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# Phylogenetic and biogeographical analyses of *Thismia* (*Thismiaceae*) support *T. malipoensis* as the eighth species in China

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**Abstract:** *Thismia* Griff. (*Thismiaceae*) is a holo-mycoheterotrophic genus with more than 100 species. In this study, phylogenetic analyses supported that *T. malipoensis* from Yunnan is a new species in *T.* sect. *Glaziocharis*. Morphologically, this new species can be distinguished from its phylogenetic sister species *T. abei* by having the annulus of the flower expanded and modified into a cucullate (hood-like) structure with zygomorphic symmetry with one opening on one side. Biogeographical inference showed that SW China to Indo-Burma and the Sunda Shelf region was suggested as the ancestral distribution region of *Thismia* s.s., then eastward to SE China and Japan, and southward to New Guinea to Australia, respectively. The Chinese species should have originated from at least two different ancestral sources, and geographical isolation caused the divergence between *T. malipoensis* and *T. abei* at 17.47 Mya.

**Keywords:** China, biogeography, conservation, new species, phylogeny, taxonomy, *Thismia*, *Thismiaceae*

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## Introduction

Heterotrophic plants exhibit distinct mechanisms for nutrient acquisition when compared to autotrophic plants. To date, more than 880 mycoheterotrophic plants that rely upon associations with fungi for their supply of organic nutrients have been documented (Merckx & al. 2013b). Due to their highly reduced leaves and lack of chlorophyll (Cameron & Leake 2007; Leake & Cameron 2010), holo-mycoheterotrophic are only visible during brief periods of flowering and fruiting. As large-scale expeditions are conducted across different seasons and remote areas, numerous leafless holo-mycoheterotrophic species have been discovered and classified as new to the field of science. Currently, most of these species are only found in small populations within one or a few locations, making them susceptible to being categorized as Critically Endangered (CR). Therefore, efforts to conserve these species are crucial (Merckx & al. 2013a).

*Thismia* Griff. is a holo-mycoheterotrophic genus with remarkable flowers in its peculiar appearance and exceptionally complicated and quite diverse floral morphology (Kumar & al. 2017; Shepeleva & al. 2020; Nuraliev & al. 2021). Traditionally, *Thismia* was treated as a member of the tribe *Thismieae* in the family *Burmanniaceae* (Maas-van de Kamer 1998; Merckx 2008; Li & al. 2020), with four other holo-mycoheterotrophic genera, i.e. *Afrothismia* Schltr., *Haplothismia* Airy Shaw, *Oxygyne* Schltr. and *Tiputinia* P. E. Berry & C. L. Woodw. Recent phylogenetic studies have supported the tribe *Thismieae* as a separate family *Thismiaceae*, because *Thismiaceae* is sister to the family *Taccaceae* and rather distantly related to the family *Burmanniaceae* s.s. (Merckx & al. 2006; Lam & al. 2016; Shepeleva & al. 2020). The most recent phylogenetic study showed that *Thismia* species are polyphyletic in that the Old World species formed five well-supported groups, and the neotropical species are clustered with *Tiputinia*, which

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probably represents a separate genus (Shepeleva & al. 2020), i.e. *Ophiomeris* Miers. In this study, we tentatively followed the traditional delimitation of *Thismia* s.l., which is characterized by having a prominent hypanthium (also called a flower tube or flower chamber) that bears six tepals and six stamens. To date, *Thismia* includes about 105 species and one variety (IPNI 2023; POWO 2023) (Supplementary appendix S1), which are distributed mainly in tropical and subtropical Asia to temperate Australia and tropical America (Shepeleva & al. 2020).

*Thismia taiwanensis* Sheng Z. Yang & al. was the first species to be described from China until 2002 (Yang & al. 2002). To date, seven species have been recognized in China (Yang & al. 2002; Ho & al. 2009; Chiang & Hsieh 2011; Li & Bi 2013; Mar & Saunders 2015; Xu & al. 2020; Li & al. 2023), and *T. guangdongensis* X. J. Li & al. was most recently described in 2023. Of these, Guangdong, Hong Kong and Taiwan have recorded two species, and Hainan and Yunnan have one species each, with *T. hongkongensis* Mar & R. M. K. Saunders found in Guangdong and Hong Kong. During botanical surveys in SE Yunnan in 2019, a unique flowering species of *Thismia* was found and collected (Fig. 1–4). After investigations on morphological characters and herbarium specimens from China and adjacent regions, as well as a literature review, we confirmed that this species was new to science, which was also supported by phylogenetic analyses using two nuclear ribosomal DNA (nrDNA) and two mitochondrial DNA (mtDNA) sequence datasets. Herein, this new species is named as *T. malipoensis* J. D. Ya & W. B. Yu by providing a morphological description, type specimen, colour photographs (Fig. 1–3) and line drawings (Fig. 4). Moreover, the phylogenetic and biogeographic significance of this new species is inferred and discussed, and conservation suggestions and recommendations are proposed.

## Material and methods

### Morphological observation

Voucher specimens of *Thismia malipoensis* were collected from the Laoshan Provincial Nature Reserve of Malipo County during a field expedition in 2019. The morphological characters of this new species were observed, measured and photographed based on living individuals. Fresh flowering specimens were identified by checking herbarium specimens and reviewing the relevant literature (Yang & al. 2002; Larsen & Averyanov 2007; Ho & al. 2009; Chiang & Hsieh 2011; Li & Bi 2013; Mar & Saunders 2015; Kumar & al. 2017; Dančák & al. 2020a; Nuraliev & al. 2020; Xu & al. 2020; Siti-Munirah & al. 2021; Li & al. 2023). DNA tissues of *T. malipoensis* were collected from flowering shoots, then dried using silica-gel. The type specimen was deposited at the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences (KUN; herbarium code following Thiers 2023+).

### Phylogenetic analyses

In order to elucidate the phylogenetic association between *Thismia malipoensis* and other species within the *Thismiaceae*, phylogenetic analyses were conducted using sequences of nrDNA 18S and ITS, as well as mtDNA *atpA* and *matR*. A comprehensive analysis was performed on a total of 48 taxa, encompassing four genera of *Thismiaceae*, with *Tacca palmatifida* Baker (*Taccaceae*) as the outgroup. Appendix 1 provides voucher information for the GenBank accession numbers associated with the sequences generated or obtained from the studies of Dančák & al. (2020b, 2020c), Merckx & al. (2017), Shepeleva & al. (2020) and Sochor & al. (2018) for this study.

Genomic DNA of the new species was isolated from silica-gel dried shoot tissues of the type collection using the CTAB method (Doyle & Doyle 1987). Library preparation for the Next Generation Sequencing followed the procedure of Zeng & al. (2018). Around 500 pg purified genomic DNA was fragmented to approximately 350 bp in size by sonication, then built into a blunt-end DNA library using the NEBNext Ultra II DNA library prep kit for Illumina (New England BioLabs) following the standard protocol. The 150 bp pair-end reads were generated using the Illumina Sequencing Platforms. Raw data were assembled de novo for the mitochondrial and nuclear ribosome DNA contigs/sequences using the GetOrganelle toolkit (Jin & al. 2020). Assembled mitochondrial and nuclear ribosome DNA sequences of the new species were annotated in Geneious (Kearse & al. 2012) using nrDNA 18S and nrITS, and mtDNA *atpA* and *matR* sequences of *Thismia* species from NCBI as references, then four targeted DNA regions were extracted from the annotated sequences, respectively.

Four DNA regions were aligned separately using MAFFT 7.505 (Katoh & Standley 2013). Then the four regions were concatenated into a supermatrix (Supplementary appendix S2) using SequenceMatrix package of TaxonDNA 1.78 (Meier & al. 2006). Bayesian inference (BI) and maximum likelihood (ML) methods were used to reconstruct phylogenies. The BI analysis was performed using MrBayes 3.26 (Ronquist & al. 2012). The total dataset was partitioned, and the DNA substitution model of the Bayesian information criterion (BIC) for two DNA regions was estimated using jModeltest 2 (Darriba & al. 2012; Darriba & al. 2019). Markov chain Monte Carlo (MCMC) analysis was performed using MrBayes for 10,000,000 generations for the total dataset, with two simultaneous runs, each run comprising four incrementally heated chains. The BI analysis was started with a random tree and sampled every 1000 generations. The ML analysis was conducted with RAxML 8.2.10 (Stamatakis 2014) using the GTR substitution model with gamma (Γ) distribution rate heterogeneity among

Fig. 1. *Thismia malipoensis* – A: plant; B, C: plants in habitat. – Source of material: *J.-D. Ya & W. Zhang 19CS18569*. – Photographed by J.-D. Ya.

sites and the proportion of invariable sites estimated from the data. Support values for nodes/clades were estimated from 1000 bootstrap replicates.

### Divergence time estimation and ancestral area reconstruction

The concatenated dataset of 18S rDNA, ITS, *atpA* and *matR* from 49 taxa was used to estimate the divergence time among *Thismia* species. According to the previous studies (Merckx & Smets 2014), we chose the secondary calibration time for two nodes: (1) 63–96 Ma for the root node between *Thismiaceae* s.s. and *Tacca* J. R. Forst. & G. Forst.; and (2) 54–86 Ma for the crown node of *Thismiaceae* age (Merckx 2008). The divergence time was estimated using the MCMCTree program in PAML 4.10.5 (Yang 2007). Using the independent rate model (clock = 2) and the GTR + Γ model (model = 7). We ran two separate MCMC iterations for 400,000 generations with sampling every 10 iterations, the first 160,000 iterations were discarded as burn-in, and the mcmcfile was used to check ESS values and convergence in Tracer 1.7.2 (Rambaut & al. 2018).

Distribution information of 44 taxa of *Thismiaceae* and the outgroup *Tacca palmatifida* was collected from POWO (2023), and that of four accessions without name just using source information of the voucher (Shepeleva & al. 2020). Ten biogeographical areas of distribution range were classified according to previous biogeographical studies (Thomas & al. 2012; Sirichamorn & al. 2014; Liu & al. 2021): (A) Japan; (B) SE China; (C) SW China to Indo-Burma (excluding the Malay Peninsula); (D) India and Sri Lanka; (E) the Sunda Shelf region; (F) Philippines; (G) Wallacea; (H) New Guinea to Australia; (I) South America; and (J) Africa (Fig. 6). The dispersal-extinction cladogenesis (DEC) model (Ree & Smith 2008), dispersal-vicariance analyses (DIVA) model (Ronquist 1997), and BAYAREALIKE model (Landis & al. 2013), as well as the other three model with “+J” parameter (founder event speciation) in the R package BioGeoBEARS (Matzke 2018) that was used to reconstruct ancestral areas of *Thismia*. The maximum number of regions was set to 2 and the lowest corrected Akaike information criterion (AICc) was considered the “best” model.

## Results and Discussion

### Phylogenetic analyses

The nrDNA 18S matrix was 1639 bp in length including 384 variable sites and 247 parsimony-informative sites. The nrDNA ITS matrix was 1012 bp in length including 721 variable sites and 613 parsimony-informative sites. The mtDNA *atpA* matrix was 1112 bp in length including 146 variable sites and 79 parsimony-informative sites. The mtDNA *matR* matrix was 1065 bp in length including 419 variable sites and 190 parsimony-informative sites. The best-fit BIC model of 18S, mrITS, *atpA* and *matR* datasets was GTR+G11, TPM1uf+G, TPM1+G11, and GTR+I+G, respectively. The major-rule consensus tree of ML analysis with support values of both ML and BI analyses is shown in Fig. 5, which is consistent with the topology in the study by Shepeleva & al. (2020). Five well-supported clades were recovered in *Thismia* s.s., and each clade can correspond to four revised sections and one subsection in the subgenus division of *Thismia* proposed by Kumar & al. (2017). In addition, six species were not placed into any clades of the five recognized clades, with two Chinese species, *T. hongkongensis* and *T. tentaculata* K. Larsen & Aver., which are well supported as a monophyletic clade (MLBS/BIPP=98/1.00).

According to the study by Shepeleva & al. (2020), the modified *Thismia* sect. *Glaziocharis* (Taub. ex Warm.) Hatus. is a monophyletic group corresponding to Clade 1, which consists of five species from E Asia (China, Japan) and mainland SE Asia (Thailand, Laos). Herein, our phylogenetic analyses supported *T. malipoensis* as a member of *T.* sect. *Glaziocharis*, and allied to *T. abei* (Akasawa) Hatus., which are both putatively as the sister to *T. gongshanensis* Hong Qing Li & Y. K. Bi with weak support by ML analysis (MLBS = 53). Of the six sampled Chinese species, four species were fell in this clade, with the exception of *T. hongkongensis* and *T. tentaculata*.

### Morphological comparisons and species delimitation

Morphologically, *Thismia malipoensis* stands out significantly from the other six species in *T.* sect. *Glaziocharis* of the Clade 1 (Fig. 5), as well as other four recognized Chinese species by having a cucullate (hood-like) and zygomorphic annulus structure of the flower that covering the apical floral tube with an opening on one side. As the phylogenetic sister species of *T. malipoensis*, *T. abei* is characterized by having connected inner tepals as a loose dome, a ring-like and actinomorphic annulus structure, short tepal appendages (5–6 mm) and glabrous stigma. To date, the cucullate annulus of has been reported only in *T. belumensis* Siti-Munirah & Suhaimi-Miloko and *T. labiata* J. J. Sm., which were supposed to be members of *T.* sect. *Glaziocharis* (Siti-Munirah & al. 2021). *Thismia malipoensis* is distinguished from *T. belumensis* in characters of the tepal appendages: both outer and inner tepal appendages are spreading; inner tepal appendages are shorter than 2 cm and equal to the outer ones; and inner tepal appendages have a fimbriate base and a subulate tip. Geographical information is also important for species delimitation between *T. malipoensis* and *T. belumensis*. *Thismia malipoensis* is distributed in Malipo, SE Yunnan, China, and grows under evergreen broad-leaved forests in limestone mountains at an elevation of 1100 m, whereas *T. belumensis* is endemic to Perak, Peninsular Malaysia, under the shade of lowland dipterocarp forests at an elevation of 260–290 m (Siti-Munirah & al. 2021). Due

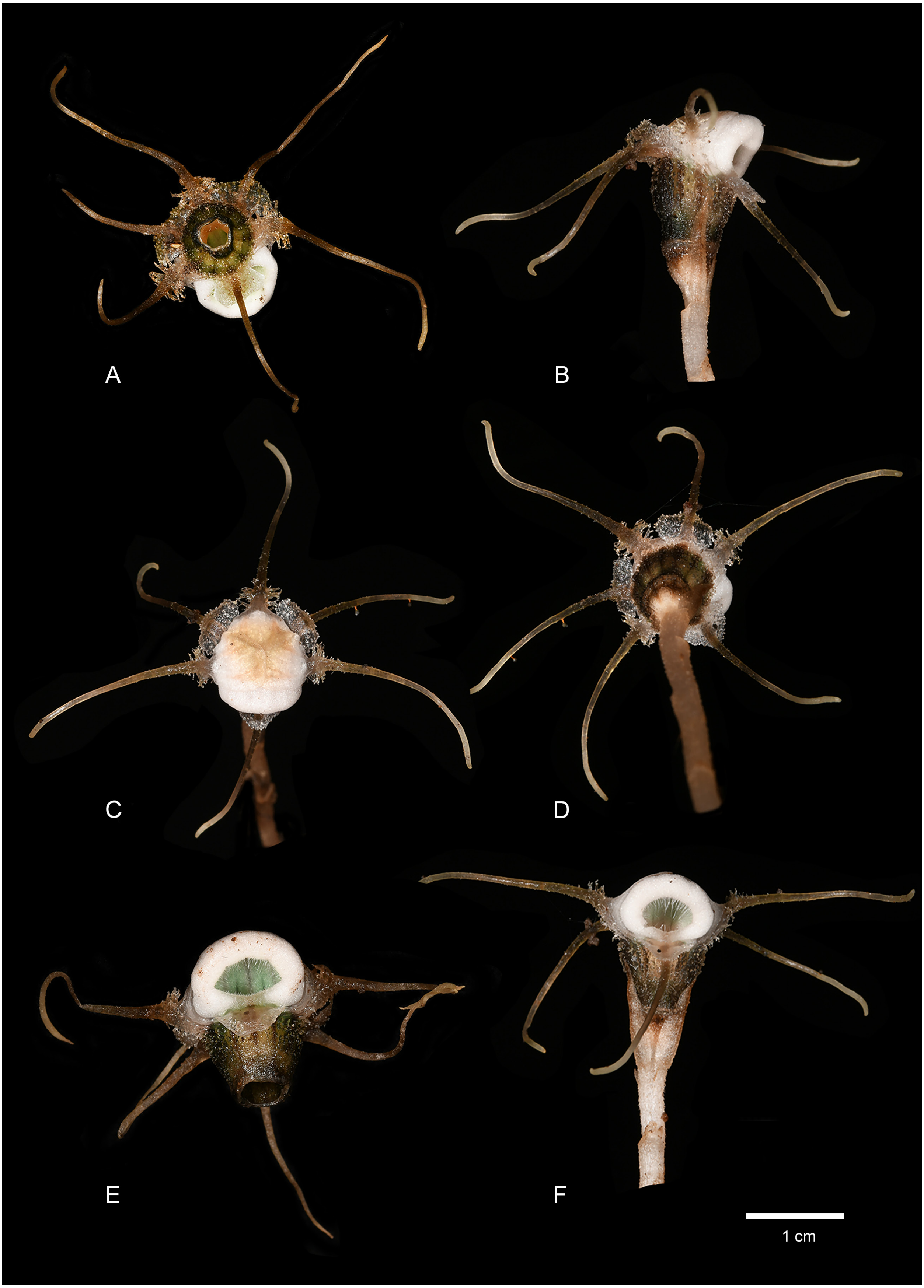

Fig. 2. *Thismia malipoensis*, different views of flower – A, D: bottom view; B: lateral view; C: top view; E, F: front view. – Source of material: *J.-D. Ya & W. Zhang 19CS18569*. – Photographed by J.-D. Ya.

to the lack of molecular data for *T. belumensis*, it is not clear whether *T. malipoensis* and *T. belumensis* are sister species or are sharing similar floral forms and structures by convergent evolution.

### Divergence time estimation and ancestral area reconstruction

The crown age of *Thismiaceae* was estimated to be 75.84 Mya (95 % HDP: 42.85–94.53 Mya), and the diversification time of *Thismia* s.s. started at 62.06 Mya (95 % HDP: 34.75–79.37 Mya) in tropical and subtropical Asia (Fig. 6). For the five major clades or sections, the diversification times varied from 14.26 Mya (95 % HDP: 6.15–26.92 Mya) in the Clade 2 to 38.91 Mya (95 % HDP: 20.16–58.05 Mya) in the Clade 1. Rapid speciation started at c. 23.80 Mya from the late Oligocene to the present. In the Clade 1, *T. thaithongiana* Chantanaorr. & Suddee diverged from the remaining six species at 38.91 Mya (95 % HDP: 20.16–58.05 Mya). Then, the two subclades, *T. malipoensis*–*T. gongshanensis* and *T. nigricoronata*–*T. taiwanensis*, separated at 31.49 Mya (95 % HDP: 16.09–48.46 Mya), and *T. malipoensis* diverged from *T. abei* at 17.47 Mya (95 % HDP: 7.23–31.34 Mya).

Ancestral area reconstruction indicated that the ancestral distribution region of *Thismiaceae* was not clear, because the earliest divergent *Oxygyne* species are found in Africa and Japan of E Asia, and the following clade *Haplothismia exannulata*–*Thismia panamensis* is mainly distributed in Central to South America, as well as the only species *Haplothismia exannulata* Airy Shaw is in India of S Asia (Fig. 6). *Thismia* s.s. is restricted in E Asia to S and SE Asia. The Sunda Shelf and SW China to Indo-Burma regions were suggested as the ancestral distribution region of *Thismia* s.s., and its common ancestor might be originated from the Sunda Shelf region at 64.95 Mya. The back-and-forth migration and dispersal between SW China to Indo-Burma (excluding the Malay Peninsula) and the Sunda Shelf region have happened at least five to six times in Clades 1, 4 and 5, which are highly associated with land-bridge connection between the SE Asia mainland and the Sunda Shelf region before 5.0 Mya (Hall 2009, 2012, 2013; Tan & al. 2020). The common ancestor of *T.* sect. *Glaziocharis* and *T.* sect. *Sarcosiphon* (Blume) Jonker should have originated in the SW China to Indo-Burma region at 38.91 Mya and 16.87 Mya, respectively, then spread eastward to SE China at 22.45 Mya and Japan at 17.47 Mya in the section *Glaziocharis* (Clade 1) and in situ diversification in *T.* sect. *Sarcosiphon* (Clade 4) started at 16.87 Mya. *Thismia* sect. *Rodwaya* (Schltr.) Jonker from New Guinea to Australia might have originated from the Sunda Shelf region at 43.50 Mya, then in situ diversification started at 14.26 Mya as New Guinea to Australia isolated from the Sunda Shelf region (Hall 2012; Zhang & al. 2023). The common ancestor of the clade *T. gardneriana* + *T. hongkongensis* + *T. tentaculata* should be from the Sunda Shelf region, but the ancestral region of *T. gardneriana* + *T. hongkongensis* + *T. tentaculata* was ambiguous, which might be caused by incomplete sampling and an unresolved relationship between *T. gardneriana* and *T. hongkongensis* + *T. tentaculata*. In addition, long-distance dispersal cannot be excluded for *T. gardneriana* spreading to India.

### Biodiversity and conservation of extremely rare *Thismia* species

*Thismia* species almost exclusively distributed in tropical and subtropical areas of Asia and America, with the exception that *T. americana* N. Pfeiff. in the C United States, which has been supposed to be extinct. Since the genus was established in 1845, species discovery progressed very slowly with only 40 species discovered until 1999 (Supplementary appendix S1). After 2011, at least one new species per year was described, and seven and 15 new species were described in 2017 and 2018, respectively. To date, there are 106 species and one variety recognized (Supplementary appendix S1). However, most *Thismia* species are found or collected only once or a few times with small population sizes (Dančák & al. 2020a; Nuraliev & al. 2020). As holo-mycoheterotrophic herbs, *Thismia* species are highly reliant on the specialized fungal host, so the distribution range might be restricted by the availability of host fungi (Merckx & Bidartondo 2008; Gomes & al. 2017; Merckx & al. 2017). Meanwhile, *Thismia* plants are usually very small, inconspicuous and of ephemeral emergence in the flowering and fruiting seasons. To date, only a few *Thismia* species have been observed in more than three locations; c. 65 % of *Thismia* species are known only from the type localities and adjacent areas; c. 45 % of them were found only by their discoverers; and some species had just a single individual (Dančák & al. 2020a; Nuraliev & al. 2020). Therefore, most *Thismia* species could be locally endemic, rare and critically endangered (CR) in accordance with the IUCN Red List categories and criteria (IUCN Standards and Petitions Committee 2022).

It is concerning that in the current geographic distribution range of eight *Thismia* species in China, six species are known only from the type locality, and only two species, *T. hongkongensis* and *T. tentaculata*, have been recorded in two or more populations. In China, *T. hongkongensis* and *T. tentaculata* were originally found in Hong Kong, the range of *T. hongkongensis* extended to Guangdong and the type locality of *T. tentaculata* was Quang Tri Province, Vietnam, but the total number of individuals was few. Moreover, *T. jianfenglingensis* Han Shu & al. is endemic to the Jianfengling National Nature Reserve, Ledong County, Hainan Island, and had only six flowering individuals when found for the first time in 2017, whereas no flowering individuals were found in 2018. Herein, *T. malipoensis* is known only from Malipo County, SW Yunnan, where only ten flowering individu-

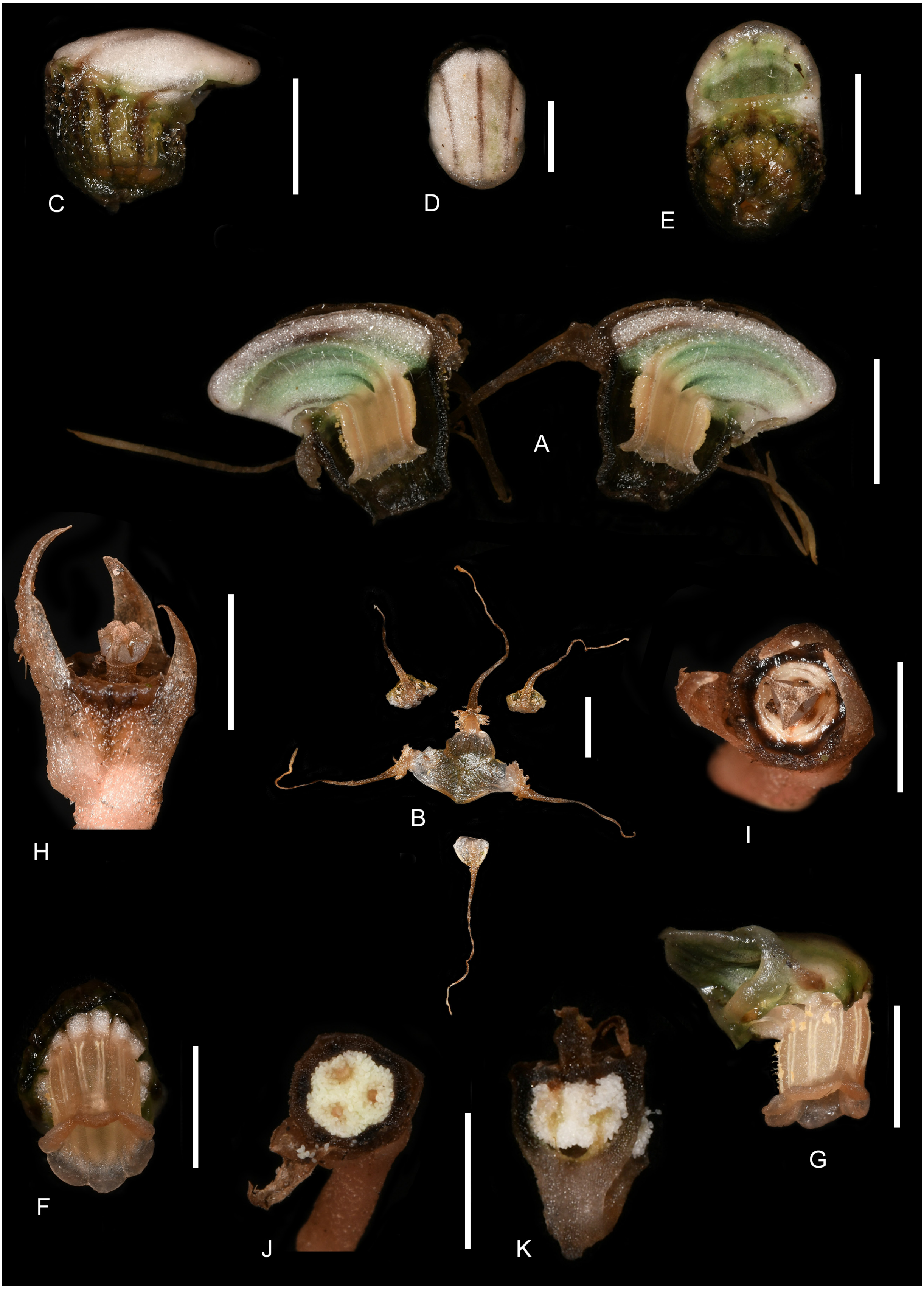

Fig. 3. *Thismia malipoensis* – A: flower, longitudinal section; B: tepals, sparsely papillate outer surface; C–E: floral tube, lateral view (C), top view (D), front view (E); F: stamens, bottom view; G: stamens, lateral view; H: stigma, lateral view; I: stigma, top view; J: ovary, cross-section; K: ovary, longitudinal section. – Source of material: *J.-D. Ya & W. Zhang 19CS18569*. – Photographed by J.-D. Ya. – All scale bars = 5 mm.

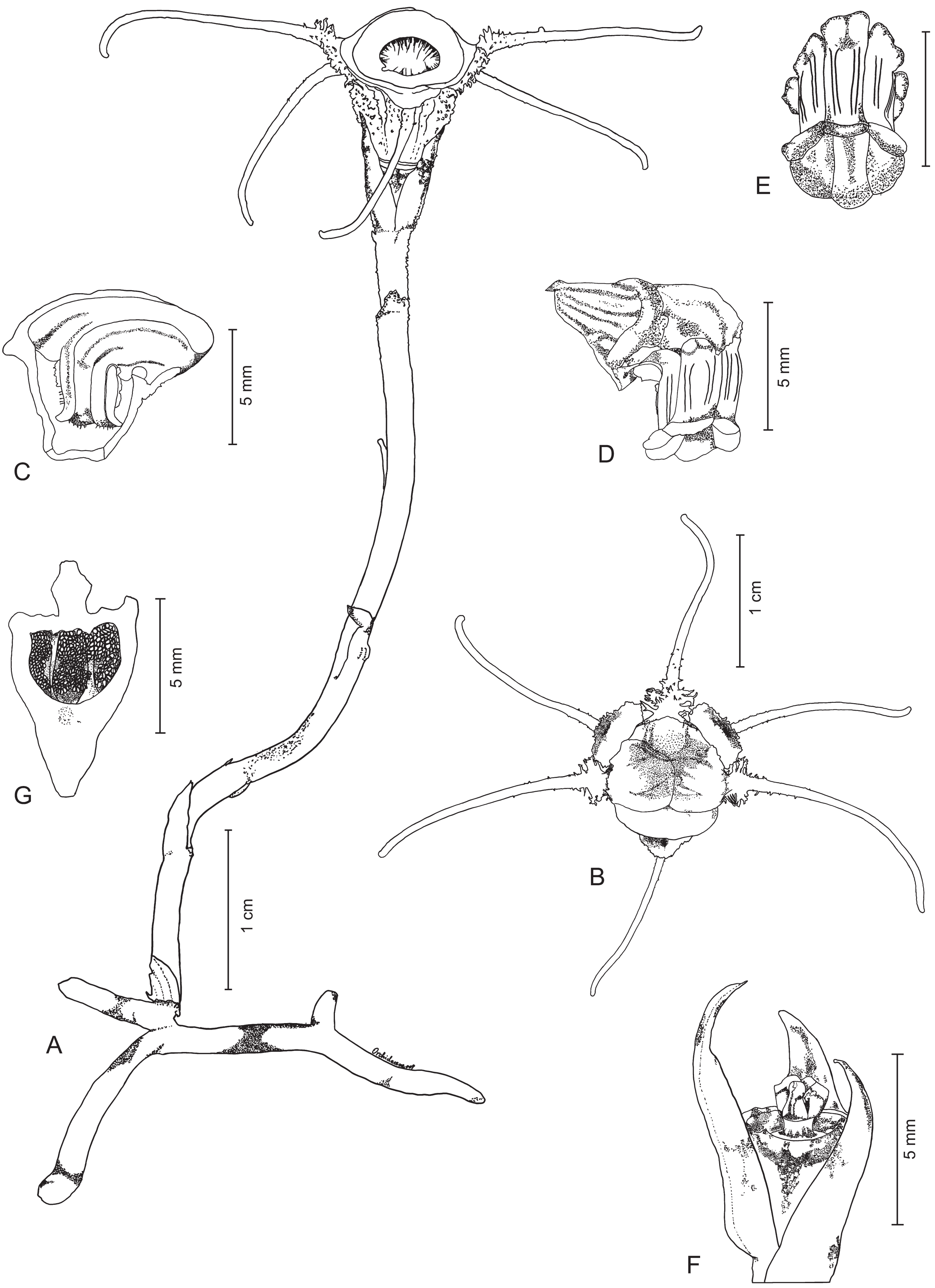

Fig. 4. *Thismia malipoensis* – A: plant; B: flower, top view; C: flower, longitudinal section; D: stamens, lateral view; E: stamens, bottom view; F: stigma, lateral view; G: ovary, longitudinal section. – Source of material: *J.-D. Ya & W. Zhang 19CS18569*. – Drawn by Z.-D. Han.

als were found in 2019. New populations of some species will be found in further investigations. However, most *Thismia* species have extremely small population sizes, which may be more sensitive to environmental changes and more vulnerable to extinction. As mentioned above, holo-mycoheterotrophic *Thismia* species are highly reliant on the specialized fungal host for seed germination and seeding development, and those fungi should be associated with the forest and soil ecosystem. Therefore, the most effective strategies are in situ conservation.

## Taxonomic treatment

***Thismia malipoensis*** J. D. Ya & W. B. Yu, **sp. nov.** – Fig. 1–4.
Holotype: China, Yunnan Province, Wenshan Prefecture, Malipo County, Tianbao Town, 1191 m a.s.l., forest on limestone, 13 Aug 2019, *J.-D. Ya & W. Zhang 19CS18569* (KUN 1584483!).

*Diagnosis* — *Thismia malipoensis* belongs to *T.* sect. *Glaziocharis* and can be distinguished from its phylogenetic sister species *T. abei* by having the annulus of the flower expanded and modified into a cucullate (hood-like) structure with zygomorphic symmetry with one opening on one side. Moreover, *T. malipoensis* can be distinguished from the morphologically similar *T. belumensis*, in that the outer and inner tepal appendages are spreading (vs erect) and equal in length by less than 2 cm (vs outer tepal appendage 1.5–2.5 cm and inner tepal appendage c. 3 cm), the inner tepal base is fimbriate at the margin (vs entire) and the inner tepal tip is subulate (vs clavate).

*Description* — *Herbs* terrestrial, achlorophyllous, c. 7 cm tall. *Roots* vermiform, creeping, branched, fleshy, terete, pale brownish. *Stems* erect, unbranched, 2–4 cm long, densely deflexed papillate hairy. *Leaves* scale-like, white, translucent, lanceolate, c. 8 × 2 mm, base appressed to stem, apex acuminate. *Involucral bracts* 3, pale brownish, lanceolate, c. 1 cm long, densely deflexed papillate hairy, base appressed, margin entire, apex acuminate. *Pedicel* c. 3 mm long (post anthesis). *Flowers* terminal, solitary, zygomorphic, c. 4.5 × 4 cm (including appendages); *hypanthium* pyriform, dark green, translucent, c. 8 mm long, c. 7 mm wide near apex, narrowed to c. 4 mm wide just above ovary, outer surface densely deflexed papillate hairy, with 12 raised dark brown longitudinal veins, inner surface smooth; *outer tepals* 3, pale brown, broadly ovate, c. 2.5 × 3 mm, 2 on opposite side of annulus opening and 1 below annulus opening, outer surface sparsely papillate, apex acute, each outer tepal with a tentacle-like spreading appendage, pale brown, 0.8–1.3 cm × c. 1 mm; *inner tepals* 3, pale brown, translucent, glabrous, broadly obovate, c. 3.5 × 4 mm, apically broadly fused and tightly adpressed and completely overlapping cucullate part of annulus, each inner tepal with a tentacle-like spreading appendage c. 1.7 cm long, pale brown, fimbriate at basal margin, subulate at apex. *Annulus* expanded and modified into a cucullate (hood-like) structure, covering apical part of floral tube and forming a lateral floral aperture; cucullate outer surface white with 3 brown lines, glabrous; cucullate inner surface light green, covered with numerous white trichomes. *Stamens* 6, light yellow, pendent from apical part of floral tube; each connective c. 3.5 mm long, outer surface with 2 linear to filiform thecae, each c. 2 mm long, inner surface smooth, outer surface and apex covered with transparent trichomes; supraconnective apex rounded and curved outward; filaments short, connected to floral tube and annulus. *Ovary* obovoid, c. 3.5 × 4.8 mm, 1-loculed, with 3 parietal placentae; style c. 0.6 mm long; stigma 3-lobed, lobes triangular-pyramidal, c. 1.2 mm long, apex truncate and densely papillate. *Fruit* cup-shaped; seeds brown.

*Phenology* — Observed flowering in August, fruiting in September.

*Distribution and habitat* — *Thismia malipoensis* is currently known only from the type locality in Laoshan Provincial Nature Reserve of Malipo County, SE Yunnan. The population consists of about ten individuals under evergreen broad-leaved forest on limestone mountains at an elevation of 1191 m a.s.l. The forest includes the *Lithocarpus tephrocarpus* (Drake) A. Camus (*Fagaceae*), *Alseodaphnopsis andersonii* (King ex Hook. f.) H. W. Li & J. Li and *Litsea yunnanensis* Y. C. Yang & P. H. Huang (both *Lauraceae*) and the bamboo *Melocalamus arrectus* T. P. Yi.

*Etymology* — The specific epithet "*malipoensis*" refers to the county name Malipo of Wenshan Prefecture, the type locality of the new species.

*Chinese name* — 麻栗坡水玉杯 (má lì pō shuǐ yù bēi).

*Conservation status* — We evaluated the conservation status of *Thismia malipoensis* according to the IUCN Red List categories and criteria (IUCN Standards and Petitions Committee 2022). The new species is known only from the type locality, our field surveys identified only one population with about ten individuals. The conservation status of the species is therefore considered to be Critically Endangered (CR A2acd; B1ab(i,iii,v)+2ab(i,iii,v); C2a(i); D).

## Key to species of *Thismia* in China

1. Corolla tube apex covered by a cucullate and zygomorphic annulus, with an opening on one side . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***T. malipoensis***
– Corolla tube apex with a ring-like and actinomorphic annulus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **2**
2. Tepals free and mitre absent . . . . . . . . . . . . . . . . . . . **3**
– Tepals connected into a loose dome or mitre . . . . . **4**

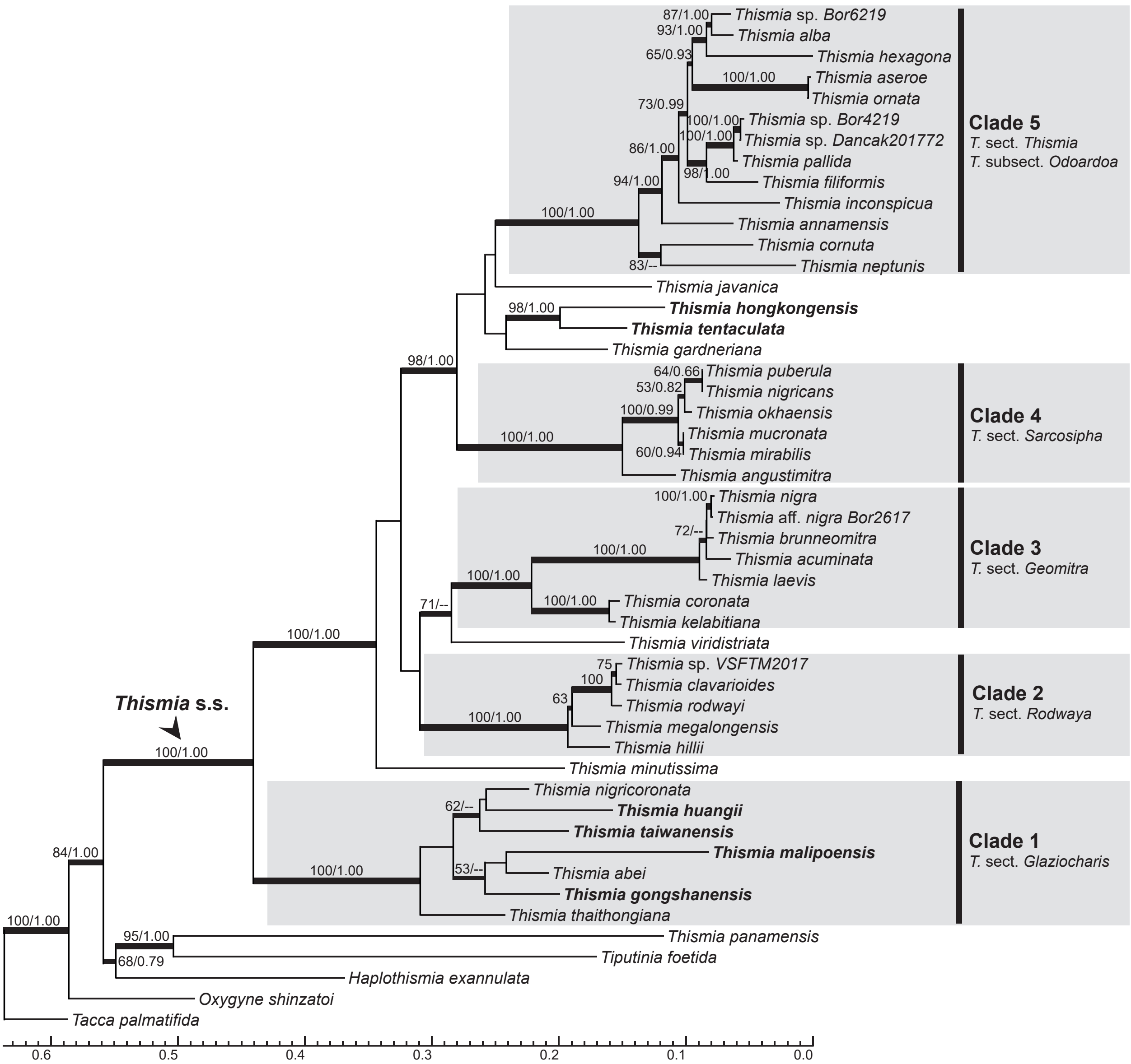

Fig. 5. Phylogeny of *Thismiaceae* inferred from the concatenated two nrDNA and two mitochondrial DNA sequences dataset. Maximum likelihood bootstrap (MLBS) and Bayesian inference posterior probability (BIPP) values are presented above the branches. The bottom scale bar represents the number of substitutions per site.

3. Inner tepal appendage c. 17 mm long, longer than perianth tube . . . . . . . . . . . . . . . . . . . . ***T. tentaculata***
– Inner tepal appendage 1–4 mm long, shorter than perianth tube . . . . . . . . . . . . . . . ***T. guangdongensis***
4. Inner tepals fused into a mitre; stigma 2-lobed . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***T. gongshanensis***
– Inner tepals forming a loose dome; stigma 3-lobed . **5**
5. Inner tepal appendage c. 30 mm long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***T. taiwanensis***
– Inner tepal appendage < 5 mm long . . . . . . . . . . . . **6**
6. Inner tepal appendage c. 1 mm long; stamen connective apex with glandular hairs . . . . . . . . . ***T. huangii***
– Inner tepal appendage 3–4 mm long; stamen connective apex without glandular hairs . . . . . . . . . . . . . . **7**
7. Perianth tube pinkish white; outer lobes separated from dome . . . . . . . . . . . . . . . . . ***T. hongkongensis***
– Perianth tube deep orange-red; outer lobes embedded in dome . . . . . . . . . . . . . . . . . . . ***T. jianfenglingensis***

## Author contributions

Ji-Dong Ya, Wen-Bin Yu and Jie Cai conceived the study; Ji-Dong Ya and Wei Zhang contributed to field surveys; Ji-Dong Ya and Wen-Bin Yu provided the species description and collected the data; Wen-Bin Yu and Hai-Yao Chen analysed the data and interpreted the results; Ji-Dong Ya, Hai-Yao Chen, Wen-Bin Yu and Jie Cai wrote and revised the manuscript; Ren-Bin Zhu and Wen-Bin Yu checked and generated the checklist of *Thismia*; all authors approved the final version of the manuscript.

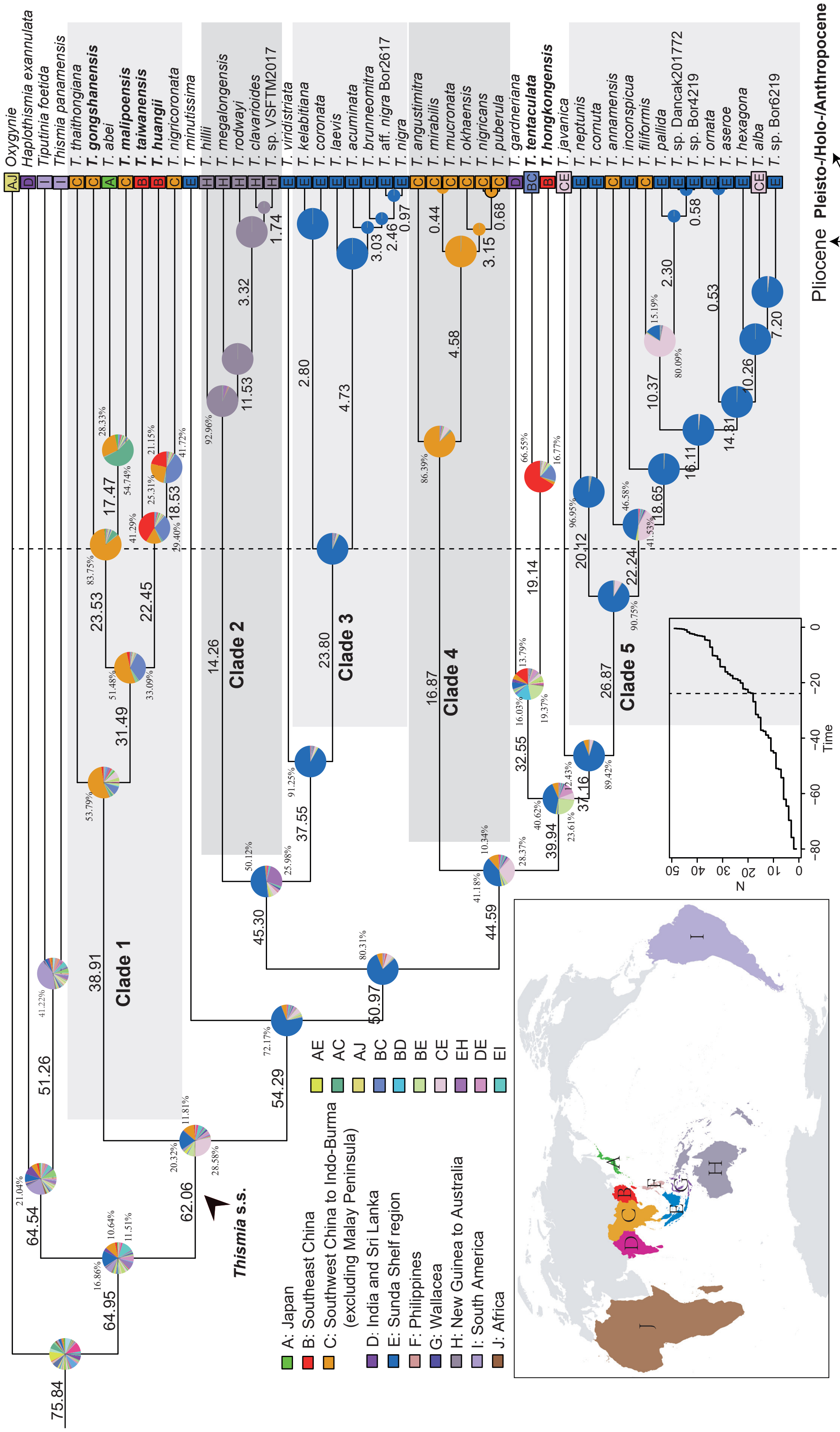

Fig. 6. Divergent time estimation and ancestral area reconstruction of *Thismiaceae*. The map shows the ten biogeographical areas. The lineages through time plot shows the diversification of *Thismiaceae*.

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## Supplemental content online

See https://doi.org/10.3372/wi.54.54102

Supplementary appendix S1. Checklist of accepted species of *Thismia* s.l. (*Thismiaceae*), including authorship(s), distribution range and publication information.

Supplementary appendix S2. Combined matrix of the four DNA markers (nrDNA 18S and ITS, mtDNA *atpA* and *matR*) in Nexus format. The matrix is partitioned by regions.

**Appendix 1**
Summary of taxon sampling for this study. Taxon names are followed by geographic origin of the sample, voucher information and GenBank accession numbers for the genes sampled: 18S, ITS, *atpA* and *matR*. Voucher information is from Dančák & al. (2020b, 2020c), Merckx & al. (2017), Shepeleva & al. (2020) and Sochor & al. (2018). Herbarium codes follow Thiers (2023+).

| **Taxon** | **Geographic origin of sample** | **Voucher information** | **GenBank accession numbers** | | | |
|---|---|---|---|---|---|---|
| | | | **18S** | **ITS** | ***atpA*** | ***matR*** |
| *Haplothismia exannulata* Airy Shaw | India | *N. Sasidharan & P. Sujanapal 30476* (KFRI) | DQ786082 | – | – | – |
| *Oxygyne shinzatoi* (Hatus.) Tsukaya | Japan: Okinawa island | *H. Tsukaya 061008* (TI) | AB437090 | – | – | – |
| *Tacca palmatifida* Baker | Indonesia | ITS: *L. Zhang ZL-003* (HITBC); 18S, *atpA* and *matR*: *M. Chase 1377* (K) | DQ786084 | JN850572 | FJ215774 | KY554903 |
| *Thismia abei* (Akasawa) Hatus. | Japan | *K. Suetsugu s.n.* (herbarium not specified) | MK356115 | MK356135 | – | – |
| *Thismia acuminata* Hroneš & al. | Malaysia: Borneo | *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & D. Atu BOR6/17* (SAR) | MG008350 | MG008338 | MG008365 | MG008392 |
| *Thismia alba* Holttum ex Jonker | Thailand | *S. Chantanaorrapint 2801* (PSU) | MK356101 | MK356123 | – | – |
| *Thismia angustimitra* Chantanaorr. | Thailand | *S. Chantanaorrapint & C. Promma 3904* (BKF, PSU) | – | MK356124 | – | – |
| *Thismia annamensis* K. Larsen & Aver. | Vietnam | *L. Averyanov, T. V. Thao & N. T. Vinh HLF 5510* (LE) | MK356119 | MK356141 | – | – |
| *Thismia aseroe* Becc. | Malaysia: Borneo | *L. Caddick 349* (SAR) | AF309404 | KY554877 | EU421048 | KY554923 |
| *Thismia brunneomitra* Hroneš & al. | Borneo | *M. Sochor, M. Dančák & M. Hroneš BOR25/19* (SAR) | MN067327 | MN067258 | MN067237 | MN067307 |
| *Thismia clavarioides* K. R. Thiele | Australia: New South Wales | *P. Jordan NSW 447624* (NSW) | KF692533 | KX790905 | KF692539 | KY554924 |
| *Thismia cornuta* Hroneš & al. | Borneo | *M. Sochor, M. Hroneš & M. Dančák BOR24/17* (SAR) | MG008352 | MG008340 | – | – |
| *Thismia coronata* Hroneš & al. | Borneo | *M. Sochor, M. Dančák & M. Hroneš BOR11/19* (SAR) | MN067320 | MN067256 | MN067234 | MN067300 |
| *Thismia filiformis* Chantanaorr. | Thailand | *S. Chantanaorrapint & C. Promma 3928* (PSU) | MK356103 | MK356126 | – | – |
| *Thismia gardneriana* Hook. f. ex Thwaites | Thailand | *S. Chantanaorrapint & C. Promma 3903* (PSU) | MK356104 | MK356127 | – | – |
| *Thismia gongshanensis* Hong Qing Li & Y. K. Bi | China: Yunnan | *Li 2008128* (HSNU) | MK356121 | MK356144 | – | – |
| *Thismia hexagona* Dančák & al. | Brunei | *M. Sochor s.n.* (SAR) | KU948543 | MG008342 | KU948541 | MG008386 |
| *Thismia hillii* (Cheeseman) N. Pfeiff. | Australia: New South Wales | *V. Merckx & al. NSW1_TH5* (NSW) | KY554861 | KX790921 | KY554871 | KY554928 |
| *Thismia hongkongensis* Mar & R. M. K. Saunders | China: Hong Kong | *S. S. Mar 3* (HK) | MK356105 | MK356128 | – | – |
| *Thismia huangii* P. Y. Jiang & T. H. Hsieh | China: Taiwan | *T. H. Hsieh & P. Y. Chiang 3031* (TAI) | KF692534 | KY554879 | KF692543 | KY554932 |
| *Thismia inconspicua* Sochor & Dančák | Brunei | *M. Sochor MS1/16* (BRUN) | KU948544 | KU948545 | KU948542 | MG008382 |

**Appendix 1** (continued from p. 61)

| | | | | | | |
|---|---|---|---|---|---|---|
| *Thismia javanica* J. J. Sm. | Myanmar | *S. Ruchisansakun 770a_4715* (L) | MK356118 | MK356136 | – | – |
| *Thismia kelabitiana* Dančák & al. | Malaysia: Borneo | *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & J. R. Pasan BOR1/17* (SAR) | MG008355 | MG008343 | MG008364 | MG008389 |
| *Thismia laevis* Sochor & al. | Malaysia: Borneo | *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & D. Atu BOR9/17* (SAR) | MG008356 | MG008344 | MG008366 | MG008390 |
| *Thismia malipoensis* J. D. Ya & W. B. Yu | China: Yunnan | *J.-D. Ya & W. Zhang 19CS18569* (KUN) | PP003243 | PP025481 | PP025350 | PP025349 |
| *Thismia megalongensis* C. A. Hunt & al. | Australia: New South Wales | *C. Hunt & G. Steenbeeke s.n.* (NSW) | KJ885661 | – | KJ885662 | KY554930 |
| *Thismia minutissima* Dančák & al. | Borneo | *M. Sochor, M. Dančák & M. Hroneš BOR63/19* (OL) | MN067315 | MN067248 | MN067228 | MN067299 |
| *Thismia mirabilis* K. Larsen | Thailand | *S. Chantanaorrapint & C. Promma 3927* (PSU) | – | MK356129 | – | – |
| *Thismia mucronata* Nuraliev | Vietnam | *M. S. Nuraliev 813* (MW) | MK356106 | MK356130 | – | – |
| *Thismia neptunis* Becc. | Malaysia: Borneo | *M. Sochor & Z. Egertová BOR51/17* (OL) | MG008357 | MG008345 | MG008368 | MG008383 |
| *Thismia nigra* Dančák & al. | Borneo | *M. Sochor, M. Hroneš & M. Dančák BOR46/17* (SAR) | MK356112 | MG008346 | MG008362 | MG008391 |
| *Thismia* aff. *nigra* Bor2617 | Malaysia: Borneo | *M. Sochor & al. BOR26/17* (SAR) | MG008351 | MG008339 | MG008361 | MG008393 |
| *Thismia nigricans* Chantanaorr. & Sridith | Thailand | *S. Chantanaorrapint & C. Promma 3897* (PSU) | MK356108 | MK356132 | – | – |
| *Thismia nigricoronata* Kumar & S. W. Gale | Laos | *Gale, Kumar, Santainsy & Phunthavong HNLKFBG 0099* (HNL) | MF589340 | – | MF589341 | – |
| *Thismia okhaensis* Luu & al. | Vietnam | *N. T. Tich, T. Gioi, D. Q. Diep, L. H. Truong & N. T. Trung KH 638B* (SGN) | – | MK356147 | – | – |
| *Thismia ornata* Dančák & al. | Borneo | *M. Sochor, M. Dančák & M. Hroneš BOR51/19* (SAR) | MN067318 | MN067255 | MN067232 | MN067302 |
| *Thismia pallida* Hroneš & al. | Malaysia: Borneo | *M. Hroneš & M. Dančák BOR62/17* (SAR) | MG008359 | MG008347 | MG008369 | MG008385 |
| *Thismia panamensis* (Standl.) Jonker | Panama | *Aizprua 2946* (LV) | DQ786081 | EU421058 | EU421050 | MT054554 |
| *Thismia puberula* Nuraliev | Vietnam | *M. S. Nuraliev 1000* (MW) | MK356109 | – | – | – |
| *Thismia rodwayi* F. Muell. | Australia: Tasmania | ITS: *V. Merckx & al. TAS1_TR1* (TAS); 18S and *atpA*: *V. Merckx & al. TAS9_TR5* (TAS); *matR*: *V. Merckx & al.* (TAS) | KY554864 | KX790888 | KY554874 | KY554926 |
| *Thismia* sp. Bor4219 | Borneo | *M. Sochor, M. Dančák & M. Hroneš BOR42/19B* (SAR) | MN067329 | MN067274 | MN067225 | MN067310 |
| *Thismia* sp. Bor6219 | Borneo | *M. Sochor, M. Dančák & M. Hroneš BOR62/19* (SAR) | MN067331 | MN067275 | MN067231 | MN067313 |
| *Thismia* sp. Dancak201772 | Brunei | *M. Dančák 2017/72* (OL) | MK356120 | MK356142 | – | – |

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| *Thismia* sp. VSFTM2017 | Australia: New South Wales | *V. Merckx NSW4_TR1* (NSW) | KY554863 | – | KY554873 | KY554925 |
| *Thismia taiwanensis* Sheng Z. Yang & al. | China: Taiwan | *S.-Z. Yang & al. 28981* (PPI) | DQ786080 | KY554880 | EU421051 | KY554933 |
| *Thismia tentaculata* K. Larsen & Aver. | China: Hong Kong | *G. Lim 31* (NY) | MK356122 | MK356145 | – | – |
| *Thismia thaithongiana* Chantanaorr. & Suddee | Thailand | *S. Chantanaorrapint 2755* (PSU) | MK356111 | MK356134 | – | – |
| *Thismia viridistriata* Sochor & al. | Malaysia: Borneo | *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & D. Atu BOR11/17* (SAR) | MG008360 | MG008348 | MG008363 | MG008387 |
| *Tiputinia foetida* P. E. Berry & C. L. Woodw. | Ecuador | *Á. J. Pérez Castañeda s.n.* (LV) | FJ215764 | – | FJ215770 | KY554910 |

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