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Rediscovery and revised description of *Thismia bifida* (Dioscoreales, Thismiaceae)

MARTIN DANČÁK[1]*, MICHAL HRONEŠ[2], MICHAL SOCHOR[2,3], ALENA UVÍROVÁ[1], VOJTĚCH TOBIAS BLAŽEK[2], SALWANA JAAFAR[4], LING CHEA YIING[5], AZLAN PANDAI[6] & RAHAYU SUKMARIA SUKRI[4]

[1]*Department of Ecology and Environmental Sciences, Palacký University, Šlechtitelů 27, Olomouc, CZ-77900, Czech Republic*
[2]*Department of Botany, Palacký University, Šlechtitelů 27, Olomouc, CZ-77900, Czech Republic*
[3]*Czech Agrifood Research Center, Šlechtitelů 29, CZ-77900 Olomouc, Czech Republic*
[4]*Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Jalan Tungku Link, BE 1410, Brunei Darussalam*
[5]*Research & Development Division, Forest Department Sarawak, Kuching 93250, Sarawak, Malaysia*
[6]*Brunei National Herbarium, Forestry Department, Jalan Menteri Besar, Bandar Seri Begawan BB 3910, Brunei Darussalam*

martin.dancak@upol.cz; https://orcid.org/0000-0002-3851-4969
michal.hrones@upol.cz; https://orcid.org/0000-0002-0380-929X
michal.sochor@volny.cz; https://orcid.org/0000-0002-6525-1295
uvirova.alena@gmail.com; https://orcid.org/0009-0000-8608-2032
vojtech.blazek03@upol.cz; https://orcid.org/0009-0006-8905-4487
salwana.jaafar@ubd.edu.bn; https://orcid.org/0000-0003-0224-9603
lingcy@sarawak.gov.my; https://orcid.org/0000-0001-9572-5319
pandaiazlan@gmail.com; https://orcid.org/0009-0001-7432-9891
rahayu.sukri@ubd.edu.bn; https://orcid.org/0000-0002-2662-399X
**Author for correspondence*

Abstract

Thismia bifida was described in 1967 from a single collection made in 1963 on Bukit Kana, Sarawak, Malaysia, and had not been recollected since, leaving uncertainties about its identity and affinities. We report the rediscovery of *T. bifida* at its type locality and document several additional populations across Sarawak and Brunei Darussalam. Based on detailed morphological examination of living material and molecular phylogenetic analysis of nuclear and mitochondrial loci, we provide a comprehensive revised description and notes on its phylogenetic relationships. The species exhibits considerable variability in flower size, colouration, length of tepal appendages, length of supraconnective appendages, and shape of stigma lobes. Our findings demonstrate that *T. bifida* is rather widespread, occurring in both lowland and montane forests. Phylogenetic reconstruction reveals that *T. bifida* is closely related to *T. pallida* from Sabah and *T. filiformis* from Thailand, together forming a well-supported clade (the *Thismia filiformis* group) within *Thismia* sect. *Thismia* subsect. *Odoardoa*. These observations clarify the taxonomic boundaries between *T. bifida*, *T. filiformis*, and *T. pallida*, and highlight the importance of revisiting historical localities of poorly known mycoheterotrophic taxa.

Key words: Brunei, conservation, mycoheterotrophy, *Odoardoa*, Sarawak, taxonomy, *Thismia filiformis*, *Thismia pallida*

Introduction

Thismia Griffith (1845: 221) (Thismiaceae) is a remarkable mycoheterotrophic genus that is rarely encountered in the field, with most species documented from only a few localities and often represented by limited collections (Dančák *et al.* 2020a). The current taxonomy of *Thismia* is based, among other characters, on the structure of the stamens and particularly the supraconnective appendages (Sochor *et al.* 2018a). However, many older collections were prepared as standard herbarium specimens, making the assessment of fine floral structures extremely difficult or impossible. As a result, the scarcity or complete absence of suitable material has substantially hampered systematic and taxonomic research. Especially in the past, this deficiency resulted in species being described on the basis of a limited or otherwise incomplete material, sometimes provided only by brief descriptions and simple illustrations lacking details that are now known to be taxonomically important, particularly those of the stamens and other characters hidden inside the floral chamber (see, e.g., Blume 1850; Ridley 1915). In recent years, renewed field exploration has led to the rediscoveries of several *Thismia* species that were known only from their original, often limited, type material. These rediscoveries

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have enabled detailed morphological reassessments based on freshly collected specimens and have resulted in refined species circumscriptions and clarification of taxonomic affinities (Sochor *et al.* 2018b; Suetsugu *et al.* 2018, 2023; Yudina *et al.* 2026; Hroneš *et al.*, *in prep.*). Together, these studies highlight the broad importance of re-examining species of *Thismia* described long ago in order to achieve a more robust and consistent taxonomy.

Thismia bifida Hotta (1967: 161) is one of the species that long remained known only from a single, poorly documented collection. It was first collected by Minoru Hirano and Mitsuru Hotta during the 1963 Kyoto University Borneo Expedition to Sarawak on the north-eastern slopes of Bukit Kana in the Bintulu Division. The species was described shortly thereafter (Hotta 1967). The type material consists of two pressed individuals, one bearing a fully open flower and the other with a single opening flower bud and one fruit. The protologue of the species is very brief, missing important morphological traits. The accompanying illustration was apparently prepared based on the dried plants, leaving some aspects of floral morphology insufficiently documented. Because no additional material became available in the following six decades and the species remained known only from the type collection, uncertainties persisted not only regarding details of its floral morphology but also concerning its identity and affinities.

In this study, we report the rediscovery of *T. bifida* at its type locality and the findings of additional populations in both Sarawak and Brunei Darussalam. We provide a revised description of the species, document its morphological variability, distribution and phylogenetic relationships.

Material and methods

Field surveys were carried out in Sarawak and Brunei Darussalam between 2019 and 2025, with two targeted expeditions to the Bukit Kana area in 2023 and 2024. Populations of *Thismia bifida* were searched through non-systematic surveys in forested habitats, with effort concentrated on sites with suitable habitat characteristics. Coordinates of each locality were recorded using GPS devices in decimal degrees. The distribution map was created in QGIS 3.12 (https://qgis.org/). Collected material was preserved in spirit (70% ethanol) or dried and processed as standard herbarium specimens, and deposited in the herbaria BRUN, OL, and SAR (herbarium acronyms according to Thiers 2026+). Morphological characters were examined using a hand lens (30–60× magnification) and stereomicroscope, and documented using macro photography. Digital measurements were performed using ImageJ 1.53k. Line drawings were prepared using Clip Studio Paint from photographs of the target organs selected from multiple populations. Final illustrations were exported as vector files and provided with scale bars based on measurements taken from the original images. DNA samples were collected from selected populations and stored in silica gel. Additionally, herbarium material of various species of *Thismia* deposited in BM, BO, BRUN, K, KEP, KYO, SAN, SAR, and SING was examined.

The preliminary conservation assessment is based on the most recent version of the guidelines of the IUCN Standards and Petitions Committee (2024). The extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCAT (https://geocat.iucnredlist.org/) following Bachman *et al.* (2011).

DNA was extracted from silica gel-dried above-ground parts of the plants using the CTAB method (Doyle & Doyle 1987), and three nuclear rDNA loci—LSU (26S rDNA; large subunit), ITS (internal transcribed spacer, including 5.8S rDNA), and SSU (18S rDNA; small subunit), plus two mitochondrial genes (*atpA*, *matR*) were sequenced following Sochor *et al.* (2018a). Apart from the newly generated sequences of *T. bifida*, a representative set of sequences covering all available species of *Thismia* sect. *Thismia* subsect. *Odoardoa* Schlechter (1921: 35) was selected from Shepeleva *et al.* (2020) and Dančák *et al.* (2025). In addition, two specimens of *T. pallida* Hroneš, Dančák & Rejžek in Hroneš *et al.* (2018: 115) and *T. filiformis* agg. from new localities were included. Sequences were edited and aligned in Geneious (ver. 7.1.7., Biomatters) using the MAFFT plugin. Bayesian phylogeny inference was computed in MrBayes (ver. 3.2.4, Ronquist *et al.* 2012) using the GTR+G (for *matR*) and GTR+I+G (for the other loci) substitution models, as determined by AICc in PartitionFinder ver. 2.1.1 (Lanfear *et al.* 2017). The analysis was run for 15 million generations in two independent runs, four chains each, sampling every 1000th generation and excluding the first 50% of generations as burn-in. The specimens included in the analysis are listed in Supplementary file 1.

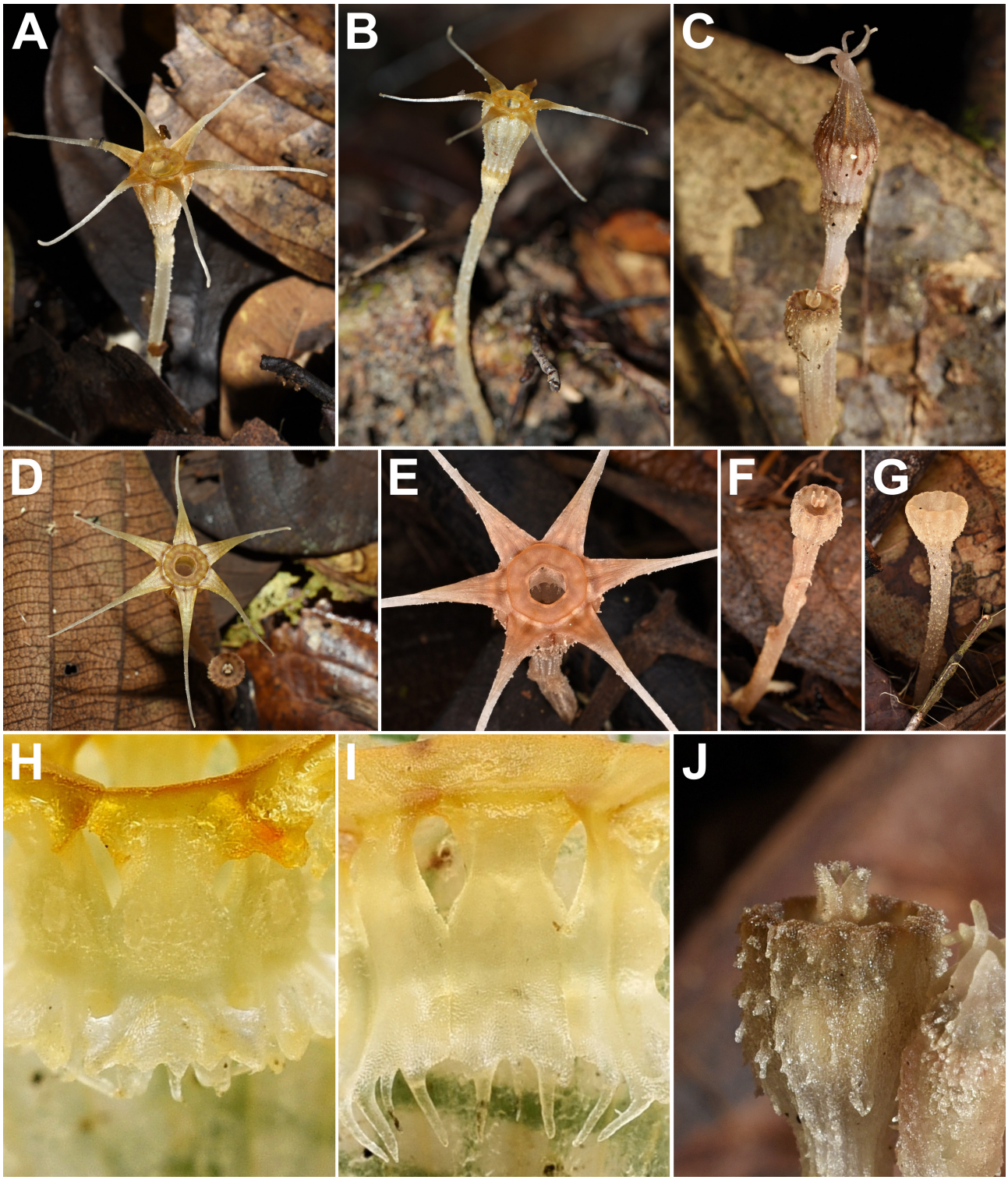

FIGURE 1. *Thismia bifida*. Plants from Bukit Kana area (broader type locality). **A, B**. General habit of anthetic plant; **C**. Detail of inflorescence and ovary with freshly fallen floral tube; **D, E**. View of the flower from above showing different shape of annulus (**D.** almost rounded, **E.** weakly hexagonal) and colour variation; **F**. Young capsule; **G**. Mature capsule; **H**. Outer view of the androecium with the connective tube, filaments, lateral appendages, interstaminal glands, and thecae; **I**. Inner view of the androecium with supraconnective appendages; **J**. Young capsule with bifid stigma lobes. **A, D, J**. *MDMH2024/7*; **B, H, I**. *MDMH2023/33*; **C, E–G**. *MDMH2024/12*. Photographs by Michal Hroneš (A, C–J) and Vojtěch T. Blažek (B).

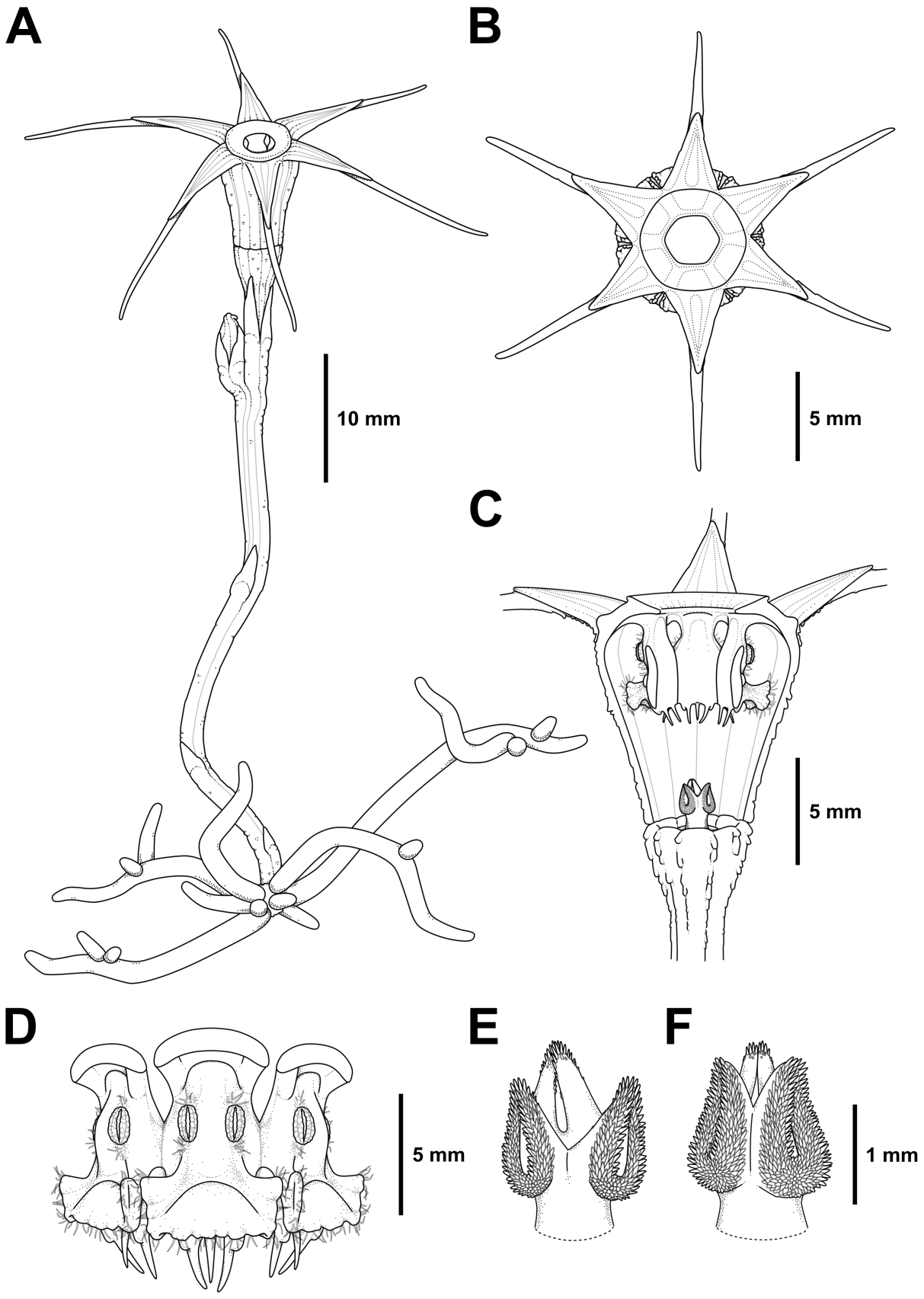

FIGURE 2. *Thismia bifida*. **A**. Habit of a plant in flower; **B**. View of the flower from above showing tepals, tepal appendages and annulus; **C**. Dissected floral tube exposing an inner view of the stamens with supraconnective appendages and style with stigma; **D**. Outer view of the androecium with the connective tube, filaments, lateral appendages, supraconnective appendages, interstaminal glands, and thecae; **E, F**. Detail of the style and stigma, illustrating variability in the depth of division of the stigma lobes. Drawn by Vojtěch T. Blažek from *Bor42/19* (A, D), *MHMD252020* (B, E), *Bor2/23* (C, F).

Taxonomy

Thismia bifida Hotta (1967: 161). Figs 1, 2, 5

Type:—MALAYSIA. Sarawak: Bintulu [District], NE slope of Bukit Kana, 600–850 m alt., 19 November 1963, *M. Hirano & M. Hotta 1269* (holotype: KYO!).

Revised description:—Achlorophyllous herb, 22.0–125.0 mm tall, mostly glabrous. **Roots** 1.1–1.8 mm thick, sparsely branched, creeping, vermiform, ± horizontal, pale brown. **Stem** 10.0–86.0 mm long, ascending to erect, ± smooth, beige to orange-brown. **Leaves** 2.8–3.4 × 1.9 mm, spirally arranged, appressed, scale-like, lanceolate to triangular, acute, entire, beige to orange-brown. **Bracts** surrounding the terminal flower 3, 2.0–5.1 × 1.3–2.1 mm, bracts of lateral flowers (if present) 1–3, 3.1–7.3 × 1.1–2.2 mm, triangular to ovate, navicular, acute, entire to erose on margins, glabrous to shortly verrucose, beige to light brown. **Pedicels** 2.0–11.0 mm long in flower, elongating up to 70.0 mm in fruit. **Flowers** 1–3 per stem, actinomorphic, 10.0–15.0 mm long, 16.0–53.0 mm in diameter; *floral tube* 8.0–11.5 × 6.0–8.6 mm, tubular-campanulate, widest in the upper fourth, then slightly narrowed to the flower opening; outer surface irregularly warty to almost smooth, cream to pale orange or rarely pinkish to reddish brown, with 12 longitudinal veins, veins basally cream turning bright orange in upper half, slightly protruding above the surface of the tube as low ribs; inner surface without transverse bars or reticulation; *annulus* well developed, circular to weakly hexagonal, slightly raised, pale orange brown, orange yellow, orange red to coral pink, sometimes with outer and inner margin more brightly coloured, with opening ca. 2.5–3.5 mm across. **Tepals** 6, all equal in shape and size, ca. 3.9–10.5 × 2.3–3.7 mm, narrowly triangular, acute, pale orange brown, orange yellow, orange red to coral pink, with 3 darker longitudinal stripes at the base; filiform appendage arising from the abaxial side of tepal apex, ca. 4.0–14.7 mm long (measured from the tepal tip), terete, apically unswollen, blunt, beige or whitish to almost translucent, sometimes lighter towards the apex. **Stamens** 6, broadly attached to the place of transition between the floral tube and the annulus; *filaments* thick, slightly curved longitudinally, free from each other and forming 6 lateral apertures visible from the opening of the floral tube, white; *connectives* flattened, laterally connate to form a tube; each connective (including supraconnective) ca. 4.2 × 2.5 mm, translucent, white; *supraconnectives* connate for over 90% of their length, rectangular in outline, with 3 apical appendages, translucent, white; paired appendages at sides of supraconnective apex 0.8–1.4 mm long, almost cylindrical, pointing centripetally; median appendage ca. 0.7–1.1 mm long, gradually tapering; appendage on the outer (adaxial) surface of supraconnective (called also lateral or skirt-like) rectangular in outline, translucent, colourless or whitish to light brown, the middle part irregularly dentate and hairy along the margin, slightly shorter than the apex of supraconnective (without appendages), laterally with two entire wings topped with a tuft of translucent hairs and with scattered hairs along the margin, with low ridge arising from the lower side of each wing and reaching up to the supraconnective apex and forming a tubercle near each of the paired supraconnective appendages; interstaminal gland inserted on the line of fusion between the supraconnectives, globose, translucent; *thecae* ellipsoid, surrounded by sparse hairs below and above. **Ovary** 2.2–4.7 × 2.5–5.1 mm, inferior, obconical, ribbed, irregularly warty, apically crenulate, unilocular, light brown, apically darker; placentas 3, column-like, central, attached to base and roof of ovary; ovules numerous, white. **Style** ca. 0.7 mm long, brown; stigma 3-lobed, lobes ca. 1.2–1.5 mm long, bifid to 1/4–2/3 of their length, papillate, light brown to whitish. **Fruit** a pyxidium, 5.0–7.2 × 4.9–8.5 mm, obconical, light brown, ribbed, warty. **Seeds** numerous, 0.5–0.6 × 0.15–0.25 mm, ellipsoid, fusiform to prolate, pale brown.

Etymology:—Although not explicitly stated in the protologue (Hotta 1967), the epithet evidently refers to the bifid stigma lobes.

Distribution:—Sarawak (Malaysia) and Brunei Darussalam (Fig. 3). The occurrence in West Kalimantan (Indonesia) is very likely due to the proximity of some western Sarawak populations to the Kalimantan border and the presence of suitable habitats in neighbouring regions.

Conservation status:—*Thismia bifida* is endemic to Borneo and currently known from nine locations (sensu IUCN 2024) and twelve populations, most recorded recently (2015–2025). Its estimated area of occupancy is very restricted (40 km²), while the extent of occurrence is wide (33,249 km²). The total number of known mature individuals is likely fewer than 250, distributed in small subpopulations, some of which occur outside protected areas. Although many subpopulations occur inside protected areas, habitat outside such areas is subject to degradation, and an overall decline in habitat quality and subpopulation numbers is expected. Based on its extremely small population size (<250 mature individuals), fragmented distribution, and inferred continuing decline, *Thismia bifida* is assessed as Endangered under criteria C2a(i) and D according to the IUCN Red List categories and criteria (IUCN 2024).

However, based on our extensive field experience, the observed spatial pattern of occurrences, the availability of numerous localities with potentially suitable habitat, and the generally low level of botanical exploration in large parts of the species' range, it is considered likely that additional subpopulations and individuals remain undiscovered. Consequently, the currently known population size probably underestimates the true abundance of the species, and the present assessment based solely on confirmed records may overestimate its extinction risk. In this context, the actual conservation status of *T. bifida* may be closer to the category Vulnerable.

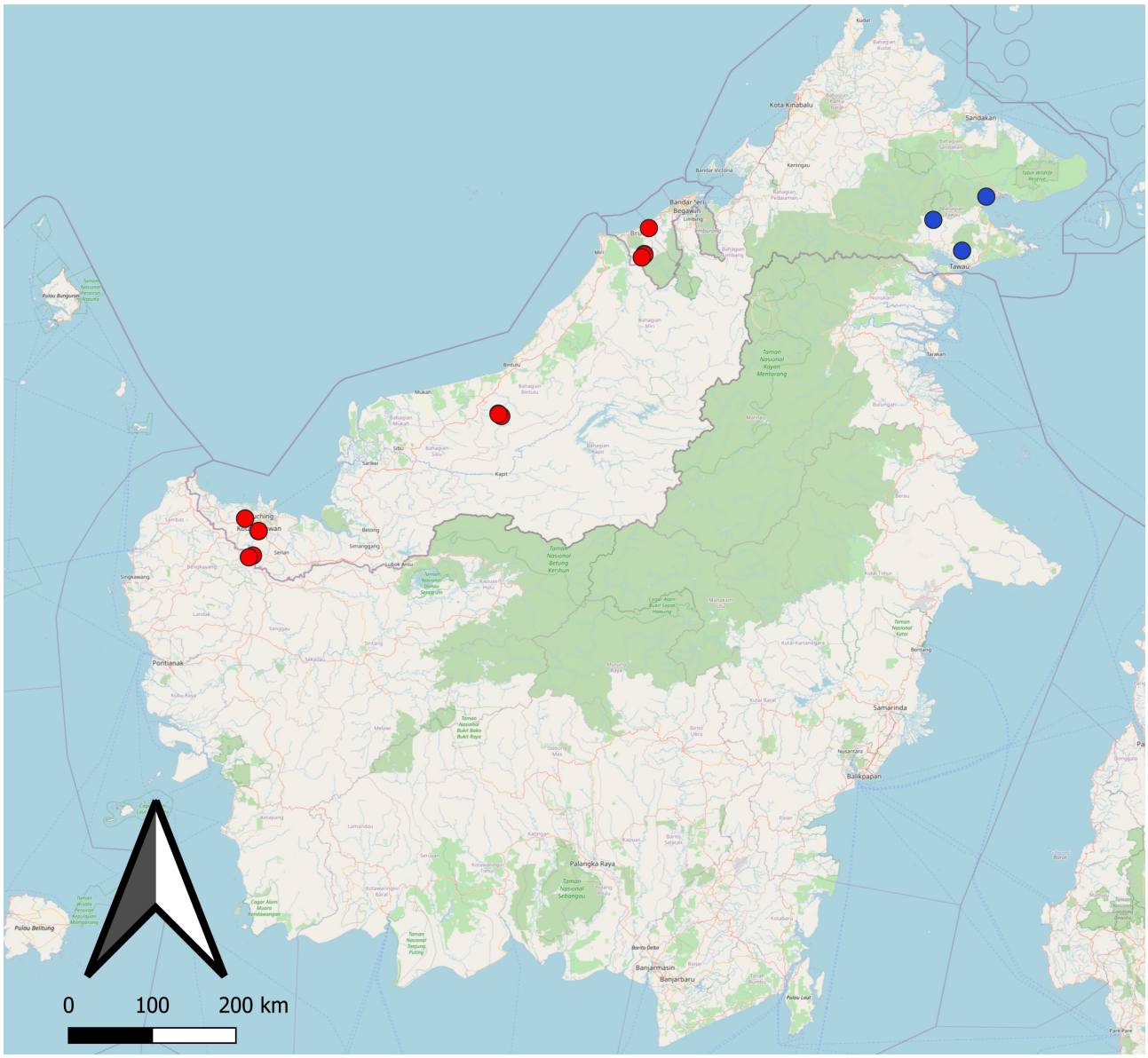

FIGURE 3. Distribution of *Thismia bifida* (red dots) and *T. pallida* (blue dots), based on the specimens studied in this paper.

Ecology and phenology:—*Thismia bifida* usually grows in humid, shaded forest microhabitats, but it can tolerate considerably drier conditions than many other *Thismia* species. It sometimes occurs in slightly disturbed forests. It is usually found in small clumps on soil or decaying wood. It occurs from lowland mixed dipterocarp forest (50 m a.s.l.) to lower montane forest (~1000 m a.s.l.). Flowering of *T. bifida* was observed between August and February.

Variability:—Populations of *Thismia bifida* differ from each other in size of floral tube and in its colouration (ranging from almost white to reddish brown; Figs 1A–E, 5A, D, G, K, 6F), length of tepal appendages, the relative length of the median supraconnective appendage, and the shape of the stigma lobes. Populations from Brunei are morphologically similar to those from the type area and show little variation in external morphology, whereas populations from western Sarawak are more variable, showing the range of variation overlapping with and exceeding the range observed in the remaining populations (Fig. 5). As the species name is derived from the bifid stigma lobes, variability in this character is of particular concern. The depth of stigma lobe division appears to be mostly stable within populations but variable among populations. While some populations, including those from the type area, have stigma

lobes that are relatively shallowly bifid (to ca. ¼, at most ½ of their length; Figs 5C, F, M, 6H), other populations have stigma lobes deeply bifid to up to ⅔ of their length (Figs 5J, 6J). However, this difference is not associated with any other morphological character and, more importantly, is not reflected in the genetic relationships among populations (Fig. 4). In one of the populations (Bukit Teraja in Brunei Darussalam), we observed plants with both types of stigma lobes (Fig. 5I), therefore we cannot exclude the possibility that the depth of division may be partially influenced by flower age. We therefore assume that the depth of stigma lobe division is not a taxonomically important character and rather represents intraspecific variability. The length of the supraconnective appendages is also rather variable in *T. bifida*, particularly the length of the median appendage relative to the outer pair. The median appendage is usually slightly shorter (70–90 % of length of the outer pair; Fig. 5E, H, K), but in some plants, it is almost as long as the outer pair of appendages (Fig. 5B).

Phylogeny:—Although the affiliation of *Thismia bifida* to *Thismia* sect. *Thismia* subsect. *Odoardoa* was already evident from the morphological data provided in the protologue and from the type material, its affinities within this group remained unclear until its rediscovery. Phylogenetic reconstruction (Fig. 4) revealed that *T. bifida* is closely related to *T. pallida* from Sabah and *T. filiformis* Chantanaorrapint (2012: 69) from Thailand. *Thismia pallida* is sister to *T. bifida*, whereas *T. filiformis* is sister to this pair. Together, these three species form a well-supported clade within *Thismia* sect. *Thismia* subsect. *Odoardoa*.

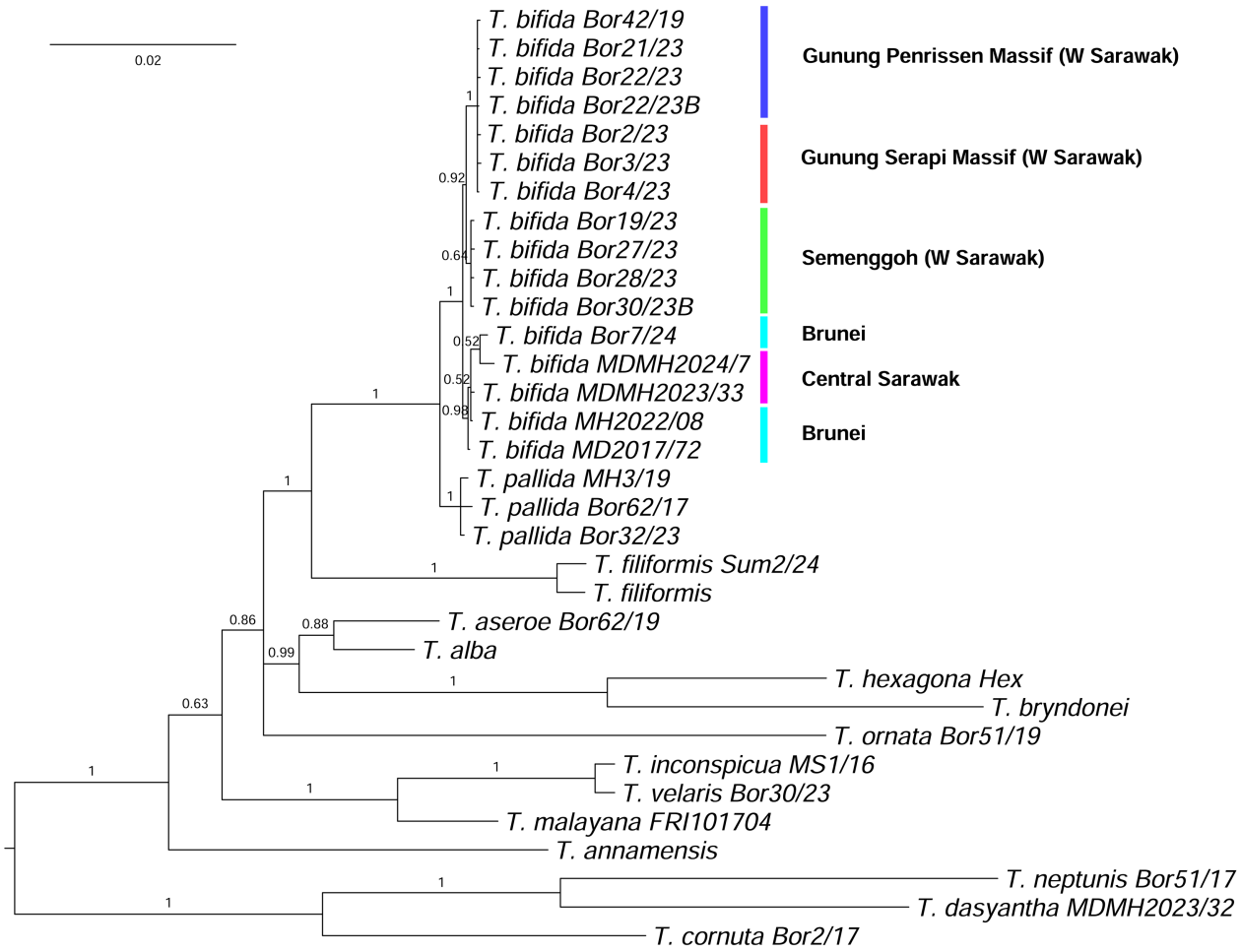

FIGURE 4. Bayesian phylogenetic tree based on five markers (LSU, ITS, SSU, *atpA*, *matR*) focused on the *Thismia filiformis* group within *Thismia* sect. *Thismia* subsect. *Odoardoa*; posterior probabilities are shown above branches. The geographic origin of *T. bifida* samples is indicated by coloured stripes. Specimens without collection code were taken from Shepeleva *et al.* (2020).

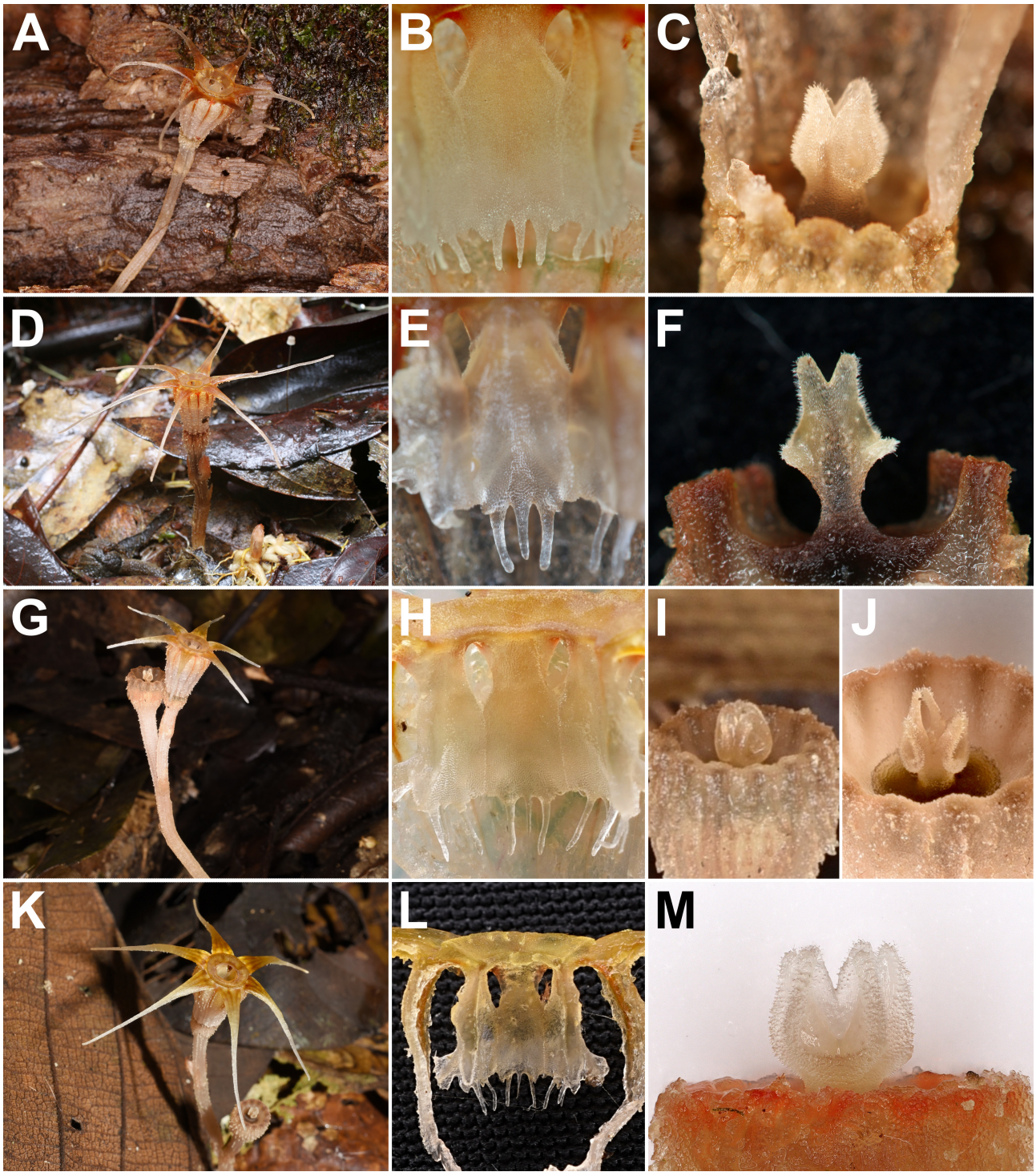

FIGURE 5. *Thismia bifida*. Variability in the general habit of flowering individuals (A, D, G, K), length of the supraconnective appendages (B, E, H, L), and shape of the stigma lobes (C, F, I, J, M). **A–C**. Sarawak, Kampung Daun (*Bor2/23*); **D–F**. Sarawak, Borneo Highland Resort (*Bor42/19*); **G–J**. Brunei Darussalam, Bukit Teraja (*MHMD252020*); **K–M**. Sarawak, Sungai Kana (*MDMH2024/7*). Photographs by Michal Sochor (A–F) and Michal Hroneš (G–M).

Discussion

Details of discovery and rediscovery of Thismia bifida

Thismia bifida was originally collected by Hirano and Hotta on 19 November 1963 on the north-eastern slope of Bukit Kana, Bintulu, Sarawak (Hotta 1967) and had not been recorded again prior to our study. To provide context for the

rediscovery reported here, it is important to briefly outline the characteristics and conservation status of the type area. Bukit Kana is a small mountain range in the Tatau District of central Sarawak, with its highest peak reaching 1,073 m a.s.l. The area was gazetted as Bukit Kana National Park in January 2015 (Sarawak Forestry Corporation 2026). Bukit Kana Hill, which gave its name to the entire range, remains predominantly forested with primary vegetation, although the surrounding foothills have been heavily impacted by large-scale logging.

Motivated by the absence of any confirmed records since the original collection, our field surveys specifically targeted the Bukit Kana range in an effort to recollect *T. bifida*. During these surveys, we rediscovered *T. bifida* at three localities within the range. One of these localities lies directly at the southern foot of Bukit Kana Hill itself. Although the type locality on the north-eastern slope could not be surveyed because of logistical, safety, and conservation constraints, the newly collected material fully matches the original description, illustration, and type specimen of *T. bifida*. Two other species of *Thismia* were also recorded at the surveyed localities, i.e., the recently described *T. dasyantha* Dančák, Sochor & Hroneš in Dančák *et al.* (2025: 122) and an undescribed species allied to *T. inconspicua* Sochor & Dančák in Sochor *et al.* (2017: 264), not corresponding to the protologue of *T. bifida* (Hroneš *et al.*, *in prep.*).

Affinities of Thismia bifida and recognition of the Thismia filiformis group

Beyond confirming the persistence of the species, the rediscovery of *T. bifida* also allowed clarification of its phylogenetic affinities. Based on both morphological and genetic evidence (Fig. 4), *T. bifida* is closely related to *T. pallida* from Sabah and *T. filiformis* from Thailand. Although the reconstructions by Shepeleva *et al.* (2020) showed a different phylogenetic position of *T. filiformis* within *Thismia* subsect. *Odoardoa*, it received low support, which was likely a result of the employment of only three loci. After inclusion of a new sample of this aggregate from Sumatra with complete data from all five loci, its close relationship with *T. bifida* and *T. pallida* became apparent. Together, these three species form a coherent *Thismia filiformis* group, which can be recognised within *Thismia* sect. *Thismia* subsect. *Odoardoa* by the following combination of characters: typically yellow, orange, or beige flowers with a floral tube that lacks transverse bars or reticulation on its inner wall and that is straight and regular (never irregularly distorted or gibbous); narrowly triangular tepals with tapering appendages; a well-developed and slightly raised annulus; and glabrous supraconnective apex bearing three appendages. Some populations here assigned to *T. bifida* were known prior to the rediscovery of the species in the type area and were previously referred to as *Thismia filiformis* agg. (e.g., Dančák *et al.* 2020a) or *Thismia* sp. "Andulau" (Shepeleva *et al.* 2020). *Thismia fumida* Ridley (1890: 338) may also belong to this complex, although this cannot be confirmed until the species is rediscovered and its stamen morphology is examined, if it has not already become extinct.

Within this group, *T. pallida* emerges as the closest relative of *T. bifida*, both phylogenetically (Fig. 4) and morphologically (Fig. 6). *Thismia pallida* is currently known only from south-eastern Sabah (Hroneš *et al.* 2018; Dančák *et al.* 2020a; Fig. 3), where it probably replaces *T. bifida*. At the time *T. pallida* was described, *T. bifida* was known only from a brief description and a simple illustration, and their affinities were therefore unrecognised.

Notes on morphology of Thismia pallida

A detailed comparison of *T. bifida* with its closest relative, *T. pallida*, reveals that some characters reported in the protologue of *T. pallida* require reinterpretation. In the original description, the diagnostic characters include the shape, length, and arrangement of the apical appendages of the supraconnective. The supraconnective apex is described as bearing five appendages arranged as follows: outer pair very short, rounded, pointing outwards; inner pair ca. 4 times longer than the outer one, ± straight, cylindrical to slightly club-shaped, obtuse, pointing inwards; the median (unpaired) appendage the longest, acute, curved. Detailed examination of material of both species revealed that the outer pair of supraconnective apex appendages of *T. pallida* actually represents the ends of low ridges arising from each wing of the adaxial appendage, reaching the supraconnective apex and forming a protuberance near each of the paired appendages. A similar structure is present in *T. bifida*, although it is less pronounced (and therefore termed a tubercle above). Consequently, both species have three appendages at the supraconnective apical margin. Then, *T. pallida* has been described as having the median (unpaired) supraconnective apex appendage "the longest", i.e., longer than the paired appendages, whereas in *T. bifida* it is usually shorter than or nearly as long as the paired appendages (Fig. 6B, D). Examination of newly collected material, however, indicates that the length of the median appendage in *T. pallida* is also rather variable and is to be more accurately characterised as longer than or nearly as long as the paired appendages. Differences between the two species also involve the shape of the stigma lobes: in *T. bifida*

they are bifid to at least one quarter of their length, whereas in *T. pallida* they are emarginate or bifid at most to one quarter of their length (Fig. 6C, E, H, J). Although both species can be distinguished based on floral micromorphology, their external morphology is very similar, and differences are subtle, involving mainly colour pattern and proportions of floral parts, making them nearly indistinguishable based on overall appearance alone.

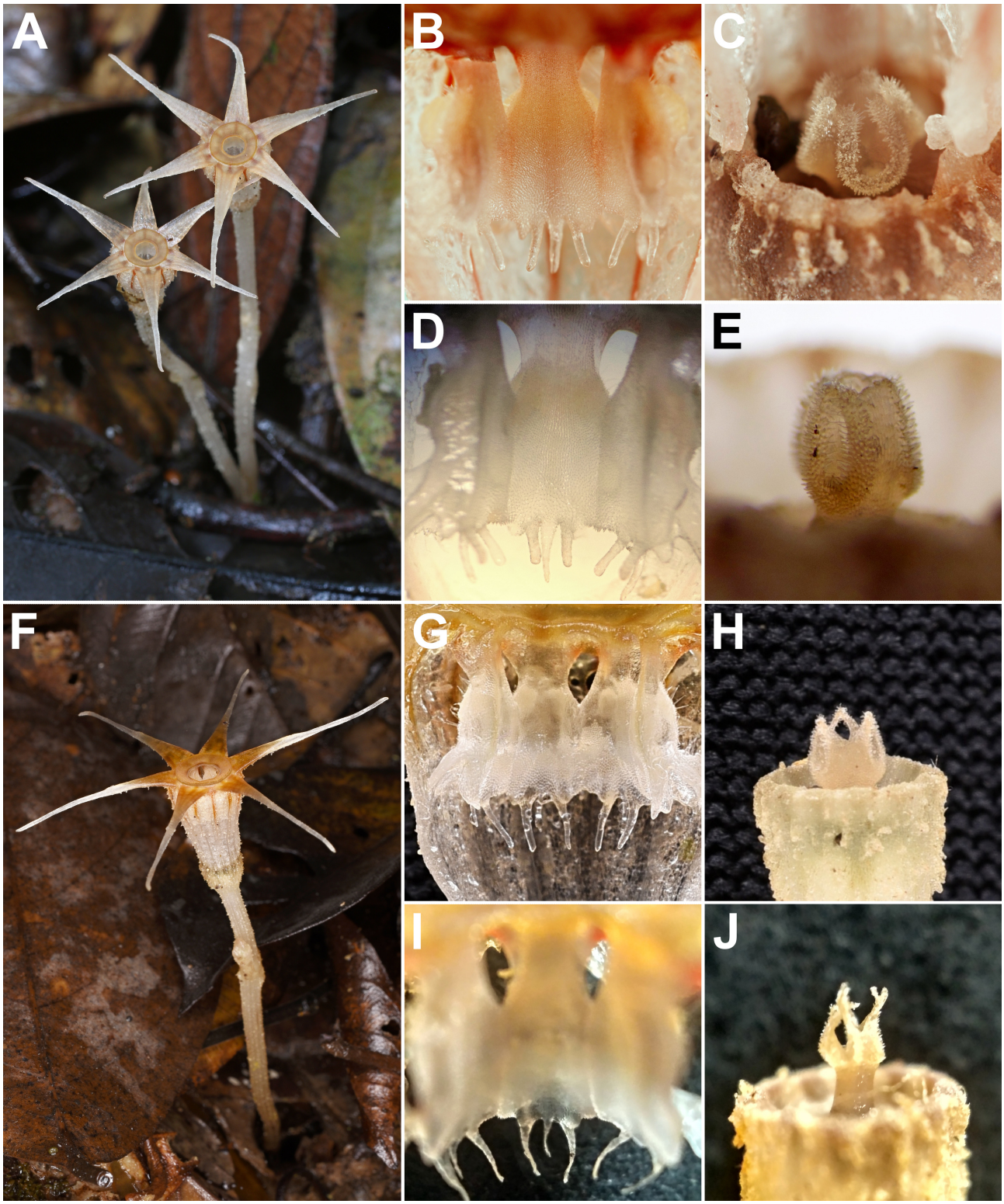

FIGURE 6. Comparison of *Thismia pallida* (A–E) and *T. bifida* (F–J) in general habit (A, F), length of the supraconnective appendages (B, D, G, I), and the shape of the stigma lobes (C, E, H, J). **A**. Sabah, Tawau Hills (*Bor46/23*); **B, C**. Sabah, Gunung Silam (*Bor32/23*); **D, E**. Sabah, SAFE Project plot (*Nilus & Svátek SAN 158204*—type); **F, G, H**. Brunei Darussalam, Bukit Teraja (*MHMD252020*); **I, J**. Brunei Darussalam, Bukit Telingan (*Bor7/24MH*). Photographs by Michal Sochor (A–C), Michal Hroneš (D–H), and Martin Dančák (I, J).

Biogeographical characteristics of Thismia bifida

The occurrences of *Thismia bifida* reported here uncover the species distribution to stretch almost 600 km across, which makes it one of the species of *Thismia* with the widest known distribution range. Also, it belongs among the few *Thismia* species with more than ten known localities (Dančák *et al.* 2020a; Suetsugu *et al.* 2025). Such species provide valuable insight into the intra- and interpopulation variation, which has rarely been studied in *Thismia* (Suetsugu *et al.* 2025).

We have shown that the morphology of *T. bifida* is mosaic-like, with some character states differing among some populations while present within another single population (e.g., the depth of stigma lobe division). Notably, there is no association between the population-specific morphology and the observed genetic structure.

The two major lineages of *T. bifida* (Fig. 4) correlate with geography, as one of them encompasses the populations from the western Sarawak and the other one comprises the central Sarawak and Brunei populations. These two regions are located on opposite sides of the Lupar Divide, which is considered an important biogeographical break, reflecting the contrasting geological histories of the areas on either side (Low *et al.* 2014; Wong & Neo 2019). Similar genetic-geographic differentiation can be observed in *T. minutissima* Dančák, Hroneš & Sochor in Dančák *et al.* (2020b: 2). The western lineage of *T. bifida* is further divided into two sublineages, one from Semenggoh Nature Reserve and the second uniting the samples from Serapi and Penrissen massifs (although the Semenggoh clade has very low statistical support, leaving considerable uncertainty in the presence of such a lineage). Such a phylogeny is not unexpected given the presumed pollination by short-range flying fungus gnats and short-distanced seed dispersal by rain splash characteristic of *Thismia*, which makes the populations isolated from each other with reduced gene flow and thus faster mutation accumulation (Mesler *et al.* 1980; Guo *et al.* 2019; Coelho *et al.* 2021; Suetsugu *et al.* 2025). Under this scenario, the population from Semenggoh would have been isolated from the remaining western Sarawak populations for longer time, allowing for its genetic differentiation. However, further floristic and population genetic research is necessary to elucidate these processes.

Key to the species of *Thismia filiformis* group

1. Floral tube 4.5–5.5 × 3.8–4.5 mm; median (unpaired) supraconnective appendage much shorter than the paired appendages (reaching ca. one third of their length) ..... *Thismia filiformis*
- Floral tube 7.5–12.0 × 6.0–8.6 mm; median (unpaired) supraconnective appendage longer, as long as, or only moderately shorter than the paired appendages (reaching or exceeding two thirds of their length) 2
2. Median supraconnective appendage shorter than or nearly as long as the paired appendages; stigma lobes bifid to at least one quarter of their length ..... *Thismia bifida*
- Median supraconnective appendage longer than or nearly as short as the paired appendages; stigma lobes emarginate, or bifid at most to one quarter of their length ..... *Thismia pallida*

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APPENDIX 1

Additional specimens examined

Thismia bifida

MALAYSIA. Sarawak: Kuching Division, Padawan Subdistrict, Semenggoh Nature Reserve, 670 m WSW of main entrance, 1.397355N, 110.319335E, 63 m a.s.l., 31 Jan 2023, *Dančák M. & Sochor M. Bor28/23* (DNA sample only); 690 m W of main entrance, 1.400256N, 110.318492E, 73 m a.s.l., 31 Jan 2023, *Dančák M. & Sochor M. Bor27/23* (OL, spirit); 700 m WSW of main entrance, 1.397009N, 110.319276E, 73 m a.s.l., 31 Jan 2023, *Dančák M. & Sochor M. Bor30/23B* (DNA sample only); 700 m WSW of main entrance, 1.398148N, 110.318838E, 92 m a.s.l., 29 Jan 2023, *Dančák M. & Sochor M. Bor19/23* (OL, spirit); near arboretum trail, 470 m W of main entrance, 1.3992761N, 110.3205414E, 65 m a.s.l., 1 Feb 2024, *Hroneš M. & Uvírová A. MHAU2024/02* (OL, SAR, spirit). Kampung Annah Rais, 350 m SSE of Gunung Merobung, 1.135196N, 110.259300E, 273 m a.s.l., 30 Jan 2023, *Dančák M. & Sochor M. Bor21/23* (OL, spirit); 370 m SSE of Gunung Merobung, 1.135016N, 110.259288E, 252 m a.s.l., 30 Jan 2023, *Dančák M. & Sochor M. Bor22/23* (OL, spirit). Borneo Highland Resort, trail to Mt. Penrissen: ca. 940 m W of summit, 1.116130N, 110.214684E, 1011 m a.s.l., 2 Feb 2019, *Dančák M., Hroneš M. & Sochor M. Bor42/19* (DNA sample only); ca. 780 m W of summit, 1.115175N, 110.215967E, 1010 m a.s.l., 2 Feb 2019, *Dančák M., Hroneš M. & Sochor M. Bor42/19B* (OL, pressed). Bau District, Kampung Daun, mountain pass in Mt. Bronang massif NW above village, 1.533171N, 110.175739E, 432 m a.s.l., 24 Jan 2023, *Dančák M. & Sochor M. Bor2/23* (OL, spirit); 1.532147N, 110.174483E, 444 m a.s.l., 24 Jan 2023, *Dančák M. & Sochor M. Bor3/23* (DNA sample only); 1.531895N, 110.174191E, 456 m a.s.l., 24 Jan 2023, *Dančák M. & Sochor M. Bor4/23* (DNA sample only). Bintulu Division, Tatau District, Rumah Agau, small patch of primary lowland mixed dipterocarp forest, 900 m NW of longhouse, 2.6346689N, 112.9343375E, 50 m a.s.l., 21 Nov 2023, *Dančák M. & Hroneš M. MDMH2023/33 with Uvírová A. & Blažek V.* (SAR, spirit). Bukit Kana National Park, river valley of Sungai Kana Kanan S of Bukit Kana summit, 2.6621817N, 112.9029350E, 120 m a.s.l., 1 Dec 2024, *Dančák M. & Hroneš M. MDMH2024/7 with Uvírová A.* (SAR, spirit); small ridge between two forest streams in side valley of Sungai Kana Kiri, ca. 0.21 km SE of Bukit Kana resort, 2.6542725N, 112.9045925E, 205 m a.s.l., 2 Dec 2024, *Dančák M. & Hroneš M. MDMH2024/12 with Uvírová A.* (SAR, spirit); northeastern slope of Bukit Kana, alt. 600–850 m, 19 Nov 1963, *M. Hirano & M. Hotta 1269* (KYO, pressed).

BRUNEI DARUSSALAM. Belait District: Sungai Liang, Andulau Forest Reserve, Compt. 8, UBD plot area, on dead log, 10 Nov 2015, *Azlan, Md. Arrifin, Watu & Jangarun E. BRUN 24429* (BRUN, spirit); UBD plot area, 4.6547222N, 114.5241667E, 55 m a.s.l., 26 Nov 2017, *Dančák M. MD2017/72* (OL, spirit). Labi village, Bukit Telingan, northern slopes, mixed dipterocarp forest, ca. 9 km NNE of Bukit Teraja summit, 4.376845N, 114.473913E, 165 m a.s.l., 25 Nov 2024, *Dančák M., Hroneš M., Sochor M. & Uvírová A. Bor7/24* (BRUN, spirit); southern slopes, bank of small stream ca. 50 m E of helipad, mixed dipterocarp forest, 4.368460N, 114.477070E, 170 m a.s.l., 6 Aug 2025, *Hroneš M. 0525 with Abdullah M.F., Pandai A. & Uvírová A.* (BRUN, spirit). Teraja village, forest on slope between Bukit Teraja summit road and Wasai Wong Kadir parking place, 4.3398672N, 114.4477119E, 100 m a.s.l., 13 Jan 2020, *Dančák M. & Hroneš M. MHMD252020* (BRUN, spirit); forest near Wasai Wong Kadir parking place, 4.3408300N, 114.4473900E, 60 m a.s.l., 30 Nov 2022, *Dančák M. & Hroneš M. MH2022/08* (BRUN, spirit).

Thismia pallida

MALAYSIA. Sabah: Lahad Datu District, Gunung Silam, 90 m WNW of the view tower, 4.965395, 118.173648, 711 m a.s.l., 3 Feb 2023, *Dančák M. & Sochor M. Bor32/23* (OL, spirit).

***Thismia filiformis* agg.**

INDONESIA. Sumatra: South Tapanuli Regency, Sitandiang village, 1.592126, 99.198364, 866 m a.s.l., 18 Nov 2024, *Dančák M., Hroneš M., Sochor M., Uvírová A. Sum2/24* (BO, spirit).

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Supplementary file 1. Collection data and GenBank accession numbers for the specimens analysed in this study.