

Observations on Orchids and Euglossine Bees in Panama and Costa Rica

by

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Bees of the tribe Euglossine were seen visiting orchid flowers by CRÜGER (9), whose observations were published shortly after the first edition of DARWIN's classic work (10). The relationship between these bees and certain orchids was not then understood; in fact, one must admit that it is even now poorly understood. This paper will present and discuss a series of observations made during a two year period in selected regions of Panama and Costa Rica.

When Crüger saw "humble-bees" swarming about the flowers of *Catasetum* and *Coryanthes*, he apparently saw that the tissues of the lip had been partly eaten (by crickets or other chewing insects), and he assumed that the bees sought food in the orchid flower. Such a relationship seemed reasonable, if not commonplace, and warranted only a brief comment alongside the unisexual flowers of *Catasetum*. As early as 1901, it was noted by DUCKE (23) that several of these orchid genera attract only the males of the euglossine bees, but he, too, believed that the bees sought food in the flowers. ALLEN (2, 3, 4, 5) later found that species of *Coryanthes*, *Cynoches*, *Gongora* and *Mormodes* were all visited only by male bees, and he noted that the *Euglossa* which he observed on *Coryanthes* did not attempt to chew on the flower (2). More recently, DODSON and FRYMIRE (16) and VOGEL (31) observed that the bees definitely do not eat the tissues of the flowers, but brush specific areas within the flowers with tufts of hair on the forefeet. Dodson and Frymire found that the bees typically brush in the flowers for a short period, hover briefly near the flower (usually downwind) and return to brush in the flower again. It was noted, further, that the bees lose their initial wariness and act as though inebriated

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after they have been brushing on the flowers for a time. The bees do not become unsteady in flight, but the coordination of their legs seems to be reduced, and the bee often slips and falls while on the flower. Dodson and Frymire (cited by VOGEL, 31) found that the symptoms of "inebriation" were induced when the liquid from a scratched orchid flower was applied to the brushes on the front feet of a bee which was tied down and could not transfer the material to other parts of the body. VOGEL (*loc. cit.*) suggested, nevertheless, that the bees might be transferring some substance from the front feet to the "scars" of their inflated hind tibiae while hovering near the flowers. Subsequent observations by Vogel, Dodson and myself indicate that this is the case. Thus contrary to several earlier reports, the bees do seem to receive some "reward" from the flowers, though not in the form of ingested food. We do not know what substance or substances the bees are gathering, nor do we know what role this substance may play in the biology of the bee.

All observers agree that it is odor which attracts male euglossine bees to orchid flowers. Dodson has found that the odors are often highly specific, and that related species of orchid may consistently attract different bee species, even when growing in close proximity. The possible importance of odor as an isolating mechanism in these orchids is, then, quite evident. Our observations repeatedly indicate that odor is the most important interspecific difference in sympatric species pairs of several orchid genera. Dr. Dodson is now undertaking analysis of the orchid odors by gas chromatograph, which should add a great deal to our knowledge of orchid-bee relationships. It has been suggested that the flowers are mimicking the sexual odors of female bees, but the evidence is inconclusive, and, in general, the behavior of the male bees does not indicate this.

Euglossine bees have been observed "brushing" on rotten wood and on seeping areas of infected living trees. It may be that they are attracted by some aromatic fungal product. Whatever the nature of the relationship, other plant groups have adapted to the biology of the male euglossine bees in the same way as have several orchid groups. Most species of *Spathiphyllum* appear to be pollinated by male euglossine bees, and a number of species of *Anthurium* show a similar relationship. I have observed males of *Eulaema meriana* (Olivier) visiting flowers of *Gloxinia perennis* (L.) Fritsch in Panama,* and males of *Eulaema nigrifacies* (Friese) visiting *Drymonia turrialvae* Hanst. in Costa Rica. It is probable that other Gesneriaceae will show the same relationship. DODSON (14) has observed instances in which at least isolated members of other plant families showed a similar relationship. Among the American Orchidaceae, the subtribes Catasetinae and Stanhopeinae and the genera *Notylia* and *Anguloa* seem to be euglossine-pollinated in their entirety. At least portions of *Lycaste*,

* This relationship was indicated by CRÜGER (9), though he identified the bee only by "the same insect visits *Coryanthes macrantha* and *Stanhopea grandiflora*", which would indicate a member of the genus *Eulaema*.

Aspasia, *Lockbartia*, *Dichaea* and the *Zygopetalum* complex show similar adaptations, and doubtless some other genera and species will prove to be adapted to pollination by male Euglossini.

The Euglossini are relatively advanced bees, being assigned to the family Apidae, but are (as far as known) solitary or, at most, gregarious, without the complex social organization of other Apidae. They are evidently most closely allied to the bumblebees, which replace them to some extent at higher elevations. They are known only from the Americas and do not extend far beyond the tropics in either hemisphere. They are fast, strong-flying animals, and usually evade the collector's net unless he makes a special study of their habits and food-plants. Many species have very long mouthparts, the folded tongue in some cases exceeding the length of the body. Thus the bees are adapted to deep, tubular flowers, and may often be found feeding on the nectar of Apocynaceae, Marantaceae, Bignoniaceae and certain Rubiaceae (especially *Sabicea*). As mentioned above, the hind tibiae of the males (the part corresponding to the pollen basket of the female) are greatly inflated, and bear characteristic "scars", slit-like openings in the chitin which are covered by closely packed hairs. There are only six genera of Euglossini, three of which are important in orchid pollination. The bees of the genus *Eulaema* are medium to large, rather villous bees, of which there are about 15 species (8 or 9 in Panama and Costa Rica). The members of the genus *Euplusia* are similar, though often smaller, but the males possess bright metallic colors on the face. Some species are quite brightly colored, and there are perhaps fifty species in all (12 to 15 in Panama and Costa Rica), many of which are very poorly represented in collections, so that their taxonomy is still unsatisfactory. The Euglossas are small to medium bees, nearly all of them of brilliant metallic colors: green, blue or bronze. There are at least 45 species in Panama and Costa Rica, some of which are still undescribed. The total number for tropical America will exceed 100. The single species of *Enfriesea*, *E. pulchra*, resembles a medium-sized *Euplusia*, with the face light green in both sexes and with a very large scutellum. It has not been observed visiting orchid flowers, but has been seen visiting an unidentified *Antbrivium* in Panama. *Exaerete* and *Aglæ* are parasitic genera (laying their eggs in the nests of *Eulaema* and perhaps *Euplusia*) in which both males and females have reduced hind tibiae. The reaction to orchid odors is present in *Exaerete*, though perhaps rudimentary. The males have been seen visiting several orchid species, though their visits are irregular and of short duration. They are not known to pollinate any orchid.

Ideally, all pollination observations would be based on plants growing undisturbed in their native habitats. In practice, this might involve living in the treetops and would impose severe geographic limitations. I have tried to obtain and cultivate many of the orchids in Panama City, or (briefly) in Turrialba. When a plant was in flower (or ideally, just before it flowered, for some of the flowers may be badly damaged in transit) it was taken to its native habitat, or as near to the native habitat as was practical. Where observations were made on plants outside of their natural ranges, this will be noted. In a few cases a

plant was taken to a "second-best" habitat, where I had never found the orchid species, but bees soon appeared bearing pollinaria of that orchid, showing that the orchid occurred naturally in the area or nearby. When I have observed a bee removing or depositing pollinia in an orchid flower, or captured the bee with pollinaria attached, I have considered that bee to be a normal pollinator of the orchid. When an orchid attracts a particular bee in great numbers and the size relationship is reasonable, the bee is considered a probable pollinator, even though pollination has not been observed. This type of observations is somewhat more frequent than desired. In the first place, male flowers of *Cycnoches*, *Catasetum* and *Mormodes* and flowers of *Gongora*, *Polycynis*, etc. suffer greatly when bounced in a car over rough roads, often losing or displacing all of the pollinaria in an inflorescence. In such a case, it is impossible for visiting bees to remove pollinaria, though the flowers may remain fragrant for a time. Another factor is the difficulty of identifying Euglossas on the wing. I have tried to catch the first few of each species to visit any orchid, so that they could be identified with some confidence (or described, if necessary).

All species of bees which are cited here are listed in MOURE's check-list (27). Most of the unpublished taxa are in press or manuscript at present. In a few cases, species are represented by one or very few specimens and have not yet been named: these bees will be cited by their collection number (*e. g.* Dressler 120). Specimens of the bees are to be found, especially, in my own collection, that of Father J. S. Moure, University of Paraná, Curitiba, Brazil, and the Snow Entomological Museum, University of Kansas, Lawrence, Kansas. I have already prepared voucher specimens of some of the critical orchid taxa, and these will be placed in the U. S. National Herbarium. In some cases this was planned for the "next season of observation". In other cases, plants which were borrowed from friends could not very well be sacrificed to the herbarium; so the documentation of the orchids is less than I had hoped for, but will be improved where possible by plants still under cultivation. Additional plants of many of the taxa reported here are now in cultivation at Fairchild Tropical Gardens, in Coral Gables, Florida.

While I have spent two years based in Panama, much less than this period was actually devoted to pollination observation, and more observations in the area are desirable in many cases. Nevertheless, my observations in Central America have been terminated for the present, and these observations are given here, as a unit. The observations in Panama and Costa Rica provide a fair sampling of an area which is especially rich in euglossine bees and euglossine-pollinated orchids, so that these observations may serve as a basis for discussion and evaluation of the phenomena involved.

The observations reported here were made in a limited number of localities. In Costa Rica most observations were made near Chitaría (formerly Chitaría), on the road between Turrialba and Siquirres, Cartago province. Other observations were made near Puerto Viejo, Heredia province; near Las Cruces, south of San Vito de Java, Puntarenas province; on the ridge above Golfito, Puntarenas province; and near Tilarán, Guanacaste province. In Panama, the hills

north of El Valle de Antón, Coclé province, are an especially favorable area, and many observations were made on Cerro Campana, in Panamá province, a similar area and closer to the Canal Zone. In the Canal Zone, the Navy Reservation (or "Pipe-line Road"), north of Gamboa, and Barro Colorado Island, are two relatively natural areas where observations were made. Some observations were made also in Diablo Heights, near the Pacific coast, and in Margarita, on the Atlantic side. On the east of the Canal Zone, a very few observations were made near Cerro Azul, Panamá province, and some of the orchid plants used were collected on the Santa Rita ridge ("East Ridge" of local orchid collectors), about 15 miles east-southeast of Colón.

The sketches (figs. 1-13), which show the mechanisms of pollination in some genera, are somewhat diagrammatic, though in most cases preserved flowers or photographs were available.

OBSERVATIONS

STANHOPEINAE.—This subtribe, of about eighteen genera, is especially well represented in the area from Nicaragua to Ecuador, nearly all of the genera occurring in this area. They are interesting because of the bizarre morphological adaptations to euglossine pollination, and because of the graded series from simple to complex which is demonstrated, for example, by *Stanhopea*. Observations are reported here for ten of the twelve genera recorded for Panama and Costa Rica.

Acineta superba (H. B. K.) Reichb.—This species is not recorded in the Flora of Panama (1), but plants are locally abundant on Cerro Campana and occasional near El Valle. The mechanism of pollination is fairly simple in *Acineta*. The flowers are somewhat campanulate, and the bees can enter and leave only beneath the column. As a bee backs out of the flower (fig. 1), the rostellum may place the viscidium beneath the bee's scutellum (aided by the large callus of the lip, which forces the bee up toward the column). When the bee enters and backs out of another flower, the pollinia are deposited in the stigma. A large plant in flower which I purchased in El Valle in September proved very attractive to males of *Euplusia concava* (Friese).* The bees were exceedingly wary, but were easily caught when they entered the flowers. One of the bees which arrived already bore a pollinarium of *Acineta superba*. This is the same species of bee observed to pollinate *Acineta chrysantha* (Morr.) Lindley in Costa Rica (DODSON, 14) and observed by myself visiting cultivated plants in central Panama. Thus, the isolation between these two species of *Acineta* would appear to be entirely geographic.

* These specimens were compared with the type, through the courtesy of Dr. E. Königsmann, of the Zoologisches Museum, Humboldt-Universität zu Berlin.

Coeliopsis hyacinthosma Reichb. f.—This species, which ranges into Costa Rica, is locally abundant in wet forests in the region of El Valle and is reported for Cerro Campana. With C. H. Dodson and H. Hills in July, I observed several plants of this species in place in El Valle and later observed the same plants on Cerro Campana. They were visited and pollinated by *Eulæma cingulata* (Fab.), *E. meriana* (Olivier), *Euplusia schmidtiana* (Friese) and another large bee which may have been *Eulæma nigrifacies* (Friese) or *E. polychroma* (Mocs.) or quite possible an *Euplusia*. Both *Euglossa dodsoni* Moure and *E. tridentata* Moure approached the flowers a few times, but are probably too small to be pollinators. As the large bees try to brush in the base of the narrow, cup-like lip (fig. 2), their faces are pushed against the column, and the pollinaria are removed on the clypeus. This species is unusual among the Stanhopeinæ in the placement of the pollinaria. Though its system of pollination is quite efficient*, the attraction of several species of bees is perhaps not conducive to speciation. The species has no close allies, as far as known.

Coryanthes maculata Hook.—A large plant collected on the Santa Rita ridge flowered repeatedly in Las Cumbres. In the Navy Reservation in February the plant attracted a number of males of *Euglossa azureoviridis* Friese, three of which bore pollinaria of *Coryanthes*. Many of these bees were attracted by the scent, but hovered near the flowers and then flew on. Perhaps the short-lived flowers were already past their prime, or had suffered from the disturbance in carrying them to the site. *Euglossa cordata* (Linnaeus) never approached the flowers, though the species is common in the Navy Reservation and at Las Cumbres, where the plant was kept. ALLEN (2) reported the pollination of *Coryanthes speciosa* Hook by *Euglossa cordata* near Palmar Sur, Costa Rica**, *Coryanthes speciosa* and *C. maculata* are similar in size and show a similar range of color variation, so that they are often confused. It is typical of the taxonomic difficulties of these organisms that I earlier reported my own observations as also being *Coryanthes speciosa* pollinated by *Euglossa cordata* (DODSON, 15). Some collections from Panama and Costa Rica do not fit either species well, and appear not to be intermediates. Their study is hampered by the scarcity of healthy, accessible plants. I have collected *Euglossa dressleri* Moure with a *Coryanthes* pollinarium in the Navy Reservation, and an *Euglossa alleni* Moure with two stipes and a complete pollinarium near Golfito, though neither of these species has yet been observed visiting *Coryanthes*.

* Many capsules are produced, but my impression is that many of them (near El Valle) are "smothered" in the wet moss which surrounds the plants, and fail to release dry, dispersible seeds.

** I have confirmed the identity of his bee specimens, which are in the collection of the U. S. National Museum. The *Coryanthes* was from northern Honduras, but I have not seen the bees which were observed there (if any were collected).

The mechanism of pollination in *Coryanthes* is well described by ALLEN (2) and DODSON (15). The attractive area is under the hood, near the base of the lip (fig. 3). The surrounding area is smooth, and bees may easily slip into the "bucket" while trying to reach the attractive portion of the lip. In the *Euglossa*-pollinated species, especially, the drops of liquid falling from the two glandular areas are an added insurance that some bees will fall into the water beneath. The liquid prevents bees from flying out, and the smooth sides of the chamber offer no foothold except beneath the apex of the column, where the viscidium is placed between the abdomen and the thorax (but seated on the base of the abdomen). The first bee to pass through has a difficult struggle to remove the pollinarium and escape. After that the passage is easily effected, and any bee bearing pollinia may pollinate the flower.

Gongora.—The *quinquenervis* complex of *Gongora* has had a checkered taxonomic career, with many species named on relatively minor morphological or color differences, often without knowledge of their geographic origin. More recently the tendency has been to lump all of this group into a single variable species, without regard to the geography of variation. While this course may be satisfactory for herbarium purposes, my observations suggest that there are about a dozen "good" species in the *quinquenervis* complex, which are distinguished by the euglossine bees. Several of these species are discussed by DRESSLER (21), and more detailed taxonomic studies are in preparation; the odors of some of these species have been analysed by DODSON and HILLS (18). In Costa Rica the *G. quinquenervis* complex includes one or more forms which appear to be good biological species, but which do not have any obvious morphological differences; and this complex requires more study. The mechanisms of pollination in this group of *Gongora* has been described by ALLEN (4) and DODSON and FRYMIRE (16). The base of the lip is the attractive portion, and the bee must cling to the lip upside down to reach this area (Fig. 4). The bee will crawl up the side of the lip to fly, if it can, but its movements are hampered by the horns and cirrhi of the lip. Thus, when the bee releases the lip to fly, or if it slips, it may fall; and its fall is so guided by the column and petals that it will slide down the column and hook the rotellum under its scutellum. The stigma is at first too narrow to receive pollinia, but the opening enlarges after the pollinarium is removed.

Gongora quinquenervis Ruiz & Pavón.—This species occurs on Barro Colorado Island (and doubtless elsewhere in the Canal Zone) and in the region of El Valle. *Gongora quinquenervis* is widespread in South America, and ranges along the Pacific slope of Costa Rica into Nicaragua in the typical form, illustrated by DRESSLER (21) and as *G. maculata* v. *alba* by TEUSCHER (30). Most plants which were observed on Barro Colorado Island, from February to April, attracted large numbers of *Euglossa tridentata* Moure, which were effective pollinators. Plants from El Valle which were cultivated in Las Cumbres attracted *Euglossa cordata* (Linnæus) and a few *E. townsendi* Cockerell. These three bee species

are so very similar that I did not at first distinguish them. Later I realized that they were distinct, and, having further found *Euglossa hemichlora* Moure with *Gongora pollinaria* in the Navy Reservation, I despaired of ever unravelling the Panamanian *Gongoras*. In April 1965, however, a large plant flowered on Barro Colorado Island (from Drayton trail 400 on the Island). This plant attracted *Euglossa tridentata*, *E. cordata*, *E. townsendi*, *E. hemichlora* and *E. cyanaspis* Moure (these additional bees, too, are "little green bees", and quite easily confused). This one plant thus neatly erased any supposed isolation between the spotted *Gongoras* of central Panama. The interesting feature here is that many plants attract only *E. cordata* or *E. tridentata*, but that other plants have an odor which attracts both of these and several others. This suggests a situation of incipient speciation and deserves careful study. *Gongora quinquenervis* was also observed near Tilarán, in March, and there it was visited only by *Euglossa cordata*. *Gongora quinquenervis* seems to be pollinated by *Euglossa cordata* wherever it is found in South America.* We have observations from Pará, Brazil (DUCKE, 23), Iquitos, Perú (DODSON, 14), and Trinidad (pollinia on bees in museum). At Iquitos, as in central Panama, other bee species are also involved. *Euglossa cordata* and *E. tridentata* are most active in visiting *Gongora* from about 9:00 AM to midday, and seem to prefer flowers in the sun. They have been observed as early as 7:30 AM and as late as 2:15 PM.

Gongora tricolor (Lindley) Reichb. f.—This species occurs commonly on the Atlantic coast of central Panama and in the central Canal Zone (Barro Colorado Island and the Navy Reservation). Though it is reported from El Valle, my informants there assure me that the plants in the market are brought in from the Atlantic coast. The flowers of *G. tricolor* are usually larger than those of *G. quinquenervis* and more boldly blotched (though some forms are nearly pure yellow). The base of the lip has large rounded knobs rather than narrow horns, and the odor is heavier than in *G. quinquenervis* (resinous in each case). Other morphological differences are minor and less consistent. *Gongora tricolor* has been observed in March and April in several areas and is consistently visited and pollinated by *Euglossa cyanura* Cockerell. This species may appear as early as 7:00 AM, and was not seen visiting the flowers after 11:00 AM, nor would it visit flowers in the sun. *Euglossa cyanura* is distinctly a forest bee and also tends to shun exposed food plants, even when they are only a few meters from the forest edge. The only other bee seen to visit *Gongora tricolor* was the par-

* I must caution here that the taxonomy of the bees is not final. The *Euglossa cordata* of Trinidad is apparently the sort described by Linnaeus as *Apis cordata*, but the bees of Panama and Iquitos are each atypical in different ways. I have very recently found what I believe to be the "Trinidad *cordata*" and the "Panamá *cordata*" sympatric in Caracas, Venezuela, which strengthens my belief that the "*E. cordata*" of Panama must be treated as a distinct species. All of the Central American bees reported in this paper as *E. cordata* are the form represented by my collection numbers 7, 157, etc. (RD 7).

asitic *Exærete smaragdina* (Guérin) (2 brief visits), which is probably too large to effect pollination and did not enter the flower properly.

Gongora unicolor Schlechter.—This species ranges from the Atlantic lowlands of Costa Rica (and possibly western Panama) north to southern Mexico. Though it tends to be a bit larger than other *Gongoras* of the area and the plant itself is slightly different in proportion, there is no obvious morphological distinction between *G. unicolor* and *G. quinquenervis*. It is easily recognizable, though, by the flesh-colored flowers and its distinctive odor of (to me, at least) freshly ground corn meal for tortillas (nixtamal). The one plant which I had available in Costa Rica in March attracted three males of *Euglossa purpurea* Friese. A bee of this same species was captured at Puerto Viejo with *Gongora pollinaria* in August. This *Euglossa* has been collected in Guatemala (A.M.N.H. specimen 28284, Stoll) and the type is from western Panama, so its known range coincides closely with that of the *Gongora*.

Gongora "El Valle".—A third Panamanian species of *Gongora* is found in the region of El Valle. It is sympatric with *G. quinquenervis*, and resembles that species, but is distinguished at once by the convex base of the hypochile, as well as other less striking differences in color and odor. This species tends to flower in October and November, while *G. quinquenervis* and *G. tricolor* have their main period of flowering in February and March (the flowering seasons, however, are ill-defined, and there is considerable overlap). This *Gongora* attracts *Euglossa gorgonensis* Cheesman in considerable numbers, both near El Valle and in other localities where I have taken it. Both *E. gorgonensis* and *E. nigrosignata* Moure, which occasionally visits this species, behave properly to function as pollinators, but I have never seen pollination in this species. *Euglossa asarophora* Moure and *E. villosa* Moure are infrequent visitors near El Valle and on Cerro Campana, but are rather large to be pollinators, and tend to brush on the sepals rather than at the base of the lip.

Gongora "yellow lip".—The commonest *Gongora* of the Turrialba area has a boldly-marked flower morphologically similar to that of *G. quinquenervis*, but differing in color pattern and odor. I believe that this will prove to be a geographic subspecies of *G. quinquenervis*, but conclusive evidence is yet lacking. These plants do not attract large numbers of bees, as do the Panamanian plants, but I observed several bees of *Euglossa cybelia* Moure and *E. gorgonensis* Cheesman and one *E. hansonii* Moure at Chitaría in February and March. Another *E. hansonii* was captured there with *Gongora pollinaria*, and *E. cybelia* was found to visit the yellow-lip *Gongora* in December near Las Cruces, where the *Gongora* is also found. Dr. Dodson, with an O.T.S. class, observed this *Gongora* near Guápiles, Limón province, where it was visited by *E. gorgonensis* and another similar, but undescribed species. This form of *Gongora* attracts more *Eulaemas* than others (excluding the South American *G. atropurpurea* Hook., which is pollinated by *Eulaema cingulata*). I have collected *Eulaema cingulata* (Fab.), *E.*

nigrifacies (Friese), *E. polychroma* (Mocs.), and *E. speciosa* (Mocs.) visiting this form, but in all cases the bees brushed on the sepals and did not behave as pollinators. It should be noted that, while *Euglossa gorgonensis* is a probable pollinator for both this and *G. "El Valle"*, there is no indication that these two *Gongoras* are sympatric. A white-lip *Gongora* is also reported in the Turrialba area, and may be biologically distinct, but I have not observed this form.

Gongora "Golfito".—A large-flowered *Gongora* is found near Golfito, which differs from *G. quinquenervis* in a number of details and which flowers in March and April. This species was observed to attract a number of *Euglossa flammea* Moure; one of this species was seen bearing a pollinarium, and there was a stipe on one of the bees captured at the *Gongora*. Dr. Dodson found both *E. flammea* and one *E. dodsoni* Moure visiting this *Gongora*, and I found one individual of *E. dodsoni* visiting a plant which was cultivated in Panama. *Euglossa dodsoni* is much smaller than *E. flammea* and may not be an effective pollinator. *Gongora quinquenervis* was not observed in flower near Golfito in late April or March, but plants collected in the area have later proven to be that species, which apparently has an earlier flowering period than *G. "Golfito"* (though they probably overlap).

Gongora "Guanacaste".—While the "yellow-lip" form of Turrialba may occasionally be a solid wine-red, there is another (consistently) wine-red *Gongora* which is sympatric with *G. quinquenervis* in northwestern Costa Rica and in adjacent Nicaragua. This form is distinctive in that the horns at the base of the lip are represented only by very small angles, and the odor is that of clove-oil. Plants from Guanacaste attracted *Euglossa viridissima* Friese* when taken to Alajuela, Costa Rica, in February. While this is outside the normal geographic range of the *Gongora*, *E. viridissima* is common in the Liberia area of Guanacaste, and so may be the normal pollinator of this very distinctive *Gongora*.

Kegeliella atopilosa L. O. Wms. & Heller.—This species is occasional in the region of El Valle. A single plant with few flowers which was observed in September attracted only a single bee of *Euplusia concava* (Friese). However, this bee bore pollinaria of *Kegeliella*, and three of the same species which visited a nearby *Acineta* at the same time also bore pollinaria of *Kegeliella*. The pollinaria were placed between the head and the prothorax (as in *Lacæna*). I did not see the removal or deposition of pollinia, but the mechanism may be similar to that *Polycynis* (though the pollinaria are placed further forward on the bee). Another species, *K. kupperi* Mansf., is occasional in Costa Rica and on the Atlantic coast of central Panama, but I have not had flowering material.

* The Costa Rican males of *viridissima* consistently show 3-dentate mandibles, while the Mexican bees include a form with 2-dentate mandibles and one with 3-dentate mandibles. No other morphological difference is evident, and both are treated as *E. viridissima* for the present.

Lacaena spectabilis (Kl.) Reichb. f.—This species is very infrequent in the region of Las Cruces, but a plant cultivated by Mr. Wilson flowered during March. The plant was attached to a tree somewhat removed from the forest, but was visited by several individuals (3-6) of *Euglossa maculilabris* Moure each day for five days. The number of visitors probably would have been higher in the forest. The flowers are pendent, with the column nearly vertical, and the bee seeks to brush near the base of the mid-lobe of the lip (probably on the callus), crawling onto the mid-lobe upside-down to reach this area (fig. 5). Pollinaria are apparently received or deposited when the bee falls. One bee was seen with a pollinarium attached between the head and prothorax, and another was caught with two stipes in this position. The relatively long life of the flowers is unusual for this subtribe.

Paphinia clausula Dressler.—I found this species to be locally frequent on a road-cut near Chitaría. Unfortunately, no observations were made at that locality when the plants were in flower. Plants taken to Puerto Viejo in August, with C. H. Dodson and H. Hills, attracted large numbers of *Euglossa gorgonensis* Cheesman and smaller numbers of *E. hansonii* Moure (5 seen), *E. asarophora* Moure (3 seen) and *E. hemichlora* Cockerell (2 seen). Some of the bees forced their way into the flower, and *E. gorgonensis* was seen to remove pollinaria on its legs, the flowers being non-resupinate, and the bees entering right-side-up. The other *Euglossas* also could reasonably function as pollinators. The half-closed flowers of this plant are probably an adaptation to pollination by small bees. Other species of *Paphinia* are pollinated by larger bees, at least to judge from their size and morphology.

Peristeria elata Hook.—The famous "Holy-ghost" or "Dove-orchid" of Panama was usually available to me as plants freshly uprooted for sale by the Indians. These were singularly unattractive to bees, though I once saw a male of *Exærete smaragdina* (Guérin) briefly brush on the flowers. Mrs. Edna Jackson caught a male of the tiny *Euglossa crassipunctata* Moure which visited both *Cynoches aureum* and *Peristeria elata*, and Dr. G. B. Fairchild photographed a larger *Euglossa* (possibly *E. tridentata* Moure) visiting a plant established in his garden. These *Euglossas* are both probably too small to pollinate *P. elata* (*E. crassipunctata* certainly so). One of the *Euplusia concava* (Friese) which visited *Acineta superba* in September bore a pollinarium of *P. elata* on the top of the head, and Dr. Fairchild has an excellent photograph of this same species visiting the *Peristeria* in his garden. It is possible that other species of *Euplusia* or *Eulama* also visit and pollinate *P. elata*, though they have not been observed. This, as other species of *Peristeria*, places the pollinaria on the bee by a sort of trap mechanism (Fig. 7). When the bee enters the flowers far enough to over-balance the hinged lip, the lip tips up and inward, throwing the bee against the column, where it is usually guided by side-lobes of the lip and/or column wings.

Peristeria species—A *Peristeria* of the *P. pendula* group, an epiphytic plant with an elongate rhizome and densely spotted flowers, occurs locally in wet forest near El Valle. I was fortunate in finding a single plant with two large inflorescences in late August. Heavy rain prevented on-the-spot observations of pollination, so the plant was removed to a similar but more accessible locality on Cerro Campana. The flowers smelled rather like a cold-remedy, "Campho-Phe-nique", and the number of different bees which they attracted was quite unexpected. A list of the bees collected follows:

- Euglossa bursigera* Moure (1)
- Euglossa cordata* (Linnaeus) (1)
- Euglossa cybelia* Moure (1, a few others seen)
- Euglossa deceptorix* Moure (12, many others seen)
- Euglossa dodsoni* Moure (3, a few others seen)
- Euglossa dressleri* Moure (1)
- Euglossa heterosticta* Moure (5)
- Euglossa imperialis* Cockerell (2, a few others seen)
- Euglossa igniventris* Friese (2)
- Euglossa maculilabris* Moure (7)
- Euglossa mixta* Friese (3, a few others seen)
- Euglossa tridentata* Moure (2)
- Eulæma nigrifacies* (Friese) (1, 2 or 3 others seen)
- Eulæma nigrita* Lep. (2, several others seen)
- Eulæma luteola* Moure or *meriana* (Olivier) - seen twice, but not captured.
- Euplusia schmidiana* (Friese) (1)

Of the last four bees listed, only *Eulæma nigrita* was strongly attracted, and all are too large to be likely pollinators. All of the *Euglossas* are potential pollinators, though *E. mixta* was seen to brush mainly on the petals, rather than entering the flowers. One *Euglossa dodsoni* arrived with three pollinaria on its thorax, and two of the *E. deceptorix* were captured with pollinaria, though all of these may have been from this same plant. These two species can be listed as pollinators with confidence. It appears, in general, that species without close sympatric allies are likely to be less specific in their pollination relationships than those with close sympatric allies. Though *Peristeria elata* occurs in the same area, it is adapted to larger bees, and is thus effectively isolated.

Polycynis gratiosa Endres & Reichb. f.—This species is frequent on Cerro Campana and occasional in wet forests near El Valle ranging into Costa Rica and Colombia. When collecting with C. H. Dodson and H. Hills in July, we found a single large plant near El Valle with two inflorescences, one of them still in good condition when found. As soon as the weather cleared a bit (about mid-day), the plant attracted about a dozen bees of *Euglossa villosa* Moure. Though the placement of the pollinaria is the same as in most other Stanhopeinæ, the mechanism is somewhat different. When the bee lands on the lip (Fig. 8), the additional weight pulls the flower down, causing the arched column to move downward, hooking the viscidium beneath the scutellum of the bee.

Sievekingia fimbriata Reichb. f.—This species is frequent on Cerro Campana and occasional in the region of El Valle. I have not observed flowering plants in either locality, but bees which visited the flowers in the Navy Reservation act as pollinators, and probably may be considered as normal pollinators. In the Navy Reservation, at least, in July and October this species attracts considerable numbers of two species that do not act as pollinators (both species do occur in El Valle and on Cerro Campana). Both *Euglossa dressleri* Moure and *E. mixta* Friese are strongly attracted (about 6 *mixta* and 10-20 *dressleri* on each morning observation), but brush only on the sepals and petals. The bees rarely tried to brush near the base of the lip, and the only time that an *E. dressleri* removed a pollinarium on its foot, this was quickly brushed off and lost. On the second day of observation, however, (in October) a few markedly smaller bees appeared and behaved in a quite different fashion. These bees quickly entered the flower upside-down (Fig. 6), often removed pollinaria on the trochanters of the middle or hind legs. Of the five smaller bees which were captured, four were *E. sapphirina* Moure, and the other an undescribed species, Dressler 120. Both species were seen removing pollinaria. Their behavior agrees with DODSON'S observation (14) on the pollination of *Sievekingia jenmanii* Reichb. f. One cannot help but wonder what olfactory or visual cue directs the proper species of bee to turn upside-down before entering the flower.

Sievekingia suavis Reichb. f.—This species is found only infrequently on the Atlantic coast of central Panama, but it is more frequent in Costa Rica, and occurs sympatrically with *S. fimbriata* in the Sarapiquí area. A plant from near Río Cuarto, in the Sarapiquí area, was observed in flower in March near Chitaría, where the species may also be expected. The flowers attracted several males of *Euglossa dodsoni* Moure, which entered the flowers. The first bee to appear quickly removed two pollinaria; unfortunately, these fell off in my hand when the bee was captured, so that their placement on the bee could not be determined. Two males of *Euglossa townsendi* Cockerell were also attracted, but these scratched on the sepals and petals, and did not enter the lip.

Stanhopea costaricensis Reichb. f.—In Panama, this species is known from Cerro Campana, where it is sympatric with *S. inodora*, and from relatively low elevations in the Canal Zone. Dodson has observed *Eulæma seabraii* Moure (or *E. luteola* Moure) visiting this species in Costa Rica (14). Five individuals of *Euplusia schmidtiana* (Friese) which visited *Stanhopea ecornuta* on Cerro Campana in July bore pollinaria of an advanced *Stanhopea* with very long stipes (one of the pollinaria still very fresh when the bee was captured). Dr. Dodson has compared these with material in his collection and finds that they match the pollinaria of *Stanhopea costaricensis*. There may be some ecological or mechanical barriers between *S. costaricensis* and *S. ecornuta*, for otherwise it is difficult to see why the interspecific hybrid is not more frequent.

Stanhopea ecornuta LEM.—This species, which ranges from Guatemala to Costa Rica, is unusual among the large-flowered Stanhopeas in the total lack of horns on the lip. Nevertheless, it is interfertile with the more ornate species, and rare hybrids do occur. (*S. lewisæ* in Guatemala and *S. ecornuta* × *costaricensis* in Costa Rica, see DODSON, 14). I did not have opportunity to observe well-established flowering plants in Costa Rica, but some of the plants flowered later in Panama and provided some useful data. The flowers, which have (to me) an odor of over-ripe cantaloupe, are very attractive to *Euplusia schmidtiana* (Friese).

Euplusia schmidtiana is known from the Atlantic slope of Costa Rica, though it is not yet recorded from other areas where *S. ecornuta* occurs. On Cerro Campana in July a plant of *S. ecornuta* with two flowers (the norm for the species) had from one to four bees in attendance from 9:00 A.M. to 1:00 P.M. (especially from 9-11), even though I was regularly harvesting specimens of this once rare bee for the museum collection. Both pollinaria were removed, but I did not see their removal. *Eulæma nigrita* Lep. showed some interest in the flowers on two or three occasions, and is also of about the right size to effect pollination, but may not occur where *S. ecornuta* is native. The bees enter the space between the lip and column from the side, where the edge of the lip is shallowly concave (Fig. 9). They often retreat from the flower by the same path, but if they shift to the center of the lip, to better reach the base of the hypochile, the knobs at each side of the apex of the lip guide the bee out beneath the column, where the apex of the lip pushes it near the projecting viscidium. This system would seem to be the evolutionary predecessor of the system in the more advanced Stanhopeas, in which the bee enters the flower from the side and may then fall through the flower. Some Euglossas, such as *E. imperialis* Cockerell, *E. allosticta* Moure and *E. tridentata* Moure, were occasionally attracted, but would not be likely to effect pollination because of their small size.

Stanhopea cirrbata Lindley.—I have not observed the pollination of this species, but a photograph taken by Mr. Orville Rigby at Las Cruces shows a large *Euglossa* of the subgenus *Glossura* in the flower. The photograph suggests *E. flammea* Moure, and this species has since been collected with a pollinarium of *S. cirrbata* in Puntarenas province (D. H. Janzen, July 1967).

Stanhopea cf. *oculata* (Lodd.) Lindley.—A pale-flowered form which appears to be referable to *S. oculata* is frequent near El Valle, where it is sympatric with *S. wardii*, but the plants which I observed were either poorly established or far from their native habitat, and I have not witnessed pollination. Nevertheless, this species is interesting for the number of non-pollinators which it attracts in the Navy Reservation. There *Euglossa crassipunctata* Moure, *E. cyanaspis* Moure, *E. flammea* Moure, *E. hemichlora* Cockerell and *E. tridentata* Moure were all collected brushing on the petals of this species in September. These Euglossas are far too small to effect pollination. This species, like the other advanced Stanhopeas, might be characterized as a "fall-through" flower (Fig. 10), and the normal pollinator is doubtless an *Eulæma* or a large *Euplusia*.

CATASETINAE.—This subtribe, of only three genera, is of special interest because of the separation of the sexes and the pollen-throwing mechanism which occur in most species.

Catasetum bicolor Kl.—This species is occasional in the central Canal Zone and on the Atlantic coast of central Panama. I have caught *Euglossa cordata* (Linnaeus) (July) and *E. cyanaspis* Moure (September and November) visiting either male or female flowers of this species, and I have caught *E. cordata* (December) and *E. tridentata* Moure (September) bearing the distinctive pollinaria. The mechanism of pollination is much the same as in the larger species of *Catasetum* (PORSCH, 28). In the male flowers, the finger-like projections position the bee (much as does the helmet-shaped lip of *C. viridiflavum*) (fig. 11-A, B). When the bee touches the antenna with its feet the viscidium is released and strikes the bee on the thorax. The stipe is hinged next to the viscidium, so that the pollinia lie back on the dorsum of the bee. As soon as the anther has fallen off, they are ready to pollinate a female flower. The female flowers, which are more fragrant and long-lasting, are similar in all *Catasetum* species with unisexual flowers. The hooded lip is uppermost and the short column beneath. The bees enter upside-down (fig. 11-D), and the pollinia hang downward, to slide into the stigma when the bee withdraws from the flower.

Catasetum viridiflavum Hook.—This very common species failed to attract pollinators in my presence for quite a long time. Then Mrs. Edna Jackson found, in September, that, when in just the right stage, the flowers attract many males of *Eulaema cingulata* (Fab.) from dawn (about 6:00 AM) to no later than 8:00 AM. Since then I have caught other males of *Eulaema cingulata* bearing the pollinaria of this species. On the available evidence, there is no isolating mechanism between *C. viridiflavum* and *C. maculatum* Kunth (*C. oerstedii* Reichb. f.) or *C. macroglossum* Reichb. f., all of which are pollinated by *E. cingulata* (and often by other *Eulaemas* as well). However, local orchid growers inform me that *C. viridiflavum* and *C. maculatum* are sympatric near Soná, without intergradation.

Catasetum warczewitzii Lindley & Paxt.—This species belongs to the small section *Clowesia*, in which the flowers are bisexual and the pollen-throwing mechanism is not or weakly developed. The plants are not infrequent at moderate elevations, especially in the region of Cerro Azul. The flowers of this species have the sides of the lip pinched in, giving a form quite different from all other species. Though the flowers are highly perfumed, I did not observe any visitors in Panama. A plant which was cultivated in Las Cruces bore several young capsules, and when the flowers of the second inflorescence opened most pollinaria were removed on the same day (but after we had left the garden). The next day, an *Eulaema nigrita* Lep. was seen on the flowers, but escaped.

Then a male of *Eulaema meriana* (Olivier)* approached and was captured. To our surprise, this bee bore three pollinaria of *Catasetum warczewitzii* on its "elbows", that is, on the distal end of the femur of the foreleg. Evidently the pinched form of the lip forces the very large bee to turn sideways to reach the attractive area, so that the joint between the femur and the tibia touches the viscidium and removes the pollinaria.

Cynoches.—Pollination of this genus has been reported by ALLEN (3) and DODSON & FRYMIRE (17). Allen has provided a taxonomic revision of the swan orchids, in which he tried to bring order to a difficult complex. It appears, though, that he went too far in the "lumping" of many taxa. His varieties of *Cynoches egertonianum* are clearly good species, and sufficient data will probably show that the plants he treated as typical *C. egertonianum* represent a number of biologically and morphologically distinct species. The separation of the sexes has been a handicap in my observation of this genus, as the female flowers show little morphological variation (much as in *Catasetum*), and there are several significant plants for which I did not see male flowers. The mechanism of pollination is a bit different in the *C. egertonianum* complex and in *C. ventricosum*, as described below under *C. aureum* and *C. ventricosum*.

Cynoches aureum Lindley.—This species, which ranges from higher elevations in central Panama into Costa Rica, is easily distinguished from other species in the *egertonianum* complex by either male or female flowers, and is sympatric with at least one other member of the complex near El Valle. The flowers attract the males of *Eulaema nigrita* Lep. wherever they occur (observed July-September), and I have seen the deposition of pollinia in the female flower. Several of these bees have been captured bearing the pollinaria of *C. aureum*. *Euglossa cyanaspis* Moure, *E. tridentata* Moure and the diminutive *E. crassipunctata* Moure are occasional visitors in Balboa and the Navy Reservation (where the *Cynoches* is not native), but they are too small to remove or deposit pollinia.

I have not seen the pollinaria removed from the male flowers, but the system must be the same as in other species of the *egertonianum* complex. The slender base of the lip is flexible, and the weight of the bee pulls it down (fig. 12.A, B), so that the abdomen of the bee touches the tip of the column. The viscidium is then released and strikes the bee near the apex of the abdomen.

* There appear to be two forms of *E. meriana* in Panama and Costa Rica. The males of the smaller form, with yellower bands and blue-black chitin on the abdomen, are the more commonly collected, but occasional males and many of the collected females are larger, with paler bands and greenish chitin on the abdomen. While I have not found a clear morphological difference between these forms, I suspect that they will prove to be distinct species. The male which visited *Catasetum warczewitzii* is of the larger form, and the only one of this form which I have found visiting orchids.

The pollinaria project straight behind the bee, and are available for pollination as soon as the stipe straightens and the anther falls off. The female flower is rigid, with a shorter column (fig 12-D). Here, however, the bee reaches the attractive area of the lip with some difficulty. It must release the grip of its hind legs and swing outward. When it does this, one of the pollinia is caught by the notched stigma and pulled off the stipe.

Cycnoches egertonianum Batem.—The form of *Cycnoches* which occurs commonly near Turrialba is apparently the typical form of *C. egertonianum*, with large, coarsely blotched dark green male flowers widely spaced on a string-like inflorescence, and wide appendages on the lip. With C. H. Dodson and H. Hills in August, I observed that this species was visited by *Euglossa ignita* Smith both near Turrialba and near Puerto Viejo, where some of the bees bore pollinaria of this species. Two of the bees collected at Puerto Viejo proved to be *E. flammea* Moure which is very similar to *E. ignita*. At Puerto Viejo another *Euglossa*, *E. purpurea* Friese, bore pollinaria of a smaller *Cycnoches*, but we did not see the plants of this other form. Typical *Cycnoches egertonianum* ranges northward to extreme southern Mexico, and *Euglossa ignita* has been collected in Guatemala (Cayuga, Guatemala, Wm. Schauss, U. S. N. M.).

Cycnoches ventricosum var. *warszewiczii* (Reichb. f.). P. H. Allen.—My observations agree with those of ALLEN (3) and DODSON and FRYMIRE (17), that this species attracts *Eulæma cingulata* (Fab.) in great numbers (observations recorded for August from plants cultivated at Diablo Heights). The geographic races recognized by Allen are all pollinated by this bee, as far as is known, and *C. lehmannii* Reichb. f., of Ecuador, might well be considered another geographic subspecies of *C. ventricosum* (17). In this species the male and female flowers are very similar in form, and the mechanism of pollinarium removal is much the same as the mechanism of deposition. The bee, clinging to the callus with its mid-feet, pivots outward and strikes the apex of the column with its abdomen.

Cycnoches sp. no. 1.—As far as I have seen there is only one form of the *C. egertonianum* complex near El Valle (except for *C. aureum*) and this form is fairly frequent. This may be the *C. densiflorum* of Schlechter. In any case, the plants have been seen to attract *Euglossa cyanura* Cockerell on several occasions in July. My earlier observations were quite unproductive, probably because I had placed the plants in the sun. I have not seen any other species visit these flowers.

Cycnoches sp. no. 2.—A *Cycnoches* of the *C. egertonianum* complex from the Santa Rita ridge was loaned to me in November by Lt. George Martin. The female flowers of this plant consistently attracted only *Euglossa tridentata* Moure. I have not seen the male flowers of this form. There was yet another form from the same area cultivated by Lt. Martin, in which the female flowers were

distinctive (ivory-cream rather than green, and with the lip distinctly ribbed). Here, again, I have not seen the male flowers, but another plant from this area and probably of the same species seems to be *C. stenodactylum* Schlechter. No bees visited this form in Margarita.

Cycnoches sp. no. 3.—Yet another of the *C. egertonianum* complex was lent to me by Henry Tooke, of Corozal, Canal Zone. The geographic origin of this plant is not certain. At El Valle the female flowers attracted a few *Euglossa bansonii* Moure in September. I later took the same plant to the Navy Reservation, and there one of the bees which came to the flowers (apparently *E. bansonii*, but it escaped) bore a pollinarium of *Cycnoches*. Thus, this is probably the form which grows in the Navy Reservation, but I have not seen the male flowers of this or any other plant from that area. Mr. Dunn tells me that the lowland plants have the male flowers even more densely clustered than the El Valle form, and he considers them to be *C. guttulatum* Schlechter.

Mormodes.—Plants of this genus, like those of *Catasetum* and *Cycnoches*, are usually found on dead wood, either standing or fallen. While they may be locally abundant, they are usually somewhat "spotty" in their occurrence, and hardly ever so omnipresent as *Catasetum*. The flowers of this genus show a peculiar torsion of the lip and column. There is great variation in color and some variation in morphology, as well. My impression is that the posture of the lip is a feature of some taxonomic importance, but this is quite lost in herbarium material, while the structure is merely badly distorted. While this genus has been considered to have perfect flowers, CORRELL (8) showed in 1941 that *M. bistrio* had dimorphic flowers. ALLEN (5) showed that these flowers were functionally "staminoid" and "pistilloid", though both types are structurally perfect. DODSON (11) found a similar condition in an Ecuadorian species, and my own observations indicate that all Panamanian species of *Mormodes* produce such "staminoid" and "pistilloid" flowers. The functionally male flowers are more numerous, short-lived, and have a narrow column. The functionally female flowers, which are usually produced by the larger, well-established plants, have a much wider column (larger stigma), which soon straightens out, parallel to the lip. These flowers are larger and longer-lasting, and the pollinia are usually discharged in a short time, even if nothing disturbs the "trigger". The lips of the female flowers of *M. skimmeri* Reichb. f. and *M. bistrio* Lind. & Reichb. f. are glabrous, but I do not know if this is the case in other species which have pilose male flowers.

The apex of the column ends in a slender appendage which remains against the lip in the male flowers (fig. 13). If a bee, walking on the lip, touches this appendage, the pollinarium is released and the viscidium arches over, striking the bee on the back. The viscidium usually strikes the thorax of the bee, but the mechanism is less precise than in *Catasetum* or *Cycnoches*, and the viscidium may strike the bee's wing, in which case the pollinia are wasted and the bee temporarily grounded. When the pollinaria are first discharged the stipe coils

tightly. As it dries, it straightens so that the pollinaria project upward from the bee's thorax. If the bee later walks under the stigma of a female flower, the pollinaria may remain in the stigmatic surface (fig. 13, D).

The nomenclature which I use here is primarily taken from Mr. G. F. J. Pabst, who has very kindly let me use his extensive notes on this genus.

Mormodes atropurpureum Lindley.—This species is known from Costa Rica and western Panama. Plants from western Panama attract *Euglossa cybelia* Moure and occasionally *E. mixta* Friese in central Panama in June. My own observations in Costa Rica were singularly unproductive, but Mr. Robert Wilson found that one of his well established plants at Las Cruces attracted numerous bees in April. The bees which he captured were *E. mixta* (5), *E. championi* Cheesman (3) and *E. cybelia* (1). It is quite probable that Champion collected the type series of *E. championi* on this or some other orchid, for he collected a series of 17 males. Since that time only 6 or 8 specimens have been collected.

Mormodes cartonii Hook.—This is the species commonly called *Mormodes igneum* in central Panama, but that epithet is applicable to another species. The present species attracts *Euglossa cordata* (Linnaeus) in large numbers (Mrs. Jackson and I once collected 35 in one morning in Diablo Heights), and this bee clearly seems to be the pollinator (observed in December and January). As with most *Mormodes*, *Euglossa mixta* is an occasional visitor, but has not been seen as a pollinator.

Mormodes colossus Reichb. f.—This species is much the most abundant *Mormodes* near Turrialba, and is frequent near San Vito de Java. Nevertheless, I do not have good pollination data for the species. The commonest visitors near Turrialba (February and March) are *Eulaema cingulata* (Fab.) and *E. meriana* (Olivier), both of which seem much too large to be pollinators. When I have observed these bees to remove pollinaria, they received the viscidia on the head or feet, and quickly removed them. Thus, the visits of these bees would seem not only useless but detrimental to the orchid species. *Euglossa mixta* is perhaps more strongly attracted to this than to most other *Mormodes* species, and *Euglossa asarophora* Moure was observed a few times. I believe that a third species of blue *Euglossa* was seen at Chitaria, but it evaded capture, and I cannot be sure. At Las Cruces, in March, the O. T. S. class collected two *Euglossa maculilabris* Moure visiting this species, and at least one other was seen. That *E. mixta* is a frequent visitor of both this and *M. atropurpureum* is in agreement with the morphological evidence of extensive hybridization between these species near San Vito de Java. I have seen other anomalous *Mormodes* in Costa Rica, perhaps also the work of this aptly named bee. In central Panama, however, the *Mormodes* species are quite distinct, and I have seen no sign of hybridization. It would be interesting to observe *Mormodes* near Potrerillos in Chiriquí, where I am told that there are six sympatric species of *Mormodes* (probably with hybridization between *M. atropurpureum* and *M. colossus* there, too).

Mormodes flavidum Kl.—Señor Alberto Pérez supplied me with a nice plant of this species (also known as *M. stenoglossum* Schltr., which is a later synonym), collected near Atenas, on the dry Pacific slope of Costa Rica. The flowers had an odor reminiscent of lemon drops, and, taken to an area near Alajuela in February, attracted only one specimen of *Euglossa viridissima* Friese (the others which were seen found a nearby *Gongora* more attractive). This species may be the pollinator, but the data are too few to be confident.

Mormodes igneum Lindley & Paxt.—This species is sometimes called *M. colossus* by orchid growers in the Canal Zone, but is quite distinct from either *colossus* or *cartoni*. The lip in this species is dark-brown (in central Panama) and typically elliptic and evenly curled under to form an unbroken arch beneath. Some forms are markedly truncate, so that the inrolled lip is more or less trumpet-shaped (but achieves this appearance in a different way than *M. buccinator*). There are many intermediates between the elliptic and the truncate extremes. *Mormodes igneum* and *M. cartonii* are sympatric and in several areas of central Panama, near El Valle and at lower elevations, as well (25), but I have seen no indication of intergradation, though each species is quite variable. This species is regularly visited and pollinated by *Euglossa igniventris* Cheesman in December and January. *Euglossa mixta* is an occasional visitor, but does not seem strongly attracted.

Mormodes powellii Schltr.—This species is the only *Mormodes* I have found on the eastern side of the Canal, on Santa Rita ridge and Cerro Azul, and on Barro Colorado Island. This is the form treated as *M. colossus* by TEUSCHER (29), but the lip is much narrower than in that species. The only plant which I saw on Barro Colorado Island (collected by that excellent naturalist, Fausto Bocanegra) flowered in February and attracted a large number of *Euglossa tridentata* Moure, which removed pollinaria in the normal fashion. I have collected other bees of this species with *Mormodes* pollinaria, presumably from *M. powellii*.

Mormodes sp.—This is probably the species reported from El Valle by ALLEN (1) as "small *M. colossus*". It differs from other species in this complex in the smaller size and the narrow, tightly inrolled lip. The clear yellow color and the tightly inrolled lip are both suggestive of Lindley's description of *M. convolutum*, but the type of that species is much more like a small *M. cartonii*. This species seems not to be native to the region of El Valle, but is occasionally brought in to the market from the Atlantic coast. I did not attempt to walk back to its native habitat with the plant, but took it to Margarita, which is, at least, on the Atlantic coast. In the short time I had there (in January) the flowers attracted only one specimen of *Euglossa cyanaspis* Moure, and no other bees were seen at the flowers, either there or at Las Cumbres.

OTHER ORCHID GENERA.—As I have concentrated my attention on the subtribes Catasetinæ and Stanhopeinæ, my observations of other genera are spotty and even more incomplete. In many cases they are limited to the observation of pollinaria on bees captured visiting the above-listed orchids or food plants. I have several times seen pollinaria of *Sobralia* on *Eulæma*, *Euplusia* and *Euglossa*, but I have not tried to identify the pollinaria to species (being unable to name *Sobralias* even with far better material), and, in all probability, the bees visit *Sobralia* to seek nectar, so that most species of *Sobralia* do not show the special relationship under discussion.

Dichæa sp.—A number of *Euglossa cordata* (Linnæus) which were collected on *Mormodes cartonii* in January in the Navy Reservation bore pollinaria of *Dichæa* on the face (at the top of the clypeus on the specimen that still retains the pollinarium). The pollinaria match those of *D. panamensis* Lindley, which is common in the area and was flowering at that time.

Kefersteinia sp?—Several of the *Euglossa deceptrix* Moure which were collected on Cerro Campana in August bore pollinaria with stipes wrapped around the bases of the antennæ. These stipes each bore four pollinia and appeared to be of *Kefersteinia* or some similar plant. I did not have an opportunity to search for the plants in flower, so I am unsure of their identity. One *Euglossa cybelia* Moure which was collected near Las Cruces had this same sort of pollinarium attached in the same way, and two males of the type series of *E. mixta* Friese each have a stipe on one antenna. It would be of interest to identify the plants involved and see how the pollinaria are placed on the bee's antennæ.

Lycaste sp.—A male of *Euglossa tridentata* Moure which was captured near Chitaría in March bore the pollinarium of a small *Lycaste*. This might have been *L. brevispatha* Kl. ex Lindley, *L. leucantha* Kl. or *L. tricolor* (Kl.) Reichb. f.

Notylia barkeri Lindley?—A plant of this complex was collected near Río Cuarto in the Sarapiquí region of Costa Rica and flowered at Turrialba in March. The flower structure agrees closely with the description of *N. turrialbæ* Schltr. At Chitaría this plant proved to be very attractive to Euglossini, and attracted many males of *Euglossa tridentata* Moure and several of *E. hansonii* Moure, both species which removed pollinaria on the face. A few individuals of *Euglossa sapphirina* Moure were attracted, but brushed on the sepals and did not remove pollinaria. *Euglossa ignita* Smith was attracted twice, but its behavior on the flowers was not observed. The attractive area in *Notylia* flowers seems to be the blade of the lip. The bees crawl on the inflorescence, and when one brushes on the lip its face (clypeus) is pushed against the apex of the column, thus removing the pollinarium.

Both *Euglossa tridentata* Moure and *E. dodsoni* Moure have been captured with *Notylia* pollinaria in Central Panama, but I do not know which species of *Notylia* they had been visiting.

Notylia panamensis Ames.—A plant found on Barro Colorado Island and cultivated there attracted a single *Euglossa hemichlora* Cockerell in June, but this was not seen to remove pollinia.

Notylia pentachne Reichb. f.—Two different persons assured me that this species was visited by a large fuzzy bee, and their description suggested *Eulæma cingulata* (Fab.). On my last visit to Panama, in March, I found *N. pentachne* to be in bud, flower and young fruit at Morgan's Garden, in Corozal. I saw an *Eulæma cingulata* visiting one of these plants, and saw that the bee bore several pollinaria on the clypeus. Though the bee escaped, there is no doubt of its identity.

Notylia sp.—Another species of the *N. barkeri* complex was cultivated by Mr. Wilson at Las Cruces and flowered in March. This species has relatively small flowers open few at a time, so that the inflorescence remains attractive to bees for a long period. Dr. Dodson and I each captured a male of *Euglossa erythrochlora* Moure, and a few others were seen, but were very wary and easily frightened.

DISCUSSION

It is becoming increasingly clear that the euglossine bees have been a major factor in the evolution of some American orchids (DRESSLER, 19). The odor of the orchids is the critical factor in attracting the bees, and thus the main isolating mechanism between sympatric species. The gas chromatograph may become as important to the student of orchid speciation as the tape recorder has to the student of Amphibia (DODSON and HILLS, 18). The isolating mechanisms depending on the interaction of bees and orchid odors are quite as subject to failure as any other sort of isolating mechanism (were this not so, speciation would surely be a much rarer event; see BAKER, 6). Thus, two or more of the *Mormodes* species in Costa Rica and western Panama show extensive hybridization, and some species of *Stanhopea* in Central America show interspecific hybridization, very rare between *S. ecornuta* and *S. costaricensis*, frequent between *S. wardii* and *S. oculata* and massive between *S. gibbosa* and *S. costaricensis* (DODSON, 13, 14). Where limited hybridization occurs, it is probable that each orchid species has two or more pollinators, but that at least one of the pollinators is either occasionally or regularly shared.

Highly specific pollination relationships, such as those described here, are very much the exception. Even in the North American deserts, where many bees are highly specialized (oligolectic), most plant species attract and are pollinated by several different species of bees, and most bee species visit two or more closely related plant species. Highly specific pollination relationships are generally considered to be evolutionarily somewhat perilous. In an obligate relationship involving food, such as *Yucca/Pronuba*, the plant and insect species are each highly dependent upon the other. This interdependence is, to some degree, side-stepped by the euglossine-pollinated orchids, since they depend on bee species which obtain their food from a variety of other flowers. The plants are, undoubtedly, highly dependent upon the bees, but being long-lived perennials, a

(purely hypothetical) scarcity of bees for one season or two would not be catastrophic for the plants. Quite definite advantages for this pollination system are that it is favorable for speciation and permits a high degree of cross-pollination, even when the plants are widely dispersed in the tree tops. The scattering of the plants is accentuated in many species by their extended flowering season and the short duration of the flowers. Even where a colony of 10-20 plants is found, it is unusual for two of the adjacent plants to be in flower at the same time. This extended flowering season may, in itself, be an adaptation which favors cross-pollination.

TABLE 1.

The number of pollinators compared with the number of closely related sympatric species for euglossine-pollinated orchids in Panamá and Costa Rica. The number of species with each combination is indicated.

Number of pollinators	Number of sympatric species					
	0	1	2	3	4	5
12	1					
5					1*	
4	2		1			
3	1					2**
2	1	2		1		
1	3	14	4	3	1*	1

1* *Gongora quinquenervis*, in which some plants attract several pollinators and others only one (listed twice).

2** *Mormodes atropurpureum* and *M. colossus*, which share at least one pollinator and hybridize in Costa Rica.

Table 1 contrasts the number of pollinators which are known to visit each orchid species with the number of closely related, congeneric species which overlap the range of each orchid species. Species which are adapted to bees of very different size (as *Catasetum bicolor* and *C. viridiflavum*) are considered as not closely related, and only the Panamanian and Costa Rican ranges are considered for questions of sympatry (considering a larger area might remove *Acineta superba* and *Peristeria elata*, for example, from the category of isolated species). The data are surely incomplete, but there is a clear indication that geographically isolated species tend to be less specific in their pollination relationships. This is, of course, a double-edged sword. Non-specific pollination relationships are not conducive to speciation. On the other hand, selection may impose more specific relationships where related species occur together. In this respect, it is interesting to compare the genus *Catasetum* in central Panama and Brazil. In central Panama there are only two species of the subgenus *Cata-*

setum, and they cannot be considered closely related with respect to pollination relationships. In Brazil there has been very active speciation in *Catasetum*, and as many as six species of the subgenus *Catasetum* may occur in a single region; many of the Brazilian *Catasetum* species must surely have more specific pollination relationships than the Panamanian species. Similarly, the quite isolated *Peristeria* in El Valle attracts a large number of different bees. The related *Peristeria pendula* Hook., in Peru, attracts only two species of *Euglossa* (DODSON, 14).

The cultivation of these orchids in areas where they are not native may provide some interesting biological tests. A plant of *Mormodes atropurpureum* which flowered in Rio de Janeiro proved very attractive to a green *Euglossa* in that area (as have all species visited by *Euglossa cybelia* in Central America). The *Euglossa* is probably true *E. cordata*, but the Panamanian "*E. cordata*" has never been observed to visit, or even to pause near, this orchid. Of more general interest, though, is the evidence that an orchid species invading a new habitat may encounter a "pre-adapted" pollinator. If the new pollinator is markedly different in size or behavior, the invading orchid population may be subjected to severe selection while yet very small. Such a situation would be very close to the "leap-frog speciation" discussed by DODSON (12). It should be noted, though, that we were very naive about the euglossine bees when the "leap-frog" model was proposed. Rather than consisting of a few large bees (*Eulama*) and a very few small ones (*Euglossa*), the tribe presents a very large array of potential orchid pollinators, ranging from about 8 mm to 30 mm in length, with the greatest number of species in the smaller size range.

Euglossine pollination would seem to provide a better model for sympatric speciation than flower constancy. As GRANT has indicated (24), flower constancy will break down when the number of flowers is low, as one would expect it to be in an incipient species arising through mutation. In the case of euglossine-pollination, however, we are dealing with innate and highly specific reactions to odor. It is not difficult to imagine a mutation which would attract a different species of pollinator, and such a mutant would probably be self-pollinated (possibly by a bee which visited on two successive days). In all probability a heterozygous mutant would attract both the new and the old pollinators, but a single self-pollination would be enough to produce several homozygous mutants. One may expect that the homozygous mutants (and the homozygous non-mutants) would be more attractive than the heterozygote (since all of the substrate could be utilized for one odor), and thus more efficient in pollination. Thus, the fixation and ethological isolation of an odor-modifying mutation without geographic isolation seems quite possible, at least in theory. If the new pollinator were of the same size as the ancestral pollinator, a new species might arise with a minimum of morphological change. As in the "leap-frog" model, however, if the new pollinator were markedly smaller or markedly larger, the new species would be subjected to very intense selection for morphological change. The *Gongora quinque nervis* complex shows a single widespread species and several more local species which are each sympatric with

G. quinquenervis. The pattern is suggestive, and intensive study might be rewarding.

It is apparent that the Euglossas, especially, supply a fertile background for speciation. The presence of fifteen to twenty bee species of similar body size, but each with specific odor preferences, provides more "niches" in one area than any orchid genus has filled. Those genera which are primarily adapted to *Euglossa* (*Cynoches*, *Gongora*, *Mormodes*, *Notylia*) tend to be rich in species. The morphological differences between these species are relatively slight, and the herbarium botanist has found all of these genera to be troublesome. Nevertheless, if one carefully studies the morphological variation, with due consideration for geography and ecology, a pattern of speciation is evident. One may find nearly or quite the same pattern of species by seeking the taxonomic opinions of the Euglossa (but the bees, unfortunately, refuse to express opinions on pressed specimens). Those orchid genera which have adapted as much to *Eulæma* and *Euplusia* as to *Euglossa* (*Stanbopea*, *Coryanthes*, *Catasetum*) show a much greater range of morphological variation. These genera, too, have proven difficult to study from the herbarium, especially because of their large, fleshy flowers and great color variation, but the morphological differences are generally more obvious than in genera which are primarily pollinated by *Euglossa*.

Both ALLEN (4) and BAKER (7) have commented on the strikingly different orchids which are pollinated by the same bee, as, for example, *Gongora quinquenervis* and *Coryanthes speciosa*. While the morphological diversity of the euglossine-pollinated orchids is impressive, there is more unity in the group than is at first evident. The attraction is always by odor, and one restricted portion of the flower is especially (or exclusively?) attractive. In the simplest cases, the bee is merely forced to crawl beneath the apex of the column, where the removal or deposition of pollinia is probable. In many other cases, in order to reach the attractive portion of the flower, the bee is required to assume an awkward position, usually on a very smooth surface. Under these circumstances, even if not somewhat drugged by the flower, the bee often slips and falls. The bee's fall is so guided that the removal or deposition of pollinia is highly probable. In these more complex orchids the placement of the bee in the flower and the placement of the pollinarium on the bee are both very precise. In these respects, the pollination systems of *Gongora* and *Coryanthes* are really similar, and, while they are strikingly different in morphology, it is surely these differences which have permitted different orchid genera to utilize the same pollinators.

BAKER has suggested that pollinators might be "shared" by taxonomically unrelated species (7), and this is certainly the case in the euglossine-pollinated orchids. Sympatric species of different genera or sympatric species which place the pollinaria on different parts of the bee (as in the different subgenera of *Catasetum*) may, and often do, utilize the same pollinator. Especially striking is the case of *Eulæma cingulata*, which is utilized by *Catasetum* (both subgenera and the anomalous *C. eburneum*), *Coryanthes*, *Cynoches*, *Gongora*, *Stanbopea*, *Notylia*, *Zygopetalum*, *Trichocentrum*, *Pescatoria* and *Aspasia*, as well as species

of *Anthurium* and *Spathiphyllum* (though not all in one region). In the area of Panama and Costa Rica, pollinator sharing is the rule, the common species, *Euglossa cordata* and *E. tridentata* each being shared by several species. In fact, of the 32 species of *Euglossa* cited here, 17 are cited as pollinators for two or more species of orchids, as are all of the cited *Eulaemas* and *Euplusias*.

It is difficult to visualize the evolution of some of the more bizarre euglossine-pollinated orchids. ALLEN (4) suggested a sort of orthogenesis, and BAKER (7) has very nearly proposed Goldschmidtian macromutation, or the fortuitous coincidence of several lesser mutations. The simpler pollination systems of *Acineta* or *Stanhopea ecornuta* seem admirably simple and effective, but, in fact, they seem to be much less efficient than *Gongora quinquenervis* or *Stanhopea oculata*. One may observe the bees entering and leaving these simpler flowers repeatedly without seeing a pollinarium removed. It would seem that a little "tighter" flower would be more efficient. I have noted, however, that the euglossine bees seem reluctant to fly or crawl through very small openings. Thus, I suspect that these simpler flowers maintain an uneasy balance between conflicting selection pressures. A more tightly closed flower would be more efficient, if the bees would only enter; and a more open flower would be more attractive to the bees, but, beyond a certain point, quite ineffective in pollination. This hypothesis could, I believe, be tested experimentally, and for me, at least, it makes the evolution of the more complex Stanhopeinae more understandable. The advanced Stanhopeas can afford to have the apex of the flower tailored to an exact fit (but not so tight as to require a struggle), because the bee falls through by accident. The bee exits from the *Coryanthes* flower, which is a very tight fit, under his own power, but is given very little choice. In most of these orchid genera there are enough simpler species in the present-day flora to aid one in visualizing the evolution of the more complex sorts. The genus *Coryanthes*, however, strains the imagination a bit. I would suggest that it is most closely related to *Stanhopea*, and especially to *S. tricornis* Lindley, rather than to *Gongora*. I can (not without some strain) visualize its evolution from a "fall-through" *Stanhopea* (*S. tricornis* is not of this sort), in which the addition of the dripping glands might aid in starting the bees on their fall. Such an evolution might include an element of "leap-frog speciation" with a shift from a large pollinator to a smaller one. Assuredly such an imaginary intermediate between *Stanhopea* and *Coryanthes* would be subject to intense selection pressure, and it is not surprising that it is not found among the living Stanhopeinae.

While the bizarre divergences between some of the euglossine-pollinated orchids is impressive, the lack of morphological divergence in others is equally striking. With isolation based primarily on odor, a functional morphology may remain quite constant in a number of related species. As groups which are relatively uniform in their structure, we may cite the *Gongora quinquenervis* complex, the *Stanhopea wardii/oculata* group and, to a lesser degree, the *S. saccata/tigrina* group, the *Notylia barkeri* group, the genus *Mormodes* and the *Cycnoches egertonianum* complex. *Catasetum* subgenus *Catasetum* is especially

curious in this respect. The male flowers vary widely in their structure, but the female flowers are nearly identical throughout the subgenus. In the male flowers, the bee must be properly positioned in relation to the column when it touches the antenna, and this may be achieved by a wide variety of lip structures. In the female flower, the bee must back out of the flower and slide the pollinia into the stigma, a function which is achieved only by a hooded lip placed above the column. As DODSON has indicated (11), selection pressure is strong only for the odor and the form of those flower parts involved in pollination. Color and the form of parts not directly involved in pollination may vary widely within populations without affecting the efficiency of the flower in pollination.

The genera of the Catasetinae differ among themselves in the placement of the pollinaria on the bee. The pollinaria of *Cycnoches* are attached near the tip of the abdomen, the pollinaria of *Catasetum* usually lie on the back, attached to the thorax, while those of *Mormodes* are attached to the same area, but stand upright. Natural hybridization between these genera would appear to be effectively impossible. There are two species of *Catasetum* which differ markedly in the placement of the pollinaria (*C. eburneum* Rolfe and *C. dilectum* Reichb. f., see DODSON, 11), but these do not show close relationship to the true *Catasetums* in any feature, and might better form a separate genus. *Catasetum warzewitzii* has a very unusual mechanism of pollination, but is closely similar to the other species of subgenus *Clowesia*, which probably place the pollinaria on the bee's thorax or beneath the scutellum. Most Stanhopeinae place the viscidium beneath the scutellum of the bee, though the mechanisms which achieve this are diverse. *Coryanthes* places the pollinarium between thorax and abdomen; *Peristeria*, *Kegeliella* and *Lacena* place their pollinaria further forward on the dorsal surface of the bee, while *Coeliopsis* places the pollinaria on the face*. *Sievekingia* departs totally from the norm for the subtribe and hooks the pollinaria on the trochanter of the leg.

It is interesting that several orchids regularly attract, not only their normal pollinator(s) but one or more bees whose size or behavior prevent their functioning as pollinators. It is clearly not safe to catch the first bee to approach a flower and list it as the pollinator. When these accessory visitors, or non-pollinators, are smaller than the normal pollinator, as in *Cycnoches aureum* or *Stanhopea* cf. *oculata*, they would seem to be of little consequence to the plant species. When they are larger, though, they may frighten or push away the normal pollinator (many of the euglossine males are quite aggressive, at least when

* The two main groups of highly evolved American orchids have, for the most part, different modes of pollination. Most members of the subtribe Oncidiinae place the pollinia on the face or head of the bee. The Maxillariinae and Stanhopeinae (which are closely allied to each other) usually place the pollinaria on the dorsum of the bee. Several anomalous groups in the Maxillariinae/Stanhopeinae alliance, such as *Coeliopsis* and *Dichaea*, approach the Oncidiinae in some morphological features, and also place the pollinaria on the face or head of the bee. The morphological parallels probably represent adaptations to a similar mode of pollination.

visiting orchid flowers) and thus be actively detrimental to the plant species. In the case of *Mormodes colossus*, the large Eulaemas can and do discharge the pollinaria, though it is unlikely that they ever effect pollination. If the bees are obtaining a substance which is in some way biologically important to them (as rather appears to be the case), then it is not illogical that some bees should turn the tables on the plants and "take advantage of" orchid species which do not benefit by their visits. Of particular interest is the behavior of accessory visitors. The striking behavioral differences between pollinator and non-pollinator in the case of *Sievekingia fimbriata* are mentioned above. In many cases, the accessory visitors do not seek the same portion of the flower as the normal pollinators. In the Stanhopeas the normal pollinators always seek to brush in the hypochile, at the base of the lip. The several *Euglossa* species that visit *Stanhopea* cf. *oculata* could easily enter the hypochile, yet they almost invariably brush on the petals. Here, again, the bees are reacting differently to the same stimulus; or more likely, the odors are composite, and different bees are reacting to different components. It is interesting to note that the occasional *Eulaema cingulata* which visits the "yellow-lip" *Gongora* in Costa Rica brushes on the sepals, yet if a flowering plant of the South American *Gongora atropurpurea* is exposed, *E. cingulata* is attracted and seeks to brush in the hypochile, though the Central American bees have no experience with *Gongora atropurpurea*.

It is often said that the complicated pollination mechanism of "the orchids" are relatively inefficient, and that very few orchid flowers actually set seed. This is undoubtedly true of some orchids, but I do not believe that it applies to the euglossine-pollinated groups (which surely include the most complicated). I have very little quantitative data on plants which remained undisturbed in one spot, without having a large proportion of their visitors snatched away before they could accomplish pollination. In the case of *Gongora quinquenervis* on Barro Colorado Island, I noted one very large clump in the forest which had produced about 12 inflorescences (perhaps 125-150 flowers) and had 12 young capsules. The same clump produced several capsules in each of the two seasons that it was cultivated near the laboratory. Two smaller but well established plants which were cultivated on Barro Colorado Island each had 45-50 flower scars and 4 or 5 capsules at the end of the flowering season*. Many of the buds are damaged by weevil larvae and fall off before anthesis, so the number of flowers available for pollination was less than 40 on each plant, and more than 10 % of the flowers were pollinated. Considering the tremendous seed production of each capsule, this would seem to be a quite effective method of pollination. In the case of other euglossine-pollinated species for which I do not have even approximately quantitative data, my impression is that a healthy plant in a favorable site is very likely to bear from one to several capsules each season. If the plant is in an unfavorable

* My notes on these plants have been lost, so the numbers are approximate.

site (too shady for sun-loving bees, or vice-versa), of course, it may go quite without visitors. Unfavorable weather is surely an important factor for these short-lived flowers; but a large plant will flower repeatedly over a long season, so that some of the inflorescences, at least, should meet favorable conditions. Indeed, the short life-span of the flowers is, in itself, evidence that the system of pollination is quite efficient. One finds a good general correlation (inverse) between the flowers' durability and their attractiveness for insects. At the moment, it seems a safe generalization to say that the commoner orchid species in any area are usually pollinated by common bee species. The abundance of the bees is difficult to judge, especially when they are being sampled largely at orchid flowers. This also makes it difficult to judge whether or not the bees are seasonal in their activity. A further generalization for which more quantitative data are much needed, is that the more specialized or advanced orchids are generally more abundant or "successful" than their less specialized relatives. In the Catasetinae, for example, most species of *Catasetum* are relatively abundant, while *Mormodes*, with a less precise pollination mechanism, tends to be spotty and unpredictable in its occurrence. Similarly, many of the advanced species of *Stanhopea* are abundant and widespread within their habitats, while the primitive species are more local (DODSON and FRYMIRE, 16). It is difficult in these comparisons, to separate features of the pollination mechanism from other aspects of the plants' biology. One finds, for example, that *Mormodes* and *Cynoches* are much more "delicate" and subject to rot in cultivation than *Catasetum*. One might argue that *Coryanthes*, with its bizarre floral adaptations, is not common, but it is restricted to ant nests, and usually occurs in tall trees, where its real abundance is very difficult to judge. Undoubtedly, the distribution of many orchid species is limited by the distribution of the pollinating bees. We need to know a great deal more about the distribution of both bees and orchids before much can be said on this subject.

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SUMMARY

Many orchid flowers and some flowers of other families produce no nectar and are visited and pollinated primarily or exclusively by male euglossine bees. These bees brush on the surface of the flower with tufts of hair on the forefeet, and gather some aromatic substance which is then placed in their inflated hind tibiae. The bees are attracted by odor, and many of the flower odors are highly specific, attracting one or few bee species. The tribe Euglossini includes *Euglossa*, *Eulaema*, *Euplusia*, *Eufriesea*, and the parasitic genera *Aglæ* and *Exaerete*. All genera of the orchid subtribe Stanhopeinae are pollinated by euglossine bees; observations are given here for *Acineta superba*, *Coeliopsis hyacinthosma*, *Coryanthes maculata*, *Gongora* (5 or 6 species), *Kegeliella atropilosa*, *Lacaena spectabilis*, *Paphinia clausula*, *Peristeria* (2 species), *Polycynis gratiosa*, *Sievekingia* (2 species) and *Stanhopea* (3 species). All members of the subtribe Catasetinae are also pollinated by euglossine bees, and observations are given for all three genera: *Catasetum* (3 species), *Cynoches* (6 species) and *Mormodes* (7 species). Other orchid genera for which observations are given here are: *Dichaea*, *Kefersteinia*, *Lycaste* and *Notylia*.

Euglossine pollination provides very effective isolating mechanisms, and has been important in the speciation of several orchid groups. Isolation by highly selective fragrance might permit sympatric speciation through odor-modifying mutation. Orchid species with sympatric close allies tend to be more specific in their pollination relationships than geographically isolated species. While the pollination relationships are highly specific, the same bee species may visit and pollinate several different (and distantly related) orchid species. In several cases, orchid flowers attract "accessory visitors", bees which do not function as pollinators because of size or behavior. In general, euglossine pollination appears to be efficient, and the more advanced orchid species appear to be more efficiently pollinated than their primitive allies.

RESUMEN

Muchas flores de orquídeas y de otras familias no producen néctar y son visitadas y polinizadas principal o exclusivamente por abejas euglosinas. Estas abejas frota la superficie de la flor con ciertos haces de pelo de las patas delanteras, y recogen alguna sustancia que colocan en las tibias traseras infladas. Las abejas son atraídas por el olor, y muchos de los perfumes florales son altamente específicos, atrayendo sólo una o pocas especies de abeja. La tribu Euglossini

comprende *Euglossa*, *Eulaema*, *Euplusia*, *Eufriesea*, y los géneros *Aglae* y *Exaerete* de abejas parásitas. Todos los géneros de la sub tribu de orquídeas Stanhopeinae se polinizan por abejas euglosinas; se presentan aquí observaciones de *Acineta superba*, *Coeliopsis hyacinthosma*, *Coryanthes maculata*, 5 o 6 especies de *Gongora*, *Kegeliella atropilosa*, *Lacaena spectabilis*, *Paphinia clausula*, 2 especies de *Peristeria*, *Polycynis gratioiosa*, 2 especies de *Sievekingia* y 3 de *Stanhopea*. Todos los miembros de la subtribu Catasetinae tienen también polinización por abejas euglosinas, y se da observaciones de los tres géneros del grupo: *Catasetum* (3 especies), *Cynoches* (6 especies) y *Mormodes* (7 especies). También se presenta datos de especies de *Dichaea*, *Kefersteinia*, *Lycaste* y *Notylia*.

La polinización por euglosinas resulta en mecanismos de aislamiento muy efectivos, y ha tenido importancia en la especiación de varios grupos de orquídeas. El aislamiento por olores muy selectivos podría permitir especiación simpátrica por mutaciones modificadoras del aroma. Las especies de orquídeas con aliados cercanos simpátricos tienden a ser más específicos en la atracción de un polinizador que las especies geográficamente aisladas.

Si bien las relaciones insecto-flor son muy específicas, la misma especie de abeja puede visitar y polinizar varias especies diferentes y poco emparentadas de orquídeas. En varios casos, las flores de orquídea atraen "visitantes accesorios", abejas que no actúan como polinizadores por su tamaño o comportamiento. En general, la polinización por abejas euglosinas parece ser eficiente, y las especies de orquídeas más avanzadas parecen tener mejores sistemas de polinización que sus aliados primitivos.

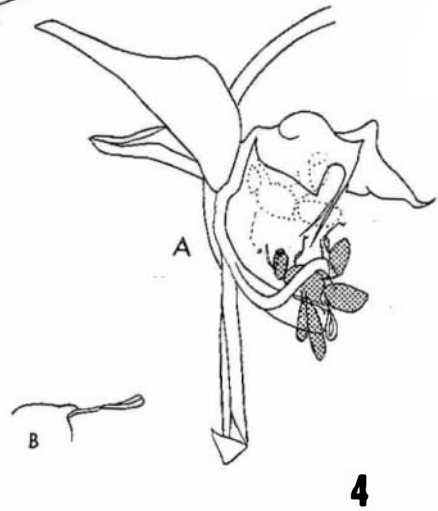
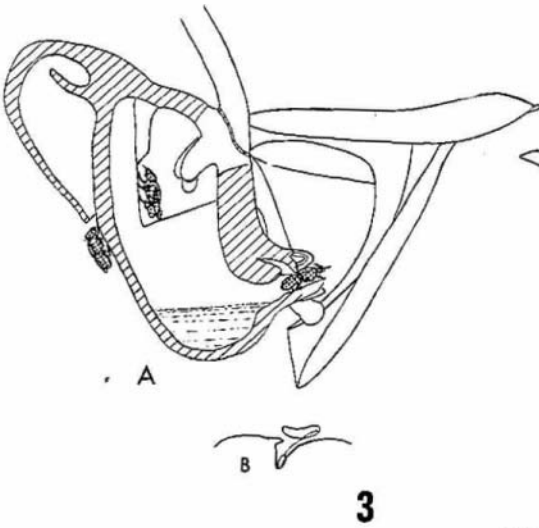
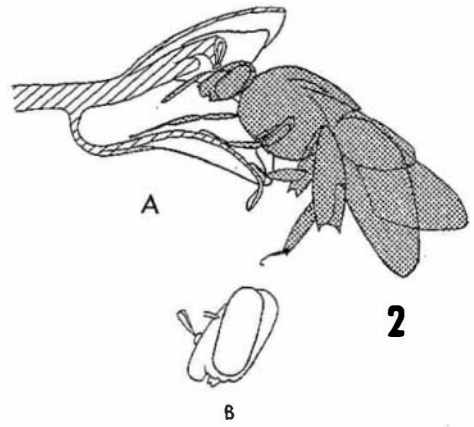
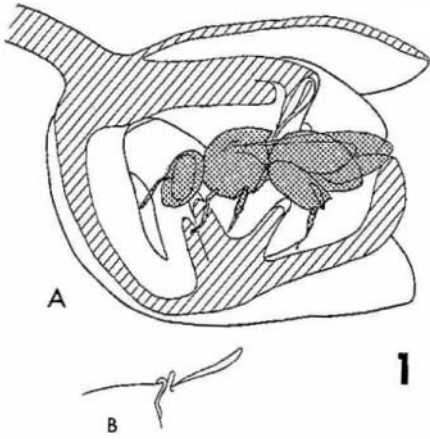
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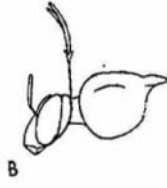
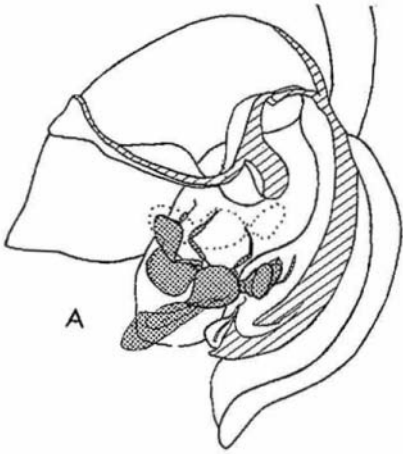
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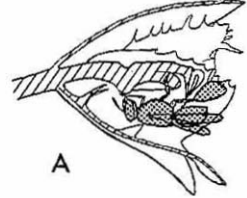
- Fig. 1. Pollination in *Acineta superba*. A. longitudinal section of the flower showing *Euplusia concava* as it backs out and receives the viscidium beneath the scutellum. B. the placement of the pollinarium on and beneath the scutellum of the bee; the thickness of the viscidium is exaggerated.
- Fig. 2. Pollination in *Coeliopsis hyacinthosma*, A. longitudinal section of the flower showing *Eulaema meriana* receiving a pollinarium on the clypeus. B. the placement of the pollinarium on the head of the bee.
- Fig. 3. Pollination in *Coryanthes maculata*, A. longitudinal section of the flower showing two *Euglossas* brushing on the lip near the hood and a third emerging beneath the apex of the column and receiving a pollinarium on the base of the abdomen. B. the placement of the pollinarium between the thorax and the abdomen.
- Fig. 4. Pollination in *Gongora tricolor*, A. the position of the bee while brushing is shown by dotted lines. When the bee falls its course is guided by the column and petals, and the pollinarium is placed beneath the scutellum. B. placement of pollinarium; the thickness of the viscidium and stipe is exaggerated.



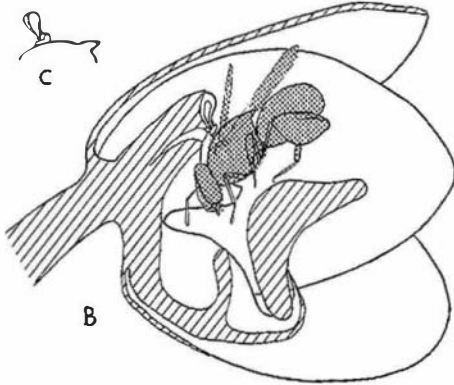
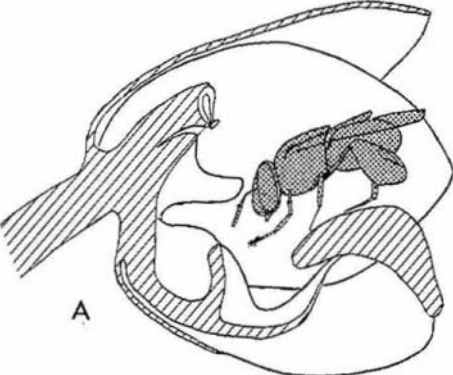
- Fig. 5. Pollination in *Lucæna spectabilis*, A. longitudinal section of the flower, the position of the bee while brushing is shown by dotted lines; when the bee falls, the pollinarium is placed between the head and prothorax. B. placement of the pollinarium.
- Fig. 6. Pollination in *Sierekingia fimbriata*, A. longitudinal section of flower with *Euglossa sapphirina* entering the flower upside-down. The hooked viscidium catches on the trochanter of the mid or hind leg. B. thorax of bee, showing the placement of the pollinarium on the trochanter of the hind leg.
- Fig. 7. Pollination in *Peristeria* species, A. longitudinal section of the flower with *Euglossa dodsoni* on the hinged lip. B. same, showing the lip overbalanced and the bee thrown against the column. C. placement of the pollinarium on the thorax.
- Fig. 8. Pollination in *Polycynis gratiosa*, A. flower in normal position. B. flower with *Euglossa villosa* on lip; the weight of the bee causes the flower to bend downward, the pollinia then being hooked beneath the bee's scutellum. C. placement of pollinarium.



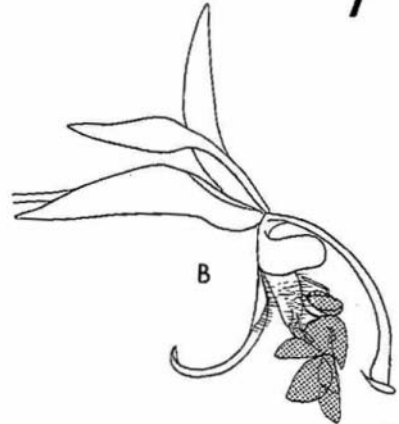
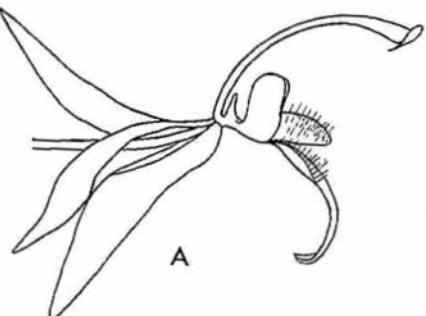
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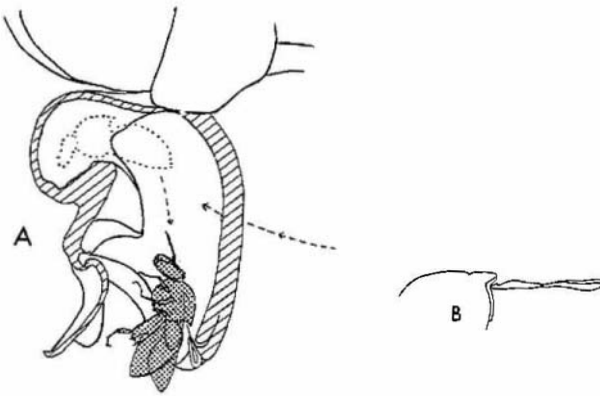
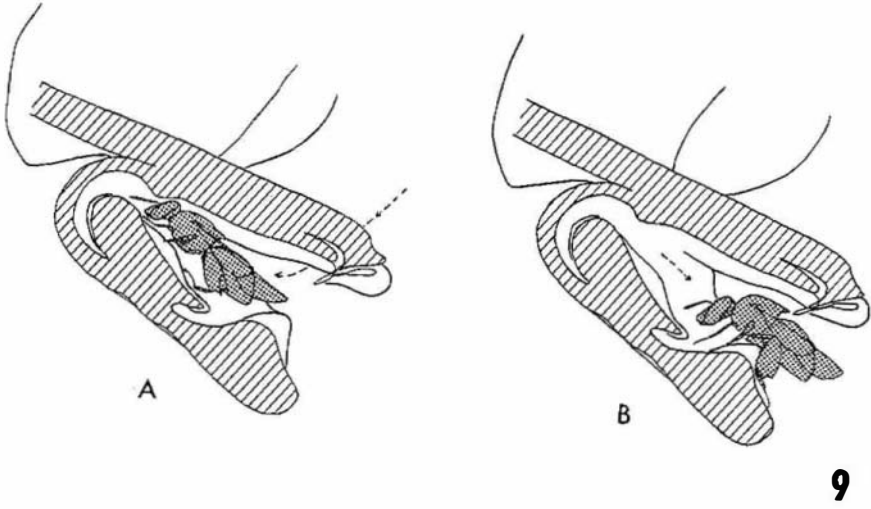


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- Fig. 9. Pollination in *Stanhopea ecornuta*. A. longitudinal section of flower with the bee brushing near base of lip (having entered from side). B. the bee backing out beneath the apex of the column. The placement of the pollinarium is probably as in figure 10, though the stipe is much shorter.
- Fig. 10. Pollination in *Stanhopea oculata* and allies. A. the bee enters from the side (arrows), brushes in the hypochile (dotted outline), and, on withdrawal, may slip and fall through the flower, the pollinarium then being placed beneath the scutellum. B. placement of *Stanhopea costaricensis* pollinarium on *Euplusia schmidtiana*; the viscidium (thickness exaggerated) is largely placed on the propodeum.



- Fig. 11. Pollination in *Catasetum bicolor*. A. longitudinal section of male flower with pollinarium in place. B. same showing *Euglossa cordata* touching the antenna and receiving the pollinarium on the thorax. C. placement of pollinarium. D. longitudinal section of female flower with bee backing out of flower and inserting a pollinium in the stigma.
- Fig. 12. Pollinia in *Cynoches aureum*. A. longitudinal section of male flower with pollinia in place. B. the weight of *Euleema nigrita* pulls the lip down and the abdomen of the bee strikes the apex of the column, causing the pollinarium to be expelled and placed near the apex of the abdomen. C. placement of pollinarium on abdomen. D. longitudinal section of female flower with the bee inserting a pollinium in the stigma. E. apex of the female column, showing the slits which catch the pollinia.
- Fig. 13. Pollination in *Mormodes ignea*. A. staminoid flower of the truncate extreme, with the pollinarium in place. B. same, with *Euglossa igniventris* touching the apex of the column and causing the pollinarium to be expelled. The viscidium usually strikes the thorax of the bee. C. placement of pollinarium. D. pistilloid flower of the elliptic extreme, with a bee passing beneath the stigma and effecting pollination.

