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Suetsugu, Kenji

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Relictithismia: An underground fairy lantern

Kenji Suetsugu[1,2]

[1]Department of Biology, Graduate School of Science, Kobe University, Kobe, Hyogo, Japan

[2]Institute for Advanced Research, Kobe University, Kobe, Hyogo, Japan

Correspondence
Kenji Suetsugu, Department of Biology, Graduate School of Science, Kobe University, Kobe, Hyogo 657-8501, Japan.
Email: kenji.suetsugu@gmail.com

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Societal Impact Statement

The discovery of a new genus within the family Thismiaceae, known as fairy lanterns, marks a significant scientific milestone in Japan, a country renowned for its botanical research. The unearthing of a new genus, especially in a well-documented flora like Japan, is both rare and monumental. Unlike other fairy lanterns that bloom under leaf litter and can be easily overlooked, the new genus and species, *Relictithismia kimotsukiensis*, often does not even emerge above the surface of the soil when flowering. This captivating characteristic not only enriches our knowledge of botanical diversity but also emphasizes the importance of preserving natural habitats that harbor such rare species.

Summary

The family Thismiaceae, known as "fairy lanterns", is distinguished by its urn- or bell-shaped, glasswork-like flowers with basally fused tepals and its dependence on specific fungi for carbon. A new genus and species, *Relictithismia kimotsukiensis*, has been discovered in southern Japan. This species is notable for its unique anther-stigma contact, hitherto unreported in the other Thismiaceae. Unlike typical fairy lanterns that bloom just above the leaf litter, *Relictithismia* often flowers beneath it. The underground habit is potentially associated with self-pollination. The discovery of *Relictithismia* enhances our understanding of evolutionary pathways within the Thismiaceae, as it possesses characteristics previously thought to be unique to *Thismia* (the annulus with drooping stamens) as well as traits found in other genera (free stamens without expanded connectives). This paper reviews the morphology, ecology, and evolutionary history of *Relictithismia*, offering insights into the peculiarities of these enigmatic plants.

KEYWORDS
arbuscular mycorrhiza, East Asia, endemic species, fairy lantern, mycoheterotrophy, Thismiaceae, underground flower

1 | INTRODUCTION

The family Thismiaceae, often referred to as "fairy lanterns" due to their distinctive, vivid, urn- or bell-shaped flowers with basally fused tepals, consists of non-photosynthetic flowering monocots primarily found in tropical regions, extending into subtropical and temperate areas (Garrett et al., 2023; Merckx & Smets, 2014; Thorogood & Mat Yunoh, 2021). These plants, engaging in mycoheterotrophy, obtain their carbon from mycorrhizal fungi. They bear a superficial resemblance to fungi more than plants and are visible above ground only during their short flowering and fruiting periods, making them easily overlooked in dense shade or concealed by leaf litter, leading to their infrequent documentation (Thorogood, 2019; Thorogood & Mat Yunoh, 2021). For instance, of the 108 accepted *Thismia* species, at least 55 are known solely from their initial discovery locations, with at least 38 documented from a single discovery event (Dančák et al., 2020; Plants of the World Online [POWO], 2024).

This family includes the monotypic genera *Haplothismia* and *Tiputinia*, as well as *Oxygyne* with six species, and *Thismia* with 108 accepted species (Merckx et al., 2006, 2009; POWO, 2024; Shepeleva et al., 2020). While *Afrothismia* was once classified within Thismiaceae, phylogenetic analysis has demonstrated it is not monophyletic with the other four genera but instead forms a sister clade with the photosynthetic Taccaceae and other Thismiaceae species (Lin et al., 2022; Merckx et al., 2009). Additionally, the ovary of *Afrothismia* is distinct, featuring a single stalked placenta, unlike other Thismiaceae species, which have three placentae (Cheek et al., 2024). Thus, *Afrothismia* has been treated as the distinct family Afrothismiaceae (Cheek et al., 2024).

In the Osumi Peninsula, southern Japan, a novel fairy lantern species exhibiting free stamens touching the stigma during anthesis—a characteristic absent in other Thismiaceae genera—has been discovered (Suetsugu et al., 2024). Typically hidden beneath the soil, locating this new species is challenging without knowing exact search areas. The first specimen was serendipitously found in June 2021 when rain exposed its entire plant body by washing away the soil (Figure 1a). The following year, careful excavation of the soil top layer led to the discovery of four additional individuals (Figure 1b,c), allowing for a detailed examination. This led Suetsugu et al. (2024) to propose a new genus, *Relictithismia*, with its monotypic species, *Relictithismia kimotsukiensis*. Considering that Japan is one of the world's most thoroughly surveyed regions botanically (Ebihara et al., 2013), the discovery of new plant species is exceedingly rare, making the identification of a new genus particularly extraordinary. The most recent discovery of a new vascular plant, simultaneously identified as a separate genus and still recognized as a distinct genus today, is *Japonolirion* (Petrosaviaceae), dating back to approximately 100 years ago (Nakai, 1930). The discovery of a new genus, *Relictithismia*, in Japan underscores the importance of continued exploration and study in even some of the most well-researched environments.

Moreover, it is interesting to note that, while fairy lanterns normally grow in deep shade under leaf litter and are easily overlooked (Thorogood & Mat Yunoh, 2021), *Relictithismia* often does not even emerge above the surface of the soil when flowering (Figure 1). Plants that flower and fruit almost exclusively below ground are exceedingly rare but have, for example, been documented in the Australian underground orchid genus *Rhizanthella* (Kuhnhäuser et al., 2023; Randi et al., 2023; Thorogood et al., 2019). This paper aims to synthesize current knowledge, including the morphology, ecology, and evolutionary history of a unique fairy lantern.

2 | MORPHOLOGY AND PHYLOGENY OF *RELICTITHISMIA*

In East Asia, the family Thismiaceae is represented by two genera, *Oxygyne* and *Thismia*, both documented in Japan. *Relictithismia* is distinguishable from *Oxygyne*, which has three stamens, by its six stamens (Cheek et al., 2018). The stamens of *Relictithismia* are free, in contrast to those of *Thismia*, which typically lack expanded connective appendages (except for paraphyletic Neotropical species belonging to subgenus *Ophiomeris* that often exhibit free stamens without expanded connectives) (Maas et al., 1986; Shepeleva et al., 2020). Although *Relictithismia* resembles *Haplothismia* in possessing a cluster of tuberous roots, *Relictithismia* is distinctive in having stamens that make direct contact with the stigma surface, a feature absent in all other Thismiaceae genera (Suetsugu et al., 2024).

Phylogenetic analysis also confirmed that *Relictithismia* is situated outside the Old World *Thismia* clade (= *Thismia* sensu strict) (Suetsugu et al., 2024). Intriguingly, all Thismiaceae genera other than the genus *Thismia*, including *Relictithismia*, exhibit poorly specialized perianths, featuring identical inner and outer perianth layers and free stamens (Airy-Shaw, 1952; Cheek et al., 2018; Shepeleva et al., 2020; Woodward et al., 2007). On the other hand, pendulous stamens emanating from the annulus are exclusive to *Relictithismia* and *Thismia* (Figure 2b,d; Suetsugu et al., 2024). Therefore, *Relictithismia* is

FIGURE 1 *Relictithismia kimotsukiensis* in its type locality. (a) A flowering individual with the entire plant body exposed due to soil erosion by heavy rain, discovered in June 2022. (b–c) Flowering individuals whose most parts or entire parts (enclosed by the dashed line) are buried in the soil, respectively, discovered in June 2023. These images were taken after removing decaying litter on the soil surface. Scale bars: 10 mm. Photographs: Yasunori Nakamura (a) and Shuichiro Tagane (b–c).

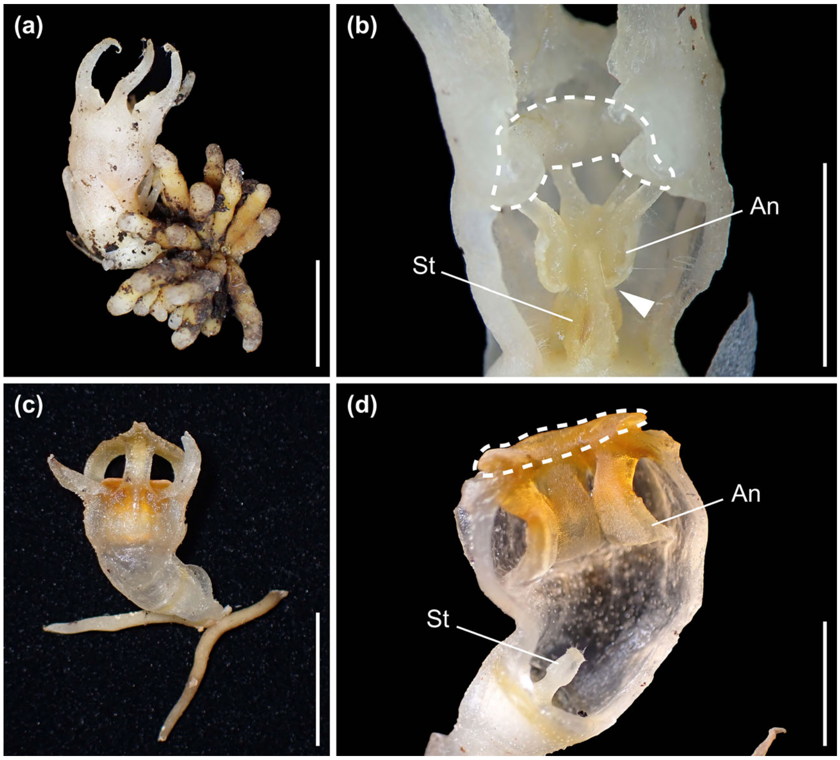

FIGURE 2 Morphological comparison between *Relictithismia* and *Thismia*. (a–b) *Relictithismia kimotsukiensis*. (c–d) *Thismia kobensis*. (a, c) Plant, lateral view. (b, d) Flower, sectional view. “An” and “St” indicate anther and stigma, respectively, while the area enclosed by the dashed line indicates the annulus. An arrow indicates direct contact between stamens and stigma. Scale bars: 10 mm (a & c) and 5 mm (b & d). Photographs: Kenji Suetsugu (a, c, d) and Shuichiro Tagane (b).

undoubtedly an intriguing species for understanding the evolution of Thismiaceae, as it possesses characteristics previously thought to be unique to *Thismia* as well as traits found in other genera. The name *Relictithismia* encapsulates its phylogenetic and morphological feature within the Thismiaceae. The genus name, derived from the Latin “relictus” meaning “left behind”, combined with the generic name *Thismia*, poignantly reflects its status as a morphological intermediary between *Thismia* and other Thismiaceae genera (Suetsugu et al., 2024). Additionally, the presence of the annulus inside the perianth mouth is a unique trait found only in *Relictithismia*, likely facilitating direct contact between stamens and stigma.

3 | DISTRIBUTION AND ITS BIOGEOGRAPHICAL SIGNIFICANCE

Relictithismia is known only from a single population within the Osumi Peninsula, southern Japan (Suetsugu et al., 2024). Spanning boreal to subtropical zones, the Japanese archipelago plays a pivotal role among the continental islands in East Asia (Kubota et al., 2017). It has been proposed as a sanctuary for Tertiary relict floras, preserving ancient plant lineages (Milne & Abbott, 2002). The present biotas of the archipelago result from a dynamic interplay of migrations, extinctions, and speciation, molded by periods of geographical isolation and connectivity (Millien-Parra & Jaeger, 1999). Moreover, the flora of Japan is particularly abundant in mycoheterotrophic plants exploiting arbuscular mycorrhizal (AM) fungi (Suetsugu et al., 2023; Suetsugu & Nishioka, 2017). To date, more than 20 AM-forming mycoheterotrophic species across four families—Petrosaviaceae, Triuridaceae, Burmanniaceae, and Thismiaceae—have been identified, often representing the northernmost distribution limits of their respective genera or families (Suetsugu et al., 2023).

Notably, Japan stands out for harboring the greatest diversity of genera within the family Thismiaceae, comprising three out of the five genera within the family. Interestingly, *Oxygyne*, being disjunct between Japan and West–Central Africa, is sister to all other Thismiaceae (Shepeleva et al., 2020; Yokoyama et al., 2008). Additionally, while *Oxygyne* is the sole member of the African Thismiaceae species, it coexists with *Relictithismia* and *Thismia* in Japan (Cheek et al., 2018; Suetsugu et al., 2019). *Relictithismia* showcases some intermediate morphological traits that potentially serve as evolutionary links between the early-branching genera in Thismiaceae such as *Oxygyne* (free stamens without expanded connectives) and the more recently diversified and species-rich genus *Thismia* (free stamens without expanded connectives) (Suetsugu et al., 2024). Furthermore, two Japanese *Thismia* species, *Thismia abei* and *Thismia kobensis*, are among the early-branching lineages within the Old World *Thismia* clade (Shepeleva et al., 2020; Suetsugu et al., 2023). These findings underscore Japan as a biodiversity hotspot and critical region for understanding the biogeography and evolutionary trajectories within Thismiaceae (Suetsugu et al., 2023).

4 | POLLINATION BIOLOGY

The production of flowers underground is a paradoxical reproductive strategy that seemingly hinders pollination (Kuhnhäuser et al., 2023). Little is known about the reproductive biology of *Relictithismia*, yet the floral architecture of this genus, particularly the stamens that contact the stigma surface during anthesis (Figure 2b), hints at an adaptation for self-pollination. This characteristic, where the anther touches the stigma, is a feature not observed in any other Thismiaceae genera except for *Afrothismia* (Afrothismiaceae), once considered under the Thismiaceae (Cheek et al., 2024). Considering the phylogenetic separation between *Afrothismia* and other Thismiaceae genera (Lin et al., 2022; Merckx et al., 2009), the emergence of free stamens touching the stigma in both lineages may represent a case of convergent evolution fostering self-pollination. Autonomous self-pollination is a beneficial trait for mycoheterotrophic plants commonly occurring in dim, understory habitats where pollinator availability is scarce (Suetsugu, 2013, 2015, 2022). The ability to achieve fruit set through self-pollination without insect intervention may have been a critical factor enabling the strongly underground habit of *Relictithismia*.

It is also noteworthy that *Relictithismia* exhibits floral traits indicative of sapromyophily, a pollination strategy aimed at attracting fly pollinators, although its flowers, buried below the surface, remain hidden from most conventional pollinators, such as bees. For instance, filiform appendages on its perianth lobes are known as an adaptation to lure fly pollinators (Suetsugu, Nishigaki et al., 2022). Interestingly, various insects, including termites, fungus gnats, flies, and wasps, have been suggested as pollinators for *Rhizanthella* (Orchidaceae) (Swarts & Dixon, 2009; Thorogood et al., 2019), another genus with underground flowers, making them plausible pollinators for *Relictithismia* as well. Fungus gnats, in particular, are plausible pollinators because they were observed to be transiently trapped inside the floral tubes of some Thismiaceae species, facilitating pollination (Guo et al., 2019; Suetsugu & Sueyoshi, 2021). Additionally, during plant dissections, we found that springtails (Collembola) had been trapped in the flowers. Given that springtails are an important component of the soil mesofauna (Nakamori & Suzuki, 2006) and sperm of mosses can also be dispersed by springtails (Rosenstiel et al., 2012), the springtail pollination system might also be plausible.

In summary, while self-pollination appears to be a probable primary pollination mode for *R. kimotsukiensis*, the potential contribution of insect-mediated pollination should not be overlooked. Further research is essential to fully unravel the complex pollination syndrome of this enigmatic plant.

5 | FUNGAL ASSOCIATIONS

Mycorrhizal associations are usually mutualistic, allowing plants to access essential minerals via their fungal partners in exchange for carbon derived from photosynthesis (Smith & Read, 2008). Conversely, similar to other fairy lanterns (Gomes et al., 2017; Guo et al., 2019; Suetsugu, Okada et al., 2022), *Relictithismia* is mycoheterotrophic, acquiring nutrients from AM fungi that forage for soil nutrients and, at the same time, is dependent on an autotrophic host for a continuous supply of carbon.

Given their strong fungal reliance, mycoheterotrophic plants have conflicting needs regarding mycorrhizal structure: (i) ample primary tissue for hyphal nourishment, (ii) extensive epidermal surface to enhance colonization chances by suitable fungi, and (iii) minimized or securely managed transportation distance for fungus-derived carbon and nutrients (Feller et al., 2022; Imhof et al., 2020). Similar to other Thismiaceae members (Feller et al., 2022), *Relictithismia* mycorrhizal structures are sophisticated (Figure 3), displaying distinct fungal configurations in different root tissue zones—preserving intact straight, coiled, and uniquely knotted hyphae in the outermost epidermal layer, while digesting others in the inner compartments. This likely maximizes the utility of limited external fungal penetrations due to the constrained root surface area (Feller et al., 2022). *Relictithismia* also possesses a warty root surface (Figure 3b–d), a trait not previously

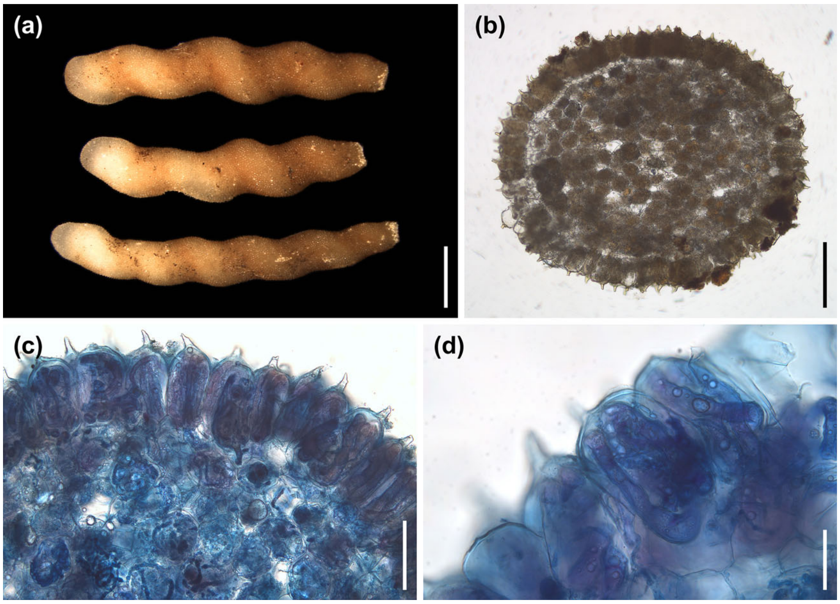

FIGURE 3 *Relictithismia kimotsukiensis* and its mycorrhizal interaction. (a) Tuberous roots. (b) Cross-section of the tuberous root. (c) Close-up of root cells with undegenerated and degenerated fungal coils stained with trypan blue. (d) Close-up of root cells with undegenerated figure-of-eight fungal coils stained with trypan blue. Scale bars: 2 mm (a), 200 μm (b), 100 μm (c), and 50 μm (d). Photographs: Kenji Suetsugu (a) and Hidehito Okada (b–d).

documented in Thismiaceae, potentially an adaptation to increase surface area facilitating colonization by appropriate fungi. Interestingly, *Relictithismia* and *T. abei*, both early-branching members within Thismiaceae, and *Oxygyne duncanii*, from the earliest-branching clade, possess a single-layered epidermis (Figure 3b–d), unlike most other *Thismia* species that develop an additional fungus-free exoepidermis (Cheek et al., 2018; Feller et al., 2022). The trait of having a single-layered epidermis is likely plesiomorphic, while species-level phylogeny and ancestral trait reconstruction would provide more conclusive evidence.

In contrast to the diffuse interactions between green plants and their mycorrhizal fungi, the connections between mycoheterotrophic plants and their fungal partners tend to be highly specific (Jacquemyn & Merckx, 2019). Members of the family Thismiaceae are especially notable for highly specialized mycorrhizal interactions, probably contributing to their rarity and often endangered status (Suetsugu et al., 2023; Thorogood, 2019; Thorogood & Mat Yunoh, 2021). Given the potentially highly specialized relationships, detailed studies on the identity of fungal partners, their evolutionary preferences, and soil requirements are essential to understanding the evolutionary history of *Relictithismia* and formulating effective conservation measures.

6 | CONSERVATION

Relictithismia kimotsukiensis has been classified as "Critically Endangered" under the IUCN Red List Categories and Criteria (International Union for Conservation of Nature [IUCN], 2022). This plant is exclusively found at a solitary site where fewer than five individuals have been discovered. Its dependency on fungal sources for sustenance complicates cultivation efforts outside natural settings, making in-situ preservation the most feasible strategy. Therefore, the primary measure to protect *Relictithismia* involves preserving its natural habitat. Given that the type locality, adjacent to a forest road and outside a protected area, features mostly young trees with a diameter at breast height of less than 13 cm, indicating recent forest clearing within the past 20–30 years, continued monitoring is essential for understanding the threats to *Relictithismia* (Suetsugu et al., 2024). Studies focusing on its population size, exploring new localities, and unveiling its ecology, such as mycorrhizal identification, will provide critical data for devising effective conservation strategies. Finally, although ex situ cultivation is difficult, it might shed light on the conservation, considering that botanic gardens have played a vital role in the conservation of mycoheterotrophic plants including *Rhizanthella gardneri* (Orchidaceae) (Swarts & Dixon, 2009; Thorogood et al., 2019).

7 | CONCLUDING REMARKS

The discovery of *Relictithismia* not only adds a new genus and species to the botanical record but also enriches our understanding of plant life strategies, highlighting mycoheterotrophic plants with underground flowers and providing a potential link between the early-diverging genera in Thismiaceae and the genus *Thismia*. Thus, the discovery of this new fairy lantern "illuminates" their enigmatic evolutionary history, despite its underground habit. The discovery also highlights the hidden diversity within well-studied regions like Japan, underscoring the importance of continuous exploration and conservation efforts.

To fully grasp the ecology of *Relictithismia*, several avenues of research are crucial, focusing on its interactions with fungal partners and pollinators. Further study, based on high-throughput sequencing technology, will provide more precise information on their phylogenetic relationships and trait evolution. Ancestral character-state reconstruction analysis, based on comprehensive sampling, will offer deeper insights into the evolution of the Thismiaceae. Nondestructive DNA analysis utilizing herbarium specimens could help achieve a comprehensive species-level phylogeny (Sugita et al., 2020), given that many species are documented from a single discovery event. Such advanced methods are essential to further illuminate the evolutionary history, including the origin, biogeographical history, floral trait evolution, and fungal interactions of this enigmatic family.

AUTHOR CONTRIBUTIONS

Kenji Suetsugu 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 conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Kenji Suetsugu https://orcid.org/0000-0002-7943-4164

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