

# CHARLES DARWIN ON CATASETINAE (CYMBIDIEAE, ORCHIDACEAE)

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**Abstract.** The background and accomplishments of Darwin's work on Catasetinae are analyzed, and issues that he and others did not resolve are discussed in detail. The segments on Catasetinae published by Darwin in the *Annals and Magazine of Natural History* in September 1869 and in the second edition of his orchid pollination opus (as Catasetidae) published in 1877, as well as his paper "On the three remarkable sexual forms of *Cataseum tridentatum*," all including the text, plates, and notes, are presented in three appendixes.

**Keywords:** Catasetinae, Catasetidae, Darwin, Orchidaceae, pollination

If I have seen further it is by standing on the shoulders of giants.  
(Isaac Newton in a letter to Robert Hooke, dated 15 February 1676)

In investigating the obscure subject of generation, additional light is perhaps more likely to be derived from a further minute and patient examination of the structure and action of the sexual organs in Asclepiadeae and Orchideae, than from that of any other department either of the vegetable or animal kingdom. (Brown, 1833)

I know of no individual of this family [Orchidaceae] which has flowers so splendid and so curious.  
(Hooker, 1824, referring to what he had described as *Catasetum tridentatum*)

The most singular Orchideous plant which has yet been seen in a cultivated state...  
(John Lindley, 1824, referring to what he had described as *Catasetum claveringii*<sup>2</sup>)

But what is impossible in nature? (John Lindley, 1843b, referring to sexual forms of *Cycnoches* Lindl.)

Who would have been bold enough to surmise that the propagation of a species should have depended on so complex, so apparently artificial, and yet so admirable an arrangement?  
(Darwin, 1862a, referring to flowers of *Cataseum tridentatum* Hook.<sup>2</sup>)

Under-sampling—in only one time slice and in one locality—can give a critically false impression of what's out there—the extent of diversity, the full quantitative and qualitative range in morphological features, and life stories and processes. (Pridgeon, 2003)

Charles Darwin's two articles and the two editions of his book on the pollination of Orchidaceae were fundamental contributions to our understanding of this perhaps most diverse of plant families. Prior to his publications (Darwin, 1862a,b, 1869, 1877a), orchids were mostly treated "morphologically," with little offered on other biological aspects of the family. There had been many publications about their pollination, some accurate (most influential to Darwin appear to be Sprengel, 1793, and Brown, 1833), some not so accurate and speculative. It was Darwin, ultimately, who carefully compiled the scattered literature and established a wide network of collaborators in England and throughout the world, especially from the Neotropics (Table 1). Most important of all, he introduced new methods—namely, careful and detailed experimentation with live plants and flowers, and

in the case of subtribe Catasetinae, with flowers preserved in spirits, an effort that would have no parallel in Orchidaceae until the 1960s, when there was a resurgence of studies on orchid pollination biology (Dodson, 1962a,b; Dodson and Frymire, 1961; Dodson and Hills, 1966; Van der Pijl and Dodson, 1966; Vogel, 1963, 1966, 1990; Dressler, 1968).<sup>3</sup> Unlike most of his contemporaries, Darwin examined the structure of orchid flowers in terms of homologies (e.g., when describing the male flowers of *Cataseum tridentatum* as "[a] deep chamber, which from its homological relations must be called the stigmatic chamber"; 1877a: 152), a critical approach needed to properly interpret the flowers of this group.

Darwin's orchid publications, particularly the last edition of his book (Darwin, 1877a), have been praised lately (Beatty, 2006; Singer, 2009; Bellon, 2009; Cameron, 2011;

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<sup>2</sup>These two species are currently considered synonyms of the earlier *Catasetum macrocarpum* Rich. ex Kunth.

<sup>3</sup>Also noteworthy are Oakes Ames's publication on the pollination of orchids through pseudocopulation (1937) and the rarely cited one on the pollination of *Coryanthes* (1941).

TABLE 1. Botanists and naturalists who interacted with Darwin in his studies of *Catasetinae* (in alphabetical order).<sup>1</sup>

IN ALPHABETICAL ORDER
Hermann Crüger (1818–1864): from 1857 until his death served as a government botanist and director of the botanical garden in Port-of-Spain, Trinidad; exchanged correspondence with Darwin
William J. Hooker (1775–1865): worked closely with Lindley in early work on <i>Catasetinae</i>
Joseph D. Hooker (1817–1911): son of William J., Darwin’s closest friend, and a supplier of orchid flowers
John Lindley (1799–1865): an early expert on <i>Catasetinae</i> , who identified some of the orchids that Darwin examined
Johann F. T. Müller (a.k.a. Fritz Müller and Müller-Desterro) (1821–1897): corresponded with Darwin; Müllerian mimicry is named after him
Robert A. Rolfe (1855–1921): a gardener at the Royal Botanic Gardens, Kew, and later in his life the leading expert on Orchidaceae
Sigismund Rucker (ca. 1809–1875): a private and successful orchid grower who supplied Darwin with flowers of <i>Catasetinae</i>
Robert H. Schomburgk (1804–1865): an explorer, naturalist, collector of plant and animal museum samples in northern South America; studied <i>Catasetum</i> in the field and sent <i>Catasetum</i> samples in spirit to the Linnean Society of London that were examined by Darwin and the bases for one of his publications (Darwin, 1862a)
James Veitch, Jr. (1792–1863): an orchid grower, member of the famous Veitch dynasty, who supplied Darwin with flowers of <i>Catasetinae</i>

<sup>1</sup> For most entries, see Cribb (2010) for more details.

Endersby, 2016), and a partial analysis of the contents of the 1877 edition was also published recently (Edens-Meier and Bernhardt, 2014). Notwithstanding, his treatment of *Catasetinae* (as “*Catasetidæ*”) has not been the focus of any recent publications, other than having been used to point out Darwin’s favorite orchids, “*Catasetidæ*” (Romero, 1990; Pérez-Escobar, 2016; Pérez-Escobar et al., 2016, 2017). As further testimony to his special interest in *Catasetinae*, a male flower of *Cycnoches ventricosum* Bateman illustrated the cover of the first edition of his orchid pollination book (Darwin 1862b; Fig. 1).

The purpose of this essay is primarily to reprint Darwin’s texts on *Catasetinae* (see Appendixes I–III), to present notes on his accomplishments, and to clarify issues that he and others did not resolve. There exists a trove of additional information on Darwin’s work on *Catasetinae* in his compiled correspondence, which falls outside the scope of this essay.<sup>4</sup>

*Catasetinae* is one of 11 currently recognized subtribes of tribe Cymbidiidae (Cribb, 2009; Li et al. 2016), in subfamily Epidendroideae of Orchidaceae. It currently includes eight genera (Table 2). However, Darwin’s *Catasetinae* included

TABLE 2. Approximate current number of species of “core” *Catasetinae*, number known by 1860, and number examined by Darwin (1877a), by genera.<sup>1</sup>

	CURRENT SPECIES	SPECIES KNOWN IN 1860	SPECIES THAT DARWIN EXAMINED
<i>Catasetum</i> Rich. (1822)	130	51	6
<i>Clowesia</i> Lindl. (1843) <sup>2</sup>	7	2	0
<i>Cycnoches</i> Lindl. (1832)	34	10	1
<i>Dressleria</i> Dodson (1975) <sup>2</sup>	13	0	0
<i>Mormodes</i> Lindl. (1836)	80	20	2

<sup>1</sup> An approximation of the number of species currently known was taken for *Catasetum* from Romero-González (2009; number reported most likely under-represents the numbered of published species); for *Cycnoches* from Pérez-Escobar (2016) and Gerlach and Pérez-Escobar (2014); for *Clowesia* from Tamayo Cen (2018); for *Dressleria* from Hills (2012) and Hills and Weber (2012); and for *Mormodes* from Salazar et al. (2016).

<sup>2</sup> Many species of *Clowesia* and *Dressleria* remained in the synonymy of *Catasetum* until Dodson (1975) revived *Clowesia* and proposed *Dressleria*. Notwithstanding, Darwin does not appear to have examined flowers of these two genera.

<sup>4</sup>See <https://www.darwinproject.ac.uk>

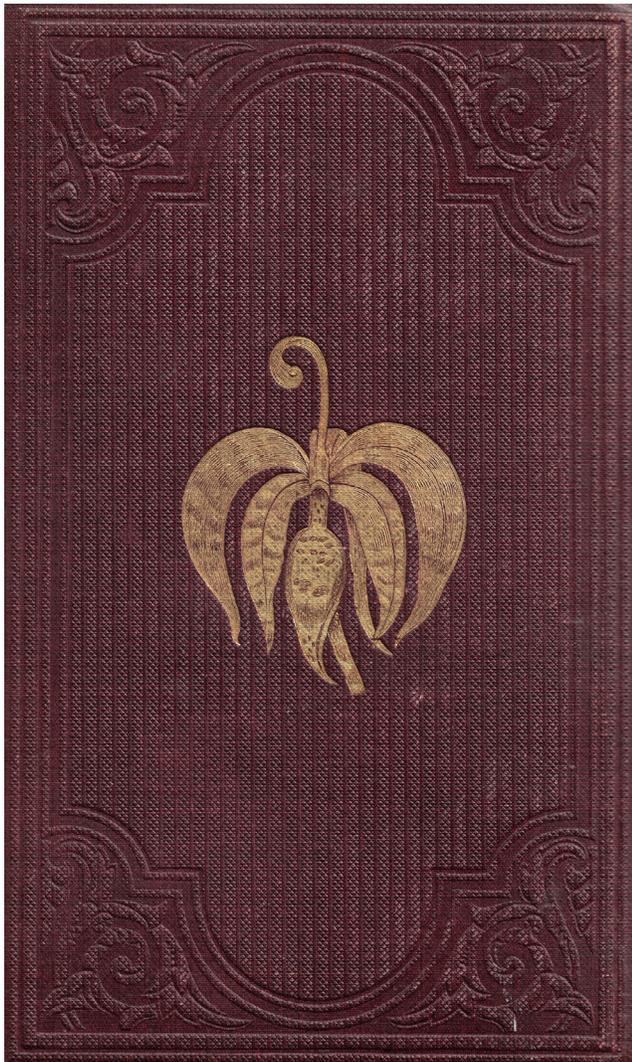


FIGURE 1. Book cover of Darwin's first edition (Darwin, 1862b), showing a male flower of *Cycnoches loddigesii* Bateman (positioned upside down). From a copy in the author's personal library.

only *Catasetum* Rich. ex H.B.K., *Cycnoches* Lindl., and *Mormodes* Lindl., genera currently included in "core" Catasetinae (e.g., Salazar et al., 2016). Core Catasetinae includes two additional genera, *Clowesia* Lindl. and *Dressleria* Dodson; the flowers of these group are characterized by the motility—that is, the active movement—of their pollinaria upon discharge (see Table 3 for terminology).<sup>5</sup>

Darwin faced a daunting challenge when trying to decipher flower function of Catasetinae. Unlike other orchid flowers he had examined before, both in the field and from cultivated plants, those of *Catasetum*, *Cycnoches*, and *Mormodes* had no parallel in Orchidaceae: the flowers borne by plants of these three genera are relatively large, exhibit unusual morphology (Fig. 3–4), have extremely mobile pollinarium discharge mechanisms, and, as Darwin later

determined, could be male (pollen bearing) or female (ovule bearing), with intermediate, nonfunctional ones in between (shown for the first time in Lindley, 1837; see Fig. 5) and, most extreme of all in Orchidaceae, exhibiting in some cases dramatic sexual dimorphism (Romero and Nelson, 1986; Fig. 6). Judging from some of the quotes cited in the beginning of this essay, other authors shared his fascination with Catasetinae.

Perhaps less critical, the names of the species, particularly in *Catasetum*, had not been well established. *Catasetum* Rich. ex Kunth had been proposed by K. (Carolus) S. Kunth in 1822 (Kunth, 1822: 330), on the basis of notes of Louis C. M. Richard (1754–1821); two species, *C. maculatum* Kunth and *C. macrocarpum* Rich. ex Kunth, were described in the same publication without illustrations (Kunth, 1822: 331). Later it was revealed that the descriptions of both *C. maculatum* and *C. macrocarpum* were largely based on rather crude sketches ("Descriptio ex schedis Humboldtianis" and "Descriptio excerpta ex schedis Richardianis," respectively; Humboldt et al. 1825: 157–158).

In the meantime, William J. Hooker published *Catasetum tridentatum* in 1824 (Fig. 7), adding,

... it was impossible to read the character given by M. Richard, of *Catasetum*, in the 1st volume of *Synopsis Plant. Æquinoct. Orbis novi* of HUMBOLDT and KUNTH, without being satisfied that it must belong to that genus. The species there given is the *Catasetum maculatum* of New Grenada... a second individual, afterwards noticed, is the *C. macrocarpum* of Richard's MSS. with blossoms of a deep purple color, and fruit four or five inches long. No figures exist of either of these (Hooker, 1824).

Hooker's species was published in March 1824, but the plates illustrating *Catasetum maculatum* Kunth and *C. macrocarpum* Rich ex Kunth did not appear until 24 December 1824 and 21 February 1825, respectively (in volume 7, plates 630 and 631 of *Nova Genera et Species Plantarum*; see Fig. 8 herein for plate 631).

Despite doubts expressed by Lindley (1824), comments about the validity of *Catasetum tridentatum* and his own *C. claverlingii* (e.g., that they may actually be synonyms of *C. macrocarpum*), and further comments by Crüger (1864), the name *C. tridentatum*, instead of *C. macrocarpum*, was used in the orchid literature until Rolfe (1890) formally reestablished the latter.

A large number of exotic orchids were cultivated in England in the 1830s, including several representatives of Catasetinae. These plants were examined, studied, described, and reported in the literature, at least morphologically, by William J. Hooker (1785–1865) and John Lindley (1799–1865) (for these two authors, see Literature Cited).

Besides the already described and known *Catasetum*, Lindley proposed two additional genera in the same

<sup>5</sup>The active movement of the pollinarium in these five genera differs tremendously, and varies from a rapid and total detachment from the column in *Catasetum* subgenus *Catasetum* to a simple flipping of the viscidium in *Clowesia*. The pollinarium itself moves hygroscopically in some genera, such as *Cycnoches* and *Mormodes*: in these two genera, the pollinarium curls tightly upon discharge, later straightening up as it becomes dry (Fig. 2). In *Mormodes*, plants can bear flowers whose columns move after the pollinaria are discharged (see fig. 1E in Salazar et al., 2016).



FIGURE 2. *Cynoches* pollinarium movement by hygroscopy. The complete movement from curled to erect depends on ambient relative humidity; in this case, at about 60%, it took approximately 6 minutes. Based on *Tamayo Cen 127* (CICY). Photographs by the author.

TABLE 3. A glossary of floral terms in Catasetinae with equivalency in Darwin's writings (1862a, 1862b, 1877).<sup>1</sup>

Antenna (antennae)	A filamentous process of the rostellum, two per flower, that triggers the discharge of the pollinarium in <i>Catasetum</i> subgenus <i>Catasetum</i>
Anther	The part of the flower that produces pollen; in Orchidaceae, the "envolture" of the pollinarium
Anther filament	A thin strap of tissue, most likely of derived from the anther, that joins the latter to the clinandrium; it is discernable in <i>Clowesia</i> and <i>Cynoches</i> , and projects beyond the apex of the column, as a tubular process, in <i>Mormodes</i> (see Romero, 1990: Figure 3); it is entirely fused to the clinandrium in <i>Catasetum</i>
Caudicle (caudicles)	A slender, elastic extension of each pollinium that connects them to the stipe
Clinandrium	The bed of the anther, prolonging into a beak-like process in flowers of some species of <i>Catasetum</i> subgenus <i>Catasetum</i> and, in <i>Mormodes</i> , beyond the apex of the column
Column (Gynostemium)	A compound organ made up of the style and the filament of one or more anthers in Orchidaceae
Curtain	A non-viscid extension of the viscidium, highly developed in <i>Cynoches</i> and <i>Dressleria</i> , which in flowers of both genera covers the stigmatic cavity
Labellum	A modified petal, facing the column, which usually serves as a landing platform in Orchidaceae
Ovarium	See ovary
Ovary	Part of the gynoecium that holds the ovules. The "Ovarium" in Darwin's writings
Pollen masses	In Darwin's writings: see pollinia
Pollinarium	A compound organ composed, in Catasetinae, of a viscidium, a stipe, and two pollinia. "Pollinium" or "pollinia" in Darwin's writings
Pollinium (pollinia)	In Darwin's writings: see pollinarium
Pollinium (pollinia)	In the current orchid literature, a compact mass of aggregated pollen grain. Pollen-mass in Darwin's writing
Rostellum	A portion of the stigma over which, in Catasetinae, the stipe is stretched taut, storing energy to discharge the pollinarium partially or completely
Sepals and petals	Homologous to sepals and petals of other plants, mostly all colored in Orchidaceae
Stigma	The sticky, receptive part of the pistil, where the pollen grains contain within each pollinium germinate. In Catasetinae, the stigma is "hidden" inside a cavity, the latter sometimes reduced to a fissure or cleft. "Stigmatic cavity" or "Stigmatic cleft" in Darwin's writings
Stipe	A strap of tissue of columnar tissue that connect the viscidium and the pollinia. "Pedicel of pollinium" or "elastic pedicel" in Darwin's writings
Viscidium	A sticky disc that serves to attach the pollinarium to the pollinator. The "disk" in Darwin's writings.

<sup>1</sup> Most entries modified from Dressler (1990: 306–316).

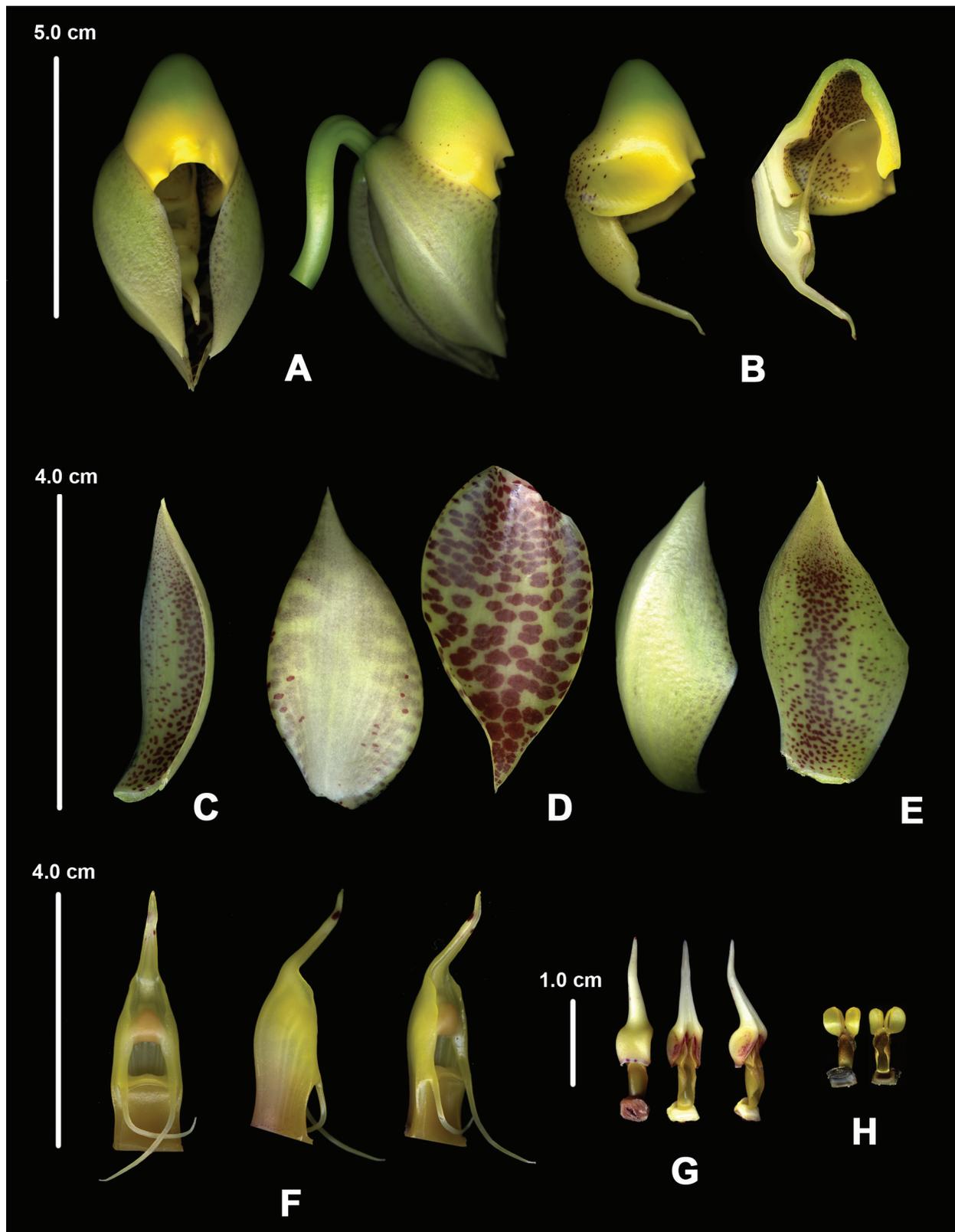


FIGURE 3. *Catasetum macrocarpum* Rich. ex Kunth. **A**, front and side view of flower; **B**, side view of flower after the removal of sepals and petals (from left to right: entire and cross-section views of the labellum); **C**, dorsal sepal; **D**, petal; **E**, lateral sepals; **F**, views of the column; **G**, views of the pollinarium and anther (from left to right: abaxial, adaxial, and side views); **H**, views of the pollinarium (from left to right: abaxial and adaxial views). Based on plant cultivated by *D. Fulop sub G. A. Romero-González s.n.* (AMES). Photographs by the author.

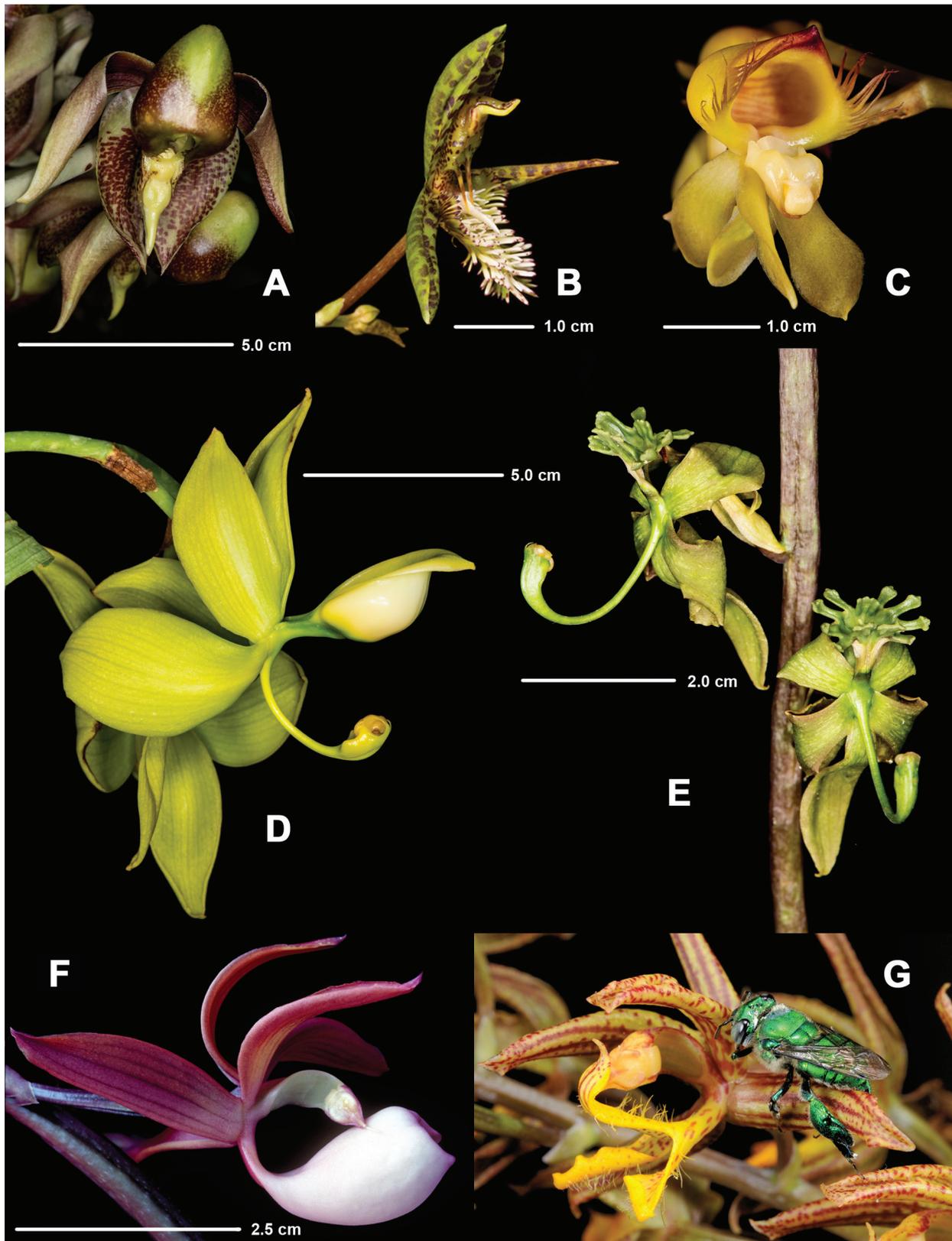


FIGURE 4. **A**, *Catasetum maculatum* Kunth (male flower); **B**, *Catasetum barbatum* (Lindl.) Lindl. (male flower); **C**, *Catasetum roseoalbum* (Hook.) Lindl. (male flower); **D**, *Cynoches ventricosum* Bateman (male flower); **E**, *Cynoches egertonianum* Bateman (male flowers); **F**, *Mormodes vernixoidea* ssp. *autanensis* Salazar & G. A. Romero (female flower); **G**, *Mormodes lineata* Lindl. with *Euglossa viridissima* Friese (male flower). A based on Guánchez 5384 (JBL); B ex Hort. Familia Aragua; C on Romero et al. 3592; D on Tamayo Cen 127 (CICY); E on Guánchez et al. 5366 (JBL); F on Romero & Guánchez 1434 (VEN); G on Carnevali 7416 (CICY).



FIGURE 5. Lindley's plate with male, female, and intermediate flowers of *Catasetum cristatum* Lindl. The hooded, green flowers in the apex of the inflorescence represent female flowers, as does flower 1 (the latter, drawn upside down, has a longer than normal clinandrum); the "cristate" ones at the bottom are male flowers, as is flower 4; flowers 2–3 are intermediate, nonfunctional flowers. From Lindley (1837). Courtesy of the Orchid Library of Oakes Ames.

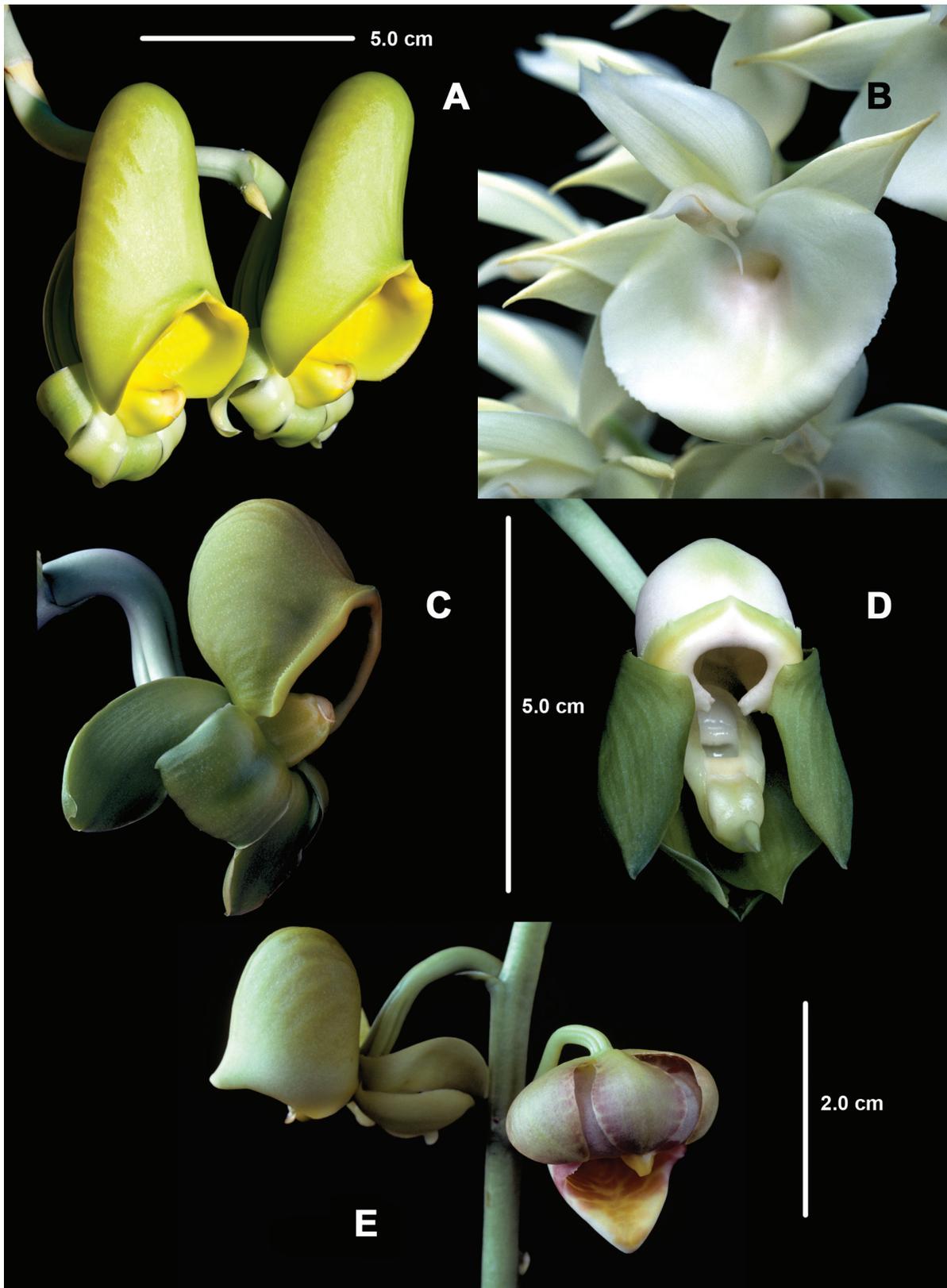


FIGURE 6. *Catasetum* sexual dimorphism. **A–B**, *Catasetum pileatum* Rchb.f. female and male flower, respectively; **C–D**, *Catasetum collare* Cogn. female and male flowers, respectively; **E**, *Catasetum bergoldianum* Foldats (from left to right: female and male flowers). A based on Romero & Gómez 3632; B on ex Hort. R. de Tomacini; C on ex Hort. R. de Tomacini; D on Romero 1155; E on Romero 1119. Photographs by the author.

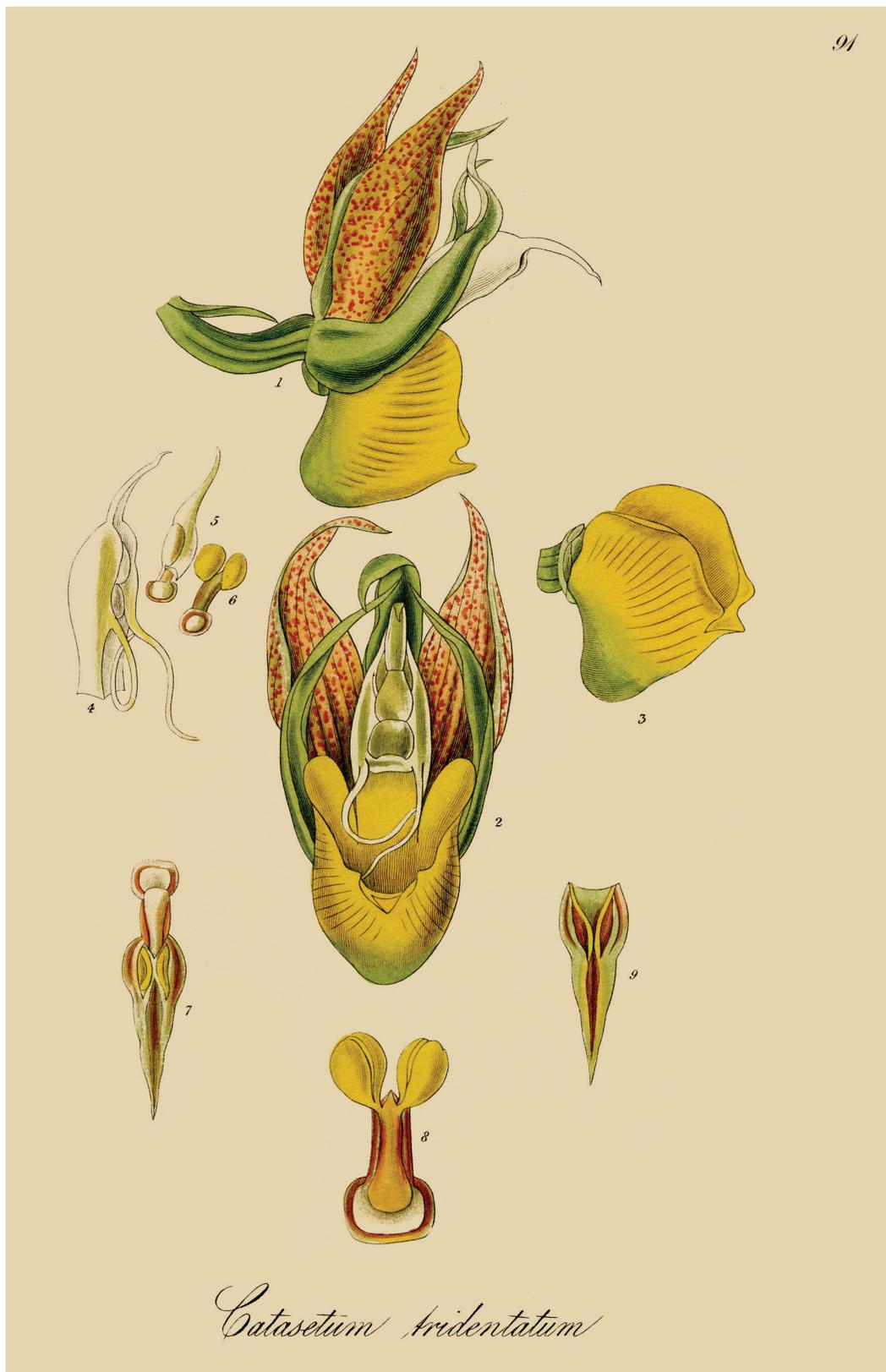


FIGURE 7. *Catasetum macrocarpum* Rich. ex Kunth (as *C. tridentatum* Hook.). From Hooker (1824: tab. 91). Quoting the text that originally accompanied the plate: 1, "Side view of flower"; 2, "Front view of same"; 3, "Side view of the lip"; 4, "Side view of column with the anther"; 5, [anther] removed"; 6, "Pollen mass" [pollinarium]; 7, "Inner view of the Anther-case, containing the pollen-mass"; 8, "Pollen-mass" [pollinarium]; 9, "Anther case, inside view." Courtesy of the Orchid Library of Oakes Ames.

Tab. 631.



L.C.M. Richard delin.

CATASETUM macrocarpum.

De l'Imprimerie de Langlois.

FIGURE 8. *Catasetum macrocarpum* Rich. ex Kunth. from Humboldt, Bonpland, and Kunth (1825: tab. 631). Courtesy of the Orchid Library of Oakes Ames.

publication (Lindley, 1832): *Myanthus* (based on *Myanthus cernuus*) and *Monachanthus* (based on *Monachanthus viridis*). Later, these genera were determined to be male flowers of *C. cernuus* and female flowers of *C. macrocarpum*, respectively. He never illustrated *Myanthus cernuus*, and the first species that appeared in the iconography was his *Myanthus barbatus* (Lindley, 1835b; Fig. 9); he did illustrate *Monachanthus viridis* (Lindley, 1835a; Fig. 10). A total of 12 new species, varieties, and combinations would be proposed in *Myanthus*, and 10 in *Monachanthus*.

Hooker (1836) was the first author to doubt Lindley's genera:

The present plant [*Myanthus barbatus*] ... is referred [by John Lindley] to *Myanthus*, without any allusion to its exceedingly close affinity with his *Catasetum cristatum*, a similarity so great, that I was at first disposed to consider our plant with a white lip the same species, differing chiefly in being furnished with a spur or tooth-like process at the base of the lip. The two plants are indeed, I doubt not, specifically distinct; but they cannot be separated generically, and perhaps Professor Lindley will agree with me in thinking, that *Myanthus* should only form a section of *Catasetum* (Hooker, 1836).

Lindley (1837), after examining the then-existing evidence, including the already cited inflorescence having a mixture of male, female, and intermediate flowers of *Catasetum cristatum* (Lindley, 1837; Fig. 5), concluded that “the necessary consequence ... is, that the supposed genera *Myanthus* and *Monachanthus* must be restored to *Catasetum*”; adding, “which of the species have their masks on, and which shew their real faces, I certainly will not at present presume to guess” (see Gerlach, 2013, for an account of Lindley's “nightmare”).

Robert H. Schomburgk (1804–1865), with the additional advantage of knowing plants in the field, had also concluded that “the genera *Monachanthus*, *Myanthus*, and *Catasetum* form but one genus” (Schomburgk, 1837).

Thus, the fact that all three genera (i.e., *Catasetum*, *Monachanthus*, and *Myanthus*) were not “sportings” (see Lindley, 1837) or “monsters” (see J. Paxton's note in Lindley, 1837), but referable to one single genus, had already been firmly established by the time Darwin expressed interest in this group of orchids.

Furthermore, Schomburgk (1837) pointed out that

We have traces of sexual difference in Orchideous flowers. I have seen hundreds of *Catasetum tridentatum* on savannahs adjacent to the Capoeya (Arabisce coast of Essequibo), without ever finding one specimen with seeds, while those bulbs, which, according to Dr. Lindley's description, belonged to *Monachanthus viridis*, astonished me by the gigantic seed-vessels.

William J. Hooker, John Lindley, and Robert H. Schomburgk had paved the way for Darwin, and Schomburgk

(1837), in particular, had alluded to the fact that “sexual difference” was involved. However, these authors had examined few species; the limited information available to them brings to our attention Pridgeon's quote in the beginning of this contribution (Pridgeon, 2003).

Darwin went on to paintakingly demonstrate that the species of *Catasetum* known thus far bore male flowers, that those of *Monachanthus* were female flowers of *Catasetum*, and, erroneously, that flowers of *Myanthus* were hermaphroditic flowers of *Catasetum*: “*Myanthus barbatus* may be considered as the hermaphrodite form of the same species, of which the *Catasetum* is the male, and the *Monachanthus* the female” (Darwin, 1877a: 156). To conduct his work on *Catasetinae* Darwin relied on fresh flowers from Joseph D. Hooker, of the Royal Botanic Gardens, Kew, James Veitch “of Chelsea,” and Mr. Sigmund Rucker “of West Hill, Wandsworth”; some of the species and flowers he examined were identified by John Lindley, the leading orchid expert at that time. Perhaps most important of all for his work, Darwin also examined an inflorescence in spirits that R. H. Schomburgk had sent to the Linnean Society of London that bore male and female flowers of *Catasetum barbatum* (Lindl.) Lindl. (illustrated in Schomburgk, 1837; Fig. 11–12); the former previously had been interpreted as being flowers of *Myanthus*, the latter as flowers of *Monachanthus* (Schomburgk, 1837; Darwin, 1862a).

It is lamentable that neither Darwin nor any of the other botanists who had worked earlier on *Catasetum* apparently ever studied the descriptions of *Catasetum macrocarpum* Rich. ex Kuth in *Synopsis Plantarum* (“*flores fusco-purpurei, labellum non ciliatum, fructus 4–5-pollicares*” [Kunth, 1822: 331]), the more detailed one in *Genera Plantarum* (1824: 158), or particularly the plate in *Genera Plantarum* (Humboldt et al., 1825: tab. 631), which shows both an inflorescence with two male flowers (one in bud) and another, borne on a second pseudobulb, with a fruit with a persistent perianth (see Fig. 13). They would have realized that plants of the genera *Catasetum* and *Cynoches* can bear male and female flowers in the same or in different flowering seasons (Dodson, 1962b; Gregg, 1975, 1982; Romero, 1992).

Rolfe (1890, 1895) partially solved the puzzle: he correctly ascertained that flowers of *Myanthus* were actually male flowers of another group of *Catasetum*, currently referred to subgenus *Catasetum* section *Isoceras*, by far the most diverse group in the genus, and definitively not hermaphroditic flowers.

A similar conundrum involved *Cynoches* Lindl. in the 1840s and 1850s, this time not involving different genera, because plants of the species then known bore generally similar flowers that could easily be referred to that genus; in this case, male and female flowers of different species were referred to the same species and male and female flowers of the same species to different ones. The first “monster” appeared on plate 40 of John Bateman's *The Orchidaceae of Mexico and Guatemala*, published in 1843 (Fig. 14). It presented, originating from the same pseudobulb, one pendent inflorescence bearing many flowers and flower buds of the new species described in the plate, *Cynoches*



FIGURE 9. *Myanthus barbatus* Lindl. Darwin (1862a,b, 1877a) incorrectly treated the flowers of this species as the hermaphroditic form of *Catasetum* from Lindley (1835b). Courtesy of the Orchid Library of Oakes Ames.



FIGURE 10. *Monachanthus viridis* Lindl. from Lindley (1835a). Darwin (1862a,b, 1877a) correctly treated the flowers of this species as the female form of *Catasetum*, and eventually it became clear that it was the female flower of *C. macrocarpum* Rich. ex Kunth. Courtesy of the Orchid Herbarium of Oakes Ames.



FIGURE 11. *Catasetum barbatum* Lindl. in Schomburgk (1837). The plate shows two inflorescences. The first is an erect one, borne at the base of the pseudobulb, showing a mixture of female flowers (the hooded ones, supposedly *Monachanthus viridis*) and male ones (the "barbate" ones, supposedly *Myanthus barbatus*); some of the female flowers show abnormally long clinandria. The second inflorescence, somewhat arcuate, bears all "barbate," male flowers. Courtesy of the Botany Libraries, Harvard University Herbaria.



FIGURE 12. *Catasetum barbatum* Lindl. in Schomburgk (1837). Again, the “hooded” flowers are female, the “barbate” ones are male. Detail redrawn by Blanche Ames and reproduced in Ames (1945). From the original drawing at the Botany Library, Harvard University Herbaria.



FIGURE 13. *Cycnoches* “monster” showing two inflorescences originating from the same pseudobulb, each bearing male flowers of two different species: in the upper left, two flowers of *Cycnoches ventricosum* Bateman; in the center, a multiflowered inflorescence with flowers of *Cycnoches egertonianum* Bateman. The line drawing shows a male flower of *C. egertonianum* with sepals and petals removed, drawn upside down. From Bateman (1843: tab. 40). Courtesy of the Missouri Botanical Garden and the Biodiversity Heritage Library.



FIGURE 14. *Cycnoches ventricosum* Bateman. The inflorescence shows six male flowers; to the right, borne in an old pseudobulb and inflorescence, there is a dehiscent fruit. From Bateman (1838: tab. 5). Courtesy of the Missouri Botanical Garden and the Biodiversity Heritage Library.

*egertonianum* Bateman, and another erect one bearing two flowers of *C. ventricosum* Bateman, a different species that had been described earlier in the same work (Bateman, 1838: tab. 5; Fig. 14 herein). Although Lindley (1843a,

1843b) had stated, in reference to this plate, "But what is impossible in nature?" we now know it is impossible that flowers of these two species could be born from the same plant.

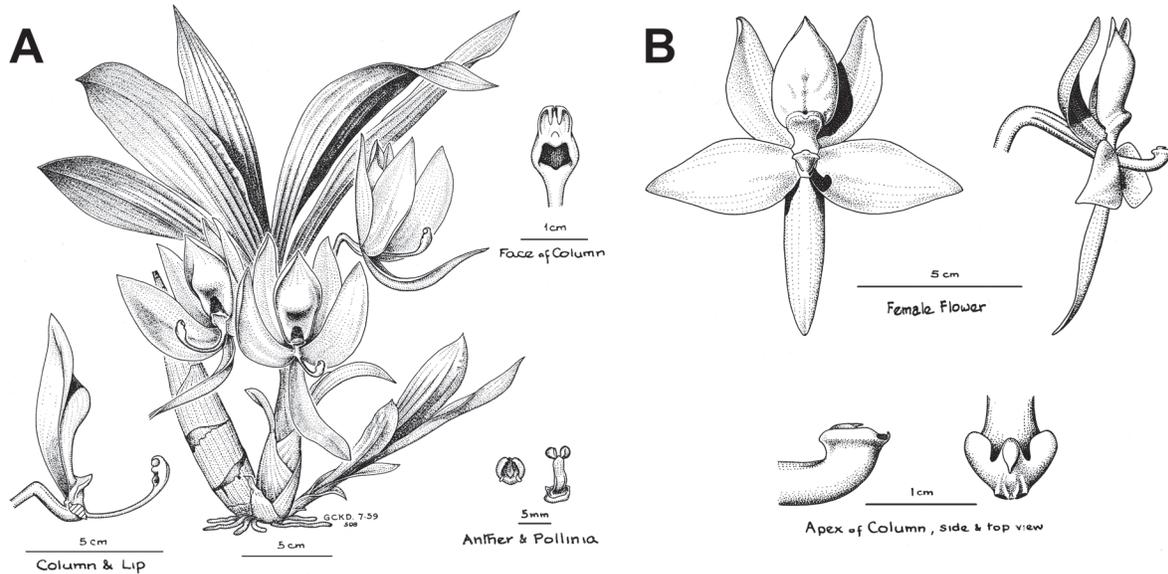


FIGURE 15. *Cynoches chlorochilon*. Klotzsch. **A**, plant bearing an inflorescence with three male flowers; **B**, female flower. Based on *G. C. K. Dunsterville 508*. From two photostats at AMES.

The following is part of the text that accompanies Bateman's plate 40:

Among Mr. Skinner's earliest Guatemala collections, attention was particularly directed to the specimens of a plant which to the habit of a *Cynoches* joined the long pendulous stems of a *Gongora*, and for the possession of which, in a living state, no small anxiety was entertained. Some plants were speedily transmitted by Mr. Skinner, but these, on flowering, proved to be merely the old *C. ventricosum*. A mistake was of course suspected, and Mr. Skinner being again applied to, sent over a fresh supply of plants, for the authenticity of which he vouched; but these were scarcely settled in the stove, when flowers of *C. ventricosum* were again produced. Mr. Skinner being importuned for the third time, and being then on the point of returning to this country, determined to take one of the plants under his special protection during the voyage, which, flowering on the passage, seemed to preclude the possibility of further confusion or disappointment. The specimens produced at sea were exhibited, and the plant itself placed in the stove at Knypersley, where it commenced growing with the utmost vigour. The season of flowering soon arrived, but brought with it a recurrence of the former scene of astonishment

and vexation, for the blossoms, instead of those of the coveted novelty, were not distinguishable from the old *C. ventricosum*. These were still hanging to the stem when the inexplicable plant sent forth a spike of a totally different character, and which was, in fact, precisely similar to the specimens gathered in Guatemala, and to those produced on the voyage.

It is, at present, impossible to attempt any explanation of so strange a phenomenon, especially on the supposition that the two forms of flower are analogous to the male and female blossoms of other tribes, for *C. ventricosum* alone not unfrequently perfects seeds. (Bateman, 1843: tab. 40).

The confusion arose because Bateman and others mistook, despite a considerable difference in size and form,<sup>6</sup> the male flower of *Cynoches ventricosum* for the female flower of *C. egertonianum*, first pointed out by Rolfe (1902: 298, 1909). The statement "*C. ventricosum* alone not unfrequently perfects seeds" (Bateman, 1843: tab. 40) resulted perhaps from the observation of a fruit borne by the same plant of *C. ventricosum* that bore male flowers (see Fig. 14).

John Lindley further confused the issue when he described, as *Cynoches cucullata*, a female flower of what he previously had described as *C. loddigesii* (Lindley, 1837, sub tab. 1951\*).

<sup>6</sup>The female flower of *Cynoches egertonianum* is much smaller than the male flower of *C. ventricosum*; see Fig. 15 for differences between male and female flowers of *Cynoches*, chiefly the shorter and thicker column of the latter, as well as the morphology of the clinandrium.

Later, Lindley (1843a) mistakenly referred male flowers and female flowers belonging to the same species to two different species, again confusing the female flowers of *Cycnoches egertonianum* with *C. ventricosum* (Fig. 16; also reproduced in Lindley, 1843b).<sup>7</sup>

He described an inflorescence of *Cycnoches egertonianum* as follows:

On the spike, No. 1 is more *Egertonianum* than *ventricosum*; the next is almost wholly *ventricosum*; that which succeeds, No. 3, is more *ventricosum* than *Egertonianum*; and 4 and 5, the last on the spike, are wholly *Egertonianum*.

Lindley, in the same publication, added his much quoted statement (i.e., Darwin, 1862a; Rolfe, 1902: 298, 1909), “What with such cases as this ... all ideas of species and stability of structure in the vegetable kingdom, are shaken to their foundation.”

By 1846 Lindley came up with another solution—plants of *Cycnoches* were “sporting”:

But what is *C. Egertonianum* itself? In our volume for 1843, at p. 77 of the miscellaneous matter [Lindley, 1843a,b], we have extracted from Mr. Bateman’s magnificent work his account of how the long-spiked small-purple-flowered *C. Egertonianum* is only the short-spiked large-green-flowered *C. ventricosum*; how the same plant at one time bears one sort of flowers, and at another time another sort; and we have shewn how the same plant, nay the same spike, is sometimes both the one, the other, and neither. *Cycnoches Egertonianum* is then a “sports,” as gardeners say, of *C. ventricosum*.

But what again is *C. ventricosum*? Who knows that it is not another “sport” of *C. Loddigesii*, which has indeed been caught in the very act of shewing a false face, something wonderfully suspicious, all things considered, and justifying the idea that it is itself a mere Janus, whose face is green and short on one side, and spotted and long on the other.

Then, if such apparently honest species as *C. Egertonianum*, *ventricosum*, and *Loddigesii* are but counterfeits, what warrant have we for regarding the other so-called species as not being further examples of plants masquerading with false faces? For ourselves we cannot answer the question; nor should we be astonished at finding some day a *Cycnoches* no longer a *Cycnoches*, but something else; perhaps a *Catasetum*. If one could accept the doctrine of the author of the “Vestiges,” it might be said that in this place we have found plants actually undergoing the changes which he assumes to be in progress throughout nature, and that they are thus subject to the most startling conditions only because their new forms *have not yet acquired stability*. (Lindley, 1846)



FIGURE 16. *Cycnoches egertonianum* Bateman from Lindley (1843a). The text accompanying this figure reads, “on the spike, No. 1 is more *Egertonianum* than *ventricosum*; the next is almost wholly *ventricosum*; that which succeeds, No. 3, is more *ventricosum* than *Egertonianum*; and 4 and 5, the last on the spike, are wholly *Egertonianum*.” All the flowers represent *C. egertonianum*: 2 represent the typical female flower and 4–5 male flowers; 1 and 3 are intermediate in color (see footnote 7 below) but apparently fully functional male flowers.

Lindley maintained the same view in 1852, when he described *Cycnoches aureum*, and, as in 1846, presented a list of all the then-known species of the genus under the title “so-called species of *Cycnoches*”; under *C. egertonianum* he added “*Sports to ventricosum*” and under *C. ventricosum* “*Sports to Egertonianum*” (Lindley, 1846, 1852, his italics). Lindley, a keen observer, did add, under *Cycnoches loddigesii*, “*Sports by producing smaller broad-lipped flowers without scent, and with a very short club-shaped column*” (again, his italics in Lindley, 1846, 1852), describing the flowers of *C. cucullata* and a typical female flower (Fig. 15B), but not realizing that the difference between the two “species” involved sexual dimorphism.

<sup>7</sup> Rolfe (1902: 298) cited, for the line drawing reproduced in Lindley (1843a, 1843b), “two purple flowers of *C. egertonianum*, one green flower, which Lindley called ‘nearly *C. ventricosum*’ ... and two flowers in a transition state so far as the shape and color of the sepals and petals are concerned.” However, the published plate does not show any color, and Rolfe perhaps had access to the original, colored plate, which is likely among the collection of plates in the Orchid Herbarium, Royal Botanic Gardens, Kew.

Darwin did not have much to add to the different “forms” or “sports” of *Cycnoches*. On page 224 of the second edition he stated (also partially in Darwin, 1862a: 269):

Therefore it appears that this *Cycnoches* [*C. ventricosum*] must be an hermaphrodite; and Mr. Bateman, in his work on the Orchideæ, says that the present species produces seeds without being, as I understand, artificially fertilised; but how this is possible is unintelligible to me.... According to Lindley *C. ventricosum* produces on the same scape flowers with a simple labellum, others with a much segmented and differently coloured labellum (viz., the so-called *C. egertonianum*), and others in an intermediate condition. From the analogous differences in the flowers of *Catasetum*, we are tempted to believe that we here have male, female, and hermaphrodite forms of the same species of *Cycnoches*.

Then, on a footnote on the same page:

Mr. Bateman also says that *C. egertonianum* has been known to produce in Guatemala and once in England scapes of a purple-flowered and widely different species of *Cycnoches*; but that it generally produces in England scapes of the common yellow *C. ventricosum*.

The mystery surrounding *Cycnoches* would remain unsolved until Rolfe (1902: 298, 1909) correctly interpreted the male and female flowers of the different species of *Cycnoches*, thus solving the riddle.

After Rolfe, one major issue remained unsolved: do plants of *Catasetum* and *Cycnoches* ever bear hermaphroditic flowers?

“Hermaphroditic flowers” in *Catasetum* and *Cycnoches* have long been reported in the orchid literature (Ames, 1945; Hoehne, 1953; Soukup, 1976; Gregg, 1975, 1982; Bicalho and Barros, 1988; Van der Cingel, 2001: 90; Cribb, 2003; Pridgeon, 2003; Arditti, 2008: 291; Domínguez, 2007; Oliveira et al., 2013), although there is incontrovertible evidence that such flowers, intermediate in morphology between male and female flowers, are actually nonfunctional (Romero, 1992; Gerlach, 2007).

Another avenue of research originated from Darwin’s work and his correspondence with two particular collaborators, Hermann Crüger (1818–1864), then stationed in Trinidad, and Johann Friedrich Theodor Müller (a.k.a. Fritz Müller, 1821–1897), who lived in Santa Catarina, Brazil. Crüger sent bees that visited *Catasetum* to Darwin: “Dr. Crüger sent me specimens of the humble-bees which he caught gnawing the labellum, and these consist of *Euglossa*

*nov. spec., cajennensis* and *piliventris*” (Darwin, 1877a: 206; see Nemésio and Rasmussen, 2011, for comments on Darwin’s correspondence with Crüger and Müller, and on work on euglossine bees prior to Darwin’s). Crüger (1864) was the first naturalist to report the pollination of certain orchids by euglossine bees, although he misinterpreted what attracted the bees to the flowers:

...that the insects are attracted at first by the smell of the flower I take from the fact that the same insect visits *Coryanthes macrantha*, *Stanhopea grandiflora*, and *Gloxinia maculata* [Gesneriaceae], all three of which have the same perfume. But the smell probably only gives notice to the insects; the substance they really come for, in the case of these Orchids, is the interior lining of the labellum, which they gnaw off with great industry, and for which there is a continual contest.

Crüger did not realize that “the substance they really come for, in the case of these Orchids, [in] the interior lining of the labellum” were actual fragrances, secreted by osmophores, which male euglossine bees actively collect (see Roubik and Knudsen, 2017, for a recent review of this pollination syndrome).

Crüger (1864) and Müller’s (1868, 1869) work was no doubt the beginning of research on orchid fragrances and pollination by euglossine bees, research that languished until the 1960s (see references in the beginning of this contribution).

Darwin’s editions of his orchid pollination books went on to be reprinted multiple times in the 1800s (see notes in Literature Cited under Darwin, 1877a), as well as in the 20th century, and translated into multiple languages (Darwin, 1870 [French translation of the first edition], 1877b [German translation of the first edition], 1883 [Italian translation of the second edition], 2007 [Spanish translation of the second edition]). His books were no doubt bestsellers!

The texts that Darwin wrote on *Catasetinae* are presented in three appendices (which include Darwin, 1862a,b, 1869, and 1877a). The texts were transcribed verbatim with the following exceptions. Darwin (1877a) and his editor wrote binomials in italics, but generic names in roman, which are here all transcribed in italics; the names of journals were written in roman and between single quotes, which are here transcribed in italics without quotes. The transcribed texts include the published illustrations. The footnotes have been renumbered, where notes were added to the original text. The numbering and order of the figures in Appendixes I and III follows that of the original text.

A fourth appendix lists the specimens cited in the illustrations presented herein.

#### LITERATURE CITED

- AMES, O. 1937. Pollination of orchids through pseudocopulation. Botanical Museum Leaflets 5(1): 1–32.
- . 1941. Pollination in *Coryanthes*. American Orchid Society Bulletin 10: 146–150.
- . 1945. The strange case of *Catasetum barbatum*. American Orchid Society Bulletin 13: 289–294.
- ARDITTI, J. 2008. *Micropropagation of Orchids*. 2nd ed. Vol. 1. Blackwell, Malden, Mass.
- BATEMAN, J. 1837–1843. *The Orchidaceae of Mexico and Guatemala*. J. Ridway and Sons, London.
- BEATTY, J. 2006. Chance variation: Darwin on orchids. *Philosophy of Science* 73(5): 629–641.

- BELLON, R. 2009. Charles Darwin solves the “riddle of the flower”; or, why don't historians of biology know about the birds and the bees. *History of Science* 47(4): 373–406.
- BERNHARDT, P. AND R. EDENS-MEIER. 2014. Darwin's orchids (1862, 1877): Origins, development, and impact. Pages 3–19 in R. EDENS-MEIER AND P. BERNHARDT, EDS., *Darwin's Orchids*. University of Chicago Press, Chicago.
- BICALHO, H. D. AND F. DE BARROS. 1988. On the taxonomy of *Catasetum* subsection *Isoceras*. *Lindleyana* 3: 87–92.
- BROWN, R. 1833. On the organs and mode of fecundation in Orchideae and Asclepiadeae. *Transactions of the Linnean Society of London* 16: 685–745, t. 34–36.
- CAMERON, K. M. 2011. A look at “The Orchid Book” in celebration of Charles Darwin's 200th birthday. *Lankesteriana* 11(3): 223–231.
- CRIBB, P. 2003. Morphology [of Orchidaceae]. Pages 13–23 in A. M. PRIDGEON, P. J. CRIBB, M. W. CHASE, AND F. N. RASMUSSEN, EDS., *Genera Orchidacearum*. Vol. 1. Oxford University Press, New York.
- . 2009. Distribution [of tribe Cymbidieae]. Page 3 in A. M. PRIDGEON, P. J. CRIBB, M. W. CHASE, AND F. N. RASMUSSEN, EDS., *Genera Orchidacearum*. Vol. 5. Oxford University Press, Oxford, U.K.
- . 2010. Orchid collections and illustrations of Consul Friederich C. Lehmann. *Lankesteriana* 10(2–3): 1–215 (“Biographies” on pages 183–206).
- CRÜGER, H. 1864. A few notes on the fecundation of orchids and their morphology. *Journal of the Proceedings of the Linnean Society of London* 8: 127–135, pl. 9.
- DARWIN, C. 1862a. On the three remarkable sexual forms of *Catasetum tridentatum*, an orchid in the possession of the Linnean Society [“Read April 3, 1862”]. *Journal of the Proceedings of the Linnean Society* 6: 151–157.
- . 1862b. *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects and on the Good Effects of Intercrossing [with illustrations]*. John Murray, London.
- . 1869. Notes on the fertilization of orchids. *Annals and Magazine of Natural History*, ser. 4, no. 21: 141–159.
- . 1870. *De la Fécondation des Orchidées par les Insectes*. C. Reinwald et C<sup>ie</sup>, Paris.
- . 1877a. *The Various Contrivances by which Orchids are Fertilised by Insects [with illustrations]*. 2nd ed., revised. John Murray, London [reprinted, with the same pagination, by John Murray in 1882, 1885, 1890, 1898, and 1899 (as “Sixth impression, second edition”), and by D. Appleton and Company, New York, in 1877, 1884, 1886, 1892, 1895, and 1898; John Murray published a “Popular edition, being the seventh impression of the second edition” in 1904].
- . 1877b. *Die verschiedenen Einrichtungen durch welche Orchideen von Insecten befruchtet werden*. E. Schweizerbart, Stuttgart.
- . 1883. *I diversi apparecchi col mezzo dei quali le orchidee vengono fecondate dagli insetti*. Unione Tipografica, Torino.
- . 2007. *La Fecundación de las Orquídeas* [traducción de Carmen Pastor, introducción de Martí Domínguez]. Editorial Laetoli, Pamplona, Spain.
- DODSON, C. H. 1962a. The importance of pollination in the evolution of the orchids of tropical America. *American Orchid Society Bulletin* 31: 525–534, 641–649, 731–735.
- . 1962b. Pollination and variation in the subtribe Catasetinae. *Annals of the Missouri Botanical Garden* 49: 35–56.
- . 1975. *Dressleria* and *Clowesia*: A new genus and an old one revived in the Catasetinae (Orchidaceae). *Selbyana* 1(2): 130–137.
- AND G. P. FRYMIRE. 1961. Natural pollination of orchids. *Missouri Botanical Garden Bulletin* 49: 133–139.
- AND H. G. HILLS. 1966. Gas chromatography of orchid fragrances. *American Orchid Society Bulletin* 35: 720–725.
- DOMÍNGUEZ, M. 2007. Introducción. Pages 7–25 in C. DARWIN, *La Fecundación de las Orquídeas* [translated by C. Pastor Gradolí]. Editorial Laetoli, Pamplona, Spain.
- DRESSLER, R. L. 1968. Observations on orchids and euglossine bees in Panama and Costa Rica. *Revista de Biología tropical* 15: 143–183.
- . 1990. *The Orchids*. Harvard University Press, Cambridge, Mass.
- EDENS-MEIER, R. AND P. BERNHARDT, EDS., 2014. *Darwin's Orchids*. University of Chicago Press, Chicago.
- ENDERSBY, J. 2016. Deceived by orchids: sex, science, fiction and Darwin. *BJHS* 49, 2, 205–229.
- GERLACH, G. 2007. The true sexual life of *Catasetum* and *Cycnoches*. *Caesiana* 28: 57–62.
- . 2013. La pesadilla de Lindley—la biología sexual de *Catasetum* y *Cycnoches*. *Lankesteriana* 13(1–2): 39–46.
- AND O. A. PÉREZ-ESCOBAR. 2014. Looking for missing swans. *Orchids* 84: 434–437.
- GREGG, K. B. 1975. The effect of light intensity on sex expression in species of *Cycnoches* and *Catasetum* (Orchidaceae). *Selbyana* 1(2): 101–113.
- . 1982. Sunlight-enhanced ethylene evolution by developing inflorescences of *Catasetum* and *Cycnoches* and its relation to female flower production. *Botanical Gazette* 143(34): 466–475.
- HILLS, H. G. 2012. Taxonomic revision of *Dressleria* (Orchidaceae, Catasetinae). *Phytoneuron* 48: 1–28.
- AND M. H. WEBER. 2012. *Dressleria morenoi* (Orchidaceae, Catasetinae): A new species from Colombia. *Phytoneuron* 103: 1–5.
- HOEHNE, F. C. 1953. Contribuição para o conhecimento do género *Catasetum* Rich. e especialmente o hermaphroditismo e trimorfismo das suas flores. *Boletim da Agricultura* (São Paulo) 33: 133–196.
- HOOKE, W. J. [March] 1824. *Catasetum tridentatum*. *Exotic Flora* 2: tab. 90–91.
- . 1836. *Myanthus barbatus* var. *labello albo*. *Curtis's Botanical Magazine* 63: tab. 3514.
- HUMBOLDT, A. VON, A. BONPLAND, AND C. S. KUNTH. 1824–1825. *Nova Genera et Species Plantarum*. Vol. 7. Gide Filium, Paris.
- KUNTH, C. S. 1822. *Synopsis Plantarum*. Vol. 1. F. G. Levrault, Paris.
- LI, M.-H., G.-Q. ZHANG, Z.-J. LIU, AND S.-R. LAN. 2016. Subtribal relationships in Cymbidieae (Epidendroideae, Orchidaceae) reveal a new subtribe, Dipodiinae, based on plastid and nuclear coding DNA. *Phytotaxa* 246(1): 37–48.
- LINDLEY, J. 1824. *Catasetum claverlingii* [as “Claveringi”]. *Botanical Register* 10: tab. 840.
- . 1832. *Myanthus* and *Monachanthus*. *Edwards's Botanical Register* 18: sub tab. 1538.
- . 1835a. *Monachanthus viridis*. *Edwards's Botanical Register* 21: tab. 1752.
- . 1835b. *Myanthus barbatus*. *Edwards's Botanical Register* 21: tab. 1778.
- . 1837. *Monachanthi et Myanthi cristati*. *Edwards's Botanical Register* 23: tab. 1947<sup>A</sup> [text sub 1951\*].<sup>8</sup>
- . 1843a. *Cycnoches ventricosum* and *Cycnoches Egertonianum*. *Edwards's Botanical Register* 29: misc. 75–77.
- . 1843b. The vagaries of flowers. *The Gardeners' Chronicle* no. 44: 775–776.

<sup>8</sup> This particular plate in *Edwards's Botanical Register* (vol. 23) has a confusing numeration due no doubt to a printing error. Plate 1947 shows *Laelia anceps* Lindl. var. *barkeriana* Lindl.; it is accompanied by the numerically matching and correct text. However, the text for plate “1947<sup>A</sup>,” cited above, was published as “1951\*,” the asterisk used surely to distinguish it from plate 1951, which shows *Trichocentrum fuscum* Lindl., which, again, is accompanied by the numerically matching and right text. Therefore, authors wishing to cite the plate of “*Monachanthi et Myanthi cristati proles biformis*” (see Fig. 5 herein) have to cite the number “1947<sup>A</sup>,” whereas those wishing to cite the text, as when citing what appears to be the protologue of *Cycnoches cucullata* Lindl., have to cite number “1951\*,” and not “1951,” as currently cited in IPNI and Tropicos.

- . 1846. *Cycnoches egertonianum* var. *viride*. Edwards's Botanical Register 32: tab. 46.
- . 1852. The Golden Swan-Orchid. Paxton's Flower Garden 3: 5–6, tab. 75.
- MÜLLER, F. 1868. Ueber Befruchtungerscheinungen bei Orchideen. Botanische Zeitung 26: 629–631.
- . 1869. Ueber Befruchtungerscheinungen (*Eschscholtzia*, *Faramea*, *Epidendrum*, *Scorzoneria*). Botanische Zeitung 27: 115: 224–226.
- NEMÉSIO, A. AND C. RASMUSSEN. 2011. Nomenclatural issues in the orchid bees (Hymenoptera: Apidae: Euglossina) and an updated catalogue. Zootaxa 3006: 1–42.
- OLIVEIRA DE, V. M., F. DE BARROS, AND E. R. FORNI-MARTINS. 2013. Chromosome numbers and karyotypes of *Catasetum* species (Orchidaceae). Plant Biosystems 148(3): 499–507.
- PÉREZ-ESCOBAR, O. A. 2016. Molecular phylogenetics, evolution of sexual systems and historical biogeography of Darwin's favourite orchids (Catasetinae) and swan orchids (*Cycnoches* Lindl.). Doctoral diss., Ludwig-Maximilians-Universität München. Munich, Germany.
- , G. CHOMICKI, F. L. CONDAMINE, J. M. DE VOS, A. C. MARTINS, E. C. SMIDT, B. KLITGÅRD, G. GERLACH, AND J. HEINRICH. 2017. Multiple geographical origins of environmental sex determination enhanced the diversification of Darwin's favourite orchids. Nature Scientific Reports 7(12878): 1–11.
- , M. GOTTSCHLING, W. M. WHITTEN, G. SALAZAR, AND G. GERLACH. 2016. Sex and the Catasetinae (Darwin's favourite orchids). Molecular Phylogenetics and Evolution 97: 1–10.
- PRIDGEON, A. M. 2003. Modern species concepts and practical considerations for conservation of Orchidaceae. Pages 43–53 in K. W. DIXON, S. P. KELL, R. L. BARRETT, AND P. J. CRIBB, EDS., *Orchid Conservation*. Natural History Publications (Borneo), Kota Kinabalu, Sabah.
- ROLFE, R. A. 1890. On the sexual forms of *Catasetum*, with special reference to the researches of Darwin and others. Journal of the Linnean Society of London, Botany 27: 206–225, tab. VIII.
- . 1894, 1900–1902. [The] History of orchid cultivation. Orchid Review 2 [1894], no. 14: 44–48; no. 15: 75–78; no. 17: 133–136; 8 [1900], no. 95: 331–335; 9 [1901], no. 99: 69–72; no. 101: 132–136; no. 102: 164–168; no. 104: 228–232; no. 107: 330–336; 10 [1902], no. 112: 108–112; no. 118: 298–305.
- . 1895. Notes on the genus *Catasetum*. Orchid Review 3(29): 138–143.
- . 1909. A revision of the genus *Cycnoches*. Bulletin of Miscellaneous Information (Kew) no. 6: 268–277.
- ROMERO, G. A. 1990. Phylogenetic relationships in subtribe Catasetinae (Orchidaceae, Cymbidieae). Lindleyana 5(3): 160–181.
- . 1992. Non-functional flowers in *Catasetum* orchids (Catasetinae, Orchidaceae). Botanical Journal of the Linnean Society 109: 305–313.
- AND C. A. NELSON. 1986. Sexual dimorphism in *Catasetum* orchids: Forcible pollen emplacement and male flower competition. Science 232(4757): 1538–1540.
- ROMERO-GONZÁLEZ, G. A. 2009. Distribution [of *Catasetum*]. Page 14 in A. M. PRIDGEON, P. J. CRIBB, M. W. CHASE, AND F. N. RASMUSSEN, EDS., *Genera Orchidacearum*. Vol. 5. Oxford University Press, New York.
- ROUBIK, D. W. AND J. T. KNUDSEN. 2017. An embellishment that became a mutualism: Inquiries on male bee tibial bouquets and fragrance-producing orchids in Panama and oceanic islands (Apidae: Apinae, Euglossini; Orchidaceae: Epidendroideae). Flora 232: 117–127.
- SALAZAR, G. A., L. I. CABRERA, G. GERLACH, E. HÁGSATER, AND M. W. CHASE. 2016. Phylogenetic relationships in *Mormodes* (Orchidaceae, Cymbidieae, Catasetinae) inferred from nuclear and plastid DNA sequences and morphology. Phytotaxa 263(1): 18–30.
- SCHOMBURGK, R. H. 1837. On the identity of three supposed genera of Orchideous epiphytes. Transactions of the Linnean Society of London 17(4): 551–552.
- SINGER, R. B. 2009. Morfología floral y polinización de orquídeas: El segundo libro de Charles Darwin. Acta Biologica Colombiana 14S: 337–350.
- SOUKUP, V. G. 1976. *Catasetum barbatum* Lindl.: Male, female, and hermaphroditic flowers. American Orchid Society Bulletin 45(7): 603–605.
- SPRENGEL, C. K. 1793. *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen*. Friedrich Vieweg, Berlin.
- TAMAYO CEN, I. 2018. Filogenia, sistemática y biogeografía de *Clowesia* Lindl. (Orchidaceae: Catasetinae). M.S. thesis, Centro de Investigación Científica de Yucatán, Mérida, Yucatán, México.
- VAN DER CINGEL, N. A. 2001. *An Atlas of Orchid Pollination*. A. A. Balkema, Rotterdam.
- VAN DER PIJL, L. AND C. H. DODSON. 1966. *Orchid Flowers—Their Pollination and Evolution*. University of Miami Press, Coral Gables, Florida.
- VOGEL, S. 1963. *Duftdrüsen im Dienste der Bestäubung: über Bau und Funktion der Osmophoren*. Akademie der Wissenschaften und der Literatur, Mainz.
- . 1966. Parfümsammelnde Bienen als Bestäuber von Orchidaceen und *Gloxinia*. Oesterreichische Botanische Zeitschrift 113: 302–361.
- . 1990. *The Role of Scent Glands in Pollination: On the Structure and Function of Osmophores*. Smithsonian Institution Libraries and National Science Foundation, Washington, D.C. [Translation; original published in 1963.]

## APPENDIX I

(Transcribed from Darwin, 1862a)

The President and Officers of the Linnean Society having kindly permitted me to examine the remarkable specimen, preserved in spirits in their collection, of an Orchid bearing flowers of two supposed genera, and known sometimes to bear the flowers of a third genus, I have thought that the Society might like to hear a short account and explanation of this singular case. The following details will hereafter appear in a small work on the "Fertilization of Orchids by Insect-agency," which I am preparing for early publication.<sup>1</sup>

Botanists were astonished when Sir E. Schomburgk<sup>2</sup> stated that he had seen three distinct forms, believed to constitute three distinct genera, namely *Catasetum tridentatum*, *Monachanthus viridis*, and *Myanthus barbatus*, all growing on the same plant.<sup>3</sup> Lindley<sup>4</sup> remarked that "such cases shake to the foundation all our ideas of the stability of genera and species." Sir R. Schomburgk affirms that he has seen hundreds of plants of *C. tridentatum* in Essequibo without ever finding one specimen with seeds,<sup>5</sup> but that he was surprised at the gigantic seed-vessels of the *Monachanthus*; and he correctly remarks that here we have traces of sexual difference in Orchideous flowers.

The general appearance of the flower of *Catasetum tridentatum*, in its natural position, is given in the diagram, p. 152 (fig. 1); but the two lower sepals have been cut off. The column is figured separately in an upright position, showing the two curious prolongations of the rostellum, or, as I shall call them, the antennae.

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A deep chamber, which from its homological relations must be called the stigmatic chamber, lies between the bases of the antennae; and the anther, with its concealed pollen-masses, is seated above. My object is not here to describe in detail the structure of the flower and its curious mechanism. But it must be observed that the ovarium is much shorter, thinner, less deeply furrowed, more solid in the centre, and the bract at its base smaller, than in the two succeeding sexual forms presently to be described. The ovarium is bent so that the bucket-like labellum stands upper-most, instead of forming the lower lip as in most Orchids.

From what I had myself observed previously to reading Sir B. Schomburgk's paper, I was led to examine carefully the female organs of this species, and, I may add, of *C. callosum* and *C. saccatum*. In no case was the stigmatic surface viscid, as it is in all other Orchids (excepting *Cypripedium*), and as is indispensable for securing the pollen-masses on the rupture of the caudicles. I carefully looked to this point in both young and old flowers of

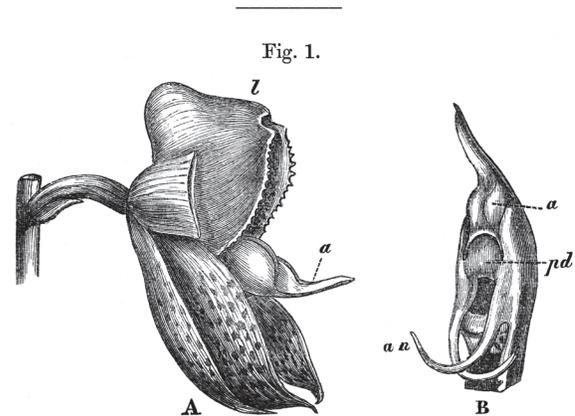
<sup>1</sup> Here Darwin was announcing the first edition of his book on orchid pollination (Darwin, 1862b) (note of the transcriber).

<sup>2</sup> "Transactions of the Linnean Society," vol. xvii. p. 522. Another account, by Dr. Lindley, has appeared in the "[Edwards's] Botanical Register," vol. xxiii. fol. 1951, of a distinct species of *Myanthus* and *Monachanthus* appearing on the same scape: he alludes also to other cases. Some of the flowers were in an intermediate condition, which is not surprising, seeing that in dioecious plants we sometimes have a partial resumption of the characters of both sexes. Mr. Rogers, of River Hill, informs me that he imported from Demerara a *Myanthus*, but that when it flowered a second time it was metamorphosed into a *Catasetum*. Dr. Carpenter (Comparative Physiology, fourth edition, p. 633) alludes to an analogous case which occurred at Bristol.

<sup>3</sup> Schomburgk (1837) never stated "that he had seen three forms, believed to constitute three distinct genera, namely, *Catasetum tridentatum*, *Monachanthus viridis*, and *Myanthus barbatus*, all growing on the same plant." He reported "a remarkable Orchideous plant, from appearance a *Monachanthus*, which on one side of the bulb produced a scape with six flowers of *Monachanthus viridis*, and two of *Myanthus barbatus*, while a second scape of the same bulb had twenty-five blossoms of the *Myanthus barbatus*" (note of the transcriber).

<sup>4</sup> *The Vegetable Kingdom*, 1853, p. 178.

<sup>5</sup> Brongniart states (*Bull. de la Soc. Bot. de France*, 1855, tom. ii. p. 20) that M. Neumann, a skilful fertilizer of Orchids, could never succeed in fertilizing *Catasetum*.

*Catasetum tridentatum*.

a. anther. an. antennae.  
pd. pedicel of pollinium. l. labellum.

A. Side view of flower in its natural position with the properly lower sepals cut off.

B. Front view of column, placed upright.

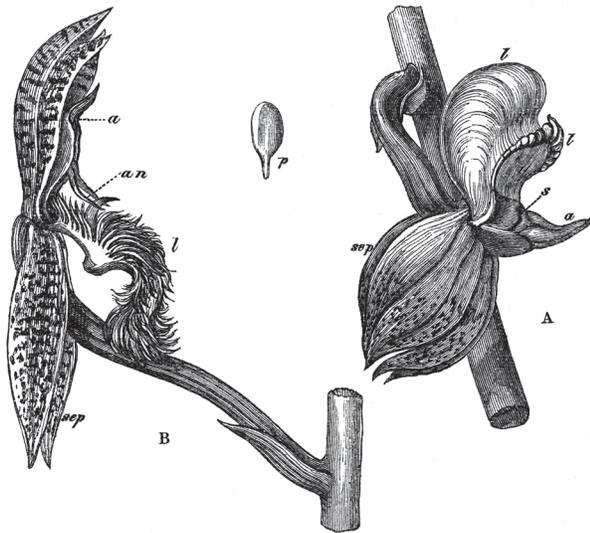
*C. tridentatum*. When the surface of the stigmatic chamber and of the stigmatic canal of the above-named three species is scraped off, after having been kept in spirits of wine, it is found to be composed of utriculi (with nuclei of the proper shape), but not nearly so numerous as with ordinary Orchids. The utriculi cohere more together, and are more transparent. I examined for comparison the utriculi of many kinds of Orchids, which had been kept in

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spirits, and in all found they were much less transparent. Again, in all three species of *Catasetum* the ovule-bearing cords are short, and the ovules present a considerably different appearance, in being thinner, more transparent, and

less pulpy than in the numerous other Orchids examined for comparison. They were, however, in not so completely an atrophied condition as in the genus *Acropera*. Although they correspond so closely in general appearance and position with true ovules, perhaps I have no strict right so to designate them, as I was unable in any case to make out the opening of the testa and the included nucleus; nor were the ovules ever inverted. From these several facts—namely, the shortness, thinness, and smoothness of the ovarium, the shortness of the ovule-bearing cords, the state of the ovules themselves, the stigmatic surface not being viscid, the empty condition of the utriculi —and from Sir R. Schomburgk never having seen *C. tridentatum* producing seed in its native home, we may confidently look at this species of *Catasetum*, as well as the other two species, as male plants.

Fig. 2.



*Myanthus barbatus*.

*Monachanthus viridis*.

a. anther.

p. pollen-mass, rudimentary.

an. antennae.

s. stigmatic cleft.

l. labellum.

sep. two lower sepals.

A. Side view of *Monachanthus viridis* in its natural position. (The shading in both drawings has been added from M. Reiss's drawing in the "Linnean Transactions.")

B. Side view of *Myanthus barbatus* in its natural position.

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With respect to *Monachanthus viridis* and *Myanthus barbatus*, these two forms are seen, in the specimen sent home by Sir R. Schomburgk, and preserved in spirits in the Society's collection, to be borne on the same spike. They are represented in the diagrams, page 153. The flower of the *Monachanthus*, like that of the *Catasetum*, grows lower side uppermost. The labellum is not nearly so deep, especially on the sides, and its edges are crenated. The other petals

and sepals are all reflexed, and are not so much spotted as in the *Catasetum*. The bract at the base of the ovarium is much larger. The whole column, especially the filament at its summit and the spike-like anther, is much shorter; and the front of the rostellum is much less protuberant. The antennae or horn-like prolongations of the rostellum are entirely absent. The pollen-masses are rudimentary: I could find no trace of a viscid disk or of a pedicel; if they exist, they must be quite rudimentary, for there is hardly any space for the imbedment of the disk. The absence of the antenna; in this Orchid, which has no pollen-masses to eject, is an interesting fact, as it accords with the view to which I have been led by an examination of three living species of *Catasetum*, namely, that the function of the antenna is to convey the stimulus of a touch to the medial part of the rostellum, causing the membrane round the disk to rupture, and consequently the liberation and ejection of the pollen-masses. Instead of a large stigmatic chamber, there is a narrow transverse cleft close beneath the small anther. I was able to insert one of the pollen-masses of the male *Catasetum* into this cleft, which, from having been kept in spirits, was lined with coagulated beads of viscid matter and with utriculi. The utriculi, differently from those in *Catasetum*, were charged (after having been kept in spirits) with brown matter. The ovarium is much longer, thicker near the base, and more plainly furrowed than in *Catasetum*; the ovule-bearing cords are also much longer, and the ovules more opaque and pulpy, as in all common Orchids. I believe that I saw the opening at the partially inverted end of the testa with a large nucleus projecting; but as the specimens had been kept many years in spirits, and were somewhat altered, I dare not speak positively. From these several facts it is almost certain that *Monachanthus* is a female plant; and Sir R. Schomburgk saw it seeding abundantly. Altogether this flower differs in a most remarkable manner from that of the male *Catasetum tridentatum*, and it is no wonder that they were formerly ranked as distinct genera.

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The pollen-masses offer so curious and good an illustration of a structure in a rudimentary condition, that they are worth description; but first I must briefly describe the perfect pollen-masses of the male *Catasetum*. These consist of a large sheet of cemented or waxy pollen-grains, folded over so as to form a sac with, an open slit along the lower surface; into this slit cellular tissue enters whilst the pollen is in the course of development in the bud. Within the lower and produced end of each pollen-mass a layer of highly elastic tissue, forming the caudicle, is attached, the other end being attached to the strap-shaped pedicel of the pollinium. The exterior grains of pollen are more angular, have thicker walls, and are yellower than the interior grains. In the early bud the two pollen-masses are enveloped in two conjoined membranous sacs, which are soon penetrated by the two produced ends of the pollen-masses, and by their caudicles; and then the ends of the caudicles adhere to the pedicel. Before the flower expands, the membranous sacs including the pollen-masses open, and leave them resting naked on the back of the rostellum.

In *Monachanthus* the two membranous sacs containing the rudimentary pollen-masses never open; they easily separate from each other and from the anther. The tissue of which they are formed is thick and pulpy. Like most rudimentary parts, they vary greatly in size and in form. The included, and therefore useless, pollen-masses are not one-tenth of the bulk of the pollen-masses of the male: they are flask-shaped, with the lower and produced end greatly exaggerated, and almost penetrating through the exterior or membranous sac. The flask is closed, and there is no fissure along the lower surface. The exterior pollen-grains are square and have thicker walls than the interior grains, just as in the proper male pollen; and what is very curious, each cell has its nucleus. Now R. Brown<sup>6</sup> states that, in the early stages of the formation of the pollen-grains in ordinary Orchids, a minute areola or nucleus is often visible; so that the rudimentary pollen-grains of the *Monachanthus* apparently have retained (as is so general with rudiments in the animal kingdom) an embryonic character. Lastly, at the base, within the flask of pollen, there is a little sheet of brown elastic tissue—that is, a vestige of a caudicle—which runs far up the produced end of the flask, but does not (at least in some of the specimens) come to the surface, and could not have been attached to any part of the rostellum. These rudimentary caudicles are, therefore, utterly useless.

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We thus see that every single detail of structure of the male pollen-masses, with some parts exaggerated and some parts slightly modified, is represented by these mere rudiments in the female plant. Such cases are familiar to every observer, but can never be examined without renewed interest.

We now come to the third form, *Myanthus barbatus*, often borne on the same plant with the two preceding forms. Its flower, in external appearance, but not in essential structure, is the most different of all. It generally stands in a reversed position, compared with *Catasetum* and *Monachanthus*—that is, with the labellum downwards. The labellum is fringed, in an extraordinary manner, with long papillæ; it has a quite insignificant medial cavity, at the hinder margin of which a curious curved and flattened horn projects. The other petals and sepals are spotted and elongated, with the two lower sepals alone reflexed. The antennæ are not so long as in the male *C. tridentatum*, and they project symmetrically on each side of the horn-like projection at the base of the labellum, with their tips (which are not roughened with papillæ as in the male flower) almost entering the medial cavity. The stigmatic chamber is of nearly intermediate size between that of the male and female forms; it is lined with utriculi, charged with brown matter. The straight and well-furrowed ovarium is nearly twice as long as in *Monachanthus*, but is not so thick where it joins the flower; the ovules are not so numerous as in the female form, but are opaque and pulpy after having been kept in spirits, and resemble them in all

respects. I believe, but dare not speak positively as in the case of the *Monachanthus*, that I saw the nucleus projecting from the testa. The pollinia are about a quarter of the size of those of the male *Catasetum*, but have a perfectly well developed disk and pedicel. The pollen-masses were lost in the specimens examined by me; but fortunately M. Reiss has given, in the “*Linnean Transactions*,” a drawing of them, showing that they are of due proportional size, and have the proper folded or cleft structure; so that there can hardly be a doubt that they are functionally perfect. As we thus see that both the male and female organs are apparently perfect, *Myanthus barbatus* may be considered as the hermaphrodite form of the same species, of which the *Catasetum* is the male, and the *Monachanthus* the female.

It is not a little singular that the hermaphrodite *Myanthus* should resemble in its whole structure much more closely the male forms of two distinct species (namely *C. saccatum* and, more especially, *C. callosum*) than either its own male or female forms.

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Finally, the genus *Catasetum* is interesting in an unusual degree in several respects. The separation of the sexes is unknown in other Orchids, excepting probably in the allied genus *Cynoches* and in one other member of the Vandææ, namely, *Acropera*.<sup>7</sup> In *Catasetum* we have three sexual forms,<sup>8</sup> generally borne on separate plants, but sometimes mingled together; and these three forms are wonderfully different from each other—much more different than, for instance, a peacock is from a peahen. But the appearance of these three forms on the same plant now ceases to be an anomaly, and can no longer be viewed as an unparalleled instance of variability.

Still more interesting is this genus in its mechanism for fertilization. We see a flower patiently waiting, with its antennæ stretched forth in a well-adapted position, ready to give notice whenever an insect puts its head into the cavity of the labellum. The female *Monachanthus*, not having pollinia to eject, is destitute of antennæ. In the male and hermaphrodite forms, namely *Catasetum* and *Myanthus*, the pollinia lie doubled up like a spring, ready to be instantaneously shot forth when the antennæ are touched. The disk end is always projected foremost, and is coated with viscid matter, which quickly sets hard and firmly affixes the hinged pedicel to the insect's body. The insect flies from flower to flower, till at last it visits a female or hermaphrodite plant; it then inserts one of the balls of pollen into the stigmatic cavity. When the insect flies away, the elastic caudicle, made weak enough to yield to the viscosity of the stigmatic surface, breaks, and leaves behind the pollen-mass; then the pollen-tubes slowly protrude, penetrate the stigmatic canal, and the act of fertilization is completed. Who would have been bold enough to surmise that the propagation of a species should have depended on so complex, so apparently artificial, and yet so admirable an arrangement?

<sup>6</sup> *Transactions of the Linnean Society*, vol. xvi. p. 711.

<sup>7</sup> A name given to a group of orchids currently treated as *Gongora* section *Acropera*, the plants of which bear hermaphroditic, proterandric flowers, that is, functioning as pollen donors first, then as pollen acceptors (note of the transcriber).

<sup>8</sup> This assertion by Darwin is incorrect: plants of *Catasetum* can bear male flowers (what up to that point had been known as *Catasetum*) and female flowers (what had been described as *Monachanthus*), but not hermaphroditic flowers (what was then known as *Myanthus*, which Darwin regarded as hermaphroditic flowers). We now know, as stated by Rolfe (1890, 1895), that species of *Myanthus* represent certain species of *Catasetum* subgenus *Catasetum* section *Isoceras* (note of the transcriber).

## APPENDIX II

(Transcribed from Darwin, 1869: 154–155)

Fertilization of *Catasetum*.—It has been highly satisfactory to me that my observations and predictive conclusions in regard to *Catasetum* have been fully confirmed by the late Dr. Crüger, the Director of the Botanic Gardens of Trinidad, in letters to me and in his paper in the *Journal of the Linnean Society* (vol. viii. Bot. 1864, p. 127). He sent me specimens of the bees, belonging to three species of *Euglossa*, which he saw gnawing the inside of the labellum. The pollinia, when ejected, become attached to, and lie flat on, the backs of the bees, on the hairy surface of the thorax. Dr. Crüger has also proved that I was correct in asserting that the sexes of *Catasetum* are separate, for he fertilized female flowers with pollen from the male plants; and Fritz Müller effected the same thing with *Catasetum mentosum* in South Brazil. Nevertheless, from two accounts which I have received, it appears that *Catasetum tridentatum*, though a male plant, occasionally produces seed-capsules;<sup>1</sup> but every botanist knows that this occasionally occurs with the males of other dioecious plants. Fritz Müller has given (*Botanische Zeitung*, Sept. 1868, p. 630) a most interesting account, agreeing with mine, of the state of the minute pollinia in the female plant: the anther never opens, and the pollen-masses are not attached to the viscid disks, so that they cannot be removed by a natural means. The pollen-grains, as so generally occurs with rudimentary organs, are extremely variable in size and shape. Nevertheless the grains of the rudimentary pollen-masses belonging to the female plant, when applied (which can never naturally occur) to the stigmatic surface, emitted their pollen-tubes!<sup>2</sup> This appears to me a very curious instance of the slow and gradual manner in which structures are modified; for the female pollen-masses, included within an anther which never opens, are seen still partially to retain their former powers and function.

*Mormodes luxatum* (p. 265).<sup>3</sup>—I have now examined another species of *Mormodes*, the rare *M. luxatum*, and I find that the chief points of structure, and the action of the different parts, including the sensitiveness of the filament, are the same as in *M. ignea*. The cup of the labellum, however, is much larger, and is not pressed down firmly on the filament on the summit of the column. This cup probably

serves to attract insects, and, as in *Catasetum*, is gnawed by them. The flowers are asymmetrical to an extraordinary degree, the right-hand and left-hand sides differing much in shape.

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*Cycnoches ventricosum* (p. 265).—The plant described in my work as a second species of *Mormodes* proves to be *Cycnoches ventricosum*. I first received from Mr. Veitch some flower-buds, from which the section (fig. XXX) was taken; but subsequently he sent me some perfect flowers. The yellowish-green petals and sepals are reflexed; the thick labellum is singularly shaped, with its upper surface convex, like a shallow basin turned upside down. The thin column is of extraordinary length, and arches like the neck of a swan over the labellum; so that the whole flower presents a very singular appearance. In the section of the flower, given in my work, we see the elastic pedicel of the pollinium bowed, as in *Catasetum* or *Mormodes*; but at the period of growth represented in the figure the pedicel was still united to the rostellum, the future line of separation being shown by a layer of hyaline tissue indistinct towards the upper end of the disk. The disk is of gigantic size, and its lower end is produced into a great fringed curtain, which hangs in front of the stigmatic chamber. The viscid matter of the disk sets hard very quickly, and changes colour. The disk adheres to any object with surprising strength. The anther is very different in shape from that of *Catasetum* or *Mormodes*, and apparently would retain the pollen-masses with greater force. A part of the filament of the anther,<sup>4</sup> lying between two little leaf-like appendages, is sensitive; and when this part is touched, the pollinium is swung upwards, as in *Mormodes*, and with sufficient force, if no object stands in the way, to throw it to the distance of an inch. An insect of large size alights probably on the labellum, for the sake of gnawing the convex surface, or perhaps on the extremity of the arched and depending column, and then, by touching the sensitive point, causes the ejection of the pollen-masses, which are affixed to its body and thus transported to another flower or plant.

<sup>1</sup> This interpretation of Darwin's is partially incorrect simply because it is not the plant or even the inflorescence that is male or female, it is the flowers. Plants of *Catasetum* and *Cycnoches* and some species of *Mormodes* can bear male flowers one year and female the next, or even during the same flowering season, and inflorescences can have a mixture of male, female, and rarely intermediate, nonfunctional flowers. However, it is true that a plant of "*Catasetum tridentatum* ... occasionally [bears female flowers and] produces seed-capsules" (note of the transcriber).

<sup>2</sup> Darwin was correct here: female and also intermediate flowers may bear fertile pollen, but the morphology of the flowers and the lack of a functional pollinarium (primarily the absence of a viscidium) keep them from placing it on a pollinator (note of the transcriber).

<sup>3</sup> Darwin cited pages and figures from the first edition of his book (Darwin, 1862b; note of the transcriber).

<sup>4</sup> The function(s) of the filament of the anther, present in all other genera of core Catasetinae (see Romero, 1990, fig. 3; in *Catasetum* it is fused to the clinandrium; see Table 3 above) is not entirely clear. It could trigger the discharge of the pollinarium in *Cycnoches*, but it is not accessible to the pollinator; it may be stimulated via a slight rotation of the anther (which the pollinator does move while collecting fragrances from the labellum; Romero-González et al., in prep.) (note of the transcriber).

## APPENDIX III

(Transcribed from Darwin, 1877a)

## CHAPTER VII.

## VANDEÆ... CATASETIDÆ

Catasetidæ, the most remarkable of all Orchids—The mechanism by which the pollinia of *Catasetum* are ejected to a distance and are transported by insects—Sensitiveness of the horns of the rostellum—Extraordinary difference in the male, female, and hermaphrodite forms of *Catasetum tridentatum*—*Mormodes ignea*, curious structure of the flowers; ejection of the pollinia—*Mormodes luxata*—*Cycnoches ventricosum*, manner of fertilisation.

I have reserved for separate description one sub-family of the Vandeeæ, namely, the Catasetidæ, which must, I think, be considered as the most remarkable of all Orchids.

I will begin with *Catasetum*. A brief inspection of the flower shows that here, as with most other Orchids, some mechanical aid is requisite to remove the pollen-masses from their cells, and to carry them to the stigmatic surface. We shall, moreover, presently see that *Catasetum* is exclusively a male form; so that the pollen-masses must be transported to the female plant, in order that seed should be produced. The pollinium is furnished with a viscid disc of huge size; but this, instead of being placed in a position likely to touch and adhere to an insect visiting the flower, is turned inwards and lies close to the upper and back surface of a chamber, which must be called the stigmatic chamber, though functionless as a stigma. There is nothing in this chamber to attract insects; and even if they did enter it, the viscid surface of the disc could not possibly come into contact with them.

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How then does Nature act? She has endowed these plants with, what must be called for want of a better term, sensitiveness, and with the remarkable power of forcibly ejecting their pollinia even to a considerable distance. Hence, when certain definite points of the flower are touched by an insect, the pollinia are shot forth like an arrow, not barbed however, but having a blunt and excessively adhesive point. The insect, disturbed by so sharp a blow, or after having eaten its fill, flies sooner or later away to a female plant, and, whilst standing in the same position as before, the pollen-bearing end of the arrow is inserted into the stigmatic cavity, and a mass of pollen is left on its viscid surface. Thus, and thus alone, can the five species of *Catasetum* which I have examined be fertilised.

In many Orchideæ, as in *Listera*, *Spiranthes*, and *Orchis*, the surface of the rostellum is so far sensitive, that, when touched or when exposed to the vapour of chloroform, it ruptures in certain defined lines. So it is in the tribe of the Catasetidæ, but with this remarkable difference, that in *Catasetum* the rostellum is prolonged into two curved tapering horns, or, as I shall call them, antennæ, which

stand over the labellum where insects alight. If these are touched even very lightly, they convey some stimulus to the membrane which surrounds and connects the disc of the pollinium with the adjoining surface, causing it instantly to rupture; and as soon as this happens the disc is suddenly set free. We have also seen in several Vandeeæ that the pedicels of the pollinia are fastened flat down in a state of tension, and are highly elastic, so that, when freed, they immediately spring up, apparently for the sake of detaching the pollen-masses from the anther-cells. In the genus *Catasetum*, on the

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other hand, the pedicels are fastened down in a curved position; and when freed by the rupture of the attached edges of the disc, they straighten themselves with such force, that not only do they drag the balls of pollen together with the anther-cells from their places of attachment, but the whole pollinium is jerked forward, over and beyond the tips of the so-called antennæ, to the distance sometimes of two or three feet. Thus, as throughout nature, pre-existing structures and capacities are utilised for new purposes.

*Catasetum saccatum*<sup>1</sup>—I will first describe the male forms, belonging to five species, which are included under the generic name of *Catasetum*. The general appearance of the present species is represented in the following woodcut, fig. 28. A side view of the flower, with all the petals and sepals excepting the labellum cut off, is shown by B; and A gives a front view of the column. The upper sepal and two upper petals surround and protect the column; the two lower sepals project out at right angles. The flower stands more or less inclined to either side, but with the labellum downwards, as represented in the drawing. The dull coppery and orange-spotted tints,—the yawning cavity in the great fringed labellum,—the one antenna projecting with the other hanging down—give to these flowers a strange, lurid, and almost reptilian appearance.

In front of the column, in the middle, the deep stigmatic chamber (fig. 28, A, s), may be seen; but this is best shown in the section (fig. 29, C, s), in which all

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the parts are a little separated from each other, in order that the mechanism may be intelligible. In the middle of the roof of the stigmatic chamber, far back (*d*, in A, fig. 28), the upturned anterior edge of the viscid disc can just be seen. The upper membranous surface of the disc, before it is ruptured, is continuous with the fringed bases of the two antennæ between which it lies. The rostellum projects over the disc and stigmatic chamber (see section C, fig. 29), and is prolonged on each side so as to form the two antennæ;

<sup>1</sup> I am much indebted to Mr. James Veitch of Chelsea for the first specimen which I saw of this Orchid; subsequently, Mr. S. Rucker, so well known for his magnificent collection of Orchids, generously sent me two fine spikes, and has aided me in the kindest manner with other specimens.

the middle part is covered by the ribbon-like pedicel (*ped.*) of the pollinium. The lower end of the pedicel is attached to the disc, and the upper end to the two pollen-masses (*p*) within the anther-cell. The pedicel in its natural position is held much bowed round the protuberant rostellum; when freed it forcibly straightens itself, and at the same time its lateral edges curl inwards. At an early period of growth, it is continuous with the rostellum, but subsequently becomes separated from it by the solution of a layer of cells.

The pollinium when set free and after it has straightened itself, is represented at D, fig. 29. Its under surface, which lies in contact with the rostellum, is shown at E, with the lateral edges of the pedicel now curled inwards. In this latter view, the clefts in the under sides of the two pollen-masses are shown. Within these clefts, near their bases, a layer of strong extensible tissue is attached, forming the caudicles, by which the pollen-masses are united to the pedicel. The lower end of the pedicel is joined to the disc by a flexible hinge, which occurs in no other genus, so that the pedicel can play backwards and forwards, as far as the upturned end (fig. D) of the disc permits. The disc is large and thick; it consists of a strong upper

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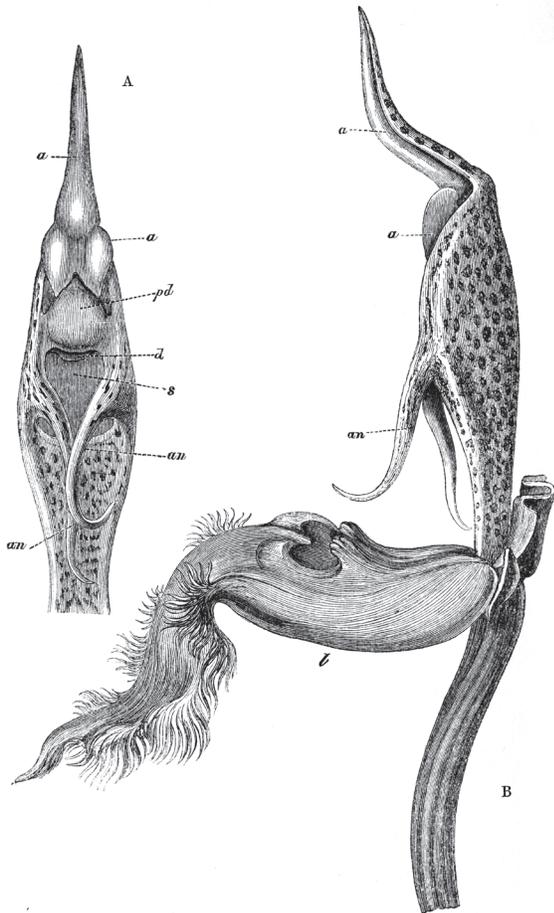


FIGURE 28. *Catasetum saccatum* Lindl.

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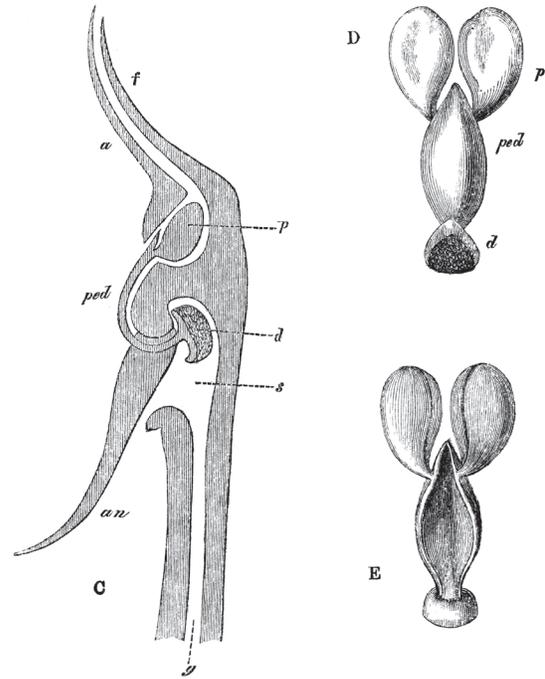


FIGURE 29. *Catasetum saccatum* Lindl.

*a.* anther. *an.* antenna; of the rostellum. *d.* disc of pollinium. *f.* filament of anther. *g.* germen or ovarium. *l.* labellum. *p.* pollen-masses. *pd.* or *ped.* pedicel of pollinium. *s.* stigmatic chamber. A. Front view of column. B. Side view of flower, with all the sepals and petals removed except the labellum. C. Diagrammatic section through the column, with all the parts a little separated. D. Pollinium, upper surface. E. Pollinium, lower surface, which before removal lies in close contact with the rostellum.

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membrane, to which the pedicel is united, with an inferior cushion of great thickness, of pulpy, flocculent, and viscid matter. The posterior margin is much the most viscid part, and this necessarily first strikes any object when the pollinium is ejected. The viscid matter soon sets hard. The whole surface of the disc is kept damp before ejection, by resting close against the roof of the stigmatic chamber; but in the section (fig. C) it is represented, like the other parts, a little separated from the roof.

The connective membrane of the anther (*a* in all the figures) is produced into a spike, which adheres loosely to the pointed end of the column; this pointed end (*f*, fig. C) is homologically the filament of the anther.

The anther has this peculiar shape apparently for the sake of leverage, so that it may be easily torn off by a pull at its lower end, when the pollinium is jerked out by the elasticity of the pedicel.

The labellum stands at right angles to the column, or hangs a little downwards; its lateral and basal lobes are turned under the middle portion, so that an insect can stand only in front of the column. In the middle of the labellum there is a deep cavity, bordered by crests. This cavity does not secrete nectar, but its walls are thick and fleshy, with a slightly sweet nutritious taste; and it will presently be shown that they are gnawed by insects. The extremity of the left-hand antenna stands immediately over the cavity, and would infallibly be touched by an insect visiting this part of the labellum for any purpose.

The antennæ are the most singular organs of the flower, and occur in no other genus. They form rigid, curved horns, tapering to a point. They consist of a narrow ribbon of membrane, with the edges curled inwards so as to touch; each horn therefore is tubular,

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with a slit down one side, like an adder's fang. They are composed of numerous, much elongated, generally hexagonal cells, pointed at both ends; and these cells (like those in most of the other tissues of the flower) have nuclei with nucleoli. The antennæ are prolongations of the sides of the anterior face of the rostellum. As the viscid disc is continuous with a little fringe of membrane on each side, and as this fringe is continuous with the bases of the antennæ, these latter organs are put into direct connection with the disc. The pedicel of the pollinium passes, as already stated, between the bases of the two antennæ. The antennæ are not free for their whole length; but their exterior edges are firmly united to and blend for a considerable space with the margins of the stigmatic chamber.

In all the flowers which I examined, taken from three plants, the two antennæ which are alike in structure occupied the same relative position. The extreme part of the left-hand antenna bends upwards (see B, fig. 28, in which the position is shown plainer than in A), and at the same time a little inwards, so that its tip is medial and guards the entrance into the cavity of the labellum. The right-hand antenna hangs down, with its tip turned a little outwards; and as we shall immediately see, is almost paralysed, so as to be functionless.

Now for the action of the parts. When the left-hand antenna of this species (or either of the antennæ in three of the following species) is touched, the edges of the upper membrane of the disc, which are continuously united with the surrounding surface, instantly rupture, and the disc is set free. The highly elastic pedicel then instantly flings the heavy disc out of the stigmatic chamber with such force, that the whole pollinium is ejected, bringing away with it the two

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balls of pollen, and tearing the loosely attached spike-like anther from the top of the column. The pollinium is always ejected with its viscid disc foremost. I imitated the action with a minute strip of whalebone, slightly weighted at one end to represent the disc; this was then bent half round a cylindrical

object, the upper end being at the same time gently held by the smooth head of a pin, to represent the retarding action of the anther, the lower end was then suddenly set free, and the whalebone was pitched forward, like the pollinium of the *Catasetum*, with the weighted end foremost.

That the disc is first jerked out of the stigmatic chamber, I ascertained by pressing the middle of the pedicel; and when I touched the antenna the disc instantly sprung forth, but, owing to the pressure on the pedicel, the pollinium was not dragged out of the anther-cell. Besides the spring from the straightening of the pedicel, elasticity in a transverse direction comes into play: if a quill be split lengthways, and the half be forced longitudinally on a too thick pencil, immediately the pressure is removed the quill jumps off; and an analogous action takes place with the pedicel of the pollinium, owing to the sudden inward curling of its edges, when set free. These combined forces suffice to eject the pollinium with considerable force to the distance of two or three feet. Several persons have told me that, when touching the flowers of this genus in their hothouses, the pollinia have struck their faces. I touched the antennæ of *C. callosum* whilst holding the flower at about a yard's distance from a window, and the pollinium hit the pane of glass, and stuck by its adhesive disc, to the smooth vertical surface.

The following observations on the nature of the

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excitement which causes the disc to separate from the surrounding parts, include some made on the following species. Several flowers were sent me by post and by the railroad, and must have been much jarred, but they had not exploded. I let two flowers fall from a height of two or three inches on the table, but the pollinia were not ejected. I cut off with a crash with a pair of scissors the thick labellum and ovarium close beneath the flower; but this violence produced no effect. Nor did deep pricks in various parts of the column, even within the stigmatic chamber. A blow, sufficiently hard to knock off the anther, causes the ejection of the pollinium, as occurred to me once by accident. Twice I pressed rather hard on the pedicel, and consequently on the underlying rostellum, without any effect. Whilst pressing on the pedicel, I gently removed the anther, and then the pollen-bearing end of the pollinium sprang up from its elasticity, and this movement caused the disc to separate. M. Meniere,<sup>2</sup> however, states that the anther-case sometimes detaches itself, or can be gently detached, without the disc separating; and that then the upper end of the pedicel, bearing the pollen-masses, swings downwards in front of the stigmatic chamber.

After trials made on fifteen flowers of three species, I find that no moderate degree of violence on any part of the flower, except on the antennæ, produces any effect. But when the left-hand antenna of *C. saccatum*, or either antenna of the three following species, is touched, the pollinium is instantly ejected. The extreme tip and the whole length of the antennæ are sensitive. In one specimen of *C. tridentatum* a touch from a bristle sufficed; in five specimens of

<sup>2</sup> *Bull. de la Soc. Bot. de France*, tom. i. 1854, p. 367.

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*C. saccatum* a gentle touch from a fine needle was necessary; but in four other specimens a slight blow was requisite. In *C. tridentatum* a stream of air and of cold water from a small pipe did not suffice; nor in any case did a touch from a human hair; so that the antennæ are less sensitive than the rostellum of *Listera*. Such extreme sensitiveness would indeed have been useless to the plant, for, as is now known, the flowers are visited by powerful insects.

That the disc does not separate owing to the simple mechanical movement of the antennæ is certain; for they adhere firmly for a considerable space to the sides of the stigmatic chamber, and are thus immovably fixed near their bases. If a vibration is conveyed along them, it must be of some special nature, for ordinary jars of manifold greater strength do not excite the act of rupture. The flowers in some cases, when they first arrived, were not sensitive, but after the cut-off spikes had stood for a day or two in water they became sensitive. Whether this was owing to fuller maturity or to the absorption of water, I know not. Two flowers of *C. callosum*, which were completely torpid, were immersed in tepid water for an hour; and then the antennæ became highly sensitive; this indicates either that the cellular tissue of the antennæ must be turgid in order to receive and convey the effects of a touch, or, as is more probable, heat increases their sensitiveness. Two other flowers placed in hot water, but not so hot as to scald my fingers, spontaneously ejected their pollinia. A plant of *C. tridentatum* had been kept for some days in a rather cool house, and the antennæ were consequently in a torpid condition; a flower was cut off and placed in water at a temperature of 100°F. (37.7°C), and no effect was immediately produced; but when it was

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looked at after an interval of 1 h 30 m the pollinium was found ejected. Another flower was placed in water at 90°F. (32.2°C), and after 25 m the pollinium was found ejected: two other flowers left for 20 m in water at 87°F. (30.5°C.) did not explode, though they were afterwards proved to be sensitive to a slight touch. Lastly, four flowers were placed in water at 83°F. (28.3°C.); two of these did not eject their pollinia in 45 m, and were then found to be sensitive; whereas the other two, when looked at after 1 hour 15 m, had spontaneously ejected their pollinia. These cases show that immersion in water raised to a temperature only a little higher than that to which the plant had been exposed, causes the membrane by which the discs are attached to rupture. A thin stream of almost boiling water was allowed to fall through a fine pipe on the antennæ of some flowers on the above plant; these were softened and killed, but the pollinia were not ejected. Nor did sulphuric acid, dropped on the tips of the antennæ, cause any action; though their upper parts which had not been injured by the acid were afterwards found to be sensitive to a touch. In these two latter cases, I presume

<sup>3</sup> M. Baillon (*Bull. de la Soc. Bot. de France*, tom. i. 1854, p. 285) states that *Catasetum luridum* ejects its pollinia always in a straight line, and in such a direction that it sticks fast to the bottom of the concavity of the labellum; and he imagines that in this position it fertilises the flower in a manner not clearly explained. In a subsequent paper in the same volume (p. 367) M. Ménérier justly disputes M. Baillon's conclusion. He remarks that the anther-case is easily detached, and sometimes naturally detaches itself; the pollinia then swing downwards by the elasticity of the pedicel, the viscid disc still remaining attached to the roof of the stigmatic chamber. M. Ménérier hints that, by the subsequent and progressive retraction of the pedicel, the pollen masses might be carried into the stigmatic chamber. This is not possible in the three species which I have examined, and would be useless. But M. Ménérier himself then goes on to show how important insects are for the fertilisation of Orchids; and apparently infers that their agency comes into play with *Catasetum*, and that this plant does not fertilise itself. Both M. Baillon and M. Ménérier correctly describe the curved position in which the elastic pedicel lies before it is set free. Neither of these botanists seems to be aware that the species of *Catasetum* (at least the five which I have examined) are exclusively male plants.

that the shock was so sudden and violent that the tissue was instantly killed. Considering the above several facts, we may infer that it must be some molecular change which is conveyed along the antennæ, causing the membrane round the discs to rupture. In *C. tridentatum* the antennæ were one inch and a tenth in length, and a gentle touch from a bristle on the extreme tip was conveyed, as far as I could perceive, instantaneously throughout this length. I measured several cells in the tissue composing the antennæ of this species, and on a rough average it appeared that the stimulus must travel through no less than from seventy to eighty cells.

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We may, at least, safely conclude that the antennæ, which are characteristic of the genus *Catasetum*, are specially adapted to receive and convey the effects of a touch to the disc of the pollinium. This causes the membrane to rupture, and the pollinium is then ejected by the elasticity of its pedicel. If we required further proof, nature affords it in the case of the so-called genus *Monachanthus*, which, as we shall presently see, is the female of *Catasetum tridentatum*, and it does not possess pollinia which can be ejected, and the antennæ are here entirely absent.

I have stated that in *C. saccatum* the right-hand antenna invariably hangs down, with the tip turned slightly outwards, and that it is almost paralysed. I ground my belief on five trials, in which I violently hit, bent, and pricked this antenna, and this produced no effect; but when immediately afterwards the left-hand antenna was touched with much less force, the pollinium was shot forth. In a sixth case a forcible blow on the right-hand antenna did cause the act of ejection, so that it is not completely paralysed. As this antenna does not guard the labellum, which in all Orchids is the part attractive, that is to insects, its sensitiveness would be useless.

From the large size of the flower, more especially of the viscid disc, and from its wonderful power of adhesion, I formerly inferred that the flowers were visited by large insects, and this is now known to be the case. The viscid matter sticks so firmly after it, has set hard, and the pedicel is so strong (though very thin and only one-twentieth of an inch in breadth at the hinge), that to my surprise a pollinium attached to an object supported for a few seconds a weight of 1262 grains, or nearly three ounces; and it supported for a considerable time a slightly less weight. When

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the pollinium is shot forth, the large spike-like anther is generally carried with it. If the disc strikes a flat surface like a table, the momentum from the weight of the anther often carries the pollen-bearing end beyond the disc, and the pollinium is thus affixed in a wrong direction for the fertilisation of another flower, supposing it to have been attached to an insect's body. The flight of the pollinium is often rather crooked.<sup>3</sup> But it must not be forgotten that

under nature the ejection is caused by the antennæ being touched by a large insect standing on the labellum, which will thus have its head and thorax placed near to the anther. A rounded object thus held is always accurately struck in the middle, and when removed with the pollinium adhering to it, the weight of the anther depresses the hinge of the pollinium; and in this position the anther-case readily drops off, leaving the balls of pollen free, in a proper position for fertilising the female flower. The utility

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of so forcible an ejection no doubt is to drive the soft and viscid cushion of the disc against the hairy thorax of the large hymenopterous insects which frequent the flowers. When once attached to an insect, assuredly no force which the insect could exert would remove the disc and pedicel; but the caudicles are ruptured without much difficulty, and thus the balls of pollen might readily be left on the adhesive stigma of the female flower.

*Catasetum callosum*.—The flowers of this species<sup>4</sup> are smaller than those of the last, but resemble them in most respects. The edge of the labellum is covered with papillae; the cavity in the middle is small, and behind it there is an elongated anvil-like projection,—facts which I mention from the resemblance in some of these points between the labellum of this species and that of *Myanthus barbatus*, the hermaphrodite form of *Catasetum tridentatum*, presently to be described. When either antenna is touched, the pollinium is ejected with much force. The yellow-coloured pedicel is much bowed, and is joined by a hinge to the extremely viscid disc. The two antennæ stand symmetrically on each side of the anvil-like projection, with their tips lying within the small cavity of the labellum. The walls of this cavity have a pleasant nutritious taste. The antennæ are remarkable, from their whole surface being roughened with papillae. The plant is a male, and the female form is at present unknown.

*Catasetum tabulare*.—This species belongs to the same type as *C. saccatum*, but differs greatly from it in appearance. The central portion of the labellum consists of a narrow, elongated, table-like projection, of

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an almost white colour and formed of a thick mass of succulent tissue, having a sweetish taste. Towards the base of the labellum there is a large cavity, which externally resembles the nectary of an ordinary flower, but apparently never contains nectar. The pointed extremity of the left-hand antenna lies within this cavity, and would infallibly be touched by an insect gnawing the bilobed and basal end of the medial projection of the labellum. The right-hand antenna is turned inwards, with the extreme part bent at right angles and pressed against the column; therefore I do not doubt that it is paralysed as in *C. saccatum*; but the flowers examined by me had lost almost all their sensitiveness.

*Catasetum planiceps* (?).—This species does not differ much from the following one, so I will describe it briefly. The green and spotted labellum stands on the upper side of the flower; it is jar-shaped, with a small orifice. The two elongated and roughened antennæ lie coiled up some little

way apart and parallel to one another, within the labellum. They are both sensitive to a touch.

*Catasetum tridentatum*.—The general appearance of this species, which is very different from that of *C. saccatum*, *callosum* and *tabulare*, is represented in fig. 30, with a sepal on each side cut off.

The flower stands with the labellum uppermost, that is, in a reversed position compared with most Orchids. The labellum is helmet-shaped, its distal portion being reduced to three small points. It cannot hold nectar from its position; but the walls are thick, and have, as in the other species, a pleasant nutritious taste. The stigmatic chamber, though functionless as a stigma, is of large size. The summit of the column, and the spike-like anther, are not so much elongated as in

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*C. saccatum*. In other respects there is no important difference. The antennæ are of greater length; their tips for about one-twentieth of their length are roughened by cells produced into papillæ.

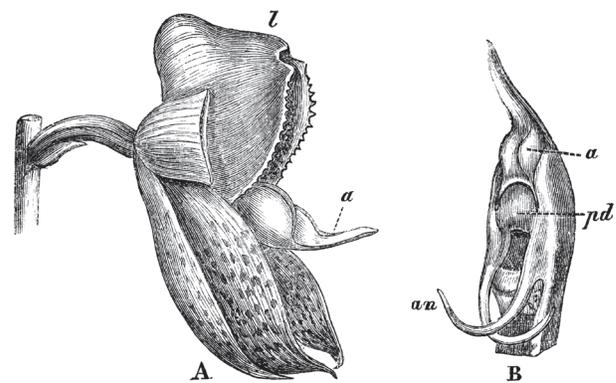


FIGURE 30. *Catasetum tridentatum*. *a*. anther. *pd*. pedicel of pollinium. *an*. antennæ. *l*. labellum. A. Side view of flower in its natural position, with two of the sepals cut off.

B. Front view of column, in position reverse of fig. A.

The pedicel of the pollinium is articulated as before by a hinge to the disc; it can move freely only in one direction owing to one end of the disc being upturned, and this restricted power of movement apparently comes into play when the pollinium is carried by an insect to the female flower. The disc is, as in the other species, of large size, and the end which when ejected first strikes any object, is much more viscid than the rest of the surface. This latter surface is drenched with a milky fluid, which, when exposed to the air, rapidly turns brown, and sets into a cheesy consistence. The upper surface of the disc consists of strong mem-

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brane formed of polygonal cells, resting on and adhering to a thick cushion, formed of irregular rounded balls of brown matter, separated from each other and embedded in a transparent, structureless, highly elastic substance. This cushion towards the posterior end of the disc graduates

<sup>4</sup> A fine spike of flowers of this species was kindly sent me by Mr. Rucker, and was named for me by Dr. Lindley.

into viscid matter, which when consolidated is brown, translucent, and homogeneous. Altogether the disc of *Catasetum* presents a much more complex structure than in the other *Vandææ*.

I need not further describe the present species, except as to the position of the antennæ. They occupied exactly the same position in all the many flowers which were examined. Both lie curled within the helmet-like labellum; the left-hand one stands higher up, with its inwardly bowed extremity in the middle; the right-hand antenna lies lower down and crosses the whole base of the labellum, with the tip just projecting beyond the left margin of the base of the column. Both are sensitive, but apparently the one which is coiled within the middle of the labellum is the more sensitive of the two. From the position of the petals and sepals, an insect visiting the flower would almost certainly alight on the crest of the labellum; and it could hardly gnaw any part of the great cavity without touching one of the two antennæ, for the left-hand one guards the upper part, and the right-hand one the lower part. When either of these is touched the pollinium is ejected and the disc will strike the head or thorax of the insect.

The position of the antennæ in this *Catasetum* may be compared with that of a man with his left arm raised and bent so that his hand stands in front of his chest, and with his right arm crossing his body lower down so that the fingers project just beyond his left side. In *Catasetum callosum* both arms are held lower down

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and are extended symmetrically. In *C. saccatum* the left arm is bowed and held in front, as in *C. tridentatum*, but rather lower down; whilst the right arm hangs downwards paralysed, with the hand turned a little outwards. In every case notice will be given in an admirable manner, when an insect visits the labellum, and the time has arrived for the ejection of the pollinium, so that it may be transported to the female plant.

*Catasetum tridentatum* is interesting under another point of view. Botanists were astonished when Sir R. Schomburgk<sup>5,6</sup> stated that he had seen three forms, believed to constitute three distinct genera, namely, *Catasetum tridentatum*, *Monachanthus viridis*, and *Myanthus barbatus*, all growing on the same plant. Lindley remarked<sup>7</sup> that "such cases shake to the foundation all our ideas of the stability

of genera and species." Sir R. Schomburgk affirms that he has seen hundreds of plants of *C. tridentatum* in Essequibo without ever finding one specimen with seeds;<sup>8</sup> whereas

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he was surprised at the gigantic seed-vessels of the *Monachanthus*; and he correctly remarks that "here we have traces of sexual difference in Orchideous flowers." Dr. Crüger also informs me that in Trinidad he never saw capsules naturally produced by the flowers of this *Catasetum*;<sup>9</sup> nor when they were fertilised by him with their own pollen, as was done repeatedly. On the other hand, when he fertilised the flowers of the *Monachanthus viridis* with pollen from the *Catasetum*, the operation never failed. The *Monachanthus* also commonly produces fruit in a state of nature.

From what I had myself observed, I was led to examine carefully the female organs of *C. tridentatum*, *callosum*, and *saccatum*. In no case was the stigmatic surface viscid, as it is in all other Orchids (except as we shall hereafter see in *Cypripedium*), and as is indispensable for securing the pollen-masses by the rupture of the caudicles. I carefully looked to this point both in young and old flowers of *C. tridentatum*. When the surface of the stigmatic chamber and of the stigmatic canal of the above-named three species is scraped off, after having been kept in spirits, it is found to be composed of utriculi (including nuclei of the proper shape), but not nearly so numerous as with ordinary Orchids. The utriculi cohere more together

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and are more transparent; I examined for comparison those of many kinds of Orchids which had been kept in spirits, and in all found them much less transparent. In *C. tridentatum*, the ovarium is shorter, much less deeply furrowed, narrower at the base, and internally more solid than in *Monachanthus*. Again, in all three species of *Catasetum* the ovule-bearing cords are short; and the ovules present a considerably different appearance, in being thinner, more transparent, and less pulpy than in the numerous other Orchids examined for the sake of comparison. Perhaps these bodies hardly ought to be called ovules, although they correspond closely in general appearance and position with true ovules, for I was unable in any case to make out the opening of the testa and the included nucleus; nor were the ovules ever inverted.

<sup>5</sup> *Transactions of the Linnean Soc.* vol. xvii. p. 522. Another account by Dr. Lindley appeared in the [*Edwards's*] *Botanical Register*, fol. 1951, of a distinct species of *Myanthus* and *Monachanthus* appearing on the same scape: he alludes also to other cases. Some of the flowers in these cases were in an intermediate condition, which is not surprising, seeing that in dioecious plants we sometimes have a partial resumption of the characters of both sexes. Mr. Rodgers of River-hill informs me that he imported from Demerara a *Myanthus*, and that when it flowered a second time it was metamorphosed into a *Catasetum*. Dr. Carpenter (*Comparative Physiology*, 4th edit. p. 633) alluded to an analogous case which occurred at Bristol. Lastly Dean Herbert informed me many years ago that *Catasetum luridum* flowered and kept true for nine years in the Botanic Garden at York; it then threw up a scape of a *Myanthus*, which as we shall presently see is an hermaphrodite, intermediate in form between the male and female. Duchartre has given a full historical account of the appearance of these forms on the same plant, in *Bull. de la Soc. Bot. de France*, vol. ix. 1862, p. 113.

<sup>6</sup> See note 3 of Appendix 1 (note of the transcriber).

<sup>7</sup> *The Vegetable Kingdom*, 1853, p. 178.

<sup>8</sup> Brongniart states (*Bull. de la Soc. Bot. de France*, tom. ii. 1855, p. 20) that M. Neumann, a skilful fertiliser of Orchids, could never succeed in fertilising *Catasetum*.

<sup>9</sup> Dr. Hance writes to me that he has in his collection a plant of *Catasetum tridentatum* from the West Indies bearing a fine capsule; but it does not appear to have been ascertained that this particular flower was that of *Catasetum*, and there is no great improbability in a single flower of *Monachanthus* being produced by a plant of *Catasetum*, as well as a whole scape, which we know has often occurred. J. G. Beer says (quoted by Irmisch, *Beiträge zu Biologie der Orchideen*, 1853, p. 22) that during three years he tried in vain to fertilise *Catasetum*, but on one occasion, by placing only the viscid disc of a pollinium within the stigma, a ripe fruit was produced; but it may be asked, Did the seeds contain embryos?

From these several facts, namely,—the shortness, smoothness, and narrowness of the ovarium, the shortness of the ovule-bearing cords, the state of the ovules themselves, the stigmatic surface not being viscid, the transparent condition of the utriculi,—and from neither Sir R. Schomburgk nor Dr. Crüger having ever seen *C. tridentatum* producing seed in its native home, or when artificially fertilised, we may confidently look at this species, as well as the other species of *Catasetum*, as male plants.

With respect to *Monachanthus viridis*, and *Myanthus barbatus*, the President of the Linnean Society has kindly permitted me to examine the spike bearing these two so-called genera, preserved in spirits, which was sent home by Sir R. Schomburgk. The flower of the *Monachanthus* (A, fig. 31) resembles pretty closely in external appearance that of *Catasetum tridentatum* (fig. 30). The labellum, which holds the same relative position to the other parts, is not nearly so deep

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especially on the sides, and its edge is crenated. The other petals and sepals are all reflexed, and are not so much spotted as in the *Catasetum*. The bract at the base of the ovarium is much larger. The whole column,

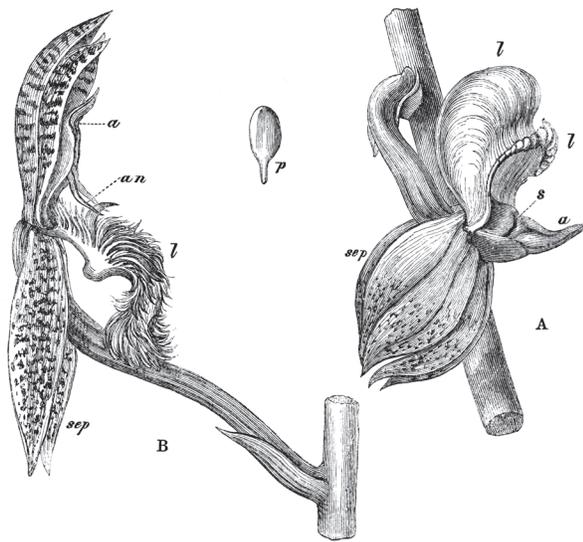


FIGURE 31. *Myanthus barbatus*.

a. anther. an. antennæ. l. labellum. p. pollen-mass, rudimentary. s. stigmatic cleft. sep. two lower sepals. A. *Monachanthus viridis*. A. Side view of *Monachanthus viridis* in its natural position. (The shading in both drawings has been added from Mr. Reiss' drawing in the Linnean Transactions.) B. Side view of *Myanthus barbatus* in its natural position.

especially the filament and the spike-like anther, are much shorter; and the rostellum is much less protuberant. The antennæ are entirely absent, and the pollen-masses are rudimentary. These are interesting

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facts, from corroborating the view taken of the function of the antennæ; for as there are no pollinia to eject, an organ adapted to convey the stimulus from the touch of an insect to the rostellum would be useless. I could find no trace of a viscid disc or pedicel, and no doubt they had been lost; for Dr. Crüger says<sup>10</sup> that "the anther of the female flower drops off immediately after the opening of the same, i.e. before the flower has reached perfection as regards colour, size, and smell. The disc does not cohere, or very slightly, to the pollen-masses, but drops off about the same time, with the anther;" leaving behind them the rudimentary pollen-masses.

Instead of a large stigmatic chamber, there is a narrow transverse cleft close beneath the small anther. I was able to insert one of the pollen-masses of the male *Catasetum* into this cleft, which from having been kept in spirits was lined with coagulated beads of viscid matter, and with utriculi. The utriculi, differently from those in *Catasetum*, were charged (after having been kept in spirits) with brown matter. The ovarium is longer, thicker near the base, and more plainly furrowed than in *Catasetum*; the ovule-bearing cords are also much longer, and the ovules more opaque and pulpy, as in all common Orchids. I believe that I saw the opening at the partially inverted end of the testa, with a large projecting nucleus; but as the specimens had been kept many years in spirits and were somewhat altered, I dare not speak positively. From these facts alone it is almost certain that *Monachanthus* is a female plant; and as already stated, Sir E. Schomburgk and Dr. Crüger have both seen it seeding abundantly. Altogether the flower differs in a most

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remarkable manner from that of the male *Catasetum tridentatum*, and it is no wonder that the two plants were formerly ranked as distinct genera.

The pollen-masses offer so curious and good an illustration of a structure in a rudimentary condition, that they are worth description; but I must first recur to the perfect pollen-masses of the male *Catasetum*. These may be seen at D and E, fig. 29, attached to the pedicel: they consist of a large sheet of cemented or waxy pollen-grains, folded over so as to form a sack, with an open slit along the lower surface, within which at the lower and produced end, a layer of highly elastic tissue, forming the caudicle, is attached; the other end being attached to the pedicel of the rostellum. The exterior grains of pollen are more angular, have thicker walls, and are yellower than the interior grains. In the early bud the two pollen-masses are enveloped in two conjoined membranous sacks, which are soon penetrated by the two produced ends of the pollen-masses and by their caudicles; and afterwards the extremities of the caudicles adhere to

<sup>10</sup> *Journ. Linn. Soc. Bot.* vol viii. 1864, p. 127.

the pedicel. Before the flower expands the membranous sacks including the two pollen-masses open; and the pollen-masses are left resting naked on the back of the rostellum.

In *Monachanthus*, on the other hand, the two membranous sacks containing the rudimentary pollen-masses never open; but they easily separate from each other and from the anther. The tissue of which they are formed is thick and pulpy. Like most rudimentary parts, the pollen-masses vary much in size and form; they are only about one-tenth of the bulk of those of the male; they are flask-shaped (*p*, fig. 31), with the lower end greatly produced so as almost to penetrate the exterior or membranous sack. There is

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no fissure along their lower surfaces for the protrusion of the caudicles. The exterior pollen-grains are square and have thicker walls than the interior grains, just as in the proper male pollen; and, what is very curious, each cell has its nucleus. Now, B. Brown states<sup>11</sup> that in the early stages of the formation of the pollen-grains of ordinary Orchids (as with other plants) a minute nucleus is often visible; so that the rudimentary pollen-grains of *Monachanthus* apparently have retained—as is so general with rudiments in the animal kingdom—an embryonic character. Lastly, at the base, within each flask-shaped pollen-mass, there is a little mass of brown elastic tissue,—that is, a vestige of a caudicle,—which runs far up the pointed end of the flask, but does not (at least in some of the specimens) come to the surface, and could never be attached to any part of the pedicel. These rudimentary and enclosed caudicles are, therefore, utterly useless. Notwithstanding the small size and almost aborted condition of the female pollen-masses, when they were placed by Dr. Crüger within the stigma of a female plant they emitted “here and there a rudimentary tube.” The petals then faded and the ovarium enlarged, but after a week it turned yellow and finally dropped off without bringing any seeds to perfection. This appears to me a very curious instance of the slow and gradual manner in which structures are modified; for the female pollen-masses, which can never be naturally removed or applied to the stigma, still partially retain their former powers and function.

Thus every detail of structure which characterises the male pollen-masses is represented in the female plant in a useless condition. Such cases are familiar to

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every naturalist, but can never be observed without renewed interest. At a period not far distant, naturalists will hear with surprise, perhaps with derision, that grave and learned men formerly maintained that such useless organs were not remnants retained by inheritance, but were specially created and arranged in their proper places like dishes on a table (this is the simile of a distinguished botanist) by an Omnipotent hand “to complete the scheme of nature.”

The third form, *Myanthus barbatus* (fig. 31, B), is sometimes borne on the same plant together with the two

preceding forms. The flowers differ greatly in external appearance, but not in essential structure, from those of both the other forms. They generally stand in a reversed position, compared with those of *Catasetum tridentatum* and of *Monachanthus viridis*, that is, with the labellum downwards. The labellum is fringed in an extraordinary manner with long papillae; it has a quite insignificant medial cavity, at the hinder margin of which a curious curved and flattened horn projects, which represents the anvil-like projection on the labellum of the male *C. callosum*. The other petals and sepals are spotted and elongated, with the two lower sepals alone reflexed. The antennæ are not so long as in the male *C. tridentatum*; they project symmetrically on each side of the horn-like process at the base of the labellum, with their tips, which are not roughened with papillae, almost entering the medial cavity. The stigmatic chamber is of nearly intermediate size between that of the male and female forms; it is lined with utriculi charged with brown matter. The straight and well-furrowed ovarium is nearly twice as long as that of the female *Monachanthus*, but not so thick where it joins the flower; the ovules are opaque and pulpy after having been kept

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in spirits, and resemble those of the female in all respects, but are not so numerous. I believe that I saw the nucleus projecting from the testa, but dare not, as in the case of the *Monachanthus*, speak positively. The pollinia are about a quarter of the size of those of the male *Catasetum*, but have a perfectly well developed disc and pedicel. The pollen-masses were lost in the specimens examined by me; but Mr. Reiss has given, in the *Linnean Transactions*, a drawing of them, showing that they are of due proportional size and have the proper folded or cleft structure, within which the caudicles are attached. Thus as both the male and female organs are in appearance perfect, *Myanthus barbatus* may be considered as an hermaphrodite form of the same species, of which the *Catasetum* is the male and *Monachanthus* the female. Nevertheless, the intermediate forms, which are common in Trinidad, and which resemble more or less closely the above described *Myanthus*, have never been seen by Dr. Crüger to produce seed-capsules.

It is a highly remarkable fact, that this sterile hermaphrodite form resembles in its whole appearance and structure the males of two other species, namely, *C. saccatum* and more especially *C. callosum*, much more closely than it does either the male or female form of the same species. As all orchids, with the exception of a few in the present small subfamily, as well as all the members of several allied groups of plants, are hermaphrodites, there can be no doubt that the common progenitor of the Orchideæ was an hermaphrodite. We may therefore attribute the hermaphrodite condition and the general appearance of *Myanthus* to reversion to a former state; and if so, the ancestors of all the species of *Catasetum* must

<sup>11</sup> *Transactions of the Linnean Soc.* vol. xvi. p. 711.

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have resembled the males of *C. saccatum* and *callosum*, for as we have just seen, it is to these two plants that *Myanthus* presents so many striking resemblances.<sup>12</sup>

Lastly I may be permitted to add that Dr. Crüger, after having carefully observed these three forms in Trinidad, fully admits the truth of my conclusion that *Catasetum tridentatum* is the male and *Monachanthus viridis* the female of the same species. He further confirms my prediction that insects are attracted to the flowers for the sake of gnawing the labellum, and that they carry the pollen-masses from the male to the female plant. He says “the male flower emits a peculiar smell about twenty-four hours after opening, and the antennæ assume their greatest irritability at the same time. A large humble-bee, noisy and quarrelsome, is now attracted to the flowers by the smell, and a great number of them may be seen every morning for a few hours disputing with each other for a place in the interior of the labellum, for the purpose of gnawing off the cellular tissue on the side opposite to the column, so that they turn their backs to the latter. As soon as they touch the upper antenna of the male flower, the pollen-mass, with its disc and gland, is fixed on their back, and they are often seen flying about with this peculiar-looking ornament on them. I have never seen it attached except to the very middle of the

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thorax. When the bee walks about, the pollen-mass lies flat on the back and wings; but when the insect enters a female flower, always with the labellum turned upwards, the pollinium, which is hinged to the gland by elastic tissue, falls back by its own weight and rests on the anterior face of the column. When the insect returns backwards from the flower, the pollinia are caught by the upper margin of the stigmatic cavity, which projects a little beyond the face of the column; and if the gland be then detached from the back of the insect, or the tissues which connect the pollinia with the caudicle, or this with the gland, break, fecundation takes place.” Dr. Crüger sent me specimens of the humble-bees which he caught gnawing the labellum, and these consist of *Euglossa nov. spec.*, *cajennensis* and *piliventris*.<sup>13</sup>

*Catasetum mentosum* and a *Monachanthus*, according to Fritz Müller,<sup>14</sup> grow in the same district of South Brazil; and he easily succeeded in fertilising the latter with pollen from the former. The pollen-masses could be inserted only partially into the narrow stigmatic cleft; but when this was done, a process of deglutition, as described under *Cirrhaea*, commenced and was slowly completed. On the other hand, Fritz Müller entirely failed in his attempts to fertilise the flowers of this *Catasetum* with its own pollen or with that from another plant. The pollinia of the female *Monachanthus* are very small; the pollen-grains are variable both in size

and shape; the anther never opens, and the pollen-masses are not attached to the caudicle. Nevertheless, when these rudimentary pollen-masses, which can never naturally be removed from their cells, were placed on the slightly viscid

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stigma of the male *Catasetum*, they emitted their tubes.

The genus *Catasetum* is interesting to an unusual degree in several respects. The separation of the sexes is unknown amongst other Orchids, except perhaps in the allied genus *Cycnoches*. In *Catasetum* we have three sexual forms, generally borne on separate plants, but sometimes mingled together on the same plant; and these three forms are wonderfully different from one another, much more different than, for instance, a peacock is from a peahen. But the appearance of these three forms now ceases to be an anomaly, and can no longer be viewed as an unparalleled instance of variability.

This genus is still more interesting in its manner of fertilisation. We see a flower patiently waiting with its antennæ stretched forth in a well-adapted position, ready to give notice whenever an insect puts its head into the cavity of the labellum. The female *Monachanthus*, not having true pollinia to eject, is destitute of antennæ. In the male and hermaphrodite forms, namely *Catasetum tridentatum* and *Myanthus barbatus*, the pollinia lie doubled up, like a spring, ready to be instantly shot forth when the antennæ are touched. The disc end is always projected foremost, and is coated with viscid matter which quickly sets hard and affixes the hinged pedicel firmly to the insect's body. The insect flies from flower to flower, till at last it visits a female plant: it then inserts one of the pollen-masses into the stigmatic cavity. As soon as the insect flies away the elastic caudicle, made weak enough to yield to the viscosity of the stigmatic surface, breaks, and leaves behind a pollen-mass; then the pollen-tubes slowly protrude, penetrate the stigmatic canal, and the act of fertilisation is completed. Who would have

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been bold enough to have surmised that the propagation of a species depended on so complex, so apparently artificial, and yet so admirable an arrangement?

I have examined three other genera placed by Lindley in the small sub-family of Catasetidæ, namely, *Mormodes*, *Cycnoches* and *Cyrtopodium*. The latter plant was purchased by me under this name, and bore a flower-stem about four feet in height with yellowish bracts spotted with red; but the flowers presented none of the remarkable peculiarities of the three other genera, with the exception that the anther was hinged to a point projecting from the summit of the column, as in *Catasetum*.

<sup>12</sup> The male of the Indian antelope (*A. bezoartica*) after castration produces horns of a widely different shape from those of the perfect male; and larger and thicker than those occasionally produced by the female. We see something of the same kind in the horns of the common ox. I have remarked in my *Descent of Man* (2nd edit. p. 506), that such cases may probably be attributed to reversion to a former state of the species; for we have good reason to believe that any cause which disturbs the constitution leads to reversion. *Myanthus*, though having the organs of both sexes apparently perfect, is sterile; it has therefore had its sexual constitution disturbed, and this seems to have caused it to revert in character to a former state.

<sup>13</sup> Check comments in Nemésio and Rasmussen (2011) about euglossine bees cited by Darwin (note of the transcriber).

<sup>14</sup> *Bot. Zeitung*, 1868, p. 630.

*Mormodes ignea*.—To show how difficult it sometimes is to understand the manner in which an Orchid is fertilised, I may mention that I carefully examined twelve flowers,<sup>15</sup> trying various experiments and recording the results, before I could at all make out the meaning and action of the several parts. It was plain that the pollinia were ejected, as in *Catasetum*, but how each part of the flower played its proper part I could not even conjecture. I had given up the case as hopeless, until summing up my observations, the explanation presently to be given, and subsequently proved by repeated experiments to be correct, suddenly occurred to me.

The flower presents an extraordinary appearance, and its mechanism is even more curious than its appearance (fig. 32). The base of the column is bent backwards, at right angles to the ovarium or footstalk,

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and then resumes an upright position to near its summit, where it is again bent. It is, also, twisted in a unique manner, so that its front surface, including

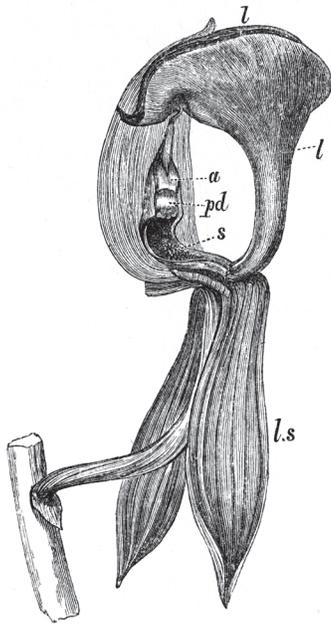


FIGURE 32. *Mormodes ignea*.

Lateral view of flower, with the upper sepal and the near upper petal cut off.

N.B. The labellum in the drawing is a little lifted up, to show the depression on its under surface, which ought to be pressed close down on the bent summit of the column. *a.* anther. *pd.* pedicel of pollinium.

*s.* stigma. *l.* labellum *l. s.* lateral sepal.

the anther, rostellum, and the upper part of the stigma faces one side of the flower; this being either to the

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right or left, according to the position of the flower on the spike. The twisted stigmatic surface extends down to the base of the column and is hollowed out into a deep cavity at its upper end. The large viscid disc of the pollinium is lodged in this cavity close beneath the rostellum; and the rostellum is seen in the drawing (*pd.*) covered by the bowed pedicel.

The anther-case (*a* in the figure) is elongated and triangular, closely resembling that of *Catasetum*; but it does not extend up to the apex of the column. The apex consists of a thin flattened filament, which from the analogy of *Catasetum* I suppose to be the produced filament of the stamen; but it may be a prolongation of some other element of the column. In the bud-state it is straight, but before the flower expands, it becomes much bent by the pressure of the labellum. A group of spiral vessels runs up the column as far as the summit of the anther-case; they are then reflexed and run some way down the anther-case. The point of reflexion forms a short thin hinge by which the top of the anther-case is articulated to the column beneath its bent summit. The hinge, although smaller than a pin's head in size, is of paramount importance; for it is sensitive and conveys the stimulus from a touch to the disc of the pollinium, causing it to separate from its place of attachment. The hinge also serves to guide the pollinium during its ejection. As it has to convey the necessary stimulus to the disc, one may suspect that a portion of the rostellum, which lies in close contact with the filament of the anther, runs up to this point; but I could not here detect any difference in structure on comparing these parts with those of *Catasetum*. The cellular tissue round the hinge is gorged with fluid, and a large drop exudes when the anther is torn from the column during the ejection

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of the pollinium. This gorged condition may perhaps facilitate the rupture of the hinge.

The pollinium does not differ much from that of *Catasetum* (see fig. 29, D, p. 183); and it lies in like manner curved round the rostellum, which is less protuberant than in that genus. The upper and broad end of the pedicel, however, extends beneath the pollen-masses within the anther; and these are attached by rather weak caudicles to a medial crest on its upper surface.

The viscid surface of the large disc lies in contact with the roof of the stigmatic cavity, so that it cannot be touched by an insect visiting the flower. The anterior end of the disc is furnished with a small dependent curtain (dimly shown in fig. 32); and this, before the act of ejection, is continuously joined on each side to the upper margins of the stigmatic cavity. The pedicel is united to the posterior end of the disc; but when the disc is freed, the lowermost part of the pedicel becomes doubly bent, so that it then appears as if attached by a hinge to the centre of the disc.

The labellum is a highly remarkable structure: it is narrowed at its base into a nearly cylindrical foot-stalk, and its sides are so much reflexed as almost to meet at the

<sup>15</sup> I must express my cordial thanks to Mr. Rucker, of West Hill, Wandsworth, for having lent me a plant of this *Mormodes* with two fine spikes, bearing an abundance of flowers, and for having allowed me to keep the plant for a considerable time.

back, forming a folded crest on the summit of the flower. After rising up perpendicularly it arches over the apex of the column, against which it is firmly pressed down. The labellum at this point is hollowed out (even in the bud) into a slight cavity, which receives the bent summit of the column. This slight depression manifestly represents the large cavity, with thick fleshy walls, which insects gnaw, on the anterior surface of the labellum in the several species of *Catasetum*. Here by a singular change of function, the cavity serves to keep the labellum in its proper position on the summit of the column, but is, perhaps,

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likewise attractive to insects. In the drawing (fig. 32) the labellum has been forcibly raised a little up, so as to show the depression and the bent filament. In its natural position it may almost be compared to a huge cocked-hat, supported by a footstalk and placed on the head of the column.

The twisting of the column, which I have seen in no other Orchid, causes all the important organs of fructification in the flowers on the left side of the spike to face to the left, and in all those on the right side to face to the right. So that two flowers taken from opposite sides of the same spike and held in the same relative position are seen to be twisted in opposite directions. One single flower, which was crowded by the others, was barely twisted, so that its column faced the labellum. The labellum is also slightly twisted: for instance, in the flower figured, which faced to the left, the midrib of the labellum was first twisted to the right-hand, and then to the left, but in a less degree, and being bent over it pressed on the posterior surface of the crooked summit of the column. The twisting of all the parts of the flower commences in the bud.

The position thus acquired by the several organs is of the highest importance; for if the column and labellum had not been twisted laterally, the pollinia, when shot forth, would have struck the overarching labellum and have then rebounded, as actually occurred with the single abnormal flower having a nearly straight column. If the organs had not been twisted in opposite directions on the opposite sides of the same crowded spike, so as always to face to the outside, there would not have been a clear space for the ejection of the pollinia and their adhesion to insects.

When the flower is mature the three sepals hang

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down, but the two upper petals remain nearly upright. The bases of the sepals, and especially of the two upper petals, are thick and swollen and have a yellowish tint; when quite mature, they are so gorged with fluid, that, if punctured by a fine glass tube, the fluid rises by capillary attraction to some height in it. These swollen bases, as well as the footstalk of the labellum, have a decidedly sweet and pleasant taste; and I can hardly doubt that they are attractive to insects, for no free nectar is secreted.

I will now endeavour to show how all the parts of the flower are co-ordinated and act together. The pedicel of the

pollinium is bowed round the rostellum, as in *Catasetum*; in this latter genus, when freed, it merely straightens itself with force, in *Mormodes* something more takes place. If the reader will look forward to fig. 34 (p. 223), he will see a section of the flower-bud of the allied genus of *Cycnoches*, which differs only in the shape of the anther and in the viscid disc having a much deeper dependent curtain. Now let him suppose the pedicel of the pollinium to be so elastic that, when freed, it not only straightens itself, but suddenly bends back on itself with a reversed curvature, so as to form an irregular hoop. The curved surface which was before in contact with the protuberant rostellum now forms the outside of the hoop. The exterior surface of the curtain, which depends beneath the disc, is not viscid; and it now lies on the anther-case, with the viscid surface of the disc on the outside. This is exactly what takes place with *Mormodes*. But the pollinium assumes with such force its reversed curvature (aided, apparently, by a transverse curling outwards of the margins of the pedicel), that it not only forms itself into a hoop, but suddenly springs away from the protuberant

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lace of the rostellum. As the two pollen-masses adhere, at first, rather firmly to the anther-case, the latter is torn off by the rebound; and as the thin hinge at the summit of the anther-case does not yield so easily as the basal margin, the pollinium together with the anther-case is instantly swung upwards like a pendulum. But in the course of the upward swing the hinge yields, and the whole body is projected perpendicularly up in the air, an inch or two above and close in front of the terminal part of the labellum. If no object is in the way, as the pollinium falls down, it generally alights and sticks, though not firmly, on the folded crest of the labellum, directly over the column. I witnessed repeatedly all that has been here described.

The curtain of the disc, which, after the pollinium has formed itself into a hoop, lies on the anther-case, is of considerable service in preventing the viscid edge of the disc from adhering to the anther, and thus permanently retaining the pollinium in the form of a hoop. This would have been fatal, as we shall presently see, to a subsequent movement of the pollinium which is necessary for the fertilisation of the flower. In some of my experiments, when the free action of the parts was checked, this did occur, and the pollinium, together with the anther-case, remained permanently glued together in the shape of an irregular hoop.

I have already stated that the minute hinge by which the anther-case is articulated to the column, a little way beneath its bent filamentary apex, is sensitive to a touch. I tried four times and found that I could touch with some force any other part; but when I gently touched this point with the finest needle, instantly the membrane which unites the disc

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to the edges of the stigmatic cavity where it is lodged, ruptured, and the pollinium was shot upwards and fell on the crest of the labellum as just described.

Now let us suppose an insect to alight on the folded crest of the labellum, and no other convenient landing-place is afforded, and then to lean over the front of the column so as to gnaw or suck the bases of the petals swollen with sweet fluid. The weight and movements of the insect would disturb the labellum and the bent underlying summit of the column; and the latter, pressing on the hinge in the angle, would cause the ejection of the pollinium, which would infallibly strike the head of the insect and adhere to it. I tried by placing my gloved finger on the summit of the labellum, with the tip just projecting beyond its margin, and then gently moving my finger it was really beautiful to see how instantly the pollinium was projected upwards, and how accurately the viscid surface of the disc struck my finger and firmly adhered to it. Nevertheless, I doubt whether the weight and movements of an insect would suffice to thus act indirectly on the sensitive point; but look at the drawing and see how probable it is that an insect leaning over would place its front legs over the edge of the labellum on the summit of the anther-case, and thus touch the sensitive point. The pollinium would then be ejected, and the viscid disc would certainly strike and adhere to the insect's head.

Before proceeding, it may be worth while to mention some of the early trials which I made. I pricked deeply the column in different parts, including the stigma, and cut off the petals, and even the labellum, without causing the ejection of the pollinium; this, however, once happened when I cut rather roughly through the thick footstalk of the labellum, the

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filamentary summit of the column no doubt having been thus disturbed. When I gently prised up the anther-case at its base or on one side, the pollinium was ejected, but then the sensitive hinge would necessarily have been bent. When the flower has long remained expanded and is nearly ready for spontaneous ejection, a slight jar on any part of the flower causes the action. Pressure on the thin pedicel of the pollinium, and therefore on the underlying protuberant rostellum, is followed by the ejection of the pollen-masses; but this is not surprising, as the stimulus from a touch on the sensitive hinge has to be conveyed through this part of the rostellum to the disc. In *Catasetum* slight pressure on this point does not cause the act of ejection; but in this genus the protuberant part of the rostellum does not lie in the course along which the stimulus has to be conveyed from the antennæ to the disc. A drop of chloroform, of spirits of wine, or of boiling water placed on this part of the rostellum produced no effect; nor, to my surprise, did exposure of the whole flower to vapour of chloroform.

Seeing that this part of the rostellum was sensitive to pressure, and that the flower was widely open on one side, and being pre-occupied with the case of *Catasetum*, I at first felt convinced that insects entered the lower part of the flower and touched the rostellum. Accordingly I pressed the rostellum with variously-shaped objects, but the viscid disc never once adhered in a proper manner to the object. If I used a thick needle, the pollinium, when ejected, formed

a hoop round it with the viscid surface outside; if I used a broad flat object, the pollinium struggled against it and sometimes coiled itself up spirally, but the disc either did not adhere at all, or very imperfectly. At the close of the twelfth trial I was in despair. The

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strange position of the labellum, perched on the summit of the column, ought to have shown me that here was the place for experiment. I ought to have rejected the notion that the labellum was thus placed for no good purpose. This plain guide was overlooked, and for a long time I completely failed to understand the structure of the flower.

We have seen that when the pollinium is ejected and swings upwards, it adheres by the viscid surface of the disc to any object projecting beyond the edge of the labellum directly over the column. When thus attached, it forms an irregular hoop, with the torn-off anther-case still covering the pollen-masses which are close to the disc, but protected from adhering to it by the dependent curtain. Whilst in this position the projecting and bowed part of the pedicel would effectually prevent the pollen-masses from being placed on the stigma, even supposing the anther-case to have fallen off. Now let us suppose the pollinium to be attached to an insect's head, and observe what takes place. The pedicel, when first separated from the rostellum, is damp; as it dries, it slowly straightens itself, and when perfectly straight the anther-case readily drops off. The pollen-masses are now naked, and they are attached to the end of the pedicel by easily ruptured caudicles, at the right distance and in a proper position for their insertion into the adhesive stigma, as soon as the insect visits another flower. Thus every detail of structure is now perfectly adapted for the act of fertilisation.

When the anther-case drops off, it has performed its triple function; namely, its hinge as an organ of sense, its weak attachment to the column as a guide causing the pollinium at first to swing perpendicularly upwards, and its lower margin, together with the curtain of the

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disc, as a protection to the pollen-masses from being permanently glued to the viscid disc.

From observations made on fifteen flowers, it was ascertained that the straightening of the pedicel does not occur until from twelve to fifteen minutes have elapsed. The first movement causing the act of ejection is due to elasticity, and the second slow movement to the drying of the outer and convex surface; but this latter movement differs from that observed in the pollinia of so many *Vandææ* and *Ophrææ*, for, when the pollinium of this *Mormodes* was placed in water, it did not recover the hoop-like form which it had at first acquired by elasticity.

The flowers are hermaphrodites. The pollinia are perfectly developed. The elongated stigmatic surface is extremely viscid and abounds with innumerable utriculi, the contents of which shrink and become coagulated after immersion for less than an hour in spirits of wine.

When placed in spirits for a day, the utriculi were so acted on that they disappeared, and this I have not noticed in any other Orchid. The ovules, after exposure to spirits for a day or two, presented the usual semi-opaque, pulpy appearance common to all hermaphrodite and female Orchids. From the unusual length of the stigmatic surface I expected that, if the pollinia were not ejected from the excitement of a touch, the anther-case would have detached itself, and the pollen-masses would have swung downwards and fertilised the stigma of the same flower. Accordingly, I left four flowers untouched; after they had remained expanded from eight to ten days, the elasticity of the pedicel conquered the force of attachment and the pollinia were spontaneously ejected, but they did not fall on the stigma and were consequently wasted.

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Although *Mormodes ignea* is an hermaphrodite, yet it must be as truly dioecious in function as *Catasetum*; for as it takes from twelve to fifteen minutes before the pedicel of an ejected pollinium straightens itself and the anther-case drops off, it is almost certain that within this time an insect with a pollinium attached to its head would have left one plant and flown to another.

*Mormodes luxata*.—This rare and fine species is fertilised in the same manner as *Mormodes ignea*, but differs in several important points of structure. The right and left sides of the same flower differ from one another even in a greater degree than in the last species. One of the petals and one of the sepals project at right angles to the column, while the corresponding ones stand upright and surround it. The upturned and twisted labellum is furnished with two large lateral lobes: of these one embraces the column, while the other stands partly open on the side where the one petal and sepal lie flat. Insects can thus easily enter the flower on this latter side. All the flowers on the left side of the spike are open on their left sides, while those on the right side are open on this side. The twisted column with all the important accessory parts, together with the rectangularly bent apex, closely resemble the corresponding parts in *M. ignea*. But the under side of the labellum does not rest on and press against the rectangularly bent apex of the column. This stands free in the middle of a cup formed by the extremity of the labellum.

I did not obtain many flowers fit for examination, as three had ejected their pollinia owing to the shocks received during their journey. I pricked deeply the labellum, column and stigma of some of the flowers without any effect; but when I lightly touched with a

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needle, not the anther-hinge as in the last species, but the apex of the column of one flower, the pollinium was instantly ejected. The bases of the petals and sepals are not swollen and succulent like those of *M. ignea*; and I have little doubt that insects gnaw the labellum, which is thick and fleshy, with the same peculiar taste as in *Catasetum*. If an insect were to gnaw the terminal cup, it could hardly

fail to touch the apex of the column, and then the pollinium would swing upwards and adhere to some part of the insect's body. The pedicels of the pollinia straighten themselves and the anther-cases are cast off, in about fifteen minutes after the act of ejection. We may therefore confidently believe that this species is fertilised in the same peculiar manner as *Mormodes ignea*.

*Cycnoches ventricosum*.—Mr. Veitch was so kind as to send me on two occasions several flowers and flower-buds of this extraordinary plant. A sketch of a flower in its natural position, with one sepal cut off, is shown at fig. 33 (p. 222), and a longitudinal section through a young bud at fig. 34 (p. 223). The labellum is thick and fleshy, with the usual taste of this organ in the *Catasetidæ*; it resembles in shape a shallow basin turned upside down. The two other petals and the three sepals are reflexed. The column is almost cylindrical, thin, flexible, elastic and of extraordinary length. It curves round so as to bring the stigma and anther opposite to and beneath the convex surface of the labellum. The apex of the column is not nearly so much produced as in *Mormodes* and *Catasetum*. The pollinia closely resemble those of *Mormodes*; but the disc is larger, and its curtain, which is fringed, is so large that it covers the whole entrance into the stigmatic chamber. The structure of these parts is best seen in the section,

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fig. 34; in which the pedicel of the pollinium has not as yet become separate from the rostellum, but the future line of separation is shown by a line (dotted in the figure) of hyaline tissue. The filament of the anther (f, fig. 34) has not as yet grown to its full length. When fully developed it bears two little leaf-like appendages which lie on the anther. Lastly, on the sides of the stigma there are two slight protuberances (fig. 33), which apparently represent the antennæ of *Catasetum*, but have not the same function.

Neither the labellum nor the protuberances on the sides of the stigma are at all sensitive; but when on three occasions I momentarily touched the filament, between the little leaf-like appendages, the pollinium was ejected in the same manner and through the same mechanism as in *Mormodes*; but it was thrown only to the distance of about an inch. If the filament had been touched by an object which had not been quickly removed, or if by an insect, the viscid disc would certainly have adhered to it. Mr. Veitch informs me that he has often touched the end of the column, and the pollinium has adhered to his finger. When the pollinium is ejected, the pedicel forms a hoop, with the exterior surface of the curtain of the disc resting on and covering the anther. In about fifteen minutes the pedicel straightens itself, and the anther-case drops off; and now the pollinium is in a right position for fertilising another flower. As soon as the viscid matter on the under surface of the disc is exposed to the air it quickly changes colour and sets hard. It then adheres with surprising force to any object. From these various facts and from the analogy of the other *Catasetidæ*, we may conclude that insects visit the flowers for the sake of gnawing the labellum:

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but it cannot be predicted whether they alight on the surface which is uppermost in the drawing (fig. 33) and

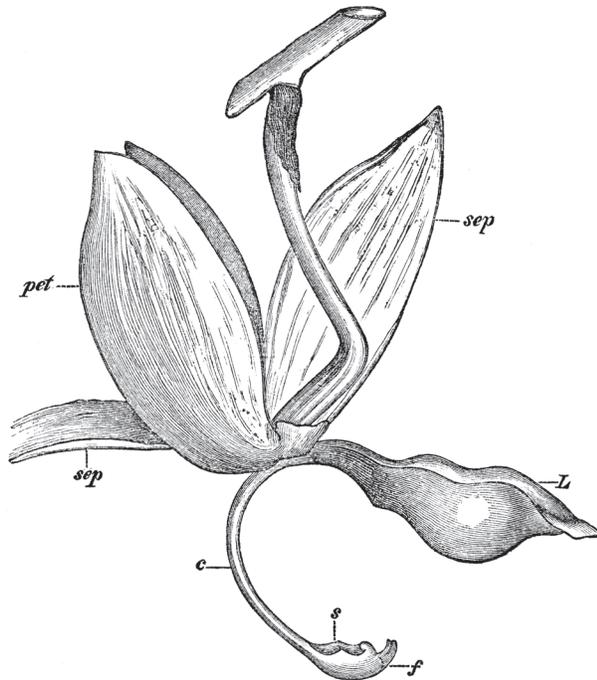


FIGURE 33. *Cycnoches ventricosum*.

Flower viewed in its natural dependent position.

*c.* column, after the ejection of the pollinium together with the anther. *f.* filament of anther. *s.* stigmatic cavity. *L.* labellum. *pet.* the two lateral petals. *sep.* sepals.

then crawl over the margin so as to gnaw the convex surface, and in doing so touch with their abdomens

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the extremity of the column, or whether they first alight on this part of the column; but in either case they would cause the ejection of the pollinia, which would adhere to some part of their bodies. The specimens which I examined were certainly

male plants, for the pollinia were well developed. The stigmatic cavity was lined with a thick layer of pulpy matter which was not adhesive. But as the flowers cannot possibly be fertilised until the pollinia have been ejected, together with the great curtain which covers the whole stigmatic surface, it may be that

<sup>16</sup> Quoted by Irmisch, *Beiträge zur Biologie der Orchideen*, 1853, p. 22.

<sup>17</sup> Lindley's *Vegetable Kingdom*, 1853, p. 177. He has also published in the [Edwards's] *Botanical Register*, fol. 1951 [1837], a case of two forms appearing on the same scape of another species of *Cycnoches*. Mr. Bateman also says that *C. egertonianum* has been known to produce in Guatemala and once in England scapes of a purple-flowered and widely different species of *Cycnoches*; but that it generally produces in England scapes of the common yellow *C. ventricosum*.

<sup>18</sup> Here Darwin surely misquoted Lindley. He was most likely referring to Lindley (1843a,b), and not to figure "fol. 1951," which was actually tab. 1947<sup>A</sup> (see Lindley, 1837, referring to *Catasetum*, not *Cycnoches*) (note of the transcriber).

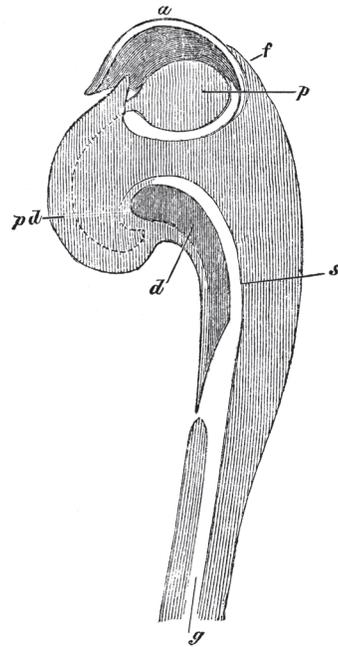


FIGURE 34. Diagrammatic Section of a Flower-bud, the column placed upright.

*a.* anther. *f.* filament of anther. *p.* pollen-mass. *pd.* pedicel of pollinium, barely separated as yet from the rostellum. *d.* disc of pollinium with the dependent curtain. *s.* stigmatic chamber. *g.* stigmatic canal leading to the ovarium.

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this surface becomes at a later period adhesive so as to secure the pollen-masses. The ovules when kept for some time in alcohol were filled with brownish pulpy matter, as is always the case with perfect ovules.

Therefore it appears that this *Cycnoches* must be an hermaphrodite; and Mr. Bateman, in his work on the Orchideæ, says that the present species produces seeds without being, as I understand, artificially fertilised; but how this is possible is unintelligible to me. On the other hand, Beer says<sup>16</sup> that the stigma of *Cycnoches* is dry, and that the plant never sets seeds. According to Lindley *C. ventricosum* produces on the same scape flowers with a simple labellum, others with a much segmented and differently coloured labellum (viz., the so-called *C. egertonianum*), and others in an intermediate condition. From the analogous differences in the flowers of *Catasetum*, we are tempted to believe that we here have male, female, and hermaphrodite forms of the same species of *Cycnoches*.<sup>17, 18</sup>

I have now finished my description of the *Catasetidæ* as well as of many other *Vandææ*. The study of these wonderful and often beautiful productions, with all their many adaptations, with parts capable of movement, and other parts endowed with something so like, though no doubt different from, sensibility, has been to me most interesting. The flowers of Orchids, in their strange and endless diversity of chape, may be compared

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with the great vertebrate class of Fish, or still more appropriately with tropical Homopterous insects, which appear to us as if they had been modelled in the wildest caprice, but this no doubt is due to our ignorance of their requirements and conditions of life.

APPENDIX IV  
SPECIMENS CITED

- Catasetum barbatum* (Lindl.) Lindl. (male flower). VENEZUELA. Amazonas: Municipio Maroa, Maroa, 2 August 2013, *ex Hort.* Familia Aragua (no voucher prepared).
- Catasetum bergoldianum* Foldats (male and female flowers). VENEZUELA. Amazonas: Municipio Atures, Río Sipapo, 5 June 1983, *G. A. Romero 1199* (AMES).
- Catasetum collare* Cogn. (female flower). VENEZUELA. Municipio Atures, río Orinoco, 27 June 1983 *ex Hort.* R. de Tomacini (no voucher prepared).
- Catasetum collare* Cogn. (male flower). VENEZUELA. Municipio Atures, El Burro, 26 November 1983, *G. A. Romero 1155* (AMES).
- Catasetum maculatum* Kunth. COSTA RICA. Cartago: Turrialba, campus of CATIE, DATE, *F. Guánchez* (JBL).
- Catasetum pileatum* Rchb.f. (female flower). VENEZUELA. Amazonas: Municipio Maroa, “Caño” San Miguel, 3 September 2007, *G. A. Romero & C. Gómez 3632* (VEN).
- Catasetum pileatum* Rchb.f. (male flower). VENEZUELA. Amazonas: Municipio Atures, Río Orinoco, 5 September 1983, *ex Hort.* R. de Tomacini (no voucher prepared).
- Catasetum roseo-album* (Hook.) Lindl. VENEZUELA. Amazonas: Municipio Maroa, Cerro Mesaque, 23 July 2006, *G. A. Romero, G. Gerlach & C. Gómez & G. Gerlach 3592* (VEN).
- Cycnoches egertonianum* Bateman. COSTA RICA: Cartago: Santa Cruz, 1200 m, 20 September 2018, *F. Guánchez, F. Cuza, G. Alvarado y G. A. Romero 5366* (JBL).
- Cycnoches ventricosum* Bateman. MEXICO. Chiapas: vicinity of Ocosingo, May 2017, *I. Tamayo Cen 127* (CICY).
- Mormodes lineata* Bateman *ex* Lindl. MEXICO: Oaxaca: Municipio San Miguel Chimalapa: Carretera El Jícara-Rodolfo Benito Juárez, 1038 m, 15 enero 2009, *G. Carnevali 7416* (CICY).
- Mormodes vernixioidea* Pabst *ssp. autanensis* Salazar & G. A. Romero: VENEZUELA. Amazonas: Río Autana, 28 November 1987, *G. A. Romero & F. Guánchez 1434* (VEN). Based on the holotype.