

Article



https://doi.org/10.11646/phytotaxa.733.1.1

Two new combinations in *Plagiobothrys* (Boraginaceae subtribe Amsinckiinae)

C. MATT GUILLIAMS^{1,3*} & RONALD B. KELLEY^{2,4}

- ¹Department of Conservation and Research, Santa Barbara Botanic Garden, Santa Barbara, California 93105, United States
- ²Department of Chemistry and Biochemistry, Eastern Oregon University, La Grande, Oregon 97850, United States
- ³ mguilliams@sbbotanicgarden.org; https://orcid.org/0000-0003-3919-8432
- *Correspondence author

Abstract

The genus *Allocarya* (Boraginaceae subtribe Amsinckiinae) was proposed by E.L. Greene in 1887 to unite 18 annual herbaceous taxa from North America and South America. Taxonomists greatly expanded the genus through the 1920s, although the more conservative taxonomic approach advocated by I.M. Johnston coupled with his transfer of *Allocarya* to the genus *Plagiobothrys* resulted in the relegation of many early *Allocarya* names to synonymy. While preparing the taxonomic treatment of genus *Plagiobothrys* for the Flora of North America project, we studied specimens that corresponded to two presently unrecognized *Allocarya* taxa, which on the basis of morphology and geographic distribution we find to be worthy of recognition. We briefly describe these two taxa and make the new combinations for them in *Plagiobothrys*.

Key words: Allocarya divaricata, Allocarya minuta, Amsinckiinae, Boraginaceae, endemic, Flora of North America, FNANM, new combination, rare, synonymy

Introduction

The genus *Allocarya* (Boraginaceae subtribe Amsinckiinae; Chacón *et al.* 2016; Guilliams 2015, Hasenstab-Lehman & Simpson 2012, Simpson *et al.* 2017) was proposed by E.L. Greene in 1887 and at that time comprised 18 minimum-rank taxa from North America and three from South America (Greene 1887a). Nine of these taxa were newly described by Greene in this paper, while the others were new combinations for taxa formerly in the genera *Echinospermum* Sw. ex Lehm., *Eritrichium* Schrad., *Krynitzkia* Fisch. & C.A. Mey., *Lithospermum* L., and *Myosotis* L. According to Greene, taxa in *Allocarya* were distinctive in having opposite, connate-perfoliate lower leaves and an expanded, turbinate pedicel proximal to the calyx that becomes indurated with age. Greene also noted that plants in *Allocarya* are ecologically similar, growing in "low moist ground". Greene continued to describe new taxa and make new combinations in *Allocarya* until 1901 (Greene 1887b, 1888, 1892, 1895a,b,c, 1896, 1901), eventually recognizing a total of 37 in the genus.

In the late 1800s and the first two decades of the 1900s, contemporaries of E.L. Greene were also at work describing new taxa and making new combinations in *Allocarya*. T.S. Brandegee and Nelson each described a new *Allocarya* in 1899 (Brandegee 1899, Nelson 1899). A new species and two new combinations were made by Jepson in the Flora of Middle California in 1901 (Jepson 1901), and Howell published a new species in the same year (Howell 1901). Piper published his first name in the genus, *Allocarya jucunda*, in 1902 (Piper 1902). Working in South America where another center of *Allocarya* diversity lies, Reiche (1907) treated nine species and 10 minimum-rank taxa for Chile. Of these, eight were new combinations. Finally, in the 1910s, J.F. MacBride began working on *Allocarya*, independently publishing four new combinations in 1916 and one new species name in 1919 (MacBride 1916, 1919). Nelson and MacBride also partnered on two new combinations (Nelson & MacBride 1916).

Two important and contrasting taxonomic treatments of *Allocarya* taxa were published in the 1920s. The first of these treatments of *Allocarya* was published in 1920 by Piper, who recognized 79 species and 80 minimum-rank taxa in the United States and Canada (Piper 1920). Forty-nine of the taxa treated by Piper were described as new. Piper briefly mentions *Allocarya* taxa that occur in Mexico, South America, and Australia, but does not formally treat them. I.M. Johnston, a contemporary of Piper and himself likely the most prolific student of the Boraginaceae, transferred the

genus to *Plagiobothrys* Fisch. & C.A. Mey. as section *Allocarya* due to "a lack of consistently diagnostic characters" (Johnston 1923). Johnston expressed concern with the great multiplication of lower taxa in Piper's *Allocarya* treatment, choosing at that time to recognize only 33 minimum-rank taxa in the section. Johnston would later (1932) recognize a greater number of species (31) and minimum-rank taxa (41) in his treatment of sect. *Allocarya* in the Western United States. Johnston's treatment of *Allocarya* as a section of *Plagiobothrys* would be followed by many later authors (e.g., Hitchcock *et al.* 1959, Cronquist 1984, Munz 1959, Messick 1993, Horn 2000, Guilliams 2015, Kelley & Guilliams 2021, but see e.g., MacBride 1927, Brand 1931, and Abrams 1951). The widespread adoption of Johnston's more conservative taxonomic approach left many of Piper's names in synonymy.

While preparing the taxonomic treatment of genus *Plagiobothrys* for the Flora of North America project (Flora of North America Editorial Committee 1993+), we encountered specimens that correspond to two of Piper's presently unrecognized *Allocarya* taxa: *A. divaricata* Piper and *A. minuta* Piper. On the basis of morphology and geographic distribution, we find them to be worthy of recognition under the morphological species concept (Cronquist 1978). We briefly describe these two taxa in the paragraphs that follow, then conclude with the new combinations.

Species Background

Allocarya divaricata was described in 1920 on the basis of a plant collected by William Palmer from the seashore in Victoria, British Columbia. It is distinctive relative to other congeners in the region in a combination of morphological features. It is branched from the base, with branches stout and widely spreading. Inflorescences are bracted at least proximally. Calyces are somewhat accrescent; corollas are small and scarcely exceed the calyx. The nutlets of this taxon are perhaps the most distinctive feature (Figure 1), being ovoid, grayish brown, and glossy. The adaxial (ventral) surface is strongly keeled, and the keel is not positioned within a groove or trough. The attachment scar is relatively small and located on the adaxial surface, near the base of the nutlet.



FIGURE 1A–C. Nutlets of *Plagiobothrys divaricatus* (Piper) Guilliams & R.B. Kelley. **A.** abaxial (dorsal) view; **B.** adaxial (ventral) view; **C.** lateral (side) view.

Piper (1920) treated *A. divaricata* in his Nitentes Group, which was intended to encompass *Allocarya* taxa with bracteate inflorescences, small corollas, and ovoid, glossy nutlets that lack an adaxial groove or trough. Johnston (1923) included *A. divaricata* as a synonym of *Plagiobothrys scopulorum* (Greene) I.M. Johnst., which he describes as "...the most common and widely distributed *Allocarya*." He also states that "a careful study [of *P. scopulorum*] will probably cause the recognition of a number of forms here submerged." Indeed, after additional study of this difficult group, Johnston later (1932) chose to recognize a number of taxa that he treated as synonyms of *P. scopulorum* in 1923, e.g., *P. bracteatus* (Howell) I.M. Johnst., *P. cusickii* (Greene) I.M. Johnst., *P. reticulatus* (Piper) I.M. Johnst., and *P. tener* (Greene) I.M. Johnst. Johnston (1932) did not elect to recognize *A. divaricata*, however, treating it as a synonym

of *Plagiobothrys medius* (Piper) I.M. Johnst. Although not explicitly discussed by Johnston, it is assumed that he believed that the names *A. divaricata* and *A. media* pertained to the same plant of the Pacific Northwest coast, and that *A. media* was the correct name for this plant based on its earlier occurrence on page 107 of Piper's 1920 treatment. In contrast, we find *A. divaricata* to be distinctive in its combination of morphological characters and separable from other *Plagiobothrys* sect. *Allocarya* taxa of the region. We suspect that plants conforming to Piper's description of *A. media* with ascending to erect stems and wide corolla limbs (4–5+ mm) might be better placed in *Plagiobothrys scouleri* (Hook. & Arn.) I.M. Johnst., pending further study.

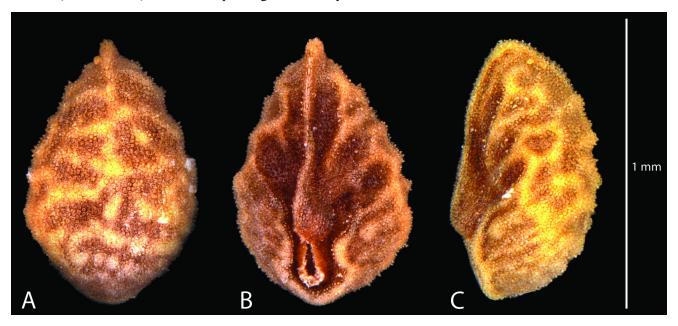


FIGURE 2A–C. Nutlets of *Plagiobothrys minutus* (Piper) Guilliams & R.B. Kelley. **A.** abaxial (dorsal) view; **B.** adaxial (ventral) view; **C.** lateral (side) view.

Allocarya minuta, also described in 1920, was based on a J.P. Tracy collection (no. 4469) from Fort Seward in Humboldt County, California. It is distinctive in having erect stems, slender inflorescence axes, a very small, non-accrescent calyx, a relatively large corolla limb (3+ mm wide), and perhaps the smallest nutlets of any section Allocarya taxon (0.6–0.8 mm long; Figure 2). This plant is only known from three collections by J.P. Tracy at the type locality, Fort Seward (nos. 4469, 13844, 13860). Ecologically, collection labels describe this plant as being "abundant in wet places" and as occurring in "wet places in level field". The last known collections of this remarkable plant were made in 1935.

Piper included A. minuta in his Sulcatae Group, which united taxa with an adaxial keel and attachment scar sunken in a groove or trough. Presently recognized members of Piper's Sulcate Group that also occur in northwestern California include P. lithocaryus (Greene) I.M. Johnst., P. reticulatus, P. strictus (Greene) I.M. Johnst., and P. undulatus (Piper) I.M. Johnst. Allocarya minuta can be easily distinguished from each of these plants on the basis of a suite of vegetative, floral, and nutlet characters. Johnston (1923) treated A. minuta as a synonym of P. scopulorum, a taxon previously described as overly broad. With further study, Johnston later (1932) treated A. minuta as a synonym of P. reticulatus, a taxon that differs in corolla limb width, nutlet size, and nutlet sculpturing. However, A. minuta also bears a resemblance to Plagiobothrys tener, a taxon with slender, erect stems, wide corolla limbs, and similarly sculptured nutlets. At least one specimen (G93596) from Tracy's first gathering (no. 4469) bears a 1915 annotation label from K. Brandegee with the determination of Allocarya tenera Greene. In returning to study this specimen in 1934, Tracy affixed a handwritten note stating that "Mrs. Brandegee's determination as A. tenera appeals to me as a closer alliance than P. reticulatus." We recognize this plant as morphologically distinct from each of the taxa listed above, but abstain from suggesting close relatives pending the results of ongoing molecular phylogenomic studies (Guilliams et al. unpublished data).



FIGURE 3. Holotype of *Plagiobothrys divaricatus* (Piper) Guilliams & R.B. Kelley (US529836).



FIGURE 4. Holotype of *Plagiobothrys minutus* (Piper) Guilliams & R.B. Kelley (UC180174).

New Combinations

We make the new combinations for Allocarya divaricata and A. minuta in the genus Plagiobothrys here:

Plagiobothrys divaricatus (Piper) Guilliams & R.B. Kelley, comb. nov.

Basionym: *Allocarya divaricata* Piper, Contributions from the United States National Herbarium 22(2): 107. 1920. **Type: CANADA. British Columbia.** Victoria: collected on exposed rocks on the seashore, June 6, 1905. *W. Palmer, s.n.*, (holotype: US digital image!; Figure 3).

Plagiobothrys minutus (Piper) Guilliams & R.B. Kelley, comb. nov.

Basionym: *Allocarya minuta* Piper, Contributions from the United States National Herbarium 22(2): 104. 1920. *Allocarya californica* var. *minuta* (Piper) Jeps. & Hoover, A Flora of California 3(2): 363. 1943. **Type: UNITED STATES. California.** Humboldt Co.: abundant in wet places, May 14, 1914. J.P. Tracy, 4469 (holotype: UC!; Figure 4).

Acknowledgements

We thank the following herbaria for providing specimens on loan for study at Santa Barbara Botanic Garden (SBBG): ASU, CAS, CONC, NDG, OBI, OSU, RBC, RM, RSA/POM, UBC, UC/JEPS, UCR, UTC, and WTU. We further thank the curators of UC and US for providing high-resolution images of the holotype specimens used herein. We appreciate José Flores of Santa Barbara Botanic Garden for his early assistance with nutlet imaging. Finally, we are grateful to the Phytotaxa subject editor Dr. Farzaneh Khajoei Nasab and two anonymous reviewers for their contributions during the review of the manuscript.

References

Abrams, L. (1951) Allocarya. Illustrated Flora of the Pacific States, Volume III. Stanford University Press, Stanford, California.

Brand, A. (1931) Borraginaceae—Borraginoideae—Cryptantheae. *In*: Engler, A. (Ed.) *Das Pflanzenreich 97*. Leipzig: Verlag von Wilhelm Engelmann.

Brandegee, T.S. (1899) New species of western plants. *Botanical Gazette* 27 (6): 444–457. https://doi.org/10.1086/327855

Chacón, J., Luebert, F., Hilger, H.H., Ovchinnikova, S., Selvi, F., Checchi, L., Guilliams, C.M., Hasenstab-Lehman, K., Sutory, K., Simpson, M.G. & Weigend, M. (2016) The borage family (Boraginaceae s.str.): a revised infrafamilial classification based on new phylogenetic evidence, with emphasis on the placement of some enigmatic genera. *Taxon* 65 (3): 523–546. https://doi.org/10.12705/653.6

Cronquist, A. (1978) Once again, what is a species? *In*: Knutson, L.V. (Ed.) *Biosystematics in Agriculture*. Allenheld Osmin; Montclair, New Jersey, U.S.A, pp. 3–20.

Cronquist, A., Holmgren, A.H., Holmgren, N.H., Reveal, J.L. & Holmgren, P.K. (1984) *Plagiobothrys*. Intermountain Flora, Volume 4. The New York Botanical Garden, Bronx, New York.

Flora of North America Editorial Committee, eds. (1993+) Flora of North America North of Mexico [Online]. 25+ vols. New York and Oxford. Available from: http://beta.floranorthamerica.org (accessed 18 September 2025)

Greene, E.L. (1887a) Some West American Asperifoliae. Pittonia 1 (1): 8-20.

Greene, E.L. (1887b) New or noteworthy species. Pittonia 1 (8): 139-143.

Greene, E.L. (1888) New or noteworthy species. II. Pittonia 1 (10): 139-176.

Greene, E.L. (1892) New or noteworthy species. XII. Pittonia 2 (11B): 222-233.

Greene, E.L. (1894) *Manual of the Botany of the Region of San Francisco Bay*. Cubery & Company, San Francisco, CA. https://doi.org/10.5962/bhl.title.57343

Greene, E.L. (1895a) Novitates occidentales.—XI. Erythea 3 (3): 44-49.

Greene, E.L. (1895b) Phytographic notes and amendments—I. Erythea 3 (4): 53-57.

Greene, E.L. (1895c) Novitates occidentales.—XVI. Erythea 3 (8): 123-126.

- Greene, E.L. (1896) New or noteworthy species. XVII. Pittonia 3 (15C): 91-116.
- Greene, E.L. (1901) New or noteworthy species. XXVIII. Pittonia 4 (24A): 233-241.
- Guilliams, C.M. (2015) Diversification, biogeography, and classification of Amsinckiinae (Boraginaceae), with an emphasis on the popcornflowers (Plagiobothrys). Doctoral Dissertation, Department of Integrative Biology, University of California, Berkeley.
- Hitchcock, C.L., Cronquist, A. & Ownbey, M. (1959) *Plagiobothrys. Vascular Plants of the Pacific Northwest*, Part 4. University of Washington Press, Seattle, Washington.
- Hasenstab-Lehman, K.E. & Simpson, M.G. (2012) Cat's eyes and popcorn flowers: phylogenetic systematics of the genus Cryptantha s.l. (Boraginaceae). *Systematic Botany* 37: 738–757.
 - https://doi.org/10.1600/036364412X648706
- Horn, N. (2000) Revision der Gattungen Plagiobothrys und Pectocarya in Chile und den angrenzenden gebieten. Doctoral Dissertation, Universität München.
- Howell, T.J. (1901) A Flora of Northwest America. Portland, Oregon.
- Jepson, W.L. (1901) *A Flora of Western Middle California*. Encina Publishing Company, Berkeley, California. https://doi.org/10.5962/bhl.title.79060
- Jepson, W.L. (1943) *Allocarya and Plagiobothrys. A Flora of California*, Volume 3, Part 2. University of California, Berkeley, California.
- Johnston, I.M. (1923) II. Studies in the Boraginaceae, 4. A synopsis and redefinition of *Plagiobothrys. Contributions from the Gray Herbarium of Harvard University* 68: 57–80.
 - https://doi.org/10.5962/p.336051
- Johnston, I.M. (1932) The *Allocarya* Section of *Plagiobothrys* in the Western United States. *Contributions from the Arnold Arboretum* 3: 1–82.
 - https://doi.org/10.5962/bhl.title.152926
- Kelley, R.B. & Guilliams, C.M. (2021) *Plagiobothrys. In:* Jepson Flora Project (eds.) *Jepson eFlora*, Revision 9. Available from: https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=38525 (accessed 19 September 2025)
- MacBride, J.F. (1916) III. Certain Borraginaceae, new or transferred. *Proceedings of the American Academy of Arts and Sciences* 51: 541–548.
 - https://doi.org/10.2307/20025598
- MacBride, J.F. (1919) II. Reclassified or new Spermatophytes, chiefly North American. *Contributions from the Gray Herbarium* 59: 28–39.
 - https://doi.org/10.5962/p.336033
- MacBride, J.F. (1927) 5. A defense of Allocarya. Field Museum of Natural History Publication 244 Botanical Series 4 (5): 119-122.
- Messick, T.C. (1993) *Plagiobothrys*. The Jepson Manual Higher Plants of California. University of California Press, Berkeley, California.
- Munz, P.A. (1959) Plagiobothrys. A California Flora. University of California Press, Berkeley, California.
- Nelson, A. (1899) New species in Oreocarya and its allies. Erythea 7 (7): 65-70.
- Nelson, A. & MacBride, J.F. (1916) Western plant studies. III. Botanical Gazette 61 (1): 35-47.
 - https://doi.org/10.1086/331878
- Piper, C.V. (1902) New and noteworthy Northwestern plants—VII. *Bulletin of the Torrey Botanical Club* 29 (11): 642–646. https://doi.org/10.2307/2478716
- Piper, C.V. (1920) A study of Allocarya. Contributions from the United States National Herbarium 22 (2): 79–113.
- Reiche, K.F. (1907) Estudios críticos sobre la flora de Chile (continuacion) Familia Borrajináceas. *Anales de la Universidad de Chile* 121: 803–835.
- Simpson, M.G., Guilliams, C.M., Hasenstab-Lehman, K.E., Mabry, M.E. & Ripma, L. (2017) Phylogeny of the popcorn flowers: use of genome skimming to evaluate monophyly and interrelationships in subtribe Amsinckiinae (Boraginaceae). *Taxon* 66 (6): 1406–1420.
 - https://doi.org/10.12705/666.8