

# Origin of floral isolation between ornithophilous and sphingophilous plant species

(mechanical isolation/ethological isolation/allopatric speciation/*Aquilegia*/*Ipomopsis*/*Diplacus*)

VERNE GRANT

Department of Botany, University of Texas, Austin, TX 78713

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**ABSTRACT** Three plant groups in temperate western North America contain closely related ornithophilous and sphingophilous species: the *Aquilegia formosa*/*Aquilegia caerulea* group (Ranunculaceae), the *Ipomopsis aggregata* group (Polemoniaceae), and the *Diplacus longiflorus* group (Scrophulariaceae). The ornithophilous and sphingophilous species are products of allopatric speciation on the diploid level. Geographical races which are adapted to one class of pollinators in one area where these pollinators are abundant and effective and to another class of pollinators in another geographically isolated area (pollination races) represent a probable intermediate stage in the process of allopatric speciation. Mechanical and ethological isolation (collectively, floral isolation) is a byproduct of the divergence in pollination systems. Selection for reproductive isolation *per se* has not played any detectable role in the origin of the floral isolation in the three plant groups.

Three genera in temperate regions of western North America contain hummingbird-pollinated species with ornithophilous floral and inflorescence characters and closely related hawkmoth-pollinated species with sphingophilous characters. The genera are *Aquilegia* (Ranunculaceae), *Ipomopsis* (Polemoniaceae), and *Diplacus* (Scrophulariaceae); and the species groups are the *A. formosa*/*A. caerulea*, *I. aggregata*, and *D. longiflorus* groups. These groups have been extensively studied by various botanists, including myself, from the standpoints of systematics, ecology, pollination, cytogenetics, and fertility relationships. Abundant information is thus available for drawing plausible conclusions about evolution in these species groups.

Floral isolation—mechanical and ethological isolation at the stage of pollination—is associated with the differentiation into ornithophilous species and sphingophilous species in *Aquilegia* and *Ipomopsis* and probably also in *Diplacus*. Therefore we can learn something about the mode of origin of floral isolation from a study of these plant groups.

Reproductive isolating mechanisms are known to arise in two ways: as byproducts of divergence and as products of selection for reproductive isolation *per se*. The first mode is general. The second mode comes into play as a reinforcement of the first mode, but does so only under special conditions, and then it affects mainly premating barriers (1, 2). Both modes have been considered as theoretical possibilities for floral isolation, but the mode of origin has never been identified and documented in any particular plant group.

The two problems—divergence in the pollination system and formation of a floral isolating mechanism—are both problems in the general field of plant speciation. Diverse modes of speciation occur in higher plants (3). The task before us is to determine what speciation processes come into play in the development of the divergent pollination systems

and the floral isolation. Each species group provides strong indications in itself. But the three distantly related groups when considered together provide a broader data base to support the conclusions.

## MATERIALS

The three species groups, though distantly related and belonging to different families, have a number of features in common. The plants are outcrossing diploid perennials with showy flowers, being either perennial herbs (*Aquilegia*, *Ipomopsis*) or soft-wooded shrubs (*Diplacus*). The three groups are widely distributed in mountainous areas of western North America. In each group, as already mentioned, some component species are ornithophilous and others are sphingophilous. The sphingophilous species generally occur in an elevational zone above the ornithophilous species in the three groups.

The ornithophilous and sphingophilous species occur sympatrically in some areas without hybridizing, but they hybridize in other areas. Internal sterility barriers between species are known to be weak in each group (4–6). Reproductive isolation between sympatric or parapatric species in nature is therefore determined mainly by external barriers. The external barriers are ecological, seasonal, and floral isolation, working in concert. They effectively prevent hybridization in some situations in nature but not in others (7, 8).

Each group is very variable and systematically complex, partly as a result of natural hybridization. The taxonomy of *Aquilegia* (9) and *Ipomopsis* (5, 10, 11) is more or less stabilized. The ornithophilous and sphingophilous taxa of these two groups are listed in Table 1. However, there is no generally accepted classification system of *Diplacus* at present. Consequently it is necessary to make some taxonomic judgments regarding *Diplacus* for use in this paper.

Taxonomic opinion is divided as to whether *Diplacus* should be treated as a section of *Mimulus* or as a small segregate genus. I follow McMinn (6) in viewing *Diplacus* as a distinctive satellite of *Mimulus* and in favoring generic segregation. Within *Diplacus*, the number of species recognized varies widely from 2 to 14, depending on the author. On this question I favor an eight-species treatment similar to but different in certain respects from that of Pennell (12). Six of the eight species that I recognize are either ornithophilous or sphingophilous and hence are relevant to the present study. These six species are listed in Table 1. The other two species are *Diplacus clevelandii* (bee-pollinated) and *Diplacus grandiflorus* (pollination mode uncertain). Discussion of the taxonomy of *Diplacus* beyond this short but necessary summary lies beyond the scope of this paper.

## RESULTS

**Pollination Systems and Floral Isolation.** The ornithophilous flowers of the three species groups have floral and inflorescence characters that correspond to the mouthparts and foraging habits of western American hummingbirds. Such

Table 1. Ornithophilous and sphingophilous taxa of the three species groups

Taxa	Range
<i>Aquilegia formosa</i> /A. <i>caerulea</i> group (Ranunculaceae)	
Ornithophilous members ( <i>A. formosa</i> subgroup)	
<i>A. formosa</i> , including <i>A. formosa</i> var. <i>truncata</i>	Alaska to Montana and California; var. <i>truncata</i> in Sierra Nevada and southern California mountains
<i>A. flavescens</i>	Alberta to Oregon and Utah
<i>A. eximia</i>	California Coast Range
<i>A. shockleyi</i>	Eastern Mojave Desert mountains
<i>A. desertorum</i>	Northern Arizona
<i>A. triternata</i>	Eastern Arizona to New Mexico
<i>A. elegantula</i>	Southern Rocky Mountains
Sphingophilous members ( <i>A. caerulea</i> subgroup)	
<i>A. pubescens</i>	Crest of Sierra Nevada, California
<i>A. scopulorum</i>	Nevada and Utah
<i>A. chrysantha</i>	Arizona, New Mexico, and northern Mexico
<i>A. longissima</i>	Southwestern Texas to northern Mexico
<i>A. chaplinei</i>	Guadalupe Mountains on the Texas–New Mexico state line
<i>A. hinckleyana</i>	Presidio Co., southwestern Texas
<i>A. caerulea</i>	Widespread in Rocky Mountain region
<i>Ipomopsis aggregata</i> group (Polemoniaceae)	
Ornithophilous members	
<i>I. aggregata</i> ssp. <i>aggregata</i>	Eastern Washington to Utah and Colorado
<i>I. aggregata</i> ssp. <i>formosissima</i>	Pacific slope and Arizona to New Mexico
<i>I. aggregata</i> ssp. <i>bridgesii</i>	Southern Sierra Nevada, California
<i>I. aggregata</i> ssp. <i>collina</i>	East slope of Rocky Mountains of Colorado and New Mexico
<i>I. aggregata</i> ssp. <i>carmenensis</i>	Coahuila, Mexico
<i>I. arizonica</i>	Pinyon–juniper zone in southwestern U.S.
Sphingophilous members	
<i>I. tenuituba</i> , including ssp. <i>tenuituba</i> and <i>latiloba</i>	Subalpine zone from eastern Oregon to Colorado and northern Arizona; ssp. <i>tenuituba</i> in northern part and ssp. <i>latiloba</i> in southern part of area
<i>I. aggregata</i> ssp. <i>candida</i>	High plains and adjacent eastern slopes of Rocky Mountains in Colorado and northern New Mexico
<i>I. macrosiphon</i> (formerly treated as a subspecies of <i>I. tenuituba</i> )	High montane zone in southern Arizona and southern New Mexico
<i>Diplacus longiflorus</i> group (Scrophulariaceae)	
Ornithophilous members	
<i>D. parviflorus</i>	Southern California islands
<i>D. puniceus</i>	Coastline of southern California and adjacent Baja California and on Santa Catalina Island
<i>D. longiflorus</i> ( <i>sensu</i> McMinn, not <i>sensu</i> other authors)	Chaparral zone of southern California
<i>D. aurantiacus</i> (including <i>D. australis</i> of McMinn as a subspecies)	Low elevations from Oregon to Baja California
Sphingophilous members	
<i>D. calycinus</i>	Middle elevations in mountains from southern Sierra Nevada to southern California
<i>D. aridus</i>	Interior mountains of San Diego Co., California, and adjacent Baja California

The sources for the taxonomic information are as follows: *Aquilegia*, ref. 9; *Ipomopsis*, refs. 5, 10, and 11; and *Diplacus*, refs. 6 and 12 and unpublished data.

characters include flower color (red, red and bright yellow, or orange), orientation of flowers in an open inflorescence, daytime nectar production, length and width of floral tube (corresponding to hummingbird mouthparts), and pollen deposition mechanism. Similarly, the flowers of the sphingophilous taxa correspond to the characteristics and habits of western American hawkmoths in many ways: in color (white or pale colors), vespertine and nocturnal nectar production, fragrance, orientation, length and width of the floral tube (suitable for a long slender proboscis), and pollen deposition mechanism.

Field observations indicate that the ornithophilous flowers of the three species groups are pollinated primarily by

western American hummingbird species, while the sphingophilous species are pollinated mainly by *Hyles lineata* and other hawkmoths (Sphingidae). The primary pollinators are listed in Table 2. Of course, the details are more complex, as described in the original literature reports (also listed in Table 2), since hummingbirds sometimes visit sphingophilous flowers, hawkmoths sometimes visit ornithophilous flowers, and bees often visit both types of flowers. These complicating details refer to secondary pollinators or nonpollinating visitors. Detailed studies in *Ipomopsis* and *Aquilegia* support the conclusion that ornithophilous and sphingophilous flowers in these groups usually have different primary pollinators as indicated above and in Table 2 (7, 17, 18, 21, 22, 28).

Table 2. Known primary pollinators of ornithophilous and sphingophilous taxa of the three species groups

Taxa grouped by pollination system	Records of hummingbird (HB) or hawkmoth pollination	Refs.
<b>Ornithophilous <i>Aquilegia</i></b>		
<i>A. formosa</i> var. <i>truncata</i>	Rufous, calliope, anna HBs	13–16
<i>A. elegantula</i>	Broad-tailed HBs	17–19
<b>Sphingophilous <i>Aquilegia</i></b>		
<i>A. pubescens</i>	<i>H. lineata</i>	13, 14, 16
<i>A. chrysantha</i>	<i>H. lineata</i> , <i>Eumorpha achemon</i> , <i>Sphinx chersis</i> , <i>Sphinx</i> sp., <i>Manduca sexta</i>	13, 20, 21
<i>A. caerulea</i>	<i>H. lineata</i> , <i>Sphinx vashti</i>	14, 17, 18
<b>Ornithophilous <i>Ipomopsis</i>*</b>		
<i>I. aggregata</i> ssp. <i>aggregata</i>	Rufous, broad-tailed, unident. HBs	19, 22, 23
<i>I. aggregata</i> ssp. <i>formosissima</i>	Rufous, broad-tailed, calliope, unident. HBs	22
<i>I. aggregata</i> ssp. <i>bridgesii</i>	Unident. HBs	22
<i>I. aggregata</i> ssp. <i>collina</i>	Rufous, broad-tailed, unident. HBs	22, 24
<i>I. arizonica</i>	Unident. HBs	22
<b>Sphingophilous <i>Ipomopsis</i>*</b>		
<i>I. aggregata</i> ssp. <i>candida</i>	<i>H. lineata</i> , <i>Sphinx</i> aff. <i>drupiferarum</i>	22, 24
<i>I. tenuituba</i> ssp. <i>latiloba</i>	<i>H. lineata</i>	22, 25
<i>I. macrosiphon</i>	<i>H. lineata</i>	22
<b>Ornithophilous <i>Diplacus</i></b>		
<i>D. puniceus</i>	Unident. HBs	26
<i>D. longiflorus</i>	Costa, unident. HBs	15, 26
<i>D. aurantiacus</i>	Anna, allen HBs	15, 27
<b>Sphingophilous <i>Diplacus</i></b>		
<i>D. calycinus</i>	<i>H. lineata</i>	26

The Latin names of the hummingbird species listed here are *Selasphorus rufus* (rufous HB), *Selasphorus platycercus* (broad-tailed HB), *Selasphorus sasin* (allen HB), *Calypte anna* (anna HB), *Calypte costae* (costa HB), *Stellula calliope* (calliope HB).

\*The older pollinator records in the *Ipomopsis aggregata* group are placed in the current classification system outlined in Table 1.

This leads to the further conclusion that the ornithophilous flowers and western hummingbirds form one coadapted system, and the sphingophilous flowers and western hawkmoths form another coadapted system (7, 20, 22, 28, 29). The concept of coadaptation does not necessarily imply total exclusiveness, species specificity, and narrow tolerances, like the coadaptation between a key and a lock, and such a narrow concept of coadaptation is out of place in the cases under consideration here. The coadapted systems with which we are dealing have moderate tolerances and therefore some flexibility.

Since the ornithophilous flowers and sphingophilous flowers have different primary pollinators and belong to different coadapted systems, one would expect floral isolation to be operative. The evidence confirms this expectation in the species groups in *Aquilegia* and *Ipomopsis* (7). We don't have sufficient evidence in the *D. longiflorus* group to say whether floral isolation plays a significant role here or not. In all species groups the floral isolation is incomplete. The primary pollinators sometimes visit the "wrong" species, and secondary pollinators may cross-pollinate the contrasting species (7). Furthermore, first-generation hybrids and hybrid populations, once formed, have flowers with intermediate

characters that can be visited and pollinated successfully by both hummingbirds and hawkmoths (8).

The floral isolation is primarily mechanical and secondarily ethological. The ornithophilous and sphingophilous flowers are adapted structurally for hummingbirds or hawkmoths, respectively, and the structural differences make the sphingophilous flowers more or less inaccessible to hummingbirds, and vice versa (mechanical isolation). The pollinating animals recognize these interspecific differences in the flowers and adjust their foraging behavior by shunning the "wrong" kind of flower (ethological isolation) (7).

**Mode of Origin.** As noted in the introduction, floral isolation could arise either as a byproduct of divergence or as a product of selection for barriers to hybridization. We have also noted that the floral characters in the ornithophilous species of *Aquilegia*, *Ipomopsis*, and *Diplacus* are adapted for hummingbird pollinating visits, and the floral characters of the related sphingophilous species are adapted for hawkmoths. The simplest explanation of the differentiation between the ornithophilous and sphingophilous floral characters is that these characters, and therefore the resulting floral isolation, are a by-product of divergence.

This conclusion is confirmed by another line of evidence. If selection for reproductive isolation is playing a role, floral isolation would be expected to be stronger in hybrid zones between the ornithophilous and sphingophilous species than in hybrid-free areas. Just the opposite is the case. The floral isolation is strongest in the hybrid-free areas and is diminished in the hybrid zones. In some areas of hybridization the original species pair with distinctive ornithophilous or sphingophilous flowers has been replaced by populations bearing intermediate flowers that are visited and pollinated by both hummingbirds and hawkmoths (8).

**Mode of Speciation.** The species of the *A. formosa/A. caerulea*, *I. aggregata*, and *D. longiflorus* groups are diploid, sexual, and outcrossing and have normal meiosis (4, 6, 13, 30–32). Therefore we can rule out various modes of speciation in their formation, namely allopolyploid speciation, hybrid speciation involving apomixis, and hybrid speciation involving permanent translocation heterozygosity or permanent odd polyploidy. The normal genetic system of the species is consistent with a mode of allopatric speciation or neighboringly sympatric speciation. (See ref. 3 for more on these modes.)

Neighboringly sympatric speciation involves divergence between populations living in different habitats in the same local area. There is circumstantial evidence for it in some groups of plants and animals (2), and it should be considered as a possibility in the species groups in *Aquilegia*, *Ipomopsis*, and *Diplacus*. However, the conditions are unfavorable for neighboringly sympatric speciation in these groups because of wide outcrossing by highly motile pollinators. In many places where the ornithophilous and sphingophilous species come into contact today they hybridize. It is difficult to conceive how the ancestral populations could diverge to the species level in a neighboringly sympatric field; the process of divergence would in all probability be reversed by hybridization at one stage or another.

It is far more likely that the ornithophilous and sphingophilous species are products of a mode of allopatric speciation which includes a stage of geographical isolation. Two allopatric modes are well known: geographical speciation, in which geographical races diverge to the species level; and quantum (or peripatric) speciation, in which the species develop out of local races (see refs. 2 and 3). The geographical distribution of racial variation within the species is consistent with one or the other of these allopatric modes.

The ornithophilous members of *I. aggregata* comprise five geographical races, treated taxonomically as subspecies, with separate areas as listed in Table 1. *I. arizonica* is

sympatric with but ecologically segregated from *I. aggregata*. A related ornithophilous species, *I. rubra*, has an allopatric distribution in the south-central and southeastern United States. The sphingophilous taxa of the *I. aggregata* group likewise have allopatric areas (Table 1). There is broad sympatry between the ornithophilous and the sphingophilous taxa.

The same pattern of allopatric distribution is found within the ornithophilous *A. formosa* subgroup and within the sphingophilous *A. caerulea* subgroup (Table 1). Here the allopatric taxa are treated taxonomically as species. We can also view them in the populational sense as allopatric semispecies. In this sense the ornithophilous entities of *Aquilegia* (listed in Table 1) are allopatric semispecies of one super-species, the *A. formosa* superspecies, and the sphingophilous entities (in Table 1) are allopatric semispecies of the *A. caerulea* superspecies. (See chapter 20 of ref. 2 for more on these categories of population systems.) Broad sympatry exists between the ornithophilous and sphingophilous super-species in *Aquilegia*.

This distribution pattern is found again in *Diplacus*. The ornithophilous taxa are allopatric (Table 1); they are treated taxonomically as species but can be regarded as semispecies in the populational sense. Marginal sympatry exists between the ornithophilous and sphingophilous species.

In short, we find an array of stages of divergence in the three plant groups, as expected if the groups have been evolving by allopatric homoploid speciation. We cannot say whether allopatric speciation followed the pathway of geographical speciation or that of quantum speciation, since evidence needed to distinguish between the two modes is not available. One line of reasoning presented below suggests that geographical speciation had a prevalent role. However, it is quite possible that both geographical and quantum speciation took place in different segments of the groups.

Pollination races represent a stage of divergence in the pollination system. Widespread species become adapted by selection to the spectrum of important pollinators in each part of the species areas. The pollinator spectrum often exhibits geographical variation. Geographical races of a plant species may be in part pollination races adapted to different sets of pollinators (22). Pollination races have been described in various species of Polemoniaceae (22) and in *A. caerulea* (18).

It seems likely that the ancestral species in each plant group developed an ornithophilous pollination race in one geographical area that was favorable for hummingbird pollination and a sphingophilous pollination race in another geographically isolated area that was favorable for sphingophily. Continued divergence with respect to pollination and secular ecological conditions led the divergent branches to the level of externally isolated species, and range expansions brought about sympatric overlap.

## DISCUSSION

I have argued that the ornithophilous and sphingophilous pollination systems in the three species groups, and the floral isolation associated with them, are products of allopatric speciation. This conclusion raises a new question: What were the pollination systems in the ancestral species in the three groups? We can draw plausible inferences about the main outlines of the phylogeny of these groups from a comparative treatment of floral morphology, pollination system, secular ecology, and geographical distribution in the extant members and their close relatives.

The center of distribution and probable center of origin of *Aquilegia* lies in Eurasia, which has the primitive spurless species *Aquilegia ecalcarata*. The North American aquilegias are evidently immigrants from Eurasia (9, 13). The

Eurasian species are bee-pollinated (33). Some of the North American species in Alaska, western Canada, and the Rocky Mountains (*Aquilegia saximontana*, *Aquilegia micrantha*, etc.) retain the ancestral condition of melittophily.

In temperate North America aquilegias came into contact with a new indigenous pollinator, hummingbirds, representing a new ecological opportunity, and gave rise to successful derived ornithophilous forms, the *Aquilegia formosa* subgroup in western North America and *Aquilegia canadensis* in eastern North America. *Aquilegia* also gave rise to the derived sphingophilous *A. caerulea* subgroup in western North America (13).

The present center of distribution of the genus *Ipomopsis* lies in northern Mexico and the American southwest. The putatively ancestral section *Phloganthea* of *Ipomopsis* occurs entirely in this area, and the section *Ipomopsis*, which includes the *I. aggregata* group and is probably derived from section *Phloganthea*, is predominantly southwestern (32).

Bee pollination prevails in section *Phloganthea* and is the probable ancestral pollination system for *Ipomopsis* (22). The two main pollination systems in section *Ipomopsis* as a whole and in the *I. aggregata* group are hummingbird pollination and hawkmoth pollination (22). Ornithophily and sphingophily are apparently derived from melittophily in *Ipomopsis* as they are in *Aquilegia*.

The small shrubby genus *Diplacus* is endemic to the Pacific slope from Baja California to Oregon. Its center of distribution and probable center of origin lie in southern California. It is related to and undoubtedly derived from the large, widespread, herbaceous, and predominantly bee-pollinated genus *Mimulus*. *D. clevelandii* with a woody base and herbaceous shoots and bee flowers is intermediate and transitional between *Mimulus* and the woody species comprising the *D. longiflorus* groups. The latter group, which contains the ornithophilous and sphingophilous taxa, is probably derived from an ancestral form like the existing *D. clevelandii* (6).

The ornithophilous and sphingophilous species thus appear to be derived from bee-pollinated ancestral species in all three groups. The shift from melittophily to the derived pollination systems goes back ultimately to speciation events. The available evidence is inconclusive as regards the number and order of branchings but does point to this general trend.

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