A REVISION OF THE *ECHIDIOCARYA* SECTION OF *PLAGIOBOTHRYS* (BORAGINACEAE)

LARRY C. HIGGINS1

Abstract.— This revision discusses two closely related species of *Plagiobothrys* (Boraginaceae) found in the southwestern United States and central Chile. One of the two species, *P. collinus*, is composed of five varieties that range from southern California and western Arizona to central Chile in South America. The following new combinations are proposed: *P. collinus* var. californicus, *P. collinus* var. gracilis, *P. collinus* var. ursinus, and *P. collinus* var. fulvescens. Detailed keys, synonymy, and descriptions are given for each entity.

The section *Echidiocarya*, as here defined, includes those species of the genus that are annuals with opposite or alternate lower leaves and that have the nutlet scar elevated on the end of a conspicuous stipe. The section *Allocarya* (to be treated in a later paper) differs mainly in that the nutlets lack the cylindrical stipe and the leaves

are nearly always oppositely arranged.

The section Echidiocarya (Gray) Johnston is composed of two species and five varieties that are confined to the western half of the American continent, ranging from central California to central Arizona and southward to northern Sonora and northern Baja California, Mexico, with an outlying population in central Chile. The habitats of the various entities occur from sea level to steep mountain slopes and are characterized by scanty rainfall, warm temperatures, and high evaporation.

In 1857 R. A. Phillipi described the first species in the section when he published *Eritrichium collinum*. In 1908 K. Reiche transferred the species to *Cryptantha* in his treatment of the Boraginaceae published serially in the *Anales de la Universidad de Chile* and in 1910 as part of his *Flora de Chile*. In 1895 Phillipi described *E*.

inconspicuum, which falls into synonymy with E. collinum.

Asa Gray (1876) proposed the genus Echidiocarya for Echidiocarya arizonica (Plagiobothrys pringlei Greene). It was characterized by the long-stiped nutlets. Gray (1877) added E. californica and (1883) E. ursina to the genus. Gray (1885), commenting on the very close relationship of his genus to Plagiobothrys, said, "The comparatively recent discovery of the preceding species [P. ursina] of this section has made it clear that both of them should fall in Plagiobothrys." He then transferred E. californica and ursina to Plagiobothrys, leaving the original species by iteslf.

Greene (1887) disposed of *Echidiocarya*, stating that it had "every aspect and every character of *Plagiobothrys*, except that there is a stipe between the scar, or point of attachment to the gynobase,

and the body of the nutlet."

Johnston (1923) placed *Echidiocarya* as one of his sections under *Plagiobothrys*. He also described two additional varieties of *P. cali-*

¹Department of Biology and Killgore Research Center, West Texas State University, Canyon, Texas 79015.

fornicus. Since Johnston's treatment only Brand (1931) and Abrams

(1951) have accepted *Echidiocarya* as a distinct genus.

During my research—which led ultimately to a complete revision of *Plagiobothrys*—a realignment of the members of this section became apparent because the South American *P. collinus* is conspecific with *P. californicus* of the southwestern United States and Mexico. Johnston (1927) was aware of the close relationship even though he never made any nomenclatural changes. He said, "the relationship between the Californian and Chilean plants is very clear and strong, so incontrovertible in fact, that some changes in the classification of the North American forms will probably be made." Those changes are the primary basis of this paper.

Special thanks are extended to the curators of the following herbaria for their loan of material for this study: BRY, CAS, GH, ND, ND-G, NY, UC, US. I also wish to thank West Texas State University and the Killgore Research Center for their support both

physical and monetary.

TAXONOMY

Plagiobothrys Fisch. and Mey. Sect. Echidiocarya (Gray) Johnston, in Contr. Gray Herb. 68:65, 1923. Echidiocarya Gray, in Benth. and Hook. Genera Pl. 2:854, 1876; Proc. Amer. Acad. Arts 11:89, 1876. Species Holotypus: (E. arizonica) P. pringlei Greene.

Annual, usually diffusely branched, herb with the lowest leaves opposite or sometimes alternate; flowers in slender spikes, usually bracteate, calyx lobes linear-lanceolate, corolla white, the throad not crested; nutlets 4, incurved, conspicuously rugulose dorsally, conspicuously keeled ventrally; scar on a slightly to prominently elevated stipe.

- 2. Corolla 4-7 mm broad; pubescence fine, appressed, usually somewhat silky; California, Arizona, and northern Mexico 2A. var. californicus
- 3. Leaves narrowly linear, 2-2.5 mm broad ______4
- 4'. Pubescence coarse, nutlets sharply rugose; Chile. 2C. var. collinus

- 5'. Racemes elongate, projecting from among the leaves and evident; southern California and Baja California, Mexico

 2E. var. fulvescens
- 1. Plagiobothrys pringlei Greene

Echidiocarya arizonica Gray, in Benth. and Hook. Genera Pl. 2:854, 1876; Proc. Amer. Acad. Arts 11:89, 1876. Not P. arizonicus (Gray) Greene; Plagiobothrys pringlei Greene, in Pittonia 1:21, 1887. Mesa Verde, Arizona, Dr. Smart sn. Holotype GH!

Stems several to many branched from near the base, prostrate or decumbent to nearly erect, slender, 1-4 dm long, spreading setose; leaves numerous below, less so above, narrowly oblanceolate, 2-4 cm long, 2-5 mm broad, rounded or obtuse to nearly acute at apex, appressed strigose or canescent to conspicuously setose; floral bracts lanceolate to narrowly oblong, 1-2 cm long; spikes elongating in age, bractless near the apices; calyx segments lance-linear, about 3 mm long in fruit, hirsute; corolla 2-3 mm broad, inconspicuous; nutlets 4, the lowermost commonly joined in pairs, the upper separate, ovate, the apex acute, 1.8-2 mm long, dorsal keel evident above fading to rather distinct tuberculations below, dorsal surface rugulose with short ridges also conspicuously tuberculate; scar elevated on a prominent stipe at least 1.3 mm long and usually as long as the nutlet, ventral keel evident; style shorter than the stipe of nutlet.—Representative collections: J. J. Thornber sn. (cas, ny); F. R. Fosberg 10663 (cas, gh); V. L. Cory 3398 (gh); Pultz and Phillips 1572 (gh, ny); I. L. Wiggins 8689, 8190 (gh); L. C. Higgins 2822 (bry, wtsu).

Distribution

Common in Cochise, Maricopa, Pima, and Pinal counties of Arizona and in northern Sonora, Mexico. Growing on sandy desert flats and mesas.

The most remarkable characteristic of Pringle's *Plagiobothrys* is the long-stiped nutlets, unique among the borages. This species is very closely related to *P. collinus* var. *fulvescens*, which it resembles in most details, except that the former has stalked nutlets and slightly longer calyx segments.

2a. Plagiobothry's collinus var. californicus (Gray) Higgins

Plagiobothrys collinus (Ph.) Johnston var. californicus (Gray) Higgins comb. nov., based on Echidiocarya californica Gray. in Proc. Amer. Acad. Arts 12:164, 1877. Plagiobothrys californicus (Gray) Greene, in Bull. Calif. Acad. Sci. 2:407, 1887. Plagiobothrys cooperi Gray, in Proc. Amer. Acad. Arts 20:285, 1885. Allocaryastrum californicum (Gray) Brand, in Pflanzenr. 4352:100, 1931. Southeastern California in San Bernardino County. 1876, Parry and Lemmon 278. Holotype GH!

Leaves numerous below, oblanceolate, 1-3 cm long, 2-5 mm broad, rounded or obtuse at apex, thinly hirsute with ascending hairs or sometimes canescent with appressed pubescence; spikes slender, at maturity elongate and remotely flowered; calyx segments 3 mm long in fruit, linear-lanceolate, hirsute to hispid; corolla 4-6 mm

broad; nutlets about 1.5 mm long, scar with a short stipe near base. —Representative collections: J. T. Howell 3935 (GH, CAS); T. S. Brandegee 1637 (GH); L. Abrams 3276 (GH); I. M. Johnston 1839 (GH).

Distribution

San Benito County, California, southward to northern Baja Cali-

fornia, Mexico.

P. collinus var. californicus is most easily recognized by its large corollas, 4-7 mm broad and the more canescent pubescence; even at this, it intergrades with varieties gracilis and fulvescens.

2b. Plagiobothrys collinus var. gracilis (Johnston) Higgins

Plagiobothrys collinus (Ph.) Johnston var. gracilis (Johnston) Higgins comb. nov., based on Plagiobothrys californicus var. gracilis Johnston, in Contr. Gray Herb. 68:73, 1923. Allocaryastrum gracile Brand, in Pflanzenr. 4252:100, 1931. Echidiocarya californica subsp. gracilis (Brand) Abrams, in Ill. Fl. Pacific Stat. 3:571, 1951. San Diego, San Diego County, California, on the mesas. 10 April 1902. T. S. Brandegee 1658. Holotype GH!

Stems slender, with spreading hispid pubescence; leaves linear-lanceolate, sparsely pubescent, with spreading setose hairs, 2-2.5 mm broad, acute or acutish; calyx segments linear, ca 2 mm long, very slender, hirsute; corolla 1.5-2 mm broad; nutlets 1-1.5 mm long, inconspicuously rugulose.—Representative collections: F. R. Fosberg 7681 (CAS, GH); I. L. Wiggins 4462 (GH); F. F. Gander 4955 (GH); Raven & Mathias 12520 (GH).

Distribution.

San Diego County, California, southward to northern Baja California, Mexico, and on the islands of Santa Cruz, Santa Catalina, and San Clemente.

The variety gracilis is differentiated from the other varieties by the sparse spreading hirsute pubescence, narrower leaves, and smaller corollas. Its closest relatives are to be found in the varieties fulvescens and collinus. Intermediates are not uncommon with variety fulvescens and are very difficult to separate from true gracilis. 2c. Plagiobothrys collinus var. collinus

Eritrichium collinum Ph. Linnaea 29:17, 1857. Cryptantha collina Reiche, in Anales Univ. Chile 121:828, 1908; Fl. Chile 5:233, 1910. Plagiobothrys collinus (Ph.) Johnston, in Contr. Gray Herb. 78:81-82, 1927. Hills, Huanta, August 1836, Gay 1623. Holotype MS! Isotype fragment and photograph GH!

Eritrichium inconspicum Ph. Anales Univ. Chile 90:534, 1895.

Cryptantha inconspicua Reiche, in Anales Univ. Chile 121:820. 1908; Fl. Chile 5:225, 1910. Coquimbo: La Serena, October 1878. Philippi s.n. Holotype MS! Fragment and photograph GH!

Stems several, mostly erect, 3-15 cm long, hispidulous-villous; leaves linear to oblance-linear, obtusish, conspicuously hispidulous, 2-4 mm broad; calyx segments 1.5-2.5 mm long, fulvescent; corolla 1-1.5 mm broad, inconspicuous; nutlets 1.2-1.5 mm long, reticulately rugose with sharp ridges; style approximating nutlets.—Representative collections: C. O. Skottsberg 1371, 723 (NY, GH); G. Montero

1895 (GH); E. Barros 6316, 6361 (GH); Worth & Morrison 16340 (GH).

Distribution

Chile, in the providence of Coquimbo. Apparently restricted to the area around Coquimbo.

This variety is most closely related to the varieties gracilis and fulvescens. It differs from the former in being coarser and in having broader obtusish more densely pubescent leaves and sharper and more prominently rugulose nutlets. From fulvescens it differs in having narrower leaves that are not so harshly pubescent, a more erect habit, and more prominently rugulose nutlets.

2d. Plagiobothrys collinus var. ursinus (Gray) Higgins

Plagiobothrys collinus (Ph.) Johnston var. ursinus (Gray) Higgins comb. nov., based on Echidiocarya ursina Gray, in Proc. Amer. Acad. Arts 19:90, 1883.
 Plagiobothrys ursinus Gray, in Proc. Amer. Acad. Arts 20:285, 1885. Plagiobothrys californicus var. ursinus (Gray) Johnston, in Contr. Gray Herb. 68:74, 1923. Echidiocarya californica var. ursina (Gray) Jepson, in Fl. Calif. 3:370, 1943. California, San Bernardino Mountains, S. B. Parish 927. Lectotype GH!

Stems much branched, dense, compact, 2-8 cm long; spikes short; flowers concealed by the hispidulous leaves and bracts which are 1-2.5 cm long; corolla 1-2 nm broad; nutlets weakly rugulose.—Representative collections: S. B. Parish 3247 (NY); P. A. Munz 5725 (GH); Munz & Johnston 4550 (GH); C. R. Orcutt 908 (GH).

Distribution

California, in the San Bernardino and the San Jacinto Mountains, growing in sandy to gravelly soils.

The caespitose, compact habit of variety *ursinus* serves best to distinguish it from all the other varieties. It also grows at a higher, more montane elevation.

2e. Plagiobothry's collinus var. fulvescens (Johnston) Higgins

Plagiobothrys collinus (Ph.) Johnston var. fulvescens (Johnston) Higgins comb. nov., based on Plagiobothrys californicus var. fulvescens Johnston, in Contr. Gray Herb. 68:74, 1923. Allocaryastrum ursinum var. fulvescens (Johnston) Brand, in Pflanzenr. 4²⁵²:101, 1931. Echidiocarya californica subsp. fulvescens (Brand) Abrams, in Ill. Fl. Pacific Stat. 3:571-572, 1951. California, Santa Barbara, 1888, T. S. Brandegee s.n. Holotype GH!

Plagiobothry's micranthus A. Nels., in Amer. J. Bot. 25:115, 1938. Arizona, Prescott, moist creek banks, 28 April 1925. A. Nelson 10232, Holotype RM! Isotype GH!

Stems slender, elongate, prostrate, hispid-pubescent, leaves oblanceolate, obtusish to acutish, hispidulous 3-5 mm broad; spikes very slender at maturity, remotely flowered; corolla about 2 mm broad.—Representative collections: Eastwood and Howell 3914, 4156 (CAS, GH); F. R. Fosberg 10706 (CAS, GH); J. T. Howell 31075 (CAS); L. Abrams 3315 (NY); T. H. Kearney s.n. (CAS); C. B. Hardham 3049, 5602, 10048 (CAS).

Distribution

Santa Barbara County, California, southward to northern Baja California, Mexico, eastward to central Arizona. Also on the islands of Santa Rosa, Santa Catalina, and Anacapa.

Most closely related to the varieties collinus and gracilis as discussed under collinus. Variety fulvescens also introgresses considerably with varieties californicus and gracilis.

LITERATURE CITED

ABRAMS, L. 1951. Illustrated flora of the Pacific states. 3. Stanford Univ., Calif.: Stanford Univ. Press.

Bentham, G., and J. D. Hooker. 1876. Genera Plantarum. 1. London: Reeve

and Co.

BRAND, A. 1931. Borraginaceae-Borraginoideae-Cryptantheae. Pflanzenr. IV. 252:100-101.

Gray, A. 1876. Contributions in North American botany, IV. Miscellaneous botanical contributions. Proc. Amer. Acad. Arts 11:89. —. 1877. Contributions in North American botany, XIV. Characters of

some little-known or new genera of plants. Proc. Amer. Acad. Arts 12:163-

164. 1883. Contributions in North American botany, I. Characters of new Compositae, with revisions of certain genera and critical notes. Proc. Amer. Acad. Arts 19:90.

—. 1885. Contributions in North American botany. A revision of some

Boragineous genera. Proc. Amer. Acad. Arts 20:285.

Greene, E. L. 1887. Some west American Asperifoliae. Pittonia 1:9-21.

Johnston, I. 1923. Studies in the Boraginaceae, IV. A synopsis and redefinition of Plagiobothrys. Contr. Gray Herb. 68:57-80.

———. 1927. Studies in the Boraginaceae, VI. A revision of the South American Asperifoliae.

can Boraginoideae. Contr. Gray Herb. 78:81-82.

Nelson, A. 1938. Rocky Mountain herbarium studies. Amer. J. Bot. 25:115. Philippi, R. 1857. Linnaea 29:17.

————. 1895. Plantas nuevas Chilenas. Anales Univ. Chile 90:534-535.

REICHE, K. 1908. Estudios críticos sobre la flora de Chile. Anales Univ. Chile.

121:820-829. -. 1910. Flora de Chile. 5:225-233.