ERYTHRINA SYMPOSIUM III.[1] *ERYTHRINA* (FABACEAE: FABOIDEAE): INTRODUCTION TO SYMPOSIUM III[2]

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ABSTRACT

About half of the approximately 110 species of *Erythrina* (Fabaceae: Faboideae), comprising New World species of six sections of subgen. *Erythrina*, are characterized by tubular flowers in which the standard is elongated and the keel and wings are reduced. These species, which are pollinated predominantly by hummingbirds, have relatively low concentrations of amino acids and high sucrose/hexose ratios in their nectar. In the remaining 12 species that occur in the New World and all but two of those of the Old World, the flowers are more or less gaping, with the standard tending to be ovate or obovate and the keel and wings more or less conspicuously exserted. These species are pollinated predominantly by medium-sized passerine birds; their flowers have relatively high concentrations of amino acids and low sucrose/hexose ratios in their nectar. In the two species of the southern African sect. *Humeanae* of subgen. *Erythrina*, the floral morphology resembles that of the New World humingbird-pollinated species. They are pollinated by small sunbirds and white-eyes. Several and perhaps all species of *Erythrina* have a large gland at the apex of the calyx that secretes nectar; ants, attracted to this nectar, patrol the plants and help to protect them from herbivores. A report of short-styled flowers in *E. leptorhiza* is reviewed, and papers providing new information on the taxonomy, alkaloids, modes of propagation, and bruchids of *Erythrina*, included in this symposium, are mentioned.

Most of the papers in the present symposium address the pollination relationships of *Erythrina*, and they add significantly to our body of knowledge concerning this interesting field. The basic division of the genus, from the standpoint of pollination biology, is between those species in which the standard tends to be ovate or obovate, and the keel and wings are more or less conspicuously exserted from the calyx, and those in which the standard is elongated and the keel and wings are reduced. In the first group of species, the corollas are often more or less gaping, the sucrose/hexose ratios are low, and the proportion of amino acids in the nectar is often extremely high. Included here are all species of the genus except some of those of the large subgen. *Erythrina*, and all species of *Erythrina* that occur in the Old World except those of the ditypic southern African sect. *Humeanae* Barneby & Krukoff of subgen. *Erythrina*. In the second group, comprising six related American sections of subgen. *Erythrina* and about half of the species of the genus, together with the two species of sect. *Humeanae* of the same subgenus, the corollas are narrow and tubular. In the American ones, the nectar has high sucrose/hexose ratios, and low proportions of amino acids.

Within the Old World, only *Erythrina zeyheri* Harvey and *E. humeana* Sprengel (sect. *Humeanae*) have relatively narrow corollas that correspond to those of the American species of subgen. *Erythrina* just mentioned. As Jacot

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Guillarmod and her collaborators have shown in this symposium, the Cape white-eye (*Zosterops pallidus*) is the most frequent visitor to the flowers of *E. humeana*, and the malachite sunbird (*Nectarina famosa*) the most important visitor to the flowers of *E. zeyheri*. Sunbirds are likewise frequent at the flowers of the introduced American *E. crista-galli* L., but in the other southern African species of the genus, which have more or less gaping corollas like those of the other species of the Old World, larger passerine birds, such as weavers, starlings, orioles, and bulbuls are the important pollinators, along with the larger sunbirds, whereas white-eyes are insignificant as pollinators.

In general, larger passerines seem to be the most important pollinators of all Old World species of the genus except the two of the southern African section *Humeanae*, and also of the dozen New World species that are not primarily pollinated by hummingbirds. As Corner (1940: 368) has pointed out for the Malayan species, "All the flowers in a whorl are open on the same day. Small birds may therefore drink their fill in a single visit, but they are too light to depress the flowers and reach the style and stamens: only heavy-bodied birds are the effective pollinators." He might have added that only the heavier-bodied birds, in consequence of their nectar requirements, were likely to move from tree to tree and thereby to effect cross-pollination (Heinrich & Raven, 1972). A similar relationship has been outlined well in this symposium for *E. fusca* Loureiro by Morton and by Feinsinger and his collaborators.

In the New World, there are, as summarized by Toledo and Hernández in this symposium, in addition to more than 50 species of subgen. *Erythrina* that have flowers like those of the second group outlined above and which are visited and pollinated by hummingbirds, an additional 12 species that have flowers like those of the first group. These belong to three subgenera, *Erythrina* (3 species), *Micropteryx* (Walpers) J. G. Baker (7 species), and *Erythraster* Barneby & Krukoff (2 species), and include all of the New World species of the two latter subgenera. Papers presented in this symposium and the literature summarized in them indicates that most of the species about which sufficient information is available, *E. fusca*, *E. poeppigiana* (Walpers) O. F. Cook, *E. breviflora* A. DC., and *E. oliviae* Krukoff, are primarily pollinated by orioles and other relatively large passerine birds, but also that they, like Old World species grown in the New World, may also be visited by and pollinated by hummingbirds. In this connection, Morton has presented the fascinating hypothesis in this symposium that the burnt-orange coloration of the apical portion of the wings of *E. fusca* in Panama has evolved there in connection with pollination by male overwintering orchard orioles, which match it in color, and that the comparable spot on the flowers of this pantropical species will be found to differ in color elsewhere. In *E. megistophylla* Diels, which occurs in the lowland tropical wet forests of Ecuador, Steiner has shown that honeycreepers are the principal visitors.

Bats have been observed visiting the flowers of a population of *Erythrina fusca* in Colombia (Helverson in Raven, 1977), but Feinsinger and his coworkers have pointed out that nectar flow in this species, in Trinidad at least, is diurnal, so that pollination by bats is unlikely to be frequent. Arroyo (1980) has suggested that bats may also pollinate the "shaving-brush" flowers of *E. velutina*, but these

flowers are relatively similar to the oriole-pollinated ones of the Mexican *E. oliveae*, described by Toledo and Hernández in this symposium. At any event, bat-pollination has not been shown to be characteristic of any species of *Erythrina*, and the single record probably simply results from opportunistic utilization by the bats of the large amounts of nectar available at the flowers of this genus. Squirrels have likewise been reported feeding at the flowers of *Erythrina* in both the Old World and the New World, and insects have also been reported as occasionally abundant (summaries in Raven, 1974, 1977). In Amazonian Peru, Janson & Terborgh (1979) reported that the flowers of *Erythrina* sp. were an important food source for the monkey *Ateles paniscus*, which however ate and did not pollinate them, in the same area where they observed effective pollination by primates of the flowers of *Ceiba*, *Quararibea*, and *Combretum*. They reported that although icterid birds were probably the normal pollinators of *Erythrina* in the Manu National Park, the monkey and also several species of parrots of the genera *Aratinga* and *Ara* regularly ate the flowers in large quantities. Similarly, Ian Tattersall (pers. comm.) has reported that the flowers of *Erythrina fusca* constitute over half of the diet of *Lemur fulvus mayottensis* in the dry season; the implication is that, as in the case of *Ateles* monkeys in Peru, the flowers were eaten and pollination did not occur. In summary, there is no evidence for nonflying mammals effectively pollinating the flowers of *Erythrina* (summary of this pollination system in Sussman & Raven, 1978) and only one authenticated record of bats making such visits. On the basis of present evidence, it may be concluded that all species of *Erythrina* are bird-pollinated, with about half of the species of the genus, representing all but twelve of the New World species of subgen. *Erythrina*, pollinated primarily by hummingbirds but occasionally also visited by passerines, and the other half, representing all Old World species and a dozen from the New World, primarily pollinated by passerines, mostly relatively large ones, but also visited by hummingbirds when they are native to or cultivated within the area where these birds occur.

The more copious nectars of the passerine-pollinated species of *Erythrina*, which are less concentrated in sugars but much richer in amino acids, both as to quantity and to number of kinds, than those of the hummingbird-pollinated species, seem to provide a food source that is complete or nearly so for their passerine visitors, which have frequently been reported to defend the flowers (Cruden & Hermann-Parker, 1977; this symposium). It may be presumed, as suggested to me by H. G. Baker, that the nectar constituency of the flowers of *Erythrina* species respectively pollinated by hummingbirds and by passerines is related to the fact that the hummingbirds are constantly feeding on insects while they are feeding, the passerines not. The tubular, closed corollas and relatively low concentrations of amino acids in the flowers of hummingbird-pollinated species of *Erythrina* are both apparently specialized features that tend to restrict visits to the flowers of these species by other kinds of birds.

It seems likely, on the basis of present evidence, that the nectars of some species of *Erythrina* are, on the bases of their included phenolics, alkaloids, and other substances, repellent to ants and other nectar-robbers (Baker & Baker, this symposium). Feinsinger & Swarm (1978) have shown that this may be the case

for *E. fusca*, but not for *E. poeppigiana*, and Baker & Baker (this symposium) have suggested that *E. herbacea* L. (hummingbird-pollinated) may have nectar that is less attractive to ants than that of *E. crista-galli* (presumably passerine-pollinated, although visited by hummingbirds). Skead (1967) has implied that the nectar of *E. caffra* Thunberg is more bitter than that of other southern African species he investigated, and Corner (1940: 368) refers to the "somewhat bitter, watery honey" of species of *Erythrina* in Malaysia (pollinated by passerines).

At any event, several of the papers in this symposium have brought back to attention an observation first made by Mattei (1925) on a species of *Erythrina* from Eritrea. In at least several, and perhaps all, species of the genus, there is at the summit of the calyx a large nectary. This extrafloral nectary secretes copious nectar, which attracts ants, and the ants that are attracted patrol the plant and protect it from many kinds of insect herbivores, in the mode outlined by Bentley (1977) for many different kinds of tropical and extratropical plants. This phenomenon should be studied throughout the genus to see if it is ubiquitous, and it would be of interest to see what kinds of relationships occur on some of the distant oceanic islands that *Erythrina* species with buoyant seeds have colonized. It might be that the heavy infestations of the Bucare twig borer, *Terastia meticulosalis*, that makes the cultivation of *Erythrina* in southern Florida almost impossible (Raven, 1974) are related to an absence of the normal protective ant fauna, either naturally or as a result of the application of pesticides, and the relationship might be important with respect to the success of the genus in cultivation. The chemical constituency of the nectars in the floral and extrafloral nectaries of *Erythrina* should be compared, especially in a species such as *E. fusca* that has been shown to have floral nectar that is somewhat distasteful to ants (Feinsinger & Swarm, 1978). Sherbrooke & Scheerens (this symposium) have already presented evidence that the high sucrose/glucose ratio in the floral nectar of this species is much lower in the extrafloral nectaries, both calycine and foliar. Feinsinger et al. (this symposium) have pointed out that while ants are characteristically abundant around the outside of the flowers of *Erythrina*, they are very rarely found within; and the reasons for this relationship would be of great interest. In addition to the large gland on the calyx, Sherbrooke & Scheerens (this symposium) have called attention to the foliar nectaries in *E. flabelliformis* Kearney, the presence of which in other species of the genus ought also to be investigated. Once again it is emphasized that a genus such as *Erythrina*, for which a great deal of chemical information is available, is an ideal subject for the investigation of predator-prey relationships and coevolution.

A final major point concerning pollination systems that has been brought out in this symposium is the observation of Hernández & Toledo that *Erythrina leptorhiza* A. DC. forms some flowers with short styles that also differ in other characteristics from the normal ones. Hernández and Toledo have reported that about 20% of the flowers they examined had short styles, shorter than the anthers; they did not obtain any seed set following the self-pollination of either kind of flower. The apparently very interesting breeding system of this species should be investigated in more detail.