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# Dactyliform appendage contributes to delayed selfing in the diminutive orchid *Stigmatodactylus sikokianus*

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## Societal Impact Statement

Understanding plant reproductive strategies is vital for conserving endangered species. This study reveals a novel self-pollination mechanism in the diminutive orchid *Stigmatodactylus sikokianus*, facilitated by the movement of a finger-like appendage beneath the stigma. While this less-than-1-mm-long structure inspired the name *Stigmatodactylus*, its ecological function remained unknown for over 130 years—until now. The findings suggest that this appendage facilitates delayed self-pollination, likely ensuring reproductive success under conditions of pollinator scarcity. Furthermore, the research highlights the value of integrating taxonomy with functional morphology to advance our understanding of pollination ecology.

## Summary

- Orchidaceae is one of the largest and most morphologically diverse plant families, largely due to intricate relationships with pollinators. However, autonomous self-pollination is relatively common, likely as an adaptation to limited pollinator availability. This study examines the reproductive mechanism of the diminutive orchid *Stigmatodactylus sikokianus*, focusing on the finger-like appendage beneath the stigma.
- The reproductive biology of *S. sikokianus* was investigated through pollination observations, artificial pollination experiments, and detailed studies of column morphology.
- Pollination experiments demonstrated that *S. sikokianus* primarily relies on autonomous self-pollination, as indicated by high fruit set in bagged flowers and no fruit set in emasculated ones. Microscopic analysis revealed that the dactyliform appendage arcs toward the stigma, maintaining its straight structure, and eventually adheres to the stigma surface, allowing contact between the appendage apex and pollinia. UV microscopy showed thick bundles of pollen tubes penetrating the appendage adhered to the stigma and reaching the base of the column. The absence of pollen tube formation before contact between the appendage apex and pollinia suggests that autogamy occurs exclusively through the appendage at a later flowering stage.

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- This study uncovers a novel self-pollination mechanism in orchids, where the movement of the stigma appendage likely facilitates delayed selfing. This mechanism ensures seed production and likely reproductive success in *S. sikokianus*, enabling it to thrive in shaded environments with limited pollinator availability. The discovery highlights the value of integrating taxonomic and ecological approaches, as morphological traits provide valuable insights into species life histories.

#### KEYWORDS

autogamy, autonomous self-pollination, column morphology, delayed selfing, pollinator limitation, reproductive assurance

## 1 | INTRODUCTION

Orchidaceae is one of the largest and most morphologically diverse plant families, comprising over 33,000 species across more than 700 genera (POWO, 2024). This remarkable diversity is partly attributed to complex relationships between orchids and their pollinators, with numerous species depending on single pollinator species (Ackerman et al., 2023). The intricate pollination strategies within Orchidaceae have fascinated naturalists for over a century (Darwin, 1862). Nearly half of all orchid species offer no reward, instead deceiving pollinators by mimicking nectar-bearing flowers or female insects to lure male pollinators into pseudocopulation (Ackerman et al., 2023).

Despite high specialization in orchid-pollinator interactions, autonomous self-pollination is relatively common, occurring in nearly 500 orchid species across all subfamilies and most tribes, accounting for about 20% of species with known pollination systems (Ackerman et al., 2023). Deceptive orchids often face pollinator limitations and achieve about half the fruit set of rewarding species ( $20.7 \pm 1.7\%$  vs.  $37.1 \pm 3.2\%$ ) (Tremblay et al., 2005). In this context, the evolution of self-pollination mechanisms may be an adaptation to overcome limited pollinator availability.

In orchids, the anther (stamen) and stigma (pistil) are typically separated by a rostellum (Chen et al., 2012). A reduced rostellum, allowing direct contact between the stigma and pollinia, is the most common self-pollination mechanism in Orchidaceae, found in about half of the self-pollinating species (Catling, 1990; Suetsugu, 2015). Other self-pollination strategies include *Holcoglossum amesianum*, where the pollinia rotate  $360^\circ$  via auto-spinning of the stipe to deposit pollen into the stigma cavity (Liu et al., 2006), and *Paphiopedilum parishii*, where the solid anther liquefies and flows onto the stigma (Chen et al., 2012).

The subtribe Acianthinae comprises roughly 200 species across five genera: *Acianthus*, *Cyrtostylis*, *Stigmatodactylus*, *Townsonia*, and *Corybas* (Chase et al., 2015; POWO, 2024). Most species in this subtribe appear to be pollinated primarily by fungus gnats, particularly from the family Mycetophilidae (Han et al., 2022; Jones, 1970, 1974). Although *Stigmatodactylus*, the least well known of these genera, was locally confined across eastern Asia from northern India and Japan to the Malay Archipelago and Solomon Islands, recent studies revealed

that many species traditionally classified under *Acianthus* actually belong to *Stigmatodactylus* based on molecular and morphological evidence (Clements & Jones, 2018; Jones & Clements, 2017; Robinson, 2021). As a result, *Stigmatodactylus* now includes 28 species, with two in Australia and 13 in New Caledonia, with its diversity centered in the New Guinea–Solomon Islands–New Caledonia arc (Robinson, 2021). Within Acianthinae, *Stigmatodactylus* is recognized by its distinctive floral traits, including a single, large, sub-entire to lobed basal callus on the labellum, a ventrally keeled or appendaged column, and axillary subterranean tubers (Robinson, 2021).

The genus *Stigmatodactylus*, with *S. sikokianus* as its type species, was first described by the Japanese botanist Makino Tomitarō in 1890. He sent specimens and illustrations to the Russian botanist C. J. Maximowicz, who remarked, “The orchid is quite a new genus. I dissected a flower bud myself and found everything just as you had figured. I have named the plant, on account of the remarkable finger-like (dactyliform) appendage beneath the stigma, *Stigmatodactylus sikokianus*” (Makino, 1905). In 1891, Makino published the illustration with only the name (*S. sikokianus* Maxim.) and location in Latin (Figure 1; Makino, 1891), which was valid under the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018), as illustrations with analysis were sufficient before January 1, 1908. Although the name refers to this appendage in the type species, its form varies within the genus, ranging from linear to hooked, and is prominent in some species, while vestigial or absent in others (Robinson, 2021).

While *S. sikokianus* retains some photosynthetic capacity (Figure 2a–c), it primarily acquires carbon from decaying litter through its mycorrhizal associations (Suetsugu et al., 2021, 2025). Due to its nearly fully mycoheterotrophic status, this orchid can survive in low-light environments; however, such conditions may hinder reproduction, as pollinator activity often relies on light availability (Suetsugu & Yamamoto, 2024). In contrast to relatively intensive studies on mycorrhizal associations (Suetsugu et al., 2021; Yagame & Yamato, 2008), the pollination biology of *Stigmatodactylus* remains unexplored across all species. Additionally, the functional role of the finger-like (dactyliform) appendage on the stigma is unknown, despite this distinctive feature inspiring the genus name, which intrigued both Makino and Maximowicz. Consequently, the present study focuses on the



**FIGURE 1** Line drawing of *Stigmatodactylus sikokianus* by Tomitaro Makino, originally published in Makino (1891). Image credit: The Kochi Prefectural Makino Botanical Gardens.



**FIGURE 2** Self-pollination mechanism of *Stigmatodactylus sikokianus*. (a) Plant approximately 1 day after anthesis. (b) Plant approximately 3 days after anthesis. (c) Plant at the fruiting stage. (d) Flower approximately 1 day after anthesis, front view. (e) Flower approximately 1 day after anthesis, lateral view. (f) Flower approximately 3 days after anthesis, front view. (g) Flower approximately 3 days after anthesis, lateral view. The appendage is no longer visible due to its completed movement in (f) and (g). (h) Column approximately 1 day after anthesis. (i) Upper part of the column, approximately 1 day after anthesis. (j) Column approximately 3 days after anthesis. (k) Upper part of the column, approximately 3 days after anthesis. (l) Epifluorescence images of the column approximately 3 days after anthesis, stained with aniline blue. The finger-like appendage on the stigma is highlighted by arrows (in all panels except k). Dashed lines in (k) and (l) indicate the finger-like appendage adhered to the stigma surface and bundles of pollen tubes elongated through it, respectively. Scale bars: 1 cm (a–c), 3 mm (d–g), 1 mm (h & j), and 500  $\mu$ m (i & k–l). Photo credit: Tetsuro Ikeda (a–b & d–g) and Kenji Suetsugu (c & h–l).

pollination biology of *Stigmatodactylus sikokianus*, one of the most iconic Japanese orchids, with particular attention to the function of the dactyliform appendage.

## 2 | MATERIALS AND METHODS

### 2.1 | Study species and site

*Stigmatodactylus sikokianus* is a diminutive terrestrial orchid found on Shikoku Island, southern Kyushu Island, and the Kii Peninsula on Honshu Island, Japan (Maekawa, 1971).

Fieldwork was conducted from late August to early September 2011 in a *Cryptomeria japonica* plantation in Tanabe City, Wakayama Prefecture, Japan. Approximately 300 flowering individuals of *S. sikokianus* were identified during the investigation. We conducted direct observations of flower visitors during daylight hours from 7:00 to 18:00, totaling approximately 25 h. To record the behavior of insect visitors, we either walked around the study area or sat near flowering plants. For each floral visitor, we documented the frequency, duration, and patterns of their visits.

### 2.2 | Artificial pollination experiments

For the pollination experiments, flower buds just before anthesis were randomly assigned to one of four treatments: (1) emasculation to test for agamospermy ( $n = 5$ ), (2) spontaneous self-pollination to evaluate autogamy ( $n = 10$ ), (3) artificial self-pollination to test self-compatibility ( $n = 10$ ), and (4) artificial cross-pollination to assess cross-compatibility ( $n = 10$ ). After treatment, flowers were bagged to prevent external pollination. Plants were monitored for approximately 3 weeks, and fruit set was recorded. Although *S. sikokianus* typically produces multiple flowers, the experiment focused on the lowest flower on each plant to minimize the effect of resource limitation. Additionally, 21 plants (40 flowers) were tagged for natural fruit development (Table 1). After fruit set, all capsules were collected, and 50 seeds from each capsule were sampled for microscopic analysis to assess seed development.

To assess the impact of pollination treatments on fruit and seed set, a generalized linear model (GLM) or generalized linear mixed model (GLMM) with a binomial error distribution (logit link) was used. “Treatment” was included as an explanatory variable, and the seed set model also incorporated “plant ID” as a random effect. Multiple comparisons were conducted using Tukey’s post hoc test.

### 2.3 | Self-pollination mechanism

Because autonomous self-pollination in orchids is often driven by column modifications (e.g., degeneration of the rostellum) (Gale, 2007; Suetsugu, 2015), the column structure of *S. sikokianus* was examined at three stages: (i) about 1 day after flower opening, (ii) about 3 days after, and (iii) about 5 days after ( $n = 5$  for each stage). Based on the results of bagging experiments and column morphology investigations, which suggested self-pollination, pollen tube elongation was observed using aniline blue staining to confirm self-pollination.

Briefly, samples were softened in 1 M KOH for 30 min at 60°C using a block heater. The columns were washed in distilled water for a few minutes and stained with 0.1% aniline blue in  $K_3PO_4$  buffer (pH 8.5) for 2 h at room temperature. After staining, the samples were briefly rinsed in distilled water and mounted in 50% glycerol. The samples were squashed and examined under a fluorescence microscope (BX60, Olympus Optical Co. Ltd., Tokyo, Japan) with blue excitation to observe pollen tube development.

## 3 | RESULTS AND DISCUSSION

This study provides compelling evidence that *Stigmatodactylus sikokianus* primarily relies on autonomous self-pollination. Despite its intricate floral morphology, which suggests potential for outcrossing, and observations of dipteran visitors (*Drosophila* spp. [ $n = 2$ ] and Calliphoridae sp. [ $n = 1$ ]) landing on the lip, none carried pollinia. In contrast, plants in both natural conditions and those bagged to exclude pollinators successfully produced fruit, while emasculated flowers did not, indicating that autogamy is the primary driver of high fruit set (Table 1). These findings support that *S. sikokianus* is predominantly autogamous (Dataset S1). Nonetheless, artificial crosses between individuals yielded high fruit set, showing that outcrossing is possible. Although pollinators were not identified in this study, the strikingly colored, relatively large flowers, in proportion to the small size of the plant, suggest that *S. sikokianus* may partially depend on insect pollinators. Identifying specific pollinators remains an objective for future research.

*Stigmatodactylus sikokianus* typically inhabits dark understories, often growing among leaf litter, and exhibits a small, cryptic vegetative state. Its self-pollination mechanism likely ensures reproductive success in this diminutive, nectarless orchid, enabling it to thrive in shaded environments where pollinator availability is limited. Previous studies suggest that mycoheterotrophic plants often favor selfing strategies (Bidartondo, 2005; Suetsugu, 2022). Given their nutritional reliance on fungi, autonomous self-pollination, which minimizes the

**TABLE 1** Effects of pollination treatment on fruit set and seed set in *Stigmatodactylus sikokianus*.

Treatment	Emasculation	Bagged	Artificial self-pollinated	Artificial cross-pollinated	Open
Fruit set (%)	–	80.0 <sup>a</sup>	80.0 <sup>a</sup>	100.0 <sup>a</sup>	80.0 <sup>a</sup>
Seed set (%)	–	93.5 ± 3.7 <sup>a</sup>	92.0 ± 4.0 <sup>a</sup>	93.4 ± 3.8 <sup>a</sup>	93.3 ± 3.9 <sup>a</sup>

<sup>a</sup>Seed set values are expressed as mean ± SD. There are no significant differences ( $p < 0.05$ ) in either fruit or seed set.

need for pollinator attractants, may offer a cost-efficient reproductive strategy for mycoheterotrophic plants (Takahashi et al., 1993; Zhang & Saunders, 2000). Additionally, self-pollination in these plants may be an adaptation to the challenges posed by low-light environments. Mycoheterotrophy is often viewed as an adaptation to low-light conditions, where competition from autotrophs is minimal (Bidartondo et al., 2004). However, such conditions can limit reproductive success, as pollinator activity often depends on light availability (Suetsugu & Yamamoto, 2024). Thus, the development of self-pollination mechanisms could be an adaptive strategy for the nearly fully mycoheterotrophic *S. sikokianus*.

While a reduced rostellum is the most common self-pollination mechanism in Orchidaceae (Catling, 1990), in *S. sikokianus*, a rostellum initially blocks autogamy. However, by 3 days after anthesis, the finger-like appendage on the posterior margin of the stigma arcs toward the stigma, maintaining its straight structure, and eventually adheres to the stigma surface, allowing contact between the appendage apex and pollinia (Figure 2d–k). UV microscopy revealed that thick bundles of pollen tubes penetrate the appendage adhered to the stigma and reach the base of the column (Figure 2l), while no pollen tube formation was observed in the stigma 1 day after anthesis. The absence of pollen tube formation before contact between the appendage apex and pollinia strongly suggests that the appendage functions as a stigma surface once positioned atop it, facilitating delayed selfing. Thus, based on available data (i.e., column morphology and UV microscopy), the movement of the stigma appendage likely contributes to self-pollination. Nonetheless, despite technical challenges due to its diminutive size, excision experiments on this appendage are needed to conclusively demonstrate its essential role in fruit set in *S. sikokianus*.

The discovery of delayed selfing in *S. sikokianus* aligns with broader evolutionary trends in flowering plants. While self-pollination likely guarantees reproductive success, repeated selfing carries the risk of inbreeding depression, which may drive the evolution of mating systems that combine the benefits of both self- and cross-pollination (Kalisz et al., 2004; Whitehead et al., 2018). Delayed selfing, where self-pollination is postponed until opportunities for outcrossing are exhausted, is likely one such adaptation (Goodwillie & Weber, 2018; Kalisz et al., 2004).

Overall, this study identifies delayed selfing in *S. sikokianus*, probably facilitated by the dactyliform (finger-like) appendage on the stigma, from which the genus name is derived. While the bending or rotation of the stipe and caudicle attached to pollinia is known to facilitate autogamy in other orchids (Catling, 1990; Liu et al., 2006), the movement of the stigma appendage represents, to the best of our knowledge, a novel self-pollination mechanism in orchids. Given that *Stigmatodactylus* includes 28 species and that this appendage, though variable in form (e.g., linear to hooked), is often present in the genus (Robinson, 2021), a similar autogamous strategy may be widespread, at least within *Stigmatodactylus*.

More broadly, this discovery not only reveals a previously unknown pollination mechanism in orchids but also underscores the importance of integrating taxonomic and ecological approaches. While

taxonomists may focus more on patterns of trait distribution than on trait function, taxonomic features can be essential for uncovering functional adaptations and species life histories. This study highlights how a detailed examination of taxonomic features can provide insights into the reproductive biology and life history of organisms. Additionally, it underscores how traditional natural history research, which once seamlessly integrated taxonomy, evolution, and ecology, continues to reveal new phenomena.

#### AUTHOR CONTRIBUTIONS

KS designed and performed the research, collected and interpreted the data, and wrote the manuscript.

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#### CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available in the supplementary material of this article.

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## SUPPORTING INFORMATION

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