

Reassignment of Species of Paraphyletic *Junellia* s. l. to the New Genus *Mulguraea* (Verbenaceae) and New Circumscription of Genus *Junellia*: Molecular and Morphological Congruence

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Abstract—Verbenaceae tribe Verbenaeae includes three major genera, *Verbena*, *Glandularia*, and *Junellia*, which form a recently diversified group. *Junellia* is a South American genus, whereas *Verbena* and *Glandularia* are distributed in temperate regions of both South and North America. Seven noncoding chloroplast regions were sequenced including intergenic spacers and/or introns in *trnD-trnT*, *trnS-trnG*, *trnS-trnfM*, *trnT-trnL*, *trnG*, *trnL*, and *trnL-trnF*; the nuclear ITS and ETS regions were also sequenced. Together with previous studies, these results suggest that *Junellia*, as traditionally conceived, is a paraphyletic group of two separate clades. *Junellia* should be restricted to the clade containing the type, *J. micrantha*, which also includes *Glandularia* subgenus *Paraglandularia* and the genus *Urbania*. Consequently *Urbania* and *Glandularia* subgenus *Paraglandularia* are reduced to synonymy under *Junellia*, and eight new combinations in *Junellia* are proposed: *Junellia ballsii*, *J. crithmifolia*, *J. fasciculata*, *J. hookeriana*, *J. lucanensis*, *J. occulta*, *J. pappigera* and *J. origenes*. The remaining *Junellia* species form a monophyletic group here designated as the new genus *Mulguraea*, with 13 new combinations: *Mulguraea arequipense*, *M. asparagoides*, *M. aspera* var. *aspera*, *M. aspera* var. *longidentata*, *M. cedroides*, *M. cinerascens*, *M. echegarayi*, *M. hystrix*, *M. ligustrina* var. *ligustrina*, *M. ligustrina* var. *lorentzii*, *M. scoparia*, *M. tetragonocalyx* and *M. tridens*. *Verbena* and *Glandularia* s. s. are both monophyletic based on ETS/ITS data, but neither is monophyletic based on cpDNA data. Relationships within each genus are still not wholly resolved, nevertheless there is evidence that South and North American *Verbena* might both be monophyletic. *Verbena* and *Glandularia* are sister groups, and together they are sister to the reconstituted *Junellia*. *Mulguraea* is sister to the group comprising all the three genera, *Verbena*, *Glandularia*, and *Junellia*.

Keywords—*Glandularia*, new combinations, *Paraglandularia*, phylogeny, taxonomy, *Verbena*, Verbenaeae.

In the most recent classification of Verbenaceae (Atkins 2004) tribe Verbenaeae Schauer comprises five genera, *Verbena* L. with 44 species (O'Leary et al. 2007a), *Glandularia* J. F. Gmel. with 84 species (Peralta 2009), *Junellia* Moldenke with 39 species (Peralta et al. 2008), and the monotypic *Urbania* Phil. and *Hierobotana* Briq. These genera, often combined under *Verbena* in early treatments (Schauer 1847; Briquet 1895; Perry 1933; Troncoso 1974; Table 1), constitute a recent and rapidly diversifying group, referred to as the “*Verbena* complex” (Yuan and Olmstead 2008a, b). All Verbenaeae share a dry schizocarpic fruit, separating at maturity into four 1-seeded mericarps. Most species of this tribe are found in temperate North or South America.

Junellia is distinguished by its shrubby habit, woody rootstock, and reduced, sometimes spiny, leaves, and a base chromosome number of $x = 10$, rarely $x = 9$ (Botta and Brandham 1993). *Glandularia* and *Verbena* are mostly leafy herbs, occasionally subshrubs, without woody rootstocks or spines. *Verbena* differs from *Glandularia* principally by its base chromosome number of $x = 7$ vs. $x = 5$ (Schnack and Covas 1944), as well as several morphological and anatomical characters (Schnack and Covas 1946; Schnack 1964; Umber 1979; Botta 1989; O'Leary et al. 2007b).

Junellia is a South American genus, distributed along the arid Andean region, from Perú, Bolivia, Chile, and Argentina, with the greatest species richness in the Andean-Patagonian domain (Cabrera and Willink 1973). *Verbena* and *Glandularia* are distributed in temperate regions of both South and North America, with several species naturalized in the Old World.

Yuan and Olmstead (2008a, b), using cpDNA and the nuclear genes *waxy*, *PHOT1*, and *PHOT2* sequence data, showed that both *Glandularia* (excluding subgenus *Paraglandularia* Schnack & Covas) and *Verbena* are monophyletic, with base chromosome numbers of $x = 5$ and $x = 7$ as putative synapomorphies, respectively. These studies also provided initial evidence that

Junellia, as currently circumscribed (Botta 1989; Peralta et al. 2008), is not monophyletic. The main objective of this study is to extend sampling of *Junellia* to provide a solid phylogenetic framework for generic realignments.

MATERIALS AND METHODS

Taxon Sampling—For phylogenetic analyses, 70 taxa of the *Verbena* complex were included; all but 20 of these taxa had been used in a previous study (Yuan and Olmstead 2008a), where detailed voucher information can be found. Information on the 20 new taxa is in Appendix 1. For the cpDNA analyses, trees were rooted using *Lippia salsa* and *Aloysia virgata* as outgroups; both belong to tribe Lantaneae, sister group of tribe Verbenaeae (Marx and Olmstead, unpubl. data). There is too much ETS/ITS sequence divergence between *Aloysia/Lippia* and the *Verbena* complex to permit an unambiguous alignment, and thus, the use of *Aloysia/Lippia* as outgroups. Subsequently, the ETS/ITS trees were rooted using the “*Junellia* II” group (Yuan and Olmstead 2008b) as a functional outgroup, based on previous studies on the *Verbena* complex (Yuan and Olmstead 2008a, b) and ongoing work towards resolving the phylogeny of the Verbenaceae family based on cpDNA (Marx and Olmstead, unpubl. data) and five nuclear pentatricopeptide (PPR) genes (Yuan et al. 2009). This “*Junellia* II” group is treated as a new genus, *Mulguraea*, in this study (see below).

DNA Extraction, Amplification and Sequencing—The material used for DNA extraction was taken from plants collected from wild populations and dried in silica gel or from herbarium specimens (taxa with asterisk in Appendix 1). For leaves dried in silica gel, DNA extraction was performed using a modified CTAB protocol by Doyle and Doyle (1987), adapted for small amounts of plant material. For herbarium material, DNA extraction was conducted using the DNeasy plant mini kit (Qiagen, Hilden, Germany). Seven noncoding chloroplast regions were amplified. The *trnS-trnG* spacer and *trnG* intron were generally amplified together as the *trnS-G* fragment, using primers *trnS* (Shaw et al. 2005) and *trnG(V)* (Yuan and Olmstead 2008a). When this was not possible internal primers *trnG-S F(V)* and *trnG-S R(V)*, designed by Yuan and Olmstead (2008a), were used to amplify the region in two fragments. The *trnT-trnL* spacer, *trnL* intron, and *trnL-trnF* spacer were amplified together as the *trnT-F* fragment using primers “a” and “f” (Taberlet et al. 1991). When this was not possible internal primers “b” and “c” (Taberlet et al. 1991) were used to amplify the region in two fragments. The *trnS-trnfM* region was amplified using primers *trnS* and *trnfM* (Shaw et al. 2005). The *trnD-trnT* region was amplified

TABLE 1. Comparison of historical treatments of *Verbena*, *Glandularia*, and *Junellia*.

Schauer (1847), Briquet (1895), Perry (1933)	Troncoso (1974)	Botta (1989), Atkins (2004), O'Leary et al. (2007a), Peralta et al. (2008), (2009)
<i>Verbena</i> L.	<i>Verbena</i>	<i>Verbena</i>
sect. <i>Verbenaca</i> Schauer		ser. <i>Verbena</i>
ser. <i>Leptostachyae</i> Schauer	sect. <i>Verbena</i>	ser. <i>Pachystachyae</i> Schauer
ser. <i>Pachystachyae</i> Schauer		
		<i>Junellia</i> Moldenke
ser. <i>Pungentes</i> Schauer		subg. <i>Junellia</i>
ser. <i>Pauciflorae</i> Briquet		sect. <i>Junellia</i>
ser. <i>Acerosae</i> Briquet		sect. <i>Junelliopsis</i> (Botta) Peralta & Múlgura
ser. <i>Junciformes</i> Briquet	sect. <i>Junellia</i> (Mold.) Tronc.	sect. <i>Guedesia</i> Botta
ser. <i>Verticilliflorae</i> Schauer		subg. <i>Thryothamnus</i> Botta
		sect. <i>Thryothamnus</i> Botta
ser. <i>Nobiles</i> Schauer	<i>Glandularia</i> J. F. Gmel.	sect. <i>Verticiflora</i> (Schauer) Botta
		sect. <i>Dentium</i> Peralta & Múlgura
sect. <i>Glandularia</i> (J. F. Gmel.) Schauer		<i>Glandularia</i>
		subg. <i>Glandularia</i>
		subg. <i>Paraglandularia</i> Schnack & Covas

using primers trnDF and trnTR (Shaw et al. 2005). When this was not possible internal primers designed by Yuan and Olmstead (2008a), trnD2T(V) and trnT2D(V), were used to amplify the region in two fragments. The internal and external transcribed spacer regions of nuclear DNA (ITS and ETS) were amplified using primers ITS-4 and ITS-5 (White et al. 1990), and primers 18S-IGS (Baldwin and Markos 1998) and ETS-B (Beardsley et al. 2003), respectively. Polymerase chain reaction and sequencing protocols followed those of Yuan and Olmstead (2008a) for their chloroplast DNA data. Some sequencing reactions were also performed by MacroGen Inc. using ABI PRISM BigDye™ Terminator Cycle Sequencing Kits with AmpliTaq DNA polymerase (Applied Biosystems, Seoul, Korea).

The initially generated ITS/ETS sequences display > 1% intraindividual polymorphic sites in one *Junellia* species and a few *Glandularia* species. For these taxa, the primer pair ITS-4 and ETS-B was used to amplify a fragment including ETS and the entire 18S, ITS1, 5.8S, and ITS2 regions, totaling ca. 3 kb. Polymerase chain reaction reactions were performed using PfuUltra™ II Fusion HS DNA Polymerase (Stratagene, La Jolla, California), following the protocol used by Yuan and Olmstead (2008a) to generate their nuclear DNA data. After purification, PCR products were cloned using the TOPO TA Cloning kit (Invitrogen, Carlsbad, California) and six to eight positive clones were sequenced for the ETS and ITS region but not the 18S DNA. The cloned ETS and ITS sequences were identified by clone numbers. All newly generated sequences from this study have been deposited in GenBank (Appendix 1).

Phylogenetic Analysis—Sequences were aligned manually using the program Se-Al version 2.0a11 (Rambaut 1996) based on the similarity criterion (Simmons 2004). Alignment matrices were submitted to TreeBASE study number S2349. Two poly-A/C regions in the *trnS-trnfM* fragment (positions 626–643, 686–693) were excluded from subsequent analyses due to uncertainty of homology assessment. Parsimony-informative gaps were coded as binary characters using the simple gap coding approach (Simmons and Ochoterena 2000; Graham et al. 2000) and were included in both parsimony and Bayesian analyses. Phylogenetic analyses were conducted on the combined cpDNA dataset and the combined ITS/ETS dataset separately. Parsimony analyses were performed using PAUP* v.4.0b10 (Swofford 2002). Heuristic searches were performed with 500 random stepwise addition replicates and TBR branch swapping with the MULTREES option in effect. Clade support was estimated by bootstrap analyses (Felsenstein 1985) using 500 pseudo-replicates. Bayesian MCMC analyses (Yang and Rannala 1997) were conducted using MrBayes v.3.1.2 (Ronquist and Huelsenbeck 2003). A mixed-model approach (Ronquist and Huelsenbeck 2003) was employed to integrate the parsimony-informative gaps as binary characters with nucleotide data. Each final dataset (cpDNA, ITS/ETS) was divided into two partitions, the “DNA” partition and “gap” partition. The Akaike information criterion (AIC; Akaike 1974) as implemented in Modeltest v.3.7 (Posada and Crandall 1998) was used to determine the model of sequence evolution that best fit the DNA partition (TVM + G and GTR + I + G for the cpDNA and ITS/ETS dataset, respectively). The restriction site (binary) model in MrBayes v.3.1.2 (Ronquist and Huelsenbeck 2003) was used for the “gap” partition, with ascertainment bias for gap characters incorporated (Iset coding = informative). We carried out two independent runs of 1,000,000 generations from a random starting tree using the default priors and four Markov chains (one cold and three heated chains), sampling one tree every 100 generations. The program Tracer v.1.4 (Rambaut and Drummond 2007) was used to

examine the output parameters from the Bayesian MCMC analyses. Stationarity was assumed when the estimated value of $-\ln L$ and all other parameters had stabilized. Trees prior to reaching stationarity were discarded as burn-in and the remaining trees from the two independent runs were pooled to calculate the majority rule consensus tree.

RESULTS AND DISCUSSION

Phylogenetic Analyses—Figure 1 represents one of the 12 maximum parsimonious (MP) trees inferred from cpDNA data and Fig. 2 represents one of the 7,137 MP trees inferred from ITS/ETS data, respectively. Bayesian analyses gave very similar results, and none of the few differences was supported by > 50% bootstrap value (BS) or > 0.95 posterior probability (PP). With more extensive sampling of *Junellia* and *Glandularia*, the cpDNA tree topology is consistent with previous results based on cpDNA data (Yuan and Olmstead 2008a). *Junellia* is paraphyletic and can be divided into two major clades (Fig. 1). The three species from *Glandularia* subgenus *Paraglandularia* are well nested within one of the *Junellia* clades. Neither *Verbena* nor *Glandularia* (excluding *Paraglandularia*) is monophyletic in the cpDNA tree, a consequence of two potential intergeneric chloroplast transfers (Yuan and Olmstead 2008a). Within *Verbena*, both the South and North American group are monophyletic (Fig. 1). The ITS/ETS tree topology is largely consistent with previous results from nuclear gene data (Yuan and Olmstead 2008a, b) in the monophyly of both *Verbena* and *Glandularia* (excluding subgenus *Paraglandularia*), and is also consistent with the cpDNA phylogeny in the paraphyly of *Junellia* and the position of *Glandularia* subgenus *Paraglandularia*. In addition, like the cpDNA data, the ITS/ETS data suggest that both South and North American *Verbena* are monophyletic.

Mulguraea a New Genus Segregated from Junellia—A recent taxonomic treatment of *Junellia* (Peralta et al. 2008) recognized two subgenera: *Junellia* and *Thryothamnus*, each composed of three sections. Subgenus *Junellia* is characterized by an enlarged style base covering the mericarp apex, whereas the style base in subgenus *Thryothamnus* is somewhat inserted between the four mericarps, as is the case in the rest of Verbenaceae. Subgenus *Thryothamnus* was initially recognized as a genus by Philippi (1895) and is distinguished by its deeply 5-sected calyx and its cylindrical stems.

Junellia as currently circumscribed (Botta 1989; Peralta et al. 2008) is not monophyletic based on previous studies using chloroplast DNA and nuclear *waxy*, *PHOT1* and *PHOT2* genes

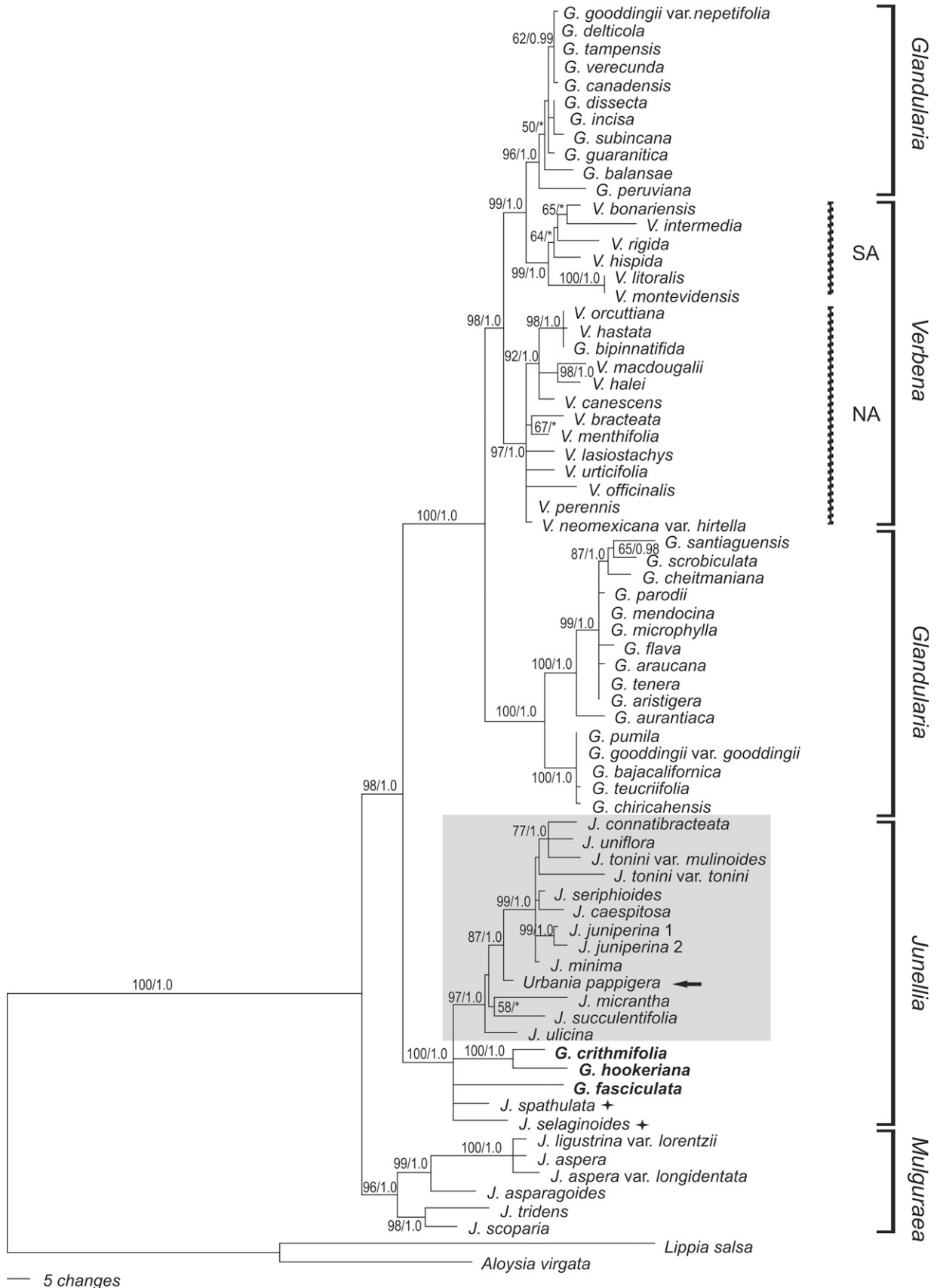


FIG. 1. One of the 12 maximum parsimony (MP) trees from the combined cpDNA data. The topology is similar to the Bayesian consensus tree. Bootstrap values (BS) and Bayesian posterior probabilities (PP) supporting the corresponding branches are shown when BS ≥ 50% or PP ≥ 0.95 (BS/PP). The asterisks indicate that BS < 50% when PP ≥ 0.95 or PP < 0.95 when BS ≥ 50% of the same branch. Numbers after *J. juniperina* designate different voucher accessions. The arrow shows the position of *Urbania pappigera*. *Glandularia* species formerly placed in subgenus *Paraglandularia* are in bold. The asterisks indicate species from *Junellia* subgenus *Thryothamnus* sect. *Thryothamnus*; *Junellia* subgenus *Junellia* species are shaded.

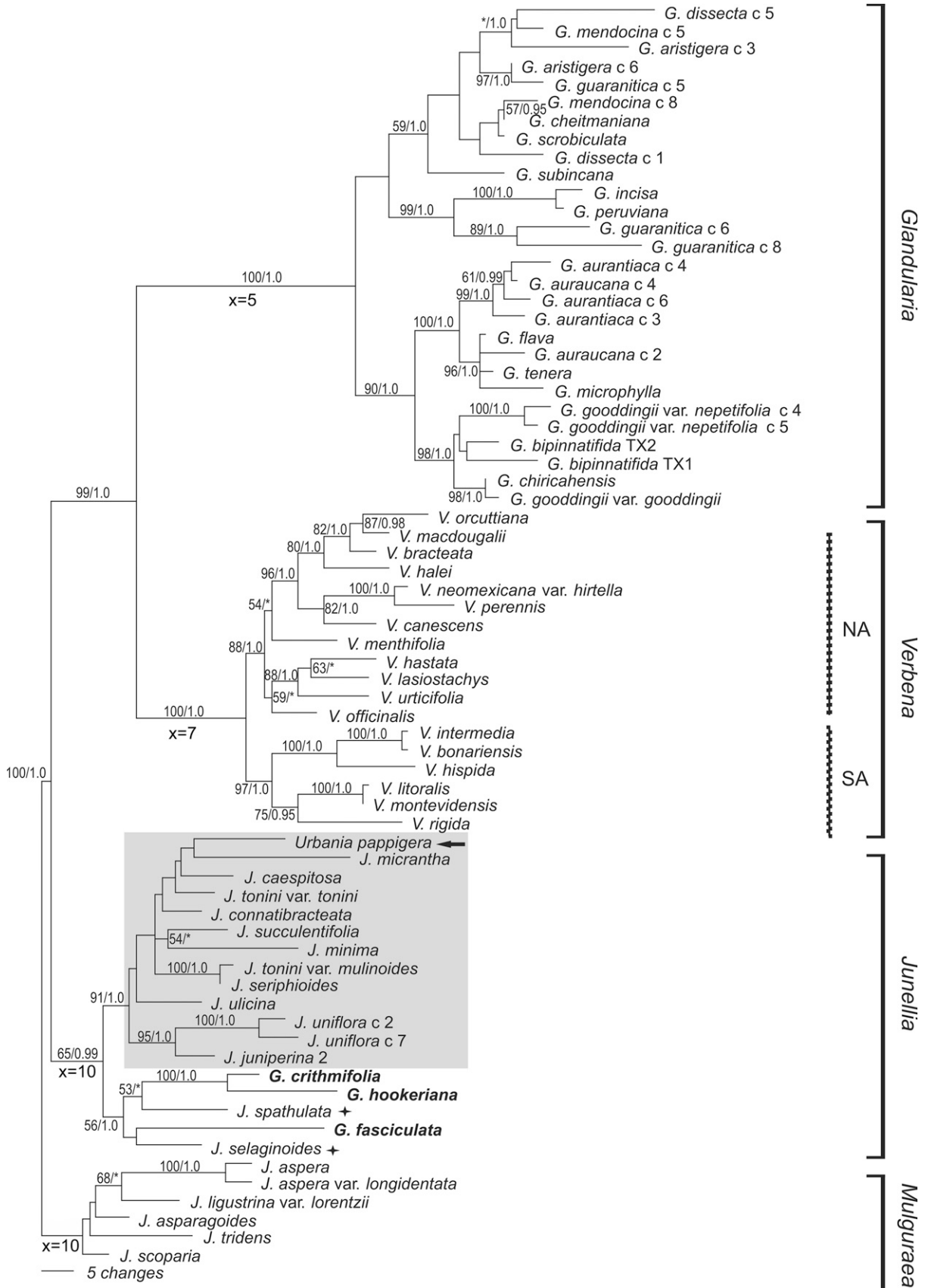


FIG. 2. One of the 7,137 maximum parsimony (MP) trees from the combined ETS/ITS data. The topology is similar to the Bayesian consensus tree. Node support (BS/PP) is shown as in Fig. 1. Clone numbers are designated after species names when the individual sampled display >1% polymorphic sites at the ETS/ITS region. Numbers after *J. juniperina* designate voucher accessions. The arrow shows the position of *Urbania pappigera*. *Glandularia* species formerly placed in subgenus *Paraglandularia* are in bold. The asterisks indicate species from *Junellia* subgenus *Thryothamnus* sect. *Thryothamnus*; *Junellia* subgenus *Junellia* species are shaded. Base chromosome numbers are represented along the branch leading to each of the four genera.

(Yuan and Olmstead 2008a, b). These results are here confirmed by our expanded chloroplast DNA data and the newly generated ETS/ITS data (see Figs. 1–2), which suggest that species from *Junellia* subgenus *Thryothamnus* sect. *Dentium* and sect. *Verticiflora* form a clade distinct from the rest of *Junellia*. Even though we sampled only six of the 13 taxa that belong to these two sections due to difficulty in obtaining material, we assume that the rest will fall within this clade based on the shared morphological synapomorphy of anther connective surpassing the theca. This character state is not found in any other *Junellia*, *Glandularia*, or *Verbena* species, all of which have anther connectives not surpassing the theca (except four *Verbena* species from ser. *Pachystachyae*). In addition, a MITE (miniature inverted-repeat transposable element) insertion in *waxy* gene intron 8 and a MITE insertion in *PHOT1* intron 13 were found in all *Verbena*, *Glandularia*, and *Junellia* s. s. species, but not in *Junellia* subgenus *Thryothamnus* sect. *Dentium* and sect. *Verticiflora* (Yuan and Olmstead 2008a, b). These MITE insertions were suggested to be a molecular signature defining the clade of *Verbena* + *Glandularia* + *Junellia* s. s. (Yuan and Olmstead 2008a, b), further corroborating the evidence that *Junellia* is not monophyletic as currently circumscribed.

Given such strong evidence from both molecular and morphological characters, species of *Junellia* subgenus *Thryothamnus* sects. *Dentium* and *Verticiflora* are here circumscribed as the new genus *Mulguraea*.

Taxonomic Position of *Glandularia* subgenus *Paraglandularia*—Schnack and Covas (1978) established *Glandularia* subgenus *Paraglandularia* to include three South American species, *G. crithmifolia* (Gillies & Hook. ex Hook.) Schnack & Covas, *G. hookeriana* Covas & Schnack, and *G. origenes* (Phil.) Schnack & Covas, which differed from the rest of the species because of their subshrubby habit, winged or subwinged mericarps and chromosome number $2n = 20$. This chromosome number is uncommon in *Glandularia*, given that all South American *Glandularia* were believed to be diploids with $2n = 10$. Botta (1992) accepted subg. *Paraglandularia* and added some defining morphological character states for this group, including glabrous corolla throat, mericarps narrowed at the base, and a fruiting calyx longer than the mericarps with non-contorted teeth. Botta (1992) also suggested that *G. ballsii* was better placed in subgenus *Paraglandularia* given the presence of these character states in this species. All species in this section are interpreted to have unbranched inflorescences, or if branched then the lateral branches briefly pedunculated (P. Peralta, pers. comm.), appearing as compressed inflorescences because of the brief basal internodes (Martínez et al. 1996). In some species internodes are so brief and lateral branches are so many, that it looks as if the flowers are arranged in heads (e.g. *G. ballsii* and *G. origenes*). *G. fasciculata* (Benth.) P. Jörg. shares this type of inflorescence as well as characters related to mericarp morphology, based on which it was also grouped into subgenus *Paraglandularia* (Peralta 2009).

All but one of the morphological characters that define subgenus *Paraglandularia* are also found in all species of *Junellia* subgenus *Thryothamnus* sect. *Thryothamnus*, the exception being the winged mericarps, which are found in only some species. The close similarity between these two groups had previously been noted by Botta (1989). Our phylogenetic analyses indicate that *G. crithmifolia*, *G. hookeriana*, and *G. fasciculata* form a clade with species belonging to sect. *Thryothamnus*, all forming a subclade within *Junellia* (Fig. 2) or all part of a basal grade within *Junellia* (Fig. 1). This is also supported by pre-

vious studies using nuclear genes *waxy*, *PHOT1* and *PHOT2* (Yuan and Olmstead 2008a,b), where *G. crithmifolia* always is nested within *Junellia*. Unfortunately, we were unable to obtain any living material from the remaining members of *Glandularia* subgenus *Paraglandularia* (*G. ballsii*, *G. lucanensis*, *G. occulta*, and *G. origenes*) mainly because they are not widespread. Two of these species are endemic to Perú (*G. lucanensis* and *G. occulta*) and one (*G. ballsii*) is from the northern Argentine province of Jujuy; herbarium specimens were not of sufficient quality for DNA extractions. However, we predict that these four other species will group with *Junellia*, given that they share the character states that differentiate this group from subgenus *Glandularia* and unite them with *Junellia* sect. *Thryothamnus*. Consequently seven new combinations are made. The inclusion of these species in *Junellia* means the chromosome number $2n = 20$ is not a tetraploid number of $x = 5$, but a diploid number of $x = 10$, as *Junellia* and *Mulguraea* species have (Botta and Brandham 1993: 147–148).

Taxonomic Position of the genus *Urbania*—*Urbania* Philippi (1891) is a monotypic genus, confined to the high Andean puna of Argentina and Chile. Its taxonomic position has been controversial, principally due to its close morphological similarity to *Junellia*, from which it has been differentiated (Troncoso 1974; Botta 1988) only by its hairy calyx with long hygroscopic hairs. Our results show that *Urbania* is nested within the *Junellia* clade (Figs. 1–2), so recognition of *Urbania* as a different genus, based only on the presence of a hairy calyx, renders *Junellia* paraphyletic. Besides, *Urbania* and *Junellia*, especially species from sect. *Guedesia*, share many morphological character states, including the cushion habit and homomorphic leaves that are imbricate, spineless, and somewhat fleshy. The transfer of *Urbania* to *Junellia* makes the presence of a hairy calyx an autapomorphy for this new species of *Junellia*, and does not justify its segregation as a different genus.

Redefinition of *Junellia* Boundaries—Our results show that *Junellia* s. s. is restricted to four of the six sections classified by Peralta et al. (2008). These are sects. *Junellia*, *Guedesia*, *Junelliopsis*, and *Thryothamnus*. Species from the remaining two sections, sects. *Dentium* and *Verticiflora*, have been transferred to the new genus *Mulguraea*. However, *Junellia* has gained seven species from *Glandularia* subg. *Paraglandularia* and one species from the monotypic genus *Urbania*. As a consequence, the recircumscribed *Junellia* comprises 36 species. The type species of *Junellia* is *Junellia serpyllifolia* (Speg.) Moldenke (1940), which is a synonym of *J. micrantha* (Phil.) Moldenke. This species was included in our analyses, and the results confirm the association of the name *Junellia* with this clade.

Species from subg. *Paraglandularia*, which have the style base inserted between the mericarps, group with species of sect. *Thryothamnus* (Figs. 1–2), which have an enlarged base style covering the apex of the mericarps. This renders the traditional division of *Junellia* into two subgenera, based upon the presence or absence of an enlarged style base, no longer correct. To further investigate if the sections within *Junellia* s. s. constitute natural groups we should sample more taxa and obtain more DNA sequence data.

Glandularia* and *Verbena—Our nuclear ETS/ITS data indicate that both *Glandularia* and *Verbena* are monophyletic, in agreement with the nuclear data in Yuan and Olmstead (2008a; 2008b). However, neither *Verbena* nor *Glandularia* are monophyletic based on chloroplast data. These results suggest two intergeneric chloroplast transfers from *Verbena* to *Glandularia* (Yuan and Olmstead 2008a).

Within *Verbena*, the North American species, treated by O'Leary et al. (unpublished results) as series *Verbena*, were recovered as monophyletic in this study (Figs. 1–2), consistent with results from the nuclear *waxy* and *PHOT1* genes but incongruent with the *PHOT2* gene (Yuan and Olmstead 2008a, b). Species of series *Verbena* are all diploids, with cortical chlorophyllous parenchyma as a continuous band and filiform or much elongated cylindrical inflorescences. South American species of *Verbena* were also suggested to be monophyletic by the chloroplast and nuclear ITS/ETS data (Figs. 1–2), consistent with *PHOT1* gene data but not with *PHOT2* or *waxy* sequence data (Yuan and Olmstead 2008a, b). These species are treated by O'Leary et al. (2007a) in series *Pachystachyae* being mostly polyploids with compressed cylindrical inflorescences.

Within *Glandularia*, relationships resolved by the chloroplast DNA (Fig. 1), nuclear ITS/ETS (Fig. 2), *waxy* (Yuan and Olmstead 2008a), *PHOT1* and *PHOT2* (Yuan and Olmstead 2008b), were largely incongruent. The incongruence is most likely due to incomplete lineage sorting or/and extensive recent gene flow. Potential gene flow among *Glandularia* species was also implied by the intraindividual heterogeneity (see Fig. 2) in the ribosomal ITS/ETS region of many diploid species. The ribosomal ITS/ETS region is expected to be homogenized rapidly in the absence of extensive gene flow, presumably by highly efficient unequal crossing over or gene conversion (Eickbush and Eickbush 2007).

Relationship Among Genera of Tribe Verbenae: *Verbena*, *Glandularia*, *Junellia* and *Mulguraea*—This study corroborates previous inferences (Yuan and Olmstead 2008a, b) that *Verbena* and *Glandularia* are sister groups, and *Junellia* as circumscribed here is sister to the *Verbena* + *Glandularia* clade. The new genus *Mulguraea* is sister to this more inclusive clade. Although *Junellia* and *Mulguraea* share many morphological symplesiomorphies, such as a base chromosome number $x = 10$, shrubby habit, unbranched inflorescences, and narrow mericarp bases, these results suggest that *Junellia* s. s. is more closely related to *Verbena* and *Glandularia* than to *Mulguraea*. Given that both *Mulguraea* and *Junellia* are restricted to South America, the origin of the *Verbena* complex is inferred to be in South America. This also indicates that the chromosome number $x = 10$ might be ancestral, and that $x = 7$ and $x = 5$ are derived from $x = 10$, as suggested by Yuan and Olmstead (2008a), in contrast with the view of Botta and Brandham (1993).

TAXONOMIC TREATMENT

Mulguraea N. O'Leary & P. Peralta, gen. nov.—TYPE: *Verbena asparagoides* Gillies & Hook. ex Hook., Bot. Misc. 1: 165. 1829. [*Mulguraea asparagoides* (Gillies & Hook. ex Hook.) N. O'Leary & P. Peralta].

Frutices caulibus cylindricis vel subcylindricis. Foliis dimorphis, raro homomorphis, macroblastorum integris aut trisectis, apice pungentibus, brachyblastorum integris, carnosus, inermis. Corolla faux glabra. Connectivum staminum quam techae longius. Inflorescentiae capitula globosa vel maturitate elongata efficientes, solitaria.

Subshrubs with cylindrical or subcylindrical stems, generally divided in macroblast and brachyblasts. Leaves dimorphic, sometimes homomorphic, macroblast leaves entire or trisected, spinescent; brachyblast leaves entire, sometimes fleshy, never spinescent. Many flowered, unbranched inflorescences,

forming cylindrical spikes or racemes, rachis elongated during maturity or not. Flowers slightly zygomorphic, calyx tubular, 4 or 5 teathed, never contorted at maturity. Corolla hypocrateriform, interior with retrorse hairs, throat pubescent or glabrous. Stamens 4, didynamous, attached towards the upper middle of corolla tube, generally inserted, anthers with connective tissue surpassing the theca, not appendaged. Ovary bicarpellate, 4 locular, 4 ovular, with a filiform style more than three times the length of the ovary, style base inserted between mericarps, bilobed stigmatic tissue. Mericarps 4, narrowed at the base, winged or not. Basic chromosome number $x = 10$.

Distribution—Eleven species and two varieties inhabiting arid zones in southern South America.

Notes—The new genus is named in honor of Prof. M. E. Múlgura (Instituto de Botánica Darwinion), who has been working on Verbenaceae for more than 20 yr and is a well-known specialist on *Junellia*. Because the species *Mulguraea asparagoides* has typical characters states that define this genus, it is designated as the type species. *Mulguraea* is sister to the clade *Verbena* + *Glandularia* + *Junellia* s. s. (Figs. 1–2.) Sections are not recognized within *Mulguraea* until more taxa have been analyzed.

See Peralta et al. (2008) for synonymies, complete description, distribution data, additional type information, and observations referred to each newly combined taxon. For a key to the species of *Mulguraea*, see key to *Junellia* sect. *Dentium* and sect. *Verticiflora* in Peralta et al. (2008).

The genus *Dipyrena* Hook. (tribe Priveae Briq.) has a subdrupaceous fruit separating into two mericarps and alternate leaves; *Junellia* has a dry fruit separating into four mericarps and opposite leaves. Ravenna (2008) transferred several *Junellia* species to *Dipyrena*, but Múlgura and Peralta (unpublished results) reject these new combinations on the basis of these morphological differences between the two genera. Three of these species, *J. arequipensis*, *J. cinerascens*, and *J. scoparia* are here transferred to *Mulguraea*.

Mulguraea arequipense (Botta) N. O'Leary & P. Peralta, comb. nov. *Verbena arequipense* Botta, Darwiniana 28: 237. [1987] 1988. *Junellia arequipense* (Botta) Botta, Darwiniana 29: 392. 1989. *Dipyrena arequipensis* (Botta) Rav., Onira 11(15): 43. 2008.—TYPE: PERÚ. Arequipa: encima de baños de Jesús, 23 Apr. 1961, 2,600–2,700 m, A. Ferreyra 14261 (holotype: SI!).

Mulguraea asparagoides (Gillies & Hook. ex Hook.) N. O'Leary & P. Peralta, comb. nov. *Verbena asparagoides* Gillies & Hook. ex Hook., Bot. Misc. 1: 165. 1829. *Junellia asparagoides* (Gillies & Hook. ex Hook.) Moldenke, Lilloa 5: 395. 1940.—TYPE: ARGENTINA. Mendoza: "near the upper ... from Portezuelo a Uspallata to the valley of Uspallata", s. f., J. Gillies s.n. (lectotype, designated by Peralta et al. 2008: 371: K photo SI!; isotype: K, photo SI!).

Mulguraea aspera (Gillies & Hook. ex Hook.) N. O'Leary & P. Peralta, comb. nov. *Verbena aspera* Gillies & Hook. ex Hook., Bot. Misc. 1: 163. 1829. *Junellia aspera* var. *aspera* (Gillies & Hook. ex Hook.) Moldenke, Lilloa 5: 393. 1940.—TYPE: ARGENTINA. Mendoza: Paramillo de Uspallata "near Los Hornillos, eastern descent from Paramillo de Uspallata", Nov. 1822, J. Gillies s.n. (lectotype, designated by Botta, 1989: 392: K, photo SI!; isotype: BM, photo SI!).

- Mulguraea aspera** var. **longidentata** (Moldenke) N. O'Leary & P. Peralta, comb. nov. *Junellia longidentata* Moldenke, *Known Geogr. Distr. Verb. Avicen.*: 77. 1942. *Verbena aspera* var. *longidentata* (Moldenke) Botta, *Darwiniana* 25: 338. 1984. *Junellia aspera* var. *longidentata* (Moldenke) Múlgura & P. Peralta, *Ann. Missouri Bot. Gard.* 95(2): 338–390. 2008.—TYPE: ARGENTINA. Tucumán. Amaicha, 2090 m, 29 Dec. 1912, *L. Castillón 2460* (holotype: LIL 31753, photo SI!).
- Mulguraea cedroides** (Sandwith) N. O'Leary & P. Peralta, comb. nov. *Verbena cedroides* Sandwith, *Kew Bull.* 1927: 184. 1927. *Junellia cedroides* (Sandwith) Moldenke, *Lilloa* 5: 394. 1940.—TYPE: ARGENTINA. Neuquén. Zapala: Zapala, 27 Nov. 1925, *H. F. Comber 189* (holotype: K, photo SI!; isotypes: BM, K, LP!, TEX).
- Mulguraea cinerascens** (Schauer) N. O'Leary & P. Peralta, comb. nov. *Verbena cinerascens* Schauer, in *DC Prodr.* 11: 545. 1847. *Diostea cinerascens* (Schauer) Moldenke, *Revista Sudameric. Bot.* 5: 1. 1937. *Junellia cinerascens* (Schauer) Botta, *Darwiniana* 29: 392. 1989. *Dipyrena cinerascens* (Schauer) Rav., *Onira* 11(15): 44. 2008.—TYPE: CHILE. IV Región. Coquimbo, 1829, *C. Gay s. n.* (lectotype, designated by Botta, 1989: 392: G, photo FM 7855!; isotypes: F, G, K, photo SI!).
- Mulguraea echegarayi** (Hieron.) N. O'Leary & P. Peralta, comb. nov. *Verbena echegarayi* Hieron., *Bol. Acad. Nac. Ci.* 4: 66. 1881. *Junellia echegarayi* (Hieron.) Moldenke, *Lilloa* 5: 395. 1940.—TYPE: ARGENTINA. San Juan. Leoncito, Jan. 1876, *S. Echegaray s. n.* (holotype: CORD!).
- Mulguraea hystrix** (Phil.) N. O'Leary & P. Peralta, comb. nov. *Verbena hystrix* Phil., *Anales Univ. Chile* 90: 610. 1895. *Junellia hystrix* (Phil.) Moldenke, *Known Geogr. Dist. Verben. Avicen.*: 77. 1942.—TYPE: CHILE. Atacama: Acerillos, desierto de Atacama, Nov. 1844, *Villanueva s. n.*, SGO 42514 (lectotype, designated by Acevedo de Vargas 1951: 55: SGO; isotype: SGO, photo SI!).
- Mulguraea ligustrina** (Lag.) N. O'Leary & P. Peralta, comb. nov. *Verbena ligustrina* Lag., *Gen. Sp. Pl.*: 18. 1816. *Lippia ligustrina* (Lag.) Britton, *Trans. New York Acad. Sci.* 9: 181. 1890. *Aloysia ligustrina* (Lag.) Small, *Flora SE United States*: 1013. 1903. *Junellia ligustrina* var. *ligustrina* (Lag.) Moldenke, *Phytologia* 2(11): 466. 1948.—TYPE: ARGENTINA. Santa Cruz. Deseado: a 107 km al S del límite con Chubut, ruta Nac. 3, 25 Feb. 1990, *M. N. Correa et al. 10256* (neotype, designated by Peralta et al. 2008: 378: SI!).
- Mulguraea ligustrina** var. **lorentzii** (Niederl. ex Hieron.) N. O'Leary & P. Peralta, comb. nov. *Verbena lorentzii* Niederl. ex Hieron., *Bol. Acad. Nac. Ci. Córdoba* 3(4): 370. 1880. *Junellia lorentzii* (Niederl. ex Hieron.) Moldenke, *Lilloa* 5: 397. 1940. *Junellia ligustrina* var. *lorentzii* (Niederl. ex Hieron.) Moldenke, *Phytologia* 47: 222. 1980.—TYPE: ARGENTINA. Río Negro. Sep.-Nov., 1874, *C. Berg 100* (lectotype, designated by Peralta et al. 2008: 379: CORD).
- Mulguraea scoparia** (Gillies & Hook. ex Hook.) N. O'Leary & P. Peralta, comb. nov. *Verbena scoparia* Gillies & Hook. ex Hook., *Bot. Misc.* 1: 161. 1829. *Diostea scoparia* (Gillies & Hook. ex Hook.) Miers, *Trans. Linn. Soc. London* 27: 104. 1869. *Junellia scoparia* (Gillies & Hook. ex Hook.) Botta, *Darwiniana* 29: 392. 1989. *Dipyrena scoparia* (Gillies & Hook. ex Hook.) Rav., *Onira* 11(15): 44. 2008.—TYPE: ARGENTINA. Mendoza: Las Heras, shrub valley near Villavicencio, *J. Gillies s. n.* (lectotype, designated by Botta, 1989: 392: K, photo SI!; isotype: K, photo SI!).
- Mulguraea tetragonocalyx** (Tronc.) N. O'Leary & P. Peralta, comb. nov. *Verbena tetragonocalyx* Tronc., *Darwiniana* 8: 481. 1949. *Junellia tetragonocalyx* (Tronc.) Moldenke, *Phytologia* 3: 167. 1949.—TYPE: ARGENTINA. Chubut. Paso de Indios: 23 km al E de El Sombrero, 6 Jan. 1948, *Soriano 2839* (holotype: SI!; isotype: K, photo SI!).
- Mulguraea tridens** (Lag.) N. O'Leary & P. Peralta, comb. nov. *Verbena tridens* Lag., *Gen. Sp. Pl.* 19. 1816. *Junellia tridens* (Lag.) Moldenke, *Lilloa* 5: 402. 1940.—TYPE: ARGENTINA. Chubut. Florentino Ameghino: a 7 km del cruce de Ruta Provincial 28 con Ruta Nacional 3, 24 Feb. 1990, *N. Correa 10227* (neotype, designated by Peralta et al. 2008: 373: SI!).
- New transfers to Junellia*—Eight new combinations under *Junellia* have resulted from this study. See Botta (1988) for synonymies, complete descriptions, distribution data, additional type information, and observations referred to each newly combined taxa of *Junellia* previously placed under *Glandularia* subgenus *Paraglandularia* or under the monotypic *Urbania*, respectively. Given that *Urbania* (Philippi 1891) has priority over *Junellia* (Moldenke 1940), a formal proposal to conserve the name *Junellia* over *Urbania* was made to the International Committee on Nomenclature and has been recently accepted (O'Leary et al. 2009).
- Junellia ballsii** (Moldenke) N. O'Leary & P. Peralta, nov. comb. *Verbena ballsii* Moldenke, *Phytologia* 1: 477. 1940. *Glandularia ballsii* (Moldenke) Botta, *Hickenia* 2: 61. 1992.—TYPE: ARGENTINA. Jujuy, Chorrú Valley, near Tilcara, 12,800 ft, 13 Feb 1939, *E. K. Balls 6036* (holotype: US; isotypes: K, US, W).
- Junellia crithmifolia** (Gillies & Hook. ex Hook.) N. O'Leary & P. Peralta, nov. comb. *Verbena crithmifolia* Gillies & Hook. ex Hook. *Bot. Misc.* 1: 169. 1829. *Glandularia crithmifolia* (Gillies & Hook. ex Hook.) Schnack & Covas, *Darwiniana* 6: 475. 1944.—TYPE: ARGENTINA. "along the foot of mountains near Mendoza and San Luis de la Punta", *J. Gillies s. n.* (lectotype, designated by Botta, 1993: 18, K; isolectotype: K).
- Junellia fasciculata** (Benth.) N. O'Leary & P. Peralta, nov. comb. *Verbena fasciculata* Benth., *Bot. Voy. Sulphur.*: 153. 1844. *Glandularia fasciculata* (Benth.) P. Jörg., *Mem. New York Bot. Gard.* 92: 463. 2005.—TYPE: PERÚ. Lima. "Huamantango", *Hinds 707* (holotype: K, isotypes: K, SI).
- Junellia hookeriana** (Covas & Schnack) N. O'Leary & P. Peralta, nov. comb. *Glandularia hookeriana* Covas & Schnack, *Revista Argent. Agron.* 12: 57. 1945. *Verbena hookeriana* (Covas & Schnack) Moldenke, *Phytologia* 2: 149. 1946.—TYPE: ARGENTINA. Mendoza. Dpto. La Paz: entre La Paz y Desaguadero, 15 Dec 1943, *G. Covas 2106* (holotype: SI).
- Junellia lucanensis** (Moldenke) N. O'Leary & P. Peralta, nov. comb. *Verbena lucanensis* Moldenke, *Phytologia* 3:

279. 1950. *Glandularia lucanensis* (Moldenke) Botta, *Hickenia* 2: 128. 1995.—TYPE: PERÚ. Ayacucho, Lucanas, between Nazca and Puquio, 1,500–2,000 msm, 19 Mar 1949, R. Ferreira 5493 (holotype: NY; isotypes: MO, US).

Junellia occulta (Moldenke) N. O'Leary & P. Peralta, nov. comb. *Verbena occulta* Moldenke, *Phytologia* 3: 280. 1950. *Glandularia occulta* (Moldenke) P. Jörg., *Mem. New York Bot. Gard.* 92: 463. 2005.—TYPE: PERÚ. La Libertad, Prov. Bolívar, cerca al Nevado Cajamarquilla, 12 Sep 1946, R. Ferreira 1298 (holotype: NY; isotypes: NY, SI)

Junellia origenes (Phil.) N. O'Leary & P. Peralta, nov. comb. *Verbena origenes* Phil., *Linnaea* 29: 20. 1857–58. *Glandularia origenes* (Phil.) Schnack and Covas, *Darwiniana* 6: 475. 1944.—TYPE: CHILE. Andium Coquimbensium, monte del Toro, Nov 1836, C. Gay 1906 (holotype: SGO 54769; isotype: SGO 54769).

Junellia pappigera (Phil.) N. O'Leary & P. Peralta, nov. comb. *Urbania pappigera* Phil., *An. Mus. Nac. Chile (Verz. Antof. Pfl.)*, 2° sect. Bot. 8: 60. 1891.—TYPE: CHILE. "ad. ped. montis Miñique, I-1885", s/leg. (lectotype, designated by Botta 1988: 480: SGO 42497).

KEY TO THE GENERA OF TRIBE VERBENEAE

1. Subshrubs or cushion plants, mericarp base narrowed, inflorescences generally unbranched (sometimes with simple branching), base chromosome number $x = 9$ or $x = 10$ 2
 2. Anther connective never surpassing the theca *Junellia*
 2. Anther connective surpassing the theca *Mulguraea*
1. Herbs, mericarp base thickened, not narrowed, branched inflorescences (at times condensed and appearing simple), base chromosome number $x = 5$ or $x = 7$ 3
 3. Style generally more than $3 \times$ longer than ovary, mature calyx usually longer than fruit and with teeth generally contorted, chromosome number $x = 5$ *Glandularia*
 3. Style never more than $3 \times$ longer than ovary, mature calyx shorter than fruit and with teeth not contorted, chromosome number $x = 7$ *Verbena*

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- APPENDIX 1. Accession data for plants included in the molecular phylogenetic analyses. Voucher information is only given for sequences generated in this study, GenBank numbers from this study are in bold, the rest were submitted prior to this study in connection with a previous paper (Yuan and Olmstead 2008a). For voucher information for species marked with ‡ see Yuan and Olmstead (2008a). GenBank accession numbers are in the following sequence: *trnS-G* / *trnD-T* / *trnS-FM* / *trnT-F* / ETS / ITS (— indicates sequence not obtained). The number in parentheses represents different clones. The taxa marked by an asterisk represent DNA extractions from herbarium specimens.
- Aloysia* Palau — *A. virgata* (Ruiz and Pav.) Juss. ‡, EF583119 / EF583172 / EF576717 / EF571570 / **FJ867545** / **FJ867398**
- Glandularia* J. F. Gmel. — *G. araucana* (Phil.) Botta‡, EF583104 / EF583157 / EF576702 / EF571555 / (c2)**FJ867576**, (c4)**FJ867577** / (c2)**FJ867429**, (c4)**FJ867430**. *G. aristigera* (S. Moore) Tronc. ‡, EF583106 / EF583159 / EF576704 / EF571557 / (c3)**FJ867570**, (c6)**FJ867571** / (c3)**FJ867423**, (c6)**FJ867424**. *G. aurantiaca* (Speg.) Botta‡, EF583103 / EF583156 / EF576701 / EF571554 / (c3)**FJ867572**, (c4)**FJ867573**, (c6)**FJ867574** / (c3)**FJ867425**, (c4)**FJ867426**, (c6)**FJ867427**. *G. bajacalifornica* (Moldenke) Umber, EF583097 / EF583150 / EF576695 / EF571548 / — / —. *G. balansae* (Briq.) N. O'Leary, Paraguay: Canindeyú, *Mulgura* 3576 (CTES, FCQ, SI), **FJ867511** / **FJ867476** / **FJ867489** / **FJ867532** / **FJ867596** / —. *G. bipinnatifida* Nutt. ‡, EF583084 / EF583137 / EF576682 / EF571535 / (TX2)**FJ867588**, (TX1)**FJ867589** / (TX2)**FJ867440**, (TX1)**FJ867441**. *G. canadensis* (L.) Nutt., EF583093 / EF583146 / EF576691 / EF571544 / — / —. *G. cheitmaniana* (Moldenke) Botta and Poggio‡, Argentina, Jujuy, Marazzi 260 (SI), **FJ867508** / **FJ867474** / **FJ867493** / **FJ867530** / **FJ867595** / **FJ867444**. *Glandularia chiricahensis* Umbert‡, EF583095 / EF583148 / EF576693 / EF571546 / **FJ867584** / **FJ867436**. *G. crithmifolia* (Gillies and Hook. ex Hook.) Schnack and Covas‡, EF583107, EF586160, EF576705, EF571558, **FJ867593** / **FJ867443**. *G. delticola* (Small) Umber, EF583090 / EF583143 / EF576688 / EF571541 / — / —.
- G. dissecta* (Spreng.) Schnack and Covas‡, EF583085 / EF583138 / EF576683 / EF571536 / (c1)**FJ867565**, (c5)**FJ867566** / (c1)**FJ867418**, (c5)**FJ867419**. *G. fasciculata* Benth.*. Perú: Ancash, *Cano* 1717 (MO), **FJ867514** / **FJ867472** / **FJ867491** / **FJ867528** / **FJ867597** / **FJ867447**. *G. flava* (Gillies and Hook. ex Hook.) Schnack and Covas‡, EF583102 / EF583155 / EF576700 / EF571553 / **FJ867575** / **FJ867428**. *G. goodingii* var. *goodingii* (Briq.) Solbrig‡, EF583096 / EF583149 / EF576694 / EF571547 / **FJ867585** / **FJ867437**. *G. goodingii* var. *neptifolia* Tidestrom. ‡, EF583089 / EF583142 / EF576687 / EF571540 / (c4)**FJ867586**, (c5)**FJ867587** / (c4)**FJ867438**, (c5)**FJ867439**. *G. guaranitica* Tronc. ‡, EF583087 / EF583140 / EF576685 / EF571538 / (c5)**FJ867581**, (c6)**FJ867582**, (c8)**FJ867583** / (c5)**FJ867433**, (c6)**FJ867434**, (c8)**FJ867435**. *G. hookeriana* Covas and Schnack, Argentina: Catamarca, RGO 2007-080 (MERL, SI, WTU), **FJ867510** / **FJ867471** / **FJ867495** / **FJ867527** / **FJ867590** / **FJ867448**. *G. incisa* (Hook.) Tronc. ‡, EF583086 / EF583139 / EF576684 / EF571537 / **FJ867567** / **FJ867420**. *G. mendocina* (Phil.) Covas and Schnack‡, EF583100 / EF583153 / EF576698 / EF571551 / (c5)**FJ867568**, (c8)**FJ867569** / (c5)**FJ867421**, (c8)**FJ867422**. *G. microphylla* (Kunth) Cabrera‡, EF583101 / EF583158 / EF576699 / EF571552 / **FJ867579** / **FJ867432**. *G. parodii* Covas and Schnack, EF583099 / EF583152 / EF576697 / EF571550 / — / —. *G. peruviana* (L.) Small, Argentina: Jujuy, RGO 2007-066 (MERL, SI, WTU), **FJ867512** / **FJ867477** / **FJ867490** / **FJ867533** / **FJ867591** / **FJ867445**. *G. pumila* (Rydb.) Umber, EF583094 / EF583147 / EF576692 / EF571545 / — / —. *G. santiaguensis* Covas and Schnack, Argentina, Salta, RGO 2007-005 (MERL, SI, WTU), **FJ867509** / **FJ867473** / **FJ867494** / **FJ867529** / **FJ867594** / —. *G. scrobiculata* (Griseb.) Tronc., Argentina, Jujuy, Marazzi 259 (SI), **FJ867513** / **FJ867475** / **FJ867492** / **FJ867531** / **FJ867592** / **FJ867446**. *G. subincana* Tronc., Argentina: Corrientes, RGO 2004-117 (WTU), EF583088 / EF583141 / EF576686 / EF571539 **FJ867580** / **FJ867442**. *G. tampensis* Small, EF583091 / EF583144 / EF576689 / EF571542 / — / —. *G. tenera* (Spreng.) Cabrera‡, EF583105 / EF583158 / EF576703 / EF571556 / **FJ867578** / **FJ867431**. *G. teucriuifolia* (Mart. and Galeotti) Umber, EF583098 / EF583151 / EF576696 / EF571549 / — / —. *G. verecunda* Umber, EF583092 / EF583145 / EF576690 / EF571543 / — / —.
- Junellia* <http://www.tropicos.org/name/40033922Moldenke> — *J. asparagoides* (Gillies and Hook. ex Hook.) Moldenke‡, EF583116 / EF583169 / EF576714 / EF571567 / **FJ867616** / **FJ867458**. *J. aspera* (Gillies and Hook. ex Hook.) Moldenke‡, EF583117 / EF583170 / EF576715 / EF571568 / **FJ867617** / **FJ867459**. *J. aspera* var. *longidentata* (Moldenke) Múlgura and P. Peralta, Argentina: Jujuy, Soza 1824 (WTU), **FJ867523** / **FJ867479** / **FJ867502** / **FJ867539** / **FJ867618** / **FJ867460**. *J. caespitosa* (Gillies and Hook. ex Hook.) Moldenke, Argentina: San Juan, Meglioli 174 (SI), **FJ867520** / **FJ867481** / **FJ867500** / **FJ867536** / **FJ867606** / **FJ867466**. *J. conatibracteata* (Kuntze) Moldenke‡, EF583108 / EF583161 / EF576706 / EF571559 / **FJ867613** / **FJ867453**. *J. juniperina* 1 (Lag.) Moldenke, EF583112 / EF583165 / EF576710 / EF571563 / — / —. *J. juniperina* 2 (Lag.) Moldenke‡, EF583113 / EF583166 / EF576711 / EF571564 / **FJ867612** / **FJ867455**. *J. ligustrina* var. *lorentzii* (Niederl. ex Hieron.) Moldenke, Argentina: Neuquén, RGO 2007-092 (MERL, SI, WTU), **FJ867522** / **FJ867486** / **FJ867504** / **FJ867542** / **FJ867603** / **FJ867468**. *J. micrantha* (Phil.) Moldenke, Argentina: Mendoza, RGO 2004-198 (MERL, SI), **FJ867524** / **FJ867482** / **FJ867498** / **FJ867537** / **FJ867602** / **FJ867462**. *J. minima* (Meyen) Moldenke‡, EF583109 / EF583162 / EF576707 / EF571560 / **FJ867611** / **FJ867454**. *J. scoparia* (Gillies and Hook. ex Hook.) Botta‡, EF583115 / EF583168 / EF576713 / EF571566 / **FJ867615** / **FJ867457**. *J. selaginoides* (Walp.) Moldenke*, Chile: Elqui, Lammers et al. 7597 (US), **FJ867518** / **FJ867485** / **FJ867505** / **FJ867541** / **FJ867604** / **FJ867463**. *J. seriphoides* (Gillies and Hook. ex Hook.) Moldenke‡, EF583110 / EF583163 / EF576708 / EF571561 / **FJ867610** / **FJ867452**. *J. spathulata* (Gillies and Hook. ex Hook.) Moldenke‡, EF583114 / EF583167 / EF576712 / EF571565 / **FJ867614** / **FJ867456**. *J. succulentifolia* (Kuntze) Moldenke*, Argentina, Bonifacio 418 (US), **FJ867517** / — / **FJ867503** / **FJ867540** / **FJ867599** / **FJ867461**. *J. tonini* var. *multinoides* (Speg.) P. Peralta and Múlgura*, Argentina: Neuquén, Kiesling 10081c (SI), **FJ867521** / **FJ867484** / **FJ867499** / **FJ867538** / **FJ867601** / **FJ867467**. *J. tonini* var. *tonini* (Kuntze) Moldenke, Argentina: Neuquén, Morrone 5756 (SI), **FJ867525** / **FJ867483** / **FJ867506** / **FJ867534** / **FJ867600** / **FJ867464**. *J. tridens* (Lag.) Moldenke*, Argentina: Santa Cruz, Bonifacio 500 (US), **FJ867516** / **FJ867487** / **FJ867501** / **FJ867543** / **FJ867605** / **FJ867465**. *J. ulicina* (Phil.) Moldenke, Argentina: Mendoza, RGO 2004-201 (MERL, SI), **FJ867519** / **FJ867480** / **FJ867497** / **FJ867535** / **FJ867607** / **FJ867469**. *J. uniflora* (Phil.) Moldenke‡, EF583111 / EF583164 / EF576709 / EF571562 / (c2)**FJ867608**, (c7)**FJ867609** / (c2)**FJ867450**, (c7)**FJ867451**.
- Lippia* L. — *L. salsa* Griseb. ‡, EF583118 / EF583117 / EF576716 / EF571569 / **FJ867546** / **FJ867399**.
- Urbana* Phil. — *U. pappigera* Phil., Argentina: Salta, RGO 2007-036 (MERL, SI, WTU), **FJ867515** / **FJ867478** / **FJ867496** / **FJ867544** / **FJ867598** / **FJ867449**.
- Verbena* L. — *V. bonariensis* L. ‡, EF583067 / EF583120 / EF576665 / EF571518 / **FJ867548** / **FJ867401**. *V. bracteata* Cav. ex Lag. and Rodr. ‡, EF583075 / EF583128 / EF576673 / EF 571526 / **FJ867555** / **FJ867408**.

V. canescens Kunth‡, EF583082 / EF583135 / EF576680 / EF571533 / **FJ867559** / **FJ867412**. *V. halei* Small‡, EF583083 / EF583136 / EF576681 / EF571534 / **FJ867556** / **FJ867409**. *V. hastata* L. ‡, EF583080 / EF583133 / EF576678 / EF571531 / **FJ867562** / **FJ867415**. *V. hispida* Ruiz and Pav., Argentina: Jujuy, Soza 1826 (WTU), — / — / — / — / **FJ867549** / **FJ867402**; Argentina: Misiones, Zuloaga 8266 (SI), **FJ867507** / **FJ867470** / **FJ867488** / **FJ867526** / — / —. *V. intermedia* Gillies and Hook. ex Hook. ‡, EF583071 / EF583124 / EF576669 / EF571522 / **FJ867547** / **FJ867400**. *V. lasiostachys* Link‡, EF583072 / EF583125 / EF576670 / EF571523 / **FJ867564** / **FJ867417**. *V. litoralis* Kunth‡, EF583069 / EF583122 / EF576667 / EF571520 / **FJ867551** / **FJ867404**. *V. macdougalii* Heller‡, EF583081 / EF583134 /

EF576679 / EF571532 / **FJ867554** / **FJ867407**. *V. menthifolia* Benth. ‡, EF583076 / EF583129 / EF576674 / EF571527 / **FJ867560** / **FJ867413**. *V. montevidensis* Spreng. ‡, EF583070 / EF583123 / EF576668 / EF571521 / **FJ867552** / **FJ867405**. *V. neomexicana* var. *hirtella* L. M. Perry‡, EF583078 / EF583131 / EF576676 / EF571529 / **FJ867557** / **FJ867410**. *V. officinalis* L. ‡, EF583074 / EF583127 / EF576672 / EF571525 / **FJ867561** / **FJ867414**. *V. orcuttiana* L. M. Perry‡, EF583079 / EF583132 / EF576677 / EF571530 / **FJ867553** / **FJ867406**. *V. perennis* Wooton‡, EF583077 / EF583130 / EF576675 / EF571528 / **FJ867558** / **FJ867411**. *V. rigida* Spreng. ‡, EF583068 / EF583121 / EF576666 / EF571519 / **FJ867550** / **FJ867403**. *V. urticifolia* L. ‡, EF583073 / EF583126 / EF576671 / EF571524 / **FJ867563** / **FJ867416**.