Plant Species Biology

WILEY | SSSO

ORIGINAL ARTICLE OPEN ACCESS

The Function of the Partially-Opened Spathe of *Pinellia pedatisecta* (Araceae) as a Pitfall Pollinator Trap

Kohei Yanagisawa[1] | Tetsuya K. Matsumoto[2]

[1]College of Science, Ibaraki University, Mito, Japan | [2]Graduate School of Science and Engineering, Ibaraki University, Mito, Japan

Correspondence: Tetsuya K. Matsumoto (arisaematsumoto@gmail.com)

Received: 24 April 2025 | **Revised:** 17 March 2026 | **Accepted:** 3 April 2026

Keywords: aroid | deceptive pollination system | introduced species | pollinator shift | trap flower

ABSTRACT

In the protogynous genus *Pinellia*, pitfall trap inflorescence typically attracts flies to the trap entrance using a floral odor, directing them into a spathe tube with a slippery surface covered by downward-pointed microstructures and imprisoning them near the female floral zone surrounded by the chamber structure (female phase). After pollen shedding, trapped insects are released as the chamber unfolds (male phase). *Pinellia pedatisecta* is an exception as it lacks a chamber structure. This species unfolds the whole spathe, and shows a high fruiting rate without pollinators. However, its spadix appendix, mostly wrapped by the spathe, emits a floral odor during the initial flowering phase, suggesting that the partially-opened cylindrical spathe functions as an ephemeral pitfall trap and that the completely unfolded spathe releases insects. To validate this hypothesis, we examined whether spathe unfolding coincided with pollen shedding (Experiment A), trapped insects could escape from the cylindrical spathe fixed by taping (Experiment B), and the microstructure of *P. pedatisecta* resembled that of its congeners with pitfall traps (Experiment C). Experiment A demonstrated phenological matching between the unfolding movement and male phase. Experiment B revealed that insects were more frequent in taped inflorescences than in the controls. The inner wall of the spathe was covered by downward-pointed microstructures in *P. pedatisecta* and two *Pinellia* species (Experiment C). Therefore, the simplified spathe of *P. pedatisecta* seemed to perform a similar pollination process as the specialized spathe of congeners, although the unfolding movement pattern differed considerably.

1 | Introduction

In the sexual reproduction of flowering plants, each flower completes the two tasks, pollen receipt and pollen removal, to achieve both maternal and paternal successes through outcrossing. Under selection pressures that promote successful cross-pollination, some plant lineages have developed unique floral traits that control pollinator behavior in various ways (Kato et al. 2003; Terry et al. 2007; Gaskett et al. 2008; Iwata et al. 2012; Gardner et al. 2018). Many elaborate pollination systems have been discovered in plants, such as using floral traps (Gibernau et al. 2004; Oelschlägel et al. 2009; Phillips et al. 2014). In the family Araceae, for example, pitfall trap inflorescence improves the probability of pollen receipt through the imprisonment of floral visitors within the cylindrical spathe (when stigma are receptive); pollen is exported by floral visitors that are released after anther dehiscence to effectively remove pollen (Lack and Diaz 1991; Bröderbauer et al. 2014; Matsumoto et al. 2023). Although pitfall trap structures have convergently evolved in different phyletic lines of angiosperm (Vogel 1965; Oelschlägel et al. 2009), the release mechanisms of captured pollinators show considerable variation, even within the family Araceae (Bröderbauer et al. 2012). The pollinator-capturing devices of aroids can be classified into six types based on their release mechanism and floral trap structure (Bröderbauer et al. 2012). In most cases, the release mechanism is shared within each genus; however, a few genera include multiple release mechanisms (Bröderbauer et al. 2012). Studying this intrageneric variation

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Plant Species Biology* published by John Wiley & Sons Australia, Ltd on behalf of The Ecological Society of Japan.

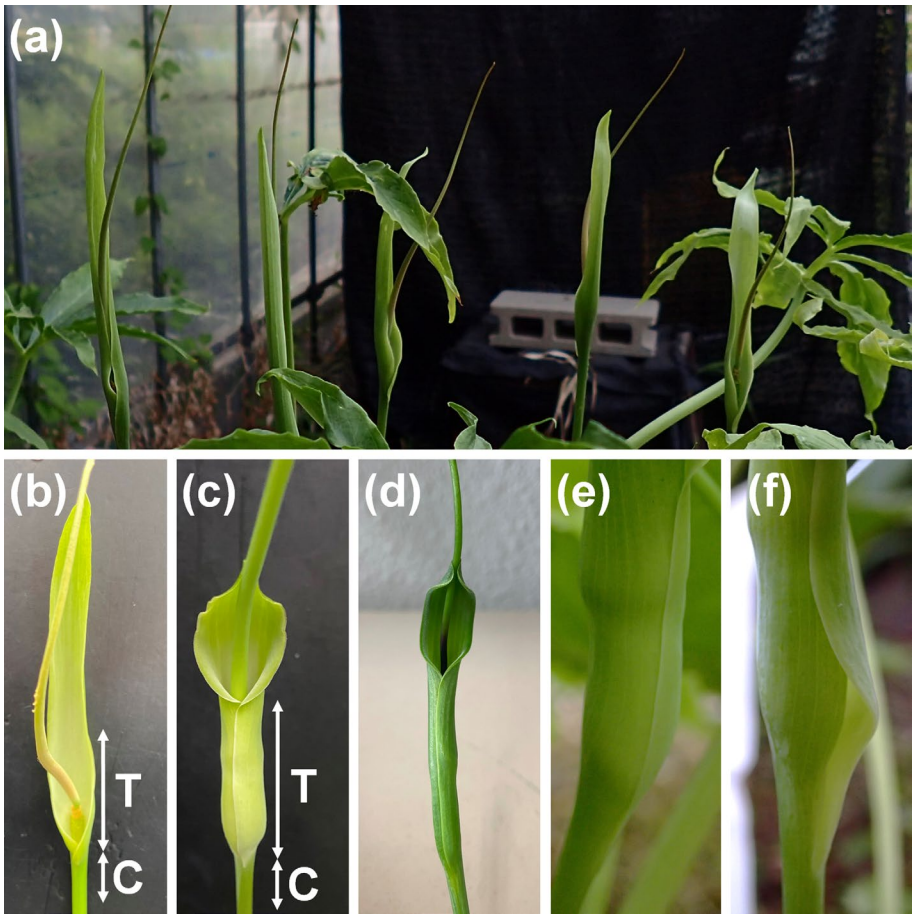


FIGURE 1 | Inflorescences of *Pinellia pedatisecta* (a and b), *P. tripartita* (c), *P. ternata* (d), and the spathe movement on the chamber structure of *P. tripartita* from female (e) to male phases (f). The highlighted regions of "T" and "C" in (b and c) were covered with the packing tape in the taping and control treatments, respectively.

contributes to our understanding of how each type of floral trap is derived from the others.

The genus *Pinellia* Tenore (Figure 1), which is endemic to East Asia (Zhu et al. 2007), shows an apparent interspecific morphological diversity in the inflorescence structure (Murata and Matsumoto 2021), suggesting that this taxon contains multiple types of floral traps. All members share several inflorescence characteristics (Figures 2–4): the female floral zone adheres to the inner surface of the basal spathe (Figure 2g,h); on the female floral zone, male florets construct a cylindrical spadix independent of the spathe wall (Figure 2e); and a whip-like spadix appendix is elongated to the outside of the spathe (Figures 1 and 2). In most *Pinellia* species, male and female floral zones are separated by a thickened spathe wall (Figure 3), which prevents autonomous geitonogamy (i.e., self-pollination) (Matsumoto et al. 2023). However, one *Pinellia* species, *P. pedatisecta* Schott, completely lacks this structure (Figures 1b, 2d, and 4; Zhu et al. 2007; Li and Bogner 2010; Murata and Matsumoto 2021).

In two *Pinellia* species with thickened walls (Figure 3), *P. tripartita* (Blume) Schott (Figure 1c) and *P. ternata* (Thunberg) Breitenbach (Figure 1d), a consistent relationship between inflorescence structure and the outcrossing process has been described in detail (Breitenbach 1879; Vogel 1965; Shida and Tominaga 2016; Matsumoto et al. 2023). When the upper part of the cylindrical spathe is opened, the spadix appendix emits a floral odor to attract dipteran pollinators. Once insects enter the spathe tube, they cannot return to the entrance because the slippery inner surface consists of numerous downward-pointed microstructures (Poppinga et al. 2010). The thickened wall between male and female floral zones has a narrow penetrating hole (Figure 3), allowing insects to enter the inflated basal space (chamber structure) surrounding the female floral zone (Figure 3). The inflorescence anthesis is protogynous in which the stigma becomes receptive at the spathe opening (female phase); subsequently, the anther dehisces after completion of the pistillate function (male phase). Autonomous self-pollination can be caused by a short overlap between the female and male phases in *P. tripartita* (Matsumoto et al. 2023) but no overlap was found in *P. ternata* (Higuchi and Okada 1996). If pollen grains are already attached to a dipteran pollinator captured during the female phase, pollen receipt will be successfully achieved as trapped insects move within the narrow inner space of the chamber (Matsumoto et al. 2023). When the male phase begins, an exit slit opens at the bottom of the chamber (Figure 1e,f); consequently, trapped insects can escape from the chamber. Some pollen grains fall into the female floral zones from male florets through the penetrating hole (Figure 3). Pollen removal is completed if the fallen pollen grains adhere to the released dipterans. Subsequently, the male phase inflorescence with the exit slit serves as a pollen source for several days.

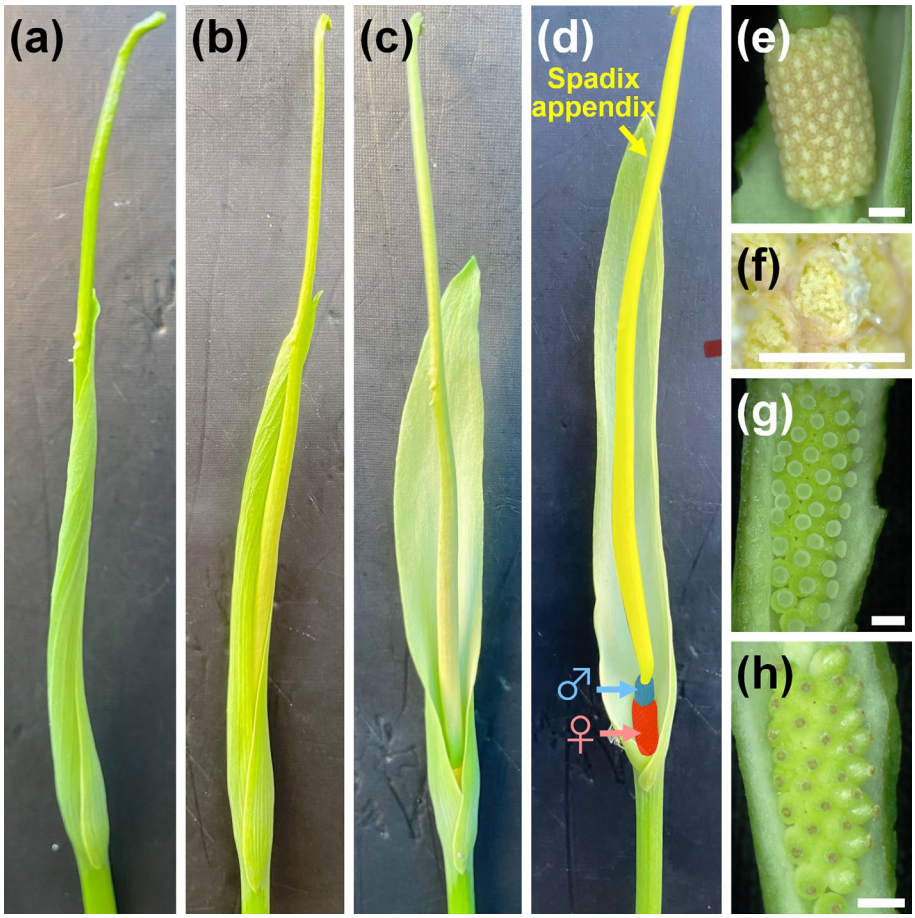


FIGURE 2 | The spathe movement (a–d) and the inflorescence component of *Pinellia pedatisecta* (e–h). The inflorescences before the anthesis (a), at female (b) and male phases (c and d). Male floral zone (♂ in d) at the female phase (e) and male florets at the male phase (f). Female floral zone (♀ in d) with receptable (g) and faded stigmas (h). Each scale bar is 1 mm.

In contrast, the whole spathe without the thickened wall gradually opened as the flowering phenology progressed in *P. pedatisecta* (Figure 2a–c), resulting in complete exposure of male and female floral zones (Figure 2d). This sequential change in spathe morphology suggests that the inflorescence of *P. pedatisecta* completely lacks the function of a pitfall trap at a later stage of the flowering period. *Pinellia pedatisecta* can achieve a high fruiting rate even when the spadix appendix is fully removed (Marshall et al. 2014), implying that this species depends considerably on autonomous selfing. Nevertheless, in our preliminary observation, the spadix appendix emitted a strong perfume even when most parts of the spathe remained closed (Figure 2), and small coleopterans stayed around the female floral zone. This is reminiscent of a type of pitfall pollinator trap (Bröderbauer et al. 2012), in which the spathe blade is slightly opened and functions as an ephemeral pollinator trap, and trapped insects are released when the spathe blade fully opens at a later phase (Bröderbauer et al. 2014). In addition, as in other congeners with pitfall trap inflorescences (Bröderbauer et al. 2012), a downward-pointed microstructure was found on the inner surface of the spathe of *P. pedatisecta* (Y. Kato, personal communication), suggesting that floral visitors cannot climb the inner wall until the spathe unfolds. Although *P. pedatisecta* completely lacks specialized floral structure (Zhu et al. 2007; Murata and Matsumoto 2021), it may have developed a different pitfall trap pollination system in which the folded spathe functions as a pitfall trap in the female phase (Figure 2a–c) and trapped insects are released via complete exposition of spadices after the start of the male phase (Figure 2d).

In this study, we conducted three experiments to examine the function of young *P. pedatisecta* inflorescences as pitfall pollinator traps. First, we observed the temporal sequences of spathe unfolding (Figure 2a–d) and the sexual phase of the spadices of *P. pedatisecta* (hereafter, Experiment A). If the ephemeral pitfall trap hypothesis is true, the spathe unfolding process should be strictly associated with the switching from female to male phases. Second, we compared the number of trapped insects between taped inflorescences (the basal spathe could not unfold) and controls (the basal spathe could unfold) for *P. pedatisecta* and *P. tripartita* using the pitfall trap pollination system (Experiment B). When the spathe was part of the trapping mechanism, more insects were imprisoned in taped inflorescences (e.g., no basal opening) than in the controls for both *Pinellia* species. Finally, we observed the morphological characteristics of the microstructures covering the inner wall of the spathe for *P. pedatisecta* and its two congeners (*P. ternata* and *P. tripartita*) using a pitfall trap pollination system (Experiment C). If the folded spathe of *P. pedatisecta* captures insects with a slippery surface, its microstructures must be pointed downward, as in other congeners (Poppinga et al. 2010). Based on these results, we estimated the pollination system of *P. pedatisecta* and

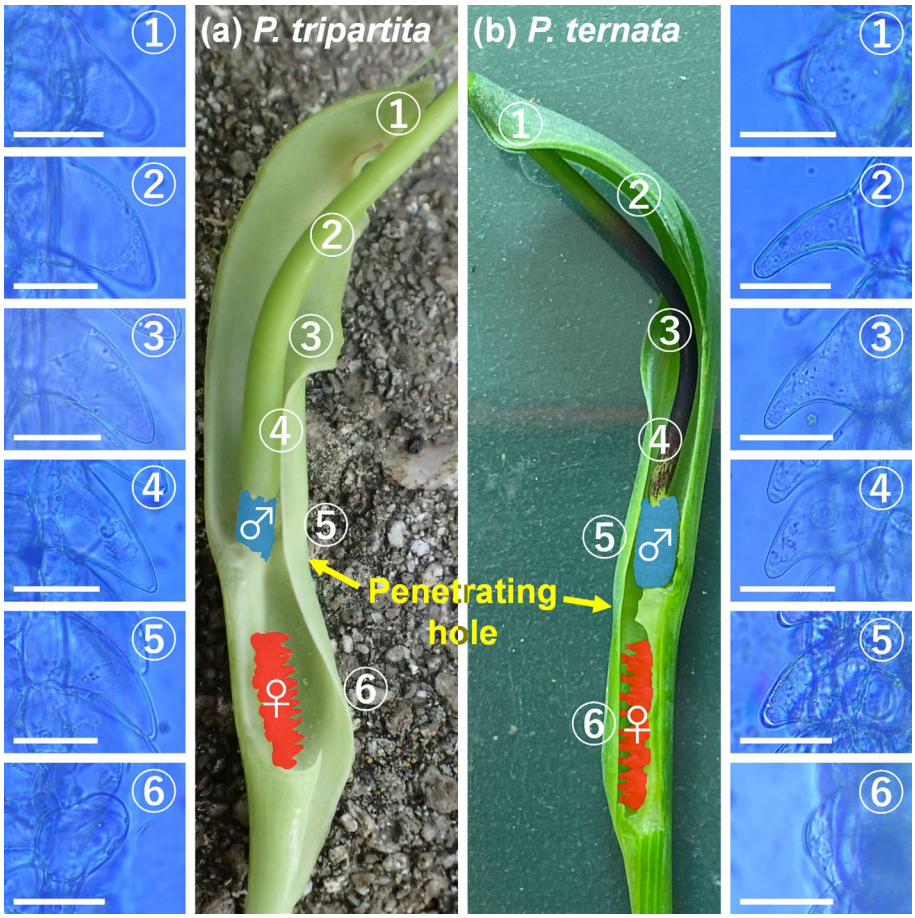


FIGURE 3 | The observed locations shown on the vertical inflorescence sections (center large panels) and microstructure morphology (left- and right-side small panels) of *Pinellia tripartita* (a) and *P. ternata* (b). Male and female floral zones are highlighted by ♂ and ♀, respectively. The number in the upper-right corner of each small panel corresponds to that on the vertical inflorescence section. Each scale bar is 50 μm.

discussed the morphological diversity of spathe in the genus *Pinellia*.

2 | Materials and Methods

2.1 | Plant Materials

The genus *Pinellia* (Araceae) consists of 11 species endemic to East Asia (Zhu et al. 2007; Chen et al. 2024). Each plant is seasonally dormant as a tuber and produces several inflorescences and leaves during the growing season. Although leaf morphology is diversified from simple to pedate (Murata and Matsumoto 2021), all species produce an inflorescence, which is a spadix bearing distinct upper male and basal female zones separated by a thickened wall (Figure 3), except for *P. pedatisecta* (Figure 4). In this study, we focused on *P. pedatisecta* and its two congeners (*P. tripartita* and *P. ternata*). For the two congener species, their pollination system has been well documented (Shida and Tominaga 2016; Matsumoto et al. 2023).

Pinellia pedatisecta (Figure 1a,b) is an understory perennial endemic to East China (Zhu et al. 2007). Pedate leaves consist of 6–11 leaflets (Zhu et al. 2007) and lack bulbils on the leaf rachis or petiole (Murata and Matsumoto 2021). The lanceolate spathe is 10–19 cm in length and lacks a thickened wall between the female and male floral zones (Zhu et al. 2007). Each plant produces cormlets around the corm (vegetative reproduction) and fruits through autonomous self-pollination. However, there is no detailed information on outcrossing (Marshall et al. 2014). The experimental plants of *P. pedatisecta* in this study were obtained from naturalized populations in the Koishikawa Botanical Garden (Botanical Gardens, Graduate School of Science, The University of Tokyo), Bunkyo Ward, Tokyo metropolitan area, eastern Japan (Murata and Matsumoto 2021).

Pinellia tripartita (Figure 1c) is an understory perennial distributed from the central to southern Japanese Archipelago (Matsumoto et al. 2023). Only one specimen has been recorded from Hong Kong (Li and Bogner 2010). The simple leaf is divided into three lobes (Zhu et al. 2007) and completely lacks bulbils on the leaf rachis or petiole (Matsumoto et al. 2023). Each plant attracts cecidomyiid pollinators for outcrossing, and partly achieves autonomous selfing owing to overlapping days between the female and male phases (Matsumoto et al. 2023). The experimental plants of *P. tripartita* in this study were derived from naturalized populations at the Medical Plant Garden of Okayama University, Okayama City, Okayama Prefecture, western Japan (Matsumoto et al. 2023).

Pinellia ternata (Figure 1d) is a perennial weed native to East Asia (China, Japan, and Korea) and naturalized in Europe,

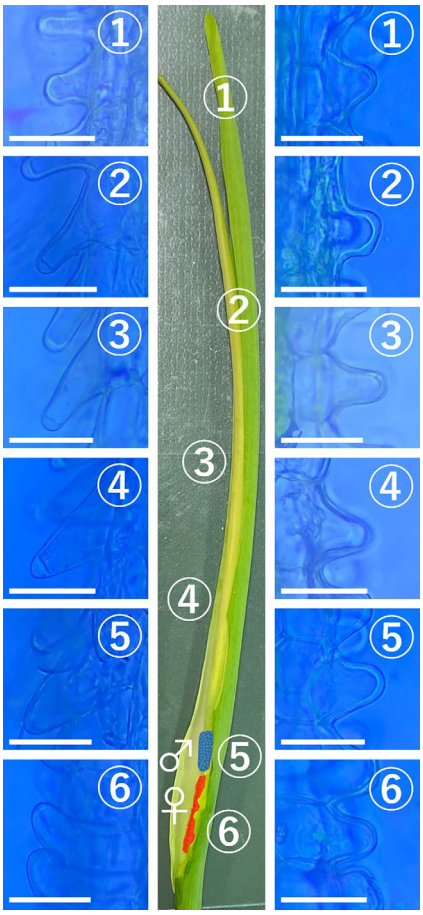


FIGURE 4 | The observed locations shown on the vertical inflorescence section (center large panel) and microstructure morphology on the spathe inner- (left-) and outer surfaces (right-side small panels) of *Pinellia pedatisecta*. Male and female floral zones are highlighted by ♂ and ♀, respectively. The number in the upper-right corner of each small panel corresponds to that on the vertical inflorescence section. Each scale bar is 50 μm.

North America, and Australia (Zhu et al. 2007). Ternate leaves produce bulbils on the rachis and petioles (Tominaga and Nakagaki 1997). Each plant lacks selfing ability because of strict protogyny (Higuchi and Okada 1996) and attracts ceratopogonid and/or cecidomyiid pollinators for outcrossing reproduction (Vogel 1965; Shida and Tominaga 2016). The experimental plants of *P. ternata* in this study were obtained from a natural population in Ochiai, Nishiki Town, Iwaki City, Fukushima Prefecture, eastern Japan (Shida and Tominaga 2016).

2.2 | Cultivation Conditions

From February 23 to 28, 2023, dormant corms of *P. pedatisecta* ($n = 21$) were embedded in ceramic pots (Daon-bachi, width: 18.5 cm, height: 15 cm, volume: 2 L) for Experiment A. At the bottom of each pot, we made a thin layer of pumice stones (Hyuga-tsuchi, Large grain, Hyuga-tsuchi Hanbai Co. Ltd., Miyakonojo, Japan) to improve draining, and added solid fertilizer (MAGAMP plus K, Medium grain, HYPONeX Japan Corp. Ltd., Osaka). On the pumice layer, we filled the pot with mixed soil consisting of two potting media (Soil for foliage plants, Rook Co. Ltd., Takahama, Japan; Soil for cuttage and seeding, PROTOLEAF Inc., Tokyo, Japan) in a ratio of 3:2. Only one corm was planted in each pot. These pots were arbitrarily arranged without intentional bias on the understory of a fragmentated stand (3.63 a) consisting of evergreen and deciduous broad-leaved trees in the experimental field of Ibaraki University, Mito City, Ibaraki Prefecture, eastern Japan (36° 24′ N, 140° 26′ E, 32 m a.s.l.). Mean annual precipitation and temperature were 1367.7 mm and 14.1°C, respectively, at Mito Meteorological Station, 3.3 km southeast of the study site (Japan Meteorological Agency, 1991–2020). Each pot was watered once the soil surface dried and fertilized with 1000× diluted liquid fertilizer (HYPONeX undiluted solution, HYPONeX Japan Corp. Ltd., Osaka, Japan) once a week during the growing season.

On February 24, 2024, the dormant corms of three *Pinellia* species (*P. pedatisecta*: $n = 32$, *P. tripartita*: $n = 32$, *P. ternata*: $n = 10$) were embedded in ceramic pots for Experiments B and C. Considering with the contrasting corm sizes among species, we selected small (width: 15.5 cm, height: 12.5 cm, volume: 1.2 L) and large pots (width: 18.5 cm, height: 15 cm, volume: 2 L) for *P. ternata* and the two remnant species, respectively. At the bottom of each pot, we placed a thin layer of pumice stones (Karuishi, Large grain, Makino Co. Ltd., Kanuma, Japan) and added a solid fertilizer (MAGAMP plus K, Medium grain). On the pumice layer, we filled the pot with mixed soil consisting of two potting media (Soil for foliage plants, Makino Co. Ltd., Kanuma, Japan; Soil for cuttage and seeding, HYPONeX Japan Corp. Ltd., Osaka, Japan) in a ratio of 3:2. Only one corm was planted in each pot. The pots were randomly arranged on plant cultivation shelves in a greenhouse in an experimental field at Ibaraki University. The greenhouse was adjacent to a fragmented stand (see previous paragraph). All flying insects had free access to the greenhouse because their side panels were always open. Each pot was watered once the soil surface dried, and fertilized with 500× diluted liquid fertilizer (HYPONeX undiluted solution) twice a week during the growing season.

2.3 | Observation of Flowering Phenology (Experiment A)

From April 2 to September 15, 2023, we observed the flowering stage of each inflorescence for 21 experimental plants of *P. pedatisecta* (a total of 83 inflorescences) once daily in the evening. We recorded the start dates of anthesis, odor emission, anther dehiscence, exposure of the male floral zone, and pollen receipt on the stigma, and finish dates of stigma fading, odor emission, and anthesis for each inflorescence. We defined that the anthesis began when each spathe blade opened more than 5 mm and/or the spadix appendix emitted noticeable floral odor (by human nose), and ended when the spadix appendix was wrinkled and faded. The "exposure of the male floral zone" refers to (at least) the tip of male zone being visible from the front of the inflorescence (Figure 2c). We investigated whether some pollen grains attached to the stigmas of each inflorescence by the direct observation to record the first date of "pollen receipt on the stigma." However, we could not distinguish the origin of these pollen grains (i.e., selfing or outcrossing). Based on these records, we estimated the apparent flowering period and durations of odor emission, female, and

male phases. The female phase corresponded from the start of anthesis to the fading of the stigma; the male phase corresponded from anther dehiscence to the end of anthesis. The collection of these sequential data was not always complete for all observed inflorescences because some were injured by fallen twigs, animals, or diseases. During the observation of flowering phenology, we also observed the presence/absence of floral visitors within the spathe daily to evaluate pollinator attraction for each inflorescence in contrasting phases (i.e., emitting odor vs. odorless and opened vs. partially-opened spathe). As most floral visitors were removed from the spathe using a handmade aspirator, no multiple counts of the same insect were expected.

2.4 | Taping Experiment (Experiment B)

We conducted a taping experiment on the two *Pinellia* species using the following procedure. First, we compared the number of trapped insects between taped inflorescences (spathe could not open) and controls (spathe could open naturally) for *P. tripartita* which is already known as a pitfall trap pollination species (Matsumoto et al. 2023). This experiment provides ideal results if the inflorescence of *P. pedatisecta* also functions as a pitfall pollinator trap. We conducted a comparative experiment on *P. pedatisecta*.

From April 25 to August 25, 2024, we tagged female phase inflorescences with folded spathes (Figures 1e and 2b) for the taped experiment (*P. tripartita*: $n = 30$, *P. pedatisecta*: $n = 31$) and the control (*P. tripartita*: $n = 31$, *P. pedatisecta*: $n = 35$). The uneven replication in each treatment was partly due to unexpected injury to inflorescences. Because the opening of the spathe differed between the two *Pinellia* species, the taping treatment was performed in different regions (Figure S1). In *P. tripartita*, which partially-opens the base of the spathe tube (Figure 1f), we fixed the whole spathe tube ("T" region in Figure 1c; see also Figure S1a,b) using the packing tape with a 2.5 cm width (No. 750, Nitoms Inc., Tokyo, Japan). In *P. pedatisecta*, which completely opens the whole spathe (Figures 1b and 2d), we fixed the region from the middle to bottom parts of the spathe (the "T" region in Figure 1b; see also Figure S1c,d). During the initial stage of flowering phenology with floral odor emission, this region tends to remain closed while the tip of spathe blade slightly opens (Figure 2b), which is reminiscent of the ephemeral pollinator trap. Hence, we were careful not to close the putative entrance (i.e., the tip of spathe blade) completely to allow pollinators to access the spathe. In both taping experiments, the tape roll was cut into 5 cm lengths and three pieces were attached to the spathe. For the control inflorescences, we also attached the packing tape with the same length to the top of the peduncle ("C" region in Figure 1b,c) because some volatiles of the packing tape may affect the insect visitation unexpectedly. We harvested taped and control inflorescences 5 days after treatment once the trap function ended. Trap function of the control inflorescences was lost during this phase due to the open spathe in both *P. tripartita* (Matsumoto et al. 2023) and *P. pedatisecta* (see results). Each collected inflorescence was immediately placed into a 50 mL Falcon tube and kept in a freezer (−20°C) overnight to fix the insects. Subsequently, we incised the frozen inflorescences to collect arthropods present within the spathe. These samples were observed under a stereomicroscope (Leica S APO, Leica Microsystems GmbH, Heerbrugg, Switzerland) and identified to the family level for dipterans based on manuals (McAlpine et al. 1981, 1987) and to the order level for other arthropods.

2.5 | Observation of Anatomical Microstructure (Experiment C)

From April 18 to August 19, 2024, we harvested whole female phase inflorescences of *P. pedatisecta* ($n = 8$), *P. tripartita* ($n = 6$), and *P. ternata* ($n = 8$). We could not obtain eight inflorescences of *P. tripartita* because the flowering season had completed prior to our observations. The peduncle of each inflorescence was then cut at the soil surface and immediately inserted into a 500 mL plastic bottle filled with tap water. For these observations, we focused on six positions on the inner and outer surface of the spathe center for each inflorescence collected (Figures 3 and 4): (1) below the tip of the spathe blade; (2) the middle of the spathe blade; (3) the lower of the spathe blade; (4) the mouth part (i.e., the entrance of pitcher trap; Figure S2) of the spathe tube; (5) neighboring part of the male floral zone; and (6) neighboring part of the female floral zone. The terminologies used for these regions are shown in Figure S2 in detail. Although the spathe morphology differed considerably between *P. pedatisecta* and the two remnant species (Figures 3 and 4), we tentatively regarded the six positions as homologous parts among them, considering the positional relationship between these parts and the spadices and the weak constriction on the spathe of *P. pedatisecta* (Figure S2), reminiscent of the rudimentary mouth organs of the two remnant species. Of the six positions, we expected to find downward-pointing microstructures between Positions 2 and 5 in the two *Pinellia* species with a thickened wall (Figure 3). Attracted insects in contact with these structures should fall into the basal floral trapping chamber. In contrast, Position 6, surrounding the female floral zone, may lack a slippery surface because the thickened wall (Figure 3) inhibits trapped insects from climbing up the spathe tube. Similarly, the slippery function may be less developed at Position 1, which is in contact with the spadix appendage (Figure 3).

The microstructures were observed according to the observation method for hand-sectioned plant materials (Kato 2024). We obtained a fragment of the spathe (*c.* 5 × 10 mm) from each position (Figures 3 and 4) using a surgical knife. Each fragment was deaired using a 5 mL syringe (GA-8, Maruhachi Industry Co. Ltd., Tokyo, Japan). We took these fragments by finger in a small dish filled with tap water and sliced them as thinly as possible from the tip to the base of the spathe using a razor blade. The thinnest cross-section in the water was picked up by tweezers and placed in a droplet laid on a glass slide. The slide overlaid with cover glass was observed using a binocular transmitted light microscope (FH, Olympus Co., Hachioji, Japan) with a 20× eyepiece and 20× objective lenses. Microscopic images of all cross-sections were captured using a smartphone (iPhone 11, Apple Inc., Cupertino, USA).

The captured images were imported into the free software ImageJ (Rasband 1997) for measurement. We focused on

five microstructures for each cross section (see Figure S3a), of which we measured five morphological traits, including four size parameters (arc, chord, base, and height) and the inclination (see Figure S3b), using the ImageJ software and a protractor. These parameters were recorded for both the inner- and outer walls of the spathe in *P. pedatisecta* but only for the inner wall in the other two species. This was because no microstructures were distributed on the outer wall of the spathes (see Section 3). Finally, we calculated the degree of curvature (arc/chord) for all microstructures as a parameter reflecting the shape.

2.6 | Statistical Analyses

All analyses were performed using the free software R ver. 4.3.1 (R Development Core Team 2023). Statistical significance was set at $p < 0.05$.

Before data processing of Experiments B and C, we verified the insect attractiveness of *P. pedatisecta* inflorescences with a partially-opened spathe during the initial flowering phase (Figure 1b) using Experiment A, as follows. To compare the ratio of inflorescences with and without odor emission between the naturally opened and the partially-opened phases, we conducted χ^2 tests using the chisq.test function in R. Similarly, we compared the ratio of inflorescences with and without insect visitation between the opened and partially-opened phases. In addition, we examined the role of floral odor in pollinator attraction in *P. pedatisecta* by comparing the ratio of inflorescences with and without insect visitation between the odorless and odor-emitting phases (determined by human nose). Then, we subdivided the data on the presence/absence of trapped insects into the inflorescence with partially-opened and opened spathes for the χ^2 tests.

To examine the effect of spathe closure on insect imprisonment in two *Pinellia* species (Experiment B), we compared the ratio of inflorescences with and without trapped insects between the taped treatment and the control by χ^2 tests. We also compared the number of insects captured in the spathe between the two treatments using the Mann–Whitney *U* test. These tests were conducted using the wilcox test function in R. Moreover, we compared the assemblage of trapped insects between the species and treatments using a two-way permutational multivariate analysis of variance (PERMANOVA) with 10 000 permutations. A distance matrix was obtained using Chao index. We then considered the species (*P. tripartita* or *P. pedatisecta*), treatment (taped or control), and their interaction as explanatory variables. A two-way PERMANOVA was conducted using the adonis2 function in the 'vegan' package (Oksanen et al. 2018) in R.

To describe microstructure morphologies of the three *Pinellia* species (Experiment C), we compared six morphological parameters (Figure S3b) among all six positions' combinations (Figures 3 and 4). Multiple comparisons were performed separately for each species. These analyses were conducted using *U* tests with Bonferroni correction, except for inclination. We used the Mardia–Watson–Wheeler tests with Bonferroni correction using the watson.wheeler.test function in the package 'circular' (Lund et al. 2017). This nonparametric test was used to examine the homogeneity of the two samples with circular data.

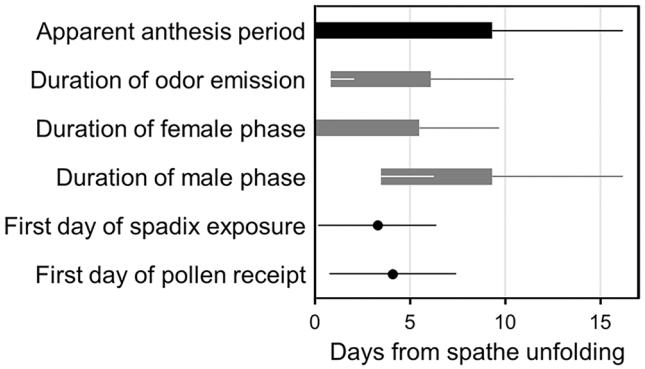


FIGURE 5 | Mean values of total flowering days (black column), the duration of each reproductive phase (gray columns), and the first days of two reproductive events (filled circles) in *Pinellia pedatisecta* during Experiment A. Error bars (black, white, and gray lines) indicate the standard deviation of each phenological event.

3 | Results

3.1 | Observation of Flowering Phenology (Experiment A)

The inflorescence anthesis duration was 9.33 ± 6.88 days (mean ± SD) in *P. pedatisecta* (Figure 5). The spadix appendix began and finished emitting the floral odor 0.84 ± 1.21 and 5.24 ± 4.37 days after the first day of the anthesis (i.e., female phase initiation), respectively (Figure 5). The male phase started with the anther dehiscence 3.48 ± 2.78 days later (Figure 5). At almost the same time (3.26 ± 3.09 days, Figure 5), the male floral zone began to be exposed (Figure 2c). Subsequently, the first pollen grain attached to the stigma at 4.07 ± 3.32 days (Figure 5), and the female phase terminated due to stigma fading (Figure 2h) at 5.49 ± 4.19 days (Figure 5).

During anthesis, the spadix appendices partly covered by the folded spathe (Figure 2b) emitted the floral odor (χ^2 tests, $\chi^2 = 23.11$, $p < 0.001$, Figure 6a) and attracted insects ($\chi^2 = 4.90$, $p = 0.03$, Figure 6b) more frequently than those exposed (Figure 2c,d). The odor emission significantly contributed to the insect attraction in both inflorescences with partially-opened ($\chi^2 = 12.37$, $p < 0.001$, Figure 6c) and opened spathes ($\chi^2 = 30.94$, $p < 0.001$, Figure 6d).

3.2 | Taping Experiment (Experiment B)

The ratio of inflorescences capturing insects in the taping treatment significantly exceeded that in the control in both *P. tripartita* (χ^2 tests, $\chi^2 = 10.27$, $p = 0.001$, Figure 7a) and *P. pedatisecta* ($\chi^2 = 5.02$, $p = 0.03$, Figure 7b). Each inflorescence of the taping treatment and the control imprisoned 3.40 ± 5.67 and 0.48 ± 0.93 insects in *P. tripartita* and 0.55 ± 0.77 and 0.29 ± 0.83 insects in *P. pedatisecta*, respectively. The number of insects captured in the taped inflorescences significantly exceeded that of the control in

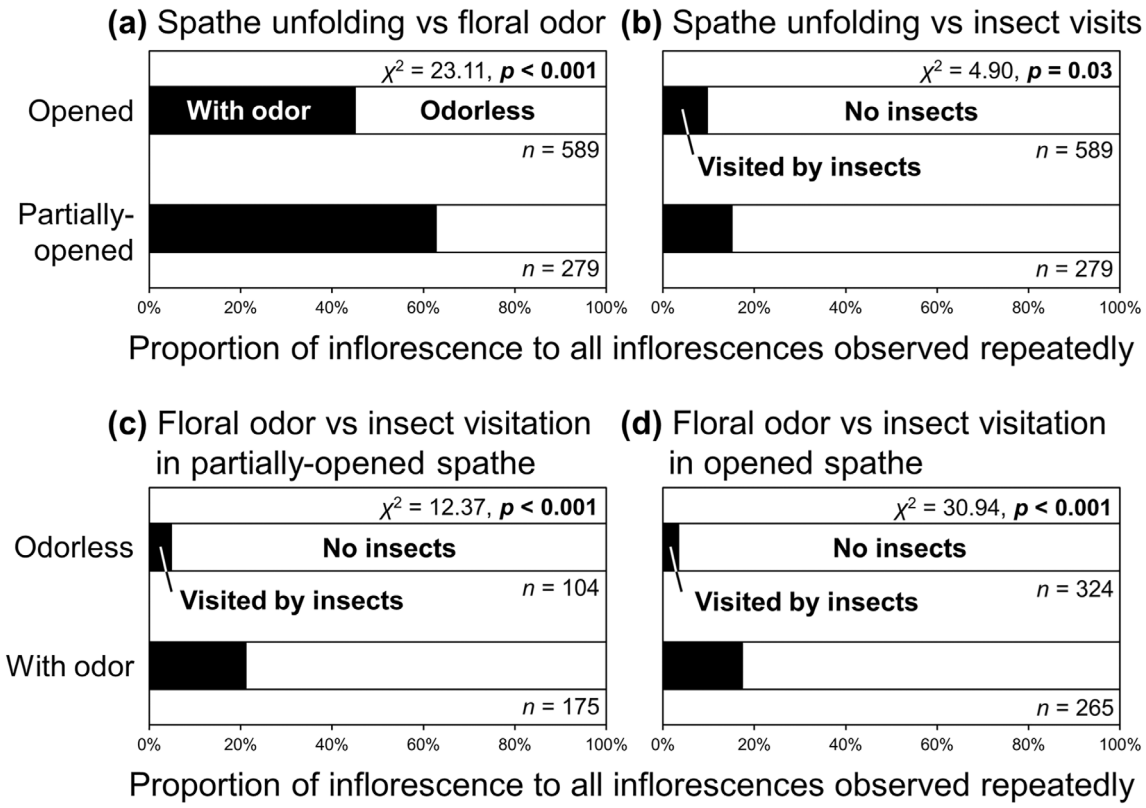


FIGURE 6 | The ratio of the number of inflorescences at contrasting states (with versus without floral odor, opened versus partially-opened spathe, and with versus without insect visitors) during Experiment A. The statistics of the χ^2 tests are indicated at the upper-right corner of each panel. The total number of inflorescences at each state is shown at the lower-right corner of each column. It includes many pseudo-replications because each tagged inflorescence had been observed repeatedly during the experiment.

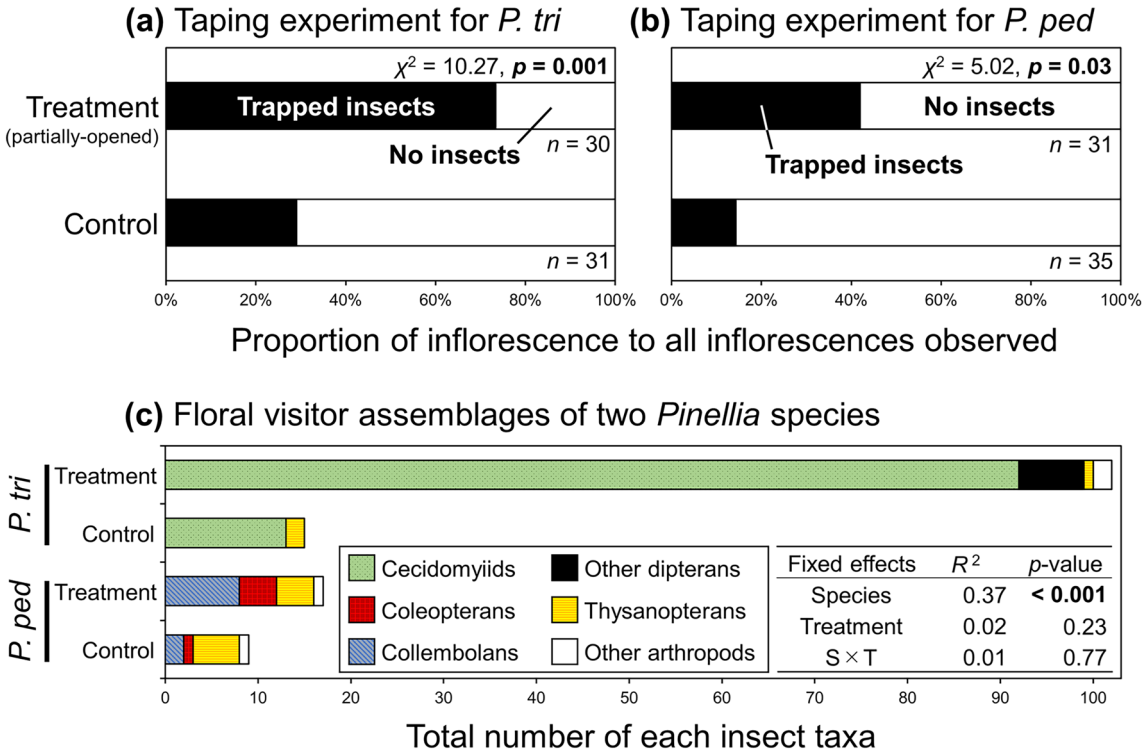


FIGURE 7 | The comparison of the ratio of inflorescences with and without trapped insects between the taped inflorescences and the controls in *Pinellia tripartita* (a) and *P. pedatisecta* (b) and the floral visitor assemblages in these treatments (c) in Experiment B. The statistics of the χ^2 tests are indicated at the upper-right corner of each panel in (a and b). The total number of inflorescences at each treatment is shown at the lower-right corner of each column in (a and b). The result of the two-way PERMANOVA is shown at the lower-right corner of (c).

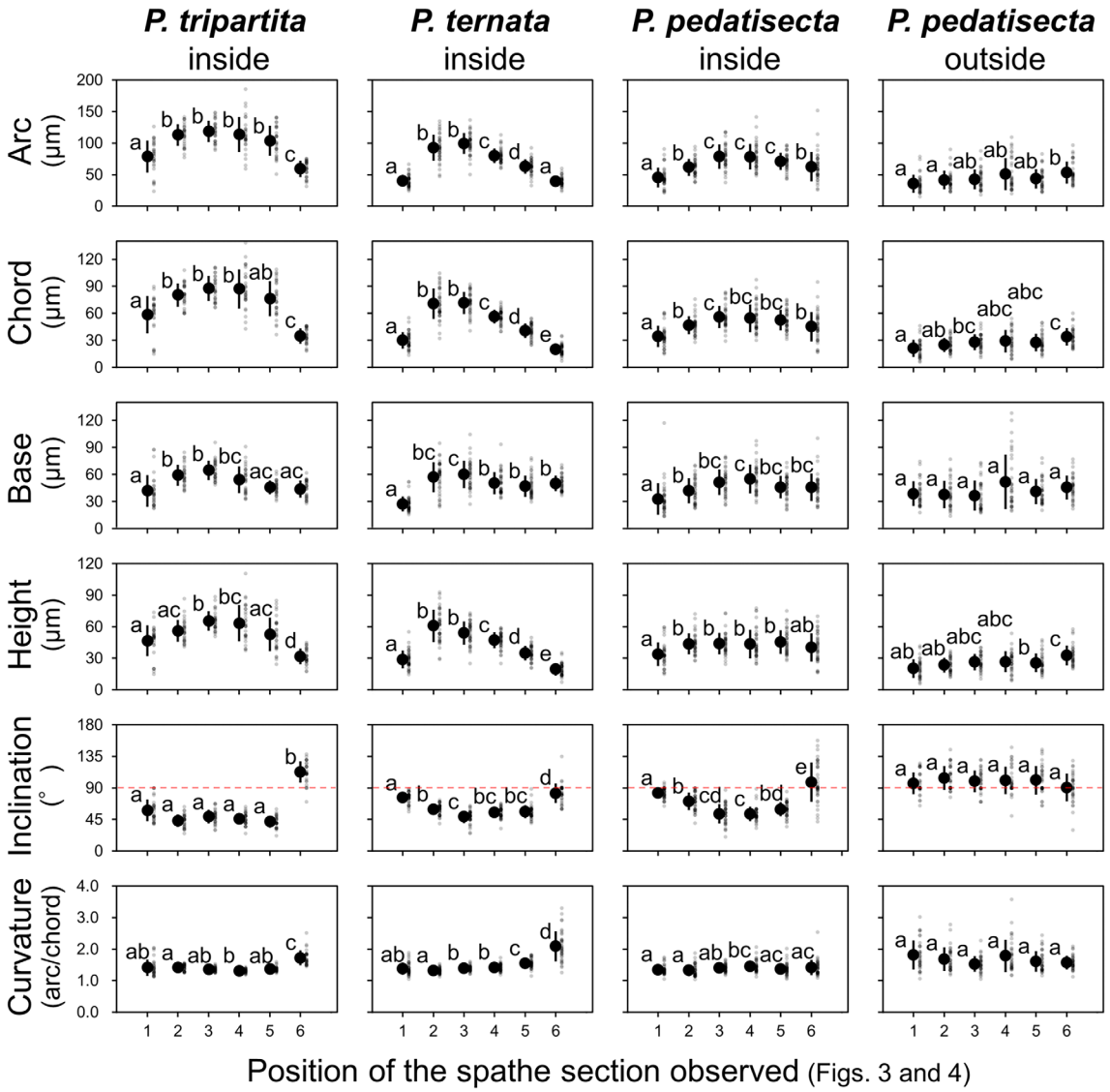


FIGURE 8 | Morphological parameters of the microstructure (Figure S3) in the three *Pinellia* species. Position of the spathe section corresponds to the enclosed number of Figures 3 and 4. Filled circles and error bars are means and standard deviations on each position. Gray small dots show the raw data. The different alphabet on each filled circle indicates significant difference between positions in the Mardia–Watson–Wheeler tests (inclination) or Mann–Whittney's *U* tests (other parameters) with the Bonferroni correction.

P. tripartita (Mann–Whitney *U* test, $W = 710.0$, $p < 0.001$) and *P. pedatisecta* ($W = 694.5$, $p < 0.001$).

The floral visitor assemblage (Figure 7c) significantly differed between the two *Pinellia* species (two-way PERMANOVA, $R^2 = 0.37$, $p < 0.001$) but not between the taped inflorescences and controls ($R^2 = 0.02$, $p = 0.23$). No interaction between species or treatments was detected ($R^2 = 0.01$, $p = 0.77$). In contrast to the floral visitors of *P. tripartita* exclusively dominated by cecidomyiid flies (Figures 7c and S4a), *P. pedatisecta* attracted a wide range of arthropods (Figure 7c), including small beetles (Figure S4b,c), thrips (Figure S4d), and spring tails (Figure S4e).

3.3 | Observation of Anatomical Microstructures (Experiment C)

In all species observed, we found microstructures on the inner wall of the spathe (Figures 3 and 4). In the two *Pinellia* species with thickened walls (Figure 3), four size parameters, except basal width (Figure S3b), were higher between Positions 2 and 5 than on the two remaining positions (Figure 8). Microstructures of the two species were usually downward-pointed between Positions 1 and 5 but tended to approach or exceed 90° at Position 6 (Figures 3 and 8). The curvature slightly increased from the distal to the proximal parts (Figure 8), although this tendency was obscured in the picture (Figure 3).

Overall, these tendencies were also observed in the morphological parameters of *P. pedatisecta*, except for height and curvature, with no meaningful patterns (Figures 4 and 8). In *P. pedatisecta*, the peak size parameters appeared to be more indistinct and shifted toward the proximate direction (Figure 8) compared to the two remnant species.

In contrast to the inner wall, we could not find any microstructures on the outer-wall of the spathe in *P. tripartita* or *P. ternata* (K. Yanagisawa, personal observation). Although the outer-wall

of the spathe was covered with many microstructures in *P. pedatisecta* (Figure 4), these morphological parameters lacked meaningful trends across all positions (Figure 8). Interestingly, the inclination of the microstructure slightly exceeded 90° at all positions (Figure 8).

4 | Discussion

4.1 | Inflorescence Structure and Function of *P. pedatisecta*

In contrast to the congeners with a specialized spathe structure (Figure 3) related to the pitfall trap pollination system (Shida and Tominaga 2016; Matsumoto et al. 2023), *P. pedatisecta* appeared to have a simplified spathe structure (Figure 1b) and unfolding movement (Figure 2a–d). This anomalous trait has attracted attention from a taxonomic perspective (Zhu et al. 2007; Li and Bogner 2010; Murata and Matsumoto 2021). Although the sexual reproduction process of *P. pedatisecta* has not been examined directly, except for autonomous selfing (Marshall et al. 2014), the odor emission of the spadix appendix indicates resource investment for outcrossing. Indeed, the floral odor was related to insect visitation in Experiment A (Figure 6c,d), and various insect taxa were obtained from Experiment B (Figures 7c and S4). Therefore, we conclude that *P. pedatisecta* is a facultative outcrosser, like *P. tripartita* (Matsumoto et al. 2023).

Similar to other aroids (Bröderbauer et al. 2012, 2014), the inflorescence with the partially-opened spathe at the initial flowering phase (Figure 2b) seemed to function as an ephemeral pitfall trap based on the odor emission from the spadix appendix covered by the spathe (Figure 6a), a high ratio of inflorescences capturing insects (Figure 7b), and an increased number of trapped insects in the taping treatment (Figure 7c). Synchronization between spadix exposure and the initiation of the male phase (Figure 5) suggests that insects captured in the female phase will be released after pollen shedding in *P. pedatisecta*, similar to other *Pinellia* species (Shida and Tominaga 2016; Matsumoto et al. 2023). This assumption is supported by similar results between *P. pedatisecta* and *P. tripartita* using a pitfall trap pollination system (Matsumoto et al. 2023) in Experiment B (Figure 7). Although the opening region differs between the two *Pinellia* species (Figures 1e,f and 2a–d), both spathe movements play a common role in protogynous plant taxa with a trap pollination system; pollinators are trapped during the female phase and released during the male phase (Vogel 1965; Oelschlägel et al. 2009; Bröderbauer et al. 2012).

The downward-pointed microstructure (Figure 3) has been regarded as the main driver of the pitfall trap function in the genus *Pinellia* (Bröderbauer et al. 2012). Therefore, the insect capture by *P. pedatisecta* inflorescences (Figure 7b,c) may be achieved in the same way. In the two *Pinellia* species with pitfall pollination systems (Shida and Tominaga 2016; Matsumoto et al. 2023), microstructures tended to be large and pointed downward along the inner spathe surface from the entrance of the pitfall trap (Position 2) to the penetrating hole (Position 5) inside the spathe tube (Figures 3 and 8). These morphological patterns suggest that the observed microstructures facilitate the spathe slippery function. In *P. pedatisecta*, although the patterns were not as clear in the other species, several parameters showed similar tendencies between Positions 3 and 5 (Figure 8), which folded tightly during the female phase (Figures 2b and 5). Interestingly, some coleopterans climbed onto the outer surface (Figure S4f) covered by the upright-pointing processes (Figure 8) before accessing the inner part. The different patterns in the microstructure morphology of *P. pedatisecta* (Figure 8) may reflect the contrasting roles of the inner (slippery) and outer (climbable) spathe surfaces during the outcrossing process. These functional aspects should be directly documented in future studies.

4.2 | Putative Pollinator of *P. pedatisecta*

Myophily has been well documented in two of the 11 *Pinellia* species (Breitenbach 1879; Vogel 1965; Shida and Tominaga 2016; Matsumoto et al. 2023). However, typical dipteran pollinators (Cecidomyiidae and Ceratopogonidae) were not collected from *P. pedatisecta* (Figure 7c), even though they were present at the study site (Figure 7c, T. K. Matsumoto, personal observation). Instead, various arthropods were trapped by *P. pedatisecta*, including spring tails, thrips, and beetles (sap and rove beetles) (Figures 7c and S4). Unfortunately, their effectiveness as pollinators could not be assessed because they were collected from male phase inflorescences that shed pollen. Although many inflorescences did not receive any pollen grains from other inflorescences during the initial female phase, pollen deposited on the stigma was observed frequently after the start of the male phase (Figure 5), implying that autonomous self-pollination occurred frequently. On the other hand, thrips and beetles are regarded as important pollinators of several aroid taxa (Rust 1980; Gibernau 2003, 2011, 2016; but see Barriault et al. 2010), and collembolan visitors are sometimes collected (Jones et al. 2013; Matsumoto et al. 2019). At least, they do not seem to be captured by chance because flower visitation was clearly correlated with floral odor (Figure 6c,d).

The wide spectrum of floral visitor (Figure 7c) might be related to the simplified spathe morphology of *P. pedatisecta* owing to the reduction of two elements; (1) the penetrating hole on the thickened wall (Figures 3 and 2), the pollinator release system via the exit slit opening (Figure 1e,f). First, the penetrating hole present in the congener species (Figure 3) may function as an insect filter, allowing only appropriate pollinators to access the female floral zone, similar to other trap flowers with similar filtering structures (Gibernau et al. 2004; Oelschlägel et al. 2009). Indeed, the size of the penetrating hole of *P. ternata* (Figure 3b) fits that of pollinating flies (Breitenbach 1879), which can reduce their body size by folding wings and legs, in contrast to beetle visitors of *P. pedatisecta* with hard elytra (Figure S4b). Second, the completely opened spathe of *P. pedatisecta* in the male phase (Figures 1b and 2d) may have contributed to the attraction of various sized insect pollinators because the trap flower cannot release trapped insects if their body size exceeds the inner diameter of the exit slit (Hayase 2019). These two exceptional inflorescence traits (Figures 1 and 2) potentially enable *P. pedatisecta* to capture and release insects with various body sizes, although we cannot conclude that these arthropods are effective pollinators.

4.3 | Contrasting Pollination Systems of the Genus *Pinellia*

We estimated that *P. pedatisecta* outcrosses using the following procedure. First, the spadix appendix begins to emit a floral odor while the spathe blade is partially-opened (Figure 2a,b) and the stigma is receptive (female phase). The attracted insects land on the outer-wall of the spathe and intrude into the slit of the spathe blade (Figure S4f). Upon reaching the middle parts of the inner spathe blade (Position 3 in Figure 3), they fall to the bottom of the spathe tube because of the slippery surface covered by downward-pointed microstructures (Figure 8). Upward-pointed microstructures (Figures 4 and 8) allow trapped insects to walk around the female floral zone. Pollen deposition on stigma can be achieved if they carry pollen grains from other inflorescences. Several days later, anther dehiscence leads to the shedding of pollen within the spathe tube (male phase), partly causing autonomous selfing (Marshall et al. 2014). The completely open spathe (Figure 2d) then releases trapped insects loaded with pollen grains.

The pollination system of *P. pedatisecta* appears to differ from that of congeners, not only in the availability of a wide pollinator spectrum but also in the high possibility of autonomous self-pollination. *Pinellia ternata*, an absolute outcrosser (Higuchi and Okada 1996), considerably reduces fruiting rate under low pollinator attractiveness conditions (Shida and Tominaga 2014, 2016). In general, autonomous selfing can ensure seed production under pollen-limited conditions (Baker 1955; Fægri and van der Pijl 1979); however, the thickened wall between male and female floral zones of typical *Pinellia* species (Figure 3) may limit passive self-pollen deposition on the stigma (Vogel 1965; Matsumoto et al. 2023; but see Uhlarz 1984). In the genus *Pinellia* with pollen limitation for outcrossing and/or selfing (Shida and Tominaga 2016; Matsumoto et al. 2023), sexual reproduction may be assured by the simplified spathe structure (Figures 1 and 2) and a wide spectrum of floral visitors (Figure 7c).

Interestingly, phylogenetic trees constructed using whole plastid genomes imply that *P. pedatisecta* may not be the most basal taxon of this genus (Cui et al. 2022), although its simplified inflorescence has been regarded as an ancestral trait. Although the phylogenetic position of *P. pedatisecta* may differ in future studies because only three species have been analyzed by Cui et al. (2022), repeated evolution of the elaborate inflorescence of the other species (Figure 4) seems improbable. Hence, it is most likely that the simplified floral structure in *P. pedatisecta* have secondarily evolved only once in the genus *Pinellia*. This speculation does not contradict the tendency for the type of pitfall trap to be shared within each aroid genus (Bröderbauer et al. 2012). Unfortunately, we could not discuss the factors underlying this simplification of the spathe morphology because our study was conducted outside the native range. To clarify its evolutionary background, future studies should examine the pollination biology of *P. pedatisecta* and its congeners in their natural habitats.

Author Contributions

Kohei Yanagisawa: conceptualization, data curation, formal analysis, investigation, methodology, visualization, and writing – original draft.

Tetsuya K. Matsumoto: conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, visualization, writing – original draft, and writing – review and editing.

Acknowledgments

We would like to thank Yuta Kato for the lecture on the preparation method of hand-sectioned plant materials and a preliminary report about the microstructure of the epidermis of *Pinellia* spp.; Kaede Iijima and Shuto Yonezawa for their support in the data collection and the cultivation of experimental plants; Ryo Hayashi, Shimpei Oikawa, and Tomoya Ono for their support in the preparation and the management of the experimental field; Ryuhei Miyazaki, Yuko Miyazaki, Yuki Numata, Ryo Takemura, and Kotone Tatano for their support in the transplanting of experimental plants; Yoshihiro Senda for his comments on the coleopteran identification; Kiichi Takahashi for seeking rare articles; Jin Murata, Takafumi Shida, and Shoko Taniguchi for providing the cultivated *Pinellia* plants.

Funding

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

References

Baker, H. G. 1955. "Self-Compatibility and Establishment After "Long-Distance" Dispersal." *Evolution* 9: 347–349.

Barriault, I., D. Barabé, L. Cloutier, and M. Gibernau. 2010. "Pollination Ecology and Reproductive Success in Jack-in-the-Pulpit (*Arisaema triphyllum*) in Québec (Canada)." *Plant Biology* 12: 161–171.

Breitenbach, W. 1879. "Die Blütheneinrichtung von *Arum ternatum* Thunbg." *Oesterreichische Botanische Zeitschrift* 29: 689–692.

Bröderbauer, D., A. Diaz, and A. Weber. 2012. "Reconstructing the Origin and Elaboration of Insect-Trapping Inflorescences in the Araceae." *American Journal of Botany* 99: 1666–1679.

Bröderbauer, D., S. Ulrich, and A. Weber. 2014. "Adaptations for Insect-Trapping in Brood-Site Pollinated *Colocasia* (Araceae)." *Plant Biology* 16: 659–668.

Chen, M. Q., N. Xu, M. Man, and R. Luo. 2024. "*Pinellia discolor*: A New Cryptic Species Distinguished *P. cordata* in Mainland China." *Nordic Journal of Botany* 2024: e04119.

Cui, N., W. Chen, X. Li, and P. Wang. 2022. "Comparative Chloroplast Genomes and Phylogenetic Analyses of *Pinellia*." *Molecular Biology Reports* 49: 7873–7885.

Fægri, K., and L. van der Pijl. 1979. "Autogamy." In *The Principles of Pollination Ecology*, edited by K. Fægri and L. van der Pijl, 3rd ed., 135–140. Pergamon Press.

Gardner, E. M., R. J. Gagné, P. E. Kendra, et al. 2018. "A Flower in Fruit's Clothing: Pollination of Jackfruit (*Artocarpus heterophyllus*, Moraceae) by a New Species of Gall Midge, *Clinodiplosis ultracrepidate* sp. Nov. (Diptera: Cecidomyiidae)." *International Journal of Plant Sciences* 179: 350–367.

Gaskett, A. C., C. G. Winnick, and M. E. Herberstein. 2008. "Orchid Sexual Deceit Provokes Ejaculation." *American Naturalist* 171: 206–212.

Gibernau, M. 2003. "Pollinators and Visitors of Aroid Inflorescences." *Aroideana* 26: 66–83.

Gibernau, M. 2011. "Pollinators and Visitors of Aroid Inflorescences: An Addendum." *Aroideana* 34: 70–83.

Gibernau, M. 2016. "Pollinators and Visitors of Aroid Inflorescences III—Phylogenetic & Chemical Insights." *Aroideana* 39: 4–22.

Gibernau, M., D. Macquart, and G. Przetak. 2004. "Pollination in the Genus *Arum*—A Review." *Aroideana* 27: 148–166.

Hayase, Y. 2019. "Variation of *Arisaema serratum* Group in Toyama Prefecture, Central Japan." *Bulletin of the Toyama Biological Society* 58: 50–59.

Higuchi, M., and M. Okada. 1996. "Studies on Cultivation of *Pinellia ternata* Breit. (Part 2) on the Mode of Pollination." *Natural Medicines* 50: 170–175.

Iwata, T., O. Nagasaki, H. S. Ishii, and A. Ushimaru. 2012. "Inflorescence Architecture Affects Pollinator Behaviour and Mating Success in *Spiranthes sinensis* (Orchidaceae)." *New Phytologist* 193: 196–203.

Jones, S., M. Davis, A. McCaskill, and F. Corotto. 2013. "Spadix Function in the Jack-in-the-Pulpit, *Arisaema triphyllum*." *Georgia Journal of Science* 71: 191–196.

Kato, M., A. Takimura, and A. Kawakita. 2003. "An Obligate Pollination Mutualism and Reciprocal Diversification in the Tree Genus *Giochidion* (Euphorbiaceae)." *Proceedings of the National Academy of Sciences of the United States of America* 100: 5264–5267.

Kato, Y. 2024. "Easy Plant Tissue Observation by the Hand Sectioning Technique." *Japanese Journal of Crop Science* 93: 79–81.

Lack, A. J., and A. Diaz. 1991. "The Pollination of *Arum maculatum* L.—A Historical Review and New Observations." *Watsonia* 18: 333–342.

Li, H., and J. Bogner. 2010. "*Pinellia*." In *Flora of China*, edited by Z. Y. Wu, P. H. Raven, and D. Y. Hong, vol. 29, 39–43. Science Press & St. Louis: Missouri Botanical Garden Press.

Lund, U., C. Agostinelli, H. Arai, et al. 2017. "R Package Circular Version 0.4-93."

Marshall, T., M. Davis, A. McCaskill, and F. Corotto. 2014. "Spadix Function in *Pinellia pedatisecta* (Araceae)." *Aroideana* 37: 89–94.

Matsumoto, T. K., Y. Miyazaki, M. Sueyoshi, Y. Senda, K. Yamada, and M. Hirobe. 2019. "Pre-Pollination Barriers Between Two Sympatric *Arisaema* Species in Northern Shikoku Island, Japan." *American Journal of Botany* 106: 1612–1621.

Matsumoto, T. K., M. Onoue, T. Miyake, et al. 2023. "Gall Midge Pollination and Ant-Mediated Fruit Dispersal of *Pinellia tripartita* (Araceae)." *Plant Ecology* 224: 59–72.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1981. *Manual of Nearctic Diptera*. Vol. 1. Research Branch Agriculture Canada.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1987. *Manual of Nearctic Diptera, Vol. 2*. Research Branch Agriculture Canada.

Murata, J., and T. K. Matsumoto. 2021. "*Pinellia pedatisecta* (Araceae) for Botanical Research." *Journal of Phytogeography and Taxonomy* 69: 51–65.

Oelschlägel, B., S. Gorb, S. Wanke, and C. Neinhuis. 2009. "Structure and Biomechanics of Trapping Flower Trichomes and Their Role in the Pollination Biology of *Aristolochia* Plants (Aristolochiaceae)." *New Phytologist* 184: 988–1002.

Oksanen, J., F. G. Blanchet, M. Friendly, et al. 2018. "R Package 'vegan' Version 2.5-2."

Phillips, R. D., D. Scaccabarozzi, B. A. Retter, et al. 2014. "Caught in the Act: Pollination of Sexually Deceptive Trap-Flowers by Fungus Gnats in *Pterostylis* (Orchidaceae)." *Annals of Botany* 113: 629–641.

Poppinga, S., K. Koch, H. F. Bohn, and W. Barthlott. 2010. "Comparative and Functional Morphology of Hierarchically Structured Anti-Adhesive Surfaces in Carnivorous Plants and Kettle Trap Flowers." *Functional Plant Biology* 37: 952–961.

R Development Core Team. 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/.

Rasband, W. S. 1997–2012. *ImageJ*. National Institutes of Health. https://imagej.net/ij/.

Rust, R. W. 1980. "Pollen Movement and Reproduction in *Arisaema triphyllum*." *Bulletin of the Torrey Botanical Club* 107: 539–542.

Shida, T., and T. Tominaga. 2014. "Sexual Reproduction of *Pinellia ternata*." *Tohoku Weed Journal* 13: 15–19.

Shida, T., and T. Tominaga. 2016. "Pollinator of *Pinellia ternata* and Their Behavior." *Tohoku Weed Journal* 15: 1–5.

Terry, I., G. H. Walter, C. Moore, R. Roemer, and C. Hull. 2007. "Odor-Mediated Push-Pull Pollination in Cycads." *Science* 318: 70.

Tominaga, T., and A. Nakagaki. 1997. "Corm Weight-Dependent Reproduction of *Pinellia ternata*." *Journal of Weed Science and Technology* 42: 18–24.

Uhlarz, H. 1984. "Is *Pinellia tripartita* (Blume) Schott an Anemophilous Self-Pollinator?" *Beiträge Zur Biologie der Pflanzen* 60: 277–291.

Vogel, S. 1965. "Kesselfallen-Blumen." *Umschau für Wissenschaft und Technik* 65: 12–17.

Zhu, G., H. Li, and R. Li. 2007. "A Synopsis and a New Species of the E Asian Genus *Pinellia* (Araceae)." *Willdenowia* 37: 503–522.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** psbi70058-sup-0001-FigureS1-S4.docx. **Figure S2:** psbi70058-sup-0001-FigureS1-S4.docx. **Figure S3:** psbi70058-sup-0001-FigureS1-S4.docx. **Figure S4:** psbi70058-sup-0001-FigureS1-S4.docx.