

**RECOGNITION OF *ERIOGONUM HARPERI* (POLYGONACEAE)  
BASED ON MOLECULAR BARCODING,  
ACHENE MORPHOLOGY, AND LIFE HISTORY**

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**ABSTRACT**

Data on the morphology, distribution, life history, and molecular barcoding using nuclear ribosomal ITS (nrITS) of the *Eriogonum longifolium* group supports recognizing *E. harperi* and *E. floridanum* as distinct species. Conservation implications are discussed, and photographs of floral and seed morphological characters for each of the three species are provided.

*Eriogonum* Michx. (Polygonaceae) is a genus of ca. 250 species most diverse in western North America. Only a few species occur in eastern North America. *Eriogonum* in eastern North America include the shale barren endemic *E. allenii* S. Wats., the Coastal Plain *E. tomentosum* Michx., and *E. longifolium* Nutt. Current circumscription of *E. longifolium* recognizes a broadly delimited species with morphologically distinctive and geographically isolated subtaxa (Reveal 1968, 1971, 1981, 2005) that are widely distributed through the south-central USA and scattered eastward.

Reveal (1981) reported difficulty in delineating the subspecies of *Eriogonum longifolium* and considered the variation on a north to south and west to east cline over which the morphology was correlated, but continuous. Despite his conclusions, the morphology of the three taxa are dissimilar to one another and they are allopatric in distribution. "In extreme individuals within the primary range of *E. longifolium*, in both the sandhill and limestone barren habitats, there are occasional overlaps in the ranges of certain salient features of the more eastern two subspecies, which has probably contributed to such a broad species concept." Possible infraspecific variation within *E. longifolium* sensu stricto is not discussed here and the total distribution of *E. longifolium* var. *longifolium* is wholly west of the Mississippi River, from southwest Missouri south to Louisiana and west to New Mexico. The varieties of *E. longifolium* occur only east of the Mississippi River — *E. longifolium* var. *harperi* (Goodman) Reveal in xeric habitats over limestone in Tennessee and Alabama (extirpated in Kentucky), and *E. longifolium* var. *gnaphalifolium* Gand. in the sandhills of Florida.

Circumscription of *Eriogonum longifolium* and recognition of its varieties varies among numerous treatments. In Alabama and Tennessee *E. harperi* Goodman is treated at specific rank (Keener et al. 2017; TFC 2015), and Weakley et al. (2022) also has treated *E. harperi* and *E. floridanum* Small at specific rank. In the USDA Plants Database (USDA 2022), The Plantlist (2022), NatureServe (2022), and FNA (Reveal 2005), both are treated at varietal rank as *E. longifolium* var. *harperi* (Goodman) Reveal and *E. longifolium* var. *gnaphalifolium* Gand. In BONAP (Kartesz 2015) both varieties are apparently treated as synonyms of *E. longifolium*. In Reveal (2005), where they are treated as subspecies, and Weakley (2015), where each is recognized at specific status, the individual taxa are well-differentiated in morphology and they are also allopatric. My familiarity with *E. longifolium* and *E. harperi* in cultivation led to an investigation into the status of the latter taxon and circumstantially to that of *E. floridanum*.

## Methods

Plants of *Eriogonum harperi* in situ in Tennessee and *E. longifolium* in Arkansas, Missouri, and Texas were studied to observe habitat and growth differences during 2009–2010. Specimen examinations at APSC, MO, and TENN and digital images of specimens on SERNEC (2017) and the Alabama Plant Atlas (Keener et al. 2017) were made to observe differentiating characters of the taxa and to obtain habitat data. Samples at TENN were photographed to show the morphology of the perianth and achenes (Fig. 1). Living collections of *E. harperi* from Tennessee were cultivated at the University of Tennessee and in the author's garden from 2005–2017 to observe the life history; samples of *E. longifolium* from Arkansas and Texas were cultivated from 2009–2013 by the author. Molecular barcoding of the nuclear ribosomal ITS was performed for one sample each of *E. harperi* and *E. floridanum* and compared to a sample of *E. longifolium* in Genbank. The primers ITS4 and ITS-Leu were used for amplification following protocols in Schilling et al. (2007). Maximum Likelihood analyses of ITS and pairwise comparisons were done for *Eriogonum* using additional samples from Genbank.

Table 1. Data from specimens at APSC, MO, and TENN, SERNEC, (*E. harperi* (n=20), *E. floridanum* (n=18), and *E. longifolium* (n= 99) [including holotypes and isotypes at MO]), from living accessions, and data in Reveal (2005). Few measurements outside Reveal's data were noted. All measurements are in millimeters.

Taxon	<i>E. harperi</i>	<i>E. floridanum</i>	<i>E. longifolium</i>
Life Cycle	monocarpic, 3–5 years	perennial	perennial
Foliage	gradually reduced	abruptly reduced	abruptly reduced
Leaf indument			
adaxial	glabrate	glabrate	pubescent
abaxial	tomentose	tomentose	tomentose
Inflorescence			
shape	broadly paniculate	paniculate	paniculate
indument	tomentose	densely tomentose	densely tomentose
involucres	3–3.5	6–7	4–6
involucre lobes	< 0.5, rounded	ca. 1 mm, narrowly deltoid, acute	0.5, deltoid obtuse
perianth	5–7	8–15	5–11
stipe	0.5–1 (-1.2)	2–4 (-7)	(0.5-) 1–2.5 (-4.5)
tepals			
shape	obovate	lanceolate	elliptic
apex	acute	acuminate-acute	obtuse
Anthers	subequal to tepals	< half tepal length	> half tepal length
Achene	exserted	included	included
vestiture	short pubescent, appressed	long pubescent, throughout	long pubescent, distal half
shape	obovate, 3-winged apically	pyriform, not winged	pyriform, not winged
length	4–4.5	5–6	4–6

Table 2. Samples newly sequenced and from Genbank for nr ITS barcoding of *Eriogonum longifolium* and its varieties *E. floridanum harperi* and *E. harperi*.

DNA 4800 *Eriogonum floridanum* Small, OQ091944, Abbot 22683

DNA 4781 *Eriogonum harperi* Goodman, OQ091945, Floden s.n., White Co., Tennessee.

*Eriogonum longifolium*, JQ352543

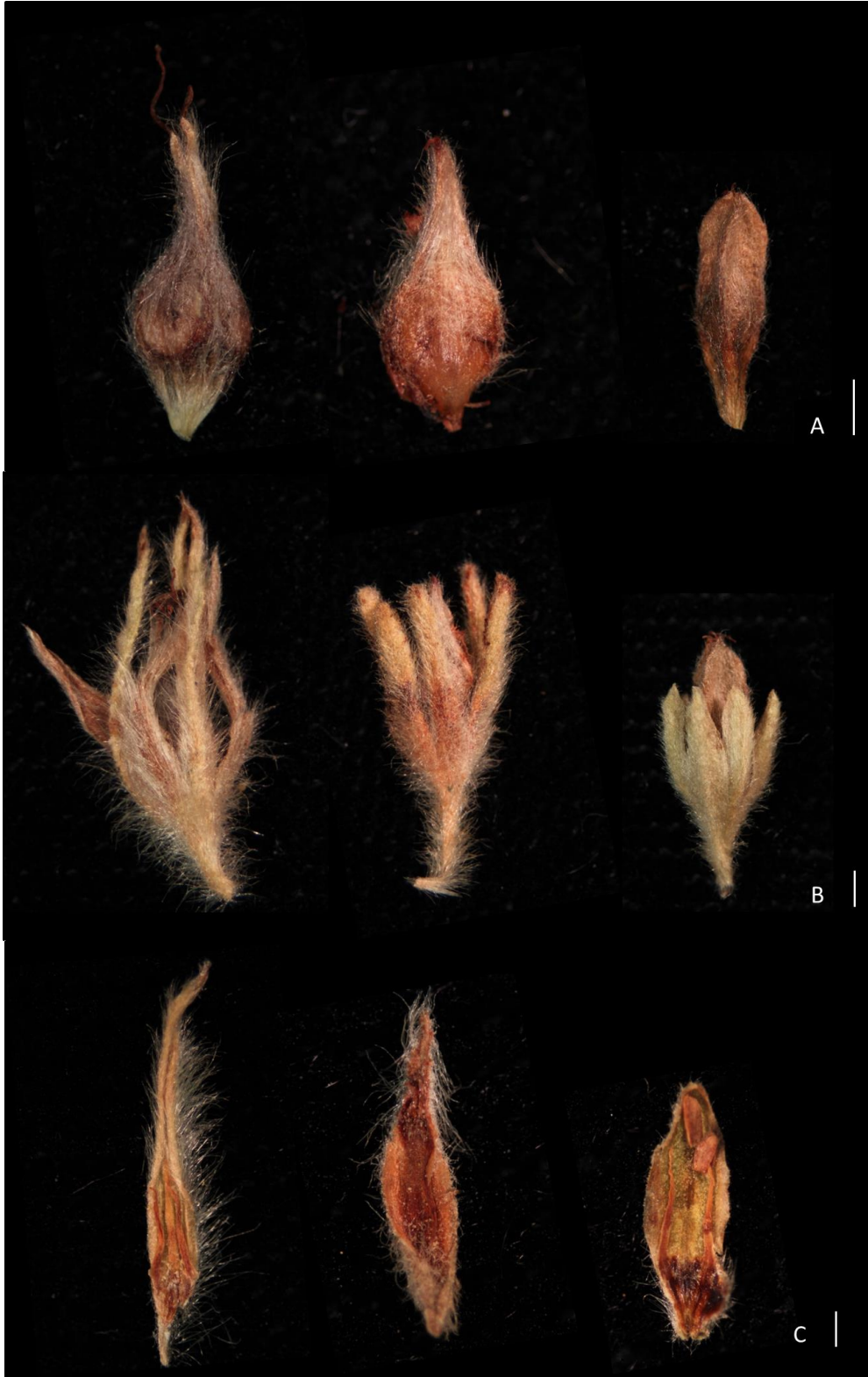


Figure 1. Representative samples of (A) achenes, (B) perianths, and (C) tepals of *Eriogonum* species. Left to right: *Eriogonum floridanum* (Slaughter 13934), *E. longifolium* (Thomas 55936), and *E. harperi* (D.H. Webb 6781). Scale bars = 1 mm.

## Results

Morphological comparison showed that the perianth (its overall length, tepal shape, size, and indument, and stipe), the shape and size of the achenes (Fig. 1, Table 1), and the habit of the plant regarding the abundance and size of the cauline leaves differed between species. *Eriogonum harperi* in fruit has achenes with three wings at the apex. Cultivation of *E. harperi* and *E. longifolium* revealed distinct differences in life cycle — the former grew as a rosette of basal leaves for 2–3 years in cultivation before it then flowered and died, thus monocarpic, whereas *E. longifolium* flowered every year from a perennial long-lived taproot. Observations in the field showed this pattern of behavior also, where flowering plants of *E. harperi* were not observed the following season.

New nrITS sequences for *Eriogonum floridanum* and *E. harperi* are reported here (Table 2). Results of the maximum likelihood analyses recovered these in a clade with *E. nealleyi* J.M. Coulter sister to these eastern species with *E. longifolium* sister to *E. harperi* + *E. floridanum* (71 BS, Fig. 2). Pairwise comparisons of the ITS sequence data revealed five bp difference of *E. harperi* compared to *E. longifolium*, and a 12 bp difference from *E. floridanum*, whereas *E. floridanum* differed by 13 bp from *E. longifolium*. Four of the different positions in *E. floridanum* were heterozygous.

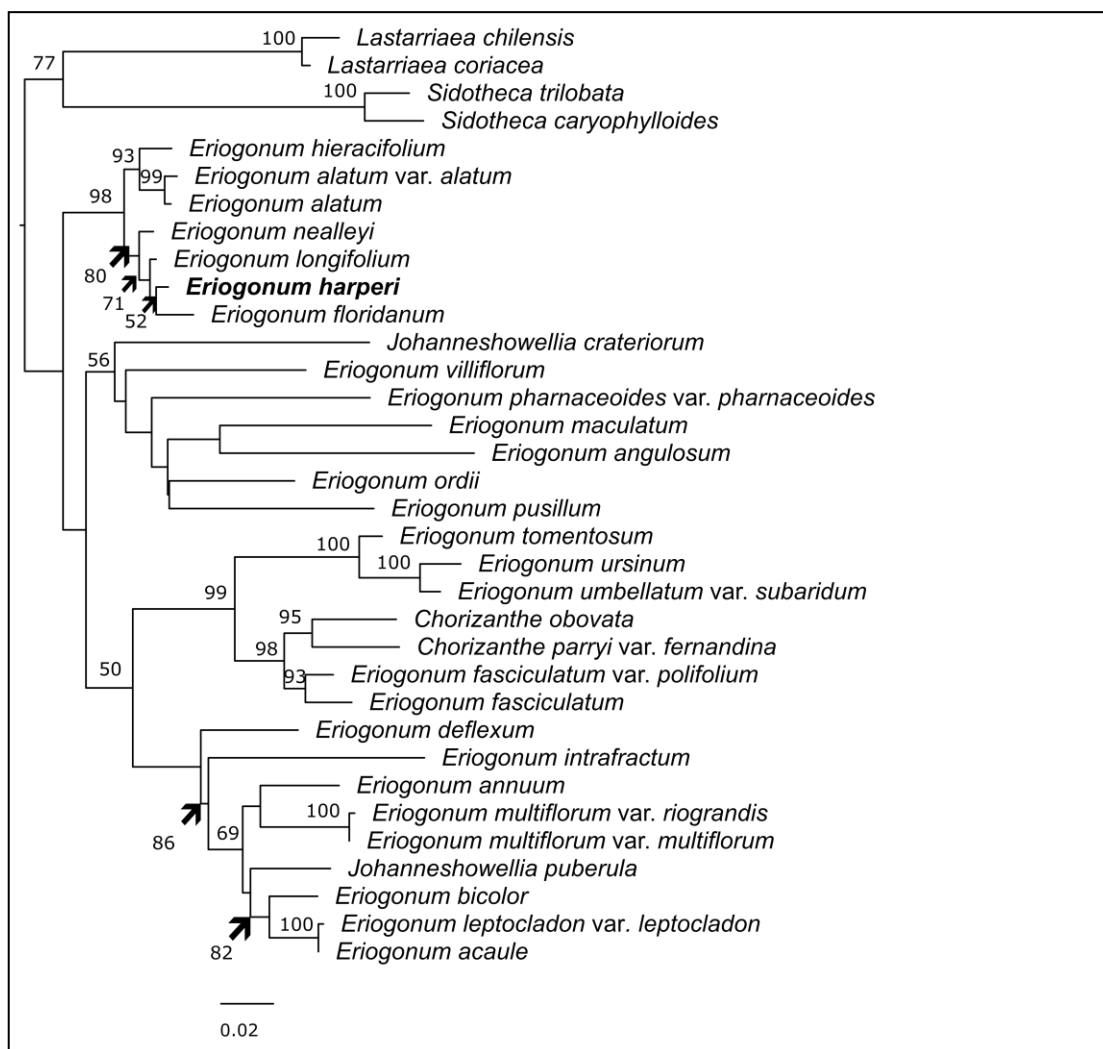


Figure 2. Phylogram of nuclear ribosomal ITS sequences produced using RaxML showing Maximum Likelihood bootstrap supports from 1000 replications showing the sister relationships *Eriogonum longifolium*, *E. harperi* and *E. floridanum*.

## Discussion

*Eriogonum harperi* is not only morphologically distinct from *E. longifolium* but also differs in its life cycle and allopatric and narrow distribution. *Eriogonum floridanum* is distinct in its morphology and disjunct from populations of *E. longifolium*. Both *E. harperi* and *E. floridanum* occur in different physiographic provinces but similarly xeric habitats: *E. floridanum* in the Florida sandhill scrub (Christman 1988; Wunderlin 1982), *E. harperi* in limestone barrens and cliffs in Tennessee and Alabama in Cedar Glades, where numerous endemic plant species occur (Baskin & Baskin 2003). Recognizing these as distinct species follows the state floras (TNFC 2015; Wunderlin 1982) and regional floristic treatments of these taxa (Weakley et al. 2022).

The life cycle of *Eriogonum harperi*, to which little attention has been paid since Goodman (1941), is important in recognizing this entity as separate from *E. longifolium*. Goodman (1947) mentioned briefly in his description of *Eriogonum harperi* that Harper was not certain, but "...believes the plant flowers but once," but Reveal (2005) stated that *E. longifolium* and its varieties are polycarpic. Life history observations of *E. harperi* and *E. longifolium* in a common garden and observations of both taxa *in situ* have shown that *E. harperi* behaves as a monocarpic, or short lived perennial, reaching flowering size in two to three years in cultivation, or three to five in habitat, flowering, and then perishing. Three generations of *E. harperi* grown from seed from a Tennessee population have flowered in cultivation in two gardens — my own private garden and in the University of Tennessee Biology gardens. All plants that have flowered have died after flowering, unless the flowering stem was cut while in flower. None of these plants have made offsets from the caudex. Seed production is abundant and germination of these seeds is plentiful in cultivation though observations in the field suggest long-term recruitment is low in habitat. In the garden copious germination below the parent and ensuing overcrowding leads to the majority of seedlings perishing within the first two seasons if these are not manually spaced out. This behavior is unlikely in the wild where I have observed plants due to the slope of the habitat where the species occurs. *Eriogonum longifolium* has flowered consecutively for three years from its Western Gulf Coastal Plain Sandhill and limestone Ozark glade ecotypes (see Reveal 1981) and seed production and germination has been limited, with the few seeds that are produced have proven recalcitrant to germination when left to disperse near the parent plant, i.e. no seedlings have been produced in the garden. No asexual propagation in individuals of *E. harperi* has been noted during five years observation. In contrast, the plants of *E. longifolium* have produced multiple growth points at the terminus of a tap root though these do not seem to be able to be removed for propagation, but in habitat over longer durations these might separate to form clonal individuals.

Reveal (2005) provided a key to the varietal taxa of *Eriogonum longifolium* noted that the morphological discontinuities with limited overlap between the typical variety and *E. harperi* as well as that of *E. floridanum* (Table 1). Goodman (1947) noted the presence of a more foliose stem with cauline leaves not abruptly reduced, glabrous to glabrate adaxially, and shorter, less densely distributed trichomes of the calyces — these characters are confirmed here. The leaves of *E. harperi* are only gradually reduced up the stem, giving the plant a more leafy appearance. *Eriogonum floridanum* and *E. longifolium* tend to have a basal rosette of leaves with cauline leaves abruptly reduced and only bract-like leaves within the inflorescence.

Recent phylogenetic analyses by Kempton (2012) have placed *Eriogonum longifolium* as a member of subg. *Pterogonum* and not in subg. *Eriogonum*, which mostly have 3-winged or ridged achenes. Reveal (2005) included it in subg. *Eriogonum*. Contrary to its phylogenetic placement, subg. *Pterogonum*, *E. longifolium* *sensu stricto* does not have winged achenes or seeds (Kempton 2012). Examination of achenes from specimens at MO and TENN shows that *E. floridanum* and *E. longifolium* have unwinged or unridged achenes. In contrast, *E. harperi* has achenes and seeds that are 3-winged or 3-ridged apically rather than merely angled (Goodman 1947) (Figure 1).

Reveal (2005) provided a key to the subspecific taxa considered here at specific rank. *Eriogonum floridanum* differs from *E. longifolium* in its larger flowers as well as longer involucre (Reveal 1981). Nonetheless, its morphology and life history are more similar to *E. longifolium* than either of those species are to *E. harperi*. On the basis of disjunct distribution of *Eriogonum harperi*, its distinct life history, and distinct morphology, the taxonomy followed by Weakley et al. (2022), TFC (2015), and Keener et al. (2017) supports recognition of *E. harperi* at specific rank. Likewise, *E. floridanum* should be treated at specific rank based on distribution, molecular differences, and discrete morphology.

The results of these initial barcoding studies using the proposed ITS barcode show distinct differences between the taxa that support recognition at specific rather than subspecific rank. *Eriogonum harperi* differs from *E. longifolium* by five bp and from *E. floridanum* by 12 in ITS pairwise comparisons. These differences are equal to or greater than some other well established Western North American *Eriogonum* species but similar to the seven bp difference for *E. nealleyi*, which is sister to these three species. The analyses places all three taxa in subg. *Pterogonum*, but only *E. harperi* has distinct ridges or wings in the distal half of the achenes. In the maximum likelihood analyses these three species form a clade with *E. longifolium* as the earliest lineage, followed by a sister pair of *E. harperi* and *E. floridanum* (Fig. 2, 71 bs).

Reveal (1981) considered the variation in *Eriogonum longifolium* to be continuous, with a small degree of difference in the involucre and perianth sizes and inflorescence shapes and he argued for varietal rank of the three species considered here. There also are differences in the involucre shape of *E. floridanum* vs. *E. longifolium*, anther size relative to the tepals, the achene shape and size between these species, the inflorescence branching structure, and the rhizome orientation (Table 1). The involucre is distinctly lobed in *E. floridanum*, with sinuses 1+ mm deep and the lobes deltoid-triangular with acute apices in comparison to the 0.5 mm sinuses and broadly deltoid rounded lobes in *E. longifolium* and with rounded short lobes in *E. harperi*. Anthers are subequal to the tepal length in *E. harperi*, less than half the tepal length (typically 1/3<sup>rd</sup>) in *E. floridanum*, and nearly subequal in *E. longifolium*. The achene shapes have been noted, but their lengths relative to the tepals is distinctly different in *E. harperi*, where the achene surpasses the tepals when mature; the achene is included in *E. floridanum* and *E. longifolium*. The inflorescence branching structure of *E. floridanum* is corymb-like in that its branches originate in close proximity to one another on the stem, whereas *E. longifolium* is branched unevenly and *E. harperi* is densely branched on the upper 1/2 to 1/3 of the stem. Last, the rhizome differs between these species — the rhizome of *E. harperi* is vertical and unbranched vs. horizontal and branching in *E. floridanum* and *E. longifolium*. In contrast to earlier observations on the stipe length, I found that many stipes in *E. longifolium* are nearly equal in length to those of *E. floridanum*.

Recent field examination in 2017 and 2018 of *Eriogonum harperi* in Tennessee did not reveal any flowering plants at two known locations, and only one site, from which the original living collection originated, revealed only a few immature plants in a road bank now dominated by *Sorghum halapense*. In previous years flowering individuals had been observed every year at this locality, with higher seedling recruitment than what was observed in 2017 and 2018.

The intermittent flowering of *Eriogonum harperi*, its monocarpic life history, and observed low seedling recruitment in situ may drastically affect population sizes, which might lead to rapid population losses of an already rare species — ranked as S1 in Tennessee and Alabama (NatureServe). In contrast *E. longifolium* is ranked G4T2 (NatureServe); in Florida *E. floridanum* is state-endangered (as *E. longifolium* var. *gnaphalifolium*; Wunderlin et al. 2018).

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