Palacký University in Olomouc Faculty of Science Department of Botany



Faculty of Science

Genus *Thismia* Griff. (Thismiaceae) in Asia and Australasia with focus on the Malesian floristic region RIGOROUS THESIS

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Abstract:

Genus Thismia contains 60 species of small mycoheterotrophic monocotyledonous plants, which belongs to the order Dioscoreales and family Thismiaceae. Members of the genus are distributed mostly in the (sub-)tropical areas of Asia, Australia and South America. Recent knowledge of the genus is very scattered, despite the fact that it represents biologically very interesting group. This state of knowledge is, however, getting better with the use of the modern biosystematic methods and more intensive field research in tropical areas in recent years.

Presented thesis summarizes state of knowledge in the end of 2015. It reviews the historical and recent knowledge about biology, cytology, evolution, ecology and taxonomy of this remarkable genus with focus mostly on the area of the Asia and Australia, with particular interest in the flora Malesiana area. Three previously published scientific papers dealing mostly with taxonomy of *Thismia* (description of the two new species and one new nomenclatural combination) are enclosed at the end of the thesis.

Keywords: mycoheterotrophy, monocots, Dioscoreales, taxonomy, phytogeography

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Abstrakt:

Rod *Thismia* zahrnuje 60 druhů drobných mykoheterotrofních jednoděložných rostlin, které jsou řazeny do řádu Dioscoreales a čeledi Thismiaceae. Rod je rozšířen především v tropických a subtropických oblastech Asie, Austrálie a Jižní Ameriky. Současné znalosti o rodu jsou stále velmi kusé i přesto, že se jedná o, z biologického hlediska, velmi zajímavou skupinu. S nástupem moderních biosystematických metod a zintenzivnění výzkumů v tropických oblastech v posledních letech se nicméně stav poznání velmi zlepšuje – jen za poslední 2 dekády bylo nalezeno a popsáno téměř 20 nových druhů, bylo publikováno několik fylogenetických či ekologických studií atd.

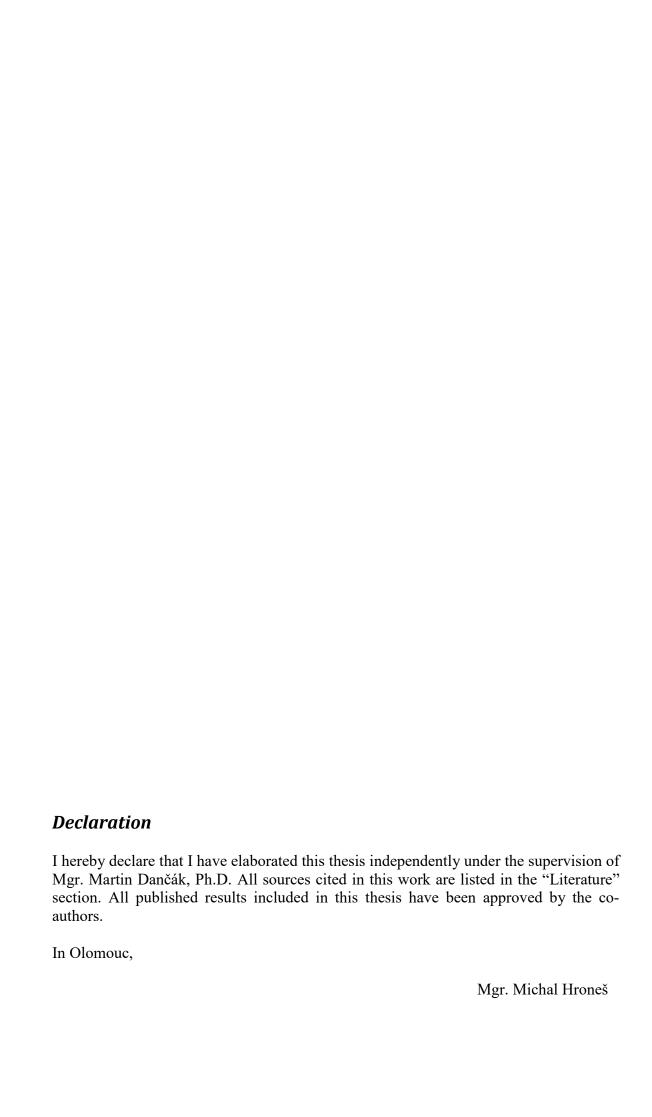
Předkládaná práce shrnuje stav poznání na konci roku 2015. Uvádí historické i recentní poznatky o biologii, cytologii, evoluci, ekologii a taxonomii zástupců tohoto zajímavého rodu. Je zaměřena na druhy rostoucí v Asii a Austrálii a zejména v Malesijské fytogeografické oblasti. Součástí práce jsou také tři publikované vědecké články, zabývající se převážně taxonomií rodu (popis dvou nových druhů a nová nomenklatorická kombinace).

Klíčová slova: mykoheterotrofie, jednoděložné rostliny, Dioscoreales, taxonomie,

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1. Introduction

Thismia Griff. is a small genus of enigmatic monocotyledonous mycoheterotrophic plants. This genus is currently placed in the oligotypic, predominantly tropical family Thismiaceae (MERCKX et al. 2006, MERCKX et al. 2013). The entire family includes five genera and approximately 80 species (MERCKX et al. 2013). With its 60 recognized species, Thismia is the largest genus in the family (DANČÁK et al. 2013, LI & BI 2013, LUU et al. 2014, MERCKX & SMETS 2014, NURALIEV et al. 2014, HUNT et al. 2014, CHANTANAORRAPINT & SIRIDITH 2015, HRONEŠ et al. 2015, NURALIEV et al. 2015). The second most species-rich genus is Afrothismia (Engl.) Schltr. (14 species) from west tropical Africa. The remaining three genera are species poor (Oxygyne Schltr. with 4 species, native to west tropical Africa and Japan) or even monotypic (Haplothismia Airy Shaw from India and Tiputinia P.E. Berry & C.L. Woodw. from the Atlantic rain forest in Brazil; MAAS et al. 1986, MERCKX et al. 2013, SAINGE et al. 2013).

The taxonomy of the family is currently experiencing considerable development – since the description of the first species in 1844 to the end of the 20th century, 49 species have been described. However, 32 additional new species have been described over the last 15 years (Fig. 1).

Many species in the genus are probably extremely rare with small, restricted distribution areas or are stenoendemic (Jonker 1938, Larsen & Averyanov 2007). Most members of the genus are also generally poorly known and have often been collected only once or a few times (Jonker 1948). They are easily overlooked in the field because of their small size and the ephemeral nature of their aboveground parts (Larsen & Averyanov 2007). Due to their rarity, most members of the genus are worthy of protection. It is also possible that many undescribed species might be still found in the understory of impenetrable tropical rain forests.

Despite the considerable taxonomical progress that has been made during the last two decades, *Thismia* remains somewhat unexplored. Little is known about its biology, cytology, ecology or genetic variability. This thesis aims to briefly summarize recent knowledge on the genus with particular focus on the species that are present in the Malesian floristic region. A contribution to the knowledge of this genus has also been made by the attached scientific papers.

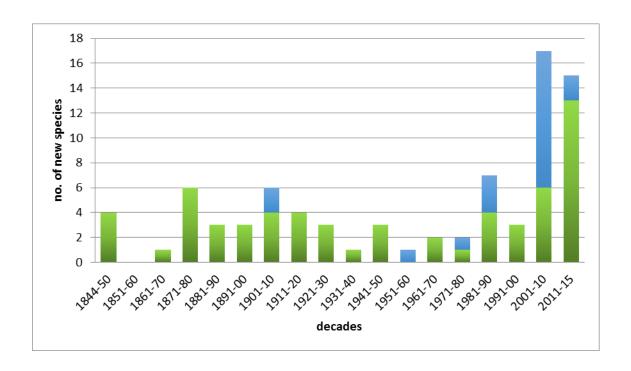


Fig. 1: Description of the new species of *Thismia* (green) and in other Thismiaceae genera (blue) by decades.

2. Material and Methods

This work is consisted of two main parts. The first part is a review of the current state of knowledge of *Thismia* and is based mostly on the available literature, type specimens (in the Jstor Global Plants database) and field data from Brunei Darussalam. The review focuses on the morphology, ecology, distribution and taxonomy of taxa from south-east Asia. The second part presents the outcomes of taxonomic and floristic research and is presented in form of the scientific papers (DANČÁK et al. 2013, HRONEŠ 2014, HRONEŠ et al. 2015).

3. Results and Discussion

3.1 Morphology

Members of the genus *Thismia* are small, perennial, achlorophyllous plants with a quite peculiar morphology. The subterranean parts (i.e., rhizomes) are persistent, variable in shape and size and lack root hairs. The roots of several species also lack root caps. Rhizomes are of three different types (JONKER 1938, MAAS et al. 1986,

IMHOF et al. 2013): i) tuberous (globose to ovoid tubers often with exogenous filiform roots or small apical tubers; this is typical for most neotropical members of the genus), ii) vermiform (endogenous, long, creeping, often branched rhizomes; the most common type of subterranean parts; Fig. 2a), iii) coralliform (reduced to cluster-like, coralloid structure; several species from south-east Asia; Fig. 2b).



Fig. 2: Underground parts of Asian *Thismia*: a) vermiform (photo M. Dančák, b) coralliform (photo F. Kolář).

Stems are usually short, simple or branched, ascending to erect, glabrous or rarely pubescent, mostly white, reddish, purplish or brown. Leaves are small, reduced to triangular or lanceolate scales, occasionally absent. Bracts are small, leaf-like, inserted below the flowers and sometimes forming an involucre enveloping the flower base.

Flowers are bisexual, actinomorphic or rarely slightly zygomorphic (e.g., in *Thismia labiata* J. J. Sm.; SMITH 1929), inserted mostly solitary on the top of the stem, rarely forming sparse terminal inflorescences. Pedicels are sometimes elongated after flowering. Hypanthium (also termed the perianth or basal tube; cf. CADDICK et al. 2000) is mostly urceolate to campanulate, variously coloured, and is sometimes covered with transverse bars (e.g., in *Thismia lauriana* Jarvie; JARVIE 1996), ended by two whorls of tepals. The morphology of the perianth is very complex and is also rather variable. The perianth comprises six tepals in two alternating circles arranged in threes. There are two major types of tepal lobe arrangements in Asian *Thismia*: i) all tepal lobes free and of equal length and size with each tepal ending as a short or long filiform appendage (i.e. tentacle; e.g. *Thismia alba* Holttum ex Jonker; CHANTANAORRAPINT 2007), ii) inner tepals noticeably larger than outer tepals, with inner tepals either free, ending with a long filiform appendage (e.g., *Thismia javanica* J. J. Sm.; SMITH 1910) or bent inwards

and imbricate but not fused (e.g., *Thismia taiwanensis* Sheng et al.; YANG et al. 2002), or connate to forming a mitre with three holes (Fig. 3a; e.g., *Thismia mucronata* Nuraliev; NURALIEV et al. 2014). On the top of the mitre there can be one (*Thismia gigantea* (Jonker) Hroneš; JONKER 1938) or three erect filiform appendages (*Thismia clavigera* (Becc.) F. Muell., *T. betung-kerihunensis* Tsukaya & H. Okada; JONKER 1948, TSUKAYA & OKADA 2012). The base of the tepal lobes is frequently fused to form a rounded or hexagonal, sometimes slightly raised, more or less prominent annulus (Fig. 3b).

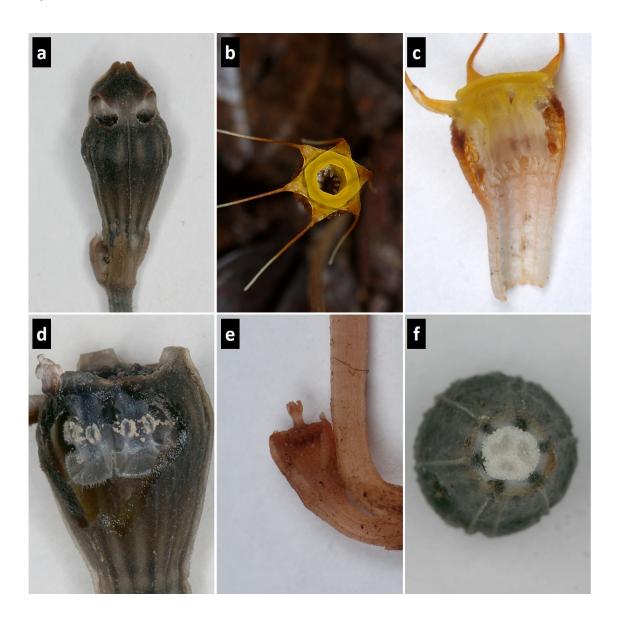


Fig. 3: Floral morphology of *Thismia*: a) perianth with lobes connate to a mitre (photo Z. Mačát), b) annulus with free perianth lobes, c) dissection of anther tube with prominent appendages at apical part (photo F. Trnka), d) connectives from adaxial side with wing-like appendage (photo Z. Mačát), e) ovary with stigma (photo F. Trnka), f) dissection of ovary showing three locules (photo Z. Mačát).

Stamens are six in number, free or usually connate to a tube, hanging from the annulus. Filaments are short, usually free, and in some neotropical species are alternated with interstaminal lobes of the perianth (MAAS et al. 1986). Connectives are flattened, ribbon-shaped, in paleotropical species connate to each other, usually with several appendages at the free apical margin (Fig. 3c) and the wing-like appendage on the outer side of the stamen (Fig. 3d). Anthers are divided into two separate thecae, which are situated above the wing-like appendage. Pollen is ovoid to globose, predominantly monoporate, sometimes with microporation (MAAS et al. 1986, JIANG & HSIEH 2011).

The ovary is obconical to obovoid, unilocular or trilocular (Fig. 3f) with three (two in *T. gongshanensis*; LI & BI 2013) placentas inserted parietally or at the bottom of the basal part of the ovary. Stigmas are usually three in number, entire or bilobed (Fig. 3e). The fruit is a fleshy, cup-shaped capsule, topped by the fleshy basal ring of the hypanthium and persistent stigmas. Seeds are ellipsoid to ovoid (MERCKX et al. 2013).

3.2 Cytology

Very little is known about the cytology and karyology of the genus. This is best illustrated by the fact that only five chromosome counts have been published to date. Data are available for only two neotropical species (*Thismia luetzburgii* Goebel & Süss. (2n=11-14) and *Thismia panamensis* (Standl.) Jonker (2n=11-13; both counts RÜBSAMEN 1986)) and for three paleotropical species (*Thismia javanica* (2n=12-16; MEYER 1909), *Thismia abei* (Akasawa) Hatus. (2n=12; AOYAMA et al. 1978) and *Thismia huangii* Jiang & Hsieh (2n=18; CHIANG & HSIEH 2011)). Given that the counts are scarce and that most of them are ambiguous (i.e., they are not sufficiently accurate), it is premature to draw conclusions regarding the basic chromosome number or occurrence of polyploidy.

The paucity of chromosome counts is probably caused by the rarity of most of these species but might also be affected by presence of inorganic crystals in the cells of the root tips (at least in some species), which prevent the tips from being properly squashed, thus rendering *Thismia* very difficult karyological material to work with (JANDOVÁ in verb.).

3.3 Distribution and phytogeography

The global range of the genus is discontinuous, with some unusual disjunctions (Fig. 4). *Thismia* is predominantly (sub)tropical, but some species occur also in temperate regions. Of currently known species, more than one third occur in the Malesian floristic region (22 species, with four species exceeding the area; JONKER 1948, TSUKAYA & OKADA 2012, DANČÁK et al. 2013, HRONEŠ et al. 2015), followed by neotropical America (15 species; MAAS et al. 1986, MANCINELLI et al. 2012) and the Indochinese floristic region (13 species, with five species exceeding the area; JONKER 1948, CHANTANAORRAPINT 2012, NURALIEV et al. 2014, CHANTANAORRAPINT & SIRIDITH 2015). Seven species are currently known to occur in the Sino-Japanese floristic region, five species occur in the Australian-Neozelandic region, one species occurs in Sri Lanka and one was known from the Chicago area in North America (Figs 4, 5; THIELE & JORDAN 2002, JIANG & HSIEH 2011, LI & BI 2013, MERCKX & SMETS 2014, HUNT et al. 2014).

Thismia is notable for its amphi-pacific (or trans-pacific) disjunction between tropical south-east Asia and South America (Fig. 4). This disjunction can be explained by the common ancestors of the Thismiaceae (excl. Afrothismia; see also chapter 7.1) existing in the ancient continent of Gondwana. Some unusual disjunctions can be found even for lower taxonomic ranks, such as the section Rodwaya (F. Muell.) Jonker (MAAS et al. 1986, MERCKX & SMETS 2014). This group comprises six species, four of which grow in Australia, Tasmania and New Zealand (Thismia rodwayi F. Muell., T. clavarioides Thiele, T. hillii (Cheeseman) N. Pfeiffer and T. megalongensis Hunt et al.), one grows in Taiwan (T. huangii), and one was historically distributed in the northern USA (T. americana Pfeiffer). Thismia americana and T. rodwayi are morphologically very similar and have been even considered as being possibly conspecific (JONKER 1938). Thus, a hypothetical disjunction exists between closely related Australian and North American species. Such distribution patterns have proved very puzzling for many authors (MAAS et al. 1986, MERCKX & SMETS 2014). A new hypothesis, suggesting that the closest relatives of T. americana may be some species from eastern Asia, was recently proposed by MERCKX & SMETS (2014). In their scenario, the occurrence of Thismia in North America can be explained by the migration of an ancestor of T. americana from eastern Asia throughout the Beringia. However, this might mean that

the Australian and North American species are probably not as closely related as was previously thought and suggests that the similar morphology of both species represents convergence (MERCKX & SMETS 2014).

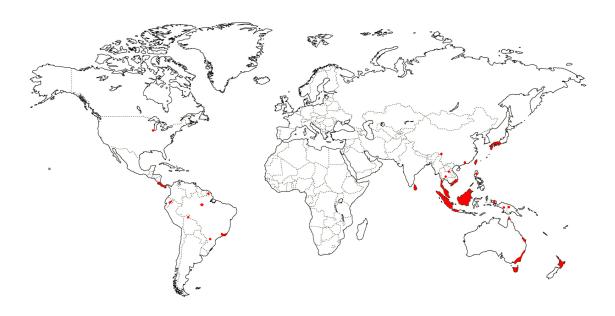


Fig. 4: Pattern of scattered distribution of the genus *Thismia*.

As noted above, most of the species in the genus have small and restricted areas of distribution. Only a few species have larger distribution ranges. Such species include *T. panamensis*, which is discontinuously distributed from Costa Rica to Ecuador, and *T. rodwayi*, which occurs in Tasmania, south-eastern Australia and New Zealand (but see chapter 6). In Malesia, only four species have a wide range and are reported from more than one geographical area: *T. alba* is distributed in peninsular Malaysia and Thailand (Jonker 1948, Chantanaorrapint & Sridith 2007), *T. clandestina* (Blume) Miq. is known from Sumatra and was recently collected also in Thailand (Jonker 1948, Chantanaorrapint et al. 2015), *T. clavigera* is found in Borneo, Sumatra, Langkawi and Thailand (Jonker 1948, Stone 1980, Chantanaorrapint & Chantanaorrapint 2009), and the range of *T. javanica* extends from Java and Sumatra to Thailand and Vietnam (Jonker 1948, Larsen 1965).

Within the Malesian floristic region, most species are restricted to the island of Borneo and to the Malay Peninsula. These areas, along with southern Thailand and Vietnam, probably represent biodiversity centres of the whole genus (Fig. 5; Chantanaorrapint et al. 2015, Hroneš et al. 2015).

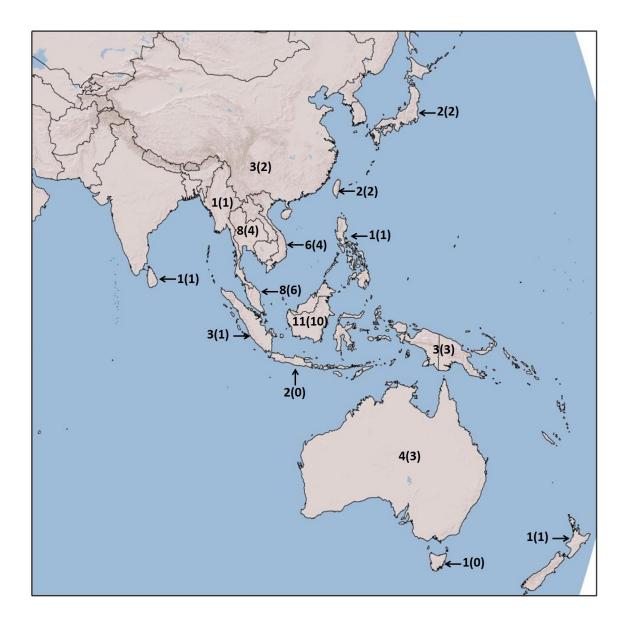


Fig. 5: Distribution of *Thismia* in Asia, Australia and New Zealand. First number display a total count of species present in particular country/island, number in parentheses display endemic species in the same area.

3.4 Ecology

3.4.1 Habitat preferences

Generally, members of the genus grow in the shaded leaf-litter covered understory of (sub)tropical rain forests. In Borneo, the common habitat is the lowland dipterocarp forest (JARVIE 1996, TSUKAYA & OKADA 2012, DANČÁK et al. 2013). However, some species reach higher altitudes, such as *Thismia goodii* Kiew which has been found in

submontane forest at 1260 m a.s.l. (KIEW 1999). In Thailand and Vietnam, bamboo forests and evergreen forests with admixed trees of the family Dipterocarpaceae are the most frequent habitats (CHANTANAORRAPINT 2008, CHANTANAORRAPINT & CHANTANAORRAPINT 2009, CHANTANAORRAPINT 2012, NURALIEV et al. 2014). An interesting insight into the vegetation associations of *Thismia* was provided by MERCKX & WAPSTRA (2013), who studied populations of *T. rodwayi* in Tasmania, where this species inhabits wet temperate sclerophylous forests dominated by eucalypts. They found that *Thismia* plants mostly associate with three shrub species *Pomaderris apetala* Labill. (Rhamnaceae), *Coprosma quadrifida* (Labill.) B. L. Rob. (Rubiaceae) and *Beyeria viscosa* (Labill.) Miq. (Euphorbiaceae). However, all three shrub species were not present in all *Thismia* stands. This observation led the authors to suggest that "*T. rodwayi* and its associated mycorrhizal fungus have a strong preference for a particular vegetation type, but not for specific plant species" (MERCKX & WAPSTRA 2013).

Remarkably, several taxonomically unrelated mycoheterotrophic species form an aggregation, which often accompanies Thismia (JONKER 1938). In Borneo, such "mycoheterotrophic assemblages" have been reported from Betung Kerihun (western Kalimantan) and Temburong (Brunei Darussalam). In both the cases, mycoheterotrophic genera Sciaphila Blume (Triuridaceae), Epirixanthes Blume (Polygalaceae), Gymnosiphon Blume (Burmanniaceae) and several species of orchids were reported (TSUKAYA & OKADA 2012, DANČÁK et al. 2013, HRONEŠ et al. 2015). A similar pattern has also been reported from Thailand (CHANTANAORRAPINT 2012), Vietnam (NURALIEV et al. 2014) or even Neotropics (JONKER 1938). This unusual aggregation can be explained by the connection of all mycoheterotrophic species to one suitable fungal associate (see the following chapter).

3.4.2 Mycoheterotrophy

Mycoheterotrophy plays an important role in the biology, morphology and distribution of the *Thismia* species. The basic definition of mycoheterotrophy implies the ability of the plants to obtain carbon sources from other plants via mycorrhizal fungi (MERCKX 2013). Due to this phenomenon, mycoheterotrophic plants do not gain carbon sources through photosynthesis. This allows mycoheterotrophs to exist hidden for the most of their life cycle in leaf litter or soil in the form of rhizomes and to save their resources for periods that are favourable for flowering. This probably explains, at least in part, the

"rarity" of these plants in nature; i.e., in particular habitats, these plants might not be as rare as thought, but remain almost undetectable to botanists.

Thismiaceae coexist with arbuscular mycorrhizal fungi from the family Glomeraceae (so called *Glomus* group A; MERCKX & BIDARTONDO 2008, MERCKX et al. 2012). Unfortunately, very few data on this phenomenon are available for *Thismia* because most available data are for the African genus *Afrothismia*. The only available record in the genus is for *T. rodwayi* (MERCKX et al. 2012). However, members of the genus *Thismia* can be expected to also associate with *Glomus* group A given that most mycoheterotrophic plants have been proven to associate with this group of fungi (HYNSON & BRUNS 2010, MERCKX et al. 2012).

3.4.3 Pollination and seed dispersal

The pollination and pollen dispersal mechanisms of *Thismia* remain generally unknown. Some authors have suggested that these plants are self-pollinated (cf. MIERS 1866). This mode appears to be unlikely for most south-east Asian members due to their stamen morphology. Most species have anthers that are situated above the large wing-like appendage that protrudes from the connective outwards to the perianth tube, and more or less isolates thecae from the stigma.

Other authors have suggested that the flowers might be pollinated by flies (myophily; STONE 1980). The strikingly coloured annulus and perianth lobes favour this hypothesis. The complex inner morphology of the perianth might serve as guidance for the pollinators to the anthers (STONE 1980, MAAS et al. 1986). Moreover, an odour resembling rotten flesh or dried fungi, which is characteristic for myophily, was recorded in *T. rodwayi* (WAPSTRA et al. 2005) and *T. brunneomitra* Hroneš et al. (HRONEŠ et al., unpublished). In agreement with previous suggestions, Li & Bi (2013) observed small members of Diptera visiting the flowers of *T. gongshanensis* Li & Bi. MAR & SAUNDERS (2015) caught small flies in the flowers of *T. hongkongensis* Mar & Saunders. These flies were identified as fungus gnats (of the family Mycetophilidae or Sciaridae). Moreover, these authors also retrieved a wing from the floral chamber, which probably belonged to a fly from the Phoridae family. Similar fly visitors were also observed in *T. hexagona* Dančák et al. (HRONEŠ et al., unpublished).

The mechanisms of seed dispersal are also poorly known. Several hypothetical modes of dispersion have been proposed so far, including dispersal by birds (CROAT

1978) or earthworms (BECCARI 1890). STONE (1980) suggested that the seeds might be dispersed by raindrops that splash the seeds from the fruit. The fruits of *Thismia* are cup-shaped, the fruiting stems elongate after anthesis in at least some species and the small seeds in the fruit are covered only by fragile membrane; given these findings, Stone's conclusions appear very likely (cf. THIELE & JORDAN 2002, YANG et al. 2002, HRONEŠ et al. 2015, MAR & SAUNDERS 2015). The presence of a mucilagineous substance surrounding the seeds, which might serve as a hydrophilic lubricant, thus facilitating the separation of seeds by rain drops also supports rain dispersal (MAR & SAUNDERS 2015).

3.5 Taxonomy and classification

3.5.1 Family classification and phylogeny

From its first description in 1844, there were no doubts that *Thismia* is a monocotyledonous plant. The genus was considered intermediate between Burmanniaceae and Taccaceae by the author of the description (GRIFFITH 1844). Later, MIERS (1847) formally placed the genus in the family Burmanniaceae and established a new tribus Thismieae. Thismiaceae was first proposed as a separate family from Burmanniaceae by J. Agardh (AGARDH 1858). However, this view was mostly ignored for almost one and a half centuries (SCHLECHTER 1921, JONKER 1938, MAAS et al. 1986, MAAS-VAN DE KAMER 1998) until molecular studies recognized Burmanniaceae including Thismiaceae as a polyphyletic group (MERCKX et al. 2006).

In the phylogeny of MERCKX et al. (2006), Thismiaceae were resolved as a monophyletic group and as a sister to Taccaceae. Some new phylogenies even suggest that Thismiaceae could be paraphyletic and must include *Tacca* J.R. Forst. & G. Forst. to be monophyletic (MERCKX & SMETS 2014). However, Thismiaceae together with Taccaceae undoubtedly form a monophyletic group that is a sister group to Dioscoreaceae.

The relationships within the family remain unclear (MERCKX et al. 2006, MERCKX & SMETS 2014). It seems that *Afrothismia* is the evolutionary oldest genus within the family, sister to *Tacca* and the rest of Thismiaceae. As noted above, this causes the whole family to be paraphyletic (MERCKX & SMETS 2014). Concerns about monophyly

do not avoid even the genus *Thismia* itself: paleotropical species appear to form one group, which is a sister to *Haplothismia*, but neotropical species probably represent a different evolutionary lineage that is more closely related to the genus *Tiputinia* (MERCKX et al. 2009, MERCKX & SMETS 2014). For a final generic resolution of the genus and family, more detailed sampling is required.

Unfortunately, there are no fossil records that can be assigned to Thismiaceae. However, molecular dating suggests that origin of the family is probably best placed in the Cretaceous. The stem group of Thismiaceae (excl. *Afrothismia*) is estimated as occurring at (92-)79(-68) m.y., and the origin of the crown group is estimated as occurring at (85-)68(-49) m.y. The stem group of *Afrothismia* appears to be even older, with an origin before (109-)95(-79) m.y. (MERCKX et al. 2010).

3.5.2 Generic classification

The genus *Thismia* was described by the British botanist William Griffith who described *T. brunonis* Griff. as the type in 1844. Mainly due to strict approach of various authors, who adopted a rather narrow generic concept, an additional 12 generic names have been established since then; these names are considered synonymous with *Thismia* today and are (in chronological order) *Ophiomeris* Miers, *Sarcosiphon* Blume, *Tribrachys* Champ. ex Thwaites, *Myostoma* Miers, *Bagnisia* Becc., *Geomitra* Becc., *Rodwaya* F. Muell., *Glaziocharis* Taub. ex Warm., *Triscyphus* Taub. ex Warm., *Triurocodon* Schltr., *Scaphiophora* Schltr. and *Mamorea* de la Sota (MAAS-VAN DE KAMER 1998). Most, or at least some, of these genera were maintained in most of the important taxonomic treatments of the genus (SCHLECHTER 1921, JONKER 1938, JONKER 1948). Finally, MAAS et al. (1986), and subsequently MAAS-VAN DE KAMER (1998), established a broader taxonomic concept of *Thismia* and merged these genera into one. The broad concept of *Thismia* is now widely accepted, although some authors continue to distinguish *Geomitra* and *Scaphiophora* as separate genera (GOVAERTS et al. 2007).

3.5.3 Infrageneric subdivision

Schlechter (1921) adopted a rather narrow taxonomic view of the genus and kept several taxa in genera that are separate from *Thismia* in *Glaziocharis*, *Myostoma*, *Ophiomeris*, *Sarcosiphon*, *Scaphiophora*, *Triurocodon* and *Triscyphus*. Schlechter divided *Thismia* into three sections: *Euthismia* Schltr., *Odoardoa* Schltr. and *Sarawakia* Schltr. To the section *Euthismia*, three species with larger inner tepal lobes than outer lobes were included; namely, *T. brunonis*, *T. gardneriana* Hook. f. ex Thwaites and *T. javanica*. The section *Odoardoa* comprised five species with tepal lobes equal in length and size (*T. aseroe* Becc., *T. chrysops* Ridl., *T. fumida* Ridl., *T. grandiflora* Ridl. and *T. ophiuris* Becc.). The last section, *Sarawakia* was monotypic and was created for *T. neptunis* Becc., which, in his view, differed from members of the section *Euthismia*. The genus *Sarcosiphon* was also divided into three sections: *Triuranthe* Schltr. (for *T. clavigera*), *Rodwaya* (for *T. rodwayi*, *T. hillii* and *T. americana*) and *Sarcosiphon* (Blume) Schltr. (for the remaining species).

In his Monograph of Burmanniaceae, JONKER (1938) partly adopted and expanded Schlechter's classification. He distinguished five sections mainly on the basis of the subterranean organs and flower morphology: Euthismia, Myostoma (Miers) Jonker, Ophiomeris (Miers) Jonker, Rodwaya and Sarcosiphon (Blume) Jonker. In Jonker's view, the sections Myostoma and Ophiomeris comprised neotropical members of the genus with tuberous underground parts, section Rodwaya included species from Australia and North America that have a vermiform root system and flowers with inner tepal lobes that are bent inwards but are usually not connate. The section Sarcosiphon in his concept united species with coralliform roots and flowers with inner tepal lobes that form a connate mitre but lack any filiform appendages on the top (Jonker treated species with appendages on the top of the flower in the separate genera Geomitra and Scaphiophora). The last and largest section, Euthismia, which exhibit vermiform roots and free tepal lobes, was divided into two subsections (Brunonithismia Jonker and Odoardoa (Schltr.) Jonker), which were equivalent to the Schlechter's sections Euthismia and Odoardoa. Finally, in Flora Neotropica, the family was divided into two separate subgenera: neotropical species in subgen. Ophiomeris (Miers) Maas & H.

Maas, and the remaining species in subgen. *Thismia*. Most from the previous classification scheme made by Jonker was retained (MAAS et al. 1986).

Given the considerable and rapid development in taxonomy and the descriptions of many new species of the genus, the infrageneric classification proposed by Jonker is currently insufficient. Thus, I propose here the use of informal groups or species complexes until a larger phylogenetic and taxonomic study encompassing most of the described species is performed. These species complexes are based mostly on a combination of several morphological traits (morphological similarity) and geographical distribution. The following nine informal groups of Old World species of *Thismia* could be recognized:

Thismia aseroe agg. – Rhizomes vermiform, tepal lobes free, all equal in length and size, usually ended by filiform appendages. Thirteen species (*T. aseroe*, *T. ophiuris*, *T. chrysops*, *T. fumida*, *T. grandiflora*, *T. racemosa* Ridl., *T. alba*, *T. bifida* M. Hotta, *T. lauriana*, *T. mullerensis* Tsukaya & H. Okada, *T. annamensis* K. Larsen & Aver., *T. filiformis* Chantanaorr., *T. hexagona*) in Borneo, the Malayan Peninsula, Thailand and Vietnam. This group overlaps very closely with Schlechter's description of the section *Euthismia*.

Thismia brunonis agg. – Rhizomes vermiform, tepal lobes free, the outer mostly reduced, inner long with filiform appendages. Eight species (*T. brunonis*, *T. hongkongensis*, *T. javanica*, *T. labiata*, *T. neptunis*, *T. gardneriana*, *T. arachnites* Ridl., *T. tentaculata* K. Larsen & Aver.) distributed from Java, Sumatra and Borneo to Vietnam, Thailand, Myanmar, Sri Lanka and Hong Kong. This group includes the type of the genus and is almost identical to the description of Jonker's subsection *Brunonithismia*.

Thismia rodwayi agg. – Rhizomes vermiform, stems rather short at the anthesis, rarely elongating later, outer tepal lobes free, triangular or with various appendages, inner tepal lobes bent inwards to form a mitre but usually not connate. Six species (*T. rodwayi*, *T. hillii*, *T. americana*, *T. clavarioides*, *T. megalongensis*, *T. huangii*) in Tasmania, south-eastern Australia, New Zealand, Taiwan and northern USA. This group matches Schlechters' Sarcosiphon sect. Rodwaya.

Thismia abei agg. – Rhizomes vermiform, flowers almost sessile, outer tepal lobes radiating outwards, with short or long appendages, inner tepal lobes apically imbricate, forming a loose mitre and terminated by filiform appendage. Three species (*T. abei*, *T. tuberculata* Hatus. and *T. taiwanensis*) known from Japan (Honshu, Shikoku

and Kyushu) and Taiwan. Some species of this group were formerly treated as the genus *Glaziocharis*.

Thismia mirabilis agg. – Rhizomes vermiform, flowers rather small, up to 3 cm tall, inner tepal lobes connate to form a mitre. Six species (*T. mirabilis* K. Larsen, *T. angustimitra* Chantanaorr., *T. okhaensis* Luu et al., *T. mucronata*, *T. nigricans* Chantanaorr. & Sridith and *T. puberula* Nuraliev) known from Thailand and Vietnam.

Thismia appendiculata agg. – Rhizomes coralliform, stems densely foliated, flowers rather large (3-6.5 cm in length), inner tepal lobes connate to form a mitre with one erect appendage on top. Two species (*T. appendiculata* Schltr., *T. gigantea*) occurr in New Guinea and the Philippines. The species were formerly separated into the genus *Scaphiophora*.

Thismia clavigera agg. – Rhizomes coralliform, stems sparsely foliated, flowers rather large (3-6 cm in length), inner tepal lobes connate to form a mitre with three erect appendages on top. Two species (*T. clavigera*, *T. betung-kerihunensis*) found in Borneo, Sumatra and the Tarutao-Langkawi Archipelago off the Malay Peninsula coast. *T. clavigera* was treated by Jonker (1948) as the separate genus *Geomitra*.

Thismia clandestina agg. – Rhizomes coralliform, flowers usually rather small (1-2.5 cm in length), inner tepal lobes connate to form a mitre without any filiform appendages on top. Seven species (*T. clandestina*, *T. brunneomitra*, *T. episcopalis* (Becc.) F. Muell., *T. crocea* (Becc.) J. J. Sm., *T. goodii*, *T. versteegii* J.J. Sm. and *T. yorkensis* Cribb) occurr in western Java, Borneo, New Guinea and northern Australia. Members of this group represent the former genus *Sarcosiphon*.

Thismia gongshanensis – A somewhat atypical species with vermiform rhizomes and inner tepal lobes connate to form a mitre but with only two carpels with two placentas (three in all other species). The species is known only from southern China.

3.6. Undescribed or unrecognized species

Several other species of *Thismia* are currently not formally recognized but will probably be distinguished in the future. These species can be classified into two groups: 1) cryptic species that have only recently been recognized using new biosystematics techniques and 2) species that are not properly known to science and await collection and/or formal description.



Fig. 6: Two undescribed species of Thismia from Borneo (photos by A. Hoffman & F. Kolář).

The first group is represented by *Thismia hillii* and *T. versteegii*. *Thismia hillii* is a species from New Zealand that is morphologically almost identical to Australian and Tasmanian *T. rodwayi*. Both species are considered conspecific in recent Floras, although some morphological differences exist between the species (Hunt et al. 2014, Merckx & Smets 2014). Moreover, a sample from New Zealand, which was used in a molecular study (labelled as *T. rodwayi*), was shown to be clearly distinct from the Australian and Tasmanian plants in the phylogenetical evaluation of the family Thismiaceae (Merckx & Smets 2014). Thus, the authors hypothesized that *T. hillii* is a distinct species that should be formally recognized. However, the formal recognition of *T. hillii* will require further morphological study. *Thismia versteegii* is currently considered conspecific with another species from New Guinea *T. crocea* (Jonker 1938, Jonker 1948, Govaerts et al. 2007). However, as briefly noted by Larsen (1965), based on comparison of illustrations in the protologues, these two species are completely different. The recollection of both species in nature or, at least, an analysis of the type material is needed to solve the problem.

The second group consists of species for which convincing evidence exists that they are new to science but for which the evidence (usually a photograph) is insufficient to construct a proper description. I am aware of at least eight undescribed species from Malesia (Fig. 6) that await formal description.

4. Conclusions

This review summarized present state of knowledge on the mycoheterotrophic monocot genus *Thismia* from family Thismiaceae. Current understanding of its biology, ecology and taxonomy is still fragmentary despite the considerable progress in recent years. The review showed that there are still major gaps in knowledge of phylogenetic affinities and cytology of many *Thismia* species probably mostly due to their rarity which results in difficult sampling.

South-east Asia and Borneo in particular belongs to the most species rich areas of the world while it is at the same time considered highly threatened by the human impact. The genus *Thismia* has mostly tropical distribution locally reaching subtropics or even temperate areas. The centre of species diversity of the genus is located in Malesian floristic region of south-east Asia where some 25 species occur. Most of the species grow in primary lowland dipterocarp forests and require undisturbed trophic webs. Thus, they could be considered as indicators of non-disturbed habitats and used for conservation assessment of these forests.

After numerous recent discoveries of new species, the traditional division of the genus into subgenera and sections is no longer sufficient. Therefore, use of informal groups based on morphology was proposed in this work which could be applied until the large-scale phylogenies including most of the species will be published. The Old World species can be divided into nine such groups. Malesian species of *Thismia* could be attributed to one of the five following complexes: *Thismia appendiculata* agg., *Thismia aseroe* agg., *Thismia brunonis* agg., *Thismia clandestina* agg. and *Thismia clavigera* agg.

Recent discoveries showed that the genus is more species-rich than was previously expected and that new species could be discovered also in relatively well surveyed areas. Examples of such new discoveries can be *Thismia hexagona* and

T. brunneomitra which were described from Temburong district of Brunei Darussalam, an area under strong research focus from early 1990's (Appendices 1 and 3). These two species represent even the first report of Thismia occurrence in the whole country. Thismia hexagona belongs to T. aseroe agg. and is characterised by prominent sharply hexagonal yellow annulus, four appendices in two rows at the tip of the connective and perianth lobes equal tapering into long filiform appendages. It was discovered in 2013. Thismia brunneomitra is characterised by inner perianth lobes connate to forming a mitre with three holes, brown to blackish perianth, presence of three short processes at the apex of the mitre, free apical margin of the stamen connective with two broad obtusely triangular lateral lobes and narrowly triangular middle lobe and large entire wing-like lateral appendage of the connective. It best fits to T. clandestina agg. and it was discovered in 2015.

Many other species still await their discovery or proper description. However, the forests of south-east Asia vanish in an unprecedented rate and it is beyond any doubt that many *Thismia* species already disappeared forever with them. For the above given reasons, the *Thismia* should be in the spotlight of researches and conservation agencies.

5. Literature

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6. Appendices

1.

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