THE CATASETUMS (ORCHIDACEAE) OF TAPAKUMA, GUYANA

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INTRODUCTION

Six to eight species of *Catasetum* occur on the coastal plain of Guyana, on the northeastern perimeter of South America. Four species — *Catasetum macrocarpum* L. C. Richard ex Kunth, *Catasetum discolor* Lindl., *Catasetum longifolium* Lindl., and *Catasetum thompsonii* Dodson — which are frequent on the coast, also occur along the Tapakuma River in the Essequibo District of Guyana. The other species occur in the inland areas, particularly in the savannah country. The four species under consideration are markedly different in their growth habits and in their habitat preferences, and are thereby easily distinguished. No natural hybrids had been recognized between the four species and it was assumed that the species had isolating mechanisms which kept them distinct even though they were known to occur together in the same regions in South America.

In this paper I wish to discuss the populations of the four species of *Catasetum* at Tapakuma. Manmade disturbance, a consequence of the building of the dam at Dawa, has altered the nature of these populations. Inundation by the resulting lake killed the trees which once bordered the Tapakuma River, and provided a habitat for a tremendous expansion of the *Catasetum* populations. The dead trees have also provided a habitat wherein natural hybrids can exist.

The basic biology of the genus *Catasetum* and its allies is covered in Dodson (1962) but a brief discussion might be of value here. Generally, *Catasetum* plants are found in association with dead trees. The genus *Catasetum* belongs to the subtribe Catasetinae and forms one of the groups which produce separate male and female flowers. The production of female flowers depends on the presence of a robust plant in full sunlight. If a plant is in partial shade or is not particularly robust, male flowers are normally produced. Study of populations of *Catasetum* (Dodson, 1962) indicated that the female flowers are produced in a considerably lower ratio than the male. Plants producing female flowers tend to be associated with dead trees, where they force their numerous roots into rotting wood and obtain considerably greater nutritional levels. Full sunlight, due to the lack of leaves on the trees, also has an effect in promoting female flowers. The male flowers are produced in much greater number and are found on plants growing on tree trunks and limbs in relatively shaded areas. These plants are often considerably less robust. Data gathered in Ecuador in 1962 indicated that approximately 25 male flowers occur for each female. This ratio was also found to hold in the populations of *Cycnoches lehmannii* Rchb. f. and *C. peruviana* Rolfe that were studied at that time. *Cycnoches* is a genus closely allied to *Catasetum* and also produces separate male and female flowers.

A given plant may produce either male or female flowers depending on the particular circumstances of its habitat. For example, if a plant is growing in shady areas for most of the season, it will almost invariably produce male flowers; however, if a plant growing in a sunny condition in a dead tree and producing female flowers, falls out of the tree into a shady situation, it will usually revert to the production of male flowers.

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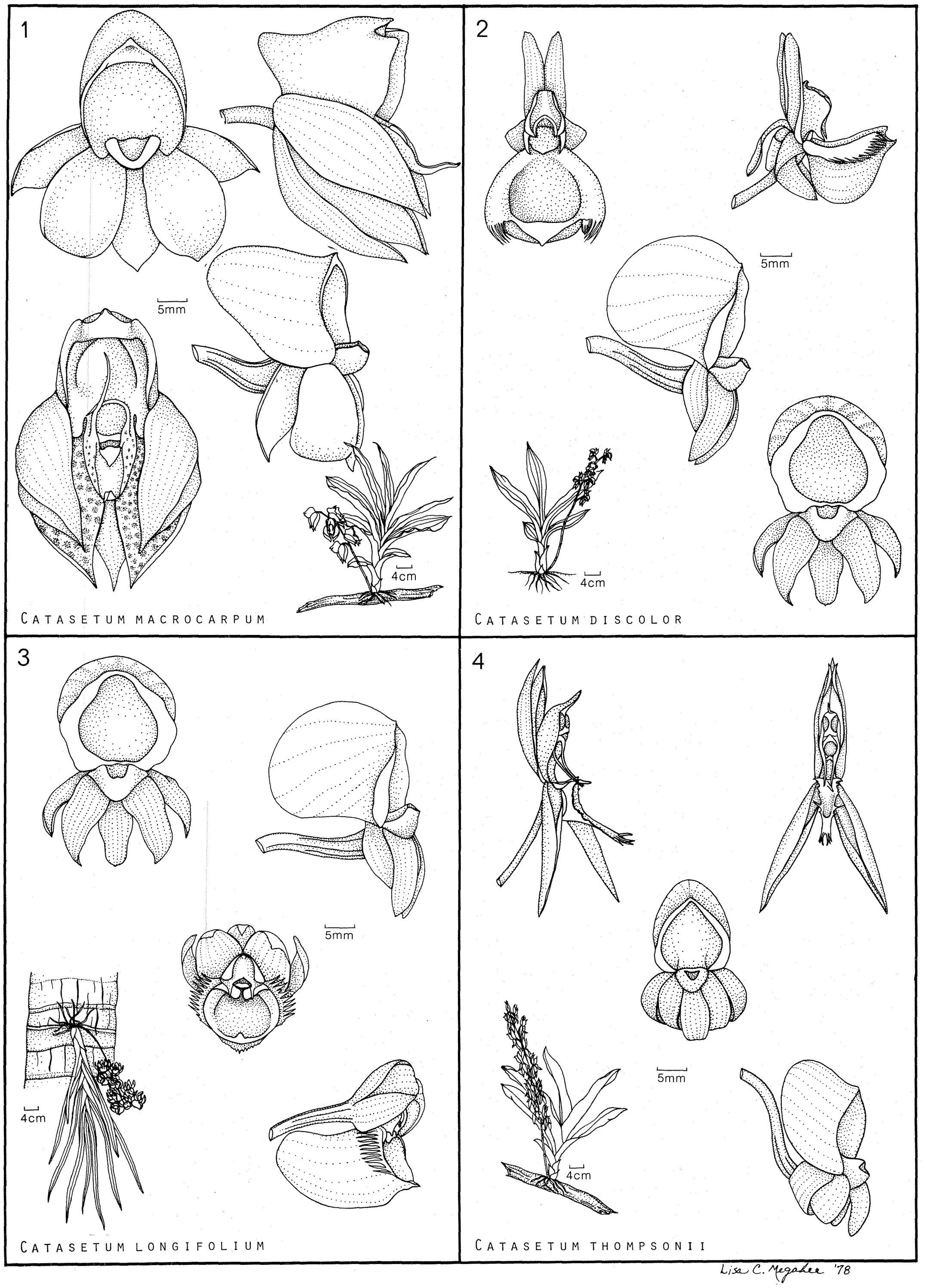
THE SPECIES AND THEIR HABITATS

Catasetum macrocarpum L. C. Richard ex Kunth is a widespread species found from the eastern slopes of the Andes in Colombia, Venezuela and through to the region of Belem in eastern Brazil. It is common along the lower Amazon and the Orinoco Rivers. The plants are normally found growing as epiphytes in the rain forest regions and are most frequent along the river banks where the female plants can occur in branches of dead trees overhanging the river. The male plants more frequently occur in living trees and in slightly shadier situations along the river banks. There seems to be little preference for particular species of trees as hosts. The lips of both the male and the female flowers are hood-shaped (Figure 1) and the column of the male flower is provided with antennae which are elongated and project up inside the hood. When touched by the pollinating insect, the antenna causes the viscidium of the pollinarium to be released. It is then thrown strongly against the dorsal part of the thorax of the visitor. In all cases the effective pollinators are large bees of the genus *Eulaema*. The male flowers are usually yellow in color, heavily blotched with red and with occasional spots of brownish red. The female flowers are yellow-green with sepals and petals often flecked like the male flowers. Both male and female flowers are strongly fragrant. The male flowers last for a very short period of time and cease to attract pollinators upon the discharge of the pollinarium. If they are not disturbed by a pollinator, they usually last only two or three days. The female flowers, on the other hand, are long-lived, frequently lasting two to three weeks if undisturbed. They close very quickly and cease to produce fragrance if pollinated. Natural hybrids (*C.* ×*splendens* Cogn.) between *C. macrocarpum* and *C. pileatum* Rchb. f. occur frequently in Venezuela. The leaves of the plants are broad and they arch downward. The pseudobulbs are ovoid.

Catasetum discolor Lindl. is normally found growing as a terrestrial in sand in savannah regions, quite frequently among the tufts of grass common to those areas. It is often found growing in the shade under low shrubby trees and bushes in the same kind of area, particularly on the edge of gallery forest. It is distributed from Colombia, Venezuela, and Peru across to eastern Brazil, but it is usually restricted to the sand savannah regions, or the higher elevation savannahs of the table top mountains. The plants normally root into the sand, leaf mold, or whatever small amount of humus may be on the surface, particularly if the plants are under small shrubs and trees. The plants which occur in grass out in the open savannah regions frequently produce female inflorescences. This is particularly so of those plants which are large and robust, or which grow in ant nests. Those plants which are found at the edge of gallery forests or under shrubs where they receive some shade typically produce male flowers. The female and male flowers of this species are more distinctive than in *C. macrocarpum.* The pale pink or greenish-red male flowers are produced in an arching inflorescence and may number as many as 20 to 25. The lip of the flower is cup-shaped (Figure 2) and is frilled around the edge. The flowers are considerably smaller than those of *C. macrocarpum.* The anther-firing mechanism is much reduced and the antennae, which extend from the edges of the column, are very short and form a central flap. This central flap, when touched, causes the pollinarium to be fired. The flowers are formed in such a way that the bee lands on them with


1
5mm
4cm
Catasetum macrocarpum
2
5mm
4cm
Catasetum discolor
3
5mm
4cm
Catasetum longifolium
4
5mm
4cm
Catasetum thompsonii
Lisa C. Megahee '78

Figures 1-4

the ventral surface of his body facing towards the column. When the anther is fired, the pollen masses are attached to the ventral part of the thorax of the bee.

The green female flowers are produced on an erect inflorescence and seldom more than three or four occur. The female flower is much larger than the male flower and it has a much deeper lip cavity. Again, the bees land on the flowers and turn the ventral surface toward the stigmatic region of the flower (Figure 2). The plant habit in *C. discolor* is distinct from any of the other species. The narrow leaves are relatively stiff and held nearly erect. The pseudobulbs are conical.

Catasetum longifolium Lindl. occurs throughout much of the Amazon basin and also in parts of Venezuela and Guyana. It is restricted to growing epiphytically in *Mauritia flexuosa*, palms which are normally found at the edges of very slow moving river systems, inundated forest regions, and shallow lakes throughout northeastern South America. *Catasetum longifolium* is different from all other species of *Catasetum* in that the plants are pendant. The plants develop in the leaf bases of the mauritia palm so that the long narrow leaves, which may at times reach two meters in length, hang down like ribbons. The species is closely allied to *C. discolor*, the flowers of which are very similar (Figure 3). The inflorescences are also pendent. The lip, however, is slightly deeper than that of *C. discolor* and the frill on the edge of the lip is perhaps less obvious and more fimbriated. The colors are usually stronger with the inside of the lip very dark yellow and the callus and outer edge of the lip dark red. The female flowers are similar to those of *C. discolor*, and the positioning of the pollinator is relatively the same.

Catasetum thompsonii Dodson is closely related to *C. barbatum* (Lindl.) Lindl. which occurs in Guyana and Brazil. Similar related forms are found from Colombia, Ecuador, Venezuela, and Trinidad, through the Amazon region to southern Peru and central southeastern Brazil. Numerous names have been proposed such as *C. cristatum* Lindl., *C. appendiculatum* Schltr., *C. randii* Rolfe, etc., some of which may prove to be valid species. The plant habit of *C. thompsonii* is quite similar to that of *C. macrocarpum*. The leaves are slightly broader and shorter and the coloring at the base of the leaf slightly more speckled with red, but it is difficult to differentiate *C. thompsonii* from *C. macrocarpum* when they are not in flower. When flowers are available, however, it is obvious that the species are quite distinct. The male flowers of *C. thompsonii* are much smaller; the lip is held in the downward position; and rather than being a hood, the lip is an open, tongue-like structure with stout papillae on its margins (Figure 4). The column is erect over the lip and the antennae are extended down along the inner surface of the lip. The inflorescence is erect and produces ten to twenty-five flowers. They are light green spotted with red and the lip is white. The female inflorescence is also erect and produces ten to twelve flowers. They are reminiscent of the female flowers of *C. macrocarpum*, but they are much smaller and very light yellow. The pollination system is basically similar to that of *C. macrocarpum*, the pollinarium being attached to the dorsal part of the thorax of the pollinator. However, the pollinators of this species are much smaller bees befitting the size of the flowers. *Catasetum thompsonii* is normally scattered among the populations of *C. macrocarpum*, growing along the river sides. Similar to *C. macrocarpum*, the plants producing female flowers are found in dead trees, and those producing male flowers usually grow in the shade.

The Habitat At Tapakuma

The natural conditions for the presence of the four species of *Catasetum* described above were unquestionably present in the region of Tapakuma prior to the development of the dam at Dawa, in 1963. When the dam closed, it caused the inundation of the forest which had surrounded the edges of the river. The trees died and within a few years became literally infested with *C. macrocarpum* and *C. thompsonii*. The other two species, C. *discolor* and *C. longifolium*, grew nearby: *C. discolor* is found in areas within three or four miles of the dam growing naturally in sand scrub regions and *C. longifolium* is present near the dam in mauritia palms. The palms were found in submerged areas along the Tapakuma River originally. The forest area around Dawa is degraded rain forest and contains — wherever the land is at all low — great quantities of mauritia palms. The huge population of catasetums now present in the dead trees is certainly much greater than any natural situation.

The clearing of the hillside around the dam by bulldozers in order to gather sand for the dam and roadways and to open space for construction of houses provided a habitat similar to the savannah country which grasses and *C. discolor* were able to invade. The result is that literally thousands of *Catasetum* plants of four species occur together in one area within distances which would certainly be possible for bees to traverse. In some instances, all four species were found wthin a radius of fifty meters.

The Reproductive Isolating Mechanisms

Since hybrids between these species had never been reported, it was assumed that even though the species occasionally occur near to one another, the reproductive isolating mechanisms were sufficiently strong to preclude hybrids. It was known that the *C. barbatum* complex (which includes *C. thompsonii*) was normally pollinated by euglossas (Dodson, 1965). Euglossas are small green or golden bees slightly larger than a housefly. *Catasetum macrocarpum* was known to be pollinated by larger eulaemas, principally *Eulaema cingulata* and *E. meriana* (Dodson, 1965). *Catasetum discolor* was known to be pollinated by *E. meriana* and also *E. cingulata* (Dressler, pers. comm.). The pollinator of *C. longifolium* was unknown. The assumption then was that another species of bee must pollinate *C. longifolium*, and that *C. macrocarpum* and *C. discolor* were probably separated more by ecological preferences than by strict attraction of different species of bees.

In April of 1970 all four species were found to be in bloom. The visitors to the flowers of the four species are tabulated in Table 1. The unexpected result of the observations was the presence of *E. cingulata* as visitor to all four species. Size relationships, however, preclude *E. cingulata* as a pollinator of *C. thompsonii* even though it very frequently visits that species (Figure 5). The smaller euglossas are able to enter and exit from the flower in such a way as to pollinate it without difficulty; however, *Eulaema cingulata* is too large to enter the flower and pollinate it effectively.

The other three species of *Catasetum* attracted essentially the same species, but the ratios of the species were strikingly different. *Catasetum macrocarpum* attracted much greater numbers of *E. cingulata* than of any other eulaemas, whereas *C. discolor* and *C. longifolium* attracted many more *E. meriana* and *E. bombiformis* than *E. cingulata.*

There was clearly a temporal difference in the visitation by the bees. The eulaemas began flying before dawn. *Eulaema cingulata* was found in great quantities on pads saturated with eugenol at dawn (about 6 a.m.) and at the same time *C. discolor* and *C. longifolium* were being visited by large numbers of *E. bombiformis* and *E. meriana.* Visitation by the bees to the pads on these plants respectively persisted until about 8 a.m. During this period, *C. macrocarpum* was rarely visited and certainly not before 7 a.m. At about 8 a.m. *C. discolor* and *C. longifolium* seemed to lose their attractiveness for the larger eulaemas, and the bees gradually left. By 8 a.m. a few had shifted to the now fragrant *C. macrocarpum* and numerous *E. cingulata* began visiting that species. From 8 a.m. to 10 a.m. *E. cingulata* came to *C. macrocarpum* in great quantity, but *C. thompsonii* which was in the same area, was not visited during these hours. At about 10:30 a.m. the fragrance of *C. thompsonii* became strong and the bees of *E. cingulata* shifted from *C. macrocarpum* to *C. thompsonii.* Some bees continued working both species, however, until 12 noon. The majority of the bees visited *C. thompsonii* after 11 a.m. Neither *E. meriana* nor *E. bombiformis* was ever seen visiting *C. thompsonii.* Along with *Eulaema cingulata* several species of *Euglossa* visited *C. thompsonii.* The smaller *euglossas* are the pollinators of the species.

Occasional bees of *Eulaema meriana* were captured which carried the pollinia of *C. discolor* or *C. longifolium* on the underside of the thorax and *C. macrocarpum* pollina on the upper side of the thorax, indicating that this bee may be the agent which carries the pollen between species, thereby causing natural hybrids.

Gas chromatography of the fragrances of the four species of *Catasetum* indicate that there is little difference between the fragrances of *C. discolor, C. longifolium* and *C. macrocarpum.* However, *C. thompsoni* has quite a distinctive fragrance. The major peak in the *C. discolor, - C. longifolium - C. macrocarpum* fragrance is alpha-pinene, which is probably not the attractant since alpha-pinene presented in pure form to the bees does not attract them. Other components of the fragrance such as benzyl acetate or d-carvone may well be the attractants. *Catasetum thompsonii* produces primarily pipertone and ocimene. Pipertone produces the major portion of the smell to the human nose and in terms of quantity probably dominates the other compounds present. Where pipertone is found in other orchids, such as *Coryanthes macranthum, Eulaema cingulata* is found to be the pollinator. The differences in the fragrances of *C. discolor - C. longifolium - C. macrocarpum* and *C. thompsonii* appear to be responsible for the presence of bees of the genus *Euglossa* visiting *C. thompsonii.* The other three catasetums attracted only a single species *(Euglossa chlorosoma)*, which is probably only an accidental visitor not functioning as a pollinator. Mixtures of the compounds found in the fragrance of *C. thompsonii* were tested at Dawa and they found to attract many bees of the species which are visitors of *C. thompsonii.*

THE HYBRIDS AT TAPAKUMA

Soon after our arrival at Dawa, we became aware of a kind of *Catasetum*, not referable to any of the four known species. This *Catasetum* was found either in mauritia palms or on dead trees. The plants were pendant and reminiscent of *C. longifolium*, but the pseudobulbs were much more massive and the leaves were broader and not as long. The flowers were

Figure 5. Male bees of *Eulaema cingulata* visiting female flowers of *Catasetum thompsonii*. The bees are too large to be effective pollinators.

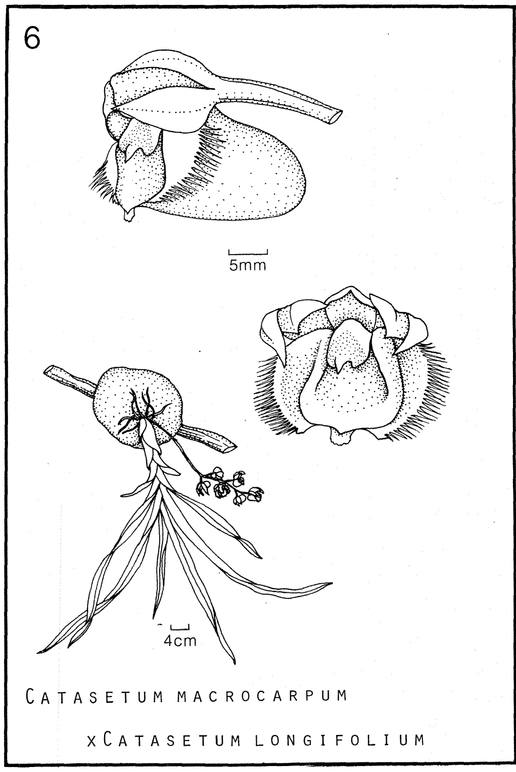


Figure 6

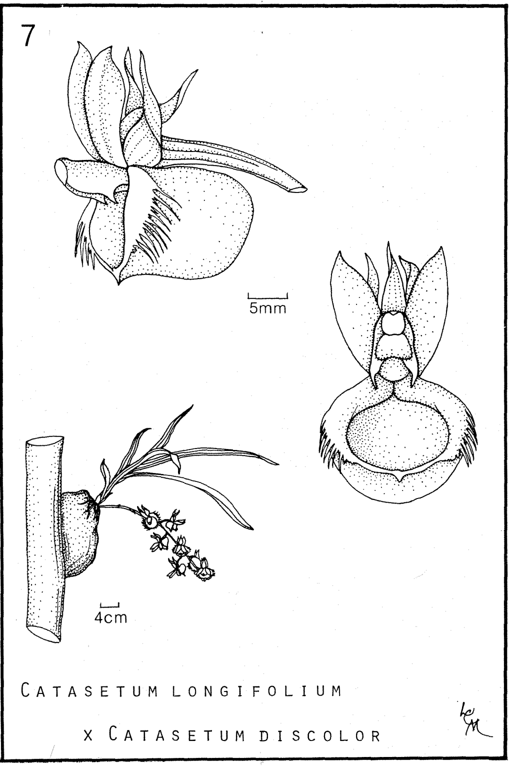


Figure 7

found to be intermediate between *C. macrocarpum* and *C. longifolium* (Figure 6). We presumed that these plants were hybrids between the two species. This was confirmed by later hybridization experiments.

Further search indicated the presence of presumed hybrids between C. *longifolium* and *C. discolor* (Figure 7). These plants were nearly always found growing in termite nests in the dead trees surrounding the lake. The plants grew erect but had relatively narrow stiff aching leaves and the flowers were intermediate between the two putative parental species. Apparent hybrids between *C. macrocarpum* and *C. discolor* were found growing on termite nests or in the grassy clearings where *C. discolor* was found. The leaves of these plants were broader and more rigid than those of *C. discolor*, but narrower than those of *C. macrocarpum*.

A certain amount of backcrossing may be occuring between the hybrids and *C. longifolium* and *C. macrocarpum*. However, there was little indication of backcrossing between the hybrids and *C. discolor*. No hybrids were found between *C. thompsonii* and any of the other three species. Curiously enough the hybrid between *C. macrocarpum* and *C. longifolium* is strikingly similar to the plant illustrated in Dunsterville and Garay's *Venezuelan Orchids Illustrated* 4:42 which is determined by Garay as *Catasetum fimbriatum* Lindl., a species distinct in many characters, and from southeastern Brazil. The plant from Venezuela probably is the hybrid between *C. macrocarpum* and *C. longifolium*. This plant was described by Reichenbach f. as *Catasetum tapiriceps*.

CONCLUSIONS

The presence of the massive population of catasetums at Dawa on Lake Tapakuma is obviously a temporary one. That is, within a matter of a few years the rotting trees will have fallen into the lake and will be gone. The sides of the lake probably will return to a situation resembling the river banks, and the conditions which have made possible the hybridization of the three species of *Catasetum* will have been removed. With conditions returned to normal, selection pressure will very likely eliminate most of the hybrids and the backcrossed individuals which approximate the hybrids.

The long range effect of the hybridization may be considerably more important. The results of natural hybridization between populations of plants have been discussed at great length, principally by Anderson (1953), Stebbins (1950), and their followers. There is no need at this time to go into this general effect, other than to say that hybridization between species which are relatively distinct followed by subsequent backcrossing to any of the parental types will introduce whole blocks of genetic material from one species to another. The end result is the addition of considerable variation into the various populations. When conditions return to normal, several things may happen. First, the intermediates and the hybrids may be eliminated. Under very rare circumstances a new kind of condition in the habitat may make it possible for a new and different species to develop which is reproductively isolated from any of the other species in the populations. The most frequent effect, however, is for variability to be incorportated into the existing species. This variability can be acted upon by selection and over a period of time will probably stabilize so that a species has a recognizable series of characteristics in a given population. If this introgressive hybridization followed by subsequent return to natural conditions occurs in several instances in widely separated geographical areas, the resulting populations — after stabilization — will probably differ one from another. The differences will depend on the presence of certain kinds of variability and the selection which has caused particular forms to be stabilized. This may explain the variability from population to population encountered in the broad geographical ranges of such species as *C. macrocarpum*, *C. discolor*, and many other species of *Catasetum*.

Quite distinctive forms may develop. For example, in Venezuela, there is a form of *C. discolor* which has been described as *C. roseo-album* (Hook.) Lindl. This form does not grow terrestrially in sandy areas nor in the savannah, but it grows epiphytically. The inflorescence arches and hangs somewhat pendantly. The flowers are generally much smaller and could utilize *Euglossa chlorosoma* as its pollinator. The floral fragrance is the same as that of typical *C. discolor*. The flower structure, however, is quite similar to that of the other forms of *C. discolor*, but it is rosier pink in color and the lacerations surrounding the margin of the lip are much larger. This form may have resulted from the action of selection on particularly variable populations resulting from hybridization between *C. discolor* and *C. longifolium*.

TABLE I. Male Euglossine bees captured at flowers of the four species of *Catasetum* at Tapakuma.

	Euglossa augaspis	*E. chlorosoma*	*E. cognata*	*E. cordata*	*E. liopoda*	*E. mixta*	*E.* sp. (UM 10)	*E.* sp. (RD 1215)	*Eulaema bombiformis*	*E. cingulata*	*E.* aff. *luteola*	*E. meriana*	*E. mimetica*	*E. peruviana*
Catasetum thompsonii	1		1	1	19	1	1	3		*69				
Catasetum discolor		*9							9				1	
Catasetum longifolium									1	2		5		
Catasetum macrocarpum									8	30	1			1

* = not effective as pollinators

SUMMARY

Hybridization has taken place between three of the four species of *Catasetum* in the circumstances described above due to manmade changes in the ecology and the habitat. These three species *(C. macrocarpum, C. discolor,* and *C. longifolium)* appear to be isolated ecologically under normal circumstances, and hybrids, even though crossing may occur, simply do not have an opportunity to become established because of the lack of a hybrid habitat. The fourth species, *C. thompsonii*, does not hybridize with the others because of its size and the consequent attraction of much smaller bees of the genus *Euglossa* rather than the large bees of the genus *Eulaema*. *Catasetum thompsonii* appears to be strongly isolated mechanically and partially isolated ethologically, for the fragrance does attract one species of *Eulaema*. The phenomenon witnessed here is apparently common to the genus *Catasetum* throughout much of its range. All the species are genetically compatible, and ecological or spatial isolation maintains the integrity of the species. Where ecological conditions keep the species separate, catastrophic events such as the manmade development of the lake at Tapakuma may

alter the conditions so that hybrids can occur. Such catastrophic events could be envisioned as occurring naturally by the damming of river systems due to landslides. The results would probably be the same. This is a different kind of situation from that discussed in Dodson (1962) where in western Ecuador, *C. platyglossum* and *C. macroglossum* hybridize to form an immense hybrid swarm. There the isolating mechanism was apparently spatial. When the habitat changed as a result of drying conditions, the two species migrated close enough together to begin to form natural hybrids. The hybrids still exist and probably will continue to exist over a long period of time. The significance of short term, massive hybridization similar to that at Dawa is the injection of variability into the parental species.

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