

CATASETUM × *DUNSTERVILLEI* (ORCHIDACEAE: CATASETINAE), A NATURAL HYBRID CONFIRMED BY ARTIFICIAL HYBRIDIZATION

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Abstract. The parentage of *Catasetum* × *dunstervillei*, a natural hybrid or nothospecies, formally proposed in 1989 from the vicinity of Puerto Ayacucho, Amazonas state, Venezuela, was confirmed *via* artificial hybridization. The originally proposed putative parents were *Catasetum pileatum* and *C. discolor*. In nature, both species are pollinated by the same male Euglossine bees, *Eulaema meriana* and *E. cingulata*, and the two orchids are found in close proximity and have overlapping flowering seasons: the hybrid is relatively common. The artificial hybrid took 44 months (January 2014–September 2017) from the time seeds were planted to the first flowering.

Resumen. El parentaje de *Catasetum* × *dunstervillei*, un híbrido natural o notoespecies propuesto en 1989 de plantas procedentes de las cercanías de Pto. Ayacucho, Amazonas, Venezuela, se confirmó *via* hibridación artificial. Las especies parentales putativas originalmente propuestas fueron *Catasetum pileatum* y *C. discolor*. En la naturaleza, las dos especies son polinizadas por las mismas abejas euglosinas, *Eulaema meriana* y *E. cingulata* y son simpátricas; además, sus periodos de floración se solapan por lo que el híbrido natural es relativamente común. El híbrido artificial tomó 44 meses (enero 2014 hasta septiembre 2017) desde el momento en que se sembraron las semillas hasta la primera floración.

Keywords: *Catasetum* × *dunstervillei*, natural and artificial hybridization, Euglossine bees, Orchidaceae

The monumental works published in six volumes by G. C. K. Dunsterville and L. A. Garay in their series *Venezuelan Orchids Illustrated* (1959–1976), and in five volumes by E. Foldats for the Flora of Venezuela (1969–1970), have long served as basic references for the orchid flora of northern South America.

These were the references available in the early 1980s when the senior author initiated a study of all *Catasetum* Rich. species and their male Euglossine bee pollinators in the vicinity of Puerto Ayacucho, the capital of Amazonas state, Venezuela. It was soon evident that there were many *Catasetum* species in the study area, often occupying the same habitat, that several were pollinated by the same male euglossine bees, and that they had overlapping flowering seasons: the chances for natural hybridization were high. Eventually, two of the authors (GAR-G. and GC) formally proposed a number of natural hybrids or nothospecies from this region (Romero and Carnevali, 1989, 1990, 1991a–b, 1992).

The first clue that helped decipher the hybrid treated here came from R. L. Dressler in a review of Dunsterville and Garay's *Venezuelan Orchids Illustrated*.

Dressler (1968) suggested that a drawing published as *Catasetum fimbriatum* (Morren) Lindl. (Dunsterville and Garay, 1966: 43; 1979: 85; Fig. 1; also partially shown in Foldats, 1970, IV: 82) was actually a hybrid between *Catasetum discolor* (Lindl.) Lindl. and *Catasetum pileatum* Rchb.f. (i.e., “*Catasetum discolor* Lindl. × *pileatum* Rchb.f.”; Dressler, 1968: 131).

It was evident that the plant drawn by Dunsterville was different from *Catasetum fimbriatum*, a species known from southern Brazil and northern Argentina (Fig. 2). The name actually had been suggested to Garay by C. Schweinfurth in 1963 (according to a note in Schweinfurth's handwriting on Garay's copy of the drawing at AMES). The plant that Dunsterville illustrated was collected in the upper Orinoco river in the early 1960s by Pablo Anduze Díaz (1902–1989), a renowned Venezuelan medical doctor, entomologist, and ethnologist, twice governor of Venezuela's Amazonas state (1960–1963 and 1974–1976), and member of the expedition that found the sources of the Orinoco in 1951. According to Dunsterville, the sepals were “pale green suffused with pink, particularly on the back,” the petals “pale green, suffused with pink at apex,” the labellum “...underside surface light green, upper surface light brown inside ‘cup,’ bordered on apical section of cup by pale cream with a soft-textured surface. Reminder (*sic*) of surface greeny-yellow with some wax-shiny pinkish suffusion on margin near base. Margin of cup tends to be yellow.” Both the column and anther were “white.” Dunsterville also pointed out that “it was very noticeable that the flowers appear in groups of three with a distinct gap along the rachis before the next group of three pedicels arise” (from Dunsterville's original notes at AMES; an edited description was published in Dunsterville and Garay, 1966: 42).

The senior author eventually collected both parents (Fig. 3–4) and the hybrid (Fig. 5) in the vicinity of Puerto Ayacucho, although *C. discolor* was extremely rare in the

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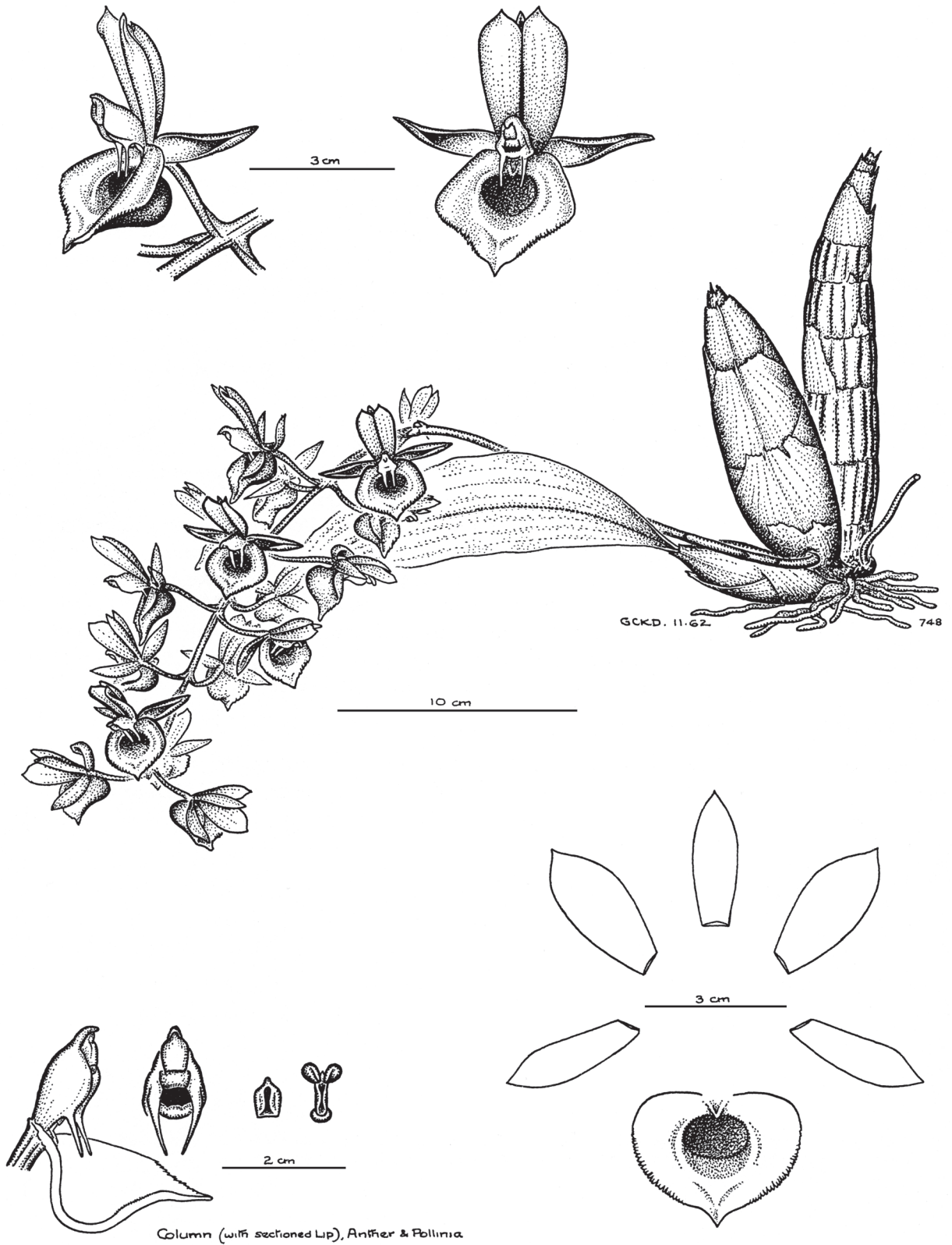


FIGURE 1. *Catasetum x dunstervillei* G.A.Romero & Carnevali originally published as *Catasetum fimbriatum* (Morren) Lindl. (1850). Drawing by G. C. K. Dunsterville based on *Dunsterville 748* (apparently not preserved; photostat copy of original drawing at AMES).

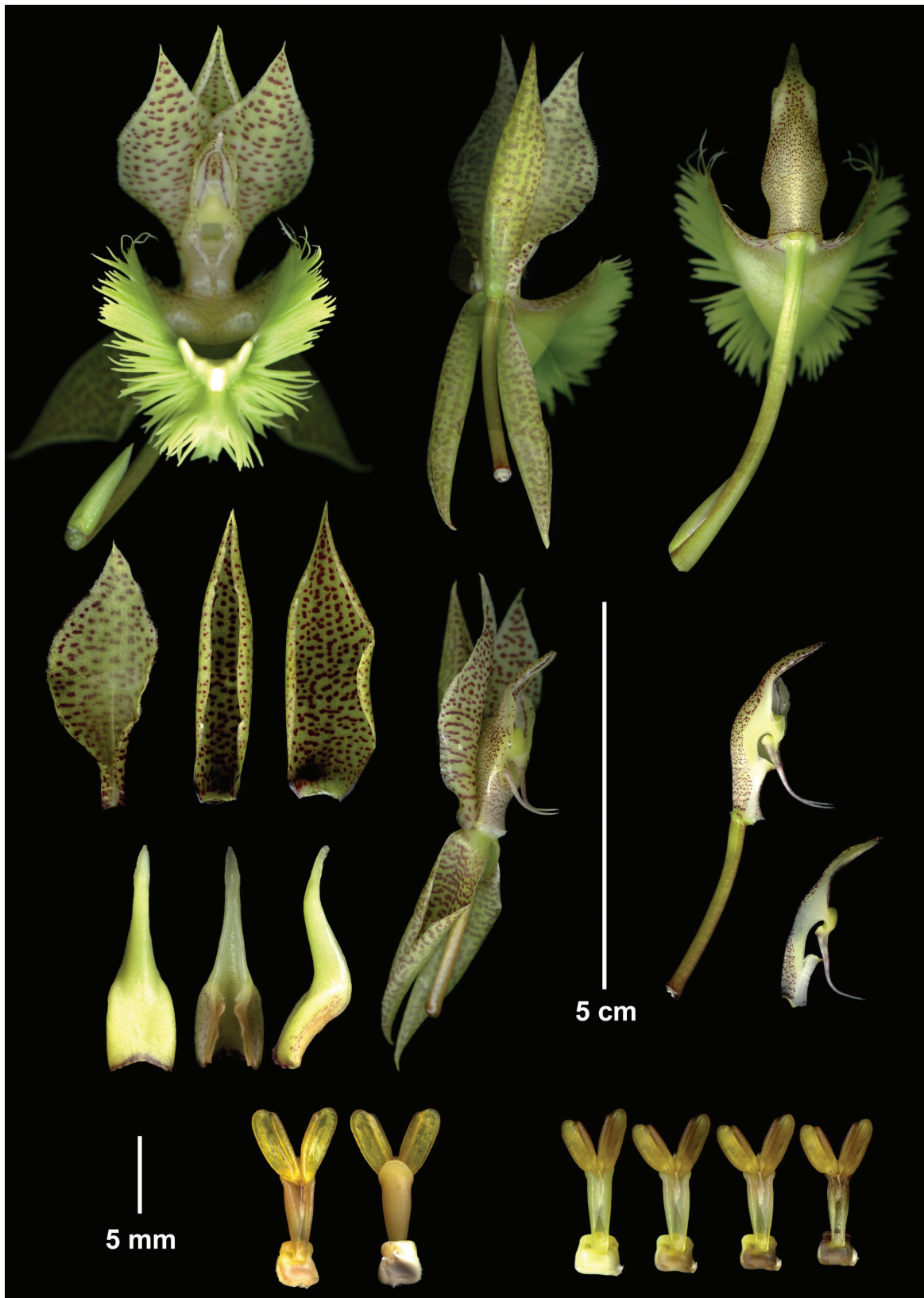


FIGURE 2. *Catasetum fimbriatum* (Morren) Lindl. Scan and composition by G. A. Romero-González based on a plant cultivated by D. Fulop at Harvard University (fragments at AMES *sub* Romero *s.n.*).

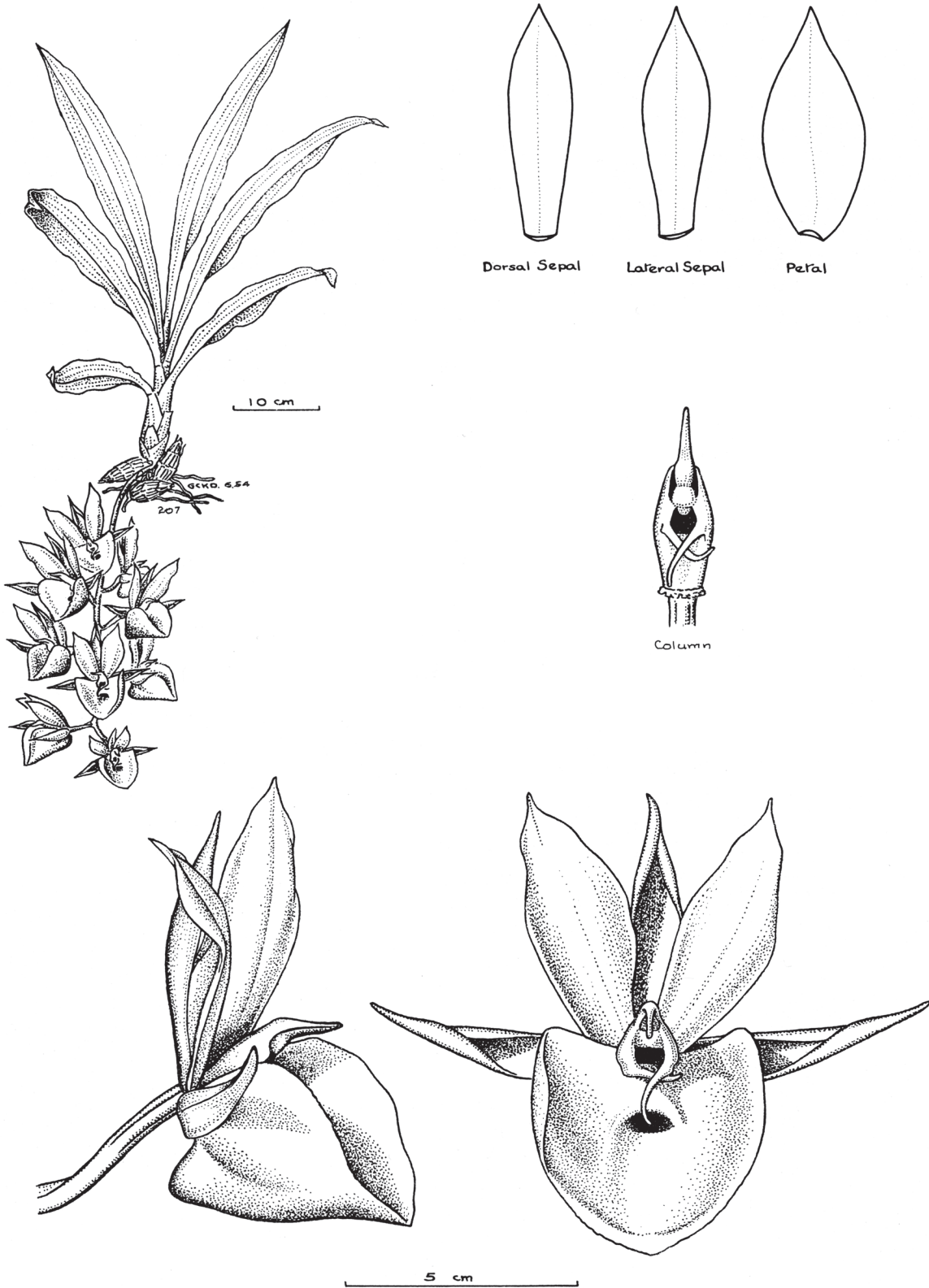


FIGURE 3. *Catasetum pileatum* Rchb.f. Drawing by G. C. K. Dunsterville based on *Dunsterville 207*, apparently not preserved, photostat copy of original drawing at AMES.

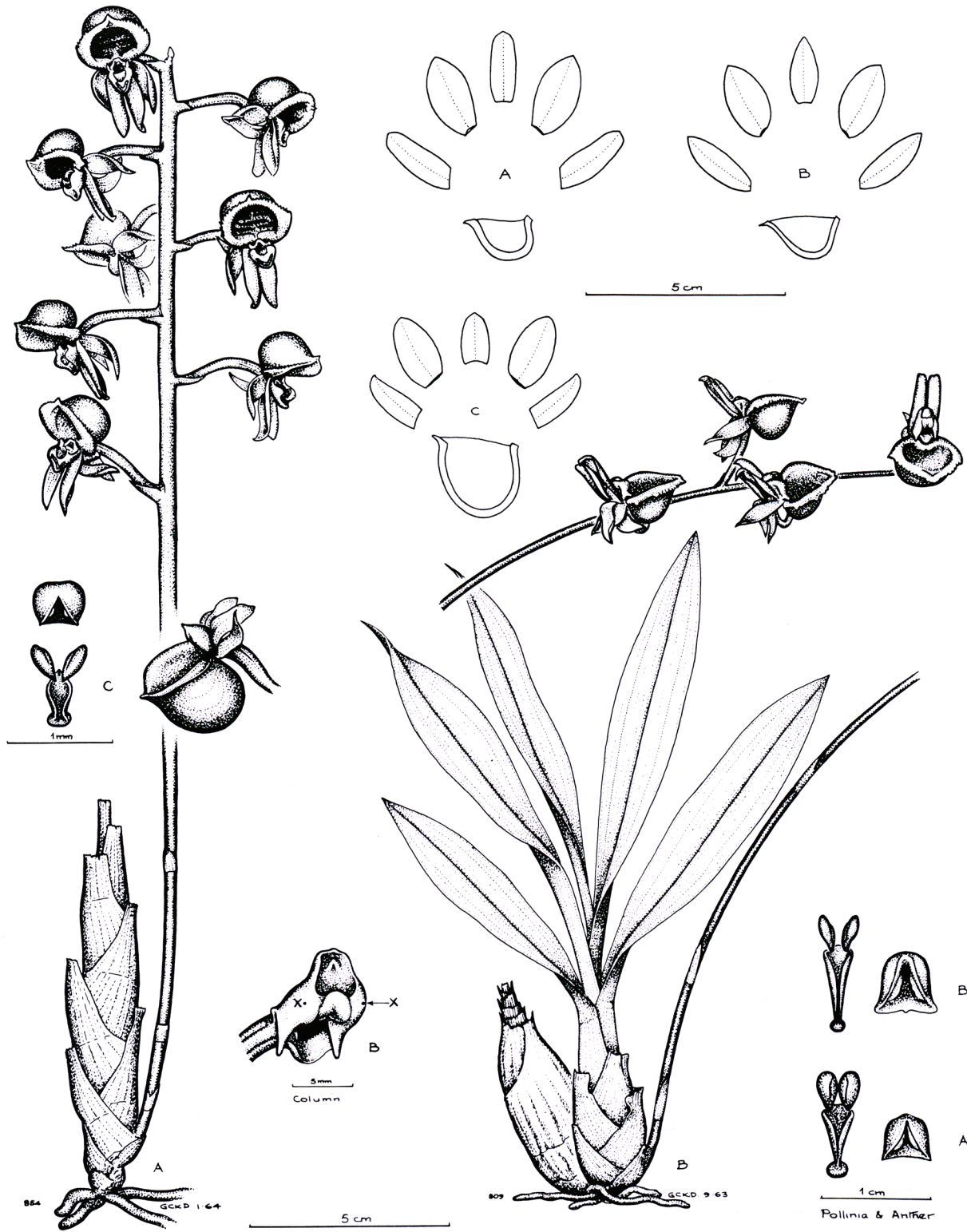


FIGURE 4. *Catasetum discolor* (Lindl.) Lindl. Drawing by G. C. K. Dunsterville based on *Dunsterville* 854, apparently not preserved, photostat copy of original drawing at AMES.



FIGURE 5. *Catasetum x dunstervillei* G.A.Romero & Carnevali. Photographed by G. A. Romero-González.

region, usually found growing in sandy soils. The natural hybrid was formally proposed by Romero and Carnevali (1989; see also 1991a). Plants of this nothospecies subsequently have been collected several times by orchid aficionados and have been in horticultural orchid collections for the past twenty years. They have also appeared from time to time in orchid shows in Venezuela and elsewhere.

The pollinators of *C. pileatum* are *Eulaema cingulata* (Fabricius), *E. meriana* (Olivier), and *E. nigrita* Lepelletier (Romero and Carnevali, 1990; Fig. 6A–B; *E. nigrita* is not shown in Fig. 6 but it does appear in Romero and Carnevali, 1990: 1219, lower figure); the pollinators of *C. discolor* are *Eulaema bombiformis* (Packard), *E. cingulata*, and *E. meriana* (Romero and Carnevali, 1991b; Fig. 6C–D).

These two *Catasetum* species, however, employ entirely different pollination mechanisms.

In *Catasetum pileatum*, bees approach the front of the resupinate male flower (Fig. 7A), flying rapidly toward and away from the flower, eventually touching the triggering antennae, whether while in flight or after crawling on the labellum, triggering the ejection of the pollinarium, which is placed always on the dorsum of the bee's abdomen (Fig. 6A–B). The “loaded” bees then fly to the non-resupinate female flower (Fig. 7B), which they enter upside-down. As the bees moves in and out of the deep labellum of the female flower, the pollinarium flexes, and eventually a pollinium is inserted in the stigmatic slit. It should be emphasized that bees are attracted to *Catasetum* flowers by particular fragrances, and that their movements inside *Catasetum* flowers have as ultimate goal the collection of these fragrances (Dodson, 1962).

In *Catasetum discolor*, bees approach the non-resupinate male flowers (Fig. 8A) and eventually land on the column; when the pollinarium is ejected, it is placed on the ventrum of the bee's thorax (Fig. 6C–D). The “loaded” bees then find the equally non-resupinate female flower, eventually landing, again, on the column, and after moving in and out of the shallow labellum of the female flower, a pollinium is inserted in the stigmatic slit.

It is more likely that in nature the pollen donor of the natural hybrid is *Catasetum discolor*. Firstly, it is unlikely that a bee carrying a pollinarium of *C. pileatum* will try to enter the shallow labellum of the female flower of *C. discolor* upside down (the only way the “loaded” bee could pollinate it, given that the pollinarium is on the dorsum of the bee); furthermore, the pollinia of *C. pileatum* is slightly too large to enter the stigma slit of the female flower of *C. discolor*. Manually, of course, a pollinium of *C. pileatum* can obviously be inserted forcefully in the stigmatic slit of a female flower of *C. discolor*, as was the case in the artificial cross we present here. In nature, this nothospecies is quite variable in color (ranging from pearly white to yellow suffused with red), and it has considerable horticultural value.

In the artificial hybrid the pollen donor was *Catasetum pileatum* (versus most likely *C. discolor* in the nothospecies). This difference did not seem to alter the resulting floral morphology: the two hybrids are undistinguishable (Fig. 5 versus Fig. 9). We perhaps would have expected differences,

as in plants all the extra-nuclear DNA (that in the chloroplasts and mitochondria) is strictly maternally inherited.

The artificial cross was performed by one of us (SPR), and the seeds were planted, *in vitro*, by another of the authors (REL). The seeds were planted January 2014 and the first flowering plants appeared in September 2017 (Fig. 9).

Of the parents of *Catasetum x**dunstervillei*, *C. discolor* has by far the widest distribution: the Guianas (Cayenne, Surinam, and Guyana), the Venezuelan Guayana, and Colombia (Carnevali et al., 2007), and perhaps occurs in Bolivia and Brazil. *Catasetum pileatum*, however, is restricted to the Orinoco river basin in Colombia and Venezuela and the upper Rio Negro basin in Brazil, Colombia, and Venezuela. The hybrid has been reported from Colombia (Bonilla et al., 2016), Venezuela (herein and in literature cited), but it surely occurs in adjacent Brazil, perhaps in the upper Rio Negro basin.

It is curious that another natural hybrid, *Catasetum x**roseoalbum* (Hook.) Lindl. (Fig. 8B), most certainly between *Catasetum discolor* and *C. longifolium* Lindl. (Fig. 10), is by far more common than *Catasetum discolor* in the area where the authors have found plants of *C. x**dunstervillei*, both growing as an epiphyte, more commonly on palms or, rarely, as a terrestrial plant growing on granite outcrops (Romero and Carnevali, 1989, 1991b).⁶ The dry pollinaria from this natural hybrid cannot be distinguished from those of *C. discolor*. This natural hybrid or nothospecies (i.e., between *Catasetum pileatum* and *x**C. roseoalbum*), was already suggested by Villegas (2002), providing a drawing and two photographs, as well as photographs of the putative parents. It would be interesting to artificially cross this other nothospecies (i.e., *Catasetum x**roseoalbum*) with *C. pileatum* to test Villegas's hypothesis.

Here we would like to add one final comment. Villegas (2002: 168) argued whether *Catasetum x**roseoalbum* was a natural hybrid or a “valid species” (“especie válida,” perhaps given “...Categoría de especie”; Villegas, 2002: 168).

First of all, *Catasetum longifolium* Lindl., which Villegas (2002: 168) doubted existed in the Colombian llanos, is a “cryptic” species, found close to the crown of *Mauritia flexuosa* palms, some of which can be up to 40 m tall; the plant of *C. longifolium* are pendent and the leaves, as the epithet implies, are long and also narrow and, from a distance, hard to distinguish from the leaves of the palm. We suspect that the distribution of *Catasetum longifolium* in northern South America, especially in Colombia, has been underestimated.

Second of all, the distinction between a “stable” nothospecies (which *C. x**roseoalbum* seems to be one) and a “species” is blurred, given that a large proportion of plant and animal species certainly seem to be of hybrid origin (Arnold, 1997; see also Lamichhaney et al., 2017). Most likely, stable natural hybrids (with a reticulate ancestry) create or invade their own, novel “adaptive peaks,” modeled by genetic drift or by local selective pressures acting over novel character combinations inherited from the parental taxa, eventually following independent evolutionary histories.

⁶ *Catasetum x**roseoalbum* in fact, displaces one of the parents around Puerto Ayacucho, *C. longifolium*, from its typical habitat on *Mauritia flexuosa*. Nearby, in the basins of the Samariapo and Sipapo rivers, as well as in the upper Río Negro basin, in the San Miguel river, where *Catasetum longifolium* is much more prevalent, always on *M. flexuosa*, *C. x**roseoalbum* is confined to other palms and rotten limbs of miscellaneous trees, and, as mentioned before, rarely found growing terrestrially on granite outcrops.

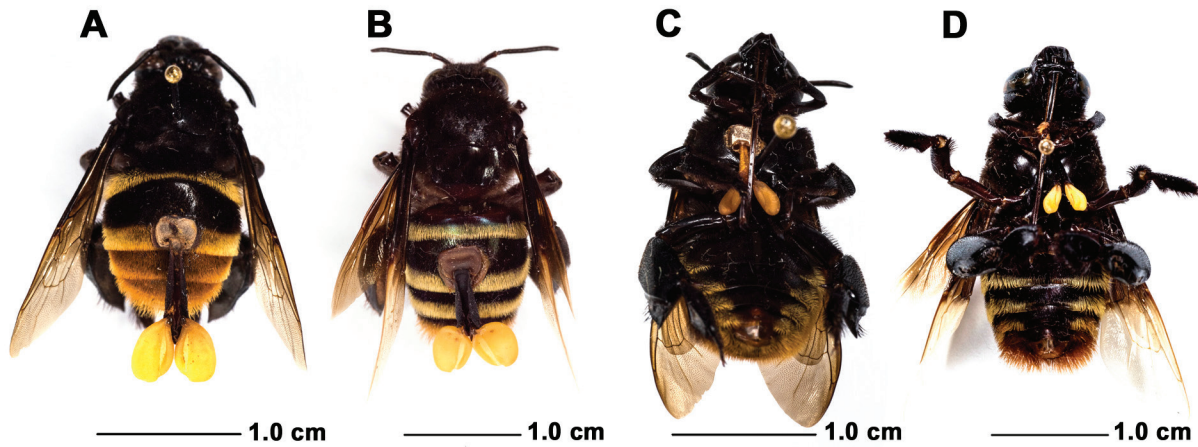


FIGURE 6. Pollinators of *Catasetum* species. A, *Eulaema cingulata* (Fabricius) bearing a pollinarium of *Catasetum pileatum* Rchb.f.; B, *E. meriana* (Olivier) bearing a pollinarium of *C. pileatum*; C, *E. cingulata* bearing a pollinarium of *C. discolor* (Lindl.) Lindl.; D, *E. meriana* bearing a pollinarium of *C. discolor*. The round, gold object in A, C, D, is the head of the entomological pin holding the bees; in C and D, the tongue or proboscis of the bees can be seen laying on top of part of the pollinaria, running along the axis of the bees from the head to the abdomen. Photographs by G. A. Romero-González based on bees in his personal collection.

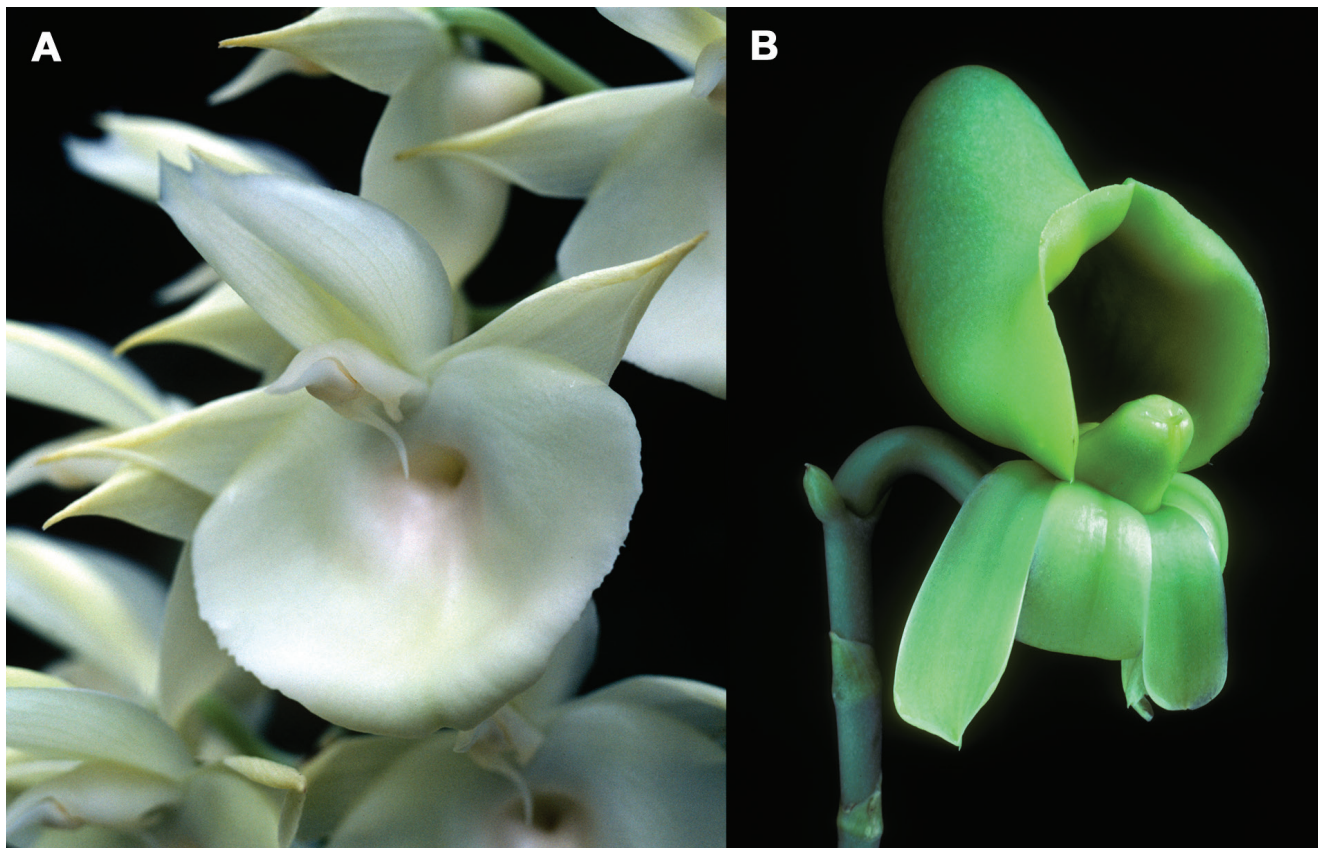


FIGURE 7. *Catasetum pileatum* Rchb.f. A, staminate (male) flower; B, pistillate (female) flower. Photographs by G. A. Romero at approximately the same scale (for precise scale, see figure 3).



FIGURE 8. *Catasetum* species and nothospecies. A, *Catasetum discolor* (Lindl.) Lindl., staminate (male) flower; B, *Catasetum* xroseo-album (Hook.) Lindl., staminate (male) flower. Photographs by G. A. Romero at approximately the same scale (for a precise scale, see figure 4).

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FIGURE 9. *Catasetum x dunstervillei* G.A.Romero & Carnevali, product of the artificial cross. Photographed by R. E. López.

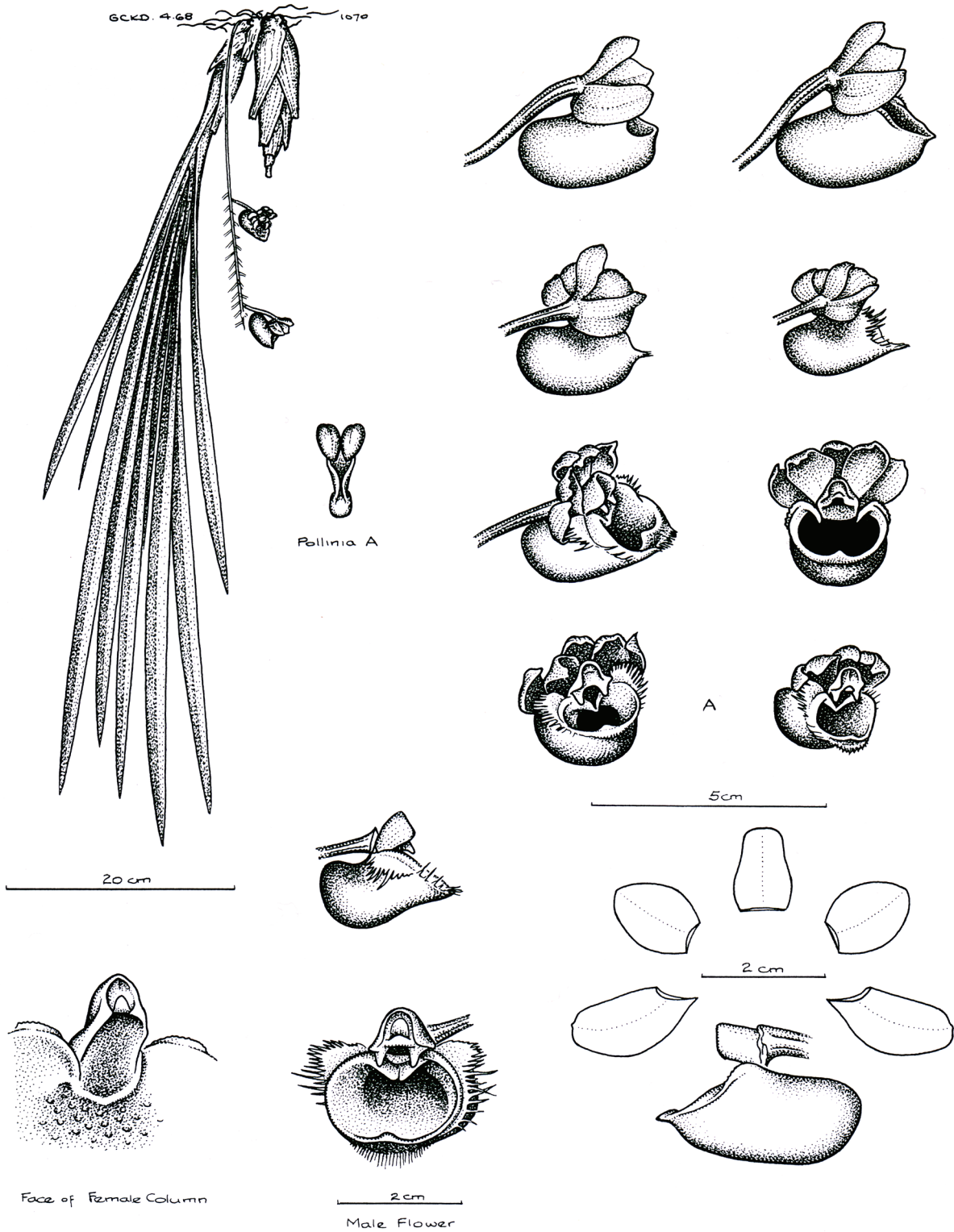


FIGURE 10. *Catasetum longifolium* Lindl. Drawing by G. C. K. Dunsterville based on *Dunsterville 1070*, apparently not preserved, photostat copy of original drawing at AMES.