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Suetsugu, Kenji
Sennikov, Alexander N.
Nuraliev, Maxim S.

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Multifaceted obscurity of *Thismia abei* (Thismiaceae): A fairy lantern with the protologue long disregarded in practice

Kenji Suetsugu^{1,2}  | Alexander N. Sennikov³  | Maxim S. Nuraliev^{4,5} 

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

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

³Botanical Museum, Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland

⁴Department of Higher Plants, Faculty of Biology, M.V. Lomonosov Moscow State University, Moscow, Russia

⁵Joint Vietnam-Russia Tropical Science and Technology Research Center, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

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

Tiny, leafless fairy lanterns are easily overlooked on the forest floor. *Thismia abei*, endemic to Japan, persists in small, unstable populations and is listed nationally as Critically Endangered. Our recent work has revealed another, less obvious form of obscurity. The original source of the scientific name has long been cited incorrectly because a later, more widely read academic account displaced an earlier, valid description in a local periodical that some taxonomists dismissed as nonacademic. The case of *T. abei* is not unique; many similar works were likely treated in the same way. This example underscores the importance of careful nomenclatural study and better access to regional publications so that plant diversity is accurately documented and properly recognized.

Summary

Thismia abei is a minute, mycoheterotrophic plant that emerges above the leaf litter in summer. Here, we present a comprehensive review of *T. abei* by integrating recent findings on its morphology, phylogenetics, ecology, and nomenclatural history. Phylogenetic analyses place *T. abei* among the early-diverging lineages of the Old World *Thismia* clade, and current taxonomy assigns it to *Thismia* sect. *Labiothismia*. Its stamens are united into a tube along part of their length, although they were previously regarded as free. This misinterpretation has hindered comparisons between Old World and New World lineages. The species exhibits high mycorrhizal specificity and is associated primarily with two *Rhizophagus* virtual taxa (Glomeraceae). The fungus gnat *Bradysia atracornea* (Sciaridae) has been observed visiting its musty-scented flowers, consistent with the hypothesis that some fairy lanterns exploit fungus-associated cues. Beyond its biological elusiveness, *T. abei* also has an obscure nomenclatural history. In a Japanese academic climate in which influential botanists shaped prevailing views of what counted as effective publication, a later and more prominent account became the standard citation for the name, obscuring the earlier protologue that had been effectively published in a regional periodical. This case suggests that substantial taxonomic information remains hidden in regional Japanese publications. In addition, the publication history of *T. abei*, involving collaboration between a local

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naturalist, Chikaichi Abe, and a professional botanist, Yoshiyuki Akasawa, illustrates how such partnerships can bring overlooked plants to scientific attention and foreshadows key features of modern citizen science.

KEYWORDS

arbuscular mycorrhizal fungi, citizen science, East Asia, Japan, mycoheterotrophy, nomenclature, phylogeny, taxonomy

1 | INTRODUCTION

Fairy lanterns (*Thismia* spp.) are remarkable for their animal-like nutrition, a life cycle that makes them easy to overlook, and highly elaborate flowers with diverse appendages, ornamentation, and intricate internal structures (Suetsugu, 2025; Thorogood & Siti-Munirah, 2021). They belong to Thismiaceae, a family composed entirely of fully mycoheterotrophic taxa. These plants rely on arbuscular mycorrhizal fungi for organic carbon (Gomes et al., 2017; Merckx et al., 2017). They emerge aboveground only during flowering and fruiting, and many species are known from a single locality or a single collection event (e.g., Dančák et al., 2020).

Thismia abei is a small Japanese fairy lantern that epitomizes this elusiveness (Figure 1). The species was first discovered in 1943 on Shikoku Island by an amateur botanist, Chikaichi Abe, who later brought it to wider attention by publishing a sketch (Abe, 1947) and calling on scientists to investigate this extraordinary plant. This discovery represented the first record of the predominantly tropical genus *Thismia* in Japan and, more broadly, in extratropical Asia, and it immediately raised questions about plant biogeography and hidden diversity within the archipelago (Honda & Tuyama, 1948; Suetsugu et al., 2023). Recognizing its broad significance, Abe, together with a local professional botanist, Yoshiyuki Akasawa, remained actively engaged in promoting the discovery, linking it to local natural history, education, and public outreach, thereby embedding *T. abei* in both scientific discourse and local culture (Abe, 1950, 1951, 1967, 1990; Akasawa, 1948a, 1948b, 1950a, 1950b). Consequently, one of its habitats was designated a nationally protected Natural Monument in 1954.

The species occurs in shaded primary and secondary broad-leaved and mixed forests, as well as Japanese cedar plantations, sometimes on limestone soils, and typically occupies humid microsites (Abe, 1950; Shin, 1974; Suetsugu & Ishida, 2011; Suetsugu & Okada, 2025). Even at flowering, individuals may remain hidden beneath the leaf litter, and unlike in some related species (e.g., Chiang & Hsieh, 2011), the stem does not elongate during fruiting (Figure 1). It often forms small colonies and flowers in summer (Asano et al., 2024; Matsumoto & Yamada, 1994; Suetsugu & Ishida, 2011). Although the species has been observed repeatedly for several decades, its floral morphology remained incompletely understood until recently (Yudina et al., 2026). The obscurity of *T. abei* extends beyond its biology and morphology to its publication history (Yudina et al., 2026): The name was consistently cited as though it had originated from a more visible academic account

(Akasawa, 1950a), despite the existence of the earlier protologue (Akasawa, 1948a), which was properly prepared and effectively published. Here, we present a comprehensive review of *T. abei* by synthesizing recent advances in its morphology, phylogenetics, ecology, and nomenclatural history.

2 | PHYLOGENETIC RELATIONSHIPS AND TAXONOMIC PLACEMENT

Molecular phylogenetic analyses demonstrate that Old World species of *Thismia* form a monophyletic group composed of five major clades (Shepeleva et al., 2020). These clades broadly reflect geographic structure. In particular, clade 1, which includes *T. abei*, is centered in East and Southeast Asia (Shepeleva et al., 2020; Suetsugu et al., 2024; Ya et al., 2024). Clade 1 is notable because it is sister to the remainder of the Old World species (Shepeleva et al., 2020). Importantly, the neotropical *T. panamensis* is not closely related to the Old World clade. Instead, it clusters with the neotropical genus *Tiputinia*, demonstrating that *Thismia*, as traditionally circumscribed, does not constitute a single lineage and that its neotropical lineage likely warrants recognition as a separate genus (Shepeleva et al., 2020; Suetsugu et al., 2024).

For many years, *T. abei* was classified in *Thismia* sect. *Glaziocharis* (Hatusima, 1976; Kumar et al., 2017; Merckx & Smets, 2014). Nuraliev and Sennikov (2024) clarified that this long-standing practice was incorrect because the name *Thismia* sect. *Glaziocharis* is typified by the neotropical species *T. caudata* and therefore applies to a neotropical lineage rather than to Asian taxa. Inclusion of any Old World species in this section would render the section polyphyletic. Once *Thismia* sect. *Glaziocharis* was correctly restricted to the Neotropics, the Asian group containing *T. abei* (i.e., clade 1) required a different sectional name. Nuraliev and Sennikov (2024) argued for treating the entire clade 1 as a single section and demonstrated that the appropriate name is *Thismia* sect. *Labiiothismia*, originally established for the unusual *T. labiata* characterized by bilabiate flowers. Based on morphological similarities, Nuraliev and Sennikov (2024) also placed several species not yet included in molecular phylogenetic studies in *Thismia* sect. *Labiiothismia*. Under the revised circumscription, *Thismia* sect. *Labiiothismia* comprises 14 species, including the only North American species of the genus (*T. americana*), with the remainder distributed from India and Japan to Sumatra (Nuraliev & Sennikov, 2024). This revised classification aligns sectional taxonomy with molecular phylogenetic evidence

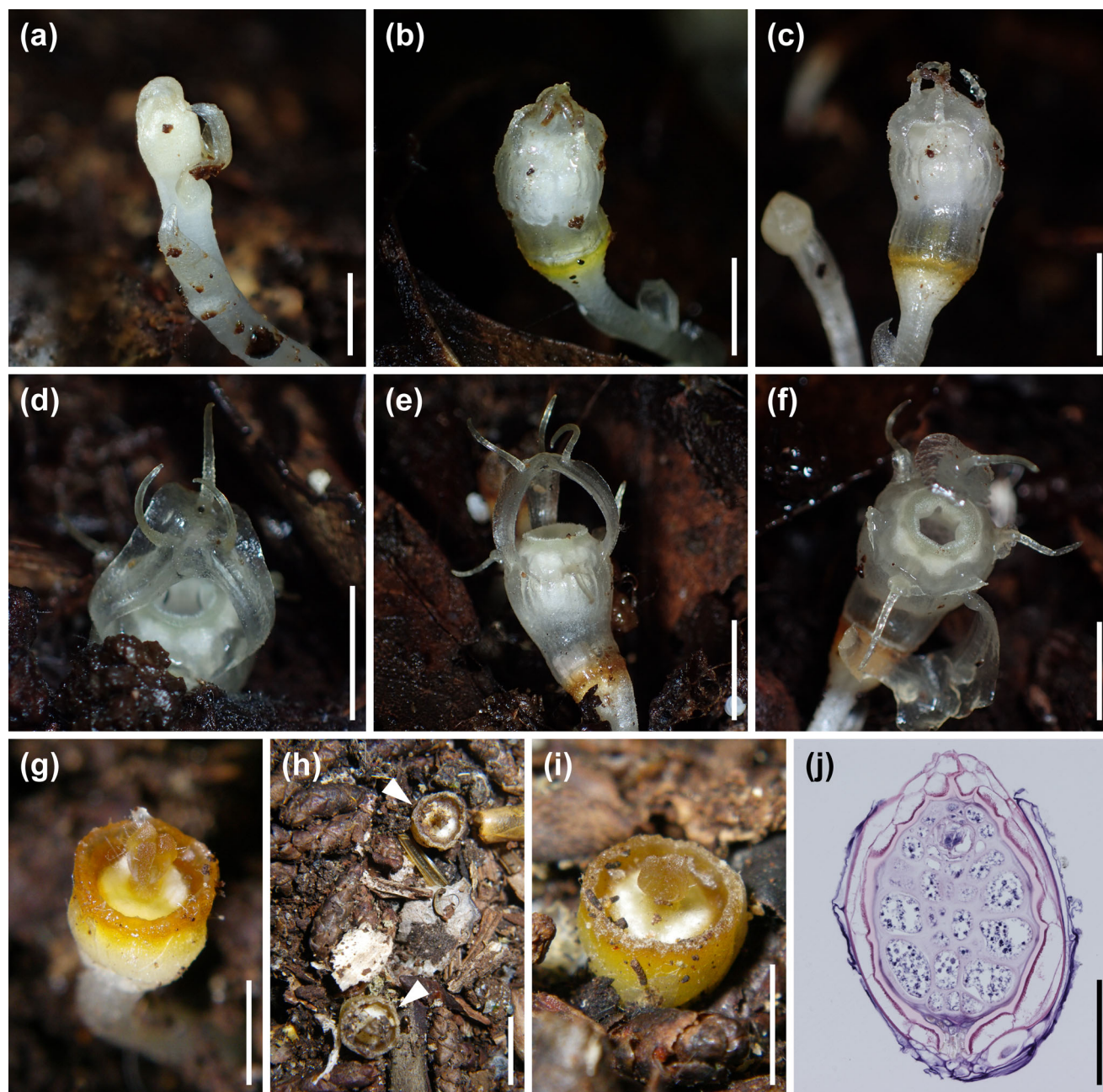


FIGURE 1 Phenological sequence of *Thismia abei*. (a) Individual at the early bud stage. (b,c) Individuals at the late bud stage, shortly before anthesis. (d,e) Individuals at anthesis. (f) Individual at late anthesis, with the mitre broken, presumably following raindrop impact. (g) Individual at the immature fruit stage. (h,i) Individuals at the mature stage before fruit dehiscence, with arrowheads indicating fruits partially embedded in the soil. (j) Seed in longitudinal section. Scale bars: 3 mm (a,g,i), 5 mm (b–f,h), and 100 μ m (j). Photographs by Kenji Suetsugu.

and resolves the long-standing misapplication of *Thismia* sect. *Glaziocharis* to Asian species (Nuraliev & Sennikov, 2024).

3 | FLORAL MORPHOLOGY

Fairy lanterns exhibit extreme reduction of vegetative organs, yet their flowers are highly elaborate, with much of the taxonomically informative morphology concealed from external view. *Thismia*

flowers have six tepals arranged in two whorls; the outer three tepals are free, whereas the inner three are either free or fused apically to form a mitre above the floral entrance (Nuraliev et al., 2021). An elongated floral tube, often referred to as a hypanthium, extends from the inferior ovary toward the tepal bases, and at its mouth, a thickening called the annulus forms a roof over the floral chamber. The annulus bears six stamens that hang into the floral chamber. Detailed developmental studies indicate that the annulus is best interpreted as a tube formed by late congenital fusion of the stamen filaments rather than

as an outgrowth of the floral tube (Nuraliev et al., 2021). The stamens are difficult to observe because they are entirely concealed within the floral chamber, yet variation in stamen structure carries substantial taxonomic significance (Sochor et al., 2018).

In *T. abei*, the presence or absence of fusion among the stamens has been described inconsistently, and this feature was documented too briefly to permit thorough assessment. Akasawa (1950a) illustrated the stamens as separate and did not mention this character in the text description, whereas Akasawa (1950b) described the connectives as united into a tube. As a result, later authors of major taxonomic treatments largely avoided describing stamen interactions (Ohwi, 1965; Tsukaya, 2016). Recent anatomical observations have resolved this ambiguity (Yudina et al., 2026): In *T. abei*, the stamens

are postgenitally united into a tube along part of their length (Figure 2). A comparable situation occurs in *T. kobensis*, another member of *Thismia* sect. *Labiothismia*. Although it was originally described as having free stamens (Suetsugu et al., 2018), later studies revealed stamen fusion (Suetsugu et al., 2023). Likewise, recent work showed that the inner tepals of *T. abei* are fused into a mitre (Yudina et al., 2026), although the dome-shaped structure was previously described as being formed by overlapping free tepals.

Thismia sect. *Labiothismia* was previously regarded as the only group within the Old World *Thismia* clade that includes species with free stamens (Nuraliev & Sennikov, 2024; Shepeleva et al., 2020). By contrast, neotropical species of the genus uniformly possess free stamens. The recently demonstrated presence of a stamen tube in *T. abei*

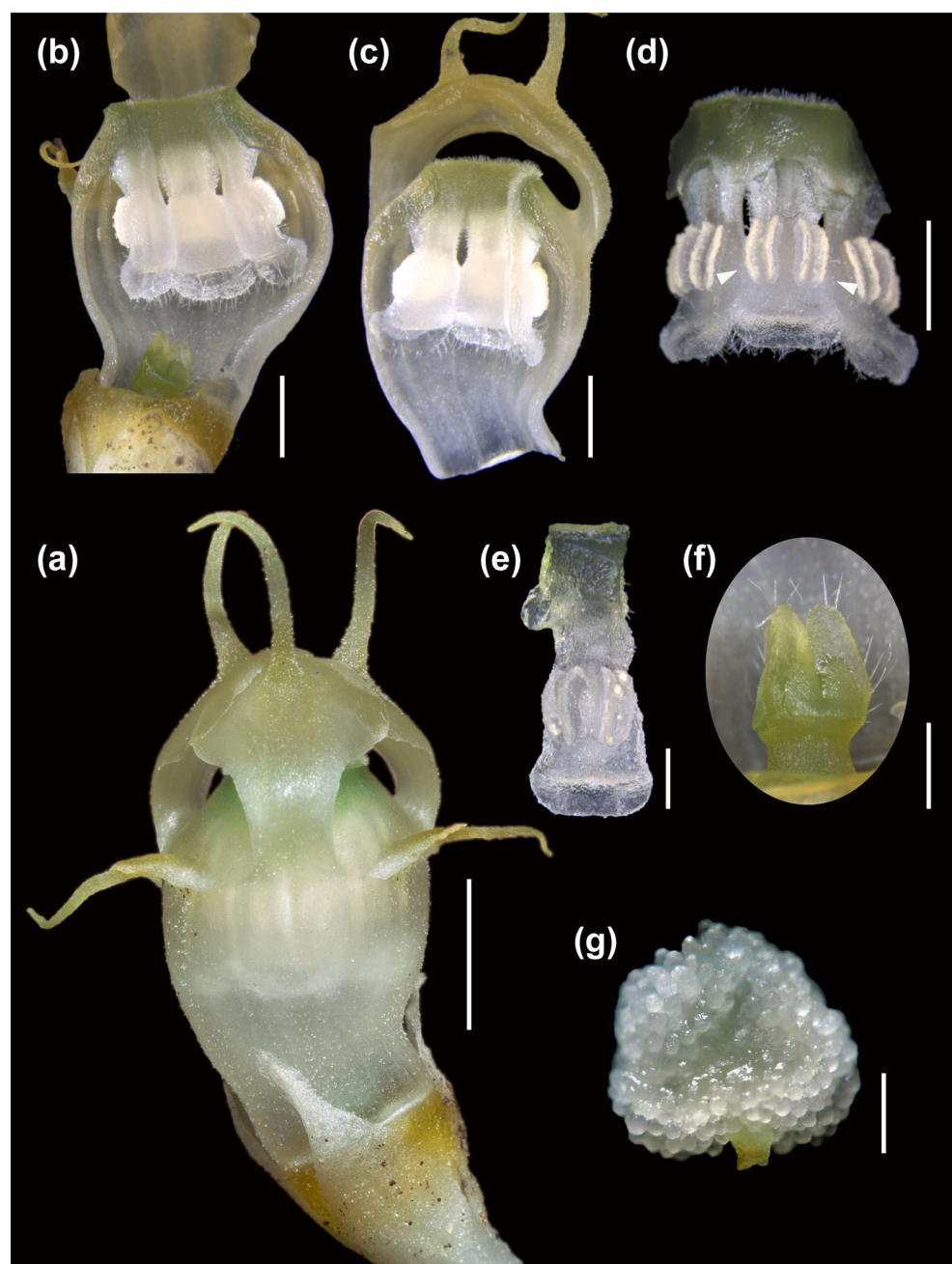


FIGURE 2 Flower of *Thismia abei*, highlighting internal floral structure. (a) Flower. (b,c) Longitudinally dissected flower. (d) Annulus and stamen tube, outer view. Arrowheads indicate the fusion sutures. (e) Stamen, outer view. (f) Stylar column and styles. (g) Placenta with ovules. Scale bars: 3 mm (a), 2 mm (b–d), 1 mm (e, f), 500 μm (g). Photographs by Kenji Suetsugu (a), Kazuma Takizawa (b–f), and Takuto Shitara (g).

and *T. kobensis* supports the hypothesis that a stamen tube characterizes the entire Old World *Thismia* clade (Nuraliev et al., 2024; Nuraliev & Sennikov, 2024). Thus, misinterpretations of androecium structure in Old World taxa have obscured morphological distinctions between the two phylogenetically separated lineages of *Thismia* and contributed to phylogenetically inconsistent sectional concepts. Although a few species in *Thismia* sect. *Labiothismia* are still assumed to have free stamens (Li & Bi, 2013) or await evaluation of this character, careful dissection and anatomical sectioning could reveal a stamen tube in these taxa as well. The examples of *T. abei* and *T. kobensis* demonstrate that reliance on simplified illustrations risks misinterpretation of this critical character.

4 | POLLINATION BIOLOGY

For many years, pollination in fairy lanterns has been inferred rather than directly observed (summarized by Severova et al., 2021; Yudina et al., 2021) because these plants are rare and emerge aboveground only briefly. In *T. abei*, direct observations remain limited but nonetheless informative. As reported by Suetsugu and Sueyoshi (2021), its flowers were visited by the fungus gnat *Bradyia atracornea* (Sciaridae, Diptera) and emitted a strong musty odor, supporting the hypothesis that some fairy lanterns attract small flies

by mimicking fungus-related cues (Figure 3a,b). This observation also represents only the second published record of *B. atracornea* in Japan (Sasakawa, 2003; Suetsugu & Sueyoshi, 2021) and highlights how studies of elusive plants can simultaneously reveal the ecology of poorly documented insects.

Publications on other *Thismia* species point to promising directions for future work on *T. abei*. In *T. mucronata* and *T. puberula*, pollination studies suggested a primary role for scuttle flies (Phoridae), together with a substantial contribution of autogamy (Yudina et al., 2021). In *T. tentaculata*, pollination biology has been investigated in more detail, revealing fungus gnat pollinators, temporary retention of visitors within the floral chamber, and self-compatibility in pollination experiments (Guo et al., 2019). Comparable approaches could clarify which visitors pollinate *T. abei*, how consistently pollination occurs across years, and how essential these interactions are for reproduction. More broadly, these fairy lanterns may mimic fungi in appearance, scent, or both, thereby exploiting sensory biases of fungus-associated insects. Testing this hypothesis will require experiments that disentangle visual and olfactory cues to determine how insects perceive and use fairy lantern flowers in the dim forest understory. Interestingly, Severova et al. (2021) showed that pollen in Asian *Thismia* has a syndrome of structural traits that does not conform to prevailing expectations for entomophily. The capacity for autonomous self-pollination in *T. abei* also warrants investigation.

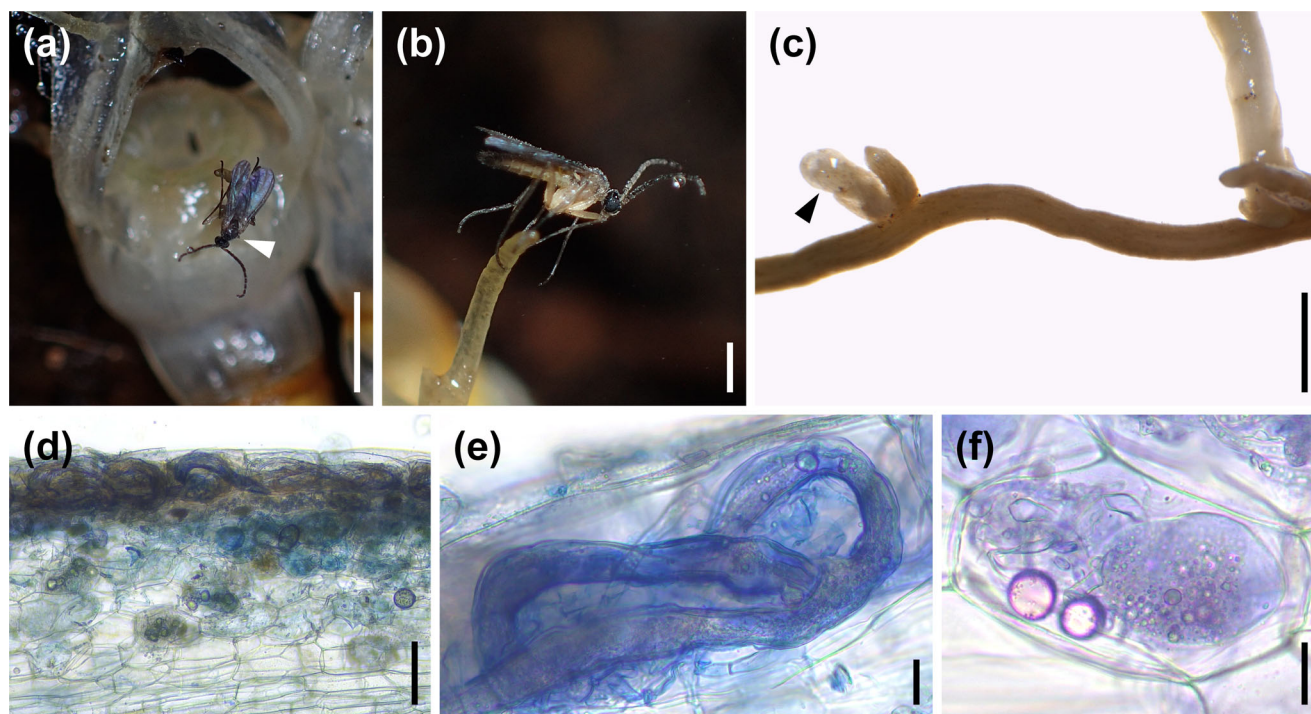


FIGURE 3 *Thismia abei* and its ecological interactions. (a) Fungus gnat *Bradyia atracornea* (arrowhead) visiting a flower. (b) Close-up of *B. atracornea* visiting a flower. (c) Root, with the arrowhead indicating an immature bud. (d) Longitudinal section of the root showing intact figure-eight hyphal coils and degenerated fungal coils stained with trypan blue. (e) Close-up of root cells containing intact figure-eight hyphal coils stained with trypan blue. (f) Close-up of root cells containing degenerated fungal coils stained with trypan blue. Scale bars: 5 mm (a), 1 mm (b), 3 mm (c), 100 μ m (d), and 20 μ m (e,f). Photographs by Kenji Suetsugu (a–c) and Hidehito Okada (d–f).

5 | FUNGAL ASSOCIATIONS

Mycorrhizal associations are typically mutualistic, enabling plants to acquire mineral nutrients from fungal partners in exchange for photosynthate-derived organic carbon (Smith & Read, 2008). In contrast, like other fairy lanterns (Gomes et al., 2017; Guo et al., 2019; Merckx et al., 2017), *T. abei* is an obligate arbuscular mycorrhizal mycoheterotroph that acquires organic carbon indirectly from surrounding photosynthetic plants via Glomeraceae fungi. Its roots are anatomically specialized for hosting and processing fungal hyphae. Cells of the single-layered epidermis contain both straight hyphae and tightly coiled structures that often form characteristic figure-eight knots (Feller et al., 2022; Suetsugu & Ishida, 2011). Within the root, intact hyphae occur near the periphery, whereas progressively degenerating coils and clumps are found toward the interior, with the inner cortex and central cylinder remaining fungus-free (Figure 3d–f; Suetsugu & Ishida, 2011; Feller et al., 2022). This organization conforms to a common pattern in Thismiaceae, in which fungi colonize root cortical cells intracellularly and are ultimately digested rather than maintained for reciprocal exchange.

Molecular analyses have further shown that *T. abei* is highly specialized in its fungal partners. High-throughput 18S metabarcoding revealed dominance by two *Rhizophagus* virtual taxa (Glomeraceae; VTX00106 and VTX00295) (Suetsugu & Okada, 2025). This pattern is consistent with the general tendency in *Thismia* toward high mycorrhizal specificity to Glomeraceae (Gomes et al., 2017; Guo et al., 2019; Merckx et al., 2017; Suetsugu et al., 2026). Together, these findings might help explain why fairy lanterns remain rare. Successful establishment likely depends on the local coexistence of suitable Glomeraceae, the surrounding photosynthetic vegetation that sustains those fungi, and appropriate humid microhabitats (Suetsugu et al., 2023; Thorogood, 2019; Thorogood & Siti-Munirah, 2021). In addition, dual specialization on fungal partners and pollinators may further constrain the distribution and population size of *T. abei* (Guo et al., 2019). For *T. abei*, future research should compare the relative abundance of *Rhizophagus* between occupied and unoccupied sites and test whether partner availability predicts long-term persistence. More broadly, current evidence still does not clarify whether establishment of this species is more strongly limited by fungal and pollinator availability, microhabitat requirements, or dispersal. This question warrants further study.

6 | CONSERVATION

Thismia abei has been provisionally assessed (Yudina et al., 2026) as Critically Endangered under multiple IUCN Red List criteria (IUCN, 2022). Its extent of occurrence is relatively large (approximately 70,000 km²) and therefore does not meet the threshold for criterion B1. By contrast, its estimated area of occupancy is extremely small, likely well below 0.1 km², which is far below the 10 km² threshold for Critically Endangered under criterion B2. This pattern reflects its small and highly localized subpopulations, each likely occupying no

more than 25 × 25 m. Fewer than 10 individuals have typically been observed at a single site at a given time, and the total number of mature individuals is inferred to be fewer than 50, consistent with criterion D (Yudina et al., 2026). This vulnerability mirrors a broader pattern among Japanese Thismiaceae, most of which are threatened yet easily overlooked (Cheek et al., 2018; Suetsugu, 2025; Suetsugu et al., 2024). Monitoring should be carefully timed to the flowering season so that true population declines can be distinguished from years in which plants fail to emerge.

In practice, conservation of *T. abei* should prioritize site protection and minimization of disturbance. The species depends on stable, humid forest-floor microhabitats, making strict protection of occupied microsites and surrounding buffer zones essential. Maintaining the surrounding biota is equally critical because *T. abei* relies on a very narrow set of mycorrhizal partners and likely also on a restricted range of dipteran pollinators. Because of its public visibility and cultural significance, *T. abei* could serve as an umbrella or surrogate species for protecting the biota of its microhabitat and, more broadly, the entire legally protected forest, as proposed for *T. kelabitiana* by Dančák et al. (2018).

Finally, although ex situ cultivation is challenging, it remains worth attempting, given successful conservation outcomes in other mycoheterotrophic plants such as *Rhizanthella gardneri* and several *Gastrodia* species (Orchidaceae; Bougoure et al., 2010; Kitahara et al., 2022; Thorogood et al., 2019).

7 | AN OBSCURE PLANT, AN EQUALLY OBSCURE PUBLICATION HISTORY

The ecological obscurity of fairy lanterns is well recognized, but *T. abei* adds another dimension because its publication history also slipped from view (Yudina et al., 2026). For decades, the species, originally described as *Glaziocharis abei*, was widely treated as if its name had been established in 1950, even though Akasawa (1948a) had already provided a Latin diagnosis and designated the type as a single specimen collected in 1943 by Chikaichi Abe, which therefore constitutes the holotype. That work was unusual in having been issued as an indelible autograph (mimeographed) journal article, but publication by indelible autograph before January 1, 1953, is effective under the International Code of Nomenclature for algae, fungi, and plants (the Code) (Art. 30.5; Turland et al., 2025).

Why, then, did the protologue published by Akasawa (1948a) remain disregarded for so long? The most plausible explanation lies in the early negative reception of the local natural history bulletin in which it appeared. Influential academic botanists Honda and Tuyama (1948) argued that mimeographed duplication and limited circulation should not confer nomenclatural validity, and this skepticism was later crystallized into a formal statement by the Japanese Society for Plant Taxonomy (1979), which declared that broad categories of domestic gray literature and non-taxonomic books and periodicals were not effectively published for nomenclatural purposes. In response to this criticism, Akasawa (1948b) subsequently noted that

his earlier paper did not assert nomenclatural priority. Shortly thereafter, Akasawa (1950a) republished the species in a more conventional academic venue for a broader readership, without reference to his earlier work (Akasawa, 1948a).

These historical reactions, however, did not override the binding provisions of the Code. Indelible autograph is excluded only for works issued on or after January 1, 1953, whereas earlier works of this type are explicitly accepted (Art. 30.5) and were not prohibited in earlier editions of the Code. Publication of nomenclatural novelties in non-taxonomic periodicals is not prohibited (although not recommended: Rec. 30A.4, 30A.5). Although effective publication also requires public or institutional accessibility (Art. 29.1), the fact that Honda and Tuyama (1948) published an immediate criticism strongly suggests that the paper was already accessible. We therefore concluded that Akasawa (1948a) constitutes the true protologue and that the long-standing citation of the 1950 publication reflects convention rather than priority (Yudina et al., 2026).

More broadly, this case illustrates that disregarded protologues can remain embedded in regional publications not only in Japan but also elsewhere (Mahood et al., 2014; Sennikov, 2024a, 2024b). Improving access to such gray literature is essential for uncovering hidden information on plant diversity and streamlining nomenclatural practice. At the same time, recommendations in botanical nomenclature have consistently encouraged authors to publish new scientific names in venues that maximize visibility and long-term accessibility in order to avoid similar confusion.

In addition, the publication history of *T. abei*, shaped by collaboration between a local naturalist, Chikaichi Abe, and a professional botanist, Yoshiyuki Akasawa, reflects an early form of public participation in scientific research (Shirk et al., 2012). Their use of regional outlets helped communicate discoveries not only to scientists but also to local communities, sustaining early conservation interest (Abe, 1951, 1967, 1990; Akasawa, 1948a, 1948b, 1950b). Today, online platforms such as iNaturalist provide powerful infrastructure for community-contributed biodiversity records that increasingly inform research and catalyze taxonomic discovery (Callaghan et al., 2022; Mesaglio et al., 2025). Because fairy lanterns emerge aboveground only briefly and are easily overlooked, discoveries and rediscoveries may depend on the number of observers and rapid communication with specialists. Recent examples in *Thismiaceae* include *Thismia paradisiaca*, described after attention was drawn to an iNaturalist record from Colombia (Guzmán-Guzmán & Plata-Torres, 2023), and *Relictithismia kimotsukiensis*, a new genus and species from Japan discovered through an initial observation by a local enthusiast followed by specialist investigation (Suetsugu et al., 2024).

8 | CONCLUDING REMARKS

Thismia abei was obscure in multiple respects, and substantial effort has been required to bring its characteristics and history to light (e.g., Yudina et al., 2026). The species spends most of the year belowground and emerges above the forest floor only briefly for flowering

and fruiting, relying entirely on fungi for organic carbon. Taxonomically, several of its diagnostic characters are also easily misinterpreted because they are concealed within the floral chamber. For example, although the stamens are fused into a tube, this important feature remained unrecognized until recently. This and other morphological findings motivate further efforts to reevaluate structural evolution within the family. Nomenclature adds another layer of complexity because valid publication of the basionym of *T. abei* was long attributed to a later and more widely read account. Renewed recognition of its long-overlooked protologue, together with sustained local engagement with the plant, underscores the important roles of regional culture and local naturalists in documenting and protecting biodiversity. Given the position taken by the Japanese Society for Plant Taxonomy (1979), many earlier effectively published plant names may still remain hidden in regional Japanese publications. Improved access to such publications and careful nomenclatural practice are therefore essential for accurate recognition of hidden plant diversity. At the same time, intensive fieldwork and detailed morphological study remain indispensable for understanding the biology of such elusive plants.

AUTHOR CONTRIBUTIONS

Kenji Suetsugu drafted the manuscript and prepared the figures. Alexander N. Sennikov and Maxim S. Nuraliev revised the manuscript. All authors approved the final version of the manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare 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>

Alexander N. Sennikov  <https://orcid.org/0000-0001-6664-7657>

Maxim S. Nuraliev  <https://orcid.org/0000-0001-8291-2633>

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