Takhtajan (1972) contended that many morphological discontinuities among related plant taxa are illusory because we commonly compare only adult forms. He suggested that we will discover a greater continuity of form within lineages if we consider ontogenies as well. The application of comparative ontogenetic data to questions of animal phylogeny has a long and sometimes tumultuous history (for review see Gould, 1977). Botanists, however, have only rarely dealt with broad theoretical aspects of the relationship of ontogeny and phylogeny in plants (Takhtajan, 1943, 1969 for review, 1972, 1976; Doyle, 1978). In this study, ontogenetic data together with phylogenetic and ecological information are interpreted in the context of models of ontogeny and phylogeny recently developed by zoologists, to address the evolution of the unique floral form of *Delphinium nudicaule*.

Gould (1977) rekindled interest in the study of ontogeny and phylogeny by his thorough historical treatment of the subject. One of Gould’s contributions was to distinguish between evolutionary processes (e.g., neoteny and progenesis), and their morphological or phylogenetic products (paedomorphosis). He also modified and simplified de Beer’s (1930) categorization of heterochrony (i.e., changes in rates or timing of development) by reducing the basic processes to relative acceleration and retardation. Building on this foundation, Alberch et al. (1979) have developed a framework using size, shape and age as independent variables to illustrate how heterochrony can account for morphological differences among related taxa (Fig. 1). Paedomorphosis (evolutionary juve-

nilization), and its opposite, peramor-

phosis (literally ‘shapes beyond’), can each be produced by three processes: paedo-

morphosis by neoteny, progenesis, and post-displacement; and peramorphosis by acceleration, hypermorphosis, and pre-displacement.

One of the strengths of the Alberch et al. methodology is that it can be applied simultaneously to many arbitrarily chosen developmental processes within an organism. This allows different components of overall form to be conceptually dissected from one another. These can then be inter-

preted in the context of the whole organ-

ism. For example, Alberch and Alberch (1981) discuss the effect of several dissociations, or decouplings, of developmental processes within and among various portions of the body, on the form of the generally progenetic salamander, *Bolitoglossa occidentalis*.

To understand the effect of hetero-

chrony on the evolution of adult forms, it is necessary to compare the size, shape, and age to maturity of related organisms. This is problematic since maturity is not a unitary concept, but rather consists of two distinct phenomena. The ability to reproduce sexually, and a culmination of growth, are separately and together termed maturity. Because of the embryonic sep-

aration of germinal cell lines from somatic tissues in the majority of metazoans, sexual maturity in most animals is a property of whole individual organisms. An animal typically reaches sexual maturity just once, and a culmination of somatic growth is often loosely associated with the onset of sexual maturity. This is not usually the case with plants because of their indeter-
terminate growth form. A single plant can be viewed as a "population" of semi-autonomous vegetative meristems, of which any can potentially become reproductive. Disregarding the problems of what constitutes an individual (ramet vs. genet; Harper, 1977), the shoot component of flowering plants has at least three levels of organization: (1) individual determinate structures, i.e., leaves and flowers (provisionally excepting the gynoecium, which may subsequently develop into a fruit); (2) individual axes, i.e., a stem and its leaves; and (3) systems of axes, i.e., the whole shoot component of a plant or parts of it. One or both notions of maturity can be applied within each level of organization. As is true of hierarchies in general, higher levels of organization of the flowering plant body have emergent properties not predicted by lower levels.

It is necessary to accommodate these and other differences between plants and animals in order to use the Alberch et al. methodology to investigate morphological evolution in plants.

To facilitate ontogenetic comparison among flowers of different species, the organization of an individual flower may be compared conceptually to that of a whole animal. Both exhibit determinate growth and have distinct reproductive and non-reproductive structures. Insofar as somatic tissues of animals can be seen as analogous to the sporophytic tissues of flowers, the germinal tissues of animals have megand microgametophytes as their floral analogs. The analogy is meant only to illustrate how both definitions of maturity can be applied to flowers; beyond this nothing is implied. That flowers are appropriate subjects for study by this methodology is a conceptual cornerstone of this investigation.

Delphinium is a large circumboreal genus noted for its strongly zygomorphic, generally blue-purple flowers specialized for pollination by bumblebees (Proctor and Yeo, 1972; Faegri and van der Pijl, 1979). In California there are two red-flowered species in separate taxonomic series (Ewan, 1945), both of which are considered not only to be specialized for pollination by hummingbirds, but also to be evolutionarily derived from bumblebee-pollinated ancestors (Grant and Grant, 1968). One of these, Delphinium nudicaule, has strongly tubular flowers that are very different in appearance from those of other larkspurs. However, they bear a striking resemblance to the buds of many other Delphinium species, for example D. decorum (Fig. 2). It is thus possible that morphological differences associated with the adaptive switch from bumblebee- to hummingbird-pollination originated as features of "juvenile" (buds) ancestors that became incorporated into the "adults" (flowers) of the derived form. If so, then D. nudicaule flowers can be considered paedomorphic.

This report has two primary goals. The first is to demonstrate quantitatively that D. nudicaule flowers are more similar to the buds than to the flowers of other, gen-
eralized blue or purple-flowered larkspurs of which *D. decorum* is a representative. The second goal is to discriminate among three alternative processes that can produce such paedomorphic descendants. Neoteny, progenesis, and post-displacement are regarded as competing explanatory hypotheses (Fig. 1), even though it is recognized that combinations of these and other processes cannot be ruled out a priori.

**MATERIALS AND METHODS**

Plants from two populations of each species were sampled in spring 1979 from southern Sonoma County, California. Both populations of *D. decorum*, on Bodega Head and in Cheney Gulch, are in the vicinity of the type locality. The range of *D. decorum* extends along the California coast from Monterey to Humboldt counties, and is entirely within the range of *D. nudicaule*. *Dephinium nudicaule* was sampled in Coleman Valley and in Crane Canyon. These are both near the middle of its range, which extends from San Luis Obispo County, California in the south, to Josephine and Curry counties of southern Oregon in the north (Ewan, 1945).

The interval of time between meiosis and anthesis of the most mature anther was inferred from logistic growth curves generated both from potted plants grown under relatively uniform conditions in Berkeley, and from naturally occurring plants in the field. Sepal spur lengths were measured daily on the potted plants in Berkeley, and two to four times per week in the field. The best fit logistic curve was fitted to the data for both potted and field grown plants of each species (Appendix). To determine the sizes of buds at which meiosis was occurring in the pollen mother cells of the largest anthers, buds were fixed in FAA, stained with acetocarmine (Radford et al., 1974), dissected and examined with a microscope (*D. decorum*, *N* = 14; *D. nudicaule*, *N* = 17). These and the spur lengths on the first day of anthesis (*N* = 19 for both species) were used to generate the relative times at which meiosis and anthesis occurred. To facilitate comparison between groups the average time at meiosis of each group was set at time zero. Advantages of this method are that no absolute time zero is necessary, and that the only data required are a series of lengths and the intervals of time between consecutive measurements. A drawback is that although the relative times are accurate, the absolute times for specific sizes are meaningless.

Measurements were taken of 20 floral characters on 30 open flowers and 22 characters on 30 buds, 15 from each population, of each species collected in April 1979 (Figs. 3, 4). Floral measurements consisted of lengths, angles, and ordered multistate information. Except for angle of flower openness, which was measured in the field, all measurements were made on material fixed in FAA. Times were calculated for each of the buds from the logistic curves of the field grown plants, and
Fig. 3. Illustrations of: front (A, E), and side (B, F) views of *D. decorum*, and *D. nudicaule* flowers; left upper petals (C, G); and left lower petals (D, H). All are to same scale, as marked on figure. The orientation of the spurs in B, and F, are the average angle of 25 flowers measured in the field (Guerrant, 1978).

The results of the discriminate function analysis of the flowers and buds of both species demonstrate that the flowers of *D. nudicaule* resemble the buds of both species more closely than they do the flowers of *D. decorum* (Fig. 5). The eight variables used to distinguish the groups are listed in the order selected, along with the coefficients of each to the three canonical variables (Table 1).

The interval of time between meiosis and anthesis in *D. nudicaule* is slightly longer than that in *D. decorum*, both in field grown plants and in potted plants grown under relatively uniform conditions in Berkeley (Fig. 6). In the field, both *D. nudicaule* and *D. decorum* took almost twice as long to mature their pollen as they did when grown in pots in Berkeley. The relationship between the species, however, is similar under both sets of growing conditions.

Allometric analyses indicate that homologous parts of the flowers of the two species have generally similar shapes at comparable sizes during ontogeny (Table 2). For example, although the right lateral sepals are significantly longer and wider in *D. decorum* flowers than in *D. nudicaule* flowers (Table 3), the slopes and intercepts of log transformed data of the sepal lengths and widths of the buds are not...
FIG. 5. Plot of the first and second canonical variables for *D. decorum* buds (hollow circles), and flowers (stippling, and solid circles), and *D. nudicaule* buds (hollow triangles), and flowers (vertical lines).

sequence, even this feature of *D. nudicaule* flowers resembles a bud stage of *D. decorum*.

Perhaps the most striking difference between the flowers of the two species is in the lower petals (Fig. 3d, h; Table 3). The petals have distinct claw and blade portions, with a "knob" at the junction. The length and width of the claw portions of

statistically separable (Fig. 7, Table 2). This means that for the range of bud sizes sampled the right lateral sepal of both species at any given size have similar shapes (i.e., length to width ratios). The difference in adult sizes and shapes can be attributed to the slower growth rate of *D. nudicaule* (Fig. 8, Table 2).

A seemingly qualitative shape difference between the mature right lateral sepal s of *D. nudicaule* and *D. decorum* is that the former species has cupped sepals, while the sepals of the latter are more planar. The sepals of *D. decorum* in the bud become increasingly more cupped until late in ontogeny when they flatten out shortly before anthesis (Fig. 9). As a con-
FIG. 6. Best fit logistic curve for *D. nudicaule* (triangles) and *D. decorum* (circles) grown in the field (36.9 and 31.6 days respectively; *t* = 2.764; *P* < .01), and under relatively uniform conditions in pots in Berkeley (17.6 and 15.8 days; *t* = 2.628; *P* < .01). The ordinate is the sepal spur length in mm, the abscissa time in days from meiosis. The circles and triangles indicate the average time of anthesis.

The lower petals cannot be separated statistically, so the difference in appearance seems to be related primarily to the difference in blade sizes. The adult blade lengths and widths have completely non-overlapping ranges. Although statistically separable, there is considerable overlap in shape of this structure between species during development (Table 2; Fig. 10). Once again, although the two species go through ap-

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**Table 2.** Regression statistics for bivariate comparisons. For those characters where regressions were run on log transformed data, the antilog of the intercept is given in mm for convenience.

| Characters                        | *D. decorum* | *D. nudicaule* | *t* (*P*) | *D. decorum* | *D. nudicaule* | *t* (*P*) |
|----------------------------------|--------------|----------------|-----------|--------------|----------------|-----------|
|                                  | Slope SE     | Slope SE       |           | (log int.) SE| (log int.) SE  |           |
| Rt. lat. sepal length (b) ×      | 0.663 0.035  | 0.616 0.023    | 1.120     | 0.087        | 0.126          | -1.237    |
| lg length (b) × lg width (c)     | (N.S.)       | 1.22           | 1.34      | (N.S.)       |                |
| Rt. lat. sepal time × length (b) | 0.350 0.012  | 0.212 0.012    | 7.998     | 1.874        | 1.898          | -0.082    |
| Lower pet. blade length (m) ×     | 1.079 0.046  | 0.878 0.056    | 2.778     | (-0.091)     | 0.024          | -2.574    |
| lg length (m) × lg width (n)     | 0.81         | 0.97           |           |              |                |
| Lower pet. blade time × length (m)| 0.195 0.010  | 0.074 0.007    | 9.471     | 0.855        | 0.531          | 1.522     |
| Nect. petal length (h) × lg spur | 0.619 0.014  | 0.655 0.018    | -1.552    | (-0.229)     | 0.200          | 1.648     |
| limb. length (i)                 | (N.S.)       | 1.69           | 1.58      | (N.S.)       |                |
| Nect. Petal time × spur length (h)| 0.592 0.023  | 0.474 0.034    | 2.848     | -1.146       | 0.346          | -0.352    |
| Nect. Petal lg spur length (h) ×  | 0.963 0.013  | 0.900 0.013    | 3.422     | (-0.287)     | 0.010          | -12.778   |
| lg nect. portion (j)             | 0.52         | 0.78           |           |              |                |

* = *P* < .05; ** = *P* < .01; *** = *P* < .001.
NEOTENIC FLOWER

proximately the same series of shapes at similar sizes, the great discrepancy in adult sizes can largely be accounted for by the slower growth rate of *D. nudicaule* (Table 2; Fig. 11).

Not all of the features of *D. nudicaule* flowers resemble developmental stages of *D. decorum*. The upper or nectariferous petal of *D. nudicaule* (Fig. 3g) is not only larger than that of *D. decorum* (Fig. 3c), but also exhibits other differences. The allometric relationships of the nectariferous (Fig. 4h) to non-nectariferous (Fig. 4i) limbs are statistically indistinguishable (Table 2). The difference in size, and therefore overall shape (ratio of limb lengths) once again can largely be explained by the different growth rates (Table 2). However, this time it is *D. nudicaule* that grows faster. Nonetheless, there is a difference within the nectariferous limb that cannot be accounted for by rate differences. A regression of the nectariferous portion of the nectariferous limb (Fig. 4j) to its total length (Fig. 4h) in buds shows both the slopes and intercepts to be different (Table 2, Fig. 12). This means that proportionately more of the nectariferous limb of *D. nudicaule* is given to the saccate portion, which is here assumed to be related to nectar production. At any given size, a petal of *D. nudicaule* will presumably be able to produce more nectar than one of *D. decorum*.

DISCUSSION

Before the primary goals can be discussed, two premises that underlie this study will be addressed. The first is that the floral form of *D. nudicaule* is likely derived from a generalized bumblebee-
### Table 3. Descriptive statistics for characters measured on fully open, mature flowers.

| Character                        | Sp.  | Mean  | St. dev. | Range          | N  | t/P   |
|----------------------------------|------|-------|----------|----------------|----|-------|
| **Angle of flower**              | nudi | 42    | 8.1      | 25–55          | 24 | 36.086|
| **Openness (u)**                 | dec  | 177   | 16.5     | 145–220        | 26 | ***   |
| in 5° intervals                  |      |       |          |                |    |       |
| **Flower width (a)**             | nudi | 10.37 | 1.11     | 8.6–13.4       | 30 | 24.637|
| **in mm**                        | dec  | 26.93 | 3.51     | 16.7–33.4      | 30 | ***   |
| **Rt. lat. sepal length (b)**    | nudi | 10.29 | 1.25     | 8.7–13.3       | 28 | 8.505 |
| **in mm**                        | dec  | 13.81 | 1.81     | 10.5–17.6      | 29 | ***   |
| **Rt. lat. sepal width (c)**     | nudi | 5.29  | 0.88     | 4.0–7.8        | 28 | 5.026 |
| **in mm**                        | dec  | 6.77  | 1.30     | 4.2–9.4        | 29 | ***   |
| **Rt. lat. sepal depth (d)**     | nudi | 1.90  | 0.42     | 1.3–2.6        | 25 | −13.664|
| **in mm**                        | dec  | 0.47  | 0.32     | −1.0–1.2       | 26 | ***   |
| **Up. sepal spur length (e)**    | nudi | 16.56 | 1.47     | 14.3–19.8      | 30 | −5.685|
| **in mm**                        | dec  | 14.38 | 1.50     | 12.0–17.6      | 30 | ***   |
| **Up. sepal hood length (f)**    | nudi | 10.65 | 1.45     | 9.0–15.0       | 30 | 5.722 |
| **in mm**                        | dec  | 13.09 | 1.84     | 10.5–16.4      | 30 | ***   |
| **Up. sepal hood width (g)**     | nudi | 8.38  | 1.59     | 5.6–11.9       | 30 | −4.344|
| **in mm**                        | dec  | 6.79  | 1.23     | 4.9–9.4        | 30 | ***   |
| **Up. petal upper limb length (h)** | nudi | 17.02 | 1.11     | 15.0–19.3      | 29 | −10.026|
| **in mm**                        | dec  | 13.62 | 1.47     | 11.5–17.0      | 30 | ***   |
| **Up. petal upper limb width (i)** | nudi | 12.56 | 0.88     | 11.0–14.1      | 30 | −13.718|
| **in mm**                        | dec  | 9.39  | 0.91     | 7.8–11.2       | 30 | ***   |
| **Upper petal angle (q)**        | nudi | 14    | 5.9      | 5–25           | 30 | 15.820|
| **in 5° intervals**              | dec  | 43    | 8.0      | 25–55          | 30 | ***   |
| **Lower petal pitch**            | nudi | 51    | 17.2     | 15–85          | 30 | 14.254|
| **Angle (s)** in 5°              | dec  | 106   | 12.0     | 80–140         | 29 | ***   |
| **Lower petal roll angle**       | nudi | 36    | 17.9     | −30–70         | 30 | 5.768 |
| **(t) in 5° intervals**          | dec  | 61    | 15.1     | 25–80          | 29 | ***   |
| **Lower petal claw length (k)**  | nudi | 5.54  | 0.59     | 4.8–7.7        | 30 | −0.854|
| **in mm**                        | dec  | 5.41  | 0.64     | 4.0–7.0        | 29 | N.S.  |
| **Lower petal claw width (l)**   | nudi | 1.24  | 0.17     | 1.0–1.7        | 30 | 1.040 |
| **in mm**                        | dec  | 1.29  | 0.22     | 0.9–1.8        | 29 | N.S.  |
| **Lower petal blade length (m)** | nudi | 3.21  | 0.41     | 2.3–4.0        | 30 | 17.888|
| **in mm**                        | dec  | 6.44  | 0.90     | 4.6–8.3        | 29 | ***   |
| **Lower petal blade width (n)**  | nudi | 2.38  | 0.35     | 1.8–3.2        | 30 | 19.513|
| **in mm**                        | dec  | 5.86  | 0.91     | 4.2–7.2        | 29 | ***   |
| **Lower petal blade Sinus (o)**  | nudi | 1.31  | 0.30     | 0.7–1.8        | 30 | 11.201|
| **in mm**                        | dec  | 2.76  | 0.63     | 1.6–3.9        | 28 | ***   |
| **Lower petal knob (v)**         | nudi | 4.2   | 1.4      | 1–7            | 30 | 19.548|
| **in “states” 1–9**              | dec  | 9.0   | 0.0      | 9–9            | 29 | ***   |

*** = \( P < .001 \).
with the predominantly neotropical distribution of hummingbirds, they suggest that within these groups hummingbird pollination is derived. Both *D. nudicaule* and *D. decorum* are members of the tuberiform series, which is almost exclusively limited to extreme western North America (Ewan, 1945). In addition to *D. decorum*, the tuberiform series also contains 12 other bumblebee-pollinated species. All of these have flowers that are very similar not only to those of one another, but also to those of many species in practically all other series in both the New and Old World. By applying the criterion of outgroup analysis (see Stevens, 1980) at the series level (using any series with flowers that resemble either of the two species in this study as the out-group), it is reasonable to conclude that within the tuberiform series, the floral form of *D. nudicaule*, which is unique within the genus, is derived and that the bumblebee-pollinated type is ancestral and generalized. This conclusion is similar to that reached by Grant and Grant (1968), who state that *D. nudicaule* "must have diverged from a bee-flowered ancestor."

Ideally, a derived taxon should be compared directly to its sister group that shows the ancestral condition. However, because the sister group of *D. nudicaule* is not known, *D. decorum* was examined as representing the hypothetical ancestral floral form. Both *D. nudicaule* and *D. decorum* are diploids with \( n = 8 \) (Lewis et al., 1951). The genetic distance between them is likely not great; naturally occurring hybrid swarms between these two species have been reported (Munz, 1959; Howell, 1970; Santana, 1975; Guerrant, 1978), and viable seed can be obtained from experimental crosses (Santana, 1975; Guerrant, unpubl.).

A typical *Delphinium* flower (Figs. 2c, 4a–d) has five widely spreading, generally blue-purple, petaloid sepals that surround the two pairs of highly modified petals which in turn conceal the stamens and pistils. The orange-red flowers of *D. nudicaule* (Figs. 2a, 4e–h) appear tubular because the sepals do not spread widely apart at anthesis, and are curved in transsection. In a typical larkspur, the greatly expanded blades of the two clawed lower petals meet along the midline of the zygomorphic flower. These are used as a landing platform by bumblebees (Laverty, 1980), and apparently serve also to deny all but the heaviest and strongest flower visitors access to the nectar. In *D. nudicaule*, the lower petals have very small (seemingly vestigial) blades, positioned off
to the side of the flower, which do not physically obstruct access to the nectar. The presumed ancestral function of excluding illegitimate flower visitors by the lower petal blades is apparently supplanted by the tubular form, red color, and downward pointing angle at which the flower is positioned. These features combine to seemingly make *D. nudicaule* nectar relatively inaccessible to bumblebees.

The initial goal of this study was to quantify the relative similarity of *D. nudicaule* flowers to the buds and flowers of *D. decorum*. A discriminant function analysis of a broad array of floral characters supports the hypothesis that *D. nudicaule* flowers are more similar to *D. decorum* buds than to its flowers. It follows that if *D. nudicaule* is actually derived from a taxon with flowers similar to those of *D. decorum* then its flowers can be considered to have become paedomorphic, or evolutionarily juvenilized in appearance.

Assuming that *D. nudicaule* flowers are generally paedomorphic, the next goal is to discriminate among the various possible processes by which this could have come about. To do this, it is necessary to compare the ages at maturity of the two taxa. *Delphinium nudicaule* required a slightly longer period to mature its pollen both under field and uniform garden conditions. It must be emphasized I do not suggest that morphological differentiation of the flowers begins with meiosis. Rather, meiosis is simply a convenient, easily distinguished, discrete early developmental event that is used as a marker. Because both progenesis and post-displacement entail a reduction in the time required to mature structures in question, (α to β interval, Fig. 1), they are effectively rejected as hypotheses. Neoteny then becomes the primary hypothesis for the process that produced the novel floral form; and this was presumably selected for by hummingbirds.

If *D. nudicaule* flowers are of “pure” neotenic origin, all sporophytic floral parts would then be expected to grow through the same series of shapes, though at a slower rate, than those of *D. decorum* (Alberch et al., 1979; Fig. 1). Those features that most noticeably distinguish *D. nudicaule* flowers from *D. decorum* and other typical larkspur flowers are its forward pointing cupped sepals and its small lower petal blades. Allometric analyses indicate that the lateral sepals of both species grow through size-shape trajectories statistically indistinguishable from one another throughout the range of sizes measured. The size-shape paths of lower petal blades, though statistically separable, overlap broadly during development. In other words, when these structures are the same size they have approximately the same shapes. Furthermore, the cupped aspect of *D. nudicaule* sepals, and their forward pointing orientation in the flower, represent conditions which in *D. decorum* are seen only in the buds. The great differences in adult sizes of these features, and to varying degrees in shape also, can be attributed to the conspicuously slower growth rate of *D. nudicaule*. Hence, neoteny accounts, to a considerable degree, for the externally visible differences in shape that distinguish the flowers of these two species.

These features, along with the red color, seem to serve both to attract hummingbirds, and make the flowers less suitable nectar sources for bumblebees. The evolution of red flower color from a blue-purple ancestor requires no explanation beyond a traditional view of selection by hummingbirds acting on existing variation. *Delphinium nudicaule* flowers contain both red and blue pigment complexes that are believed to be based respectively on the anthocyanidins pelargonidin and delphinidin (Guerrant, 1978). Hypothetically its immediate ancestor contained these also, though with relatively more blue than red pigment, compared to *D. nudicaule*.

Though similar, *D. nudicaule* flowers are not identical to the buds of *D. decorum*. This should come as no surprise since mosaic patterns of evolution, in which different portions of organisms evolve separately, are widely acknowledged (Mayr, 1963; Dobzhansky et al.,
Whereas the externally visible portions of the flowers seem generally neotenic, the nectariferous petals, which produce the pollinators' reward, are not. The nectariferous and non-nectariferous limbs have a comparable allometric relationship to one another in both species. However, those of *D. nudicaule* are larger and have a different shape (ratio of nectariferous to non-nectariferous limb lengths) since they grow faster than those of *D. decorum*. This can be interpreted as a peramorphic change that occurred by a combination of the processes of acceleration and hypermorphosis (Fig. 1). Within the nectariferous limb, both the slope and intercept are different between species in a regression of the nectariferous portion to the total length. This means that the nectariferous petals of *D. nudicaule* are not only larger in absolute terms, but proportionally more of them are devoted to nectar production. Additionally, while both the sepal spurs and nectariferous limbs of the upper petals of *D. nudicaule* are longer than those of *D. decorum*, the petals seem to have become disproportionately larger. Although the differences are not statistically significant, the average petal spur lengths are greater than the sepal sacs that contain them in *D. nudicaule*, while they are smaller in *D. decorum*. This suggests that either there were differential selective pressures on these structures, or they had different sources and magnitudes of variation associated with their origin.

Together these differences should account for the greater nectar production in *D. nudicaule* which is consistent with its pollination syndrome. Hummingbird-pollinated flowers characteristically produce more nectar per flower than do bumblebee-pollinated flowers (Baker and Baker, pers. comm.). The concentration and composition of sugar in the nectar of *D. nudicaule* are also consistent with predictions based on a large sample of nectar from flowers with many different pollination syndromes (Baker and Baker, 1979, in press). *Delphinium nudicaule* produces copious dilute (34% sucrose equivalents, wt. to total wt.), sucrose-dominated nectar (Guerrant, 1978). Although 34% is near the upper limit of sugar concentrations found in hummingbird-pollinated species, *D. nudicaule*, and *D. cardinale*, the other red-flowered hummingbird pollinated larkspur, have the lowest nectar sugar concentrations found in all larkspurs surveyed (Baker and Baker, 1979, in press, and pers. comm.; Guerrant, unpubl.). Many of the bumblebee-pollinated species, for example *D. decorum* (47%), have nectar that averages around 50% sugar.

In summary, the juvenile appearance of *D. nudicaule* flowers relative to those of *D. decorum*, can in part be accounted for, and was most likely produced by, the process of neoteny. In other words, although the flowers of both species have comparable times to maturity, those of *D. nudicaule* do not progress as quickly through their mutual series of shapes, so their flowers end up looking like buds of *D. decorum*. The resulting tubular flower shape represents convergent evolution onto a floral form that is commonly visited by hummingbirds. The ability to produce the increased nectar reward, which seems clearly associated with the switch from bumblebee to hummingbird pollination, can be attributed to a localized combination of the processes of acceleration and hypermorphosis of the nectariferous petal. In addition, the morphological trend toward greater nectar production potential has been augmented by a novel allometric reorganization of the nectariferous limb of the nectariferous petal.

Implicit in this study is an opportunity to provide a first approximation evaluation of the Alberch et al. (1979) methodology at elucidating morphological evolution in plants. Perhaps the most immediately apparent value of this methodology is that it provides a clear definition of, and therefore distinction among, components of form. Using these sorts of developmental parameters in conjunction with allometry, 'null' hypotheses of expected forms can be generated. Comparing these to empirical results in an ecolog-
ical and phylogenetic context may then provide further insight into the nature and role of adaptation and natural selection in evolution (see Alberch et al., 1979; Alberch, 1981).

At least in this case, the morphological changes in structures mediated by different processes correspond closely to their presumed changes in function. It can be hypothesized that if an initial neotenic event occurred, it would simultaneously have created the tubular shape characteristic of hummingbird-pollinated flowers, and rendered the nectar less accessible to bumblebees. This, in a sense, may have constituted the 'key' adaptation to hummingbird pollination. It would have provided the basic framework upon which subsequent selection by hummingbirds has fine tuned the change in pollination syndromes. Comparative developmental studies, it seems, provide a rich conceptual bridge between ecology and evolution, in a manner that approaches Van Valen's (1974) aphorism, "evolution is the control of development by ecology."

Finally, although Alberch et al. did not present their methodology as a 'theory of ontogeny and phylogeny', it does provide a coherent framework, which when taken in conjunction with ecological and phylogenetic information, can be used to generate falsifiable hypotheses about the origin of novel forms and the evolution of shape in general. For example, it has been hypothesized that a reduction in the time required to flower and produce seed was a primary selective force that led to the evolution of autogamy in species of Clarkia, (Moore and Lewis, 1965), Leavenworthia (Lloyd, 1965; Solbrig and Rollins, 1977), and Limnanthes (Arroyo, 1973). If so, it is possible that the small flowers that characterize these and some other derived autogamous species may simply be a result of a progenetic origin (Fig. 1). An increased appreciation of the constraints development imposes on morphological evolution may ultimately yield insights into the origins of morphological variation, and in turn, the nature and relationship of adaptations and their consequences (see Gould and Lewontin, 1979).

**Summary**

The flowers of the derived hummingbird-pollinated *D. nudicaule* resemble the buds of the generalized bumblebee-pollinated species much more closely than they do their flowers. *Delphinium nudicaule* flowers then may be considered paedomorphic, in that the adults (flowers) of the derived species resemble the juveniles (buds) of the ancestral type. This study brings to bear current ideas, developed by zoologists, about the relationship of ontogeny and phylogeny in an attempt to explain the processes by which the morphological differences that accompanied the evolution of *D. nudicaule* flowers may have originated. Comparative allometric and growth rate data suggest that relatively few developmental perturbations are required to account for the bulk of the morphological differences observed. The externally visible portions of the flower, which apparently function both to attract hummingbirds and make the nectar less accessible to bumblebees, seem generally neotenic in origin. However, the nectariferous petal, which produces the pollinator's reward, is not juvenilized. Rather, it has recapitulated the ancestral shape and become peramorphic by a combination of the processes of acceleration and hypermorphosis. It is suggested that the dissection of component processes that accompany morphological change during evolution, when used in an ecological and phylogenetic context, allows a more critical understanding of the origin of morphological variation and the nature of adaptations and their consequences.

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APPENDIX

The growth of the sepal spur in length can be described by the logistic:

\[ y = \frac{k}{1 + be^{-at}} \]

where \( y \) is sepal spur length in mm; \( k \), the ceiling length of \( y \); \( a \), growth parameter; \( b \), the time shift parameter; and \( t \), the time in days. Logarithmic differentiation yields

\[ \frac{dy}{dt} = \frac{a}{k} - \frac{ay}{k} \]

Because the sepal lengths were measured at discrete intervals of time, the left hand side was approximated by

\[ \frac{y_t + \Delta t - y_t}{\Delta t} = \frac{1}{2} \left( \frac{y_t + \Delta t - y_t}{2} \right) \]

Then ordinary least squares was used on the model

\[ z_t = \beta + \gamma y_t + u_t \]

where \( \beta \) is the estimate of \( a \), \( -\beta/\gamma \) estimates \( k \), and \( u_t \) is a random error term.

Given the estimated logistic curve, to each length at meiosis was associated at time of meiosis and similarly with anthesis. Since \( t_{\text{anath}} - t_{\text{melo}} \) was the only variable of concern, the time shift factor \( (b) \), which positions the logistic curve on the time axis, was irrelevant to the analysis.

Given that the \( t \) of anthesis and the \( t \) of meiosis are distributed with approximately equal variances, a standard t-test was used to compare \( t_{\text{anath}} - t_{\text{melo}} \) interval between the two species. This test presupposes that meiosis and anthesis are independent events within and between species. Lack of correlation between species is clear. However, it is not possible to test for correlation of \( t_{\text{anath}} - t_{\text{melo}} \) within a species since observing \( t_{\text{melo}} \) kills the flower.