NOTES ON VARIATION AND GEOGRAPHY IN RAYJACKSONIA PHYLLOCEPHALA (ASTERACEAE: ASTEREAE)

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ABSTRACT

Inflorescences of *Rayjacksonia phyllocephala* in the disjunct Florida population system are characterized by heads on peduncles with leaves mostly reduced to linear bracts; heads in inflorescences of the Mexico-Texas-Louisiana system are immediately subtended by relatively unreduced leaves. The difference is consistent and justifies recognition of the Florida system as *R. phyllocephala* var. *megacephala* (Nash) D.B. Ward. Scattered waifs between the two systems are identified here as one or the other variety, directly implying their area of origin. In the eastern range of var. *phyllocephala*, at least from Brazoria County, Texas, eastward about 300 miles to central Louisiana, leaf margins vary from entire to deeply toothed-spinulose. In contrast, margins are invariably toothed-spinulose in var. *megacephala* as well as in the rest of southeastern Texas (from Brazoria County southwest) into Tamaulipas, Mexico. In some of the populations with variable leaf margins, 70-95% of the individuals have entire to mostly entire margins.

KEY WORDS: *Rayjacksonia*, morphological variation, leaf margins, disjunction, waifs

Rayjacksonia phyllocephala (DC.) Hartman & Lane (Gulf Coast camphor-daisy) is an abundant and conspicuous species of the shore vegetation around the Gulf of Mexico. In the present paper, we record observations on its distribution and morphology not made in previous pertinent literature (e.g., Correll & Johnston 1970; Kawaguchi 1996; Lane & Hartman 1996; Nesom 2006).

Rayjacksonia phyllocephala is distributed nearly continuously from northern Tamaulipas northward along the coastal strand through Texas into central Louisiana (Fig. 10). Except for an apparent waif in Mississippi and one historical collection from panhandle Florida, the species apparently then is absent eastward until it reappears along the coast Gulf Coast of central peninsular Florida, from Levy County to Big Pine Key and Middle Torch Key of Monroe County.

Characteristic habitat of *Rayjacksonia phyllocephala* in Texas and Louisiana is along the back shore to primary dunes (Fig. 1). At least in some of these localities, it is by far the most abundant species in such habitats and plants of *R. phyllocephala* at many sites often are densely arranged, with only a few millimeters separating their bases. Individuals can be single-stemmed or produce a number of decumbent-ascending branches from the base. The species also occurs infrequently on spoil banks, marsh edges, salt flats, and in other sandy sites along canal banks.

In Florida, in contrast, characteristic habitat of *Rayjacksonia phyllocephala* is in palmetto and palmetto-scrub oak communities, slash pine-thrinax woodland, and old fields and roadsides. It also occurs in woods-marsh ecotone, hammock and marsh edges, canal banks, and salt flats and barrens.



Figure 1. Population of *Rayjacksonia phyllocephala* var. *phyllocephala* at Holly Beach, Louisiana. The population (plants of lower stature) is from arrow to arrow and grows similarly westward along the beach nearly continuously, along the Texas coast eventually to northeastern Mexico. Photo by David Rosen, 6 July 2013.



Figure 2. *Rayjacksonia phyllocephala* var. *phyllocephala* at Galveston Island State Park, Texas. The taproot is characteristic of the species and genus. Photo by David Rosen, 1 July 2013.

Plants of *Rayjacksonia phyllocephala* are annual, developing a deep taproot (Fig. 2) and flowering more or less continuously from May or June until December and then sporadically for the rest of the year. Germination also may occur sporadically through the season, judging from the wide range of sizes in both immature and flowering individuals.

Recognition of the Floridian var. megacephala

The Florida plants have been formally named as *Eriocarpum tracyi* Gand. and *Eriocarpum megacephalum* Nash — recently treated by Ward (2012) as *Rayjacksonia phyllocephala* var. *megacephala* (Nash) D.B. Ward. Only a single species without formal variants was recognized by Kawaguchi (1996), Lane and Hartman (1996), and Nesom (2006). Ward's revivification simply referred to the plants as the "larger-headed Florida native." The original description of the Floridian *Eriocarpum megacephalum* by Nash did not contrast it with any other — he did not mention or even allude to plants west of the Mississippi. Apparently the only published contrast between the two geographic systems has been by Small (1903), whose taxonomic treatment of *Sideranthus* included both as separate species. The following contrast is drawn from Small's descriptions.

1. Stems 8–12 dm tall; involucres ca. 10 mm long, outer bracts linear-lanceolate to linear

Sideranthus megacephalus

Sitems 1–4 dm tall; involucres 6–9 mm, outer bracts more or less foliaceous

Sideranthus phyllocephalus

In the current study, we are unable to confirm distinctions in plant height or involucral size, but the difference in "outer bracts" referred to by Small is more evident, if by outer bracts he was referring to the peduncular bracts immediately subtending the head. Figures 5 and 6 show characteristic arrays of variation in inflorescence morphology of the two population systems — heads in Florida are on peduncles with leaves mostly reduced to linear bracts, while heads of the Mexico-Texas-Louisiana system are immediately subtended by relatively unreduced leaves. The two systems also differ in ecology. In view of these apparently consistent differences and the geographic disjunction between the two population systems, formal recognition of the Florida plants is justified, and they are maintained here at varietal rank within a single species. It is plausible that gene flow occurs between the two systems through long-distance dispersal (comments below on waifs).

RAYJACKSONIA PHYLLOCEPHALA (DC.) Hartman & Lane, Amer. J. Bot. 83: 369. 1996. Haplopappus phyllocephalus DC., Prodr. 5: 347. 1836. Aplopappus rubiginosus var. phyllocephalus (DC.) A. Gray, Syn. Fl. N. Amer. 1(2): 130. 1884. Aster phyllocephalus (DC.) Kuntze, Revis. Gen. P1. 1: 316. 1891. Eriocarpum phyllocephalum (DC.) Greene, Erythea 3: 15. 1895. Eriocarpum rubiginosum var. phyllocephalum (DC.) A. Heller, Contr. Herb. Franklin Marshall Coll. 1: 101. 1895. Sideranthus phyllocephalus (DC.) Small, Fl. S.E. U.S. 1185. 1903. Machaeranthera phyllocephala (DC.) Shinners, Field & Lab. 18: 40. 1950. Type: MEXICO: Tamaulipas. Between San Fernando and Matamoros, 1832, J.L. Berlandier 2278 (holotype: G-DC photo: TEX!; isotypes: G, GH, K, NY digital image! and Fig. 3).

a. RAYJACKSONIA PHYLLOCEPHALA var. PHYLLOCEPHALA

Aplopappus rubiginosus Torr. & Gray, Fl. N. Amer. 2: 240. 1842. Eriocarpum rubiginosum (Torr. & Gray) Britt., Mem. Torrey Bot. Club 5: 316. 1894. Sideranthus rubiginosus (Torr. & Gray) Britt. in Rydb., Bull. Torrey Bot. Club 27: 621. 1900. Aplopappus phyllocephalus DC. var. rubiginosus (Torr. & Gray) Blake, Contr. Gray Herb. 52: 22. 1917. Type: USA. Texas. [Austin Co.]: San Felipe de Austin, 1835, T. Drummond 110 (holotype: GH digital image! via JSTOR; isotypes: GH, K).

Eriocarpum glaucum Gand., Bull. Soc. Bot. France 65: 41. 1918. **Type: USA. Texas.** [Galveston Co.]: Galveston Island, 22 Sep 1901, *S.M. Tracy* 7365 (holotype: LY; isotypes: F digital image!, G, GH, US).

Eriocarpum floridanum Gand., Bull. Soc. Bot. France 65: 41. 1918. **TYPE**: **USA**. **Florida**. [Escambia Co.]: Pensacola, 29 Oct 1903, *S.M. Tracy* 8515 (holotype: LY; isotypes: F digital image!, GH digital image! via JSTOR, ND-G, SMU!, US).



Figure 3. *Haplopappus phyllocephalus*, Tamaulipas, Mexico, NY isotype. One plant of two on the sheet.

b. RAYJACKSONIA PHYLLOCEPHALA var. MEGACEPHALA (Nash) D.B. Ward, Phytologia 94: 467. 2012. Eriocarpum megacephalum Nash, Bull. Torrey Bot. Club 23: 107. 1896. Haplopappus megacephalus (Nash) Hitchc., Trans. Kansas Acad. Sci. 16: 131. 1899. Sideranthus megacephalus (Nash) Small, Fl. S.E. U.S., 1185. 1903. Haplopappus phyllocephalus var. megacephalus (Nash) Hitchc., Publ. Carnegie Inst. Wash. 389: 59. 1928. Machaeranthera phyllocephalus var. megacephalus (Nash) Shinners, Field & Lab. 18: 40. 1950. Haplopappus phyllocephalus var. megacephalus (Nash) Waterfall, Rhodora 62: 321. 1960. LECTOTYPE (Ward 2012, p. 467): USA. Florida. Manatee Co.: Sneed's Island, near the mouth of the Manatee River, 21-23 Aug 1895, G.V. Nash 2432 (US digital image!; isolectotypes: F digital image!, K, MICH digital image! and Fig. 4, MO digital image!, ND-G, NY digital image!, P, PH digital image!). Lane and Hartman (1996) cited the NY specimen as "holotype" but Nash did not specify a herbarium; Ward (2012) designated the US specimen as 'lectotype" without comment. Citations of duplicates not seen are fide Lane and Hartman.

Eriocarpum tracyi Gand., Bull. Soc. Bot. France 65: 41. 1918. **TYPE**: **USA**. **Florida**. Manatee Co.: Palmetto, Sneed's Island, 9 Sep 1899, *S.M. Tracy* 6354 (holotype: LY; isotypes: GH, US digital image!).



Figure 4. *Eriocarpum megacephalum*, Manatee Co., Florida, MICH isotype. The US holotype and F, MO, NY, and PH isotypes have relatively immature inflorescences with unelongated peduncles appearing more leafy.

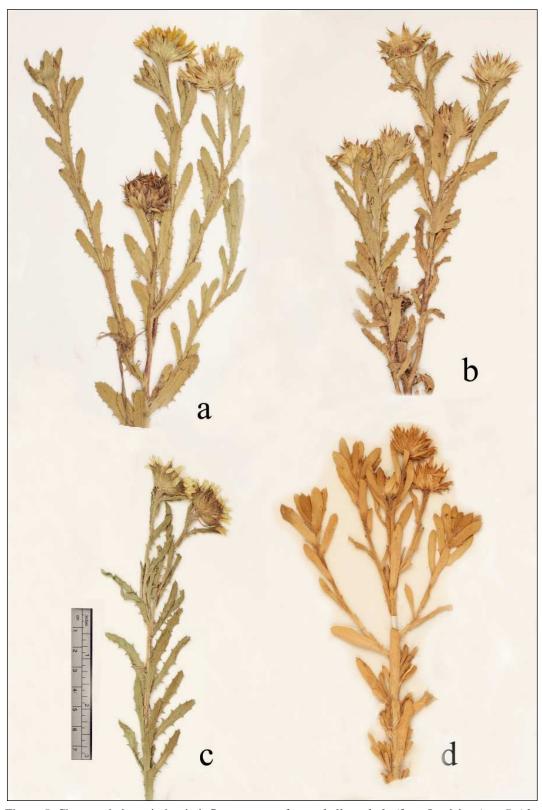


Figure 5. Characteristic variation in inflorescences of var. *phyllocephala* (from Louisiana): a. *Reid* 5182, Cameron Par. (LSU); b. *Powers* 80, Cameron Par. (LSU); c. *Ferguson* 211, Cameron Par. (LSU); d. *Correll* 9618, Cameron Par. (LSU).

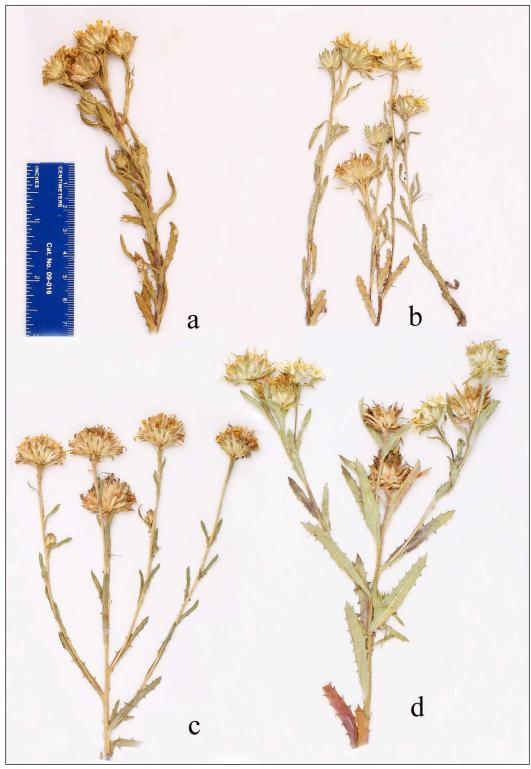


Figure 6. Characteristic variation in inflorescences of var. *megacephala* (from Florida): a. *Todd 174*, Hillsborough Co. (USF); b. *King 76*, Hillsborough Co. (USF); c. *Bradley & Woodmansee 1320*, Monroe Co. (USF); d. *Semple 11713*, Pasco Co. (USF).



Figure 7. Probable waif of var. megacephala from Terrebone Par., Louisiana.



Figure 8. Probable waif of var. phyllocephala from Escambia Co., Fla. Eriocarpum floridanum isotype, SMU.



Figure 9. Probable waif of var. phyllocephala from Jackson Co., Mississippi.

Several collections appear to represent populations geographically juxtaposed between var. phyllocephala and var. megacephala (Fig. 10), but these are isolated and likely were made from plants established as waifs, perhaps from hurricane winds. Among these is the type of *Eriocarpum* floridanum Gand., from the vicinity of Pensacola in Florida's westernmost county, but in contrast to the peninsular Florida plants, those from Pensacola have leafy-congested peduncles (Fig. 8) more like plants of var. phyllocephala (entire-margined). Those in Jackson Co., Miss., are typical var. phyllocephala (Fig. 9). Peduncles of the Terrebonne Parish, La., plants have linear bracts on elongate, linear-bracteate peduncles (Fig. 7) and are identified here as var. megacephala.

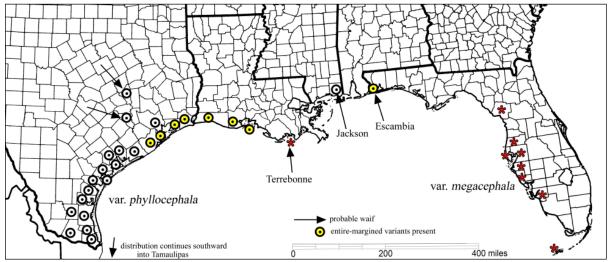


Figure 10. Geographic distribution by county of Rayjacksonia phyllocephala, showing the two varieties, occurrence of probable waifs, and known area of variants with entire to subentire leaf margins discussed in text.

Collections mapped as probable waifs. Texas. Austin Co.: Hwy 36, 8 mi NW of Sealy, sand, 19 Mar 1971, Cary 48 (TAMU); San Felipe de Austin, 1835, T. Drummond 110 (the type of Aplopapus rubiginosus). Brazos Co.: 2 mi S of College Station, sand, 30 Mar 1970, Gavlsk 16 (TAMU). Louisiana. Terrebonne Par.: Timbalier Island, dune/swale area, after severe overwash from Hurricane Andrew, 7 Nov 1992, Buras 398 (LSU digital image!, Fig. 7). Brown 19951 (LSU) from "Rockefeller Refuge" in extreme eastern Cameron Par. is similar to Buras 398 and also might be a waif. Mississippi. Jackson Co.: Pascagoula, vicinity of Bayou Casottem beyond city animal shelter at S end of Louise St, 0.4 mi S of Washington Ave., heavily disturbed fill area, clay soil with oyster shell fragments, locally abundant, 16 Oct 1994, MacDonald & Bryson 7972 (MISS digital image!); Greenwood Island, W of Pte. aux Chenes, sandy open area, 7 Nov 1990, Schiefer s.n. (MISS-2 sheets digital images!). Florida. Escambia Co.: Pensacola, 29 Oct 1903, S.M. Tracy 8515 (the type of Eriocarpum floridanum, Fig. 8).

Leaf variation in var. phyllocephala

Populations in the eastern range of var. phyllocephala produce a high percentage of individuals with entire to nearly entire margins — these are known roughly from Brazoria County eastward to central Louisiana (Fig. 10); field observations might extend the known range of these variants southward. Such plants have an notably different aspect compared to those typical for the species. Figure 11 shows a plant with elliptic-obovate leaves and almost complete entire margins; Figure 12 shows an area of young plants in which most of the plants have entire margins.

Characteristic leaf variation in populations at Galveston Island (Galveston Co., Texas), Holly Beach (Cameron Par., Louisiana), and Sabine Pass (Jefferson Co., Texas) is documented in Figures 13, 14, and 15, respectively. Each leaf represents a single plant.

At Galveston Island State Park, a measure of the variability was obtained by counting individuals in six randomly selected 1-meter-square quadrats. 91% of the population produces entire to subentire leaf margins (Table 1; Fig. 13). We counted flowering and non-flowering plants but included only individuals greater than 5 mm high. In any case, margin morphology appears to be expressed even in the youngest plants and leaf morphology on a single plant is relatively constant. Most of the other populations we studied and inspected, including Holly Beach (Fig. 14), also had large proportions of entire to subentire-margined (scored as "entire") plants. The Sabine Pass population (Fig. 15) was distinctive in having a higher proportion of toothed-margined individuals.

Table 1. Entire-margined vs. toothed-margined individuals of Rayjacksonia phyllocephala var. phyllocephala in meter-square quadrats at Galveston Island State Park.

	TOTAL	ENTIRE	TOOTHED	% Entire
Quadrat 1	174	165	9	95
Quadrat 2	117	113	4	97
Quadrat 3	50	47	3	94
Quadrat 4	48	40	8	83
Quadrat 5	22	18	4	82
Quadrat 6	143	130	13	91
Quadrat 7	31	21	10	68
Total	585	534	51	Avg. 91%



Figure 11. Mostly entire-margined plant of var. phyllocephala at Galveston Island State Park, Texas. Photo by David Rosen, 1 May 2013.

Leaves in subtribe Machaeranthinae (Astereae) generally are characterized by spinulosemargins (Nesom 1994). Nesom (2006) described leaf margins of Rayjacksonia as "coarsely serrate (teeth bristle-tipped), rarely entire," noting that the genus is "coherent in vestiture, spinulose leaf teeth, heads borne singly, and rays with prominent, yellow laminae." Correll & Johnston (1970, under Machaeranthera phyllocephala) described the leaves R. phyllocephala as "usually oblanceolate to narrowly obovate, firm or even fleshy, 15-50 mm long, on each side with 5-8 prominent salient teeth or short lobes." Type specimens for R. phyllocephala (e.g., Figs. 3, 4, 8) and all of its synonyms (as cited above) have regularly and deeply spinulose-toothed leaf margins. Lane and Hartman (1996 did not provide descriptions or comments on individual species.



Figure 12. Area of young plants of var. phyllocephala at Holly Beach, Louisiana. Almost all are entiremargined. Photo by David Rosen, 1 July 2013.

Vouchers for populational leaf variation shown Figs. 13, 14, and 15. Louisiana. Cameron Par.: Near the town of Holly Beach, on and S of Hwy 82, ca. 400 m W of its intersection with Hwy 27, abundant multi-branched annual with decumbent stems on beach backshore and dunes with Panicum antidotale, Panicum repens, Sesuvium portulacastrum, Spartina patens, Eustoma sp., Distichlis spicata, and Heliotropium curassavicum, 12 Jul 2013, Rosen 6098 with Nesom (TEX, others to be distributed). Texas. Galveston Co.: Galveston Island State Park, near SE boundary of the park, ca. 0.5 km E of the visitor's center, abundant annual of beach backshore (but beyond the swash zone) to the berm in front of the dunes, 29°11'44.97" N, 94°56'58.03" W, with Cakile geniculata, Sesuvium portulacastrum, Heterotheca subaxillaris, Croton punctatus, and Distichlis spicata, 9 May 2013, Rosen 6030 with Lawrence (MO, TEX, VSC). Jefferson Co.: On and S of Hwy 87, ca. 20 km W of Sabine Pass, just W of the entrance to Sea Rim State Park, abundant multi-branched annual with decumbent stems on beach backshore and dunes with Panicum antidotale, Sesuvium portulacastrum, Spartina patens, Distichlis spicata, and Heliotropium curassavicum, 12 Jul 2013, Rosen 6099 with Nesom (TEX, others to be distributed). Vouchers for Brazoria Co. populations with entire to subentire leaf margins are these: Brazoria Co.: Near village of Surfside, S of Bluewater Hwy, ca 4.5 km NE of intersection with Hwy 332, abundant on beach backshore and dunes with Sesuvium portulacastrum, Tidestromia lanuginosa, Salicornia bigelovii, Distichlis spicata, Amaranthus greggii, 27 Jul 2013, Rosen 6104 and 6105 with Lawrence (TEX).

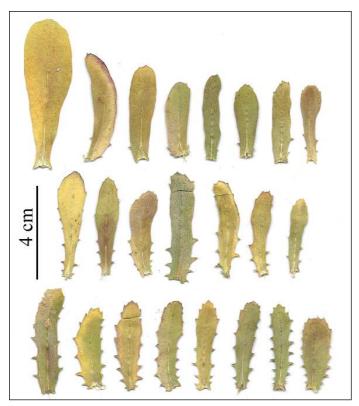


Figure 13. Characteristic leaf variation in var. phyllocephala from a population at Galveston Island State Park, Texas. Leaves like those in the top two rows were scored in Table 1 measurements as "entire."

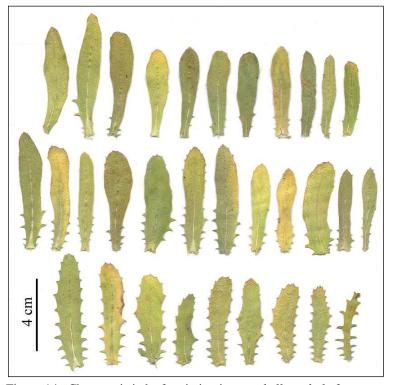


Figure 14. Characteristic leaf variation in var. phyllocephala from a population at Holly Beach, Louisiana.

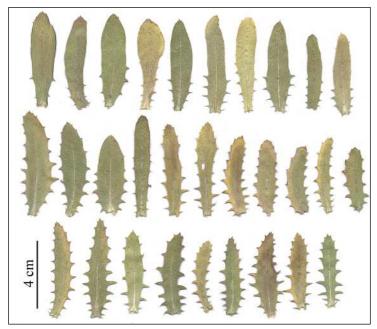


Figure 15. Characteristic leaf variation in var. phyllocephala from a population at Sabine Pass, Texas.

Remarkably, a recently opened website (Bowling 2012) shows variability in leaf margins of Rayjacksonia phyllocephala that parallels and precedes our own observations. Also, some collections at LSU (e.g. Brown 5883, Urbatsch 5955), which have plants of both leaf margin extremes, suggest that the collectors were aware of the variation.

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