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ALKALOIDAL RELATIONSHIPS IN THE GENUS *ARCTOMECON* (PAPAVERACEAE) AND HERBIVORY IN *A. HUMILIS*

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ABSTRACT.—The previously reported alkaloids (including protopines, benzophenanthridines, tetrahydrobenzylisoquinolines, and protoberberines) of the genus *Arctomecon* (Papaveraceae) are discussed in relation to their distribution in the plant kingdom, in the Papaveraceae, and among the three species of *Arctomecon*. The biological activity of these alkaloids is discussed, and possible implications for herbivore and plant-insect interactions in *A. humilis* are presented.

Key words: Arctomecon, *Papaveraceae, alkaloids, herbivory.*

The Papaveraceae genus *Arctomecon* contains only three species, all rare endemics in the western United States. The geographic distribution of the bear or desert poppies, *Arctomecon* spp., is shown in Figure 1. The great bear poppy (*A. merriamii* Coville) is the most common of these species, extending from the Las Vegas area of southern Nevada to the Death Valley region of southeastern California. *A. californica* Torr. & Fremont, the yellow bear poppy, was once common in the vicinity of Las Vegas and the Lake Mead region of southern Nevada and northwestern Arizona, but numbers have rapidly declined due to habitat loss. The dwarf bearclaw poppy (*A. humilis* Coville) is disjunct from the other species, growing exclusively in Washington County, Utah. *A. humilis* has been declared an endangered species by the U.S. Fish and Wildlife Service under the Endangered Species Act of 1973 as amended, while both *A. merriamii* and *A. californica* are presently under consideration for such protection. Habitat requirements and ecological relations of *A. humilis* and *A. californica* have been studied by Meyer (1986, 1989) and Nelson (1989). Both are obligate gypsophiles. Unlike the other two species, *A. merriamii* is not restricted to gypsum-rich soils but often occurs on shallow soils derived from limestone.

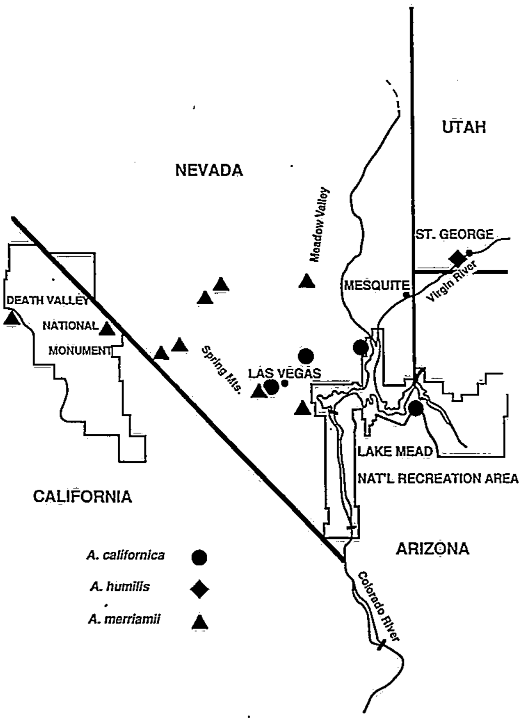

Fig. 1. Distribution of *Arctomecon* (Papaveraceae).

We have reported elsewhere (Raynie et al. 1990) the alkaloid chemicals found in this genus. Sixteen different isoquinoline alkaloids from four classes were found, and the structural details (for 14 of those alkaloids) were determined. The structures of the alkaloids known for these species are shown in Figure 2. The alkaloids identified include the protopines allocryptopine, protopine, cryptopine, and 12-methoxyallocryptopine; the benzophenanthridines chelerythrine,

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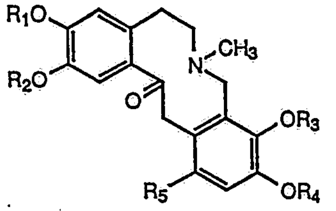
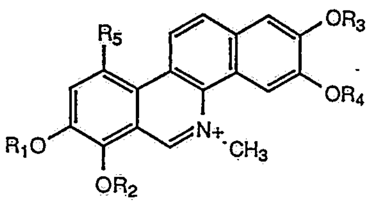
PROTOPINES

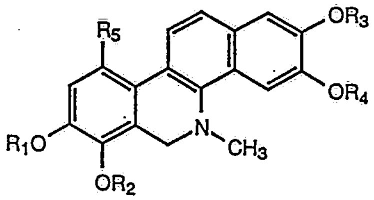


Allocryptopine: R_1-R_2 = CH_2 R_3 = R_4 = CH_3 R_5 = H
Protopine: R_1-R_2 and R_3-R_4 = CH_2 R_5 = H
Cryptopine: R_1 = R_2 = CH_3 R_3-R_4 = CH_2 R_5 = H
12-Methoxyallocryptopine: R_1-R_2 = CH_2 R_3 = R_4 = CH_3 R_5 = OCH_3

BENZOPHENANTHRIDINES



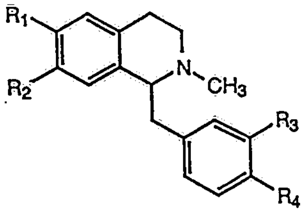
Chelerythrine: R_1 = R_2 = CH_3 R_3-R_4 = CH_2 R_5 = H
Sanguinarine: R_1-R_2 and R_3-R_4 = CH_2 R_5 = H
Sanguirubine: R_1-R_2 = CH_2 R_3 = R_4 = CH_3 R_5 = OCH_3



Dihydrochelerythrine
Dihydrosanguinarine

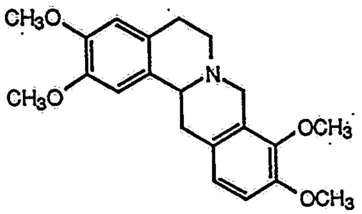
Fig. 2. Structures of alkaloids found in *Arctomecon* (Papaveraceae).

TETRAHYDROBENZYLISOQUINOLINES



Reticuline: R_1 = R_4 = OCH_3 R_2 = R_3 = OH
Pseudolaudanine: R_1 = OH R_2 = R_3 = R_4 = OCH_3
Armepavine: R_1 = R_2 = OCH_3 R_3 = H R_4 = OH

PROTOBERBERINES



Tetrahydropalmatine
N-Methyltetrahydropalmatine

Fig. 2 continued.

sanguinarine, sanguirubine, dihydrochelerythrine, and dihydrosanguinarine; the tetrahydrobenzylisoquinolines armepavine, pseudolaudanine, and reticuline; and the protoberberines tetrahydropalmatine and N-methyltetrahydropalmatine. One of these, 12-methoxyallocryptopine, was reported for the first time in our earlier study (Raynie et al. 1990). In this contribution, the alkaloids of *Arctomecon* are compared with the alkaloids of other genera of Papaveraceae. The possible values of these alkaloids to the species that produce them are also discussed.

DISTRIBUTION AND PHYSIOLOGICAL ACTIVITY OF *ARCTOMECON* ALKALOIDS

The presence of alkaloids (i.e., the ability to synthesize or accumulate alkaloids) occurs in many lineages within the plant kingdom, especially among the dicotyledons. A brief summary of the distribution in the plant kingdom of the alkaloid types reported in *Arctomecon* and their known physiological activity follows.

Cordell (1981) reviewed the phylogenetic distribution and pharmacological activity of alkaloids. In addition to the Papaveraceae, the protopines are found in four plant families (Berberidaceae, Fumariaceae, Ranunculaceae, and Rutaceae) and are represented by about 20 compounds. The physiological effects of the protopines on mammals include active dilation of coronary vessels and local anesthetic effects (Preininger 1975). The benzophenanthridines are limited to the

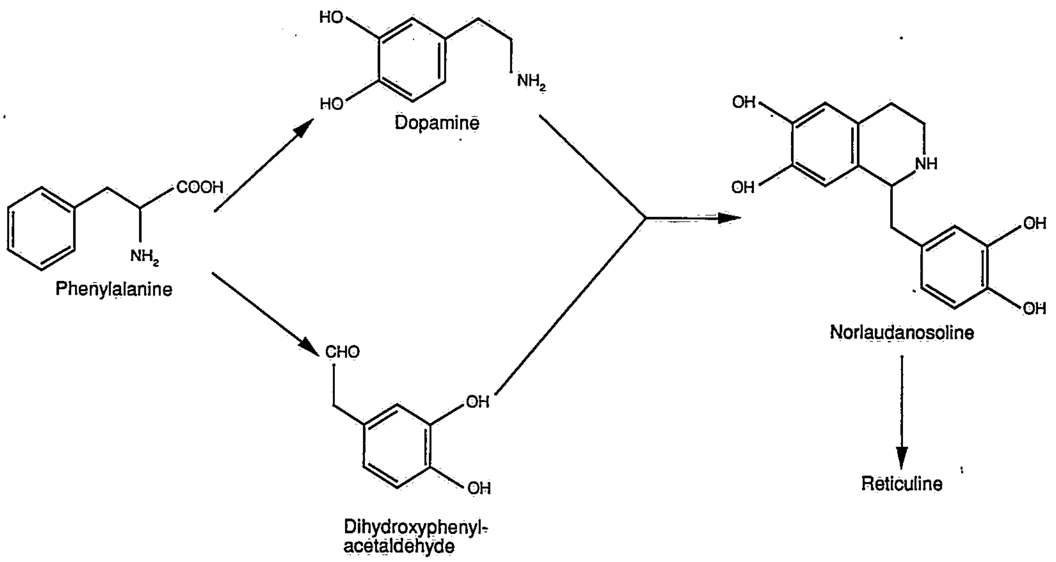


Fig. 3. Initial steps in biosynthetic scheme of Papaveraceae alkaloids from phenylalanine (after Preininger 1986).

Papaveraceae, Fumariaceae, and Rutaceae. Chelerythrine and sanguinarine, representative benzophenanthridines found in *Arctomecon,* are reported to have cytotoxic, antifungal, antiprotozoal, antibacterial, and potential anticancer activity (Cordell 1981). The tetrahydrobenzylisoquinolines, especially reticuline, are best known as biosynthetic intermediates for many other alkaloids. The protoberberines are among the most widely distributed of the isoquinoline alkaloids, occurring in nine plant families, including Annonaceae, Berberidaceae, Fumariaceae, Lauraceae, Menispermaceae, Papaveraceae, and Rutaceae. Over 40 protoberberines are known. They display at least three types of biological activity; antimicrobial, stimulation of uterine contractions, and antileukemic and antineoplastic.

RELATIONSHIP OF *ARCTOMECON* ALKALOIDS IN THE PAPAVERACEAE

The Fumariaceae and Papaveraceae are closely related families in the order Papaverales. According to Cronquist (1981), the poppy family, Papaveraceae, contains 25 genera and about 200 species. This family is unusual in that all of its species are reported to contain alkaloids (Pelletier 1970). A major feature of both the Fumariaceae and the Papaveraceae is the presence of alkaloids derived from tetrahydroisoquinolines (Preininger 1986). Preininger (1986) has reviewed, by genus, the alkaloids of the Papaveraceae and demonstrated how the biodiversity of the poppy family is reflected in its chemical diversity. The isoquinoline alkaloids can be biosynthesized from the amino acid phenylalanine by the condensation of dopamine with 3,4-dihydroxyphenylacetaldehyde followed by the Mannich condensation, yielding norlaudanosoline. From norlaudanosoline, intermediates such as reticuline and orientaline are formed in the biosynthesis of a variety of isoquinoline types (Preininger 1986). This biosynthetic scheme is shown in Figure 3.

According to Preininger's review (1986), protoberberines, benzophenanthridines, and protopines are the most widespread alkaloids in the Papaveraceae, present in almost all genera. Quaternary tetrahydroprotoberberines serve as intermediates in the biosynthetic processes that produce the foregoing alkaloids. Consequently these alkaloids were considered as a chemotaxonomically significant characteristic of the Papaveraceae. As discussed earlier, alkaloids from each of these classes, as well as tetrahydrobenzylisoquinoline alkaloids, occur in *Arctomecon.* Table 1 shows the distribution of the alkaloids found in *Arctomecon* among other Papaveraceae

TABLE 1. Distribution of alkaloids known to occur in *Arctomecon* among other genera of the Papaveraceae. The numbers at the head of each column represent *Arctomecon* alkaloids, each of which is identified in the footnote.

	Alkaloid												
	A[a]			B					C			D	
Genus	1	2	3	4	5	6	7	8	9	10	11	12	13
Argemone	x	x	x	x	x	x	x		x			x	
Bocconia	x	x		x	x	x	x						
Chelidonium	x	x		x	x	x	x						
Dendromecon	x	x				x	x						
Dicranostigma	x	x		x		x							
Eschscholtzia	x	x	x	x	x	x							
Glaucium	x	x	x	x	x	x	x			x		x	
Hunnemannia	x	x		x		x							
Hylomecon	x	x		x		x							
Macleaya	x	x		x		x							
Meconella		x											
Meconopsis	x	x	x			x							
Papaver	x	x	x	x		x	x		x	x			
Platystemon		x		x		x							
Roemeria		x											
Romneya		x		x		x	x			x			
Sanguinaria	x	x		x		x		x					
Stylomecon	x	x	x	x		x							
Stylophorum	x	x	x	x		x							

[a]Key: A = protopines, B = benzophenanthridines, C = tetrahydrobenzylisoquino lines, D = protoberberines, 1 = allocryptopine, 2 = protopine, 3 = cryptopine, 4 = chelerythrine, 5 = dihydrochelerythrine, 6 = sanguinarine, 7 = dihydrosanguinarine, 8 = sanguirubine, 9 = armepavine, 10 = reticuline, 11 = pseudolaudanine, 12 = tetrahydropalmatine, 13 = N-methyltetrahydropalmatine. Compiled from Preininger (1986), Raffauf (1970), Stermitz (1989), Willaman and Li (1970), and Willaman and Schubert (1961).

genera. The alkaloids of the Papaveraceae genera *Canbya* and *Eomecon* have yet to be studied; thus those genera are not included in Table 1. The alkaloids 12-methoxyallocryptopine, pseudolaudanine, and N-methyltetrahydropalmatine are found in the Papaveraceae only in *Arctomecon* at this time. The tetrahydrobenzylisoquinolines and the protoberberines of *Arctomecon* are shared only with *Argemone* and *Romneya* (tetrahydrobenzylisoquinolines only) among the genera endemic to western North America (*Argemone, Dendromecon, Eschscholtzia, Platystemon,* and *Romneya*). The tetrahydrobenzylisoquinolines and the protoberberines are also shared with the genera *Glaucium* (European) and *Papaver* (tetrahydrobenzylisoquinolines only), a genus widespread in the Northern Hemisphere. It is interesting to note that protopine is found in all and allocryptopine, chelerythrine, and sanguinarine in nearly all genera of Papaveraceae. According to Santavy (1970), sanguinarine-type benzophenanthridines are the most widely distributed alkaloids in the Papaveraceae. As indicated in Table 1, *Meconella* and *Roemeria* are the only genera that do not contain at least one of the five benzophenanthridines reported in *Arctomecon*. *Dendromecon* and *Meconopsis* are the only genera in which sanguinarine is reported in the absence of chelerythrine; however, the results for *Dendromecon* are preliminary, and benzophenanthridines other than those reported in Table 1 (i.e., sanguinarine and dihydrosanguinarine) may be present in trace amounts (F. R. Stermitz, unpublished data, 1989). It is not surprising that the dihydro- analogues of benzophenanthridines (i.e., dihydrochelerythrine and dihydrosanguinarine) are reported only in the presence of the parent compounds. Among the *Arctomecon* alkaloids, 12-methoxyallocryptopine, pseudolaudanine, and N-methyltetrahydropalmatine have not been reported elsewhere in the Papaveraceae. As stated earlier, 12-methoxyallocryptopine is a new alkaloid reported only in *Arctomecon*. It is interesting that 12-methoxyallocryptopine occurs in significant quantities in all species of *Arctomecon* but is absent in all other Papaveraceae genera. Other protopines are widespread in the Papaveraceae. We previously speculated (Raynie et al. 1990) that a new biosynthetic pathway for 12-methoxyallocryptopine may be present in *Arctomecon*, evidenced by an accumulation of protopine-type alkaloids and a relatively low content of benzophenanthridines in *Arctomecon* relative to related genera. The absence of pseudolaudanine and N-methyltetrahydropalmatine in other Papaveraceae is not too surprising, since they are present in *Arctomecon* in minor amounts and in only one or two species. Due to the role of tetrahydrobenzylisoquinolines and tetrahydroprotoberberines as biosynthetic intermediates, it would not be unreasonable to expect the presence of pseudolaudanine and n-methyltetrahydropalmatine in other Papaveraceae genera in amounts too small to be detected.

ALKALOID DISTRIBUTION IN *ARCTOMECON* AND POSSIBLE IMPLICATIONS

Absolute quantities of endogenous alkaloids are expected to vary with such factors as stage of plant development, tissue considered, and environmental factors, as well as

TABLE 2. Tissue distribution of alkaloids found in *Arctomecon*.

Alkaloid	*A. humilis*				*A. californica*				*A. merriamii*			
PROTOPINES												
Protopine	C[a]	R	L	O	C	R	L	O	C	R	L	O
Allocryptopine	C	R	L	O	C	R	L	O	—	R	L	—
12-Methoxyallocryptopine	C	—	—	—	—	R	—	—	C	R	—	—
Cryptopine	—	R	—	—	—	—	—	—	—	—	—	—
BENZOPHENANTHRIDINES												
Unknown	—	R	—	—	—	R	—	—	—	R	—	—
Sanguinarine	—	R	—	—	—	R	—	—	—	R	—	—
Dihydrosanguinarine	—	R	—	—	—	R	—	—	—	R	—	—
Chelerythrine	—	R	—	—	—	—	—	—	—	—	—	—
Dihydrochelerythrine	—	R	—	—	—	—	—	—	—	—	—	—
Sanguirubine	—	R	—	—	—	—	—	—	—	—	—	—
Unknown	—	—	—	—	—	R	—	—	—	—	—	—
TETRAHYDROBENZYLISOQUINOLINES												
Armepavine	C	—	—	O	—	—	—	—	—	—	—	O
Reticuline	C	—	—	O	—	—	—	—	—	—	—	—
Pseudolaudanine	—	—	—	—	—	—	—	—	—	—	—	O
PROTOBERBERINES												
N-methyltetrahydropalmatine	—	—	L	—	—	—	L	—	—	—	—	—
Tetrahydropalmatine	—	—	L	O	—	—	—	—	—	—	—	—

[a]Key: C = capsule, R = root, L = leaf, O = other (primarily stalk, also flowers and buds). Compiled from Raynie et al. (1990)

genetic differences. For this reason, absolute statements concerning the alkaloid content of *Arctomecon* must be made with the warning that these statements may be only partially correct, since our determination of the alkaloid content of *Arctomecon* is best construed as a "snapshot in time" rather than a truly definitive study. This warning was articulated by Robinson (1979):

> This ontogenic variation should be a warning to anyone who searches for a role of alkaloids in ecological interactions, for it is the alkaloid content at the exact time and place of any presumed interaction that must be determined. . . . For the field ecologist it is important to recognize that one population of a species may have a different alkaloid content than another population growing at a different location.

In an early study on the alkaloids of *A. californica*, Stermitz and Muralidharan (1967) reported that protopine and allocryptopine were present in approximately equal amounts, accounting for around 95% of the total alkaloid content. Muralidharan (1969) also reported that the total alkaloid content in *A. californica* was 0.4% and that, in addition to protopine and allocryptopine, at least three additional basic alkaloids and one quaternary alkaloid were present. However, these alkaloids were not identified. These results are similar to those we have reported (Raynie et al. 1990). In all species of *Arctomecon*, divided by tissue type, allocryptopine and protopine combined to account for 60–100% of the total alkaloid content. With the exception of *A. californica* capsule and root tissues, allocryptopine is present at much higher levels than protopine, and, in *A. merriamii*, root tissue is the only significant source of protopine.

A general rule of alkaloid distribution in plants is that they tend to accumulate in actively growing tissues and latex vessels and that alkaloid content increases rapidly at the time of cell enlargement and vacuolization and then declines slowly during senescence (Robinson 1979). The alkaloid distribution in *Arctomecon* is presented by tissue type in Table 2. Our results for *Arctomecon* showed that the highest concentration of alkaloids was in the capsule and the lowest was in the root, although for *A. californica* the amount of total alkaloids was more evenly distributed among tissues. Although the alkaloid content of the root material was lower than in other tissues, root tissue was found to contain the greatest variety of different alkaloids, and the benzophenanthridine alkaloids were limited exclusively to root tissue. Other generalizations from our limited sample include the facts that the allocryptopine/protopine ratio is greater in the leaf and stalk tissues than in capsule and root tissues and that *A. californica* and

A. merriamii are much simpler, in terms of alkaloid makeup, than *A. humilis*. The tetrahydrobenzylisoquinolines and tetrahydroprotoberberines, possible biosynthetic intermediates, were found scattered in trace amounts in all tissues except the root. However, conclusions cannot be drawn from this observation, since it is well known that the site of alkaloid accumulation is often not the site of synthesis.

Robinson (1979) has suggested that alkaloids in leaf and stem tissue render those tissues less palatable to herbivores. A population of over 400 individuals of *A. humilis* has been inventoried at four- to six-week intervals (and with greater frequency during the flowering season) from February 1987 to the present (Nelson 1989). Other *A. humilis* populations were observed less regularly during this same time period. At each observation period, we searched for evidences of herbivore predation in all individuals. Herbivory was found to be uncommon in *A. humilis* plants, and such herbivory as was noted was attributed to two-sources: rabbits and insects. In the late summer and fall of 1987, considerable use by rabbits was observed. Rabbit herbivory has been observed in only a few isolated incidents since that time. Typically, leaves were clipped near the base, and a pile of "harvested" leaves usually occurred near the plant. In all cases clipped leaves were accompanied by rabbit feces located within 40–50 cm of the affected plant. Of the 84 plants exhibiting herbivory, 82% died. While overall mortality in the population was high (58%) during 1987, mortality among the rabbit-damaged plants was significantly greater than among ungrazed plants. Nevertheless, it is not possible to attribute a cause-and-effect relationship to such data. While it may seem apparent that herbivory was the cause of mortality, it is possible that decadence of the foliage rendered the tissue more palatable to rabbits.

Robinson (1979) also noted the role of alkaloids, especially steroidal alkaloids, in plant-insect interactions. Insect damage to *A. humilis* was minimal on the study plot throughout the three years of observation. The most commonly observed insect was a small mealybug tentatively identified as *Spilococcus atriplicis* at the California Department of Food and Agriculture (Riley Nelson, personal communication, 1990). The organism itself is very minute and rudimentary, unable to fly or walk. Its infestation is marked by a cottony mass that shelters a few of the insects at the base of individual leaves. The infection sites are buried well into the thatch of leaves. The first infestations of this type were noted in April 1989. Twenty plants, in two subpopulations, harbored the insect. In July only 14 plants displayed the cottony masses. Only 8 plants harbored the insects in October. The number of infected plants increased to 13 in December 1989. Effects of the insect on *A. humilis* plants appear to be variable, but in most cases an increase in the amount of decadent leaf tissue was observed. *Spilococcus* spp. are sucking insects known to feed on plant juices. Affected leaves gradually turn brown and abscise. Of the 20 plants infected in April 1989, 3 had died by December; each of these individuals had exhibited less than 30% decadent tissue at the first sign of infestation. Only 4 of the 20 infected plants exhibited greater than 50% decadent tissue in April, but 12 had greater than 50% dead tissue by December. The condition of three plants seemed to improve after infestation. Infestations moved from plant to plant through time; only 7 of the 20 plants infected in April still showed signs of infestation in December.

McKenzie (1967) notes that the Southern California mealybug (*S. atriplicis*) infects *Baccharis* spp., *Eriogonum inflatum*, *Pleuchea sericea*, *Haplopappus* spp., and *Eriogonum* spp. in California and *Atriplex canescens* in New Mexico. To our knowledge, none of these hosts are reported to contain significant amounts of alkaloids. However, *Spilococcus* is morphologically similar to the mealybug genera *Phenacoccus* and *Pseudococcus*. *Phenacoccus eschscholtziae* and *Pseudococcus obscurus* are both known to infect the California poppy (*Eschscholtzia californica*).

Mealybugs are known to have a host of symbiotic relationships with various ants (McKenzie 1967). Seed-offering experiments (D. R. Nelson and K. T. Harper, unpublished data, 1989) have shown that ants appear to be the principal biological dispersal agent of *A. humilis* seeds. Thus ants are regularly associated with *A. humilis* plants, and ants have been reported to sometimes move mealybugs from one host plant to another (McKenzie 1967). It is thus possible that ants spread the infestation from plant to plant across the barren gypsum soil.

CONCLUSIONS

Arctomecon species are similar to most other Papaveraceae genera in respect to protopine and benzophenanthidine alkaloids, but they also contain tetrahydrobenzylisoquinoline and protoberberine alkaloids that have not been reported for most other poppy genera. The tetrahydrobenzylisoquinoline-type alkaloids are also known from the genera *Argemone* (primarily western North American), *Glaucium* (European), *Papaver* (circumboreal), and *Romneya* (southern California and adjacent Mexico). The protoberberine alkaloids are known only for the genera *Argemone* and *Glaucium* in the Papaveraceae. The diverse alkaloid content of the *Arctomecon* species may be related to the light herbivory observed on these evergreen species in the desert environment.

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