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(Citation)
Phytotaxa,585(2):102-112

(Issue Date)
2023-02-27

(Resource Type)
journal article

(Version)
Version of Record

(URL)
https://hdl.handle.net/20.500.14094/0100479355

Phytotaxa 585 (2): 102–112
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.585.2.2

Rediscovery of the presumably extinct fairy lantern *Thismia kobensis* (Thismiaceae) in Hyogo Prefecture, Japan, with discussions on its taxonomy, evolutionary history, and conservation

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Abstract

Thismia (commonly known as fairy lanterns) is a genus of strange-looking, elusive, and non-photosynthetic plants. *Thismia kobensis* was first discovered in Kobe City, Hyogo Prefecture, Japan in 1992, but it was believed to be extinct, given that its type locality was destroyed during the construction of an industrial complex. Here, we have reported the rediscovery of *T. kobensis* in Sanda City, Hyogo Prefecture, which is located approximately 30 km from the type locality. The new locality of *T. kobensis* is the northernmost distributional limit of Asian Thismiaceae species. As the original description of the species was based on a single museum specimen that lacked two of the three inner perianth lobes, we have provided an amended description of *T. kobensis*, highlighting its differences from the morphologically similar species *T. huangii*. Specifically, our morphological re-examination has revealed that *T. kobensis* is distinguishable from *T. huangii* by its short but expanded annulus and many short hairs on each stigma lobe. We have also demonstrated that the genetic distance between these taxa is comparable to that between other closely related species pairs. Finally, we have provided brief notes on the taxonomy, biogeography, evolutionary history, and conservation of *T. kobensis* and its closely related species, including an enigmatic species *T. americana.*

Keywords: conservation, emended description, extinct species, fairy lanterns, mycoheterotrophy, phylogenetic relationship, rediscovery, taxonomic revision

Introduction

Thismia Griffith (1844: 221) (commonly known as fairy lanterns) is a genus of mycoheterotrophic monocot plants with an unusual semi-subterranean habit, occasionally causing it to be mistaken for a fungus (Dančák *et al.* 2020; Roberts *et al.* 2003). The common name aptly describes the appearance of the brightly colored flowers that occur just above the soil and are usually covered by fallen leaves (Roberts *et al.* 2003). Mycoheterotrophic plants are non-photosynthetic, depending on associated fungi for all their nutritional demands. Because most mycoheterotrophic plants obtain their carbon indirectly from photosynthetic plants via shared mycorrhizal networks, they are highly dependent on the activities of both the fungi and trees that sustain them (Gomes *et al.* 2017; Suetsugu *et al.* 2022b). Consequently, they are particularly sensitive to environmental disturbances, often rendering them both rare and endangered. Fairy lanterns are renowned for their extreme rarity and highly localized occurrence (Thorogood & Mat Yunoh 2021). Currently, ca. 90 species have been described, of which at least 55 are known only from their type localities and at least 38 only from their discovery, in extreme cases, as a single individual [e.g., *T. bokorensis* Suetsugu & Tsukaya (2018: 65), *T. kobensis* Suetsugu (2018: 121), and (Dančák *et al.* 2020; Nuraliev *et al.* 2015)]. A plausible explanation for their extreme rarity and highly localized distribution could be that they show high host specificity for associated mycorrhizal fungi, whose occurrences restrict their distribution, and they prefer soil that is extremely low in nutrients (Gomes *et al.* 2017, 2019).

Accepted by Pankaj Kumar: 5 Feb. 2023; published: 27 Feb. 2023

Notably, given that (i) the preferred habitat (primary forest) is in unprecedented decline worldwide, and (ii) a substantial number of *Thismia* species appear to be stenoendemic and are known only from type collections, several species may already be extinct (Dančák *et al.* 2018, 2020; Sochor *et al.* 2018; Suetsugu *et al.* 2018a). One example, albeit atypical in habitat and distribution, is *T. americana* N. Pfeiffer (1914: 123), which has not been found since a few years after its first discovery in a wet prairie in Chicago, Illinois in 1912 (Merckx & Smets 2014). Nonetheless, some *Thismia* species may have additional unrecognized localities, considering that (i) they get easily covered by fallen leaves because of their dwarf habit, (ii) their flowers usually appear only during a short period of the year (the wet season), and (iii) an isolated population occurring in an area of few square meters is unlikely to survive for long periods (Dančák *et al.* 2020; Thorogood & Mat Yunoh 2021). Therefore, although *Thismia* species that have not been reported for long periods are considered extinct, it is often difficult to determine whether a focal species is truly extinct. In fact, *T. neptunis* Beccari (1878: 251), described by Beccari (1878), was rediscovered after 151 years (Sochor *et al.* 2018). Furthermore, Dančák *et al.* (2020) revealed that several *Thismia* species occur in multiple localities over relatively large geographical areas rather than having expected unusually narrow distributions. Future botanical surveys focusing on these tiny mycoheterotrophs will promote the discovery of new distributional records and provide critical data for conservation.

Here, we have reported a new locality for the presumably extinct species *T. kobensis*, discovered during a field survey in Sanda City, Hyogo Prefecture, Japan. *Thismia kobensis* was known from only a single individual collected at Kobe City, Hyogo Prefecture, Japan. The specimen was collected from a forest dominated by *Quercus serrata* Murray (1784: 858) in Linnaeus & Murray (1784) and *Q. glauca* Thunberg (1784: 858) on June 10, 1992. Although intensive surveys were conducted at the type locality from 1992 to 1999, additional *T. kobensis* plants were not discovered. After the destruction of the area during the construction of an industrial complex in 1999, several enthusiasts searched the surrounding intact areas for over dozens of years; however, *T. kobensis* individuals were not found (Suetsugu *et al.* 2018a). Therefore, Suetsugu *et al.* (2018a) determined that this taxon is no longer extant. Nonetheless, in June 2021, it was unexpectedly rediscovered by the second author Kohei Yamana in a coniferous plantation in Sanda City, Hyogo Prefecture, which is ca. 30 km away from the type locality. Because the original description of *T. kobensis* was based on only one museum specimen that was missing two of the three inner perianth lobes, this paper has provided an amended description and color photographs of *T. kobensis*, with short notes on its taxonomy, phylogenetic relationship, and conservation.

Materials and methods

Morphological observation

We collected three *T. kobensis* individuals from a newly discovered population. The flowers were carefully dissected to determine inner floral morphology because previous studies have shown that precise identification of *Thismia* species requires analysis of floral characteristics within the perianth tube. Morphological variation was investigated by reviewing the holotype deposited at HYO. The structures were observed and measured under a stereomicroscope (M165C; Leica Microsystems, Cambridge, UK). Morphological characteristics of *T. kobensis* were compared with those of its putative closest relative, *T. huangii* P.Y. Jiang & T.H. Hsieh (2011: 139), based on detailed images of the *T. kobensis* holotype specimen and additional specimens from the type locality (provided by Tsung-Hsin Hsieh and Tian-Chuan Hsu) (Chiang & Hsieh 2011).

DNA extraction, PCR amplification, and sequencing

Total DNA was extracted from the desiccated material of the aboveground parts of a *T. kobensis* individual using the cetyltrimethylammonium bromide method.

We amplified fragments of mitochondrial *atp1* sequences (New England Biolabs, Ipswich, MA, USA) (primer set *atp1*-F/*atp1*-R), and 18S rRNA sequences [primer set 18S-F/18S-R] using the Q5 mix, as described by Shepeleva *et al.* (2020). These primer sets have been successfully used for phylogenetic analysis of *Thismia* species (Dančák *et al.* 2020; Shepeleva *et al.* 2020). The PCR products were purified using ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA, USA), and the purified PCR products were used to perform separate forward and reverse sequencing using the BigDye™ Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems, Foster City, CA, USA) on an ABI3500 capillary sequencer (Applied Biosystems, Foster City, CA, USA). Sequence chromatograms were compared to correct for base-calling errors using ATGC v. 4.3 (Genetyx Co., Tokyo, Japan). The obtained sequences were deposited in the International Nucleotide Sequence Database Collaboration (INSDC) database under accession numbers LC742154–LC742155.

Sequence alignment and phylogenetic analysis

The *T. kobensis* sequences obtained were queried against the INSDC database based on BLAST searches, and several phylogenetically close sequences and other representative sequences of Thismiaceae and Taccaceae were downloaded (Table S1). Multiple sequence alignments were performed separately for the two phylogenetic markers (18S and *atp1*) using the MAFFT v7.475 (Katoh & Standley 2013), with linsi option. Each alignment was trimmed by trimAl (Capella-Gutiérrez *et al.* 2009) v1.2 with -gt 0.9 option (removes all positions in the alignment with gaps in 10% or more of the sequences). Next, the best evolutionary models were selected by ModelFinder (Kalyaanamoorthy *et al.* 2017) based on AIC (18S: TIM2+F+R2, *atp1*: GTR+F+R2). Phylogenetic reconstruction was performed using concatenated alignments of the two markers by IQ-TREE v1.6.12 (Nguyen *et al.* 2015) with 1000 ultrafast bootstraps (Hoang *et al.* 2018).

Taxonomic treatment

Thismia kobensis Suetsugu emend. Suetsugu (Figs. 1, 3–4)

Type:— JAPAN, Hyogo Prefecture, Kobe City, Nishi-ku, Oshibedani-cho, Komi, 34°44′ N, 135°05′ E, alt. 200 m, June 10, 1992, *Nakanishi & Kobayashi 22380* (holotype: HYO!, spirit collection).

Terrestrial, achlorophyllous, mycoheterotrophic herbs. Roots creeping, vermiform, branched, ca. 1 mm in diameter, white when young, pale brown when old. Stem erect, ca. 1 mm long. Leaves glabrous, translucent white, scale-like, narrowly triangular to ovate, 1.0–7.6 × 0.4–3.0 mm, apex obtuse to acute; largest leaves just below a flower. Involucral bracts, translucent white, similar to upper leaves. Flower solitary, slightly zygomorphic, subsessile, pubescent. Perianth tube translucent white to pale orange, hexagonal prismatic apically and urceolate basally, 8.0–8.9 × 3.4–7.9 mm, basally bent or inclined at an angle to the ovary; upper part of the perianth thus displaced from the ovary axis, narrowest just above the ovary, widest at the upper apex; inner surface without transverse bars; apex with a broad annulus. Perianth of 6 lobes fused apically; inner perianth lobes 3, larger than outer perianth lobes, translucent white to pale orange, 5.4–6.3 × 1.3–3.5 mm, arching inward distally and connate apically to resemble a mitre hat, apex obtuse, dorsal keel ending in a 1-mm long, erect, finger-like appendage; outer perianth lobes 3, translucent white to pale orange, 3.8–4.0 × 1.3–1.7 mm, apex acuminate. Stamens 6, adnate, forming a tube around the style, pendulous from the annulus, annulus dark orange or red, connective orange or yellow, dilated and adnate along mediolateral margins forming a tube; each connective rectangle-to-trapezoid, 2.7–2.8 × 1.9–2.0 mm, skirt-like appendage absent, apex with long hairs; thecae attached at the base of connective, each theca oblong, 0.5–0.6 × 0.1 mm; nectariferous gland absent. Ovary inferior, cup-shaped, 2.2–2.5 × 1.4–1.5 mm, pubescent; style 0.45–0.58 mm long; stigma trilobed, 1.0–1.1 mm long; stigma lobes triangular or arrow-shaped with many short hairs on each lobe.

Additional specimens examined:— JAPAN. Hyogo Pref.: Sanda City, Kamihonjo, May 26, 2021, *Kohei Yamana T1-1* (HYO, KYO), loc. cit., May 29, 2021, *Kohei Yamana & Hidehito Okada T1-2* (HYO, KYO), loc. cit., May 31, 2021, *Kenji Suetsugu* & *Kohei Yamana T1-3* (HYO, spirit collection).

Distribution: Japan (currently known only from Sanda City, Hyogo Pref). *Thismia kobensis* was considered extinct because the type locality was destroyed, and intensive searches of surrounding intact areas has failed to rediscover the plant (Suetsugu *et al.* 2018a). However, we found it at another locality, ca. 20 km north of the type locality. The new locality is rather far north, given that the majority of Thismiaceae species are distributed tropically in Asia, Australia, and South America (Merckx 2013). However, the wet subtropical to temperate Japanese forest is a habitat for many arbuscular mycoheterotrophs that otherwise have primarily tropical distributions (Merckx 2013). Notably, the new locality of *T. kobensis* is the northernmost distributional limit of eastern Asian Thismiaceae species.

Morphological and biogeographical notes: Morphological observations indicated no distinct differences between the *T. kobensis* holotype and the newly discovered individuals reported here. As indicated by Suetsugu *et al.* (2018a), *T. kobensis* is most similar to *T. huangii* from Taiwan in having a dark orange annulus, yellow and truncate connectives with hairs, stigma lobes with hairs, and no nectaries. Nonetheless, Suetsugu *et al.* (2018a) noted that *T. kobensis* is distinguished from *T. huangii* by its hexagonal prismatic and less hairy perianth tube (vs. an urn-shaped and densely hairy perianth tube) and white (vs. pale orange to yellow) perianth lobes.

FIGURE 1. *Thismia kobensis* at the new locality. (A–C) Flower, lateral view. (D–F) Flower, upper view. (G) Flower without perianth lobes. (H) Flower with broken perianth tube and exposed stigma. Scale bars: 5 mm. Photographed by Kenji Suetsugu.

Further examination, however, revealed that *T. kobensis* is morphologically closer to *T. huangii* than previously assumed. We showed that the perianth tube hair density and lobe color varied within the newly recorded population of *T. kobensis*, covering an area of less than 20 m^2 (Fig. 1). In addition, although Suetsugu *et al.* (2018a) noted that *T. kobensis* differs from *T. huangii* in having stamens free from each other (vs. adnate), the dehiscence zone of *T. kobensis* that forms at the boundaries of each stamen often remains incomplete and each stamen was often fused in the middle (Fig. 3–4). Nonetheless, *T. kobensis* is distinguishable from *T. huangii* by morphological differences that have not been emphasized. For example, at the perianth tube mouth, *T. kobensis* has a short but expanded annulus (ca. 1.3 mm wide, 0.4 mm tall), whereas, *T. huangii* has an erect annulus (ca. 0.4 mm wide, 0.7 mm tall) (Figs. 1–4). Furthermore, *T. kobensis* individuals (including both the newly collected samples and the holotype) have many short hairs on each stigma lobe (Fig. 3I & 4G). Notably, a long hair on each stigma lobe is a stable trait of *T. huangii* (Fig. 2E). Therefore, given that inner floral morphology is considered essential for *Thismia* classification (Merckx & Smets 2014; Shepeleva *et al.* 2020), these differences support interspecific distinction between *T. kobensis* and *T. huangii.*

FIGURE 2. *Thismia huangii* at the type locality. (A) Habit. (B) Flower, upper view. (C) Flower, lateral view. (D) Longitudinal section of perianth tube with stamens, style, and stigma. (E) Style and stigma. Arrows indicate a long hair on each lobe. Scale bars: 20 mm (A), 5 mm (B–D), and 1 mm (E). Photographed by Tsung-Hsin Hsieh (A, D–E) and Tian-Chuan Hsu (B–C).

It is noteworthy that not only the gross outline but also the inner floral morphology, such as the absence of connective appendages and interstaminal glands and the presence of many short hairs on each stigma lobe, of *T. kobensis* resembles that of the only North American *Thismia* species, *T. americana* (Merckx & Smets 2014; Pfeiffer 1914), whereas *T. kobensis* differs from *T. americana* by its coloration of perianth tube (white to pale orange vs. blue-green) and annulus (dark orange vs. white). As the northernmost known Eastern Asian *Thismia* species, *T. kobensis* may provide valuable insights into the systematic affinity and biogeography of *T. americana*, which is now believed to be related to some Australia-New Zealand species such as *T. rodwayi* Mueller (1890: 115) (Merckx & Smets 2014). However, the striking similarity in their inner floral morphology suggests that *T. americana* has a closer relationship to *T. kobensis* than *T. rodwayi* (See also "phylogenetic and evolutionary notes"). Close relationships between plant species in eastern Asia and North America are not uncommon, and the disjunct distribution across these regions can frequently be attributed to migration through the Beringia land bridge (Donoghue & Smith 2004; Merckx & Smets 2014). Consequently, it is possible that *T. kobensis* is indeed the closest relative of *T. americana*, and their disjunct distribution might be attributable to migration via Beringia.

Phylogenetic and evolutionary notes: We have identified significant molecular differences between *T. kobensis* and *T. huangii*, as evidenced by their comparable genetic distance to other closely related species pairs (Fig. 5). Thus, both morphological and molecular data support the recognition of *T. kobensis* and *T. huangii* as distinct species.

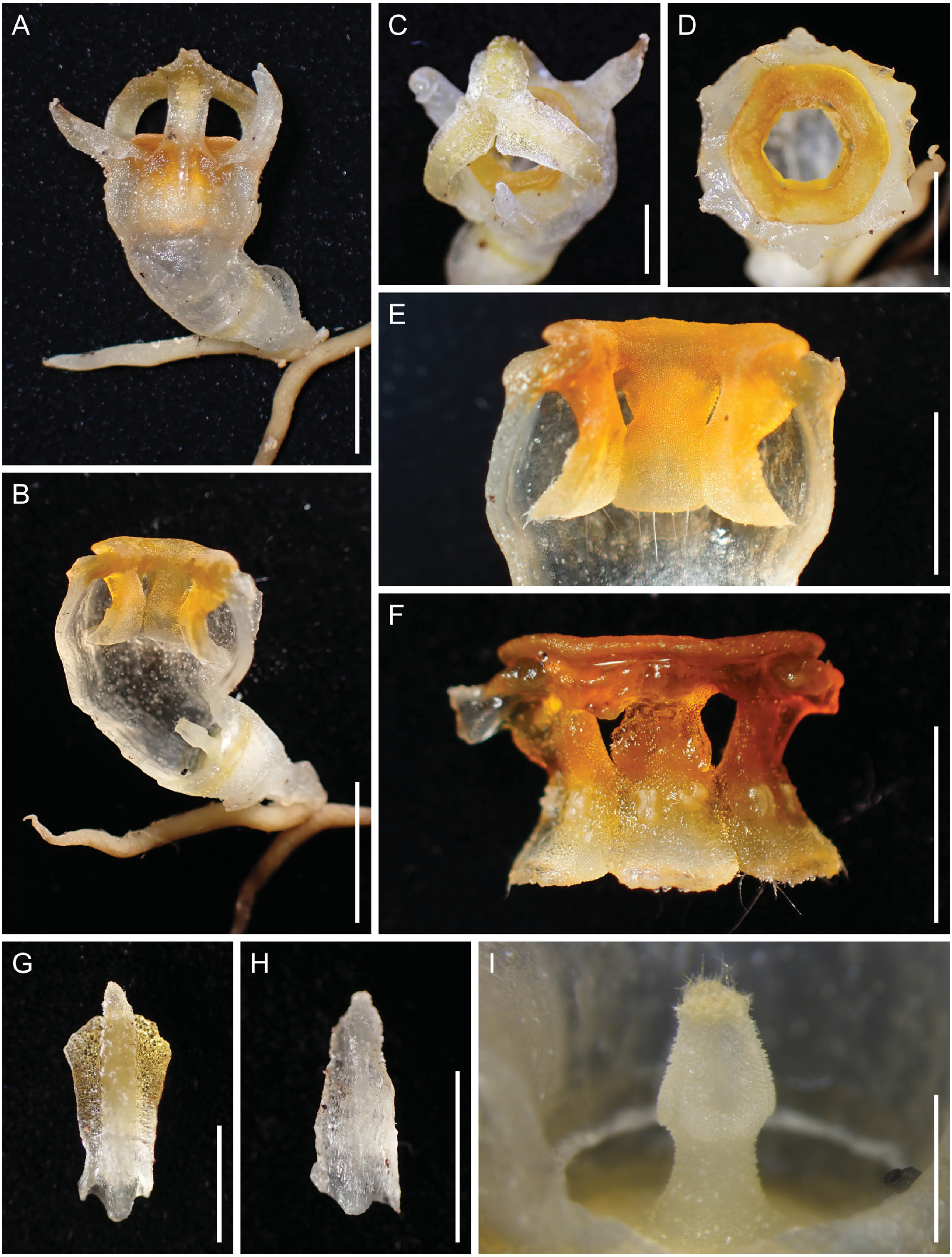

FIGURE 3. *Thismia kobensis* (*Kenji Suetsugu & Kohei Yamana T1-3*, HYO). (A) Habit. (B) Longitudinal section of perianth tube with stamens, style, and stigma. (C) Flower, upper view. (D) Flower with perianth lobes removed. (E) Stamens, inner view. (F) Stamens, upper view. (G) Inner perianth lobe. (H) Outer perianth lobe. (I) Style and stigma. Scale bars: 5 mm (A–B), 3 mm (C–H), and 1 mm (I). Photographed by Kenji Suetsugu.

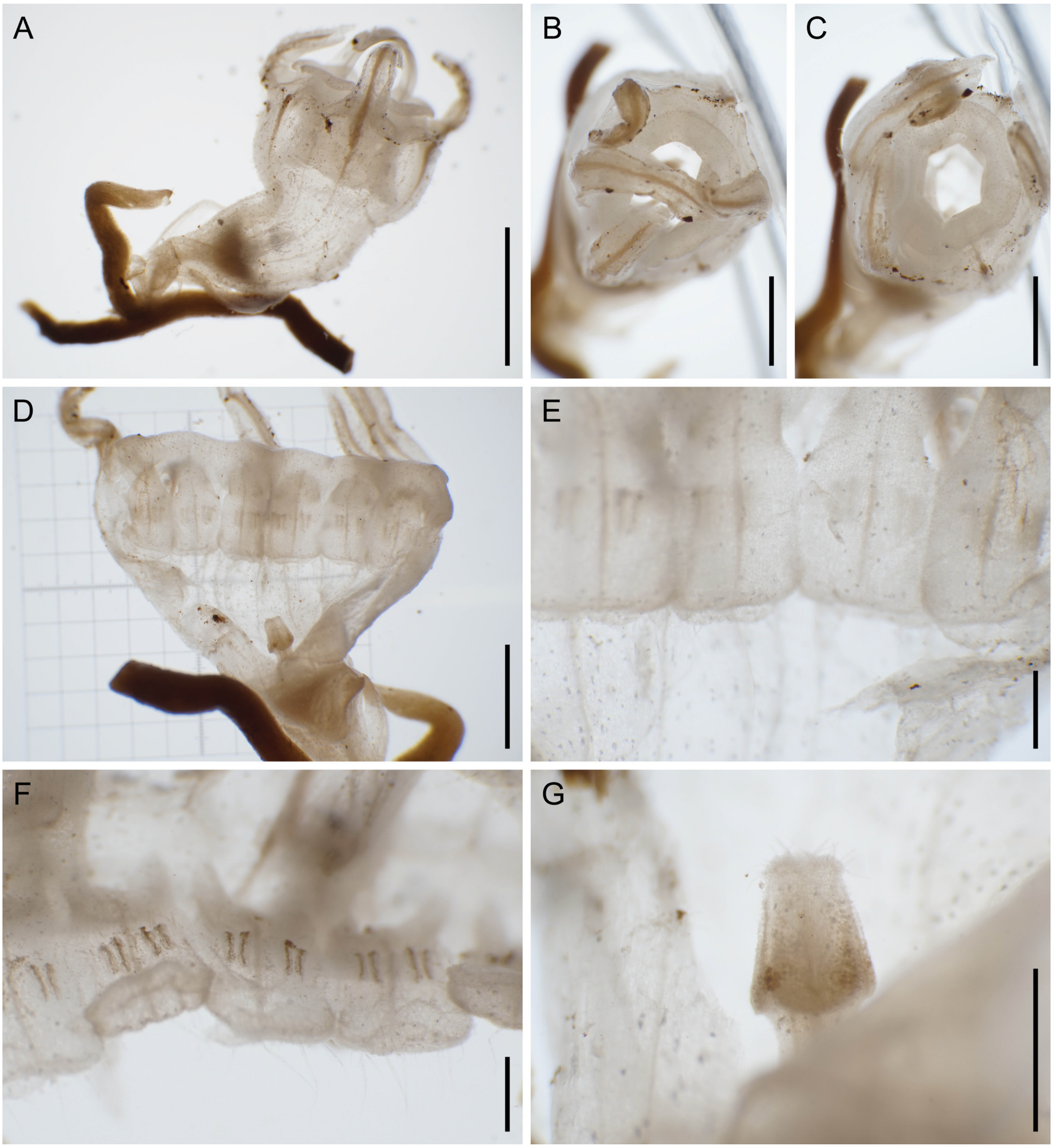

FIGURE 4. *Thismia kobensis* (holotype). (A) Habit. (B–C) Flower, upper view. (D) Flattened perianth tube. (E) Stamens, inner view. (F) Stamens, outer view. (G) Stigma. Scale bars: 5 mm (A–B), 3 mm (C–D), and 1 mm (E–G). Photographed by Kumi Hamasaki.

Our molecular phylogenetic reconstruction suggests that *T. kobensis* and *T. huangii* are sister species, which is consistent with morphological data (Fig. 5). In addition, the molecular analysis provides strong support for placing *T. kobensis* and *T. huangii* in a clade with other members of the section *Glaziocharis* (Taubert ex Warming 1901: 175) Hatusima (1976: 4). Both *Thismia* taxa were previously assigned to section *Rodwaya* Schlechter (1921: 38) based on their outer perianth lobes without free filiform appendages (Chiang & Hsieh 2011; Kumar *et al.* 2017; Shepeleva *et al.* 2020; Suetsugu *et al.* 2018a). Although perianth lobe morphology is historically a diagnostic character of *Thismia*, several recent studies have suggested that perianth appendages are of little phylogenetic significance in *Thismia* species delimitation (Kumar *et al.* 2017; Merckx & Smets 2014; Shepeleva *et al.* 2020). Given that many *Thismia* species are probably pollinated by dipteran visitors (Guo *et al.* 2019; Suetsugu & Sueyoshi 2021), and that filiform appendages are considered adaptations to attract fly pollinators (Suetsugu *et al.* 2022a), these appendages may have evolved convergently, based on pollinator preferences. Notably, the transfer of Asian and North American species of section *Rodwaya*—*T. kobensis*, *T. huangii* and *T. americana*—to section *Glaziocharis* and of the only Australian species of section *Glaziocharis*—*T. clavarioides* K. Thiele (2002: 766)—to section *Rodwaya*, likely renders these sections monophyletic (Fig. 5).

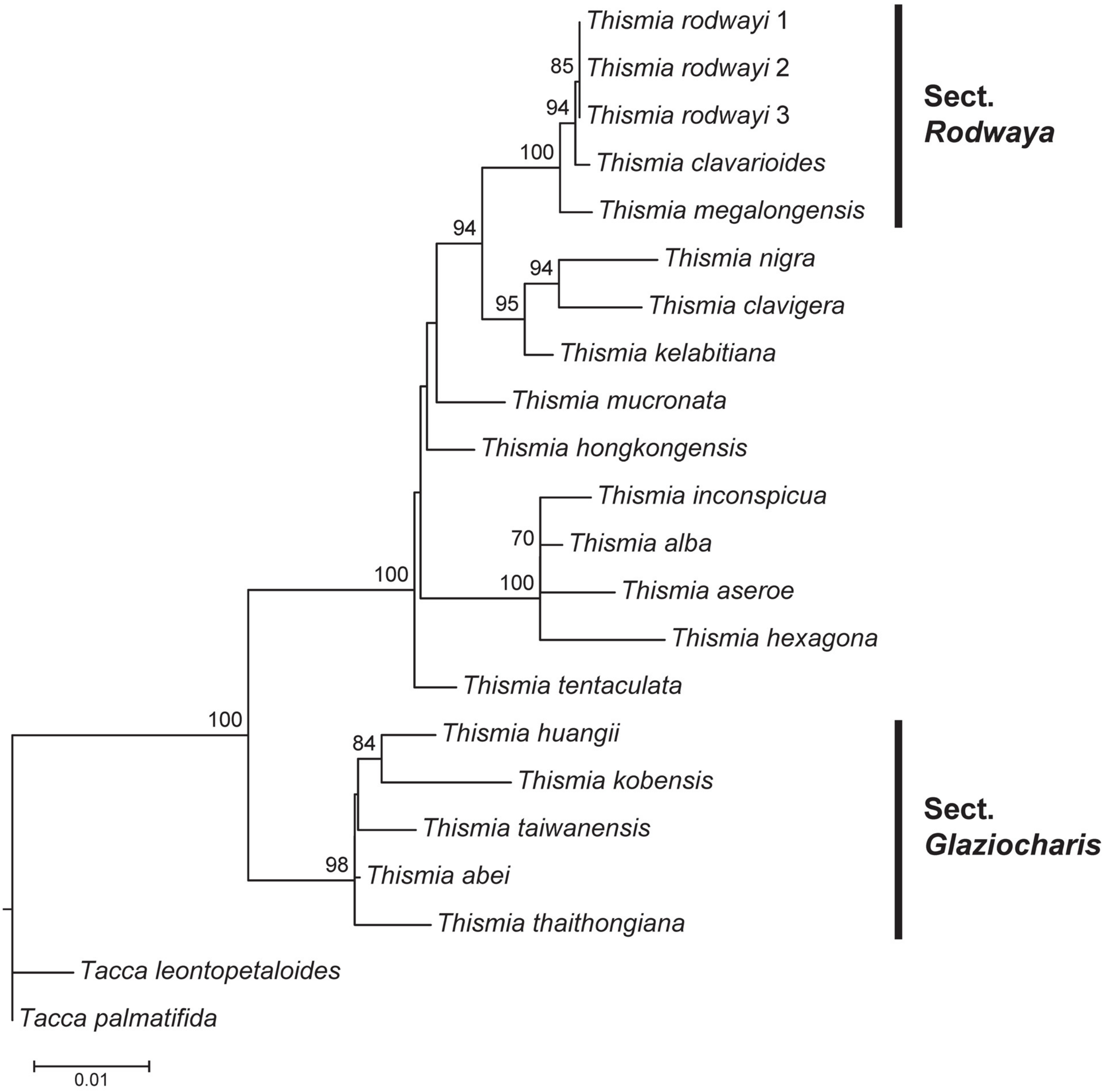

FIGURE 5. Maximum-likelihood phylogenetic tree of the combined 18S rDNA and *atp1* sequences from *Thismia kobensis* and its related taxa. Node values indicate bootstrap support (1000 replicates) of ≥ 70%. The scale bar indicates the number of substitutions per site.

This modification of sectional taxonomy is further consistent with the inner floral morphological traits, namely the absence of connective appendages and interstaminal glands in *T. kobensis*, *T. huangii*, *T. americana*, and other *Glaziocharis* species and their presence in *T. clavarioides* and other Oceanian *Rodwaya* species (Shepeleva *et al.* 2020). These results indicate that inner floral morphology, rather than outer floral appearance, is vital for *Thismia* classification. Therefore, precise taxonomic classification of *Thismia* species, including *T. americana*, which remains somewhat elusive in terms of its sectional placement, requires detailed examination of floral organs hidden within the perianth tube. Additionally, molecular data obtained from a museum specimen of *T. americana* will enhance our understanding of the enigmatic evolution within the genus *Thismia*.

Conservation status and conservation implications: We assess *T. kobensis* as "Critically Endangered" following the IUCN Red List Categories and Criteria [CR B1ab(iii)+ C2a(i)+B2ab(iii)+D1]. *Thismia kobensis* is currently extant in a newly recorded population covering an area of less than 20 m^2, where fewer than 20 individuals have been observed in total. Despite the authors' long-term search around the population during the flowering season, this species has not been discovered elsewhere. This lack of additional discovery during surveys specifically targeting *T. kobensis* suggests that it exhibits a highly patchy distribution, which is consistent with the fact that only one individual was found at the type locality. Nonetheless, given its highly cryptic growth habit and ephemeral flowering phenology, *T. kobensis* might occur in other areas. Our rediscovery of *T. kobensis* over 30 km away from the type locality suggests that more extensive surveys during the flowering season could provide critical insight into its distribution and rarity, with implications for conservation.

The new locality is located on a trail within a forest dominated by *Cryptomeria japonica* (Thunberg ex Linnaeus 1782: 42) D.Don (1839: 167), which renders the plant at a high risk of disturbance owing to the human footfall in the habitat. Their reliance on fungi for energy makes mycoheterotrophic plants difficult to culture under artificial conditions; hence, *in situ* conservation remains the only realistic conservation approach. Members of the *Thismia* species usually prefer primary forests, which are currently facing unprecedented levels of destruction. Although *Thismia* species plants are tiny and inconspicuous, they have been described as one of the most curious and extraordinary genera in the plant kingdom (Thorogood & Mat Yunoh 2021), and their odd appearance and life strategy make them exceptional among herbs (Dančák *et al.* 2018). Owing to its bright orange coloration, *T. kobensis* could become a particularly iconic species in Japan. Although the forests around the newly recorded population are almost completely disturbed by logging, the discovery of *T. kobensis* may provide momentum to local initiatives to obtain official protection for these forests, as proposed for other *Thismia* species (Dančák *et al.* 2018).

Finally, although *ex situ* cultivation is difficult, it might shed light on the conservation of *T. kobensis*, considering that botanic gardens have played a vital role in the conservation of mycoheterotrophic orchids such as *Rhizanthella gardneri* Rogers (1928: 1) through successful propagation (Swarts & Dixon 2009; Thorogood *et al.* 2019). The *ex situ* propagation of *T. kobensis* could provide an intriguing opportunity for establishing its conservation priorities and understanding its enigmatic natural history.

Acknowledgments

We thank Tsung-Hsin Hsieh and Tian-Chuan Hsu for providing helpful information and pictures of *Thismia huangii*. We would like to thank Editage (www.editage.com) for English language editing. We are also grateful to Takako Shizuka, Kumi Hamasaki and Kazuma Takizawa for technical assistance. This study was financially supported by the JST PRESTO (JPMJPR21D6).

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