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CURRENT PROBLEMS IN RESEARCH

Evolutionary Mechanisms in Pollination Biology

Origins and functions of floral systems are being elucidated by genetical and ecological studies.

H. G. Baker

The angiosperms, or flowering plants, now dominate the land surfaces of the earth even though they are relative newcomers in the plant world, having a fossil record which cannot be traced back with certainty much beyond the Cretaceous period. Their most obvious distinguishing feature is the production of seeds in closed carpels (angiospermy); consequently, it is appropriate to study the mechanisms involved in seed production in these plants in case these mechanisms may provide clues to the evolutionary success of the group as a whole (*1*).

Of particular interest in this connection is the suggestion made by Whitehouse (*2, 3*) that incompatibility between carpel tissue and pollen from the same plant (determined by a multiple-allele system) was the primary cause of the evolution of the closed carpel as well as of the success of the angiosperms over their gymnospermous (naked-seeded) predecessors. In this theory, a gymnospermous ancestor to the angiosperms is presumed, one with a nearly closed carpel. Thus, instead of germinating on the surface of the ovule, if the pollen grain of such a plant should germinate on the carpel tissue and the male gametes should be conveyed to the embryo sac by the pollen tube, an incompatibility system could arise. Whitehouse postulates the appearance of a multiple-allele system, although this hypothesis requires the chance occurrence of at least three alleles at the appropriate locus before the incompatibility system can begin to function, an extremely unlikely event. Once established, however, and in the conditions of a changing environment where natural selection would favor a high degree of cross-fertilization (or outbreeding), a multiple-allele system would prove superior to any other because, while it provides full self-incompatibility, there is a minimum chance of cross-incompatibility between plants. By this means, the angiosperms would rise to dominance over the "less efficient" gymnosperms which depend upon dioecism or monoecism for outbreeding. Dioecism involves the separation of pollen- and seed-bearing tissue on different plants; in monoecism the separation is to distinct parts of the same plant. Later, "when the angiosperms had become dominant and comparative [environmental] stability was reached, a marked retardation on the rate of the angiosperm evolution might occur" (*2*, p. 209) and, by this time, self-compatible variants might have the adaptive advantage except where local conditions, once again, favor a return to outbreeding.

Any attempted explanation of the seemingly sudden rise to a dominant position by the angiosperms must be speculative as long as the ancestry of this group remains, as Darwin (*4*) called it, an "abominable mystery." Nevertheless, other explanations are possible than that given by Whitehouse. The ability of the angiosperms to develop an herbaceous habit and shorter life cycles may have played a significant role, especially as seasonal climatic extremes became increasingly prominent in the Tertiary period. It is difficult to believe that the advantage of the outbreeding system of the angiosperms over systems employed by gymnosperms was great enough to be the whole explanation. After all, monoecism provides outbreeding while allowing complete interfertility between adjacent plants, and roughly two-thirds of the Coniferales are monoecious, with lesser proportions in other groups of gymnosperms (*2*, p. 211).

More recent studies of incompatibility systems have shown that several different kinds of multiple-allele systems exist (*5, 6*), thus rendering the Whitehouse theory of a single origin of multiple-allele incompatibility unlikely. In the Solanaceae, two systems are even to be found in one family (in the genera *Physalis* and *Nicotiana,* for examples) (*5*). Other systems, such as the two-allele heteromorphic kinds (which Whitehouse believes could evolve more frequently, and, therefore, assumes to be a secondary development), are no more scattered among the angiosperms than are multiple-allele systems (*6*).

Consequently, we should now examine other possible explanations for the apparent dominance of flower- (and fruit-) bearing plants in competition with cone-bearing gymnosperms. The flexibility in seed dispersal mechanisms made available by the development of the fruit is one such possibility. Even if we restrict our attention to the

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The author is professor of botany and director of the Botanical Garden at the University of California, Berkeley.

circumstances under which pollination takes place, we should note that, as far as we can tell from the poor fossil record, the rise to dominance of the angiosperms coincided rather closely with the vast proliferation of potential pollen vectors—insects, birds, and bats. Leppik (*7*) has reviewed the evidence on the correlation between the development of the sensory capabilities of flower-visiting insects and the evolution of flower types (from amorphic flowers, which may no longer exist, through several stages to special types of zygomorphic flowers, such as those of the figwort family, the Scrophulariaceae). Beetles, as first postulated by Diels (*8*), led the way, and the sequence culminates in bees of various sorts.

Flowers appear to have been more adaptable than cones to the evolution of pollination by animal agency. Unlike woody cones, the soft, thin petals of flowers may be colored brightly, with translucence and surface effects sometimes playing a part in making them attractive. The development of correlated "honey-guide" color patterns and scent patterns as well as specialized flower shapes is also made possible. The production of nectar, although not necessarily a feature of the most primitive flowers, where solid food was probably presented to insect visitors in the form of fleshy parts and pollen (*9*) (Fig. 1), was unquestionably a very important factor in tying the pollination of flowers to the feeding habits of animals.

For the angiosperms, the activities of the animals, as they seek out the flowers and carry the pollen, provide a real advantage over the broadcasting of pollen into the air to be wafted only by chance to an appropriate stigma. The advantage is measured by increased certainty of seed production and results in an economical expenditure of energy by reduction in the amount of pollen produced in relation to the number of seeds. Only later, when large stands of specialized vegetation dominated by one or a few species of flowering plant (temperate forests, grasslands, and so forth) became established, would the disadvantages of wind pollination be removed, allowing a return to this mode of pollen transfer. The efficiency of pollen transfer by animals is increased still further if, when the pollen is brought into the flower and laid down on the stigma, a further supply is picked up from the anthers. In this manner, the close association of the "hermaphrodite" flower with pollination by animals would be expected to develop (*10, 11*).

With the evolution of the hermaphrodite flower as a consequence of pollination by animals, the outbreeding propensities of monoecism and dioecism possessed by the gymnosperms are lost. At the same time, however, the presence of a style and of pollen-tube growth through it provide an opportunity for the control of fertilization by a different means, the sieving of pollen tubes. Thus, physiological incompatibility systems are not only possible but are likely to confer a selective advantage upon their possessors if they should arise. This may explain why it is that we see numerous separately evolved (and somewhat different) incompatibility systems among the angiosperms. Bateman (*12*) has reviewed the different kinds of incompatibility systems which are theoretically possible, and an impressive proportion of them has been discovered, even though there is not one major family of angiosperms for which we have more than a skeletal knowledge.

Fig. 1. Nectarless flower of *Argemone munita* subsp. *rotundata* (Papaveraceae) with small pollen-collecting bees. Summit of Monitor Pass, Sierra Nevada, California.

Specialized Mechanisms

For convenience, species are sometimes classified as bearing "moth-flowers," "bumble-bee flowers," and so forth, often on the basis of their gross morphology and coloration (not always observed in the living condition). This can lead to errors of interpretation (*13*) (Fig. 2), apart from the fact that a one-to-one restriction of a particular flower to a particular class of pollinator is probably the exception rather than the rule (*14*). Even while the nearly world-wide coincidence of the geographical-distribution patterns of the monkshood genus *Aconitum* (Ranunculaceae) and the bumble-bee genus *Bombus* (*15*) may be significant, we should not jump to the conclusion that the absence of the plants from South Africa and Australia is due to the absence of the potential pollinator. After all, *Bombus* occurs in South America while *Aconitum* fails to penetrate south of the equator anywhere in the world. Similarly, the alleged barrier to the further spread of *Calystegia sepium*, the hedge bindweed (Convolvulaceae), in the British Isles, because it has reached the limits of distribution of its "necessary" pollinator, the convolvulus sphinx moth (*Sphinx convolvuli*) (*16*), is fallacious since the flowers of this species are quite adequately pollinated by other insects that fly during the day (*17*).

Similarly, the effectiveness of adaptation to separate classes of pollinator as a barrier to natural crossing between two closely related species of flowering plants appears to require substantiation in each case for which it is suspected (*18*). However, there are sometimes rather high degrees of specialization. Sprague (*19*) has pointed out that the red flowers of the lousewort, *Pedicularis densiflora* (Scrophulariaceae), have purple overtones in coastal California, where they are visited by Anna hummingbirds which have gorgets of the same shade. In the Sierra Nevada, where pollination depends upon rufous hummingbirds with orange-red gorgets, the color of the flower is a corresponding orange-red. This specialization may be compared with the observation by van der Pijl (*20*) that the flowers of some tropical trees which are visited by bats smell rather similar to the bats themselves, a fact which suggests that the relationship between flower and pollinator may have been initiated by a direct sexual stimulus.

This kind of pollinator attraction reaches its greatest degree of sophistication in the Orchidaceae. Here, the studies by Kullenberg (*21*) and Stebbins and Ferlan (*22*) on *Ophrys*, in the Mediterranean region, have fully confirmed the extraordinary syndrome that includes the stimulation of visiting male hymenoptera into attempts at copulation with the flower, which has an insect-like appearance (*23*). After alighting on the lip of the flower, the bee is roused to copulatory activity by the stimulus of contact with hairs on its surface. In the process the bee picks up or deposits pollinia. The same observers have shown how, by variations in the color, shape, pubescence, and scent of various parts of the flowers, speciation in the plants may accompany adaptation to different species of visitor.

Thus, for a general mechanism which is already in existence, such as this "pseudocopulation," Darwinian evolutionary processes involving the accumulation of small changes appear very likely to be operative in producing the differences to be seen between species. The big question is whether or not the basic mechanism can *arise* in such a manner.

Sudden Origins

Tropical epiphytic orchids provide some of the most intricate pollination systems, and these can only be operated successfully by particular insects. They represent the ultimate in reliance upon floral mechanisms for the promotion of outbreeding and might be expected, on a basis of Darwinism, to show to a high degree correlation of floral evolution with differentiation in the insect visitors. Unfortunately, in some cases, at least, this is not so.

In the tropical American orchid *Gongora maculata*, the pollinator is a small bee, *Euglossa cordata* (*24*). The male bee is attracted to a flower by its fragrance, the source of which is a deep cleft at the base of the lip. If, in attempting to reach this, the bee clambers onto the keel-like, slippery plates of the lip, it may fall, slide on its back over the smooth concave surface of the column, strike the tip of the anther, and remove the pair of pollinia. Insertion of these pollinia from the back of the insect into the very narrow stigmatic cleft is possible only after a rather protracted period and, in this way, cross-pollination is more likely to occur than selfing.

Another orchid, *Coryanthes speciosa*, operates an equally complex but entirely different mechanism (*25*). Here again, male bees are attracted by the fragrance. As it alights on the mesochile, the bee maintains its position by the vigorous use of its wings. Ultimately, these hit against a drop of fluid (secreted by the glands at the base of the column) which had been hanging over the head of the bee. This dislodged drop then carries the bee with it into the liquid-filled bucket formed by the epichile. The struggle of the bee to free itself from this prison is likely to be prolonged and is successful only when it pushes its way up past the anther and emerges through the lateral opening of the lip, with two pollinia attached to its back. By this time the fragrance of the flower has vanished and the bee flies away. However, the next day, fragrance and the secretion of the droplets of fluid return, and a bee, presumably already carrying pollinia, may go through the process again and leave a pollinium on the stigma.

The punch line to this story of two elaborate but entirely dissimilar mechanisms is that the bee involved in each case is of the same species, *Euglossa cordata*. Apparently the multiplicity of characteristics in each kind of flower (including the appropriate timings of glandular secretions and fragrance) have evolved without any obvious evolutionary change in the bee. This suggests that one or both of these systems for the pollination of orchids is the product of recent, sudden evolution. In any case, it is very difficult to

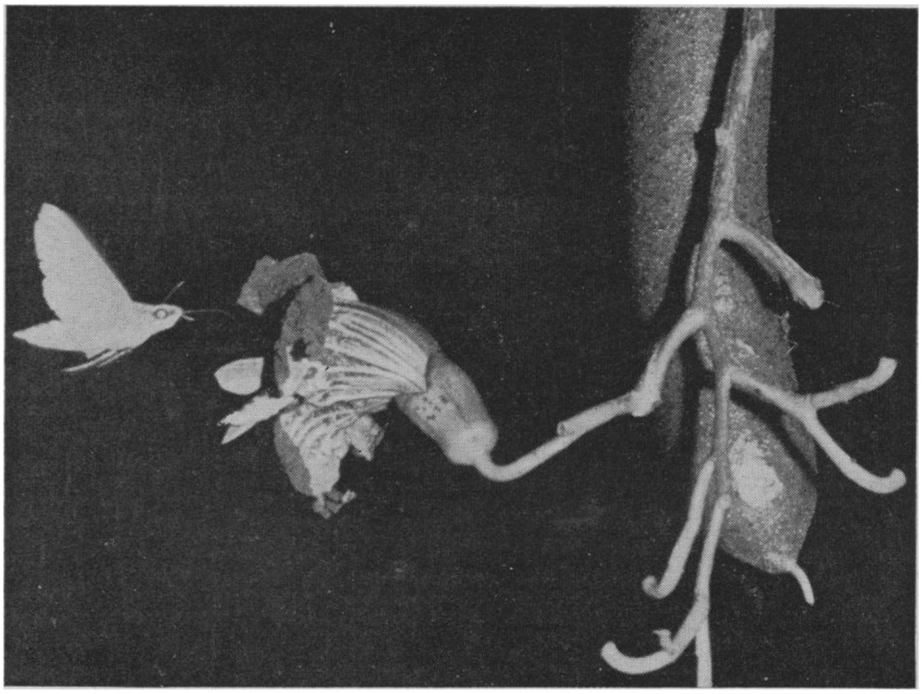

Fig. 2. Although wrongly referred to in the literature as bird-pollinated, *Kigelia africana* (Bignoniaceae) is visited by hawkmoths (*Nephele vau*) at dusk. One moth has crawled into the nocturnally-opening flower which has a reddish-purple color and a nauseous odor (not a combination of characters traditionally associated with moth-pollination). These flowers are also visited by bats [Harris and Baker (*13*)]. Legon, Ghana.

Fig. 3. Flowers of *Ceiba pentandra* (Bombacaceae) visited after nightfall by the fruit-bat *Eidolon helvum* which laps nectar and chews anthers but also conveys pollen on its fur [Baker and Harris (*33*)]. Achimota, Ghana.

imagine how they could have been built up gradually, and one is tempted to see in them the result of fortuitous but apparently successful variation of a number of characters at the same time. This is not to deny the probability that innumerable unsuccessful "mutations," or "fortuitous recombinations," occurred before the efficient one was produced, or that each system has been brought to its present degree of perfection by subsequent minor modifications and elaborations. Although flowers and insects may both be evolving, there is no need to suppose that the steps taken by each will necessarily be contemporaneous.

The related genus *Stanhopea* contains at least two strikingly different pollination mechanisms, one of which (in *S. bucephalus*) resembles that of *Gongora*, although the visitors are male bees of the genus *Elaema (26)*. In *Gongora, Coryanthes,* and *Stanhopea* the scent appears to be the most important attractant for insects, and it remains constant within a species, as does the morphology of those flower parts which are concerned with the pollination mechanism. Color and the morphology of unessential parts, however, vary widely, the difference here indicating that, whether or not the mechanism originates by way of a selective process, its essential features are certainly maintained thereby.

The fact that only male bees visit the flowers and appear to get no benefit from their calls could explain the lack of evolutionary development in the bees, in contrast to the elaborate floral changes. The male bees are attracted by the scent of the flowers, but, as there is no reward for them in the shape of food, there is no selection pressure which might result in an increase in their powers of discrimination. No selection against their fascination for the scent need necessarily occur either, for, although their time appears to be wasted, most often they have no other use for it. The females, however, are concerned with food gathering and nest building; for them to be lured into a pointless concern with the flowers would be penalizable inefficiency. Significantly, they do not possess the same chemoreceptive hairs on the tarsi of their front legs, and consequently they are not attracted by the various secretions of the flowers (*26*).

The sudden origin of characters with adaptive significance for pollination is most likely to be detectable and genetically interpretable when the situation is not as complicated as in the orchids discussed above. Thus, in the columbine genus *Aquilegia* (Ranunculaceae) one floral character that plays a significant role in the pollination system is the nectariferous spur. Prazmo has shown that when a spurred plant of *A. vulgaris* is crossed with a spurless one (as in the probably primitive Asiatic species *A. ecalcarata*), the F_1 generation is spurred and a 3:1 ratio may be extracted from the F_2. A single gene is involved (*27*).

In this case, we may suppose that the appearance of the spur is a previously spurless stock was a fortuitous major event which restricted the attractiveness of the flowers so that only insects with long tongues could acquire the nectar at the end of the spur. Because the discriminatory powers of these insects enable them to recognize and confine their visits to such flowers, a mutually advantageous relationship between plants and animals would be favored in selection. Thus the stage would be set for variation upon this theme through the action of other genes which might affect spur length, flower color, and the angle at which flowers are held. All of these variations have been effective in adapting individual species of *Aquilegia* to bees, hummingbirds, and sphingid moths (*28*).

In the snapdragon genus, *Antirrhinum* (Scrophulariaceae), the usually two-lipped flower can be converted to a radially symmetrical form by the mutation of a single gene (*29*). If this means that a reverse change could have been the origin of their bilateral symmetry, the foxglove family Scrophulariaceae, as a whole, may owe this salient feature to a single mutation. Sudden origin of a different sort has been postulated for another member of the Scrophulariaceae, *Penstemon spectabilis* (*30*). This species appears to have arisen by hybridization between *P. centranthifolius* (with red, tubular flowers, pollinated by hummingbirds) and *P. grinellii* (with two-lipped blue flowers, visited by large carpenter bees of the Megachilidae). *Penstemon spectabilis* has purplish-blue, rather two-lipped flowers and is pollinated by wasps of the genus *Pseudomaris*.

Although the genetical situations in the orchids may have little in common with these simple models from the Ranunculaceae and Scrophulariaceae, the latter may help to substantiate the possibility of their evolution in only a restricted number of stages.

In the case of *Aquilegia* and *Penstemon*, the assumption has been made that suitable pollen vectors were available when the new types of flower evolved suddenly. The converse is suggested in other cases. Thus, the fossil record of the bats (Chiroptera) does not reach back beyond the Paleocene epoch, and the flower- and fruit-visiting Megachiroptera appear to have evolved too late to be able to enter the New World from the Old World tropics. In the New World tropics, nectar-lapping bats appear to have evolved relatively recently from an insectivorous microchiropteran stock. On the other hand, the tree genus *Parkia* is pantropical; its South American species have been separated from those of the Old World since the Eocene epoch at the latest. Nevertheless, *Parkia* trees have been shown to be pollinated by bats in Southeast Asia (*31*), West Africa (*32*), and South America (*33*), and the same specialized adaptations exist in each area. Thus we have a real problem; the plants appear to have been ready for the bats before the bats were available. What could have been the nature of their visitors before the bats took over?

A similar problem is presented by the nocturnally flowering kapok tree, *Ceiba pentandra* (Bombacaceae), which is pollinated by bats in West Africa (*34*) (Fig. 3) and South America (*33*).

Gradual Origins

The cases cited above suggest that fortunate accidents, in the shape of the preadaptation by either flowers or visitors to flowers, have been a necessary part of the rapid evolution of specialized pollination systems. In addition, a mechanism exists whereby new relationships may be built up gradually by a process of "bridging" (*14*). As has been emphasized already, even where quite specialized flowers are concerned, pollinators of more than one class are usually to be found making visits. For example, a species of four o'clock, *Mirabilis froebelii* (Nyctaginaceae), which is often thought of as having "moth-flowers" because they open at night, is also visited by hummingbirds and butterflies, as well as pollen- and nectar-seeking bees (*14*). Even the scarlet "hummingbird flowers" of the monkey flower, *Mimulus cardinalis* (Scrophulariaceae) receive visits from a hawk moth, *Celerio lineata* (*35*). Flowers of *Zauschneria* spp. (Onagraceae), visited by hummingbirds for nectar (Fig. 4), are also called upon by pollen-collecting bees, despite the red color of their petals. Such versatility allows the possibility of gradual change whereby adaptation primarily to one pollinator may give way to adaptation mostly to another without an interval during which the flower is adapted to neither.

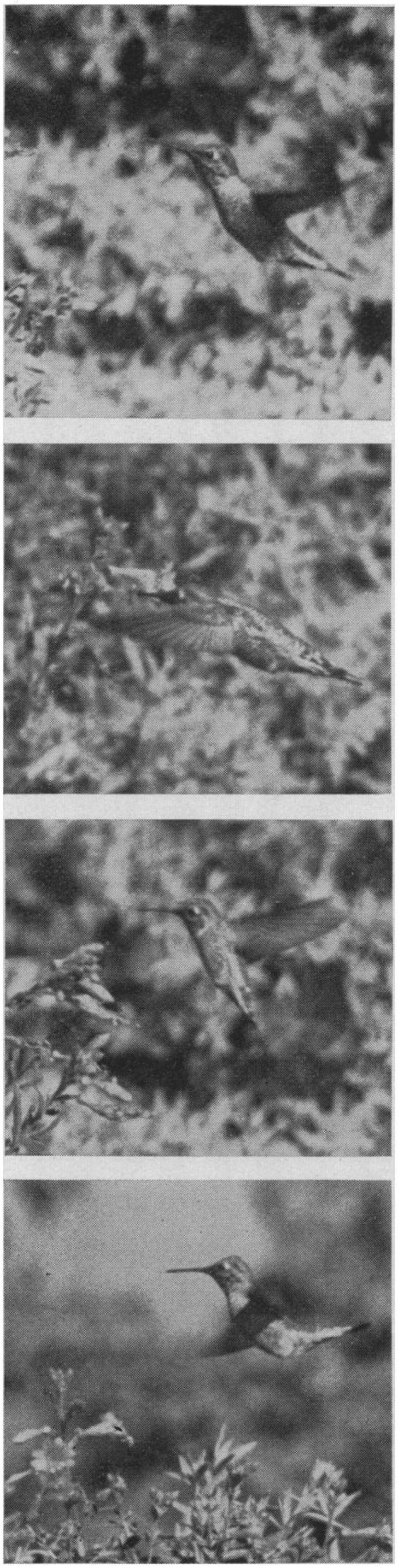

Fig. 4. Anna hummingbirds (*Calypte anna*) visiting, taking nectar, backing away from and leaving *Zauschneria* flowers (Onagraceae). Berkeley, California.

Gradual transitions need not be restricted to various kinds of pollination by animals but may also include the change-over from insect pollination to wind pollination. This may be seen in the meadow rue genus *Thalictrum* (Ranunculaceae) (*36*). Some species, like *T. aquilegifolium*, produce fragrant flowers with erect and conspicuously colored filaments to the stamens. These flowers are pollinated by insects. Others, like *T. alpinum*, bear nonfragrant flowers with drooping filaments and are pollinated by wind. A third, intermediate group, containing *T. flavum* and *T. minus*, appears to utilize both means of pollen transfer (*36*). The converse, the adoption of insect pollination by a member of characteristically wind-pollinated family, is shown by the tropical sedge *Dichromena ciliata* (Fig. 5) (*7*), but wind pollination probably still can occur in this plant.

Pollination on a Community Basis

At their simplest, evolutionary studies have been concerned with the elucidation of the phylogenies of single characters. Nevertheless, compensation between characters within the organ or the individual is possible, even usual. Consequently, it is unrealistic to treat characters or even organs by themselves; individual animals or plants, at least, are the units of natural selection. More recently, there has been an emphasis upon population studies, for many adaptations seem to be related to the survival of populations rather than to the advantage of the particular mortal individuals which carry them. Thus the evolution of outbreeding pollination systems has not been promoted by any advantage to the individual plants which bear the flowers (*37*). But now that we know more about population biology we should be moving toward the ultimate stage in

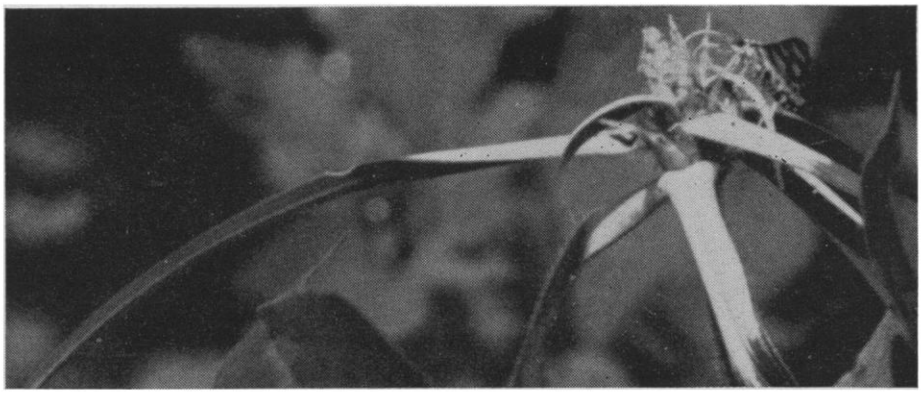

Fig. 5. *Dichromena ciliata* (Cyperaceae). The white bases to the leaves surrounding the inflorescence have the biological effect of a flower. Insects are attracted, such as this lepidopteran, but only pollen-feeders find food. St. Augustine, Trinidad.

synthesis, the consideration of such interactions as may occur between representatives of the taxa that occur together in natural communities.

There has been very little study of pollination biology on a community basis. Evidence of parallel reactions by plants of unrelated taxa to externally applied forces has been brought forward. In the Faeroe Islands self-pollination mechanisms have been developed in otherwise cross-pollinating species, presumably in response to the persistent strong winds which cut down the numbers and activities of insect pollen vectors (*38*). However, this is not interaction, a process which is more likely to operate in sheltered situations where relations with animals which carry pollen are more nearly stablized.

In establishing a basis of theory, we must recognize that two apparently opposing processes may be in operation. The first, proposed by Grant (*39*), is that a couple of species adapted to different pollinators may be able to coexist more successfully in the same territory than two species with the same kind of pollinator, through the avoidance of competition. This may be thought of as comparable with the vegetational phenomenon of "layering" which permits a restricted area of forest to be populated by more plants than could be accommodated if all were of comparable height. On the other hand, it is not out of the question that, where the supply is adequate, there will be a sharing of pollinators by taxonomically unrelated species. This second idea is worthy of further exploration.

In regions of the world where the pollinating animals have a long season of activity (during which they must continue to feed) and each plant species has a relatively restricted flowering season, either the pollinator must migrate or there must be a series of plant species to provide continuous nourishment. This may be expected to foster adaptations in plants whose flowers are visited by this pollinator, so that the plants will grow where the animals live. There is very little information on the subject as yet, although investigations are in progress (*40*). In particular, it seems likely that it will be in relation to the larger flower visitors that pollinator sharing will be detected, if it is real. For the flower- and fruit-visiting bats in tropical forests and woodlands, there is such a succession of available flowers and fruit (*14, 41*).

The analogy of layering has another, more direct connection with the subject under discussion, for there is layering in forests in relation to pollinators (*42*) and to seed dispersal (*43*). For the emergent and canopy trees which are exposed to wind, both pollination by wind and dispersal of seeds by currents of air are important. However, the significance of wind as an agent in the dispersal of pollen and seeds decreases as one descends to ground level through the shrub and herb layers, and the importance of animals increases correspondingly.

The development of natural history in north temperate regions of the world has led to the widespread acceptance of an unnatural view of forests as if they are always dominated by one or at least a very few species of outbreeding, wind-pollinated trees. By contrast, in tropical rain forests, floristic diversity is the rule and here pollination by species-specific animals (together with an insurance reserve of self-compatibility) is usual (*42*). An examination should be made of the diversified assemblages of tree species which occur in the hardwood forests of the southeastern United States to see if the same sort of situation prevails.

Pollination on a Taxonomic Basis

Another appraisal of the significance of pollination systems in evolution may be made by analyzing the different kinds of systems present in a plant family as well as their proportions and the circumstances in which they are found. Very few attempts have been made to do this, but notable exceptions are the studies by Grant (*39*) of the Polemoniaceae and Porsch (*44*) of the Cactaceae.

Despite the inadequacy of the data available for many families, some generalizations are possible. Thus, the list given by Fryxell (*45*) shows that 97 families are known to contain either self-incompatible species or dioecious species, but only 13 contain both (*42*). The latter are almost all very large families, and the different types of outbreeding systems are confined to separate genera. Even dioecism and monoecism seem to be mutually exclusive; although they may be found in the same family, they tend not to be found in the same genus. Exceptions to this rule, such as in *Mercurialis* (Euphorbiaceae) and *Atriplex* (Chenopodiaceae) may sometimes be related to a change in habit, the dioecious perennials having given rise to the monoecious annuals which may have greater need of the possibility of selfing which is provided by monoecism.

Gynodioecism

The first serious interpretation of the relatively high proportions of "male-sterile" plants which occur in some populations of species otherwise characterized by hermaphrodite flowers was made by Darwin (*46*), who referred to such a population structure as "gynodioecious." Darwin found that the seeds from the male-sterile plants were produced in greater numbers and were heavier than those from the hermaphrodites, and he thought that this constituted the benefit of gynodioecism to the species. Apparently this greater output was rendered possible by the concentration of the resources of the male-sterile plants on the production of seed.

Much more recently, Jain (*47*) has reinterpreted the value of male-sterility to otherwise inbred taxa as providing for the maintenance of hybridity optima. However, some species of flowering plants in which the gynodioecism is well established also possess a well-defined incompatibility system. In *Plantago lanceolata* (see cover photograph) as much as 70 percent of some populations consist of male-sterile plants, yet, even the hermaphrodites need to be cross-pollinated. From the point of view of outcrossing the gynodioecism appears to be superfluous. If the reproductive output of male-sterile and hermaphrodite plants were equal, the former world contribute only one-third as many nuclear genes to the next generation as the latter and might be expected to be eliminated in the course of time. However, in the wild marjoram, *Origanum vulgare* (Labiatae), Lewis and Crowe (*48*) have shown how the lethality and reduced production of some genotypes, as well as the lower output of seed by the hermaphrodites, may maintain the proportions of the male-sterile plants in the populations. Nevertheless, in self-incompatible species like *Plantago lanceolata* it is hard to see any "adaptive advantage" to gyndioecism unless it is in the larger seeds or in some, as yet undiscovered, pleiotropic effect of the gene or genes responsible for male-sterility.

The sort of reproductive system represented by gynodioecism is susceptible both to genetic analysis and to ecological assessment, for the genetics is relatively simple and the phenotypes are easily recognized. Another such system is heterostyly (*46*), and already this has been exploited in phytogeographical, genecological, and historical studies (*49*). Further investigations of rather simple mechanisms seem to hold out the best prospect of improving our understanding of the nature and evolutionary role of pollination systems. From them we may hope to build back to a real comprehension of the complexities of such groups as the orchids, with which Darwin (*1*) began the study of pollination biology 100 years ago.

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