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Integrating Biotic and Abiotic Factors to Elucidate Reproductive Success in *Rafflesia zollingeriana* Koord

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1 **Integrating Biotic and Abiotic Factors to Elucidate Reproductive Success in *Rafflesia***
2 ***zollingeriana* Koord.**

3
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17

18 **Abstract**

19

20 **Background and aims** - The pollination mechanism of *Rafflesia* remains a mystery due to its
21 dioecious nature, as male and female flowers rarely bloom simultaneously in the same location.
22 This study examined the reproductive biology of *Rafflesia zollingeriana* Koord., an endemic
23 species of East Java, by analyzing flower morphology, phenology, and pollen viability, alongside
24 field observations on microclimate conditions and pollinator visitation.

25 **Material and methods** - Pollen samples were collected every six hours, stained with 1% TTC
26 solution, and examined using a Dinolite microscope, while morphological analysis was performed
27 using a Scanning Electron Microscope. Microclimate parameters, including temperature and
28 humidity at different floral structures, were recorded using a thermo-hygrometer and a lux meter.
29 Pollinator activity was monitored hourly from 08:00 to 16:00 throughout anthesis. The highest
30 light intensity and temperature were recorded between 11:00 and 13:00, with the perigone
31 exhibiting the highest temperature.

32 **Key results** – The flower has a brief blooming time, only 5 days, but the pollen can remain viable
33 for up to 8 days. Four fly species from the families Sarcophagidae, Muscidae, and Calliphoridae
34 were identified as primary pollinators, with *Chrysomya rufifacies* being the most frequent visitor.
35 The highest visitation occurred midday on days 1–2, followed by a decline on days 3–4. Pollinator
36 visitation is influenced not only by biological traits and floral cues but is also significantly affected
37 by environmental factors, particularly temperature and light intensity. Pollination is most likely to
38 occur when female flowers bloom within one to seven days after male flowers, as pollen remains
39 viable for up to eight days, allowing effective pollen transfer. However, the limited survival and
40 lifespan of pollinators may contribute to the low reproductive success of this species.

41

42 **Keywords:** *Rafflesia zollingeriana*, flower, pollination, flies

43

44 **INTRODUCTION**

45

46 *Rafflesia*, a genus comprising 50 species (POWO 2025), is only found in Southeast Asia, namely
 47 Thailand, Malaysia, Indonesia, Brunei, and the Philippines. *Rafflesia* is the biggest single flower,
 48 which holoparasite of the vine stems or roots of the *Tetrastigma* genus (Vitaceae) (Wicaksono et
 49 al. 2016; Kusuma et al. 2018; Latiff 2018). Indonesia is regarded as one of the centers of diversity
 50 for *Rafflesia*, with at least 15 acknowledged species documented (Malabrigo et al. 2023),
 51 distributed in the three biggest islands and the small islands surrounding: Sumatra, Java,
 52 Indonesian Borneo (Kalimantan), Anambas, Nusa Kambangan, and Simeuleu. Three species are
 53 thought to be endemic to Java Island: *R. patma* Blume (endemic to West and Central Java), *R.*
 54 *rochussenii* Teijsm. & Binn. (endemic in West Java), and *R. zollingeriana* Koord. (endemic to East
 55 Java) (Kusuma et al. 2018).

56 Initially, *R. zollingeriana* was believed to be confined to protected areas such as Meru Betiri
 57 National Park and the Watangan Nature Reserve only. However, recent studies have revealed a
 58 broader and more fragmented distribution (Lestari and Susatya, 2022; Susatya et al. 2023), with
 59 numerous populations occurring outside conservation zones. Both protected and unprotected
 60 habitats are subject to mounting anthropogenic pressures, including harvesting for traditional
 61 medicine (Lestari and Rianto 2019) and deforestation, as well as biological and ecological stressors
 62 (Nurchayati et al. 2025). As a result, the population size of *R. zollingeriana* is in progressive
 63 decline (Lestari et al. 2014).

64 There is an urgent need for conservation interventions targeting this species. However, the
 65 development of effective conservation strategies is impeded by several unresolved fundamental
 66 questions concerning the biology of *R. zollingeriana*. Although several studies have focused on
 67 the ecological aspects of *R. zollingeriana*, research into its biological and reproductive processes
 68 remains limited.

69 Pollination is a crucial subject of study in the biology of *Rafflesia* due to its status as an
 70 obligate holoparasitic plant. In addition to relying entirely on a host organism for its nutritional
 71 needs, *Rafflesia* also depends on external agents for successful pollination (Beaman et al. 1988).
 72 This reliance is particularly significant given its dioecious floral structure, with male and female
 73 flowers occurring on separate individuals. Pollinators are essential in completing the pollination
 74 process (Hor et al. 2021). Thus, the male and female flowers must bloom at the same time for
 75 carrion flies to pollinate them effectively (Latiff 2018).

76 Pollination biology remains one of the least understood aspects of the genus. The extremely
 77 brief anthesis period, coupled with the inaccessibility of its habitats, has rendered this process
 78 difficult to observe. More than two centuries after the first *Rafflesia* species (*R. arnoldii*) was
 79 documented in 1818, its pollination mechanisms remain largely enigmatic. To date, empirical
 80 studies on *Rafflesia* pollination have begun to be elucidated in several species, particularly in *R.*
 81 *kerrii* and *R. pricei*, with key contributions from Beaman et al., (1988) and Bänziger (1991).

82 In contrast to other *Rafflesia* species whose pollination has been partially elucidated—such
 83 as *R. pricei* and *R. kerrii*—*R. zollingeriana* presents a markedly different floral morphology. Its
 84 fully opened flowers lack the translucent “windows” or white speckling on the underside of the
 85 diaphragm (Susatya et al., 2023), morphological features that Beaman et al., (1988) suggested
 86 function to visually guide flies in the floral chamber. The absence of such structures in *R.*
 87 *zollingeriana* may indicate an alternative pollination strategy or sensory mechanism involved in
 88 fly attraction and orientation. It is anticipated that findings from this study will provide new

89 insights into the pollination dynamics of this species and contribute to a broader understanding of
 90 reproductive adaptations within the genus *Rafflesia*.

91 Previously, Anggunira et al. (2019) observed the potential pollinators for *R. zollingeriana*.
 92 Yansen et al. (2023) identified *Lucilia sericata* and *Oecophylla* sp. as the visitors of *R. gadutensis*,
 93 and Hor et al. (2021) observed *R. kerrii* potential pollinator. However, this study aims to go beyond
 94 merely identifying the pollinators of *R. zollingeriana*. We explored how floral traits, phenology,
 95 pollinator behavior, and environmental factors interact to influence the reproductive success of
 96 this species. Previous studies have concluded that *Rafflesia* flowers exhibit elevated temperatures
 97 to attract flies (Patiño et al. 2002). Based on the information, we observed floral temperature while
 98 also assessed additional microhabitat parameters, including relative humidity and light intensity,
 99 to better understand the environmental conditions that shape pollinator activity and reproductive
 100 success in this species.

101 MATERIALS AND METHODS

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103 Study Site

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105 The observation was conducted in the secondary forest area of the Northern Banyuwangi Forest
 106 Management Unit (Perhutani Banyuwangi Utara), RPH Gombeng, BKPH Ketapang, located near
 107 Sumber Nanas, Kalipuro, 11 km northeast of Banyuwangi City.

108

109 Phenological and morphological observation of *R. zollingeriana* flower

110

111 In this study, we focused on observing the phenological flowering phase of a male flower. The
 112 observation was conducted from the first day of anthesis and monitored daily to document its
 113 phenological changes, continuing until visible signs of senescence, such as colour changes and
 114 tissue decay, were observed. Meanwhile, the morphological characteristics were measured and
 115 documented by comparing specimens encountered during this study with those recorded in the
 116 previous research in 2022. For each flower we found, all floral parts were measured and recorded
 117 through both detailed morphological descriptions and photographic documentation.

118

119 Pollen Morphology and Viability Analysis

120

121 To characterize the pollen morphology of *R. zollingeriana*, pollen samples were collected from the
 122 underside of the disc of a male flower. The samples were then examined using a Scanning Electron
 123 Microscope (SEM) JSM IT200 to observe their form and size. For the pollen viability test using
 124 staining techniques, pollen was collected and stained with a 1% solution of 2,3,5-
 125 triphenyltetrazolium chloride (TTC), prepared by dissolving 0.2 g of TTC and 12 g of sucrose in
 126 20 mL of distilled water, following the method described by Sulusoglu and Cavusoglu (2014). A
 127 drop of liquid pollen was placed on a microscope slide, to which the TTC solution was added. The
 128 slide was then covered with a coverslip. Pollen grains exhibiting red coloration were considered
 129 viable. This procedure was conducted every six hours, starting from the first day of blooming.
 130 Observations were performed using both a Dino Lite AM4113T Digital Microscope (USB2.0)
 131 1.3MP Res. 10x~200x Magnification and a light microscope Olympus CX31.

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133 Microclimate data collection

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135 We observed microhabitat parameters based on the method employed by Patiño et al. (2002), with
136 certain modifications. Microclimate parameters were recorded hourly from 08:00 to 16:00 to
137 assess environmental conditions influencing pollination. Parameter measurements included light
138 intensity, temperature, and humidity in the immediate surroundings of the flower. Additionally,
139 microclimate data were collected at three specific floral locations: on top of the perigone, above
140 the disk, and below the disk, to evaluate variations in microhabitat conditions within the flower
141 structure.

142

143 **Pollinator observation and identification**

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145 Pollinator observations were carried out simultaneously with microclimate measurements from
146 08:00 to 16:00. An insect was classified as a pollinator if pollen grains were visibly attached to its
147 body, whereas visitors were insects that only visited flowers without attaching pollen to their
148 bodies. Each insect visiting the flowers was recorded, and high-resolution photographs were taken.
149 Lastly, the insects were captured by hand, placed into vials, and preserved in 70% ethanol for
150 identification purposes. Specimens were identified by taxonomic experts provided by ELSA of the
151 Indonesian Research and Innovation Agency (BRIN).

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153 **Statistical analysis**

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155 Statistical analysis was performed on R (version 4.3.2).

156 **RESULTS**

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158 **Morphology of the female and male flowers of *Rafflesia zollingeriana***

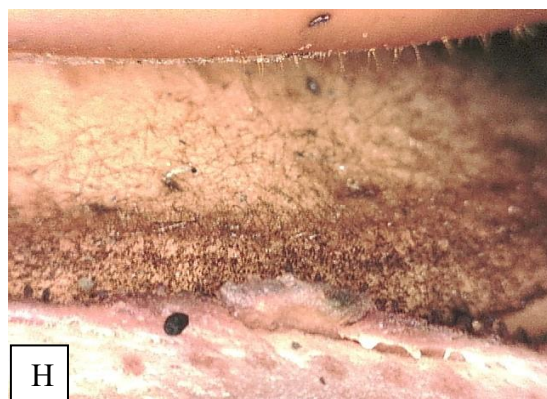
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160 *Rafflesia zollingeriana* is a dioecious flower; the female and male flowers are separate on different
161 plants. The fully opened male flower of *R. zollingeriana* measured 35×42 cm, with a diaphragm
162 width of 3×4 cm and an aperture size of 10×9 cm. The flower consisted of five perigone ranging
163 from 10 to 17 cm in length and 13 to 15 cm in width and featured a total of 40 processes arranged
164 in 4 concentric rings. Meanwhile, the fully opened female flower of *R. zollingeriana* measures
165 39×40 cm in length and width, with an aperture of 4×5 cm. The diaphragm is 11×2.5 cm, consisting
166 of five perigones ranging from 13 – 18 cm. The flower height is 18 cm.

167

168 The external morphological features of the male and female flowers exhibited notable
169 distinctions. First, lies in the appearance of the warts on the perigone. In female flowers, the white
170 warts are more prominent, larger, and have a smoother surface compared to those on male flowers,
171 that dominated by smaller nodules randomly dispersed in the spaces between the warts (Fig. 1C
172 and 1D). Nevertheless, both flowers share a dominant orange background color. Second, a distinct
173 contrast in disc coloration was observed in male flowers, where the disk base appears significantly
174 lighter—often whitish—compared to the bristled processes. This contrast is absent or much less
pronounced in female flowers (Fig. 1E–F). When observed closely, there were yellow bristles on

175 the apex of the processes, as well as the tip and underside of the disk rim (Fig. 1G–H); this
176 characteristic is present in both male and female flowers.
177



178 Figure 1. Floral morphology of *R. zollingeriana*. (A) Female flower. (B) Male flower. (C) Perigone
179 dwarf of the female flower. (D) perigone dwarf of the male flower. (E) Disc and processi of the
180 female flower. (F) Disc and processi of the male flower. (G) Bristle in disc rim and processi tip
181 male flower. (H) bristles in the underside of the disk rim, the lower part of the floral column in
182 female flowers bears fine hairs and trichomes.

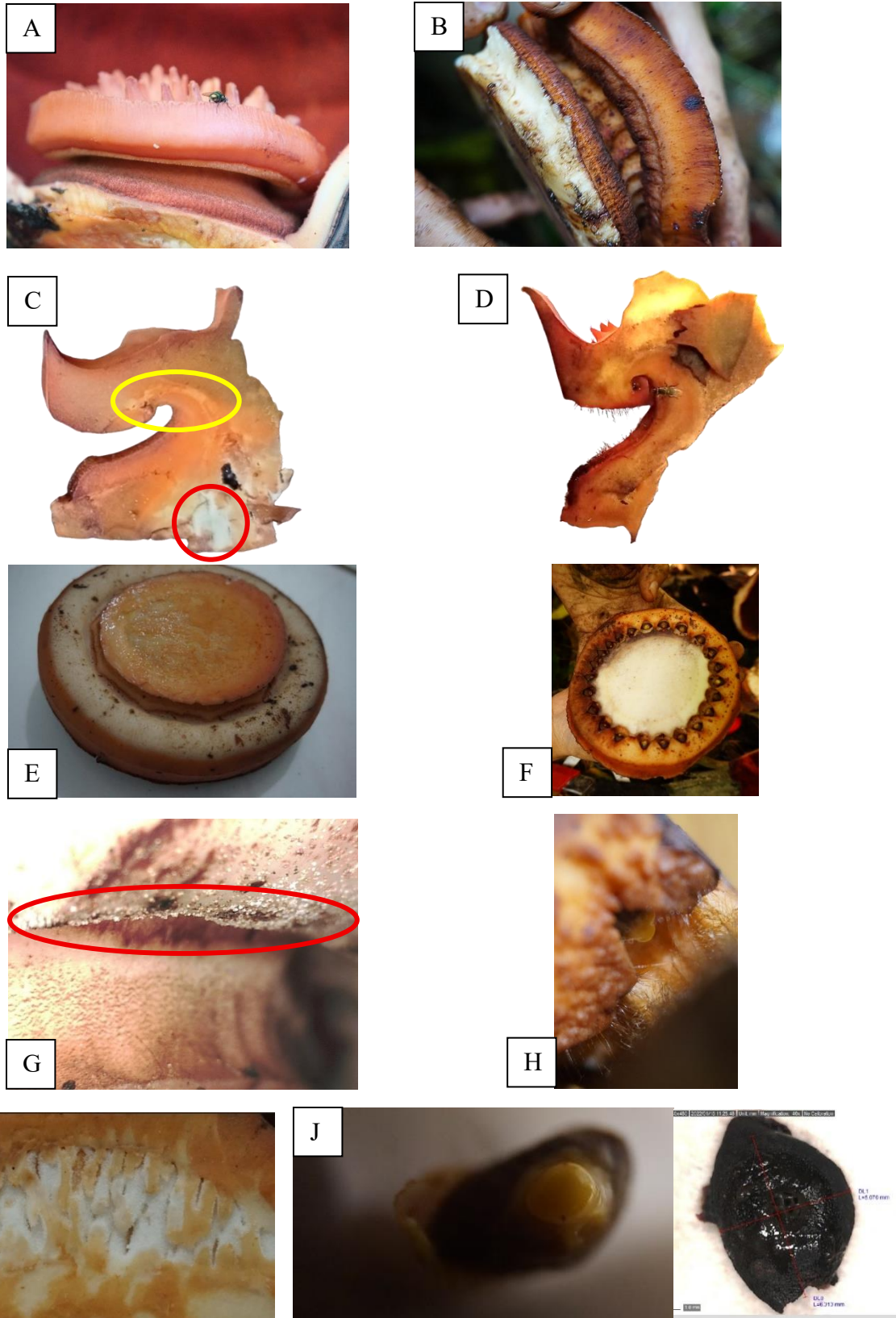
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184 The third morphological difference could be found in the region below the disk (Fig. 2A–J).
185 Under the disks, the stigma and ovary are present, while in male flowers, this area bears pollen..
186 Both sexes have an annulus at the base of the column, covered with a dense layer of fine hairs. The
187 column in female flowers lacks a pronounced depression, whereas in males, a deep groove is
188 present and bears hairs at its apex. The underside of the disk in male flowers is uneven, with
189 reddish-yellow color, bearing fine protuberances with dense hairs and a conspicuous cavity with
190 an 8 – 9mm diameter, near the supporting column, where 40 pollen tubes are attached. In female
191 flowers, the underside of the disk is relatively flat, glabrous, and white, bearing the stigma papillae
192 (Fig. 2G) including the presence of a style connecting the stigma to the ovary (Fig. 2C). These
193 papillae are connected to the ovary below via a distinct style (see details Fig. 2G–H). The presence
194 of the stigma beneath the disk has previously been reported by Bänziger (1991) and Francis Ng
195 (2019), and is further confirmed by this study.

196

197 In this study, we identified the dense hairs covering the lower part of the column beneath
198 the disk as the primary floral features emitted the odor. These hairs function as specialized sites
199 for scent release, producing the strong odor that attracts pollinators, while the pollen itself was
200 found to be odorless.

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232 Figure 2. Comparative Floral Structure in Male and Female Flowers of *R. zollingeriana* (A)
233 Column of female flower. (B) Column of male flower. (C) In female flowers, no deep depression

234 is present beneath the disk; fine hairs are confined to the upper annulus only. Style (shown by a
235 yellow circle) connected stigmatic papillae to the ovary (shown by a red circle). (D) There is a
236 deep groove behind the male flower disc, and fine hairs are evenly distributed from the top of the
237 annulus to around the cavity adjacent to the anther tube on the male flower. (E) The lower surface
238 of the disk in female flowers is white, glabrous, and lacks any fine hairs. (F) In contrast, male
239 flowers possess a conspicuous depression beneath the disk, which is uneven and undulating in
240 texture, reddish-yellow in color, and densely covered with fine hairs. This depression serves as the
241 attachment site for the pollen tube. (G) Stigmatic papillae (shown by a red circle) are clearly
242 visible, covering the entire underside of the disk in female flowers. (H) The lower surface of the
243 male disk, including the cavity, is densely covered with fine hairs. (I) White ovules densely occupy
244 the ovary cavity. (J) Upper: Liquid pollen on the first day of flowering, Lower: pollen tube with 4-
245 5mm in diameter, there were 8 apertures directed horizontally towards the column, functioning as
246 exit points for pollen exudation.

247

248 In females, hairs are confined to the upper margin of the annulus; the stalk and underside of
249 the disk are glabrous. These hairs are relatively sparse, unlike in male flowers, where hairs are
250 more extensively distributed, covering the top of the annulus, the disk-supporting column, the
251 ridge, and the disk surface, including areas around the pollen tube openings and densely covering
252 the entire column, the ridge of the vertical groove, and even beneath the base of the disk (Fig. 2H).

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254 **Flowering Phenology and Blooming Duration**

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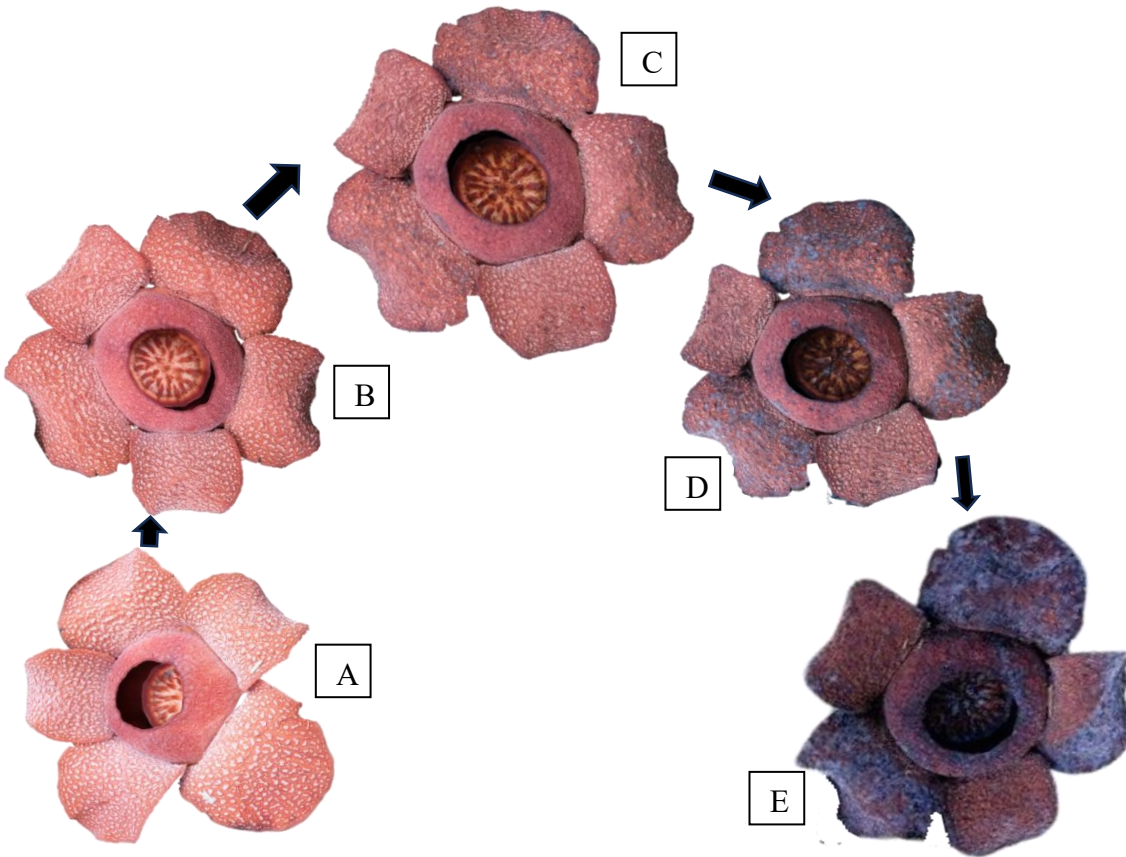
256 Several individuals of *R. zollingeriana* at different developmental stages were recorded within the
257 population. These included two male flowers in bloom—one of which had started to turn black,
258 while the other was the focus of this observation. Three buds at the bracteal phase were recorded
259 with diameters of 13 cm, 8 cm, and 4.75 cm, respectively. One flower at the copula phase measured
260 3.25 cm in diameter. Additionally, two post-anthesis male flowers were observed in a decayed
261 stage.

262

263 On the first and second days of blooming, the flower emitted a strong, unpleasant odor.
264 According to our observations, the scent of the male flower closely resembles that of liquefied
265 petroleum gas, exhibiting a sulfur-like odor. This is consistent with previous studies on the floral
266 scent of male *R. cantleyi*, which identified dimethyl disulfide and dimethyl trisulfide as the
267 dominant volatile compounds of *R. cantleyi* blooming flowers (Wee et al. 2018). The sulfur-
268 containing dimethyl disulfide is only detected on the full bloom flowers, and it is mainly
269 responsible for the rotten smell of the flowers. Its synthesis only takes place when the aperture is
270 fully open, and the flies are able to access the sex organs (Bascos et al., 2024). On the second day,
271 the odor was detectable from a greater distance compared to the first day. Time of day also
272 appeared to influence odor intensity, with the smell being stronger at midday than in the morning
273 or late afternoon. This phenomenon is also mentioned by Bascos et al., 2024 that between 10.00-
274 14.00 when the sun light penetrated the canopy the *R. consulaceae* emit the strongest odor.
275 However, still no explanation for whether this strongest smell is triggered by the light intensity or
276 temperature, further detailed studies are required to better understand this phenomenon.

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Figure 3. Flower changes during anthesis in male flowers of *Rafflesia zollingeriana*. (A) First day of flowering. (B) Second day of flowering. (C) Third day of flowering. (D) Fourth day of flowering. (E) Fifth day of flowering.

285 We found the color changes in the perigone occur rapidly (Fig. 3A-E). On the first and second
286 days of blooming, the perigone displayed a bright orange coloration. By the second day, the edges
287 of the perigone lobes adjacent to the ground began to darken, indicating early signs of senescence.
288 By the third day, as the perigone darkened to a maroon red, the apices of the processes also began
289 to darken. Simultaneously, black spots appeared on the surface of the perigone. On the fourth and
290 fifth days, a marked decline in both color intensity and odor emission was observed, suggesting a
291 reduction in reproductive activity and pollinator attraction. Fungi appear to dominate in the
292 perigone, diaphragm, processii, wall of the flower tube, and discus. By the fourth day, the scent
293 began to fade and was no longer as intense as on the previous day. On the fifth day, the
294 characteristic sulfurous odor was no longer detectable and had been replaced by a musty or damp
295 smell. However, the scent could only be perceived at proximity, directly above the aperture of the
296 flower.

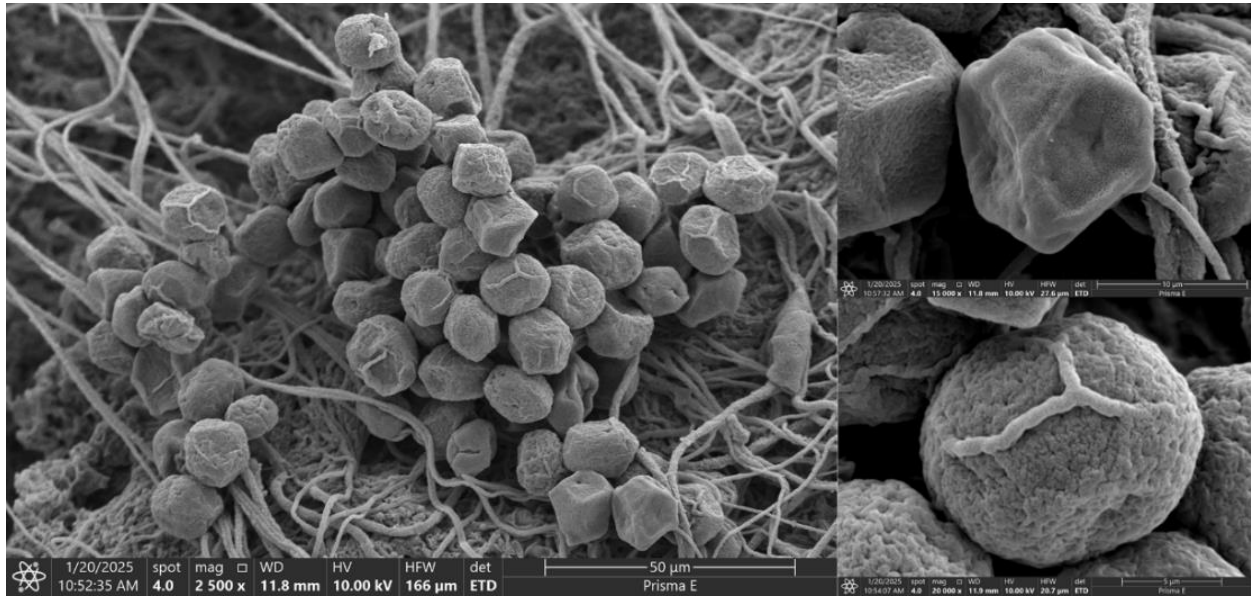
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Pollen Morphology and Viability

301 The anthers of *Rafflesia* are located on the underside of the disc of the flower. The androecium
 302 consists of dome-shaped sessile stamens evenly arranged in a circular pattern beneath the margin
 303 of the disc. The pollen grains of *Rafflesia* are fluid and are extruded through pores in the anthers
 304 (see Fig. 2J) as viscous liquid masses, within which individual pollen grains have a polygonal
 305 shape due to mutual adhesion (Ng 2019; Ng 2025).

306 The pollen of *R. zollingeriana* occurs as monads (single grains) and is generally spheroidal
 307 in form, although some grains appear irregular or show infoldings (Fig. 4). Pollen size is relatively
 308 small, typically ranging from 11 to 16 μm in diameter. The surface is scabrate, characterized by a
 309 rough or irregularly textured ornamentation, which may enhance adhesion to pollinators or
 310 facilitate attachment to stigma surfaces. Although the pollen grains observed in this study were
 311 relatively similar in size and shape, our findings differ slightly from previous reports. Earlier
 312 studies on several *Rafflesia* species: *R. tuan-mudae*, *R. hasseltii*, *R. azlanii*, *R. cantleyi*, *R. keithii*,
 313 *R. kerrii*, and *R. lawangensis*—described their pollen as having a smooth surface (Sofiyanti &
 314 Chee Yen, 2012).

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316
 317 Figure 4. Pollen grains of *Rafflesia zollingeriana*.

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320 Table 1. The viability of pollen of *Rafflesia zollingeriana*. Pollen remaining in the anthers and free
 321 of water remains viable for 120 hours.

Time	Viability
24 hours	Viable
48 hours	Viable
72 hours	Viable
96 hours	Viable
120 hours	Viable
144 hours	Viable
168 hours	Viable
192 hours	Viable

322 Successful pollination is closely associated with the viability of pollen during anthesis, as pollen
 323 viability serves as a key indicator of the potential for effective fertilization. In *R. zollingeriana*,
 324 this parameter is particularly critical due to its short flowering period and dependence on highly
 325 specific and time-sensitive pollinator interactions. Our result showed that pollen remains viable
 326 for up to eight days from the onset of anthesis (Table 1). This extended viability period implies
 327 that, despite the short duration of floral display, the effective timing for fertilization may extend
 328 slightly longer, especially if pollinator visits occur early in the anthesis phase.

329

330 **Insect Visitation, Pollinator Diversity, and Visitation Patterns**

331 Observations conducted throughout the flowering period revealed that several insect species
 332 visited the flower during the day. A total of 17 insect individuals and two different species of
 333 Arachnida were recorded (Fig. 5A). However, not all these insects played a role in the pollination
 334 of *R. zollingeriana*. Most of them merely used the flower as a resting place, mating without
 335 contacting the underside of the disk and thus had no potential to carry pollen.

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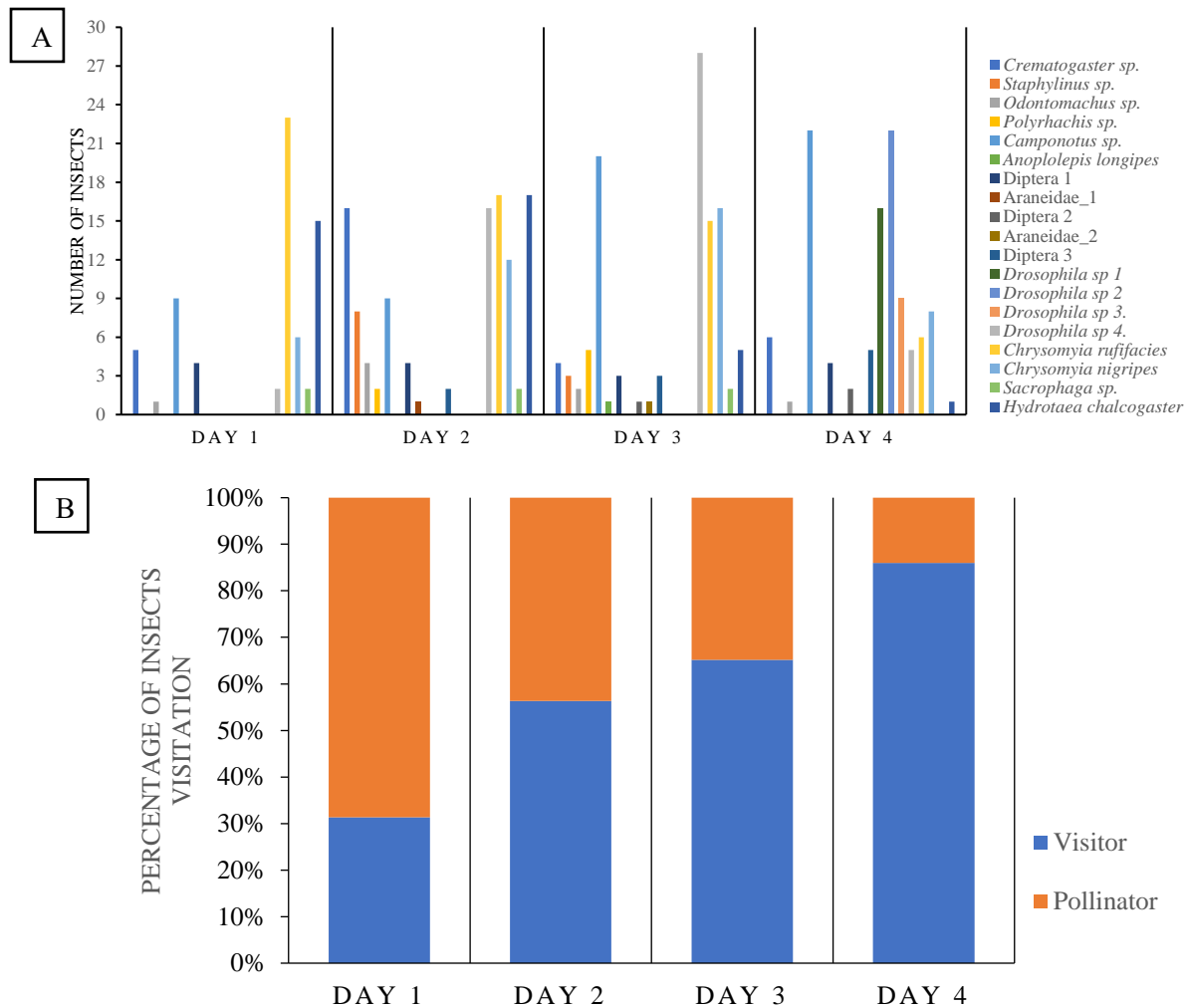
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357 Figure 5. The total number and percentage composition of floral visitors compared to confirmed
 358 pollinators. (A) Total number of insect and arachnid visits to the flower. (B) Percentage
 359 composition of floral visitors and confirmed pollinators.

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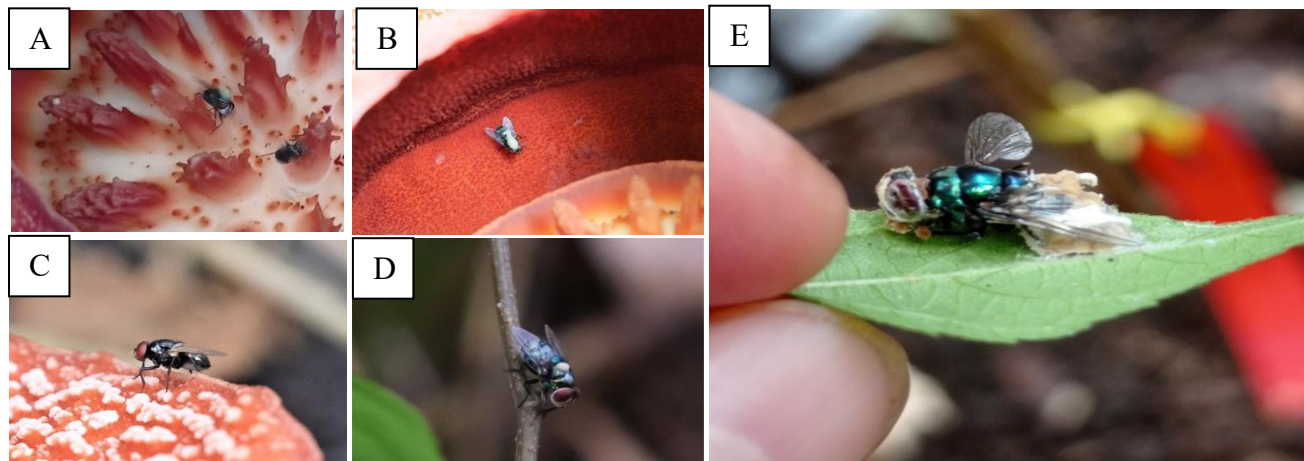
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We categorized the insects into two functional groups: (1) visitors, which interacted with the flower without carrying pollen, and (2) pollinators, which were observed bearing pollen on their dorsal surfaces. Observations on the first day of anthesis indicated that 69% of insect visitation recorded consisted of pollinators, while the remaining 31% were non-pollinating visitors (Fig. 5B). The proportion of effective pollinators declined markedly over the subsequent days, with pollinator visitation dropping to 44% and 35% on the second and third days, respectively. By the fourth day, pollinators accounted for only 14% of total insect visitors. On days 3 and 4, the insect visitors were non-pollinating insects, predominantly *Drosophila* spp. The increased abundance of *Drosophila* on the third and fourth day indicates that the flower had entered the decomposition phase, as this genus is commonly attracted to decaying organic matter such as rotting fruit.

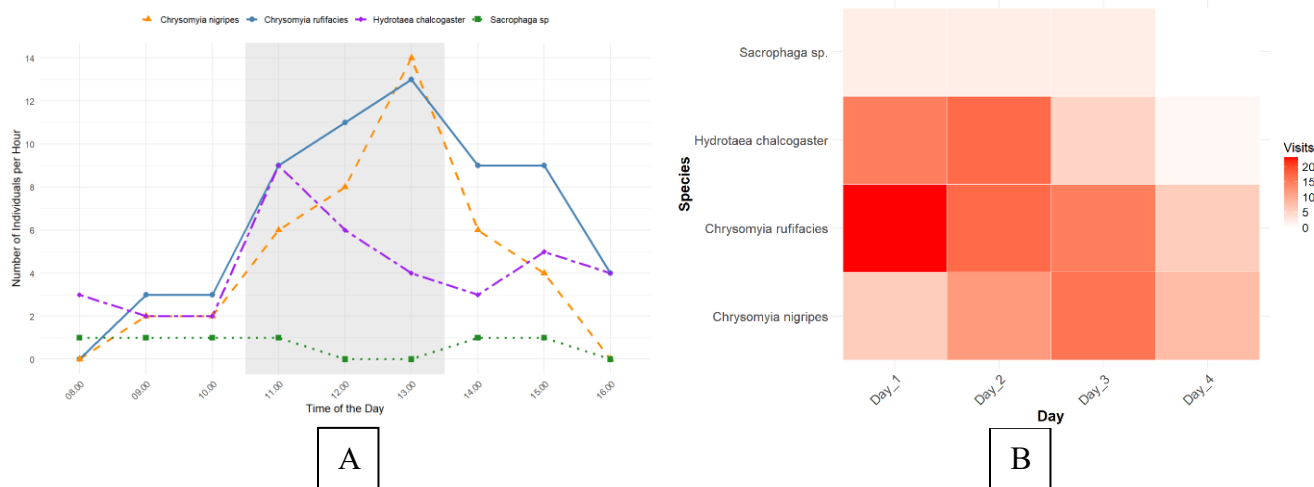
A total of four dipteran species were identified as pollinators of *R. zollingeriana*: *Sarcophaga* sp., *Chrysomya rufifacies*, *Hydrotaea chalcogaster*, and *C. nigripes* (Fig. 6A–D). These species belong to the families Sarcophagidae (flesh flies), Calliphoridae (blow flies), and Muscidae (house flies), all of which are members of the Calyptrata group. They are recognized as important scavengers, exploiting carrion, human waste, animal feces, and decaying animal matter as their

376 primary resources. This scavenging behaviour is closely aligned with their attraction to carrion-
 377 mimicking floral odors, such as those emitted by *Rafflesia*. They were observed carrying liquid
 378 sticky pollen masses on their dorsal surfaces. In some individuals, sticky pollen also adhered to
 379 the wings, indicating direct contact with the anther during floral visitation.
 380



381 Figure 6. The pollinator species found in *Rafflesia zollingeriana*. (A) *Sarcophaga* sp. (B)
 382 *Chrysomya rufifacies*. (C) *Hydrotaea chalcogaster*. (D) *Chrysomya nigripes*. (E) Deceased (non-
 383 surviving) pollinator.
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385 In several instances, a dead pollinator was recorded near the flowers (Fig. 6E.). The individual
 386 appeared to have succumbed to the burden imposed by the viscous and adhesive properties of the
 387 pollen. In fresh condition, the pollen was liquid, sticky, and relatively heavy, adhering to the bodies
 388 and wings of visiting flies. This excessive pollen load not only caused physical encumbrance but
 389 also disrupted wing movement and balance. Over time, the pollen desiccated, further impairing its
 390 mobility. The physical properties of *R. zollingeriana* pollen not only aid in pollen adherence and
 391 transfer but may also present mechanical challenges that influence pollinator survival.

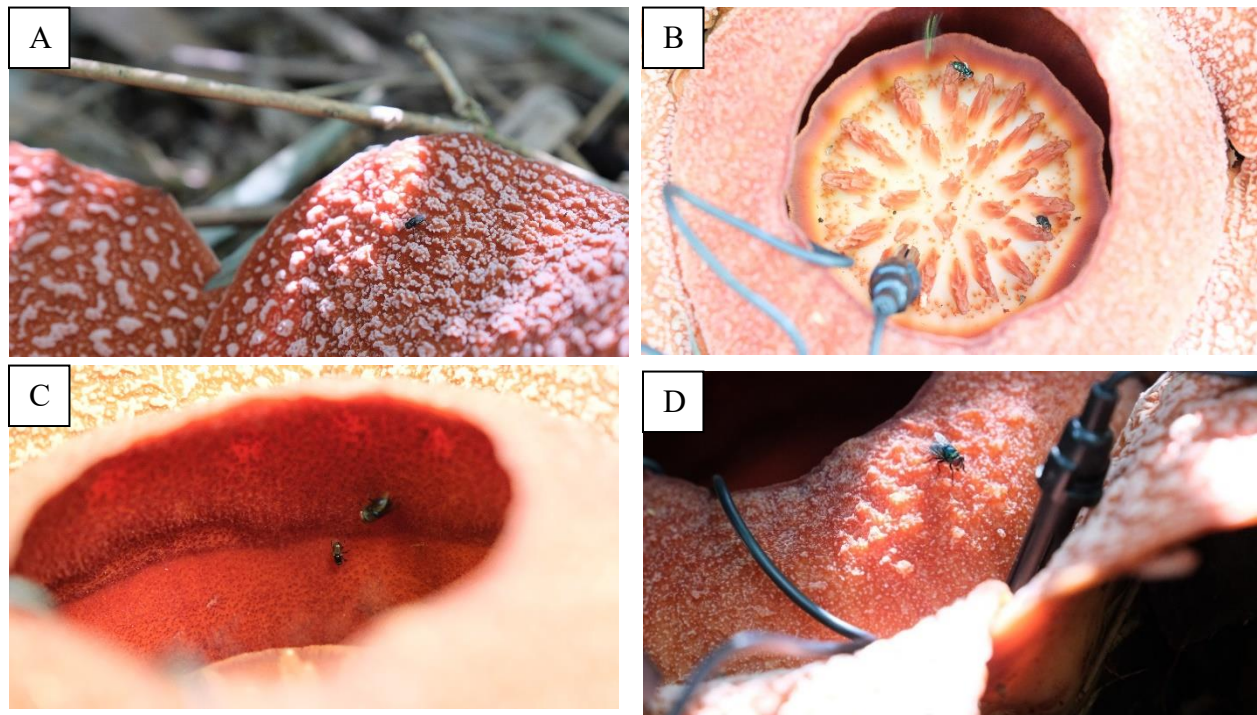


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 393 Figure 7. Pollinator visitation pattern. (A) Hourly distribution of pollinator visits during a single
 394 day. Grey bars indicate peak visitation periods. (B) Heatmap showing the total number of visits by
 395 each pollinator species across observation days.

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The total visitation of these fly species varied throughout each hour of the day. Observations conducted across four consecutive days revealed that visitation activity was initially low at 08:00, with only two species—*Sarcophaga* sp. and *H. chalcogaster*—present in small numbers. From 09:00 to 13:00, the number of visits steadily increased, reaching a peak between 11:00 and 13:00 (Fig. 7A). Following this peak period, visitation gradually declined until 16:00. Among all recorded species, *H. chalcogaster* was the only one consistently observed throughout the entire daily observation window (08:00–16:00), although in lower numbers compared to *C. rufifacies*. During the peak visitation hours, *C. rufifacies* and *C. nigripes* recorded the highest number of total visits, indicating their significant contribution to pollination activity during this period.

In addition to hourly patterns, a declining trend in pollinator visitation was observed over the anthesis period. The highest visitation rates occurred on the first and second days of anthesis, followed by a marked decline on the third and fourth days. Among the identified fly species, *C. rufifacies* exhibited the highest total visitation, suggesting its potentially significant role in the pollination of *R. zollingeriana*. Conversely, *Sarcophaga* sp. was recorded at the lowest visit, indicating a comparatively minor contribution to pollination during the observation period.



413 Figure 8. Pollinator flies in many parts of *Rafflesia zollingeriana*. (A) Perigone. (B) Beyond and
 414 above the disk. (C) Upper tube and middle tube rameta. (D). Diaphragma
 415

416 We also observed the behaviour of pollinators. During the first and second days of
 417 observation, numerous flies were recorded bearing pollen on their dorsal thorax and other regions
 418 of the body. At midday, pollen grains were observed adhering to the tips of the processes. We
 419 suspect that these are residual deposits originating from pollen previously attached to the dorsal
 420 surface of visiting flies. On the third day of observation, the pollen beneath the disk appeared to
 421 have transitioned from a liquid to a more compact or solid state.

422 During field observations, the flies did not immediately land on the flower itself, but instead
 423 alighted on surrounding structures such as branches and twigs in the vicinity. They gradually
 424 approached the perigone lobes of the flower, landing and moving laterally across its surface. After
 425 this exploratory phase, they entered the floral tube and exhibited active flight within the chamber.

426 Inside the flower tube, the flies were observed landing sequentially on various floral
 427 structures: first on the processus, followed by hovering on the inner floral walls lined with dense
 428 ramenta, then beneath the diaphragm, onto the processes again, and finally beneath the central disk
 429 (Fig. 8). They continued to move within the chamber, flying intermittently between floral tissues.
 430 After some time, they exited the floral tube, briefly returned to the perigone surface, and
 431 subsequently flew back into the surrounding habitat. This pattern of movement was repeated across
 432 multiple individuals. The repeated transitions between external and internal floral structures,
 433 combined with prolonged activity within the floral chamber, likely enhance the potential for
 434 effective pollen deposition and transfer.

435

436 **Microclimate Conditions and Their Influence on Pollination**

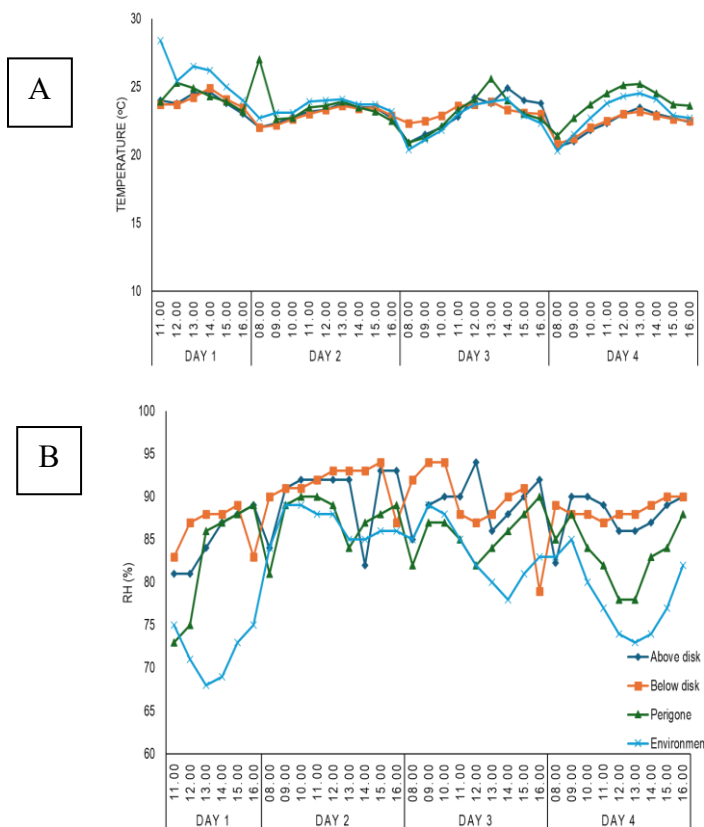
437 Environmental microclimate data recorded showed distinct temporal variation in temperature,
 438 relative humidity (RH), and light intensity between 08:00 and 16:00. The temperature ranged from
 439 a minimum of 21.13°C at 08:00 to a peak of 24.78°C at 11:00. Relative humidity values fluctuated
 440 between 76.50% and 87.67%, with the highest RH observed at 09:00 and the lowest at 13:00 and
 441 14:00 (Table 1.). Light intensity increased progressively from morning to midday, reaching its
 442 maximum value of 859.75 lux at 13:00, before declining in the late afternoon. The lowest light
 443 intensities were recorded at 08:00 (184.67 lux) and 16:00 (236.25 lux). These results indicate that
 444 both temperature and light intensity reached their highest levels between 11:00 and 13:00,
 445 coinciding with the period of maximum solar radiation received.

446

447 Table 2. Average temperature, relative humidity, and light intensity of environmental microclimate
 448 variation during anthesis

Time	T (°C)	RH (%)	Light intensity (Lux)
08.00	21.13	84.00	184.67
09.00	21.90	87.67	560.00
10.00	22.53	85.67	518.00
11.00	24.78	81.25	752.75
12.00	24.35	78.75	569.75
13.00	24.75	76.50	859.75
14.00	24.53	76.50	572.00
15.00	23.63	79.25	470.25
16.00	23.05	81.50	236.25

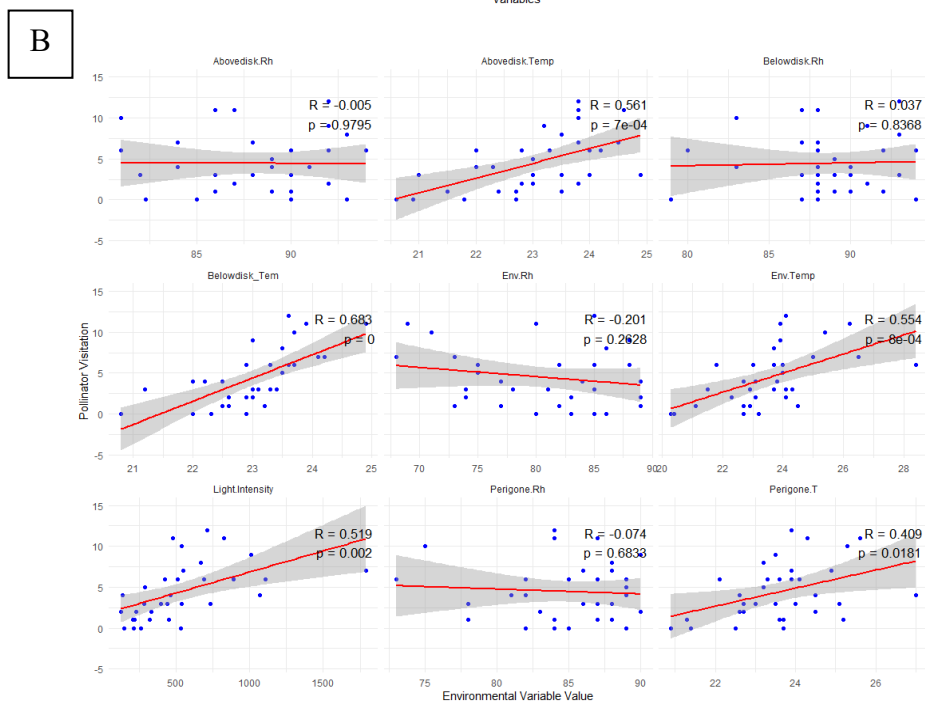
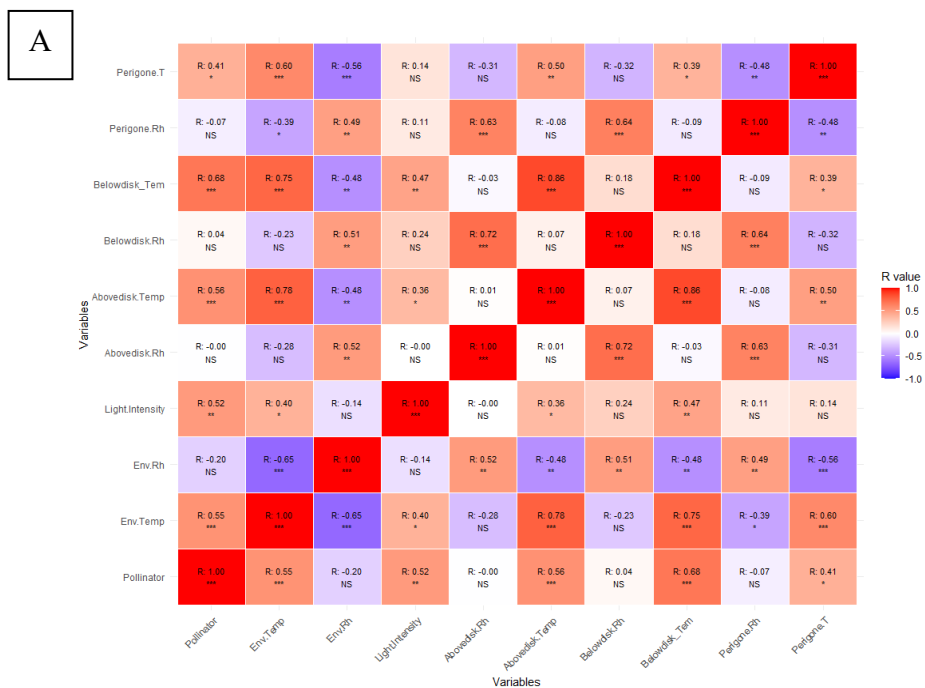
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Figure 9. Comparison of (A) temperature and (B) relative humidity between environmental conditions and floral structures at three morphological parts: above the disk, below the disk, and the perigone.

Floral surface temperature measurements taken during the same time interval showed significant spatial variation across different floral regions. Notably, the perigone consistently exhibited higher surface temperatures compared to the areas above and below the disk. During the peak environment temperature (11:00–13:00), the average surface temperature of the perigone ranged from 23.80°C to 24.90°C, whereas the regions above and below the disk recorded average temperatures of 23.90°C and 23.73°C, respectively. These results indicate a differential pattern of heat accumulation among floral structures. Meanwhile, the highest humidity was recorded in the area below the disk, likely due to the tubular floral morphology that traps moisture in this region.



481
 482 Figure 10. Relationships between pollinator visitation and microclimatic variables (A) Pearson
 483 Correlation Matrix of Pollinator Visitation and Microclimatic Variables (significance codes NS
 484 $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$); (B). Relationships Between Pollinator Visitation and
 485 Microclimatic Environmental Variables

486
 487 A Pearson correlation analysis was conducted to evaluate the relationship between pollinator
 488 visitation and various environmental parameters (Fig. 10A). The heatmap illustrates the strength

489 and direction of pairwise correlations among variables, with the level of significance indicated by
490 asterisks (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, NS = not significant). Pollinator visitation was
491 significantly and positively correlated with temperature, including above and below disk
492 temperature, perigone temperature, and environmental temperature. A significant positive
493 correlation was also observed with Light Intensity. These results suggest that both thermal
494 conditions and light availability play important roles in influencing pollinator activity.

495 To further examine these relationships, linear regression analyses were performed between
496 pollinator visitation and each environmental variable (Fig. 10B.). The regression plots showed
497 strong and statistically significant positive trends for Below disk Temperature ($R = 0.683$, $p <$
498 0.001), Environmental Temperature ($R = 0.561$, $p < 0.001$), Above disk temperature ($R = 0.561$, p
499 $= 0.001$), Perigone Temperature ($R = 0.409$, $p = 0.0181$), and Light Intensity ($R = 0.519$, $p = 0.002$).
500 In contrast, relative humidity in each of the floral parts, such as perigone, below disk, above disk,
501 and also the environment, showed weak or negligible correlations with pollinator visitation, and
502 none were statistically significant.

503

504 DISCUSSION

505

506 Based on our observation, the anthesis period of the male flower of *R. zollingeriana* was brief,
507 lasting only five days. This duration is similar to that of other *Rafflesia* species that remain in full
508 bloom for only 1–8 days. For instance, the blooming period of *R. cantleyi* ranges from 1–7 days,
509 depending on weather conditions (Wee et al. 2024). *R. hasseltii* can remain in bloom for 4–8 days
510 (Sofiyanti et al. 2007), while *R. patma* blooms for 3 to 5 days (Hidayati et al. 2000). *R. arnoldii*
511 typically blooms for 5–8 days, and *R. rochussenii* flowers last for approximately seven days
512 (Susatya 2020). *R. meijerii* has an even shorter blooming period, lasting about three days
513 (Sihombing and Sinery 2022).

514 In one population, we observed there were three flowers (one in anthesis and two post-
515 anthesis), all of which were male. When compared with the study by Nurchayati et al. (2025),
516 whose observed population also recorded a similar pattern—being dominated by flowers of the
517 same sex—it can be tentatively concluded that each population tends to produce flowers of a single
518 sex. Such a mechanism may serve as an evolutionary strategy to encourage inter-population
519 outcrossing, which could help sustain or enhance genetic diversity within the species. This may
520 help explain why the genetic diversity of *Rafflesia* species, as reported by Pelsner et al. (2018),
521 remains high despite the species' extremely small and fragmented populations.

522 The specific window of floral attractiveness is with pollinator activity concentrated during
523 the early anthesis phase. The vivid coloration and strong odour observed during the first two days
524 likely play a critical role in attracting pollinators, whereas their rapid decline in subsequent days
525 showed the limited lifespan of the flower. Our observations of the visual and olfactory traits of
526 *Rafflesia* support the conclusions of Beaman et al. (1988) and Wee et al. (2018), who mentioned
527 that olfactory cues alone may not be sufficient to elicit pollinator landing; the attraction relies on
528 a combination of visual and olfactory signals.

529 The synchronized peaks of scent intensity and vivid coloration during the first two days of
530 anthesis may represent the maximal effort of the flower to attract pollinators. By the third day,
531 signs of decay are apparent. We also observed that the absence of a floral window does not appear
532 to disorient flies navigating entry or exit from the floral tube. Instead, the contrasting coloration of

533 the disk relative to the perigone lobes, diaphragm, and ramenta likely functions as a visual guide,
 534 complementing olfactory cues in directing pollinators toward appropriate landing sites.

535 In this study, we found that the odour of *Rafflesia* was coming from hair-like structures
 536 distributed at the base of the floral tube. Male flowers have more extensive distribution of these
 537 hairs than female flowers. The odour produced by these hairs, particularly those located around
 538 the pollen region, guides fly deeper into the pollen chamber in male flowers.

539 This finding also helps explain the results of an earlier experiment, in which no flies entered
 540 the floral chamber when the base of the flower (the region beneath the disk) was flooded, thereby
 541 preventing odour emission (Beaman et al., 1988). The absence of pollinator visitation under such
 542 conditions strongly supports the role of these hairs in scent emission and highlights their
 543 importance in mediating pollinator attraction and ensuring reproductive success.

544 In contrast, female flowers possess relatively sparse hairs compared to male flowers, and the
 545 scent they produce is correspondingly weaker. This observation may help explain scepticism
 546 regarding the foul odour of *Rafflesia* flowers reported by Ng (2024), whose specimen was
 547 described as scentless. Examination of the photographic evidence suggests that the specimen was
 548 a female flower, which, based on our observations, indeed has fewer hairs and therefore emits a
 549 much weaker odour than male flowers. With this finding, we suggest that further research is needed
 550 to investigate these hair-like structures and their potential role in odor emission, thereby expanding
 551 upon previous studies that analyzed floral volatiles from the central disk of *Rafflesia cantleyi* (Zain
 552 et al., 2020).

553 Morphologically, female flowers typically exhibit a shallower floral cavity; the gap between
 554 the underside of the disc and the base of the column is not as recessed, allowing flies to come into
 555 contact with the stigmatic surfaces which located around the underside of the disc, without needing
 556 to enter as deeply. The possibility of fertilization without pollen, as proposed by Nais (1997),
 557 appears to warrant further investigation, particularly regarding the viability of the resulting seeds.

558 This structural differentiation between male and female flowers may reflect a functional
 559 specialization that enhances pollination efficiency. While male flowers appear adapted to
 560 maximize pollen attachment to visiting flies, female flowers may facilitate effective pollen
 561 deposition onto the stigmatic surfaces. Such spatial and morphological differences could represent
 562 an adaptive strategy to optimize reproductive success.

563 The effectiveness of these pollinators is further enhanced by pollen morphology. The small
 564 size and adhesive nature of the pollen grains facilitate their accumulation in large quantities on the
 565 dorsal surfaces of visiting flies. This morphology enhances pollen transfer to floral regions that are
 566 more accessible to pollinators, thereby increasing the likelihood of successful pollen dispersal
 567 (Wicaksono et al. 2016). In addition, the scabrate surface texture of the pollen promotes adhesion,
 568 increasing the success pollen deposit and transport from male flowers to the stigmas of female
 569 flowers. However, despite these apparent advantages, our observations indicate a potential cost of
 570 excessive pollen accumulation. High pollen loads on the dorsal surface and wings can impair flight
 571 performance and may lead to pollinator mortality, which could reduce reproductive success in *R.*
 572 *zollingeriana*.

573 Pollen viability is also a key factor influencing reproductive success. Previous studies have
 574 reported that moisture content strongly affects pollen longevity, with viability declining to zero
 575 within 24 hours when exposed to water, whereas in dry conditions, pollen may remain viable for
 576 up to 120 hours (Nais, 2001; Ng, 2025). However, based on our observations, pollen remained
 577 viable for up to eight days, even though the flowers began to decay after five days. This suggests
 578 that pollen longevity may extend beyond the lifespan of the male flower. In a closely related taxon,

579 *Sapria himalayana*, pollen viability has been reported to persist for up to three weeks (Bänziger et
 580 al., 2022), further indicating that long pollen longevity may represent a common reproductive
 581 strategy within this lineage.

582 In addition to the biological traits of the flower, morphological compatibility between
 583 flowers and pollinators, particularly pollinator body size, is a critical determinant of effective
 584 pollen carry and transfer. In *Rafflesia kerrii*, for example, the body size of *Chrysomya* sp. closely
 585 matches the dimensions of the floral canal leading to the anther chamber, allowing direct contact
 586 with the reproductive organs and facilitating efficient pollen transfer (Hor et al. 2021). Similarly,
 587 *Chrysomya megacephala* (the Oriental latrine fly) has been reported as the most frequent visitor
 588 to *R. lagascae* flowers (Ireneo 2018). We observed there were four fly species identified as
 589 pollinators of *R. zollingeriana*: *Sarcophaga* sp., *Chrysomya rufifacies*, *Hydrotaea chalcogaster*,
 590 and *Chrysomya nigripes*. These taxa are relatively large dipterans, making them morphologically
 591 compatible with the deep position of pollen within the floral chamber. In contrast, smaller flies
 592 were observed merely hovering around the perigone surface, likely attracted by visual cues such
 593 as the orange-to-reddish coloration of the floral lobes (Beaman et al. 1988), but without effective
 594 contact with the reproductive structures. Larger-bodied flies are likely to be more effective
 595 pollinators, as their greater surface area enables the accumulation of higher quantities of pollen
 596 grains on their dorsal surfaces during floral visits. This increased pollen load may enhance the
 597 probability of successful pollen deposition on receptive stigmas, thereby improving overall
 598 pollination efficiency.

599 Two species within the genus *Chrysomya*: *C. rufifacies* and *C. nigripens* were the most
 600 frequent visit *R. zollingeriana* flower during anthesis. Genus of *Chrysomya* have also been
 601 reported as a primary pollinator in other *Rafflesia* taxa. For example, *Chrysomya* sp. was
 602 documented in *R. kerrii*, *Chrysomya megacephala* in *R. lagascae*, and *Chrysomya chani* as a
 603 pollen carrier in *R. cantleyi* (Beaman et al., 1988; Wee et al., 2018; Lit, Jr., 2018; Hor et al. 2021).
 604 The effectiveness of this genus as a pollinator was also mentioned by previous studies including
 605 *Hydrotaea chalcogaster* (Cook et al., 2020). The lifespan of calliphorid flies ranges from
 606 approximately 24 to 45 days, depending on species and whether longevity was measured under
 607 laboratory or field conditions (Pérez et al., 2016; Yanmanee et al., 2016). Under natural field
 608 conditions, adult lifespan is estimated to average around four weeks, although it remains strongly
 609 influenced by temperature and nutritional availability. Especially in higher temperatures, the
 610 lifespan decreases (Bosly, 2021; Pérez et al., 2016; Yanmanee et al., 2016).

611 Given that pollen in this species remains viable for up to eight days, even after floral
 612 senescence, living adult flies may have sufficient time to transfer viable pollen to receptive female
 613 flowers within their lifespan. This temporal overlap between pollen longevity and pollinator
 614 survival may partially offset low visitation rates and enhance the probability of successful
 615 fertilization,

616 Along with the life span, the survival of the pollinator also affected the reproductive success
 617 of *R. zollingeriana*. In our study, we observed that pollinator visitation in *R. zollingeriana* was
 618 significantly influenced by microclimatic conditions, particularly temperature and light intensity,
 619 which regulate the temporal patterns of pollinator activity during anthesis. The activity of
 620 pollinators increased under conditions of specific temperature and optimal light, suggesting that
 621 these factors act as important environmental cues.

622 Notably, *Rafflesia* has been described as partially endothermic, with heat production
 623 occurring in the central column (Patiño et al., 2002). Consistent with this findings, we recorded
 624 higher temperatures within the perigone compared to the surrounding environment. This

625 endogenous heat production may function as an adaptive trait to attract flies by creating a favorable
626 thermal microenvironment. Although the flower is capable of producing endogenous heat, ambient
627 environmental temperature remains a key determinant of pollination visitation. Internal heat
628 production alone may not be sufficient to ensure effective pollinator attraction if external thermal
629 conditions are suboptimal. The synchronization of pollinator activity with optimal light and
630 temperature conditions appears to enhance pollen transfer efficiency and thereby promote
631 reproductive success. Furthermore, the emission of floral odor in *Rafflesia* appears to be influenced
632 by environmental cues, potentially including temperature and solar radiation. These abiotic factors
633 may regulate the intensity or timing of volatile release. However, further investigation is required
634 to elucidate the physiological mechanisms underlying odor emission and its relationship with
635 environmental conditions.

636 Nevertheless, the dependency on specific microclimatic conditions, combined with limited
637 pollinator availability and short floral longevity, may impose significant constraints on
638 reproductive output. Such ecological sensitivity likely contributes to the consistently low fruit set
639 observed in natural populations and underscores the vulnerability of this species to environmental
640 variability and climatic fluctuations. From a conservation perspective, this dependence on
641 narrowly defined ecological conditions suggests that even subtle habitat alterations, such as canopy
642 disturbance or shifts in microclimate, could disproportionately affect reproductive success.
643 Therefore, conservation strategies should prioritize the maintenance of intact microhabitats and
644 stable pollinator assemblages to sustain long term population viability.

645

646 CONCLUSION

647 The visual and olfactory cues of *Rafflesia* are widely recognized as key drivers of pollinator
648 attraction to the *Rafflesia* flower, yet these factors alone are insufficient to ensure successful
649 pollination. Floral morphological traits further facilitate pollen transfer by guiding fly movement
650 within the floral chamber. The scabrate surface of the pollen enhances its attachment to pollinators,
651 and its viability of up to eight days after anthesis represents novel information, especially
652 considering that male flowers of *R. zollingeriana* bloom for only five days and pollinator visitation
653 declines thereafter. Thus, despite the asynchronous and spatially separated blooming of male and
654 female flowers, pollination can still occur as long as pollen remains viable and pollinators persist.
655 The pollinator activity also depends strongly on temperature and sunlight; the microclimate
656 disturbances, such as climate change or land-use change, could affect pollinator visitation. Further
657 research is required to elucidate these interactions in greater detail.

658

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