

INFRAGENERIC CLASSIFICATION OF *VERBENA* (VERBENACEAE)

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ABSTRACT

The genus *Verbena* sensu stricto in the present account includes 70 species (6 currently in the process of description). The genus is divided into three sections: 1. Sect. **VERBENA**, type *V. officinalis* (including 10 series: ser. *Verbena*; ser. **Haleae** Nesom, ser. nov., type *V. halei*; ser. **Plicatae** Nesom, ser. nov., type *V. plicata*; ser. **Simplices** Nesom, ser. nov., type *V. simplex*; ser. **Connaticarpae** Nesom, ser. nov., type: *V. carnea*; ser. *Leptostachyae* Schauer, lectotype (designated here) *V. urticifolia*; ser. **Candelabrae** Nesom, ser. nov., type *V. stricta*; ser. **Bracteatae** Nesom, ser. nov., type *V. bracteata*; ser. **Californicae** Nesom, ser. nov., type *V. californica*; and ser. **Tricesimae** Nesom, ser. nov., type *V. canescens*); 2. Sect. **AMPHEPEIROS** Nesom, sect. nov., type *V. glabrata* (including 2 series: ser. **Austrobrasilienses** Nesom, ser. nov., type *V. hirta*; and ser. **Pacificae** Nesom, ser. nov., type *V. glabrata*); and 3. Sect. **VERBENACA** Walpers, lectotype (designated here) *V. bonariensis* (including 2 series: ser. *Pachystachyae* Schauer, type *V. bonariensis*; and ser. **Litorales** Nesom, ser. nov., type *V. litoralis*). The three sections are delimited primarily on the basis of inflorescence structure.

KEY WORDS: *Verbena*, Verbenaceae, infrageneric classification, sections, series

The only inclusive, critical study of North American *Verbena* L. sensu stricto has been provided by Perry (1933). Moldenke's contributions "toward a monograph of the genus" (1961–1964) covered all of the taxa, but they were oriented toward nomenclature and literature and did not provide evaluation of patterns of variation; nor did Moldenke provide a key to species, except in a few regional floristic accounts. Since a recent overview by Sanders (2001), most of the native South American taxa have been examined in revisionary detail (O'Leary et al. 2007; Nesom 2010a); certain groups of the North American species have been studied in detail (Nesom 2010b, 2010c, 2010f, 2010g). O'Leary et al. (2010) present a revision of the species they consider to represent lineages apart from the primary ones of South America—included are species native to the USA, Mexico, South America, and Europe. The Flora of North America treatment (Nesom submitted) includes the native and naturalized species of North America north of Mexico.

Verbena in the account here includes 70 species. Other recent estimates (e.g. Sanders 2001, "40 to 50" species; O'Leary et al. 2007 and 2010, 45 and 44 species, respectively) have been generally similar, but Atkins (2004) estimated between 200 and 250 species, even though she treated both *Glandularia* Gmelin and *Junellia* Moldenke as segregates of *Verbena*. The species of *Verbena* series *Pachystachyae* Schauer (sensu O'Leary et al. 2007) are native to South America; five of these are naturalized elsewhere in the world. Most of the remaining species are North American and Central American, except for two European species, *V. supina* L. and *V. officinalis* L., which apparently are most closely related to North American natives. Australian segregates of *V. officinalis* have been recognized (Michael 1997; Munir 2002; comments in Nesom 2010b). Two species of northwestern South America also are hypothesized here to be closely related to *V. officinalis*.

Tribe Verbenae Schauer includes *Verbena*, *Glandularia* (ca. 100 species), *Junellia* (ca. 30 species, including the monotypic *Urbania* Phil.), and *Mulguraea* O’Leary & Peralta (19 species) (O’Leary et al. 2009). *Hierobotana* Briq. (1 species, *H. inflata* (Kunth) Briq.) also has been included among these (e.g., Atkins 2004), but its status apparently remains unresolved—its disposition was not mentioned in O’Leary et al. (2009), even under the subheading “Relationship among genera of Tribe Verbenae: *Verbena*, *Glandularia*, *Junellia* and *Mulguraea*.” This group is characterized by fruits that separate into four 1-seeded mericarps, mostly parallel anther thecae often with dilated and glandular connective, and 2-lobed styles with the anterior lobe stigmatic. *Glandularia* has its center of diversity in South America and *Junellia* and *Mulguraea* occur only in that area. The largest number of *Verbena* species occurs in Mexico and the USA. Botta (1989) included *Tamonea* Aublet (6 species) as part of this group, but Atkins (2004) and O’Leary et al. (2008) have placed it in tribe Casselieae. *Verbena carnea* Medik. has been treated as the monotypic genus *Stylodon* Raf., based primarily on its mericarps that are connate at maturity, but in other features, *V. carnea* is similar to North American species of *Verbena* and the connation of mericarps is interpreted here as a derived feature within the genus. Recent DNA studies of the Verbenae (Marx et al. in prep., Dick Olmstead pers. comm.) indicate that both *Hierobotana* and *Stylodon* evolved from within the evolutionary matrix of *Verbena* sensu stricto.

Phylogenetic reconstructions by Yuan and Olmstead (2008a, 2008b) indicate that *Glandularia* and *Verbena* are monophyletic sister groups, together having a sister relationship to *Junellia* sensu stricto (O’Leary et al. 2009). Phylogenetically basal to tribe Verbenae is the newly described *Mulguraea*, a genus, like *Junellia*, primarily of the arid Andean region.

The close relationship between *Verbena* and *Glandularia* is emphasized by the discovery (Yuan & Olmstead 2008a) that two independent intergeneric chloroplast transfers have occurred, both from *Verbena* to *Glandularia*. “One is from a diploid North American *Verbena* species [*V. hastata* or *V. orcuttiana*, as sampled] to a polyploid North American *Glandularia* species [*G. bipinnatifida* (Nutt.) Nutt., as sampled]. The other is more ancient, from the South American *Verbena* group [sect. *Verbenaca*] to the common ancestor of a major *Glandularia* lineage [including *G. canadensis* (L.) Nutt.], which has radiated subsequently in both South and North America.”

Most infrageneric classifications of *Verbena* have included *Glandularia* and/or *Junellia*, and *Verbena* species have mostly been grouped in series or unranked groups (Walpers 1845; Schauer 1847; Briquet 1895; Small 1933; Troncoso 1974). Moldenke (1961) simply repeated the system of Walpers. O’Leary et al. (2007) studied only South American species, placing them all in 2 subseries within series *Pachystachyae* Schauer. O’Leary et al. (2010) divided the remaining species (ser. *Verbena*) among three unranked groups: *Verbena*, *Hastatae*, and *Bracteosae*. Sanders (2001) arranged the species of the southeastern USA into five informal groups. Among the few (14) species of *Verbena* sensu stricto sampled in a molecular phylogenetic studies by Yuan and Olmstead (2008a, 2008b) and Yuan et al. (2010), essentially two main species groups are evident, corresponding essentially to South American and North American species. Cladistic positions of the few-sampled North American species are inconsistent among data sets and types of analyses.

In their classification of *Verbena*, O’Leary et al. (2007, 2010) have divided the species between two groups, emphasizing two basic types of stem anatomy: Type A—cortical parenchyma continuous and discrete along the circumference, not interrupted at the stem angles by columns of sclerenchyma (their Fig. 2C); and Type B—cortical parenchyma interrupted at the stem angles by thick columns of sclerenchyma joined to the angular tissue (their Fig. 2D). Type B anatomy is characterized externally by a sharply 4-angled appearance and more prominent development of the angular nerves. All of the species except *V. rigida* of their “subser. *Pachystachyae*” (= ser. *Pachystachyae* in the present arrangement) are characterized by Type B anatomy. All of these are South American. O’Leary et al.

placed South American species with Type A anatomy (except for *V. rigida*) within subseries *Pseudoracemosae*, a morphologically heterogeneous group dispersed here among ser. *Austrobrasilienses* and ser. *Verbena*. Native North American species have Type A anatomy, fide O’Leary et al. (2010).

In preparation of a taxonomic treatment of *Verbena* for the Flora of North America North of Mexico, I have attempted to delimit natural groups within the genus.

The three sections are recognized within *Verbena*, primarily based on inflorescence structure.

- 1. Inflorescence paniculate, with spikes solitary or irregularly arranged, not in definite 3’s; spikes not subtended by prominent foliaceous bracts, all spikes pedunculate; stem anatomy Type A sect. **Verbena**
- 1. Inflorescence cymose, with spikes in definite 3’s; spikes subtended or not by foliaceous bracts, middle spike sessile or subsessile to pedunculate; stem anatomy Type A or B.
 - 2. Spikes not subtended by foliaceous bracts; stems usually sharply 4-angled or (in ser. *Litorales*) some not; leaves indistinctly petiolate through attenuate leaf bases; stem anatomy mostly Type B sect. **Verbenaca**
 - 2. Each spike subtended by foliaceous bracts; stems not sharply 4-angled; leaves distinctly petiolate from truncate to cuneate leaf bases; stem anatomy Type A sect. **Amphepeiros**

A character of fruit morphology appears to be predictive, as inferred from its consistent correlation with others in the distinction of natural groups. In some species, the developing fruit is essentially flat at the apex, and the style base is inserted at that level, at the juncture of the four nutlets. When the nutlets separate at maturity, the commissural faces appear to extend to the very tip of the nutlets. In other species, the style base is inserted in a depression in the middle of the nutlets, and when the nutlets separate at maturity, the dorsal side (the outer) of the nutlets is higher than the ventral side (the inner, with the commissural face), giving the appearance that the commissural face does not reach the nutlet apex.

Basis of the study

Thirty-two species occur in the FNANM flora area, and I also have studied representatives of almost all of the rest of the species. The present report summarizes observations based on study of the entire collections of *Verbena* sensu stricto (all geographic areas) from the following institutions: ARIZ (800 collections), BRIT-SMU (ca. 1000), MO (ca. 1800), NLU (ca. 800), and TEX-LL (ca. 1200, the Moldenke Verbenaceae collection). The ability to study additional type specimens through online images from F, GH, NY, US, and others has been especially useful. In addition to the FNA treatment (32 species, submitted), documentation is provided for various taxonomic decisions in a series of collateral papers (Nesom 2010a, 2010b, 2010c, 2010d, 2010e, 2010f, 2010g).

The native geographic range of each species is broadly characterized below as USA, Mexico, Central America, or South America. If a species occurs in more than one of these areas, the area of widest distribution is listed first.

VERBENA L., Sp. Pl. 1: 18. 1753; Gen. Pl. ed. 5, 12. 1754. **LECTOTYPE** (Jarvis et al., List Linn. Gen. Names Types, 98, 1993): *Verbena officinalis* L.

1. SECTION *VERBENA*

Stems not sharply 4-angled; leaves broad to narrow, petiolate or basally attenuate, lobed or unlobed, margins serrate; inflorescence paniculate, with spikes usually not in definite 3's; spikes not subtended by foliaceous bracts, all spikes usually pedunculate; fruits remote to densely overlapping at maturity. Stem anatomy Type A.

1a. Series *VERBENA*

Verbena [unranked] *Schizophyllae* Walpers, Repert. Bot. Syst. 4: 23. 1845. **LECTOYPE** (designated here): *Verbena officinalis* L.

Verbena [unranked] *Officinales* Small, Man. S.E. Fl. 1135. 1933. **TYPE**: *Verbena officinalis* L.

Plants taprooted or fibrous-rooted; stems erect at the base, sometimes apparently strongly 4-angled (perhaps similar to those of sect. *Verbenaca*?); leaves petiolate to subpetiolate, lobed to unlobed, blades thin, veins not impressed adaxially, margins serrate with acute teeth, not revolute; spikes solitary to few, with a tendency to occur in pairs, especially at the proximal 1–2 nodes of the inflorescence, fruits remote or becoming remote proximally; floral bracts usually shorter than the calyx or equal; rachis glandular or eglandular; commissural faces reaching the nutlet tip.

Verbena officinalis L. Europe; $2n = 14, 28, 42, 56$

Verbena supina L. Europe; $2n = 14$

Verbena gaudichaudii (Briquet) P.W. Michael Australia

Verbena macrostachya F. Mueller Australia

Verbena sororia D. Don Australia/Africa

Verbena madrensis Nesom Mexico

Verbena menthifolia Bentham Mexico, USA; $2n = 42$

Verbena grisea Rob. & Greenm. South America (Galapagos Islands)

Verbena demissa Moldenke South America (Ecuador)

Verbena caniuensis Moldenke South America (s Brazil)

Verbena filicaulis Schauer South America (Brazil, São Paulo)

Verbena gracilescens (Chamisso) Herter South America (Argentina, Bolivia, Paraguay, Uruguay); $2n = 42$

Verbena swiftiana Moldenke South America (Argentina, Misiones; Brazil, Rio Grande do Sul)

Verbena townsendii Svenson South America (Ecuador, Galapagos Islands)

The widely dispersed nativity of ser. *Verbena*, as constituted here, is unusual compared to other groups of the genus, which are geographically more coherent, and suggests that the geographical subsets need to be examined for the possibility of greater evolutionary independence. Significant differences between *V. officinalis* and *V. supina* suggest that even they are not most closely related to each other. The South American species placed here also constitute a heterogeneous group, morphologically and geographically.

Munir (2002) treated a group of morphologically and geographically distinct Australian population systems at varietal rank within *Verbena officinalis*. Michael (1997) recognized three of these taxa at specific rank (as above), distinct from naturalized *V. officinalis*, and the other two probably should be treated similarly (see comments in Nesom 2010b). One of these Australian entities is naturalized in Africa (or vice versa); another may be naturalized in Mexico (Chiapas) and Guatemala, or else the latter plants represent an undescribed species (Nesom 2010b). Reported variability in ploidy level (diploid, tetraploid, hexaploid, octoploid) gives plausibility to the view that

differentiation within *V. officinalis* sensu lato may include discrete evolutionary entities appropriately recognized by formal nomenclature.

O'Leary et al. (2010) have indicated that *Verbena sororia* D. Don and *V. officinalis* var. *natalensis* Hochst. ex C. Krauss are the correct names at specific and varietal rank for the taxon treated in recent literature as *Verbena africana* (R. Fernandes & Verdcourt) P.W. Michael and *V. officinalis* var. *africana* (R. Fernandes & Verdcourt) Munir. O'Leary et al. treat it at varietal rank but have included other segregates, including the Australian taxa, as synonyms of typical *V. officinalis*.

Verbena grisea, an endemic of the Galapagos Islands, is distinct in its small, highly dissected leaves evenly distributed along the stems, stems and leaves and stipitate-glandular and grayish with densely hispid-hirsute vestiture, spikes elongate and very slender, and tiny flowers and fruits (corolla limb ca. 2 mm in diam., calyces 1.8–2 mm long, nutlets 1–1.2 mm long) slightly overlapping in fruit and relatively compactly arranged. The spikes mostly in pairs are like those of ser. *Verbena*, as are the nutlet commissural faces reaching the very tip. Its placement here is provisional but provides a basis for a hypothesis regarding its occurrence in the Galapagos, especially since it would be anomalous within any of the South American groups. In addition to images of the holotype and isotype (GH!), I have examined the following: Galápagos Islands: Duncan Island, rare around 1250 ft, 15 Aug 1905-06, *Stewart 3316* (CAS photo-LL!); Pinzon [Isla Pinzon = Duncan Island], near summit, 1200 ft, rare, fls light blue, to 70 cm, Sep 1975, *van der Werff 2322* (LL!).

Verbena demissa is endemic to Andean Ecuador (known from provinces Azuay, Cañar, and Pichincha). It is distinctive in morphology: stems numerous, prostrate and sometimes apparently rooting at the nodes, radiating from a thick, woody taproot; stems and rachises sparsely strigillose and sparsely stipitate-glandular; leaves small (6–20 mm), short-petiolate, obovate or elliptic-obovate to oblanceolate, the margins serrate with 2–3(–5) pairs of coarse teeth or shallow lobes; spikes relatively short (1–7 cm) and few-flowered, mostly solitary, less commonly with paired proximal spikes, the fruits becoming remote and somewhat divergent; flowers small (limbs ca. 2 mm in diam.); and fruits 1.6–1.8 mm, with commissural faces reaching the nutlet tips. *Verbena demissa* is similar to other species of the group in features of habit, stem anatomy (fide O'Leary et al. 2010) and morphology, glandular vestiture, the mostly solitary, short and few-flowered spikes, and nutlet morphology.

Verbena caniuensis is distinctive in its creeping habit and inflorescence reduced to a single spike, habitual features shared with the geographically similar *V. filicaulis*. O'Leary et al. (2007) further discussed the distinctive inflorescence of *V. caniuensis*. On the other hand, its ovate-orbicular, coarsely serrate, narrowly petiolate leaves are unusual in ser. *Verbena*.

Verbena filicaulis is unusual among species of South American *Verbena* in its deeply 3-parted or pinnately 5-parted leaves, especially in combination with its apparently rhizomatous habit, solitary spikes, and larger flowers and fruits,. O'Leary et al. (2007) allied *V. filicaulis* with the species placed here in sect. *Ampepeiros* ser. *Austrobrasilienses*.

Verbena swiftiana Moldenke is similar to *V. filicaulis* in its deeply 3-lobed (with narrow divisions) to coarsely toothed lower and mid-cauline leaves and short, few-flowered, mostly unbranched spikes with remote fruits. The stems are glabrous, mostly unbranched, and often procumbent and rooting at the nodes. The type (isotype: NY digital image!) and the few other known collections from northeastern Argentina (Misiones), with one collection from immediately adjacent Brazil (Rio Grande do Sul).

Verbena gracilescens is a common and abundant species of central and southeastern South America (Argentina, Bolivia, Paraguay, Uruguay). It characteristically produces relatively short

(mostly 5–15 cm), very slender spikes with remote fruits extending to the base or nearly so (essentially without peduncles). The inflorescence is dichotomously branched, but often irregularly so. The stems are branching, sometimes decumbent and nodally rooting, and glabrous or very sparsely strigillose along the angles. Flowers are very small (calyces 1.2–1.5 mm), and the leaves are sharply serrate and often tripartite, especially the basal to mid-cauline.

In their characteristic morphology, *Verbena swiftiana* and *V. gracilescens* are conspicuously different, but O’Leary et al. (2010) have treated them as conspecific varieties, apparently emphasizing several cited specimens (without locality data) that are said to represent “una gradación continua” between the two. I have not seen the putative intergrades, but interspecific hybrids are not unusual in *Verbena* and such have not been interpreted in other instances as evidence of conspecificity. O’Leary et al., however, did not include Misiones, Argentina, or any of Brazil in the range of *V. gracilescens*, thus its geographic range, apparently allopatric with that of *V. swiftiana*, would preclude hybridization. The putative intergrades cited possibly may be populational variants within *V. gracilescens*.

Moldenke (1968, 1971) recognized *Verbena townsendii*, *V. galapagosensis* Moldenke, *V. stewartii* Moldenke, and *V. glabrata* var. *tenuispicata* Moldenke as native taxa of the Galapagos Islands. From study in herbarium and field, Van der Werff (1977) concluded that they all belong to one single, extremely variable species (by far the most variable in the whole genus, in my observations of collections at MO and TEX-LL), the oldest name being *V. townsendii*. According to Van der Werff, differences in leaf width and lobing apparently result from habitat differences, position on the stem, and maturation of the plants—juvenile leaves usually are broader. Forms of *V. townsendii* are very similar to *V. gracilescens*.

1b. Series SIMPLICES Nesom, ser. nov. Type: *Verbena simplex* Lehm.

Foliis sessilibus angustis nonlobatis, spicis 1 vel paucis fructibus dense superpositis, vestimento eglanduloso, et nuculis superficiebus commissuralis apices attangentibus distinctus.

Plants taprooted; leaves linear to narrowly lanceolate or narrowly oblong-oblancheolate, sessile, unlobed, margins few-toothed, not revolute, blades thick with veins not impressed adaxially; spikes mostly 1 or few from proximal branches, fruits remaining dense and overlapping; floral bracts shorter than the calyces; rachis eglandular; commissural faces apparently extending completely to the nutlet tips.

***Verbena simplex* Lehman** USA; $2n = 14$

Verbena simplex has no apparent close relatives, at least in eastern North America. It is similar to *V. carnea* in its tendency to produce sessile, unlobed leaves and fruits with commissural faces extending completely to the nutlet tips.

O’Leary et al. (in press) have treated *Verbena orcuttiana* as conspecific with *V. simplex*. The two differ in growth habit, vestiture, leaf arrangement, and floral features; they are very different in ecology and their native geographic ranges at their closest point are disjunct by more than 1100 miles. *Verbena orcuttiana* has many similarities with *V. californica* and *V. abramsii*, and those three species are treated here as ser. *Californicae*. Given the apparently isolated position of *V. simplex* in the eastern USA, it would be reasonable, at least as a hypothesis, to consider the possibility that it is closely related to ser. *Californicae*.

1c. Series CONNATICARPAE Nesom, ser. nov. TYPE: *Verbena carnea* Medikus

Duratione perenni habitu rhizomato, foliis sessilibus, spicis plerumque solitariis, floribus relative amplis distinctus, et nuculis connatis non discedentibus ad maturitatem.

Plants rhizomatous; leaves sessile, oblong-spatulate, unlobed, margins closely serrate to irregularly crenate-serrate, revolute, blades thick with veins impressed adaxially; spikes mostly 1 or few, slender, fruits becoming remote; floral bracts usually shorter than the calyx or equal; rachis eglandular; nutlets connate, not separating at maturity, commissural faces apparently extending completely to the nutlet tips.

***Verbena carnea* Medikus USA**

Sanders (2001) hypothesized that *Verbena carnea* is close to *V. stricta* (here placed in ser. *Candelabrae*), but the rhizomatous habit and the thickened, unlobed leaves with closely serrate margins are without a close match elsewhere in the genus. The reduced inflorescence and the connate nutlets are specialized features, suggesting that *V. carnea* is derived from some North American group. There is a tendency in a number of North American species for the nutlets to remain adherent until very late in ontogeny, and the developmental persistence of this feature in *V. carnea* is hardly a character that would justify segregation at generic rank.

O'Leary et al. (2010) have adopted *Verbena caroliniana* Michx. (1803) as the correct name for this species, as preferred over the earlier *V. carnea* Medikus (1784). Comments and a neotype justifying retention of the Medikus name are provided by Nesom (2010d).

1d. Series LEPTOSTACHYAE Schauer in DC., Prodr. 11: 545. 1847. LECTOTYPE (designated here): *Verbena urticifolia* L. Troncoso (1974, p. 311) designated *Verbena officinalis* as the lectotype of series *Leptostachyae*, but *V. officinalis* is automatically the type of series *Verbena*.

Plants taprooted or fibrous-rooted; leaves petiolate, unlobed, margins serrate with acute teeth, blades thin with veins not impressed adaxially; spikes numerous, often strictly in 3's at lower nodes, slender, fruits distantly remote; floral bracts usually shorter than the calyx or equal; rachis eglandular; commissural faces extending to very tip of nutlets.

***Verbena carolina* L.** Mexico, sw USA, Central America; $2n = 14$

***Verbena ehrenbergiana* Schauer** Mexico; $2n = 14$

***Verbena scabra* Vahl** USA, West Indies, Mexico

***Verbena urticifolia* L.** USA; $2n = 14$

The plants of ser. *Leptostachyae* are easily recognizable by their eglandular vestiture, numerous, long, very slender spikes with remote fruits, tiny corollas, and nutlets with commissural faces extending to very tips (see Nesom 2010 c).

1e. Series CANDELABRAE Nesom, ser. nov. TYPE: *Verbena stricta* Ventenat

Verbena [unranked] *Hastatae* Small, Man. S.E. Fl. 1135. 1933. **TYPE: *Verbena hastata* L.**

Foliis latis grosse serrato et spicis numerosis crassiusculis fructibus dense superpositis distinctus.

Plants taprooted or fibrous-rooted; leaves distinctly petiolate to subsessile, unlobed, margins usually coarsely serrate to incised with acute teeth, blades thickened with veins impressed adaxially; spikes numerous and clustered from distal nodes, thick, fruits densely overlapping; floral bracts usually shorter than the calyx or equal; rachis eglandular; commissural faces extending to very tip of nutlets.

Verbena hastata L. USA; $2n = 14$

Verbena macdougalii Heller USA, Mexico; $2n = 14$

Verbena stricta Ventenat USA; $2n = 14$

Verbena xutha Lehman USA; $2n = 42$

Verbena stricta and *V. macdougalii* are very similar between themselves and probably related as sister species. *Verbena hastata* stands apart in its reduced vestiture and relatively long-petiolate leaves with serrate margins; a close relationship with ser. *Leptostachyae* should be investigated. *Verbena xutha* is provisionally placed here, emphasizing its eglandular vestiture, spikes arising from distal branches and often remaining relatively compact, and nutlets with commissural faces extending to very tip of nutlets. The lacinate leaves of *V. xutha*, however, are more similar to some of those of ser. *Plicatae*. The polyploid chromosome number of *V. xutha* at least allows the possibility that it incorporates more than one genome.

1f. Series BRACTEATAE Nesom, ser. nov. TYPE: *Verbena bracteata* Lag. & Rodr.

Verbena [unranked] *Bracteosae* Small, Man. S.E. Fl. 1135. 1933. **TYPE:** *Verbena bracteata* Lag. & Rodr. (incl. *Verbena bracteosa* Michx.)

Foliis latis serrato-incisis, spicis densis bracteis longi-protrusis, et fructibus ad maturitatem plus minusve remotis distinctus.

Plants taprooted or fibrous-rooted; leaves petiolate to subsessile, often 3-lobed, margins serrate to deeply incised with acute teeth, blades relatively thin, veins not impressed adaxially; spikes few, thick, fruits densely overlapping but sometimes becoming somewhat remote at maturity; floral bracts becoming much longer than the calyx and corolla; rachis eglandular; commissural faces extending to very tip of nutlets.

Verbena bracteata Lagasca & Rodr. USA, Mexico; $2n = 14, 28$

Specializations of *Verbena bracteata* in habit (prostrate) and inflorescence (mostly solitary, elongate spikes with greatly enlarged bracts and relatively large fruits) give the species a distinctive appearance. The petiolate, incised leaves, eglandular vestiture, and nutlets with commissural faces extending completely to the tip are similar to those of *V. xutha*.

1g. Series HALEAE Nesom, ser. nov. TYPE: *Verbena halei* Small

Foliis crassibus venis adaxialiter impressis marginibus revolutis caulium lobatis et spicis numerosibus fructibus late remotis ad maturitatem distinctus.

Plants taprooted; leaves petiolate to subpetiolate, basal lobed to unlobed, cauline lobed, margins serrate with acute teeth, blades thick, veins impressed adaxially; spikes numerous, slender, fruits becoming remote; floral bracts usually shorter than the calyx or equal; rachis eglandular; commissural faces ending below the nutlet tips.

Verbena halei Small USA, Mexico; $2n = 14$

Verbena halei has been treated as element of *V. officinalis*, as *V. halei* subsp. *halei* (Small) S. Barber, but the two rarely if ever have the opportunity even to hybridize, much less to intergrade. The consistent morphological differences and continental disjunction in native range support the treatment of *V. halei* at specific rank.

An individual of *Verbena menthifolia* from Arizona studied by Yuan and Olmstead (2008b) was heterozygous at both the PHOT1 and PHOT2 nuclear gene loci, and the gene trees indicated that the individual was of hybrid origin, with *V. halei* as one of the putative parental species.

1h. Series *PLICATAE* Nesom, ser. nov. TYPE: *Verbena plicata* Greene

Foliis latis plerumque 3-lobatis segmentis inciso-dentatis venis saepe abaxialiter prope margines albidis et spicis 1 vel paucis distinctus.

Plants taprooted; leaves usually petiolate, relatively broad (oblong-ovate or obtusely elliptic-ovate), cauline sometimes subclasping, often 3-parted, margins coarsely serrate to incised-serrate or pinnately lobed-serrate, blades thick, veins impressed adaxially, often whitish abaxially near the margins; spikes 1 or few, dense with overlapping fruits to elongate and slender with fruits becoming remote; floral bracts usually shorter than the calyx or equal; rachis usually glandular; commissural faces ending below the nutlet tips (except in *V. xutha*).

Verbena cloverae Moldenke USA; $2n = 14$

Verbena plicata Greene USA, Mexico; $2n = 14$

Verbena runyonii Moldenke USA; $2n = 14$

Verbena lasiostachys Link (incl. *V. robusta* Greene, *V. prostrata* W.T. Ait.) USA, Mexico; $2n = 14$

Among these species, *Verbena plicata* and *V. cloverae* share a distinctive feature of the nutlets—the commissural faces are bullate with low plates densely packed and perhaps connate, forming essentially an unbroken white surface. The Californian *V. lasiostachys* appears to belong in ser. *Plicatae* but is distinct in geography compared to the others, which are mostly in the south-central USA. O’Leary et al. (2010) treated *V. runyonii* as a synonym of *V. neomexicana* var. *hirtella* Perry.

1i. Series *CALIFORNICAE* Nesom, ser. nov. TYPE: *Verbena californica* Moldenke

Foliis plerumque oblanceolatis dentatis, fructibus dense imbricatis vel remotis, rhachidibus calycibusque glandulosis, et nuculis superficiebus commissuralis apices attengentibus distinctus.

Plants taprooted; leaves elongate, not lobed, without distinct petioles, margins toothed, revolute, surfaces not glossy, veins impressed adaxially; spikes 1 or 2–5 from medial to distal branches, relatively thin, fruits not overlapping or densely overlapping but becoming remote proximally; floral bracts shorter than the calyx or equal; rachises and calyces glandular; commissural faces extending completely to the nutlet tips

Verbena abramsii Moldenke USA

Verbena californica Moldenke USA

Verbena orcuttiana Perry Mexico

These three species are very similar in aspect to those of ser. *Tricesimae*. Their recognition here as a separate group emphasizes the distinctive nutlet morphology and their Californian geography (Nesom 2010 f, in manuscript).

1j. Series *TRICESIMAE* Nesom, ser. nov. TYPE: *Verbena canescens* Kunth

Foliis elongatis pinnatifidus vel penitus dentatis, laminis incrassatis venis adaxialiter impressis marginibus revolutis, spicis 1 vel paucis relative tenuibus fructibus plerumque proxime remotis distinctus.

Plants taprooted; leaves elongate, pinnatifid to deeply toothed (incised-pinnatifid or incised dentate, varying to subentire), blades thickened, veins impressed adaxially, margins revolute, surfaces glossy; spikes 1 or few, relatively thin, fruits becoming remote proximally; floral bracts shorter than the calyx or equal; rachises glandular or eglandular; commissural faces not reaching the nutlet apex.

- Verbena canescens** Kunth Mexico, USA; $2n = 14$
- Verbena gracilis** Desfontaines Mexico, USA
- Verbena hirtella** (Perry) Nesom, ined. Mexico, USA; $2n = 14$
- Verbena jessicae** Nesom & Hinton, ined. Mexico
- Verbena johnstonii** (Moldenke) Nesom Mexico
- Verbena livermorensis** Turner & Nesom, ined. USA, Mexico
- Verbena moranii** Nesom, ined. Mexico
- Verbena neomexicana** Small Mexico, USA; $2n = 14$
- Verbena nitens** Nesom, ined. Mexico
- Verbena perennis** Wooton USA; $2n = 14$
- Verbena pinetorum** Moldenke Mexico, USA
- Verbena subuligera** Greene Mexico
- Verbena xylopoda** (Perry) Nesom, ined. USA, Mexico

The sectional epithet alludes to the 30th parallel, which most of the species are near. *Verbena canescens* and *V. gracilis* have wide ranges compared to the others, from the southwestern USA to south-central Mexico. *Verbena abramsii*, *V. californica* and *V. orcuttiana*, at the northwestern corner of this group, stand apart from the other species in their elongate, serrate leaves and commissural faces of the nutlets extending completely to the nutlet tips—these perhaps represent a distinct group. The species of ser. *Tricesimae* are treated in detail in Nesom (2010g, in manuscript) and Nesom and Hinton (2010, in manuscript; *V. jessicae*), where the species noted above as “ined.” will be formally described or delimited.

Sanders (2001) hypothesized that *Verbena neomexicana* is part of the species group that includes *V. mentifolia*, and indeed they have similarities in habit. *Verbena mentifolia*, however, and its putatively close relative *V. madrensis* have thinner leaves with non-revolute margins and veins not impressed adaxially, and the commissural faces generally extend completely to the nutlet tips.

2. SECTION AMPHEPEIROS Nesom, sect. nov. TYPE: *Verbena glabrata* Kunth

Inflorescentiis cymosis spicis in 3s, quoque spica per folia vel bracteas foliaceas subtenta, et foliis latis distincte petiolatis e basi truncatis vel cuneatis marginibus grosse serratis distinctus.

Stems not sharply 4-angled (Type A anatomy); leaves broad, distinctly petiolate from truncate to cuneate leaf bases, unlobed, margins coarsely serrate; inflorescence cymose, with spikes in definite 3's; each spike subtended by foliaceous bracts, often with the middle spike sessile or subsessile to short-pedunculate; fruits usually densely overlapping at maturity.

2a. Series PACIFICA Nesom, ser. nov. TYPE: *Verbena glabrata* Kunth

Distributione geographica plerumque secus oceanum pacificum distinctus.

- Verbena glabrata** Kunth South America (Bolivia, Ecuador, Columbia, Peru)
- Verbena macrodonta** Perry Mexico (Baja California Sur)
- Verbena recta** Kunth Mexico
- Verbena sedula** Moldenke South America (Galapagos Islands)

Species of ser. *Pacificae* are autochthonous to both the South American and North American continents (also see ser. *Pachystachyae* regarding *V. sphaerocarpa*; ser. *Verbena* is the only group hypothesized here to be more widespread). The separation of ser. *Brasilienses* and ser. *Pacificae*, based on geography, hypothesizes that other distinctions remain to be discovered; a clear morphological difference is not apparent, but the geographically-based names provide reference to the groups. It also is acknowledged that the separation may be arbitrary.

Verbena macrodonta is one of a number of endemic species of the oak and pine-oak woodlands of the Sierra de la Laguna of Baja California Sur. Pine-oak forests closest to those of the Sierra de la Laguna are in the trans-volcanic ranges of southeast and south-central Mexico, the “Serranias Meridionales” floristic province, fide Rzedowski (1978). Pine-oak forests of northern Baja California (Sierra Juarez, Sierra San Pedro Mártir) are more closely related floristically to the USA.

I have seen only the holotype (MO!) and isotype (US digital image!) of *Verbena macrodonta*, but the distinctive leaf morphology and inflorescence structure, as well as its geography, justify its placement among these species. The leaves are large, broadly lanceolate to oblong-lanceolate with coarsely serrate margins and truncate or rounded bases and distinct petioles, and the spikes are dense, subtended by bracts, and distinctly in 3's. *Verbena macrodonta* and *V. recta* both are unusual in sect. *Amphypeiros* because of their pedunculate spikes. O'Leary et al. (2010) have placed *V. macrodonta* as a synonym of *V. officinalis*.

Verbena glabrata is native to western South America. O'Leary et al. (2007) identified and cited far-disjunct collections from Mexico (Michoacan, Puebla, and Veracruz) as *V. glabrata*, but these Mexican plants are *V. recta*. O'Leary et al. (2010) have recognized *V. recta* as distinct but without clarifying their earlier equation of it with *V. glabrata*. I have seen collections of *V. recta* from the Mexican states of Distrito Federal, Edo. México, Michoacan, Morelos, Nuevo León, Oaxaca, and Puebla. The populations in Nuevo León appear to be disjunct from the others but morphologically inseparable.

Collections identified as *Verbena glabrata* from the southernmost portion of its range (Depto. Arequipa in Peru) are of prominently glandular plants with trilobed and more elongate leaves than characteristic elsewhere. It is probable that these represent an undescribed species.

2b. Series AUSTROBRASILIENSES Nesom, ser. nov. TYPE: *Verbena hirta* Sprengel

Distributione geographica plerumque in Brasilia australi distinctus.

Verbena hirta Sprengel South America (s Brazil, ne Argentina)

(tentatively including var. **hirta** and var. **gracilis** Dusén)

Verbena lobata Velloso South America (s Brazil)

(tentatively including var. **lobata** and var. **glabrata** Moldenke)

Verbena subpetiolata N. O'Leary South America (s Brazil)

All three species of ser. *Austrobrasilienses* are centered in southernmost states of Brazil, Paraná, and Rio Grande do Sul, hence the series epithet. This is a morphologically heterogeneous assemblage needing further study.

3. SECTION VERBENACA Walpers, Repert. Bot. Syst. 4: 14. 1845. **LECTOTYPE** (designated here): *Verbena bonariensis* L. Sect. *Verbenaca* of Walpers included *Verbena*, *Glandularia*, and *Junellia*. The lectotype is chosen here to represent to restrict the section to *Verbena* sensu stricto. Schauer (1847) followed Walpers in his broad concept of sect. *Verbenaca*, placing *V. officinalis* within sect. *Verbenaca* series *Leptostachyae*.

Stems usually sharply 4-angled (Type B anatomy); leaves broad to narrow, indistinctly petiolate through attenuate leaf bases, unlobed, margins coarsely serrate to subentire; inflorescence cymose, with spikes in definite 3's; spikes not subtended by foliaceous bracts, often with the middle spike sessile or subsessile to pedunculate; fruits densely overlapping or becoming remote at maturity.

3a. Series PACHYSTACHYAE Schauer in DC., Prodr. 11: 539. 1847. **LECTOTYPE** (Troncoso 1974, p. 311): *Verbena bonariensis* L. O'Leary et al. (2007, p. 580) cited "serie *Pachystachyae* subserie *Pachystachyae* Schauer," perhaps supposing that the subseries was automatically established. "Subseries *Pachystachyae*" is not a legitimate name.

Verbena [unranked] *Foliosae* Walpers, Repert. Bot. Syst. 4: 18. 1845. **LECTOYPE** (designated here): *Verbena bonariensis* L.

Verbena [unranked] *Micranthae* Walpers, Repert. Bot. Syst. 4: 18. 1845. **LECTOYPE** (designated here): *Verbena bonariensis* L.

Verbena [unranked] *Holophyllae* Walpers, Repert. Bot. Syst. 4: 18. 1845. **LECTOYPE** (designated here): *Verbena bonariensis* L.

Verbena [unranked] *Bonarienses* Small, Man. S.E. Fl. 1135. 1933. **TYPE**: *Verbena bonariensis* L.

Verbena [unranked] *Venosae* Small, Man. S.E. Fl. 1135. 1933. **TYPE**: *Verbena rigida* Spreng.

Fruiting spikes relatively short and thick, the central sessile to subsessile, with fruits usually densely overlapping at maturity. Leaves unlobed.

Verbena alata Otto ex Sweet South America

Verbena bangiana Moldenke South America

Verbena bonariensis L. South America; $2n = 14, 28$

Verbena brasiliensis Velloso (incl. *V. intercedens* Briquet) South America

Verbena ephedroides Chamisso South America

Verbena goyazensis Moldenke South America

Verbena hispida Ruiz & Pavon South America; $2n = 14$

Verbena incompta P.W. Michael South America

Verbena intermedia Gillies & Hooker ex Hooker South America; $2n = 28, 35, 56$

Verbena lindbergii Moldenke South America

Verbena ovata Chamisso South America; $2n = 72$

Verbena rigida Sprengel South America; $2n = 42$

Verbena sagittalis Chamisso South America

Verbena sphaerocarpa Perry Mexico (Socorro Island)

Verbena valerianoides Kunth South America

Verbena rigida was observed by O'Leary et al. (2007) to have Type B stem morphology, unlike the rest of the section. It also is unusual in its rhizomatous habit, but in features of the inflorescence it is similar to the species placed here in ser. *Verbenacae*.

Verbena sphaerocarpa is tentatively recognized at specific rank (Nesom 2010a). It is endemic to Socorro Island (about 600 kilometers west of the coast of Colima, Mexico) but is very similar to *V. brasiliensis* and probably derived from it.

Verbena valerianoides is a distinctive species apparently endemic to montane Colombia (the type from Bogotá, P. fide!) It produces sessile, non-clasping, narrowly lanceolate to oblong-lanceolate, entire leaves and short, thick spikes, the central one sessile. O'Leary et al. (2007) considered this a "doubtful taxon" but I have seen recent collections from the departments of Boyacá, Cundinamarca, and Nariño.

Verbena bangiana was treated by O’Leary et al. (2007) as *V. hispida* var. *obovata* (Moldenke) O’Leary, who noted that they did not consider differences in vestiture and floral dimensions between the two taxa as “sufficiently important in *Verbena*” to separate them as distinct species. Collections of each are numerous and intermediates appear to be rare, suggesting that the two are reproductively isolated.

Verbena goyazensis (Bull. Torrey Bot. Club 77: 404. 1950. **TYPE: Brazil.** Goiás. Rio do Peixe, 8 Jul 1949, G. Hashimoto 663 [holotype: SP, fragment-NY digital image!]) has broad, sessile, serrate leaves and very short, congested spikes in 3’s—it appears to be remarkably distinct in its leaves with deeply reticulate-excavate abaxial surfaces. It has been included by O’Leary et al. (2010) as a “doubtful taxon.”

3b. Series LITORALES Nesom, ser. nov. TYPE: *Verbena litoralis* Kunth

Spicis fructiferis relative elongatis gracilibusque fructibus proximalibus remotis ad maturitatem et foliis nonlobatis distinctus.

Fruiting spikes elongate and slender, the central pedunculate, with fruits becoming remote at maturity, at least proximally; leaves unlobed.

***Verbena litoralis* Kunth** South America (western); $2n = 28, 42, 56$

***Verbena montevidensis* Sprengel** South America (southeastern); $2n = 21, 42$

Both of these species, as currently identified, appear to be polymorphic. Potential correlations between ploidy level and morphology apparently have not been investigated.

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LITERATURE CITED

- Atkins, S. 2004. Verbenaceae. In K. Kubitzki (ed.), *The Families and Genera of Vascular Plants*, Vol. 7: 449–468.
- Botta, S.M. 1989. Studies in the South American genus *Junellia* (Verbenaceae, Verbenoideae) I. Delimitation and infrageneric divisions. *Darwiniana* (San Isidro) 29: 371–396.
- Briquet, J. 1895. Verbenaceae. In A. Engler & K. Prantl (eds.), *Naturalischen Pflanzenfamilien* IV, 3a. 1915, Nachtr. 3,4: 132–182.
- Martinez, S., S. Botta, y M.E. Mulgura. 1996. Morfología de las inflorescencias en Verbenaceae-Verbenoideae. I: Tribu Verbenae. *Darwiniana* 34: 1–17.
- Michael, P.W. 1997. Notes on *Verbena officinalis* s.s. and *V. macrostachya* (Verbenaceae) with new combinations in two closely related taxa. *Telopea* 7: 293–297.
- Moldenke, H.N. 1961–1965. Materials toward a monograph of the genus *Verbena*. I. *Phytologia* 8: 95–104. 1961. II. *Phytologia* 8: 108–152. 1962a. III. *Phytologia* 8: 175–216. 1962b. IV. *Phytologia* 8: 230–272. 1962c. V. *Phytologia* 8: 274–323. 1962d. VI. *Phytologia* 8: 371–384. 1962e. VII. *Phytologia* 8: 395–453. 1962f. VIII. *Phytologia* 8: 460–496. 1963a. IX. *Phytologia* 9: 8–54. 1963b. X. *Phytologia* 9: 59–97. 1963c. XI. *Phytologia* 9: 113–181. 1963d. XII. *Phytologia* 9: 189–238. 1963e. XIII. *Phytologia* 9: 267–336. 1964a. XIV. *Phytologia* 9: 351–407. 1964b. XV. *Phytologia* 9: 459–480. 1964c. XVI. *Phytologia* 9: 501–

505. 1964d. XVII. *Phytologia* 10: 56–88. 1964e. XVIII. *Phytologia* 10: 89–161. 1964f. XIX. *Phytologia* 10: 173–236. 1964g. XX. *Phytologia* 10: 271–319. 1964h. XXI. *Phytologia* 10: 406–416. 1964i. XXII. *Phytologia* 10: 490–504. 1964j. XXIII. *Phytologia* 11: 1–68. 1964k. XXIV. *Phytologia* 11: 80–141. 1964l. XXV. *Phytologia* 11: 155–213. 1964m. XXVI. *Phytologia* 11: 219–287. 1965a. XXVII. *Phytologia* 11: 290–357. 1965b. XXVIII. *Phytologia* 11: 400–422. 1965c. XXIX. *Phytologia* 11: 435–507. 1965d.
- Moldenke, H.N. 1968. The vervains collected on the Galapagos Islands by Charles Darwin during the voyage of the “Beagle.” *Phytologia* 16: 340–342.
- Moldenke, H.N. 1971. *Verbena*. Pp. 503–509, in I.L. Wiggins and D.L. Porter. *Flora of the Galapagos Islands*. Stanford University Press, Stanford, California.
- Munir, A.A. 2002. A taxonomic revision of the genus *Verbena* L. (Verbenaceae) in Australia. *J. Adelaide Bot. Gard.* 20: 21–103.
- Nesom, G.L. 2010a. Taxonomic notes on *Verbena bonariensis* (Verbenaceae) and related species in the USA. *Phytoneuron* 2010-12: 1–16.
- Nesom, G.L. 2010b. A new species of *Verbena* (Verbenaceae) from northeastern Mexico and an overview of the *V. officinalis* group. *Phytoneuron* 2010-13: 1–14.
- Nesom, G.L. 2010c. Taxonomy of *Verbena urticifolia* (Verbenaceae) and its close relatives. *Phytoneuron* 2010-14: 1–12.
- Nesom, G.L. 2010d. Neotypification of *Verbena carnea* Medikus (Verbenaceae). *Phytoneuron* 2010-15: 1–3.
- Nesom, G.L. 2010e. Typification of *Verbena spuria* L. (Verbenaceae). *Phytoneuron* 2010-16: 1–3.
- Nesom, G.L. 2010f. Taxonomy of the *Verbena californica* group (Verbenaceae). *Phytoneuron*, to be published.
- Nesom, G.L. 2010g. Taxonomic overview of the *Verbena neomexicana* group (Verbenaceae), including new species. *J. Bot. Res. Inst. Texas*, in manuscript, to be submitted.
- Nesom, G.L. and G.S. Hinton. 2010. *Verbena jessicae* (Verbenaceae), a new species from Nuevo León, Mexico. *Phytologia*, in manuscript, to be submitted.
- O’Leary, N., M.E. Múlgura, and O. Morrone. 2007. Revisión taxonómica de las especies del género *Verbena* (Verbenaceae): serie *Pachystachyae*. *Ann. Missouri Bot. Gard.* 94: 571–621.
- O’Leary, N., P. Peralta, and M.E. Múlgura. 2008. A taxonomic revision of the genus *Tamonea* (Verbenaceae). *Bot. J. Linn. Soc.* 157: 357–371.
- O’Leary, N., Y.-W. Yuan, A. Chemisquy, and R.G. Olmstead. 2009. Reassignment of species of paraphyletic *Junellia* s.l. to the new genus *Mulguraea* (Verbenaceae) and new circumscription of genus *Junellia*: Molecular and morphological congruence. *Syst. Bot.* 34: 777–786.
- O’Leary, N., M.E. Múlgura, & O. Morrone. 2010. Revisión taxonómica de las especies del género *Verbena* (Verbenaceae). II. Serie *Verbena*. *Ann. Missouri Bot. Garden*, in press.
- Perry, L.M. 1933. A revision of the North American species of *Verbena*. *Ann. Missouri Bot. Gard.* 20: 239–363.
- Rzedowski, J. 1978. *Vegetación de Mexico*. Editorial Limusa, Mexico, D.F.
- Sanders, R.W. 2001. The genera of Verbenaceae in the southeastern United States. *Harvard Pap. Bot.* 5: 303–358.
- Schauer, J.C. 1847. Verbenaceae. In A.P. De Candolle (ed.), *Prodr.* 11: 522–700.
- Small, J.K. 1933. *Manual of the Southeastern Flora*. Univ. of North Carolina Press, Chapel Hill.
- Troncoso, N.S. 1974. Los generos de Verbenáceas de Sudamérica extratropical (Argentina, Chile, Bolivia, Paraguay, Uruguay, y Sur de Brazil). *Darwiniana* (San Isidro) 18: 295–412.
- van der Werff, H. 1977. Vascular plants from the Galapagos Islands: New records and taxonomic notes. *Bot. Not.* 130: 89–100.
- Walpers, W.G. 1845. Verbenaceae. *Repert. Bot. Syst.* 4: 3–134. Addendum in 6: 686–693. 1847.
- Yuan, Y-W. and R.G. Olmstead. 2008a. A species-level phylogenetic study of the *Verbena* complex (Verbenaceae) indicates two independent intergeneric chloroplast transfers. *Molec. Phylog. Evol.* 48: 23–33.

- Yuan, Y.-W. and R.G. Olmstead. 2008b. Evolution and phylogenetic utility of the *PHOT* gene duplicates in the *Verbena* complex (Verbenaceae): Dramatic intron size variation and footprint of ancestral recombination. *Amer. J. Bot.* 95: 1166–1176.
- Yuan, Y.-W., C. Liu, H.E. Marx, and R.G. Olmstead. 2010. An empirical demonstration of using pentatricopeptide repeat (PPR) genes as plant phylogenetic tools: Phylogeny of Verbenaceae and the *Verbena* complex. *Molec. Phylogen. Evol.* 54: 23–35.