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TAXONOMIC REVISION OF ARCTOMECON TORR. & FREM.

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ABSTRACT

The genus Arctomecon Torr. & Frem. is reviewed, its three species, A. humilis Coville, A. californica Torr. & Frem., and A. merriamii Coville, are provided with a diagnostic key, described, and discussions of their peculiar habitat requirements and other pertinent information are included.

Key Words: Arctomecon, A. humilis, A. californica, A. merriamii, habitats, geography, Mohave Desert

INTRODUCTION

The genus Arctomecon Torr. & Frem. (Papaveraceae) is composed of three distinctive species: Arctomecon californica Torr. & Frem., A. humilis Coville, and A. merriamii Coville. All are gypsophilous species endemic to northern portions of the Mojave Desert regions of the southwestern United States, where their distributions are restricted to peculiar edaphic situations. Plants of all of the species are perennial herbs with long taproots, woody caudices, and tufts of basal leaves. Flowers are large and showy with petals white or yellow. All three species are considered to be rare, but only A. humilis is presently listed under stipulations of the Endangered Species Act of 1973 as amended (USFWS, 1979). Recent inventories of populations of A. californica and A. merriamii revealed losses in habitat, due primarily to development and urban expansion in the Las Vegas area, which has resulted in elimination of entire subpopulations. Need for pro-

tection of all species in the genus under the Endangered Species Act is indicated.

The generic name Arctomecon was regarded as neuter by Torrey, hence the name californicum. It is regarded here as feminine, following the example for Greek nouns with the "-on" termination cited in Stern's Botanical Latin (1983, p. 84), and the termination of the specific epithets agree with that gender. When included in quotes the original form, as treated by Torrey and others, is followed.

HISTORY

The type of the genus Arctomecon (Greek arktos, of bear; and mekon, a poppy, from the fancied resemblance of the hairy leaves with the lobes armed with a long trichome to a bear's foot), and its initial species californica (of Alta California, then a portion of Mexico), was collected by John Charles Fremont on his second expedition of exploration of the American West. On 3 May 1844 they reached the springs at "las Vegas [The Meadows]-a term which the Spaniards use to signify fertile or marshy plains, in contradistinction to *llanos*, which they apply to dry and sterile plains. Two narrow streams of clear water, four or five feet deep gush suddenly, with a quick current, from two singularly large springs; these and other waters of the basin, pass out in a gap to the eastward. The taste of the water is good, but rather too warm to be agreeable; the temperature being 71° in the one, and 73° in the other. They, however, afforded a delightful bathing place" (Fremont, 1845, p. 266). There he collected the plant that became the type specimen "on the banks of a creek." The water from the two springs coalesced into a stream - the only one in the vicinity (Welsh, 1993).

In 1874, Charles Christopher Parry collected, near St. George, Utah, a "showy Papaveraceous plant with nodding white flowers" (Parry, 1875). Parry identified this plant as *A. californica*, but recognized that it differed from Fremont's earlier, solitary collection, in its "less hairy leaves, four (not six) valved capsule and more caespitose habit." Parry forwarded a portion of his collection (he took plants in sets for later distribution through exchange or sale) to Dr. Asa Gray at Harvard University. Dr. Gray also identified the Parry materials as *A. californica* (Gray, 1877). Neither Parry nor Gray had noted that the Fremont materials were described as having yellow petals. Parry's materials were noted as distinctive by Coville (1892) who published them as belonging to a newly erected species, *A. humilis* Coville, but not until two years following the death of Parry (Welsh, 1988). In that same publication (Coville, 1892) a second species with white flowers, *A. merriamii* Coville, was proposed for the genus. It was based on specimens taken by Vernon Bailey west of Vegas Ranch in Lincoln County, Nevada in 1891 (Mozingo and Williams, 1980). Thus, the genus, as it is currently recognized, was fully constituted by 1892.

TAXONOMIC AFFILIATIONS

Arctomecon differs from other papaveraceous genera present in the Mojave Desert (Argemone, Platystemon) in general habit and gross morphologic features. Its species are the only members of the poppy family, in North America at least, recognized as gypsum restricted. The three species share ample characters to readily demonstrate their affinity, while the differences between the species are substantial enough to provide clear taxonomic units. All three species can be readily recognized by their foliage; the dense rosette of relatively long, broad, green leaves appears very "extravagant" in comparison to that of most plants of the warm desert regions. Affinities of the genus to others of the American southwest have not been resolved.

The species differ morphologically from each other on the basis of arrangement of flowers in the inflorescence, flower color, status of the petals following anthesis, number of locules per ovary, outline of apical margins of the leaf, amount and kind of foliar vestiture, and the overall stature of the plant. Distinct morphological differences, when taken with the geographic isolation of the species from each other, suggest that the separation of the taxa was not a recent event.

Raynie et al. (1990) report alkaloid content of the three Arctomecon species. Total number of alkaloids was greatest for A. humilis, with 14 unique alkaloids. Eight were detected in the tissues of A. californica and five in A. merriamii. Three alkaloids were found to be common to all species of the genus. Allocryptopine and protopine were major alkaloids in all species, while 12-methoxyallocryptopine (a new protopine-type alkaloid isolated during the study and presently known only from Arctomecon)

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was found in lesser quantities. It is uncertain what clues alkaloid composition can provide to understanding the evolutionary relationships between this genus and other Papaveraceae, and between the species in the genus. The larger numer of alkaloids in *A. humilis* may suggest that the species is ancestral to the others (Raynie et al., 1990). To date, the chemical and morphological criteria have not provided evidence of a close relationship of this genus to others in the family.

DISTRIBUTION

All species of Arctomecon are endemic to the northern margin of the Mojave Desert regions of the southwestern United States (Figure 1). The range of A. humilis is the most restricted of the three. It is presently known to be limited to an archipelago of less than a dozen sites, all within a few miles of St. George, Utah. Plants are strictly limited to gypsic outcrops of the Moenkopi Formation, primarily to the Shnabkaib Member, but occasionally extending downward to the Middle Red Member and upward to the Upper Red Member. The low, rolling terrain formed by these gypsum outcrops makes these areas popular for off-road vehicle use. All accessible sites are heavily impacted by off-road vehicular traffic which rapidly destroys cryptogamic soil crusts and compacts the substrate. It is noted that Kearney and Peebles (1960) cite A. humilis from northern Arizona, and an equivocal specimen cited from there is present at BRY, but probably it came from Utah. Recent investigations, including those by the authors, have not located this species in Arizona, although it has been found within one km of the Utah-Arizona boundary.

The ranges of A. californica and A. merriamii appear to overlap in the Las Vegas area, but the species do not occur together, probably due to differences in habitat requirements. In the Las Vegas area A. californica occurs on Quaternary Alluvium, often on ancient gypsic playa remnants. To the east, near Lake Mead, it is on other alluvium, but also on the Moenkopi Formation, and, in adjacent Arizona, it evidently occurs on gypsic limestones. In comparison, A. merriamii seems to prefer the gypsic limestones and gravels, and mainly occurs in numerous, small, disjunct subpopulations. Many habitats that appear to be habitable by the species of this genus do not support any of the plants. The reasons for the paucity of the plants are unknown. Several known sites



Figure 1. Habit sketch of Arctomecon humilis Coville.

of former habitation of both *A. californica* and *A. humilis* have been obliterated by construction, with pavement and structures now occupying the sites. It is believed that some other populations may have recently disappeared, especially in the Las Vegas area. The California bearclaw poppy occurred as recently as the mid

1980's in a vacant lot in a subdivision along Craig Road in Las Vegas, growing on an evidently saline playa remnant.

The range of *Arctomecon merriamii* extends from Death Valley on the west to the Spring Mountains of Nevada on the east. The species has been reported from approximately 20 sites within Death Valley National Monument, and from three or four mountain ranges in Nevada and near Ash Meadows, Nevada. One population is known from within the Las Vegas, Nevada, city limits. This population has been closely monitored by the authors and presently includes 15 individuals. The site is heavily impacted by construction on adjacent lots and its future is in doubt.

ECOLOGY

All three species of *Arctomecon* have been observed on heavily gypsic substrates. Since all records of occurrence of *A. humilis* and *A. californica* have been from such substrates, it seems reasonable to assume that this affinity to gypsum is obligate for these species. The situation with *A. merriamii* is not so clear. It is known from both definitely gypsic sites and from limestones where the presence of gypsum has not been demonstrated. Thus, it might be considered a facultative gypsophile.

Gypsum content of soils at four sites occupied by *A. humilis* was determined to be from 27 to 51 percent by weight (Nelson, 1989) and at five *A. californica* sites ranged from 36 to 69 percent (Meyer, 1987). Gypsum content of soils at four sites occupied by *A. merriamii* was determined to be from 2 to 8 percent by weight. The soils on sites occupied by *A. humilis* and *A. californica* tend to have very low bulk densities due to the presence of sponge gypsum and often have a heavy cover of cryptogams (Meyer, 1987; Nelson, 1989). It has been suggested that the unique chemistry of gypsic sites, especially the high sulfur content, is a primary factor responsible for the evolution of gypsophile endemics (Parsons, 1976). Meyer (1986) found gypsophiles to occur only where gypsum content was sufficiently great to effect physical properties of soil, while much smaller amounts of gypsum would still create high sulfate levels.

Because of their apparent obligate affiliation with gypsic soils, both *A. californica* and *A. humilis* are not found growing in close association with the creosote bush-dominated desert shrub community typical of the Mojave Desert (Meyer, 1987; Nelson, 1989). They are, instead, found with a complement of other gypsumtolerant species, including shadscale [Atriplex confertifolia (Torr. & Frem.) Wats.], burrobush (Hymenoclea salsola T. & G.), indigo bush [Psorothamnus fremontii (Torr.) Barneby], ephedra (Ephedra torreyana Wats.), and Anderson wolfberry (Lycium andersonii Gray). Plant species associated with A. merriamii are much more diverse. It has not only the widest geographic range, and the broadest tolerance with regard to substrate, but it also has the broadest elevational tolerance (610 to 1710 m). The elevational range of A. humilis is 750 to 1070 m, and that of A. californica is between 550 and 950 m. A solitary record of A. californica is known from Utah, from the Moenkopi Formation, on the Coalpits Wash road, where it might have been recently introduced.

All of the species flower in April and May, with *A. humilis* reaching the peak of flowering in early May, somewhat later than for the other species. Pollinating agents observed at flowers of low bearclaw poppy include both honey bees (*Apis mellifera*) and native ground nesting bees. Experimental hand pollinations have shown that this species relies almost exclusively on outcrossing with neighboring plants (Nelson, 1989). Information on pollination ecology of the other species is lacking.

Large plants of *Arctomecon humilis* may produce as many as 400 flowers, of which 70–75 percent are expected to mature fruit. Capsules generally produce at least 23 fully developed seeds. Petals of this species are persistent, surrounding the developing capsule as they dry. The mature capsule abscisses from the pedicel several millimeters below the mature ovary and the fruit enfolded by marcescent petals falls free. Some seeds, those falling from capsules still attached to the plant, are deposited among the leaves of the rosette and elsewhere near the plant base. Other seeds are scattered for some distance from the plant when the fruit abscisses and is tumbled across the land surface, propelled by the wind against its petal "wings."

Studies of populations of A. californica (Meyer, 1987) and A. humilis (Nelson, 1989) demonstrate drastic year-to-year fluctuations in population density. Data suggest that, for both species, such volatile cycles are primarily the result of a relatively short lifespan (individuals surviving the first year may be expected to live an average of four to five years) coupled with irregular occurrence of germination events. Meyer (1987) found that years

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with sufficient winter rainfall to assure significant establishment of *A. californica* seedlings may occur as much as nine years apart. During a four year study of populations of *A. humilis* only a single germination event was observed (Nelson, 1989). Both species appear to rely on high reproductive output and the maintenance of a large reservoir of long-lived seed in the soil in order to persist. Separation of organic material from soil collected near *A. humilis* plants, using a flotation technique, revealed a large quantity of seed "entrapped" within cryptogamic soil crusts. This suggests the importance of protecting these soil surfaces in order to maintain soil seedbanks critical to the survival of populations. Dynamics of population densities in *A. merriamii* have not been documented.

TAXONOMY

Arctomecon Torr. & Frem. in Frem. Rep. Expl. Exped. Oreg. & N. Calif. 312. 1845.

Type species: Arctomecon californica Torr. & Frem. in Frem.

Perennial herbs from a subligneous caudex and long taproot, subacaulescent, caulescent, or subscapose; leaves mostly in a basal rosette, some typically cauline, usually cuneate, long-hirsute, mostly toothed apically and the teeth spinulose-tipped; flowers large and showy, solitary, or borne in leafy-bracteate cymes, nod-ding in bud, becoming erect at anthesis; sepals 2 or 3, caducous; petals 4 or 6, white or yellow; anthers basifixed, oblong, opening longitudinally; pistil 1, the carpels 4 or 5 (6), the styles obsolete or united and less than 1.5 mm long, the stigmas connate, with 4–6 lobes; ovary unilocular; capsules acrocidal along 4–6 sutures; seeds strophiolate.

- Petals 4; plants scapose; flowers 2–5 in a paniculiform cyme; plants of Washington County, Utah A. humilis
- Petals 6; plants subacaulescent; flowers 1 or 2 (3-7) in a greatly shortened cyme, the elongated pedicels scapose;

^{1.} Flowers white, solitary or 2-5 (7); plants variously distributed

Arctomecon humilis Coville Proc. Biol. Soc. Wash. 7: 67. 1892. (Figure 1)

Low or dwarf bearclaw poppy.

Type locality: "In 1874 Dr. C. C. Parry collected in the vicinity of St. George, Utah, an *Arctomecon*, which Dr. Gray referred to *A. californicum*. The material now at hand shows that it is distinct both from the original plant of Fremont and from the species just described [i.e., *A. merriamii*]. It differs from the former in its smaller size throughout, less hairy leaves, fewer flower parts, white petals, dilated filaments, and the presence of a style; from *A. merriamii* in its smaller size and more scanty hairs, more than 1-flowered peduncles, fewer flower parts, persistent petals, and obovate, several times shorter than the capsule" (Coville, 1892).

Type: "Flora of Southern Utah, &c. Arctomecon humile, Coville, non Arctomecon Californicum Torr. & Fremont, C. C. Parry 6, 1874" (HOLOTYPE GH; ISOTYPE NY!; frag. US!).

Plants forming rounded clumps, 1.5-2.5 dm tall, from a branching caudex, this clothed with brown to ash colored, marcescent leaf bases, caulescent to apparently subscapose; stems glabrous to scabrous with crisped trichomes; basal leaves 0.5-8 (8.5) cm long, 4-16 mm wide, cuneate to obovate, usually 3- or 4-toothed or -lobed apically, glaucous and hirtellous as well as sparingly long pilose; cauline leaves typically the shorter and wider, cuneate to narrowly obovate, commonly deeply 3-lobed apically and each with an acerose bristle 1-5 mm long; cyme subcorymbose to paniculiform, bracteate; flowers mainly 3-5, on pedicels 2-9 cm long; sepals 2-8 mm long, usually 2, glabrous; petals 4-6, white, 1.5-4 cm long, usually as wide as long, oval to obovate, persistent on and falling with the mature fruit; stamens surpassed by the stigma; anthers 2 mm long, the filaments somewhat dilated; carpels 3 or 5, astylous or the style to 1 mm long; capsules obovoid, 8-13 mm high, 6-9 mm wide, acrocidal along the sutures, splitting 1/3 to 1/2 the height of the capsule; fruit soon abscissing following dehiscence; seeds shiny black, 2.5-3 mm long, ca. 1.2 mm thick, conspicuously arilate.

This plant is endemic on gypsiferous outcrops of the Moenkopi Formation (primarily the Shnabkaib Member, but also the Middle Red, and Upper Red members) in Washington County, Utah.

The mature capsules, with marcescent petals attached, fall from the plant soon after maturity and serve to aid dispersal by being carried by wind.

As irreplaceable portions of our natural heritage all members of the genus should be regarded a national prize, as jewels of great price, and protected for future generations, whose advocacy this generation must represent. The low bearclaw poppy (*A. humilis*) is being impacted by off-road vehicles and by urban sprawl in the vicinity of St. George. It is legitimately cited as endangered under stipulations of the Endangered Species Act of 1973, as amended. Despite that listing and attempts by concerned federal and state agencies, and many private individuals, the habitat is being systematically impacted by off-road traffic. Only prudent preservation of the habitat will guarantee survival of this species into the future.

Representative specimens: United States. Utah, Washington County, St. George, 23 June 1937, W. P. Cottam 7238 (BRY!); W side Warner Ridge, 11 April 1983, E. Neese 12896 (BRY!); 1.5 km E of Bloomington, 1 May 1981, S. L. Welsh 20388 (BRY!); ca. 5 km S of St. George, 3 May 1970, S. L. Welsh & N. D. Atwood 9695 (BRY!); S of St. George, 18 May 1971, L. C. Higgins 4210 (BRY!); Bloomington, Price Hills, 26 May 1983, L. C. Higgins & B. Welsh 13423 (BRY!).

Arctomecon californica Torr. & Frem. *in* Frem. Rep. Expl. Exped. Oreg. & N. Calif. 312. 1845. (Figure 2)

California bearclaw poppy.

Type locality: "This remarkable plant was found in only a single station in the Californian mountains, on the banks of a creek; flowering early in May. The soil was sterile and gravelly. Although very near *Papaver*, it differs so much in habit and in the strophiolate seeds, as well as in other characters that it must be a distinct genus" (Fremont, 1845).

Type: "Fremont's Expedition to California, 1843-4. No. 429, May 3, 1844" (NY!) (l.c.).

Plants forming tall to rounded clumps, subscapose, 2.5–6 dm tall, from a branching caudex, this clothed with ash to straw-colored marcescent leaf bases; basal leaves, 5–14 cm long, 3–25 mm wide, cuneate, usually with 3–5 apical teeth each with an acerose bristle 4-10(12) mm long, hirtellous as well as moderately





long pilose with barbellate trichomes to ca. 10 mm long; stems sparsely pilose and scabrous, glabrous above; pedicels 7–17 cm long; cymes paniculiform, 5- to 20-flowered, 10–30 cm long, with only 1 or 2 foliose bracts, these long pilose; sepals 3, 8–15 mm long, glabrous or sparingly pilose; petals 4 or 6, yellow, 1.5–3.2 cm long, slightly longer than wide; stamens equaling or slightly surpassing the stigma; anthers 2–3 mm long, the filaments filiform; carpels 4 or 5, astylous; capsules ovoid to obconic, 12–23 mm long, 7–10 mm wide, acrocidal along 4 or 5 sutures, splitting not more than ¹/₄ the length of the capsules; seeds shiny black, 2.5–3 mm long, ca. 1.2 mm thick, conspicuously arilate.

The plants occur in gypsic substrates in Clark County, Nevada, and also in Mohave County, Arizona, east of Lake Mead. The populations fluctuate numerically, and often dramatically, in response to rainfall patterns (Meyer, 1987), "disappearing" from sites for several years and reappearing *en masse* (Welsh et al., 1987).

The type of this specimen (LECTOTYPE NY!) consists of a drawing and a fragment envelope containing an immature fruit and portions of a second one. The data on the label are as follows: "Fremont's Expedition to California, 1843-4. No. 429, May 3, 1844. Arctomecon Californicum. Torr. 'Specimen lost by Nick Pooleyor the Lithographer. It was the only one collected by Fremont! Found at a place called Las Vegas, near the Rio Virgen in Southern Utah-Lat. 36°10'." The drawing has the notation, "(original drawing) by Nick Pooley-Arctomecon californicum." It is evident that Mr. Pooley was one of several artists occasionally employed by Dr. John Torrey in the 1840's to provide illustrations for publication. The surviving illustration shows a plant remarkable for its completeness and beauty, a fact not often in evidence in numerous other Fremont flood-damaged collections from the troubled second expedition (Welsh, 1993). Pooley's illustration will serve as frontispiece in the published version of the work by Welsh (1993) to be published later. The note in Torrey's hand demonstrates a degree of frustration that the specimen was lost. The epithet californica denotes the historical designation of the area where the plant was collected, i.e., Alta Californica, then a portion of Mexico (Welsh, 1993). Alta California included not only present California, but Nevada, Utah, Arizona, and portions of Colorado and New Mexico as well. The epithet was well chosen.

Representative specimens: United States. Arizona, vicinity of

Lake Meade, 25 Mar. 1981, R. K. Gerrisch 4816 (BRY!). Nevada, Clark County, 2 mi. W of Las Vegas, 19 April 1938, I. W. & C. B. Clokey 8347 (BRY!); 2 mi. S of old town of St. Thomas, W shore of Lake Meade, 4 May 1941, V. M. Tanner s.n. (BRY!); do, North of Las Vegas on Hwy 91-93, milepost 38, 4 April 1970, N. D. Atwood 2387 (BRY!); do, ca. 2 mi. NE of Frenchmans Mt. and ca. 4 mi. NE of Las Vegas, 5 April 1981, J. C. Stimson 439 (BRY!); do, ca. 18 mi. S of Overton, 21 April 1982, N. D. Atwood & S. L. Welsh 8605 (BRY!); do, Jct of Cheyenne and Lamb Blvds, Las Vegas, 27 April 1978, D. Williams s.n. (BRY!); do, North Las Vegas, Craig Rd., 7 April 1983, S. L. & S. L. Welsh 21539 (BRY!); do, North-bound lane of I-15, near Nellis Air Force Base, 30 April 1988, D. Nelson & K. T. Harper 305 (BRY!). Utah, Washington County, Clint Isom Ranch on Coalpits Mesa road, 20 June 1986, R. B. Warrick 2039 (BRY!).

Arctomecon merriamii Coville Proc. Biol. Soc. Wash. 7: 66. 1892. (Figure 3)

Merriam bearclaw poppy.

Type locality: "Type specimen in the United States National Herbarium, No. 1890, Death Valley Expedition; collected May 1, 1891, a few miles west of Vegas Ranch, Lincoln County, Nevada, by C. Hart Merriam and Vernon Bailey" (l.c.).

Type: "Vegas Valley, Lincoln Co., Nevada, between Cottonwood Cr. & Vegas ranch, *Vernon Bailey 1890*, May 1, 1891" (HOLOTYPE US!; ISOTYPE US!).

Plants clump-forming, 1–4 dm tall, subacaulescent, from a caudex clothed with ash-colored marcescent leaf bases; stems very short; leaves clustered at the base, 3.5–12 cm long, cuneate to obovate, the base cuneate-attenuate, with 3–12 apical teeth (or sometimes merely crenate), each tooth with an acerose bristle 5–12 mm long, moderately to densely long pilose, especially dense near the apex, the trichomes 1–12 mm long, barbellate; inflorescence axis much shortened, cymose, with 1–6 scapose pedicels per stem, these (7) 15–36 cm long; sepals 2–3, 14–20 mm long, pubescent like to the leaves; petals 6, white, 2.5–4 cm long, 2–3 cm wide; anthers 4–5 mm long, the filaments somewhat dilated above; carpels usually 6, astylous; capsule linear-oblong, 2.5–4 cm long, 7–11 mm wide, dehiscing ¼ the length of the capsule along 6 sutures.



Figure 3. Habit sketch of Arctomecon merriamii Coville.





This plant grows on gypsic and limestone substrates in Death Valley (Inyo Co., California) and eastward into Nye, Clark, and southern Lincoln counties, Nevada.

The label of the type specimen bears only the name of Vernon

Bailey as collector, but the type is attributed to Merriam, party director, and Bailey. Is it probable that Dr. C. Hart Merriam had no hand in its collection? And, if so, why was it not named for Bailey? There is a hint of playing politics, or of personal distrust or dislike, in the selection of the specific epithet. Coville should have honored collector Bailey with the name.

Representative specimens: United States. California, Inyo County, Racetrack Valley road, ca. 18 km S of Ubehebe crater, 1 April 1982, *Thorne et al.* 1595, 1 April 1982 (BRY!); do, Funeral Mts, road to Chloride, ca. 8 km from Beatty road, 6 April 1983, *K. Thorne & B. Ratcliffe 2342* (BRY). Nevada, Clark County, South of Indian Springs, 26 April 1939, *I. W. Clokey 8238* (BRY!). Lincoln County, Rainbow Canyon road, 10 km E of Hwy 93, 22 April 1988, *D. Nelson 284* (BRY!); do, 10 km E of Hwy 73, along Caliente road, 4 September 1981, *E. Neese & S. Clark 10994* (BRY!); do, Meadow Valley Mts, ca. 23 mi. SW of Elgin, 19 April 1982, *N. D. Atwood & S. L. Welsh 8553* (BRY!).

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