

FOUR NEW SUBTRIBES: ALLOLEPIINAE, JOUVEINAE, KALINIINAE, AND SOHNSIINAE IN THE CYNODONTEAE (POACEAE: CHLORIDOIDEAE)

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ABSTRACT

Allolepis, *Jouvea*, *Kalina*, and *Sohnsia* are small (only *Jouvea* contains two species), often overlooked genera that are morphologically and genetically isolated within the tribe Cynodonteae. We present a molecular phylogeny using sequence data from seven plastid markers (*ccsA*, *ndhA* intron, *ndhF*, *rpl32-trnL*, *rpoC2*, *rps16-trnK*, and *rps16* intron) and the nuclear ribosomal internal transcribed spacer regions (ITS 1 & 2). Since *Allolepis*, *Jouvea*, *Kalinia*, and *Sohnsia* do not align within any of the 21 existing Cynodonteae subtribes, we describe **Allolepiinae**, **Jouveinae**, **Kaliniinae**, and **Sohnsiinae** as new. In addition, we provide descriptions, habitat, distribution, and comments for each subtribe.

Allolepis texana (Vasey) Scribn., *Jouvea pilosa* (J. Presl) Scribn, *J. straminea* E. Fourn., and *Sohnsia filifolia* (E. Fourn.) Airy Shaw are dioecious, caespitose grasses, whereas *Kalinia obtusiflora* (E. Fourn.) H.L. Bell & Columbus has 4–8 mm wide, sharp-pointed rhizomes and perfect florets. Historically, these western hemisphere grasses were placed in other genera, i.e., *Brizopyrum* (Presl, 1830; Fournier 1886), *Calamochloa* (Fournier 1877), *Distichlis* (Lamson-Scribner 1899), *Eragrostis* (Lamson-Scribner 1897), *Poa* (Kunth 1833; Vasey 1890b), and *Rhachidospermum* (Vasey 1890a), until recently being aligned within the Cynodonteae (Columbus 2007; Peterson et al. 2010, 2016). An early molecular phylogeny of the subfamily Chloridoideae placed *Allolepis*, *Jouvea*, and *Sohnsia* within the tribe Cynodonteae (Columbus et al. 2007). Later molecular studies have confirmed that these three genera, along with *Kalinia*, are members of the supersubtribe Boutelouodinae, a primarily Western Hemisphere clade within the Cynodonteae that includes six subtribes: Boutelouinae, Hilariinae, Monanthochloinae, Muhlenbergiinae, Scleropogoninae, and the Traginae (Bell et al. 2013; Peterson et al. 2010; 2016; Soreng et al. 2017). However, these four genera do not align within any of the existing 21 subtribes of Cynodonteae (Peterson et al. 2010; 2016; Soreng et al. 2017) or within the six subtribes of Boutelouodinae. *Allolepis*, *Jouvea*, and *Sohnsia* are strictly dioecious whereas *Kalinia* is hermaphroditic. All four genera are endemic or centered in México (one extending into Texas, another into Arizona and New México, one other extending south to Panama in Central America, and Ecuador in South America), emphasizing the morphological diversification of the Boutelouodinae in this region and the correlation of outcrossing breeding systems with this diversification. We present a molecular phylogeny using sequence data from seven plastid markers (*ccsA*, *ndhA* intron, *ndhF*, *rpl32-trnL*, *rpoC2*, *rps16-trnK*, and *rps16* intron) and a single nuclear marker (ITS) emphasizing these four genera, and describe four new, monotypic subtribes within the Boutelouodinae.

MATERIALS AND METHODS

The phylogram (Fig. 1) was generated with existing data from Peterson et al. (2010, 2016) and we added three samples, one for *Allolepis*, *Jouvea pilosa*, and *Sohnsia*. Voucher information and GenBank numbers for the four genera are given in Table 1. The methods for DNA extraction, primers, amplification, sequencing, and phylogenetic analysis are given in Peterson et al. (2010, 2016). We estimated the phylogeny among members of these four genera and the Cynodonteae based on the analysis of eight molecular markers (nuclear ITS 1&2 and plastid *ccsA*, *ndhA* intron, *ndhF*, *rpl32-trnL*, *rpoC2*, *rps16-trnK*, and *rps16* intron DNA sequences). To make the phylogram smaller, taxa already placed in existing subtribes or tribes are depicted only at that level.

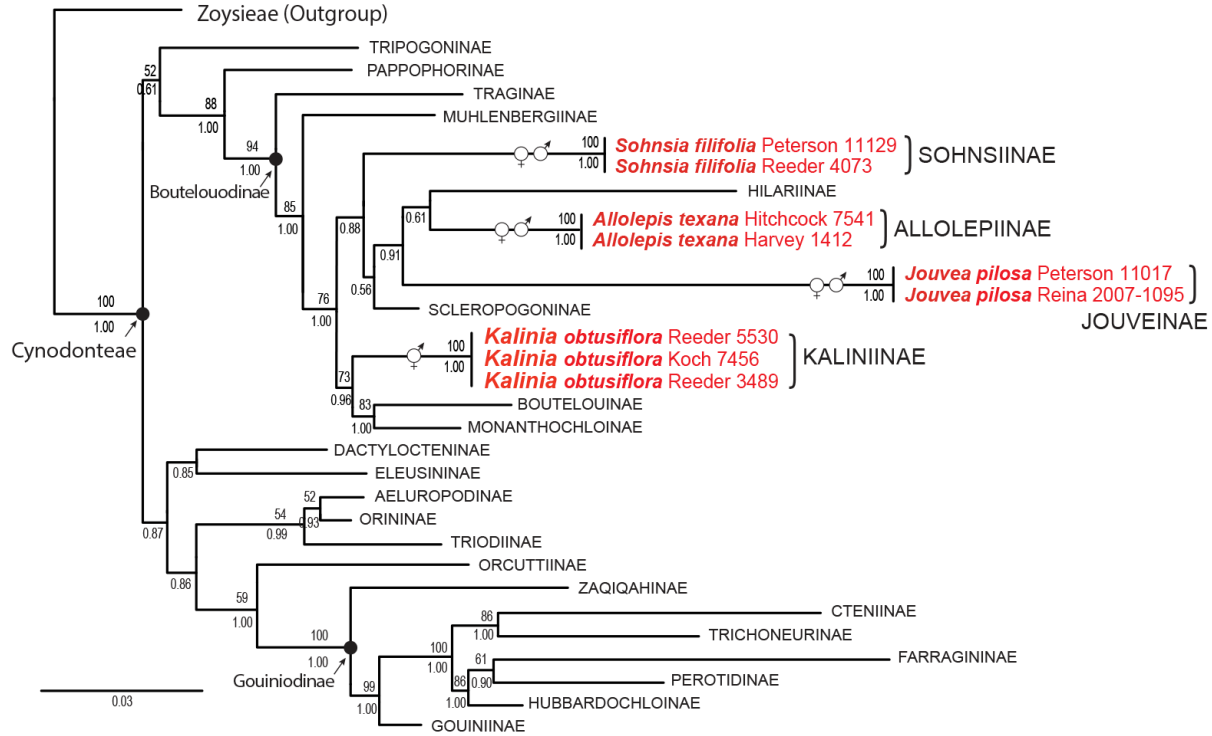


Figure 1. Maximum-likelihood tree inferred from combined plastid (*ccsA*, *ndhA* intron, *ndhF*, *rpl32-trnL*, *rpoC2*, *rps16-trnK*, and *rps16* intron) and ITS sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; vertical bars indicate our classification; circle with a cross = female plants; circle with an arrow = male plants; circle with cross and arrow indicates plants with perfect flowers; scale bar = 3%.

RESULTS AND DISCUSSION

The maximum-likelihood tree from the combined analysis of seven plastid regions (*ccsA*, *ndhA* intron, *ndhF*, *rpl32-trnL*, *rpoC2*, *rps16-trnK*, and *rps16* intron) and ITS depicts *Allolepis*, *Jouvea*, *Kalinia*, and *Sohnsia* in separate clades embedded within the supersubtribe Boutelouodinae clade (Fig. 1). The species within each of the four genera form strongly supported clades [bootstrap (BS) = 100, posterior probability (PP) = 1.00]. *Kalinia* is moderately supported as sister to the Boutelouinae–Monanthochloinae clade (BS = 73, PP = 0.96). *Allolepis* is unsupported as sister to the Hilariinae (PP = 0.61), *Jouvea pilosa* is unsupported as sister to the *Allolepis*–Hilariinae clade (PP = 0.91), and *Sohnsia* is unsupported as sister to the Scleropogoninae–*Jouvea*–*Allolepis*–Hilariinae clade. Successive sisters to the aforementioned lineage are the Muhlenbergiinae (near, BS = 76, PP = 1.00) and the Tragiinae (next, PP = 85, PP = 1.00). The Cynodonteae phylogeny based on analysis of 389 samples in 213 species presented in Peterson et al. (2016) is identical with our new phylogeny.

Table 1. List of sampled specimens of the genera *Allolepis*, *Jouvea*, *Kalinia*, and *Sohnsia*; taxon voucher (collector, number; all specimens housed at the United States National Herbarium), country and state of origin, and GenBank accession for DNA sequences is given.

Taxon	Voucher	Country	ITS	ccsA	ndhA intron	ndhF	rpl32-trnL	rpoC2	rps16-trnK	rps16 intron
<i>Allolepis texana</i> (Vasey) Soderstr. & H.F. Decker	Hitchcock 7541	México, Durango	GU359264	JQ345048	GU359388	GU359577	GU360015	–	GU360573	GU360318
<i>Allolepis texana</i> (Vasey) Soderstr. & H.F. Decker	Harvey 1412	México	GU359265	–	GU359387	GU359588	GU360016	–	GU360572	GU360306
<i>Jouvea pilosa</i> (J. Presl) Scribn.	Peterson 11017 & Annable	México, Colima	GU359144	JQ345095	GU359433	GU359737	GU359812	KX582800	GU360696	GU360379
<i>Jouvea pilosa</i> (J. Presl) Scribn.	Reina 2007-1095, Van Devander, Chamberland & Bertelsen	México, Sonora	KJ768884	KX582279	KX582475	KX582538	KJ768979	KX582801	KX582972	KX582905
<i>Kalinia obtusiflora</i> (E. Fourn.) H.L. Bell & Columbus	Koch 7456	México, Lago de Texcoco	KX582380	–	–	KX582539	KX582656	–	KX582973	KX582906
<i>Kalinia obtusiflora</i> (E. Fourn.) H.L. Bell & Columbus	Reeder 3489, Reeder & Soderstrom	México, Chihuahua	KX582381	–	–	KX582540	KX582657	–	KX582974	KX582907
<i>Kalinia obtusiflora</i> (E. Fourn.) H.L. Bell & Columbus	Reeder 5530 & Reeder	USA, Arizona	KX582382	–	–	KX582541	KX582658	–	KX582975	KX582908
<i>Sohnsia filifolia</i> (E. Fourn.) Airy Shaw	Peterson 11129 & Annable	México, San Luis Potosi	GU359204	JQ345145	GU359531	GU359612	GU359918	KX582839	GU360634	GU360350
<i>Sohnsia filifolia</i> (E. Fourn.) Airy Shaw	Reeder 4073 & Reeder	México	GU359205	–	GU359532	GU359614	GU359917	–	GU360633	GU360332

In the taxonomy section below we describe each of these four genera as subtribes (Allolepiinae, Jouveinae, Kaliniinae, and Sohnsiinae) since they do not align within any existing Cynodonteae subtribes.

In the Boutelouodinae, dicliny occurs in the Allolepiinae, Boutelouinae (*Bouteloua*), Jouveinae, Monanthochloinae (*Distichlis*), Scleropogoninae (*Blepharidachne*, *Munroa*, and *Scleropogon*), and the Sohnsiinae. There are at least 15 diclinous species found in four sections of *Bouteloua*: *Buchloe*, *Cyclostachya*, *Opizia*, and *Triplathera* (Kinney et al. 2007; Peterson et al. 2015; Schrager-Lavelle et al. 2017). Within Chloridoideae, dicliny is apparently restricted to the western hemisphere (Connor 1979).

TAXONOMY

Allolepiinae P.M. Peterson, Romasch., & Y. Herrera, **subtribe nov.**

TYPE: *Allolepis* Soderstr. & H.F. Decker, Madroño 18: 36. 1965.

Dioecious, caespitose perennials with stolons 5–25 cm long, 1–4 mm wide. **Culms** 10–70 cm tall. **Leaf** sheaths shorter than flowering culm internodes with smooth margins; ligules 0.5–1.4 mm long, a ciliate membrane; blades 5–30 cm long, 2.5–6 mm wide, sometimes involute towards apex. **Panicles** 3–23 cm long, 1–6 cm wide, narrow; primary branches appressed to main axis (usually floriferous to base), terminating in a spikelet with appressed secondary branches; pedicels glabrous, smooth; disarticulation above glumes, lemma and palea falling as a unit; rachilla glabrous. **Staminate** spikelets 9–23 mm long, 3–8 mm wide, 4–14(–20)-flowered, ovate to lanceolate-linear, solitary, stramineous, terete, coriaceous; glumes 4–5 mm long, broadly ovate; lower glumes 1-veined; upper glumes 1 or 3-veined, a little longer than the lower; lemmas 5–5.5 mm long, 3-veined, glabrous, shiny; paleas equal or slightly longer than the lemma; stamens 3, anthers 3–3.5 mm long, yellow. **Pistillate** spikelets 10–30 mm long, 2.5–3.5 mm long, 5–10-flowered, slightly laterally compressed with sterile florets present above fertile, coriaceous; glumes 5–12 mm long, glabrous; lower glumes 5–10 mm long, 1-veined with 4 or 5 additional faint veins; upper glumes 6–12 mm long, 3-veined, sometimes with 2 or 4 additional faint veins; lemmas 5–11 mm long, 3-veined, coriaceous, glabrous, midvein scabrous above, margins irregular and scarious; paleas slightly shorter than the lemma, keels ciliate; lodicules 3, cuneate; stigmas 2. **Caryopsis** ellipsoid, with a fused pericarp adherent. $2n = 40$ (Gould, 1966).

Included taxon—*Allolepis texana* (Vasey) Soderstr. & H.F. Decker [syn. *Poa texana* Vasey; *Sieglingia wrightii* Vasey; *Distichlis texana* (Vasey) Scribn.].

Habitat—Sandy and silty soils but not in alkaline areas; 900–2000 m.

Distribution—Known from the Big Bend region of southwestern Texas, USA (Jeff Davis and Presidio counties) and Chihuahua, Coahuila (Municipio Satillo), Durango (Municipio Ocampo), and Tamaulipas, México (Powell 1994). Based on a *Hitchcock 7541* (US-913782, US-913783) collection label that states “Torreón, Durango,” this species was reported as occurring in Durango by Soderstrom and Decker (1965) and Powell (1994). *Hitchcock 7540* was collected from Torreón-Durango border and *Hitchcock 7542 & 7543* was also collected from Torreón, Durango. It seems likely that Hitchcock knew what state he was in, and collected these plants in Torreón de Cañas, Durango and not Torreón, Coahuila.

Comments—Vasey (1890b) first described this *Allolepis texana* in *Poa* L. and later, based on a different collection, described the same species in *Sieglingia* Bernh. (Vasey 1893). Based on having a dioecious habit, a paniculate inflorescence, subcoriaceous glumes, exerted styles, and grains enclosed by a palea base, Lamson-Scribner (1899) transferred this species to *Distichlis*. *Allolepis* is very similar to *Distichlis*, sharing the dioecious habit, a ciliate membrane for a ligule, disarticulation above the glumes, and many florets per spikelet (Clayton & Renvoize 1986; Peterson

et al. 1995, 1997). Soderstrom and Decker (1965) found that *Allolepis* can be distinguished from *Distichlis* in having stolons and the absence of rhizomes, non-distichous leaf blade arrangement, heteromorphic staminate and pistillate spikelets, non-sunken bicellular microhairs, and occurrence in sandy soils (not alkaline).

Jouveinae P.M. Peterson, Romasch., & Y. Herrera, **subtribe nov.**

TYPE: *Jouvea* E. Fourn., Bull. Soc. Roy. Bot. Belgique 15: 475. 1876.

Dioecious, caespitose perennials with stolons, often with scaly buds. **Culms** 20–60 cm tall, decumbent or mat forming, glabrous. **Leaf** sheaths shorter or longer than internodes with smooth margins; ligules 0.5–1 mm long, a line of hairs; blades 1–15 cm long, 1–4 mm wide, flat becoming involute, pungent. **Inflorescences** 2–3 cm long, of 1-many spikelets in fascicles of 1–5 in pistillate plants; inflorescence a panicle 2–6 cm long in staminate plants; inflorescence exserted (smooth in staminate plants) or fully included (pistillate plants spikelets are embedded in sponge-like tissue of rachilla, only summit of florets free); primary branches appressed to main axis terminating in a spikelet; disarticulation above the glumes, lemma and palea falling as a unit. **Spikelets** 8–40 mm long (15–40 mm long in staminate spikelets) or in clusters (pistillate spikelets), (3–)5–25-flowered, laterally compressed, sessile, sterile florets present about fertile florets; rachilla glabrous; glumes present or absent, shorter than spikelets (in staminate spikelets), smooth, glabrous; lower glume unveined; upper glume shorter than lower lemma, 1-veined; lemmas 3-veined, coriaceous, glabrous, smooth; paleas chartaceous, glabrous, smooth, margins not enfolding the fruit; lodicules absent; stamens 3 or rudimentary, anthers yellow or reddish purple; stigmas 2 or rudimentary, exserted. **Caryopsis** ellipsoid, terete, with a fused pericarp. $2n = 20$ (Pohl & Davidse 1971)

Included taxa—*Jouvea pilosa* (J. Presl) Scribn. [syn. *Brizopyrum pilosum* J. Presl; *Poa preslii* Kunth; *Rhachidospermum mexicanum* Vasey]; *Jouvea straminea* E. Fourn.

Habitat—Near the immediate coast on sand dunes and unprotected beaches forming densely foliaceous mounds (*J. pilosa*) and in saline mud flats forming loosely interspersed culms (*J. straminea*) [Pohl & Davidse 1994].

Distribution—The genus occurs in México (Baja California Sur, Chiapas, Colima, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, Sinaloa, Sonora), Central America (Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama), and Ecuador (*J. straminea*) [Pohl & Davidse 1994; Espejo Serna et al. 2000; Dávila et al. 2006].

Comments—Pilger (1956) recognized the unique morphological features by erecting the tribe Jouveae Pilg. (Pilger 1956), referring to Weatherwax's (1939) comments, "but the weight of evidence at present favors placement in the Festuceae." Although Weatherwax did indicate that the staminate spikelets of *Jouvea* resembled those found in *Distichlis*. Pistillate plants are characterized by an inflorescence that consists of 2–5 spikelets embedded in a sponge-like tissue of the rachilla, with only the summit of the florets free (Peterson et al. 1997). Clayton and Renvoize (1986) placed *Jouvea* near *Distichlis* in the Monanthochloinae as treated then along with *Allolepis* and *Swallenia* Soderstr. & H.F. Decker. *Jouvea* and *Distichlis* share distichously arranged leaves and the dioecious habit (Peterson et al. 1997). Molecular studies clearly place *Swallenia* within the Scleropogoninae (Peterson et al. 2010; 2016).

Kalininae P.M. Peterson, Romasch., & Y. Herrera, **subtribe nov.**

TYPE: *Kalinia* H.L. Bell & Columbus, Aliso 30(2): 91–93, f. 9. 2012.

Hermaphroditic perennials with scaly, sharp-pointed rhizomes, with innovations, sometimes stoloniferous, the sharp-tipped rhizomes 4–8 mm thick. **Culms** 15–40(–50) cm tall, erect, stiff, hard, glaucous below the nodes. **Leaf** sheaths hairy at the apices, hairs to 2 mm long; ligules 0.2–0.4 mm

long, membranous, ciliate; blades 2–15 cm long, (1–)2–4 mm wide, involute, arcuate, glabrous abaxially, scabrous adaxially, apices sharply pointed. **Panicles** 6–20(–24) cm long, 2–8(–12) cm wide, ovate, open or contracted; primary branches 1–8(–15) cm long, appressed or diverging up to 50° from the rachises; pedicels 0–8 mm long, appressed, lower pedicels on each branch shorter than 1 mm long. **Spikelets** 8–14 mm long, 1.4–3 mm wide, ovate to lanceolate, stramineous with a reddish-purple tinge, with 5–10 florets; disarticulation basipetal, glumes 1(3)-veined, persistent; glumes unequal, chartaceous; lower glumes 2.4–3.6 mm long, 1-veined; upper glumes 3–4.5 mm long, sometimes 3-veined; lemmas 3.8–4.5 mm long, ovate, leathery, 3-veined, lateral veins evident, greenish, upper margins hyaline, apices acute to obtuse, usually erose; paleas 3.8–4.5 mm long, membranous, keels scabridulous, apices obtuse to truncate; stamens 3, anthers 2–2.4 mm long, purplish to yellowish. **Caryopses** 1.6–2 mm long, ellipsoid, with a fused pericarp, dorsally flattened, with a shallow adaxial groove, striate, reddish-brown. $2n = 40$ (Reeder 1977).

Included taxon—*Kalinia obtusiflora* (E. Fourn.) H.L. Bell & Columbus [syn. *Brizopyrum obtusiflorum* E. Fourn., Mexic. Pl. 2: 120. 1886; *Eragrostis obtusiflora* (E. Fourn.) Scribn.].

Habitat—It grows in dry or wet alkali flats and playas, often in association with *Distichlis* and *Sarcobatus*; 900–1400 m.

Distribution—*Kalinia obtusiflora* is native to the USA in southeastern Arizona and southwestern New México and occurs in the following Mexican states: Chihuahua (municipios Ascensión and Saucillo), Coahuila, Distrito Federal, Guanajuato, Jalisco, México (municipios Ecatepec de Morelos, Montecillo, Texcoco, and Tezoyuca), Michoacán (Municipio Cuitzeo), Nuevo León, Oaxaca, Sonora (municipios Bacoachi and Cananea), and Veracruz (Espejo Serna et al. 2000; Peterson 2003; Dávila et al. 2006; Valdés Reyna 2015).

Comments—The type species was first described by Fournier (1886) in *Brizopyrum* Link along with other species that are now included in *Distichlis* (= *D. spicata* subsp. *stricta* Thorne), *Jouvea*, and *Uniola* (*U. pittieri* Hack.). Ogden (1897) performed an anatomical survey of four grasses, *Kalinia obtusiflora*, *Jouvea pilosa*, *J. straminea*, and *Distichlis spicata* (L.) Greene, all inhabitants of saline environments in southwestern North America. Ogden had originally thought that *Kalinia obtusiflora* was conspecific with *Jouvea*. While all three of these species appear to be C₄ NAD-ME grasses, there are few unique anatomical features among each of these species (Peterson et al. 2005). *Kalinia obtusiflora* has a crown of colorless cells above each vein that is absent from the other three genera. Even though Fournier (1886) and later Ogden (1896) noticed affinities of *Kalinia* with *Distichlis*, *Jouvea*, and *Uniola*, all American agrostologists have followed Lamson-Scribner's (1897) placement of this species in *Eragrostis* until Bell et al. (2013) erected *Kalinia* for it. *Kalinia* appears to differ from other species of *Eragrostis* in having leaf blades with papillae located in the intercostal zones on the abaxial surface, stomata on the lemma surface, and the lack of interruption of the bundle sheath with sclerenchyma (known in *E. pergracilis* S.T. Blake) [Bell et al. 2013]. Bell et al. (2013) also found that *Kalinia* differs from *Distichlis* in having a bundle sheath extensions of colorless cells (absent in *Distichlis*) and wide metaxylem cells (narrow in *Distichlis*). *Distichlis* and *Kalinia* do share sunken bicellular microhairs on the surface of the leaf blades (Bell et al. 2013).

Sohnsiinae P.M. Peterson, Romasch. & Y. Herrera, **subtribe nov.**

TYPE: *Sohnsia* Airy Shaw, Kew Bull. 18(2): 272. 1965.

Diocious, caespitose perennials with short rhizomes forming tough clumps. **Culms** 30–100 cm tall, pubescent below the nodes. **Leaf** sheaths sometimes auriculate, hairy at summit margins; ligules 0.7–1.1 mm long, a line of hairs; blades flat becoming involute upon drying, antrorsely scabrous. **Panicles** 7–21 cm long with 6–18 branches alternately inserted along the main axis, main axis pubescent; disarticulation above the glumes. **Spikelets** 5–12 mm long, 3–5-flowered, laterally compressed; rachilla prolonged above upper floret; callus pilose; glumes 2.8–7 mm long, the lower

usually shorter than the upper, 1-veined, the apex often mucronate; lemmas 5–7 mm long, 3-veined, the veins extending as mucros (mostly staminate plants) or into subulate awns (mostly pistillate plants), the awns 1–4 mm long, pilose on margins and each side of the midvein, apex cleft; palea as long as lemma or slightly shorter, with a narrow membranous wing on each keel (staminate plants); lodicules 2, membranous; stamens 3, anthers 2–3 mm long (staminate plants), reddish-purple; ovary glabrous, styles 2, free to base. **Caryopsis** with a fused pericarp. $2n = 24$ (Reeder, 1967).

Included taxon—*Sohnsia filifolia* (E. Fourn.) Airy Shaw (1965) [syn. *Calamochloa filifolia* E. Fourn. (1877), nom. illeg. hom. for *Calamochloë* Rchb. (1828); *Eufornia filifolia* (E. Fourn.) Reeder (1967)].

Habitat—Calcareous, rocky slopes usually on north- or east-facing slopes associated with thorn-scrub vegetation with *Muhlenbergia*, *Bouteloua*, *Erioneuron*, *Aristida*, *Eragrostis*, *Quercus*, *Rhus*, *Croton*, *Mimosa*, *Dalea*, *Salvia*, *Tagetes*, *Agave*, *Yucca*, *Stevia*, and *Allium*; 1100–2100 m.

Distribution—Known only from the two Mexican states: Querétaro (municipios Arroyo Seco, Cadereyta de Montes, Ezequiel Montes, Peñamiller, and Toliman) and San Luis Potosí (Municipio Guadalcázar).

Comments—Fournier (1877) originally described the genus *Calamochloa* as containing a single species, *C. filifolia*. Airy Shaw (1965) transferred the species to a new genus, *Sohnsia*, because it is confusingly similar, differing by only a single letter to *Calamochloë*, an earlier homonym (Article 53.3, ex. 14 of the International Code of Botanical Nomenclature; McNeill et al. 2006). The 3-awned nature of the lemma in *Sohnsia* is also found in the Boutelouinae, Scleropogoninae, and the Triraphideae (Peterson et al. 1997, 2016). Hitchcock (1913) did not include *Sohnsia* in his Mexican grasses simply because no material was available at this time to study in the US National Herbarium. Although, Hubbard (1934) and Sohns (1956) had aligned *Sohnsia* with the tribe Pappophoreae, now subtribe Pappophorinae in the Cynodonteae (Peterson et al. 2016). Reeder (1967) found meiotic irregularities, such as formation of 10 bivalents and four univalents at diakinesis and suggested a basic chromosome number of 10, a common number for the tribe. *Sohnsia filifolia* was collected by PMP west of Guadalcázar in 1991 [*Peterson & Annable 11129* (US)], 2010 [*Peterson, Saarela & Romaschenko 23359* (US)], and 2012 [*Peterson & Romaschenko 24675* (US)]. In 2012, only sterile specimens were found, suggesting that it does not flower every year. This may contribute to the paucity of collections for this Mexican endemic.

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