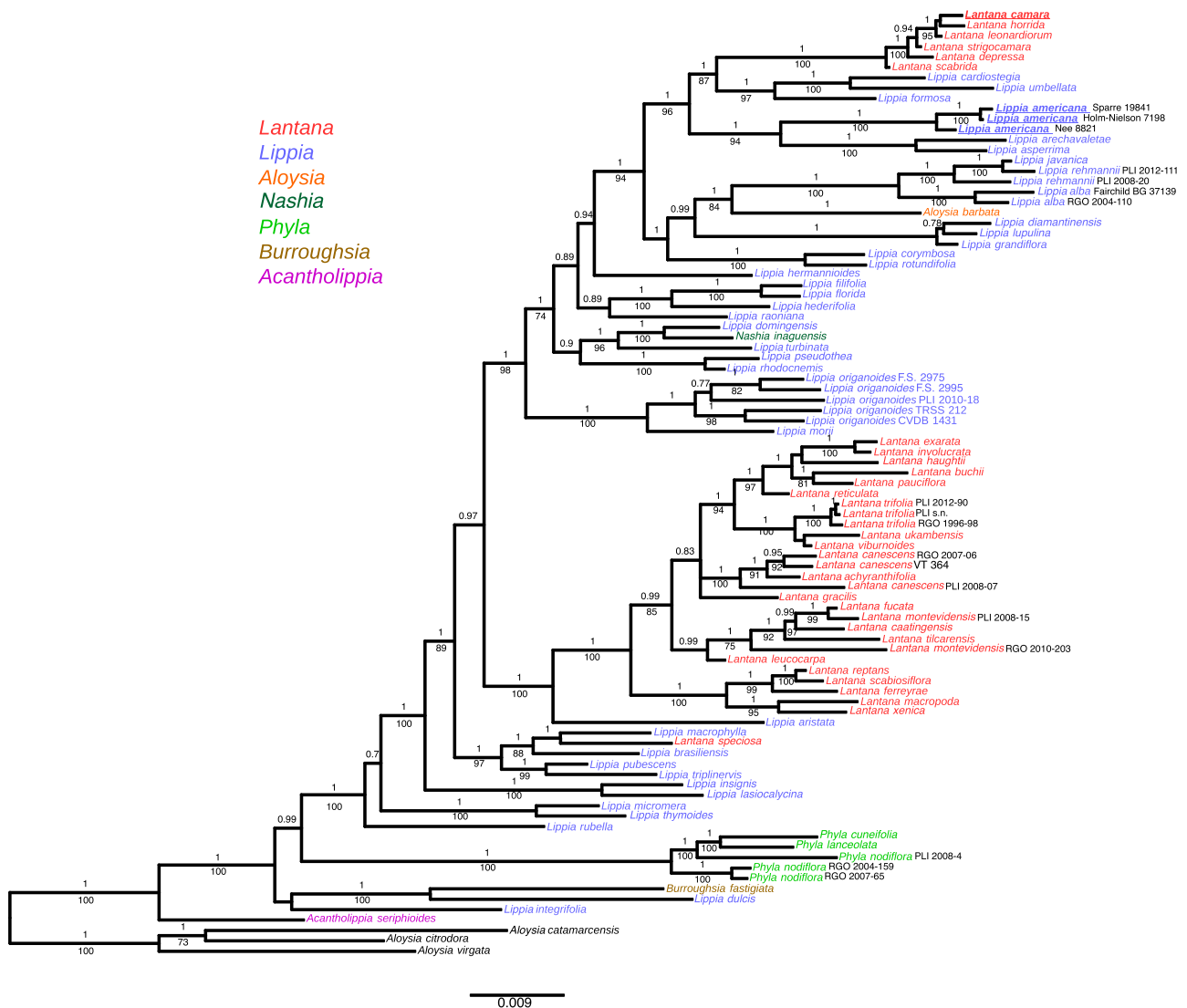|	ETS	ITS	PPR11	PPR81	PPR90	PPR97	PPR123
Length	480	762	1277	1162	986	747	1122
Accessions	81	80	80	76	76	63	76
Model	GTR + Γ	GTR + I + Γ	GTR + Γ	GTR + I + Γ	HKY + I + Γ	HKY + I + Γ	HKY + I + Γ

FIGURE 2 Phylogeny inferred from the combined sequences of seven nuclear loci. Bayesian posterior probability and ML bootstrap values >0.7 (or 70%) are indicated above and below branches, respectively. Species names are color coded according to current generic classification. The type species of *Lantana* and *Lippia* are in bold and underlined

The ML and BI analyses of the concatenated matrix resulted in similar topologies that differ only in one well-supported instance (Figure 2; Appendix S2). Most branches in the Bayesian topology were supported by posterior probabilities >0.90 with six exceptions, mostly in terminal clades among closely related species (Figure 2). The species tree inferred from all data using the coalescent-based approach implemented in *BEAST included high posterior probabilities for major clades, but less confidence in lower-order branches (Figure 3). The *BEAST coalescent tree and the Bayesian tree from the concatenated data have very similar topologies and are consistent with respect to major clades, but differ with respect to some details within those clades where support was moderate or weak in one or both
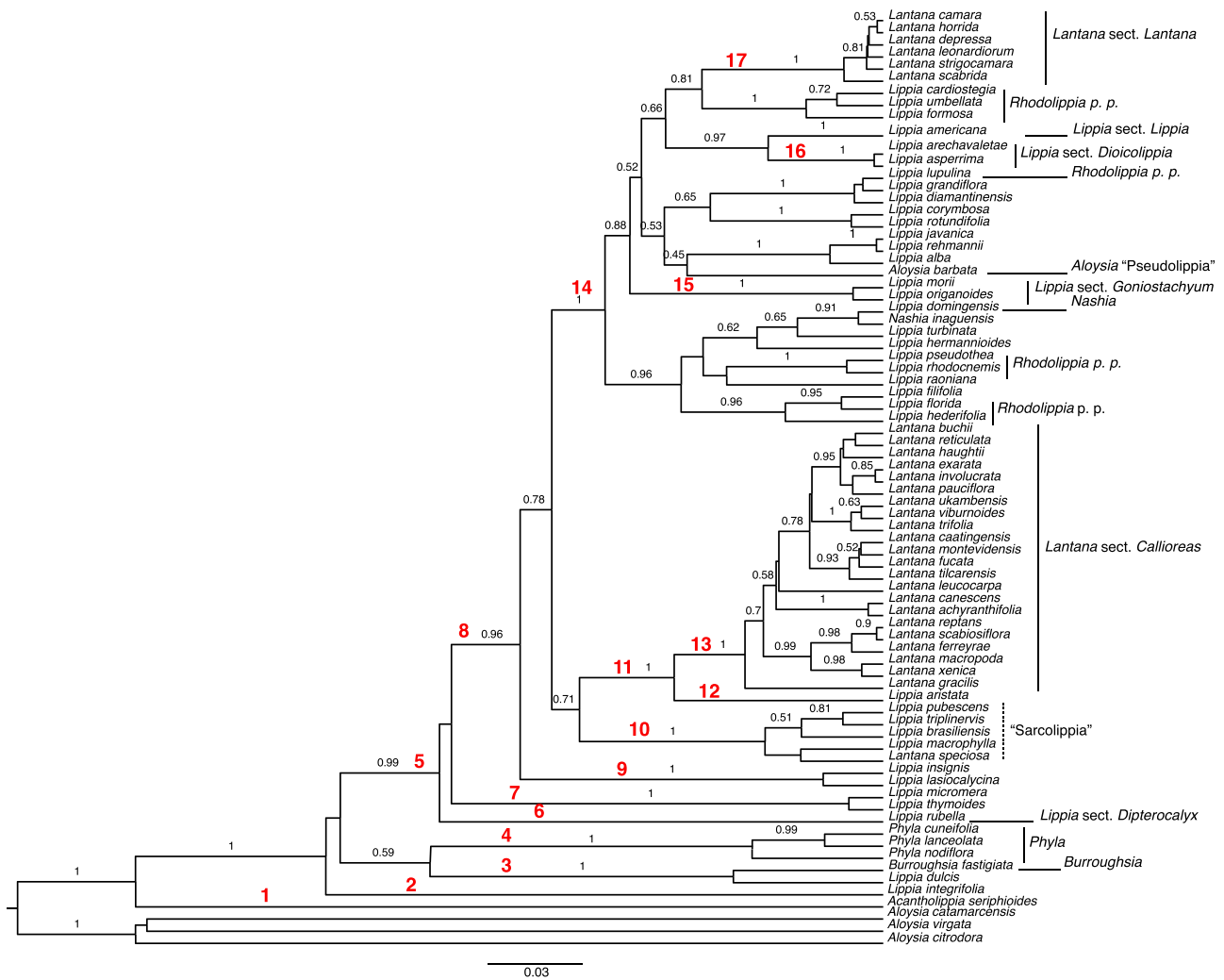
FIGURE 3 Species tree inferred using the multispecies coalescent, as implemented in *BEAST, from sequence data from six independent nuclear loci (ITS and ETS are linked in the ribosomal repeat and considered as one locus for this analysis). Genus and sectional designations for groups in *Lantana* and *Lippia* are indicated to the right; unlabeled species are *Lippia* section *Zappania*. Posterior probability values >0.5 are shown above branches. Numbers in red identify clades enumerated in the text

trees. The major difference between the *BEAST tree and the concatenated tree is in the branching order near the base of the tree after the divergence of *Acantholippia seriphioides*, with the former placing *Lippia integrifolia* (Griseb.) Hieron. sister to the rest of the *Lantana/Lippia* clade followed by a clade comprising *Phyla* sister to *Burroughsia* and *Lippia dulcis* Trevir., and the latter placing *L. integrifolia* sister to *Burroughsia* and *L. dulcis* in a clade that is sister to the rest of the *Lantana/Lippia* clade. However, these relationships are weakly supported in both trees.

We identify 17 clades (some comprising individual species) that are consistently obtained in both the MrBayes and *BEAST trees (Figures 2 and 3). The order of branches from the base of the *Lantana/Lippia* clade is consistent in all trees, except for clades 2–4: (1) *Acantholippia seriphioides*, (2) *Lippia integrifolia*, (3) a clade comprising *Lippia dulcis* and *Burroughsia*, (4) *Phyla*, and (5) the "core" Lantana/Lippia clade, which contains (6) *Lippia rubella* (Moldenke) T.R.S. Silva, (7)

Lippia micromera Schauer and *L. thymoides* Mart. & Schauer, and (8) a clade comprising all other *Lantana, Lippia,* and *Nashia* species. Within the latter clade, nine additional clades are consistently obtained: (9) *Lippia insignis* Moldenke and *L. lasiocalycina*, (10) a clade with *Lantana speciosa* and four species of *Lippia*, including three species of "Sarcolippia" and *L. triplinervis* Gardner, (11) the inclusive clade comprising clades (12) *Lippia aristata* Schauer and (13) a large clade of *Lantana* species comprising section *Callioreas*, and (14) a large clade made up primarily of *Lippia* species, which includes (15) *Lippia* sect. *Goniostachyum*, (16) *Lippia* sect. *Dioicolippia*, and (17) *Lantana* sect. *Lantana*. African members of *Lantana* and *Lippia* form clades nested within clades 13 and 14, respectively.

For the fruit ancestral state reconstructions, the ER (AIC = 48.83545) and SYM (AIC = 48.83545) models were equally ranked by AIC score and were significantly better than ARD (AIC = 50.53699) in ancestral state reconstruction of fruit type. Under both the ER and SYM models,

stochastic character mapping supports the same hypothesis. The ER (AIC = 38.66185) and SYM (AIC = 40.12464) models were again equally ranked by AIC scores and were slightly better than ARD (AIC = 38.66185) in the ancestral state reconstruction of seed units. Stochastic character mapping under both models yielded the same hypothesis (Figure 4). Under this scenario, correspondence between fleshy fruits and fruits with a single, undivided seed-bearing structure, variously referred to as a pyrene or cluse, is strong, but not universal, with species assigned to "Sarcolippia" having fleshy fruits that are divided into two units.

The biogeographic reconstruction identified the origin of the *Lantana/Lippia* clade and most of the backbone of the tree as occurring in South America (Figure 5). *Phyla* and the *Burroughsia/Lippia dulcis* clade, which form a weakly supported clade in the *BEAST tree (but not supported in the concatenated analysis; Figure 2) represent an early expansion into Central and North America. From ancestors in South America, at least four dispersal or expansion events resulting in clades of one or more species have led to range expansions into both Central/North America and the Caribbean and two into Africa from South America, in addition to several species of widespread distribution between continents.
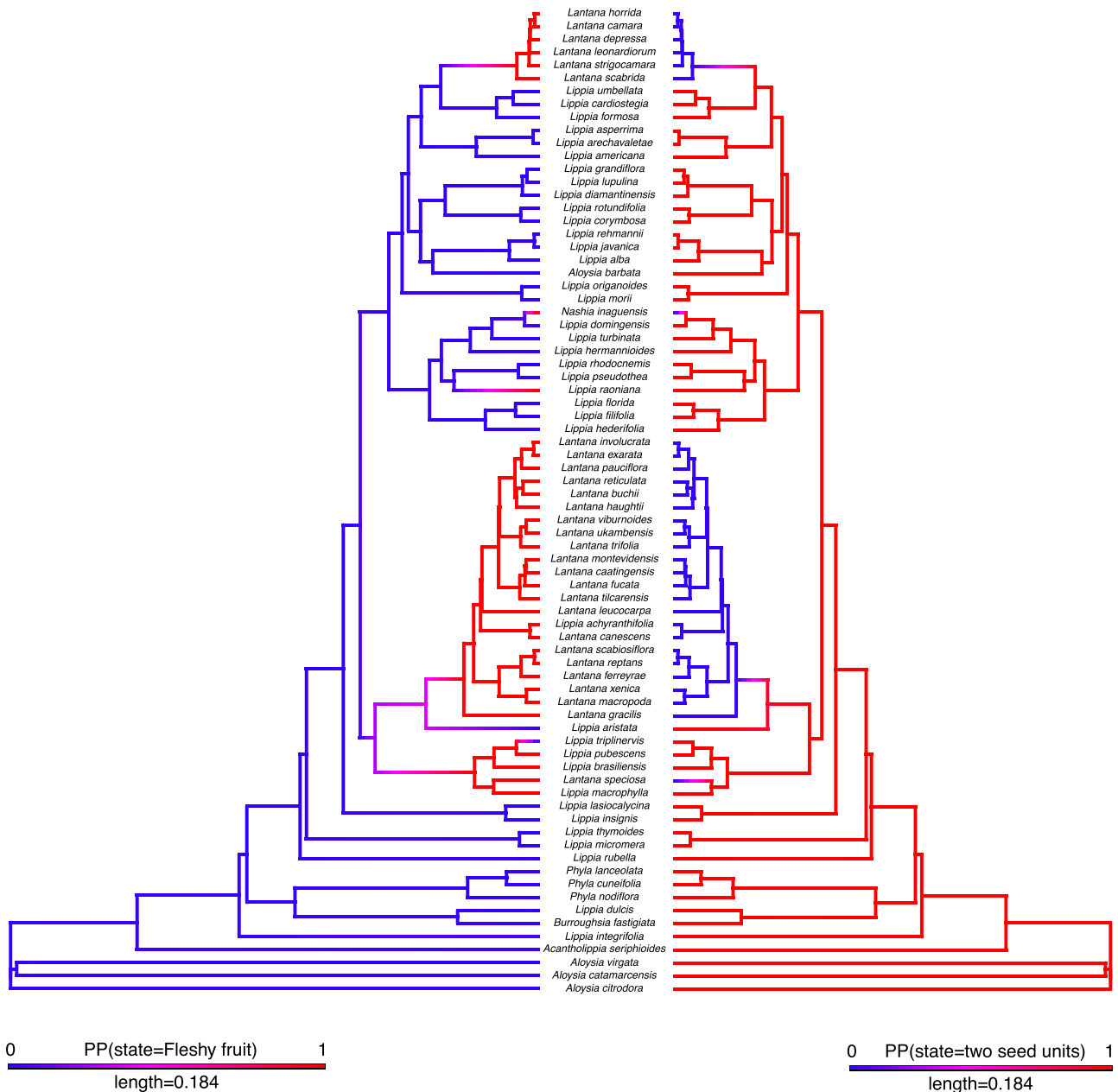

FIGURE 4 Stochastic character-mapping results for seed type (left: blue = dry vs. red = fleshy) and seed dispersal units (right: blue = one vs. red = two) under the equal rates (ER) model and using the species tree generated in this study; 1000 character maps are summarized. The posterior probability along branches for the character states is shown by shading
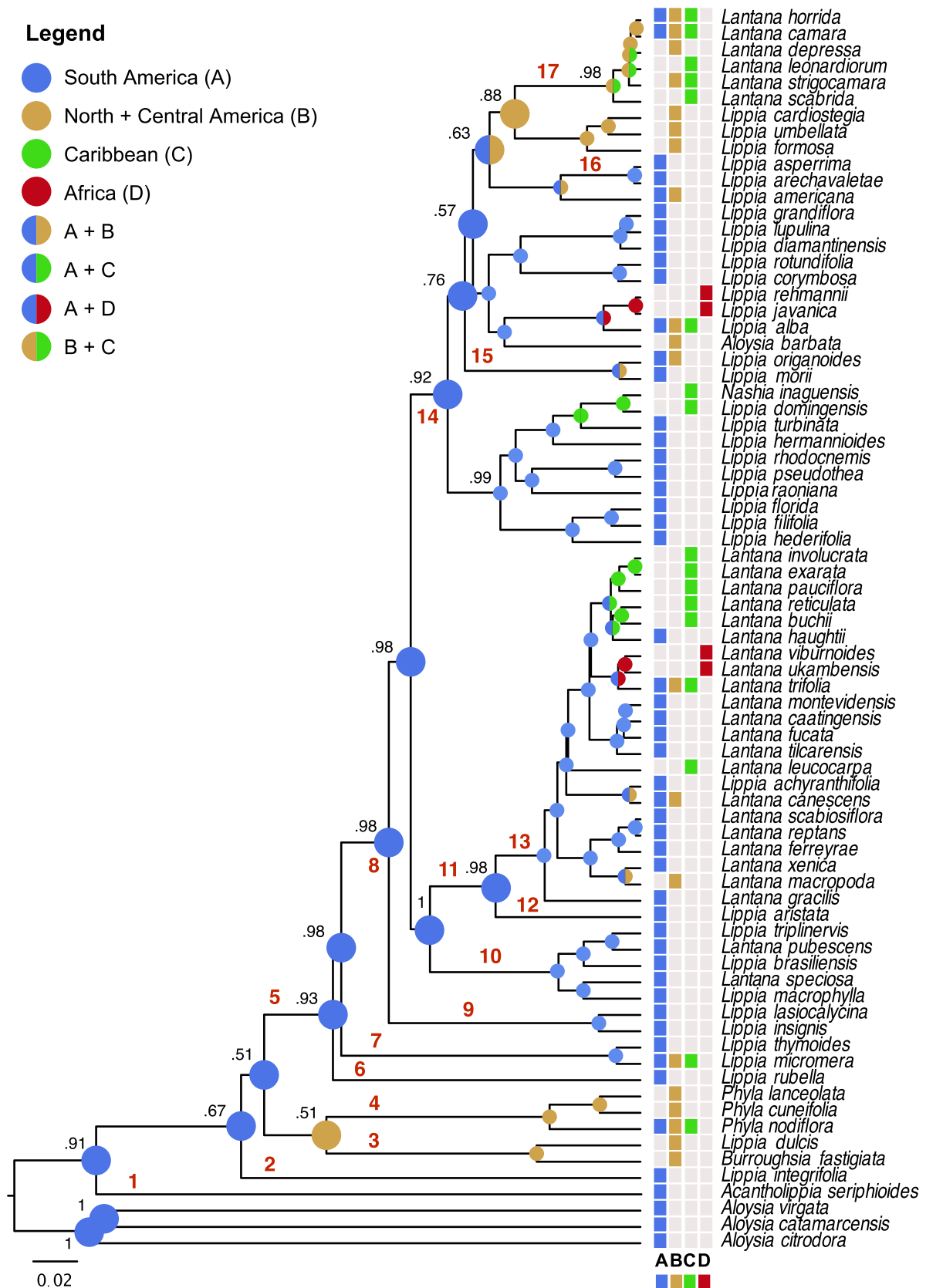
FIGURE 5 Species tree inferred using *BEAST with ancestral state estimates reconstructed using DEC in Lagrange. Colored circles indicate the ancestral range with the highest posterior probability (PP), with range state according to the legend. Terminals are coded according to their current distribution. Black numbers are PP for the most likely ancestral state of the nodes along the backbone of the tree; numbers in red identify clades enumerated in the text

DISCUSSION

Evidence from previous studies of Verbenaceae and tribe Lantaneae suggests that plastid DNA loci are not sufficiently variable to provide resolution among species within Lantaneae (Marx et al., 2010; Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014). For the present study, seven nuclear loci were considered to be suitably variable to sequence for all of the sampled accessions (Appendix S1). These loci were successful in resolving phylogenetic relationships among the species of the *Lantana/Lippia* clade. In addition to the ITS and ETS regions, which are linked as part of the nuclear ribosomal repeat, the remaining loci are members of the pentatrichopeptide repeat (PPR) gene family, which have proven useful for phylogenetic inference in plants (Yuan et al., 2009a, 2009b; Lu-Irving and Olmstead, 2013; Crowl et al., 2014; Lu-Irving et al., 2014; Chau et al., 2017, 2018), including in targeted sequence capture approaches using next-generation sequencing methods, where they exceed other commonly used targeted sequence markers in terms of both average sequence length and variability (Chau et al., 2018).

As expected, some differences in phylogenetic reconstruction from different loci were observed (Appendix S2), with two possible causes that are not mutually exclusive: (1) the relatively small number of variable sites in individual loci can result in inadequate data to resolve trees with confidence (Olmstead and Sweere, 1994), and (2) different phylogenetic histories among loci owing to the effects of lineage sorting or ancient hybridization. The tree topology inferred using a total evidence approach (concatenating all sequence data) is supported by high confidence values throughout most of the tree (Figure 2), whereas the species tree inferred under a coalescent model to account for differences in branching history among the several loci has low to moderate posterior probabilities for many nodes, especially near branch tips (Figure 3). However, trees from both the concatenated data and the coalescent analysis are consistent in the major clades obtained by each, with most differences only found in moderate or weakly supported nodes in the two large and species-rich clades 13 and 14 and among some of the early diverging clades.

In this and previous studies with limited sampling of the *Lantana/Lippia* clade (Lu-Irving and Olmstead, 2013; Marx et al., 2020), the same major lineages within the group are consistently obtained. These include several clades corresponding to taxa recognized in traditional classifications: *Phyla* (sensu O'Leary and Múlgura, 2011), *Lantana* sect. *Lantana* (sensu Sanders, 2006; equal sect. *Camara* sensu Chamisso, 1832), *Lantana* section *Callioreas* (sensu Rotman, 2012, including sections *Callioreas* sensu Chamisso, 1832, and *Rhytidocamara* sensu Briquet, 1904), *Lippia* sect. *Dioicolippia* (Múlgura, 2000), and *Lippia* sect. *Goniostachyum* (O'Leary et al., 2012b). With only one species sampled in each, there was insufficient evidence confirming monophyly of *Burroughsia*, *Nashia* s.l., and *Lippia* sections *Dipterocalyx* and *Lippia*.

A single species each of *Nashia* s.l. and *Burroughsia* was included. *Nashia inaguensis* Millsp. represents this Caribbean endemic group of nine species recently partitioned into three genera (Greuter and Rodriguez, 2016) and is sister to *Lippia domingensis* Moldenke forming a Caribbean clade nested within the large clade 14. *Burroughsia*, segregated from *Lippia* by Moldenke (1940) because of its glandular appendage on the ventral stamen pair, occurs near the base of the *Lantana/Lippia* clade sister to *Lippia dulcis*. Consistent with previous studies (Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014), *Acantholippia seriphioides* appears in all trees as sister to the rest of the *Lantana/Lippia* clade, with which it shares a bilabiate calyx and condensed axillary inflorescences.

Previously (Lu-Irving et al., 2014), a clade of three Mexican *Aloysia* species (*A. barbata* (Brandegee) Moldenke, *A. chiapensis* Moldenke, *A. sonorensis* Moldenke) was found to be nested among species of *Lippia*. Two additional Mexican species known only from the type specimens (*A. coalcomana* Siedo, *A. nahuire* Gentry & Moldenke) also likely belong to this group (Siedo, 2012), informally named "Pseudolippia" by Siedo (2006). This clade is distinct from other *Aloysia* in having a bilobed calyx, a synapomorphy of the *Lantana/Lippia* clade, yellow flowers, otherwise not observed in *Aloysia*, in somewhat shortened inflorescences compared to other *Aloysia* species, and additional calyx and corolla traits that are more similar to species of *Lippia* (Siedo, 2006). This clade is represented here by *Aloysia barbata*, where it occurs in a clade with the widespread species *Lippia alba* (Mill.) N.E. Br. ex Britton & P. Wilson and the African species of *Lippia* in clade 14. Of the five species in the "Pseudolippia" group, only *Aloysia barbata* has another valid name in *Lippia* (*L. barbata* Brandegee).

The remaining species are assigned to *Lippia* sections *Rhodolippia* and *Zappania* and to "Sarcolippia," none of which are monophyletic. These species are found primarily in two regions of the tree, as a grade at the base of the *Lantana/Lippia* clade (clades 2, 3, 7, 9, 10, 12 in Figure 3) and again as a grade in clade 14, from which *Nashia*, *Lippia* sections *Dioicolippia*, *Goniostachyum*, and *Lippia*, and *Lantana* sect. *Lantana* are derived. Species assigned to *Rhodolippia* occur on four subclades all within clade 14. The large section *Zappania* has been divided into three series, *Axilliflorae*, *Corymbosae*, and *Paniculatae*, based on inflorescence morphology (Schauer, 1847; Troncoso, 1974). However, with multiple representatives of *Axilliflorae* and *Corymbosae* included here (*Paniculatae* is unsampled), neither is monophyletic, suggesting that the artificial nature of section *Zappania* extends to its included series. The three "Sarcolippia" species form a clade with one species each of *Lantana* (*L. speciosa*) and *Lippia* (*L. triplinervis*).

Morphological traits that characterize taxa

Morphological traits used to characterize the primary genera *Lantana* and *Lippia*—fleshy fruits with a single pyrene

for *Lantana* and schizocarpous fruit or a leathery drupe with two pyrenes for *Lippia*—are found not to be unique synapomorphies for clades in the phylogeny of the *Lantana/Lippia* clade (Figure 4). In contrast, diagnostic traits that have been used to characterize taxa inferred here to be monophyletic include (1) *Phyla*—malpighiaceous hairs and a trailing herbaceous habit; (2) *Lantana* sect. *Lantana* (Figure 1A)—yellow to orange corollas, dark blue-black drupes, and moderately conspicuous narrow floral bracts; (3) *Lantana* sect. *Callioreas* (Figure 1B, C, D)—lavender to purple corollas, white or purplish drupes, and ovate to reniform conspicuously imbricate floral bracts; (4) *Lippia* sect. *Dioicolippia* (Figure 1I)—dioecy (rare in Verbenaceae), xylopodial perennial plants with yellow flowers; and (5) *Lippia* sect. *Goniostachyum* (Figure 1J)—numerous axillary florescences (except *L. morii* Moldenke with one axillary florescence), tetrastichous floral bracts becoming fused near the apex of the inflorescence.

Lippia section *Dipterocalyx* (Figure 1L) is a distinctive taxon characterized by inflorescences with both terminal and axillary unbranched florescences (other sections have axillary florescences only) and winged calyces that suggest monophyly, but a single sample does not permit a test of monophyly in our analysis. Similarly, *Lippia* sect. *Lippia* is a small clade, most similar morphologically to *Dipterocalyx*, from which it was distinguished by Troncoso (1974) by inflorescences in dense globose heads and a compressed, bilobed calyx without wings; but, with a single species in our analysis, it cannot be evaluated for monophyly. The single representatives of these sections do not come out together on our tree.

Lippia sections *Rhodolippia* and *Zappania*, as well as "Sarcolippia," are not monophyletic. The traits that characterize the large sect. *Zappania* (Figure 1E, G, H, K), dense axillary or terminal florescences solitary or united in racemes or corymbs, large pluriseriated floral bracts, and membranaceous calyx, are a combination of generalized and plesiomorphic traits for the *Lantana/Lippia* clade (Troncoso, 1974). In contrast to the apparent plesiomorphic traits characterizing sect. *Zappania*, *Lippia* sect. *Rhodolippia* seems to be characterized by convergent derived traits. Section *Rhodolippia* (Figure 1F) is characterized by distinctive large, colored, floral bracts, which appear to have arisen multiple times independently (also in *Lippia macrophylla*, not assigned to *Rhodolippia*), perhaps as a modification for pollinator attraction. Colorful floral bracts that function in attracting pollinators are found throughout angiosperms (e.g., *Bougainvillea*, *Castilleja*, *Cornus*, *Euphorbia*) but are otherwise unknown in Verbenaceae. "Sarcolippia" is characterized by leathery drupaceous fruits with two pyrenes. Emphasis on the drupes, rather than the number of pyrenes, led to the inclusion of "Sarcolippia" in *Lantana* originally. Our results demonstrate that evolutionary lability in fruit fleshiness is widespread in the *Lantana/Lippia* clade (Figure 4) and that the two species that share clade 10 with "Sarcolippia" (*Lantana speciosa* and *Lippia triplinervis*) may have further

modifications from "Sarcolippia" ancestors that led to their being more similar to *Lantana* and *Lippia* sect. *Zappania*, respectively. A newly recognized species, *Lippia raoniana* P.H. Cardoso & Salimena., with fruit anatomy characteristic of "Sarcolippia," is distant from the other "Sarcolippia" species.

Several of the species at or near the base of the tree (*Acantholippia seriphioides*, *Burroughsia*, *Lippia integrifolia*, *L. micromera*, and *L. thymoides*) share the trait of an anther connective extension on the ventral stamen pair (not observed in *L. dulcis*, *L. rubella*, or *Phyla*). This trait is found elsewhere in Verbenaceae, including tribe Verbeneae, the sister group to Lantaneae. The occurrence of this trait only among the earliest branches of the *Lantana/Lippia* clade suggests that it may be an ancestral trait in the group, but the distribution of taxa without this trait among other species that exhibit it in this part of the tree makes any such conclusion speculative. These taxa from the basal grade also share several noteworthy morphological traits: axillary spikes or capituliform florescences, commonly small leaves in fascicles, and white flowers.

Fruit evolution and taxonomic confusion

The classification of *Lantana* and *Lippia* has been based on two associated, but not fully congruent, fruit traits. The two genera have commonly been distinguished by fleshy indehiscent fruits in *Lantana* and by dry schizocarpous fruits in *Lippia* (e.g., Schauer, 1847; Troncoso, 1974). In most species, there is a strict association of fleshiness with indehiscence of the seed-bearing structure and, thus, a single dispersal unit (vs. a dry fruit with dehiscence into two dispersal units). However, a handful of species are fleshy outside and schizocarpous inside. These species were assigned to *Lantana* sect. *Sarcolippia* by Schauer, who weighted the fleshy nature of the fruit in his assignment to *Lantana*, but have been transferred to *Lippia* by Silva and Salimena (2002), who emphasized the separation into two seed-bearing units. There are four instances of strict correspondence between these traits: *Lantana* sects. *Lantana* and *Callioreas*, *Lantana speciosa*, and *Nashia* (Figure 4). The phylogenetic proximity of the "Sarcolippia" group with *Lantana* sect. *Callioreas* leaves open the possiblity that they shared fleshy fruits from a common ancestor (Figure 4) and that fusion of dispersal structures came later in *Callioreas*. The clade that includes three species of "Sarcolippia" also includes one species characterized by classic *Lippia*-like fruits (*Lippia triplinervis*), suggesting a unique loss of fleshiness in the *Lantana/Lippia* clade, and one with classic *Lantana*-like fruits (*Lantana speciosa*), indicating another case of fusion of the seed-bearing units. Two instances of fleshy fruits with divided seed-bearing structures ("Sarcolippia" and *Lippia raoniana*), and no examples of the opposite combination, suggests that fleshiness is a precursor to fusion of the seed-bearing structures in the *Lantana/Lippia* clade.

Biogeography

The *Lantana/Lippia* clade is widely distributed in the New World from southern Argentina to southern Canada. Whereas a few species venture into temperate latitudes (*Phyla* in North America and *Acantholippia seriphioides* in South America), all of the rest are constrained to predominantly frost-free zones in the Neotropics and tropical Africa (Olmstead, 2013).

The most closely related clades in Verbenaceae to *Lantana/Lippia* are either entirely South American in distribution (Neospartoneae, *Rhaphithamnus*) or originated in South America (*Aloysia*, Verbeneae), except *Coelocarpum*, which is distributed in Madagascar, Socotra, and adjacent Somalia, suggesting that the clade originated in South America (Marx et al., 2010; Olmstead, 2013; Lu-Irving et al., 2014). All of the early diverging lineages in the *Lantana/Lippia* clade (except the small clade 3) occur in South America or are restricted to South America. This implies that multiple lineages, perhaps as many as four or more (Figure 5), have reached North/Central America and an equal number have reached the Caribbean from South American ancestors. These estimates do not include the several individual widespread species (e.g., *Lantana camara*, *Lippia alba*, *Phyla nodiflora*) with distributions in both North and South America, which represent additional range expansions between the continents.

Sampling a species-rich clade with broad geographic distribution can always introduce bias in the outcome of biogeographic interpretations. In the present study, the emphasis in sampling was on the center of greatest diversity in Argentina and Brazil, with significant sampling also in the Antilles, and relatively reduced sampling elsewhere in South America and Central America. Given the prior evidence that the origin of the *Lantana/Lippia* clade was in South America (Lu-Irving and Olmstead, 2013; Olmstead, 2013) and that our sampling emphasized taxonomic diversity, the confidence in the conclusions regarding the ancestral areas of nodes along the backbone of the tree is likely to be greater than that for nodes near the tips where sampling within sections, for example, favored South America. Hence, ancestral areas along the backbone of the tree are emphasized in Figure 5.

Several of the clades identified here are widely distributed throughout the Neotropics, including *Phyla* (clade 4), *Lantana* sect. *Callioreas* (clade 13), *Lantana* sect. *Lantana* (clade 17), and *Lippia* sect. *Goniostachyum* (clade 15). Sampling bias is likely to have influenced the ancestral area reconstruction for all of these except section *Callioreas*. Section *Goniostachyum* is distributed from Argentina to Mexico (O'Leary et al., 2012b), but only two species from Brazil were sampled here. The biogeographic analysis with Lagrange identified the ancestral area for *Phyla* as Central/North America, but the widespread species *Phyla nodiflora* is sister to or paraphyletic with respect to the rest of *Phyla* (Figures 2 and 3) and the support for the small *Burroughsia/Lippia dulcis* clade as its sister group is weak (and not

obtained in the concatenated sequence analysis; Figure 2). Thus, the inferred ancestral area for *Phyla* is equivocal.

Lantana sect. *Lantana* (clade 17) is represented here only by U.S. and Caribbean specimens, but prior studies (Marx et al., 2010; Lu-Irving and Olmstead, 2013; Lu-Irving et al., 2014) included accessions from Argentina, Brazil, and the southwestern United States. Section *Lantana* is sister to a clade of species from the southeastern United States and Central America with moderate support, but the inclusive clade is nested among South American species. The biogeographic analysis interprets the origin of sect. *Lantana* to be in Central/North America or the Caribbean. However, the poor resolution within sect. *Lantana* and the limited and biased sampling across its widespread distribution makes any inference regarding its geographic origin here uncertain.

African species are restricted to two clades, one each in *Lantana* and *Lippia* (Figure 5). In each case, the sister to the African clade is a widespread New World species, *Lantana trifolia* (now also a widespread weed in Africa) and *Lippia alba*, respectively. Two specimens of *Lippia rehmannii* were collected in South Africa as *L. rehmannii* and *L. wilmsii*; the latter is considered a synonym of the former (Fernandes, 1986).

We also identified two clades within clade 14 comprising mostly species occurring in the *campos rupestre* of the Espinhaço Range, including the *Lippia* species *L. hederifolia*, *L. filifolia*, and *L. florida* in one and *L. lupulina* (Cerrado endemic), *L. diamantinensis*, and *L. grandiflora* (previously misidentified as *L. pusilla*; Lu-Irving and Olmstead, 2013) in the other. These species have in common a well-developed xylopodium and flower after fires. Similarly, the species in clade 10 (members of "Sarcolippia" and two related species) are endemic to eastern Brazil, where they occur in the Serra do Mar, Mantiqueira Range, and Espinhaço Range chains associated with Atlantic Forest vegetation.

Taxonomic implications

Despite extensive transfers of names between *Lantana*, *Lippia*, and the other small genera sometimes recognized in Lantaneae since Linnaeus (1753) first applied these names (e.g., Millspaugh, 1906; Moldenke, 1940, 1941; Silva and Salimena, 2002; O'Leary and Múlgura, 2011), none of the previous circumscriptions for *Lantana* or *Lippia* align with monophyletic groups based on our current understanding of phylogeny. Both of the currently recognized sections of *Lantana* (Rotman, 2012) are monophyletic (with the exception of the recently described *Lantana speciosa*, which falls in the "Sarcolippia" clade), as are the small genus *Phyla*, the "Pseudolippia" clade of *Aloysia* species (Lu-Irving et al., 2014), and at least two recognized sections of *Lippia* (*Dioicolippia* and *Goniostachyum*), but all of these groups are nested within the inclusive *Lantana/Lippia* clade. Two sections of *Lippia*, sects. *Rhodolippia* and *Zappania*, plus "Sarcolippia" are not monophyletic, although a clade is obtained corresponding to species recognized as "Sarcolippia"

(clade 10) with a couple of additional species. *Rhodolippia* appears to be a polyphyletic group of species sharing the convergent trait of large, colorful floral bracts, whereas *Zappania* represents a paraphyletic group characterized by plesiomorphic or generalized traits, among which clades representing virtually all other taxa named at the genus or section rank are nested. Species recognized as "Sarcolippia" have a history of ambiguity with respect to generic assignment, initially being described in *Lantana*, but subsequently transferred to *Lippia* (Silva and Salimena, 2002). In our tree, *Lantana speciosa* and *Lippia triplinervis* occur in a clade with species of "Sarcolippia."

Adhering to the contemporary convention of recognizing and assigning names only to monophyletic groups in classification, revising these genera under the International Code (Turland et al., 2018) will require extensive changes, regardless of how genera are circumscribed. Two contrasting approaches to resolving the taxonomy of Lantaneae are possible.

In one approach, an effort to retain both *Lantana* and *Lippia* would require that several small clades be recognized as genera, many without clear defining traits. The type species of *Lantana* (*L. camara*) and *Lippia* (*L. americana* L.) occur in small clades that are sister to each other (type species in bold in Figure 2). So, even if retaining both names is a desired outcome, recircumscribing *Lantana* and *Lippia* will result in small genera bearing those names, and most species currently placed in each genus would need to be assigned to other genera. A few valid generic names are available, but with the exception of *Tamonopsis* Griseb. (= *Lantana* sect. *Callioreas*), these would also only apply to small clades in our phylogenetic tree, requiring that large numbers of species be assigned to new genera.

Thus, trying to construct a classification that retains both *Lantana* and *Lippia* would require establishing numerous new genera of dubious usefulness for field botanists. Also, with representative but limited sampling present in this study, it is likely that additional evidence will uncover more distinct lineages requiring yet more names or suggest combining some lineages that now appear to be distinct, resulting in more names abandoned to synonymy. A second, simpler alternative is to recognize a single large genus. Both *Lantana* and *Lippia* are available names, having first appeared in Species Plantarum (Linnaeus, 1753). *Lantana* is perhaps the more widely recognized name, due to the number of widely cultivated species, and the global impact of *Lantana camara* as a cosmopolitan weed in tropical regions (Day et al., 2003), whereas keeping *Lippia* would require fewer name changes, since many species of *Lantana* and most of the species in the small segregate genera already have names in *Lippia*. A third compromise option might be to establish new genera for *Acantholippia seriphioides* and *Lippia integrifolia*, expand *Burroughsia* to include *Lippia dulcis*, and retain *Phyla*, while placing the rest into a single large *Lantana* or *Lippia*. We are currently preparing a taxonomic revision.

A complementary taxonomy could be drafted using the principles of phylogenetic nomenclature as detailed in PhyloCode (Cantino and de Queiroz, 2020). A phylogenetic classification would permit defining and naming well-supported clades without the constraint of rank. In such a classification, all of the clades that correspond to named groups at the rank of genus (e.g., *Burroughsia, Nashia, Phyla*) or section (e.g., *Callioreas, Camara, Goniostachyum*) within *Lantana* or *Lippia* could be recognized, as well as any other clades it would be useful to name in order to enhance communication about diversity in Lantaneae (e.g., "Pseudolippia" for the clade of Mexican species presently assigned to *Aloysia*, or the African clades of *Lantana* and *Lippia*). For example, any of the 17 clades that were obtained consistently between the concatenated Bayesian analysis and the coalescent *BEAST analysis could be defined and named, along with others. In our opinion, this strategy would provide the greatest consistency with current taxonomy by recognizing clades based on shared morphology within the *Lantana*/*Lippia* clade, while retaining the identity of the group as a whole, without the constraints of equivalence of names within ranks. PhyloCode does not provide for the application of species names, so a revision based on the conventional code also would be needed.

CONCLUSIONS

The species of the *Lantana*/*Lippia* clade are closely related and, based on the inability to resolve relationships in prior chloroplast DNA studies, appear to be recently diversified, belying their remarkable morphological diversity and wide geographic distribution. The close relationships between them can be resolved using DNA sequence data of sufficient variability, and in sufficient quantity, but care should be taken in interpreting the results, due to the possible confounding effects of gene tree/species tree incongruence. Revising generic boundaries within the *Lantana*/*Lippia* clade will not be straightforward; we recommend absorbing most, if not all, of its species into an expanded *Lantana* or *Lippia*, and exploring a rank-free classification scheme to retain widely used names for many recognized groups.

AUTHOR CONTRIBUTIONS

P.L.-I. and R.G.O. conceptualized the overall project. All authors participated in collecting material in the field or obtaining material from herbaria. A.M.B., C.B., and P.L.-I. did most of the DNA sequencing, and A.M.B. and P.L.-I. did the data analyses. F.R.S., T.R.S.S., V.T., P.H.C., and N.O. contributed knowledge of diversity and taxonomy of the group and confirmed identifications and nomenclature. P.L.-I., A.M.B., and R.G.O. drafted the manuscript, to which all others contributed comments and edits.

DATA AVAILABILITY STATEMENT

All collections used in this study are deposited in publicly accessible herbaria (Appendix) and all DNA sequences have been deposited in GenBank. All herbarium specimens that are vouchers for DNA and deposited in Brazilian herbaria are registered with SISGEN.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information tab for this article.

Appendix S1. Pairwise distances between representative members of the *Lantana/Lippia* clade, used to gauge variability of loci to select data sources for phylogenetic analysis. All pairwise comparisons with *Lantana trifoliata*.

Appendix S2. Individual gene trees obtained by Bayesian analysis (ETS, ITS, PPR 11, PPR 81, PPR 90, PPR 97, PPR 123). Posterior probability values above branches.

APPENDIX 1

TABLE A1: Table of vouchers and GenBank accession numbers accompanying sequence data used in this study

Species	Voucher	Section	Origin	ETS	ITS	PPR 11	PPR 81	PPR 90	PPR 97	PPR 123
Acantholippia seriphioides (A. Gray) Moldenke (=*Lippia seriphioides* A. Gray)	Olmstead 2004-146; WTU	–	Argentina	JX966793	MW292718	JX966651	JX966696	MW397314	MW397399	JX966747
Aloysia barbata (Brandegee) Moldenke (=*Lippia barbata* Brandegee)	Carter & Ferris 3902 A; TEX	–	Mexico	JX966794	MW292719	JX966652	JX966697	MW397315	ns	JX966748
Aloysia catamarcensis Moldenke	Olmstead 2007-82; WTU	–	Argentina	KF688828	MW292720	MW397465	ns	MW397316	MW397400	Excluded
Aloysia citrodora Palàu	Olmstead 2007-13; WTU	–	Argentina	JX966795	MW292721	JX966653	JX966698	MW397317	MW397401	JX966749
Aloysia virgata (Ruiz & Pav.) Pers.	Olmstead 2004-133; WTU	–	Argentina	KF688852	MW292722	ns	ns	ns	MW397402	Excluded
Burroughsia fastigiata (Brandegee) Moldenke (=*Lippia fastigiata* Brandegee)	Sikes & Babcock 294; TEX	–	Mexico	JX966800	MW292723	JX966658	ns	ns	MW397403	JX966754
Lantana achyranthifolia Desf.	Salimena 2989; CESJ	*Callioreas*	Brazil	JX966818	MW292760	JX966673	JX966719	MW397353	ns	JX966769
Lantana buchii Urb.	Lu-Irving 2012-107; WTU	*Callioreas*	Dominican Republic	MW296957	MW292724	MW397466	MW397264	MW397318	MW397404	MW397214
Lantana caatingensis Moldenke	S.F.Conceição 92; HUEFS	*Callioreas*	Brazil	MW296958	MW292725	ns	ns	MW397319	ns	MW397215
Lantana camara L.	Lu-Irving 2012-37; WTU	*Lantana*	Puerto Rico	MW296959	MW292726	MW397467	MW397265	MW397320	MW397405	MW397216
Lantana canescens Kunth	Thode 364; ICN	*Callioreas*	Brazil	MW296977	ns	MW397484	MW397234	MW397341	ns	MW397234
Lantana canescens Kunth	Olmstead 2007-06; WTU	*Callioreas*	Argentina	JX966806	MW292727	FJ549096	JX966708	MW397321	MW397406	FJ549274
Lantana canescens Kunth	Lu-Irving 2008-7; WTU	*Callioreas*	Cultivated	MW296960	MW292728	MW397468	MW397266	MW397322	ns	MW397217
Lantana depressa Small	Lu-Irving 2012-1; WTU	*Lantana*	Florida	MW296961	MW292729	MW397469	MW397267	MW397323	MW397407	MW397218
Lantana exarata Urb. & Ekman	Lu-Irving 2012-49; WTU	*Callioreas*	Puerto Rico	MW296962	MW292730	MW397470	MW397268	MW397324	MW397408	MW397219
Lantana ferreyrae Moldenke	Lu-Irving s.n; WTU	*Callioreas*	Peru	MW296963	MW292731	MW397471	MW397269	MW397325	MW397409	MW397220
Lantana fucata Lindl.	Salimena 2952; CESJ	*Callioreas*	Brazil	JX966808	MW292732	JX966663	JX966710	MW397326	ns	JX966759
Lantana gracilis T.R.S. Silva	T.R.S.Silva 228; HUEFS	*Callioreas*	Brazil	MW296964	MW292733	ns	ns	MW397327	ns	MW397221
Lantana haughtii Moldenke	Lu-Irving 2009-34; WTU	*Callioreas*	Peru	MW296965	MW292734	MW397472	MW397270	MW397328	MW397410	MW397222
Lantana horrida Kunth	Lu-Irving 2012-61; WTU	*Lantana*	Dominican Republic	MW296966	MW292735	MW397473	MW397271	MW397329	MW397411	MW397223
Lantana involucrata L.	Lu-Irving 2012-13; WTU	*Callioreas*	Florida	MW296967	MW292736	MW397474	MW397272	MW397330	MW397412	MW397224

TABLE A1 (Continued)

Species	Voucher	Section	Origin	ETS	ITS	PPR 11	PPR 81	PPR 90	PPR 97	PPR 123
Lantana leonardiorum Moldenke	Lu-Irving 2012-102; WTU	*Lantana*	Dominican Republic	MW296968	MW292737	MW397475	MW397273	MW397331	MW397413	MW397225
Lantana leucocarpa Urb & Ekman ex Moldenke	Lu-Irving 2012-70; WTU	*Callioreas*	Dominican Republic	MW296969	MW292738	MW397476	MW397274	MW397332	ns	MW397226
Lantana macropoda Torr.	Nesom & Mayfield 7355; TEX	*Callioreas*	Mexico	JX966810	MW292739	JX966665	JX966712	ns	ns	JX966761
Lantana montevidensis (Spreng.) Briq.	Lu-Irving 2008-15; WTU	*Callioreas*	Texas	JX966813	MW292740	JX966668	JX966715	MW397333	ns	JX966764
Lantana montevidensis (Spreng.) Briq.	Olmstead 2010-203; WTU	*Callioreas*	Brazil	MW296970	MW292741	MW397477	MW397275	MW397334	MW397414	MW397227
Lantana pauciflora Urb.	Lu-Irving 2012-106; WTU	*Callioreas*	Dominican Republic	MW296971	MW292742	MW397478	MW397276	MW397335	MW397415	MW397228
Lantana reptans Hayek	Lu-Irving 2009-14; WTU	*Callioreas*	Peru	MW296972	MW292743	MW397479	MW397277	MW397336	MW397416	MW397229
Lantana reticulata Pers.	Lu-Irving 2012-66; WTU	*Callioreas*	Dominican Republic	MW296973	MW292744	MW397480	MW397278	MW397337	ns	MW397230
Lantana scabiosiflora Kunth	Lu-Irving 2009-1; WTU	*Callioreas*	Peru	MW296974	MW292745	MW397481	MW397279	MW397338	MW397417	MW397231
Lantana scabrida Aiton	Lu-Irving 2012-89; WTU	*Lantana*	Dominican Republic	MW296975	MW292746	MW397482	MW397280	MW397339	MW397418	MW397232
Lantana speciosa Salimena & T. Silva	Dittrich 1654; CESJ	*Callioreas*	Brazil	MW297003	MW292792	MW397503	MW397302	MW397384	MW397452	MW397256
Lantana × *strigocamara* R.W. Sanders	Lu-Irving 2012-22; WTU	*Lantana*	Puerto Rico	MW296979	MW292749	MW397486	MW397283	MW397343	MW397419	MW397236
Lantana tilcarensis Tronc.	Olmstead 2007-18; WTU	*Callioreas*	Argentina	MW296980	MW292750	MW397487	MW397284	MW397344	MW397420	MW397237
Lantana trifolia L.	Lu-Irving s.n. (cult from seed from Lu-Irving 2009-59); WTU	*Callioreas*	Peru	MW296982	MW292752	MW397489	MW397286	MW397346	MW397422	MW397239
Lantana trifolia L.	Lu-Irving 2012-90; WTU	*Callioreas*	Dominican Republic	MW296981	MW292751	MW397488	MW397285	MW397345	MW397421	MW397238
Lantana trifolia L.	Olmstead 1996-98; WTU	*Callioreas*	Cultivated	JX966815	MW292753	JX966670	JX966716	MW397347	MW397423	JX966766
Lantana ukambensis (Vatke) Verc.	Mawi 80; MO	*Callioreas*	Tanzania	MW296983	MW292754	MW397490	ns	MW397348	MW397424	ns
Lantana viburnoides Vahl	Miyazaki 991013R29; TEX	*Callioreas*	Saudi Arabia	JX966816	MW292755	JX966671	JX966717	MW397349	MW397425	JX966767
Lantana xenica Moldenke	Soza 1838; WTU	*Callioreas*	Argentina	MW296985	MW292756	MW397491	MW397287	MW397350	MW397426	MW397240

(Continues)

TABLE A1 (Continued)

Species	Voucher	Section	Origin	ETS	ITS	PPR 11	PPR 81	PPR 90	PPR 97	PPR 123
Lippia alba (Mill.) N.E. Br. ex Britton & P. Wilson	Fairchild BG 37139; FTG	*Zappania*	Cultivated	JX966817	MW292757	JX966672	JX966718	MW397351	MW397427	JX966768
Lippia alba (Mill.) N.E. Br. ex Britton & P. Wilson	Olmstead 2004-110; WTU	*Zappania*	Argentina	MW296986	MW292758	MW397492	MW397288	ns	MW397428	MW397241
Lippia americana L.	Nee 8821; NY	*Lippia*	Panama	MW297012	ns	ns	MW397311	MW397397	MW397462	Excluded
Lippia americana L.	Sparre 19841; NY	*Lippia*	Ecuador	MW297014	ns	ns	MW397313	MW397398	MW397464	Excluded
Lippia americana L.	Holm-Nielson 7198; NY	*Lippia*	Ecuador	MW297013	ns	ns	MW397312	ns	MW397463	Excluded
Lippia archavaletae Herter ex Moldenke	Thode 54; ICN	*Dioicolippia*	Brazil	MW296987	MW292759	MW397493	ns	MW397352	MW397429	ns
Lippia aristata Schauer	Salimena 2361; CESJ	*Zappania*	Brazil	JX966821	MW292767	JX966676	JX966722	MW397359	MW397434	JX966772
Lippia asperrima Cham.	Olmstead 2004-140; WTU	*Dioicolippia*	Argentina	ns	MW292761	MW397494	MW397289	MW397354	MW397430	ns
Lippia brasiliensis (Link) T. Silva	Salimena 2996 CESJ	"Sarcolippia"	Brazil	JX966819	MW292762	JX966674	JX966720	MW397355	MW397431	JX966770
Lippia cardiostegia Benth.	Grose 144; HULE	*Rhodolippia*	Nicaragua	MW296988	MW292763	MW397495	MW397290	ns	ns	MW397242
Lippia corymbosa Cham.	Salimena et al. s/n CESJ 34741	*Zappania*	Brazil	MW296989	MW292764	MW397496	MW397291	MW397356	MW397432	MW397243
Lippia diamantinensis Glaz.	Salimena 2943; CESJ	*Rhodolippia*	Brazil	JX966820	MW292765	JX966675	JX966721	MW397357	ns	JX966771
Lippia domingensis Moldenke	Lu-Irving 2012-80; WTU	*Zappania*	Dominican Republic	MW296990	MW292766	MW397497	MW397292	MW397358	MW397433	MW397244
Lippia dulcis Trevir.	Lu-Irving 2013-2; WTU	*Zappania*	Cultivated	MW296991	MW292768	ns	ns	MW397360	MW397435	ns
Lippia dulcis Trevir.	Olmstead 1998-56; WTU	*Zappania*	Cultivated	JX966822	ns	FJ549095	JX966723	ns	ns	FJ549273/ M-W397245
Lippia filifolia Mart. & Schauer	Thode 352; ICN, WTU	*Zappania*	Brazil	JX966823	MW292769	JX966677	JX966724	MW397361	MW397436	JX966773
Lippia florida Cham.	Salimena 2945; CESJ	*Rhodolippia*	Brazil	MW296992	MW292770	MW397498	MW397293	MW397362	MW397437	MW397246
Lippia formosa Brandegee	Ocampo 1764; WTU	*Rhodolippia*	Cultivated	MW296993	MW292771	MW397499	MW397294	MW397363	ns	MW397247
Lippia grandiflora Mart. & Schauer (misidentified as *L. pusilla* T.R.S. Silva in Lu-Irving & Olmstead (2013))	Thode 337; ICN	*Zappania*	Brazil	JX966831	MW292785	JX966685	JX966732	MW397377	MW397446	JX966781
Lippia hederifolia Mart. & Schauer	Salimena s/n CESJ 48274	*Rhodolippia*	Brazil	JX966824	MW292772	JX966678	JX966725	MW397364	MW397438	JX966774
Lippia hermannioides Cham.	Thode 389; ICN, WTU	*Zappania*	Brazil	JX966825	MW292773	JX966679	JX966726	MW397365	MW397439	JX966775

TABLE A1 (Continued)

Species	Voucher	Section	Origin	ETS	ITS	PPR 11	PPR 81	PPR 90	PPR 97	PPR 123
Lippia insignis Moldenke	S.F.Conceição 98; HUEFS	*Zappania*	Brazil	MW296994	MW292774	ns	MW397295	MW397366	ns	MW397248
Lippia integrifolia (Griseb.) Hieron.	Olmstead 2007-78; WTU	*Zappania*	Argentina	MW296995	MW292775	MW397500	MW397296	MW397367	MW397440	MW397249
Lippia javanica Spreng.)	Lu-Irving 2012-1 A; WTU	*Zappania*	South Africa	JX966826/ MW296996	MW292776	JX966680	JX966727	MW397368	MW397441	JX966776/ M-W397250
Lippia lasiocalycina Cham.	Thode 363; ICN, WTU	*Zappania*	Brazil	MW296997	MW292777	MW397501	MW397297	MW397369	MW397442	MW397251
Lippia lupulina Cham.	Salimena 2941; CESJ	*Rhodolippia*	Brazil	JX966827	MW292778	JX966681	JX966728	MW397370	ns	JX966777
Lippia macrophylla Cham.	Thomas 13474; CESJ	"*Sarcolippia*"	Brazil	JX966828	MW292779	JX966682	JX966729	MW397371	ns	JX966778
Lippia micromera Schauer	Olmstead 1992-225; WTU	*Zappania*	Cultivated	JX966829	MW292780	JX966683	JX966730	MW397372	MW397443	JX966779
Lippia morii Moldenke	C. van den Berg, 1427; HUEFS	*Goniostachyum*	Brazil	MW296999	MW292782	ns	MW397299	MW397374	ns	MW397253
Lippia organoides Kunth	Lu-Irving 2010-18; WTU	*Goniostachyum*	Cultivated	MW297000	MW292783	JX966684	JX966731	MW397375	MW397444	JX966780
Lippia organoides Kunth (original det as *L. microphylla* Schauer)	T.R.S.Silva 212; HUEFS	*Goniostachyum*	Brazil	MW296998	MW292781	ns	MW397298	MW397373	ns	MW397252
Lippia organoides Kunth (original det as *L. rigida* Schauer)	C. van den Berg, 1431; HUEFS	*Goniostachyum*	Brazil	MW297002	MW292788	ns	MW397301	MW397380	ns	MW397255
Lippia organoides Kunth (original det as *L. salviifolia* Cham.)	Salimena 2975; CESJ	*Goniostachyum*	Brazil	JX966836	MW292791	JX966690	JX966736	MW397383	MW397451	JX966786
Lippia organoides Kunth (original det as *L. velutina* Schauer)	Salimena 2995; CESJ	*Goniostachyum*	Brazil	JX966838	MW292797	JX966692	JX966738	MW397389	MW397454	JX966788
Lippia pseudothea Schauer	Salimena 2940; CESJ	*Rhodolippia*	Brazil	MW297001	MW292784	MW397502	MW397300	MW397376	MW397445	MW397254
Lippia pubescens (Moldenke) T. Silva	Salimena 2981; CESJ	"*Sarcolippia*"	Brazil	MW296976	MW292747	MW397483	MW397281	MW397340	ns	MW397233
Lippia rehmannii H. Pearson (coll. as *L. wilmsii* H. Pearson)	Lu-Irving 2012-111 (cult from seed of Lu-Irving 2008-29); WTU	*Zappania*	South Africa	MW297007	MW292798	MW397506	MW397306	MW397390	MW397455	MW397259
Lippia rehmannii H. Pearson	Lu-Irving 2013-1; WTU (probably from seed from PLI 08-20)	*Zappania*	South Africa	JX966832	MW292786	excluded	ns	MW397378	MW397447	Excluded
Lippia raoniana P.H. Cardosa & Salimena	Thode 386; ICN		Brazil	MW296978	MW292748	MW397485	ns	MW397342	ns	MW397235
Lippia rhodocnemis Mart. & Schauer	Salimena 1385; CESJ	*Rhodolippia*	Brazil	JX966833	MW292787	JX966687	JX966733	MW397379	MW397448	JX966783

(Continues)

TABLE A1 (Continued)

Species	Voucher	Section	Origin	ETS	ITS	PPR 11	PPR 81	PPR 90	PPR 97	PPR 123
Lippia rotundifolia Cham.	Salimena 2958; CESJ	*Zappania*	Brazil	JX966834	MW292787	JX966688	JX966734	MW397381	MW397449	JX966784
Lippia rubella (Moldenke) T.R.S. Silva	F. Salimena 2987; CESJ	*Dipterocalyx*	Brazil	JX966835	MW292790	JX966689	JX966735	MW397382	MW397450	JX966785
Lippia thymoides Mart. & Schauer	M.C.Dorea, 61; HUEFS	*Zappania*	Brazil	MW297004	MW292793	ns	MW397303	MW397385	ns	MW397257
Lippia triplinervis Gardner	Mota 2456; BHCB	*Zappania*	Brazil	MW297005	MW292794	MW397504	MW397304	MW397386	ns	MW397258
Lippia turbinata Griseb.	Olmstead 2007-74; WTU	*Zappania*	Argentina	JX966837	MW292795	JX966691	JX966737	MW397387	MW397453	JX966787
Lippia umbellata Cav.	Van Devender 06-194; TEX	*Rhodolippia*	Mexico	MW297006	MW292796	MW397505	MW397305	MW397388	ns	ns
Nashia inaguensis Millsp. (= *Lippia inaguensis* (Millsp.) Urban)	Cultivated; no voucher		Cultivated	JX966839	MW292799	JX966693	JX966739	MW397391	MW397456	JX966789
Phyla cuneifolia (Torr.) Greene	Olmstead 1992-134; WTU		Colorado	MW297008	MW292800	ns	MW397307	MW397392	MW397457	MW397260
Phyla lanceolata (Michx.) Greene	Lu-Irving 2008-16; WTU		Texas	MW297009	MW292801	MW397507	MW397308	MW397393	MW397458	MW397261
Phyla nodiflora (L.) Greene	Olmstead 2004-159; WTU		Argentina	MW297010	MW292802	ns	MW397309	MW397394	MW397459	MW397262
Phyla nodiflora (L.) Greene	Olmstead 2007-65; WTU		Argentina	JX966841	MW292803	JX966694	JX966741	MW397395	MW397460	JX966790
Phyla nodiflora (L.) Greene	Lu-Irving 2008-4; WTU		Texas	MW297011	MW292804	MW397508	MW397310	MW397396	MW397461	MW397263

Note: "Section" refers to conventional classification. GenBank numbers beginning with "MW" are newly obtained for this study.

Abbreviation: ns, no sequence.