FLORAL VISITATION, POLLEN REMOVAL, AND POLLEN TRANSPORT OF *TACCA CRISTATA* JACK (DIOSCOREACEAE) BY FEMALE CERATOPOGONID MIDGES (DIPTERA: CERATOPOGONIDAE)

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Premise of research.   *Tacca* is a monocot genus characterized by an unusual reproductive display, with plants possessing umbelliform inflorescences subtended by highly conspicuous leafy bracts and filiform bracteoles with colors ranging from dark maroon to white. Paradoxically, previous studies indicated very low levels of outcrossing in some showy *Tacca* species, implicating self-pollination as the primary reproductive strategy.

Methodology.   We describe visual observations and collections made of floral visitors to flowering individuals of *Tacca cristata* Jack in Singapore.

Pivotal results.   Female ceratopogonid midges were observed to visit the flowers at anthesis and were collected with pollen specifically placed on their dorsal thoracic region. A significant proportion of flowering plants was attacked by florivores.

Conclusions.   These findings suggest that at least some showy species of *Tacca* may be pollinated to some extent through insect visitation. The reproductive biology of *Tacca*, including inflorescence display, is discussed in the context of its natural history.

Keywords: floral orientation, fly pollination, mixed mating, myiophily, pollinator sex bias, reproductive display.

Online enhancement: video.

Introduction

The morphology of angiosperm flowers provides clues to their reproductive biology, as convergence in floral traits has long been thought to indicate the most effective class or functional group of pollination vector (reviewed in Johnson and Steiner 2000; Fenster et al. 2004; Ollerton et al. 2009). Most animal-pollinated flowers are pollinated by well-studied groups such as bees and birds (Rosas-Guerrero et al. 2014), with which they are usually associated through characteristic suites of floral traits that indicate how they attract and are foraged on by their pollinators (Bradshaw and Schemske 2003; Castellanos et al. 2004; Fenster et al. 2004; Reynolds et al. 2009). In other plants, such traits may be more generalized, or pollinator affinities may be difficult to predict, particularly when the pollinators belong to lineages that are relatively overlooked, highly diverse, and/or morphologically variable. A prime example would be the many families of pollinating flies (Diptera), which are ecologically and

behaviorally diverse and which, accordingly, may visit flowers for manifold reasons, from seeking nectar and pollen to seeking brood sites or mates (Kearns 2001; Larson et al. 2001; Ssymank et al. 2008; Woodcock et al. 2014; Orford et al. 2015). In such cases, our knowledge may not yet be sufficient to allow the accurate prediction of pollinator class based on floral morphology (Stökl et al. 2011; Oelschlägel et al. 2015).

One such example is *Tacca*, a pantropical genus of approximately 20 described species with known diversity concentrated in Malesia (Drenth 1972). Counter to the general trend in the family Dioscoreaceae, plants in genus *Tacca* are robust, acaulescent herbs that are usually found in forest understories, although some species (notably *Tacca leontopetaloides* (L.) Kuntze) can be found in coastal habitats, or as agricultural weeds in highly disturbed areas. In showy *Tacca*, the inflorescences are unique and easily identify plants as members of this genus. Flowers are colored from white to yellow-gray to greenish-purple or black, which is highly unusual in general but can be common in plants with brood-site mimicry (Sakai and Inoue 1999; Urru et al. 2011; Jürgens et al. 2013; Chen et al. 2015). The reproductive display further consists of conspicuous sterile elements, including two pairs of showy involucral bracts and profuse filiform bracteoles subtending the umbelliform inflorescence, which gives the genus its common name, the bat lilies (fig. 1A).

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Fig. 1   *A*, *Tacca cristata*. Note erect and pendent flowers, showy involucral bracts, and whisker-like filiform bracteoles. *B*, Cross section of a *Tacca* flower. Note the hooded, reflexed anthers with bright yellow sticky pollen. They are tightly appressed to the mushroom-shaped stigma at anthesis. Scale bar = 1 mm.

Due to its unique coloration and morphology, which does not readily indicate how the inflorescence display is attractive to or worked by pollinators, previous authors considered the flowers of *Tacca* to be indicative of sapromyiophily, in which flowers mimic the visual and/or chemical traits of rotting substrates including feces, carrion, and fungi (Vogel 1978; Dafni 1984). This diagnosis was primarily based on inflorescence coloration, which is similar to other well-known examples of sapromyiophilous plants (van der Pijl 1961; Drenth 1972; Faegri and van Der Pijl 1979; Saw 1993). Specifically, Vogel (1978) suspected that the pollinators were likely to be gnats, as carrion flies are too large to be able to access the pollen thecae, which are hidden behind hooded, reflexed anthers (fig. 1*B*).

On the other hand, population studies suggest that outcrossing in *Tacca* may be rare. Recent analyses of molecular markers in two showy species, *Tacca integrifolia* Ker Gawl. and *Tacca chantrieri* André, demonstrate a very high degree of geographical population stratification, consistent with a hypothesis of self-pollination (Zhang et al. 2005; Zhang 2006; Zhao and Zhang 2015). Furthermore, an exhaustive study on the reproductive biology of *T. chantrieri* in Yunnan showed little evidence of pollinator visitation, and plants were highly capable of autonomous selfing under field and experimental conditions (Zhang et al. 2005).

These results present a paradox: why would showy *Tacca* species risk the energetic and ecological costs of conspicuous floral display, such as increased predation by florivores (McCall and Irwin 2006), if they are primarily self-pollinating? Furthermore, other *Tacca* species (e.g., *Tacca plantaginea* (Hance) Drenth) are not showy and instead produce small, green, inconspicuous, and mostly hidden inflorescences that are more consistent with the expectations of autogamous reproduction (Doubleday et al. 2013). How are the conspicuous and apparent reproductive displays of showy *Tacca* species reconciled with the observations that selfing may be their predominant mode of reproduction? In plant reproductive biology, there is an expectation that species capable of self-pollination will trend toward increased selfing due to the fitness advantages of serving as both parents, as long as the offspring are not exposed to an excess of homozygous deleterious traits (Barrett 2014). However, the phenomenon of persistent mixed mating often occurs in plants that are superficially assumed to be either outcrossing (*Datura* [Motten and Antonovics 1992], *Collinsia* [Kalisz et al. 2004]) or selfing (*Ephedra* [Bolinder et al. 2016]) based on their morphological characteristics. The maintenance of both selfing and outcrossing mechanisms appears to be a more prevalent reproductive strategy than has been appreciated, and mixed mating has only recently been considered to be an evolutionarily stable strategy (Goodwillie et al. 2005; Winn et al. 2011; Dart et al. 2012; Yin et al. 2016). This can be understood in the context of reproductive assurance (Fenster and Marten-Rodriguez 2007; Ruan and Silva 2012), encompassing pollinator effectiveness and abundance as well

as florivory (Steets et al. 2007; Penet et al. 2009; Cardel and Koptur 2010).

Here we document multiple observations of floral visitation by female ceratopogonid midges to one species of showy *Tacca* (*T. cristata*) in Singapore. While Drenth (1972) considered this species to be a synonym of *T. integrifolia*, there is evidence that this species is distinct, based on molecular data (Zhang et al. 2011), as well as morphological characters, i.e., narrow, decurrent leaves and spathulate inner showy bracts in *T. cristata* versus oblong leaves and obovate inner showy bracts in *T. integrifolia*. Additionally, we describe sophisticated chronobiological floral behavior in concert with the timing of insect visitation and discuss how this may contribute to outcrossing in some cases. These observations may provide clues to a fuller understanding of the evolution of showy inflorescences in this and related *Tacca* species.

Material and Methods

Species Description and Study Sites

Tacca cristata is a perennial herbaceous monocot commonly found in primary to disturbed secondary forest understory areas in Singapore and Malaysia (Jack 1821). Plants are robust, rhizomatous, and acaulescent, forming rosettes of elongate ovate leaves that trap leaf litter between clasping petioles. During flowering season, they produce one or two peduncles in succession. The terminal umbelliform inflorescence stands erect over the leafy rosette (fig. 1*A*). The inflorescence is subtended by two pairs of leafy bracts, which are colored red-violet, fading to white. The first pair of leafy bracts forms the protective sheath for the emerging inflorescence, while the second pair of leafy bracts is large and showily pigmented (fig. 1*A*). The inflorescence is umbelliform, arranged in a double cincinnus (Eichler 1879) in which each flower is subtended by two long filiform bracteoles (Limpricht 1902). Flowers are fleshy, hermaphroditic, actinomorphic, and usually colored in shades of violet. The stamens are adnate to a shallow hypanthium, hooded, and reflexed, with anthers hooded, reflexed, introrse, and appressed tightly against a mushroom-shaped stigma (fig. 1*B*). The exposed surface of the stigma is waxy, while the section within the inner hypanthial space is mucilaginous with a papillate surface. Anthesis of flowers in the inflorescence is diurnal and sequential. Inflorescences may persist through the middle of the calendar year, gradually developing into decumbent infructescences. Despite the flowers' appearance, they do not have a noticeable scent to the human nose.

Populations of *T. cristata* in Singapore are separated by the road network and land use patterns, which, for the purposes of this study, can be referred to as the Bukit Timah Nature Reserve (BTNR; lat. 1°20′50″N, long. 103°46′35″E) and Lower Pierce (lat. 1°22′10″N, long. 103°49′23″E) populations; the former is mostly composed of primary forest while the latter, mixed secondary forest (fig. 2). Plants were most common in highly disturbed areas (e.g., trails and pipelines), habitats with patchy light, moderate understory vegetation, and dense leaf litter, which sometimes partially obscured the rosette. Here we located individuals of *T. cristata* for study and tagged plants with inflorescences for consequent observations and pollinator traps.

Field Observations and Collections

Experiments were conducted from June to July of 2012, during the flowering season of *T. cristata*. No observations or trapping experiments were conducted on days with rain. Inflorescence maturation and floral anthesis in *T. cristata* are associated with characteristic changes in flower orientation, similar to those observed in *Tacca chantrieri* by Zhang et al. (2005). We describe floral orientation with the terminology proposed by Fenster et al. (2009). Field observations were made from sunup to sundown (~0800–1700 hours), corresponding with anthesis and cessation of movement of first-day flowers. On alternate days, collar traps (fig. 3) made with Catchmaster Clear Bug and Fly Window Traps (AP&G, Brooklyn, NY) and twine were placed around flowers on inflorescences. A control trap was placed nearby at the same height aboveground, in order to trap ambient fauna. These traps are transparent, in order to control for color being an attractant to insects. Traps were checked once daily in the evening, in order to allow the immediate surroundings to reacclimate after human disturbance caused by tagging, setting up traps, and taking photographs. Less frequent collections resulted in the loss of samples due to exposure and fungal growth. For other plants, visual observations were made of floral visitors, taking note of what arrived, the manner of their arrival, and which part of the inflorescence they approached. Representative plants with inflorescences have been vouchered at the Bailey Hortorium (BH) under G.L. 8–10.

Data Analysis

Identification of the insect fauna below family was difficult, due to the lack of regional expertise, published keys, and the rapidity with which specimens deteriorated. Trapped flies were keyed morphologically to family (Oosterbroek 1998) whenever possible. For midges, antennal morphology was used to determine whether individuals were male or female, as it is sexually dimorphic in many nematoceran flies. Where identification was difficult due to the glue adhering to taxonomically important characters, insects were removed from flypaper with drops of Goo Gone orange oil solvent (Weiman Products, Gurnee, IL) and were stored in 70% ethanol.

Further analysis was focused on individuals collected with pollen on their thoraxes. These were imaged using light and confocal microscopy while still attached to the traps. They were then clipped, placed into individual PCR tubes, and DNA bar-coded still glued to the traps, according to the methods of Wong et al. (2014). Successfully amplified sequences were queried against two Barcode of Life Data Systems (BOLD) databases: All Barcode Records, which includes records without species identification, and Species Level Barcodes, which is the subset of the former containing only records with species-level identification (last accessed May 16, 2016).

Results

Populations at Study Sites

The distribution of *Tacca cristata* at our study sites is patchy, with plants usually located in clusters <25 m away from their nearest neighbor, while the distance between clusters was usually more than double that. Many mature plants were attached
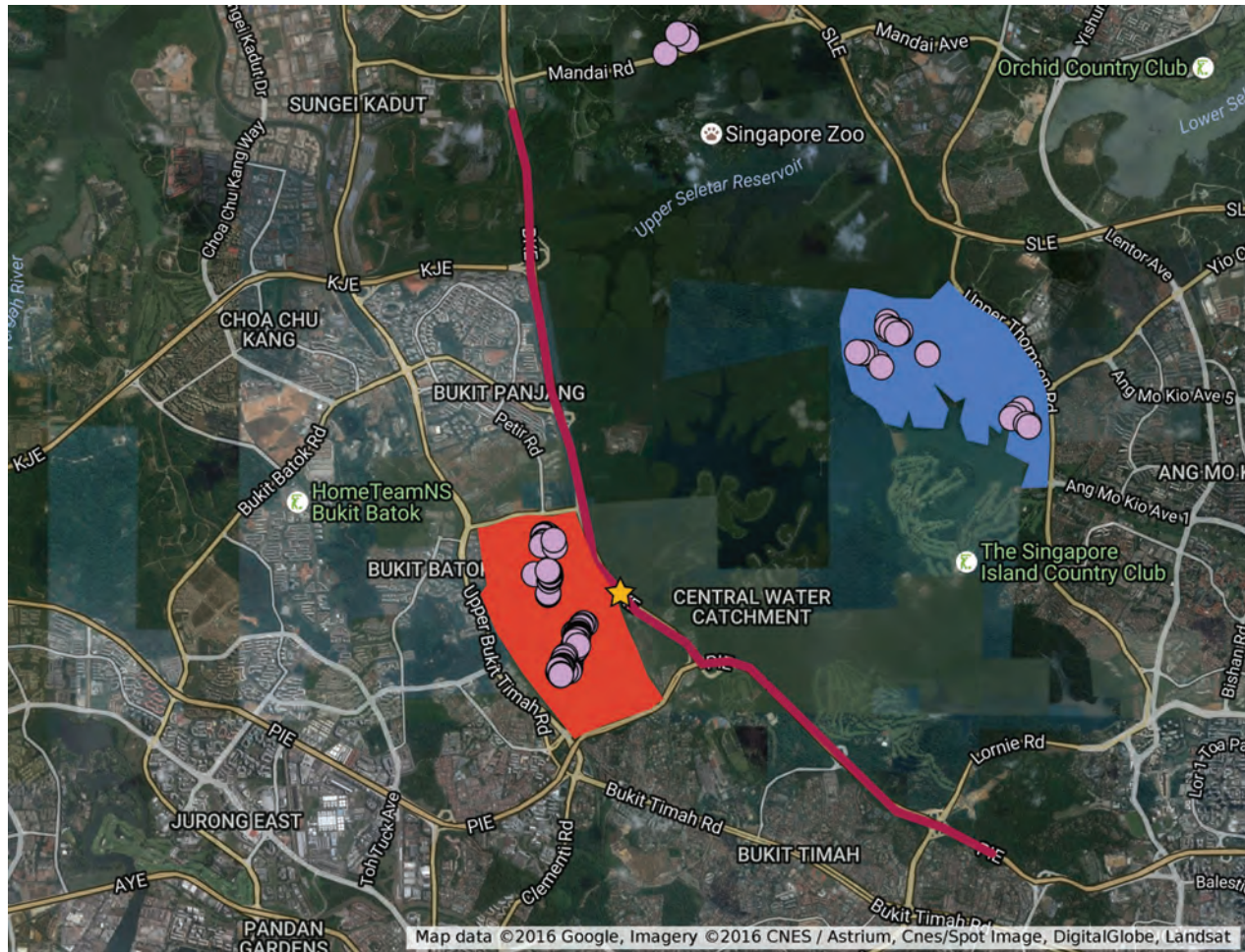
Fig. 2 Map of populations and individuals studied. The Bukit Timah population (red) was separated from the Lower Peirce population (blue) on the right by the Bukit Timah Expressway (BKE; pink line) until recently, when the Eco-Link@BKE (star) was built.

to smaller rhizomatous clones. A total of 189 individuals were surveyed in both populations. This excludes clonal individuals found next to mature plants, as well as seedlings with fewer than five mature leaves. Most plants (133) were sterile (non–sexually reproductive). Thirty-eight plants had infructescences of varying maturity, while 20 plants were surveyed with blooming inflorescences during the time of study. Of these, eight were consequently damaged or destroyed through herbivory in situ. This was likely caused by mammalian fauna such as macaques or rodents, based on evidence such as teeth marks and snapped peduncles (fig. 4).

Plant abundance was lower in Lower Peirce than in Bukit Timah, and there were greater signs of rhizome herbivory, likely by wild boar, which were prevented from accessing the latter population by the Bukit Timah Expressway (BKE; fig. 2), as the wildlife link had not yet been built at the time of study.

Floral Behavior

Flowers within *T. cristata* inflorescences, being arranged in two compact cincinni, mature consecutively, starting with the primary flowers in the center of the display and proceeding laterally in both directions. Flower buds are horizontal to the ground, becoming erect just before anthesis. Flowers opened at dawn, with the corolla elevated above the horizontal position, up to vertical (fig. 5). Through the rest of the day, the pedicel slowly drooped such that the flower became pendent by sunset. Older flowers remain pendent, and this posture persists as the fruits develop. As the infructescence develops, the peduncle becomes flaccid and eventually deliquesces, causing the now-mature berry fruits to rest on the ground, where, based on teeth marks, we infer that they have been gnawed on by small mammals.

Floral Visitors

Of 12 intact inflorescences sampled with sticky traps, two were lost to vandalism, while six yielded collections of female biting midges (Ceratopogonidae) carrying *T. cristata* pollen (table 1; figs. 3, 5, 6). One plant (individual 91, BTNR population) was particularly attractive, luring more than half of all biting midges sampled in this study, as well as other arthropod fauna.

Fig. 3 *A*, Collar trap on erect flowers of *Tacca cristata*. *B*, Midges trapped on upper edge of collar trap.

These consisted of infrequent collections of ants, spiders, beetles, and collembolans, as well as other small Diptera. In addition, lepidopteran scales were found on two of the traps. Control traps were removed/lost 30% of the time but when collected were devoid of insect fauna (one was found on the ground with feathers, likely the victim of a bird strike).

Visual observations of the inflorescences on alternating days indicated that insect visitation was sporadic, with clouds of midges present during daytime hours on clear days around some individual plants but not on others. No midges were observed on overcast days. Ants and other crawling insect fauna were present but rarely on the inflorescence. When midges approached the flowers, they appeared to target the vertical first-day flowers (figs. 3, 5), approaching from the air in a zigzag trajectory (video 1). They were therefore trapped unequally at one edge of the collar trap (fig. 3*B*).

Molecular Analysis

Of the 12 pollen-carrying midges selected for DNA barcoding, seven were successfully amplified. All specimens came back unidentified beyond the family level Ceratopogonidae, highlighting the lack of taxonomic information available for this family in Malesia. The sequence data can be accessed in the BOLD database (specimen records TAC001-17, TAC002-17, TAC003-17, TAC004-17, TAC005-17, TAC006-17, TAC007-17), listed under DS-taccafly.

Discussion

Findings

This study revealed three novel aspects that further our understanding of reproductive ecology in *Tacca cristata* and offer interesting points of similarity and divergence to the observations of Zhang et al. (2005) for *Tacca chantrieri*. First, we observed the presence of insect visitors, specifically, female biting midges (Ceratopogonidae), to some (but not all) flowering individuals. This differs from the most commonly observed pollen-carrying visitors of *T. chantrieri*, which were *Trigona* bees (Zhang et al. 2005). The midges are much smaller and are able to enter the hypanthial chamber between the hooded anthers (fig. 1*B*) and contact the thecae beneath them. As evidence of this, we photographed the removal and transport of pollen through specific (nototribic) placement on the dorsal thoracic region of the flies. In the case of *T. chantrieri*, *Trigona* bees appeared to remain on the surface of the flower (Zhang et al. 2005). Pollen grains were documented as adhering to the legs of these bees, but it is not clear how they were transferred or collected, as the pollen thecae are well hidden behind the hooded anthers and fleshy stigma. Second, the midges were specifically attracted to the vertical flowers, which had assumed this position on their first day of anthesis, rather than to buds or older pendent flowers. This, combined with the unique floral anatomy in *Tacca*, with its recurved stamens and hidden receptive stigmatic surface, may fa-

Fig. 4   Inflorescences of *Tacca cristata* that have been damaged or eaten by mammals, based on the pattern of damage.

cilitate pollen transfer between midge and flower upon anthesis. The minute size of the visiting midges indicates that single receptive flowers of *T. cristata* function as chamber flowers, providing a protected space in which further pollinator behavior affecting pollen transfer is likely. As flowers age, the change of posture from vertical to pendent would provide autogamous reproductive assurance by increasing the odds of dehisced self-pollen contacting the stigma within the floral chamber. Third, we observed high levels of mammalian florivory, likely from rodents and macaques native to this habitat, as well as relatively heavy rhizome herbivory in an exposed population, putatively due to recently reintroduced wild boar. These observations are examples of some of the ecological costs of floral display and apparency in *T. cristata*. In extreme cases, such selective pressure would be predicted to favor reduced floral displays and strict autogamy, as we infer is the norm for related species such as *Tacca plantaginea*.

Floral Visitors and Inference of Pollen Transport

Based on the faunal assemblage obtained, we do not find support for the proposed hypothesis of sapromyiophily in this ge-nus, at least for *T. cristata*, as its flowers did not attract unambiguously saprophagous insects, such as those that use rotting fungi, fruits, feces, or carrion as brood sites (Jürgens et al. 2013). The absence of such visitors is consistent with the findings of Zhang et al. (2005) for *T. chantrieri* in southern China. Instead, about half of all monitored flowers were visited by ceratopogonid midges, whose approach flights were characteristic of orientation toward an odor plume (Vickers 2000). The sex ratio of midges that were trapped on flypaper was overwhelmingly female, suggesting a sex-specific element in their attraction to the flowers. Female-biased fly pollination exhibited by ceratopogonid midges also has been recorded in *Theobroma cacao* (Saunders 1959; Winder 1977; Young et al. 2011). The family Ceratopogonidae comprises approximately 5000 species of small flies, of which both sexes feed on nectar; however, females generally require blood meals to complete egg production and consequently have biting mouthparts to prey on both invertebrate and vertebrate hosts (Downes and Wirth 1981; Borkent 2005). Some pest species are important vectors of human and livestock diseases (Boorman 1993; Borkent 2005). It is likely that in *Theobroma*, as with *T. cristata*, floral attraction may be based on the production of stimuli that mimic the cues used by blood-
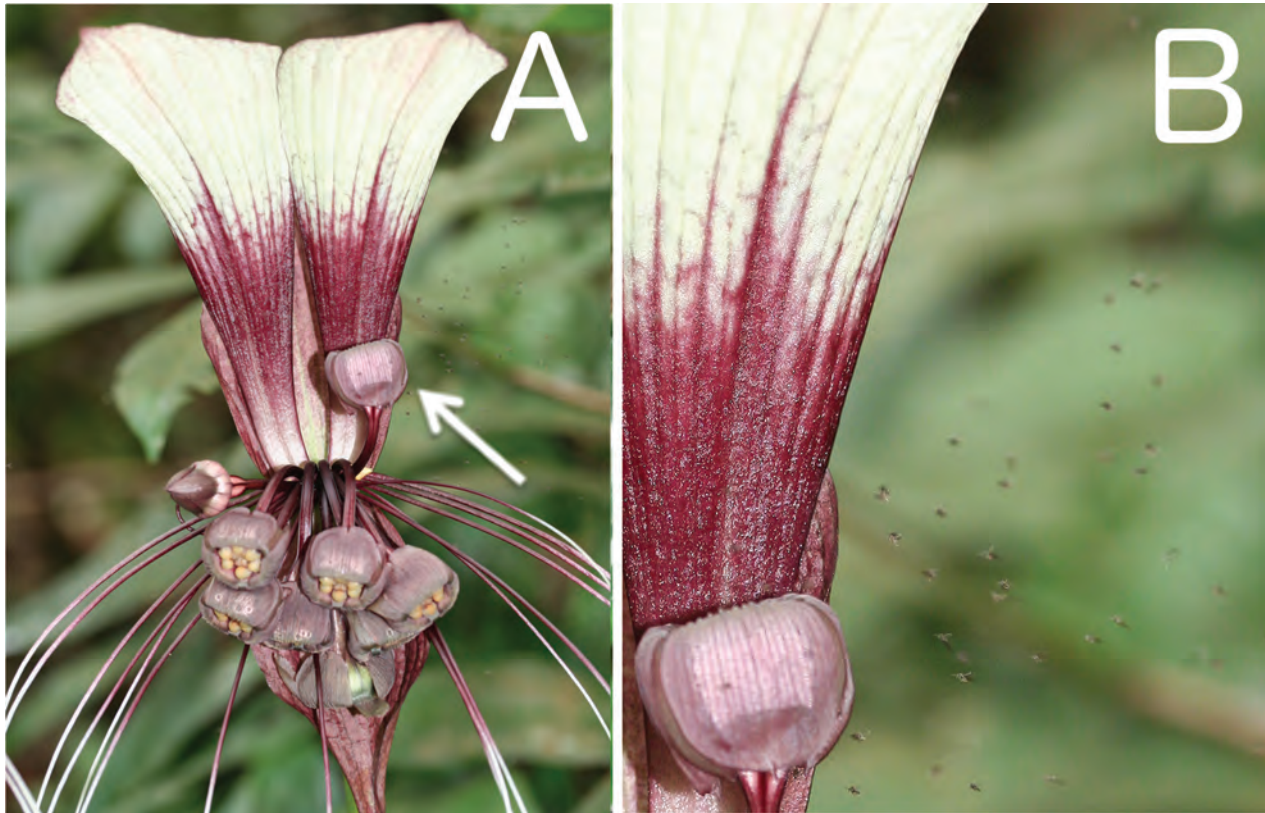
Fig. 5   *A*, Inflorescence of *Tacca cristata* showing the positions adopted by flowers of varying maturity. Buds are parallel, the first day-of-anthesis flower is vertical, and older flowers are pendent. Biting midges are swarming the newly opened vertical flower (arrow). *B*, Magnification of this erect flower to better visualize the swarming midges. Photo provided by Marcus Ng.

or hemolymph-seeking female ceratopogonids. Mimicry of prey has been documented in two other fly-pollinated species, *Aristolochia rotunda* (family Aristolochiaceae; Oelschlägel et al. 2015) and *Ceropegia dolichophylla* (family Apocynaceae; Heiduk et al. 2010, 2015), in each case driven by extremely specific chemical mimicry.

In *T. cristata*, some of the trapped female ceratopogonids captured emerging from the flowers possessed characteristic mono-sulcate *Tacca* pollen adhering to the dorsal surface of their thorax (fig. 6). While this observation is insufficient to determine whether they are successfully transferring pollen from the anthers to the stigma within a flower (facilitated autogamy), or between flowers from different individuals (xenogamy) of *T. cristata*, it clearly indicates successful pollen transfer from the plant to an insect whose size and behavior would be conducive to successful pollination.

Table 1

Visitors to *Tacca cristata* Inflorescences

Visitors	No. collected	Fraction present in collections	Percentage trapped with pollen (%)
Ant spp. (workers and alates)	4	.2	0
Arachnid spp.	2	.2	0
Coleoptera sp.	1	.1	0
Collembolan sp.	1	.1	0
Lepidoptera spp.	2 (scales only)	.2	0
Ceratopogonidae spp. (all females[a])	124	.6	9.6
Phoridae sp.	1	.1	0
Cecidomyiidae sp.	1[b]	.1	0
Unidentified insect (parts)	3	.2	0

[a] Based on the morphology of the antennae.

[b] One individual was collected by sweep netting around an inflorescence tagged for visual observation.
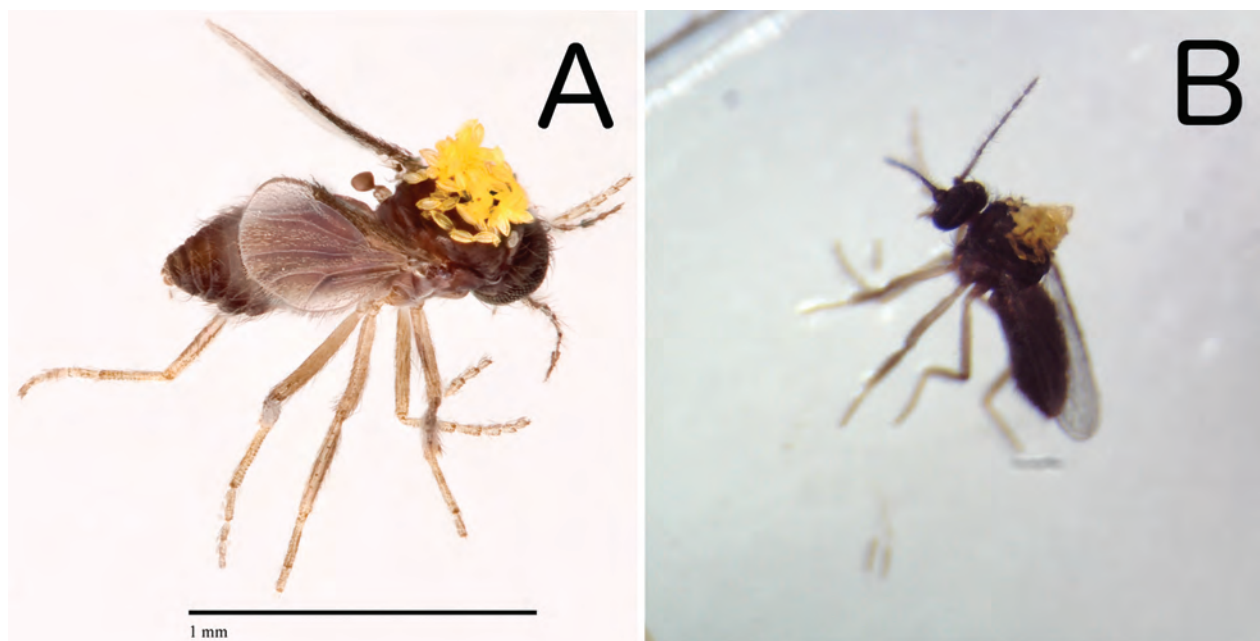
Fig. 6   Photos of two ceratopogonid females carrying monosulcate *Tacca cristata* pollen taken via confocal microscope (*A*; courtesy Yuchen Ang) and light microscope (*B*). Note the specific placement of the large sticky pollen. Flies are photographed at the same scale.

Floral Behavior and Morphology

As reviewed by Fenster et al. (2009), floral orientation is a source of information to pollinators. Floral orientation is known to impact pollinator partitioning (Eisikowitch and Rotem 1987; Botes et al. 2009), reproductive isolation (Fulton and Hodges 1999), and pollinator effectiveness (Wang et al. 2014).

We observed changing floral orientation in *T. cristata* as flowers matured from bud (horizontal) to anthesis (vertical) and beyond (pendent) as they senesced. This also occurs in other showy species, i.e., *T. chantrieri* (Zhang et al. 2005), which appeared to those authors to facilitate autogamous selfing, as pollen from dehisced thecae would accumulate at the bottom of the hypanthial chamber during the vertical phase, becoming depos-

Video 1   Still image from a video (available online) documenting approach and entry of *Tacca cristata* flowers and transport of their pollen by ceratopogonid midges. In the video, a pollen-carrying midge can be seen at 0:15 on the erect, open flower in the foreground and another at 0:18 on the one farther to the back; the latter eventually enters the floral chamber.

ited on the receptive surface of the stigma as the flower became pendent. Hence, floral orientation may be a component in autogamous selfing as a form of reproductive assurance in unvisited flowers of *Tacca* that display flower movement.

In *T. cristata*, we observed a possible second aspect of floral orientation in pollination, i.e., specific attraction of female ceratopogonid midges to the vertically oriented flowers during their first day of anthesis but not to pendent flowers or buds. As pendent flowers and erect flowers look similar, this suggests that production of a nonvisual component of floral display that is attractive from longer distances lasts only during the first day of anthesis. Additional studies will be needed to determine whether floral volatiles are released according to this diel pattern. Fenster et al. (2009) discuss the importance of floral orientation with regard to increasing specificity of pollinator directionality, an idea that has been investigated in multiple plant-pollinator associations (Huang et al. 2002; Imamura and Ushimaru 2007; Wang et al. 2010; Rands et al. 2011). The kettlefall trap, most commonly exemplified by members of the family Araceae, as well as the genera *Aristolochia* (Aristolochiaceae) and *Ceropegia* (Apocynaceae), is strongly associated with fly pollination (Kunze 1991; Bröderbauer et al. 2012). The hypanthial space of *Tacca* flowers may form such a chamber, with one important difference being that ceratopogonid midges, particularly females, are generally considered not to be saprophagous but ectoparasitic blood feeders (Borkent 2005).

Selective Herbivory and Community Impact

The conspicuous floral displays of showy *Tacca* species are not apparent only to pollinators. We observed high rates (eight out of 20 inflorescences, or 40%) of floral or inflorescence loss (fig. 4) during our period of study due to predation. These observations support the hypothesis that showy reproductive displays are at higher risk of florivory (Strauss and Whittall 2006; Teixido et al. 2011), whether from arthropods or from vertebrates (Knight 2004; Kessler et al. 2013). The parts of the plants most often consumed or damaged included flowers and rhizomes and were likely performed by different mammals such as rodents, monkeys, or pigs. In the former case, inflorescences were denuded of only flowers/buds at all developmental stages, while the bracts were usually left behind (fig. 4). Tooth marks on pedicels indicate that they had been nipped. Wild boars were likely the cause of rhizome predation, as they were reported at Lower Pierce but not in the Bukit Timah Nature Reserve, which at the time of study was separated by the BKE. These populations have now been connected with the Eco-Link@BKE ecological bridge, which was built for the purpose of restoring wildlife traffic between two nature reserves. Rhizome predation was characterized by patches of churned-up soil, with leaves of *T. cristata*

flung about (having been separated at the base of the rosette). In two cases, small clonal individuals were observed to be sprouting from the base of the frayed petioles of *T. cristata* leaves.

Beyond the specific case of *T. cristata*, mammalian herbivory patterns have great impact on populations of long-lived herbs by altering not just population sizes but also reproductive fitness (Strauss and Armbruster 1997; Knight 2004). In the fragmented forests of Singapore, they may have disproportionate long-term impact on forest dynamics, by altering understory composition and species population structure due to selective predation on plants of favored species and size (Halpern and Underwood 2006; Maron and Crone 2006; Kolb 2008; Knight et al. 2009; Vázquez et al. 2010). Invasive herbivores dramatically increase the hypothetical minimum number of plants that are required for viable populations, which have to be factored into conservation management, especially for patchy forest fragmentation (McGraw and Furedi 2005). In the specific case of Singapore's forested patches, understory plant communities may be relatively undefended against wild boar foraging, as they have been absent for a period of time (Pisanu et al. 2012; Martin et al. 2015).

Conclusion

Here, we add a new dimension to the reproductive biology of *Tacca*. Initially posited to be fly pollinated (Vogel 1978; Dafni 1984) based on the visual similarity between the dark-colored flowers and accessory bracts to those of sapromyiophilous plants, later studies (Zhang et al. 2005, 2007; Zhang 2006) demonstrated that populations of showy *Tacca* appeared to be predominantly selfing. We have outlined the potential for outcrossing in *T. cristata* and observe that inflorescence morphology and behavior facilitate ceratopogonid midge visitation, pollen removal, and transport specifically in first-day flowers. We conclude that the pollination biology of *T. cristata* may be an example of cryptic myiophily embedded within a mixed mating system.

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