A SYSTEMATIC AND ECOLOGICAL STUDY
OF DELPHINUM LUTEUM HELLER
(RANUNCULACEAE)

by
Edward O. Guerrant, Jr.

A thesis submitted to
Sonoma State College

in partial fulfillment of the requirements
for the degree of

MASTER OF ARTS

in

Biology

Dr. Charles F. Quibell, Chairman

Dr. Robert S. Sherman

Dr. Joseph Powell

Date
Mar. 8, 1978
A SYSTEMATIC AND ECOLOGICAL STUDY
OF DELPHINIUM LUTEUM HELLER (RANUNCULACEAE)

A thesis by
Edward O. Guerrant, Jr.

ABSTRACT

Purpose of the Study:

Delphinium luteum, the yellow-flowered larkspur, is a narrowly restricted endemic consisting of two small populations near Bodega Bay, Sonoma County. Early workers suggested that this taxon is most closely related to the widespread, red-flowered D. nudicaule. Munz and others report that the blue-flowered D. decorum occasionally hybridizes in nature with D. nudicaule, giving rise to individuals with flowers ranging from purple to yellow.

The purpose of this study is to determine the evolutionary position of D. luteum within the tuberiform series of the genus Delphinium.

Procedure:

To determine the evolutionary affinities of D. luteum, this study has used a combination of ecological, chemical (nectar constituents, floral and foliar pigments) and morphological information. In addition, chromosomes were counted, hybridization and pollinator exclosure experiments were conducted, and pollen vector activity was monitored.

Findings:

Delphinium luteum was found to be intermediate between D. nudicaule and D. decorum in almost every morphological character measured in both absolute values and in the ratios between characters. The three taxa have many nectar constituents, and floral and foliar pigments in common, with D. luteum occupying an intermediate condition. It also occupies a habitat intermediate in many ways between those of D. nudicaule and D. decorum.

Conclusions:

The two most likely hypotheses to account for the origin of D. luteum are that it was derived solely from D. nudicaule, or that it was derived from hybridization between D. decorum and D. nudicaule. The data do not support the first hypothesis, and offer strong circumstantial evidence that D. luteum had its origin in a series of hybridizations between D. nudicaule and D. decorum.
ACKNOWLEDGMENTS

I would like to take this opportunity to thank a small portion of the many people who have assisted me in the course of this study.

To begin, I thank my major professor, Chuck Quibell, who introduced me to *Delphinium luteum*, and who has assisted me in every phase of the research and writing of this thesis. I am grateful for the feedback and needed perspective that I have received from Bob Sherman and Joe Powell, the other members of my thesis committee. Chuck Stasek has been instrumental in assisting me to expand my horizons in many endeavors, not the least of which are exhibited in my enhanced ability to write and illustrate this paper due to our interaction. Herbert and Irene Baker of the Department of Botany at the University of California at Berkeley have been and continue to be two of the most generous and giving people I have ever had the pleasure of knowing. They kindly analyzed many nectar samples for me and gave freely of their time and expert advice.

The existence of this paper is in a very real way due to the continuous encouragement and support that I have always received from my parents, Edward and Charlotte Guerrant. In addition, special thanks to my mother for typing this manuscript.
### TABLE OF CONTENTS

**INTRODUCTION** .............................................. 1

**MATERIALS AND METHODS** .................................... 2
- Sources of Materials ........................................... 2
- Geographical Distribution,
  Morphological and Ecological Information .................. 3
- Examination of Chromosomes ................................... 3
- Hybridization Experiments ..................................... 3
- Pollen Vectors ............................................... 4
- Pollinator Exclosures .......................................... 4
- Chromatography ................................................ 4
- Flavonoid Aglycones ........................................... 5
- Floral Anthocyanins and Floral and Foliar Flavonoids ....... 6
- Nectar Amino Acid and Sugar Determinations ................ 6

**OBSERVATIONS AND RESULTS** .................................. 8
- Floral Morphology and Biology ................................. 8
- Vegetative Morphology and Biology ............................ 16
- Range .................................................................. 24
- Habitats ................................................................ 24
- Pollinator Exclosures and Experimental Hybridization ...... 27
- Pollen Vectoring .................................................. 27
- Chromosomes ..................................................... 29
- Foliar Flavonoids ............................................... 29
- Floral Pigments .................................................. 29
- Nectar Sugars ..................................................... 30
- Nectar Amino Acid Content ..................................... 35

**DISCUSSION** ...................................................... 37

**CONCLUSIONS** .................................................... 42

**LITERATURE CITED** .............................................. 43
LIST OF FIGURES

1. Statistical information about morphological characters and pollinator exclosure results. ............. 10
2. Scatter diagram of ratios of morphological characters. .... 12
3. Illustrations and statistics of floral characters .............. 14
4. Illustration of Delphinium decorum ..................... 18
5. Illustration of Delphinium luteum ......................... 20
6. Illustration of Delphinium nudicaule ..................... 22
7. Range map .................................................. 26
8. Diagrams of chromatograms of floral pigments ............. 32
9. Nectar constituents ......................................... 34
INTRODUCTION

*Delphinium luteum* Heller is a yellow-flowered larkspur which is now known to occur only in two small populations near Bodega Bay, Sonoma County, California. This species has been considered on morphological grounds to be most closely related to the widespread, red-flowered *D. nudicaule* T. & G. since its original circumscription by Heller in 1903. *Delphinium nudicaule* is known to hybridize in nature with *D. decorum* F. & M., a blue-flowered species, and yellow-flowered individuals are reported to be occasionally present in hybrid swarms (Munz, 1959; Howell, 1970).

The nature of the relationships among species of delphinium has long been the subject of speculation and investigation. Ewan (1945) stated that within the tuberiform series, to which these three species belong, certain unspecified taxa have arisen through interspecific hybridization. Lewis and Epling (1959) provided convincing evidence that within the spiciform series, *D. gypsophilum* Ewan arose following a series of hybridizations between *D. hesperium* Gray ssp. *pallescens* (Ewan) Lewis & Epling and *D. recurvatum* Greene. They cite other probable examples of this mode of speciation within the spiciform series and go on to suggest that speciation resulting from interspecific hybridization may be a general phenomenon in the genus *Delphinium*.

This study has incorporated morphological, chemical, and ecological information about *D. luteum*, *D. nudicaule* and *D. decorum* in an attempt to place *D. luteum* in an evolutionary and systematic perspective within the tuberiform series.
MATERIALS AND METHODS

A wide variety of approaches was employed, including: examination of floral and vegetative morphology; observations of habitat characteristics; examination of chromosomes; hybridization, and pollinator exclosure experiments; observations of pollen vectoring; and chromatographic analyses of floral and foliar flavonoids, and of floral anthocyanins. In addition, floral nectar was assayed for both amino acid content, and sugar content and concentration.

Sources of Materials

Herbarium sheets of all three species from the following herbaria were examined: JEPS; NCC; POM; RSA; UCB; and UCLA.

Living materials of all three species were sampled from two populations each, all in Sonoma County, California. The only two known populations of D. luteum are in Cheney Gulch, approximately 1.1 km and 2.3 km inland from Bodega Bay. They are located on west-facing rocky outcroppings south of California Highway One near milepost 7.55, and between mileposts 8.10 and 8.28. The sampled populations of D. nudicaule are located on north-facing road cuts along Crane Canyon Road, approximately 1.9 km from Petaluma Hill Road, and also next to Occidental Road, approximately 0.5 km west of its junction with Joy Road. One of the sampled populations of D. decorum occurs on a west-facing grassy slope between the two populations of D. luteum in Cheney Gulch, across from milepost 7.77. The other occurs on a grassy knoll approximately 200 m north of the highest point on Bodega Head. Care was taken to avoid sampling in areas of suspected natural hybridization. Herbarium vouchers of representative specimens of each of these populations will be placed in the North Coast Herbarium (NCC), Department of Biology, Sonoma State College.
Geographical Distribution, Morphological and Ecological Information

Geographical distribution information was obtained from labels on herbarium specimens. Measurements of floral and vegetative features were taken from both living and herbarium specimens. Twenty vegetative features were measured from a minimum of twenty-five herbarium specimens of each taxon. All floral measurements, as well as corroborative measurements of total plant height, leaf width, and pedicel length, were taken from a minimum of twenty-five randomly selected individuals from each of the previously listed populations. Ecological observations of the habitat and soil conditions, as well as of any interactions between the delphiniums and animals, were also made.

Examination of Chromosomes

Chromosome counts were made from materials collected at each of the above-mentioned populations. To obtain buds in various stages of development, whole immature racemes, 10-15 mm long, were collected. These were fixed in 100% ethanol and acetic acid (3:1 v/v), and rehydrated to 70% ethanol for storage (Radford et al., 1974). Whole anthers were placed in a drop of aceto-carmine and the sporogenous tissue excised with iron dissecting needles. Buds 2-4 mm wide were found to have the highest frequencies of meiotic figures. Hoyers mounting medium was used to make the slides semi-permanent.

Hybridization Experiments

Hybridization experiments were conducted both in the lath house and in the field. In the lath house individual flowers were emasculated before anther dehiscence. When the stigmas were judged to be receptive, whole dehiscing anthers from known sources were rubbed on them and the individual flowers were then bagged in cheesecloth and labelled. In the field, individual flowers, all of whose anthers but one or two had dehisced, were emasculated and their as yet non-receptive stigmas brushed clean and examined with a 10X lens to be certain they were free of pollen. Dehiscing anthers of the prospective male parent were removed with forceps and deposited on stigmas which were expected to be receptive within two to four days.
Pollen Vectors

Direct observation and application of an insect-trapping adhesive as well as of a light yellow fluorescent dye were used in an attempt to discover something of the pollen vector(s) of *D. luteum*. Over seventy hours of direct observations of individuals of this species were conducted on various occasions throughout the blooming period of March to June in 1976 and 1977. Observations were conducted throughout the period from before sunrise, (5:30 a.m.) to well after sunset (11:30 p.m.). "Tangle-trap" (Tanglefoot Company), a viscous jelly-like insect-trapping substance, was placed in 5 ml syringes equipped with broken-off 18 ga needles, and applied directly as strands across the faces of the flowers of ten plants. A light yellow particulate dye, Resoform Fluorescent Blue UV (General Dyestuff Company), was applied with a small watercolor brush to the entire inner surfaces of all of the flowers of two plants in one population. This population was subsequently checked one and two weeks later, during the day for adhering insects, and after dark with a portable "black light" for the presence of dye on flowers.

Pollinator Exclosures

To determine the potential for autogamy, pollinator exclosures were constructed around three separate plants of each species. Each exclosure consisted of three wooden stakes driven into the ground around a plant with unopened flowers, with a cheesecloth tube placed around them and sewn shut top and bottom. The plants remained in their exclosures until the follicles had completely ripened, at which time the total number of follicles and the number containing seed were noted.

Chromatography

Three separate chromatographic procedures were used to isolate the following three groups of compounds: flavonoid aglycones (flavonols and anthocyanidins); foliar flavonoids; and floral flavonoids including anthocyanins. Each procedure involved standard chromatographic techniques with Watman #1 chromatographic paper. Flavonoid aglycones were obtained from hydrolyzed flower and leaf extracts and run in one direction. Alcoholic extracts of flavonoids and
anthocyanins were subjected to two-dimensional separation; first in an alcoholic solvent system, and then in an aqueous one.

All chromatograms were viewed in visible and ultraviolet light and all spots were circled with pencil and their colors noted. The chromatograms were then fumed with ammonium hydroxide and again viewed in visible and ultraviolet light; any color changes were noted.

Flavonoid Aglycones

Flavonols and anthocyanidins were extracted from flowers and leaves following a method described by Harborne (1973). Individual dried flowers or leaves were placed in a test tube with 3 ml of 2N hydrochloric acid and heated in a boiling water bath for 30-40 minutes. The extract was cooled and decanted; 3 ml of ethyl acetate was added, shaken vigorously, and the mixture allowed to separate. The upper ethyl acetate layer contained the flavonols, the lower aqueous layer the anthocyanidins. The upper layer was removed with a pipette and saved for flavonol determination.

To isolate the anthocyanidins the lower layer was again heated to remove all traces of ethyl acetate and then cooled and re-extracted with 3 ml of amyl alcohol. The resulting alcoholic layer was concentrated to dryness in vacuo, the residue suspended in 1-3 drops of 1% methanolic HCl (methanol, concentrated HCl, 100:1 v/v), and spotted on chromatography paper.

The original flavonol-containing ethyl acetate layer was also concentrated to dryness in vacuo, the flavonols resuspended in 1-3 drops of 95% ethanol, and spotted on chromatography paper.

The chromatograms were run in the descending direction in conjunction with standards in two separate solvent systems: forestal (acetic acid, concentrated HCl, water 10:3:30 v/v/v) and BAW (n-butanol, acetic acid, distilled water 4:1:5 v/v/v). The anthocyanidins: cyanidin (K. and K. Laboratories); delphinidin; and pelargonidin were used as standards. Delphinidin and pelargonidin could not be commercially obtained but were isolated from eggplant skins and Pelargonium sp. petals respectively, by the process described above. Compounds were identified by comparing experimentally derived Rf values with those of the known compounds and
with published values (Dunn and Arditti, 1968; Harborne, 1973).

Floral Anthocyanins and
Floral and Foliar Flavonoids

Floral anthocyanins and flavonoids were isolated with ascending chromatography using a process modified from Bloom (1976). The perianths of ten flowers of each species were homogenized in 50 ml of 1% methanolic hydrochloric acid in a blender and allowed to soak overnight in the dark. The solution was then filtered through Watman #1 filter paper and the volume reduced to 1-3 ml in a flash evaporator at 40° C. The concentrate was then applied at a spot 2.5 cm from each edge in one corner of a 23 x 28.5 cm sheet of chromatography paper. The sheets were first run in the long direction in BAW and then in the perpendicular direction in acidified water (distilled water, concentrated HCl, 97:3 v/v).

Foliar flavonoids were isolated with descending chromatography using a method modified from Harborne. To obtain these in solution, leaves that had been torn into 1 cm² sections or less were first placed in 30 ml of diethyl ether overnight to remove the chlorophyll, and then moved to 50 ml of absolute methanol and placed on a shaker for a similar period. The resulting solution was decanted and reduced to 1-3 ml in a flash evaporator at 40° C. The extract was spotted 9-10 cm from the edges in one corner of a 46 x 57 cm sheet of chromatography paper. The chromatograms were developed in two dimensions, first in the long direction in BAW and then in the short direction in HOAc (glacial acetic acid, distilled water, 15:85 v/v).

Nectar Amino Acid and
Sugar Determinations

Nectar was withdrawn from the nectaries of flowers of all three species with a 5 µl pipette and spotted on Watman #1 filter paper and sent to Dr. H. G. Baker and I. Baker of the University of California at Berkeley for determinations of amino acid content, and of qualitative and quantitative sugar analysis. Standard descending paper chromatographic techniques were used to separate the sugars, and relative quantities were determined by fluorometry (Baker and Baker, 1978). Amino acid content was determined with
two-dimensional thin-layer chromatography by a process described in Baker and Baker (1976a).

Sugar concentration in the nectars was determined by collecting samples in 5 µl pipettes, sealing both ends with "Tube-seal", measuring the refractive index with a refractometer, and then extrapolating to sucrose-equivalent concentrations.
OBSERVATIONS AND RESULTS

Floral Morphology and Biology

Delphinium flowers are strongly zygomorphic, usually blue to purple, have five petaloid sepals, four petals, three multi-ovulate pistils, and many stamens. The upper sepal is on the mid-line of the bilaterally symmetrical flower and forms a sheath which envelopes the paired upper saccate nectariferous petals. The paired lower petals are generally clawed with the relatively broad blades arched over, concealing the essential parts of the flower and the entrance to the nectaries.

The flowers, borne in racemes, are protandrous with their approximately twenty stamens dehiscing a few at a time in such a way that each flower is functionally male for a total of seven to ten days. Filaments of the immature stamens are curved downward. Immediately preceding anther dehiscence each becomes upcurved, positioning the anthers just under the lower petals at the entrance to the floral tube. After dehiscence the stamens wither and again become downcurved. A day or two after the last anther withers the three previously downcurved styles simultaneously bend upward, positioning the stigmas in approximately the same position as that previously occupied by the deshiscing anthers. The stigmas apparently then become receptive for one to three days, as evidenced by the presence of a glistening liquid exudate.

The most conspicuous differences among the species with which this study is concerned are in the floral characters. Delphinium luteum was found to be intermediate in all characters except color and the length-to-width ratio of the lower sepals, a character in which D. nudicaule was found to be intermediate (Fig. 1 C). A scatter diagram incorporating two sets of ratios indicates the intermediacy of D. luteum (Fig. 2).

The blue-purple flowers of D. decorum (Fig. 3 A-D) can be considered typical within the genus. The sepals are arranged in a
Figure 1.

(A-F: Mean, range, standard deviation and standard error of the mean for various morphological traits. N = 25 for all except D where N = 50.)

A. The angle at which the upper petal is bent at its point of attachment to the receptacle.

B. The arc that is subtended between lines from the receptacle to the tips of the upper sepal and lower sepals as viewed from the side.

C. Length-to-width ratio of the lower sepals measured at their longest and widest points.

D. Plant height in cm from ground level to the point of attachment at the highest pedicel to the main stem.

E. Leaf width in cm at the widest point.

F. Length of the lowest pedicel.

G. Results of pollinator exclosure experiments with the number of follicles in the enclosures and the number and percent that set seed.
Upper Petal Angle

Flower Openness

Lower Sepal I/w

Plant Height

Leaf Width

Pedicel Length

Pollinator Exclosures

Legend

<table>
<thead>
<tr>
<th>Legend</th>
<th>Pollinator Exclosures</th>
<th>number of follicles</th>
<th>fruits set</th>
<th>percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D. nudicaule</td>
<td>36</td>
<td>7</td>
<td>19.4</td>
</tr>
<tr>
<td></td>
<td>D. luteum</td>
<td>42</td>
<td>5</td>
<td>11.9</td>
</tr>
<tr>
<td></td>
<td>D. decorum</td>
<td>24</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 2.

Scatter diagram showing the relationship of the angle of the flower openness (Figs. 1B, 3B, F, J) divided by the angle of spur orientation relative to horizontal (Fig. 3B, F, J, N) to the ratio of plant height to leaf width (Fig. 1D, E).
Plant Height: Leaf Width

D. decorum
D. luteum
D. nudicaule

1.6 1.5 1.4 1.3 1.2

3 4 5 6 7 8 9 10

Flower Openness: Spur Orientation
Figure 3.

A, E, I. Front view of flowers showing five bilaterally arranged sepals and paired upper (nectariferous) and lower petals.

B, F, J. Side view of flowers showing saccate portions of the single upper sepals and their average orientations in space.

C, G, K. Left upper (nectariferous) petals. Note the saccate portion (left) where nectar is produced, and the average angles at which the petals are bent at their points of attachment to the receptacle.

D, H, L. Lower petals showing pubescence and proportions of claw to blade.

M, N, O. Mean, range, standard deviation, and standard error of the mean for flower diameter, orientation of the spurs in space, and width of lower petals at widest point of the blade (N = 25).
D. decorum

D. luteum

D. nudicaule

Flower Diameter

Spur Orientation

Lower Petal Width
rotate manner, giving a total frontal diameter of slightly more than 30 mm (Fig. 3 A, M). The reddish orange flowers of *D. nudicaule* (Fig. 3 I-L) have a tubular appearance due to the forward-pointing sepals, and are only one-third as wide in frontal diameter as those of *D. decorum* (Fig. 3 M). *Delphinium luteum* has pale yellow flowers with the sepals spread in a cup-like fashion (Fig. 3 E-H), giving a frontal diameter mid-way between *D. decorum* and *D. nudicaule* (Fig. 3 M).

The flowers of each species have characteristic orientations in space regardless of the positioning of the inflorescences. The plane of bilaterallity always remains vertical in all three species, but the angle of the spur relative to horizontal was seen to differ (Fig. 3 B, F, J, N). The spurs of *D. decorum* are almost horizontal, those of *D. nudicaule* are steeply up-pointing, and those of *D. luteum* have an intermediate attitude.

The strongly clawed lower petals of *D. decorum* have the typical form for the genus (Fig. 3 D). Their blades average 6.3 mm wide (Fig. 3 O), have deep sinuses, and are adaxially pubescent. Each is bent at an acute angle from the axis of its claw, and is oriented in such a manner that the two lower petals meet along the mid-line of the flower face (Fig. 3 A), thereby covering the anthers and obstructing the entrance to the nectaries. In contrast, the relatively straight lower petals of *D. nudicaule* (Fig. 3 L) have little expression of a claw, are glabrous, and have an average blade width which is less than half that of *D. decorum* (Fig. 3 O). The sinus, which is so prominent in *D. decorum*, is shallow and occasionally absent in *D. nudicaule*.

The lower petals of *D. luteum* are intermediate in blade width (Fig. 3 H-O) and share features in common with those of both *D. nudicaule* and of *D. decorum*. Like those of *D. decorum*, they have a distinct claw, a deep sinus, and to a lesser degree are adaxially pubescent. They are similar to those of *D. nudicaule* in that the blade is not bent sharply from the axis of the claw. There is, however, a wide range of variation in their orientations. Most are centrally located and some are laterally displaced, but in neither case do they obscure the anthers or the entrances to the nectaries as completely as do those of *D. decorum* (Fig. 1 E).
Delphinium decorum again represents the more typical condition in the genus in the morphology of its nectariferous petals (Fig. 3 C). These typically have a bend of approximately $45^\circ$ at their point of attachment to the receptacle (Figs. 3 C, 1 A). Aside from color, the most strikingly atypical feature of the flowers of D. nudicaule is the relative straightness of the nectariferous petals, which bend less than $14^\circ$ at their point of attachment (Figs. 1 A, 3 C, G, K). The nectariferous petals of D. luteum bend $22^\circ$ at this point and in this regard closely resemble only those of D. nudicaule and D. cardinale Hook. (Delphinium cardinale has not been treated in this study but herbarium samples and my own collections have been analyzed for this particular feature.)

Vegetative Morphology and Biology

All three species are spring-ephemeral herbaceous perennials having tuberous roots and one or more flowering stems (Figs. 4, 5, 6). Total plant height from ground level to the point of attachment of the highest pedicel, length of longest pedicel, and width of the largest leaf were measured in the field. The plants and leaves of D. nudicaule are largest, those of D. decorum smallest, and those of D. luteum intermediate (Fig. 1 D, E). Delphinium decorum has small more or less spherical roots (Fig. 4), while D. luteum and D. nudicaule have tuberous roots that are long and thin (Figs. 5, 6).

The leaves of D. nudicaule and D. luteum, but generally not those of D. decorum, have distinct red margins, a feature which is most pronounced in the rosette stage. The red margin is most prominent in D. luteum and was found in all leaves of this species which were examined. The majority of individuals of D. nudicaule examined had leaves with red margins, but this condition is not as pronounced as it is in D. luteum. Delphinium decorum essentially lacks this feature, with only two of the plants examined having any red in their leaf margins. An anthocyanidin, believed to be petunidin, (no standards were available for comparison) was found to be present in the leaves of D. nudicaule and D. luteum, but was not detected in those of D. decorum.
Figure 4.

*Delphinium decorum:* note the compact knobby root and compare with those of *D. luteum* (Fig. 5) and *D. nudicaule* (Fig. 6).
Figure 5.

*Delphinium luteum*: note the long, thin, tuberous root and multiple flowering stems.
Figure 6.

*Delphinium nudicaule:* notice the long, thin, tuberous root and that adjacent flowering stems can have a common root.
Delphinium luteum and D. nudicaule were found to suffer a lower rate of leaf predation than did D. decorum. Surveys were conducted on March 1, 1977 and April 22, 1977, to determine how many leaves each plant had, and how many of these had either portions of blades or the entire blades missing. Individuals of D. luteum suffered the least leaf predation with 13.7% of 226 leaves damaged, those of D. nudicaule had 20.5% of 216 leaves damaged, and D. decorum had 39.4% of 132 leaves suffering from predation.

The leaves of all three species are predominantly basal, but in each some cauline leaves occur which show transitions into bracts toward the top of the plant. In stature, D. decorum is the smallest of the three, averaging 11.3 cm in height, and individual plants are often difficult to see in their grassland habitat. The largest leaves average just over 3 cm in width, and are quickly replaced above by three-lobed to simple lanceolate bracts. Delphinium nudicaule is a conspicuous plant, and is the largest of the three species, averaging 69 cm in height. This taxon also has the largest leaves, averaging over 8 cm in width. These get progressively smaller toward the top of the plant, but are often not modified so much as those of D. decorum. Delphinium luteum is also a conspicuous plant and is intermediate in total height (30 cm) and in leaf width (5 cm). Its leaves are mostly basal, with some upper cauline leaves being reduced to bracts.

Delphinium decorum has small, more or less spherical, knobby roots that are typical of the tuberiform series. The long, thin, branching tuberous roots of D. luteum and D. nudicaule are unique in this series. The roots of D. decorum have been found to be up to 2 cm in diameter, and have many fine roots growing from their knobby protrusions. These thin lateral roots are apparently short-lived, perhaps living for only a single season. The main tuberous portion of the roots of D. luteum and D. nudicaule have been found to be up to 30 cm long and up to 1 cm in diameter. Root branching has been observed in both species, with the result that rosettes which are at least within 10 cm of each other may represent parts of single individuals. This character has not been observed in D. decorum.
Range

*Delphinium nudicaule* has the most extensive range of the three species studied (Fig. 7), extending from San Luis Obispo County in the south, to Josephine and Curry counties in southern Oregon in the north, and extending across northern California in Siskiyou, Shasta and Modoc counties and south to Butte and Plumas counties in the Sierra Nevada. Several herbarium specimens from as far south as Yosemite National Park, and Stanislaus County were examined.

*Delphinium decorum* is in a state of taxonomic chaos with individuals being reported from the Sierra Nevada and other places. This paper accepts a concept of *D. decorum* as described in Munz (1959) and considers only those plants from southern Sonoma County that closely resemble this circumscription of the taxon. This entity is found in grassy places near the coast from northern Monterey County in the south to the middle of Humboldt County in the north.

*Delphinium luteum* has the most restricted range of the three, being endemic to a single locality in southwestern Sonoma County.

Habitats

Each of the three species occurs in its own characteristic habitat, with soil texture appearing to be an important factor. *Delphinium nudicaule* and *D. luteum* are found growing in rocky places, often in areas subject to active rock sliding, while *D. decorum* is a plant of open grasslands which have a more well-developed soil.

*Delphinium luteum* is today known only from two colonies inhabiting rocky areas in the North Coastal Scrub Community (Munz, 1959) near Bodega Bay. The outcroppings which produce these conditions are known as Franciscan knockers, and are associated with a soil of the Kneeland series derived from Franciscan Greywacky (United States Department of Agriculture, 1972). In the more inland site, *D. luteum* is found growing on an active rock slide. The slope varies from 37° to 45° with no A horizon present. The Larkspur Hill site is more stabilized, but the plants even there are growing in shallow rocky soil or in broken rock, some of which forms periodically active slides.

*Delphinium nudicaule* is found usually in rocky soils. The Coleman Valley population is on a slope of approximately 30° in a very
Figure 7.

Map showing general distribution of the three taxa.
D. nudicaule

D. decorum

> D. luteum

100 mi.
gravelly loam of the Hugo series, which is a moderately fractured green schist. In this location the roots pervasively penetrate only the upper 45 cm of the ground. *Delphinium nudicaule* is apparently adapted to disturbed habitats and is thus frequently seen growing on road cuts, often in the lower scree slopes.

The sites in which *D. decorum* was studied are in typical open grasslands of the North Coastal Scrub Community. The site in Cheney Gulch is on a 25° to 30° slope, which has a better-developed soil than either of the habitats of the other two species. The soil of this site is also of the Kneeland series.

**Pollinator Exclosures and Experimental Hybridization**

A program of experimental hybridization was undertaken, and a series of pollinator exclusures was constructed in order to determine fertility relationships and the potential for autogamy in each of the three species.

All reciprocal crosses within and among all taxa were successful, and some quantity of normal-shaped seed was obtained in each case.

Pollinator exclusures were constructed in the field around three immature plants of each species. No seed was set in any of the follicles of *D. decorum*. In *D. luteum*, 12 percent of the follicles set some seed, and in *D. nudicaule*, 20 percent of the follicles set some seed (Fig. 1 C). There were no formal control plants, but virtually all of the follicles in each of the taxa set seed.

**Pollen Vectoring**

Direct observation, and application of insect-trapping adhesive and of fluorescent dye were used in an attempt to discover something of the pollen vector(s) of *D. luteum*. During the 1976 blooming season, over fifty hours were spent observing groups of individuals of this species, covering the period from before sunrise until well after dark. The only visitor seen during this period is believed to have been an Allen's hummingbird, observed once just before sunset. During the blooming season of 1977, an additional twenty man-hours was spent observing groups of *D. luteum* individuals, emphasizing the period from 6:00 p.m. until after dark. On two occasions, one week apart,
hummingbirds (again believed to be Allen's) were seen visiting the flowers. Both visits occurred after the sun had disappeared from view behind low hills, but before dark. In the first instance five flowers on three plants were visited, and in the second contact was made with eight flowers on five plants. On the second occasion the bird was seen to fly past and not visit a robust, profusely flowering *Diplacus aurantiacus* Jeps. between visits to much smaller and fewer-flowered plants of *D. luteum* that were at least ten meters apart.

The two indirect methods of monitoring pollen vector activity, involving placing adhesive strands or a fluorescent dye on the flowers, met with variable success. No insects were caught over a two week period on any of ten plants to which "Tangle-trap" insect trapping adhesive was applied. The fluorescent dye, however, was found to have been transferred from the marked flowers to many others within the same population. In each case the dye was observed in a "ring" on the inner surfaces of the petals on most of the flowers within ten meters of the two marked plants. It is significant that this was the only pattern in which transferred dye was found, the implication being that the vector(s) contacted the flowers only in that central area, and did not alight on or make contact with the sepals while foraging for nectar. Only vectors such as hummingbirds or hawk moths that can hover and feed at the same time would seem to be capable of producing such a pattern.

No systematic observations were made of the visitors to *D. nudicaule* or *D. decorum*, but visits of potential pollinators were noted in the course of other field work. Unidentified hummingbirds were repeatedly seen to visit the flowers of *D. nudicaule* in several populations in southern Sonoma and northern Marin counties. One hummingbird was seen to visit flowers of thirty-eight plants consecutively in a hybrid swarm believed to consist of *D. nudicaule* x *decorum*. This bird started with nudicaule-like individuals and proceeded to visit diverse hybrid types and decorum-like individuals. In addition, large unidentified bees have been seen to visit the flowers of *D. decorum* in Cheney Gulch.
Chromosomes

The vast majority of the North American species of Delphinium are diploids with n = 8 (Fedarov, 1969). The karyotype was reported to be constant within the genus with two long chromosomes having submedian centromeres, and four medium and two short chromosomes having sub-terminal centromeres (Lewis et al., 1951). Both D. nudicaule and D. decorum are reported to be diploids, however there is one report of a tetraploid D. decorum (Kurita, 1965). The chromosome number of the former species was reported by Lawrence (1936), and both species by Lewis et al. (1951) and Legro (1961). No published counts for D. luteum Heller have been found.

Chromosome counts were made from materials collected from two populations of each species. All plants were found to be diploid with n = 8. The diploid condition of D. luteum has twice been corroborated by Dr. John Strother of the University of California at Berkeley, Department of Botany.

Foliar Flavonoids

The results of the investigations into the foliar flavonoids are not entirely clear, but they do provide two significant pieces of information. The first is that all three species have several compounds in common; the second is that there is at least one compound present in the leaves of D. luteum and D. decorum that does not occur in those of D. nudicaule.

All three species have at least three spots in common and one spot, visible only under ultraviolet light, is present in D. luteum and D. decorum but not in D. nudicaule. These three species, in addition, seem to share many poorly resolved compounds, all of which have an Rf of less than 50 in BAW, and greater than 50 in HOAc. A subjective comparative analysis of this quadrant of each of the chromatograms indicates that although there is much here that is characteristic of all three taxa, D. luteum and D. nudicaule are more similar to each other than either is to D. decorum.

Floral Pigments

Perianth parts of each species were subjected to chromatographic analysis to ascertain the presence of anthocyanins and flavonoids.
Delphinium luteum was found to possess a sub-set of those pigments that occur in Delphinium nudicaule, and neither was found to have specific pigments in common with Delphinium decorum (Fig. 8).

Delphinium luteum contained ten unidentified flavonoids and no anthocyanins in its flowers. Two flavonoids, designated b and j, were present in some but not all of the flowers tested.

Delphinium nudicaule was found to possess all ten of the floral flavonoids found in Delphinium luteum, and eight pigments that were not. One of these, j, is an unidentified flavonoid. Spots k, l, and m are all orange and are thought to be derivatives of pelargonidin. Spots n, o, p and q are blue, and are thought to be derivatives of delphinidin. The darker nature of the orange as compared with the blue spots is believed to indicate relatively higher concentrations of the pelargonidin-based pigments. The presence of spot b was found to be variable as in Delphinium luteum; however, unlike in the former case, spot j was found in all individuals of Delphinium nudicaule tested.

Delphinium decorum has a much smaller array of floral pigments than do either of the other species. This includes three unidentified flavonoids and one bimodal derivative of delphinidin (v) that is different from those found in Delphinium nudicaule. Spots s and t were not present in every sample of Delphinium decorum tested.

Nectar Sugars

Nectar sugar concentrations were found to be most variable in Delphinium nudicaule, slightly less so in Delphinium decorum, and most variable in Delphinium luteum (Fig. 9C). In addition to having less variability in this regard, Delphinium nudicaule was found to have the most dilute nectar, while that of Delphinium decorum was the most concentrated. These two species had non-overlapping ranges of sugar concentrations, with a gap between them equal to four standard deviations of that of the more variable Delphinium decorum. Although the nectar of Delphinium luteum has an intermediate average sugar concentration, it was found to be so variable that the range encompassed by one standard deviation to either side of its mean exceeds the maximum and minimum values for Delphinium decorum and Delphinium nudicaule respectively.
Figure 8.

Drawing of chromatograms of floral pigments of the three species of Delphinium. Equivalent letters indicate presumed equivalent compounds. Spots a-j and s-u are unidentified flavonoids, k-m are derivatives of pelargonidin, and n-q plus v are derivatives of delphinidin.
Figure 9.

Nectar constituents:

A. Amino acids present in nectar from *D. luteum*, *D. nudicaule*, *D. decorum* and from a naturally occurring putative hybrid, *D. nudicaule x decorum*. Amounts are relative.

B. Sugar concentrations in nectar expressed as sucrose-equivalent—weight of sugar to total weight of solution.

C. Average relative amounts of the different sugars present in nectars of the different species, and the ratio of the amount of sucrose to the combined amount of the hexoses, glucose and fructose. Extremes and averages are given for the sucrose-to-hexose ratios.
### A. AMINO ACIDS PRESENT IN NECTAR SAMPLES

<table>
<thead>
<tr>
<th></th>
<th>ALA</th>
<th>ARG</th>
<th>CYS</th>
<th>GLY</th>
<th>PRO</th>
<th>SER</th>
<th>THR</th>
<th>TYR</th>
<th>ASP</th>
<th>TRY</th>
<th>VAL</th>
<th>ILE</th>
<th>LEU</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>D. luteum</strong></td>
<td>+</td>
<td>++</td>
<td>±</td>
<td>±</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td></td>
</tr>
<tr>
<td><strong>D. nudicaule x decorum</strong></td>
<td>++</td>
<td>++</td>
<td>±</td>
<td>±</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
</tr>
<tr>
<td><strong>D. decorum</strong></td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
</tr>
<tr>
<td><strong>D. nudicaule</strong></td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>(+)</td>
<td>(+)</td>
<td>+</td>
<td>±</td>
<td>±</td>
<td></td>
</tr>
</tbody>
</table>

### B. NECTAR SUGAR CONCENTRATION

<table>
<thead>
<tr>
<th></th>
<th><strong>X</strong></th>
<th><strong>s.d.</strong></th>
<th><strong>N</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>D. nudicaule</strong></td>
<td>34.5 %</td>
<td>± 0.53 %</td>
<td>5</td>
</tr>
<tr>
<td><strong>D. luteum</strong></td>
<td>41.7 %</td>
<td>± 8.24 %</td>
<td>15</td>
</tr>
<tr>
<td><strong>D. decorum</strong></td>
<td>47.0 %</td>
<td>± 1.70 %</td>
<td>6</td>
</tr>
</tbody>
</table>

### C. NECTAR SUGARS

<table>
<thead>
<tr>
<th></th>
<th><strong>D. nudicaule</strong></th>
<th><strong>D. luteum</strong></th>
<th><strong>D. decorum</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>raffinose</td>
<td>----</td>
<td>----</td>
<td>.054</td>
</tr>
<tr>
<td>sucrose</td>
<td>.761</td>
<td>.766</td>
<td>.473</td>
</tr>
<tr>
<td>glucose</td>
<td>.157</td>
<td>.104</td>
<td>.188</td>
</tr>
<tr>
<td>fructose</td>
<td>.064</td>
<td>.130</td>
<td>.285</td>
</tr>
<tr>
<td>Sucrose to Glucose plus Fructose Ratio</td>
<td><strong>X</strong></td>
<td>3.44</td>
<td>3.27</td>
</tr>
<tr>
<td></td>
<td>(range)</td>
<td>(2.04-15.39)</td>
<td>(1.5-5.56)</td>
</tr>
<tr>
<td></td>
<td><strong>N</strong></td>
<td><strong>N = 3</strong></td>
<td><strong>N = 5</strong></td>
</tr>
</tbody>
</table>
Qualitatively, the nectar samples were found to contain mixtures of sucrose, glucose and fructose (Fig. 9 B). The nectars of *D. nudicaule* and *D. luteum* were found to be strongly sucrose-dominant, both having ratios of the concentrations of sucrose-to-glucose-plus-fructose of in excess of 3.25:1. *Delphinium decorum* was found to have a generally lower average sucrose-to-hexose ratio (1:1), but had one of the widest ranges of variation in this regard of any species yet tested (Baker and Baker, personal communication), with an almost twentyfold difference between the extremes.

Baker and Baker (1978) have demonstrated in a broad spectrum of plant taxa that the qualitative and quantitative aspects of the sugar content of floral nectars can be correlated with their respective pollinator syndromes. Hummingbird-pollinated taxa characteristically have a relatively dilute nectar (Baker, 1975) that is sucrose-dominant.

The nectars of bumblebee-pollinated taxa are generally more concentrated; the ratio of sucrose to the hexoses is generally less than that for hummingbird-pollinated taxa, although more work is needed to overcome the relative paucity of bumblebee-pollinated taxa for which this information is known.

The total sugar concentration, sucrose-to-hexose ratios, and the observed pollinators for these three species are consistent with the general patterns discovered by Baker and Baker (1978).

**Nectar Amino Acid Content**

The amino acid content of the nectars of each of the three taxa was found to be species-distinctive and constant within each taxon (Fig. 9 A). Analyses indicate that each of the three species, plus a naturally occurring putative hybrid (*D. nudicaule* x *decorum*) have the following seven amino acids in common: proline; serine; alanine; arginine; cystine; glycine; and threonine. *Delphinium nudicaule* has in its nectar only those seven amino acids that are shared by all three species. The nectar of *D. decorum* has tyrosine, aspartic acid, tryptophan, and valine in addition to the basic seven. The putative hybrid has all of the amino acids found in *D. decorum* plus isoleucine and leucine. The amino acid complement of the nectar of *D. luteum* closely resembles that of the putative hybrid, lacking only tryptophan.
Baker and Baker (1976b) have shown that qualitative amino acid content of floral nectar in the vast majority of cases is consistently uniform within any given species. In addition, experimentally produced F1 hybrids were almost without exception found to possess nectars with all of the amino acids that are present in both parental species. In subsequent experimentally produced generations and in naturally occurring hybrid swarms, all of the amino acids present in both parental taxa are potentially represented; however, due to segregation it is likely that not all of the individuals will each have the entire complement.
DISCUSSION

In his synopsis of the North American species of the genus Delphinium, Ewan (1945) described thirteen main evolutionary trends, designating each a series. The three species with which this study is most concerned are in the tuberiform series, which consists of fifteen ostensibly closely related species found principally in maritime and lowland areas of the western United States. The tuberiformae are spring-ephemeral herbaceous perennials that become dormant in early summer and reappear in late autumn-to-spring as rosettes. They are distinguished by having tuber-like roots, and are cited as being well adapted for survival in areas of summer drought (Stebbins, 1974).

*Delphinium decorum* is typical of this series in having compact, more or less spherical, knobby roots. *Delphinium nudicaule* and *D. luteum* have root systems which are unlike those of any other taxa in the series. Both have long, thin, tuberous roots and are usually found growing in rocky soil, rock slides, or crevices. Weaver (1919) found that plants growing in his "gravel slide community" characteristically have long, thin, tuberous roots, a root form which appears to confer a selective advantage under these circumstances.

The genus *Delphinium* is considered to have evolved with, and the vast majority of its species are adapted for, pollination by large hymenoptera, especially *Bombus* ssp. (Epling and Lewis, 1952; Grant and Grant, 1968; Lewis and Epling, 1959; and Macior, 1975). Of the three species with which this study is concerned *D. decorum* is morphologically the most representative of the genus. It has blue-purple flowers and is the only one of the three that is known to be bumblebee-pollinated. Its nectar has a relatively low sucrose-to-glucose-plus-fructose ratio, a characteristic that has been recently correlated on a wide scale with various insect pollination syndromes (Baker and Baker, 1978). *Delphinium nudicaule* and *D. luteum* have sucrose-dominated nectars, which consequently have much higher sucrose-to-glucose-plus-fructose ratios. This condition has been
found to be associated with hummingbird-pollinated taxa.

Outcrossing herbaceous perennial genera with prominent floral differences among their species commonly have only low to moderate post-fertilization reproductive barriers (Grant, 1971). Twenty-eight species of larkspurs are known from the California flora and, among these, twenty-one naturally occurring putative hybrid combinations have been reported (Ewan, 1945; Lewis and Epling, 1954; Munz, 1959; and Santana, 1975). There is one report of three species being represented in one hybrid swarm; *D. nudicaule* and *D. decorum* F. & M. ssp. *Tracyi* Ewan of the tuberiform series, and *D. trollifolium* Gray of the oxysepaloid series (Santana, 1975). Hybridization in the California larkspurs, however, appears to be a localized phenomenon that is generally associated with disturbed habitats. I have found no evidence, either in the field or in the literature, that broad areas of introgression exist even though there is considerable sympatry among the many species in California. Species differences are presumably maintained by a combination of factors such as habitat preferences, differential flowering times, and pollinator specificity, at least between the hummingbird-pollinated taxa and bumblebee-pollinated taxa.

Ewan hypothesized that within the tuberiform series speciation has occurred in unspecified cases as a result of interspecific hybridization. Lewis and Epling (1959) developed a strong case for the hypothesis that a series of hybridizations between two species within the spiciform series, and subsequent establishment of a recombinant type was the probable evolutionary origin of *D. gypsophilum*. The putative parental taxa are *D. hesperium* ssp. *pallescens*, which inhabits the oak-woodlands of the Coast Ranges of central California, and *D. recurvatum* of the Atriplex-dominated western San Joaquin Valley. *Delphinium gypsophilum* is morphologically intermediate and occupies an ecologically intermediate habitat, the narrow zone of grasslands between the salt flats and oak-woodlands. Although all three species are diploid, interfertile, intercompatible, have pollen vectors in common, and have overlapping flowering times, they are genetically isolated by their distinct and different habitat preferences. Other possible examples of this mode of speciation in the spiciform series are cited by these same authors who propose that it is very
possibly a common phenomenon among larkspurs.

Grant and Grant stated that *Delphinium nudicaule* and *D. cardinale* must have been evolutionarily derived from bee-pollinated precursors. *Delphinium* is one of nineteen genera in the western United States which are primarily bee-pollinated, but which have one or a few hummingbird-pollinated species. These latter and many other hummingbird-pollinated taxa are part of a large, co-evolved complex in which the taxonomically diverse species have undergone convergent evolution of floral signals; they typically have red, tubular flowers.

The reddish orange flowers of *D. nudicaule* were found to have a predominance of pelargonidin, a red anthocyanidin, and low concentrations of delphinidin, a blue pigment. Many delphinium species are purple and could very possibly also have both red and blue components to their pigmentation. Hummingbirds with their known proclivity for visiting red flowers, may well have provided a selective mechanism for the derivation of red-flowered species from purple-flowered precursors.

*Delphinium luteum* has been considered to be most closely related to *D. nudicaule* since its original circumscription by Heller in 1903. Ewan concurred with this opinion and my data also support the contention that they are closely related. Both of these species share many features, some of which are otherwise unique in the series. The possession of long, thin, tuberous roots is restricted to these two species. Both have relatively straight nectariferous petals, a character that to my knowledge is shared only with *D. cardinale*, the only other hummingbird-pollinated species of the genus. They also have very similar floral and foliar flavonoid complements. The ten flavonoid pigments which comprise the yellow pigmentation of the flowers of *D. luteum* are all present in the flowers of *D. nudicaule*, but the latter has two anthocyanidin-based pigment complexes which mask the yellow, and result in red flowers. Some unexposed portions of the flowers of *D. nudicaule* are a yellow similar to that of the flowers of *D. luteum*.

A relatively simple hypothesis that could account for the origin of a red-flowered *D. nudicaule* from a purple-flowered precursor
involves the mechanism of active selection of red flower color by hummingbirds. There is no such simple explanation that will account for an independent origin of *D. luteum* directly from a presumed blue-purple-flowered precursor, and at the same time satisfactorily account for the many striking similarities it has with *D. nudicaule*. It therefore appears that *D. nudicaule* is in some manner an evolutionary precursor of *D. luteum*. There are two ways in which this could have occurred. *Delphinium luteum* could have arisen directly from *D. nudicaule* through genetic drift, or it could be of hybrid origin with *D. nudicaule* as one of the parents.

The first hypothesis is that *D. nudicaule* is the sole evolutionary precursor of *D. luteum*. This path finds conceptual support in the existence of occasional yellow-flowered individuals in populations of normally red-flowered *D. cardinale* (Lewis et al., 1951; and personal observation). This hypothesis presumes that a permanent genetic change involving the loss of red and blue pigments in at least one individual of *D. nudicaule*, such that a yellow-flowered progeny result. This hypothesis, however, has serious shortcomings. There are at least two differences between *D. luteum* and *D. nudicaule* for which it fails to account. First, it fails to explain the origin of certain floral morphological characteristics of *D. luteum* such as wide bladed lower petals, and more importantly, genetic drift will not account for more amino acids in the nectar of *D. luteum* than are found in *D. nudicaule*.

The second hypothesis, that *D. luteum* is of hybrid origin, with *D. nudicaule* as one parent, is more consistent with the data. Additionally, *D. decorum* appears for several reasons to be the most likely candidate for the second parent. However, due to taxonomic confusion among the blue-flowered tuberiformae, the choice of *D. decorum* as one of the parental taxa is far less certain than that of *D. nudicaule* as the other putative parent. Evidence in support of the hybrid origin hypothesis takes the following two forms. First, *D. nudicaule* and *D. decorum* are indeed interfertile as evidenced by experimental hybridization, and that hybrid offspring are viable and fertile was indicated by the wide range of variation of floral types found in a naturally occurring hybrid swarm ostensibly involving these two species. Secondly, occasional yellow-flowered individuals have
been reported from hybrid swarms of putative *D. nudicaule* x *decorum* parentage in southern Sonoma and northern Marin counties. In addition, this investigation shows that *D. luteum* occupies an intermediate position between *D. nudicaule* and *D. decorum* in morphological, chemical, and ecological characteristics as the following summary shows.

*Delphinium luteum* is intermediate between *D. nudicaule* and *D. decorum* in almost every morphological feature measured, in both absolute size and ratios between features. The foliar flavonoid complements are very similar for all three species, and there is at least one compound shared by *D. luteum* and *D. decorum* that was not found to be present in *D. nudicaule*. The nectar amino acid data are also consistent with the hypothesis of a hybrid origin of *D. luteum* as all of the amino acids in its nectar are found in *D. nudicaule* and three additional ones are found in *D. decorum*. Both *D. luteum* and a putative natural hybrid have two additional amino acids in their nectars that have not been found in either *D. nudicaule* or *D. decorum*. Finally, *D. luteum* occupies a habitat that has characteristics in common with both those of *D. nudicaule* and *D. decorum*. The two known populations of *D. luteum* are in the North Coastal Scrub Community within thirty meters of individuals of *D. decorum*, but are limited to two rocky outcroppings with rock slides that resemble the substrate in which *D. nudicaule* is found to occur.
CONCLUSIONS

The tuberiform series of the genus Delphinium is a group of primarily blue-purple flowered, bumblebee-pollinated, summer-dormant, herbaceous perennials characterized by globose-tuberous roots. Delphinium luteum and D. nudicaule have many characteristics in common that clearly separate them from the rest of the tuberiformae. The many striking differences that separate these species from the more typical members of the series provide strong circumstantial evidence that they represent a coherent evolutionary offshoot within the tuberiformae.

It is reasonable to assume that D. nudicaule became distinct and reproductively isolated from the rest of the tuberiformae by the action of active selection by hummingbirds for red flower color. Hybridization and subsequent fixation of a recombinant type is the most plausible explanation that is both consistent with the data, and which will account for the evolution of a yellow-flowered larkspur in the tuberiform series. I therefore suggest that D. luteum originated as a stabilized recombinant resulting from naturally occurring hybridization involving D. nudicaule and probably D. decorum.


United States Department of Agriculture. 1972. Soil Survey, Sonoma County, California. United States Forest Service and Soil Conservation Service with the University of California Agricultural Experimental Station, pp. 188.