POLLINATION SYSTEMS AS ISOLATING MECHANISMS IN ANGIOSPERMS

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The opinion, once held rather widely by biologists, that related species are generally, if not universally, separated by barriers to reproduction involving incompatibility and hybrid sterility has undergone some qualifications in recent years. The modification of the time-honored view has been in part a consequence of the discovery that species of higher plants, which occupy the same range in nature without evident hybridization, may nevertheless yield fertile progeny when crossed in the breeding plot (Anderson, 1948). Two sets of processes are now known whereby intercompatible and interfertile species of flowering plants can occur sympatrically and still maintain their distinctness. The first of these is the non-establishment of the hybrid seedlings, due to the lack of an available ecological niche; the second is the non-production of hybrids, due to the failure of interspecific pollination. The effect of ecological factors on the isolation of interfertile, sympatric species has been dealt with in several recent publications (Epling, 1947a, 1947b; Stebbins, Matzke, and Epling, 1947; Anderson, *op. cit.*). The purpose of the present paper is to investigate the occurrence and distribution in angiosperms of isolating mechanisms operating at the critical stage of pollination.

THE NATURE OF FLORAL ISOLATING MECHANISMS

Interspecific pollination in a mixed population consisting of two intercompatible species of angiosperms, which are normally pollinated by animals rather than by wind or water, may be prevented in one of two ways. Either the floral mechanisms of the two species may differ in certain details so that the animals which pollinate one species are unable to enter the flowers of the other species, and, if they succeed in making their entrance, fail to touch the stigmas with pollen. Or it may happen that the pollinating animals themselves confine their visits to one kind of flower, which they recognize by its form and markings, and do not stray from species to species; this type of behavior has long been recognized in certain insects, particularly bees (Frisch, 1914). We may accordingly distinguish between barriers to interspecific pollination which arise from the floral mechanism itself, and those which owe their effectiveness to the habits of the pollinators. If the prevention of interspecific pollination comes about as a result of the structural contrivances of the flower, we have mechanical isolation (Dobzhansky, 1937); if cross-pollination between two species is mechanically possible, but does not occur owing to the constancy of the pollinating animals to one kind of flower, we may speak of ethological isolation. (The latter term, which was applied by Mayr (1948) to preferential mating in animals, may perhaps be expanded to include the selective fertilization of some flowering plants by their pollinators.)

Either mechanical or ethological isolation presupposes a certain level of complexity of both the flower and its agent of pollination. The structural complexity of the flower has the dual function of debarring all but certain types of animals access to the stores of nectar and pollen, and of rendering pollination impossible by those unwanted visitors that do find their way into the flower. The complexity of the animal vector of pollination consists of morphological adaptations for working the floral mechanism, sucking the nectar,

and collecting the pollen, and, in some insects at least, also of specialized instincts of flower constancy, etc., which improve the efficiency of the worker. Flowering plants pollinated promiscuously by wind, water, or unspecialized insects will probably be incapable of developing barriers to interspecific pollination. We may expect the operation of floral isolating mechanisms to be confined, therefore, to those groups of angiosperms possessed of flowers sufficiently complex to insure their non-promiscuous pollination.

A peculiarity of floral isolating mechanisms, in distinction from all other systems of isolation known in angiosperms, is that they operate only between species which differ in the morphological characters of their flowers. It follows that closely related species of non-promiscuous angiosperms should be separated taxonomically in large measure by floral characters of the sort that serve as barriers to interspecific pollination or as recognition features for insects. In promiscuously pollinated angiosperms, by contrast, the morphological differences between species should involve no unduly great emphasis on floral characters.

In order to determine whether non-promiscuous groups of angiosperms are in fact more differentiated into species on floral characters than promiscuous angiosperms, the author drew up, from Knuth (1906–1909), Robertson (1928), Porsch (1926–1930), and other sources, a list of those genera of flowering plants for which pollination records are available. The genera were grouped into the following seven pollination classes: (a) bird plants; (b) butterfly and moth plants; (c) bee plants; (d) bee and long-tongued fly plants (Syrphidae, Bombyliidae in part); (e) promiscuous plants (miscellaneous bees, wasps, flies, etc.); (f) wind-pollinated plants; (g) water-pollinated plants. Then, turning to a wide variety of taxonomic treatments, the author noted for each genus the diagnostic characters that have been used to separate pairs of species in the ultimate divisions of the

keys. The results of this survey, which is admittedly only as adequate as the taxonomic treatments and pollination records on which it is based, are summarized in table 1.

To facilitate comparison between the different pollination classes, the data from table 1, column 5 have been extracted and represented as a bar diagram (fig. 1). There are certain combinations and one omission in this figure; thus the totals for bee plants and bee and long-tongued fly plants have been combined, as have the totals for wind- and water-pollinated plants. Due to the relatively small sample of butterfly and moth plants represented in the survey, and the correspondingly great possibility of sampling errors, that class has been omitted from the bar diagram. The mean percentage of floral
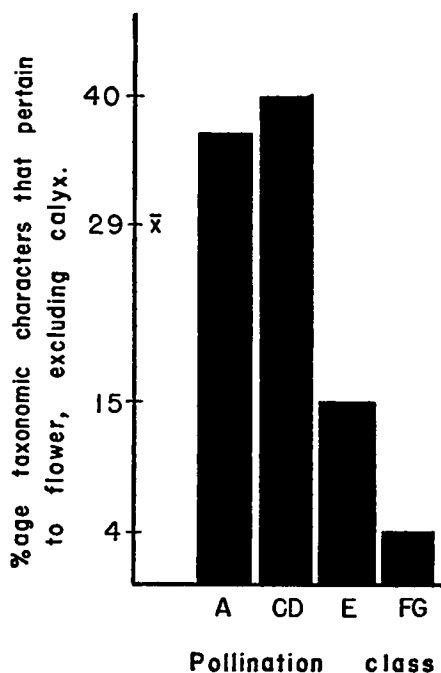

FIG. 1. The relative taxonomic importance of floral characters, as correlated with mode of pollination in angiosperms.
(A) Bird-pollinated plants; (CD) Bee and long-tongued fly plants; (E) Plants pollinated promiscuously by unspecialized insects; (FG) Wind and water-pollinated plants; (x) Mean for all classes.

characters, exclusive of calyx, for the 416 genera and 5289 characters considered in the survey is 29 per cent, as shown in figure 1. It is the best estimate we have at present of the taxonomic importance of floral characters in the angiosperms as a class, though no doubt it is biased with genera of the temperate zones.

When bird, bee, and bee and long-tongued fly plants are compared with "the average angiosperm," it appears that a correlation between non-promiscuous pollination and preponderance of floral characters does indeed exist. By contrast with these latter groups, closely related species of promiscuous plants are seen to be separated relatively little by floral characters. The difference between the means of bee and long-tongued fly plants and of promiscuous plants, when subjected to the appropriate t test (cf. Snedecor, 1946), was shown to be highly significant; that is, the probability that these percentage differences are due to

TABLE 1. *Frequency distribution of taxonomic characters among the various parts of the plant in Angiosperms; data grouped according to agent of pollination*

1 Pollination class / 2 Taxonomic category*	3 Regions**	4 No. genera*	5 Flower (except calyx)	6 Calyx (except where petaloid)	7 Inflorescence	8 Fruit, seed	9 Habit, leaf, pubescence	10 Total no. characters
A—BIRD PLANTS (Trochilidae, Nectariniidae, Drepanididae, Meliphagidae, etc.)								
Rubiaceae	Peru	52	35	0	22	4	39	218
Fuchsia	S. Amer.	1	48	0	14	7	31	58
Salvia (in part)	Mex.-S. Am.	1	28	27	9	0	36	185
Leguminosae	Peru, Austral.	6	40	3	16	11	30	37
Epacridaceae	Austral.	18	41	11	8	0	40	225
Proteaceae	Aust., S. Afr.	28	27	0	21	7	45	540
Liliaceae	S. Africa	2	31	0	17	0	52	35
Iridaceae	S. Africa	2	67	0	5	0	28	36
Musaceae	world	3	39	0	15	14	32	41
Campanulaceae-Lobelioideae	Hawaii	5	50	9	12	2	27	107
Totals for Bird Plants		123	37	5	16	4	38	1562
B—BUTTERFLY AND MOTH PLANTS								
Caryophyllaceae-Sileneae	Cal.; C. Eur.	2	38	15	3	8	36	39
Lilium	Cal.; C. Eur.	1	78	0	11	0	11	9
Lonicera	Cal.; e. N. A.	1	62	0	8	7	23	13
Totals for Butterfly and Moth Plants		7	54	10	6	5	25	81
C—BEE PLANTS								
Boraginaceae	C. Eur.	4	48	14	7	0	31	29
Fumariaceae	Cal.; C. Eur.	3	47	0	13	20	20	15
Labiatae	Cal.; Eur.	9	49	8	9	0	34	83
Leguminosae-Papilionatae	N. Am.; Eur.	15	31	8	13	11	37	360
Orchis	C. Eur.	1	61	0	9	0	30	23
Ranunculaceae	w. N. A.; C. Eur.	3	33	5	10	19	33	21
Scrophulariaceae	Cal.; e. N. A.; C. Eur.	13	41	12	6	10	31	203
Viola	Cal.; C. Eur.	1	46	3	5	3	44	39
Totals for Bee Plants		49	38	9	10	9	34	773
D—BEE AND LONG-TONGUED FLY PLANTS (Syrphidae, Bombyliidae in part)								
Boraginaceae	C. Eur.	4	62	4	8	9	17	24
Epilobium	Cal.; C. Eur.	1	27	0	5	9	59	22
Ericaceae	N. A.; C. Eur.	4	32	4	8	20	36	50
Geraniaceae	N. A.; C. Eur.	2	35	5	14	8	38	86
Hydrophyllaceae	Cal.	5	45	3	5	8	39	38
Labiatae	Cal.; C. Eur.	5	13	23	13	3	48	31
Liliaceae	Cal.	2	57	0	7	4	32	28
Malvaceae	Cal.; C. Eur.	2	33	10	19	9	29	21
Polemoniaceae	w. N. A.; world	9	58	5	11	6	20	149
Scrophulariaceae-Verbasceae &-Veroniceae	Cal.; e. N. A.	2	28	4	13	20	35	46
Totals for Bee & Long-tongue Fly Plants		39	42	6	10	9	33	523
Combined totals for Classes C & D		87	40	7	10	9	34	1296

TABLE 1.—*Continued*

1 Pollination class / 2 Taxonomic category*	3 Regions**	4 No. genera*	Distribution of key characters used in separating closely related species, by percentage of total number of characters					10 Total no. characters
			5 Flower (except calyx)	6 Calyx (except where petaloid)	7 Inflorescence	8 Fruit, seed	9 Habit, leaf, pubescence	
E—PROMISCUOUS PLANTS (Miscellaneous Insects)								
Acer	world	1	10	2	12	23	53	51
Caryophyllaceae-Alsineae	Cal.; C. Eur.	5	20	4	23	6	47	51
Cruciferae-Brassiceae & -Sisymbrieae	world	52	19	3	10	33	35	298
Euphorbia	Cal.; C. Eur.	1	0	0	26	26	48	31
Ranunculus	Cal.; C. Eur.	1	27	0	3	19	51	37
Rosaceae	N. A.	5	12	5	11	10	62	148
Salix	N. A.; C. Eur.	1	24	0	12	5	59	42
Umbelliferae	N. A.	21	6	3	23	23	45	287
Saxifraga	Cal.; C. Eur.	1	33	3	6	6	52	33
Totals for Promiscuous Plants		92	15	3	15	21	46	1000
				Scale, perigyn., spikelet	Catkin, spike panicle	Fruit, seed, involucre		
F—WIND-POLLINATED PLANTS								
Betulaceae	world	5	2	30	20	3	45	40
Cyperaceae	N. A.; world	2	3	47	16	7	27	469
Fagaceae	N. A.	2	0	0	0	32	68	31
Gramineae	Cal.	24	0	50	22	0	28	94
Juglandaceae	N. A.	2	0	0	6	44	50	18
Juncaceae	Cal.	2	39	0	22	17	22	18
Potamogeton	N. A.	1	4	0	8	28	60	25
Totals for Wind-pollinated Plants		39	4	40	16	8	32	697
G—WATER-POLLINATED PLANTS								
Naiadaceae	N. A.; world	3	11	0	0	28	61	18
Combined totals for Classes F & G		42	4	39	16	9	32	715
Grand totals for all classes		416	29	11	14	9	37	5289

* for list of genera considered cf. appendix i.
** for list of taxonomic treatments used cf. appendix ii.

errors of random sampling represents a chance of much less than one in a hundred. We may conclude that the data drawn from a wide series of angiosperms are not at variance with the hypothesis of floral isolation.

Species Differences in Wind-pollinated Angiosperms

It will be instructive to consider the types of taxonomic characters separating closely related species of oaks and grasses, which can probably not be isolated by their mode of pollination. The suggestion of Stebbins (in press) that species of oaks are isolated, not by genetic barriers to hybridization but by ecological barriers to the establishment of the hybrid seedlings, finds an interesting commentary in the emphasis on leaf characters in the genus Quercus, which here constitute 58 per cent of the total number of taxonomic characters.

The absence of stamen and style characters in the Gramineae, in constrast with the diversity of characters of the spikelet, which encloses the seed in that family, is in line with another idea of Stebbins. He has pointed out (*op. cit.*) that the conditions of pollination are very uniform for all grasses and that selective pressures are correspondingly weak at the stage of flowering; but selective pressures are strong at the stage of dispersal, with the result that the important permutations in the Gramineae concern almost solely those modifications of spikelets, awns, joints,

etc. which characterize the different dispersal mechanisms of grasses.

Mechanical and Ethological Isolation in Butterfly and Moth Plants

The mutual adaptations of certain moths and orchids constitute a classical case of a mechanical relationship in flower pollination; but to what extent moths and butterflies are also instinctively flower constant is not clear. Knoll (1921–1926, pp. 374–375) believes that a Lepidopteran will remain constant if there is an abundance of nectar in one place, but will otherwise wander about at random. This might explain why Christy (1883) observed a group of butterflies (*Vanessa, Colias, Parnassius, Pieris*) making predominantly (75 per cent) single species visits, while Bennett (1883) found the same kinds of butterflies making predominantly (78 per cent) interspecific visits.

The hawkmoths (Sphingidae), by contrast with butterflies, have acquired a reputation for flower constancy (Loew, 1886; Lovell, 1918). Knoll (*op. cit.*, pp. 215–216) observed *Macroglossa stellatarum* L. to remain constant on Linaria during over a hundred visits, while paying no attention to Pelargonium. Much more work needs to be done on pollination by Lepidoptera; the proper designation of the type or types of floral isolating mechanisms in plants pollinated by these long-tongued insects is a nice problem for future research. Then perhaps an explanation will be forthcoming for the interesting contrast, as regards the relative importance of floral characters, between the Lepidopteran-pollinated Sileneae and the promiscuous Alsineae of Caryophyllaceae (with 38 per cent and 20 per cent of floral characters respectively, cf. table 1).

Mechanical Isolation in Bird Plants

How can we account for the importance of floral characters in bird plants? The case for flower constancy in birds is weak. To be sure, hummingbirds will remain on one species of plant if it is abundant and nothing else is to be had, as the au-

thor has observed in the Sierra Nevada of California with Rufous hummingbirds (*Selasphorus rufus*) and *Pentstemon newberryi* Gray; but it is equally true that in Berkeley gardens the Allen hummingbird (*Selasphorus alleni*) goes freely from one kind of flower to another. Bené (1941, 1945, 1946) has shown that the feeding behavior of hummingbirds is complex; they do form habits, conditioned by their experience, and may remain constant to a certain kind of syrup for a time (1941); yet this constancy is tempered by choice and caprice.

It may be objected that these observations are based solely on temperate zone hummingbirds which are known to be unspecific (Wagner, 1946). The scanty equivalent data available for tropical hummingbirds, however, lead to the conclusion that those birds, too, are unmethodical and inconstant in their visits to flowers (Fr. Müller, 1873; Bates, 1895). The author has succeeded in finding one clear statement regarding the pollinating habits of Australian honeyeaters (Meliphagidae). It is stated that *Meliphaga virescens versicolor* "darts out with a fluster from among the hibiscus bushes on the beach away up to the top of the melaleuca tree; pauses to sample the honey from the yellow flowers of the gin-gee, and down to the scarlet blooms of the flame tree, across the pandanus palms . . ." (quoted in Mathews, 1923–1924, p. 471).

Though flower-visiting birds may flit from one kind of blossom to another, their effective pollinating activity may be limited to those plants whose corolla-tubes are of the right proportion for their bill. Now, the most important floral characters separating South American species of Fuchsia and Salvia are those relating to the length of the floral tube. The Andean species of hummingbirds, moreover, unlike their North American relatives, have very diverse bill proportions. Again in the Hawaiian Lobelioideae the most important floral character separating closely related species is the length, curvature, and shape of the corolla-tube; and their pollinators,

the Hawaiian honeycreepers (Drepanididae), likewise exhibited marked variation in the proportions and curvature of the mandible (Perkins, 1913, pp. 385 ff.). The frequency of characters referring to the proportions of the floral tube in Fuchsia, Salvia and Lobelioideae is 18 per cent of the total number of characters, and alone nearly accounts for the difference between those plants and promiscuous plants. These facts suggest that a mechanical isolating factor may be operative in some ornithophilous plants.

If Perkins (*op. cit.*) and Rock (1919) were correct in their belief that the Hawaiian honeycreepers were the only pollinators of the lobeliads, the extinction of those birds must have placed a great selective value on autogamy, or automatic self-pollination, in the plants that they formerly pollinated. Rock (*op. cit.*, p. 31) did in fact note that the flowers of Hawaiian lobeliads may be autogamously self-pollinated; and Skottsberg (1927) found that *Cyanea hirtella* Rock is both autogamous and self-compatible. The persistence and continued seed set of the lobeliads in areas where drepanid birds are extinct perhaps finds its explanation in this process of autogamy.[1]

Mechanical Isolation in Bee Plants and Wasp Plants

Mechanical relationships are not wanting among such typical bee plants as the Papilionatae. It is well known that the flowers of alfalfa, clover, and other legumes cannot be pollinated except by bees of the right body weight or tongue length. The trigger device in the flowers of one member of the Papilionatae is currently the source of some concern to the alfalfa growers of California, who are not getting the normal set of seeds for the reason that bees of the right size and weight are not visiting the alfalfa fields (Linsley and MacSwain, 1947). It has recently been

shown (Dunn, in press) that closely related species of Lupinus may have slightly different floral mechanisms, so that one species is visited by bees and the other is not.

The flower constancy exhibited by the pollinating bees in the foregoing cases does not lessen the fact that we are here dealing with mechanical isolation, according to the definitions proposed on page 82, since the barrier to interspecific pollination would exist whether the bees were constant or not. This conclusion is borne out by the existence of mechanical isolation in flowering plants that are normally pollinated by inconstant wasps and ichneumon flies. The clip and slot device in the flowers of the milkweeds (Asclepiadaceae), for example, which has secured them against the production of taxonomically "difficult" species (Woodson, 1941), even though they are pollinated by inconstant wasps (Hurd, 1948) and flies, identifies that family as one where mechanical factors have been influential in isolation. The pollination of some orchids by the pseudocopulation of male Hymenopterans (Scoliidae, Ichneumonidae) with their flowers (Ames, 1937) provides another evident case of mechanical isolation.

THE FLOWER CONSTANCY OF BEES AND LONG-TONGUED FLIES

A general classification of bees on the degree of their flower constancy was proposed by Loew in 1884. According to this classification a distinction was made between bees that go indifferently to very diverse flowers (polytropic bees), bees that visit a few allied species of plants (oligotropic bees), and bees that visit the flowers of but a single species of plant (monotropic bees). Since Loew's terms were applied to all bees, males and inquilines as well as females, and to nectar visits as well as pollen visits, Robertson (1925) introduced the parallel terminology of polylectic, oligolectic and monolectic bees, to refer specifically to the pollen-gathering visits. These distinctions apply at the level of species of bees, but in-

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[1] The extensive literature on ornithophily has been thoroughly reviewed by Melin (1935); cf. also the writings of Porsch cited in the bibliography of the present paper.

dividual bees, even of the polylectic class, may remain constant to one species of plant throughout a series of flights.

This habit of the honey bee has been known since the time of Aristotle. Recent investigations into the flower constancy of the honey bee have been conducted from the points of view of insect psychology (v. Frisch, 1914, 1919), floral ecology (Clements and Long, 1923), and agriculture (Brittain and Newton, 1933; Crane and Mather, 1943; Butler, 1945; Bateman, 1947), to cite but a few of the numerous papers on the subject. Data on the flower constancy of various wild bees, based on the examination of their pollen loads, are given by Bennett (1874), Clements and Long (*op. cit.*), Brittain and Newton (*op. cit.*), Linsley and Mac-Swain (1942, 1947), *inter alia.*

Loew (1886) believed that long-tongued flies of the families Syrphidae and Bombyliidae have, like bees, evolved habits of efficiency and constancy to complement their structural adaptations for rifling flowers with concealed nectar. Knoll subsequently (1921–1926, pp. 97 ff.) described a case of flower constancy in *Bombylius fuliginosus* Wied. That long-tongued fly remained true to the flowers of *Muscari racemosum* Lam. et DC., while skirting an individual of *M. comosum* Mill. Lovell (1918), on the other hand, observed the syrphid fly *Mesograpta germinata* to be somewhat irregular in its flower visits.

Observations and Experiments with Gilia and Antirrhinum

During the spring of 1947 the author grew in a garden in Berkeley, California, three subspecies of *Gilia capitata* (Polemoniaceae). The three subspecies were: *Gilia capitata capitata*, a tall and slender annual with light blue flowering heads from the Coast Ranges in Napa County, California; *Gilia capitata chamissonis*, a short and stocky, glandular, sand-dune plant with deep blue flowers from Point Reyes Peninsula north of San Francisco Bay; and *Gilia capitata tomentosa*, also

from the area north of San Francisco Bay.[2] The three subspecies were represented in the garden by about eighty individuals each. They were planted in one-foot rows, with complete randomization. The flowers were pollinated by honeybees, and it was soon noticed that the bees did not stray over the garden at random. If a bee alighted on a plant of *G.c.chamissonis* she remained with that subspecies, passing over if necessary several individuals of *G.c.capitata* or *G.c.tomentosa* before stopping at another *G.c.chamissonis* plant. The manner in which the bee on *G.c.chamissonis* carefully investigated a flower of *G.c.capitata* or *G.c.tomentosa* without entering it left no doubt that discrimination was being exercised.

Other bees, working meanwhile on *G.c. capitata* and *G.c.tomentosa,* and freely circulating between these two subspecies, were likewise observed not to go over to *G.c.chamissonis;* and this isolation of the two groups of gilias remained in force throughout the spring. As the summer advanced, however, and the supply of blossoms diminished, the constancy of the bees became less rigorous. In late summer bees were seen on more than one occasion to fly from *G.c.capitata* and *G.c. tomentosa* to *G.c.chamissonis* and *vice versa;* but even then this behavior did not become customary.

Bulk seed was collected from each of the three strains in the garden and was sown in 1948. The progeny were then classified as subspecies or hybrids. This method would give an unbiased estimate of the movements of the bees only if the three subspecies of gilia were perfectly intercompatible. As a matter of fact, they are not fully intercompatible. With certain exceptions, female parents of one subspecies artificially crossed to the other subspecies in the greenhouse set only

[2] These names are based on described species and varieties of other authors, which the present author recognizes as subspecies. The proper nomenclatorial changes have been made in a monographic study of the group which will shortly be in press.

about half as many seeds per capsule as did plants used for *inter se* crosses under the same conditions. This leads one to surmise that, in the event of a bee bringing a mixed load of pollen to one stigma, the foreign pollen tube, or hybrid embryo, etc., would be at some disadvantage in competition with the products of the domestic pollen. The bees will therefore have made more inter-subspecific visits than are revealed by the progeny test.

TABLE 2. *Contamination of three subspecies of* Gilia capitata *grown intermixed in a garden and pollinated by honeybees*

Parental sub-species	No. progeny grown	Hybrid types in progeny, by per cent	
G.c.chamissonis	145	× G.c.tomentosa × G.c.capitata	19.6% 2.1
G.c.capitata G.c.tomentosa	134	× G.c.chamissonis	0.0
G.c.capitata		× G.c.tomentosa	58.7

The results of the progeny test, which are recorded in table 2, indicate 0 per cent contamination of the progeny of *G.c.capitata* and *G.c.tomentosa* by pollen from *G.c.chamissonis,* and, conversely, 2.1 per cent contamination of the progeny of *G.c. chamissonis* from hybridization with *G.c. capitata,* but 19.6 per cent contamination of *G.c.chamissonis* from *G.c.tomentosa.* These figures can be correlated in part with the compatibility relationships of the gilias, the rather complicated details of which are being presented elsewhere (Grant, 1949). The much greater frequency of hybrids of *G.c.chamissonis* ♀ × *G.c.tomentosa* (19.6 per cent) than of *G.c.tomentosa* ♀ × *G.c.chamissonis* (0 per cent) may be accounted for by reciprocal differences in incompatibility between these two entities. The greater proportion of F₁ hybrids of *G.c.chamissonis* ♀ × *G.c.tomentosa* (19.6 per cent) as compared with *G.c.chamissonis* ♀ × *G.c.capitata* (2.1 per cent) may again be due to the fact that the former cross is somewhat easier to make than the latter. These considerations fail to explain, however, why the

quite compatible cross *G.c.capitata* ♀ × *G.c.chamissonis* was not carried out. Indeed, when all due allowances are made for the reduced compatibilities between the different strains, the following conclusions stand out from the data of table 2. Pollination between *G.c.capitata* and *G.c. tomentosa* was at random, but pollination between *G.c.capitata* and *G.c.chamissonis* occurred very infrequently. In order to explain fully the results of the progeny test, therefore, it is necessary to consider the factors that determined the system of non-random pollination by the bees.

The bees had been observed to discriminate between *G.c.chamissonis* on the one hand, and *G.c.capitata* and *G.c.tomentosa* on the other, in the garden. The question arises as to how and by what characters the bees were able to recognize the two groups of gilias. There are several vegetative characters separating the two groups: the dissection of the leaves, the glandulosity of the stems. There is the shape of the calyx lobes. But the behavior of the bees did not indicate that they were guided by these characters. It was only after they had investigated the entrance to the flower that they accepted or rejected it. There must be some floral characters, other than the calyx, by which the bees were able to distinguish between the two groups of gilias. There are very obvious color differences. The corolla of *G.c.capitata* and *G.c.tomentosa* is pale lavender-violet; the corolla of *G.c.chamissonis* is deep bluish-violet. But since bees cannot distinguish one shade of blue from another, or blue from violet or purple (Frisch, 1914), they cannot have identified the subspecies of *Gilia capitata* by the colors of their corollas.

This leaves us with two possible characters, both well within the known field of perception of bees. The fragrance of the flower is different in each subspecies. The flowers of *G.c.capitata* and *G.c.tomentosa* are sweet-scented; those of *G.c.chamissonis* are creosote-scented. Bees do have a well developed sense of smell, and be-

come habituated to certain odors, as was shown experimentally by Frisch (1919). The second character which might have served as the basis for the flower constant behavior of the bees is the shape of the corolla lobes. In *G.c.capitata* and *G.c. tomentosa* the lobes are linear; in *G.c. chamissonis* they are oval (cf. fig. 2). This is the most important character used by botanists to separate the two groups of gilias; and since bees have a keen sense of form and a good memory for geometrical figures (Frisch, 1914), it is reasonable to suppose that they too perceived this character.

Mather (1947) has arrived at quite similar conclusions from experiments with two species of Antirrhinum, which differ in the size and markings of the corolla. Almost a hundred plants each of *Antirrhinum glutinosum* Boiss. and *A. majus* L. were grown intermixed in a garden and pollinated by honeybees. In the following season the progeny of *A. glutinosum* showed only 2.9 per cent contamination from *A. majus*, notwithstanding complete compatibility between the two species. However, these same *A. glutinosum* plants manifested as much as 4.2 per cent con-

tamination from a group of various hybrid derivatives of *A. glutinosum* × *majus*, differing from the species mainly in flower color. This case is very interesting for our purposes, because the foreign pollen here had to travel across a distance of four hundred feet. Pollination between *Antirrhinum glutinosum* and *A. majus* in their common garden-bed was thus opposed by a barrier more potent than microgeographical separation. That barrier was the flower constancy of the pollinating bee, founded, as in the gilia experiments, on the perception of likenesses and differences in the corolla.

ETHOLOGICAL ISOLATION IN BEE AND LONG-TONGUED FLY PLANTS

We must next inquire whether there is any evidence for the hypothesis of ethological isolation by bees and long-tongued flies under natural conditions. It may be indeed that we should speak of *clues* rather than *evidence* at the present time. There is, for example, the interesting case described by Epling (1947a) in the bee plant, Delphinium, where three interfertile species manage to coexist in the same
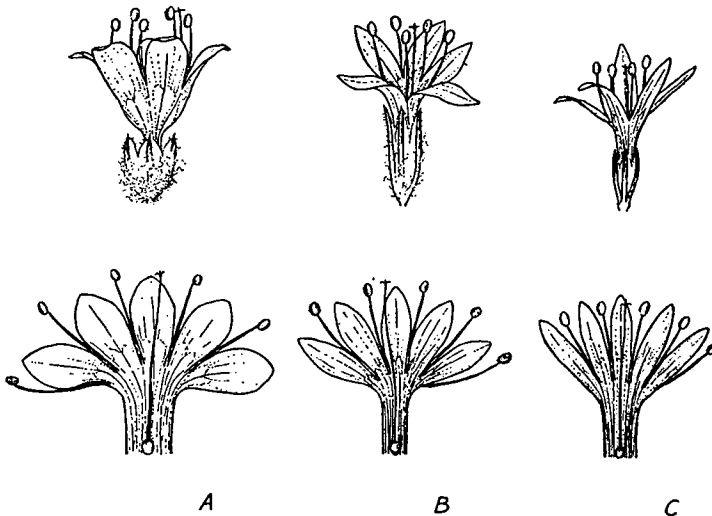

A   B   C

FIG. 2.   Drawings of the flowers of three subspecies of *Gilia capitata*.
   (A) *G.c.chamissonis;* (B) *G.c.tomentosa;* (C) *G.c.capitata.*
   Above, habit sketches of flower; below, form and venation of corolla lobes (both × 4).

territory without losing their specific distinctness.

"With [their high] degree of compatibility it is difficult to understand how these three species maintain themselves. But more than that, despite careful search in mixed colonies, we have as yet found no evidence even of initial hybridization, although the F_1s would readily be detected. The ecological differences are slight, incomplete study of the pollinators by our colleague, Professor Gorton Linsley, indicates no marked insect preference. The potential flow of genes seems assured, yet it is apparently not realized, or if so, to an extent far less than might be expected in view of the compatibility of the species. We can as yet offer no satisfactory explanation of the factors involved." (Epling, *op. cit.*) The three species of larkspur, as Dr. Epling has kindly informed the author, are *Delphinium hesperium* Gray, *D. parryi* Gray, and *D. variegatum* Torr. and Gray. As might be expected, they are separated by the size, shape, and hair-markings of the showy sepals, and by some other floral characters.

The chief evidence for the hypothesis of ethological isolation is the existence in our temperate floras of a large contingent of bee and long-tongued fly plants, distinguished one from another, for bees as well as for botanists, by visible markings of the flowers. The floral structure is sufficiently generalized in many of these plants, for instance *Gilia capitata* and its allies, so that a bee mechanically able to pollinate one species could pollinate the next one as well. In such cases ethological rather than mechanical factors must be the main ones producing floral isolation. Here then, among the less highly specialized groups of bee and long-tongued fly plants, is the potential sphere of influence of ethological isolation.

THE RELATION BETWEEN FLORAL ISOLATION AND SPECIATION IN BEE PLANTS

Two evolutionary roles may, on *a priori* grounds, be postulated for floral isolation in bee plants. In the first place, ethological isolation may operate to reinforce an isolation originally set up by geographical and ecological factors. Its effect in this case will be to minimize the interbreeding between sympatric populations which have acquired different floral characters during a previous period of geographical separation. There are general reasons for supposing that this effect, namely the augmentation of the efficiency of allopatric speciation, may constitute the primary evolutionary role of ethological isolation in bee plants (Mayr, 1947, and in correspondence with the author).

In the second place, ethological isolation may itself conceivably determine, under certain conditions, the original divergence of populations. This might be the case, for example, when a mutation affecting the shape or markings of the floral organs, etc., arises in a population of bee plants. Let us suppose that the mutation is recessive and that a single mutant individual becomes segregated out in the population. The fixation of certain bees on the new kind of flower would impel them to return to the mutant individual at the beginning of each foraging flight (H. Müller, 1882; Buzzard, 1936; Butler, Jeffree and Kalmus, 1943); the insufficient supply of blossoms on this one individual, however, would lead these bees to visit other individuals and so to cross-pollinate the mutant individual with the normal types. In this manner the new factor might spread through the population in the heterozygous condition.

The next important stage in the history of this floral mutation would occur after it had reached a critical frequency in the population. The segregation, then, in one generation of a large number of mutant individuals might insure that at least some of them would be isolated due to the flower constancy of the bees. The new line, remaining thus reproductively isolated from the main body of the population, might now accumulate other factors making for its differentiation. It would develop, in short, under the influence of

its own genic materials. The establishment of a new and distinct population within the limits of an old population is thus at least a hypothetical possibility in bee plants.

It must be admitted that evidence for sympatric speciation by ethological isolation has not as yet been found in any group of bee plants. In Gilia and Antirrhinum, for example, the data at present available suggest that new and distinct populations have first been allopatric before they have become sympatric (Grant, 1949; Baur, 1932). Powerful arguments have been advanced by Mayr (1947), moreover, against the hypothesis of sympatric speciation in general. The important role of ethological isolation in evolution would appear, in the light of present knowledge, to consist, not in the determination of sympatric speciation, but in the reinforcement of allopatric speciation.

A system of non-random mating has nevertheless been shown to exist in some flowering plants habitually pollinated by bees. That system of non-random mating, moreover, as we have seen from the data of Mather (1947), is capable of producing more effective isolation than microgeographical distances. The author has concluded, from the foregoing facts and deductions, that sympatric speciation in bee plants is by no means a theoretical impossibility.

If floral isolation is a factor in the evolutionary divergence of angiosperms, we might expect to find, especially in areas rich in bees, a greater diversification of bee plants than of promiscuous plants. That such is indeed the case is indicated by the following facts. In Southern California, an arid to semi-arid land with a great concentration of endemic bees, there are, according to a survey of the genera listed in Munz's Manual (1935), a mean number of 3.38 species per genus in promiscuous, entomophilous angiosperms, and 5.94 species per genus in bee plants. The means are based on 143 genera of promiscuous plants and 141 genera of bee plants;

the individual genera are approximately the same as, or comparable to, those listed in Appendix I. The difference between 3.38 and 5.94 is highly significant, and can scarcely be due to chance alone. This relatively great diversification of bee plants in Southern California is what we might expect if floral isolation is an effective factor in speciation (whether allopatric, sympatric, or both) in bee plants.

These considerations and the data presented in Table 1 do not suggest that floral isolation has played a lone hand in speciation in bee plants. In many groups it may have played a very minor role, or no role at all. For instance, in some Papilionatae closely related species appear to be isolated primarily by the inviability of the hybrid embryo. All attempts over a period of several years to intercross seventeen species of Lathyrus thus met with complete failure (Senn, 1938). A second case, illustrating a very different situation within the group of plants pollinated by bees, is the Polemoniaceae. In the genus Gilia, and probably in some other genera as well, unpublished evidence of the author indicates that hybridization has been very active in the compounding of new floral structures out of older types. The young family, Polemoniaceae, thus places before us the problem of natural hybridization in bee plants, which has never been examined in the light of the phenomenon of flower constancy. These two examples will suffice to illustrate the point, which no one doubts, that the problem of speciation has many facets.

In view of the abundant repertoire of isolating mechanisms in nature, as has been emphasized by several writers (Dobzhansky, 1937; Mayr, 1948; Stebbins, in press), it cannot be imagined that floral isolation has enjoyed a monopoly in the origin of species of bee plants. The data of Table 1 and the figures just presented, however, are not in disagreement with the hypothesis that floral isolating mechanisms have in fact played a role in the evolution of bee plants.

SUMMARY

Floral isolating mechanisms consist of barriers to interspecific pollination in angiosperms imposed by structural contrivances of the flowers which prevent the pollen of one species from being conveyed to the stigmas of the other (mechanical isolation), or imposed by the constancy of the pollinators to one kind of flower (ethological isolation). A necessary precondition for the rise of floral isolating mechanisms in any group of angiosperms is that the plants shall be non-promiscuous, that is, pollination shall be effected exclusively by certain types of animals. Such non-promiscuous plants are shown to be differentiated into species on floral characters to a greater extent than angiosperms pollinated promiscuously by miscellaneous insects. 40 per cent of the taxonomic characters in bee and long-tongued fly plants pertain to the floral parts exclusive of calyx, and the corresponding figure in bird plants is 37 per cent, as compared with only 15 per cent of floral characters in promiscuous, entomophilous angiosperms, and 4 per cent in wind-pollinated angiosperms (cf. table 1). The great importance of floral characters for the classification of non-promiscuous angiosperms may perhaps be a consequence of the operation of floral isolating mechanisms.

Floral isolation of the mechanical type may exist in plants pollinated by birds, butterflies, moths, bees, or long-tongued flies. Ethological isolation must be confined to plants pollinated by those insects which exhibit habits of flower constancy, chiefly bees, but also some long-tongued flies and hawkmoths.

As an example of ethological isolation under artificial conditions some observations and experiments with *Gilia capitata* (Polemoniaceae) are reported. Three subspecies of *Gilia capitata*, two with linear corolla lobes and sweet-scented nectar, and one with oval corolla lobes and creosote-scented nectar, were grown intermixed in a garden where they were pollinated by honeybees. The bees were observed in general to remain either with the linear-lobed or the oval-lobed subspecies, and not to cross-pollinate them; in the progeny of the garden plants a low percentage (0 to 21.7 per cent) of F_1 hybrids between the two groups of gilias was encountered. The most probable conclusion that can be drawn from existing knowledge of bee psychology, from the known characters of the plants, and from the observed behavior of the bees on the flowers is that the bees were distinguishing the two groups of gilias by the form and venation of their corolla lobes and/or by the odor of their nectar.

Ethological isolation may have two roles in the evolution of bee plants: the initiation of a primary evolutionary divergence as a result of the selective pollination of mutant floral types arising within a population; and the prevention or reduction of interbreeding between sympatric populations which have acquired different floral characters during a previous period of geographical separation. In the light of present knowledge, the latter role, or the augmentation of the efficiency of allopatric speciation, is probably of considerable evolutionary importance; whereas the former role, the initiation of sympatric speciation, is largely of academic interest. In any case, bee plants, in so far as they possess a method of isolation not available to promiscuous plants, are in a position to undergo more rapid evolution than the less specialized groups

of angiosperms. There are, in the flora of Southern California, an average number of 5.94 species per genus in bee plants, as opposed to 3.38 species per genus in promiscuous, entomophilous angiosperms.

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APPENDIX I

List of Genera considered in Table 1

A—Bird Plants.—ONAGRACEAE.—Fuchsia (Hummingbirds [Trochilidae]). RUBIACEAE.—Albertia, Amaioua, Anisomeris, Arcytophyllum, Bathysa, Bertiera, Borreria, Cephaelis, Chimarrhis, Chomelia, Cinchona, Coccocypselum, Condaminea, Coussarea, Diodia, Duroia, Exostema, Faramea, Galium, Geophila, Gonzalagunia, Guettarda, Hamelia, Hillia, Hippotis, Hoffmannia, Isertia, Ixora, Joosia, Laidenbergia, Machaonia, Macrocnemum, Manettia, Mitracarpus, Oldenlandia, Palicourea, Pentagonia, Phitopis, Posoqueria, Psychotria, Randia, Relbunium, Retiniphyllum, Richardia, Rondeletia, Rudgea, Sabicea, Sickingia, Spermacoce, Tocoyena, Uncaria, Warscewiczia (many Rubiaceae of American tropics pollinated by Hummingbirds, but detailed information is wanting for the foregoing genera). SCROPHULARICEAE.—Castilleja, Pentstemon (in part) (Hummingbirds). LABIATAE.—Salvia, sect. Calosphace (Hummingbirds). LEGUMINOSAE.—Albizzia, Bauhinia, Brachysema, Kennedya (the foregoing genera by Honeyeaters [Meliphagidae] *inter alia*), Brownea, Erythrina (the foregoing two genera by Hummingbirds). CAMPANULACEAE-LOBELIOIDEAE.—Clermontia, Cyanea, Delissea, Lobelia, Rollandia (Hawaiian Honeycreepers [Drepanididae]). PROTEACEAE.—Adenanthos, Banksia, Conospermum, Dryandra, Franklandia, Grevillea, Hakea, Helicia, Isopogon, Lambertia, Lomatia, Macadamia, Orites, Petrophila, Persoonia, Stenocarpus, Stirlingia, Synaphea (the foregoing Australian genera pollinated by Honeyeaters, etc.), Diastella, Faurea, Leucadendron, Leucospermum, Mimetes, Nivenia, Protea, Serruria, Sorocephalus, Spatalla (the foregoing South African genera pollinated by Sunbirds [Nectariniidae]). LORANTHACEAE.—Loranthus (Sunbirds). EPACRIDACEAE.—Acrotriche, Andersonia, Archeria, Astroloma, Brachyloma, Coleanthera, Conostephium, Cyathodes, Dracophyllum, Epacris, Leucopogon, Lysinema, Melichrus, Monotoca, Richea, Sprengelia, Styphelia, Trochocarpa (Honeyeaters etc.). LILIACEAE.—Aloe, Kniphofia (Sunbirds). IRIDACEAE.—Antholyza, Gladiolus (Sunbirds). AMARYLLIDACEAE.—Anigozanthos (Honeyeaters etc.). MUSACEAE.—Heliconia (Hummingbirds), Musa, Strelitzia (foregoing two genera by Sunbirds). ORCHIDACEAE.—Disa (Sunbirds).

B—Butterfly and Moth Plants.—CAPRIFOLIACEAE.—Lonicera (also pollinated by Hummingbirds). CARYOPHYLLACEAE-SILENEAE.—Dianthus, Silene. LILIACEAE.—Lilium. ORCHIDACEAE.—Habenaria. SOLANACEAE.—Datura, Nicotiana.

C—Bee Plants.—BORAGINACEAE.—Anchusa, Echium, Pulmonaria, Symphytum. FUMARIACEAE.—Corydalis, Dicentra, Fumaria. LABIATAE.—Ajuga, Ballota, Galeopsis, Lamium, Prunella, Salvia (some California species are Hummingbird flowers), Scutellaria, Stachys (in part), Teucrium. LEGUMINOSAE-PAPILIONATAE.—Astragalus, Colutea, Cytisus, Hedysarum, Genista, Lathyrus, Lotus, Lupinus, Medicago, Melilotus, Ononis, Ornithopus,

Phaseolus, Trifolium, Vicia. ORCHIDACEAE.—Orchis. RANUNCULACEAE.—Aconitum, Aquilegia, Delphinium (foregoing three genera are bumblebee plants). SCROPHULARIACEAE.—Antirrhinum, Aureolaria (bumblebees), Chelone (bumblebees), Collinsia, Digitalis, Euphrasia, Gerardia, Gratiola, Linaria, Mimulus, Pedicularis (bumblebees), Pentstemon (in part), Rhinanthus (bumblebees). VIOLACEAE.—Viola. (Long-tongued flies and Lepidopterans may exceptionally work the floral mechanism in some of the foregoing bee plants.)

D—Bee and Long-tongued Fly Plants.—BORAGINACEAE.—Cynoglossum, Heliotropium, Lithospermum, Myosotis. CRASSULACEAE.—Sempervivum. FRICACEAE.—Arctostaphylos, Azalea, Pyrola, Vaccinium. GERANIACEAE.—Erodium, Geranium. HYDROPHYLLACEAE.—Hydrophyllum, Miltitzia, Nama, Nemophila, Phacelia. LABIATAE.—Lycopus, Mentha, Satureja, Stachys palustris and sylvaticus, Thymus. LILIACEAE.—Allium, Fritillaria. LYTHRACEAE.—Lythrum. MALVACEAE.—Malva, Sphaeralcea. ONAGRACEAE.—Epilobium. POLEMONIACEAE.—Collomia, Eriastrum, Gilia, Langloisia, Leptodactylon, Linanthus, Navarretia, Phlox, Polemonium. RANUNCULACEAE.—Helleborus. SCROPHULARIACEAE.—Verbascum, Veronica (chiefly Syrphid-flies).

E—Promiscuous Plants—ACERACEAE.—Acer. BERBERIDACEAE.—Berberis. CARYOPHYLLACEAE-ALSINEAE.—Arenaria, Cerastium, Sagina, Spergularia, Stellaria. CRUCIFERAE-BRASSICEAE and -SISYMBRIEAE.—Aphragmus, Arabidopsis, Brassica, Brassicella, Braya, Brayopsis, Chrysochamela, Conringia, Cossonia, Crambe, Descurainia, Didesmus, Diplotaxis, Enarthocarpus, Eruca, Erucaria, Erucastrum, Eudema, Eutrema, Fortuynia, Halimolobus, Harmsiodoxa, Heterothrix, Huguenina, Maresia, Micromystria, Microsisymbrium, Moricandia, Onuris, Orychophragmus, Parlatoria, Phryne, Physorrhynchus, Pseuderucaria, Raphanus, Rapistrum, Sarcodraba, Schouwia, Sinapidendron, Sinapis, Sisymbrium, Smelowskia, Sobolewskia, Sophiopsis, Stenodraba, Taphrospermum, Thellungiella, Torularia, Vella, Weberbauera, Xerodraba, Zilla. EUPHORBIACEAE.—Euphorbia. LILIACEAE.—Veratrum. RANUNCULACEAE.—Ranunculus. RHAMNACEAE.—Rhamnus. ROSACEAE.—Crataegus, Geum, Potentilla, Prunus, Sanguisorba. SALICACEAE.—Salix. SAXIFRAGACEAE.—Saxifraga (fly flowers). SCROPHULARIACEAE.—Scrophularia (wasp flowers). UMBELLIFERAE.—Angelica, Apium, Arracacia, Cicuta, Cymopterus, Donnellsmithia, Eryngium, Hydrocotyle, Ligusticum, Lilaeopsis, Lomatium, Oenanthe, Oreoxis, Osmorhiza, Oxypolis, Perideridia, Prionosciadum, Pteryxia, Rhodosciadium, Sanicula, Tauschia.

F—Wind-pollinated Plants.—BETULACEAE.—Alnus, Betula, Carpinus, Corylus, Ostrya. CYPERACEAE.—Carex, Scirpus. FAGACEAE.—Castanea, Quercus. GRAMINEAE.—Agrostis, Aira, Aristida, Agropyron, Bouteloua, Bromus, Calamagrostis, Chaetochloa, Danthonia, Echinochloa, Elymus, Eragrostis, Festuca, Glyceria, Hordeum, Lolium, Melica, Muhlenbergia, Oryzopsis, Panicum, Phalaris, Sitanion, Stipa, Trisetum. JUGLANDACEAE.—Carya, Juglans. JUNCACEAE.—Juncus, Luzula. NAIADACEAE.—Potamogeton. PLATANACEAE.—Platanus.

G—Water-pollinated Plants.—NAIADACEAE.—Naias, Ruppia, Zostera.

APPENDIX II

List of Taxonomic Treatments used in Table 1

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