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Thismia nigricoronata, a new species of Burmanniaceae (Thismieae, Dioscoreales) from Vang Vieng, Vientiane Province, Laos, and a key to subgeneric classification

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Abstract

Thismia nigricoronata is described as a new species in family Burmanniaceae. Both morphological and phylogenetic analyses indicate that this new Lao endemic is allied to *T. taiwanensis* in section *Glaziocharis*, and it can be differentiated on the basis of its longer vestigial stem leaves, reflexed free outer perianth lobes and ornamented, vibrantly coloured outer surface of the perianth tube. The infrageneric taxonomy of *Thismia* is reviewed, the genera *Geomitra* and *Scaphiophora* are officially reduced to sectional status in *Thismia*, and all species are enumerated in systematic order. A key to all currently accepted subgenera, sections and subsections is presented to facilitate further examination of their phylogenetic integrity in light of apparent conflict between the traditional morphology-based system and the emerging DNA-based classification.

Key words: achlorophyllous plants, Dioscoreaceae, holomycoheterotrophs, Laotian flora, Thismiaceae

INTRODUCTION

Burmanniaceae Miers (1847: 129) are a widely recognised family of mycoheterotrophic flowering plants (Chase *et al*. 1995, Chase *et al*. 2000, Woodward *et al*. 2007, Merckx 2013, Merckx & Smets 2014, Truòng *et al*. 2014). DNA analyses have indicated that the five genera typically included in tribe Thismieae, namely, *Thismia* Griffith (1845: 221), *Afrothismia* Schlechter (1906: 138), *Oxygyne* Schlechter (1906: 140), *Haplothismia* Airy Shaw (1952: 277) and *Tiputinia* Berry & Woodward (2007: 158), all fall outside Burmanniaceae (Merckx & Smets 2014), but their specific placement within the order Dioscoreales remains unclear (Merckx *et al*. 2009, Merckx & Smets 2014). In particular, tree topologies recovered in recent analyses revealed *Tacca* Forster & Forster (1776: 69) to be sister to core Thismieae species representing the genera *Thismia*, *Oxygyne*, *Haplothismia* and *Tiputinia*, but with *Afrothismia* sister to both (Merckx *et al*. 2009, Merckx & Smets 2014). Despite this apparent polyphyly, however, Thismieae are readily distinguished from *Tacca* on the basis of pollen morphology (Cranwell 1953, Chakrapani & Raj 1971), and the two have hence been treated as separate from Burmanniaceae within Dioscoreales by APG IV, in the hope that this taxonomic issue will be resolved by further study (APG, 2016).

Thismia comprises small mycoheterotrophic, ground dwelling herbs that are for the most part poorly studied (Mar & Saunders 2015). The genus is the largest of the tribe, being represented by c. 56 species (Merckx & Smets 2014, Govaerts *et al*. 2007) distributed from warm temperate and tropical Asia, eastern and southeastern Australia, New Zealand, southern North America and South America (Govaerts *et al*. 2007). Of these, 37 species are found in tropical and temperate Asia, including 12 species in the Indo-Burma Biodiversity Hotspot (Govaerts *et al*. 2007). *Thismia* is characterised by the presence of an urceolate perianth tube that is formed by the fusion of the tepals that bear two whorls with apically free lobes (Caddick *et al*. 2000, Mar & Saunders 2015). Anther morphology, presence of a mitre (a hat-like structure formed from overlapping of the inner perianth lobes that covers the annulus) and morphology of mitral appendages and perianth lobes have been used as diagnostic characters in species delimitation, although Merckx & Smets (2014) suggested that the perianth appendages may carry little phylogenetic significance in accurately assessing species relationships within the genus.

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According to the latest generic classification proposed by Merckx & Smets (2014), *Thismia* is divided into two subgenera: *Ophiomeris* (Miers 1847: 328) Maas & Maas (1986: 144), which is characterised by connate anther thecae, and *Thismia*, which is characterised by free anther thecae. Subgenus *Ophiomeris* is further divided into three sections, namely, *Myostoma* (Miers 1866: 57) Maas & Maas (1986: 158), *Ophiomeris* (Miers 1847: 328) Maas & Maas (1986: 145) and *Pyramidalis* Maas & Maas (1986: 161), whereas subgenus *Thismia* is further divided into six sections, namely, *Thismia* (*Euthismia* Schlechter, 1921: 34, which cannot be used under Article 21.3 of the Melbourne code, McNeill *et al*. 2012), *Sarcosiphon* Blume (1850: 65) Jonker (1938: 251), *Glaziocharis* (Taubert ex Warming 1901: 175) Hatusima (1976: 4), *Rodwaya* (Schlechter 1921: 38) Maas & Maas (1986: 166), *Geomitra* and *Scaphiophora*; however, sections *Geomitra* and *Scaphiophora* have never been formally published. Section *Thismia* is further divided into subsections *Odoardoa* Schlechter (1921: 34) and *Brunonithismia* Jonker (1938: 242).

The genus has received a lot of botanical interest lately with the publication of 16 new species from Asia and the Pacific (Thiele & Jordan 2002, Yang *et al*. 2002, Tsukaya & Okada 2005, Larsen & Averyanov 2007, Chantanaorrapint 2008, Chiang & Hsieh 2011, Chantanaorrapint 2012, Tsukaya & Okada 2012, Dančák *et al*. 2013, Li & Bi 2013, Nuraliev *et al*. 2014, Truòng *et al*. 2014, Mar & Saunders 2015, Nuraliev *et al*. 2015, Chantanaorrapint & Sridith 2015), as well as several new records (Chantanaorrapint & Sridith 2007, Chantanaorrapint & Chantanaorrapint 2009, Ho *et al*. 2009) in the last 15 years alone.

During a field survey in Laos in April 2012, the first two authors came across a population of a terrestrial herb in *Thismia*. After a thorough literature survey, it was found to be an undescribed species in section *Glaziocharis*, described here as *T. nigricoronata*.

MATERIALS AND METHODS

Morphological data

Morphological study was conducted on living as well as preserved specimens collected in the field in Laos. Voucher specimens were deposited at Herbier National du Laos (HNL). A detailed taxonomic description was prepared, and critical comparison with allied species was undertaken. In order to clarify morphological features used to define infrageneric taxa and facilitate subsequent systematic studies of Thismiaceae, a unified key to the subgenera, sections and subsections of *Thismia* was compiled and is presented here.

Phylogenetic analysis

Sampling:—Sequence data (nuclear ribosomal 18S DNA and mitochondrial *atp1*) for 13 accessions representing ten species of Thismieae (Table 1). Given recent phylogenetic evidence to suggest that *Afrothismia* is an independent clade sister to the other four genera typically included in Thismieae (*Thismia*, *Oxygyne*, *Haplothismia* and *Tiputinia*) plus *Tacca* (Merckx & Smets 2014), *Afrothismia* was excluded from our analysis. The plants discovered in Laos were sequenced using standard protocols as described below. Two species, *Tacca leontopetaloides* (Linneì 1753: 313) Kuntze (1891: 704) and *Tacca parkeri* Seemann (1866: 102), were chosen as outgroups following Merckx & Smets (2014).

DNA extraction and phylogenetic analysis:—Total DNA was extracted from a dried flower of the collection from Laos using the QIAGEN DNeasy® plant DNA kit (Hilden, Germany) according to the manufacturer's instructions. Using the primers NS1, NS2, NS3, NS4, NS5 and NS8 (White *et al*. 1990), 18S rDNA was amplified, and mitochondrial *atp1* was amplified with the primers and conditions described by Eyre-Walker & Gaut (1997). PCR was performed in a total reaction mixture of 25 µl containing 1 µl of template DNA (2–10 ng), 5 µl of 5 × Phire® reaction buffer with MgCl2, 0.5 µl 10 mM of dNTP mix, 0.5 µl of Phire® hot start II DNA polymerase (Finnzymes, Finland) and 10 pmol of each primer (Beijing Genomics Institute). The thermal cycler programme consisted of an initial denaturation step of 30 s at 98°C, followed by 35 cycles of 5 s at 98°C, 10 s at 60°C for 18S rDNA and 10 s at 55°C for *atp1*, 20 s at 72°C, and a final extension of 1 min at 72°C. Amplification products were purified using a DNA purification Kit (Beijing Genomics Institute). Purified PCR products were sequenced using an ABI 3730 DNA Sequencer (Beijing Genomics Institute, Hong Kong).

Alignment was conducted using the MAFFT multiple alignment plugin in Geneious v6.1.6 (Drummond *et al*. 2011), with subsequent adjustment by eye. An incongruence length difference (ILD) test (Farris *et al*. 1995) was performed in PAUP* v4.0b10 (Swofford 2003) to assess whether the 18S rDNA and *atp1* data sets reflect similar potential trees; 1,000 replicates, each with 1,000 random addition sequence replicates and TBR branch swapping, were performed in each test, and a P value of < 0.05 was considered significant (Sullivan 1996, Darlu & Lecointre 2002).

A "hard" incongruence test was also performed by directly comparing respective topologies and resolution for each of the clades generated in the separate analyses, with bootstrap percentages (BP) of ≥ 85 (Chase *et al*. 2000) and posterior probabilities (PP) of ≥ 0.95 (Martínez-Azorín *et al*. 2011) being taken as evidence of strong support.

Phylogenetic analysis of individual and multilocus alignments were carried out using maximum parsimony (MP) in PAUP* v4.0b10 and Bayesian inference (BI) in MrBayes v3.2 (Huelsenbeck & Ronquist 2003). For MP analyses, heuristic searches were conducted with 1,000 random addition replicates followed by tree bisection-reconnection branch swapping. All characters were unordered and equally weighted with gaps (including unavailable sequences) treated as missing data. Topological robustness was assessed using 1,000 bootstrap replicates. For BI analyses, each DNA region was assigned its own model of nucleotide substitution, as determined by the Akaike information criterion (AIC) in Modeltest v3.06 (Posada & Crandall 1998). Four simultaneous Monte Carlo Markov Chains (MCMC) were run, with sampling one tree every 1,000 generations for 3,000,000 generations, starting with a randomly generated tree. Majority rule (> 50%) consensus trees were constructed after removing the first 25% of sampled trees as burn-in.

Conservation status

A conservation assessment was carried out using the criteria of IUCN (2012).

TABLE 1. A list of samples.

Species	GenBank accession numbers	
	18S nrDNA	***atp1***
Thismia aseroe	AF309404	EU421048
Thismia clavarioides	KF692533	KF692539
Thismia clavigera	AF309405	EU421049
Thismia huangii	KF692534	KF692543
Thismia javanica	KF692535	-
Thismia hillii (accessioned as *Thismia rodwayi*)*	AF309403	AY299849
Thismia rodwayi (TAS1)	KF692536	KF692540
Thismia rodwayi (TAS2)	KF692537	KF692542
Thismia rodwayi (VIC)	KF692538	KF692541
Thismia taiwanensis	DQ786080	EU421051
Thismia nigricoronata sp. nov.	MF589340	MF589341
Haplothismia exannulata	DQ786082	EU421037
Tiputinia foetida	FJ215764	FJ215770
Tacca leontopetaloides	EU420999	AF039252
Tacca parkeri	EU421001	JN850562

*Merckx & Smets (2014) explain use of this name.

RESULTS

Morphological analysis

Examination of the plants collected from Vang Vieng, Laos, revealed them to possess free anther thecae, placing them in subgenus *Thismia*, and an urceolate perianth tube bearing a mitre with prominent outer perianth lobes and long filiform appendages arising from the free part of the inner perianth lobe, suggesting they belong to section *Glaziocharis*. The same combination of characters closely allies it to *Thismia taiwanensis* (Yang *et al*. 2002: 485), which also belongs to section *Glaziocharis*. However, the plants are distinct from *T. taiwanensis* in having longer vestigial stem leaves, reflexed free outer perianth lobes and an ornamented, vibrantly coloured outer surface of the perianth tube.

Phylogenetic analysis

Statistics relating to the phylogenetic analysis for 18S rDNA and *atp1* sequence data were newly generated for the Lao *Thismia* and the combined data set are given in Table 2. Tree topologies generated for the 18S rDNA data partition using BI (Fig. 1) were approximately congruent with those using MP. Given this, the 13 samples of family Thismiaceae included here formed a strongly supported clade (BP 100, PP 1.00) within which the genus *Thismia*, represented by 11 samples, formed a strongly supported clade (BP 81, PP 1.00). The 11 *Thismia* samples were clearly resolved into two distinct clades: one comprising *T. hillii*, *T. clavarioides*, *T. rodwayi*, *T. clavigera*, *T. javanica* and *T. aseroe* that received moderate BP (82) and strong PP (1.00) support, and another comprising *T. taiwanensis, T. huangii* and the collection

from Laos, which was also strongly supported (BP 99, PP 1.00). Within this clade, the collection from Laos fell sister to *T. huangii*, although support for this relationship was very weak (BP 53, PP 0.53).

TABLE 2. Statistics relating to the DNA data sets used in this study.

Information	18S rDNA	*atp*1	Combined 18S rDNA and *atp1* data sets
Aligned length	1,620	1,186	2,806
No. of variable characters	111	53	164
Parsimony-informative characters	172	63	235
Tree length	510	149	661
Consistency index	0.68	0.89	0.73
Retention index	0.69	0.90	0.74
Best-fit model determined by AIC in Modeltest	GTR+I+G	TIM+I+G	GTR+I+G

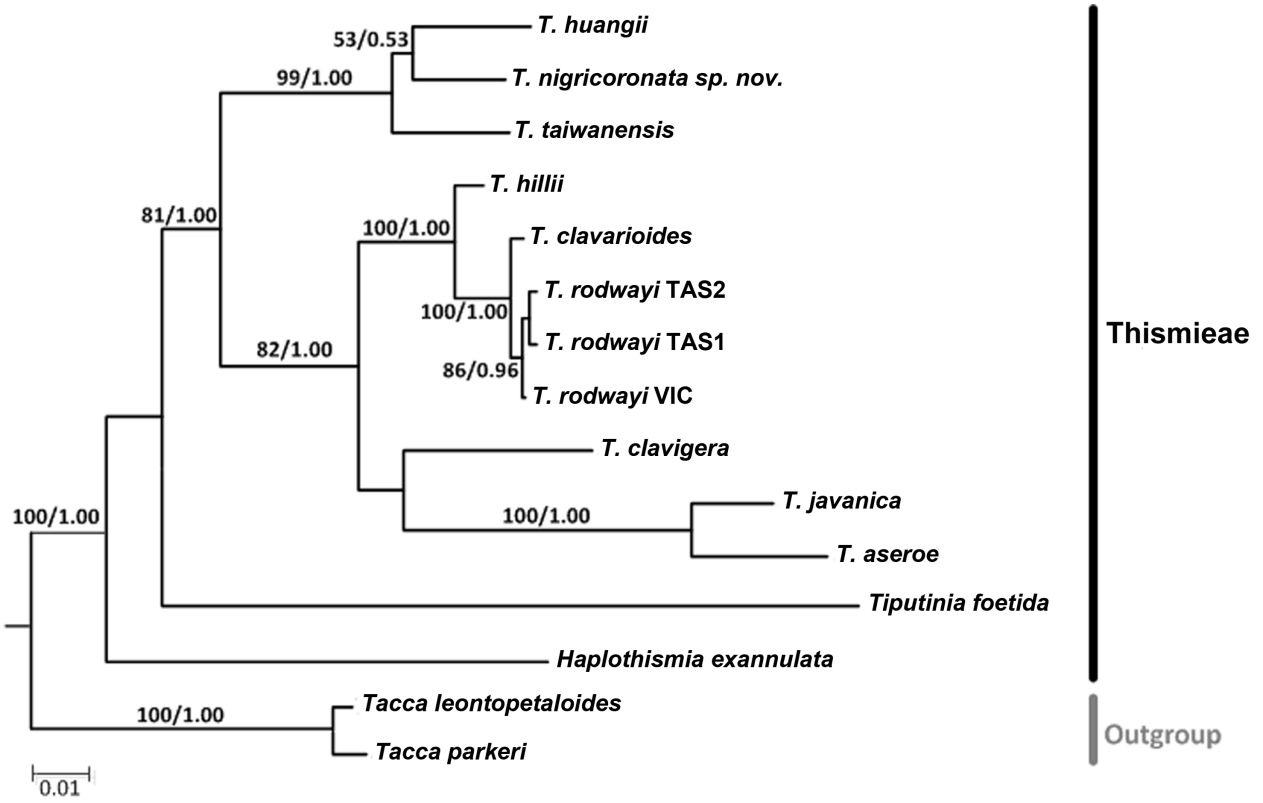

FIGURE 1. Bayesian inference (BI) tree from analysis of 18s rDNA data. Numbers at the nodes indicate MP bootstrap percentages and Bayesian posterior probabilities, respectively.

The topology of the *atp1* tree (Fig. 2) was mostly concordant with the 18s rDNA phylogram. The 12 Thismiaceae samples formed a strongly supported clade (BP 100, PP 1.00), within which the ten samples representing genus *Thismia* again formed a strongly supported clade (BP 99, PP 1.00) composed of two discrete subclades, each comprising the same samples as in the 18s rDNA analysis, except that *T. javanica* was not included in this analysis because *atp1* sequence data were not available for this taxon. A clade comprising *T. taiwanensis*, *T. huangii* and the Lao material was again strongly supported (BP 98, PP 1.00), with a sister relationship between the latter two receiving moderate support (BP 64, PP 0.89).

A homogeneity test for the 18S rDNA and *atp1* data sets gave a *P* value of 0.76, indicating that there was no significant incongruence between the two regions. Moreover, visual node-by-node comparisons of trees generated for each region individually revealed no major disparity in topology for nodes of BP ≥ 85 or PP ≥ 0.95. Given this, we combined the two regions into a single analysis. Tree topologies generated by BI (Fig. 3) and MP analyses were consistent. This combined analysis resulted in greater resolution as compared with the separate analyses.

Thismiaceae formed a strongly supported clade (BP 100, PP 1.00) with the 11 *Thismia* samples forming two distinct clades composed of samples consistent with the individual 18s rDNA and *atp1* trees. Within the strongly supported clade (BP 100, PP 1.00) comprising *T. taiwanensis*, *T. huangii* and the collection from Laos, the latter two again fell sister to one another with weak support (BP 72, PP 0.77).

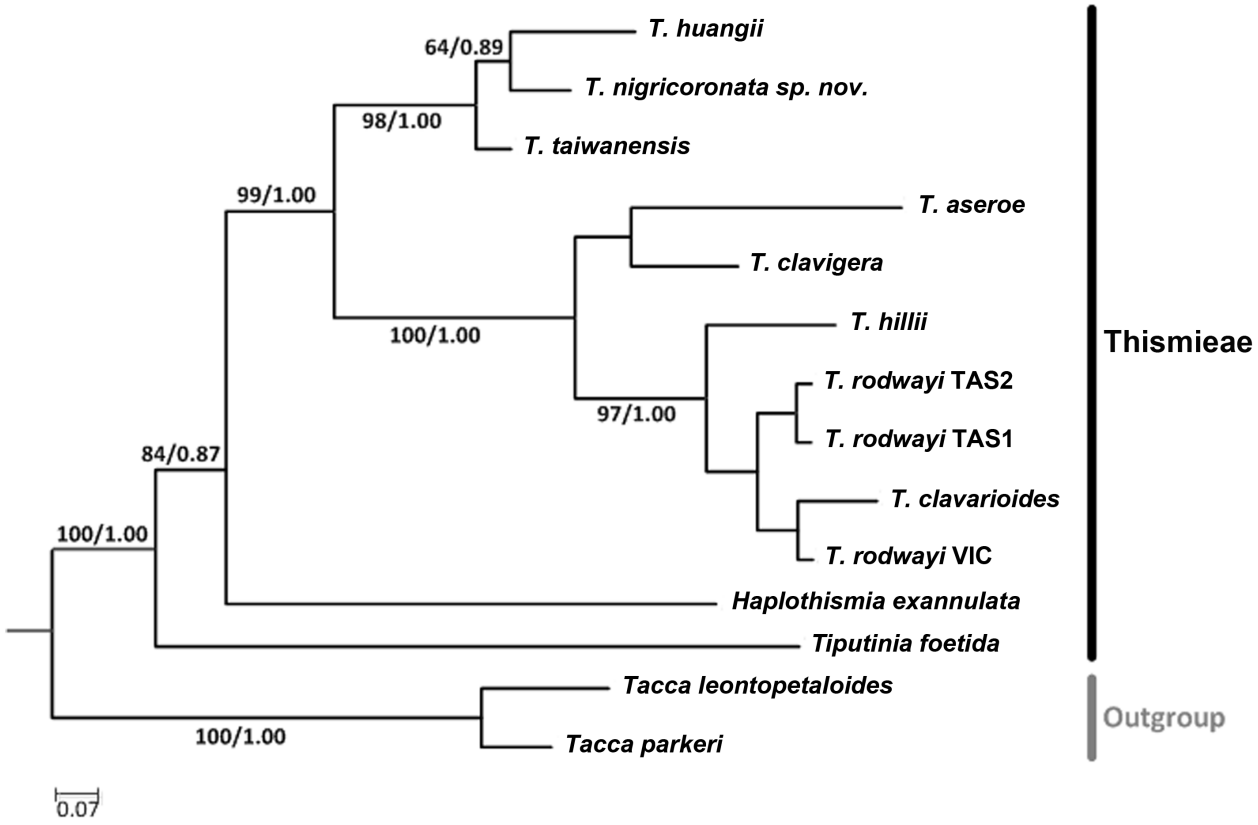

FIGURE 2. Bayesian inference (BI) tree from analysis of *atp1* data. Numbers at the nodes indicate MP bootstrap percentages and Bayesian posterior probabilities, respectively.

DISCUSSION

A specific combination of floral characters places the Lao plants unequivocally in *Thismia* section *Glaziocharis*. Given the significance of the characters that then distinguish them from *T. taiwanensis*, morphologically the most similar, it appears justified to regard them as an undescribed new species.

Molecular phylogenetic reconstruction also retrieves strong support for the placement of this taxon in a clade containing *T. taiwanensis*. However, within this clade, the new species falls sister to the morphologically distinct *T. huangii*, which has previously been assigned to section *Rodwaya* on account of its free anther thecae and its outer perianth lobes that lack filiform appendages. Furthermore, *T. clavarioides*, the other member of section *Glaziocharis* included in this study, does not associate with either *T. taiwanensis* or the Lao collection in our trees. This outcome corresponds with Merckx & Smets (2014) and corroborates their conclusion that the presence of perianth appendages may not be a phylogenetically informative character. The basis for incongruence between the morphology-based classification and the relationships inferred through molecular phylogenetic analysis requires further study. These appendages may be tracking pollinator relationships rather than phylogenetic relationships.

At present, sampling within tribe Thismieae for phylogenetic reconstruction remains low, limiting the taxonomic conclusions that can be drawn. The emerging picture suggests that the floral characters traditionally emphasised in defining infrageneric divisions may not reflect phylogeny, but it is also plausible that the two regions currently sequenced simply do not provide adequate resolution. To facilitate reappraisal of the current classification as more evidence becomes available, below we present a key to the subgenera and sections of *Thismia*, highlighting the critical morphological characters previously used to distinguish them and underscoring the need for broader sampling in molecular studies with which to evaluate infrageneric relationships.

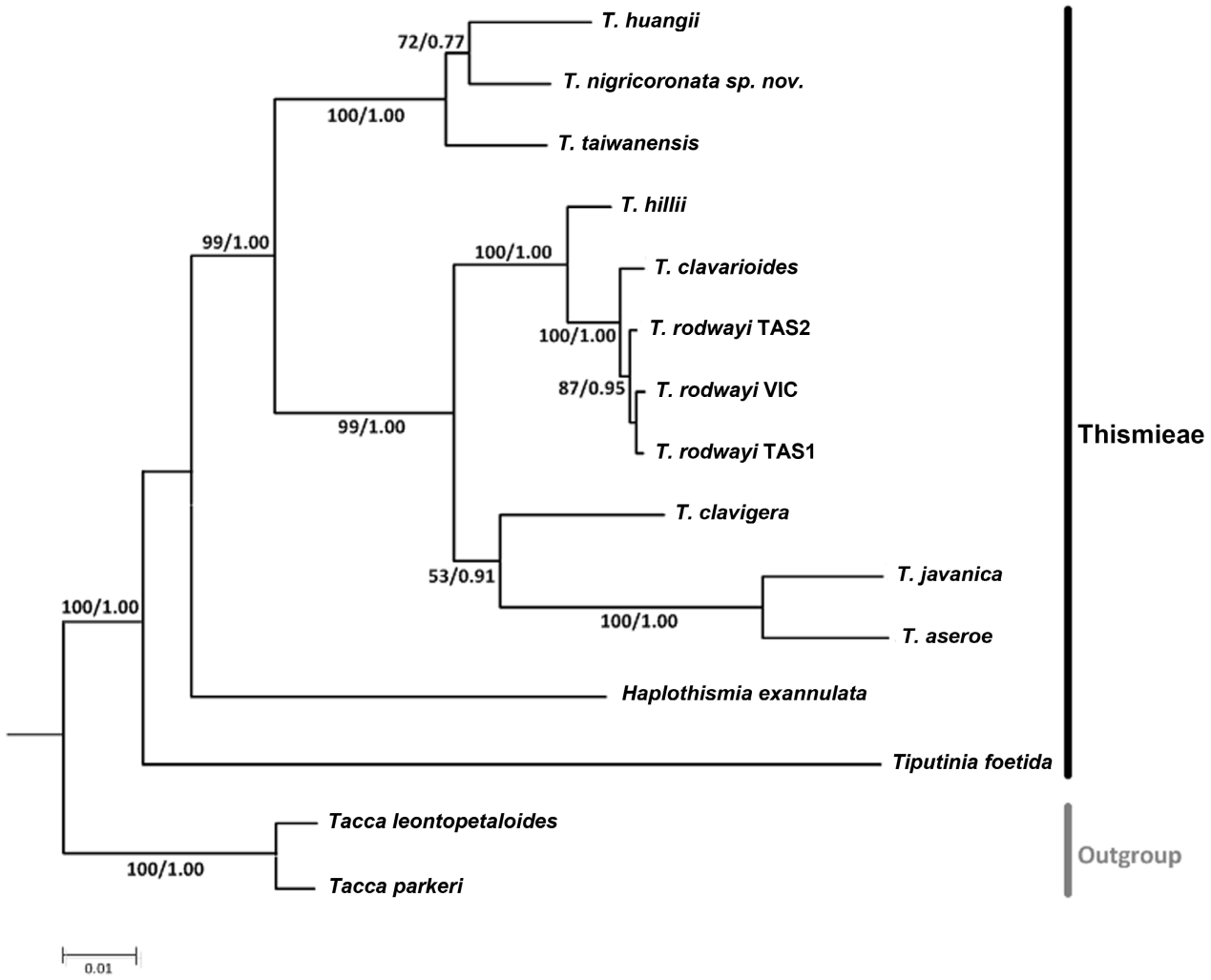

FIGURE 3. Bayesian inference (BI) tree from analysis of the combined 18s rDNA and *atp1* data. Numbers at the nodes indicate bootstrap percentages and Bayesian posterior probabilities, respectively.

TAXONOMIC TREATMENT

Thismia Griffith (1845: 221).

Ophiomeris Miers (1847: 328), *Sarcosiphon* Blume (1849: 65), *Tribrachys* Champion ex Thwaites (1864: 325) nom. inval., *Myostoma* Miers (1866: 474), *Bagnisia* Beccari (1878: 249), *Geomitra* (Beccari 1878: 250), *Rodwaya* Mueller (1890: 116) nom. inval., *Triscyphus* Taubert (1895: 66), *Glaziocharis* (Taubert ex Warming 1901: 175), *Scaphiophora* Schlechter (1921: 39), *Triurocodon* Schlechter (1921: 41), *Mamorea* de la Sota (1960: 43).

Type:—*Thismia brunonis* Griffith (1845: 221).

Terrestrial, mycoheterotrophic herbs with tubers or coralloid roots. Stems unbranched. Leaves present or absent; if present, vestigial, scaly and colourless. Inflorescence terminal, solitary or more than 1, cymose or paniculate. Flowers actinomorphic or zygomorphic, often vibrantly coloured or colourless. Perianth campanulate, forming an urceolate, cylindrical or obconical tube. Tepals 6, free or inner 3 fused to form a mitre above the floral tube. Stamens 6, rarely 3, epipetalous, suspended inside the perianth tube, forming a staminal tube or reflexed outside, thecae connate or fused, dehiscing longitudinally, connective adnate. Ovary inferior, unilocular with 3 parietal placentas, ovules numerous, style short, thick; stigma 3, free or fused. Fruit cupular or a dry capsule. Seeds numerous, attached to the 3 parietal placentae, dust-like. Embryo undivided, homogeneous.

Key to identification of the subgenera, sections and subsections of *Thismia*

1. Anther thecae connate (subgenus *Ophiomeris*) 2
- Anther thecae free (subgenus *Thismia*) 4
2. Rootstock vermiform, stem terete, vestigial stem leaves present, mitre present, stamen connective touching or fused to formstaminal tube ..... section *Pyramidalis*
- Rootstock tuberous, stem sulcate, stem leaves absent, mitre absent, stamen connective free 3
3. Anthers sagittate with single tip ..... section *Myostoma*
- Anthers sagittate with double tip ..... section *Ophiomeris*
4. Mitre present 5
- Mitre absent (section *Thismia*) 9
5. Outer perianth lobes less than 2 mm long or absent 6
- Outer perianth lobes more 2 mm long 8
6. Mitre without filiform appendages ..... section *Sarcosiphon*
- Mitre with filiform appendages 7
7. Central mitral appendages free from each other ..... section *Geomitra*
- Central mitral appendages fused into a column ..... section *Scaphiophora*
8. Outer perianth lobes with filiform appendages ..... section *Glaziocharis*
- Outer perianth lobes without filiform appendages ..... section *Rodwaya*
9. Free perianth lobes of similar shape and size ..... subsection *Odoardoa*
- Free perianth lobes distinctly dissimilar in shape and size ..... subsection *Brunonithismia*

INFRAGENERIC CLASSIFICATION OF GENUS *THISMIA*

Thismia subg. ***Ophiomeris*** (Miers) Maas & Maas (1986: 165). [basionym: *Ophiomeris* Miers (1847: 328)].

Type:—*Thismia macahensis* (Miers) Mueller (1891: 232). [basionym: *Ophiomeris macahensis* Miers (1847: 329)].

Thismia subg. ***Ophiomeris*** sect. ***Ophiomeris*** (Miers) Maas & Maas (1986: 145).

[basionym: *Ophiomeris* Miers (1847: 328)].

Type:—*Thismia macahensis* (Miers) Mueller (1891: 232). [basionym: *Ophiomeris macahensis* Miers (1847: 329)].

Species included:

T. espiritosantensis Brade, *Revista Brasil. Biol.* 7: 286 (1947).

T. glaziovii Poulsen, *Rev. Gén. Bot.* 1: 549 (1889).

T. iguassuensis (Miers) Warm., *Overs. Kongel. Danske Vidensk. Selsk. Forh. Medlemmers Arbeider* 1901(6): 182 (1902).

T. janeirensis Warm., *Overs. Kongel. Danske Vidensk. Selsk. Forh. Medlemmers Arbeider* 1901: 183 (1902).

T. luetzelburgii Goebel & Suess., *Flora* 117: 56 (1924).

T. macahensis (Miers) F.Muell., *Pap. & Proc. Roy. Soc. Tasmania* 1890: 232 (1891).

T. panamensis (Standl.) Jonker, *Monogr. Burmann.*: 234 (1938).

T. prataensis Mancinelli, C.T.Blum & E.C.Smidt, *Syst. Bot.* 37: 879 (2012).

T. saulensis H.Maas & Maas, *Brittonia* 39: 376 (1987).

Thismia subg. ***Ophiomeris*** sect. ***Myostoma*** (Miers) Maas & Maas (1986: 158). [basionym: *Myostoma* Miers (1866: 474)].

Type:—*Thismia hyalina* (Miers) Benth. & Hook.f. ex Mueller (1891: 234). [basionym: *Myostoma hyalinum* Miers (1866: 25)].

Species included:

T. hyalina (Miers) Benth. & Hook.f. ex F.Muell. *Pap. & Proc. Roy. Soc. Tasmania*1890: 234 (1891).

Thismia subg. ***Ophiomeris*** sect. ***Pyramidalis*** Maas & Maas (1986: 161).

Type:—*Thismia caudata* Maas & Maas (1986: 162).

Species included:

T. caudata Maas & H.Maas, *Fl. Neotrop. Monogr.* 42: 162 (1986).

T. fungiformis (Taub. ex Warm.) Maas & H.Maas, *Fl. Neotrop. Monogr.* 42: 165 (1986).

T. melanomitra Maas & H.Maas, *Opera Bot.* 92: 141 (1987).

T. singeri (de la Sota) Maas & H.Maas, *Fl. Neotrop. Monogr.* 42: 166 (1986).

Thismia subg. ***Thismia***

Type:—*Thismia brunonis* Griffith (1845: 221).

Thismia subg. ***Thismia*** sect. ***Thismia***

Type:—*Thismia brunonis* Griffith (1845: 221).

Note: Originally published as "*Euthismia*" (Schlechter 1921: 34), but the prefix "*Eu*-" is no longer permitted (McNeill *et al*. 2012, Article 21.3).

Thismia subg. ***Thismia*** sect. ***Thismia*** subsect. ***Brunonithismia*** Jonker (1938: 242).

Type:—*Thismia brunonis* Griffith (1845: 221).

Species included:

T. arachnites Ridl., *J. Straits Branch Roy. Asiat. Soc.* 44: 197 (1905).

T. brunonis Griff., *Proc. Linn. Soc. London* 1: 221 (1845).

T. gardneriana Hook.f. ex Thwaites, *Enum. Pl. Zeyl.*: 325 (1864).

T. hongkongensis Mar & R.M.K.Saunders, *PhytoKeys* 46: 23 (2015).

T. javanica J.J.Sm., *Ann. Jard. Bot. Buitenzorg* 23: 32 (1910).

T. labiata J.J.Sm., *Bull. Jard. Bot. Buitenzorg*, sér. 3, 9: 220 (1927).

T. neptunis Becc., *Malesia* 1: 251 (1878).

T. tentaculata K.Larsen & Aver., *Rheedea* 17: 16 (2007).

Thismia subg. ***Thismia*** sect. ***Thismia*** subsect. ***Odoardoa*** Schlechter (1921: 34).

Type:—*Thismia aseroe* Beccari (1878: 252), **designated here**.

Species included:

T. alba Holttum ex Jonker, *Fl. Males.* 4: 23 (1948).

T. annamensis K.Larsen & Aver., *Rheedea* 17: 13 (2007).

T. aseroe Becc., *Malesia* 1: 252 (1878).

T. bifida M.Hotta, *Acta Phytotax. Geobot.* 22: 161 (1967).

T. chrysops Ridl., *Ann. Bot. (Oxford)* 9: 323 (1895).

T. hexagona Dancák, Hroneš, Kobrlová & Sochor, *Phytotaxa* 125: 34 (2013).

T. hexagona var. grandiflora Tsukaya, Suleiman & H.Okada, *Acta Phytotax. Geobot.* 65: 142 (2014).

T. filiformis Chantanaorr., *Kew Bull.* 67: 69 (2012).

T. fumida Ridl., *J. Straits Branch Roy. Asiat. Soc.* 22: 338 (1890).

T. grandiflora Ridl., *Ann. Bot. (Oxford)* 9: 324 (1895).

T. lauriana Jarvie, *Blumea* 41: 259 (1996).

T. mullerensis Tsukaya & H.Okada, *Acta Phytotax. Geobot.* 56: 129 (2005).

T. ophiuris Becc., *Malesia* 1: 252 (1878).

T. racemosa Ridl.. *J. Straits Branch Roy. Asiat. Soc.* 68: 13 (1915).

Notes:—*Thismia aseroe* Becc. is selected as the type in accordance with Article 10.2 of the Melbourne Code (McNeill *et al.*, 2012).

Thismia subg. ***Thismia*** sect. ***Sarcosiphon*** (Blume) Jonker (1938: 251). [basionym: *Sarcosiphon* Blume (1849: 65)].

Type:—*Thismia clandestina* (Blume) Miquel 616 (1859: 616). [basionym: *Sarcosiphon clandestinum* Blume (1849: 65)].

Species included:

T. angustimitra Chantanaorr., *Blumea* 53: 524 (2008).

T. brunneomitra Hrones, Kobrlová & Dancák, *Phytotaxa* 234: 173 (2015).

T. clandestina (Blume) Miq., *Fl. Ned. Ind*. 3: 616 (1859).

T. crocea (Becc.) J.J.Sm., *Nova Guinea* 8 (1): 193 (1909).

T. episcopalis (Becc.) F.Muell., *Pap. & Proc. Roy. Soc. Tasmania* 1890: 235 (1891).

T. goodii Kiew, *Gard. Bull. Singapore* 51: 179 (1999).

T. mirabilis K.Larsen, *Dansk Bot. Ark.* 23: 171 (1965).

T. mucronata Nuraliev, *Phytotaxa* 167: 246 (2014).

T. nigricans Chantanaorr. & Sridith, *Phytotaxa* 217: 294 (2015).

T. okhaensis Luu, Tich, G.Tran & Dinh, *Phytotaxa* 164: 190 (2014).

T. puberula Nuraliev, *Phytotaxa* 234: 135 (2015).

T. yorkensis Cribb, *Queensland Naturalist* 33: 51 (1995).

Thismia subg. ***Thismia*** sect. ***Glaziocharis*** (Taub. ex Warm.) Hatusima (1976: 4). [basionym: *Glaziocharis* Warming (1901: 175)].

Type:—*Thismia abei* (Akasawa) Hatusima (1976: 7). [basionym: *Glaziocharis abei* Akasawa (1950: 193)], **designated here**.

Species included:

T. abei (Akasawa) Hatus., *J. Geobot.* 24: 7 (1976).

T. clavarioides K.R.Thiele, *Telopea* 9: 766 (2002).

T. gongshanensis Hong Qing Li & Y.K.Bi, *Phytotaxa* 105: 25 (2013).

T. nigricoronata Kumar & S.W.Gale *sp. nov.*

T. taiwanensis Sheng Z.Yang, R.M.K.Saunders & C.J.Hsu, *Syst. Bot.* 27: 485 (2002).

T. tuberculata Hatus., *J. Geobot.* 24: 4 (1976).

Notes:—Warming (1901) described a single species, *Glaziocharis macahensis* Taub. ex Warm., in his genus *Glaziocharis*, but this was an illegitimate name [(Article 11.1, Melbourne Code (McNeill *et al.*, 2012)] due to the prior existence of *T. macahensis* (Miers) Mueller (1891: 232) and is now considered a synonym of *Thismia caudata* Maas & Maas (1986: 162). The latter species possesses connate anther thecae, a character of subgenus *Ophiomeris*, and has hence been transferred to subgenus *Ophiomeris* as the type of section *Pyramidalis* (Maas & Maas 1986). When describing section *Glaziocharis*, Hatusima (1976) included three species, namely, *T. abei* (Akasawa) Hatus., *T. tuberculata* Hatus. and *T. macahensis* (Taub. ex Warm.) Hatus., of which two remain in the section and might therefore be considered as candidate types. In accordance with Article 10.2 of the Melbourne Code (McNeill *et al.*, 2012), we designate *Thismia abei* (Akasawa) Hatus. as the type for this section because it clearly exhibits features characteristic of section *Glaziocharis* and due to the presence of a detailed description and illustration in the protologue.

Thismia subg. ***Thismia*** sect. ***Rodwaya*** (Schlechter 1921: 38) Maas & Maas (1986: 166). [basionym: *Thismia* sect. *Rodwaya* Schlechter (1921: 38) ≡ *Rodwaya* Mueller (1890: 116), nom. inval.].

Type:—*Thismia rodwayi* Mueller (1890: 115).

Species included:

T. hillii (Cheesem.) N.Pfeiff., *Bot. Gaz.* 57: 122 (1914).

T. americana N.Pfeiff., *Bot. Gaz.* 57: 123 (1914).

T. huangii P.Y.Jiang & T.H.Hsieh, *Taiwania* 56: 139 (2011).

T. rodwayi F.Muell.. *Vict. Naturalist* 7: 115 (1890).

Thismia subg. ***Thismia*** sect. ***Geomitra*** (Becc.) Kumar & S.W. Gale, ***comb. nov.*** [basionym: *Geomitra* Beccari (1878: 250) ≡ *Bagnisia* sect. *Geomitra* (Becc.) Engler (1888: 48)].

Type:—*Thismia clavigera* (Becc.) Mueller (1891: 235) [basionym: *Geomitra clavigera* Beccari (1878: 251)], designated by Jonker (1938: 255).

Species included:

T. clavigera (Becc.) F.Muell., *Pap. & Proc. Roy. Soc. Tasmania* 1890: 235 (1891).

T. betungkerihuensis Tsukaya & H.Okada, *Syst. Bot.* 37: 56 (2012).

Notes:—Beccari established the genera *Bagnisia* (based on *B. crocea* Beccari (1878: 249)) and *Geomitra* (based on *G. episcopalis* Beccari (1878: 250) and *G. clavigera* Beccari (1878: 251)) in 1878, but Bentham & Hooker (1883) later suggested that the two were congeneric on account of both sharing a fleshy, leafless habit. Engler (1888) accordingly reduced *Geomitra* to sectional rank within *Bagnisia* but without designating a type, simultaneously making the new combination *B. episcopalis* (Beccari 1878: 250) Engler (1888: 48) and creating *B.* sect. "*Eubagnisia*" (not validly published: Art. 21.3) to accommodate *B. crocea*. Mueller (1891) subsequently transferred both *Geomitra* and *Bagnisia* to the genus *Thismia*, judging the difference in perianth lobe morphology that separates them (united in the former two, free in the latter) to be too minor for recognition at generic level. Jonker (1938) nevertheless treated *Geomitra* at genus level and selected *G. clavigera* as its type. Various authors have since either maintained *Geomitra* as a separate genus (Govaerts *et al*. 2007) or synonymised it under *Thismia* (Stone 1980; Merckx *et al*. 2006; Chantanaorrapint & Chantanaorrapint 2009; Hunt *et al*. 2014; Merckx & Smets 2014). Most recently, Merckx & Smets (2014) listed *Geomitra* as one of six sections within *Thismia* subg. *Thismia* but without formally making the combination. We therefore validate *Geomitra* as a section within *Thismia* here.

Thismia subg. ***Thismia*** sect. ***Scaphiophora*** (Schltr.) Kumar & S.W.Gale ***comb. & stat. nov.*** [basionym: *Scaphiophora* (Schlechter 1921: 39)].

Type:—*Thismia appendiculata* Schlechter (1918: 202) ≡ *Scaphiophora appendiculata* (Schltr.) Schlechter (1921: 39).

Species included:

T. appendiculata Schltr., *Bot. Jahrb. Syst.* 55: 202 (1918).

T. gigantea (Jonker) Hroneš, *Phytotaxa* 172: 55 (2014).

Notes:—Schlechter (1918) described the species *Thismia appendiculata* (Schlechter 1918: 203) from New Guinea. He later proposed the new genus *Scaphiophora* (Schlechter 1921: 39) along with the new combination *S. appendiculata* (Schlechter 1918: 202) Schlechter (1921: 39), highlighting the connate appendages of the perianth lobes as one of the main characters to differentiate *Scaphiophora* from *Thismia* (in which the perianth lobe appendages are free). Jonker (1938) accepted the new genus and added one more species, *S. gigantea* (Jonker 1938: 257), which was later transferred to *Thismia* as *T. gigantea* (Jonker 1938: 257) Hroneš (2014: 55), following Merckx *et al*. (2013) and Merckx & Smets (2014). This new combination has been accepted and followed thereafter (Govaerts *et al*. 2007). Based on morphological and DNA analysis, Merckx & Smets (2014) informally reduced *Scaphiophora* to sectional rank within *Thismia* but without validly publishing the sectional name. It is therefore formally validated here.

NEW SPECIES

Thismia nigricoronata Kumar & S.W.Gale, *sp. nov.* (Figs. 4, 5)

Type:—LAOS. Vientiane Province: Vang Vieng District, Nam Pae Village, elevation 544 m, 28 April 2012, *Gale, Kumar, Santainsy & Phunthavong HNL-KFBG 0099* (holotype: HNL, spirit).

Thismia nigricoronata is morphologically similar to *Thismia taiwanensis* but can be differentiated on the basis of its longer vestigial stem leaves (more than 6 mm long in the former versus less than 6 mm in the latter); its reflexed free outer perianth lobes (versus erect and projecting upwards in the latter); the ornamented outer surface of its perianth tube, which is verrucose below and papillose above (versus smooth and glabrous in the latter); and its vibrantly coloured perianth tube (versus translucent white in the latter).

Terrestrial, mycoheterotrophic herbs, erect, ca. 5.5 cm tall. Roots clustered, prostrate, unbranched, pale yellow-brown, vermiform, 3.2–7.5 × 0.8–1.5 mm, tapering towards apex. Stem erect, 10.3–14.5 × 1.2–1.5 mm at the base, ca. 2.5–3.0 mm wide near the apex; unbranched, off-white, somewhat translucent, covered with the bases of sheathing vestigial leaves. Leaves entire, white, translucent, shiny, scattered along the stem, obovate, upper ones 6.0–7.5 × 1.0–1.5 mm at base, lower ones up to 5.0–5.3 mm long, acute, margin smooth. Pedicel white, ca. 0.50 × 1.75 mm, finely and irregularly verrucose. Flowers solitary, actinomorphic, 25–40 mm long, 7.0–7.5 mm wide; tepals fused to form an urceolate perianth tube with a whorl of 3 inner and 3 outer free apical perianth lobes. Perianth tube obovoid, clearly divisible into upper and lower parts by the point of placement of the free perianth lobes; lower part of perianth tube ca. 4.5 mm long, narrower towards the base (ca. 4.5 mm in diameter), wider above (ca. 5.5 mm in diameter), white tinged yellow-green, densely covered with longitudinally arranged irregularly sized verrucae, with 12 depressed green ribs of which 6 alternate ribs run from the base of the tube to the mouth of the annulus on the upper half of the perianth tube, inner wall smooth with a protruding ring-like structure just below the stigma; upper part of perianth tube 3.5–4.0 mm long, wider at the base (ca. 5.5 mm in diameter), narrower at the annular opening (ca. 2.7 mm in diameter), bright yellow-green with 6 dark green ribs terminating at the annulus, covered with densely arranged papillae on the outer surface except on the ribs, inner wall smooth. Free part of outer perianth lobes white, translucent, triangular, 2.5–3.0 mm long, reflexed, ca. 1 mm wide at the base, gradually tapering. Free part of inner perianth lobes distinctly divisible into 2 parts: lower obliquely spathulate bases and upper flagelliform appendages; obliquely spathulate bases 3, black, rough and irregularly carbunculate, ca. 1 mm wide at the point of attachment to the perianth tube, broadening above (ca. 4 mm wide) and then fused with one another in a contorted aestivation to form a crown-like structure arching over the annulus with a concavity in the centre and an aperture directly above the annulus aperture, surrounded by flagellate appendages that arise at the base of the concavity; flagelliform appendages 3, erect, immotile, black and carbunculate towards the base, becoming translucent white and smooth above, 7.2–17.7 mm long, ca. 0.8 mm wide towards the base but abruptly narrowing towards the apex to less than 0.2 mm wide. Stamens 6, 4.8–5.5 mm long, 0.7–0.9 mm wide, quadrangular; filaments partially fused, arranged radially and forming a staminal tube that originates from the opening of the annulus at the base (ca. 1 mm in diameter) and is continuous with the connective towards the apex; suspended

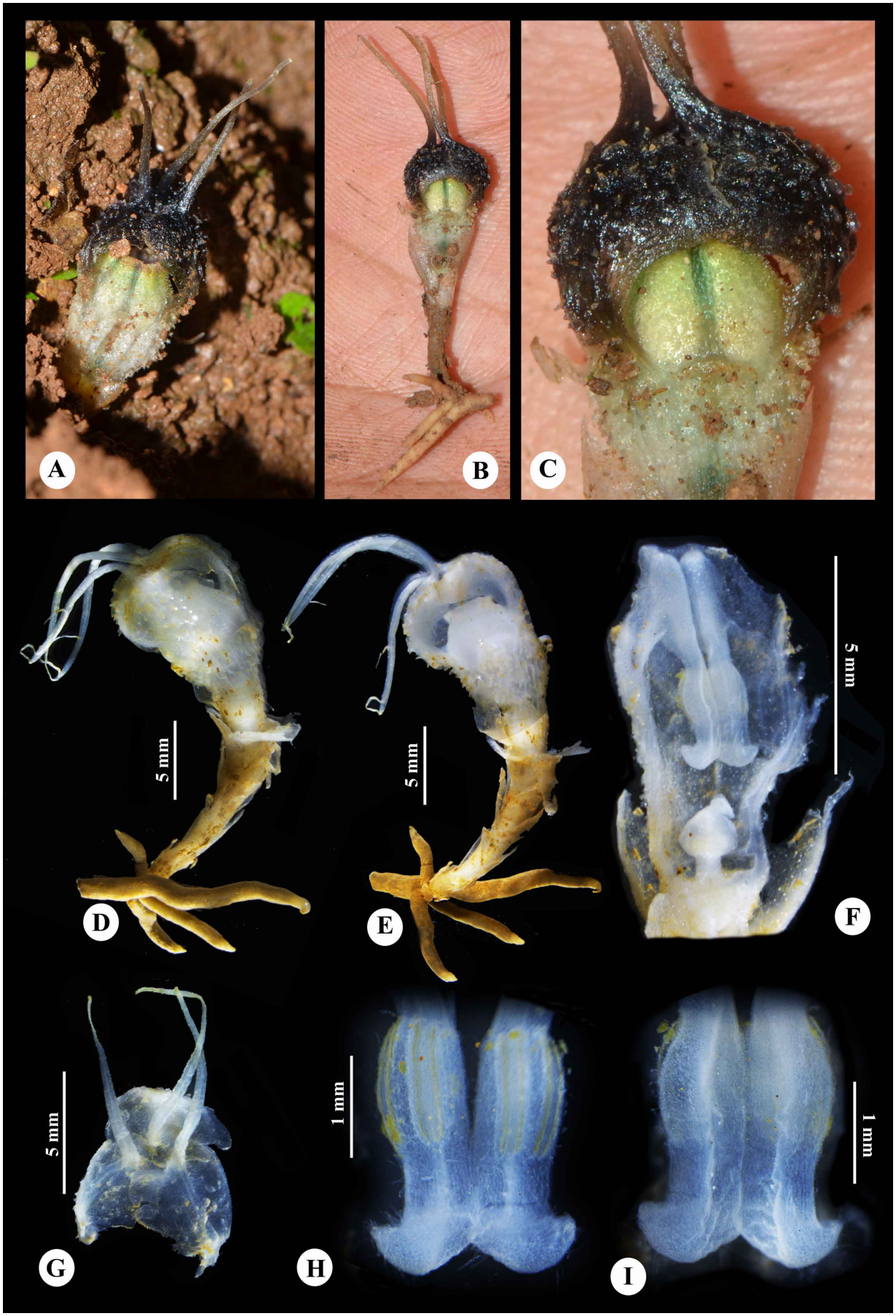

FIGURE 4. *Thismia nigricoronata*. A. Plant in habitat. B. Habit. C. Close-up of the crown. D. Whole plant showing the structure of the crown. E. Whole plant showing the structure of the annulus. F. Transverse section of the perianth tube. G. Dorsal view of the crown. H. Stamens showing the anther locules. I. Stamens showing the connectives and staminal tube.

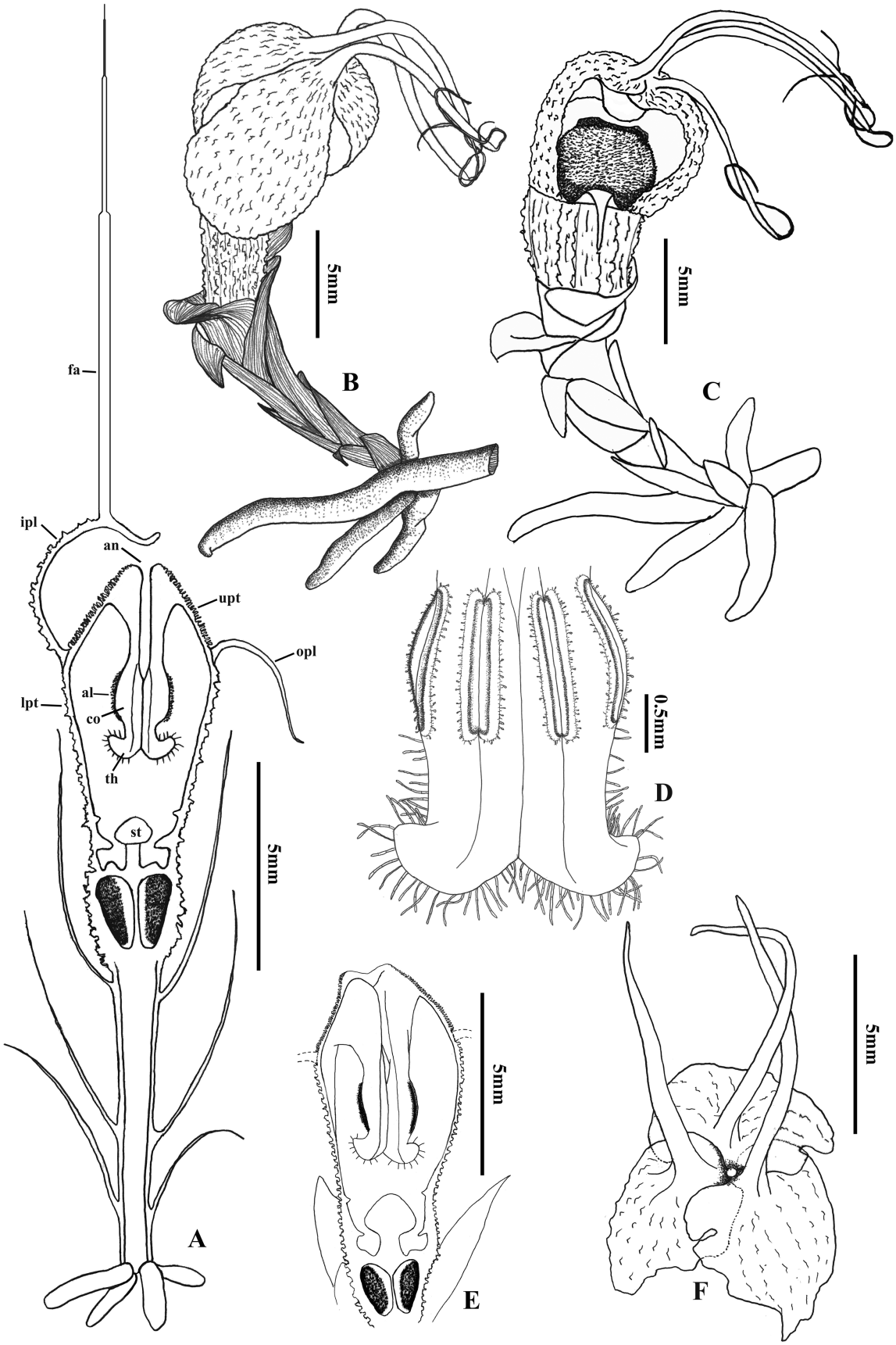

FIGURE 5. *Thismia nigricoronata*. A. Whole plant in longitudinal section showing the internal parts (fa, flagellate appendage; ipl, free part of inner perianth lobe; an, annulus; upt, upper part of perianth tube; al, anther locule; opl, free part of outer perianth lobe; co, connective; lpt, lower part of perianth tube; th, thecae; st, stigma). B. Whole plant showing the mitre. C. Whole plant showing the upper part of perianth tube. D. Staminal tube showing anther locules and connectives. E. Longitudinal section of the perianth tube showing stamen and ovary. F. Mitre. (Drawn by P. Kumar from preserved specimen *HNL-KFBG 0099*.)

above the stigma; connectives laterally connate and forming a narrow opening (0.4–0.5 mm in diameter); anthers ca. 2.5 × 0.5 mm wide, mounted on fused connectives, thecae free, positioned ca. 2.5 mm below the annulus, opening with longitudinal slits facing the inner wall of the perianth tube, covered with sparse glandular trichomes especially along the longitudinal slit; connectives protruding ca. 0.75 mm beyond the anther locules with the apical 1/3 bent at 90° towards the inner wall of the perianth tube, sparsely covered with multicellular cilia. Ovary inferior, unilocular, obconical, outer wall longitudinally verrucose, ca. 3.5 mm long; style cylindrical, ca. 0.75 mm long, ca. 0.70 mm wide; stigmas 3, fused together and forming a dome-like structure, ca. 1 mm long and wide.

Flowering:—April, fruits not seen.

Habitat:—*Thismia nigricoronata* was discovered on a steep slope of a limestone mountain, growing among leaf litter in clayey soils under a dense evergreen canopy.

Etymology:—The species epithet refers to the black, crown-like structure formed above the annulus by the fusion of the three inner perianth lobes. Hence the taxon may informally be referred to as 'the black-crowned thismia'.

Specimens examined:—**LAOS**. Vientiane Province: Vang Vieng District, Nam Pae Village, elevation 544 m, 28 April 2012, *Gale, Kumar, Santainsy & Phunthavong HNL-KFBG 0099* (HNL, spirit).

Taxonomic notes:—With diagnostic characters including the free anther thecae, the fused inner perianth lobes that form a mitre with prominent outer perianth lobes and long filiform appendages, there is little doubt that *Thismia nigricoronata* is presently best placed in section *Glaziocharis*. However, as noted above, the circumscription of this (and other sections) requires reappraisal, with phylogenetic analysis placing the morphologically distinct *T. huangii*, a member of section *Rodwaya*, as sister to our new species. Additionally, it is noteworthy that *T. nigricoronata* is the only species known so far in section *Glaziocharis* to have such a vibrantly coloured perianth tube, with that of all other previously described members of the section (namely, *T. abei*, *T. clavarioides*, *T. taiwanensis* and *T. tuberculata*) being whitish and somewhat translucent. Further study is required to assess whether or not this pigmentation is related to photosynthetic activity.

Conservation assessment:—Only ca. 10 individuals were observed at the site at a single locality on the lower slopes of a limestone mountain in Nam Pae Village of Vang Vieng District in central Laos. *Thismia nigricoronata* is an inconspicuous plant not easily observed in the field due to its small size and short flowering period. However, the area continues to be subjected to intense local pressures in the form of forest clearance for agriculture on the plains and selective logging on steeper slopes, cattle grazing and limestone mining for cement factories. Habitat destruction is therefore regarded as a very real threat to the long-term persistence of *T. nigricoronata* in this area. Although we recommend more surveys to confirm its occurrence in adjacent areas, we assess *T. nigricoronata* as critically endangered (B1+B2ab(iii); D) (IUCN 2012). The discovery of this apparently highly restricted endemic in the limestone karst landscape of central northern Laos underscores the need to ensure better protection of this biologically invaluable but highly threatened ecoregion.

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REFERENCES

Agardh, J.G. (1858) *Theoria systatis plantarum*. Gleerup, Lund, 404 pp.

Airy Shaw, H.K. (1952) A new genus and species of Burmanniaceae from south India. *Kew Bulletin* 7: 277–279. https://doi.org/10.2307/4109280

Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1–20. https://doi.org/10.1111/boj.12385

Beccari, O. (1878) Burmanniaceae. *In: Malesia: raccolta di osservazioni botaniche intorno alle piante dell'arcipelago Indo-Malese e Papuano pubblicata da Odoardo Beccari, destinata principalmente a descrivere ed illustrare le piante da esso raccolte in quelle regioni durante i viaggi eseguiti dall'anno 1865 all'anno 1878*, *volume 1*. Genova, Tip. del R. Instituto sordo-muti, pp. 240–254.

https://doi.org/10.5962/bhl.title.79357
Bentham, G. & Hooker, J.D. (1883) Burmanniaceae. *In: Genera plantarum: ad exemplaria imprimis in Herberiis Kewensibus servata definite*, volume 3, part 2. Reeve, London, pp. 455–460.
Blume, C.L. (1849) *Sarcosiphon* Blume. *In: Museum botanicum Lugduno-Batavum, sive, Stirpium exoticarum novarum vel minus cognitarum ex vivis aut siccis brevis expositio et description* 1 (5): 65.
Caddick, L.R., Rudall, P.J. & Wilkin, P. (2000) Floral morphology and development in Dioscoreales. *Feddes Repertorium* 111: 189–230. https://doi.org/10.1002/fedr.20001110313
Chakrapani, P. & Raj, B. (1971) Pollen morphological studies in the Burmanniaceae. *Grana* 11: 164–179. https://doi.org/10.1080/00173137109430491
Chantanaorrapint, S. & Chantanaorrapint, A. (2009) *Thismia clavigera* (Thismiaceae), a new record for Thailand. *Thai Forest Bulletin* 37: 27–31.
Chantanaorrapint, S. & Sridith, K. (2007) *Thismia alba* (Thismiaceae), a new record for Thailand. *Thai Forest Bulletin (Botany)* 35: 34–37.
Chantanaorrapint, S. & Sridith, K. (2015) *Thismia nigricans* Chantanaorr. & Sridith, a new species of Thismiaceae from southern Thailand. *Phytotaxa* 217: 293–297. https://doi.org/10.11646/phytotaxa.217.3.7
Chantanaorrapint, S. (2008) *Thismia angustimitra* (Thismiaceae), a new species from Thailand. *Blumea* 53: 524–526. https://doi.org/10.3767/000651908X607477
Chantanaorrapint, S. (2012) *Thismia filiformis*, a new species of Thismiaceae (formerly Burmanniaceae) from Thailand. *Kew Bulletin* 67: 69–73. https://doi.org/10.1007/s12225-012-9340-1
Chase, M.W., Stevenson, D.W., Wilkin, P. & Rudall, P.J. (1995) Monocot systematics: a combined analysis. *In*: Rudall, P.J., Cribb, P.J., Cutler, D.F. & Humphries, C.J. (Eds.) *Monocotyledons: systematics and evolution*. London, Kew Publishing, pp. 475–487.
Chase, M.W., Soltis, D.E., Soltis, P.S., Rudall, P.J., Fay, M.F., Hahn, W.H., Sullivan, S., Joseph, J., Molvray, M., Kores, P.J., Givnish, T.J., Sytsema, K.J. & Pires, J.C. (2000) Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification. *In*: Wilson, K.L. & Morrison, D.A. (Eds.) *Monocots: systematics and evolution*. Commonwealth Scientific and Industrial Research Organisation Publishing, Melbourne, pp. 3–16.
Cheeseman, T.F. (1908) A new species of Burmanniaceae from New Zealand. *Bulletin of Miscellaneous Information, Royal Gardens, Kew* 1908: 419–421. https://doi.org/10.2307/4113219
Chiang, P.Y. & Hsieh, T.H. (2011) *Thismia huangii* (Thismiaceae), a new species from Taiwan. *Taiwania* 56: 138–142. http://dx.doi.org/10.6165/tai.2011.56(2).138
Cranwell, L.M. (1953) New Zealand pollen studies. The monocotyledons: a comparative account. *Bulletin of the Auckland Institute and Museum* 3, Harvard University Press, 91 pp.
Dančák, M., Hroneš, M., Sochor, M., Kobrlová, L., Hédl, R., Hrázsky, Z., Vildomcová, A., Sukri, R.S. & Metali, F. (2013) A new species of *Thismia* (Thismiaceae) from Brunei Darussalam, Borneo. *Phytotaxa* 125: 33–39. https://doi.org/10.11646/phytotaxa.125.1.5
Darlu, P. & Lecointre, G. (2002) When does the incongruence length difference test fail? *Molecular Biology and Evolution* 19: 432–437. https://doi.org/10.1093/oxfordjournals.molbev.a004098
de la Sota, E.R. (1960) *Mamorea singeri*: un nuevo género y especie de Burmanniaceae. *Darwiniana* 12: 43–47. http://www.jstor.org/stable/23211935
Drummond, A.J., Ashton, B., Buxton, S., Cheung, M., Cooper, A., Duran, C., Field, M., Heled, J., Kearse, M., Markowitz, S., Moir, R., Stones-Havas, S., Sturrock, S., Thierer, T. & Wilson, A. (2011) Geneious v6.1. Available from: http://www.geneious.com (accessed 1 September 2017)
Engler, A. (1888) Burmanniaceae. *In:* Engler, A. & Prantl, K. (Eds.) *Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten, insbesondere den Nutzpflanzen, unter Mitwirkung zahlreicher hervorragender Fachgelehrten begründet*. volume 2, part 6. Engelmann, Leipzig, pp. 44–51.
Eyre-Walker, A. & Gaut, B.S. (1997) Correlated rates of synonymous site evolution across plant genomes. *Molecular Biology and Evolution* 14: 455–460. https://doi.org/10.1093/oxfordjournals.molbev.a025781
Farris, J.S., Källersjö, M., Kluge, A. & Bult, G.C. (1995) Constructing a significance test for incongruence. *Systematic Biology* 44: 570–572. https://doi.org/10.1093/sysbio/44.4.570
Forster, J. R. & Forster, G. (1775) *35. Tacca*. *In*: Forster, J.R., Elmsly, P., White, B. & Cadell, T. (Eds.) *Characteres generum plantarum,*

quas in itinere ad insulas maris Australis: collegerunt, descripserunt, delinearunt, annis 1772-1775. White, Cadell & Elmsly, London, pp. 69–70.
https://doi.org/10.5962/bhl.title.4448

Govaerts, R., Wilkin, P., Saunders, R.M.K., Raz, L., Valdés, O.T., Maas-van de Kamer, H., Maas-van de Kamer, P. & Zhang, D.X. (2007) *World checklist of Dioscoreales, yams and their allies*. Kew Publishing, Royal Botanic Gardens, Kew, Richmond, 65 pp.

Griffith, W. (1845) On the root parasites referred by authors to Rhizantheae, and their allies. *Proceedings of the Linnean Society of London* 1: 216–221.

Hatusima, S. (1976) Two new species of Burmanniaceae from Japan. *Journal of Geobotany* 24: 2–10.
https://doi.org/10.11646/phytotaxa.105.1.4

Ho, G.W.C., Mar, S.S. & Saunders, R.M.K. (2009) *Thismia tentaculata* (Burmanniaceae tribe Thismieae) from Hong Kong: first record of the genus and tribe from continental China. *Journal of Systematics and Evolution* 47: 605–607.
https://doi.org/10.1111/j.1759-6831.2009.00037.x

Huelsenbeck, J.P. & Ronquist, F. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180

Hunt, C.A., Steenbeeke, G. & Merckx, V.S.F.T. (2014) *Thismia megalongensis* (Thismiaceae), a new species of *Thismia* from New South Wales. *Telopea* 16: 165–174.
https://doi.org/10.7751/telopea20147809

IUCN (2012) *IUCN red list categories and criteria, version 3.1*. IUCN Species Survival Commission, Gland, 41 pp.

Jonker, F.P. (1938) A monograph of the Burmanniaceae. *Mededeelingen van het Botanisch Museum en Herbarium van de Rijks Universiteit te Utrecht* 51: 1–279.

Kuntze, O. (1891) Taccaceae. *In: Revisio generum plantarum:vascularium*. Felix, Leipzig, 704 pp.

Larsen, K. & Averyanov, L.V. (2007) *Thismia annamensis* and *T. tentaculata*, two new species of Thismiaceae from central Vietnam. *Rheedea* 17: 13–19.

Li ,H.Q. & Bi, Y.K. (2013) A new species of *Thismia* (Thismiaceae) from Yunnan, China. *Phytotaxa* 105: 25–28.
https://doi.org/10.11646/phytotaxa.105.1.4

Linneì, C. (1753) *Species plantarum 1*. Salvius, Stockholm, 560 pp.

Maas-van de Kamer, H. (1998) *Burmanniaceae*. *In*: Kubitzki, K., Huber, H., Rudall, P.J., Stevens, P.S. & Stützel, T. (Eds.) *The families and genera of vascular plants, vol. III, Monocotyledons: Lilianae (except Orchidaceae)*. Springer, Berlin, pp. 154–163

Maas, P.J.M., Maas-Van De Kamer, H., Van Benthem, J., Snelders, H.C.M. & Bsamen, T.R. (1986) Burmanniaceae. *Flora Neotropica* 42: 1–189.

Mar, S.S. & Saunders, R.M.K. (2015) *Thismia hongkongensis* (Thismiaceae): a new mycoheterotrophic species from Hong Kong, China, with observations on floral visitors and seed dispersal. *Phytokeys* 46: 21–33.
https://doi.org/10.3897/phytokeys.46.8963

Martínez-Azorín, M., Crespo, M.B., Juan, A. & Fay, M.F. (2011) Molecular phylogenetics of subfamily Ornithogaloideae (Hyacinthaceae) based on nuclear and plastid DNA regions, including a new taxonomic arrangement. *Annals of Botany* 107: 1–37.
https://doi.org/10.1093/aob/mcq207

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme Van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012) *International code of nomenclature for algae, fungi, and plants (Melbourne Code)*. Gantner, Regnum Vegetabile 154.

Merckx, V.S.F.T., Schols, V., Maas-van de Kamer, H., Maas, P., Huysmans, S., & Smets, E. (2006) Phylogeny and evolution of Burmanniaceae (Dioscoreales) based on nuclear and mitochondrial data. *American Journal of Botany* 93: 1684–1698.
https://doi.org/10.3732/ajb.93.11.1684

Merckx, V.S.F.T., Bakker, F.T., Huysmans, S. & Smets, E. (2009) Bias and conflict in phylogenetic inference of myco-heterotrophic plants: a case study in Thismiaceae. *Cladistics* 25: 64–77.
https://doi.org/10.1111/j.1096-0031.2008.00241.x

Merckx, V.S.F.T. & Smets, E.F. (2014) *Thismia americana*, the 101st anniversary of a botanical mystery. *International Journal of Plant Sciences* 175: 165–175.
https://doi.org/10.1086/674315

Merckx, V.S.F.T., Freudenstein, J.V., Kissling, J. Christenhusz, M.J.M., Stotler, R.E., Crandall-Stotler, B., Wickett, N., Rudall, P.J., Maas-van de Kamer, H. & Maas, P.J.M. (2013) Taxonomy and classification. *In*: Merckx, V.S.F.T. (Ed.) *Mycoheterotrophy: the biology of plants living on fungi*. Springer, New York, pp. 19–102.
https://doi.org/10.1007/978-1-4614-5209-6_2

Miers, J. (1847) On a new genus of plants of the family Burmanniaceae. *Proceedings of Linnean Society of London* 1: 328–329.

Miers, J. (1866) On *Myostoma*, a new genus of Burmanniaceae. *Proceedings of Linnean Society of London* 25: 461–476. https://doi.org/10.1111/j.1096-3642.1865.tb00195.x

Miquel, F.A.W. (1859) Thismiaceae. *Flora van Nederlandsch Indie¨*3: 615–616

Mueller, F.J.H.V. (1890) Description of new Australian plants with occasional, other annotations. *The Victorian Naturalist* 7: 114–116.

Mueller, F.J.H.V. (1891) Notes on a new Tasmanian plant of the order Burmanniaceae. *Papers and proceedings of the Royal Society of Tasmania* 1890: 232–235.

Nuraliev, M.S., Beer, A.S., Kuznetsov, A.N. & Kuznetsova, S.P. (2014) *Thismia mucronata* (Thismiaceae), a new species from Southern Vietnam. *Phytotaxa* 167: 245–255. https://doi.org/10.11646/phytotaxa.167.3.3

Nuraliev, M.S., Beer, A.S., Kuznetsov, A.N. & Kuznetsova, S.P. (2015) *Thismia puberula* (Thismiaceae), a new species from southern Vietnam. *Phytotaxa* 234: 133–142. https://doi.org/10.11646/phytotaxa.234.2.3

Pfeiffer, N.E. (1914) Morphology of *Thismia americana*. *Botanical Gazette* 57: 122–135. https://doi.org/10.1086/331235

Posada, D. & Crandall, K.A. (1998) MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818. https://doi.org/10.1093/bioinformatics/14.9.817

Schlechter, F.R.R. (1906) Burmanniaceae africanae. *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie* 38: 138.

Schlechter, F.R.R. (1918) Eine neue papuasische Burmanniacee. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 55: 202–203.

Schlechter, F.R.R. (1921) Die Thismieae. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 8: 31–45.

Seemann, B. (1866) *Tacca parkeri*. *Flora vitiensis: a description of the plants of the Viti or Fiji islands, with an account of their history, uses, and properties* 1: 102.

Smith, J.J. (1910) Zur Systematik von *Thismia javanica* J.J.S. *Annales du Jardin botanique de Buitenzorg* 23: 32–35.

Stone, B.C. (1980) Rediscovery of *Thismia clavigera* (Becc.) F.v.M. (Burmanniaceae). *Blumea* 26: 419–425.

Sullivan, J. (1996) Combining data with different distributions of among-site rate variation. *Systematic Biology* 45: 375−380. https://doi.org/10.1093/sysbio/45.3.375

Swofford, D.L. (2003) *PAUP* phylogenetic analysis using parsimony (and other methods) v4.* Sinauer, Sunderland.

Taubert, P. (1895) Ueber die Verbreitung der Burmanniaceen und zwei neue Gattungen dieser Familie. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* 36: LXVI.

Thiele, K.R. & Jordan, P. (2002) *Thismia clavarioides* (Thismiaceae), a new species of fairy lantern from New South Wales. *Telopea* 9: 765–771. https://doi.org/10.7751/telopea20024015

Thwaites, G.H.K. (1864) Burmanniaceae. *In:* Thwaites, G.H.K. & Hooker, J.D. (Eds.) *Enumeratio plantarum Zeylaniae.* Dulao, London, 325 pp. https://doi.org/10.5962/bhl.title.574

Truòng, L.H., Tich, N.T., Gioi, T., Diêp, D.Q., Long, V.N., Bách, N.L.X., Dung, N.T.T. & Trung, N.T. (2014) *Thismia okhaensis* (Thismiaceae)—a new fairy lantern from Vietnam. *Phytotaxa* 164: 190–194. https://doi.org/10.11646/phytotaxa.164.3.4

Tsukaya, H. & Okada, H. (2005) *Thismia mullerensis* (Burmanniaceae), a new species from Muller Range, central Kalimantan. *Acta Phytotaxonomica et Geobotanica* 56: 129–133.

Tsukaya, H. & Okada, H. (2012) A new species of *Thismia* (Thismiaceae) from West Kalimantan, Borneo. *Systematic Botany* 37: 53–57. https://doi.org/10.1600/036364412X616639

Warming, E. (1901) Sur quelques Burmanniacées recueillies au Brésil par le Dr. A. Glaziou. *Oversigt Over Det Kgl. Danse Videnskabernes Selskabs Forhandlinger* 1901: 173–188.

White T.J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In*: Innis, M., Gelfand, D., Sninsky, J. & White, T.J. (Eds.) *PCR protocols: a guide to methods and application*. Academic Press, San Diego, pp. 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Woodward, C.L., Berry, P.E., Maas-van de Kamer, H. & Swing, K. (2007) *Tiputinia foetida*, a new mycoheterotrophic genus of Thismiaceae from Amazonian Ecuador, and a likely case of deceit pollination. *Taxon* 56: 157–162.

Yang, S.Z., Saunders, R.M.K. & Hsua, C.J. (2002) *Thismia taiwanensis sp. nov.* (Burmanniaceae tribe Thismieae): first record of the tribe in China. *Systematic Botany* 27: 485–488.