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Review

Modes and origins of mechanical and ethological isolation in angiosperms

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ABSTRACT **Mechanical and ethological isolation between species is widespread in angiosperms with specialized animal-pollinated flowers, being recorded in 29 species groups belonging to 27 genera and 16 families. Mechanical isolation occurs in two forms. (*i*) The common type, designated the *Salvia* type, operates when two or more species of flowers are adapted for different groups of pollinators with different body sizes and shapes. (*ii*) In the *Pedicularis* type two flower species have the same species of pollinator but pick up pollen from different parts of the pollinator's body. Four forms of ethological isolation are recognized. (*i*) In the *Aquilegia* type, which is widespread, ethological isolation is a side effect of mechanical isolation. (*ii*) The flower-constancy type, as the name suggests, is based on flower-constant foraging behavior. (*iii*) In the *Ophrys* type, floral scents attract male bees or wasps and play a role in their mating behavior; different species of flowers, often orchids, have different scents and attract different sets of hymenopteran species. (*iv*) The monotropy type occurs in plants pollinated by hymenopterans with species-specific or group-specific flower preferences for nutritive purposes (monotropic and oligotropic bees and fig wasps). Three modes of origin of floral isolation are confirmed by evidence: (*i*) mechanical and ethological isolation arising as a by-product of allopatric speciation, (*ii*) ethological isolation developing by selection for reproductive isolation *per se*, and (*iii*) mechanical isolation arising as a by-product of character displacement. Mode of origin *i* accounts for the *Salvia* and *Aquilegia* types of isolation in nine known species groups and for the *Ophrys* type in one group. Mode of origin *ii* accounts for the flower-constancy type of ethological isolation in two species groups. Mode of origin *iii* explains mechanical isolation in two groups. Sympatric origin of floral isolation by hybrid speciation and by flower constancy has been proposed, but these modes are undocumented and improbable.**

The possibility that differences between related plant species in flower structure may function as a mechanical isolating mechanism was suggested by Dobzhansky (1, 2) and Stebbins (3) in the period 1937–1950. Building on these early works, I showed that the preconditions for reproductive isolation at the stage of pollination are widespread in angiosperms with complex floral mechanisms (4).

My early paper (4) recognized ethological as well as mechanical isolation in angiosperms. Mechanical isolation can occur when two or more plant species have different flower structures that reduce or prevent interspecific pollination. Ethological isolation takes place when specialized flower-visiting animals make preferential visitations to one species of flower which they recognize by its specific shape, color, markings, and/or scent. Mechanical and ethological isolation are likely to be combined in actual cases, making it useful to group them in a collective mode, floral isolation.

After 1950 opinion regarding floral isolation was divided between support (5) and skepticism (6). It was obviously necessary to document floral isolation between sympatric species in nature. This was done by my students and myself in the next few years (1952–1964) in *Aquilegia* (7), *Penstemon* (8), *Pedicularis* (9), and *Salvia* (10). In these cases the floral isolation is primarily mechanical but is supplemented by ethological isolation.

Since that period a much larger body of evidence has been obtained from more plant groups. One of the purposes of this paper is to present the broader data base that now exists. The broader data base makes it possible to recognize different modes of mechanical and ethological isolation. A second purpose of this review is to outline these modes.

A question which remains problematical is the origin of floral isolation. This subject was discussed in a preliminary way in my early paper (4), where both allopatric and sympatric models were considered, but the models were theoretical. What is needed is a modern analysis of the problem on the basis of our present expanded data base and in the light of our current understanding of speciation. Such an analysis is presented here.

The breakdown of the diverse phenomena of floral isolation into different forms is helpful in relation to a discussion of the origin of floral isolation. We find, as might be expected, that no one mode of evolution will account for every form of floral isolation in every plant group. Thus this paper will examine the diverse origins of floral isolation.

Broad Evidence for Floral Isolation

Examples of floral isolation in nature have now been reported in many plant groups in many geographical areas. The cases known to me are listed in Table 1. These cases occur in 29 species groups in 16 families. They leave little doubt that floral isolation is a real barrier to gene exchange between species in many animal-pollinated plant groups.

Floral isolation depends on floral specializations. It will be noted that all but a few of the cases in Table 1 occur, as would be expected, in genera and families with complex floral mechanisms. The Scrophulariaceae and Orchidaceae together account for 10 of the 29 known examples.

One family with complex flowers that is missing from Table 1 is the Asclepiadaceae. Years ago it was cited as a group in which mechanical isolation was well developed (3, 4, 47). But later students have downgraded mechanical isolation in the genus *Asclepias* to a process of secondary or negligible importance (48, 49). This is a group in which the early predictions were plausible but have not stood up under closer inspection. Since an expectation of mechanical isolation in the Asclepiadaceae is still warranted, further search for valid examples is desirable.

Mechanical isolation is the main mode in many of the examples in Table 1. Ethological isolation is often complementary to mechanical isolation (e.g., in *Aquilegia, Polygala, Penstemon, Pedicularis*), confirming the usefulness of the collective mode, floral isolation. Ethological isolation plays a primary role in several groups (*Hedysarum, Cercidium, Phlox, Ophrys*).

The strength of the floral isolation varies over a wide range. It is very

Table 1. Groups of related species which are mechanically (M) and/or ethologically (E) isolated in nature, listed by family

Species group	Area	Pollinators	Mode of isolation	Refs.
Ranunculaceae				
Aquilegia formosa subgroup and *A. caerulea* subgroup	W. North America	Hummingbirds (*A. f.*), hawkmoths (*A. c.*)	M, E	7, 11, 12
Berberidaceae				
Epimedium grandiflorum, *E. sempervirens*, and *E. trifoliatobinatum*	Japan	Bees	E	13
Papaveraceae				
Papaver rhoeas, *P. dubium*, and three other species	Great Britain	Bumblebees, honeybees	E (inferred)	14
Leguminosae				
Cassia leiophylla and *C. bicapsularis*	Mexico	Bumblebees and other large bees (*C. b.*), smaller *Ptiloglossa* bees (*C. l.*)	M	15
Cercidium floridum and *C. microphyllum*	California	Bees	E	16
Hedysarum boreale and *H. alpinum*	Alaska	Bumblebees, *Megachile* bees	E	17
Polygalaceae				
Polygala vauthieri and *P. monticola*	Brazil	Bees	M	18
Onagraceae				
Fuchsia encliandra and *F. parviflora*	Mexico	Hummingbirds (*F. e.*), bumblebees (*F. p.*), where sympatric	M, E	19
Euphorbiaceae				
Dalechampia brownsbergensis and *D. fragrans*	Surinam	Male euglossine bees	E	20
Balsaminaceae				
Impatiens capensis and *I. pallida*	E. North America	Hummingbirds (*I. c.*), bumblebees (*I. p.*)	M	21
Polemoniaceae				
Phlox pilosa and *P. glaberrima*	Illinois and Indiana	Butterflies	E	22, 23
Phlox drummondii and *P. glaberrima*	Illinois (synthetic population)	Butterflies	E	23–25
Ipomopsis aggregata and *I. tenuituba*	W. North America	Hummingbirds (*I. a.*), hawkmoths (*I. t.*)	M, E	12, 26
Solanaceae				
Solanum grayi and *S. lumholtzianum*	Mexico	Large bees (*S. l.*), small bees (*S. g.*), where sympatric	M	27
Scrophulariaceae				
Mimulus cardinalis and *M. lewisii*	W. North America	Hummingbirds (*M. c.*), bumblebees (*M. l.*)	M	28
Diplacus puniceus, *D. longiflorus*, and *D. calycinus*	California	Hummingbirds (*D. p.*, *D. l.*), hawkmoths (*D. c.*)	M (inferred)	29, 30
Penstemon centranthifolius, *P. grinnellii*, and *P. spectabilis*	California	Hummingbirds (*P. c.*), carpenter bees (*P. g.*), wasps (*P. s.*)	M, E	8
Pedicularis groenlandica and *P. attollens*	California	Bumblebees	M, E	9, 31, 32
Rhinanthus minor and *R. serotinus*	Europe	Bumblebees	M, E	33
Labiatae				
Salvia apiana and *S. mellifera*	California	Carpenter bees (*S. a.*), medium-sized and small bees (*S. m.*)	M, E	10
Monarda didyma and *M. clinopodia*	E. North America	Hummingbirds (*M. d.*), bumblebees (*M. c.*)	M, E	34
Campanulaceae				
Lobelia cardinalis and *L. siphilitica*	E. North America	Hummingbirds (*L. c.*), bumblebees (*L. s.*)	M, E	35, 36
Haemodoraceae				
Anigozanthos manglesii and *A. humilis*	Australia	Wattle birds (Meliphagidae)	M, E	37
Musaceae				
Heliconia umbrophila, *H. irrasa*, and other species	Costa Rica	Hermit and nonhermit hummingbirds	M	38, 39
Orchidaceae				
Ophrys insectivora, *O. speculum*, and other species	Europe and North Africa	Male bees and wasps	M, E	40, 41
Ophrys fusca and *O. lutea*	Algeria	Male *Andrena* bees	M, E (inferred)	42
Platanthera bifolia and *P. chlorantha*	Europe	Moths	M, E	43
Stanhopea tricornis and *S. bucephalus*	Ecuador	*Eulaema* bees	M, E	44, 45
Angraecum compactum and *Neobathiea grandidierana* (closely related though placed in different genera)	Madagascar	Hawkmoths	M, E	46

strong in *Ophrys* (41), *Mimulus* (28), and *Pedicularis* (9, 31, 32). In *Aquilegia* and *Ipomopsis*, on the other hand, the floral isolation in itself brings about only a reduction in interspecific gene exchange; however, it does not act alone but rather in combination with ecological and seasonal isolation, and the ensemble of all external barriers is highly effective (12).

Types of Mechanical Isolation

Mechanical isolation occurs in two forms. In the first, which we will call the *Salvia* type for ease of reference, the contrasting plant species have flowers adapted to different kinds of pollinating animals with bodies of different size and shape, such as bees vs. birds or large bees vs. small bees. In the second type, to be denoted the *Pedicularis* type, the contrasting plant species are pollinated by the same species of animal, but the floral mechanism deposits and picks up the pollen on different parts of the pollinator's body. The floral differences responsible for mechanical isolation reside mainly in the pollination mechanism in the *Pedicularis* type. In the *Salvia* type, on the other hand, all or nearly all features of the floral mechanism, including those involved in attraction, reward, and exclusiveness as well as pollen delivery, come into play.

The *Salvia* type of mechanical isolation is illustrated by *Salvia apiana* and *Salvia mellifera*. The flowers of these species differ in size and conformation. *S. apiana* is adapted for and pollinated by large carpenter bees (*Xylocopa*) and *S. mellifera* by various medium-sized and small bees (*Anthophora, Osmia*, etc.). Each *Salvia* species is visited and pollinated by its normal set of bees with only rare exceptions. Conversely, the floral differences between the species set up a barrier to successful visitation and pollination of *S. apiana* by the smaller bees and of *S. mellifera* by the large bees (10).

Another example is the hummingbird-pollinated *Mimulus cardinalis* and bumblebee-pollinated *Mimulus lewisii*. These interfertile species occur sympatrically in some sites in the Sierra Nevada, CA. No natural hybrids are found. Progeny tests of seeds collected on open pollinated plants in sympatric colonies yielded no hybrids. Cross-pollination between the two species is also extremely rare in the experimental garden (28).

Other examples of the *Salvia* type of isolation are found in *Aquilegia, Fuchsia, Impatiens, Ipomopsis, Penstemon, Monarda*, and *Lobelia* (Table 1).

The *Pedicularis* type of mechanical isolation is illustrated by the species pair *Pedicularis groenlandica* and *Pedicularis attollens*. Both species have bumblebee flowers and are pollinated by the same species of *Bombus* (*B. bifarius* and *B. flavifrons*). However, the differences between the *Pedicularis* species in their pollination mechanism are such as to bring about dorsal (nototribe) pollination in *P. groenlandica* and forehead pollination in *P. attollens* (9, 31, 32). The *Pedicularis* type is found also in *Polygala* (18), *Rhinanthus* (33), and *Heliconia* (38, 39).

The *Aquilegia* and Flower-Constancy Types of Ethological Isolation

Four forms of ethological isolation can be recognized. First, ethological isolation may be a side effect of the *Salvia* type of mechanical isolation. If species A is adapted for hummingbird pollination and species B for hawkmoth pollination, the birds may be unable to forage effectively on species B. They assess the difficulties and shun species B if an adequate supply of hummingbird flowers is available. The hawkmoths make a parallel adjustment in relation to species A. Examples of this type of ethological discrimination are found in species groups in *Aquilegia* and *Ipomopsis* which contain hummingbird-pollinated species and hawkmoth-pollinated species (12, 50). For ease of reference we will call this common mode the *Aquilegia* type of ethological isolation.

A second type of ethological isolation is a product of flower constancy such as occurs in bees, lepidopterans, and to a lesser extent in long-tongued flies. Individual insects become fixed on one kind of flower, which they recognize by its specific color, shape, markings, or scent, and then forage preferentially on that flower type during a succession of visitations. Flower-constant behavior increases the foraging efficiency of the insects when visiting flowers with complex floral mechanisms, since once an individual has learned how to work a given floral mechanism it can work other flowers of the same type rapidly. As a corollary of this, flower constancy is a behavioral tendency, not an absolute rule. If it does not improve foraging, as when one type of flower is present in inadequate numbers, the insects switch to another and better source. The result of interest to us here is that different individuals of the same bee species may be foraging in the same two-species colony of plants, but some individual bees visit exclusively or primarily one species of flower, while other individual bees visit the other flower species. (For more on flower constancy see refs. 51–54.)

Cases of ethological isolation based on flower constancy are well known in the experimental garden and were reported in the early years in *Antirrhinum* (55), *Gilia* (4), *Clarkia* (56), *Papaver* (14), and *Lantana* (57), and more recently in artificial flowers (58). Flower-constant pollination separating species in nature has since been found in *Epimedium, Cercidium, Hedysarum, Phlox, Pedicularis, Rhinanthus, Platanthera*, and *Angraecum*/*Neobathiea* (Table 1).

Pedicularis groenlandica and *P. attollens* grow and flower together in the same alpine meadows in the Sierra Nevada, CA. Both species are pollinated by bumblebees but are mechanically isolated, as noted earlier. The mechanical isolation is reinforced by strong ethological isolation based on flower constancy. Individuals of *Bombus bifarius* distinguish the two *Pedicularis* species by their floral features (Fig. 1). Some individual bumblebees visit *P. groenlandica* selectively, bypassing plants of *P. attollens* in their rounds, while other individual bees forage exclusively on *P. attollens* (9, 32). Lapses of flower constancy in which an individual bumblebee crosses over from one *Pedicularis* species to the other occur but are rare (9, 32).

The *Ophrys* and Monotropy Types of Ethological Isolation

In the third type of ethological isolation, the *Ophrys* type, floral scents attract male bees or wasps and play a role in their mating behavior. Two subtypes are recognized.

In the genus *Ophrys* the flowers simulate female hymenopterans in their visual and olfactory features, and they sexually stimulate male bees (*Andrena, Eucera*, etc.) and wasps (Vespidae, Sphecidae, Scoliidae), which land on and attempt to copulate with the flowers. Each species of *Ophrys* has its distinctive floral markings and scent. Different species of *Ophrys* attract mainly different sets of hymenopteran

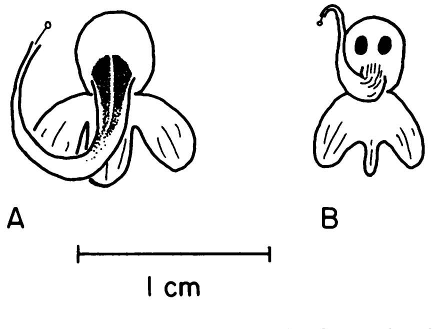

FIG. 1. Front view of corolla of two related species of *Pedicularis*, showing lower lip, upper hood, and beak extending outward and upward from hood. The stigma protrudes through the tip of the beak. The beak is displaced to the left in *B* to show the two purple spots. (*A*) *P. groenlandica*. (*B*) *P. attollens*.

pollinator species. The males of one or several hymenopteran species have a mating preference for one kind of *Ophrys* flower only, while males of other pollinator species are attracted sexually to a different kind of *Ophrys* flower. The *Ophrys* flowers thus enlist the species-specific mating preferences of male hymenopterans in the service of species-specific pollination. Some mechanical isolation is associated with the ethological isolation (41).

Male bees of the genera *Euglossa, Eulaema*, etc. (Apidae, tribe Euglossini) in the American tropics visit flowers of orchids and other plant families for perfume. They collect liquid droplets of aromatic substances (terpenes, etc.) from the scent glands of the flowers, store them by capillarity on their hind legs, and use them, apparently in a transformed state, as sex pheromones (20, 45, 59–61). A given orchid species often attracts only one or a few species of male bees, and the sets of bee pollinators differ from one orchid species to the next (44, 45, 60). Two sympatric species of the euphorb genus *Dalechampia* attract different sets of male euglossine bees in nature. This differential attraction and pollination holds up to a statistically significant extent in an experimental mixture of the *Dalechampia* species (20).

The fourth type of ethological isolation, designated the monotropy type, involves monotropy and related conditions in hymenopterans. In many genera of bees, especially among solitary bees, the species restrict their foraging to a single taxonomic group of plants. The plant group may be a tribe, genus, species group, or species. Monotropic bee species collect nectar and pollen from a single plant species; oligotropic bees collect flower food from a supraspecific group. Monolectic and oligolectic bees visit a species or larger group, respectively, for pollen, but they may forage more widely for nectar. Ten species of *Perdita* (Halictidae) collect pollen from *Calochortus* (Liliales) and mostly from different species or species groups. Thus *Perdita calochorti* collects pollen from *Calochortus nuttallii, Perdita leucostoma* from *Calochortus leichtlinii*, and *Perdita californica* from *Calochortus splendens, Calochortus kennedyi*, and *Calochortus concolor* (62). Among other bee genera with monotropy/oligotropy are *Andrena* (Andrenidae) and *Diadasia* (Anthophoridae) (62–66).

The terminology of monotropy, oligotropy, etc. is applied to bees, but perhaps the best example of flower host specificity is provided by the fig wasps (Agaonidae). Many species of *Ficus* have a single species of wasp pollinator; some *Ficus* species have two species of wasp pollinators, and the wasp species usually differ from one *Ficus* species to another (67–69). One would predict ethological isolation based on the floral preferences of the fig wasps.

The relation between monotropy/oligotropy in bees and ethological isolation in plants is complex and little studied. Monotropy and oligotropy obviously channel pollen distribution within taxonomic limits in a plant community. However, this does not necessarily bring about ethological isolation between congeneric species. Oligotropic bees are group specific but not species specific, and they might or might not discriminate between related plant species in a sympatric colony. Furthermore, monotropic bees are often not the primary pollinators of the plants they visit, their host flowers being pollinated mainly by other bees or other insects. The crucial factor is then the flower-visiting behavior of the primary pollinators. If these are not species-specific, floral isolation does not exist, and monotropy in the secondary pollinators is more or less irrelevant. These are limitations on the potential of monotropy/oligotropy for isolation.

After allowing for these factors, the possibility remains that monotropy/oligotropy in bees may contribute positively to ethological isolation in some situations. Oligotropic *Andrena* species foraging in mixed colonies of *Oenothera* have been observed to visit some *Oenothera* species more often than others, but they also cross over from one species to another (66).

The question of ethological isolation by monotropic bees and fig wasps requires further study.

The Modes of Ethological Isolation Summarized

The phenomena of flower-visiting behavior that result in ethological isolation can be grouped in several modes. It has seemed best to me to group them in the four modes presented above, but alternative groupings into three or five types are also possible. Each mode is characterized by a certain predominant pattern of flower-visiting behavior. It may be useful to summarize briefly these behavior patterns here.

In the *Aquilegia* type of ethological isolation, pollinators visit preferentially a flower species on which they can forage successfully, but shun a plant species in the same colony in which the floral reward is inaccessible or difficult of access. Put another way, the pollinators exhibit preference for a plant species with a flower structure which permits a high ratio of foraging benefits to foraging costs, and they discriminate against a flower species with a low benefit-to-cost ratio in foraging. In the flower-constancy mode of ethological isolation, individual foragers of a polytropic insect species become fixed on one flower type in a mixed plant colony, even though they could forage successfully on the other types of flowers. In the *Ophrys* and monotropy modes of ethological isolation a whole species of insect has a preference for a particular species of flower. The insects are foraging female hymenopterans in the monotropy mode, and sexually interested male hymenopterans in the *Ophrys* mode.

Origin of Floral Isolation as a By-Product of Allopatric Speciation

Reproductive isolating mechanisms arise in two ways: as by-products of divergence and as products of selection for reproductive isolation *per se*. The first process is general and ubiquitous. The second process comes into play under special conditions as a reinforcement of the reproductive isolation produced by the first mode. It affects mainly premating barriers (5, 70, 71). Both processes can be expected to play a role in the development of floral isolation. We can expect further to find cases in which the first process has acted alone and other cases in which both processes have been involved.

Floral isolation between hummingbird-pollinated and hawkmoth-pollinated species of *Aquilegia* and *Ipomopsis* can be explained as a by-product of divergence without invoking selection for reinforcement (30). The floral and inflorescence characters which bring about the floral isolation in these two groups are adaptive in relation to one type of pollinator or the other and are maladaptive in the opposite flower-pollinator combination. There are no floral features in these plant groups that point to selection for isolation. In fact, this process can be ruled out. If selection for isolation had played a role in the development of floral isolation in *Aquilegia* and *Ipomopsis*, the floral isolation should be enhanced in zones where the ornithophilous and sphingophilous species hybridize as compared with hybrid-free areas. The actual pattern is the opposite; floral isolation is diminished in the hybrid zones (30).

The pattern in *Diplacus* is parallel in most respects to that in *Aquilegia* and *Ipomopsis* with one exception. We do not have enough evidence to say whether the ornithophilous and sphingophilous species of *Diplacus* are florally isolated to any significant extent. Otherwise the facts and conclusions are the same as for *Aquilegia* and *Ipomopsis*. The ornithophilous and sphingophilous characters of contrasting species in *Diplacus* are by-products of divergence. Selection for isolation has played no detectable role in this development (30).

The next question is the mode of speciation involved in divergence of the contrasting ornithophilous and sphingophilous species of *Aquilegia, Ipomopsis*, and *Diplacus*. Diverse modes of speciation are known in plants (71, 72). Most of these can be ruled out in the species groups in *Aquilegia, Ipomopsis*, and *Diplacus* (30). This reduces the possibilities to allopatric speciation on the diploid level. The biogeographical patterns are consistent with a course of divergence by allopatric speciation (30).

There are two modes of allopatric speciation: geographical speciation and quantum (or peripatric) speciation. In the first mode the divergence passes through an intermediate stage of spatially isolated geographical races; in the second mode the intermediate stage is a peripherally isolated local race. The two modes thus differ in the pathway followed at the racial level of divergence. In dealing with mature species groups, in which the speciation process has run to completion, it is usually difficult if not impossible to determine which pathway was taken in the historically past stage of racial divergence. Consequently, in most actual species groups, we do not have sufficient evidence to distinguish between the two modes of allopatric speciation (71).

This is as true in *Aquilegia, Ipomopsis*, and *Diplacus* as it is in most other groups. However, one factor favors the pathway of geographical speciation in *Aquilegia, Ipomopsis*, and *Diplacus*. The contrasting ornithophilous and sphingophilous species in these genera are pollinated by highly motile animals with substantial food requirements and wide foraging ranges. A small isolated local race will probably be an inadequate resource base for the development of either an ornithophilous or sphingophilous pollination system. However, geographical races can become pollination races which are adapted for one set of pollinators in an area where those pollinators are abundant and for a different set in another area. Such geographical/pollination races are known (73). It seems likely that the ornithophilous and sphingophilous species in *Aquilegia, Ipomopsis*, and *Diplacus* went through an intermediate stage of geographical/pollination races (30).

Comparable evidence for six other groups in temperate North America—*Impatiens, Mimulus, Penstemon, Salvia, Monarda*, and *Lobelia* (Table 1)—suggests that floral isolation in these groups is also a by-product of allopatric speciation. The speciation is on the diploid level in the first five groups, as it is in *Aquilegia, Ipomopsis*, and *Diplacus*, and is on a tetraploid homoploid level in *Monarda*.

The nine plant groups mentioned in this section all have the *Salvia* type of mechanical isolation combined with the *Aquilegia* type of ethological isolation.

Origin of Floral Isolation in *Ophrys*

We can speculate about the origin of floral isolation in *Ophrys*. *Ophrys* races and species living in different areas probably evolve visual and olfactory floral features that are attractive to males of hymenopteran species in those areas, and along with these, also evolve structural characters fitting the body parts of the local hymenopteran pollinators. The particular floral characters and the corresponding species of male hymenopterans originally have an allopatric distribution, but may become sympatric as a result of range extensions. The floral isolation would then be a by-product of allopatric divergence of floral characters in relation to the species-specific mating preferences of the male bees and wasps. This hypothesis states in effect that the origin of floral isolation in *Ophrys* is a special case of floral isolation arising as a by-product of allopatric speciation as discussed in the preceding section.

Selective Origin of Ethological Isolation

If interspecific hybridization between two plant species results in wastage of their reproductive potential, and if this loss of reproductive potential is selectively disadvantageous, selection is expected to build up barriers to hybridization (5, 70–72). The conditions necessary for bringing selection for reproductive isolation into play are not present in many plant groups. Correspondingly, we find no evidence of the action of selection for isolation in *Aquilegia, Ipomopsis, Diplacus*, and other groups, as pointed out previously. In some groups, however, the essential preconditions may exist, and selection for reproductive isolation can be expected to go into action.

A barrier to hybridization that can be built up by selection for isolation, if the preconditions exist, is the flower-constancy type of ethological isolation. This mode of isolation is based on species-specific recognition features in flowers pollinated by flower-constant bees and lepidopterans. Visual and olfactory floral features that differ between plant species and are recognized by flower-constant bees and lepidopterans are widespread (4). It is probable that some of these recognition features are products of selection for ethological isolation. However, we have little independent evidence to support this plausible suggestion.

I previously described the ethological isolation between *Pedicularis groenlandica* and *Pedicularis attollens* based on flower constancy of bumblebees. The flower constancy is based in turn on floral differences between the two species which the bees recognize, differences that include size and shape of floral parts, markings, and scent (Fig. 1). Some of these character differences, such as the length and shape of the beak, are functional in the pollination mechanism; these characters are set aside for the present discussion. But other characters serve no apparent primary function in pollination. *P. attollens* has two large purple spots in the upper front part of the hood; *P. groenlandica* lacks such spots but has a purple area in the lower basal part of the beak (Fig. 1). These purple markings are not nectar guides; the flowers are nectarless. It seems likely that they are species-specific recognition marks for the bumblebees, and they may have been developed by selection for ethological isolation. The same suggestion can be made for the differences in floral scent between the two species.

Phlox glaberrima and *Phlox pilosa* have overlapping ranges in eastern North America. Their usually pink flowers are pollinated by butterflies. A white-flowered morph occurs in *P. pilosa*. This morph is rare in most parts of the area of *P. pilosa* but is predominant in the zone of sympatric overlap with pink-flowered *P. glaberrima*. Here it would of course favor species discrimination by butterflies. Analysis of pollen grains on floral stigmas shows that butterflies do transfer significantly less pollen between pink *P. glaberrima* and white *P. pilosa* than between *P. glaberrima* and pink *P. pilosa*. Production of hybrid seeds of *P. pilosa* ♀ × *P. glaberrima* is also reduced in the combination of white *P. pilosa* × *P. glaberrima* as compared with pink *P. pilosa* × *P. glaberrima*. The flower color in the white morph of *P. pilosa* thus has a selective advantage and enhances ethological isolation under conditions of sympatry between *P. pilosa* and *P. glaberrima* (22, 23).

Origin of Mechanical Isolation as a By-Product of Character Displacement

Two species with overlapping distribution areas are often more highly differentiated in their sympatric zone than in their allopatric areas. The morphological and physiological characters involved usually relate to secular or nonreproductive ecology. The differentiation in the sympatric zone (character displacement) is generally explained as a result of interspecific competition and selection for divergence with respect to secular factors in the environment. However, the same process of selection for ecological divergence can also come into play in the stage of pollination and bring about reproductive character displacement.

A case of reproductive character displacement is found in the species *Solanum lumholtzianum* and *Solanum grayi*, which occur in Arizona and Mexico with an overlap in their ranges. In their allopatric areas both species have large flowers and are pollinated by large bees (*Bombus*, *Xylocopa*, etc.); in the sympatric area *S. lumholtzianum* continues to have large flowers, whereas the flowers of *S. grayi* are small and are pollinated by small bees (*Nomia*, etc.). Mechanical isolation occurs in the sympatric zone. It appears to be a product of selection for ecological divergence in relation to pollinators (27). A parallel case of reproductive character displacement occurs in the species pair *Fuchsia encliandra* and *Fuchsia parviflora* (19).

Selection for ecological divergence and selection for reproductive isolation as discussed in the preceding section are different selection modes. However, they both take place in a sympatric field, and both can produce floral isolation. The floral isolation develops in the area of sympatric overlap of two species. It may be difficult to say which mode is operating in any given case. Indeed, both modes could well be operating simultaneously in the same species pair.

Effects of Hybridization

A pair of florally isolated species is often reproductively isolated in one area of sympatric contact but hybridizes in another area. This pattern has been found in *Aquilegia, Epimedium, Phlox, Ipomopsis, Diplacus, Penstemon, Rhinanthus, Salvia, Heliconia, Ophrys*, and *Platanthera* (Table 1 and references cited therein). What are the later-generation effects of the hybridization? There are several possibilities.

Let us restrict this discussion to floral isolation composed of the *Salvia* type of mechanical isolation combined with the *Aquilegia* type of ethological isolation. The contrasting plant species have different kinds of pollinating animals. Mechanical isolation between them depends on structural differences and ethological isolation depends on signaling differences in their flowers. Hybridization generally produces floral characters in the intermediate range. Individual F_1 hybrids with intermediate floral characters bridge the gap between the parental species for the pollinators, and the floral isolating barrier breaks down. The extent and direction of the evolutionary changes in the hybrid population in later generations are determined among other factors by the pollinators themselves.

The pollinators exert selective pressures on the hybrid population. If the normal pollinators of parental species A are abundant, active, and effective in the area of the hybrid population, and the normal pollinators of species B are less so, the later-generation progeny of the hybrids can be expected to revert toward the characters of species A. Or if the two different sets of normal pollinators are approximately the same in number of flower visits and pollination effectiveness, their combined selective pressures should produce later-generation derivatives with intermediate floral characters suited for both types of pollinators (74). Species groups in *Aquilegia, Ipomopsis*, and *Diplacus* have populations and population systems of hybrid derivation that exemplify these alternative courses of development (74).

Hybridization between florally isolated but interfertile species can also be expected to engender some recombination types for floral characters in F_2 and later generations. Most recombination types will probably have a floral mechanism that is not well adapted for any available pollinator, but this is not the only possible fate of a new type, as we will see.

Origin of Floral Isolation by Hybrid Speciation

One of the known modes of speciation in plants is hybrid speciation with the segregation of external barriers. Most examples involve secular ecological isolating barriers (72). We are interested here in a possible parallel process involving floral isolating barriers.

Straw (75) suggested that some particular recombination types for floral characters in a hybrid population might be preadapted for a flower-visiting animal that occurs in the area of the hybrid population and is different from the normal pollinators of the parental species. The new flower type and new pollinator could then develop into a separate isolated species with a distinctive pollination system of its own.

Straw (75) described a case in a diploid species group in *Penstemon* which seemed to conform to this model. The hummingbird-pollinated *Penstemon centranthifolius* and carpenter-bee-pollinated *Penstemon grinnellii* hybridize sporadically. Some hybrid progeny resemble a third species, *Penstemon spectabilis*, which is pollinated by pseudomasarid wasps. Furthermore, *P. spectabilis* is ecologically and morphologically intermediate between *P. centranthifolius* and *P. grinnellii*. Straw (75) suggested, therefore, that *P. spectabilis* originated as a diploid hybrid segregate from *P. centranthifolius* × *P. grinnellii* which captured a new and different pollinator and developed into a new florally isolated species.

This hypothesis has been widely cited. I accepted it years ago. However, the premise of a hybrid origin of *Penstemon spectabilis* is not supported by strong evidence and is inconsistent with some old and some recent evidence. First, *P. spectabilis* is a member of a group of five species (*Penstemon pseudospectabilis*, etc.) with a widespread distribution from interior southern California to Arizona. This group represents a branch of *Penstemon* commensurate with the *P. centranthifolius* and *P. grinnellii* groups. An alternative hypothesis which should be considered is that *P. spectabilis* originated in the common way, by allopatric speciation on the diploid level, and that its resemblance to some hybrid progeny of *P. centranthifolius* × *P. grinnellii* is coincidental.

Second, a recent allozyme study of this group of penstemons by Wolfe and Elisens (76) has identified enzyme alleles characteristic of *P. centranthifolius* and of *P. grinnellii*. These alleles are not present in *P. spectabilis* in the frequencies expected if *P. spectabilis* is a product of hybrid speciation of *P. centranthifolius* × *P. grinnellii*. According to Wolfe and Elisens (76) the allozyme evidence is consistent with allopatric speciation and subsequent introgression in the group but not with any recent events of hybrid speciation.

The formation of a new floral isolating barrier by hybridization and recombination requires a rare coincidence in space and time between a novel flower type and a new available pollinator. This is possible but must be very rare in nature, and its occurrence remains to be demonstrated.

Sympatric Origin by Flower-Constant Pollination

Flower-constant behavior in pollinating animals brings about positive assortative mating in a plant population. Assortative mating can theoretically lead to sympatric speciation. Models of sympatric speciation resulting from flower-constant pollination have been considered (4, 58). The flower characters used as cues by flower-constant pollinators could start as polymorphic variants in the population and go on to develop into species-distinguishing characters within a sympatric field.

This is a theoretical possibility which is beset with great theoretical difficulties. The model requires complete assortative mating, which in turn requires complete flower constancy over a sequence of flowering seasons. But flower constancy is subject to lapses, especially when one type of flower becomes an inadequate source of food. The lapses can occur in any flowering season or plant generation and prevent the sympatric speciation process from going through to completion.

Evidence for the occurrence of this mode of sympatric speciation in plants is lacking. However, the possibility warrants further study, as Wells *et al.* (58) suggest.

Conclusions

The *Salvia* type of mechanical isolation is often combined with the *Aquilegia* type of ethological isolation. The evidence indicates that this common pattern of floral isolation is a product of allopatric speciation in *Aquilegia, Impatiens, Ipomopsis, Mimulus, Diplacus* (with certain reservations), *Penstemon, Salvia, Monarda,* and *Lobelia.*

The unique type of ethological and mechanical isolation found in the genus *Ophrys* may also develop by allopatric speciation, although this question requires further study.

Selection for reproductive isolation *per se* will account for many cases of ethological isolation of the flower-constancy type. The evidence that it does so is largely circumstantial. Visual and olfactory features that distinguish related species, and have no other discernable function, are widespread in bee-pollinated and lepidopteran-pollinated angiosperms. Detailed evidence supporting a selective origin of ethological isolation, however, is available in only a few cases (mainly *Phlox*), and more such evidence is needed.

Where plant species compete for a limited supply of pollinators in a common sympatric area, selection for ecological divergence may go into action and promote a partitioning of the pollinators by size and type. Mechanical isolation is a byproduct of this process in *Solanum* and *Fuchsia*.

Two sympatric modes of origin of floral isolation have been proposed and discussed in the literature. One is hybrid speciation followed by the segregation of a new flower form that captures a new type of pollinator. The other is the separation of a polymorphic variant for floral characters from other members of its population by flower-constant behavior and assortative mating. These modes are theoretically possible but also theoretically difficult, improbable, and unknown in any actual plant group.

Many questions remain. It is not clear how the *Pedicularis* type of mechanical isolation originates. Also unclear is the mode of origin of ethological isolation in orchids and other plant groups pollinated by perfume-collecting euglossine bees. The contribution of monotropy/oligotropy to floral isolation is poorly understood. There is good evidence for phylogenetic coevolution between *Ficus* and fig wasps, but we know little about the origin of wasp–flower relationships at the species level in *Ficus*.

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