

Specialized fly pollination in *Apoballis mutata* (Araceae): high reproductive success in the absence of a trap system

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Abstract

Background and aims – While some plants achieve reproductive success through wind or deceptive pollination strategies, many animal-pollinated species depend on mutualistic interactions with pollinators, supported by floral cues, rewards, and microstructural adaptations. Despite the diversity within Araceae, pollination ecology remains poorly characterized for most species.

Material and methods – To address this gap, this study investigates the flowering biology and pollination dynamics of *Apoballis mutata*, with particular focus on pistillate, transitional, and staminate phases of anthesis, followed by infructescence development and seed dispersal. Seeds germination trials were conducted on cotton wool in sealed Petri dishes, and fruit set was quantified from pistillate flower and berry counts. Scanning Electron Microscopy (SEM) was used to examine staminate floral structures and pollen distribution on pollinators.

Key results – Three legitimate pollinators were identified, *Colocasiomyia* sp. 2 aff. *bogneri*, *C. sp. 34* aff. *bogneri*, and *C. sp. 17* aff. *bogneri*, along with two non-pollinating insect visitors, forming a co-occurring assemblage. Echinate pollen consistently adhered to the bodies of *Colocasiomyia* flies, confirming their role as effective pollinators. Unlike trapping system observed in some aroids, spathe movements in *A. mutata* regulated pollinator behaviour, allowing repeated visits and efficient pollen transfer. Pollinator diversity declined from the pistillate to staminate phases, with *C. sp. 2* aff. *bogneri* remaining dominant, particularly in creamy green-spathed inflorescences. Overall fruit set exceeded 90%, with creamy melon-red spathes achieving 77.90% and creamy green spathes surpassing 100%.

Conclusion – These findings reveal a specialized, non-trapping pollination system in *A. mutata*, enhancing understanding of its mutualistic relationship with *Colocasiomyia* flies and contributing new insights into the pollination ecology of Araceae.

Keywords

Araceae, Diptera, echinate pollen ornamentation, floral scent, plant-pollinator interactions

INTRODUCTION

Pollination is a fundamental ecological process that underpins the reproductive success and genetic diversity of flowering plants. Approximately 90% of flowering plants depend on pollinators for successful reproduction (Stephens et al. 2023; Tong et al. 2023), underscoring the importance of these interactions in maintaining ecosystem stability. Plant-pollinator relationships are

remarkably complex, often arising through independent or convergent evolution to enhance the fitness of both partners. Such interactions have contributed significantly to biodiversity and resilience of food webs (van der Kooi et al. 2021).

Over evolutionary time, these associations have driven the diversification of a wide array of floral traits, with natural selection favouring features that improve pollination efficiency. Variations in floral colour, shape,

scent, and timing of flowering (Fenster et al. 2004) have evolved as specialised responses to pollinator preferences and behaviours. Pollinators are primarily attracted to flowers by scent and visual cues (Wright and Schiestl 2009; van der Kooi et al. 2023). Although flowers or inflorescences may appear outwardly uniform, they often conceal structural adaptations finely tuned to attract specific pollinators. Attributes such as floral tube length, pistil and stamen morphology, and the spatial arrangement of floral organs can strongly influence pollinator effectiveness and thus promote reproductive success (Alexandersson and Johnson 2002; Nattero et al. 2010; Solís-Montero and Vallejo-Marín 2017; De Jager and Peakall 2019).

In tropical plant families such as Araceae, plant-pollinator interactions often achieve a high degree of specialization. Members of this family possess a characteristic inflorescence composed of a spadix, which bears the flowers, and a surrounding spathe, which can function in visual or olfactory attraction (Mayo et al. 1997). Certain genera, including *Anthurium* Schott, *Monstera* Adans., and *Spathiphyllum* Schott, exhibit distinct adaptations to specific insect pollinators (Gibernau 2016). Three main pollination strategies are recognised in Araceae (Chartier et al. 2014): two are mutualistic where insects receive rewards such as pollen, and/or reproductive sites for mating and oviposition, while the third is antagonistic, relying on deceptive pollination where inflorescences mimic oviposition sites or reproductive resources to attract pollinators without offering actual benefit. These strategies occur across Araceae with both bisexual and unisexual flowers: bisexual-flowered with floral rewards, whereas unisexual flowers are often associated with trap-type or deceptive pollination systems (Chartier et al. 2014; Díaz Jiménez et al. 2019). Studies in tropical Asia have documented a diverse array of Araceae pollinators and insect visitors, including beetles from Hydrophilidae Latreille (*Cycreon* Orchymont, 1919), Chrysomelidae Latreille, and Scarabaeidae Latreille (*Parastasia* Westwood, 1842 spp., *Peltonotus* Burmeister, 1847 spp.); as well as drosophilid flies exclusively in the genus *Colocasiomyia* Meijere, 1914 (Takenaka 2006; Gibernau 2016; Arriaga-Varela et al. 2018). Pollination systems involving *Colocasiomyia* are mutualistic, providing nutritive and reproductive rewards to flower-breeding flies (Sultana et al. 2006; Takenaka 2006; Takenaka Takano et al. 2012). These flies visit inflorescences primarily to feed, mate, and oviposit within the floral chamber, where floral scents attract them to the female zone; pollen becomes attached to their bodies as they exit and visit subsequent inflorescences, thereby transferring pollen between flowers and facilitating fertilization in their host plants (Yafuso 1993; Miyake and Yafuso 2003; Takenaka Takano et al. 2012). Within this system, insect behaviour and pollination is “forced” by a combination of morphotemporal changes in the spathe, including its temporary closure during the female phase and reopening during the male phase, as well as

associated changes in colour, scent emission, and surface properties that regulate insect movement and timing of release (Bröderbauer et al. 2012; Ulrich et al. 2012). Structural diversity of the spadix, including variation in staminate flowers and thecae horns, is thought to further enhance pollinator visitation and pollen acquisition (Low et al. 2016; Low and Wong 2022).

Pollination efficiency can also depend on how pollen is extruded and deposited on pollinators (Koski et al. 2018), traits closely linked to pollen surface ornamentation. Within Araceae, pollen morphology is highly variable, including psilate, echinate (spiny), reticulate, and verrucate, each likely adapted to different pollinator group (Grayum 1992; van der Ham et al. 1998). Although pollen-pollinator interactions are often taxon-dependent (Sannier et al. 2009), echinate pollen is frequently associated with fly pollination (Grayum 1986; Sannier et al. 2009).

Within the tribe Schismatoglottideae, *Apoballis* Schott, an Asian genus with bisexual flowers, is distinctive as the only genus bearing echinate pollen (Thanikaimoni 1969; Ulrich et al. 2012), whereas other genera, including *Schismatoglottis* Zoll. & Moritz possess smooth pollen surfaces (Cusimano et al. 2011; Low and Wong 2022). Despite comprising 12 accepted species, the pollination ecology of *Apoballis* remains poorly documented. Existing research has focused mainly on *Apoballis acuminatissima* (Schott) S.Y.Wong & P.C.Boyce, particularly in spathe movements and pollen morphology (Ulrich et al. 2012). Evidence from other aroids suggests that pollen often adheres to pollinators’ bodies during staminate anthesis (Maia et al. 2010; Takenaka Takano et al. 2012; Gottsberger et al. 2020). In *Alocasia macrorrhizos* (L.) G.Don, flies are attracted to female-phase flowers. They feed, mate, and oviposit, and on the second day, when pollen is released, they leave the inflorescence covered in pollen for transfer to the next receptive flower (Takenaka Takano et al. 2012). Yet, detailed microscopic documentation of where pollen adhered on the insects’ bodies remains scarce. The presence of echinate pollen in *Apoballis* suggests a potential specialisation, where pollinator attraction and efficient pollen transfer could enhance reproductive success. A comprehensive synthesis of *Apoballis* pollination, similar to studies on other Schismatoglottideae taxa (Low et al. 2016; Low and Wong 2022), is therefore needed. Moreover, unlike many aroids, *Apoballis* appears to attract rather than trap insects, with visitors seemingly “choose” to stay within the inflorescence, making behavioural observations especially valuable for understanding mutualistic dynamics.

Building on this context, the present study investigates pollination interactions between *A. mutata* and *Colocasiomyia* flies, with emphasis on floral traits that facilitate pollinator attraction, pollen distribution, and reproductive success. Scanning Electron Microscopy (SEM) was used to examine staminate floral microstructures and pollen grains of *A. mutata*, as well as pollen loads on *Colocasiomyia* flies. In addition, seed

germination trials were performed to assess reproductive success beyond pollination. Together, this study aims to improve understanding of plant-pollinator relationships in tropical ecosystems and highlight ecological strategies that sustain diversity within the Schismatoglottideae.

MATERIAL AND METHODS

Study site

Fieldwork on *Apoballis mutata* was carried out along the forest edge adjoining farmland in Cameron Highlands, Pahang, Malaysia. The study population comprised approximately 150 mature terrestrial plants, typically occurring in mesophytic habitats and occasionally near muddy stream banks. Observations on flowering biology were conducted between February and April 2016, with peak flowering likely in late February, as inferred from the abundance of developing infructescences in March.

Observations on anthesis, pollination, seed dispersal, and seed germination

Anthesis was recorded and floral visitors of *A. mutata* were observed during the pistillate, transitional, and staminate phases. Detailed observations focused on floral traits such as spathe movements, the presence or absence of perceptible floral scent, and the behaviour of pollinators and other floral visitors. These qualitative observations were conducted during field visits across all three floral phases in the 10 inflorescences monitored for flowering and pollinator behaviour. Particular attention was given to whether spathe constriction or staminode expansion occurred during anthesis, based on qualitative visual observations. Spathe opening was measured only at the onset of anthesis, while subsequent changes in spathe and staminode form were monitored observationally, as these features in some aroids restrict insect movement.

In total, 59 inflorescences were randomly selected from different individuals, which were temporarily marked to ensure that each plant was sampled only once. Of these, 10 were monitored for flowering and pollinator behaviour during both daytime and nocturnal field observations, while 49 (27 at pistillate anthesis and 22 at staminate anthesis) were bagged for insect sampling. During this study, brief field observations indicated approximately equal occurrence of creamy green and creamy melon-red spathe morphs within the population. For each morph, insect visitation rates were recorded and analysed using generalized linear models equivalent to a two-way ANOVA in R v.4.5.0 (R Core Team 2025).

To test whether the upper spadix alone attracted the same insect species, three pistillate-phase inflorescences had their upper spadices and spathe limbs excised and placed approximately 100 m from the mother plants. All insects collected from the bagged inflorescences and excised spadices were preserved in 70% ethanol and identified to species level. Fly specimens were sorted into

morphotypes and gender and compared to the reference material and descriptions in the DrosWLD database (<https://evolgen.biol.se.tmu.ac.jp/DrosWLD/modules/stdb/>). Undescribed morphotypes were assigned tentative species names (see also Sultana et al. 2006; Fartyal et al. 2013; Toda unpublished database) pending formal taxonomic treatment.

Infructescence development was monitored in 20 post-staminate inflorescences, comprising 10 from the intensively observed group and 10 randomly selected in the field, each from a separate individual, until seed dispersal. For seed germination trials, 600 seeds taken randomly from three infructescences were cultivated on cotton wool in sealed Petri dishes.

Reproductive success

Because flowering and fruiting were not synchronous, reproductive success was assessed using separate sets of individuals: 20 pistillate inflorescences and 20 infructescences. Fruit set was calculated as the ratio of berries to pistillate flowers. As pistillate flower and berry counts were obtained from different individuals, calculated fruit set values could exceed 100%; therefore, fruit set values were normalised to a maximum of 100% to facilitate comparative analyses across individuals. Seed counts per berry and infructescence were not determined because the infructescences were only partially mature. All collected flowers and infructescences were preserved in 70% ethanol.

Scanning Electron Microscopy (SEM)

Five randomly selected staminate flowers of *A. mutata* from the 49 bagged inflorescences were dissected under a stereomicroscope and dehydrated through an ethanol series to absolute ethanol (Low et al. 2016). Samples were transferred to pure acetone and dried using a critical point drier (BALTEC CPD030) with CO₂ as the transitional medium. Dried specimens were mounted on aluminium plate, sputter-coated with gold using an Auto Fine Coater (JEOL JFC-1600), and imaged with a JEOL JSL-6390LA SEM (JEOL, Peabody, MA, USA). Images were captured at 10 kV accelerating voltage, with a working distance of 10–13 mm and magnifications ranging from 30× to 10,000×.

To visualise pollen distribution on pollinators, two to three randomly selected specimens of *Colocasiomyia* spp. collected at pistillate and staminate anthesis were similarly mounted, gold-coated, and scanned under SEM.

RESULTS

Floral morphology of *Apoballis mutata*

The synflorescence of *Apoballis mutata* produced up to four sequential inflorescences blooming consecutively. Inflorescences were borne on erect peduncles; and the

spathe showed a constriction aligned with the sterile zone between the pistillate and staminate flowers zones. The spathe comprised an upper spathe limb and a lower pollination chamber (Fig. 1D, E). Two spathe colour morphs occurred at roughly equal frequency within the population: creamy green and creamy melon-red, which matched the petiole colour of the respective plant. In the creamy green morph, prominent white, stalk-like staminodes larger than the pistils were interspersed among the pistillate flowers (Fig. 1B). These staminodes varied in form between clavate to mushroom-shaped or globose, were arranged 3–4 rows above the pistillate zone. In contrast, the creamy melon-red morph lacked staminodes within the pistillate region, showing only a partial row above it (Fig. 1C). Both morphs contained a naked sterile interstice with scattered atypical bisexual flowers (ABF), usually occurring in cluster of 2–4 flowers. The staminate zone consisted of dense stamens with truncated, rectangular to dumbbell-shaped surfaces and slightly grooved connectives. The spadix terminated in an appendix bearing irregular polygonal staminodes (Fig. 1B, C).

Anthesis and pollination strategy

Stigma receptivity in *Apoballis mutata* typically began around 08:30 (local time, UTC +8.00), coinciding with initial spathe opening (approximately 5 cm × 5 mm) at the intermediate spadix zone (Fig. 1D–F). This marked the onset of the pistillate phase. During this period, the appendix emitted a sweet fruity scent that may help to attract pollen-bearing *Colocasiomyia* flies. These flies entered along the spathe margin into the lower chamber, where they contacted receptive pistillate flowers (Fig. 1D–G). Occasionally, the *Colocasiomyia* flies were observed feeding on the inner spathe surface, possibly on secretions of tissues. *Cycreon* beetles were also present (Fig. 1H), but they remained on the spathe margin or upper inner spathe and did not access the pollination chamber. By the afternoon the transitional phase began, stigma receptivity was lost, and floral scent diminished, and *Colocasiomyia* flies moved upward to the inner spathe surface. No spathe constriction or staminode expansion were observed during the pistillate or transitional phases; the spathe remained inflated and open, allowing free insect movement.

Anthesis of *A. mutata* lasted approximately 26 h. The staminate phase began on the following morning. Around 08:00, the spathe began to tighten (Fig. 1I, J), accompanied by faint scent release, and pollen dehiscence commenced from the staminate flowers. At this stage, *Colocasiomyia* flies congregated near the staminate zone or on the outer spathe, where powdery pollen was released from the thecae pores, covering their bodies (Fig. 1I, J).

After anthesis, the upper spathe and spadix abscised within five days, initiating fruit development within the lower spathe (Fig. 1K). Berries of approximately 2 mm in length matured over approximately one month, turning

from light green to light yellow as the spathe split open (Fig. 1L).

Randomly selected seeds of *A. mutata* were cultivated immediately after infructescence dehiscence on cotton wool in sealed Petri dishes (Fig. 1M). Germination began after three weeks (Fig. 1N), indicated by the emergence of the first leaf. The majority of the seeds germinated successfully, indicating high viability.

Insect visitors and pollinator composition

From the 49 bagged *A. mutata* inflorescences, a total of 3041 *Colocasiomyia* sp. 2 aff. *bogneri* (mean ± SD: 62.06 ± 38.65 individuals per inflorescence; Fig. 2B), 320 *C. sp. 17* aff. *bogneri* (6.53 ± 6.66; Fig. 2C), 729 *C. sp. 34* aff. *bogneri* (14.86 ± 10.52; Fig. 2D), and 2 *C. sp. 1* aff. *bogneri* (0.04 ± 0.20; Fig. 2A) were collected (Table 1; Suppl. material 1). The overall sex ratio of *Colocasiomyia* spp. was approximately 1:1 (1919 ♀; 2173 ♂; Fig. 2G; Table 1). Based on counts summarised in Table 1, *C. sp. 2* aff. *bogneri* occurred in comparable proportions during pistillate (53.24%) and staminate (46.76%) phases. In contrast, *C. sp. 17* aff. *bogneri* and *C. sp. 34* aff. *bogneri* declined markedly from the pistillate to the staminate stage: *C. sp. 17* aff. *bogneri* from 79.69% to 20.31%, and *C. sp. 34* aff. *bogneri* from 74.86% to 25.24%. *Colocasiomyia* sp. 1 aff. *bogneri* was incidental, represented by a single individual at each anthesis phase. Per-inflorescence abundances across species, anthesis phases, and spathe colour are illustrated in Fig. 2E and are consistent with these patterns. Three dissected pistillate-phase inflorescences showed the predominance of *C. sp. 2* aff. *bogneri* both in the lower chamber and in the upper spathe (Table 1). *Cycreon* beetles were rare visitors (38 in total; Table 1; Fig. 2E; Suppl. material 1).

Visitation patterns to the two spathe colour morphs showed minimal differences across anthesis phases. In creamy melon-red spathes, *C. sp. 2* aff. *bogneri* was abundant and occurred in broadly comparable proportions during pistillate (1172 individuals; 58.08%) and staminate (846 individuals; 41.92%) phases (Fig. 2E; Table 2; Suppl. material 1). *Colocasiomyia* sp. 17 aff. *bogneri* (79.82%) and *C. sp. 34* aff. *bogneri* (77.71%) both decreased substantially in the staminate phase (20.18% for *C. sp. 17* aff. *bogneri*, and 22.29% for *C. sp. 34* aff. *bogneri*) irrespective of spathe colour (Fig. 2E; Table 2; Suppl. material 1). In creamy green spathes, *C. sp. 2* aff. *bogneri* increased slightly from pistillate (447 individuals; 43.70%) to staminate (576 individuals; 56.30%) phases. Generalised linear models revealed no significant effects of spathe colour on visitation rates for any *Colocasiomyia* species or *Cycreon* beetles (all *p* values > 0.05; Fig. 2F). Predicted mean numbers of insect visitors were similar between creamy melon-red and creamy green spathes at both anthesis phases, indicating that spathe colour does not significantly influence *Colocasiomyia* abundance in *A. mutata*.

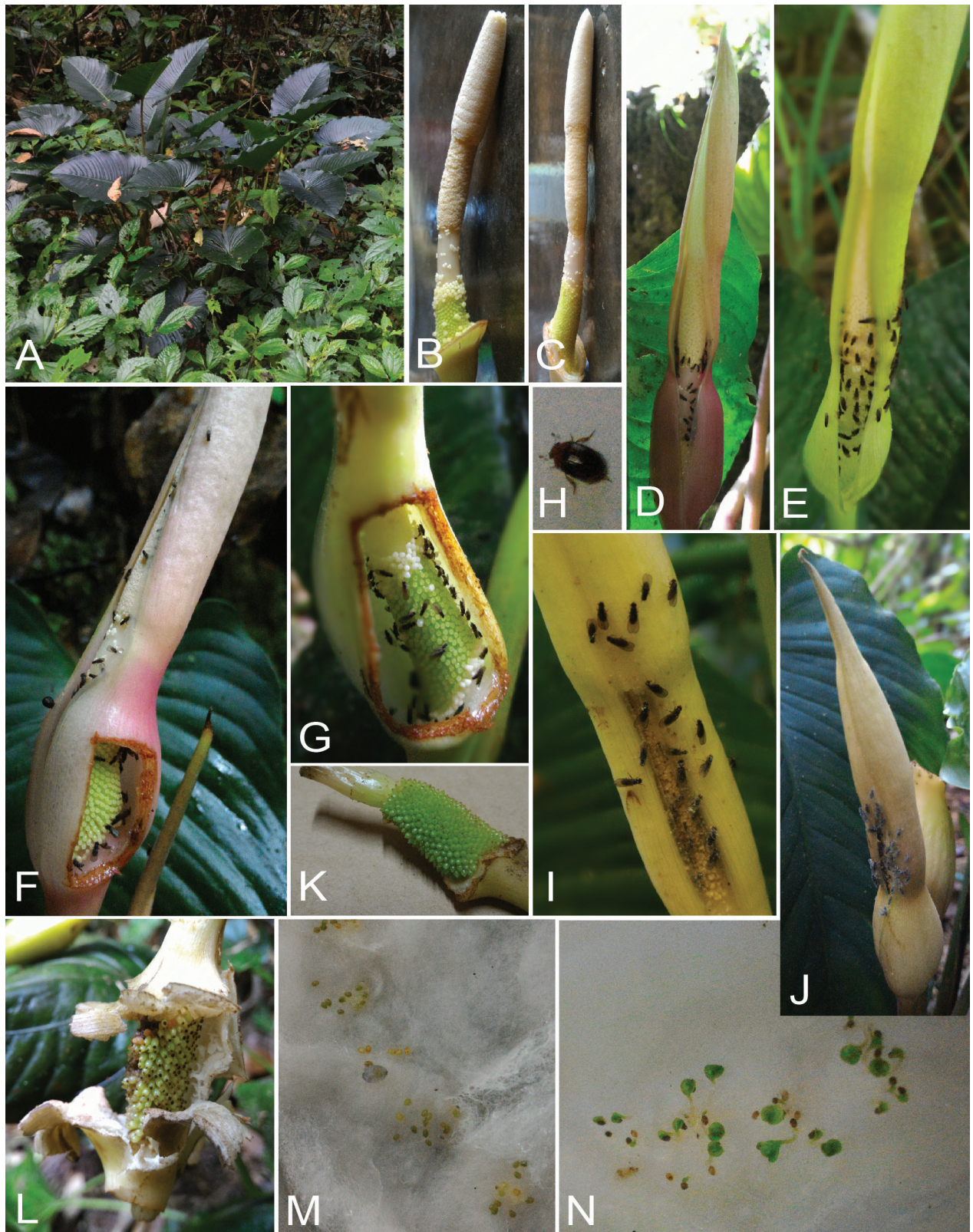


Figure 1. Habitat, flowering mechanism, pollinators and insect visitors, seed dispersal, and seedling establishment in *Apoballis mutata*. A. Individual plant in the wild. B, C. Spadix features associated with green spathe (B) and melon-red spathe (C). D, E. Inflorescences at the onset of pistillate anthesis. F, G. Windows cut to reveal the behaviour of pollinators at pistillate anthesis. H. *Cycreon*. I, J. Inflorescences at staminate anthesis; note the *Colocasiomyia* covered with pollen. K. Developing infructescence. L. Infructescence shedding fruits. M. Seeds on cotton wool. N. Seedlings.

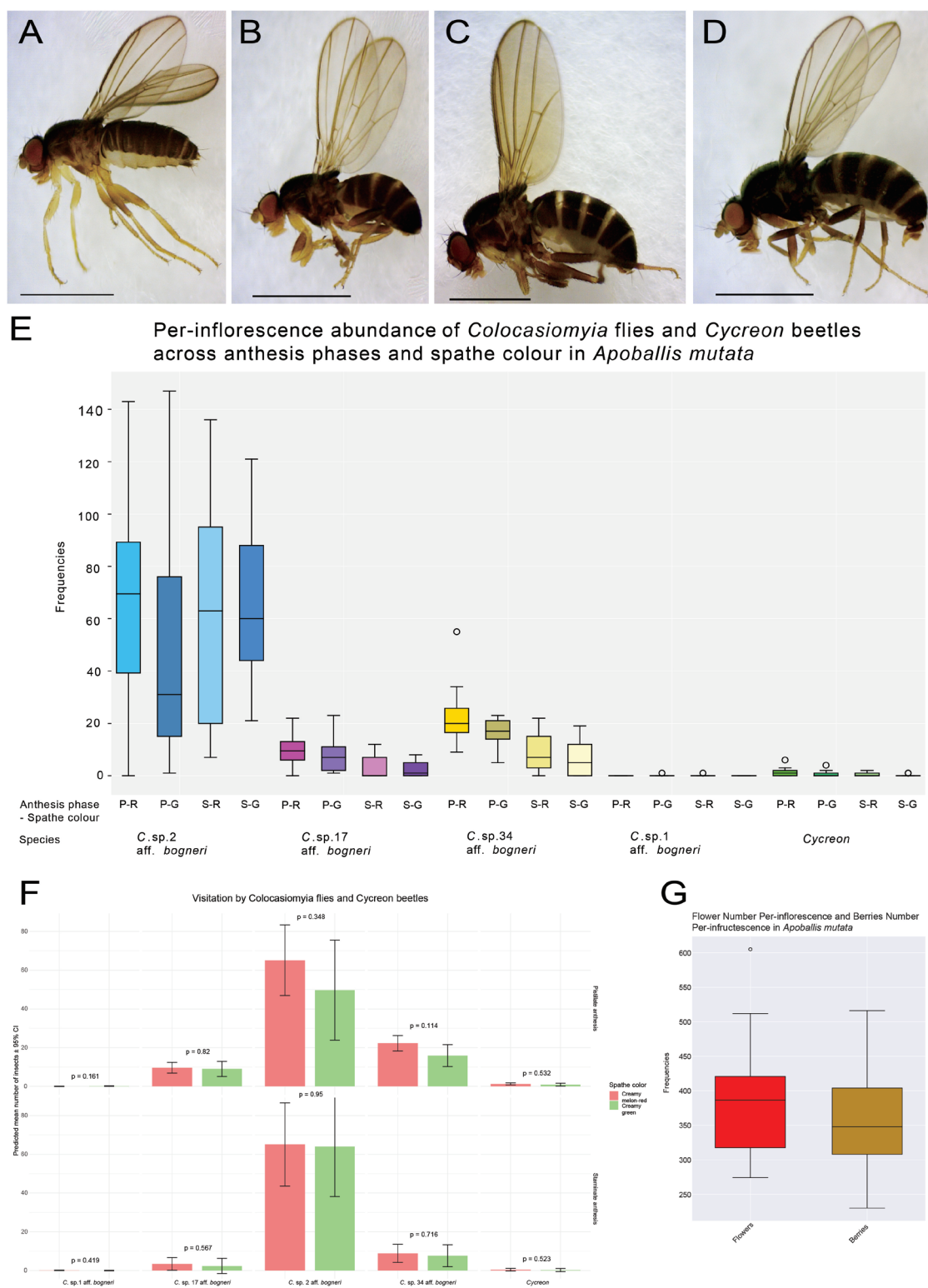


Figure 2. *Colocasiomyia* species and their occurrence frequencies in the inflorescences of *Apoballis mutata*. **A.** *Colocasiomyia* sp. 1 aff. *bogneri*. **B.** *Colocasiomyia* sp. 2 aff. *bogneri*. **C.** *Colocasiomyia* sp. 17 aff. *bogneri*. **D.** *Colocasiomyia* sp. 34 aff. *bogneri*. **E.** Number of *Colocasiomyia* flies and *Cycreon* beetles per *A. mutata* inflorescence categorized by anthesis phases (P: pistillate, S: staminate) and spathe colour (R: creamy melon-red, G: creamy green). **F.** Mean numbers ($\pm$ SD) of individual *Colocasiomyia* species and *Cycreon* beetles recorded per inflorescence during pistillate and staminate anthesis. P values indicate the statistical significance of differences between spathe colour morphs for each insect taxon. **G.** Number of pistillate flowers per inflorescence and number of berries per infructescence of *Apoballis mutata* (N = 20). Scale bars: A–D = 1 mm. Photos A–D by Masonori J. Toda.

Table 1. Pollinator and insect visitors found on the inflorescences of *Apoballis mutata* (N = 49 inflorescences).

Anthesis phase	Sex of insect visitor	<i>Colocasiomyia</i> sp. 2 aff. <i>bogneri</i>	<i>Colocasiomyia</i> sp. 17 aff. <i>bogneri</i>	<i>Colocasiomyia</i> sp. 34 aff. <i>bogneri</i>	<i>Colocasiomyia</i> sp. 1 aff. <i>bogneri</i>	<i>Cycreon</i>
Pistillate anthesis	Female	686	111	270	1	29
	Male	784	134	229		
Staminate anthesis	Female	610	37	85	1	7
	Male	812	28	99		
Dissected upper spathe and spadix – Pistillate anthesis	Female	65	1	4	0	0
	Male	41	2	8		
Dissected lower spathe and spadix – Pistillate anthesis	Female	24	5	19	0	2
	Male	19	2	15		
Total		3041	320	729	2	38
Mean $\pm$ SD		62.06 $\pm$ 38.65	6.53 $\pm$ 6.66	14.86 $\pm$ 10.52	0.04 $\pm$ 0.20	0.76 $\pm$ 1.22
Range (min–max)		0–147	0–23	0–55	0–1	0–6
% at pistillate anthesis		53.24	79.69	74.86	50	81.58
% at staminate anthesis		46.76	20.31	25.24	50	18.42
Sex ratio (♀ : ♂) in total		1385 : 1656	154 : 166	378 : 351	2 : 0	-
Sex ratio (♀ : ♂) at pistillate anthesis		775 : 844	117 : 138	293 : 252	1 : 0	-
Sex ratio (♀ : ♂) at staminate anthesis		610 : 812	37 : 28	85 : 99	1 : 0	-

Table 2. Pollinator and insect visitors found in the inflorescences of *Apoballis mutata*. The inflorescences are categorized according to the anthesis phases and spathe colour.

Anthesis phases / spathe colour	<i>Colocasiomyia</i> sp. 2 aff. <i>bogneri</i>	<i>Colocasiomyia</i> sp. 17 aff. <i>bogneri</i>	<i>Colocasiomyia</i> sp. 34 aff. <i>bogneri</i>	<i>Colocasiomyia</i> sp. 1 aff. <i>bogneri</i>	<i>Cycreon</i>
Pistillate anthesis / creamy melon-red spathe (N = 18)	1172	174	401	0	23
Means $\pm$ SD	65.11 $\pm$ 34.79	9.67 $\pm$ 6.19	22.28 $\pm$ 10.83	0	1.28 $\pm$ 1.56
Staminate anthesis / creamy melon-red spathe (N = 13)	846	44	115	1	5
Means $\pm$ SD	65.08 $\pm$ 43.74	3.38 $\pm$ 4.81	8.85 $\pm$ 7.36	0.08 $\pm$ 0.28	0.39 $\pm$ 0.65
% at pistillate anthesis / creamy melon-red spathe	58.08	79.82	77.71	0	82.14
% at staminate anthesis / creamy melon-red spathe	41.92	20.18	22.29	100	17.86
Pistillate anthesis / creamy green spathe (N = 9)	447	81	143	1	8
Means $\pm$ SD	49.67 $\pm$ 48.05	9.00 $\pm$ 8.76	15.89 $\pm$ 6.05	0.11 $\pm$ 0.33	0.89 $\pm$ 1.36
Staminate anthesis / creamy green spathe (N = 9)	576	21	69	0	2
Mean $\pm$ SD	64 $\pm$ 31.58	2.33 $\pm$ 2.96	7.67 $\pm$ 7.38	0	0.22 $\pm$ 0.44
% at pistillate anthesis / creamy green spathe	43.70	79.41	67.45	100	80
% at staminate anthesis / creamy green spathe	56.30	20.59	32.55	0	20

Table 3. Numbers of pistillate flowers and of fruits, and the percentage fruit set in inflorescences and infructescences with creamy melon-red or creamy green spathe of *Apoballis mutata*.

	<i>Apoballis mutata</i> (N = 20)	Creamy melon-red spathe (N = 10)	Creamy green spathe (N = 10)
Total pistillate flowers (N = 20)	7756	4258	3488
Mean $\pm$ SD	387 $\pm$ 82	425.8 $\pm$ 80.99	348.8 $\pm$ 64.72
Total berries (N = 20)	7164	3317	3847
Mean $\pm$ SD	358 $\pm$ 73	331.7 $\pm$ 56.79	384.7 $\pm$ 81.00
% Fruit set	92.49	77.90	110.29

Reproductive success

Reproductive success was assessed using separate sets of individuals, comprising 20 pistillate inflorescences and 20 infructescences. Across 20 pistillate inflorescences, a total of 7746 pistillate flowers were counted, with a mean 387 ± 82 (SD) pistillate flowers per inflorescence. Twenty infructescences yielded 7164 berries, averaging 358 ± 73 (SD) berries per infructescence. Based on these averages, overall fruit set was 92.49% (Table 3; Fig. 2G; Suppl. material 2).

When analysed by spathe colour, creamy melon-red spathes averaged 425.8 ± 80.99 pistillate flowers per infructescence and 331.7 ± 56.79 berries per infructescence, corresponding to a fruit set of 77.90%. Creamy green spathes averaged 348.8 ± 64.72 SD pistillate flowers and 384.7 ± 81.00 SD berries (Fig. 2G), although the unnormalized berry-to-flower ratio resulting in a calculated fruit set of 110.29%, values were normalised to a maximum of 100% (Table 3).

Scanning Electron Microscopy

SEM revealed similar stamen morphology in both spathe morphs in *A. mutata* (Fig. 3A–E). Stamens exhibited smooth papilla surfaces with few stomata (Fig. 3C). Thecae pores were membranous and sealed during pistillate anthesis (Fig. 3B), rupturing prior to pollen release in the staminate phase (Fig. 3D). Dense spiny pollen extruded from the pore slits adhered to papillae or lodged between papilla cells (Fig. 3E). Pollen grains were spiny, globose, and approximately 15 μ m in diameter (Fig. 3F).

During staminate anthesis, spiny pollens were found deposited on multiple parts of *Colocasiomyia* flies' bodies, including the mouthparts, thorax, abdomen, wings, legs, and head (Fig. 3G–O).

DISCUSSION

Flowering biology and pollination strategy

Consistent with other unisexual-flowered genera in the tribe Schismatoglottideae (Low et al. 2014, 2016; Hoe and Wong 2016; Hoe et al. 2018; Low and Wong 2022), *A. mutata* exhibits a short protogynous anthesis

sequence. The brief overlap of pistillate and staminate phases, approximately 30 minutes, minimizes the gap between pollen release and stigma receptivity, improving pollen transfer efficiency, a key feature in tropical Araceae (Soonthornkalump et al. 2020). Pollen longevity varies within the family. For example, in neotropical Araceae with bisexual flowers, such as *Anaphyllopsis americana* (Engl.) A.Hay, small pollen grains remain viable for several days due to long flowering cycles (Barabé et al. 2008). In contrast, in unisexual species with short flowering cycles, such as *Montrichardia arborescens* Schott, pollen viability drops by half within 24 h (Barabé et al. 2008). *Apoballis mutata* also possesses unisexual flowers and exhibit a comparatively short anthesis lasting approximately 26 h. The relatively large, spiny pollen grains of *A. mutata* and its short anthesis suggests an adaptation for rapid and effective pollen transfer within a narrow temporal window. Similar associations between short flowering duration, pollen morphology, and fly pollination have been reported in other aroids pollinated by dipterans, including *Arisaema* Mart. and *Colocasia* Schott species, where pollen is transferred during brief staminate phases by flower-breeding or visiting flies (Sultana et al. 2006; Takenaka 2006).

The sweet fruity fragrance emitted during anthesis appears to be the main attractant for *Colocasiomyia* flies. This differs from the benzaldehyde almond oil-like scent reported in *Apoballis acuminatissima* (Ulrich et al. 2010), however, whether this scent also specifically attracts *Colocasiomyia* flies remains unknown. Such variation in scent likely explains differences in pollinator assemblages between species. For example, in *Arum maculatum* L., population-level scent differences were associated with shifts in dominant pollinator guilds (Gfrerer et al. 2023). Thus, scent chemistry may play a central role in mediating pollinator specificity in *Apoballis*. In *A. mutata*, multiple *Colocasiomyia* species were recorded sharing inflorescences. This synhospitolic behaviour, where several fly species occupy a single inflorescence, has also been reported in other aroids such as *Alocasia odora* (Rob. ex Lodd., G.Lodd. & W.Lodd.) Spach (Toda et al. 2022). However, the scent profile of *A. odora* differs from that of *A. mutata*, and synhospitality in these systems appears to be driven by shared use of floral resources rather than similarity in floral odour.

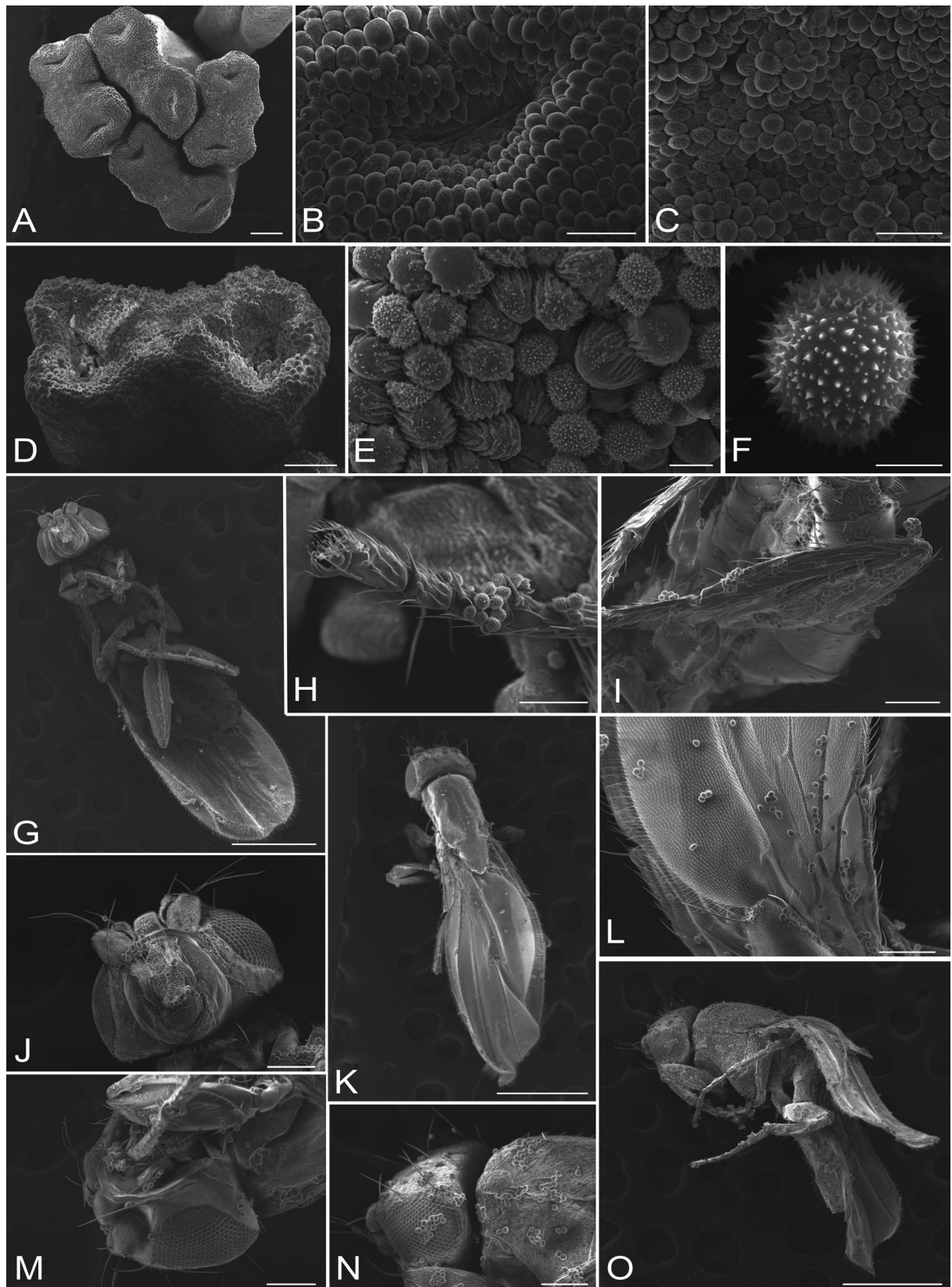


Figure 3. Microstructures of stamens, and pollinators in *Apoballis mutata* at staminate anthesis. **A.** Stamens at pistillate anthesis, each with two sealed thecae pores. **B.** Sealed thecae pore. **C.** Smooth papilla cell surface with several stomata. **D.** Stamen at staminate anthesis; note the ruptured thecae pores revealing pollen extrusion. **E.** Adherent pollen on the papilla cells. **F.** Pollen. **G.** Ventral surface of *Colocasiomyia* fly covered with pollen. **H, I.** Pollen adherent on legs. **J, M.** Pollen adherent on the head and mouth parts. **K.** Dorsal surface covered with pollen. **L.** Pollen on wings. **N, O.** Side surface covered with pollen. Scale bars: A = 200 μm ; B, C, H = 50 μm ; D, I, J, L–N = 100 μm ; E = 10 μm ; F = 5 μm ; G, K, O = 500 μm .

Like *Phymatarum* M.Hotta and *Schottarum* P.C.Boyce & S.Y.Wong (Low et al. 2016), the pale spathe colours of *A. mutata* are unlikely to be primary visual attractants. Instead, the strong floral scent likely the key attractant (Díaz Jiménez et al. 2019; Gfrerer et al. 2023). Nonetheless, intraspecific variation in spathe colour may reflect genetic or ecological diversity, potentially influencing subtle aspects of pollinator interaction.

The interaction between *A. mutata* and *Colocasiomyia* flies is best described as mutualistic, aligning with findings in related taxa (Sultana et al. 2006; Takenaka 2006; Takenaka Takano et al. 2012). In these plants, the flies obtain resources while ensuring pollen transfer. Although experimental test is lacking, repeated visits to pistillate flowers during anthesis, combined with revisits to staminate flowers, strongly suggest cross-pollination and gene flow (Hu and He 2006). It is possible that *Colocasiomyia* sp. 2 aff. *bogneri* is a pollinivorous species consuming pollen while facilitating dispersal (Fig. 3J).

The adaptations observed in *A. mutata*, such as pollen morphology, and the timing of pollen release relative to pollinator activity, are consistent with strategies reported in other Araceae to maximise pollen attachment and transfer. In *Anthurium acutifolium* Engl., bees (*Paratetrapedia chocoensis* Anguier & Melo, 2011) carry pollen on their abdomens and legs (Etl et al. 2017), whereas in *Anthurium acutangulum* Engl., gall midge (Cecidomyiidae Newman) transfer pollen via head contact (Etl et al. 2022b). In *Arisaema*, fungus gnats (Mycetophilidae Newman and Sciaridae Billberg) are dusted with pollen as they escape the spathe tube (Vogel and Martens 2000; Suetsugu et al. 2021, 2022; Zeng et al. 2023). Heavy pollen loads have also been documented in *Parastasia* beetles (*Amorphophallus napalensis* (Wall.) Bogner & Mayo; Chaturvedi 2017), Neella bugs (*Syngonium hastiferum* (Standl. & L.O.Williams) Croat; Etl et al. 2022a), and *Colocasiomyia* flies (*Schottarum*; Low et al. 2014). The pollen of these species varies in ornamentation: *A. acutifolium* has small, smooth pollen; *A. acutangulum* has slightly ornamented pollen; *Arisaema* species produce fine, smooth pollen; and beetle- or bug-pollinated species such as *A. napalensis* and *S. hastiferum* typically have granular to slightly sticky pollen. Likewise, *Colocasiomyia* visitors of *A. mutata* are often coated with spiny pollen during staminate anthesis, suggesting efficient attachment. In some aroids, sticky resinous exudates further aid adhesion (Hoe et al. 2016; Gibernau et al. 2021), though none were observed here.

Pollinator assemblage and visitation behaviour

The principal pollinators of *A. mutata* were three *Colocasiomyia* species: *Colocasiomyia* sp. 2 aff. *bogneri* (74.32% of visits; Fig. 2B), *C. sp. 34* aff. *bogneri* (17.82%; Fig. 2D), and *C. sp. 17* aff. *bogneri* (7.82%; Fig. 2C). *Colocasiomyia* sp. 1 aff. *bogneri* was an incidental visitor, with only two observed visits (Table 1; Fig. 2E, F). *Cycreon* beetles were occasional visitors and likely acted as food

foragers rather than pollinators, a role seen in *Phymatarum* and *Schottarum* (Low et al. 2016). Visitation rates of *Colocasiomyia* flies did not vary between spathe colours morphs (Fig. 2F), indicating that spathe colour does not influence pollinator attraction or visitation intensity in *A. mutata*. Instead, pollinator behaviour appears to be driven by inflorescence architecture, anthesis timing, scent emission, access to reproductive or nutritive resources, factors known to be more important than visual cues in many fly-pollinated Araceae (Gibernau 2011).

Inflorescences in the Schismatoglottideae typically attract insect visitors from Hydrophilidae (*Cycreon*), Chrysomelidae (Coleoptera), and Drosophilidae (Diptera, genus *Colocasiomyia*) (Takenaka 2006; Gibernau 2016; Arriaga-Varela et al. 2018). Multiple pollinator species can co-occur within the same inflorescence but remain reproductively isolated through behaviours such as mate discrimination (Tanaka et al. 2022). During pistillate anthesis, *Colocasiomyia* flies were seen feeding on stigmatic secretions, moving freely between floral structures and facilitating pollen transfer. They later collected food from the inner spathe and pollen from staminate flowers (Fig. 3J). Observations were consistent across visits, although fine-scale behaviour of each species requires more targeted study.

Host specificity is well known in *Colocasiomyia* (Sultana et al. 2006; Xiao et al. 2022). Geographic isolation of aroid hosts may promote specialisation through host-associated ecological divergence (Matsubayashi et al. 2010), although overlap among host ranges occurs. For example, the dominant *Colocasiomyia* sp. 2 aff. *bogneri* is also recorded from *Anadendrum microstachyum* (de Vriese & Miq.) Backer & Alderw, *Aglaonema simplex* Blume, and *Schismatoglottis rupestris* Zoll. & Moritz ex Zoll. *Colocasiomyia* sp. 17 aff. *bogneri* also visits *S. rupestris*, while *C. sp. 1* aff. *bogneri* occurs on *Aglaonema pictum* Kunth and *Schismatoglottis* sp. (Takenaka 2006). In contrast, *C. sp. 34* aff. *bogneri* has not yet been recorded as a pollinator of other aroids.

Reproductive success and fruit set

The high fruit set observed (> 90%) indicates efficient pollination in *A. mutata*. Creamy melon-red spathes averaged 77.90% fruit set, while creamy green spathes exceeded 100% (Table 3). Values exceeding 100% likely reflect sampling differences, as pistillate flowers and infructescences were counted on separate individuals.

Given that *Colocasiomyia* flies represented 99% of all recorded insect visitors (Table 1) and were present exclusively in pollination chamber, their role as primary pollinators is strongly supported.

Pollen morphology and pollinator interactions

The pollen of *A. mutata* is echinate (spiny) and ~15 µm in diameter, slightly larger than that of *A. acuminatissima* (~10–12.5 µm; Ulrich et al. 2012). This echinate structure contrasts with the smooth (psilate), inaperturate pollen

found in other Schismatoglottideae (Thanikaimoni 1969; Grayum 1992; Hesse 2005; Ulrich et al. 2012; Low et al. 2016; Low and Wong 2022).

Pollen traits are often linked with pollination systems and pollinator types (Sannier et al. 2009). Spinose pollen in *Apoballis* is frequently linked to fly pollination (Grayum 1992). SEM confirmed that *Colocasiomyia* flies carried pollen during staminate anthesis, with pollen grains found on multiple body parts and no other pollen types detected. Distribution appeared incidental rather than targeted, with spines aiding attachment, supporting the interpretation of *Colocasiomyia* as specialised but opportunistic pollen carriers.

CONCLUSION

This study provides a detailed account of the pollination dynamics of *Apoballis mutata*, emphasising its close association with *Colocasiomyia* flies and highlighting floral traits that support this mutualism. The findings demonstrate that *A. mutata* departs from the typical trapping strategies of many Araceae by employing a non-trapping system. This allows repeated visitation by pollinators and likely contributes to its exceptionally high fruit set. The timing of anthesis, subtle structural changes, and the emission of a sweet fruity fragrance appear to be the key drivers of pollinator attraction. Three main *Colocasiomyia* species, *C. sp. 2* aff. *bogneri*, *C. sp. 34* aff. *bogneri*, and *C. sp. 17* aff. *bogneri*, form a specialized yet coexisting assemblage, effectively transferring pollen as evidenced by the consistent recovery of a single pollen type on their bodies. Their pollen loads and body-wide adherence patterns suggest an efficient but largely opportunistic transport mechanism.

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SUPPLEMENTARY MATERIALS

Supplementary material 1

Numbers of *Colocasiomyia* flies and *Cycreon* beetles recorded from 49 bagged inflorescences of *Apoballis mutata*. Note: 10 additional inflorescences were used exclusively for pollination observations and are not included in these counts.

<https://doi.org/10.5091/plecevo.169286.suppl1>

Supplementary material 2

Counts of pistillate flowers and berries obtained from separate sets of inflorescences and infructescences of *Apoballis mutata* collected from different individuals.

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