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Mykoheterotrofní rostliny v tropických deštných lesích Bornea

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Martin Dančák: *Mykoheterotrofní rostliny v tropických deštných lesích Bornea*

Obsah

1 Úvod

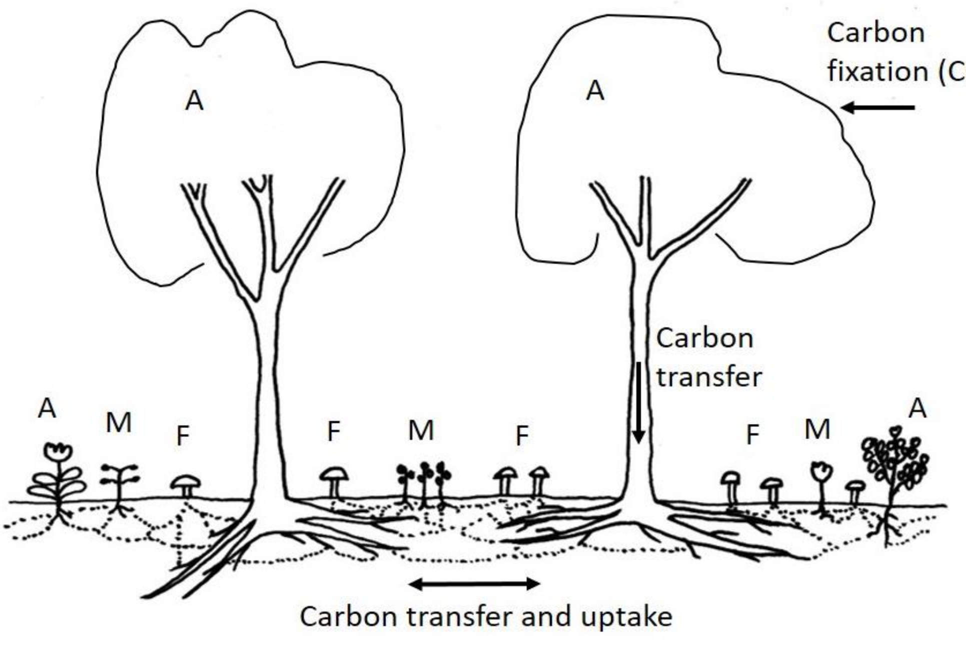
Nezelené rostliny odjakživa poutaly pozornost botaniků díky jejich zvláštnímu vzhledu, relativní vzácnosti, ale zejména neobvyklému způsobu výživy. Vedle parazitických rostlin byly tradičně rozlišovány také rostliny saprofytní. Již na konci 19. století začalo být zjevné, že tyto rostliny se neživí saprotrofně, tedy aktivním rozkladem odumřelých těl organismů (podobně jako některé houby), ale využívají mykorizních sítí, z nichž odčerpávají organický uhlík. Teprve až v 90. letech 20. století J. R. Leake (Leake 1994) zavedl termín mykoheterotrofní rostliny, který odráží skutečný způsob jejich výživy. Leakeho monografie pak vnesla nový impulz do studia těchto rostlin, zejména jejich biologie. Rozvoj výzkumu biologie mykoheterotrofů pak nutně přinesl i rozvoj ve výzkumu jejich systematiky, taxonomie a rozšíření.

Mykoheterotrofní rostliny se vyskytují převážně v lesním prostředí a přestože jsou rozšířené i v mírných zeměpisných šířkách, jejich největší diverzita je soustředěna do tropických deštných lesů. Jednou z hlavních oblastí rozšíření tropických deštných lesů na Zemi je jihovýchodní Asie, zejména Malesijská fytogeografická oblast, která zahrnuje Malajské souostroví a Malajský poloostrov. Největšími z ostrovů této oblasti jsou Nová Guinea a Borneo, které jsou zároveň druhým a třetím největším ostrovem světa (po Grónsku). Oba ostrovy jsou dodnes pokryty rozsáhlými plochami tropických deštných lesů a zároveň relativně málo botanicky prozkoumané. To dokládá také to, že téměř každoročně je z těchto ostrovů popisováno několik nových druhů rostlin (viz také Cámara-Leret et al. 2020). Zejména Borneo však v posledních desetiletích ztratilo značné procento svých primárních deštných lesů (Gaveau et al. 2016). Těžba lesů a jejich přeměna na zemědělskou půdu je dnes hlavním faktorem, který způsobuje úbytek biodiverzity na ostrově. Vzhledem k vysokému rostlinnému endemismu v bornejských deštných lesích pak vyvstává otázka, kolik rostlinných druhů Bornea vyhynulo či vyhyne, aniž bychom se kdy dozvěděli, že vůbec existovaly. Tato otázka se může zdát nepodstatná, zejména v současnosti, kdy je upřednostňován aplikovaný výzkum, před výzkumem základním. Na druhou stranu úbytek biodiverzity je v současnosti považován za jeden z nejvýznamnějších problémů, kterým lidstvo čelí a bude čelit. A abychom druhy ohrožené vyhynutím mohli účinně chránit, musíme si jejich existence být vědomi.

V této práci se zabývám mykoheterotrofními rostlinami Bornea. Jedná se o výsledky dlouhodobého výzkumu, který jsem měl možnost na Borneu od roku 2007 provádět v primárních tropických deštných lesích, zejména v Brunejském sultanátu a malajských státech Sarawak a Sabah, v menší míře také v Indonéských provinciích Východní a Severní Kalimantan. Počáteční spolupráce na výzkumu lesní dynamiky (viz např. Hédl et al. 2009, Qie et al. 2017, Sullivan et al. 2018, Sullivan et al. 2020) se postupně posunula ke studiu bylinného patra tropického deštného lesa, v němž se pravidelně uplatňují i mykoheterotrofní rostliny.

2 Mykoheterotrofie a mykoheterotrofní rostliny

Mykoheterotrofní rostliny jsou nezelené rostliny, které získávají uhlík prostřednictvím mykorhizních hub napojených na jejich kořeny (Leake 1994). Tento uhlík pochází převážně z okolních zelených rostlin (Selosse et al. 2002), se kterými mykorhizní houby tvoří symbiózu a společně tvoří tzv. mykorhizní trofickou síť (Selosse et al. 2016; obr. 1). Tím se mykoheterotrofní rostliny liší od rostlin parazitických, u kterých je parazit napojen na hostitelskou rostlinu přímo pomocí haustorií (Merckx 2013). Zda je mykoheterotrofie vztah více parazitický než symbiotický, není zcela jisté (Merckx 2013), i když v poslední době se hromadí důkazy pro spíše parazitický vztah (Perez-Lamarque et al. 2020). Některé mykoheterotrofní rostliny (prokázáno to bylo zatím jen u vstavačovitých) tvoří interakci se saprotrofními houbami a získávají tedy organický uhlík, který pochází nikoli přímo z okolních živých rostlin, ale z mrtvé biomasy (Suetsugu et al. 2020a, Yamashita et al. 2020). Mykoheterotrofní způsob výživy umožnil rostlinám existenci v podmínkách s výrazným nedostatkem světla a naprostá většina mykoheterotrofních druhů skutečně roste v lesním prostředí (Bidartondo 2005).



Obrázek 1. Mykorhizní trofická síť zobrazující vztahy mezi jejími jednotlivými složkami. A: autotrofní rostlina, M: mykoheterotrofní rostlina, F: houba. Tečkovaně jsou znázorněny hyfy hub.

Výzkumu biologie mykoheterotrofních rostlin je vzhledem k jejich odlišnosti od autotrofních rostlin přirozeně věnována poměrně velká pozornost, o to méně jsou však studovány po taxonomické stránce. K tomu také přispívá fakt, že v současnosti není taxonomický výzkum téměř vůbec podporován organizacemi financujícími vědecký výzkum, a to ani v oblastech s vysokým zastoupením nepopsaných či málo známých druhů, které jsou navíc bezprostředně ohrožené vyhynutím, jako například tropické deštné lesy. V této práci se proto zabývám výhradně taxonomickou problematikou mykoheterotrofních rostlin.

2.1 Formy mykoheterotrofie

Mykorhiza je mezi rostlinami všeobecně rozšířeným jevem, při němž mykorhizní houby získávají organický uhlík vyrobený fotosyntézou od zelených rostlin (van der Heijden et al. 2015). U mykoheterotrofních rostlin došlo k obrácení tohoto toku, takže tyto rostliny naopak získávají organický uhlík z mykorhizních hub. Jak je ve skutečnosti mezi rostlinami závislost na uhlíku získávaném prostřednictvím hub rozšířená, stále není zcela známé (Selosse & Cameron 2010). Také proto je termín mykoheterotrofie vnímán různým způsobem, obvykle podle toho, jak hluboce je konkrétní druh na mykotrofní výživě závislý. Zpravidla jsou rozlišovány rostliny iniciálně, částečně a plně mykoheterotrofní (Merckx et al. 2009). Jednotlivých forem, či stupňů mykoheterotrofie je však více a lze je rozdělit následovně.

Skupina A. Rostlina je ve všech stádiích svého života zcela nezávislá na vnějším přísunu uhlíku, je tedy plně autotrofní. Tímto způsobem se vyživuje většina vyšších rostlin. Do této kategorie náleží také nezelené gametofyty semenných rostlin, které jsou vyživovány sporofytem a nezelené sporofyty některých mechorostů, které jsou naopak vyživovány gametofytem. Tyto rostliny tedy nejsou mykoheterotrofní.

Skupina B. Rostlina je po krátké a přechodné vývojové stádium závislá na vnějším přísunu uhlíku prostřednictvím mykorhizy a bez něj nemůže uskutečnit svůj životní cyklus. Typicky se tato forma mykoheterotrofie objevuje ve stádiu klíčení a semenáčku, např. u většiny vstavačovitých (*Orchidaceae*) nebo hruštičkovitých (*Pyrolaceae*). Tato forma je označována jako iniciální mykoheterotrofie.

Skupina C. Rostlina je po celý svůj život nebo jeho podstatnou část závislá na vnějším přísunu uhlíku prostřednictvím mykorhizy, přičemž je ale stále schopná si část uhlíku zajišťovat i vlastní fotosyntézou. Tento způsob výživy byl prokázán u některých vstavačovitých (*Orchidaceae*), hruštičkovitých (*Pyrolaceae*) a hořcovitých (*Gentianaceae*). Tato forma je označována jako částečná mykoheterotrofie.

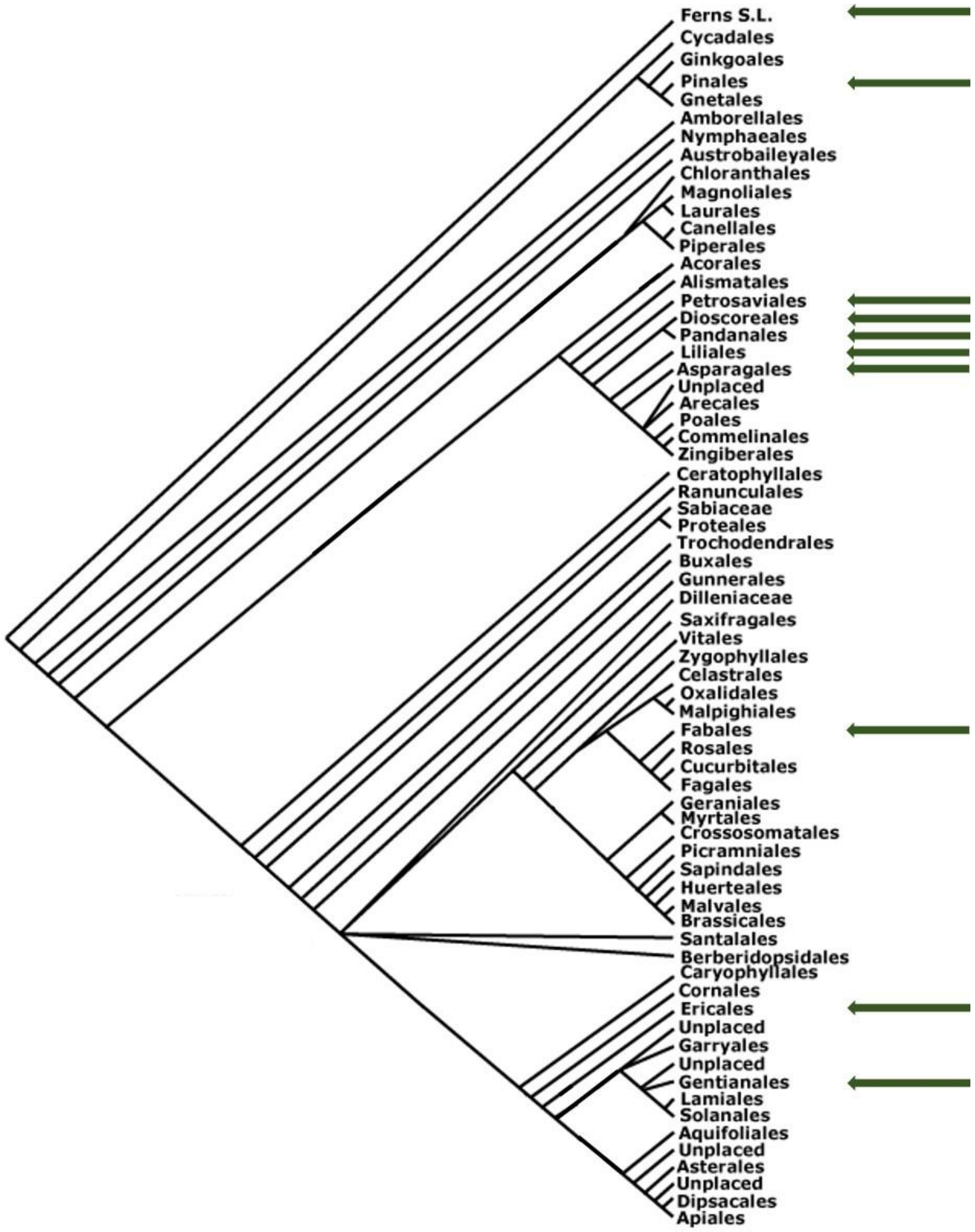
Skupina D. Rostlina je v jedné části svého životního cyklu, typicky ve stádiu gametofytu, zcela neschopná fotosyntézy a plně závislá na vnějším přísunu uhlíku prostřednictvím mykorhizy. Sporofyt je buď plně, nebo částečně autotrofní. Typicky se tato forma mykoheterotrofie vyskytuje u některých výtrusných rostlin se samostatně žijícím gametofytem a sporofytem, např. u plavuňovitých (*Lycopodiaceae*), hadilkovitých (*Ophioglossaceae*) nebo prutovkovitých (*Psilotaceae*).

Skupina E. Rostlina není v žádném vývojovém stádiu ani fázi životního cyklu schopná fotosyntézy, a je proto plně závislá na vnějším přísunu uhlíku. Tato a předchozí forma jsou označovány jako úplná mykoheterotrofie.

Termínem mykoheterotrof jsou obvykle označovány jen rostliny úplně mykoheterotrofní (skupiny D a E v přechozím textu) a v tomto pojetí je termín používán i zde. V řadě prací jsou však výtrusné mykoheterotrofní rostliny (skupina D) opomíjené a termín mykoheterotrof se zužuje jen na skupinu E, případně je těmto rostlinám věnovaná disproporčně větší pozornost (viz např. Merckx et al. 2013a). Někdy, zejména u vstavačovitých, nelze některé druhy jednoznačně zařadit do výše uvedených kategorií, například proto, že nezelení jsou jen juvenilní jedinci, kteří později v dospělosti zezelenají (rod *Pseudovanilla*) nebo jsou nezelení jen někteří jedinci v populaci (*Corybas cheesemanii* (Hook.f. ex Kirk) Kuntze).

2.2 Mykoheterotrofie u rostlin

Mykoheterotrofie se mezi rostlinami vyskytuje poměrně vzácně. Mykoheterotrofních je něco přes 1100 druhů vyšších rostlin (tab. 1), tedy asi jen 0,3 % z jejich odhadovaného celkového počtu (Christenhusz et al. 2017). V průběhu evoluce se vyvinula opakovaně a vyskytuje u většiny hlavních skupin vyšších rostlin (obr. 2), i když u některých je velmi vzácná, zejména mezi mechorosty a nahosemennými. Nejvíce rozšířená je naopak mezi jednoděložnými rostlinami, které tvoří asi 45 % všech mykoheterotrofních rostlin (tab. 1). Zajímavý je výskyt mykoheterotrofie u monilofytních rostlin, které jsou úplně mykoheterotrofní výhradně v gametofytní fázi životního cyklu. Mykoheterotrofie se u nich zřejmě vyvinula nejméně dvakrát nezávisle v průběhu evoluce, neboť se vyskytuje jednak u všech zástupců dvou evolučně spřízněných řádů eusporangiátních kapraďorostů, *Ophioglossales* a *Psilotales,* ale také u několika zástupců leptosporangiátních kapradin řádů *Gleicheniales* a *Schizaeales*, většina jejichž zástupců má ale gametofyty zelené, autotrofní, stejně jako všechny ostatní kapradiny.



Obrázek 2. Výskyt plně mykoheterotrofních druhů u cévnatých rostlin (šipkou). Fylogeneze řádů dle APG IV (2016).

Tabulka 1. Výskyt mykoheterotrofie u vyšších rostlin. Většina údajů je převzata z práce Merckx et al. (2013a) a aktualizována ke stavu v roce 2020, údaje označené hvězdičkou (*) jsou převzaty z PPG I (2016).

vyšší jednotka	**řád**	**počet druhů**	**taxony**
Marchantiophyta	*Jungermanniales*	1	*Cryptothallus mirabilis*
Lycopodiophyta	*Lycopodiales*	388*	všechny druhy řádu
Monilophyta	*Ophioglossales*	112*	všechny druhy řádu
	Psilotales	17*	všechny druhy řádu
	Gleicheniales	1*	*Stromatopteris moniliformis*
	Schizaeales	15*	*Actinostachys* (všechny druhy rodu)
Pinophyta	*Cupressales*	1	*Parasitaxus ustus*
Liliopsida	*Petrosaviales*	4	všechny druhy řádu
	Dioscoreales	162	*Burmanniaceae* (52), *Thismiaceae* (110)
	Pandanales	50	*Triuridaceae* (všechny druhy čeledi)
	Liliales	27	*Corsiaceae* (všechny druhy čeledi)
	Asparagales	287	*Orchidaceae* (285), *Geosiris* (2)
Rosopsida	*Fabales*	7	*Epirixanthes* (všechny druhy rodu)
	Ericales	17	*Monotropaceae* (16), *Pyrolaceae* (1)
	Gentianales	25	*Gentianaceae* (čtyři rody)
	celkem	**1114**	

2.3 Mykoheterotrofní rostliny v mírných pásech a v tropech

Výrazná většina mykoheterotrofních rostlin, asi 75 %, se vyskytuje v tropech, přičemž jejich preferovaným biotopem je tropický deštný les (Merckx et al. 2013b). Vyskytují se ale také v subtropických, mírných a ojediněle dokonce i v severských oblastech. V temperátním podnebném pásu je nejbohatším regionem severní Amerika, kde roste celkem 30 plně mykoheterotrofních krytosemenných druhů rostlin, následovaná Asií s více jak 20 druhy (Merckx et al. 2013b). Evropa je dosti chudší a například v České republice, pomineme-li výtrusné rostliny, se vyskytuje šest plně mykoheterotrofních druhů rostlin náležejících do dvou čeledí (*Ericaceae* a *Orchidaceae*) a pěti rodů (*Corallorhiza*, *Epipogium*, *Limodorum*, *Monotropa* a *Neottia*; Kaplan et al. 2019).

V tropech je zdaleka nejbohatší oblastí jihovýchodní Asie, kde se vyskytuje kolem 200 druhů mykoheterotrofních rostlin (aktualizovaný údaj z práce Merckx et al. 2013b), následovaná tropickou Amerikou a Australasijskou oblastí; Afrika je naopak dosti chudá, přestože má druhou největší rozlohu deštných lesů ze všech kontinentů (Merckx et al. 2013b). V rámci jihovýchodní Asie je pak diverzita mykoheterotrofů soustředěna zejména do Malesijské fytogeografické oblasti, zvláště pak na Malajský poloostrov a Sundské ostrovy, ke kterým patří i Borneo.

3 Flóra Bornea

Flóra Bornea je výrazně ovlivněna nejen jeho velmi dobře známou čtvrtohorní geologickou historií (např. Hunt et al. 2012), ale také jeho současnými přírodními podmínkami. Ostrov, jehož rozloha činí 746 000 km^2, je geograficky velmi členitý, i když převážně nížinný s centrální vrchovinou, jejíž nejvyšší vrcholy dosahují obvykle výšek kolem 2000–2500 m (MacKinnon et al. 1996). Tomu se vymyká pouze nejvyšší hora Bornea, Kinabalu, která je o víc jak 1000 m vyšší než všechny ostatní hory ostrova a s nadmořskou výškou 4095 m jen také nejvyšší horou mezi Himálajem a Novou Guineou (Beaman 2005). Klima je tropické, velmi vlhké a většinu ostrova tedy pokrývá stálezelený tropický deštný les (Slik et al. 2003). Nelesní biotopy jsou vzácné, omezené převážně na mořská pobřeží, nejvyšší hory, velké řeky, vápencové masívy, hadcové oblasti, ojedinělá přirozená jezera a centrální části rašelinišť. Výjimkou je pouze nejjižnější cíp ostrova, který je sušší a pokrytý savanou (MacKinnon et al. 1996). Flóra Bornea je tedy převážně lesní s diverzitou koncentrovanou do nížinných až podhorských tropických deštných lesů (Raes et al. 2009).

Borneo je součástí Malesijské fytogeografické oblasti Paleotropické květenné říše (Takhtajan 1986). Jeho flóra je extrémně bohatá a ostrov patří ke světovým centrům rostlinné diverzity (Raes et al. 2009). Flóra Bornea čítá odhadovaných 14 500 původních druhů rostlin (Roos et al. 2004), tedy víc, než například rozlohou třikrát větší Demokratická republika Kongo (Buttler 2019). Endemismus cévnatých rostlin je odhadován na cca 28 % (Roos et al. 2004), přičemž nejvyšší diverzita i endemismus jsou predikovány pro severní část ostrova (Raes et al. 2009). Borneo je rovněž světovým centrem diverzity pro několik významných čeledí tropických rostlin, zejména dřevinných jako dvojkřídláčovité (*Dipterocarpaceae*) a zederachovité (*Meliaceae*; van Welzen & Slik 2009), z bylinných čeledí pravděpodobně zázvorovité (*Zingiberaceae*), begóniovité (*Begoniaceae*) a další.

Zajímavé jsou fytogeografické vztahy Bornea k holarktické flóře. Na Borneu se překvapivě vyskytuje několik převážně Holarktických rodů rostlin, které se jinde v oblasti jihovýchodní Asie buď nevyskytují vůbec, nebo jsou velmi vzácné. Tyto rody se většinou vyskytují jen v nejvyšších horských polohách, obvykle v masívu Mt. Kinabalu a jsou zde glaciálními relikty (van Steenis 1964). Na Borneu se tak můžeme setkat s rody, které důvěrně známe ze střední Evropy, jako například *Avenella*, *Euphrasia*, *Potentilla*, *Ranunculus* aj. Zajímavý je rod *Platanthera*, který je ve střední Evropě zastoupen dvěma druhy, zatímco na Borneu rostou čtyři druhy, z nichž jeden, *Platanthera saprophytica,* je endemický a zároveň jediný známý plně mykoheterotrofní zástupce rodu (viz tabule 4, obr. M.).

Z floristického hlediska jsou tropické deštné lesy hyperdiverzním prostředím, především pokud jde o dřeviny, zejména pak stromy (Slik et al. 2015). Bornejské deštné lesy jsou v globálním měřítku druhé nejbohatší a v počtu druhů stromů na hektar jen těsně zaostávají za Amazonií (Condit et al. 2005). Stromová složka vegetace je také nejvíce studovanou, zejména v posledních desetiletích v souvislosti s jejich schopností vázat oxid uhličitý z ovzduší a ovlivňovat tak klimatickou rovnováhu (Qie et al. 2017, Sullivan et al. 2018, Sullivan et al. 2020). Bylinné rostliny jsou na druhou stranu dosti opomíjené. Studovány jsou zejména atraktivní skupiny, jako jsou begónie, láčkovky či zázvorovité rostliny. Jmenované skupiny jsou shodou okolností na Borneu rovněž hyperdiverzní a ostrov je světovým centrem jejich diverzity. Například rod begónie (*Begonia*) je na ostrově zastoupen asi 250 popsanými druhy, přičemž je odhadováno, že počet dosud nepopsaných druhů převyšuje výrazně počet popsaných. Celkově je počet druhů begónií na Borneu odhadován na zhruba 600 (Sang & Kiew 2014, Hughes et al. 2020), tedy víc než u kteréhokoliv jiného rostlinného rodu vyskytujícího se na ostrově. Rovněž u rodu láčkovka (*Nepenthes*) je z ostrova známo 41 druhů, tedy zhruba 25 % celosvětového počtu (asi 160 druhů), přičemž jsou stále objevovány druhy nové (např. Robinson et al. 2019, Golos et al. 2020). *Zingiberaceae* jsou na ostrově zastoupeny 19 rody (z nich 4 endemické) a cca 250 druhy, což představuje zhruba 17 % jejich globálního počtu (Lamb et al. 2013), přičemž i u této čeledi jsou z ostrova stále popisovány nové druhy (např. Meekiong 2016, Ooi et al. 2017, Aimi Syazana et al. 2018).

V tomto kontextu jsou mykoheterotrofní rostliny zcela okrajovou součástí celkové biodiverzity tropických deštných lesů Bornea, což je zřejmě také jeden z důvodů, proč jim dosud nebyla věnována větší pozornost. Nicméně v globálním kontextu rozšíření mykoheterotrofních rostlin je Borneo rovněž jejich světovým centrem diverzity.

4 Mykoheterotrofní rostliny Bornea

Diverzita mykoheterotrofních rostlin v tropických deštných lesích Bornea je enormní. Zahrnuje 29 rodů náležejících do 23 čeledí s nejméně 125 popsanými druhy. Toto číslo představuje víc jak 11 % globální biodiverzity mykoheterotrofních rostlin. U semenných rostlin s 21 rody náležejících do sedmi čeledí s nejméně 89 popsanými druhy je to pak dokonce 16 % (viz také tab. 1). Nejvíc bornejských mykoheterotrofů patří mezi vstavačovité (*Orchidaceae*) s 37 druhy ve 14 rodech, které jsou následovány hvězdnatkovitými (*Thismiaceae*) s 24 druhy v jednom rodě. Některé rody (např. *Didymoplexiella*, *Didymoplexis*, *Epirixanthes*, *Thismia* a *Sciaphila*) mají na Borneu svá centra diverzity (obr. 6, 10).

4.1 Přehled druhů mykoheterotrofních rostlin Bornea

Taxonomické pojetí a nomenklatura v tomto přehledu primárně korespondují s databází Plants of the world online (POWO 2019) s výjimkou taxonů, u kterých se aktuální stav poznání neshoduje s údaji v této databázi (např. byly popsány nové druhy, které zatím do databáze nebyly zařazeny). Seznam odpovídá stavu přibližně v polovině roku 2020.

ČELEĎ *LYCOPODIACEAE*

Rod *Huperzia*

Huperzia australiana (Herter) Holub, Folia Geobot. Phytotax. 20(1): 70 (1985).

Huperzia beccarii (Alderw.) Holub, Folia Geobot. Phytotax. 20(1): 71 (1985).

Huperzia carinata (Desv. ex Poir.) Trevis., Atti Soc. Ital. Sci. Nat. 17(2): 247 (1874).

Huperzia dalhousieana (Spring) Trevis., Atti Soc. Ital. Sci. Nat. 17(2): 247 (1874). Tabule 1, obr. A.

Huperzia goebellii (Nessel) Holub, Folia Geobot. Phytotax. 20(1): 73 (1985).

Huperzia goliathensis (Alderw.) Holub, Folia Geobot. Phytotax. 20(1): 73 (1985).

Huperzia horizontalis (Herter ex Nessel) Holub, Folia Geobot. Phytotax. 20(1): 73 (1985).

Huperzia javanica (Sw.) Fraser-Jenk., Taxon. Revis. Indian Subcontinental Pteridophytes 10 (2008).

Huperzia nummulariifolia (Blume) Chambers, Jermy & Crabbe, Brit. Fern Gaz. 10: 176. 1971.

Huperzia phlegmaria (L.) Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 62 (1944)

Huperzia phyllantha (Hook. & Walker-Arnott) Holub, Folia Geobot. Phytotax. 20(1): 75 (1985).

Huperzia pinifolia Trevis., Atti Soc. Ital. Sci. Nat. 17(2): 247 (1874).

Huperzia prolifera (Blume) Trevis., Atti Soc. Ital. Sci. Nat. 17(2): 247 (1874).

Huperzia setifolia (Alderw.) Holub, Folia Geobot. Phytotax. 20(1): 76 (1985).

Huperzia squarrosa (G. Forst.) Trevis., Atti Soc. Ital. Sci. Nat. 17(2): 247 (1874). Tabule 1, obr. B.

Huperzia tetrasticha (Kunze ex Alderw.) Holub, Folia Geobot. Phytotax. 20(1): 77 (1985).

Huperzia verticillata (L. f.) Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 60 (1944).

Rod *Lycopodiella*

Lycopodiella cernua (L.) Pic. Serm., Webbia 23: 166 (1968).

Rod *Lycopodium*

Lycopodium casuarinoides Spring, Bull. Acad. Roy. Sci. Bruxelles 8: 521 (1841). Tabule 1, obr. C.

Lycopodium clavatum L., Sp. Pl. 2: 1101 (1753).

Lycopodium platyrhizoma J. H. Wilce, Nova Hedwigia 3(1): 99 (1961).

Lycopodium scariosum G. Forst., Fl. Ins. Austr. 87 (1786).

Lycopodium volubile G. Forst., Fl. Ins. Austr. 86 (1786).

Lycopodium wightianum Wall. ex Grev. & Hook., Enum. Filic. 379 (1831).

ČELEĎ OPHIOGLOSSACEAE

Rod *Botrychium*

Botrychium daucifolium Wall. ex Hook. & Grev., Icon. Filic. 2 (9): pl. 161. (1830). Tabule 1, obr. D.

Rod *Helminthostachys*

Helminthostachys zeylanica (L.) Hook., Gen. Fil. [Hooker]: pl. 47 (1842). Tabule 1, obr. E.

Rod *Ophioglossum*

Ophioglossum gramineum Willd., Abh. Kurfürstl.-Mainz. Akad. Nützl. Wiss. Erfurt. 5(2): 18 (1802).

Ophioglossum intermedium Hook., Icon. Pl. 6: pl. 995 (1854).

Ophioglossum pendulum L. Sp. Pl. (ed. 2) 2: 1518 (1763).

Ophioglossum petiolatum Hook., Exot. Fl. 1: 56 (1823).

Ophioglossum reticulatum L., Sp. Pl. 2: 1063 (1753). Tabule 1, obr. F.

ČELEĎ PSILOTACEAE

Rod *Psilotum*

Psilotum nudum (L.) P. Beauv., Prodr. Aethéogam. 112 (1805).

Psilotum complanatum Sw., J. Bot. (Schrader) 1800(2): 110 (1801). Tabule 1, obr. H.

ČELEĎ SCHIZAEACEAE

Rod *Actinostachys*

Actinostachys digitata (L.) Wall., Numer. List [Wallich] n. 1 (1828). Tabule 1, obr. I.

Actinostachys inopinata (Selling) C. F. Reed, Bol. Soc. Brot. sér. 2, 21: 130 (1948).

Actinostachys wagneri (Selling) C. F. Reed, Bol. Soc. Brot. sér. 2, 21: 131 (1948).

ČELEĎ BURMANNIACEAE

Rod *Burmannia*

Burmannia championii Enum. Pl. Zeyl. [Thwaites] 325 (1864). Tabule 2, obr. A.

Burmannia lutescens Becc., Malesia 1: 246 (1878). Tabule 2, obr. B.

Burmannia malasica Jonker, Monogr. Burmann. 152 (1938). Tabule 2, obr. C.

Burmannia sphagnoides Becc., Malesia 1: 246 (1878).

Rod *Gymnosiphon*

Gymnosiphon aphyllus Blume, Enum. Pl. Javae 1: 29 (1827). Tabule 2, obr. D.

ČELEĎ GENTIANACEAE

Rod *Exacum*

Exacum tenue (Blume) Klack., Bot. Jahrb. Syst. 126(4): 478 (2006). Tabule 3, obr. A.

ČELEĎ ORCHIDACEAE

Rod *Aphyllorchis*

Aphyllorchis kemulensis J. J. Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 11: 84 (1931).

Aphyllorchis maliauensis Suetsugu, Suleiman & Tsukaya, Phytotaxa 367(1): 85 (2018).

Aphyllorchis montana Rchb. f., Linnaea 41(1): 57 (1876). Tabule 4, obr. C.

Aphyllorchis pallida Blume, Tab. Pl. Jav. Orchid. ad f. 77 (1825).

Aphyllorchis siantanensis J. J. Sm., Repert. Spec. Nov. Regni Veg. 30: 327 (1932).

Aphyllorchis spiculaea Rchb.f., Linnaea 41(1): 58 (1876).

Aphyllorchis striata (Ridl.) Schltr., Bull. Herb. Boissier ser. 2, 6: 299 (1906). Tabule 4, obr. A.

Rod *Cyrtosia*

Cyrtosia javanica Blume, Bijdr. Fl. Ned. Ind. 8: 396 (1825).

Rod *Cystorchis*

Cystorchis aphylla Ridl., J. Linn. Soc., Bot. 32: 400 (1896). Tabule 4, obr. D.

Cystorchis saprophytica J. J. Sm., Mitt. Inst. Allg. Bot. Hamburg 7: 23 (1927).

Rod *Didymoplexiella*

Didymoplexiella borneensis (Schltr.) Garay, Arch. Jard. Bot. Rio de Janeiro 13: 33 (1954). Tabule 4, obr. E.

Didymoplexiella cinnabarina Tsukaya, M. Nakaj. & H. Okada, Acta Phytotax. Geobot. 56(3): 208 (2005).

Didymoplexiella forcipata (J. J. Sm.) Garay, Arch. Jard. Bot. Rio de Janeiro 13: 33 (1954).

Didymoplexiella kinabaluensis (Carr) Seidenf., Dansk Bot. Ark. 32(2): 175 (1978).

Didymoplexiella ornata (Ridl.) Garay, Arch. Jard. Bot. Rio de Janeiro 13: 33 (1954). Tabule 4, obr. F.

Didymoplexiella trichechus (J. J. Sm.) Garay, Arch. Jard. Bot. Rio de Janeiro 13: 34 (1954).

Rod *Didymoplexis*

Didymoplexis cornuta J. J. Sm., Bull. Inst. Bot. Buitenzorg 7: 1 (1925). Tabule 4, obr. G.

Didymoplexis latilabris Schltr., Bull. Herb. Boissier, sér. 2, 6: 300 (1906).

Didymoplexis obreniformis J. J. Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 14: 26 (1914).

Didymoplexis pallens Griff., Calcutta J. Nat. Hist. 4: 383, pl. 17 (1844).

Didymoplexis striata J. J. Sm., Icon. Bogor. pl. 104 B (1906). Tabule 4, obr. H.

Rod *Epipogium*

Epipogium roseum (D. Don) Lindl., J. Proc. Linn. Soc., Bot. 1: 177 (1857).

Rod *Erythrorchis*

Erythrorchis altissima (Blume) Blume, Rumphia 1: 200, pl. 70 (1837).

Rod *Eulophia*

Eulophia zollingeri (Rchb. f.) J. J. Sm., Fl. Buitenz. 6: 228 (1905).

Rod *Galeola*

Galeola nudifolia Lour., Fl. Cochinch. 2: 520 (1790)

Rod *Gastrodia*

Gastrodia effusa P. T. Ong & P. O'Byrne, Malesian Orchid J. 10: 11 (2012).

Gastrodia grandilabris Carr, Gard. Bull. Straits Settlem. 8: 179 (1935).

Gastrodia javanica (Blume) Lindl., Gen. Sp. Orchid. Pl. 384 (1840).

Gastrodia maliauensis Suetsugu, Suleiman & Tsukaya, Phytotaxa 367(1): 78 (2018).

Gastrodia sabahensis J. J. Wood & A. L. Lamb, Malesian Orchid J. 1: 139 (2008).

Gastrodia spatulata (Carr) J. J. Wood, Orchids Mount Kinabalu 2: 355 (2011).

Rod *Lecanorchis*

Lecanorchis malaccensis Ridl., Trans. Linn. Soc. London, Bot. 3: 371 (1893). Tabule 4, obr. K.

Lecanorchis multiflora J. J. Sm., Bull. Jard. Bot. Buitenzorg, sér. 2, 26: 8 (1918). Tabule 4, obr. L.

Lecanorchis sarawakensis Suetsugu & Naiki, Phytotaxa 338(1): 135 (2018).

Rod *Platanthera*

Platanthera saprophytica J. J. Sm., Mitt. Inst. Allg. Bot. Hamburg 7: 12 (1927). Tabule 4, obr. M.

Rod *Stereosandra*

Stereosandra javanica Blume, Mus. Bot. 2: 176 (1856).

Rod *Tropidia*

Tropidia connata J. J. Wood & A. L. Lamb, Check-list Orchids Borneo 47 (1994)

Tropidia nagamasui (Tsukaya, M. Nakaj. & H. Okada) Ormerod & Juswara, Harvard Pap. Bot. 24(1): 30 (2019).

Tropidia saprophytica J. J. Sm., Mitt. Inst. Allg. Bot. Hamburg 7: 27 (1927). Tabule 4, obr. N.

ČELEĎ PETROSAVIACEAE

Rod *Petrosavia*

Petrosavia stellaris Becc., Nuovo Giorn. Bot. Ital. 3: 8 (1871). Tabule 6, obr. G.

ČELEĎ POLYGALACEAE

Rod *Epirixanthes*

Epirixanthes confusa Tsukaya, Suleiman & H. Okada, Phytotaxa 266(2): 147 (2016).

Epirixanthes cylindrica Blume, Catalogus 82 (1823).

Epirixanthes elongata Blume, Catalogus 82 (1823). Tabule 3, obr. B.

Epirixanthes kinabaluensis T. Wendt, Fl. Males. 10: 491 (1988). Tabule 3, obr. C.

Epirixanthes pallida T. Wendt, Fl. Males. 10: 492 (1988). Tabule 3, obr. D.

Epirixanthes papuana J. J. Sm., Repert. Spec. Nov. Regni Veg. 10: 486 (1912). Tabule 3, obr. E.

ČELEĎ THISMIACEAE

Rod *Thismia*

Thismia acuminata Hroneš, Dančák & Sochor, Pl. Syst. Evol. 304(5): 705 (2018). Tabule 5, obr. B.

Thismia aseroe agg.

Thismia betung-kerihunensis Tsukaya & H. Okada, Syst. Bot. 37(1): 56 (2012).

Thismia bifida M. Hotta, Acta Phytotax. Geobot. 22: 161 (1967). Tabule 5, obr. J.

Thismia brunneomitra Hroneš, Kobrlová & Dančák, Phytotaxa 234(2): 173 (2015). Tabule 5, obr. A.

Thismia bryndonei Tsukaya, Suetsugu & Suleiman, Phytotaxa 312(1): 135 (2017).

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

Thismia cornuta Hroneš, Sochor & Dančák, Pl. Ecol. Evol. 151(1): 111 (2018). Tabule 5, obr. I.

Thismia coronata Hroneš, Dančák & Sochor, Willdenowia 50(1): 71 (2020).

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

Thismia filiformis agg.

Thismia goodii Kiew, Gard. Bull. Singapore 51: 179 (1999). Tabule 5, obr. C.

Thismia hexagona Dančák, Hroneš, Kobrlová & Sochor, Phytotaxa 125(1): 34 (2013). Tab. 5, obr. J.

Thismia inconspicua Sochor & Dančák, Phytotaxa 295(3): 264 (2017).

Thismia kelabitiana Dančák, Hroneš & Sochor, PLoS ONE 13(10): e0203443 (3) (2018). Tabule 5, obr. D.

Thismia kinabaluensis T. Nishioka & Suetsugu, Phytotaxa 360(2): 174 (2018).

Thismia laevis Sochor, Dančák & Hroneš, Pl. Syst. Evol. 304(5): 708 (2018).

Thismia lauriana Jarvie, Blumea 41: 259 (1996).

Thismia minutissima Dančák, Hroneš & Sochor, Kew Bull. 75(2)-29: 2 (2020). Tabule 5, obr. F.

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

Thismia neptunis Becc., Malesia 1: 251 (1878). Tabule 5, obr. G.

Thismia nigra Dančák, Hroneš & Sochor, Pl. Syst. Evol. 304(5): 711 (2018).

Thismia ophiuris Becc., Malesia 1: 252 (1878).

Thismia ornata Dančák, Hroneš & Sochor, Willdenowia 50(1): 66 (2020). Tabule 5, obr. H.

Thismia pallida Hroneš, Dančák & Rejžek, Pl. Ecol. Evol. 151(1): 115 (2018).

Thismia viridistriata Sochor, Hroneš & Dančák, Pl. Syst. Evol. 304(5): 714 (2018). Tabule 5, obr. E.

ČELEĎ TRIURIDACEAE

Rod *Sciaphila*

Sciaphila alba Tsukaya & Suetsugu, Phytotaxa 170(4): 284 (2014). Tabule 6, obr. C.

Sciaphila arfakiana Becc., Malesia 3: 337 (1890). Tabule 6, obr. E.

Sciaphila atra Dančák, Hroneš & Sochor, Phytotaxa 472(3): 278 (2020). Tabule 6, obr. A.

Sciaphila betung-kerihunensis Tsukaya & H. Okada, Syst. Bot. 38(3): 600 (2013).

Sciaphila brevistyla Tsukaya & H. Okada, Syst. Bot. 38(3): 602 (2013).

Sciaphila densiflora Schltr., Bot. Jahrb. Syst. 49: 87 (1912).

Sciaphila inouei Tsukaya & Suetsugu, Phytotaxa 170(4): 284 (2014).

Sciaphila maculata Miers, Trans. Linn. Soc. London 21: 48 (1852).

Sciaphila major Becc., Malesia 3: 332 (1890). Tabule 6, obr. D.

Sciaphila micranthera Giesen, Pflanzenr. Heft 104: 54 (1938).

Sciaphila tenella Blume, Bijdr. Fl. Ned. Ind. 514 (1825). Tabule 6, obr. B.

Sciaphila winkleri Schltr., Bot. Jahrb. Syst. 48: 88 (1912). Tabule 6, obr. F.

5 Současná taxonomická problematika u vybraných skupin myko-heterotrofních rostlin Bornea

Taxonomický výzkum mykoheterotrofních rostlin je komplikován řadou okolností. V první řadě je to výrazně redukovaná stavba těla, která se vyvinula jako reakce na mykoheterotrofní způsob výživy. Tato redukce logicky nejvíce postihla asimilační orgány, tedy především listy, které se staly zbytečnými. Listy, u autotrofních rostlin nositelé celé řady taxonomicky zásadních znaků (např. počet, stavba, tvar, seratura, žilnatina, odění aj.), jsou u mykoheterotrofních rostlin zakrnělé, obvykle šupinovité a jen málokdy poskytující významnou taxonomickou informaci. Redukce je patrná také v celkové velikosti těl těchto rostlin, které jsou zpravidla velmi malé, obvykle zřetelně menší než jejich autotrofní příbuzní (existují-li). Ostatní základní orgány (květ, plod, stonek a kořen) obvykle redukovány nejsou, i když například květy mohou být u některých skupin extrémně malé (např. rody *Sciaphila* nebo *Gymnosiphon*) v souvislosti s malou velikostí celého těla rostliny. Další významnou okolností komplikující výzkum mykoheterotrofů je způsob jejich života. U mnoha taxonů (např. typicky rod *Thismia*) je mykoheterotrofie spojena s tím, že nadzemní části rostliny se objevují jen sezónně a po relativně krátkou dobu, a to i v oblastech se stálým tropickým klimatem, což významně komplikuje dostupnost studijního materiálu. Nedostupnost studijního materiálu je dále zesílena nemožností mykoheterotrofní rostliny pěstovat. Výzkum mykoheterotrofních rostlin v tropických oblastech je rovněž komplikován nadměrnou administrativou a byrokracií spojenou se získáváním povolení k výzkumu, sběru materiálu a jeho exportu. V neposlední řadě je nutné zmínit i globální neochotu poskytovatelů dotací na vědecký výzkum financovat základní popisnou vědu (Christenhusz & Byng 2016), přestože zejména v tropických oblastech zůstává významná část biodiverzity nepopsaná a navíc bezprostředně ohrožená vyhubením.

V této kapitole shrnuji poznatky, které se týkají vybraných taxonomicky zajímavých skupin mykoheterotrofních rostlin Bornea, získané terénním výzkumem během expedic uskutečněných do různých částí Bornea v letech 2007–2020. Část zde diskutovaných problémů vyústila v publikace, které jsou buď součástí této habilitační práce, anebo jsou citovány v textu. U některých skupin (*Ophioglossaceae, Burmanniaceae* a *Orchidaceae*) jde výhradně o dosud nepublikovaná zjištění, většinou z důvodu nutnosti dalšího výzkumu v těchto skupinách.

5.1 Čeleď *Ophioglossaceae*

Čeleď *Ophioglossaceae* (hadilkovité) představuje významnou skupinu výtrusných rostlin, které jsou plně mykoheterotrofní jen ve stádiu gametofytu (Merckx et al. 2013a). Rovněž sporofytní fáze si u mnoha druhů zachovává v různé míře závislost na mykorhizních houbách, i když žádný zcela nezelený druh, plně mykoheterotrofní i ve stádiu sporofytu, neexistuje (Hynson et al. 2013, Suetsugu et al. 2020b). Celosvětově je tato čeleď tvořena asi 112 druhy v 10 rodech (PPG I 2016), na Borneu se vyskytuje nejméně 7 druhů ve třech rodech (*Botrychium*, *Helminthostachys* a *Ophioglossum*, viz Tabule 1). Rody *Botrychium* a *Helminthostachys* jsou na Borneu zastoupeny každý pouze jedním druhem (viz kapitola 4.1) a jsou taxonomicky zřejmě nezajímavé, zatímco rod *Ophioglossum* má na tomto ostrově nejméně pět známých druhů (Wieffering 1964, POWO 2019). Tento rod je navíc taxonomicky komplikovaný kvůli značné plasticitě řady druhů kombinované s velmi jednoduchou tělesnou stavbou (Patel & Narsimha 2019) a z toho vyplývajících obtížích při delimitaci taxonů. To dokumentuje také fakt, že pro některé druhy jsou uváděny poměrně rozsáhlé, ale přitom velmi nesouvislé areály zahrnující i několik kontinentů (viz POWO 2019).

5.1.1 Rod *Ophioglossum*

Z Bornea je různými prameny uváděno až sedm druhů tohoto rodu, ačkoliv databáze POWO (2019) akceptuje jen pět (viz kapitola 4.1). Vedle epifytního paleotropického druhu *Ophioglossum pendulum* a druhu *O. intermedium*, který může růst epifytně i terestricky, jsou všechny ostatní terestrické. *Ophioglossum gramineum* je druh s dosti disjunktním paleotropickým rozšířením (POWO 2019) v Malesijské oblasti ale dosti častý (Wieffering 1964). *Ophioglossum reticulatum* je druh s velmi rozsáhlým pantropickým areálem zasahujícím až na okraje mírných pásů (POWO 2019). *Ophioglossum intermedium* je naopak druh omezený jen na Malesijskou oblast s přesahem do severní Austrálie (POWO 2019). *Ophioglossum petiolatum* je druh nověji akceptovaný jako samostatný (Barcelona 2011, Lindsay & Middleton 2012), i když v dřívějších pracích byl spojován s velmi podobným druhem *O. reticulatum* (viz např. Wieffering 1964). Je rozšířen tropické a subtropické Asii, Austrálii a rovně ve střední Americe (POWO 2019). *Ophioglossum parvifolium* Grev. & Hook je druh popsaný z Indie a rozšířený v tropických a subtropických oblastech Asie, Austrálie a Jižní Ameriky (POWO 2019) a některými prameny uváděný i z Bornea (Wieffering 1964, pod synonymním jménem *O. nudicaule* var. *macrorrhizum*

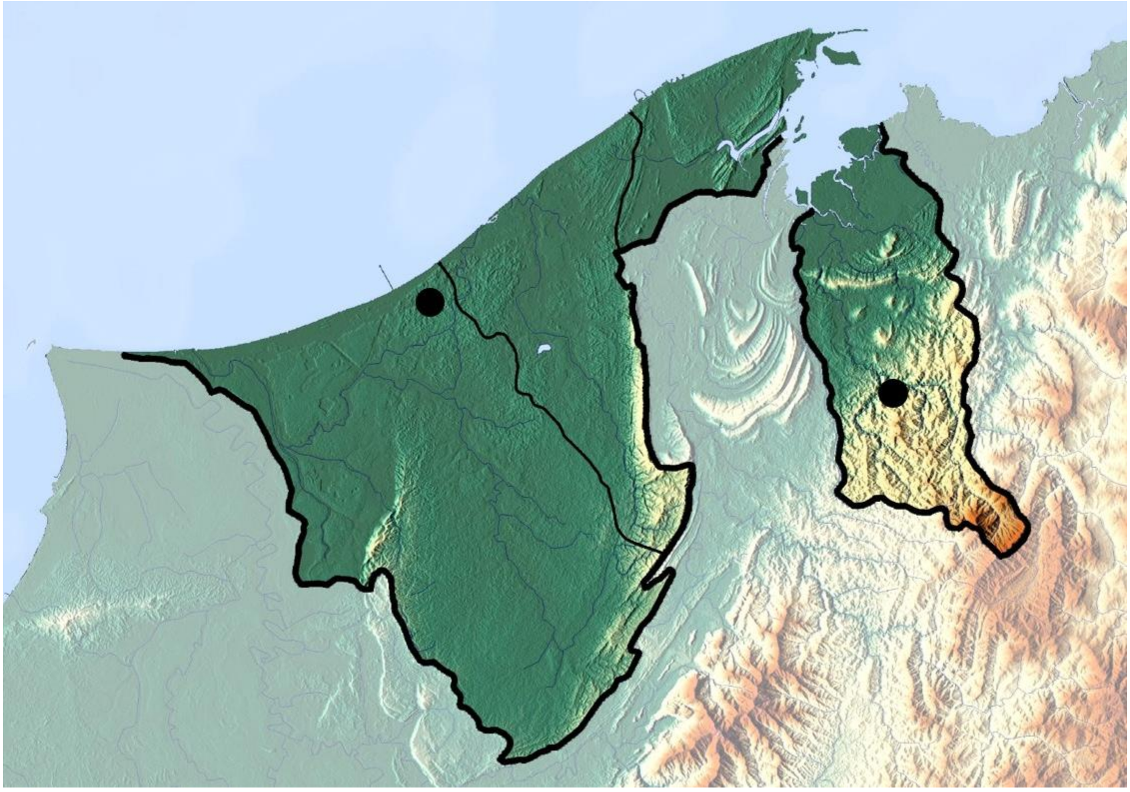
(Kze) Clausen)). *Ophioglossum simplex* Ridley je druh popsaný ze Sumatry a databází POWO (2019) je považován za endemický pro tento ostrov, přestože jej Wieffering (1964) uvádí mimo jiné rovněž z Bornea.

Kromě víc jak půl století staré práce Wiefferinga (Wieffering 1964) neexistují žádné souhrnné revize či monografie tohoto rodu v celé Malesijské oblasti včetně Bornea. Zejména v souvislosti s využitím molekulárních metod, prochází v současnosti taxonomie rodu poměrně významným vývojem. Dochází ke změnám ve vymezení některých taxonů i popisům taxonů nových (Patil & Dongare 2014, Rajput et al. 2016, Patel & Narsimha 2019). Lze tedy usuzovat, že v budoucnu dojde k dalším změnám v seznamu druhů vyskytujících se na ostrově.

Jeden z možných nových druhů, nejen pro Borneo, ale zřejmě i celkově, by mohly představovat morfologicky velmi specifické rostliny nalezené (Dančák, Hroneš & Sochor, nepublikováno) na dvou relativně vzdálených lokalitách v Bruneji (obr. 3), v této práci provizorně nazývané *Ophioglossum* sp. Brunei. Tyto rostliny mají výrazně až zcela redukovanou sterilní část listu (Příloha 1, Tabule 1G) a jsou tedy snadno odlišitelné od všech ostatních druhů z Bornea dosud uváděných. Vzhledem k tomu, že v celé Malesijské oblasti je znám výskyt pouze osmi druhů rodu (POWO 2019) a žádný z nich není tomuto podobný, jedná se skutečně s největší pravděpodobností o nepopsaný druh (viz tab. 2). Těmto rostlinám je morfologicky nejbližší druh *Ophioglossum simplex*, protože také zpravidla postrádá sterilní část listu. Nelze vyloučit, že Wiefferingovy údaje o výskytu *O. simplex* z Bornea (Wieffering 1964, neakceptované v databázi POWO) jsou založeny právě na těchto rostlinách. Skutečností je, že stavba fertilní části listu je u obou druhů výrazně odlišná, neboť *O. simplex* má obvykle větší počet výtrusnic a ty jsou umístěné i na vrcholu fertilní části listu, který má zaokrouhlený tvar (viz také Bower (1901) a tab. 2). *Ophioglossum* sp. Brunei má naopak menší počet výtrusnic a vrchol fertilní části listu je krátce zašpičatělý, bez výtrusnic (Příloha 1, Tabule 1G).

Tabulka 2. Porovnání základních morfologických charakteristik všech malesijských druhů rodu *Ophioglossum* s *Ophioglossum* sp. Brunei. Údaje jsou převzaty z protologů jednotlivých druhů, popřípadě přímo z typového materiálu.

druh	**živ. forma**	**vrchol sterilní části čepele**	**sterilní část čepele**	**fertilní část čepele**
O. costatum	terestrická	bez výtrusnic	vejčitá	vyrůstá z řapíku
O.gramineum	terestrická	bez výtrusnic	úzce kopinatá	vyrůstá z řapíku
O. intermedium	terestrická i epifytní	s výtrusnicemi, tupý	čárkovitá až kopinatá	vyrůstá ze sterilní části čepele
O. parviflorum	terestrická	bez výtrusnic	vejčitě kopinatá	vyrůstá z řapíku
O. pendulum	epifytní	s výtrusnicemi, tupý	úzce kopinatá, často vidličnatě větvená	vyrůstá ze sterilní části čepele
O. petiolatum	terestrická	bez výtrusnic, dlouze špičatý	vejčitá	vyrůstá z řapíku
O. reticulatum	terestrická	bez výtrusnic	vejčitě kopinatá	vyrůstá z řapíku
O. simplex	terestrická	s výtrusnicemi, zaokrouhlený	chybí nebo zakrnělá	vyrůstá z řapíku
O. sp. Brunei	terestrická	bez výtrusnic, krátce špičatý	široce čárkovitá, často chybí	vyrůstá z řapíku



Obrázek 3. Rozšíření *Ophioglossum* sp. Brunei (●) v Brunejském sultanátě.

5.2 Čeleď *Burmanniaceae*

Čeleď *Burmanniaceae* je druhově relativně nepočetná čeleď jednoděložných rostlin s pantropickým rozšířením, v úzkém pojetí (tedy nezahrnující *Thismiaceae*) tvořená téměř 100 druhy v 8–9 rodech (Christenhusz et al. 2017, Merckx 2020). Všechny rody, kromě rodu *Burmannia*, zahrnují výhradně mykoheterotrofní rostliny. Na Borneu je tato čeleď zastoupena rody *Burmannia* a *Gymnosiphon* (Jonker 1948).

5.2.1 Rod *Burmannia*

Rod *Burmannia* (v češtině existuje pro tento rod jméno olachan, které se však nevžilo) má pantropické rozšíření s centrem diverzity v tropické Asii (Maas et al. 1986, Maas-van de Kamer 1998). Tento rod je pozoruhodný tím, že zhruba dvě třetiny jeho druhů jsou zelené a jedna třetina nezelená. Některé zelené druhy jsou přitom plně autotrofní, jiné do různé míry mixotrofní (Merckx et al. 2013a). U tohoto rodu tedy existuje prakticky plynulý přechod od plně autotrofní výživy k plně mykoheterotrofní. Plně mykoheterotrofní druhy jsou vázány na lesní prostředí a v tropických deštných lesích Bornea je znám výskyt nejméně čtyř (POWO 2019) až pěti (Jonker 1948) druhů. Vzhledem k tomu, že tomuto rodu nebyla dosud věnována na Borneu žádná zvláštní pozornost, je velmi pravděpodobné, že počet mykoheterotrofních druhů zde rostoucích bude vyšší. Mykoheterotrofní zástupci rodu na Borneu tvoří dvě morfologicky vyhraněné skupiny. Skupina kolem *Burmannia championii* (Příloha 1, Tabule 2A) se vyznačuje květenstvím hustě na vrcholu nahloučených obvykle drobných květů bez podélných křídel, zatímco skupina kolem *B. lutescens* (Příloha 1, Tabule 2B,C) se vyznačuje volným květenstvím tvořeným spíše relativně velkými květy popřípadě jednokvětými rostlinami s křídlatou květní trubkou. Druhy rodu *Burmannia* se na Borneu vyskytují jak v nížinných tak i horských tropických deštných lesích.

5.2.1.1 Skupina *Burmannia lutescens*

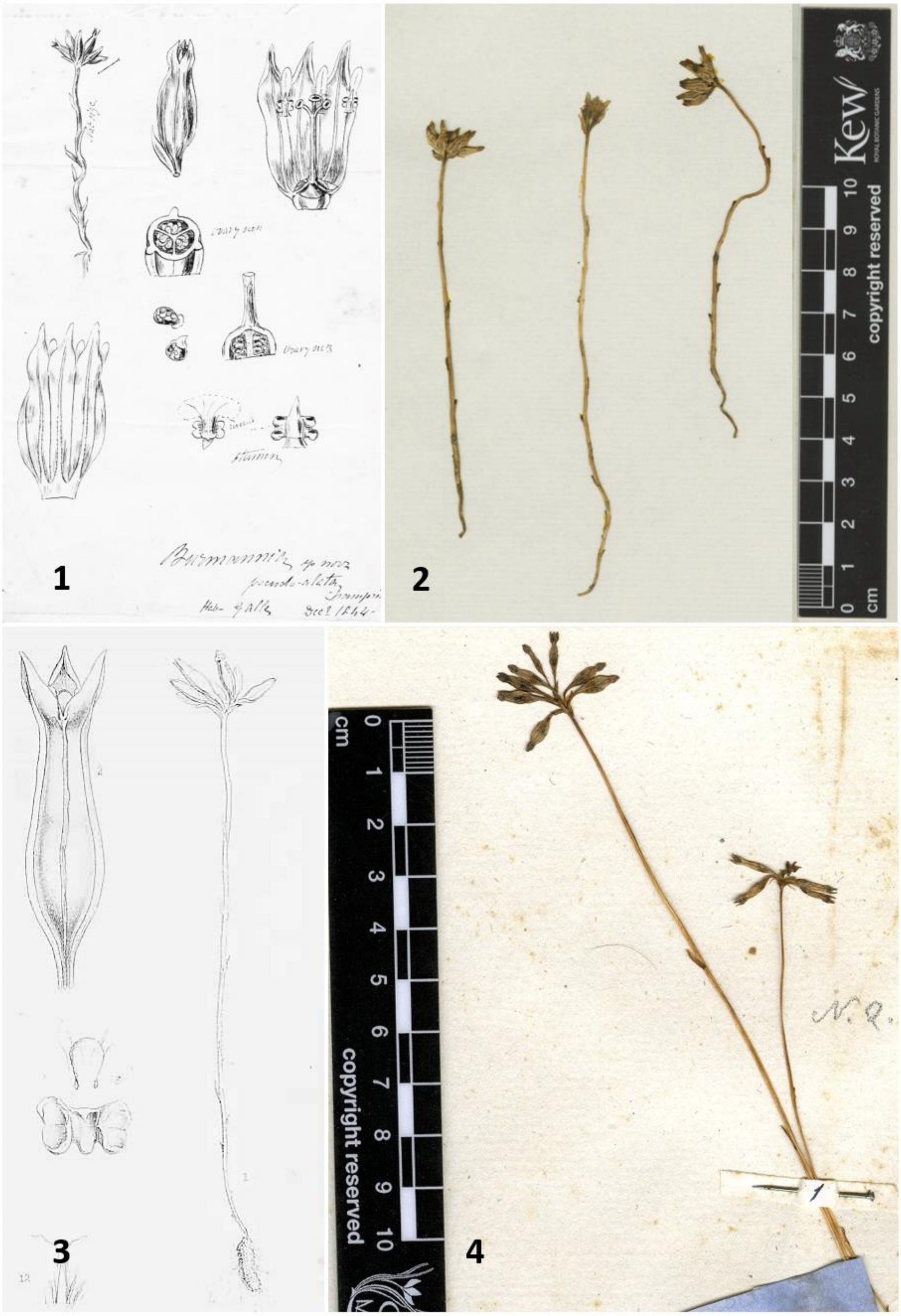
Na Borneu je tato skupina zastoupena pouze dvěma akceptovanými druhy, *Burmannia lutescens* a *B. malasica* (POWO 2019). Z ostrova byl popsán také další druh, *B. tridentata* Beccari, který je všeobecně považován za identický s *B. lutescens* (Jonker 1948, Govaerts et al. 2007). V tomto případě je ovšem kuriózní, že jak *B. lutescens,* tak *B. tridentata* popsal tentýž autor v téže práci a na téže stránce (Beccari 1878). Odoardo Beccari byl vynikající taxonom, který z Bornea i dalších oblastí Malesijské oblasti popsal stovky druhů rostlin. Oba druhy znal nepochybně z autopsie, protože typové lokality leží v území, kde řadu měsíců prováděl terénní výzkum (Sochor et al. 2018a). Stěží lze proto přijmout myšlenku, že tímto způsobem popsal pod různými jmény identický druh. Rovněž protology obou druhů ukazují, že těmito dvěma jmény označoval rostliny, které se skutečně diametrálně liší. Ve skutečnosti je *B. tridentata* morfologicky mnohem bližší druhu *B. malasica*. Jaká je tedy skutečná identita *B. tridentata*, bude nutné zjistit dalším studiem.

5.2.1.2 Skupina *Burmannia championii*

Druh *Burmannia championii* má velký areál zahrnující značnou část tropické a subtropické Asie (Jonker 1948). I na tak rozsáhlém území se zdá být nepříliš variabilní (viz např. Hsieh & Ohashi 2000, Aoyama & Tsubotha, Suetsugu et al. 2014, Van Son et al. 2015). Na Borneu se vyskytují jak rostliny odpovídající originálnímu popisu druhu (Příloha 1, Tabule 2A), tak nejméně jeden další zřetelně odlišný morfotyp. Tyto rostliny se od *B. chamipionii* liší vyšším vzrůstem, obvykle větším počtem květů, které jsou delší a stopkaté a šestihrannou květní trubkou a velmi dobře odpovídají druhu popsanému z Bornea O. Beccarim v 19. století pod jménem *B. tuberosa* (Beccari 1878). Toto jméno je ovšem nyní považováno za synonymum *B. championii* (Jonker 1948, POWO 2019). Jméno *B. tuberosa* synonymizoval se jménem *B. championii* již Jonker (1938) a od té doby to nebylo zpochybněno. Na základě studia rostlin z několika lokalit napříč Borneem, protologů a typového materiálu obou jmen ale vyplývá, že jméno *B. tuberosa* označuje rostliny zřetelně odlišné od *B. championii* (tab. 3, obr. 4) a mělo by tak být vyjmuto z jeho synonymiky. Oba druhy se liší především počtem žeber na květní trubce, což je v taxonomii rodu *Burmannia* jeden z nejvýznamnějších znaků (Jonker 1938). Zatímco *B. championii* má jen tři nepříliš výrazná žebra, *B. tuberosa* má šest žeber (tři výrazná a tři nevýrazná, obr. 4).

Tabulka 3. Morfologické srovnání *Burmannia championii* a *B. tuberosa* (Thwaites 1864, Beccari 1878 a typový materiál).

	květy	počet květů	délka květů	květní trubka
B. championii	přisedlé	9–12	cca 6,5 mm	3žebrá
B. tuberosa	stopkaté	2–18	9–14 mm	6žebrá



Obrázek 4. Srovnání ilustrací z protologů a typového materiálu *Burmannia championii* (1, 2) a *B. tuberosa* (3, 4).

5.2.2 Rod *Gymnosiphon*

Rod *Gymnosiphon* má pantropické rozšíření s centrem diverzity v tropické Americe (Maas et al. 1986, Maas-van de Kamer 1998). Všichni jeho zástupci jsou plně mykoheterotrofní rostliny (Merckx et al. 2013a). V Malesijské fytogeografické oblasti se vyskytuje osm druhů (Pelser et al. 2019), přičemž na Borneu je uváděn pouze jediný, široce rozšířený druh. *G. aphyllus* (Jonker 1948).

5.2.2.1 Skupina *Gymnosiphon aphyllus*

Druh *Gymnosiphon aphyllus* byl popsán z Jávy (Blume 1827), ale jeho areál údajně sahá až do Thajska, na Tchaj-wan a Novou Guineu (Jonker 1938, POWO 2019). Jonker (1948) jeho výskyt uvádí jako jediného zástupce rodu i na Borneu, kde se rostliny odpovídající popisu tohoto druhu skutečně vyskytují (Příloha 1, Tabule 2Da). Kromě nich lze na ostrově rozlišit nejméně další dva výrazné morfotypy (Příloha 1, Tabule 2Dbc), které se od typického *G. aphyllus* liší zbarvením, obvykle nevětveným chudokvětým květenstvím i tvarem a zbarvením okvětí. Navzájem se pak tyto dva morfotypy zřetelně liší zbarvením (bílé vs. fialové rostliny) a tvarem okvětí (krátké a tupé na okraji hrubě vroubkované cípy vs. dlouhé a špičaté téměř celokrajné cípy). Tyto morfotypy vyžadují další studium, jehož cílem bude zjistit, zda jde o extrémní projevy variability druhu *G. aphyllus*, anebo jiné ať už popsané nebo nepopsané taxony. V posledních letech byly popsány dva nové druhy rodu z Filipín (Pelser et al. 2019, Nickrent 2020), odkud předtím žádný druh rodu nebyl znám. Vzhledem k příbuznosti flór obou oblastí, nelze vyloučit, že některý z těchto nově popsaných druhů by se mohl vyskytovat i na Borneu. Zejména jeden z obou nově popsaných druhů, *G. syceorosensis* Nickrent, se velmi podobá jednomu z bornejských morfotypů (Příloha 1, Tabule 2Db). K uspokojivému zodpovězení otázky kolik druhů rodu roste na Borneu a jaká jsou jejich správná jména, bude také nutné vyřešit taxonomickou identitu *G. borneensis*, druhu popsaného O. Beccarim (Beccari 1878) ze Sarawaku a nyní považovaného za identický s *G. aphyllus* (Jonker 1948). Sám Beccari si byl vědom značné podobnosti s *G. aphyllus* a za základní rozdíl mezi těmi druhy uvádí vytrvalost, neboť *G. aphyllus* je v originálním popise charakterizován jako jednoletá rostlina (Blume 1827). To je ale zřejmě omyl, protože jednoletost je u těchto rostlin pravděpodobně jen zdánlivá, daná mykoheterotrofním způsobem života, kdy po jeho značnou část rostlina roste skrytě. Ve skutečnosti je délka života u tohoto rodu zcela neznámá.

5.3 Čeleď *Orchidaceae*

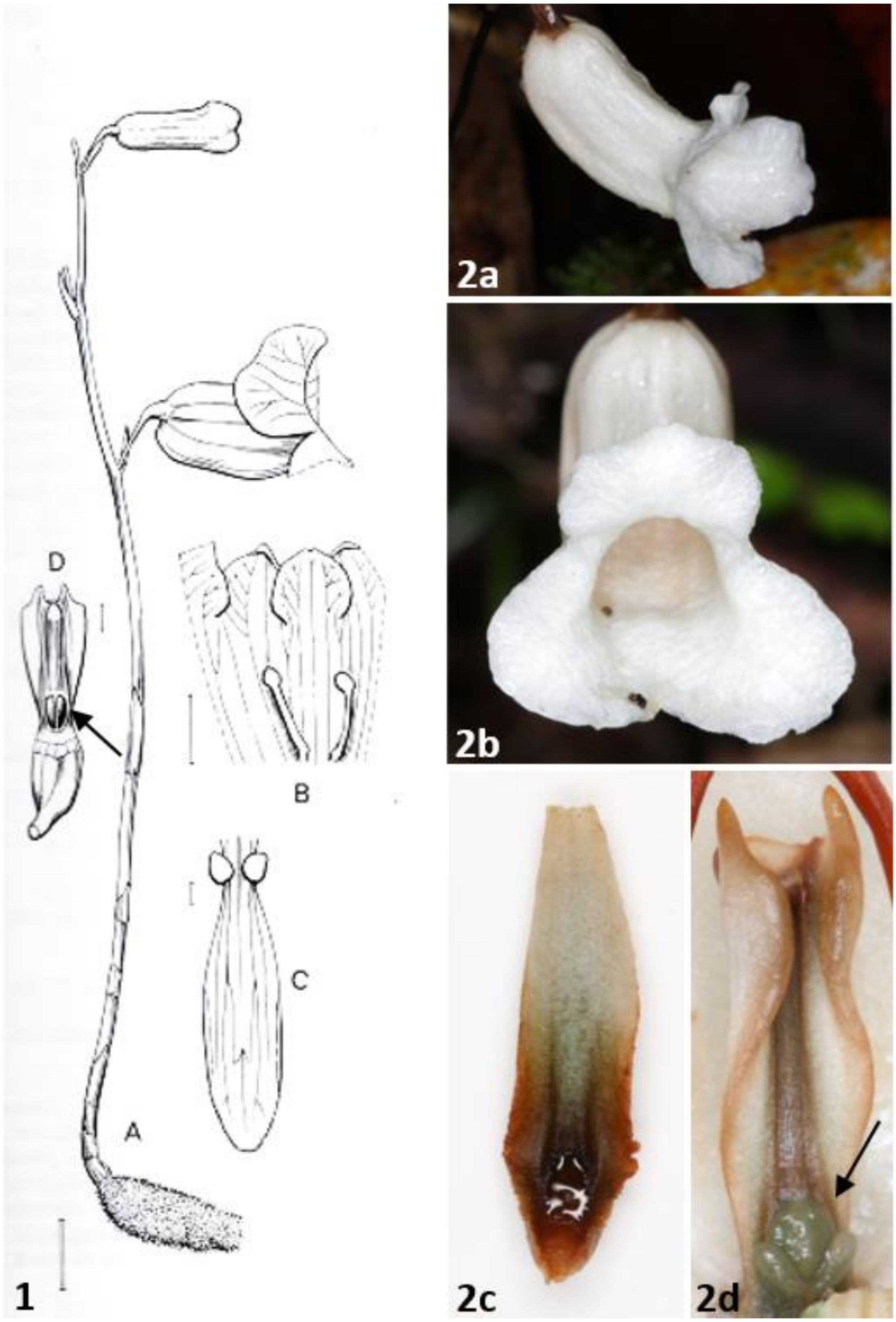
Čeleď *Orchidaceae* (vstavačovité) je druhově nejpočetnější čeledí cévnatých rostlin s kosmopolitním rozšířením výrazně koncentrovaným do tropů (Christenhusz et al. 2017). Tato čeleď je také zdaleka druhově nejbohatší skupinou mykoheterotrofních rostlin Bornea. Z ostrova je znám výskyt nejméně 37 druhů ve 14 rodech (viz kapitola 4.1), přičemž je velmi pravděpodobné, že se zde vyskytují další dosud nepopsané druhy. Až donedávna byl pro ostrov uváděn také jeden endemický rod, *Kalimantanorchis* Tsukaya, M. Nakaj. & H. Okada (Tsukaya et al. 2011), který byl ovšem nově synonymizován s rodem *Tropidia* (Ormerod & Juswara 2019, Kikuchi et al. 2020). Mykoheterotrofní *Orchidaceae* patří dnes k nejméně prozkoumaným skupinám rostlin na Borneu, což je jednak dáno velkým počtem druhů a obtížnou taxonomií některých skupin, ale zřejmě také faktem, že výzkum této skupiny je zatížen nadměrnou administrativou. Všechny *Orchidaceae* jsou zařazeny na seznamu CITES a získat úřední povolení k práci s organismy na tomto seznamu je v zemích jihovýchodní Asie velmi složité a časově náročné. Také z těchto důvodů je v této práci tato skupina, přestože na Borneu nejbohatší, diskutována jen ve velmi omezeném rozsahu.

5.3.1 Rod *Aphyllorchis*

Rod *Aphyllorchis* je rozšířen v tropické a subtropické Asii a Austrálii (Suetsugu et al. 2018a). Na Borneu je zastoupen sedmi popsanými druhy (POWO 2019), z nichž je zdaleka nejhojnější *A. pallida* (vlastní pozorování). Zbývající druhy jsou vzácné a čtyři z nich (*A. kemulensis*, *A. maliauensis*, *A. siantanensis* a *A. spiculaea*) pak dokonce endemity ostrova (Suetsugu et al. 2017, 2018a), některé pravděpodobně nalezené pouze svými objeviteli a nikdy poté znovunalezené. Vzhledem k tomu, že zejména ke dříve popsaným druhům neexistuje ani obrazový materiál a typový materiál je neznámo kde, je velmi obtížné jakýmkoliv způsobem interpretovat nálezy rostlin, jejichž morfologický popis neodpovídá ani běžnému *A. pallida* ani dalším relativně hojnějším druhům, *A. montana* a *A. striata*. To je také případ rostliny, kterou jsme nalezli v jižním Sarawaku (Dančák, Hroneš et Sochor, nepublikováno) a která by mohla právě patřit k jednomu z endemických druhů (Příloha 1, Tabule 4B). Zajímavý je také ze Sabahu recentně popsaný endemický druh, *A. maliauensis* (Suetsugu et al. 2018a), který je ovšem velmi podobný druhu *A. montana*. *Aphyllorchis montana* je uváděn z rozsáhlého areálu, od Cejlonu až po Indonésii a Japonsko (Suetsugu et al. 2018a), přičemž popsán byl z Cejlonu (Reichenbach 1876). Přirozeně se nabízí otázka, zda rostliny z tak vzdálených území, jako je Borneo, jsou pak skutečně identické s typovými populacemi druhu a zda není *A. montana* v tomto území nahrazen jinými podobnými druhy, stejně jako v případech jiných zde diskutovaných rodů (např. *Burmannia* a *Sciaphila*), jejichž zástupci byli rovněž popsáni z Cejlonu.

5.3.2 Rod *Gastrodia*

Gastrodia je rod sdružující přibližně 90 druhů s širokým rozšířením v Paleotropech a přesahem do subtropických až temperátních oblastí Asie a Austrálie (Bandara et al. 2020). V Malesijské fytogeografické oblasti se vyskytuje 19 druhů z toho šest také na Borneu (POWO 2019) a z nich dva, *G. grandilabris* a *G. maliauensis*, jsou endemické (Suetsugu et al. 2017, 2018b). Druhy rostoucí na ostrově náleží do sekcí *Codonathus* a *Gastrodia* (sensu Schlechter 1911). Nominátní sekce je zde zastoupena pouze jedním relativně nedávno ze severní části ostrova (z oblasti nejvyšší hory ostrova, Kinabalu) popsaným druhem, *G. spatulata* (Wood 2008). Na ostrově však roste ještě nejméně jeden další druh této sekce (Dančák, Hroneš et Sochor, nepublikováno, Příloha 1, Tabule 4I), který je s největší pravděpodobností nepopsaný. Tento druh nalezený v oblasti Kelabitské vysočiny v severním Sarawaku se od *G. spatulata* liší zejména odlišným tvarem pysku a utvářením sloupku (tedy znaky u vstavačovitých taxonomicky zásadními, obr. 5), ale i zbarvením květu. Květy *G. spathulata* mají bílou květní trubku, oranžové okvětní cípy a hnědý pysk (Wood 2008), zatímco u nepopsaného druhu ze Sarawaku jsou květní trubka i cípy okvětí čistě bílé a pysk má hnědobílou barvu. Rozdíly mezi oběma druhy jsou zobrazeny na obrázku 5. Také sekce *Gastrodia* je na ostrově zastoupena nejméně jedním dalším pravděpodobně nepopsaným druhem, který se vyskytuje v Bruneji (Dančák, Hroneš et Sochor, nepublikováno, Příloha 1, Tabule 4J). Od ostatních druhů sekce, zejména od velmi podobných druhů, které mají hnědé, baňkovité, z vnější strany bradavičnaté okvětí, *G. grandilabris*, *G. maliauensis* a *G. sabahensis*, se kromě stavby sloupku a tvaru pysku na první pohled liší velmi výrazně vyvinutými polštářky houbovitého pletiva na vnitřní straně postranních okvětních lístků (Příloha 1, Tabule 4J).



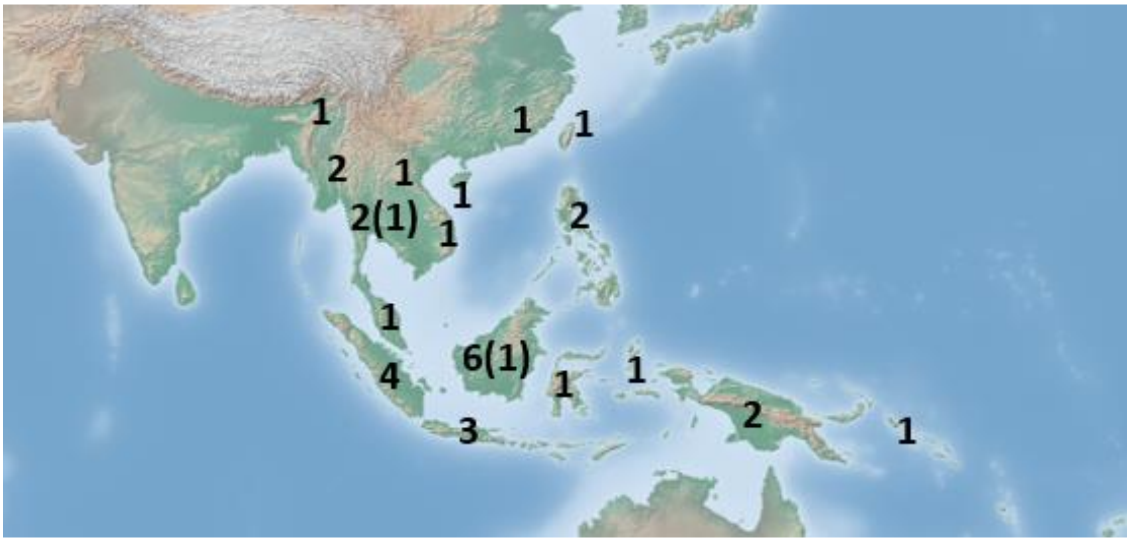
Obrázek 5. Srovnání *Gastrodia spathulata* (1) a *Gastrodia* sp. nov. (2). Zřetelně rozdílný je tvar pysku (1c vs. 2c) a tvar bliznové plochy (1d vs. 2d, označeno šipkami). Kresba převzata z práce Wood (2008), foto M. Sochor.

5.4 Čeleď *Polygalaceae*

Čeleď *Polygalaceae* (vítodovité) je druhově relativně početná čeleď o zhruba 900 druzích ve 26 rodech s kosmopolitním rozšířením (Christenhusz et al. 2017). Na Borneu je tato čeleď zastoupena šesti rody, především pak stromovým rodem *Xanthophyllum*, jehož zástupci se hojně vyskytují v nížinných tropických deštných lesích (van der Meijden 1988). Mykoheterotrofní je jen jediný rod, *Epirixanthes* (Merckx et al. 2013a), jehož nejbližší příbuzní, rod *Salomonia*, jsou plně autotrofní rostliny (Mennes et al. 2015) rovněž se vyskytující na Borneu (van der Meijden 1988).

5.4.1 Rod *Epirixanthes*

Rod *Epirixanthes* je rozšířen pouze v jižní a jihovýchodní Asii s centrem diverzity v Malesijské oblasti (van der Meijden 1988, obr. 6). Je známo jen 7 druhů rodu, přičemž 6 z nich se vyskytuje na Borneu (Dančák et al. 2017). Tento rod je zajímavým kontrastním patternem rozšíření vůči většině ostatních mykoheterotrofních rodů Bornea, protože jeho zástupci jsou zpravidla široce rozšířené druhy nejen na tomto ostrově, ale zasahují také do dalších oblastí, zejména na Sumatru a Jávu. Nejrozsáhlejší areál má druh *E. elongata*, který roste od Indie až po Moluky (Pendry 2010). Pouze jeden z bornejských druhů, *E. confusa*, je považován za endemický (Tsukaya et al. 2016). Tento druh je ale z taxonomického hlediska problematický, protože je velmi podobný široce rozšířenému druhu *E. elongata* a je možné, že se jedná jen o jeho varietu.



Obrázek 6. Světové rozšíření a diverzita rodu *Epirixanthes* s počtem druhů pro každý region a počtem endemických druhů v závorce (upraveno podle Dančák et al 2017).

U mnoha druhů je stále neúplně známé jejich skutečné rozšíření, což je způsobeno jednak malým zájmem o bylinné patro v tropických deštných lesích, relativní nenápadností rostlin, ale také determinačními omyly (viz např. Dančák et al. 2017) vycházejícími mj. z výběru ne zcela vhodných znaků do klíče publikovaného v díle Flora Malesiana (van der Meijden 1988). Jednotlivé druhy rodu jsou si navzájem velmi podobné a jejich určování činí potíže, o čemž svědčí nejen poměrně vysoká chybovost určení u herbářových dokladů, ale také chyby ve flórových dílech. Např. v seznamu cévnatých rostlin Bruneje (Coode et al. 1996) jsou uvedeny tři druhy (*E. cylindrica, E. elongata* a *E. pallida*), přičemž jak zjistili Dančák et al. (2017), na území státu se vyskytují další dva druhy (*E. kinabaluensis* a *E. papuana*) a jeden byl naopak uváděn omylem (*E. pallida*). Dančák et al. (2017) také publikovali nový klíč k určování druhů rodu založený na znacích, které jednotlivé druhy umožňují spolehlivě rozlišit.

5.5 Čeleď *Thismiaceae*

Čeleď *Thismiaceae* je druhově relativně nepočetná čeleď jednoděložných rostlin z řádu *Dioscoreales* s pantropickým rozšířením, tvořená víc jak 100 druhy (POWO 2019) s kolísajícím počtem rozlišovaných rodů od 5 do 8 (viz např. Merckx et al. 2013a, Christenhusz et al. 2017, Merckx 2020). Všechny rody zahrnují výhradně mykoheterotrofní rostliny. Fylogenetické vztahy v rámci řádu *Dioscoreales* a postavení čeledi *Thismiaceae,* zejména její vztahy k čeledím *Burmanniaceae* a *Taccaceae* patří k nejdiskutovanějším systematickým otázkám posledních desetiletí (např. Caddick et al. 2002, Merckx et al. 2009, Lam et al. 2016). Velmi často jsou *Thismiaceae* spojovány s *Burmanniaceae* (např. APG IV 2016, Christenhusz et al. 2017), se kterými jsou ovšem zřejmě jen vzdáleně příbuzné (Lam et al., 2016, 2018). Nicméně i čeleď *Thismiaceae* v současném pojetí je parafyletická, protože nezahrnuje rod *Tacca*, který fylogeneticky stojí mezi rodem *Afrothismia* a zbytkem čeledi (Merckx & Smets 2014). Východiskem by mohlo být zahrnutí současných *Thismiaceae* do *Taccaceae* (vzhledem k tomu, že toto jméno má nomenklatorickou prioritu). Čeleď *Taccaceae* ovšem zahrnuje morfologicky velmi odlišné, autotrofní rostliny, a proto takové řešení nenachází všeobecnou podporu. Dalším řešením by mohlo být odštěpení rodu *Afrothismia* do samostatné čeledi (Hunt et al. 2014, Givnish et al. 2018). I přesto, že toto řešení se nabízí jako nejlépe odrážející realitu, dosud nebyly provedeny žádné nomenklatorické změny související s vyčleněním rodu *Afrothismia* do samostatné čeledi (Shepeleva et al. 2020). Čeleď *Thismiaceae* tak v současném pojetí odpovídá tribu *Thismieae*, který v rámci čeledi *Burmanniaceae* vyčlenil Miers (1847) a upřesnil Jonker (1938), i když jeho vnitřní členění je dnes již překonané a rody *Haplothismia* a *Tiputinia* nebyly v době publikace Jonkerovy monografie známé.

Tak, jak je diskutabilní postavení čeledi v rámci řádu, neexistují jednotné názory ani na vnitřní členění čeledi. Například přijímaný počet rodů se liší od 5 (*Afrothismia, Haplothismia, Oxygyne, Thismia* a *Tiputinia*; např. Stevens 2001) po 8 (*Afrothismia, Desmogymnosiphon, Geomitra, Haplothismia, Oxygyne, Scaphiophora, Thismia* a *Tiputinia* v práci Christenhusz et al. 2017). Jak ale ukazují poslední studie (např. Shepeleva et al. 2020) rodové pojetí v rámci čeledi *Thismiaceae* zřejmě dozná značných změn. Už nyní je zřejmé, že rody *Geomitra* a *Scaphiophora* lze stěží považovat za samostatné (Sochor et al. 2018b) a naopak rod *Thismia* bude zřejmě nutné rozdělit na *Thismia* s. str. sdružující druhy Starého světa a *T. americana* N. Pfeiff. a rod *Ophiomeris*, který sdružuje druhy neotropické (Shepeleva et al. 2020). Rovněž u rodu *Oxygyne* existuje možnost, že bude rozdělen na *Oxygyne* s. str. sdružující druhy africké a rod *Saionia* sdružující druhy asijské (Ohashi 2015), i když situaci komplikuje extrémní vzácnost afrických druhů a z toho vyplývající nedostupnost studijního materiálu (Cheek et al. 2018). Jak už bylo diskutováno výše, rovněž udržení rodu *Afrothismia* v čeledi *Thismiaceae* se dle současných poznatků zdá nereálné. Výzkum fylogenetických vtahů uvnitř i vně čeledi *Thismiaceae* je ale velmi pomalý a komplikovaný především již zmíněnou extrémní vzácností mnoha druhů a s tím spojenou nedostupností experimentálního materiálu.

Na Borneu je tato čeleď zastoupena jen rodem *Thismia* (Jonker 1948).

5.5.1 Rod *Thismia*

Rod *Thismia* čítá (ke konci roku 2020) téměř 90 druhů (Chantanaorrapint & Seelanan 2021, Dančák et al. 2020a, Xu et al. 2020) rozšířených převážně v tropické a subtropické Asii až temperátní Austrálii a převážně tropické Americe. Jak už bylo zmíněno, v posledních desetiletích se hromadí důkazy, že rod je v současném pojetí parafyletický a neotropické druhy nejsou blízce příbuzné s druhy Starého světa. Zdá se tedy pravděpodobné, že v budoucnu dojde k vyčlenění neotropických druhů do samostatného rodu *Ophiomeris* Miers 1847 (viz např. Shepeleva et al. 2020). V současné době by však taková změna byla předčasná, protože neotropické druhy jsou ve fylogenetických studiích zastoupeny pouze jedním druhem (*Thismia panamensis* (Standl.) Jonker) a není tak jasné, jaké jsou příbuzenské vztahy ostatních neotropických druhů nejen ke druhům Starého světa, ale ani k *Thismia panamensis*. Nedávno byl také publikován nový návrh vnitrorodového členění (Kumar et al. 2017), který nahradil původní, již dávno překonaný Jonkerův (Jonker 1938). Toto nové členění je ale zčásti zcela umělé a nezohledňuje fylogenetické vztahy mezi jednotlivými druhy či skupinami. To se týká především sekce *Sarcosiphon*, která nyní sdružuje dvě zcela nepříbuzné skupiny druhů a také sekcí *Rodwaya* a *Glaziocharis*, jejichž druhy jsou navzájem pomíchané. Tato klasifikace také nezahrnuje některé význačné nově popsané druhy a některé morfologicky unikátní druhy klasifikuje do existujících sekcí. Proto zde navrhuji nové vnitrorodové členění pro podrod *Thismia*, které má nejen oporu ve fylogenezi rodu (Shepeleva et al. 2020), ale také reflektuje tradiční skupiny.

5.5.1.1 Návrh vnitrorodového členění *Thismia* subg. *Thismia* (= *Thismia* s. str.)

Tento návrh přináší několik změn, které se ukázaly jako nezbytné vzhledem k prohloubení znalostí o fylogenetických vztazích uvnitř rodu a objevům nových druhů, nezařaditelných do současního systému. Hlavní změnou je vymezení nových skecí *Mirabilis* a *Minuta*, pro indočínské druhy z příbuzenstva druhu *T. mirabilis* a druh *T. minutissima* z Bornea. Obnovena byla sekce *Labiothismia* pro druhy s výrazně asymetrickými květy. Pro skupinu *Odoardoa* je nově narhován rank sekce (namísto podeskce) a pro skupinu *Geomitra* rank podsekce sekce *Sarcosiphon*.

Thismia* subg. *Thismia

Typový druh: *Thismia brunonis* Griff.

Thismia* subg. *Thismia* sect. *Glaziocharis (Taub. ex Warm.) Hatus.

Diagnostické znaky: chybí interstaminální žlázy a boční přívěsek konektivu, stěna hypanthia bez příčných přehrádek; rozšíření ve východní Asii a Sev. Americe (obr. 8).
Typový druh: *Thismia abei* Hatus.
Ostatní druhy: *Thismia americana*, *T. gongshanensis* Hong Qing Li & Y. K. Bi, *T. huangii* P. Y. Jiang & T. H. Hsieh, *T. kobensis* Suetsugu, *T. nigricoronata* Kumar & S. W. Gale, *T. taiwanensis* Sheng Z. Yang, R. M. K. Saunders & C. J. Hsu, *T. thaithongiana* Chantanaorr. & Suddee, *T. tuberculata* Hatus.

Sekce *Glaziocharis* v pojetí přijatém v této práci je ve většině recentních fylogenetických studií jedním z hlavních kladů rodu a v rámci podrodu *Thismia* jeho bazální skupinou (viz např. Sochor et al. 2018b, Shepeleva et al. 2020, obr. 7). Tomu pak odporuje vymezení sekce tak, jak byla provedena v práci autorského kolektivu Kumar et al. (2017), protože zahrnuje i jeden druh (*T. clavarioides* K. R. Thiele), který ve zde přijatém vymezení náleží do sekce *Rodwaya,* a sekce *Rodwaya* naopak obsahuje dva druhy (*T. americana* a *T. huangii*), které jsou zde zařazeny do sekce *Glaziocharis*. Pro druh *T. americana* neexistují molekulární data, ale na základě morfologie, zejména absence interstaminálních žláz a bočního přívěsku konektivu, je její příslušnost do sekce *Glaziocharis* zjevná.

Thismia* subg. *Thismia* sect. *Rodwaya (Schltr.) Jonker

Diagnostické znaky: vnitřní okvětní lístky srostlé v mitru, kořeny plazivé, nenahloučené, vnější okvětní lístky s přívěsky, boční přívěsek konektivu ve tvaru křesla; rozšíření v Austrálii a na Novém Zélandě (obr. 8).

Typový druh: *Thismia rodwayi* F. Muell.

Ostatní druhy: *Thismia clavarioides, T. hillii* (Cheeseman) N. Pfeiff., *T. megalongensis* C. A. Hunt, G. Steenbee. & V. Merckx.

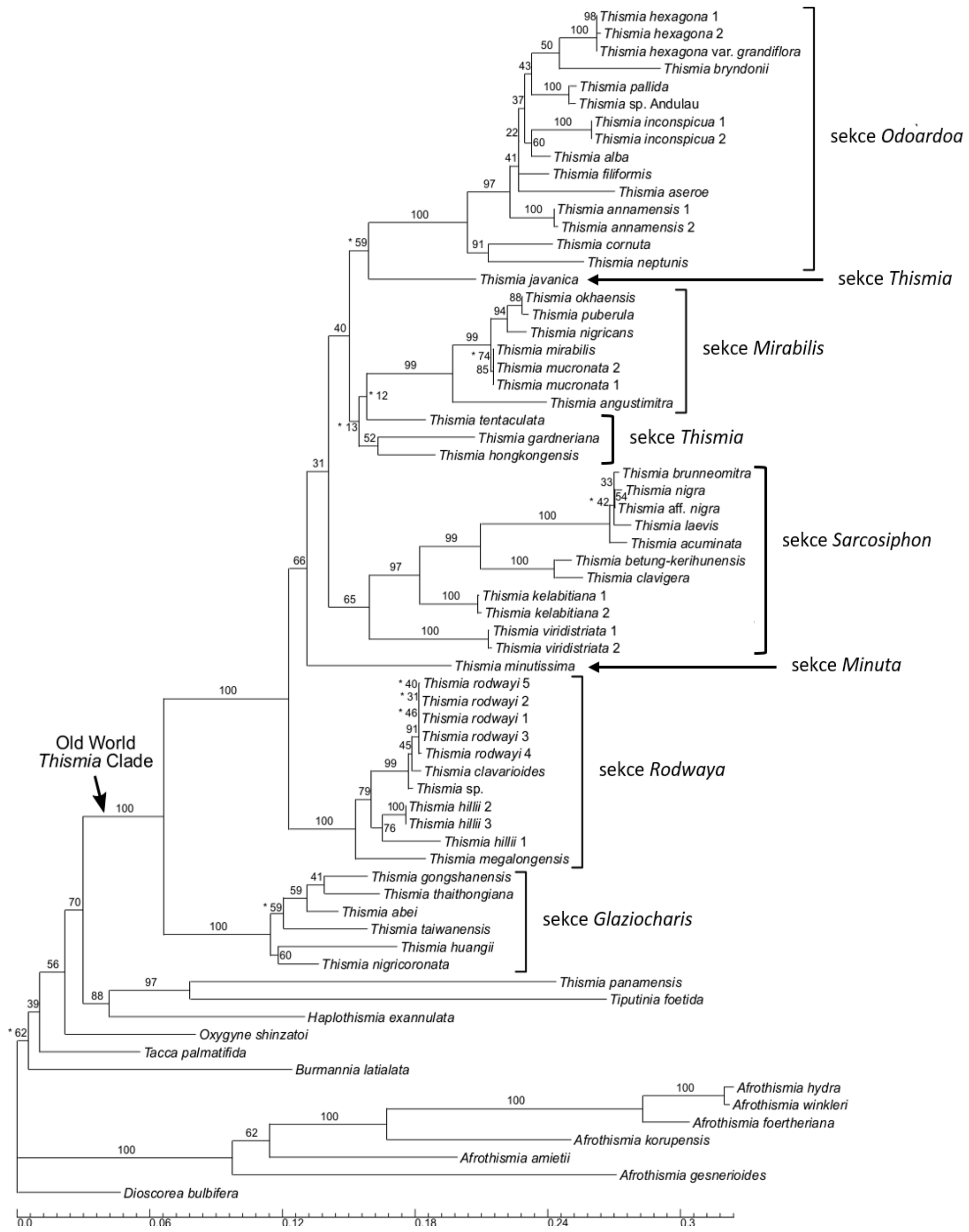
Tato sekce je ve zde přijatém vymezení tvořena čtyřmi druhy s australsko-novozélandským rozšířením (obr. 8). Většinou do této sekce byl dříve řazen (např. Jonker 1938, Kumar et al. 2017) i vyhynulý severoamerický druh *T. americana*, který ale sdílí základní diagnostické znaky (zejména absence interstaminálních žláz a bočního přívěsku konektivu) s druhy sekce *Glaziocharis*, a je proto ve zde přijatém pojetí její součástí.

***Thismia* subg. *Thismia* sect. *Minuta*,** ined.

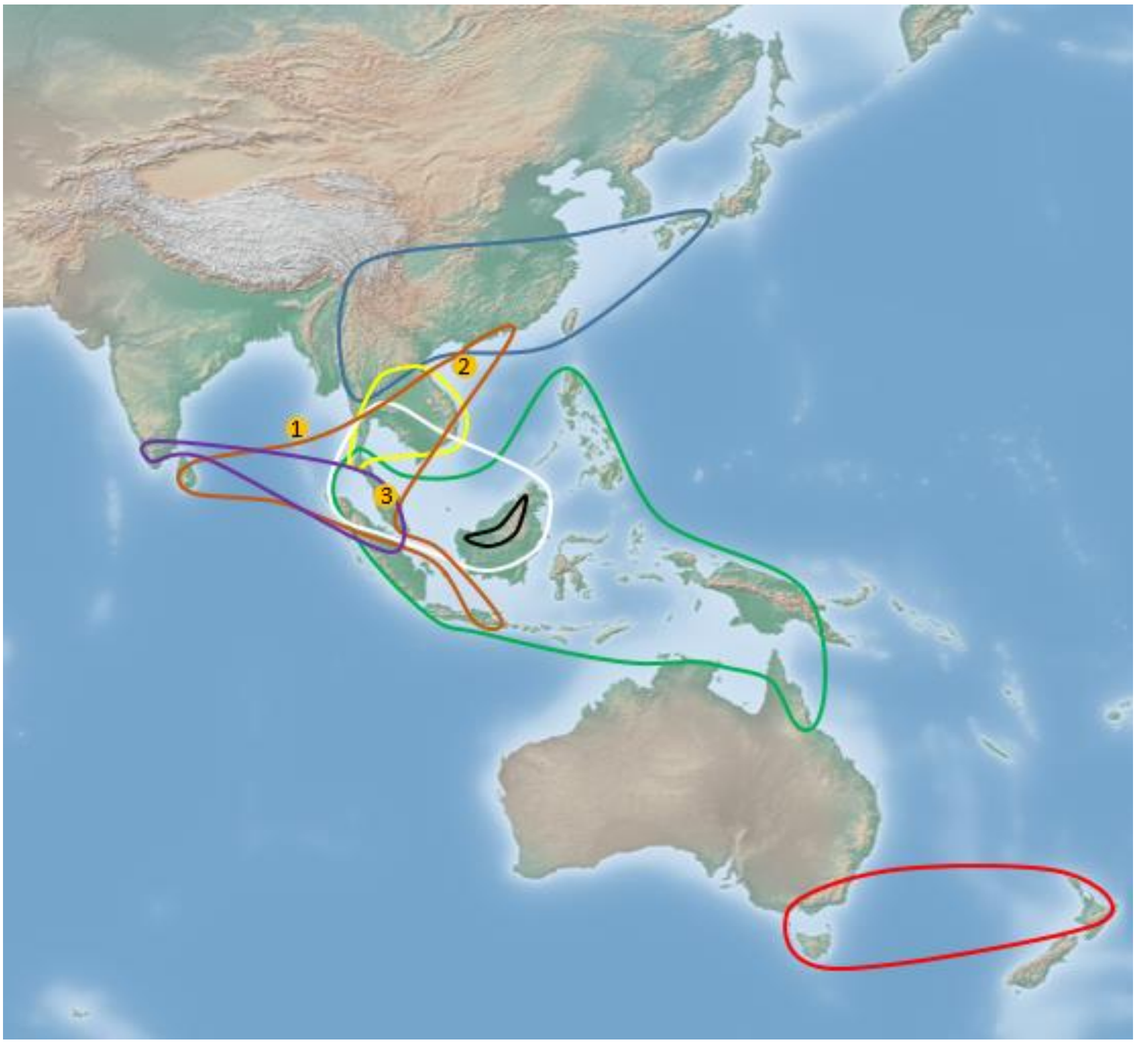
Diagnostické znaky: vnitřní okvětní lístky srostlé v mitru, kořeny plazivé, nenahloučené, vnější okvětní lístky bez přívěsků, boční přívěsek konektivu ve tvaru rybího ocasu; rozšíření na Borneu (obr. 8).

Typový druh: *Thismia minutissima* (monotypická sekce).

Tato sekce zahrnuje pouze jediný morfologicky unikátní druh z Bornea. Nejpodobnější je druhům sekce *Rodwaya,* od kterých se liší dobře vyvinutou lodyhou a tvarem bočního přívěsku konektivu (který je pro *T. minutissima* jedinečný). Tento druh také ve fylogenetických rekonstrukcích obvykle tvoří samostatnou větev (obr. 7).



Obrázek 7. Fylogram rodu *Thismia* založený na třílokusovém datasetu (ITS+18S+atp1; hodnoty posteriorních pravděpodobností jsou uvedeny nad jednotlivými větvemi) s vyznačením sekcí v pojetí navrženém v této práci. Převzato a upraveno z Shepeleva et al. (2020). Všechny zde vymezené sekce s výjimkou sekce *Thismia* tvoří monofyletické skupiny. Chybí zástupci sekce *Labiothismia*, která je ale velmi vyhraněná morfologicky.



Obrázek 8. Rozšíření sekcí *Thismia* subg. *Thismia* v Asii a Austrálii. Modře – sect. *Glaziocharis* (areál druhu *T. americana* nezobrazen); Červeně – sect. *Rodwaya*; Zeleně – sect. *Sarcosiphon*; Žlutě – sect. *Mirabilis*; Bíle – sect. *Odoardoa*; Hnědě – sect. *Thismia*; Fialově – sect. *Labiothismia*; Černě – sect. *Minuta*; Oranžově – 1 *T. aurantiaca*, 2 *T. jianfenglinensis*, 3 *T. terengganuensis*.

Thismia* subg. *Thismia* sect. *Sarcosiphon (Blume) Jonker

Diagnostické znaky: vnitřní okvětní lístky srostlé v mitru, kořeny koraloidní; rozšíření v Malesii a severní Austrálii (obr. 8).

Subsect. *Sarcosiphon*

Diagnostické znaky: konektivy na vnitřní straně bez podélného žebra, vnější okvětní lístky chybějí.

Typový druh: *Thismia clandestina* Miq.

Ostatní druhy: *Thismia acuminata, T. brunneomitra, T. brunneomitroides* Suetsugu & Tsukaya, *T. crocea* (Becc.) J. J. Sm., *T. episcopalis, T. laevis, T. lanternata* W. E. Cooper, *T. nigra, T. verstegii* J. J. Sm.

Subsect. *Geomitra* [Becc. (1878: 250) pro genus], ined.
Diagnostické znaky: konektivy na vnitřní straně s výrazným podélným žebrem, vnější okvětní lístky vyvinuty.
Typový druh: *Thismia clavigera*.
Ostatní druhy: *Thismia betung-kerihunensis, T. clavigeroides* Chantanaorr. & Seelanan, *T. goodii, T. kelabitiana, T. kelantanensis* Siti-Munirah, *T. coronata, T. sumatrana* Suetsugu & Tsukaya.

Druhy s nejistým zařazením do podsekcí: *Thismia appendiculata* Schltr., *T. gigantea* (Jonker) Hroneš, *T. hawkesii* W. E. Cooper, *T. tectipora* Cowie, *T. viridistriata, T. yorkensis* Cribb.

Významnou synapomorfií sekce *Sarcosiphon* je koraloidní kořenová soustava, která se nevyskytuje u žádné jiné skupiny rodu (Shepeleva et al. 2020). Nezařazené druhy *Thismia appendiculata, T. gigantea, T. hawkesii, T. tectipora* a *T. viridistriata* se vyznačují charakteristickým dlouhým výrůstkem na vrcholu mitry. Tento znak vedl dřívější autory k vytvoření samostatné sekce či dokonce rodu *Scaphiophora* (viz např. Schlechter 1921, Jonker 1938, Jonker 1948, Kumar et al. 2017), jak ale prokázali Sochor et al. (2018b) a Shepeleva et al. (2020), tento znak s největší pravděpodobností není systematicky významný. Mnohem větší váhu má naopak charakter kořenové soustavy, která je u těchto druhů koraloidní. Proto jsou ve zde přijatém pojetí součástí sekce *Sarcosiphon*, společně se všemi ostatními druhy s koraloidní kořenovou soustavou. Současný stav poznání nicméně neumožňuje jejich jednoznačné zařazení ani do jedné ze dvou výše uvedených subsekcí. Jednou z možných variant je také vytvoření samostatné podskece, kerá by tyto druhy sdružovala. Poslední nezařazený druh, *T. yorkensis*, kombinuje znaky obou výše uvedených podsekcí (přítomost vnějších okvětních lístků charakteristická pro subsect. *Geomitra* a hladké vnitřní stěny konektivů charakteristické pro subsekci *Sarcosiphon*). Sekce *Sarcosiphon* zasahuje z Filipín a Malajského polostrova až do severní Austrálie a má tak největší areál ze všech sekcí podrodu (obr. 8), pomineme-li to, že sekce *Glaziocharis* zasahuje díky druhu *T. americana* až do Severní Ameriky.

Thismia subg. *Thismia* sect. *Mirabilis*, ined.

Diagnostické znaky: vnitřní okvětní lístky srostlé v mitru, kořeny plazivé, nenahloučené, vnější okvětní lístky bez přívěsků, ústí květní trubky výrazně konvexní; rozšíření v Indočíně (obr. 8).

Typový druh: *Thismia mirabilis* K. Larsen.

Ostatní druhy: *Thismia angustimitra* Chantanaorr., *T. mucronata* Nuraliev, *T. nigricans* Chantanaorr. & Sridith, *T. okhaensis* Luu, Tich, G. Tran & Đinh, *T. puberula* Nuraliev, *T. submucronata* Chantanaorr., Tetsana & Tripetch.

Druhy této sekce začaly být objevovány teprve až ve druhé polovině 20. století a jako úplně první byla popsána *Thismia mirabilis* v roce 1965 (Larsen 1965). Nemohly se proto objevit v žádném přechozím vnitřním členění rodu. Jako první tyto druhy do vnitrorodového členění proto zařadili až Kumar et al. (2017), bohužel ale zcela nevhodně do sekce *Sarcosiphon*, se kterou nejsou blízce příbuzné (viz např. Shepeleva et al. 2020, obr. 7). Vzhledem k tomu, že tvoří morfologicky unikátní skupinu s jasně definovaným areálem a i ve fylogenetických rekonstrukcích formují monofyletickou skupinu a jeden z hlavních kladů rodu (Shepeleva et al. 2020), je zjevné, že tvoří vlastní svébytnou sekci.

Thismia subg. *Thismia* sect. *Odoardoa* Schltr.

Diagnostické znaky: všechny okvětní lístky nesrostlé, s přívěsky; rozšíření na Borneu, Sumatře a v Indočíně (obr. 8).

Subsect. *Odoardoa*

Diagnostické znaky: všechny okvětní lístky stejného tvaru a velikosti.

Typový druh: *Thismia aseroe* Becc.

Ostatní druhy: *Thismia alba* Holttum ex Jonker, *T. annamensis* K. Larsen & Aver., *T. bifida, T. bryndonei, T. chrysops* Ridl., *T. claviformis* Chantanaorr. & J. Wai, *T. cornuta, T. domei* Siti-Munirah, *T. filiformis* Chantanaorr., *T. fumida* Ridl., *T. grandiflora* Ridl., *T. hexagona, T. inconspicua, T. kinabaluensis, T. lauriana, T. mullerensis* , *T. ophiuris, T. ornata, T. pallida, T. racemosa* Ridl.

Subsect. *Sarawakia* [Schltr. (1921: 35) pro sectione], ined.

Diagnostické znaky: vnější okvětní lístky jiného tvaru a velikosti než vnitřní.

Typový druh: *Thismia neptunis* (monotypická podsekce)

Sekce *Odoardoa* je jedna z tradičních sekcí (popř. podsekcí) rodu, která je zároveň dobře morfologicky i geneticky vymezená. Ve fylogenetických rekonstrukcích rodu obvykle tvoří jeden z jeho hlavních kladů (viz např. Sochor et al. 2018b, Shepeleva et al. 2020, obr. 7). Z fytogeografického hlediska má výrazná centra diverzity na Borneu a Malajském polostrově. Zajímavé je postavení druhu *Thismia neptunis*, který byl dříve považován za součást sekce *Thismia* (= *Brunonithismia*), a byl by tedy jediným známým druhem této skupiny na Borneu. Geneticky je ovšem tento druh spřízněn s druhy sekce *Odoardoa,* a proto je zde zařazen v této sekci a vzhledem k tomu, že je morfologicky unikátní, byla pro něj vyhrazena samostatná subsekce *Sarawakia*, kterou jako samostatnou skupinu (sekci) vyčlenil už Schlechter (1921).

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

Diagnostické znaky: všechny okvětní lístky nesrostlé, vnější okvětní lístky bez přívěsků; rozšíření Cejlon, Indočína, Sumatra, Jáva, jižní Čína (obr. 8).

Typový druh: *Thismia brunonis* Griff.

Ostatní druhy: *Thismia arachnites* Ridl., *T. bokorensis* Suetsugu & Tsukaya, *T. breviappendiculata* Nob. Tanaka, *T. gardneriana* Hook. f. ex Thwaites, *T. hongkongensis* Mar & R. M. K. Saunders, *T. javanica* J. J. Sm., *T. tentaculata* K. Larsen & Aver.

Typová sekce rodu je zároveň také její neproblematičtější skupinou, jejíž vymezení a systematické postavení pravděpodobně ještě dozná dalších změn. Ve fylogenetických rekonstrukcích rodu založených na různých molekulárních markerech či jejich kombinacích jsou zástupci této sekce obvykle jen chudě zastoupeni a jejich pozice je navíc nejasná (obr. 7), což je zřejmě způsobeno tím, že použité markery u této skupiny nenesou fylogenetický signál. Tato sekce je zde tedy vymezená zejména na základě morfologie. Jediný druh, který se poněkud morfologicky vymyká je *T. hongkongensis*, ten je ovšem fylogeneticky zjevně spřízněný s *T. tentaculata*, tedy druhem s typickým vzhledem pro tuto sekci.

Thismia* subg. *Thismia* sect. *Labiothismia J. J. Smith

Diagnostické znaky: květy výrazně zygomorfní, ústí květní trubky umístěné bočně, boční přívěsek konektivu a interstaminální žlázy chybí; rozšíření v Indii, na Sumatře a Malajském poloostrově (obr. 8).

Typový druh: *Thismia labiata* J. J. Smith.

Ostatní druhy: *Thismia sahyadrica* Sujanapal, Robi & Dantas.

Sekce *Labiothismia*, přestože byla popsána už v roce 1927 (Smith 1927), nebyla uznávána ani monografem rodu Jonkerem (Jonker 1938), ani nebyla přijata v nejnovějším vnitrorodovém členění (Kumar et al. 2017). Dva druhy, které jsou do ní zařazené v této práci, jsou ale natolik morfologicky specifické, že by je nebylo možné zařadit do žádné jiné sekce. Kromě sekce *Glaziocharis* je to jediná skupina rodu, které chybí postranní přívěsky konektivů a interstaminální žlázy. To přirozeně vede k otázce, zda tyto dvě skupiny nejsou nějak blíže spřízněné. Přesto, že toto nelze vyloučit, neboť ve fylogenetických rekonstrukcích rodu se dosud žádný druh sekce *Labiothismia* neobjevil, je výrazně zygomorfní stavba květu s postranním ústím u celého podrodu naprosto výjimečný znak.

Druhy nezařazené do žádné ze sekcí

Thismia aurantiaca Hareesh & M. Sabu
Thismia jianfenglinensis Han Xu, H. J. Yang & S. Q. Fang
Thismia terengganuensis Siti-Munirah

Nezařazené druhy, všechny popsané v posledních letech, představují morfologicky unikátní typy, jejichž zařazení do existující vnitrorodové klasifikace není možné jen na základě morfologie. Druh *Thismia terengganuensis* (Siti-Munirah & Dome 2019) by mohl patřit do sekce *Thismia*, i když jeho morfologická stavba je dosti jedinečná, především v tom, že jeho vnitřní okvětní lístky tvoří mitru. Zcela unikátní jsou pak další dva druhy, *T. aurantiaca* (Hareesh et al. 2018) a *T. jianfenglinensis* (Xu et al. 2020), které jsou zřejmě fylogeneticky izolované a mohly by tak tvořit vlastní sekce.

5.5.1.2 Klíč k určení sekcí a podsekcí *Thismia* subg. *Thismia*

Výše vymezené sekce podrodu *Thismia* je možné určit dle následujícího klíče.

1a Boční přívěsek konektivu a interstaminální žlázy chybějí … 2

1b Boční přívěsek konektivu a interstaminální žlázy přítomny … 3

2a Květy výrazně zygomorfní … **sect. *Labiothismia***

2b Květy aktinomorfní … **sect. *Glaziocharis***

3a Kořenový systém koraloidní; vnitřní okvětní lístky srostlé v mitru … **sect. *Sarcosiphon***

01a Vnitřní strana konektivu bez výrazného podélného žebra; vnější okvětní lístky chybějí; vrchol mitry vždy bez přívěsků (> 2 mm) … **subsect. *Sarcosiphon***

01b Vnitřní strana konektivu s výrazným podélným žebrem; vnější okvětní lístky přítomny, vrchol mitry bez nebo s přívěsky … **subsect. *Geomitra***

3b Kořenový systém tvořený chudě větvenými plazivými kořeny; vnitřní okvětní lístky volné nebo srostlé … 4

4a Všechny okvětní lístky volné, opatřené přívěsky … **sect. *Odoardoa***

01a Všechny okvětní lístky stejného tvaru a velikosti … **subsect. *Odoardoa***

01b Vnitřní okvětní lístky se tvarem a velikostí liší od vnějších … **subsect. *Sarawakia***

4b Okvětní lístky volné nebo srostlé, ale pokud volné, pak vnější bez přívěsků … 5

5a Vnitřní okvětní lístky volné, rozestálé nebo se nad ústím květu překrývající ale nesrostlé, vždy opatřené přívěsky; vnější okvětní lístky (tvarem a velikostí odlišné od vnitřních) vždy bez přívěsků … **sect. *Thismia***

5b Vnitřní okvětní lístky srostlé v mitru, bez nebo s přívěsky; vnější okvětní lístky bez nebo s přívěsky … 6

6a Ústí květní trubky výrazně konvexní; vrchol mitry bez přívěsků, někdy s nápadnými jamkami … **sect. *Mirabilis***

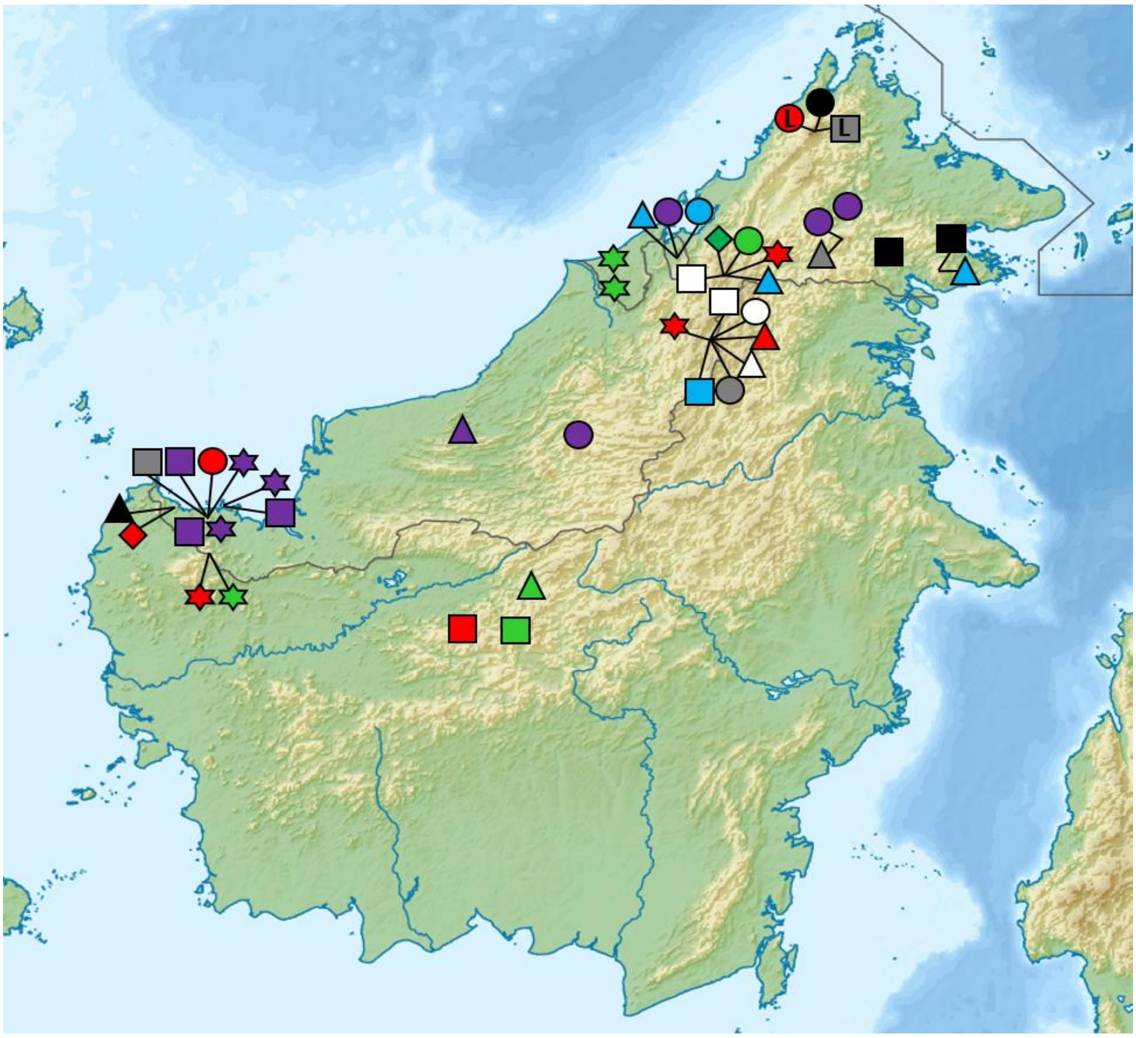
6b Ústí květní trubky ±ploché; vrchol mitry s alespoň krátkými přívěsky, vždy bez jamek … 7

7a Boční přívěsek konektivu ve tvaru rybího ocasu … **sect. *Minuta***

7b Boční přívěsek konektivu ve tvaru křesla … **sect. *Rodwaya***

3.5.1.3. Rod *Thismia* na Borneu

Na Borneu je v současnosti (rok 2020) znám výskyt 25 druhů rodu (Dančák et al. 2020a, 2020b) a dalších dvou druhových agregátů (Dančák et al. 2019), přičemž ještě v roce 2012 to bylo jen osm druhů. Za posledních 8 let se tedy počet známých druhů ostrova víc jak ztrojnásobil. Například jen pro Brunejský sultanát, který zaujímá zlomek rozlohy Bornea, byly objeveny čtyři druhy (Dančák et al. 2013, Hroneš et al. 2015, Sochor et al. 2017, Dančák et al. 2019), přičemž před rokem 2013 z této země nebyl výskyt rodu vůbec znám (cf. Coode et al. 1996). Na ostrově byla rovněž objevena řada nových lokalit druhů dříve považovaných za stenoendemické či dokonce vyhynulé (Dančák et al. 2020c). Aktuální stav rozšíření jednotlivých druhů rodu na Borneu je patrný z obr. 9.



Obrázek 9. Rozšíření druhů rodu *Thismia* na Borneu. ▲ *T. acuminata*, ◆ *T. aseroe* agg., ▲ *T. betung-kerihunensis*, ▲ *T. bifida*, ▲ *T. brunneomitra*, ▲ *T. bryndonei*, ▲ *T. clavigera*, △ *T. cornuta*, ◆ *T. coronata*, ● *T. episcopalis*, ✡ *T. filiformis* agg., ● *T. goodii*, ● *T. hexagona* (incl. *grandiflora*), ● *T. inconspicua*, ● *T. kelabitiana*, ● *T. kinabaluensis*, ○ *T. laevis*, ■ *T. lauriana*, ✶ *T. minutissima*, ■ *T. mullerensis*, ■ *T. neptunis*, ■ *T. nigra*, ■ *T. ophiuris*, ✶ *T. ornata*, ■ *T. pallida*, □ *T. viridistriata*. Upraveno podle Dančák & Hroneš (2019) a Dančák et al. (2020c). Zahrnuty jsou jen popsané druhy a druhové agregáty.

Přestože počtem druhů je Borneo globálně nejbohatším územím (Dančák et al. 2020a), fylogenetická diverzita v rámci rodu je na tomto ostrově o něco nižší, než je v sousedních oblastech ležících západním směrem. Na Borneo zasahují jen tři sekce rodu, přitom například do severní části Sumatry a na Malajský poloostrov zasahují 4 sekce (obr. 8). Zajímavá je absence sekce *Thismia* na Borneu, protože tato sekce je zastoupena na Jávě, Sumatře i Malajském poloostrově, tedy v územích, jejichž flóra je fytogeograficky s Borneem blízce spjatá. Dominantní sekcí je zde sekce *Odoardoa*, která je zastoupena 13 popsanými druhy. Pro ostrov je pak endemická její podsekce *Sarawakia*, zastoupená druhem *T. neptunis*. Počtem druhů pak následuje sekce *Sarcosiphon* s 11 popsanými druhy, přičemž na ostrově jsou zastoupeny obě její podsekce i nezařazený druh *T. viridistriata*. Jak sekce *Odoardoa*, tak sekce *Sarcosiphon* mají centra diverzity právě na Borneu. Třetí sekce zastoupená na ostrově je endemická a monotypická sekce *Minuta*.

Současných 25 druhů rodu známých z Bornea jistě není konečné číslo. Řada oblastí ostrova zůstává neprozkoumaná a nálezy nových druhů lze očekávat i v relativně prozkoumaných a dobře přístupných oblastech, jak dokládá např. popis druhu *T. ornata* (Dančák et al. 2020a) jehož typová lokalita leží jen 20 km od velkoměsta Kuching, v národním parku Kubah, kde působila řada botaniků, počínaje O. Beccarim v letech 1865–1868 (Sochor et al. 2018a).

5.5.1.4 Klíč k rodu *Thismia* na Borneu

Vzhledem k tomu, že poslední úplný klíč pro určení druhů rodu na Borneu byl publikován v roce 2017 (Sochor et al. 2017) bylo potřeba sestavit nový klíč doplněný o 12 druhů popsaných z ostrova od roku 2017.

1a Okvětní lístky volné, navzájem nesrostlé; kořeny plazivé, nenahloučené ... 2

1b Alespoň některé okvětní lístky srostlé nad ústím květní trubky; kořeny nahloučené, koraloidní nebo nenahloučené, plazivé ... 14

2a Všechny okvětní lístky stejného tvaru a velikosti ... 3

2b Vnitřní a vnější okvětní lístky se výrazně liší tvarem i velikostí, vnější na bázi s výběžkem ve tvaru drápu směřujícím do ústí květní trubky a velmi dlouhými vzpřímenými přívěsky … ***Thismia neptunis***

3a Mezi okvětními lístky vyrůstá z okraje květní trubky 6 krátkých, ale zřetelných zoubků … 4

3b Mezi okvětními lístky nejsou žádné zoubky přítomny … 5

4a Stěna květní trubky s příčnými přehrádkami … ***Thismia aseroe*** agg.

4b Stěna květní trubky bez příčných přehrádek … ***Thismia ophiuris***

5a Rostliny bezlodyžné nebo s lodyhou kratší než 1,5 cm; květní trubka výrazně esovitě prohnutá … 6

5b Rostliny obvykle se zřetelně vyvinutou lodyhou delší než 1,5 cm; květní trubka přímá nebo jen nevýrazně prohnutá … 8

6a Květní trubka cca 15 mm dlouhá; okvětí bílé v horní části s 12 světle růžovými proužky, ústí květní trubky růžové; na vrcholu konektivu dva přívěsky … ***T. cornuta***

6b Květní trubka cca 7 mm dlouhá; okvětí světle modré nebo hnědé, ústí květní trubky oranžové nebo hnědooranžové; na vrcholu konektivu 3-4 přívěsky … 7

7a Okvětí světle modré; přívěsky okvětních lístků cca 6 mm dlouhé; na vrcholu konektivu 3 přívěsky … ***T. kinabaluensis***

7b Okvětí hnědé; přívěsky okvětních lístků cca 2 mm dlouhé; na vrcholu konektivu 4 přívěsky … ***T. inconspicua***

8a Vnitřní strana květní trubky pokryta výraznou oranžově zbarvenou síťkou, příčné přehrádky ve stěně květní trubky chybí … ***Thismia ornata***

8b Vnitřní strana okvětí není pokryta síťkou, příčné přehrádky ve stěně květní trubky vyvinuty nebo chybí … 9

9a Vrchol konektivů se 2 přívěsky … 10

9b Vrchol konektivů se 3 a více přívěsky … 12

10a Přívěsky okvětních lístků až 70 mm dlouhé … ***T. lauriana***

10b Přívěsky okvětních lístků kratší než 20 mm … 11

11a Květní trubka bílá se světle oranžovými pruhy, přívěsky okvětních lístků 10-11 mm dlouhé; ústí květní trubky je lemováno vyniklým tupě šestihranným prstencem … ***T. bryndonei***

11b Květní trubka bílá s hnědofialovými pruhy; přívěsky okvětních lístků cca 17 mm dlouhé; ústí květní trubky není lemováno vyniklým prstencem … ***T. mullerensis***

12a Vrchol konektivů s nejméně 4 přívěsky; ústí květu lemováno vyniklým šestihranným prstencem … ***T. hexagona***

01a Přívěsky okvětních lístků 7-18 mm dlouhé … ***T. hexagona* var. *hexagona***

01b Přívěsky okvětních lístků 29-43 mm dlouhé ... ***T. hexagona* var. *grandiflora***

12b Vrchol konektivů s 3 nebo 5 přívěsky, ústí květu není lemováno vyniklým šestihranným prstencem (***T. filiformis* agg.**) … 13

13a Okvětní lístky bez přívěsků cca 5 mm dlouhé, přívěsky okvětních lístků kratší jak 5 mm, vrchol konektivu s 5 přívěsky … ***T. pallida***

13b Okvětní lístky bez přívěsků 2-2,5 mm dlouhé, přívěsky okvětních lístků cca 15 mm dlouhé, vrchol konektivu s 3 přívěsky … ***T. bifida***

14a Kořeny nenahloučené, plazivé; stonky i květní a plodní stopky bílé; květy bez přívěsků 6-9 mm dlouhé; boční přívěsek konektivu tvaru rybího ocasu … ***T. minutissima***

14b Kořeny koraloidní; stonky i květní a plodní stopky světle až tmavě hnědé; květy bez přívěsků 10-28 mm dlouhé; boční přívěsek konektivu tvaru křesla … 15

15a. Vrchol mitry s 1-3 přívěsky zřetelně delšími než 2 mm … 16

15b. Vrchol mitry bez přívěsků nebo jen velmi krátkými do 2 mm dlouhými výstupky … 18

16a. Vrchol mitry se 3 přívěsky … 17

16b. Vrchol mitry s 1 přívěskem (sloupkem), někdy na vrcholu trojlaločným … ***T. viridistriata***

17a. Okvětí žlutooranžové až růžově červené; vrchol konektivu trojúhelníkovitý, špičatý … ***T. clavigera***

17b. Okvětí modrozelené; vrchol konektivu okrouhlý až mělce vykrojený … ***T. betung-kerihunensis***

18a. Vnější okvětní lístky přítomny … 19

18b. Vnější okvětní lístky nepřítomny … 21

19a. Mitra jasně modrá nebo modrozelená … ***T. goodii***

19b. Mitra oranžová nebo žlutá až žlutavě hnědá … 20

20a Vnější okvětní lístky celokrajné s jediným krátkým zubem ve středu … ***T. coronata***

20b Vnější okvětní lístky dřípené … ***T. kelabitiana***

21a Semeník, žebra květní trubky i mitry pokryté bradavičnatými výrůstky; žebra na vnitřní straně okvětí výrazně vystouplá a zčásti odtržená od stěny trubky … ***Thismia viridistriata***

21b Semeník, žebra květní trubky ani mitry nejsou pokryté bradavičnatými výrůstky; žebra na vnitřní straně okvětí nejsou vystouplá ani zčásti odtržená od stěny trubky … 22

22a. Boční přívěsek konektivu zřetelně přesahuje vrchol konektivu … 23

22b. Boční přívěsek konektivu nepřesahuje vrchol konektivu … 24

23a. Květy 13–17 mm dlouhé; vrchol konektivu s 2 širokými, tupě trojúhelníkovitými postranními laloky a jedním úzce trojúhelníkovitým prostředním lalokem, každý lalok se štětičkou žláznatých chlupů … ***T. brunneomitra***

23b. Květy 10–12 mm dlouhé; vrchol konektivu s 2 drobnými postranními laloky a několika dlouhými jednoduchými průhlednými chlupy uprostřed … ***T. nigra***

24a. Vrchol konektivu mělce vykrojený, zcela hladký bez chlupů či zubů … ***T. laevis***

24b. Vrchol konektivu nevykrojený, chlupatý nebo zubatý … 25

25a. Vrchol konektivu hustě chlupatý až plstnatý s 4–5 krátkými laloky nepravidelného tvaru; okvětí v různých odstínech hnědé … ***T. acuminata***

25b. Vrchol konektivu lysý až řídce chlupatý s 3 špičatými trojúhelníkovitými zuby; okvětí žlutooranžové … ***T. episcopalis***

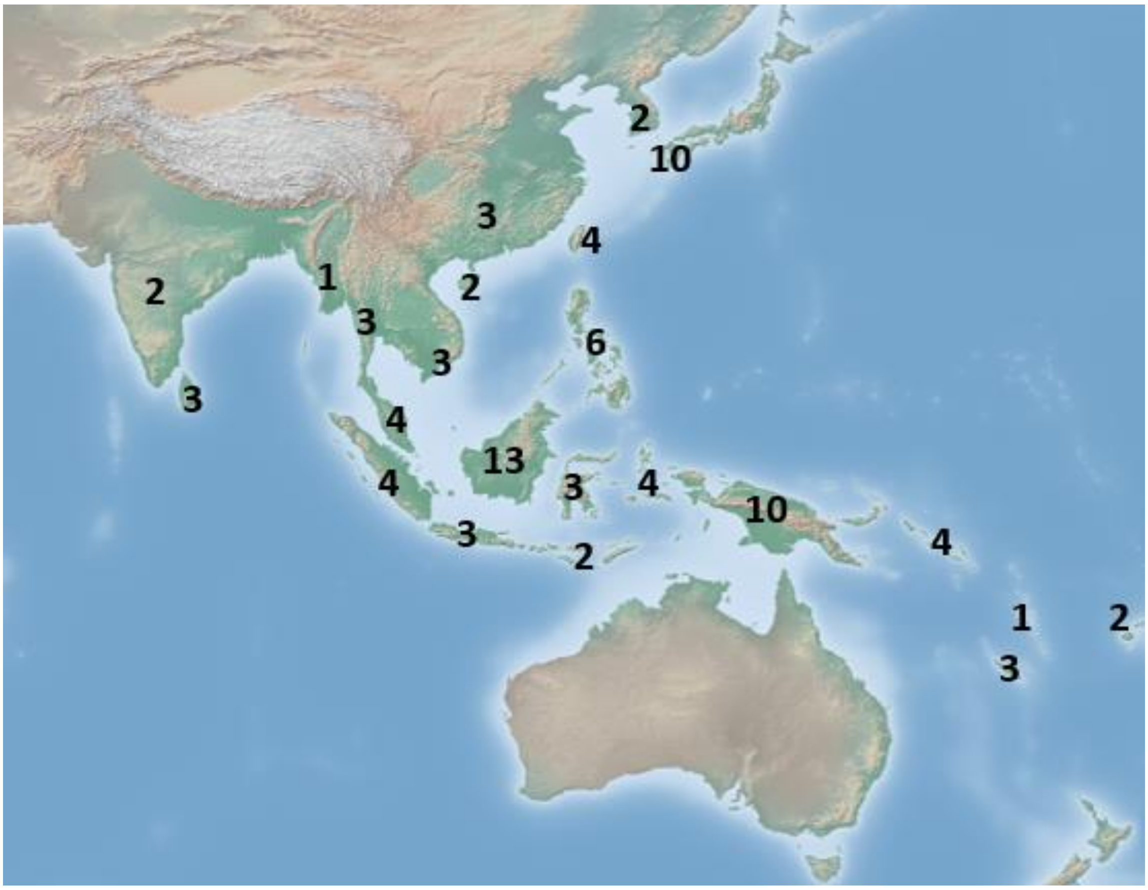
5.6 Čeleď *Triuridaceae*

Čeleď *Triuridaceae* je druhově nepočetná čeleď o zhruba 60 druzích rozšířená v tropech celého světa a lokálně zasahující až do subtropických oblastí (Maas & Rübsamen 1986, Maas-van de Kamer & Weustenfeld 1998). Zahrnuje výhradně mykoheterotrofní rostliny obvykle velmi malé velikosti (Merckx et al. 2013a). Ačkoli centrum její taxonomické diverzity leží v Neotropické oblasti (šest rodů z celkových osmi), druhová diverzita je nejvyšší v jihovýchodní Asii (30 druhů), kde se vyskytují pouze zástupci jediného rodu, *Sciaphila* (van de Meerendonk 1984).

5.6.1 Rod *Sciaphila*

Rod *Sciaphila* patří k nejméně prozkoumaným a taxonomicky nejobtížnějším rodům mykoheterotrofních rostlin Bornea (Dančák et al. 2020). To je dáno jednak redukovanou stavbou jejich těla umocněnou malou velikostí a pak také neudržitelným taxonomickým konceptem přijatým ve stěžejním díle Flora Malesiana (van de Meerendonk 1984, Suetsugu et al. 2020c). Taxonomicky významné znaky těchto rostlin jsou v převážné míře na květech, které dosahují velikosti jen několika milimetrů, přičemž například prašníky, jejichž stavba je zásadní, měří obvykle méně jak 1 mm. Navíc rostliny často tvoří jen jeden či dva květy, které lze pro určení nebo popis využít a ty jsou navíc u herbářových položek nezřídka zdeformované či poškozené.

Z Malesijské oblasti bylo celkem popsáno několik desítek druhů, značná část z nich ale nebyla později, v díle Flora Malesiana, akceptována a jsou uvedena pouze jako synonyma 14 akceptovaných druhů (van de Meerendonk 1984). V tomto pojetí jsou pak některé druhy extrémně variabilní a mají rozsáhlé areály. Typickým příkladem je druh *Sciaphila secundiflora* pospaný z Cejlonu a dle díla Flora Malesiana rozšířený od Cejlonu na západě po Japonsko a Koreu na severu a Šalamounovy ostrovy na východě (van de Meerendonk 1984, Ohashi et al. 2008). V rámci tohoto areálu jsou pak rostliny přiřazované k tomu druhu velmi variabilní a s velkou pravděpodobností jde v některých případech spíše o samostatné druhy (viz např. Suetsugu et al. 2019, Suetsugu et al. 2020c). V případě Bornea se s velkou pravděpodobností jedná o nejméně tři svébytné druhy, přičemž pravá *S. secundiflora* se zde vůbec vyskytuje (Dančák et al. 2020). Jedním z těchto druhů je *Sciaphila major*, popsaná O. Beccarim ze Sarawaku (Suetsugu et al. 2020c) či *Sciaphila atra* recentně popsaná rovněž ze Sarawaku (Dančák et al. 2020). Jak se ukazuje také na několika recentně popsaných druzích, jež jsou endemiti relativně malých území (Suetsugu et al. 2016, Suetsugu & Nishioka 2017, Suetsugu & Kinoshita 2020), rozsáhlé areály zahrnující různé fytogeografické oblasti zřejmě nebudou u tohoto rodu pravidlem. Další překážkou komplikující taxonomické studium rodu je fakt, že současná taxonomie stále z velké části stojí na analýze morfologie rostlin a prozatím nevyužívá molekulárních markerů (ale viz např. Suetsugu et al. 2019). Bez jejich využití bude stěží možné přikročit k revizi rodu nejen v Malesii ale i v mnohem menších územích. To se týká i Bornea, které patří vedle Nové Guineje a jižního Japonska s více jak 10 druhy k centrům diverzity rodu (obr. 10).



Obrázek 10. Druhová diverzita rodu *Sciaphila* v asijské části areálu (zkompilováno dle POWO 2019 a vlastních dat).

Na Borneu je v současnosti znám výskyt 13 popsaných druhů rodu, z toho je 8 endemických (POWO 2019). Několik z těchto druhů bylo popsáno až v posledních 10 letech, i když přírůstek druhů není taky výrazný jako u předchozího rodu *Thismia*. Z ostrova jsou ale uváděny také druhy, jejichž výskyt je přinejmenším nejistý. Kromě výše zmíněného druhu *S. secundiflora* je to také *S. thaidanica* (Tsukaya & Okada 2013), druh popsaný z Thajska (Larsen 1961). Jak diskutují Dančák et al. (2020), rostliny, na nichž je tento údaj založen, pravděpodobně nejsou totožné se *S. thaidanica*, ale patří k jinému (zřejmě nepopsanému) druhu, který je znám také z Bruneje, kde byl mylně označován jménem *S. secundiflora* (Coode et al. 1996).

5.6.1.1 Klíč k určení druhů rodu *Sciaphila* na Borneu

Tento klíč je převzat a upraven z práce Dančák et al. (2020). Nezahrnuje dva druhy (*S. thaidanica* a *S. secundiflora*), jejichž výskyt na Borneu není jistý a naopak zahrnuje i dosud taxonomicky nejasný (zřejmě nepopsaný) druh uváděný z Bornea pod jmény *S. thaidanica* a *S. secundiflora* (zde je pojmenován pracovním jménem *Sciaphila* sp. Brunei).

1a Rostliny s květy oboupohlavnými i jednopohlavnými … 2

1b Rostliny s výhradně jednopohlavnými květy … 4

2a Okvětní lístky 4(-5); tyčinky 2 … ***S. betung-kerihunensis***

2b Okvětních lístků 6; tyčinky 3-6 … 3

3a Samčí i oboupohlavné květy se 3 tyčinkami … ***S. maculata***

3b Samčí květy s 6 tyčinkami, oboupohlavné květy s (3-)6 tyčinkami … ***S. tenella***

4a. Samčí květy s 6 tyčinkami … ***S. densiflora***

4b. Samčí květy s 2-3 tyčinkami … 5

5a. Okvětní lístky samčích květů na vrcholu lysé … 6

5b. Okvětní lístky samčích květů na vrcholu chlupaté … 10

6a. Čnělka vyrůstá těsně pod vrcholem semeníku, za plodu zřetelně delší než semeník; okvětní lístky samčích květů na vrcholu kyjovitě ztloustlé … ***S. arfakiana***

6b. Čnělka vyrůstá z báze nebo boku semeníku, za plodu zřetelně kratší než semeník; okvětní lístky samčích květů na vrcholu neztloustlé, špičaté … 7

7a. Samčí květy s četnými bradavčitými pistillodii; rostliny 3,5-7 cm vysoké, tmavě fialové, květy téměř černé … ***S. atra***

7b. Samčí květy bez pistillodií; rostliny obvykle 7-30(-35) cm vysoké, bílé nebo červenofialové … 8

8a Plně rozkvetlé květy v průměru 6-8 mm; rostliny obvykle bílé, vzácně světle červenofialové, (10-)15-25(-35) cm vysoké … 9

8b Plně rozkvetlé květy v průměru 3-4,5 mm; rostliny červenofialové, 7-15 cm vysoké … ***Sciaphila* sp. Brunei**

9a. Plně vyvinutá květenství 8–14 cm dlouhá; květy obvykle v počtu převyšujícím 20, obvykle s 6 okvětními lístky … ***S. alba***

9b. Plně vyvinutá květenství 3–6 cm dlouhá; květy obvykle v počtu nedosahujícím 20, obvykle s více jak 6 okvětními lístky … ***S. major***

10a. Prašníky čtyřlaločné … ***S. micranthera***

10b. Prašníky dvojlaločné … 11

11a. Prašníky přisedlé … 12

11b. Prašníky na zřetelných nitkách … 13

12a Květenství spirálně uspořádané; stopky květů krátké … ***S. brevistyla***

12b Květenství jednostranné; stopky květů velmi dlouhé … ***S. lambirensis***

13a Okvětní lístky tupé; lůžko samčího květu nápadně ztlustlé … ***S. inouei***

13b Okvětní lístky špičaté; lůžko samčího květu neztlustlé … ***S. winkleri***

6 Shrnutí přínosu uchazeče k problematice habilitační práce a možné směry budoucího výzkumu

Mykoheterotrofní rostliny Bornea jsou v současnosti po taxonomicko-chorologické stránce intenzívněji studovány jen dvěma vědeckými týmy, které spolu navíc vzájemně spolupracují. Vedle týmu japonských botaniků (K. Suetsugu, H. Tsukaya a další) je to také tým z Univerzity Palackého v Olomouci (M. Dančák, M. Hroneš a M. Sochor). Český tým se soustředí na rody *Epirixanthes, Sciaphila* a zejména *Thismia*. Publikoval celou řadu prací s taxonomickou a fytogeografickou tématikou, jako jsou popisy nových druhů (např. Dančák et al. 2020a, b), taxonomicko-nomenklatorické práce (Hroneš 2014, Suetsugu et al. 2020c), fylogenetické studie (Sochor et al. 2018b), rodové revize (Dančák et al. 2017) a práce zabývající se rozšířením a endemismem (Dančák et al. 2020c).

Pro rod *Epirixanthes* byla zpracována jediná dosud existující synopse celého rodu společně s jeho revizí pro Brunejský sultanát (Dančák et al. 2017). V této práci byl zároveň publikován přepracovaný klíč k určování druhů tohoto rodu, který je založen na exaktnějších znacích, než dosud publikované klíče a s jehož pomocí je tedy určení jednotlivých druhů výrazně přesnější. Tento klíč je také dosud jediný existující, který zahrnuje všechny druhy rodu *Epirixanthes*.

Rod *Sciaphila* je studován ve spolupráci s japonským výzkumným týmem a v současnosti byla publikována studie (Suetsugu et al. 2020c), která se zabývá některými spornými taxony uváděnými z ostrova, určité z nich pak z jeho flóry vylučuje (*S. thaidanica*) a jiné naopak znovu navrací, respektive vyjímá ze synonymiky (*S. major*). Kromě této studie pak byl také publikován objev nového druhu (*S. atra*) z Malajské části ostrova (Dančák et al. 2020). Součástí posledně zmíněné práce je i výrazně přepracovaný úplný klíč k druhům tohoto rodu rostoucím na ostrově, který je podobně jako u předchozího rodu založen na exaktnějších znacích a umožňuje tedy přesnější určování (viz též klíč uvedený zde v kapitole 5.6.1.1).

Rod *Thismia* je v současnosti nejintenzivněji studovaný mykoheterotrofní rod Bornea. Do roku 2013 byl z ostrova znám výskyt pouhých osmi druhů rodu, přičemž v současnosti je to 25, z toho 23 endemických. Z těchto 23 endemických druhů bylo českým výzkumným týmem objeveno a vědecky popsáno 14. Dalším významným přínosem bylo znovuobjevení ikonického druhu *T. neptunis*, a to po více jak 150 letech (Sochor et al. 2018a). Tento druh byl považován za vyhynulý a jeho znovuobjevení má značný význam pro studium fylogeneze rodu *Thismia*, protože jde o druh morfologicky unikátní a izolovaný. Důsledkem jeho znovuobjevení bylo mj. přeřazení druhu ze sekce *Thismia* do sekce *Odoardoa,* v rámci které pak tvoří monotypickou podsekci (viz kap. 5.5.1.1). Velmi významným přínosem pro výzkum tohoto rodu pak mělo také zjištění, že jeho druhy, které dosud byly obvykle považovány za extrémně vzácné, nezřídka stenoendemické rostliny, mohou mít ve skutečnosti i poměrně rozsáhlé areály podobně jako některé jiné bylinné druhy bornejských tropických deštných lesů (Dančák et al. 2020c). To vedlo také k upřesnění míry ohrožení u některých druhů včetně návrhů na nová hodnocení dle mezinárodní klasifikace IUCN. Posledně zmíněná práce přichází rovněž s poznatky, které ukazují na velmi zajímavý průběh mikroevoluce v tomto rodě. Genetická variabilita některých druhů je totiž podstatně vyšší než variabilita morfologická a genetická vzdálenost mezi některými morfologicky téměř nerozlišitelnými populacemi může být stejná jako mezi populacemi dvou různých jiných druhů. Jaké mikroevoluční mechanismy stojí za tímto fenoménem, bude jedním z témat budoucího výzkumu rodu *Thismia*.

Obecně se výzkum mykoheterotrofních rostlin Bornea bude v následujících letech ubírat nejen směrem objevování nových dosud nepopsaných druhů (jejichž existence se předpokládá), ale také směrem kritických taxonomických revizí těchto rodů, revizí jejich skutečných areálů a rovněž fylogenetických vztahů v rámci jednotlivých rodů. Ty jsou dnes například již relativně dobře známy u rodu *Thismia,* ale prakticky neznámé jsou u rodů *Sciaphila* a *Epirixanthes*. Zejména rod *Epirixanthes* dosud stál relativně na okraji zájmu, o čemž svědčí také velmi malý počet prací, které se tomuto rodu věnovaly. Kromě výše zmíněných rodů by si ale podobnou pozornost zasloužily také další méně studované skupiny, zejména v textu habilitační práce (kapitoly 5.1, 5.2 a 5.3) diskutované rody *Burmannia* a *Gymnosiphon* z čeledi *Burmanniaceae,* rod *Ophioglossum* z čeledi *Ophioglossaceae,* ale také druhově nejpočetnější skupina mykoheterotrofních rostlin Bornea, čeleď *Orchidaceae*.

Výzkum taxonomie, rozšíření, evoluce a fylogeneze mykoheterotrofních rostlin není přirozeně možné omezit jen na Borneo a jednotlivé skupiny je nutné studovat v co největších částech jejich areálů. To předpokládá dobrou znalost flór sousedních území. V případě Bornea jde zejména o Jávu, Sumatru a Malajský poloostrov, které mají vlastní velmi bohaté mykoheterotrofní flóry. Zejména Sumatra patří nejen k floristicky nejméně prozkoumaným územím Malesijské fytogeografické oblasti, ale zároveň také k nejvíce ohroženým úbytkem tropických deštných lesů.

Z vědeckého hlediska by bylo jistě zajímavé i žádoucí využít dosavadní poznatky v nadstavbových studiích, zejména větších fylogenetických studiích (na kterých ostatně již spolupracujeme, viz např. Shepeleva et al. 2020). Za situace, kdy s největší pravděpodobností dosud neznámým a nepopsaným druhům hrozí bezprostřední vyhubení v důsledku komerční těžby dřeva a konverze tropického deštného lesa na zemědělskou půdu, by mělo být odpovídající úsilí věnováno rovněž na objevování a možnou záchranu těchto druhů.

7 Závěr

Mykoheterotrofní rostliny jsou významnou složkou biodiverzity tropických deštných lesů Bornea, i když vzhledem k jeho enormní rostlinné diverzitě tvoří pouze její zlomek. V globálním měřítku lze Borneo považovat za jedno z center diverzity mykoheterotrofních rostlin, neboť na ostrově je znám výskyt zhruba 125 druhů, tedy asi 11 % jejich celkové známé globální diverzity.

Taxonomický výzkum mykoheterotrofních rostlin na Borneu v posledních 10 letech výrazně akceleroval. Jen od roku 2011 bylo z ostrova nově popsáno 28 druhů, přičemž v období 1950–2010 to bylo jen 11 druhů. Pozornost je věnována především rodům *Thismia, Sciaphila* a *Epirixanthes*. Naopak zejména rody čeledi *Orchidaceae* jsou studovány jen marginálně a víceméně náhodně. Zcela okrajová pozornost je věnována také výtrusným mykoheterotrofním rostlinám.

K hlavním problémům, kterým současný taxonomický výzkum mykoheterotrofních rostlin, nejen na Borneu, ale v celé Malesijské oblasti, čelí, patří a) chybějící revize některých skupin (např. *Ophioglossaceae* a *Orchidaceae*), b) neudržitelně široký druhový koncept přijatý při zpracování některých rodů v díle Flora Malesiana (např. u rodů *Burmannia, Gymnosiphon* a *Sciaphila*), c) neochota grantových agentur financovat základní popisný výzkum d) administrativní zátěž spojená se získáváním výzkumných povolení, e) vzácnost mnoha druhů a s tím spojená obtížná dostupnost studijního materiálu, f) redukovaná stavba těla a nepravidelný životní cyklus rostlin.

Budoucí výzkum mykoheterotrofních rostlin na Borneu by měl být zaměřen nejen na objevování dosud nepopsaných druhů, které jsou nezřídka bezprostředně ohrožené vyhubením kvůli ničení jejich přirozeného biotopu, ale také na obecnější studium jejich taxonomie, rozšíření, evoluce a fylogeneze.

8 Poděkování

Děkuji všem, kteří se, ať již přímo či nepřímo, podíleli na tom, že jsem dostal příležitost studovat tropické mykoheterotrofní rostliny.

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Příloha 1 Obrazové tabule

Tabule 1. Výtrusné mykoheterotrofní rostliny. A: *Huperzia dalhousieana* (Indonésie, Severní Kalimantan), B: *Huperzia squarrosa* (Malajsie, Sarawak), C: *Lycopodium casuarinoides* (Indonésie, Severní Kalimantan), D: *Botrychium daucifolium* (Malajsie, Sarawak), E: *Helminthostachys zeylanica* (Malajsie, Sarawak), F: *Ophioglossum reticulatum* (Malajsie, Sarawak), G: *Ophioglossum* sp. (Brunej), H: *Psilotum complantaum* (Malajsie, Sabah), I: *Actinostachys digitata* (Brunej). (A–D, F foto M. Dančák; E, G, I foto M. Sochor, H: foto T. Ballinger).

Tabule 2. Burmanniaceae. A: *Burmannia championii* (Indonésie, Východní Kalimantan) B: *Burmannia lutescens* (Malajsie, Sarawak), C: *Burmannia malasica* (Indonésie, Východní Kalimantan), D: *Gymnosiphon aphyllus* (Da Indonésie, Východní Kalimantan, Db a Dc Brunej). (A, Ba, C, Da, Dc foto M. Sochor, Bb foto M. Dančák, Dc foto Z. Špíšek).

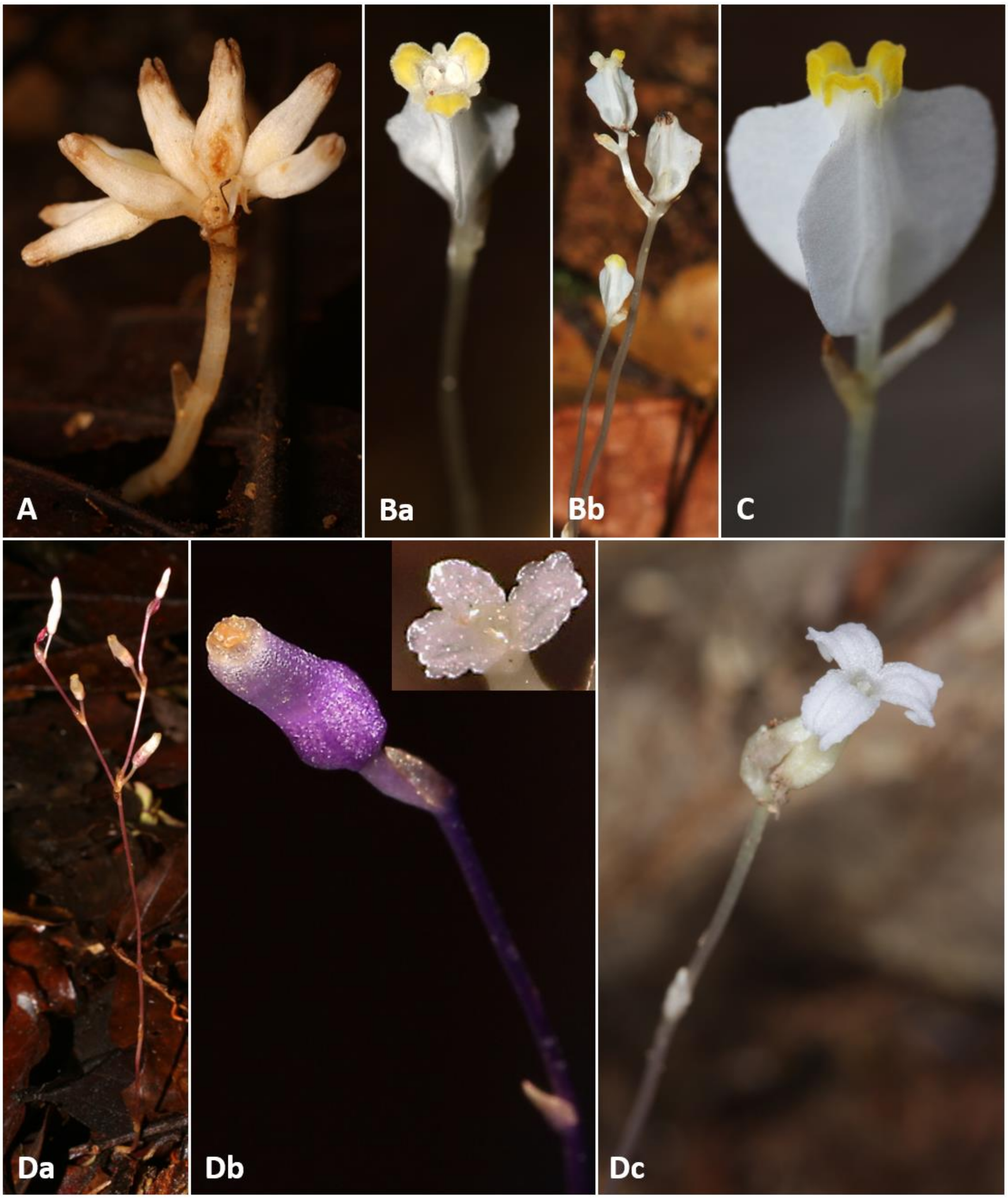
Tabule 3. Gentianaceae a Polygalaceae. A: *Exacum tenue* (Malajsie, Sarawak), B: *Epirixanthes elongata* (Malajsie, Sarawak), C: *Epirixanthes kinabaluensis* (Malajsie, Sarawak), D: *Epirixanthes pallida* (Malajsie, Sarawak), E: *Epirixanthes papuana* (Indonésie, Východní Kalimantan). (A, C, D, E foto M. Sochor, B foto M. Dančák).

Tabule 4. Orchidaceae. A: *Aphyllorchis striata* (Brunej), B: *Aphyllorchis* sp. (Malajsie, Sarawak), C: *Aphyllorchis montana* (Malajsie, Sarawak), D: *Cystorchis aphylla* (Malajsie, Sarawak), E: *Didymoplexiella kinabaluensis* (Indonésie, Východní Kalimantan), F: *Didymoplexiella ornata* (Malajsie, Sarawak), G: *Didymoplexis cornuta* (Malajsie, Sarawak), H: *Didymoplexis* aff. *striata* (Malajsie, Sarawak), I: *Gastrodia* sp. (Malajsie, Sarawak), J: *Gastrodia* sp. (Brunej), K: *Lecanorchis malaccensis* (Indonésie, Východní Kalimantan), L: *Lecanorchis multiflora* (Malajsie, Sarawak), M: *Platanthera saprophytica* (Malajsie, Sarawak), *Tropidia saprophytica* (Brunej). (A, C, D, M foto M. Dančák, B, E–N foto M. Sochor).

Tabule 5. Thismiaceae. A: *Thismia brunneomitra* (Malajsie, Sarawak), B: *Thismia acuta* (Malajsie, Sarawak), C: *Thismia goodii* (Malajsie, Sarawak), D: *Thismia kelabitiana* (Malajsie, Sarawak), E: *Thismia viridistriata* (Malajsie, Sarawak), F: *Thismia minutissima* (Malajsie, Sarawak), G: *Thismia neptunis* (Malajsie, Sarawak), H: *Thismia ornata* (Malajsie, Sarawak), I: *Thismia cornuta* (Malajsie, Sarawak), J: *Thismia bifida* (Brunej), K: *Thismia hexagona* var. *grandiflora* (Malajsie, Sabah). (A, B, D–I foto M. Sochor, C foto M. Dančák, J foto M. Hroneš, K foto T. Utteridge).

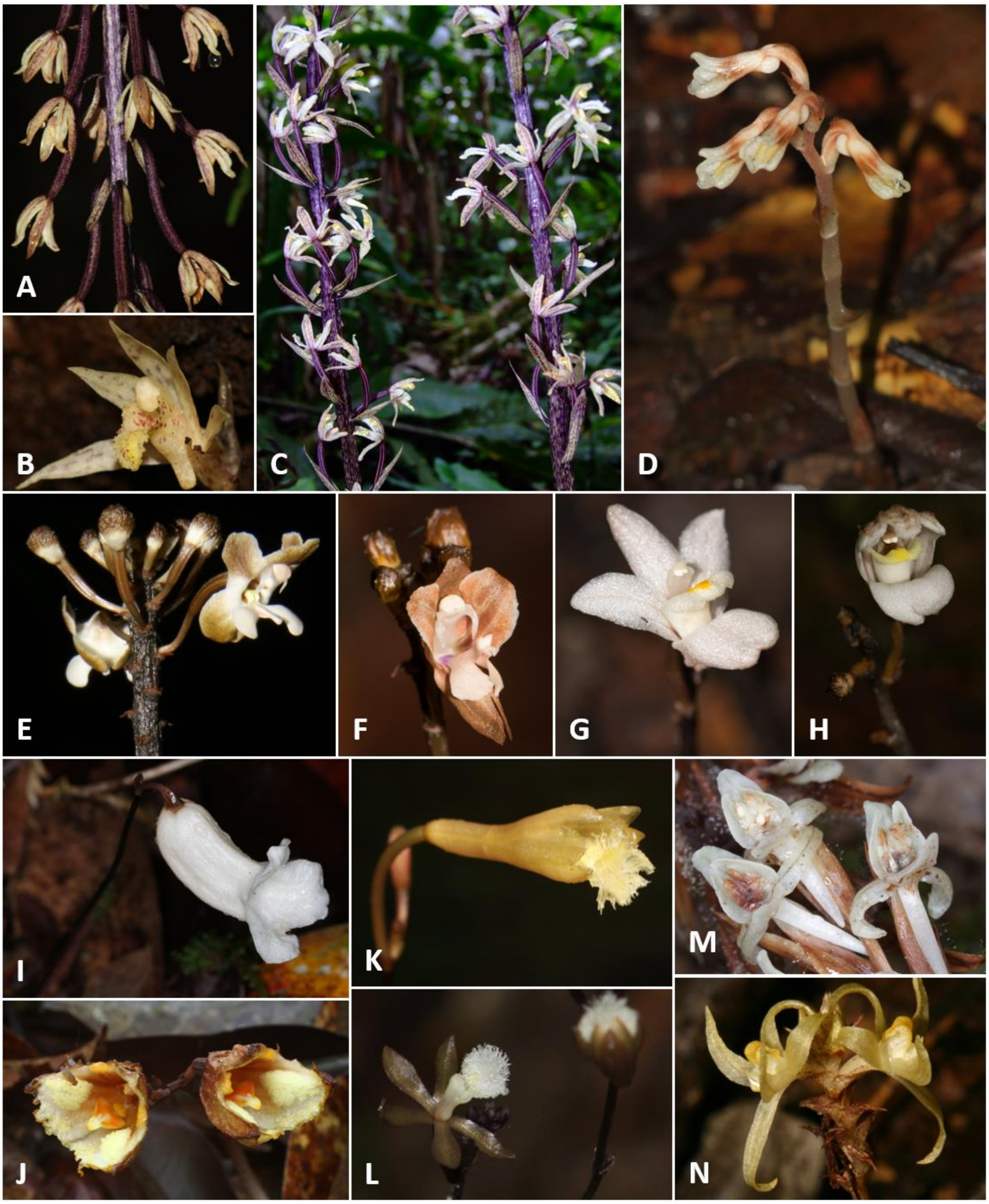
Tabule 6. Petrosaviaceae a Triuridaceae. A: *Sciaphila atra* (Malajsie, Sarawak), B: *Sciaphila tenella* (Malajsie, Sarawak), C: *Sciaphila alba* (Brunej), D: *Sciaphila major* (Malajsie, Sarawak), E: *Sciaphila arfakiana* (Malajsie, Sarawak), F: *Sciaphila winkleri* (Malajsie, Sarawak). G: *Petrosavia stellaris* (Malajsie, Sabah). (A, D, E, F foto M. Sochor, B foto M. Dančák, C foto M. Hroneš, G foto R. van Vugt).

Tabule 1. Výtrusné mykoheterotrofní rostliny. A: *Huperzia dalhousieana* (Indonésie, Severní Kalimantan), B: *Huperzia squarrosa* (Malajsie, Sarawak), C: *Lycopodium casuarinoides* (Indonésie, Severní Kalimantan), D: *Botrychium daucifolium* (Malajsie, Sarawak), E: *Helminthostachys zeylanica* (Malajsie, Sarawak), F: *Ophioglossum reticulatum* (Malajsie, Sarawak), G: *Ophioglossum* sp. (Brunej), H: *Psilotum complantaum* (Malajsie, Sabah), I: *Actinostachys digitata* (Brunej). (A–D, F foto M. Dančák; E, G, I foto M. Sochor, H: foto T. Ballinger).

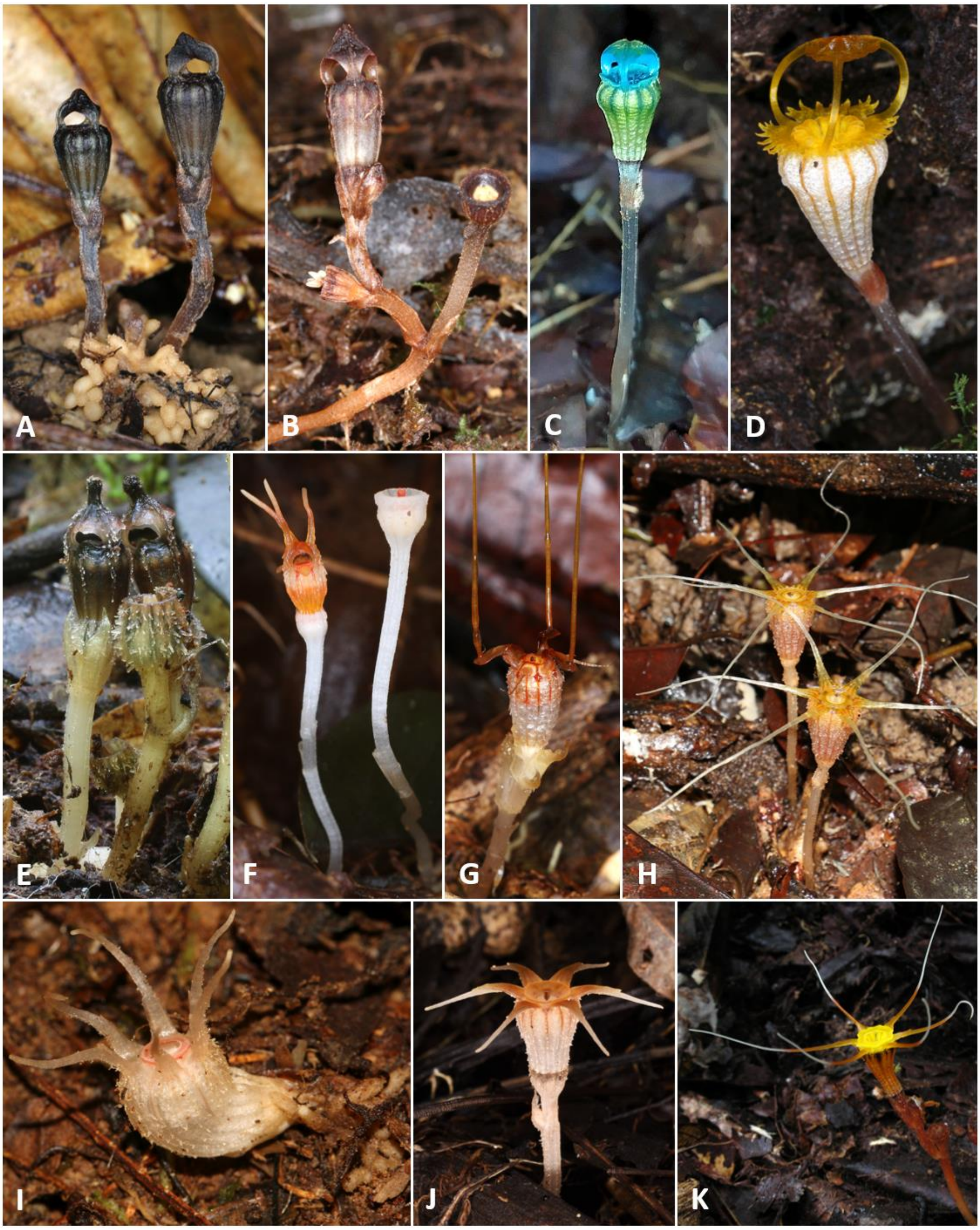


Tabule 2. Burmanniaceae. A: *Burmannia championii* (Indonésie, Východní Kalimantan) B: *Burmannia lutescens* (Malajsie, Sarawak), C: *Burmannia malasica* (Indonésie, Východní Kalimantan), D: *Gymnosiphon aphyllus* (Da Indonésie, Východní Kalimantan, Db a Dc Brunej). (A, Ba, C, Da, Dc foto M. Sochor, Bb foto M. Dančák, Dc foto Z. Špíšek).

Tabule 3. Gentianaceae a Polygalaceae. A: *Exacum tenue* (Malajsie, Sarawak), B: *Epirixanthes elongata* (Malajsie, Sarawak), C: *Epirixanthes kinabaluensis* (Malajsie, Sarawak), D: *Epirixanthes pallida* (Malajsie, Sarawak), E: *Epirixanthes papuana* (Indonésie, Východní Kalimantan). (A, C, D, E foto M. Sochor, B foto M. Dančák).



Tabule 4. Orchidaceae. A: *Aphyllorchis striata* (Brunej), B: *Aphyllorchis* sp. (Malajsie, Sarawak), C: *Aphyllorchis montana* (Malajsie, Sarawak), D: *Cystorchis aphylla* (Malajsie, Sarawak), E: *Didymoplexiella kinabaluensis* (Indonésie, Východní Kalimantan), F: *Didymoplexiella ornata* (Malajsie, Sarawak), G: *Didymoplexis cornuta* (Malajsie, Sarawak), H: *Didymoplexis* aff. *striata* (Malajsie, Sarawak), I: *Gastrodia* sp. (Malajsie, Sarawak), J: *Gastrodia* sp. (Brunej), K: *Lecanorchis malaccensis* (Indonésie, Východní Kalimantan), L: *Lecanorchis multiflora* (Malajsie, Sarawak), M: *Platanthera saprophytica* (Malajsie, Sarawak), *Tropidia saprophytica* (Brunej). (A, C, D, M foto M. Dančák, B, E-N foto M. Sochor).



Tabule 5. Thismiaceae. A: *Thismia brunneomitra* (Malajsie, Sarawak), B: *Thismia acuta* (Malajsie, Sarawak), C: *Thismia goodii* (Malajsie, Sarawak), D: *Thismia kelabitiana* (Malajsie, Sarawak), E: *Thismia viridistriata* (Malajsie, Sarawak), F: *Thismia minutissima* (Malajsie, Sarawak), G: *Thismia neptunis* (Malajsie, Sarawak), H: *Thismia ornata* (Malajsie, Sarawak), I: *Thismia cornuta* (Malajsie, Sarawak), J: *Thismia bifida* (Brunej), K: *Thismia hexagona* var. *grandiflora* (Malajsie, Sabah). (A, B, D–I foto M. Sochor, C foto M. Dančák, J foto M. Hroneš, K foto T. Utteridge).

Tabule 6. Petrosaviaceae a Triuridaceae. A: *Sciaphila atra* (Malajsie, Sarawak), B: *Sciaphila tenella* (Malajsie, Sarawak), C: *Sciaphila alba* (Brunej), D: *Sciaphila major* (Malajsie, Sarawak), E: *Sciaphila arfakiana* (Malajsie, Sarawak), F: *Sciaphila winkleri* (Malajsie, Sarawak). G: *Petrosavia stellaris* (Malajsie, Sabah). (A, D, E, F foto M. Sochor, B foto M. Dančák, C foto M. Hroneš, G foto R. van Vugt).

Příloha 2 Vybrané práce s tématikou mykoheterotrofních rostlin Bornea

1. **Dančák M.**, Hroneš M., Sukri R. S., Metali F. & Joffre A. A. (2017): Novitates Bruneienses, 9. A synopsis of *Epirixanthes* (Polygalaceae) in Brunei Darussalam. – Gardens' Bulletin Singapore 69(2): 179-187.

2. **Dančák M.**, Hroneš M., Sochor M., Kobrlová L., Hédl R., Hrázský Z., Vildomcová A., Sukri R. S. & Metali F. (2013): A new species of *Thismia* (Thismiaceae) from Brunei Darussalam, Borneo. – Phytotaxa 125(1): 33-39.

3. Hroneš M., Kobrlová L., Taraška V., Popelka O., Hédl R., Sukri R. S., Metali F. & **Dančák M.** (2015): *Thismia brunneomitra,* another new species of *Thismia* (Thismiaceae) from Ulu Temburong, Brunei Darussalam. – Phytotaxa 234(2): 172-178.

4. Sochor M., Sukri R. S., Metali F. & **Dančák M.** (2017): *Thismia inconspicua* (Thismiaceae), a new mycoheterotrophic species from Borneo. – Phytotaxa 295(3): 263-270.

5. Hroneš M., Rejžek M., Sochor M., Svátek M., Kvasnica J., Egertová Z., Pereira J. T., Nilus R. & **Dančák M.** (2018): Two new species of *Thismia* subsect. *Odoardoa* (Thismiaceae) from Borneo. – Plant Ecology and Evolution 151(1): 110-118.

6. Sochor M., Egertová Z., Hroneš M. & **Dančák M.** (2018): Rediscovery of *Thismia neptunis* (Thismiaceae) after 151 years. – Phytotaxa 340(1): 71-78.

7. **Dančák M.**, Hroneš M., Sochor M. & Sochorová Z. (2018): *Thismia kelabitiana* (Thismiaceae), a new unique Fairy Lantern from Borneo potentially threatened by commercial logging. – PLoS ONE 13(10): e0203443.

8. **Dančák M.**, Hroneš M. & Sochor M. (2020): *Thismia ornata* and *T. coronata* (Thismiaceae), two new species from Sarawak, Borneo. – Willdenowia 50(1): 65-76.

9. **Dančák M.**, Hroneš M. & Sochor M. (2020): *Thismia minutissima*, a new remarkable new species from Borneo. – Kew Bulletin 75: 29.

10. Sochor M., Hroneš M. & **Dančák M.** (2018): New insights into variation, evolution and taxonomy of fairy lanterns (*Thismia*, Thismiaceae) with four new species from Borneo. – Plant Systematics and Evolution 304(5): 699-721.

11. **Dančák M.**, Hroneš M. & Sochor M. (2020c): *Thismia*: the rarest of the rare? Ranges of some Bornean species are much larger than previously believed. – Phytotaxa 455(4): 245-261.

12. **Dančák M.**, Hroneš M. & Sochor M. (2020): *Sciaphila atra* (Triuridaceae), a new mycoheterotrophic species from Borneo. – Phytotaxa 472 (3): 277-282.

13. Suetsusgu K., **Dančák M.**, Hroneš M., Naiki A., Tagane S. & Yahara T. (2020): Resurrection and emended description of *Sciaphila major*. – Phytotaxa 459(1): 25-38.

Gardens' Bulletin Singapore 69(2): 179–187. 2017
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Novitates Bruneienses, 9. A synopsis of *Epirixanthes* (Polygalaceae) in Brunei Darussalam and notes on species elsewhere

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ABSTRACT. The genus *Epirixanthes* Blume is revised for Brunei Darussalam. Four species are recognised for the country: *Epirixanthes cylindrica* Blume, *E. elongata* Blume, *E. kinabaluensis* T.Wendt and *E. papuana* J.J.Sm., with the two latter species being newly recorded for the Brunei flora. A single collection from Brunei that was formerly identified as *Epirixanthes pallida* T.Wendt is now confirmed as *E. papuana*. A revised key for the genus is included.

Keywords. Distribution, herbs, Malesia, mycoheterotrophic plants, north-western Borneo, taxonomy, understorey

Introduction

Epirixanthes Blume is a species-poor genus of holomycoheterotrophic herbaceous plants from the family Polygalaceae which inhabit the understorey of tropical rainforests (Van der Meijden, 1988; Merckx et al., 2013). It is sister to the autotrophic genus *Salomonia* Lour. with which it shares several synapomorphies such as spike-like terminal inflorescence and three antesepalous stamen primordia (Van der Meijden, 1988; Mennes et al., 2015). Members of the genus are generally tiny plants with reduced bract-like leaves and dense spike-like inflorescences (Van der Meijden, 1988). Due to the reduction of vegetative organs as a result of mycoheterotrophy, the set of morphological characters useful for species determination is very limited and includes mostly reproductive organs (i.e., bracts, bracteoles, sepals and fruits). Currently, only seven species of *Epirixanthes* are recognised worldwide, and all of them are endemic to Indo-Malesia (Van der Meijden, 1988; Pendry, 2010; Tsukaya et al., 2016). The centre of its taxonomic diversity lies in Borneo where six of the species co-occur, with one of them apparently endemic to the island (Fig. 1). In the *Checklist of the Flowering*

Fig. 1. Global distribution and diversity of *Epirixanthes* with number of species for each region and number of endemic species in parentheses.

Plants and Gymnosperms of Brunei Darussalam (Coode et al., 1996), three species of *Epirixanthes* are reported from the country, namely *E. cylindrica* Blume, *E. elongata* Blume and *E. pallida* T.Wendt. During our recent ecological research activities in Kuala Belalong (Ulu Temburong National Park, Temburong district), we frequently encountered *Epirixanthes* plants in the lowland dipterocarp forest understorey. However, some of the observed plants did not match with any of the three species reported from Brunei Darussalam by Coode et al. (1996), indicating they possibly belong to unrecorded species. We therefore decided to clarify the taxonomic status of these plants and present a revision of *Epirixanthes* in the country.

Material and methods

We examined specimens deposited in BRUN (Brunei National Herbarium) as well as our field collections from Brunei Darussalam deposited in OL (Herbarium of the Department of Botany at Palacký University in Olomouc). Available duplicates kept in K (Royal Botanic Gardens Kew) and AAU (Science Museums, Aarhus University) were also seen. The identification of each specimen was checked and the identifications updated when necessary. All cited specimens have been seen. Bruneian localities from herbarium labels are sorted below according the current administrative districts of Brunei Darussalam.

Results

Four species of *Epirixanthes* were found to occur in Brunei Darussalam, namely *E. cylindrica*, *E. elongata*, *E. kinabaluensis* T.Wendt and *E. papuana* J.J.Sm. The two former species were previously known from the country while the two latter species are new additions to the country's flora. *Epirixanthes pallida* should be excluded from the Brunei checklist as all three duplicates (deposited in BRUN, K, and AAU) of the single collection (*Poulsen* 3) cited in Coode et al. (1996) consist of misidentified plants of *E. papuana*. All four species co-occur in the Lowland Mixed Dipterocarp forest of the Ulu Temburong National Park in the Temburong district, which further highlights the floristic and conservation significance of this area.

The *Epirixanthes* species of Brunei Darussalam

1. ***Epirixanthes cylindrica*** Blume, Cat. Gew. Buitenzorg 82 (1823). (Fig. 2A)

Global distribution. Its range includes Myanmar, Sumatra, Java, Borneo and New Guinea (Van der Meijden, 1988).

Distribution in Brunei Darussalam. It is documented only from the Temburong district in a few localities in Kuala Belalong – Bukit Belalong area. Its known elevational range in Brunei Darussalam is from c. 100 m a.s.l. up to 850 m a.s.l.

Specimens examined. BRUNEI DARUSSALAM: **Temburong:** Amo, Ulu Belalong, L.P. 382, north-facing slopes below campsite, 18 Jan 1994, *Coode 7845* (BRUN); Amo, Bukit Belalong, hill dipterocarp forest on Setap Shales ridgetop, 24 Feb 1992, *Dransfield 1246* (BRUN); Amo, Bukit Belalong, hill dipterocarp forest steep slope near valley bottom, 25 Feb 1992, *Dransfield 1266* (BRUN); Bukit Belalong, east ridge, 20 Jul 1989, *de Vogel 8989* (BRUN); Batu Apoi Forest Reserve, ridge between K. Belalong and Bt. Belalong, Jalan Tengga, damp, flat area below Bukit Belalong, 21 Mar 1992, *Poulsen 304* (AAU, BRUN); Kuala Belalong, Batu Apoi Forest Reserve, upstream the Sungai Belalong river from the Kuala Belalong Field Studies Centre, along path, 10 Nov 1991, *Hansen 1540* (BRUN); Kuala Belalong, E ridge of Sungai Belalong, ca. 0.9 km ESE from its confluence with Sungai Temburong, ecological plot 1, 13 Jan 2014, *Dančák 2014/161* (OL); ibidem, 30 Jan 2016, *Dančák 2016/367* (OL).

Notes. This species is distinguished by a rather short and thick inflorescence. The apex of the inflorescence is covered by imbricate bracts. As most of the specimens come from middle altitudes this species seems to be rare in true lowlands.

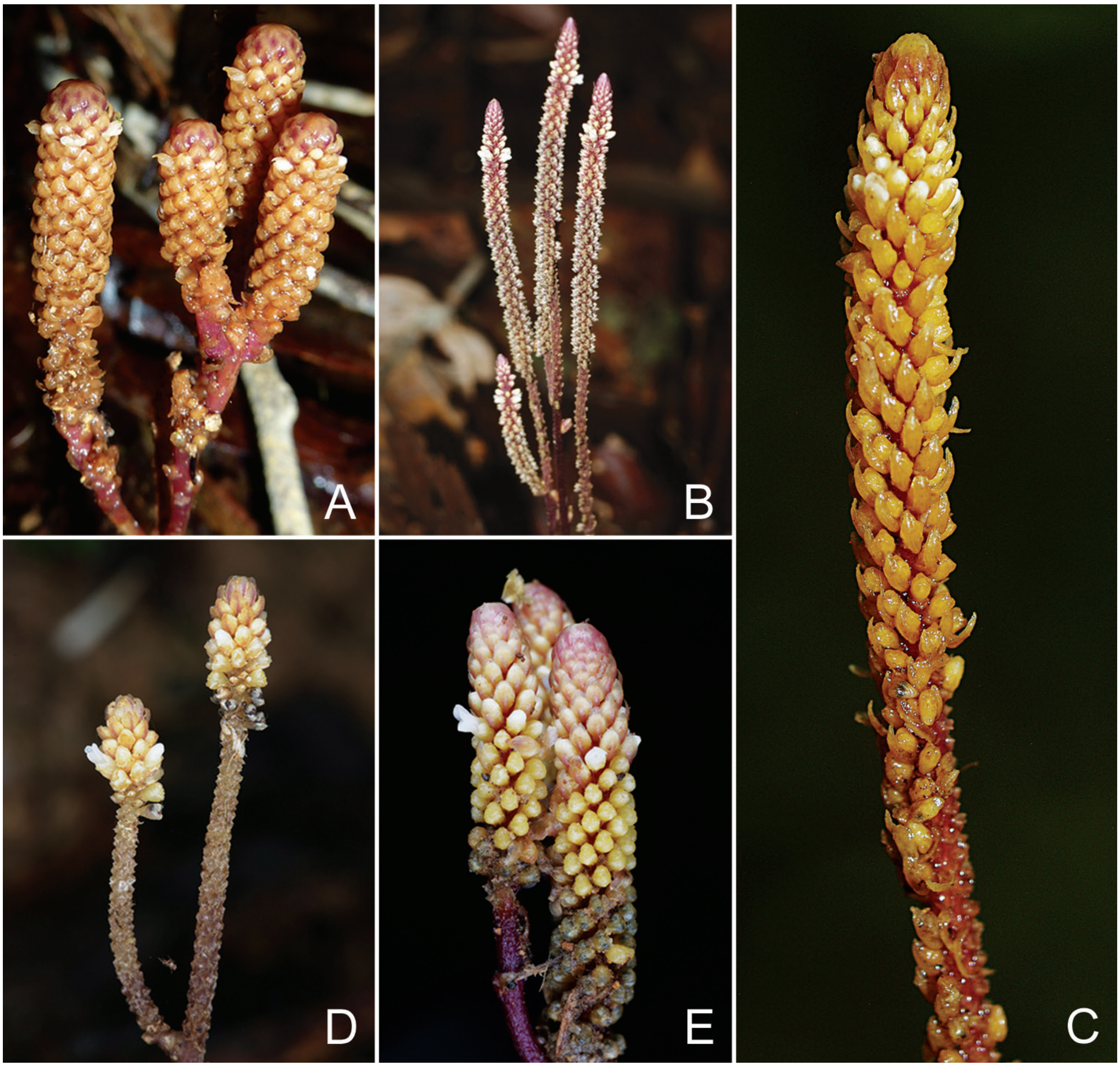

Fig. 2. *Epirixanthes* species of Brunei Darussalam. **A.** *Epirixanthes cylindrica* Blume. **B.** *E. elongata* Blume. **C.** *E. kinabaluensis* T.Wendt. **D.** *E. papuana* J.J.Sm. **E.** *E. pallida* T.Wendt. A–D, all from Kuala Belalong, Brunei Darussalam; E from Kelabit Highlands, Sarawak. (Photos: A: Ondřej Popelka, B, C: Michal Hroneš, D, E: Michal Sochor)

2. *Epirixanthes elongata* Blume, Cat. Gew. Buitenzorg 82 (1823). (Fig. 2B)

Global distribution. The species range extends from eastern India and southern China to the Moluccas (Van der Meijden, 1988; Chen et al., 2008).

Distribution in Brunei Darussalam. It is documented from various locations across the Temburong district. Outside Temburong, it has only been collected from a single locality around Labi in the Belait district. Its known elevational range in Brunei Darussalam is from c. 40 m a.s.l. up to 420 m a.s.l.

Specimens examined. BRUNEI DARUSSALAM: **Belait:** Labi, Sungai Rampayoh, ca. 3.5 km above road towards Waterfall No. 2, 9 Jan 1994, *Coode 7784* (BRUN). **Temburong:** Batu Apoi Forest Reserve, ridge W of Kuala Belalong Field Studies Centre, in Danish Plot, mixed dipterocarp forest, 1991, *Poulsen 224* (AAU, BRUN); Kuala Belalong, E ridge of Sungai Belalong, ca. 1.5 km SE from its confluence with Sungai Temburong, depression NW of ecological plot 2, 13 Feb 2015, *Hédl & Chudomelová RH132015* (OL); Kuala Belalong, E ridge of Sungai Belalong, ca. 0.9 km ESE from its confluence with Sungai Temburong, ecological plot 1, 13 Jan 2014, *Dančák 2014/6* (OL); ibidem, 13 Jan 2014, *Dančák 2014/125* (OL); ibidem, 13 Jan 2014, *Dančák 2014/160* (OL); ibidem, 13 Jan 2014, *Dančák 2014/180* (OL); ibidem, 4 Feb 2015, *Hroneš & Kobrlová 702015* (OL); Sungai Temburong at Kuala Belalong, 23 Jun 1989, *Dransfield 1007* (BRUN); Apan, ridge to the north of the river, 13 Jul 1993, *Sands 5786* (BRUN); Amo, southeast of LP 297 Bkt. Lutut, 6 Apr 2004, *Ariffin et al. BRUN 20797* (BRUN); Labu, Peradayan F. R., 5 Feb 2002, *Ariffin et al. BRUN 19913* (BRUN).

Notes. This is the most common species of *Epirixanthes*. It is locally abundant elsewhere in Borneo, and is presumably also common in Brunei Darussalam. In Kuala Belalong it is almost ubiquitous and by far the most abundant species of *Epirixanthes*. This species is easily recognised among Bruneian *Epirixanthes* as its bracts are shed well before the flowers open and the inflorescence is very long and narrow. One of the specimens studied (*Hroneš & Kobrlová 702015*) is a very pale-coloured plant conspicuously different from the typical brownish-purple plants of *E. elongata*. Such pale ivory individuals are known to occur within populations of *E. elongata* and they were described from West Kalimantan as *E. elongata* f. *alba* Tsukaya & H.Okada (Tsukaya & Okada, 2012).

3. ***Epirixanthes kinabaluensis*** T.Wendt, Fl. Males., Ser. 1, Spermat. 10(3): 491 (1988). (Fig. 2C)

Global distribution. The species is found in Sumatra and Borneo (Van der Meijden, 1988).

Distribution in Brunei Darussalam. It is known only from two locations in the immediate vicinity of the Kuala Belalong Field Studies Centre in the Temburong district. Its known elevational range in Brunei Darussalam is very narrow as it is recorded only from altitudes around 100 m a.s.l., even though its type locality, the slopes of Mt. Kinabalu in Sabah, lies at around 900–1200 m a.s.l. We have observed the species in the Kelabit Highlands of Sarawak up to c. 1300 m a.s.l.

Specimens examined. BRUNEI DARUSSALAM: **Temburong:** Kuala Belalong, Sungai Esu valley, at its confluence with Sungai Belalong, 9 Jan 2014, *Dančák 2014/162* (OL); ibidem, 18 Jan 2014, *Dančák 2014/343* (OL); Kuala Belalong, Sungai Esu, clayey bank near its confluence with Sungai Belalong, 21 Jan 2017, *Dančák 2017/46* (BRUN); Kuala Belalong, Earthwatch ecological plot ca. 0.3 km W from the Kuala Belalong Field Studies Centre, 28 Jan 2016, *Dančák 2016/292* (OL).

Notes. This species is the most robust of all Bruneian *Epirixanthes*, although *E. elongata* is usually taller. It has a rather thick inflorescence with long bracts which sometimes persist on the axis of the inflorescence after the fruits are shed.

4. *Epirixanthes papuana* J.J.Sm., Repert. Spec. Nov. Regni Veg. 10: 486 (June 1912). (Fig. 2D)

Global distribution. It is distributed throughout Malesia from Sumatra to the Solomon Islands (Van der Meijden, 1988).

Distribution in Brunei Darussalam. It is known only from a few locations immediately surrounding the Kuala Belalong Field Studies Centre in Temburong district and one locality in the Bukit Sawat area in Belait district. However, its actual distribution in the country could be much more extensive. Like most of the other species of *Epirixanthes*, this species is likely to be overlooked by collectors and therefore poorly represented in herbaria. Its known elevational range in Brunei Darussalam is rather narrow, reaching from c. 20 m a.s.l. up to 180 m a.s.l. However, the species might potentially also occur at higher elevations because the type collection from New Guinea comes from altitudes from 500 m a.s.l. up to 1800 m a.s.l.

Specimens examined. BRUNEI DARUSSALAM: **Belait:** Labi, Bukit Sawat, Sungai Malayan, 10 Jun 2003, *Ariffin et al. BRUN 20353* (BRUN). **Temburong:** Batu Apoi Forest Reserve, ridge W of Kuala Belalong Field Studies Centre, mixed dipterocarp forest, 18 Mar 1991, *Poulsen 3* (AAU, BRUN, K); Kuala Belalong, in Sungai Mata Ikan gorge near its confluence with Sungai Belalong, 26 Jan 2015, *Hroneš & Kobrlová 662015* (OL); ibidem, 21 Jan 2017, *Dančák 2017/55* (BRUN); Kuala Belalong, Sungai Mata Ikan valley ca. 0.5 km WNW from Kuala Belalong Field Studies Centre, 28 Jan 2016, *Dančák, M. 2016/291* (OL); Kuala Belalong, Sungai Baki valley near its confluence with Sungai Temburong, 18 Jan 2014, *Dančák 2014/342* (OL); Kuala Belalong, Sungai Esu, clayey bank near its confluence with Sungai Belalong, 21 Jan 2017, *Dančák 2017/47* (BRUN).

Notes. This species is distinguished by its paler colour (creamy brownish) and the rather short and narrow inflorescence with patent bracts that are turned-up at their apices.

Notes on other species of *Epirixanthes*

Epirixanthes pallida T.Wendt, Fl. Males., Ser. 1, Spermat. 10(3): 492 (1988). (Fig. 2E)

Global distribution. The species is found in Borneo and Sulawesi (Van der Meijden, 1988).

Notes. The species was included in the Brunei Checklist (Coode et al., 1996) based on a single collection (*Poulsen 3*) originally identified as *Epirixanthes pallida* but which has been reidentified as *E. papuana*. Therefore *Epirixanthes pallida* should be excluded from the flora of Brunei Darussalam. *Epirixanthes pallida* is readily distinguished from the Bruneian species by large and very early caducous whitish or pinkish bracts. It seems that *Epirixanthes pallida* is a highland species and thus probably does not grow in lowland rainforests. Its known altitudinal range is from c. 600 m a.s.l. at the type locality up to c. 1200 m a.s.l. in the Kelabit Highlands of Sarawak. As its type locality (slopes of Gunung Api in Sarawak, Malaysia) is just a few kilometres from Brunei's borders, it might potentially occur at higher altitudes in the Temburong district. It is, however, unlikely that *Epirixanthes pallida* occurs in the Tutong and Belait districts because of the generally lower terrain in these areas. Even though the type locality is on a limestone bedrock, we have observed the species in the Kelabit Highlands in Sarawak at several localities on sandstone bedrock.

Epirixanthes confusa Tsukaya et al., Phytotaxa 266(2): 147 (2016).

Global distribution. It is endemic to Borneo (Tsukaya et al., 2016).

Notes. This species is a recent addition to the genus and was described from Imbak Canyon in Sabah, Malaysia (Tsukaya et al., 2016). It undoubtedly belongs to the group of species with free sepals and wide fruits which also includes *Epirixanthes elongata*, *E. pallida* and *E. compressa* Pendry, but differs by its long-persistent bracts. So far it is known only from the type locality.

Epirixanthes compressa Pendry, Thai Forest Bull., Bot. 38: 184 (2010).

Global distribution. It is endemic to Thailand (Pendry, 2010).

Notes. This biogeographically remarkable species is narrowly distributed in south-eastern Thailand (Chanthaburi Province) and is, therefore, the only member of the genus which does not occur in Malesia. Like the previous species, it belongs to the group of *Epirixanthes* with free sepals and wide fruits.

Key to the species of *Epirixanthes*

The following key is adapted from Van der Meijden (1988), Pendry (2010) and Tsukaya et al. (2016).

1a. Sepals free; fruit wider than long 2
1b. Sepals connate for ¼–¾; fruit longer than wide or equal 5

2a. Bracts caducous before the flowers open 3
2b. Bracts persistent at least until the fruits mature 4

3a. Both leaves and bracts hairy with glandular hairs; inflorescence apex ± pointed, not fully covered by bracts; bracts narrowly triangular, c. 1.2 mm long and 0.5 mm wide, brown with central purple stripe .... *E. elongata*
3b. Both leaves and bracts glabrous; inflorescence apex ± rounded, completely covered in imbricate bracts; bracts ovate, 2–3 mm long and 1–1.5 mm wide, whitish or pinkish .... *E. pallida*

4a. Bracts glabrous, some of them persistent after the fruits have fallen; inflorescence elongate, 2–6 cm long; corolla caducous; endemic to Sabah .... *E. confusa*
4b. Bracts minutely ciliate, all of them shed with fruits; inflorescence shortly cylindrical, up to 2.5 cm long; corolla persistent; endemic to Thailand .... *E. compressa*

5a. Each flower subtended by a bract and pair of subulate bracteoles; bracts ± patent during anthesis, linear with sharply upturned obtuse apex; fruit longer than wide, much shorter than sepals .... *E. papuana*
5b. Each flower subtended only by a bract, bracteoles absent; bracts ± erect during anthesis, with straight acute or slightly curved apex; fruit as long as wide, as long as sepals or longer 6

6a. Bracts lanceolate, 2–2.5 mm long and 0.5–0.6 mm wide, brown with purple central stripe, usually persistent after the fruits have fallen; inflorescence apex not completely covered by bracts; fruit as long as sepals .... *E. kinabaluensis*
6b. Bracts ovate, 1.5–2 mm long and 0.8–1.2 mm wide, brown with basal purple patch, usually shed with fruits; inflorescence apex completely covered by imbricate bracts; fruit longer than sepals .... *E. cylindrica*

Conservation status of *Epirixanthes*

The forests of Borneo, including Brunei, Sabah and Sarawak, harbour the highest diversity of *Epirixanthes*. Six species have so far been reported from this island (Van der Meijden, 1988; Coode et al., 1996; Tsukaya et al., 2016). Similar to other mycoheterotrophic plants, all species of *Epirixanthes* are closely tied to primary or very lightly logged forests and as such are threatened by continuing deforestation. However, published data on their distribution and ecology are very scarce and most of the species are poorly represented in herbaria. For these reasons, we propose that all species of *Epirixanthes* in this study be evaluated as data deficient (DD, IUCN Standards and Petitions Subcommittee, 2016) which emphasises the need for further study and sampling.

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A new species of *Thismia* (Thismiaceae) from Brunei Darussalam, Borneo

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Abstract

A new species of *Thismia* (Thismiaceae) from Borneo is described. *Thismia hexagona* was discovered in 2013 in lowland mixed dipterocarp forest in Ulu Temburong, Brunei Darussalam. The species is circumscribed, illustrated and its position within the Malesian species of the genus is characterised by insertion into the existing determination key. Its most conspicuous feature is bright yellow, sharply hexagonal flower annulus.

Kew words: tropical rain forest, mycoheterotrophy, Malesia, Burmanniaceae

Introduction

The Family Thismiaceae (Dioscoreales) is a small group of achlorophyllous mycoheterotrophic herbaceous plants, formerly treated as a tribe Thismieae in the family Burmanniaceae (Merckx *et al.* 2006). It contains five genera: *Afrothismia* Schlechter (1907: 138), *Haplothismia* Airy Shaw (1952: 277), *Oxygyne* Schlechter (1907: 140), *Thismia* Griffith (1844: 221) and *Tiputinia* Berry & Woodward in Woodward *et al.* (2007: 158). Its distribution covers tropical and subtropical zones globally, with a few species extending to temperate regions (Maas-van de Kamer 1998, Woodward *et al.* 2007).

The genus *Thismia*, comprising about 50 species, is the most widespread and species-rich genus of the family Thismiaceae. It has a pantropical distribution, with two main centres of biodiversity: the Atlantic Rain Forest of South America and Southeast Asia (Jonker 1948, Mancinelli *et al.* 2012). Members of the genus are small herbs with reduced, scale-like leaves, actinomorphic or zygomorphic, urceolate to campanulate flowers. Perianth lobes are six, free or three inner lobes connivent at the apex forming erect mitre with three holes (Jonker 1948). After Jonker (1938), Southeast Asian species with mitre-like flowers are treated as section *Sarcosiphon* (Blume) Jonker (1938: 251) while species with free perianth lobes as section *Thismia*. The latter section is divided into two subsections: *Odoardoa* Schlechter (1921: 34) including species with all perianth lobes that are equal in length and size, and *Brunonithismia* Jonker (1938: 242) including species with inner perianth lobes that are larger than outer lobes.

Members of the genus *Thismia* are generally poorly-known, often collected only once or a few times. They are easily overlooked in the field because of their small growth form and the ephemeral nature of their aboveground parts (Larsen & Averyanov 2007). Many species are also likely extremely rare, with scattered distributions. As a result of these factors, it is highly possible that undescribed species can still be found in Southeast Asia (Larsen & Averyanov 2007, Chantanaorrapint 2012).

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During our field work at Kuala Belalong Field Studies Centre (KBFSC) in the Temburong District of Brunei Darussalam in February 2013, we found a species of *Thismia* clearly belonging to the sect. *Thismia*. The section is represented by five species on the island of Borneo, but no species has been reported from Brunei Darussalam until now (Jonker 1948, Coode *et al.* 1996, Jarvie 1996, Tsukaya & Okada 2005). In their general appearance and coloration, the plants resembled *Thismia bifida* M. Hotta (1967: 161) from Sarawak, but differed in several important morphological characters from other previously described species of the genus. We therefore report this as a first record of the family for Brunei Darussalam and describe it here as a new species for science.

Description

Thismia hexagona Dančák, Hroneš, Kobrlová & Sochor*, sp. nov*., Fig. 1

Thismia hexagona differs from congeneric species in having the following combination of morphological traits: all perianth lobes equal, tapering into long filiform tentacles, stigmas bifid, yellow hexagonal annulus and four anther appendages.

Type:—BRUNEI DARUSSALAM. Temburong Distr.: Kuala Belalong, eastern ridge of Sungai Belalong, near its confluence with Sungai Temburong. Coordinates WGS 84: N 04° 32.952'; E 115° 09.792', elevation ca. 320 m a.s.l., 13 February 2013. *M. Dančák*, *M. Hroneš*, *M. Sochor* & *L. Kobrlová* 2013/17 (holotype BRUN [herbarium specimen, accession number 23947], isotype OL [herbarium specimen, accession number 23093]).

Terrestrial, achlorophyllous, mycoheterotrophic herb. Roots thick, hardly branched, vermiform, creeping, whitish. Stem erect, simple or poorly branched in upper part, brown, glabrous, 1.7–7.0 cm tall; stem branches usually unequal in length. Leaves few, appressed, scale-like, narrowly triangular, ca. 4 mm long, ca. 2 mm wide at the base, acute at the apex. Floral bracts one or two, similar in shape to the leaves, ca. 7 mm long, ca. 2.0 – 2.5 mm wide at the base. Flowers solitary at the top of each branch. Perianth actinomorphic with 6 tepals fused into urceolate perianth tube with free, equal apical lobes; perianth tube ca. 1.0–1.5 cm long, pale brownish with lower part usually white, with 12 faint brownish longitudinal streaks and brown-purple apical stripe, widest at the upper quarter, at the apex with broad bright yellow, clearly hexagonal annulus (Fig. 1B); inner surface of the perianth tube with 12 faint longitudinal ribs and densely covered with short horizontal bars; perianth lobes brown-yellowish, equally triangular, abruptly ended with long filiform appendages 7–18 mm long, brown-yellowish at the base, white at the top. Stamens 6, borne on thickened margin of the perianth tube; filaments curved downwards, connective broad, connate to form a tube, with two distinct teeth-like appendages at the free apical margins and two thick cylindrical finger-shaped appendages positioned slightly above the marginal ones (Fig. 1C, D, 2D). Stigma 3-lobed, lobes shortly bifid (Fig. 1E); ovary cup-shaped usually with brown- purple stripe at the top. Fruit cup-shaped brown capsule. Seeds ellipsoid.

Habitat and ecology:—*Thismia hexagona* grows amongst leaf litter and on rotten logs in the lowland mixed dipterocarp forest. It prefers humid places in gullies formed by small episodic streams (Fig. 3). A total of 21 flowering individuals were found within the 1-ha permanent forest plot (Plot 1) belonging to Kuala Belalong Field Studies Centre of Universiti Brunei Darussalam (Hédl *et al.* 2009).

Distribution:—Species is known only from the type locality: eastern ridge of Sungai Belalong, near its confluence with Sungai Temburong. It is also the first record of the genus and family from Brunei Darussalam (cf. Coode et al. 1996, J. A. Ahmad, pers. comm.).

Conservation status:—The studied population occurs within the designated research zone of Ulu Temburong National Park, to which public access is restricted. The habitat, type locality and its surroundings are thus protected from logging and similar destructive anthropogenic activities. However, it is impossible to assess the current conservation status of this species because there is no information on its population size and dynamics. Therefore, we suggest to evaluate the species as data deficient (DD) according to the IUCN Red List Categories and Criteria (IUCN 2012).

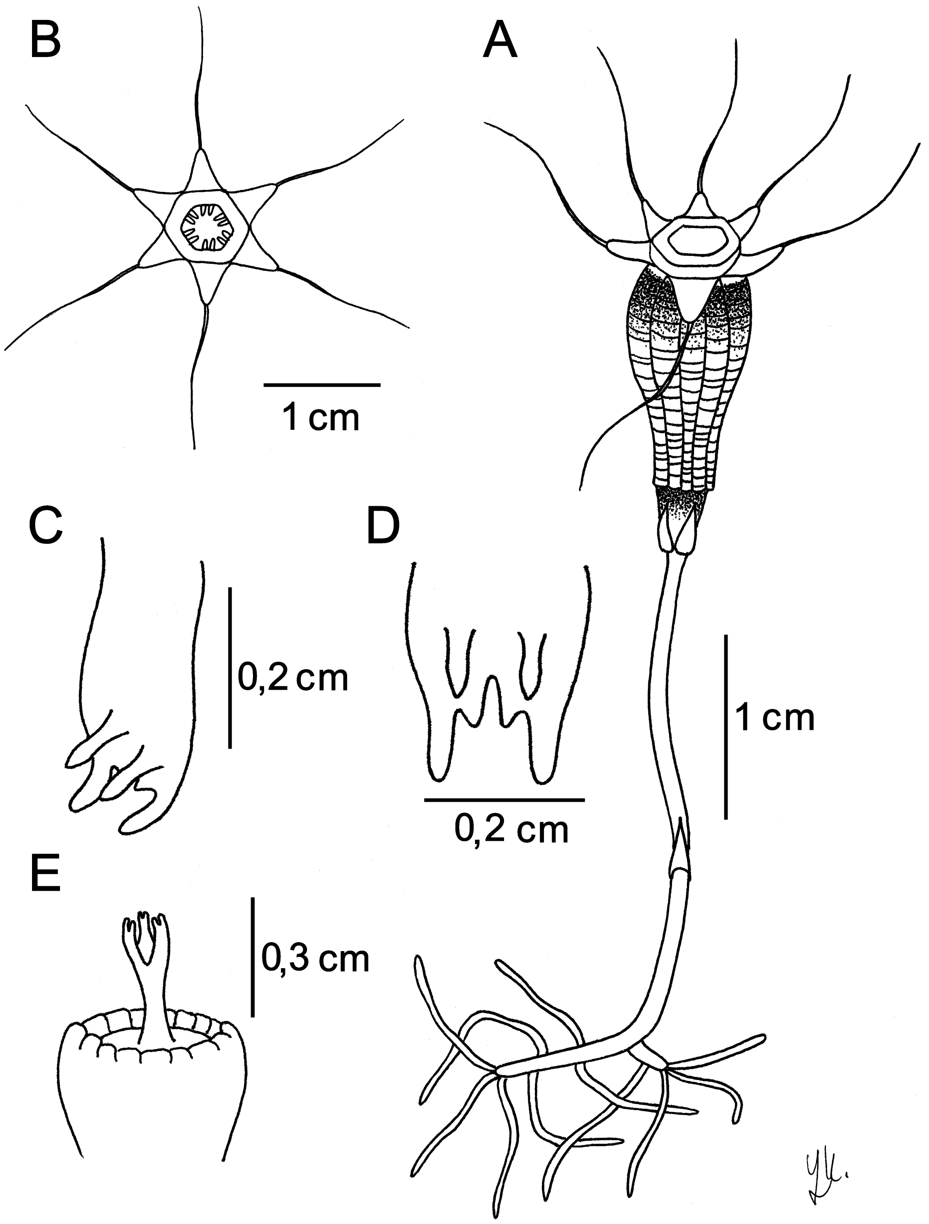

FIGURE 1. *Thismia hexagona*. A. Habit of the plant. B. View of perianth tube mouth with annulus and perianth lobes. C. Connective with anther appendages, side view. D. Apical margin of connective with anther appendages, front view. E. Stigma.

Etymology:—Named after the conspicuous shape of flower annulus.

Variability:—The population as a whole was uniform, with no considerable morphological variation. Most of the individuals were one-flowered, only few two-flowered and one individual with three flowers. Some variability was observed in the colour of the perianth tube. A typical individual had an almost white lower part of the perianth tube, with the upper part brownish and a more or less conspicuous brown-purple stripe at the top just beneath the annulus (Fig. 2A). We found two flowering shoots, probably originating from the same root system with a yellow stripe instead of the brown-purple one (Fig. 2B), which we suggest is a result of mutation. Few individuals had perianth tubes that were brownish throughout with almost no white basal portion. Most of the plants also had a brown-purple stripe at the top of ovary, which made an impression of two-purple-striped perianth tube.

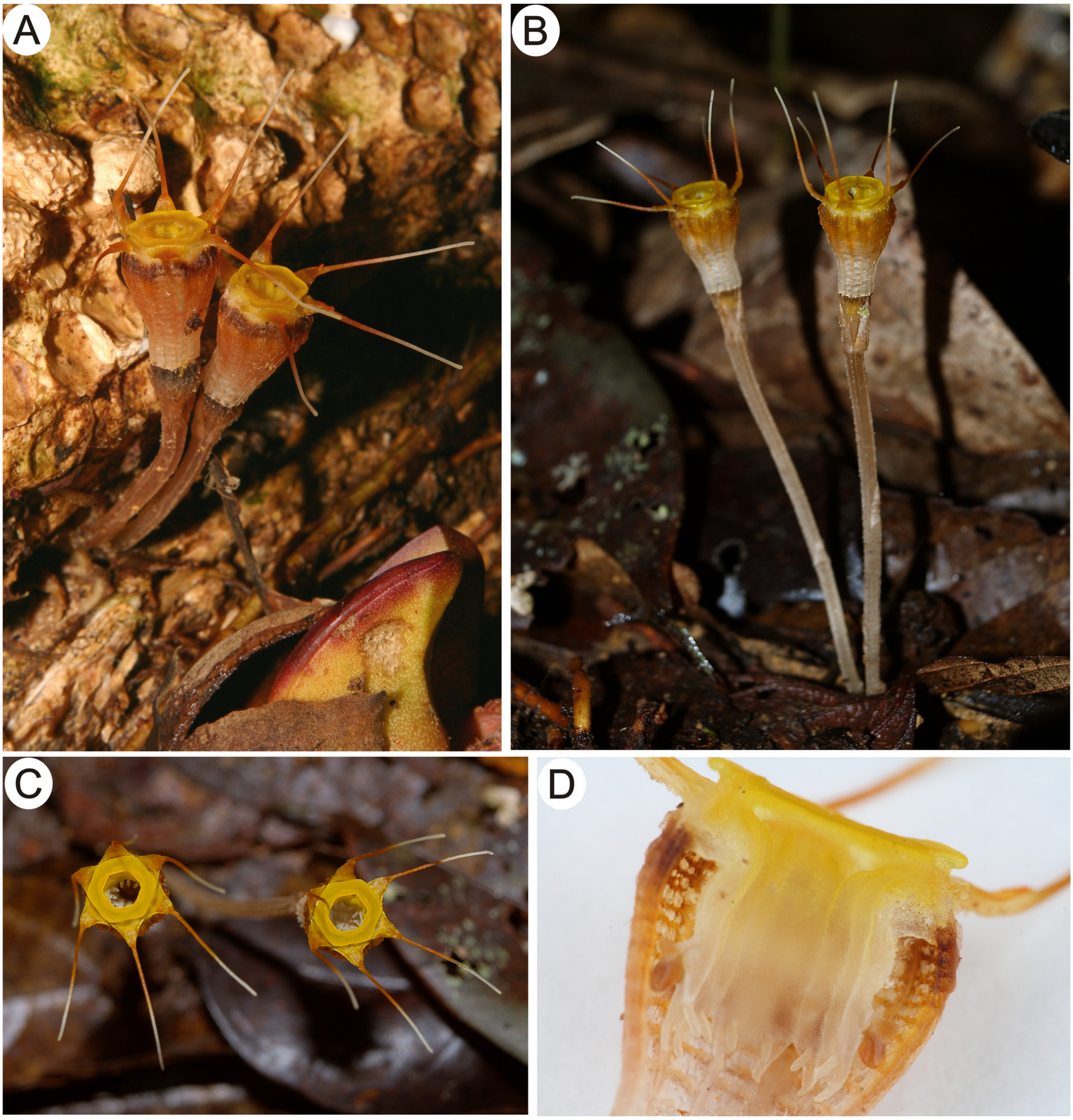

FIGURE 2. *Thismia hexagona*. A. Plant with typical coloration of perianth tube. B. Plant lacking brown-purple stripe at the top of perianth tube. C. Perianth tube mouth with annulus and perianth lobes. D. Longitudinal section of anther tube with anther appendages.

Discussion

It is believed by several researchers that some members of the genus *Thismia* could be very rare (Stone 1980, Larsen & Averyanov 2007, Chantanaorrapint 2012). However, some of these presumed rare species may actually be neglected. The recent discoveries of *Thismia alba* Holttum ex Jonker (1948: 23) and *T. clavigera* (Beccari) F. Mueller (1891: 235) from Thailand (Chantanaorrapint & Sridith 2007, Chantanaorrapint & Chantanaorrapint 2009) indicate that these inconspicuous ephemeral plants tend to be overlooked or under-collected. Most *Thismia* species do seem to be extremely rare, usually collected only once. If this is a true observation and not an artefact of collection effort, this rarity could be caused especially by a combination of two mechanisms: (1) the tight bond of the plant with its host fungus and, (2) a specific mode of seed dispersion. Merckx & Bidartondo (2008) discovered host-specific associations between members of a closely related African genus *Afrothismia* and arbuscular fungi from the genus *Glomus* Tulasne & C. Tulasne (1845: 63). A similar pattern could also be expected in *Thismia* where the scarcity and limited distribution range of its fungal host may lead to the rarity of plants in this genus. With respect to seed dispersal, Stone (1980) suggested that seeds of *Thismia* are dispersed out of their capsules by rain-splash, thus implying that the seeds are dispersed over very short distances. These hypotheses need further studies and additional observations to be eventually accepted as plausible explanations for *Thismia* rarity.

From the morphological point of view, *Thismia hexagona* is clearly distinct from other *Thismia* species of the Malesian region through a combination of following traits: 1. perianth lobes all equally sized, 2. conspicuous hexagonal raised annulus, 3. bifid stigmas and 4. four anther appendages. Species that are morphologically closest to *Thismia hexagona* are members of sect. *Thismia* subsect. *Odoardoa* with perianth lobes triangular at the base and tapering into filiform appendages: *Thismia bifida*, *T. lauriana* Jarvie (1996: 259) and *T. mullerensis* Tsukaya & Okada (1995: 129) from Borneo, *Thismia aseroe* Beccari (1877: 252) from Peninsular Malaysia and *Thismia alba* from Peninsular Malaysia and Thailand. Members of this morphologically invariable group have a round annulus, thus the hexagonal annulus of *T. hexagona* is unique within the group. Also, the number of anther appendages (four) differs from the other members of subsect. *Odoardoa* varying from 1 (*T. alba*) to 3 (*T. aseroe* and *T. bifida*). As the shape and general appearance of anthers provide useful characters for taxonomy of *Thismia* (Thiele & Jordan 2002), we consider the four anther appendages in *T. hexagona* as an important diagnostic feature. Some species of the subsection could be superficially similar to *T. hexagona* due to the pattern of their coloration (*Thismia alba*, *T. aseroe* and *T. bifida*). However, they differ by some further morphological traits: *Thismia alba* and *T. aseroe* do not have bifid stigmas and have small perianth appendages alternating the perianth lobes while *T. bifida* lacks transverse bars throughout the perianth tube.

Similarly bright yellow, distinctly raised hexagonal annulus is also observed in *Thismia javanica* Smith (1910: 32) from the Malesian region, Thailand and Vietnam and *Thismia tentaculata* Larsen & Averyanov (2007: 16) from Vietnam and China. However, these two species clearly differ from *T. hexagona*, being members of subsect. *Brunonithismia*, as the inner perianth lobes are larger than the outer lobes.

Identification key

The species position within Malesian species is shown by insertion into the modified key of Malesian species published by Tsukaya & Okada (2012):

- Perianth lobes triangular at the base, tapering into long, filiform tentacles 7
7. Stigmas bifid 8
- Stigmas not bifid .... 11 (no. 10 in Tsukaya & Okada 2012)
8. Transverse bars found only in the basal part of the perianth tube. Anther appendages 3 .... *Thismia bifida*
- Transverse bars found throughout the perianth tube inside. Anther appendages 2 or 4 9
9. Annulus bright yellow, sharply hexagonal; perianth tube brownish with lower part usually white, with 12 faint brownish longitudinal streaks and dark brown-purple apical horizontal stripe; anthers with 4 finger-shaped appendages: 2 upper and 2 lower at the free apical margin of the connective .... ***Thismia hexagona***
- Annulus pale purple, round or weakly hexagonal; perianth tube white with 12 white or brownish purple longitudinal streaks; anthers with 2 appendages 10
10. Perianth white with brownish purple streaks; lobes with tentacles ca. 17 mm .... *Thismia mullerensis*
- Perianth white with white streaks; lobes with tentacles ca. 70 mm .... *Thismia lauriana*

FIGURE 3. Habitat, Kuala Belalong, Brunei Darussalam.

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Thismia brunneomitra, another new species of *Thismia* (Thismiaceae) from Ulu Temburong, Brunei Darussalam

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Abstract

A new species of *Thismia* (Thismiaceae) from northwest Borneo is described and illustrated. *Thismia brunneomitra* was discovered in 2015 in lowland mixed dipterocarp forest in the Ulu Temburong National Park, Temburong district of Brunei Darussalam. The new species is characterized by brown to blackish flowers with twelve darker vertical stripes on the perianth tube, inner tepal lobes that are connate to form a mitre with three very short processes at the apex, three-toothed apical margin of the connective and large wing-like appendage of the connective. An updated determination key of *Thismia* species found in Borneo is included.

Key words: mycoheterotrophy, Malesia, mixed dipterocarp forest, *Sarcosiphon*

Introduction

Primary tropical rainforests of Borneo are one of the most species-rich ecosystems in one of the world's biodiversity hotspots (Myers *et al.* 2000). The island harbours some 15,000 vascular plant species in an area of 743,330 km^2, of which ca. 37% are endemic (Raes *et al.* 2009). The lowland mixed dipterocarp forest represents the dominant natural forest habitat in Borneo (Primack & Corlett 2005). Unfortunately, these forests are threatened by large-scale timber extraction, as they contain several economically important tree species (Bryan *et al.* 2013). Thus, a combination of unique biodiversity and rapid deforestation has highlighted Borneo as a priority for nature conservation.

One of the most intriguing inhabitants of the primary tropical forests of Borneo are small mycoheterotrophic herbs from the genus *Thismia* Griffith (1844: 221; Thismiaceae, or alternatively Burmanniaceae; for discussion see Merckx *et al.* 2006). Species of this genus are achlorophyllous plants with very specific and complex morphology.

Currently, almost 60 species are recognized in the genus (Hroneš 2014, Hunt *et al.* 2014, Mar & Saunders 2015, Chantanaorrapint & Sridith 2015). Species of *Thismia* have scattered distribution through the (sub-)tropical areas of the Asia, Australia, New Zealand and South America (Jonker 1938, Maas *et al.* 1986, Hunt *et al.* 2014). Along with Thailand, Borneo represents one of the species diversity centres of the genus (Dančák *et al.* 2013, Chantanaorrapint *et al.* 2015).

According to Jonker (1938), Bornean species with free perianth lobes and creeping rhizomes are treated as section *Thismia*, while species with connate perianth lobes forming mitre-like flowers and dense coralliform rhizomes are treated as section *Sarcosiphon* (Blume 1850: 65) Jonker (1938: 251). In Borneo, two species from this section are known: *T. episcopalis* (Beccari 1877: 250) F. Mueller (1891: 235) and *T. goodii* Kiew (1999: 179).

During our recent expedition to Ulu Temburong in January and February 2015, we found a species of *Thismia* with fused tepals, which turned out to be another taxonomic novelty. This finding is only the second record of the family Thismiaceae for Brunei Darussalam (see Dančák *et al.* 2013).

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Material & Methods

This study is based on material collected during February 2015 in the vicinity of the Kuala Belalong Field Studies Centre (KBFSC), Brunei Darussalam. Morphological characters were studied using stereo microscope and high-resolution macro photography. Collected specimens were thoroughly compared with original drawings and descriptions given in protologues of *Thismia* sect. *Sarcosiphon* and also with high-resolution image of *Thismia episcopalis* type specimen (Beccari 1504 deposited in FI).

Description

Thismia brunneomitra Hroneš, Kobrlová & Dančák, *sp. nov.*, Fig. 1

Similar to *Thismia episcopalis*, but differing in having 1–2 flowers per individual, 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, large entire wing-like lateral appendage of the connective and brown to blackish colour of the perianth tube (Table 1).

Type:—BRUNEI DARUSSALAM. Temburong distr.: Kuala Belalong, right bank of the stream Sungai Mata Ikan, ca. 150 m NW from the Kuala Belalong Field Studies Centre. Coordinates WGS 84: N 04°32′51.2″; E 115°09′24.5″; elevation ca. 105 m a.s.l., 3 February 2015. *Hroneš & Kobrlová 402015* (holotype BRUN! [herbarium specimen, accession number B031129], isotype OL! [herbarium specimen, accession number 31594]).

Description:—Perennial achlorophyllous mycoheterotrophic herb, 6.2–8 cm tall. Roots coralliform, slightly branched towards the apex, whitish. Stem 4.5–6.5 cm tall, ascending to erect, simple, one or two flowered, sparsely shortly hairy, mostly pale brown (Figs 1A, 2A, B), blackish when young (Fig. 2C); pedicel dark brown to blackish and elongating after anthesis (Fig. 2D). Leaves 6–7, spirally arranged, well-spaced, scale-like, triangular, acute, entire, 3.5–5 mm long, 2–3 mm wide at base, pale brown, glabrous. Floral bracts three, similar in shape to leaves but slightly larger, 5.5–7 mm long, 3–3.5 mm wide at base, keeled, enveloping base of flower, pale brown. Flowers bisexual, actinomorphic, 1.6–1.7 cm long, 0.9–1 cm wide at top of perianth tube; perianth tube urceolate, of 6 fused tepals; outer surface with six longitudinal ribs, dark brown to blackish when young, later pale brown to brown with 12 vertical dark brown stripes; outer tepal lobes absent; inner tepal lobes well-developed, connate at top and forming mitre with three holes, 5–7 mm tall; holes reniform-elliptic to almost rounded, 4–6 mm wide, 2–4 mm high; mitre dark brown to blackish when young, at maturity dark brown with paler brown to reddish-brown apex and margins of holes, topped by three short obtuse processes (Figs 1B, 2E). Annulus absent. Stamens 6, hanging from top of perianth tube, bluish to purplish (Figs 2G–I); connectives flattened, ribbon shaped, connate to form tube; individual connective with two tufts of glandular hairs on adaxial side and three lobes on free apical margin; lateral lobes wide, obtusely triangular; middle lobe narrowly triangular (Figs 1D, 2I); each lobe terminated by tuft of glandular hairs; lateral appendage of connective flattened, large, wing-like, protruding outwards to the perianth tube, with marginal glandular hairs; thecae whitish (Figs 1C, 2G). Style trifid, papillose, terminated by very shallowly notched stigmas (Fig. 2F); ovary obconical, with six vertical ribs on surface and blackish horizontal line at apex. Capsule cup-shaped, brown to dark brown, sparsely hairy, topped by basal ring of perianth tube and withered style (Fig. 2D). Seeds not seen.

Variability:—The basic colour of the perianth tube and the mitre varies from almost black to brown-reddish. The number of flowers in one individual varies from one to rarely two.

Habitat and ecology:—Shaded understory of lowland mixed dipterocarp forest. The only known site is in a ravine of a small stream. The terrain is steep, rocky and somewhat disturbed, with patches of bare mineral soil. Plants were found primarily in these bare patches with several individuals growing on a rock crevice just next to the stream in association with *Diplazium cordifolium* Blume (1828: 190), *Epipremnum falcifolium* Engler (1898: 11), *Mapania monostachya* Uittien (1935: 194), *Schismatoglottis asperata* Engler (1879: 297) and *Selaginella involvens* agg. Several other mycoheterotrophic species were recorded around, within a distance of 5 m: *Epirixanthes elongata* Blume (1823: 82), *E. papuana* J.J.Smith (1912: 486), *Sciaphila densiflora* Schlechter (1912: 87), *S. secundiflora* Thwaites ex Bentham (1855: 10) and *Gymnosiphon aphyllus* agg.

Distribution:—*Thismia brunneomitra* was found near the Kuala Belalong Field Studies Centre in the Temburong district of Brunei Darussalam. The only known population occurs on the right bank of the small stream Sungai Mata Ikan, approximately 100 m from its confluence with the Belalong River and near the "Ashton trail" forest circuit.

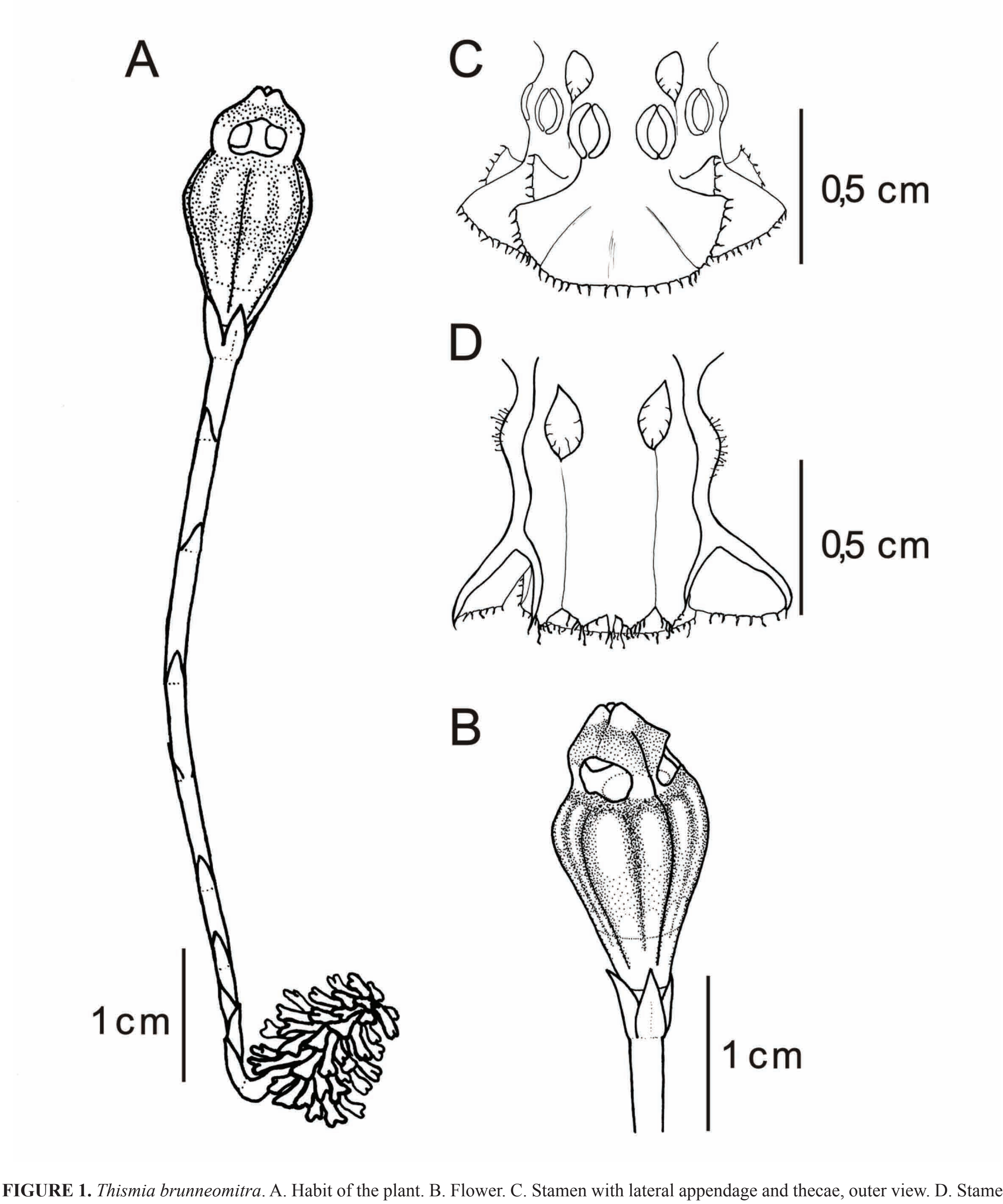

FIGURE 1. *Thismia brunneomitra*. A. Habit of the plant. B. Flower. C. Stamen with lateral appendage and thecae, outer view. D. Stamen with apical lobes, inner view. Drawn by K. Janošíková.

Conservation status:—Population of *T. brunneomitra* occurs within the designated research zone of Ulu Temburong National Park, to which public access is restricted. The type locality and its surroundings are thus protected from logging or other destructive anthropogenic activities. However, given that after a thorough search, no more than 15 individuals were noticed, and that the population is situated near relatively frequented forest trail, we suggest evaluating the species as critically endangered (CR) according to the IUCN Red List Categories and Criteria (IUCN 2012).

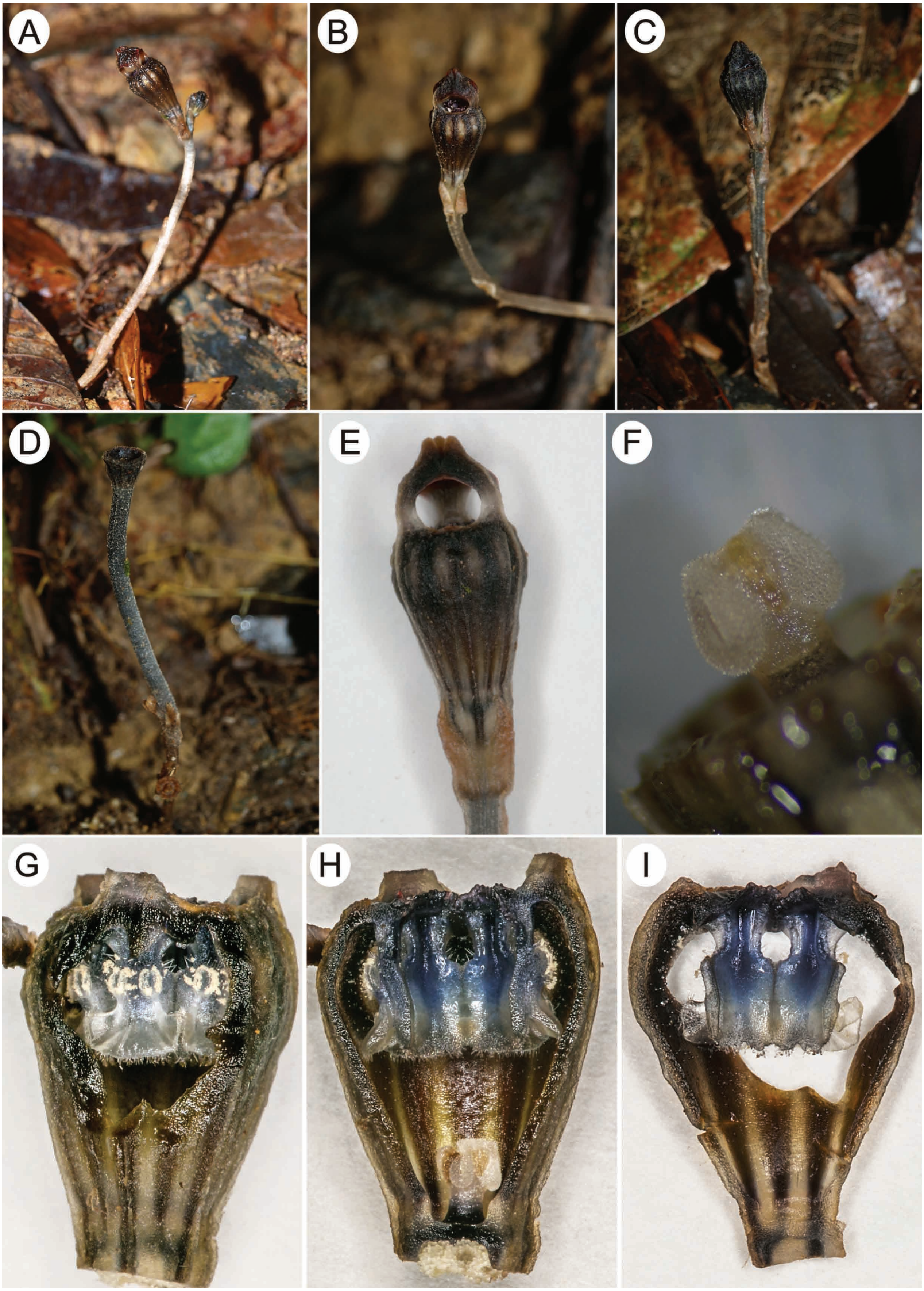

FIGURE 2. *Thismia brunneomitra*. A–B. Habit of the plant. C. Habit of the immature plant. D. Elongated stem with a capsule after the anthesis. E. Flower. F. Style. G. Perianth with removed mitre and proximal part showing stamens with anthers and lateral appendage. H. Longitudinal section of perianth tube with anthers and style. I. Section of the perianth and anther tube showing apical anther appendages.

Etymology:—Name of the species is composed from Latin words *brunneus* (brown) and Greek *mitra*, referring to the typical colour and shape of the flowers.

Taxonomic affinities

Thismia brunneomitra belongs to the section *Sarcosiphon*. Members of this section share several characteristics, such as coralliform rhizomes, three floral bracts enveloping the base of the flower and inner tepal lobes fused at the top and forming a mitre. Up to now, this section included five species, *Thismia clandestina* (Blume 1850: 65) Miquel (1855: 616) from western Java, *T. crocea* (Beccari 1877: 249) J. J. Smith (1909: 193) from West Papua, *T. episcopalis* and *T. goodii* Kiew (1999: 179) from Sarawak and *T. yorkensis* Cribb (1995: 51) from northern Australia. Moreover, two other species, *T. clavigera* (Beccari 1877: 251) F. Mueller (1891: 235) and *T. betung-kerihunensis* Tsukaya & Okada (2012: 56), both known from western Borneo, are sometimes included to this section (Tsukaya & Okada 2012). *Thismia brunneomitra* is readily distinguished from the two last species by the absence of the long clavate segments on the apex of the mitre. Flowers of *T. yorkensis* are white with well developed outer perianth lobes and inner perianth lobes wide, forming hemispherical mitre (Cribb 1995). *Thismia crocea* flowers have much longer perianth tube with a distinct constriction in the middle, stamen tube inserted near the constriction inside and the mitre with small triangular holes formed by wide inner perianth lobes (Beccari 1877). The remaining species from Java and Borneo are therefore morphologically most similar. *Thismia goodii* differs by the blue colour of the flowers and glabrous stamens, and *T. clandestina* differs by its conspicuous annulus, shorter mitre and two (or sometimes three) asymmetrical lobes on the free apical margin of the connective (Smith 1911, Jonker 1938, Kiew 1999). This leaves *T. episcopalis* the most similar to *T. brunneomitra* (see Table 1).

TABLE 1. Main morphological differences among members of *Thismia* sect. *Sarcosiphon* (*T. betung-kerihunensis* and *T. clavigera* excluded) from Borneo and Java.

	T. brunneomitra	*T. clandestina*	*T. episcopalis*	*T. goodii*
number of flowers	1(–2)	1–3	1–7	1(–2)
perianth coloration	brown to blackish with 12 longitudinal dark brown stripes	pale brown to dark greenish gray with 12 longitudinal dark brown stripes	orange-yellow	white with faint dark green tinge and narrow dark blackish green longitudinal stripes
outer perianth lobes	absent	absent	absent	distinct
height of mitre (mm)	5–7	ca 2(–4)	ca 5	(5–)7(–9)
mitre apex	not fully connate with three short erect obtuse projections	obtusely acuminate without any projections	obtuse without any projections	acuminate without any projections
teeth on free apical part of connective	3; middle lobe narrowly triangular, lateral lobes larger, obtusely triangular	2–3; asymmetrical, with additional several bristle-like laciniae	3; all teeth obtusely triangular, all similar in shape and size	3; middle lobe wide, triangular, lateral lobes smaller
hairs on apical part of connective	present	present	present	absent
lateral appendage of the connective	large, entire, exceeding whole apical part of the connective	dentate, not exceeding apical part of the connective	entire, slightly undulated, not exceeding apical part of the connective	? (not stated in the protologue)

The colour of the perianth tube of *T. episcopalis* is described as "*luteo-crocei*" by O. Beccari, i.e. yellow-orange, whereas in our species perianth tube is brown to blackish. Number of flowers is generally higher in *T. episcopalis*, in which varies from 1 to 7, than in *T. brunneomitra*, in which only one or rarely two flowers per individual plant were recorded. The mitre of *T. episcopalis* has round holes and entire, blunt apex in comparison with *T. brunneomitra*, in which mitre holes are rather reniform-elliptic and there are three short erect obtuse projections on the apex, which represent tips of the perianth lobes. Differences between these two species also exist in the size and shape of the stamens. Free apical margin of connective in both species bear three teeth. However, the teeth architecture differs—all three teeth are ± similar in shape and size in *T. epicopalis*, but in *T. brunneomitra* the two lateral teeth are noticeably larger and obtusely triangular while the central tooth is narrowly triangular. Lateral appendage of the connective is much larger, exceeding whole apical part of the connective when viewed from the outside of the flower in *T. brunneomitra*, while the appendage of *T. episcopalis* is noticeably shorter than the apex of the connective (Table 1).

Revised key of genus *Thismia* in Borneo modified after Tsukaya & Okada 2012

1. Perianth lobes free; roots creeping, vermiform 2
- Perianth lobes connate above the mouth of the perianth tube; roots clustered, coralliform 7
2. All perianth lobes simple, of the same length and size 3
- Inner perianth lobes simple, outer perianth lobes consisting of three parts ..... *Thismia neptunis*
3. Perianth tube with distinct transverse bars at least at the base; stigmas bifid 4
- Perianth tube without transverse bars; stigmas not bifid ..... *Thismia ophiuris*
4. Transverse bars found only in the basal part of the perianth tube; anther appendages 3 ..... *Thismia bifida*
- Transverse bars found throughout the perianth tube; anther appendages 2 or 4 5
5. Annulus bright yellow, sharply hexagonal; anthers with 4 finger-shaped appendages: 2 upper and 2 lower at the free apical margin of the connective ..... *Thismia hexagona*
- Annulus pale purple, round or weakly hexagonal; anthers with 2 appendages 6
6. Perianth tube white with brownish-purple streaks; lobes with appendages ca. 17 mm ..... *Thismia mullerensis*
- Perianth tube white; perianth lobes with appendages ca. 70 mm ..... *Thismia lauriana*
7. Inner perianth lobes form three free, long, almost erect, clavate appendages above the mitre; free apical margin of the connective entire or slightly emarginate 8
- Inner perianth lobes lack any elongated appendages; free apical margin of the connective clearly trilobed 9
8. Flowers yellow-orange to pink-red; free apical margin of the connective triangular, acute ..... *Thismia clavigera*
- Flowers blue-green; free apical margin of the connective rounded to slightly emarginate ..... *Thismia betung-kerihunensis*
9. Flowers blue; outer perianth lobes distinct; free apical margin of the connective glabrous, without any hairs or ciliae ..... *Thismia goodii*
- Flowers yellow, orange, brown or blackish; outer perianth lobes not distinct; free apical margin of the connective hairy 10
10. Perianth tube yellow-orange; apex of the mitre obtuse without any projections; free apical margin of the connective with lobes of the ± same length and size ..... *Thismia episcopalis*
- Perianth tube brown to blackish; apex of the mitre acuminate with three very short projections; free apical margin of the connective with lateral lobes larger, obtusely triangular and the middle lobe narrowly triangular ..... *Thismia brunneomitra*

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Thismia inconspicua (Thismiaceae), a new mycoheterotrophic species from Borneo

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Abstract

A new species belonging to the mycoheterotrophic genus *Thismia* is described and illustrated. *Thismia inconspicua* was found in a lowland mixed dipterocarp forest in Ulu Temburong National Park, Brunei Darussalam. It is characterized by its sepia-brown perianth with free equal lobes with very short terminal appendages, two pairs of appendages on connective apices, perianth tube displaced from the ovary axis and short stem. DNA sequence data from commonly studied nuclear and mitochondrial loci are provided. Phylogenetic analysis confirmed the close relationship with other members of section *Thismia*, subsection *Odoardoa*. An updated determination key of *Thismia* species of Borneo is included.

Key words: *atpA,* Burmanniaceae, Malesia, SSU rDNA

Introduction

Tropical rain forests of Southeast Asia in general and Borneo in particular belong to the most threatened and richest biodiversity hotspots in the world (de Bruyn *et al.* 2014, Myers *et al.* 2000). Their anthropogenic destruction is currently at an unprecedented rate (Wilcove *et al.* 2013), whereas research activities are still being blocked by multiple obstacles in many countries (Brunei Darussalam being a rare exception within the region). Therefore, our knowledge of the diversity of organisms in these valuable tropical ecosystems is far from complete.

Mycoheterotrophic plants are one of the least explored ecological groups due to their inconspicuous appearance and the ephemerality of their above-ground organs, which makes them predominantly visible only in the rainy seasons of the year (Merckx *et al.* 2006), i.e. in the periods usually avoided by field botanists. Moreover, some of them are believed to be extremely rare as a result of specificity of biotic interactions (Merckx & Wapstra 2013). Although most mycoheterotrophic plant taxa can associate with a wide range of arbuscular mycorrhizal fungi, some, such as *Arachnitis*, *Petrosavia* and most Thismiaceae species only associate with a single or few fungal species (Merckx et al. 2012). Not surprisingly, mycoheterotrophic herbs are thus found mainly in humid primary forests with undisturbed biotic networks (Merckx *et al.* 2006) and their diversity often reflect floristic richness of these habitats (Tsukaya *et al.* 2014). On the other hand, the specific association with a fungal symbiont does not imply an association with any particular autotrophic host taxa (Merckx & Wapstra 2013).

The genus *Thismia* Griffith (1844: 221; family Thismiaceae, order Dioscoreales; Merckx *et al.* 2009, Merckx & Smets 2014) is a good example of such a taxon containing species with scattered distributions and rare occurrence. To date, around 60 species have been described worldwide (Nuraliev *et al.* 2015), of which only a few have been found more than once; most species are therefore known only from the type locality and some are even considered extinct (Merckx *et al.* 2006, Merckx & Smets 2014). Recent interest in the genus has led to the discovery and description of many new species during the past few years, especially from Southeast Asia which includes the main centres of *Thismia* diversity (Averyanov & Larsen 2007). Furthermore, many findings still await to be published. In this paper, we report a third finding of the family Thismiaceae in Brunei Darussalam (Dančák *et al.* 2013, Hroneš *et al.* 2015). This discovery turned out to be another taxonomic novelty and we describe it as a new species.

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Material and Methods

The study is based on a single population found in Brunei Darussalam in January 2016 that comprised 10 individuals (one in full flower, two in bud stage and seven in different stages of fruit, including two plants with detached yet preserved perianths). Morphological characters were studied using stereomicroscope (40× magnification) and macrophotography. The observed characters were compared with original drawings and descriptions in protologues of species of *Thismia* sect. *Thismia*.

DNA was extracted from silica gel-dried fruit pedicel using the CTAB method (Doyle and Doyle 1987) and molecular sequence data were generated from two loci. The small subunit of ribosomal DNA (SSU rDNA) and internal transcribed spacers (ITS) were amplified and sequenced with primers NS1, NS4, NS5 and ITS4 (White *et al.* 1990), with an additional internal primer ITS2 used for sequencing only. The mitochondrial gene *atpA* was amplified and sequenced with primers developed by Eyre-Walker & Gaut (1997). PCR was performed with Kapa polymerase (Kapa Biosystems) following a standard protocol with 37 cycles and annealing temperature of 56°C. The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25 M NaCl in the precipitation mixture) and sequenced from both directions by Sanger method at Macrogene Europe. Sequences were edited and aligned in GENEIOUS (ver. 7.1.7., Biomatters). The data obtained for *T. inconspicua* and *T. hexagona* Dančák *et al.* (2013: 34) from the type localities and all available sequences of other relevant taxa from NCBI Genbank were analysed using maximum parsimony methods and tested by 1000 bootstrap replicates in MEGA (ver. 5.2.2; Tamura *et al.* 2011). All sequences were deposited in NCBI Genbank (accession numbers KU948541–KU948545).

Description

Thismia inconspicua Sochor & Dančák, sp. nov., Fig. 1.

Thismia inconspicua differs from congeneric species in having the following combination of morphological traits: short stem, all perianth lobes free and equal, tapering into very short terminal appendages, perianth tube displaced from the ovary axis, two pairs of dimorphic appendages on connective apices, three-lobed stigma with lobes entire or bifid.

Type:—BRUNEI DARUSSALAM. Temburong Distr.: Kuala Belalong, a ridge between Temburong and Belalong river valleys ca. 1.4 km SE of their confluence. Coordinates WGS 84: N 04°32’33”; E 115°09’59”, elevation ca. 280 m a.s.l., 27 January 2016. M. Sochor MS1/16 (holotype BRUN [accession number B 031 202], isotype OL [accession number 33410]).

Description:—Terrestrial achlorophyllous mycoheterotrophic herb, 1.6 to ca. 5 cm tall when flowering and to 8.5 cm tall when fruiting (Figs 1A, 2A–C). Roots ca. 0.75 mm thick, hardly branched, vermiform, creeping, cream-coloured. Stem erect, ascending, horizontal or almost missing, simple or simply branched, whitish, glabrous, usually less than 1.5 cm (or to 3.8 cm when fruiting) long. Leaves 0–3, appressed, scale-like, same colour as stem, narrowly triangular with acute apex, (2–)5–8 mm long and ca. 2 mm wide at the base (Fig. 2E), margins decurrent and forming long thin lamellae on the stem (stem thus ribbed). Floral bracts two or three, similar to leaves in shape and size, often indistinguishable from them. Flowers solitary. Perianth actinomorphic with 6 tepals fused into an urceolate perianth tube with free, equal apical lobes; perianth tube ca. 7 mm long and 7 mm wide below the apex, (light) brownish with 12 sepia-brown longitudinal ribs, both ribs and background gradually darkening toward the apex; basal part of perianth tube inclined at an angle to the ovary, thus the upper part of the perianth displaced from the ovary axis; Figs 1A, 2A); inner surface of the perianth tube with 12 longitudinal ribs and faint, pale horizontal bars; apical annulus raised moderately, 4 mm in diameter with opening ca. 2.3 mm wide, sepia-brown on the outer margin, brownish-orange to light orange on the inner margin and grayish in between, inner margin with three shallow notches situated in extensions of the axes of the inner perianth lobes (Fig. 2B); perianth lobes sepia-brown, narrowly triangular, 2.5 mm wide at base and 6–6.5 mm long (including 2 mm long terminal appendages arising from the abaxial side of each lobe). Stamens 6, borne on thickened apical margin of the perianth tube; filaments free, short, curved downwards, connectives broad and flattened, laterally connate to form a tube, with two pairs of appendages at the free distal margin – each pair consisting of a club-shaped appendage pointing centripetally and a tooth-shaped appendage pointing centrifugally (Figs 1D, 2G); outer side of connective with box-shaped lateral appendage on the distal end protruding towards perianth tube (Figs 1E, 2F). Style short, stigma 3-lobed, papillose, lobes longitudinally furrowed (Figs 1B, 2D) and sometimes split from the top (then stigmas shallowly to deeply bifid; Fig. 1C). Capsule cup-shaped, pinkish-brown, on elongated pedicel (to 6 cm long). Seeds beige, ellipsoid, ca. 0.7 × 0.2 mm (Fig. 2H).

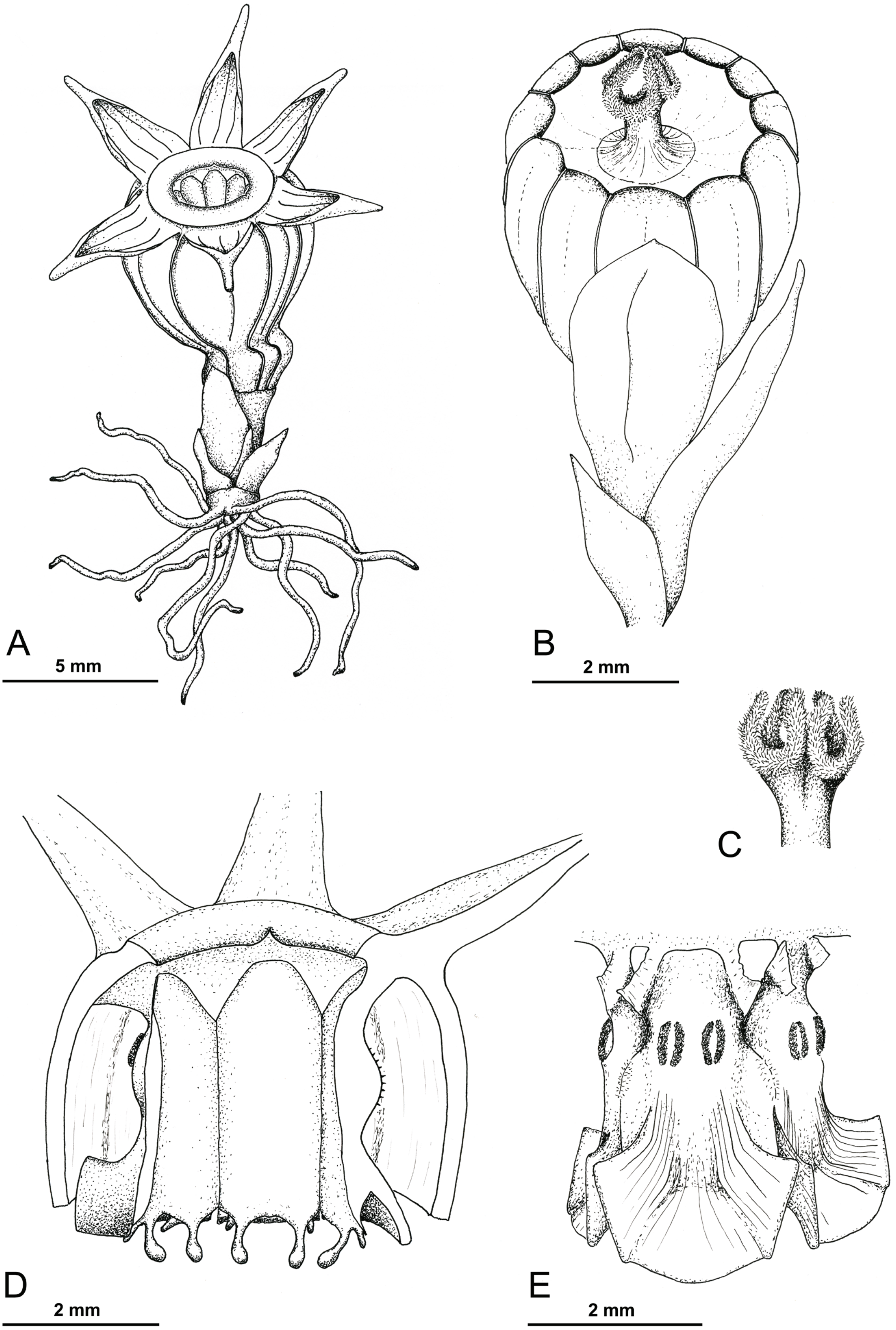

FIGURE 1. *Thismia inconspicua*: flowering plant (A), immature capsule with stigma (B), bifid type of stigma (C), longitudinal section of perianth tube (D) and outer view of stamens (E). Drawn by K. Janošíková.

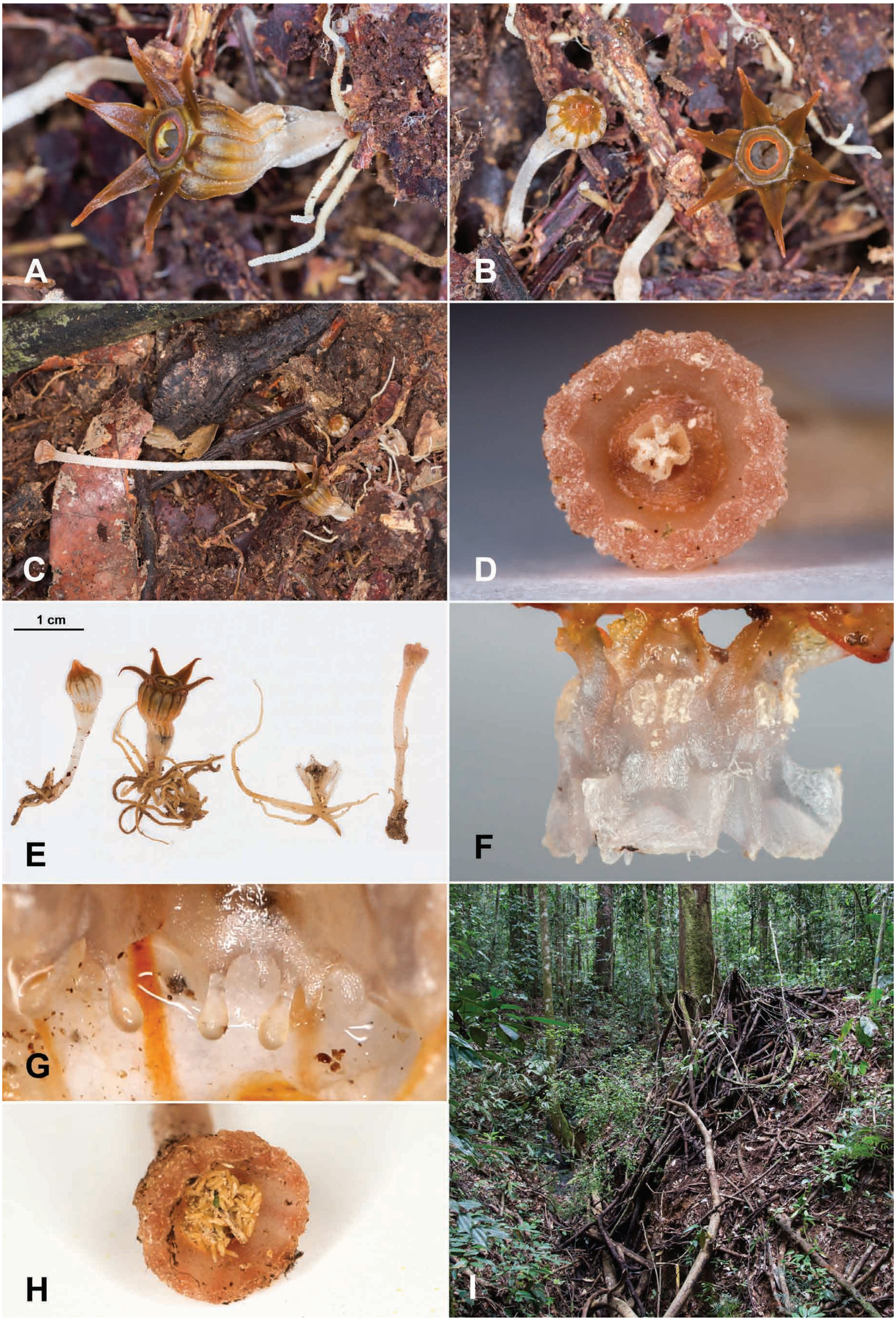

FIGURE 2. *Thismia inconspicua*: flowering plant (A), plants in different developmental stages (B, C, E), capsule with stigma (D), outer view of stamens (F), appendages on connective apices (G), mature capsule with seeds (H) and the type locality (I).

Variability:—The studied population exhibited very low morphological variability. The most prominent variation was observed for stem length; some plants were almost acaulescent (with leaves and floral bracts forming a single rosette) while the stem of one individual was as long as 3.8 cm. Only small differences were detected in the number of flowers (one or two per individual plant), number of leaves (none to three) and floral bracts (two or three). Due to the limited number of fully developed flowers, variation in generative characters could not be evaluated. Differences in flower coloration, shape of stigma (lobes entire or bifid) and fruit pedicel length (0.5–6 cm) could be ascribed to different developmental stages of each plant and/or plasticity.

Habitat and ecology:—The only known locality of the species is situated in primary lowland mixed Dipterocarp forest in a relatively light gap with a dead standing tree (Fig. 2I). *Thismia inconspicua* grows on decaying fallen branches, lianas and epiphytes, and on organic matter formed after their decomposition. A few individuals were found growing on the lower side of rotten branches. During our study, the locality was still being disturbed by falling limbs and branches, which resulted in slow vegetation restoration. Several other mycoheterotrophic plant taxa were found within 20 m—*Epirixanthes elongata* Blume (1823: 82), *Tropidia saprophytica* Smith (1927: 27), *Gastrodia* sp. and *Gymnosiphon* sp.

Distribution:—The species is known only from the type locality, 0.9 km ESE of the Kuala Belalong Field Studies Centre, Universiti Brunei Darussalam in the Temburong District, Brunei Darussalam.

Conservation status:—The population of *T. inconspicua* is protected against logging and other anthropogenic disturbance thanks to its location in Ulu Temburong National Park. Despite intensive botanical and ecological research on the locality in the past decades, the species was discovered only recently and by accident. The possibility of its presence being overlooked elsewhere in Brunei or Sarawak thus cannot be precluded due to its inconspicuous appearance and ephemeral growth. Therefore, we suggest evaluating the species provisionally as data deficient (DD) according to the IUCN Red List Categories and Criteria (IUCN 2012).

Etymology:—The specific epithet reflects the inconspicuous colour and appearance of the plants on decaying wood during flowering period.

Taxonomic affinities

With its creeping vermiform roots and free and equal perianth lobes, *T. inconspicua* is clearly placed in section *Thismia*, subsection *Odoardoa* Schlechter (1921: 34). It is distinguished from other members of this subsection by the following traits: i) two pairs of appendages on connective apices; ii) very short terminal appendages on perianth lobes; iii) short (sometimes almost absent) stem; iv) three-lobed stigma with lobes entire or bifid; v) perianth tube displaced from ovary axis; vi) notched inner margin of annulus (although this trait was clearly observed only in a single flower).

The morphologically most similar species is *T. chrysops* Ridley (1895: 323) described from the Malay Peninsula. Both taxa share several traits, such as perianth tube displaced from its axis, the four anther appendages, sepia-brown perianth lobes, and three-lobed stigma. Also, both species seem to be ecologically similar as they were found on rotten wood in lowland forests. Nevertheless, *T. chrysops* differs significantly in possessing longer and ciliate terminal appendages on its perianth lobes, few additional processes on the connective apices, a bright yellow annulus, dark brown perianth tube, short black pedicels and long stems.

A superficially similar species to *T. inconspicua* is *T. filiformis* Chantanaorrapint (2012: 69) from Thailand. Both taxa share the brown colour of perianth (although different in shade) and relatively short tentacles (although longer in the latter species). Nevertheless, *T. filiformis* differs by, for example, possessing three apical anther appendages, tuberculate longitudinal ribs on a straight perianth tube, long stems, larger flowers and thicker branched roots.

The other known Bornean species of subsection *Odoardoa* – *T. bifida* Hotta (1967: 161), *T. hexagona*, *T. lauriana* Jarvie (1996: 259), *T. mullerensis* Tsukaya & Okada (2005: 129) and *T. ophiuris* Beccari (1877: 252) differ in most characters (shape of anthers and stigma, colour, overall appearance) and probably form different evolutionary lineages.

Molecular phylogenetic analysis

DNA sequencing resulted in three continuous reads in *T. inconspicua* of total length of 3,479 bp. Two reads comprised almost 2.4 kbp long SSU–LSU rDNA region which was nevertheless interrupted by a ca. 80 bp gap around NS4/

NS5 primer binding sites. ITS and the adjacent part of SSU rDNA could not be read in *T. hexagona* due to unknown technical difficulties. Phylogenetic analyses were thus performed only on *atpA* (alignment of 1132 bp) and part of SSU rDNA (1042 bp alignment). Both *T. inconspicua* and *T. hexagona* formed a strongly supported clade with *T. aseroe* and *T. javanica* (Fig. 3), although relationships between these four species could not be determined due to only limited data of unknown quality for *T. javanica* and a number of ambiguous sequence positions in SSU of *T. aseroe*. The highest pairwise sequence identity of *T. incospicua* was 97.7 % with *T. hexagona* in SSU rDNA and 99 % with *T. aseroe* in *atpA*. The sequences of *T. incospicua* were deposited in NCBI Genbank (accession numbers KU948542, KU948544 and KU948545).

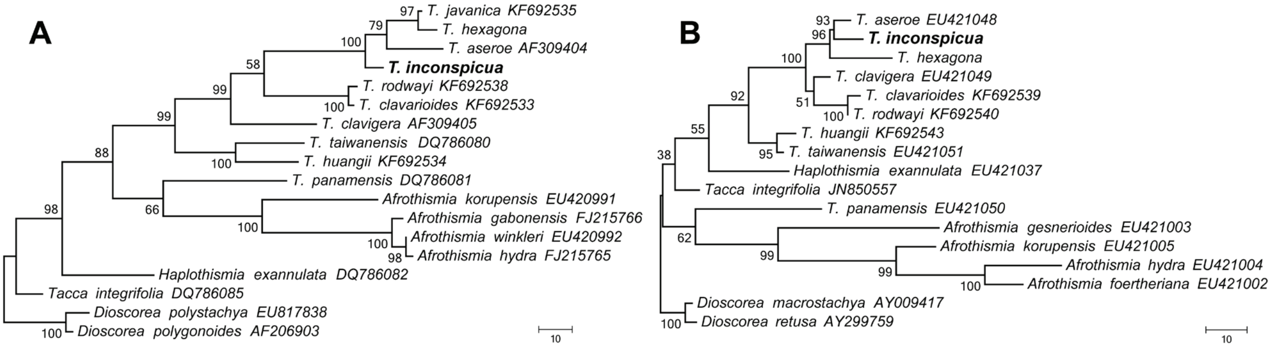

FIGURE 3. Phylogenetic position of *T. inconspicua* in Thismiaceae and related taxa based on SSU rDNA (A) and *atpA* mitochondrial gene (B). Branch length corresponds to number of mutational changes, bootstrap values shown at the branches.

Key of genus *Thismia* in Borneo (modified after Hroneš *et al.* 2015)

1.	Perianth lobes free; roots creeping, vermiform ...	2
-	Perianth lobes connate above the mouth of the perianth tube; roots clustered, coralliform ...	8
2.	All perianth lobes simple, of the same length and size ...	3
-	Inner perianth lobes simple, outer perianth lobes consisting of three parts ...	*Thismia neptunis*
3.	Free distal margin of connective with 2 club-shaped and 2 tooth-shaped appendages, stem very short or missing (usually less than 1.5 cm), perianth sepia-brown, appendages of perianth lobes ca. 2 mm, subconical, perianth tube displaced from ovary axis ...	***Thismia inconspicua***
-	Connective with 2, 3 or 4 finger-shaped or filiform appendages, stem distinct (usually more than 3 cm), perianth white or at least partly yellow, appendages of perianth lobes longer than 7 mm, filiform, perianth tube ± straight ...	4
4.	Perianth tube with distinct transverse bars at least at the base; stigmas bifid ...	5
-	Perianth tube without transverse bars; stigmas not bifid ...	*Thismia ophiuris*
5.	Transverse bars found only in the basal part of the perianth tube; anther appendages 3 ...	*Thismia bifida*
-	Transverse bars found throughout the perianth tube; anther appendages 2 or 4 ...	6
6.	Annulus bright yellow, sharply hexagonal; anthers with 4 finger-shaped appendages: 2 upper and 2 lower at the free apical margin of the connective ...	*Thismia hexagona*
-	Annulus pale purple, round or weakly hexagonal; anthers with 2 appendages ...	7
7.	Perianth tube white with brownish-purple streaks; lobes with appendages ca. 17 mm ...	*Thismia mullerensis*
-	Perianth tube white; perianth lobes with appendages ca. 70 mm ...	*Thismia lauriana*
8.	Inner perianth lobes form three free, long, almost erect, clavate appendages above the mitre; free apical margin of the connective entire or slightly emarginate ...	9
-	Inner perianth lobes lack any elongated appendages; free apical margin of the connective clearly trilobed ...	10
9.	Flowers yellow-orange to pink-red; free apical margin of the connective triangular, acute ...	*Thismia clavigera*
-	Flowers blue-green; free apical margin of the connective rounded to slightly emarginate ...	*Thismia betung-kerihunensis*
10.	Flowers blue; outer perianth lobes distinct; free apical margin of the connective glabrous, without any hairs or ciliae ...	*Thismia goodii*
-	Flowers yellow, orange, brown or blackish; outer perianth lobes not distinct; free apical margin of the connective hairy ...	11
11.	Perianth tube yellow-orange; apex of the mitre obtuse without any projections; free apical margin of the connective with lobes of the ± same length and size ...	*Thismia episcopalis*
-	Perianth tube brown to blackish; apex of the mitre acuminate with three very short projections; free apical margin of the connective with lateral lobes larger, obtusely triangular and the middle lobe narrowly triangular ...	*Thismia brunneomitra*

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REGULAR PAPER

Two new species of *Thismia* subsect. *Odoardoa* (Thismiaceae) from Borneo

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Background – Two new species of the sect. *Thismia* subsect. *Odoardoa*, *Thismia cornuta* Hroneš, Sochor & Dančák and *Thismia pallida* Hroneš, Dančák & Rejžek, from Malaysian Borneo are described and illustrated. The former species is distributed in the Bario area of the Kelabit Highlands of Sarawak, and the latter occurs in the SAFE (Stability of Altered Forest Ecosystem) Project area, northwest of Tawau in Sabah.
Methods – This study is based on field observations in several forest localities in Sarawak and Sabah and herbarium material deposited in SAN, SAR and OL. Both conventional herbarium techniques and comparison with protologues of described species were applied.
Results – *Thismia cornuta* is morphologically closely related to *T. inconspicua* Sochor & Dančák from Brunei Darussalam and *T. chrysops* Ridl. from the Malay Peninsula but it differs from both species by the presence of only two appendages at apical margin of the connective, by horn-like projection on each side of the lateral appendage and by white colour of perianth tube. It was found at three localities and is preliminarily treated as endangered (EN). *Thismia pallida* is morphologically close to *T. filiformis* Chantanaorr. from Thailand but differs by the presence of five appendages at apical margin of connective, by box-shaped lateral appendage exceeding apex of connective and by shorter filiform appendage of perianth lobe. It was found at a single locality within twice logged secondary forest and it is preliminarily treated as critically endangered (CR). This is only the second record of *Thismia* species inhabiting secondary forests in tropical Asia.

Key words – Malesia, mycoheterotrophy, Sabah, Sarawak, tropical rain forest.

INTRODUCTION

Thismia Griff. (family Thismiaceae, sometimes included also into Burmanniaceae; Merckx et al. 2006, The Angiosperm Phylogeny Group 2016) is a genus of delicate mycoheterotrophic monocot plants. The genus comprises about 70 accepted species (Nuraliev et al. 2015, Chantanaorrapint et al. 2016, Cowie & Liddle 2016, Kumar et al. 2017, Sochor et al. 2017, Suetsugu et al. 2017, Sujanapal et al. 2017, Tsukaya et al. 2017) and is distributed mostly in the tropical regions of Asia, Australia and South America and extending into the subtropical or even temperate regions of Japan, New Zealand, Australia and the USA (Maas et al. 1986, Merckx et al. 2013). Two main centres of its diversity in Southeast Asia are located in the Malay Peninsula and Borneo, both with thirteen recognized species (Jonker 1948, Chantanaorrapint et al. 2016, Sochor et al. 2017, Suetsugu et al. 2017, Sujanapal et al. 2017). Ranges of the majority of species are very small areas and most of the species are even reported as being steno-endemic (Jonker 1948, Jarvie 1996, Dančák et al. 2013, Mar & Saunders 2015). It is also commonly believed that *Thismia* species are confined to primary virgin rainforests where they grow in the leaf litter and therefore may be

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easily overlooked (Stone 1980, Merckx et al. 2006, Chantanaorrapint et al. 2016, Sochor et al. 2017).

Vegetative organs of *Thismia* are highly modified due to the full mycoheterotrophy and the individuals are probably able to persist underground for a considerable period during the year gaining all nutrients from their fungal "symbiont" (Stone 1980, Mar & Saunders 2015). Aboveground parts probably emerge only for a short period of time during the rainy season (Stone 1980). Flowers of *Thismia* are highly specialized, most likely for the pollination by small flies (Stone 1980, Mar & Saunders 2015). Stamens of Old World species usually have flattened connectives which are fused together and forming a "tunnel" for the pollinators. The connectives are furnished by variously shaped appendages, which possibly direct the move of the pollinator and restrict self-pollination (Mar & Saunders 2015). These appendages are generally considered species-specific and are used as discriminating morphological character for separating the species (e.g. Ridley 1895, Jonker 1948, Chantanaorrapint 2012, Dančák et al. 2013, Chantanaorrapint et al. 2016, Sochor et al. 2017).

Current infrageneric classification of the genus is based mostly on the morphology of the roots and perianth lobes (Jonker 1948, Kumar et al. 2017). Two subgenera (Old-World *Thismia* subgen. *Thismia* and neotropical *Thismia* subgen. *Ophiomeris* (Miers) Maas & Maas) and seven to eight sections are recognized (Maas et al. 1986, Kumar et al. 2017). Four major groups are recognized in the Old World: *Thismia* sect. *Thismia* with vermiform creeping roots and free perianth lobes, *Thismia* sect. *Rodwaya* (F.Muell.) Schltr. and *Thismia* sect. *Gaziocharis* (Taub. ex Warm.) Hatusima with vermiform roots and outer perianth lobes fused together to form a mitre, and *Thismia* sect. *Sarcosiphon* (Blume) Jonker with clustered coralloid roots and outer perianth lobes also fused together to form a mitre. The first section is further divided into two subsections: *Thismia* subsect. *Brunonithismia* Jonker with perianth lobes of two different sizes and shapes and *Thismia* subsect. *Odoardoa* Schltr. with perianth lobes all equal in shape and size (Jonker 1948, Dančák et al. 2013, Hroneš 2014, Hunt et al. 2014, Hroneš et al. 2015).

During our field trips to Pulong Tau National Park in the Kelabit Highlands of Sarawak and experimental plots of SAFE project in Sabah (both Malaysian Borneo) in early 2017, we have discovered two species of *Thismia* clearly belonging to the sect. *Thismia* subsect. *Odoardoa* by their vermiform roots and all six perianth lobes free and of same length and size. However, the combination of their morphological characters did not match any of the described taxa and we, therefore, describe them here as new species.

MATERIALS AND METHODS

Material

This study is based on material collected during January and February 2017 in the Bario area, Kelabit Highlands, Sarawak and in LFE block of the SAFE (Stability of Altered Forest Ecosystem) Project (Ewers et al. 2011) near Tawau, Sabah. Morphological characters were studied using hand lens (30–60× magnification), stereo microscope and macro photography. Collected specimens were thoroughly compared with original drawings and descriptions given in protologues of representatives of *Thismia* sect. *Thismia*. Herbarium vouchers for this study are deposited in SAN, SAR and OL.

Terminology

Morphological terminology used to describe *Thismia* flowers is sometimes confused as various authors use different terms for the same floral part, e.g. adaxial appendage vs. abaxial appendage vs. lateral appendage. We prefer to use the term lateral appendage as it describes the structure which is attached to the flat surface of the connective (although not on its margin) in contrast to apical appendages which occur on the apical margin of the connective. Strictly the use of the term lateral is not correct but it is perfectly understandable and established (see e.g. Mar & Saunders 2015). On the other hand, the term adaxial appendage suggested by several authors (e.g. Nuraliev et al. 2015) is confusing as the connective was turned down during evolution from his original erect position so that its adaxial side became abaxial.

While describing the perianth tube sometimes the term hypanthium (or floral tube) is used. However, this is not generally accepted, as hypanthium should include also ovary and vegetative tissues (i.e. upper part of floral receptacle, e.g. Hickey & King 2000, Beentje 2010). In *Thismia* the ovary and peduncle are clearly free from the rest of the flower and moreover the perianth tube is caducous. It is thus formed only by tepals and anther filaments. Therefore, we prefer use of the term perianth tube.

TAXONOMIC TREATMENT

Thismia cornuta Hroneš, Sochor & Dančák, **sp. nov.**

It differs from its congeners by the combination of following morphological characters: stem very short or absent, flower slightly zygomorphic, perianth tube white and verrucose outside, annulus pinkish, only two appendages at apical margin of the connective and small horn-like projection arising from each side of the lateral appendage. – Type: Borneo, Sarawak (Malaysia), Kelabit Highlands, Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village, 3°42′1″N, 115°31′28″E, 1195 m alt., 13 Jan. 2017, *Sochor et al.* BOR2/17, whole plant in spirit (holo-: SAR) and pressed (iso-: OL).

Small perennial achlorophyllous herbs. Roots creeping, vermiform, ± horizontal, hardly branched, pale brown. Stem very short or absent, white, 0–15 mm long, ascending, glabrous. Leaves spirally arranged, reduced, scale-like, triangular, acute, c. 3 mm long, 1–3 per stem. Bracts 3, similar to leaves but larger, 6–7 mm long. Flowers usually solitary (rarely 2), slightly zygomorphic, sessile. Perianth of 6 tepals fused to form perianth tube apically with 6 free tepal lobes. Perianth tube urceolate, c. 15 mm long, 9 mm wide at upper third, translucent-white, sometimes with 12 inconspicuous pinkish longitudinal stripes in the upper part, without transverse bars inside, verrucose outside, basally bent or inclined at an angle to the ovary, thus the upper part of the perianth displaced from the ovary axis. Apex of perianth tube fused with stamen bases to form thin, pinkish, circular, slightly raised annulus 3 mm in diameter. Perianth lobes 6, all equal in shape and size, long triangular, 5–6 mm long, 2–3 mm wide at base, white, tapering into white, filiform appendage, 8–10 mm long. Stamens 6, pendent from the annulus, translucent; filaments short, free, curved downwards; connectives laterally connate, forming a tube; each connective with 2 club-shaped appendages of the same shape and size inserted at apical margin and large cap-shaped lateral appendage on the distal part protruding towards perianth tube; lateral appendage with irregularly dentate apex and 2 horn-like projections arising from the middle part of each side; projections apically with cluster of hairs. Style short, stigma 3-lobed, papillose, lobes apically shallowly bilobed. Ovary white, inferior, cup-shaped, almost entirely surrounded by bracts. Fruit a cup-shaped white capsule, 5 mm long, 4.5–9 mm in diameter, topped by withered style and borne on elongated, 35–85 mm long, white fruiting pedicel. Seeds not seen. Figs 1 & 2.

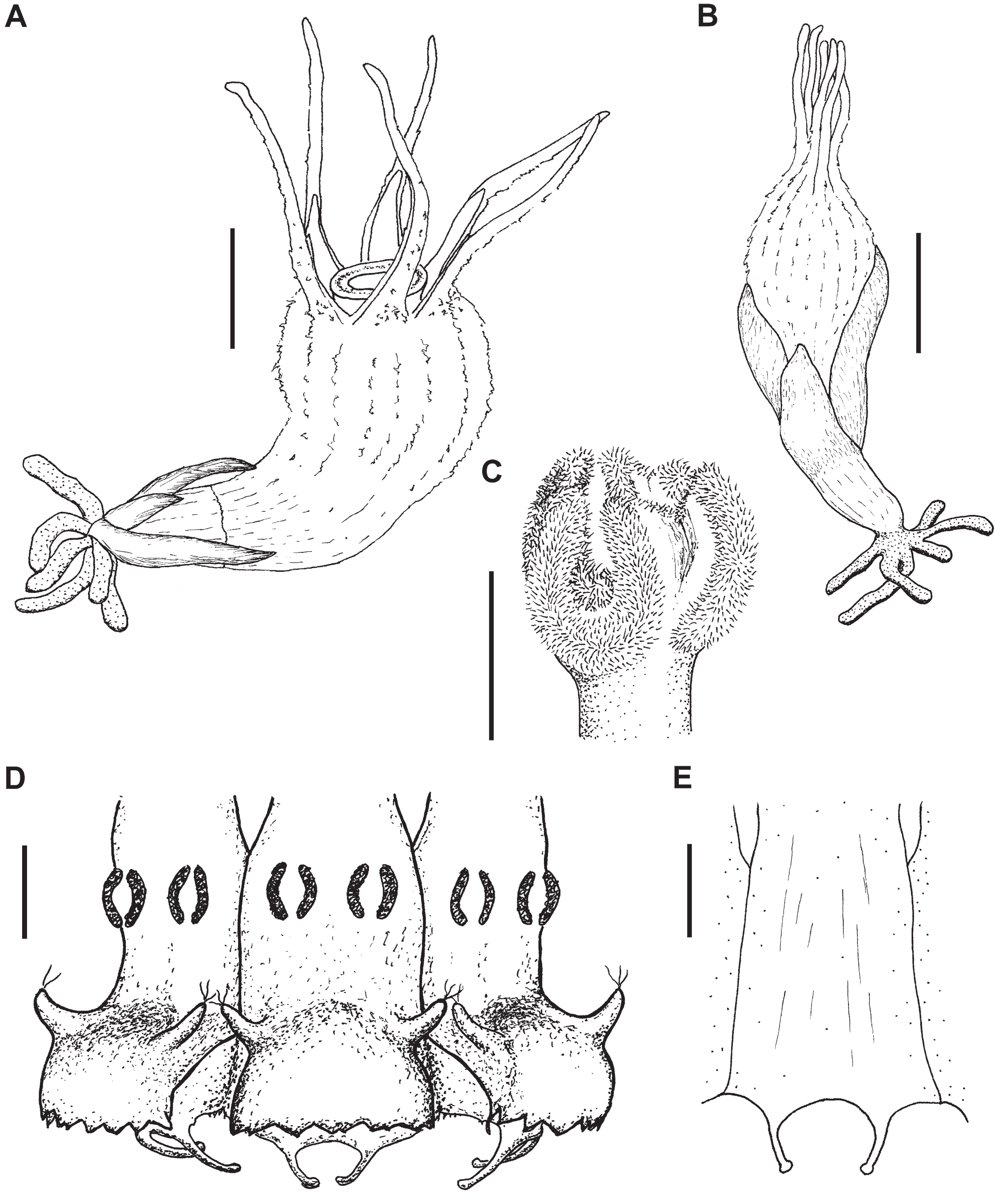

Figure 1 – *Thismia cornuta*: A, habit of flowering plant; B, habit of plant with flower bud; C, style with stigma; D, outer view of stamens; E, inner view of stamen. Scale bars: A & B = 5 mm, C–E = 1 mm. Drawn by Kateřina Janošíková. A from *Sochor et al.* BOR10/17; B–E from *Sochor et al.* BOR2/17 (type).

Additional specimens examined – **Borneo, Sarawak (Malaysia)**: Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.3 km N of the village, 3°50′22″N, 115°30′57″E, 1218 m alt., 15 Jan. 2017, *Sochor et al.* BOR24/17 (SAR); Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.1 km N of the village, 3°50′18″N, 115°31′06″E, 1136 m alt., 16 Jan. 2017, *Sochor et al.* BOR10/17 (OL).

Distribution and habitat – So far known only from the Bario area, Kelabit Highlands, Sarawak, north-western Borneo (possibly endemic). Although most of the *Thismia* species are reported from a single locality (e.g. Jonker 1948, Stone 1980, Chantanaorrapint 2012), we have discovered *T. cornuta* in two valleys which are located 15 km apart. This naturally raises a question on its real distribution. As we found the two sites more or less by chance and a plenty of similar localities exist across the Bario area, we believe it might occur elsewhere in this region. The habitat of the species was the same in both localities – river ravine in the primary rainforest, in humus-rich soil, at elevations c. 1190–1220 m a.s.l. (fig. 2I).

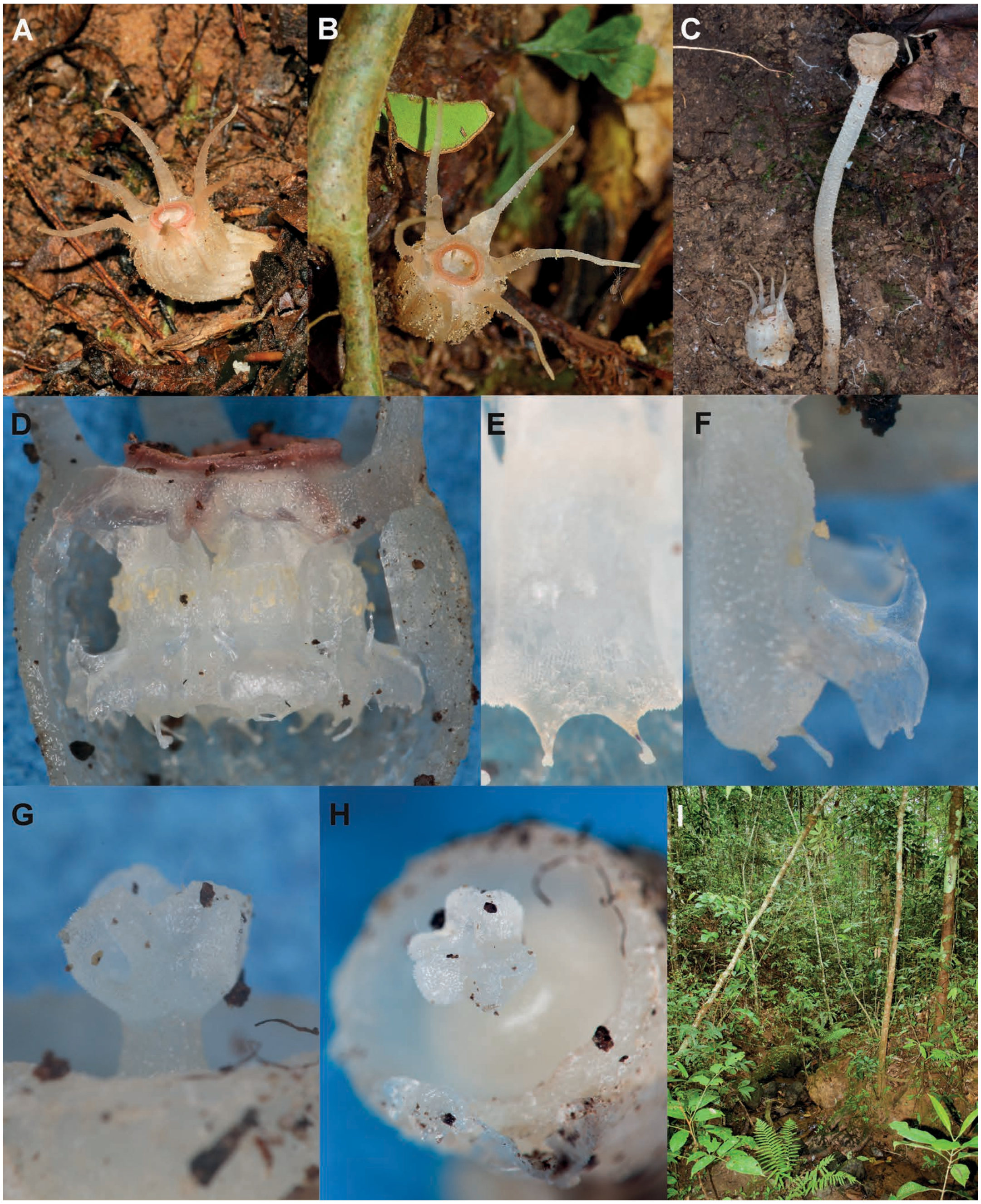

Figure 2 – *Thismia cornuta*: A & B, habit of flowering plant; C, habit of flowering and fruiting plant; D, perianth tube with removed part showing stamens with anthers and lateral appendages; E, apical part of connective with appendages; F, horn-like projection on lateral appendage; G & H, style with stigma; I, type locality. Photographs: Michal Sochor (A & C–H), Michal Hroneš (B & I). A from *Sochor et al.* BOR10/17; B from *Sochor et al.* BOR24/17; C–H from *Sochor et al.* BOR2/17 (type).

Preliminary conservation status – Endangered [EN 2ab(iii,v)]. The extent of occurrence (EOO) of *T. cornuta* was not estimated but its minimal area of occupancy (AOO) could be estimated to be 12 km^2 (within the limits for Endangered status under the criterion B2). *Thismia cornuta* is endemic to Borneo and is known from three specimens. Two were collected in protected forests of Pulong Tau National Park, without immediate threats, but the third one was collected outside the national park, and might be potentially threatened by commercial logging. The species is thus known from three specimens that represent three subpopulations. These three subpopulations represent a total of two "locations" (*sensu* IUCN 2012), falling within the limit for Endangered status. We project that the ongoing loss of its habitat will induce a continuous decline in the number of subpopulations and mature individuals. *Thismia cornuta* is therefore assigned a preliminary status of EN 2ab(iii,v).

Etymology – From the Latin *cornutus* (horned). The name points to the horn-like projections on lateral appendage re-

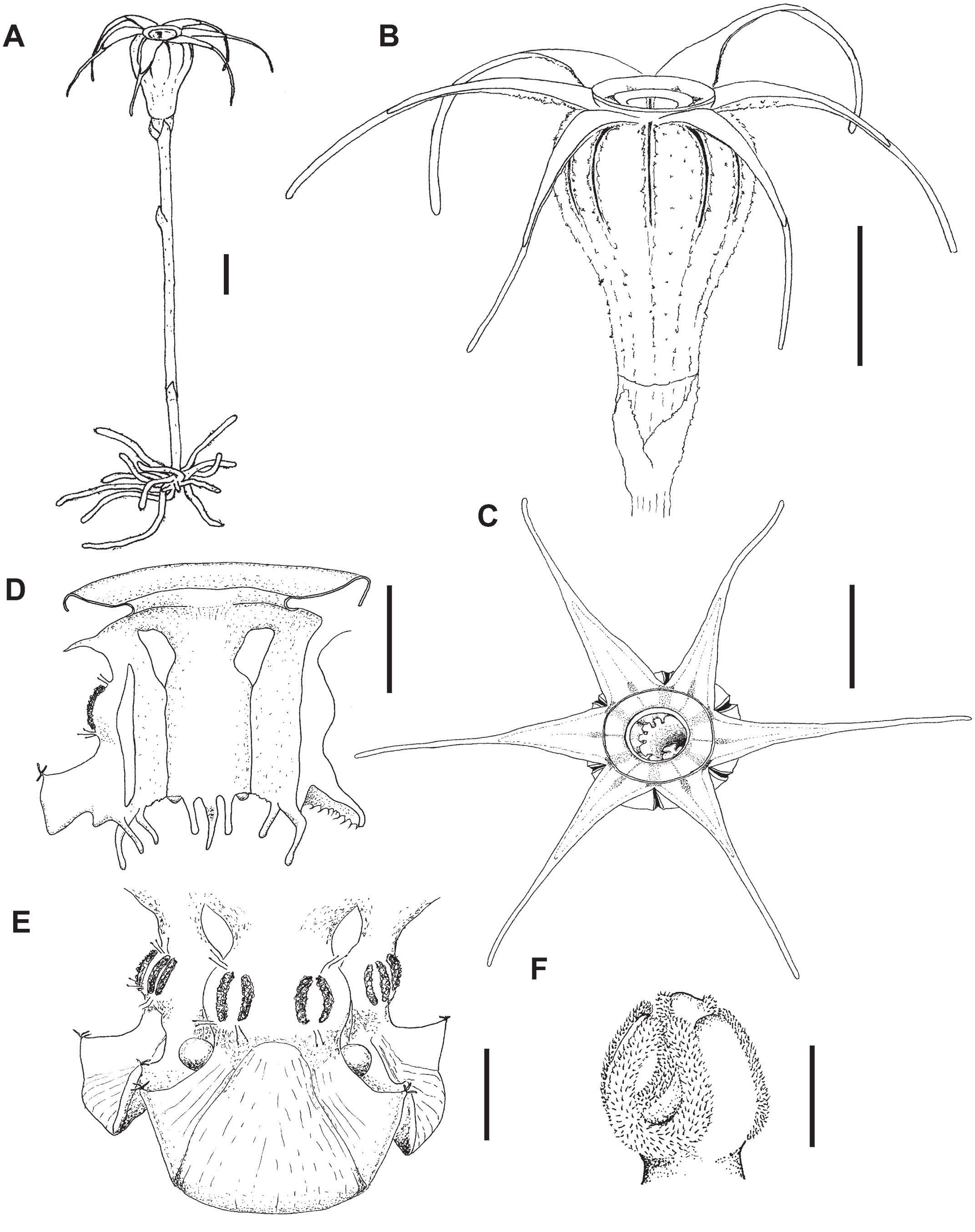

Figure 3 – *Thismia pallida*: A, habit of flowering plant; B, side view of flower; C, top view of flower; D, inner view of stamens; E, outer view of stamens; F, style with stigma. Scale bars: A–C = 5 mm, D–F = 1 mm. Drawn by Kateřina Janošíková. A–F from *Nilus & Svátek* SAN 158204 (type).

sembling horns on a Viking helmet, a morphological trait so far not known in the genus.

Thismia pallida Hroneš, Dančák & Rejžek, **sp. nov.**

Similar to *Thismia filiformis* Chantanaorr. but differs in the presence of 5 (vs. 3) appendages at apical margin of the connective, by box-shaped lateral appendage exceeding apex of the connective, by longer perianth tube and shorter appendages of the perianth lobes. – Type: Borneo, Sabah (Malaysia), Kalabakan, SAFE project, plot LFE-10, 4°44′36.41″N, 117°35′16.93″E, c. 485 m alt., 3 Feb. 2017, *Nilus & Svátek* SAN 158204, whole plant in spirit (holo-: SAN).

Small perennial achlorophyllous herbs. Roots creeping, vermiform, ± horizontal, hardly branched, pale brown. Stem white to pale cream brown, 25–45 mm tall, erect, glabrous. Leaves spirally arranged, reduced, scale-like, triangular, acute, 2–3 mm long, 5–6 per stem. Bracts 3, similar to leaves but 4–5 mm long, lanceolate-triangular, acute, surrounding the base of the ovary. Flowers solitary (rarely 2) at the top of the stem, actinomorphic, sessile. Perianth of 6 tepals fused to form perianth tube apically with 6 free tepal lobes. Perianth tube urceolate, c. 9 mm long, cream to pale brown, sparsely verrucose, with 12 vertical grooves on outer surface, apically with 12 orange-brown longitudinal stripes, without transverse bars inside. Apex of perianth tube fused with stamen bases to form fleshy, circular to weakly hexagonal funnel-shaped, yellow-brown to pale brown annulus. Perianth lobes 6, all equal in shape and size, narrowly triangular, c. 5 mm long, c. 2 mm wide at base, cream brown, tapering into a filiform appendage, c. 3 mm long. Stamens 6, translucent, pendent from the annulus; filaments free, short, curved downwards; connectives broad and flattened, laterally connate, forming a tube; each connective with 5 appendages at apical margin, large box-shaped lateral appendage on the distal part protruding towards perianth tube and interstaminal gland inserted on the line of fusion between connectives; appendages on the apical margin arranged as follows: outer pair of appendages very short, rounded, pointing outwards, inner pair ca. 4 times longer than the outer one, ± straight,

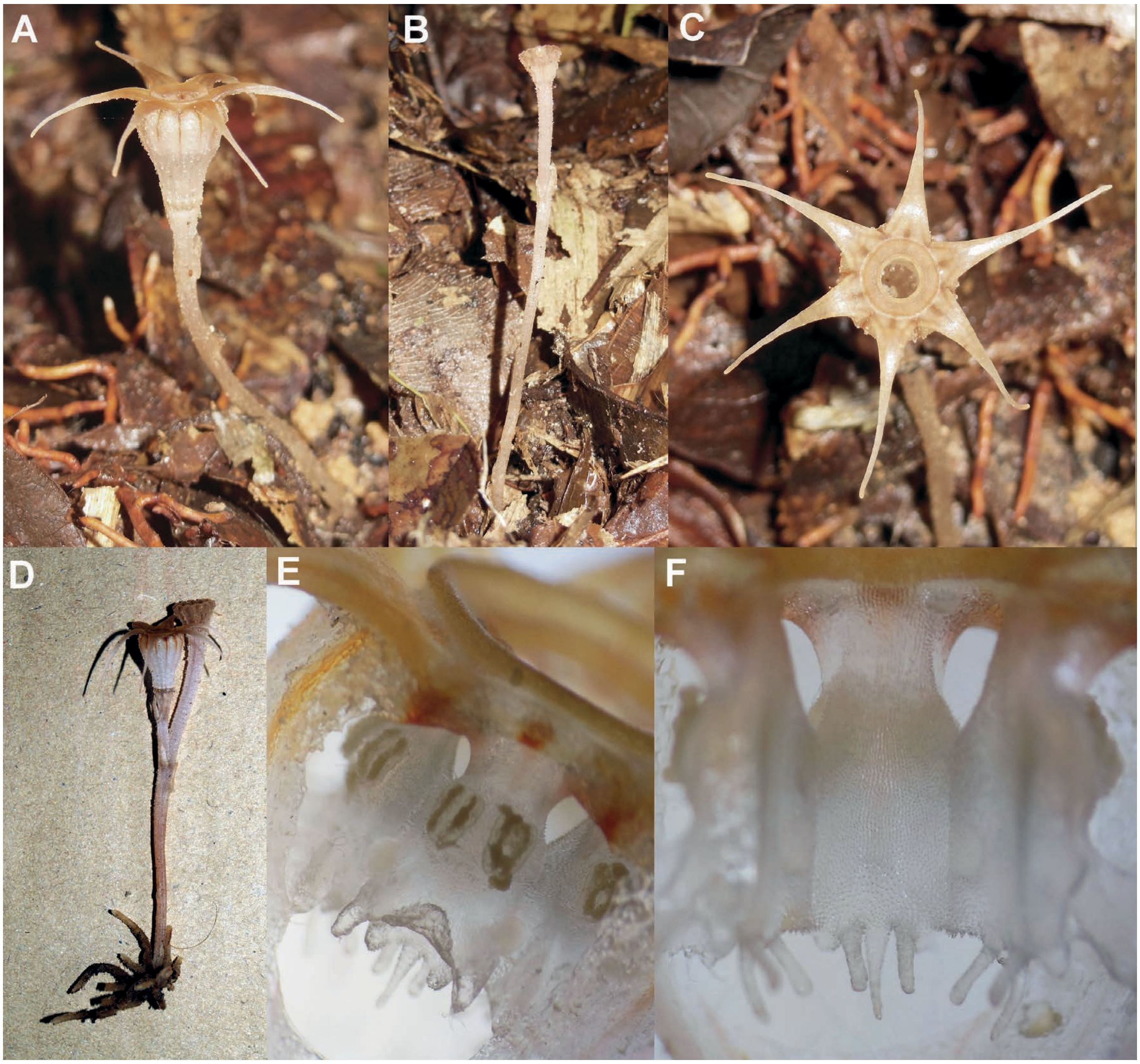

Figure 4 – *Thismia pallida*: A, habit of flowering plant; B, habit of fruiting plant; C, top view of flower showing annulus and perianth appendages; D, two-flowered plant with root system; E, outer view of stamens; F, inner view of stamens. Photographs: Michal Hroneš (A–F). A–F from *Nilus & Svátek* SAN 158204 (Type).

Table 1 – **Comparison of morphological characteristics in *Thismia cornuta*, *T. chrysops* (Ridley 1895) and *T. inconspicua* (Sochor et al. 2017).**

	Thismia cornuta	***Thismia chrysops***	***Thismia inconspicua***
length of perianth tube	c. 15 mm	c. 8 mm	c. 7 mm
perianth coloration	translucent-white, with 12 pale pinkish longitudinal stripes in the upper part	rose pink with longitudinal stripes, in the upper part chocolate-brown	(light) brownish with 12 sepia-brown longitudinal stripes
annulus protrusion degree, shape and coloration	slightly raised, pinkish, circular	slightly raised, bright yellow, hexagonal	moderately raised, sepia-brown on the outer margin, brownish-orange to light orange on the inner margin and greyish in between, circular
length of perianth appendages	8–10 mm	c. 7 mm	c. 2 mm
appendages at apical margin of connective	2 club-shaped	2 club-shaped and several shorter	2 club-shaped and 2 tooth-shaped

Table 2 – **Comparison of morphological characteristics in *Thismia pallida* and *T. filiformis* (Chantanaorrapint 2012).**

	Thismia pallida	***Thismia filiformis***
length of perianth tube	c. 9 mm	4.5–5.5 mm
perianth coloration	cream to pale brown, apically with 12 orange-brown longitudinal stripes	creamy white, with 12 pale brown to orange-brown longitudinal stripes
annulus coloration	yellow-brown to pale brown	orange-brown
length of perianth appendages	c. 3 mm	5–8 mm
number and length of appendages at apical margin of connective	5; middle one the longest	3; middle one the shortest
lateral appendage of connective	box-shaped, exceeding apex of connective	skirt-like, with central lobe notched, not exceeding apex of connective

cylindrical to slightly club-shaped, obtuse, pointing inwards, the middle (unpaired) appendage longest, acute, curved. Style short, stigma 3-lobed, papillose. Ovary pale brown, inferior, obconical, indistinctly ribbed. Fruit a conical to cup-shaped pale brown, ribbed capsule, 4–5 mm long, topped by withered style, borne on elongated, 7–20 mm long fruit stalk. Seeds small, fusiform, brown. Figs 3 & 4.

Distribution and habitat – So far known only from small population of seven individuals in twice selectively logged forest near SAFE Project base camp (LFE blocs), south of Danum Valley Conservation Area and northwest of Tawau, Sabah, at elevation c. 485 m a.s.l. Secondary forest species of *Thismia* are very rare globally. Among Neotropical species only *T. pannamensis* (Standl.) Jonker is reported to grow also in secondary or fragmented forests (Guilherme et al. 2016). Among Old World species only two species were reported from secondary forests: *T. rodwayi* F.Muell. often occurs at sites that have been subjected to intensive and relatively recent human activities, including clear-cutting and regeneration burns (Roberts et al. 2003) and *T. hongkongensis* Mar & R.M.K.Saunders is only known from the secondary forest in Hong Kong (Mar & Saunders 2015). Therefore, *T. pallida* is probably only the second *Thismia* species discovered in a secondary forest in tropical Asia.

Preliminary conservation status – The species is given a Red List status of Critically Endangered [CR B2ab(iii, v)]. The extent of occurrence (EOO) of *T. pallida* cannot be estimated because the species is only known from the type collection. Its area of occupancy (AOO) is estimated to be 4 km^2, which falls within the limits for Critically Endangered status under criterion B2. The only known subpopulation is from non-protected forest on a logging concession, so it might be potentially threatened by commercial logging. This subpopulation represents thus one location (*sensu* IUCN 2012), which is the upper limit for Critically Endangered status under subcriterion ‘a’ of criterion B2. The site where *T. pallida* has been collected was recently included into a research area which should be prevented from logging in the future (Ewers et al. 2011), however the past destruction of its habitat has probably already affected the population. Then, even if the species might be more widespread in the region, the loss of the habitat of *T. pallida* has led to a continuing decline in the number of mature individuals. We then assigned to *T. pallida* a preliminary status of CR B2ab(iii, v).

Etymology – From the Latin *pallidus*. The name refers to the pale colour of the whole plant.

DISCUSSION

Borneo harbours about 15 000 vascular plant species with c. 37% being endemic (Raes et al. 2009). Among them 20 genera are mycoheterotrophic (e.g. Tsukaya et al. 2011, Tsukaya & Suetsugu 2014, Dančák et al. 2017) and *Thismia* with its thirteen species being one of the largest (Sochor et al. 2017, Tsukaya et al. 2017). From the systematic point of view, five species belong to the sect. *Sarcosiphon*, one species to the sect. *Thismia* subsect. *Brunonithismia* and seven species to the sect. *Thismia* subsect. *Odoardoa*, respectively (Jonker

1948, Hroneš et al. 2015, Sochor et al. 2017, Tsukaya et al. 2017). Both new species described here have creeping vermiform roots and free equal perianth lobes, therefore they belong to sect. *Thismia* subsect. *Odoardoa* as well.

Given its unusual morphology, *Thismia cornuta* is well separated from all known *Thismia* species. *Thismia inconspicua* Sochor & Dančák from Brunei Darussalam and *T. chrysops* Ridl. from the Malay Peninsula seems to be morphologically closest to *T. cornuta* as they share several morphological traits, such as perianth tube bent or displaced from its axis resulting in flower zygomorphy and presence of club-shaped appendages at apical margin of the connective (Ridley 1895, Sochor et al. 2017; table 1). Moreover, flowers of *T. cornuta* are almost sessile like in *T. inconspicua*. However, *T. cornuta* differs substantially from both species by its white perianth, by only slightly raised pinkish annulus, by presence of only two appendages (vs. at least four in *T. inconspicua* and *T. chrysops*) at the apical part of the connective (fig. 2E) and by the presence of a pair of horn-like projections on lateral appendage (fig. 2F) which has not been reported for any *Thismia* species so far. *Thismia chrysops* and *T. grandiflora* Ridl. may have similar projections according to their illustrations (Ridley 1895) although it is not mentioned in written descriptions. However, it is almost impossible to judge from the illustrations if the depicted structures are identical with those seen in *T. cornuta*.

Flowers of *T. cornuta* open just above the ground and they are sometimes almost completely covered by the leaf litter or even soil. Mar & Saunders (2015) reported that the flowers of *T. hongkongensis* were visited by small dipteran flies. In the case of *T. cornuta*, the pollinators may as well be some small ground invertebrates, however we failed to observe any visitors of the flower.

The second discovered species, *Thismia pallida*, resembles *T. filiformis* Chantanaorr. from Thailand by its indistinctive pale brown colour and rather short perianth appendages (Chantanaorrapint 2012). However, these two species differ in the inner architecture of the flower. While the connective of *T. filiformis* bears three appendages on its apical margin, the middle one being the shortest, *T. pallida* bears five appendages of three different shapes, the middle one being the longest (figs 3D & 4E). Both species also differ in shape and size of lateral appendage of connective which is box-shaped and exceeding apical part of the connective in *T. pallida* (vs. skirt-like appendage with central lobe notched and not exceeding apex of the connective in *T. filiformis*). While *T. filiformis* has perianth tube up to 5.5 mm long and perianth appendages 5–8 mm long, *T. pallida* has perianth tube up to 9 mm long and much shorter perianth appendages (c. 3 mm long; table 2). Other two somewhat similar species from sect. *Thismia* subsect. *Odoardoa* that occur in Borneo are *T. bifida* M. Hotta and *T. ophiuris* Becc. (Beccari 1878, Hotta 1967). Both species differ from *T. pallida* by having a lower number of appendages at apical margin of the connective (three and two, respectively), by more prominent annulus, longer perianth appendages (more than 10 mm) and also by colour (the perianth tube is mostly yellow to yellow-orange).

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Rediscovery of *Thismia neptunis* (Thismiaceae) after 151 years

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Abstract

Thismia neptunis, as many of its congeners, is a poorly understood species that has only been known from the type collection and its limited original description. In January 2017 it was rediscovered in the type area in the Gunung Matang massif, western Sarawak, Borneo, Malaysia. The paper provides the amended description and drawings of the species, very first available photographs and short notes on taxonomy and historical context of Beccari's work on *Thismia*.

Key words: *Brunonithismia,* Burmanniaceae, fairy lanterns, Kubah, Monte Mattán, Sarawak

Introduction

Thismia Griffith (1844: 221; fairy lanterns, Thismiaceae, or Burmanniaceae s.l.) is a genus of small mycoheterotrophic plants with the main centre of diversity in tropical Asia. Although the genus in the taxonomic sense exists since 1844, many species or populations have been being discovered only in the last decade. For instance, out of total of ca 76 species, 30 have been described since 2011 (Hunt *et al.* 2014, Chantanaorrapint *et al.* 2016, Cowie & Liddle 2016, Cooper 2017, Kumar *et al.* 2017, Sochor *et al.* 2017, Suetsugu *et al.* 2017, Sujanapal *et al.* 2017, Tsukaya *et al.* 2017, Chantanaorrapint & Suddee 2018, Hroneš *et al.* 2018, Suetsugu *et al.* 2018, Sochor *et al.* 2018) and several others (ca >10) await formal description. The real diversity of fairy lanterns is therefore being uncovered only recently. At the same time, their preferred habitats, i.e. mostly primary tropical rainforests, have been facing unprecedented worldwide decline. Quite many species may therefore be already extinct now, particularly when we consider the fact that very many species appear to be stenoendemic, usually known just from the type collections. An illustrative example (although atypical in habitat and distribution) is *T. americana* Pfeiffer (1914: 123), which was observed in the type area for a few years after its first discovery in 1912, but has then never been found again despite many intensive searches (Merckx & Smets 2014). Therefore, it may seem somewhat paradoxical that new localities of formerly described taxa, although still not numerous, are being discovered mainly recently, in the time of massive landscape changes and conversions (e.g. Chantanaorrapint & Sridith 2007, Chantanaorrapint & Chantanaorrapint 2009, Tsukaya *et al.* 2014). Nevertheless, it is often unclear whether the new findings belong to some known, or rather to a new species (e.g. Tsukaya *et al.* 2014, Chantanaorrapint *et al.* 2015). One of the problems is insufficient description and documentation for the old names. In some extreme cases, e.g. *Thismia clandestina* (Blume 1850: 65) Miquel (1859: 616) which was described based on a fruiting specimen, unambiguous interpretation of the name becomes impossible (Suetsugu *et al.* 2017).

One of the species with incomplete documentation is *T. neptunis* Beccari (1878: 251). Its original description is restricted to external appearance and so is the original drawing, otherwise very detailed (Fig. 1). Other characters, particularly structure of connectives, which is crucial for *Thismia* species delimitation (Sochor *et al.* 2018), were unknown. In January 2017, the species was discovered in the type area, possibly the type locality, 151 years after its type collection. To our knowledge, it is only the second finding of the species in total. We therefore provide its amended description, inclusive internal characters, and very first photographic documentation of this iconic and, due to its peculiar appearance and also the name, almost mythical plant.

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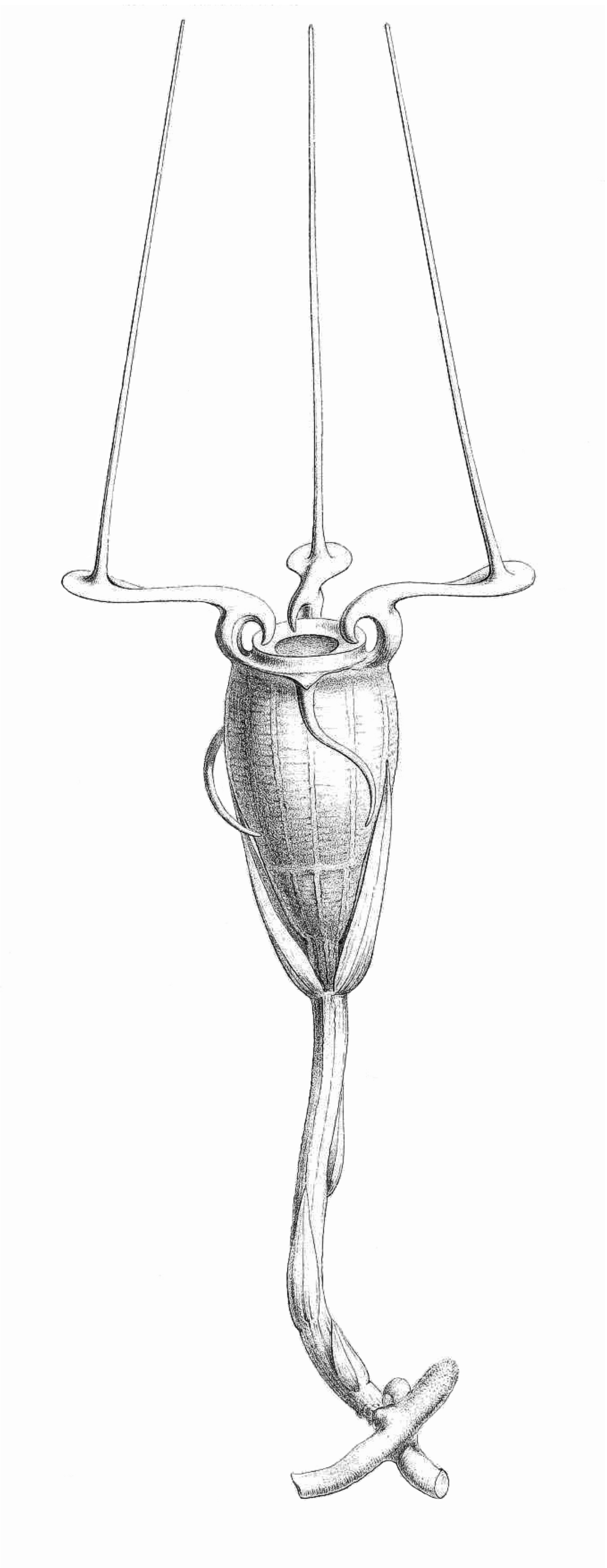

FIGURE 1. Original Beccari's drawing of *Thismia neptunis* (from Beccari 1878).

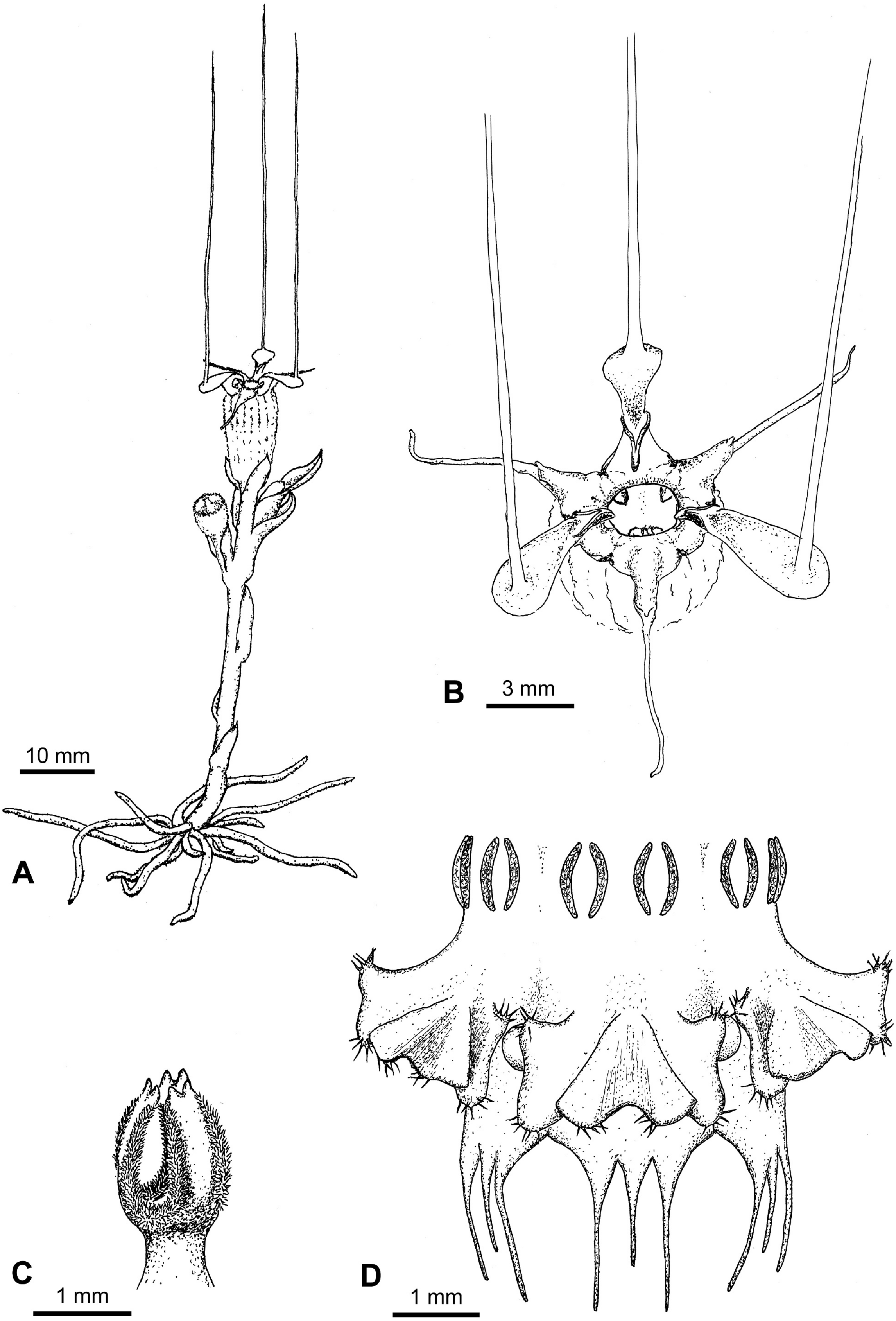

FIGURE 2. *Thismia neptunis*: flowering plant (A), upper view of flower (B), stigma (C), outer view of connective tube (D). Drawn by K. Janošíková.

Material and Methods

The studied population consisted of two flowering individuals and one bud. Morphological characters were studied using hand lens (30–60× magnification) and macro photography. Collected specimen was thoroughly compared with original drawing (Fig. 1) and description given in protologue of *T. neptunis* and with digital image of holotype in FI via JSTOR Global Plants (2017) initiative.

Taxonomic treatment

Thismia neptunis Beccari (1878: 251), Figs 1–3

Type:—MALAYSIA. Ragiato di Sarawak, Mattang. April 1866. *O. Beccari p.b. 1508* (holotype FI-B 013453!)

Description:—Terrestrial achlorophyllous herb, ca. 9 cm tall when flowering. *Roots* ca. 0.7–1.5 mm thick, hardly branched, vermiform, creeping, cream-coloured to light brown. *Stem* ascending, simple or simply branched, ribbed, whitish or creamy, glabrous, ca. 4 cm long. *Leaves* 3–5, appressed to erecto-patent, scale-like, of the same colour as stem, narrowly triangular with acute apex, entire, with prickle-like transparent processes on abaxial side, 5–8 mm long and ca. 2 mm wide at the base. *Floral bracts* 3, similar to leaves, but larger and slightly curved, up to 12 mm long. *Flowers* 1–3. Perianth actinomorphic with 6 tepals fused into an urceolate perianth tube with free, unequal apical lobes; perianth tube 12 mm long and 7 mm wide at the widest point, whitish, partly transparent (upper part therefore seemingly orange due to connectives shining through), with 12 thin longitudinal ribs and ca. 12 transverse bars; longitudinal ribs white in lower half and dark orange in upper half, widened between bases of filaments and forming dark orange to reddish ± rhombic spots between perianth lobes; perianth tube apex ± flat, without prominently raised annulus, opening 2.2 mm in diameter; outer perianth lobes ± conical, pointed, ca. 10 mm long, including a 7 mm long filiform appendage arising from the abaxial side; inner lobes with a complex three-segment structure; proximal segment claw-shaped, pointed towards the perianth tube opening, reddish-brown; middle segment ± flat (basally triangular in section), obovate in outline, growing horizontally from central abaxial part of the proximal segment; distal segment growing vertically from centre of the middle segment, filiform, gradually tapering towards apex, yellowish-brown, 4.5 cm long. *Stamens* 6, hanging against perianth lobes; filaments short, flat, reddish on sides, otherwise yellow adaxially and whitish with orange longitudinal stripe abaxially; connectives broad and flattened, laterally connate to form a tube, almost glabrous (long hairy only around thecae and on lateral appendage), shortly papillose, vivid orange in the proximal part to orange-red at the distal end; interstaminal glands prominent, hemispherical, placed between bases of lateral appendages; appendages at the distal margin of connective three, filiform, two longer (1.6 mm), one in the middle shorter (1.1 mm long); lateral appendage not reaching the connective apex, hairy and reddish at margins, composed of three lobes, lateral lobes (vertical) obtusely fishtailed, central lobe wavy (with a distinct longitudinal ridge between two furrows). *Ovary* obconical to cup-shaped, whitish to light beige, almost completely surrounded by bracts. *Style* light beige, ca. 1 mm long, stigma 3-lobed with lobes long, flat, erect, bicuspidate and reddish on top. *Capsule* cup-shaped, whitish to light beige, on elongated pedicel. *Seeds* not seen.

Additional specimens examined:—MALAYSIA. Sarawak, Kuching, Kubah National Park, 0.4 km NE of Matang Wildlife Centre. Coordinates WGS 84: 1°36’41”N, 110°9’48”E, elevation 38 m, 26 January 2017. *M. Sochor and Z. Egertová BOR51/17* (OL 35279).

Habitat and ecology:—The only known locality is in primary lowland mixed dipterocarp forest on a river alluvium. *Thismia* species are generally accompanied by other mycoheterotrophic plants; in this case it was *Sciaphila* cf. *alba* Tsukaya & Suetsugu (2015: 284). Albeit pollination ecology was not studied, ca. seven flies of family Sciaridae (Diptera) and one individual of family Braconidae (Hymenoptera) were observed being stuck on inner perianth lobes of the two flowers (Fig. 3A, D, E, F). Although the braconid was probably only a coincidental victim, the flies may represent potential pollinators, as several dipteran taxa have been reported as visitors and probable pollinators of fairy lanterns (Li & Bi 2013, Mar & Saunders 2015). Nevertheless, why had they been attracted to and finally trapped on the perianth lobes surface can only be speculated. Tepals are apparently hydrophilic (possibly as a mean of maintaining turgor in the long thin appendages) as indicated by a number of rain drops persisting on them long after the rain. But they do not appear to be sticky and no other particles tended to be trapped on them either in the field or during our manipulation. Therefore, the insects seem to have been attracted by smell (or other signals) of the flowers and accidentally drowned on the wet surface of perianth lobes.

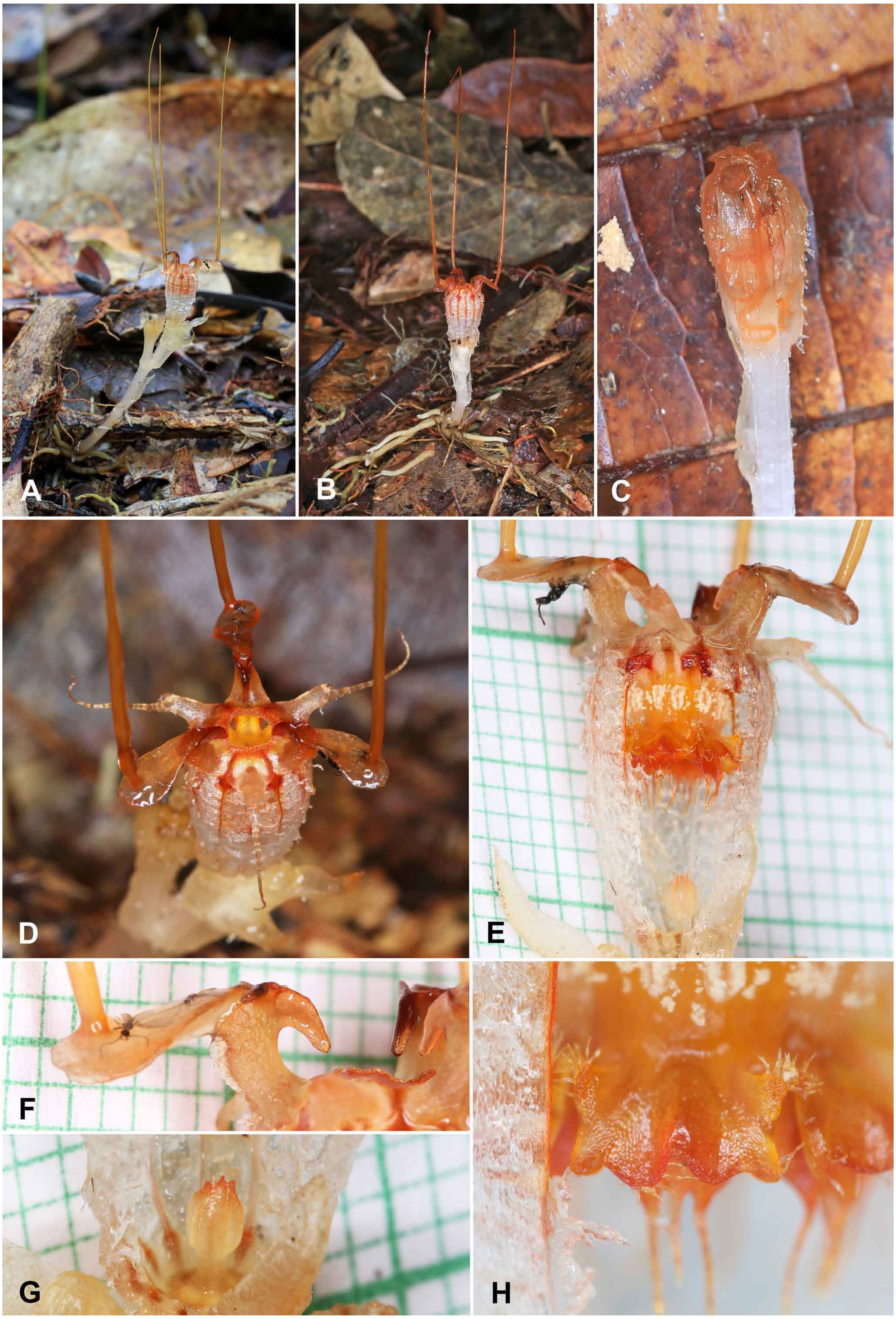

FIGURE 3. *Thismia neptunis*: flowering plants (A, B), bud (C), detail of flower (D), section of floral tube and outer view of connective tube (E), detail of inner perianth lobe (F), stigma (G), lateral appendage (H).

Distribution:—The species is known from a restricted area in western Sarawak, Borneo, Malaysia. Beccari (1878) described the locality simply as "Monte Mattán" or "Mattang", which is an area now generally known as Matang massif which Kubah National Park is part of it. The present locality is placed at the park's western border and may be identical or close to that of Beccari.

Conservation status:—The extent of occurrence (EOO) and the area of occupancy (AOO) of *T. neptunis* cannot be estimated because the species is only known from the type area/locality. Its inconspicuous appearance may potentially contribute to our limited knowledge on its distribution as it may be easily overlooked in the field. Nevertheless, due to the facts that 1. it is probably restricted to primary lowland rainforests, i.e. a habitat that has experienced a significant reduction in Sarawak in the last decades; 2. the only known population occurs in a primary forest just around 100 m from its edge and the whole locality is therefore susceptible to changes in plant community composition due to edge effect (Qie *et al.* 2017); and 3. its known population can be estimated to just a few (<50) individuals, it fulfils criteria B2, C2 and D of critically endangered species (CR) according to the IUCN Red List Categories and Criteria (IUCN 2012).

Taxonomic affinities:—Having free perianth lobes of unequal length and shape, *T. neptunis* belongs to section *Thismia* (*Euthismia* Schlechter, 1921: 34), subsection *Brunonithismia* Jonker (1938: 242). This group comprises nine species (Kumar *et al.* 2017, Suetsugu *et al.* 2018) of very diverse morphology as for symmetry of perianth, modification of perianth lobes and structure of connectives. Half of the species are, nevertheless, only poorly documented. *Thismia neptunis* is unique among other fairy lanterns in the very complex three-segmental structure of inner perianth lobes that are terminated by long filiform appendage pointing vertically upwards. This striking morphology led Schlechter to creation of monotypic section *Sarawakia* Schlechter (1921: 35) within his system of *Thismia* (Schlechter 1921). However, his approach has not been generally accepted (Jonker 1938, Kumar *et al.* 2017).

Beccari was also well aware of morphological uniqueness of *T. neptunis*. In the protologue (Beccari 1878), he stated that *T. neptunis* seems to have connectives similar to *T. brunonis* Griffith (1844: 221). However, *T. brunonis* have apical part of the connective covered by numerous short teeth (Griffith 1845) while *T. neptunis* have only three rather long appendages. Nevertheless, Beccari himself was not absolutely sure about the character of connectives as he studied only two pressed and dried plants. In having whitish perianth tube with 12 orange streaks *T. neptunis* superficially resembles *T. javanica* Smith (1910: 32) and *T. arachnites* Ridley (1905: 197). Both of them, nevertheless, differ in having short rounded outer perianth lobes and simpler spreading inner perianth lobes, and the latter species also in having “numerous short teeth” at the apical end of connectives. Connectives of *T. javanica*, although similar at a first glance, differ from those of *T. neptunis* in colour (white vs. orange, respectively) and three short teeth at the apex, each bearing 1–2 long hairs of similar length (vs. three unequal filiform appendages in *T. neptunis*). *Thismia neptunis* is so far the only known member of subsection *Brunonithismia* occurring in Borneo.

Odoardo Beccari as a collector of *Thismia*

Odoardo Beccari (1843–1920) was an Italian botanist who is considered one of the founding figures of biological research in Sarawak (Boyce & Wong 2007). He spent three years (1865–1868) in Borneo and another four years (1872–1876) in other Sunda Islands, mainly New Guinea (Pichi Sermolli & van Steenis 1983). Although his main object of interest was palms (Arecaceae), he collected and described hundreds of other plant species, among them also six species of *Thismia*, the number not yet surpassed by any other collector. One of these species originates from New Guinea (*Thismia crocea* (Beccari 1878: 249) Smith (1909:193)), one from Singapore (*Thismia aseroe* Beccari (1878: 252)) and the others from Sarawak (*Thismia clavigera* (Beccari 1878: 251) Mueller (1891: 235), *T. episcopalis* (Beccari 1878: 250) Mueller (1891: 235), *T. neptunis* and *T. ophiuris* Beccari (1878: 252)). Interestingly, three of these species come from one locality in southwestern Sarawak called by Beccari as “monte Mattán”. This refers to Gunung Matang, a mountain massif included in present-day Kubah National Park, northwest of Kuching. This area was Beccari’s favourite place during his stay in Sarawak in 1865–1868 and he spent many months in a forest hut called “Vallombrosa” on eastern flanks of the massif (Beccari 1902). Beccari himself gave only very limited information about collecting localities of the three *Thismia* in Matang which was however a common practise in those times. On the other hand, he gave an interesting description of ecological requirements of *Thismia* species, probably the first of its kind. He writes in his book *Nelle foreste di Borneo* (Beccari 1902) that *Thismia* and other achlorophyllous plants were a reward for his patient and careful search in places where the forest was thickest, the shade densest and the soil richest. This unambiguously illustrates that Beccari was aware of ecology of *Thismia* and he probably systematically searched for them in Matang. The current locality of *T. neptunis* is on the other side of the Matang massif than Beccari’s hut used to exist and it is hard to say if it is identical with the *locus classicus*. The massif itself is not huge and it is not difficult for experienced person to walk across it. As the forests of the Matang massif has been preserved almost unaltered since Beccari’s stay, we believe that the chance for rediscovery of the two remaining species described by Beccari from this locality, i.e. *Thismia episcopalis* and *T. ophiuris* is still high.

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PLOS ONE

RESEARCH ARTICLE

Thismia kelabitiana (Thismiaceae), a new unique Fairy Lantern from Borneo potentially threatened by commercial logging

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Abstract

Thismia kelabitiana, a new unique species from the Sarawak state of Malaysia in the island of Borneo is described and illustrated. This new species is not similar to any species of *Thismia* described so far especially by having a unique form of mitre and outer perianth lobes deeply divided into 8–10 acute lobes and forming striking fringe around perianth tube opening. The species appears to be critically endangered due to ongoing logging activities in the region. It may potentially become a surrogate species for lower montane forests of the region and thus help protect them against further destruction.

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Introduction

Mycoheterotrophs, i.e. achlorophyllous plants able to obtain carbon via the mycorrhizal fungi associated with their roots, are important components of primary tropical rain forest biodiversity across the globe [1]. The island of Borneo is still covered with significant primary forests, although their area has been rapidly decreasing in the past decades [2]. Commercial logging and subsequent land conversion (mostly for oil palm plantations) drastically reduced the area of pristine old-growth forest from 55.8 Mha in 1973 to 20.6 Mha in 2015 [3].

Borneo's rainforests host enormous diversity of mycoheterotrophic plants: twenty genera belong to seven families with at least 70 described species, i.e. 17% of the global biodiversity of mycoheterotrophs, orchids with 13 genera and more than 30 species being the richest family. Most of them have been poorly studied, and the knowledge on their taxonomy (as well as ecology and distribution) has been increasing only in recent years, e.g. [4], [5], [6], [7], [8].

An excellent example of this group may be *Thismia*, a genus of more than 75 species of mycoheterotrophic plants distributed mainly in tropical regions of Asia and the Americas, Borneo with 19 species [9], [10] being its centre of diversity. *Thismia* species usually prefer primary tropical rainforests–a habitat that faces unprecedented destruction in Borneo. Nature conservation efforts in this region could be potentially supported by discoveries of charismatic organisms that easily attract attention of the public, e.g. [11]. Such species may become

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surrogate species, i.e. species that are used to represent other species or aspects of the environment to attain a conservation objective [12]. Surrogate species are widely used in nature conservation as a shortcut for conservation planning [13] especially in regions where detailed data on biodiversity are lacking [14]. Umbrella and flagship species are generally known examples of such surrogate species. They are usually large mammals such as apes, pachyderms and carnivores or other distinctive animals as birds of prey and butterflies [15] that attract attention of the general public. Among plants, notable examples are orchids and parasitic *Rafflesia* [16] famous thanks to its large flowers which appear in tropical forests of Asia. Although *Thismia* species are tiny and usually inconspicuous plants in comparison to large mammals or *Rafflesia*, in close view they are fairly strange-looking and some of them are attractive and colourful. Their odd appearance, together with their peculiar life strategy and strong links to the primary forests, makes them exceptional among rainforest herbs. Thus, they are potential candidates for good surrogate species.

A few years ago, we received photographs of an unknown achlorophyllous plant, which was accidentally discovered by a group of our colleagues on a hike to the Kelabit Highlands of Sarawak in 2010. The pictures showed an undoubtedly undescribed striking species of *Thismia*. In 2017, we therefore launched an expedition to find the locality and the plant from these photographs. The successfully discovered plant with a series of unique traits is described here as a new species. Owing to its size, colour and distinctive morphology, this species is among the most eye-catching representatives of the genus.

Materials and methods

Ethic statement

The new species reported in this study was collected from a forest site located outside any protected area of Sarawak State of Malaysia. The research as well as collection and export of plant material was permitted and approved by relevant Sarawak authorities. Since this species is currently undescribed, it is inevitably not yet included in any of the existing Red Lists and lists of protected species.

Morphological observations

Morphology of the new species was studied in a field camp using hand lenses (20×–60× magnification) and macrophotography. Specimens of whole plants were taken from the type subpopulation in form of pressed herbarium and alcohol (70% ethanol) specimen and deposited in SAR and OL.

Nomenclature

The electronic version of this article in Portable Document Format (PDF) in a work with an ISSN or ISBN will represent a published work according to the International Code of Nomenclature for algae, fungi, and plants, and hence the new names contained in the electronic publication of a PLOS ONE article are effectively published under that Code from the electronic edition alone, so there is no longer any need to provide printed copies.

In addition, the new name contained in this work has been submitted to IPNI, from where it will be made available to the Global Names Index. The IPNI LSIDs can be resolved and the associated information viewed through any standard web browser by appending the LSID contained in this publication to the prefix http://ipni.org/. The online version of this work is archived and available from the following digital repositories: PubMed Central, LOCKSS.

Results

Taxonomic treatment

Thismia kelabitiana Dančák, Hroneš & Sochor, *sp. nov.* [urn:lsid:ipni.org:names: 77187919–1] (Figs 1, 2 and 3).

Type. MALAYSIA, Sarawak: Kelabit Highlands, Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village. Coordinates WGS 84: N 03˚42'; E 115˚31', Elevation 1195 m a.s.l., 13 January 2017. M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & J.R. Pasan BOR1/17 (holotype SAR [in spirit and herbarium specimen, accession number Sochor/BOR-1/17], isotype OL [35272]).

Diagnosis. *Thismia kelabitiana* differs significantly from all congeneric species by the combination of the following traits, e.g., flowers large (up to 2.8 × 1.8 cm), outer perianth lobes deeply divided into 8–10 acute lobes and forming striking fringe around perianth tube opening, mitre relatively small and flat elevated by three long filiform pillars, connectives with prominent longitudinal rib and three appendices on apical margin.

Description. Achlorophyllous herb, *ca.* 5–18 cm tall. Roots short, clustered, coralliform, light brown. Stem 1.5–16 cm long and 2 mm in diameter, erect (or sometimes ascending), simple or sparsely branched in upper part (branches developing after anthesis), longitudinally ribbed, dark pinkish to reddish brown (to almost grey or orange); bearing 1 or 2(–3) flowers. Leaves (3–)6–10, spirally arranged, scale-like, triangular, acute to acuminate, entire, 4.5–5.5 mm long and 1.8–2 mm wide at base, light brown to pinkish. Bracts 3, widely triangular to ovate, entire to irregularly dentate and often deeply torn, *ca.* 6–8 × 2.5–4 mm, pinkish to brown. Flowers sessile, actinomorphic, 2.6–2.8 cm long; perianth tube of 6 fused tepals, funnel-shaped in the basal part, urceolate at the apical part, widest (1.2–1.3 cm) at its upper quarter, white to bright yellow at the top, with six brownish non-prominent longitudinal ribs and six yellow to brown longitudinal stripes on outer surface, inner surface net-like structured; outer perianth lobes falcate in outline, much wider than long, *ca.* 9 mm wide and 5 mm long, deeply divided into 8–10 acute lobes, bright yellow, arranged in one plane and together forming striking fringe around mouth of perianth tube, 1.6–1.8 cm in diameter; inner perianth lobes bright yellow to brownish-yellow, turned upwards, connate at the end and forming mitre, the proximal part of the lobe filiform, bent upwards, pillar-like, *ca.* 1.2 cm long and 0.8–1.0 mm wide in diameter, the distal part of the lobe ± flat, rhombic in outline, with central rib and two tetrahedral depressions on upper surface of each lobe; the lobes joined to form almost flat mitre, roundly triangular in outline, 7–8 mm wide. Stamens 6, pendent from the apical margin of the perianth tube; annulus absent; filaments yellow, curved downwards, with bases slightly emerged above perianth tube apex, not connate and forming six apertures apparent from upper view; connectives broad, laterally connate to form a tube, *ca.* 7 mm long, each with prominent longitudinal rib extending along the whole length of the inner side of the connective, apex of each connective with one central lobe (extension of the rib) and two smaller lobes pointing somewhat centrifugally and bearing one transparent trichome each; lateral appendage box-shaped, protruding towards perianth tube, not reaching the apex of the connective, shallowly dentate and sparsely hairy on free margins; thecae whitish, surrounded by tufts of hairs; interstaminal glands inserted on the line of fusion between connectives. Style short, stigma 3-lobed, papillose, lobes ± rectangular, longitudinally furrowed; ovary inferior, obconical, dark brown-reddish, covered by bracts. Capsule cup-shaped, 5–7 mm in diameter, dark brown to blackish or reddish before maturity, later pinkish, on very short pedicel; seeds numerous, brown, ellipsoid, *ca.* 0.3 × 0.5 mm.

Variability. The species is rather uniform, although only *ca.* 20 individuals were seen altogether. Stem is rather variable in colour and its length varies from 1.5 cm to 16 cm, which may

Fig 1. *Thismia kelabitiana*. **A**, Plant with flower bud. **B**, Plant with young flower. **C**, Plant with mature flower. **D**, Whole plant with root system. **E**, Detail of mitre and perianth opening. Photos Michal Sochor.

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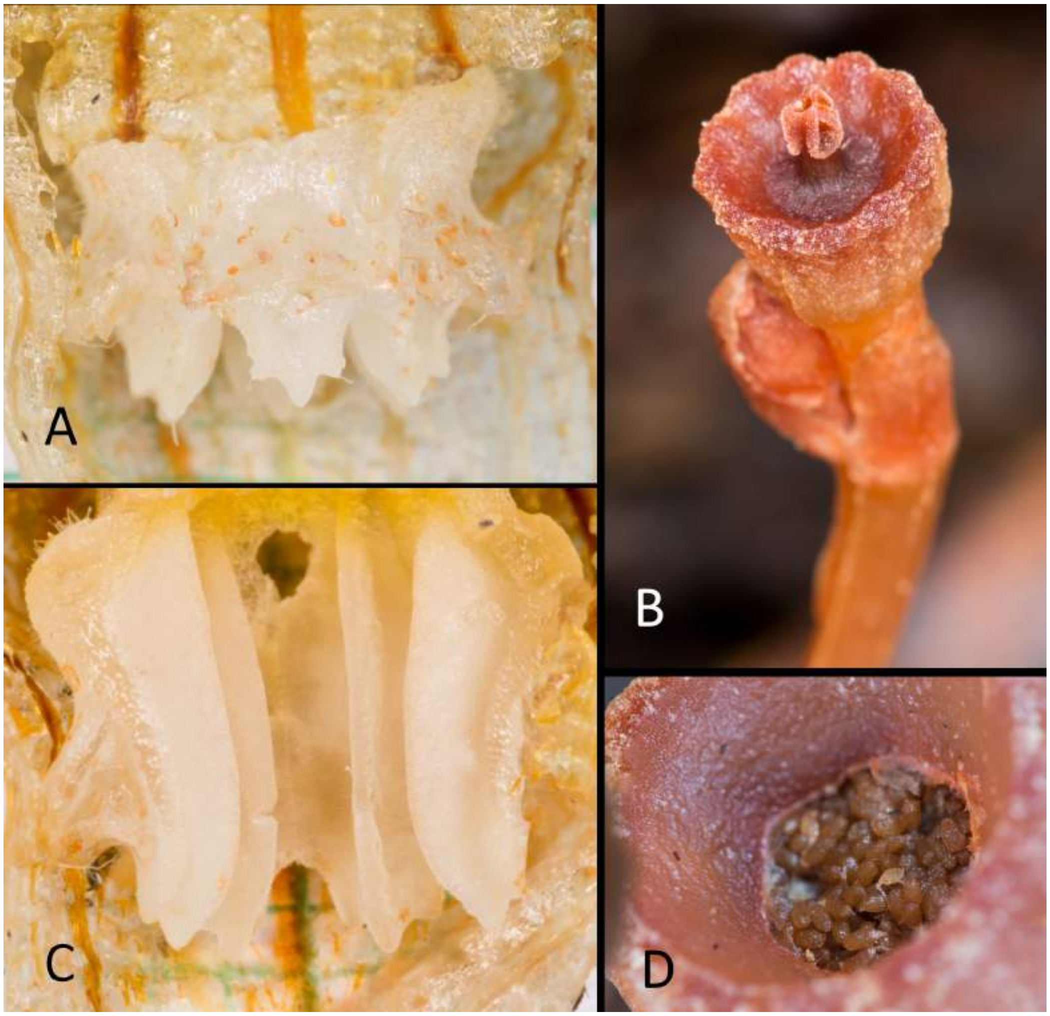

Fig 2. ***Thismia kelabitiana*****. A**, Outer view of stamens showing the lateral appendages and apical parts of connectives. **B**, Young capsule with persistent stigma. **C**, Inner view of stamens showing ribbed connectives. **D**, Seeds inside mature capsule. Photos Michal Sochor.

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be attributed to phenotypic plasticity likewise in many other species of the genus. The number of flowers is usually two, a few three-flowered individuals were also observed. Almost no variability was detected in flower size, colour and structure.

Habitat and ecology. The species occurs in lower montane primary tropical rainforest at an altitude around 1200 m a. s. l. It was found in humid stream ravines as well as in relatively drier open forest sites (Fig 4). A variety of other mycoheterotrophic species were abundant at the type locality, including *Aphyllorchis pallida*, *Burmannia lutescens* agg., *B*. *championii*, *Cystorchis aphylla*, *Gymnosiphon aphyllus* agg., *Epirixanthes kinabaluensis*, *Exacum tenue*, *Platanthera saprophytica*, *Sciaphila arfakiana*, *S*. cf. *nana*, *S*. *tenella*, *Thismia cornuta*, *T*. *minutissima* ined., *T*. aff. *nigra* and *T*. *viridistriata*. Herbaceous vegetation was otherwise sparse. *Thismia kelabitiana* seems not to prefer any particular environmental conditions at the locality as it occurs in various aspects of slopes with various inclinations either in rugged ravines or relatively flat terrain in various distances from a stream.

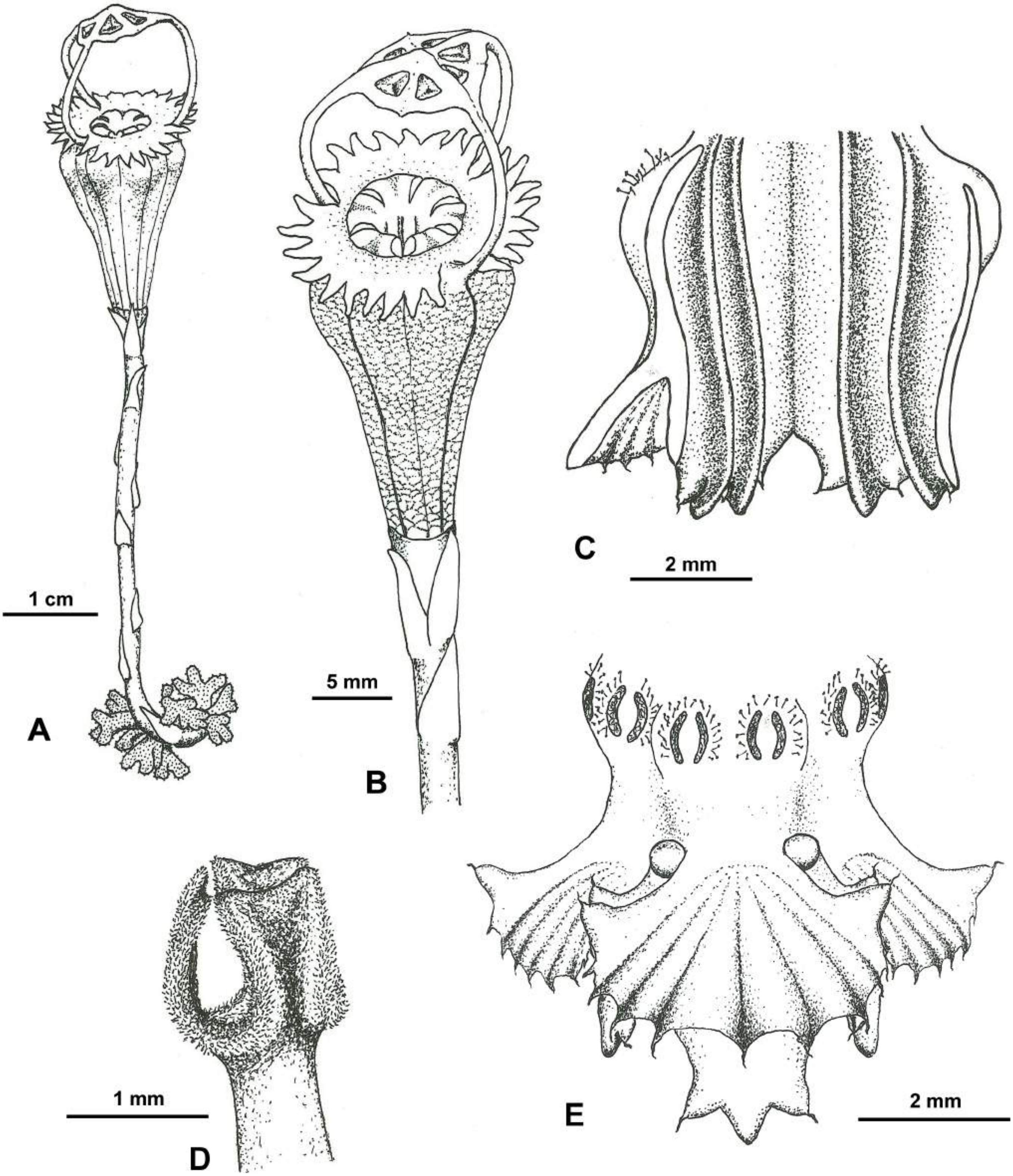

Fig 3. ***Thismia kelabitiana.*** **A**, Habit of flowering plant. **B**, Side view of flower. **C**, Inner view of stamens. **D**, Style with stigma. **E**, Outer view of stamens. Drawn by Kateřina Janošíková.

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Fig 4. Habitat of *Thismia kelabitiana*. Ravine of a small stream in lower montane tropical rain forest. Photo Michal Sochor.

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Distribution. The species is known only from the type locality and the other, 600 m distant locality, where plants have only been photographed. Both localities are found on a ridge southeast from Pa'Umor village in the Bario district of Sarawak (Malaysia).

Etymology. The specific epithet reflects the geographical origin of the species in the Kelabit Highlands, the land of the Kelabit people.

Common name. Pa'Umor Fairy Lantern. There is no widely accepted generic common name for the genus *Thismia*. The recent wave of interest as well as potential conservational employment, nevertheless, calls for this name. Sometimes the name Fairy Lantern is used [17], [18] which has originally belonged to *Thismia rodwayi* (either in singular or plural form as Fairy Lanterns). Since the name has already been used for a few other *Thismia* species, we follow this approach. We suggest calling *Thismia kelabitiana* Pa'Umor Fairy Lantern. The name is derived from Pa'Umor village community in whose forest the species occurs.

Conservation status. Both known subpopulations occur in primary rainforest that does not have any official protection status and falls under logging concessions [19]. Although the species may be locally common and the possibility of its occurrence in neighbouring regions of Sarawak and Indonesia cannot be excluded, its distribution is probably limited and scarce. It is one of the most robust *Thismia* species so far recorded, with conspicuous yellow flower and attractive appearance. Despite this, it was not recorded from nearby national parks Pulong

Tau and Kayan Mentarang. The extent of occurrence (EOO) of *T*. *kelabitiana* cannot be estimated because the species is only known from the type collection. The sites of the two subpopulations represent one location (*sensu* IUCN [20]; a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the taxon present) and its area of occupancy (AOO) is estimated to be 4 km^2, which falls within the limits for Critically Endangered status under criterion B2 of IUCN Red List Categories and Criteria [20]. Moreover none of the subpopulations contains more than 50 mature individuals. The species therefore fulfils criteria CR B2ab (iii,iv,v) and C2a(i), as well.

Discussion

Taxonomic affinities

Having coralliform roots and three perianth lobes that are connate at the top to form a mitre, the species clearly belongs to *Thismia* sect. *Sarcosiphon* [21]. However, it is unique among the known *Sarcosiphon* species in having several unparalleled traits. The flowers are relatively large among *Thismia* species, with almost 3 cm in length and nearly 2 cm in width are among the most robust in the whole genus. The form of mitre is also unique as it is relatively small, flat and positioned high above the perianth opening elevated by three filiform pillars. Furthermore, the presence of striking fringe around the perianth opening, apparently representing the outer perianth lobes, is very distinctive. Ribbed connectives are rare in the whole genus as well. Undoubtedly the most similar of all species of *Thismia* is *T*. *goodii* from Sabah [22]. In this species the outer perianth lobes are also extremely wide and short (although they are entire on margin) thus they form a discontinuous ring around the opening of the perianth tube and its mitre is structurally similar to that of *T*. *kelabitiana* as well. Although the drawing of connectives is not so detailed in the protologue of *T*. *goodii*, it is clear from the description that they are likewise very similar to those of *T*. *kelabitiana*. Interestingly, *Thismia clavigera* has extremely similar inner structure of the flower, though it was once classified in family monographs [23], [24] to another genus *Geomitra* on the basis of three long appendages arising from the top of the mitre. The only other known member of the former *Geomitra*, *Thismia betung-kerihunensis* shows some similarities to *T*. *goodii* as well (and hence also to *T*. *kelabitiana*), especially in the form of mitre. However, the rather poor description of connectives in the protologue of *T*. *betung-kerihunensis* [25] does not allow for comparison with the other species. These four species therefore might be in fact closely related and the presence of mitre appendages could be variable among them. Another pair of *Thismia* species, *T*. *gigantea* and *T*. *appendiculata*, i.e. genus *Scaphiophora* sensu Jonker, also shows some similarities to *T*. *kelabitiana*, especially in the form of the mitre. Nevertheless, they have a single erect appendage arising from the apex of the mitre. This pair of species belongs, however, among the least known species of *Thismia*, both being collected only once in the Philippines and New Guinea, respectively [23].

Conservational implications

We believe that *T*. *kelabitiana* may well become a surrogate species for lower montane primary tropical rainforest of the Bario part of the Kelabit Highlands. Thanks to its distinctive look, it is readily recognizable and thus may serve as a flagship species. As the only effective way of its protection is the conservation of its habitat, it is also a good candidate for an umbrella species. Forests in the southern part of the Kelabit Highlands have been almost completely disturbed by a dense network of logging and connection roads and subsequent selective logging. The nearest, newly-built road is less than 3 km from the type locality. However, the relatively small area (dozens of km^2) of primary forests between Pa'Umor village and abandoned village of

Pa'Main remains intact and the local community makes a remarkable effort to protect their land despite the fact that it is still under the logging concession. One possible way of helping to save at least some aspects of the traditional way of life of the Kelabit people that does not hamper socioeconomic development is ecotourism. Besides orchids and carnivorous plants, which traditionally attract public attention, *Thismia kelabitiana* may be another plant species that will increase the attractiveness of the region for ecotourism. As a flagship species, *T*. *kelabitiana* may then help local initiatives in obtaining any official protection status for the Pa'Umor forests, from Community Forest to a National Park.

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Thismia ornata and T. coronata (Thismiaceae), two new species from Sarawak, Borneo

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Thismia ornata and *T. coronata* (*Thismiaceae*), two new species from Sarawak, Borneo

Abstract: *Thismia ornata* and *T. coronata* (*Thismiaceae*), two new species from Sarawak (Malaysian Borneo) are described and illustrated. *Thismia ornata* belongs to *T.* sect. *Thismia* subsect. *Odoardoa* and occurs at several localities in western Sarawak around the city of Kuching. This species has been misidentified as *T. aseroe* until now, although the two species differ considerably. The species is assigned a preliminary conservation status of VU according to IUCN criteria. *Thismia coronata* belongs to *T.* sect. *Sarcosiphon* and has been found at only one site near the village of Long Tuyo in Lawas district of northern Sarawak. It is related to *T. goodii* and *T. kelabitiana*. The species is assigned a preliminary conservation status of CR.

Key words: Borneo, Malesia, mycoheterotrophy, new species, Sarawak, *Thismia*, *Thismia aseroe*, *Thismiaceae*, tropical rain forest

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Introduction

Thismia Griff. (*Thismiaceae*) is a genus of monocotyledonous plants that typically inhabit the understorey of tropical and subtropical forests. The genus comprises about 85 species (Dančák & al. 2018; Suetsugu & al. 2018b) and is distributed mostly in the tropical regions of Asia, Australia and South America and extending into subtropical and temperate regions of Japan, New Zealand, Australia and the USA (Merckx & al. 2013). Two main centres of *Thismia* diversity in Southeast Asia are located on the Malay Peninsula and in Borneo, with 16 and 22 recognized species, respectively (Jonker 1948; Chantanaorrapint 2018; Dančák & al. 2018; Nishioka & al. 2018; Siti-Munirah 2018; Tanaka & al. 2018; Siti-Munirah & Dome 2019; Dančák & al. 2020). The number of described species has been increasing rapidly over the last few years, which is probably one of the highest rates among angiosperms (Stevens 2001+). For example, 14 species were described in 2018 alone (Chantanaorrapint & Suddee 2018; Dančák & al. 2018; Hroneš & al. 2018; Nishioka & al. 2018; Siti Munirah 2018; Sochor & al. 2018; Suetsugu & al. 2018a, 2018b, 2018c; Tanaka & al. 2018).

During our field trip to Sarawak (Malaysian Borneo) in January and February 2019 we found two new species of *Thismia* and describe them in this article, which brings the number of Bornean species to 24.

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Material and methods

This study is based on material collected during January and February 2019 in Limbang and Kuching Divisions of Sarawak. Morphological characters were studied using a hand lens (30–60× magnification), stereo microscope and macro photography. Collected specimens were thoroughly compared with original drawings and descriptions given in protologues of representatives of *Thismia* sect. *Thismia* and *T.* sect. *Sarcosiphon* (Blume) Jonker. Herbarium vouchers for this study are deposited in SAR and OL. Because *Thismia* populations are sometimes composed of a few or even a single reproductive individual, voucher specimens were not always collected to prevent unnecessary harm to the population. In these cases only DNA samples were taken because for DNA analysis substantially less material is needed than for useful herbarium specimens. Also, herbarium vouchers were not collected if the only plants available were not in full bloom. In both cases plants were documented by photographs. Additionally, herbarium material deposited in K and SAR was studied (herbarium codes according to Thiers 2019+).

DNA was extracted by the CTAB method (Doyle & Doyle 1987) from a silica gel-dried piece of tissue from one individual per population. Sequence data were generated for three nuclear and two mitochondrial loci. The small subunit of ribosomal DNA (SSU rDNA) was amplified and sequenced with primers NS1 and NS6, internal transcribed spacers of ribosomal DNA (ITS) with primers ITS1 and ITS4 (White & al. 1990) and large subunit of ribosomal DNA (LSU rDNA) by primers N-nc26S6 and 2134rev (Kuzoff & al. 1998). The mitochondrial genes *atpA* and *matR* were amplified and sequenced with primers developed by Eyre-Walker & Gaut (1997) and primers 26F and 1002R (Meng & al. 2002), respectively. All PCRs were performed with Kapa polymerase (Kapa Biosystems) following a standard protocol with 37 to 40 cycles and annealing temperature of 56°C (rDNA, *atpA*) or 47 °C (*matR*). The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25 M NaCl in the precipitation mixture) and sequenced in both directions by Sanger method at Macrogene Europe. The most variable locus, ITS, was sequenced in all collections to screen variation, whereas the other loci were only analysed in selected specimens.

Sequences were edited and aligned in Geneious 8 (Biomatters) and deposited in NCBI GenBank under accession numbers MN067232–MN067237, MN067250–MN067259, MN067281–MN067283, MN067288, MN067290, MN067300, MN067302, MN067303, MN067307, MN067309, MN067318–MN067320, MN067327 and MN067328. The newly generated sequences were added to the dataset from Sochor & al. (2018) and Dančák & al. (2020), which included nine species whose sequences were downloaded from NCBI GenBank. The alignments are provided as supplemental content online. Bayesian phylogeny inference from concatenated data from the five loci (or four in the GenBank accessions) was computed in MrBayes (ver. 3.2.4; Ronquist & al. 2012) with 2×10^7 generations, sampling every 3000th generation, in two independent runs, each with four chains; the first 10^7 generations (50%) were excluded as burn-in. The substitution model for each locus was used as determined by Sochor & al. (2018; ITS1, ITS2 and 5.8S rDNA were treated as separate partitions).

Results and Discussion

Thismia ornata Dančák, Hroneš & Sochor, **sp. nov.** – Fig. 1 & 2.
Holotype: Malaysia, Sarawak, Kubah National Park, 0.8 km NE of Matang Wildlife Centre, WGS 84: 01°36'49"N, 110°09'57"E, elevation 60 m a.s.l., 7 Feb 2019, *Sochor, Hroneš & Dančák BOR51/19* (SAR! [in spirit]; isotype: OL! [pressed specimen]).

Diagnosis — *Thismia ornata* differs from the most similar known species, *T. filiformis* Chantanaorr., by flower size (to c. 10 cm in diam. vs to c. 3 cm including tepal appendages), inner surface of floral tube (with very fine bright orange reticulum inside vs lacking any reticulum), length of tepal appendages (to 35 mm vs to 8 mm), appendages on apical margin of connective (five of three different shapes vs three of two different shapes) and shape of lateral appendage (with small horn-shaped projection arising from each side of the lateral appendage vs lacking any horn-shaped projections).

Description — Achlorophyllous herb, 7–11 cm tall. *Roots* creeping, vermiform, ± horizontal, poorly branched, pale brown. *Stem* white to pale cream-brown, 4.5–8 cm tall, erect, ribbed, verrucose, bearing 1 or 2 (or 3) flowers. *Leaves* spirally arranged, appressed, scale-like, narrowly triangular, acute, entire, 4–6 mm long, light brown to pinkish. *Bracts* 3, similar to leaves, surrounding base of ovary, lanceolate-triangular, acute, entire, verrucose, to 10 mm long, light brown to pinkish. *Flowers* (sub)sessile, actinomorphic, 1.7–2.2 cm long; *floral tube* funnel-shaped toward base, slightly urceolate at apex, widest (0.9–1.1 cm) in upper quarter, with 12 orange longitudinal ribs and conspicuous bright orange reticulum on inner surface, outer surface pinkish with 12 thin reddish brown longitudinal stripes, verrucose. *Annulus* circular, outer margin markedly raised and brownish yellow, inner margin bright yellow, middle part brownish orange. *Tepals* 6, all equal in shape and size, narrowly triangular, 6–10 mm long, c. 4 mm wide at base, yellow with 3 longitudinal red stripes, tapering into a white filiform appendage 20–35 mm long. *Stamens* 6, connate and forming a tube, pendent from floral tube aperture, translucent; *filaments* free, short, curved downward; *connectives* broad and flattened, each connective with 5 appendages at apical margin and a large box-shaped lateral append-

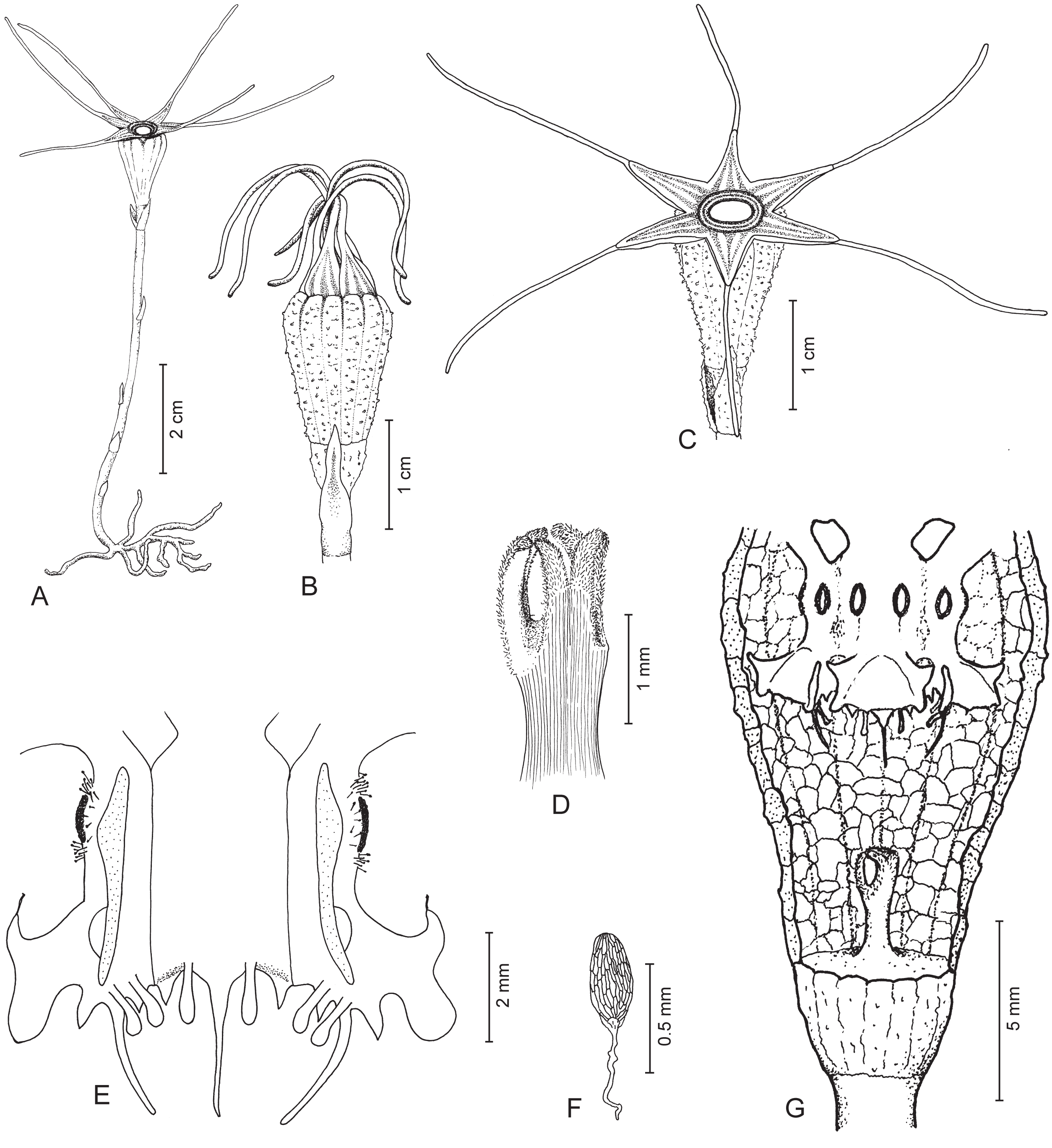

Fig. 1. *Thismia ornata* – A: habit of flowering plant; B: flower bud; C: detail of flower, apical view; D: stigma; E: inner view of stamens,; F: seed; G: outer view of stamens and inside of floral tube. – From *Sochor & al. BOR 51/19* (A, C–E, G), *BOR54/19* (B), *BOR 56/19* (F). – Drawn by Kateřina Janošíková.

age on distal part protruding toward floral tube with an interstaminal gland inserted on line of fusion between connectives; lateral appendage dark brown, with small horn-shaped projection arising from both sides, appendages on apical margin arranged as follows: outer pair of appendages directed outward, triangular, c. 0.8 mm long, apex acute; inner pair inserted above margin and directed inward, cylindric, c. 1 mm long, ± straight, apex domed; central solitary appendage caudate, c. 1.8 mm long, ± pendent. *Ovary* inferior, obconic, indistinctly ribbed, verrucose, whitish to pale brown, darker on apex; *style* c. 1.5 mm long; *stigma* 3-lobed, lobes bifid, hairy, c. 1.2 mm long. *Fruit* an obconical to cup-shaped pale brown ribbed capsule, 4–5 mm long, borne on very short fruit stalk. *Seeds* ellipsoid, beige with fine brown reticulum, 0.38–0.45 mm long, 0.17–0.21 mm wide.

Distribution — *Thismia ornata* occurs in western Sarawak in a number of locations surrounding Kuching, including Kubah National Park, Santubong National Park, Dered Krian National Park and Fairy Cave Nature Reserve (Fig. 3).

Fig. 2. *Thismia ornata* – A, B: overall appearance; C: detail of flower, apical view; D: ovary, stigma and inner surface of floral tube (background grid spacing = 1 mm); E: seeds; F: inner view of stamens; G: lateral view of connective after cutting off neighbouring connective; H: outer view of stamen. – From *Sochor & al. BOR53/19* (A), *BOR51/19* (B–D, F–H) and *BOR56/19* (E).

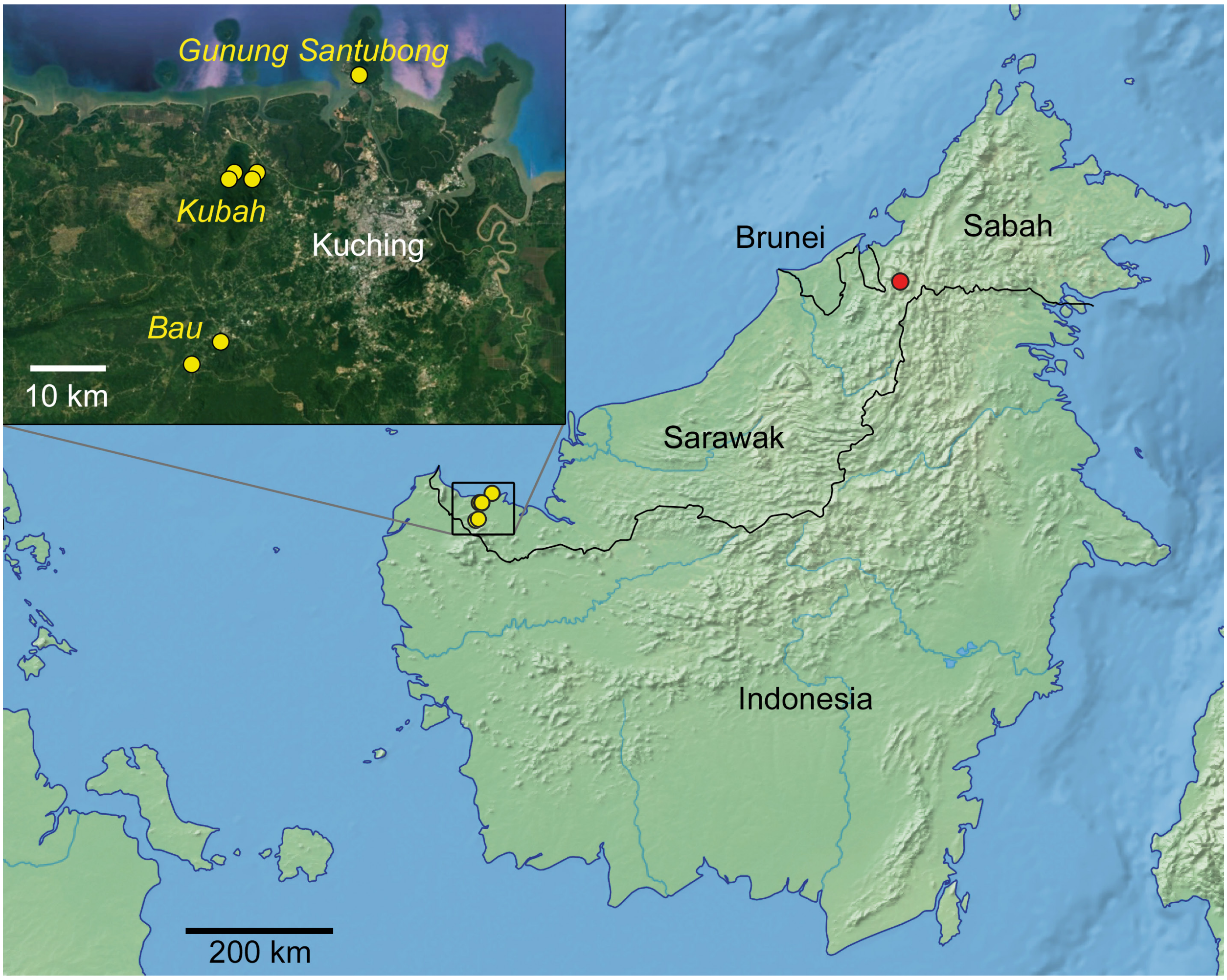

Fig. 3. Distribution of *Thismia ornata* (yellow circles) and *T. coronata* (red circle). – Aerial image modified from Google Earth (https://www.google.com/earth/).

Habitat — *Thismia ornata* inhabits a wide range of tropical lowland rain forest habitats with an altitudinal range from 40 m to c. 300 m a.s.l. It is known from rather dry limestone outcrops, lowland mixed dipterocarp forests, riverine forests including forests with some anthropogenic disturbance.

Conservation status — *Thismia ornata* is endemic to Borneo. Most, if not all, known populations occur within national parks and other protected areas. While the extent of occurrence (EOO) is c. 270 km^2, its minimal area of occupancy (AOO) could be estimated to be 30 km^2. It is known from several populations, which represent three locations (sensu IUCN 2012). *Thismia ornata* is therefore assigned a preliminary conservation status of VU (D1+2) according to the IUCN Red List categories and criteria (IUCN 2012).

Etymology — The specific epithet is the feminine form of the Latin adjective *ornatus* (ornate or decorated), whichreflects the colourful flowers and very fine bright orange reticulum inside the floral tube that resembles lace.

Remarks — *Thismia ornata* is not completely unknown to the scientific community; it has been collected several times (see Additional material examined) and many of its photographs circulate on the internet, especially from limestone outcrops around Bau town (e.g. Fehland 2019). However, it has been misidentified as *T. aseroe* Becc., a superficially morphologically similar but not closely related species (unpublished data). *Thismia ornata* was also studied under the name of *T. aseroe* in an extensive study of floral morphology and development in *Dioscoreales* (Caddick & al. 2000) and is adequately described and illustrated in that work. Correspondingly, the DNA sequence entries in GenBank that are based on the specimen *Caddick 349* (K, SAR!) and stored under the name *T. aseroe* belong to *T. ornata* (see Fig. 4).

Thismia ornata belongs to *T.* sect. *Thismia* subsect. *Odoardoa* Schltr. on account of its having six free tepals of the same size and shape. Relationships of *T. ornata* within this section however are unclear. Its morphology is rather unique although it superficially resembles *T. filiformis* (and its relatives). The inner morphology of the flower is different. The bright orange reticulum in-

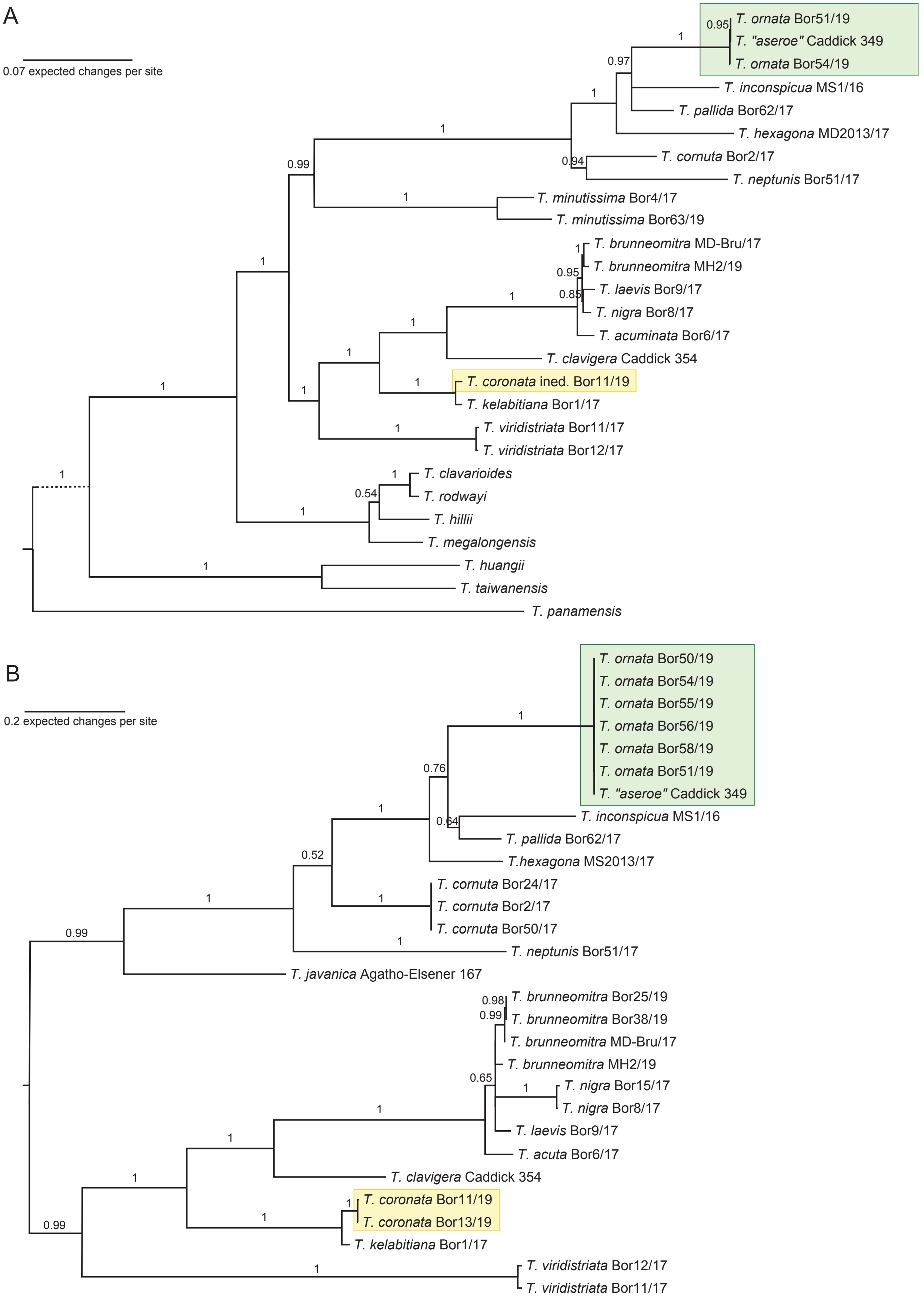

Fig. 4. A: Bayesian phylogeny tree based on five-locus analysis of a wider Old World species set. – B: Bayesian phylogeny tree of *Thismia* sect. *Thismia* and *T.* sect. *Sarcosiphon* based on ITS sequences. – Posterior probabilities are shown above the branches.

side the floral tube is absent in other Bornean species of *Thismia*, with the exception of *T. kelabitiana* Dančák, Hroneš & Sochor, which is somewhat reticulated. For *T. ornata*, the apical margin of the connective bears five appendages of three different sizes and shapes. The single central appendage is the longest while the remaining appendages are considerably shorter. One pair of these appendages sits directly on the apical margin of the connective while the other pair is shifted upward to the surface of the connective and resembles appendages known in *T. hexagona* Dančák, Hroneš, Kobrlová & Sochor and *T. bryndonii* Tsukaya, Suetsugu & Suleiman (Dančák & al. 2013; Tsukaya & al. 2017). Although it has been frequently misidentified as *T. aseroe*, the two species are different. *Thismia aseroe* has a prominently raised annulus and small teeth alternating with the tepals, which make it appear different to the naked eye. The structure of the connectives is also strikingly different between the two species (for comparison see Groom 1895 and Fig. 2).

Although no variation was detected among the seven studied specimens (six of them from Kubah) at the ITS locus (see also Fig. 4B), one SNP was detected at each of the SSU and *matR* loci in the Santubong population (Fig. 4A). Such a small difference, of course, cannot have consequences in taxonomy, but it implies that the species exhibits some small geographical genetic variation. Nevertheless, no significant variability in phenotype was observed.

Additional material examined — Borneo, Sarawak (Malaysia): 1st Division, Bau, Tai Ton, 2 Jan 1977, *P. J. Martin 38504* (SAR); 1st Division, Bau, limestone hill behind lake, 11 Nov 1989, *P. Cribb 89/16* (K); Bau, Seburan, 8 Jun 1966, *J. A. R. Anderson 25524* (SAR); Matang National Park, Sungai Rayu, 150 m a.s.l., 21 Oct 1998, *L. Caddick, V. B. Kasik, D. Jude, M. Kapi LRC 349* (SAR); Kubah National Park, Matang Wildlife Centre, near the crocodile cage, WGS 84: 01°36'31"N, 110°09'42"E, 45 m a.s.l. 9 Feb 2019, *Sochor, Hroneš & Dančák BOR55/19* (only DNA material, no voucher specimen); Kubah National Park, 0.8 km SW of headquarters, WGS 84: 01°36'25"N, 110°11'30"E, 235 m a.s.l., 9 Feb 2019, *Sochor, Hroneš & Dančák BOR56/19* (only DNA material, no voucher specimen); Kubah National Park, 30 m SW of Park hostel, WGS 84: 01°36'42"N, 110°11'43"E, 170 m a.s.l., 9 Feb 2019, *Sochor, Hroneš & Dančák BOR58/19* (only DNA material, no voucher specimen); Gunung Santubong, along contour trail, WGS 84: 01°43'55"N, 110°19'34"E, c. 300 m a.s.l., 8 Feb 2019, *Sochor, Hroneš & Dančák BOR54/19* (OL).

Thismia coronata Hroneš, Dančák & Sochor, **sp. nov.** – Fig. 5, 6 & 7.
Holotype: Malaysia, Sarawak, Limbang Division, Lawas District, Long Tuyo village, primary forest between camps 1 and 2 on trail to Paya Maga mountain plateau, WGS 84: 04°26'37"N, 115°33'07"E, elevation 1305 m a.s.l., 29 Jan 2019 *Sochor, Hroneš & Dančák BOR11/19* (SAR! [in spirit]; isotype: OL! [pressed specimen]).

Diagnosis — *Thismia coronata* differs from *T. kelabitiana* by the shape of outer tepals (entire with a single tooth in the middle vs deeply divided into several acute lobes), mitre apex (without tetrahedral depressions on upper surface vs with tetrahedral depressions on upper surface), smaller size of flower (1.8–2.3 cm vs 2.6–2.8 cm long) and flower colour (dark yellow to orange across whole flower vs white floral tube and bright yellow upper parts).

Description — Achlorophyllous herb, 4.5–8 cm tall. *Roots* coralliform, short, clustered, light brown. *Stem* 2.4–4.2 cm long, erect (or sometimes ascending), unbranched or sparsely branched in upper part (branches developing after anthesis), indistinctly longitudinally ribbed, reddish brown to orange, bearing 1–6 flowers. *Leaves* 4–11, spirally arranged, appressed, scale-like, triangular, acute to acuminate, entire, 2–5 mm long, 1–2 mm wide at base, light brown to reddish. *Bracts* 3, lanceolate-triangular, entire to irregularly dentate, 4–8 × 2–3 mm, reddish to brown. *Flowers* sessile, actinomorphic, 1.8–2.3 cm long; *floral tube* funnel-shaped toward base, urceolate at apex, widest (0.7–1 cm) in upper quarter, dark yellow to orange throughout, with 6 brown-orange prominent longitudinal ribs alternating with 6 brown-orange longitudinal stripes on outer surface, inner surface with a weakly net-like pattern, especially toward apex. *Tepals* 6; outer 3 tepals falcate, c. 2 mm long, 6–7 mm wide, entire or slightly sinuate at margin, sometimes somewhat wavy, usually with a single tooth in centre, bright orange, arranged in one plane and together forming fringe around mouth of floral tube, 0.9–1.2 cm in diam.; inner 3 tepals orange, pillar-like and arched over floral tube, connate at apex and forming a rather flat triangular mitre 5–7 mm wide, proximal part of tepal 0.5–0.9 mm long, c. 1 mm wide, distal part of tepal ± flat with 3 joined ribs. *Annulus* absent. *Stamens* 6, pendent from floral tube aperture; *filaments* orange, curved downward, with bases slightly protruding above floral tube apex, not connate and forming 6 lateral apertures visible from upper side; *connectives* broad, laterally connate to form a tube, 5–6 mm long, each with prominent longitudinal rib extending along whole length of inner side of connective, apex of each connective white to bluish, with 1 central lobe (extension of rib) and 2 smaller lobes, each lobe bearing 1 very long transparent trichome; lateral appendage box-shaped, protruding toward floral tube, not reaching apex of connective, shallowly dentate and hairy on apical margin, with tufts of hairs on lateral margins, yellow-tinted; thecae creamy, surrounded by tufts of glandular hairs; interstaminal glands inserted on line of fusion between connectives. *Ovary* inferior, obconic, dark brown, covered by bracts, placentae 3, ovules nu-

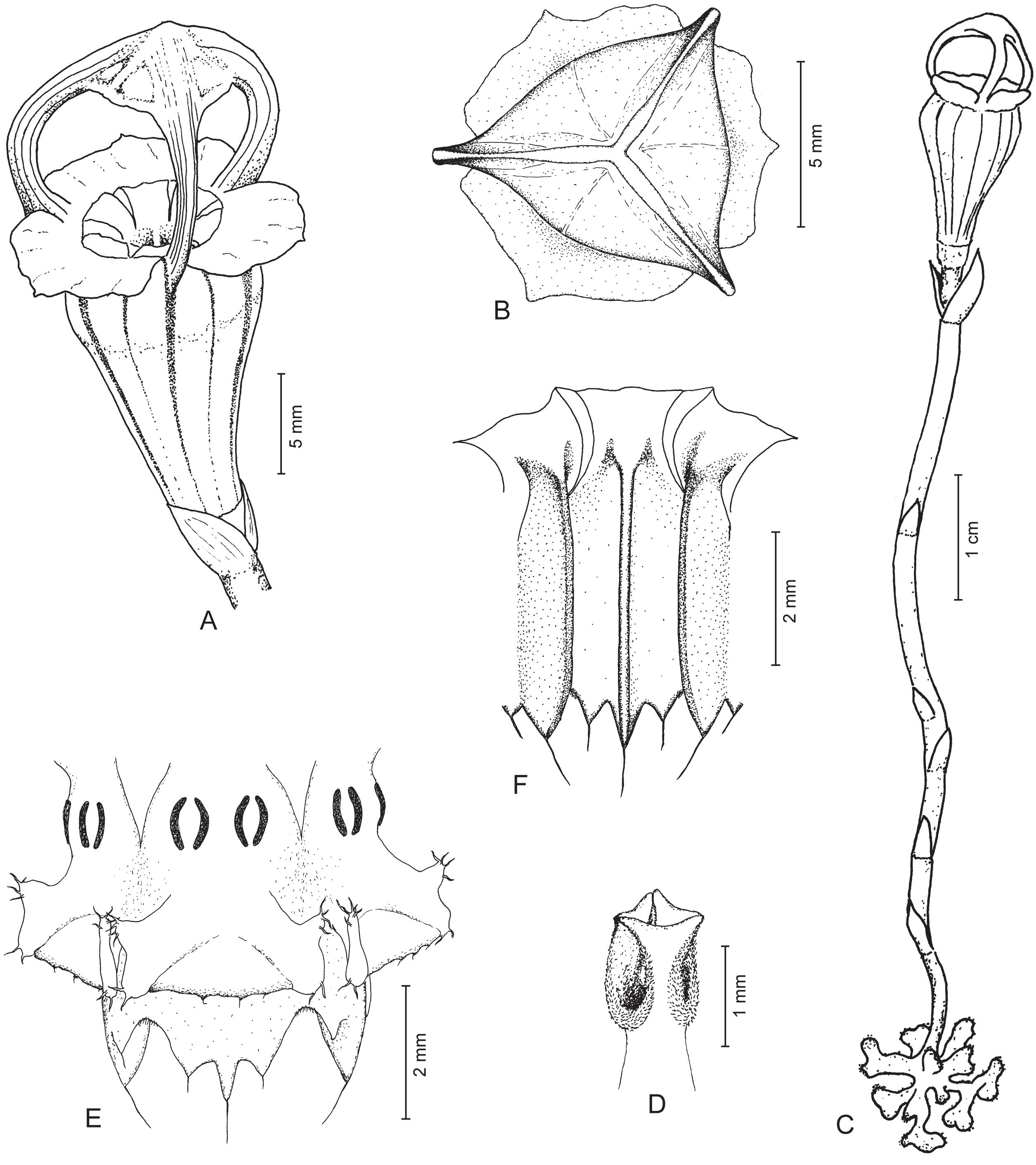

Fig. 5. *Thismia coronata* – A: lateral view of flower; B: apical view of flower; C: habit of flowering plant; D: stigma; E: outer view of stamens; F: inner view of stamens. – From *Sochor & al. BOR11/19* (A–H). – Drawn by Kateřina Janošíková.

merous, anatropous; *style* short; *stigma* 3-lobed, papillose, lobes ± rectangular, longitudinally furrowed. *Capsule* cup-shaped, 5–7 mm in diam., pale brown to reddish at maturity; fruiting pedicel 10–25 mm long. *Seeds* numerous, light brown, ellipsoid.

Distribution — *Thismia coronata* is known only from the type locality and its close surroundings in the Paya Maga mountain range in northern Sarawak (Fig. 3). At least 40 individuals were recorded at the locality.

Habitat — *Thismia coronata* occurs in lower montane primary tropical rainforest at an altitude around 1300 m a.s.l. It was found in relatively humid forest with dense understorey (Fig 7C). A variety of other mycoheterotrophic species were abundant at the type locality and surroundings, including *Burmannia lutescens* Becc. agg. (*Burmanniaceae*), *Cystorchis aphylla* Ridl. (*Orchidaceae*), *Epirixanthes kinabaluensis* T. Wendt, *E. pallida* T. Wendt (both *Polygalaceae*), *Exacum tenue* (Blume) Klack. (*Gentianaceae*), *Lecanorchis multiflora* J. J. Sm.

Fig. 6. *Thismia coronata* – A: flower prior to anthesis; B, C, D: overall appearance; E: apical view of flower; F: stigma; G: roots; H: outer bottom view of stamen. – Finest grid spacing in D and G = 1 mm. – From *Sochor & al. BOR11/19* (A–H).

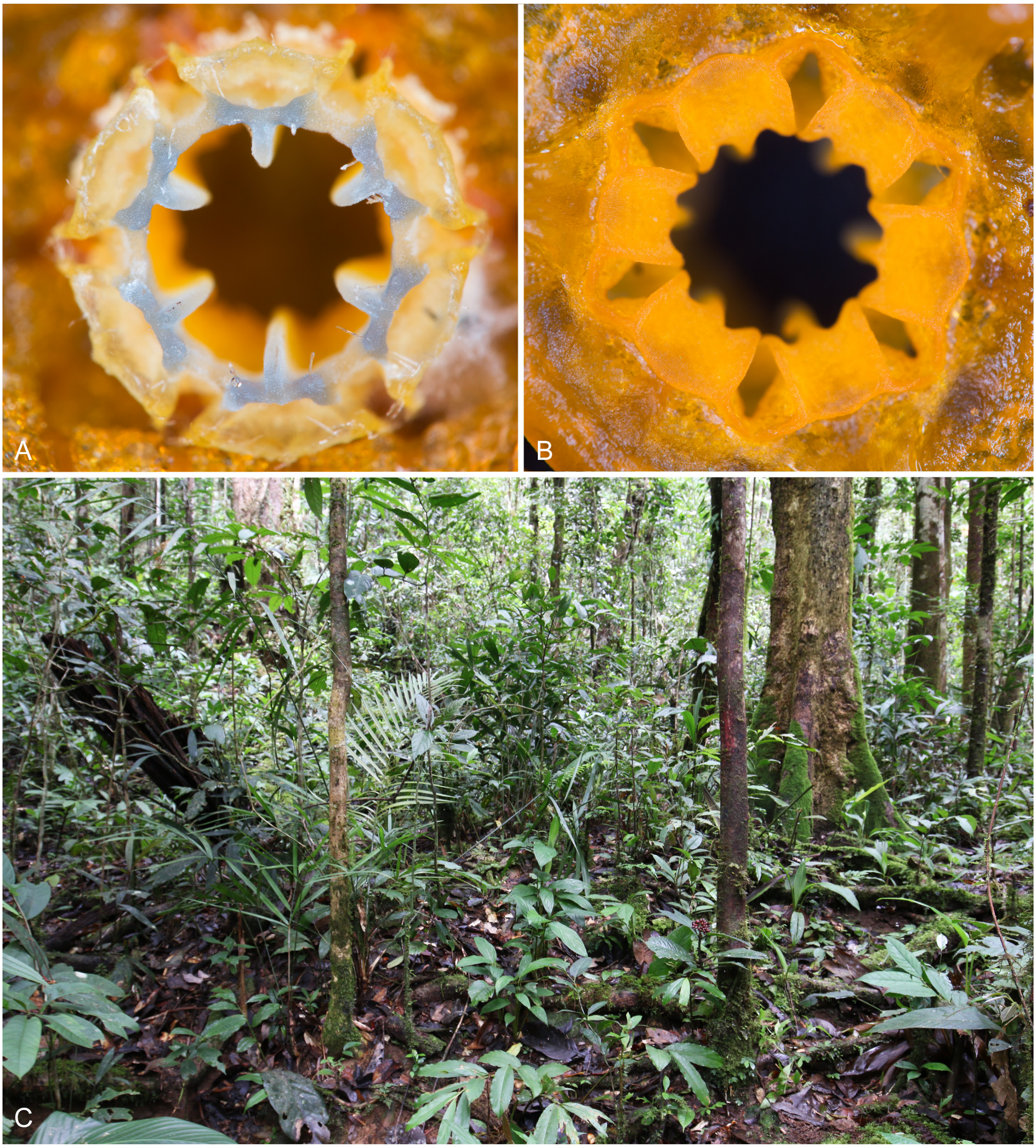

Fig. 7. *Thismia coronata* – A: connective tube viewed from lower side; B: floral tube apex and opening showing 6 lateral apertures between stamens; C: type locality, 29 Jan 2019, photograph by M. Sochor. – From *Sochor & al. BOR11/19* (A–C).

(*Orchidaceae*), *Sciaphila arfakiana* Becc., *Sciaphila* sp. (both *Triuridaceae*) and *Thismia viridistriata* Sochor, Hroneš & Dančák. Herbaceous vegetation was otherwise sparse.

Conservation status — *Thismia coronata* is endemic to Borneo and the only known population occurs outside national parks and other protected areas. The number of mature individuals observed is fewer than 50. The extent of occurrence cannot be estimated because the species is known only from the type locality and its area of occupancy (AOO) is estimated to be only 4 km^2. *Thismia coronata* is therefore assigned a preliminary status of CR (B2ab(iii); D) according to the IUCN Red List categories and criteria (IUCN 2012).

Etymology — The specific epithet is the feminine form of the Latin adjective *coronatus* (crowned), which reflects the shape and colour of the tepals resembling a royal crown.

Remarks — *Thismia coronata* superficially resembles *T. kelabitiana* mostly by its colour, which is, nevertheless, darker and nearly homogeneous across the flower. However, the flower shape is similar to *T. goodii* Kiew, which differs in colour (blue tepals and white floral tube with a green tinge), smaller mitre and hairless apex of the connective. These three species (*T. coronata*, *T. goodii* and *T. kelabitiana*) are clearly closely related (see also Fig. 4), forming a morphologically distinct group within *T.* sect. *Sarcosiphon*. They share the well-developed outer tepals that are wider than long, trilobed apex of the connective and a prominent central rib along the inner side of the connective. *Thismia goodii* is almost sympatric with *T. coronata*: it is known from a nearby site only 1.5 km away (Ampeng & al. 2013). All three species occur in the highlands of northern Borneo and have no apparent relatives outside this region. Interestingly, this group bears some similarities to the group of *T. clavigera* (Becc.) F. Muell. (see also Dančák & al. 2018). Although both groups are superficially rather different, primarily due to the three mitre appendages present in the *T. clavigera* group, the structure of the stamens is somewhat similar in both groups because the filaments reach the floral opening (which has no annulus) and the connectives have a prominent central rib along their inner side.

Additional material examined — Borneo, Sarawak (Malaysia): Limbang Division, Lawas District, Long Tuyo village: primary forest between camps 1 and 2 on trail to Paya Maga Mountain plateau, WGS 84: 04°26'36"N, 115°33'04"E, elevation c. 1280 m a.s.l., 29 Jan 2019 *Sochor, Hroneš & Dančák BOR13/19* (only DNA material, no herbarium specimen).

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Thismia minutissima (Thismiaceae), a remarkable new mycoheterotrophic species from Sarawak, Borneo

Martin Dančák[1], **Michal Hroneš**[2] & **Michal Sochor**[3]

Summary. *Thismia minutissima*, a distinctive minute species of the mycoheterotrophic genus *Thismia* is described and illustrated. It was found in several localities in mountain areas of Sarawak, Malaysia. The new species is superficially similar to members of *Thismia* sect. *Rodwaya* from Australia and New Zealand but differs by several distinctive morphological traits, including a fishtail-like lateral connective appendage and a perfect mitre. Its ecology, distribution and taxonomic status, as well as phylogenetic placement, are discussed.

Key Words. Burmanniaceae, funiculus, fairy lantern, Malesia, rainforest, seed, taxonomy.

Introduction

Fairy lanterns, *Thismia* Griff. (Thismiaceae, or alternatively Burmanniaceae sensu APG IV; The Angiosperm Phylogeny Group 2016), are non-photosynthetic mycoheterotrophic herbs of mainly tropical distribution. The number of known species in the genus has been increasing rapidly in recent years, with 85 species recognised at the end of 2018 (e.g. Chantanaorrapint & Suddee 2018; Dančák *et al.* 2018; Hroneš *et al.* 2018; Siti-Munirah 2018; Sochor *et al.* 2018b; Suetsugu *et al.* 2018a; Suetsugu *et al.* 2018b; Tanaka *et al.* 2018). New records of the genus have recently been published for Lao PDR, the Andaman Islands and peninsular India (Kumar *et al.* 2017; Sujanapal *et al.* 2017; Hareesh *et al.* 2018) as well as rediscoveries of some earlier described taxa (Chantanaorrapint 2018; Sochor *et al.* 2018a).

The infrageneric taxonomy of *Thismia* still remains controversial despite the current progress (e.g. Kumar *et al.* 2017; Sochor *et al.* 2018b). Four main groups are recognised in the Old World: sect. *Thismia*, sect. *Sarcosiphon* (Blume) Jonker, sect. *Rodwaya* (Schltr.) Jonker and sect. *Glaziocharis* (Taub. ex Warm.) Hatus. (Kumar *et al.* 2017). However, several species cannot be placed into the current infrageneric system, e.g. *T. sahyadrica* Sujanapal, Robi & Dantas (Sujanapal *et al.* 2017; Shepeleva *et al.* 2020).

During our recent field trips to Sarawak (Malaysian Borneo), several populations of a unique *Thismia* were discovered. They are distinct from all previously described species, both in their morphology and molecular markers. We describe these populations as a species new to science here.

Material and Methods

Morphology was studied in the field using hand lenses (20 – 60× magnification) and macrophotography. Specimens were preserved in the form of pressed herbarium and alcohol (70% ethanol) specimens and deposited in SAR and OL; a piece of tissue from one individual per population was silica gel-dried for subsequent DNA extraction.

DNA was extracted by the CTAB method (Doyle & Doyle 1987) and sequence data were generated for three nuclear and two mitochondrial loci. The small subunit of ribosomal DNA (SSU rDNA) was amplified and sequenced with primers NS1 and NS6, internal transcribed spacers of ribosomal DNA (ITS) with primers ITS1 and ITS4 (White *et al.* 1990) and the large subunit of ribosomal DNA (LSU rDNA) by primers N-nc26S6 and 2134rev (Kuzoff *et al.* 1998). The mitochondrial genes *atpA* and *matR* were amplified and sequenced with primers developed by Eyre-Walker & Gaut (1997) and primers 26F and 1002R (Meng *et al.* 2002), respectively. All PCRs were performed with Kapa polymerase (Kapa Biosystems) following a standard protocol with 37 – 40 cycles and

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an annealing temperature of 56°C (rDNA, *atpA*) or 47°C (*matR*). The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25 M NaCl in the precipitation mixture) and sequenced in both directions by the Sanger method at Macrogen Europe.

Sequences were edited and aligned in GENEIOUS 8 (Biomatters) and deposited in NCBI GenBank. The newly generated sequences were added to the dataset from Sochor *et al.* (2018b), which included nine species whose sequences were downloaded from NCBI GenBank (for a complete list of analysed specimens, see Electronic Supplementary Material S1). Bayesian phylogeny inference from concatenated data from the five loci (or four in the case of GenBank accessions) was computed in MRBAYES (ver. 3.2.4; Ronquist *et al.* 2012) with 2×10^7 generations, sampling every 3000th generation, in two independent runs, each with four chains; the first 10^7 generations (50%) were excluded as burn-in. A substitution model for each locus was used as determined by Sochor *et al.* (2018b; ITS1, ITS2 and 5.8S rDNA were treated as separate partitions).

Taxonomic Treatment

Thismia minutissima *Dančák, Hroneš & Sochor* **sp. nov.** Type: Malaysia, Sarawak, Kelabit Highlands, Miri Division, Bario Subdistr., Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village, 03°42'01"N, 115°31'28"E, alt. 1195 m, 13 Jan. 2017, *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & J. R. Pasan* BOR4/17 (holotype SAR! [in spirit, accession number Sochor/BOR-4/17]; isotype OL! [in spirit, accession number 35278]).

Achlorophyllous *herb*, 2.5 – 5 cm tall. *Roots* vermiform, creeping, sparsely branched, c. 1 mm thick, whitish to light brown. *Stem* 1.5 – 2 cm tall, ascending (then up to 5 cm long) to erect, unbranched, single-flowered, 1.5 mm thick, whitish. *Leaves* 2 – 4, spirally arranged, triangular to narrowly triangular, scale-like, acute, entire, 3 – 5 mm long, c. 1 mm wide at base, whitish. *Bracts* 3, similar to leaves but slightly larger. *Pedicel* 3 – 5 (– 12) mm long, elongating after anthesis, white. *Flowers* terminal, actinomorphic, 6 – 9 mm long (excluding free perianth appendages), 2.5 – 4 mm wide in the upper ⅓ of floral tube; floral tube urceolate, 3 – 4 (– 5) mm long, outer surface with 6 low, longitudinal ribs, orange, with 6 small, oblong, red spots going down from between perianth lobes and larger whitish, diffuse spots between ribs in the upper ½ of floral tube; inner surface smooth without transverse bars and other ornamentation; outer perianth lobes free, small, often rather inconspicuous, broadly triangular or rounded to tongue-like, 0.3 – 1 mm long, orange, with several teeth-like protrusions on abaxial side; inner perianth lobes well-developed, inseparably fused and forming dome-like mitre leaving three holes and each bearing narrowly conical to filiform appendage arising from the central rib on its outer surface; mitre c. 1.5 mm tall, bright red to dark orange, with distinct to indistinct lines of fusion, holes more or less rounded; mitre appendages 3.5 – 6 (– 8) mm long, orange, with distinct warts spread from the base of the appendages down to the upper part of floral tube mainly along ribs; annulus crenate, formed by 12 short lobes, densely hairy, bright red. *Stamens* 6, pendent from the apical margin of the floral tube, ± colourless or pale orange-pink to orange, densely covered with transparent hairs all over, the hairs on connectives short, on filaments and around anthers long; filaments free, short, curved downwards; connectives broad and flattened, laterally connate to form a tube, c. 1.8 mm long, with ± unlobed to shallowly irregularly dentate apex bearing several transparent, ± cylindrical, c. 0.1 mm long single-celled trichomes; outer side of connective with bilobed, fishtail-like lateral appendage protruding towards floral tube, not exceeding the apex of connective, mostly bright red, bearing dense, long, transparent hairs on margins, each stamen with 2 thecae (dehiscing towards inner surface of floral tube, c. 0.55 mm long); interstaminal glands translucent, inserted on the line of fusion between connectives at the level of attachment of appendages. *Ovary* inferior, unilocular, slightly urceolate to cup-shaped, white; placentas 3, free, forming columns and arising from the bottom of the ovary; ovules anatropous, numerous. *Style* c. 1 mm long (twice the length of the stigma), pale orange; stigma papillose, 3-lobed, with lobes ± rectangular, bright orange to orange-red. *Fruit* a cup- to (later) funnel-shaped capsule, 4.5 – 6.5 mm in height and diam., white to creamy, borne by an elongated pedicel up to 47 mm long. *Seeds* whitish, ellipsoid, c. 0.9 (incl. thickened part of funiculus) × 0.4 mm, dorsally encircled by, and on the chalazal pole covered by, a thickened, light brownish funiculus. Figs 1 – 3.

RECOGNITION. *Thismia minutissima* differs from all its congeners by the following combination of traits: roots vermiform; stem and fruiting pedicel very thin, pure white; floral tube orange, short, 3 – 4 (– 5) mm long; outer perianth lobes very short; inner perianth lobes inseparably fused into a mitre with three appendages, with the lateral appendage of the connective fishtail-like.

VARIABILITY. The species is not noticeably variable in phenotype and shows only slight variability in quantitative traits like stem and pedicel length, size of the flower etc. both within and among populations. Observed differences in the colour of the connectives (± colourless or pale orange-pink to orange) can be probably attributed to flower age and refraction of light (connectives are partly translucent). Plants from the single very distant population found in Gunung Penrissen (Fig. 2C) are slightly larger than the plants from northern Sarawak (e.g. length of floral tube mostly 4 – 5 mm vs 3 – 3.7 mm), have slightly

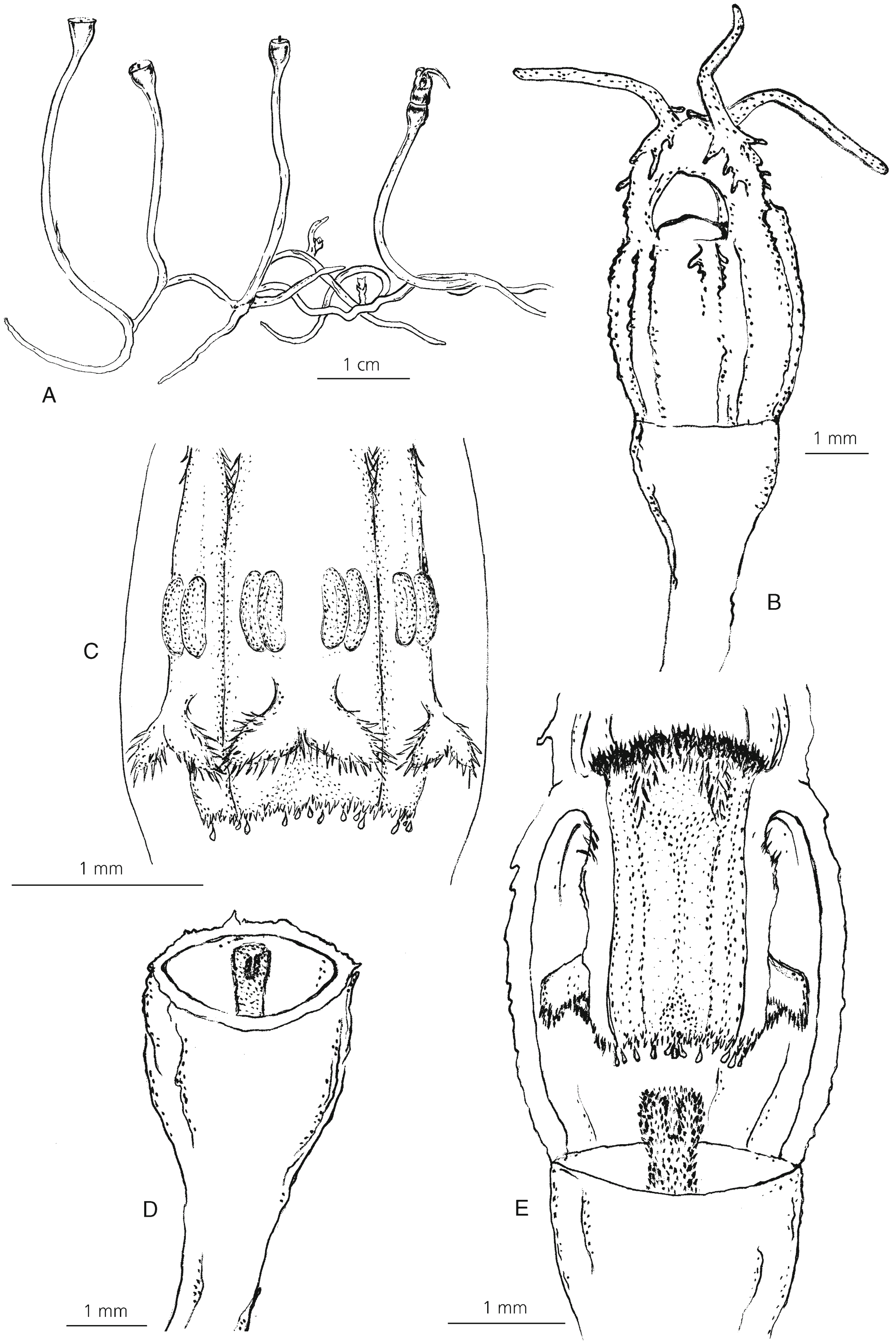
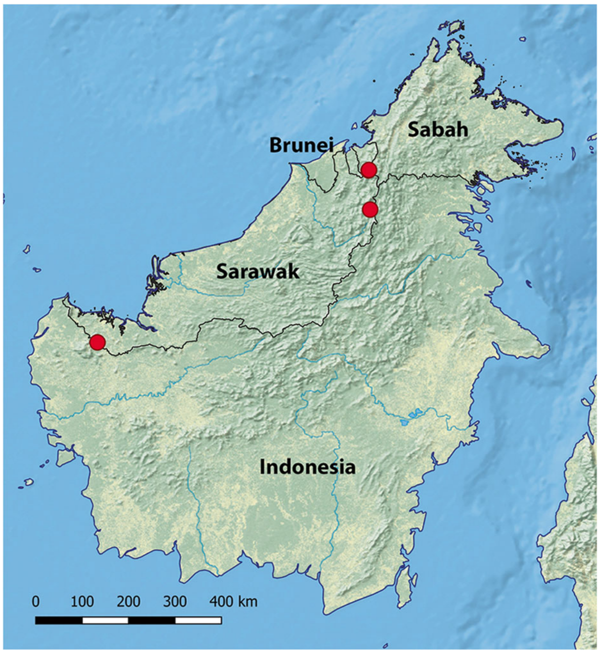


Fig. 1. *Thismia minutissima*. **A** overall appearance of flowering and fruiting plants; **B** flower; **C** outer view of connective tube; **D** ovary with stigma; **E** flower with longitudinally dissected floral tube showing connective tube. **A, B, D** from *Sochor et al.* BOR4/17; **C, E** from *Sochor et al.* BOR5/17. DRAWN BY R. MELICHÁRKOVÁ.

Fig. 2. *Thismia minutissima*. **A** plant at pre-anthesis stage; **B** – **D** overall appearance; **E** detail of flower. **A** from *Sochor et al.* BOR4/17; **B, D** from *Sochor et al.* BOR28/19; **C** from *Sochor et al.* BOR63/19; **E** from *Sochor et al.* BOR5/17.

more erect and longer mitre appendages (5 – 8.5 mm vs 3.5 – 5 mm) and distinct outer perianth lobes (tongue-like, 0.8 – 1 mm long vs shortly triangular or rounded, 0.3 – 0.5 mm long). Some individuals from Gunung Penrissen are also less warty at the base of the mitre appendages and in the upper part of floral tube. Otherwise they are identical with the type population and all the populations from northern Sarawak. However, the population from Gunung Penrissen differs significantly at each of the studied DNA loci, with pair-wise difference being 0.4% at *atpA* (plus a 3bp indel), 1% at SSU, 2.1% at *matR* (plus three indels of 13 bp), 2.7 – 3% at LSU, and 25.1 – 25.4 % at ITS (plus 17 indels of 30 bp) from the northern Sarawak populations.

DISTRIBUTION. The species is known from three regions of Sarawak across the central highlands of Borneo (Map 1). The northernmost group of localities occurs south of the village of Long Tuyo (Lawas district) in north-eastern Sarawak. The middle group is found in the Kelabit Highlands, south of the village of Pa'Umor (Bario subdistrict). The southernmost population is located in the Gunung Penrissen area of south-western



Map 1. Distribution of *Thismia minutissima* in Sarawak, Borneo.

Sarawak, SW of the village of Annah Rais (Kuching district).

SPECIMENS EXAMINED. MALAYSIA. Sarawak, Kelabit Highlands, Miri Division, Bario Subdistr., Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village, 03°42'01"N, 115°31'28"E, 1195 m, 13 Jan. 2017, *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & J. R. Pasan* BOR4/17 (holotype SAR!, isotype OL!); Sarawak, Kelabit Highlands, Miri Division, Bario subdistr., Pa'Umor village: 4.4 km S of the village, 03°41'58"N, 115°31'08"E, 1258 m, 13 Jan. 2017, *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & J. R. Pasan* BOR5/17 (SAR!); Sarawak, Limbang Division, Lawas Distr., Long Tuyo village: primary forests S of the Tuyo R., 04°27'24"N, 115°29'18"E, 610 m, 30 Jan. 2019, *M. Sochor, M. Hroneš & M. Dančák* BOR28/19 (OL!, SAR!); Sarawak, Limbang Division, Lawas Distr., Long Tuyo village: primary forests S of the Tuyo R., 04°27'55"N, 115°29'46"E, 540 m, 31 Jan. 2019, *M. Sochor, M. Hroneš & M. Dančák* BOR39/19 (OL!); Sarawak, Kuching Division, Padawan subdistr., Annah Rais village, Borneo Highland Resort, at the trail to Mt Penrissen, 01°06'58"N, 110°13'02"E, 1020 m, 3 Feb. 2019 *M. Sochor, M. Hroneš & M. Dančák* BOR63/19 (OL!).

HABITAT AND ECOLOGY. The species inhabits primary, undisturbed lowland to lower-montane tropical rainforests and its known elevational range is from c. 540 – c. 1260 m. In all cases observed, the species co-occurred with some other mycoheterotrophic plants, such as species of the genera *Epirixanthes* Blume (Polygalaceae), *Sciaphila* Blume (Triuridaceae) and also other species of *Thismia* (see also Sochor *et al.* 2018b).

CONSERVATION STATUS. *Thismia minutissima* is believed to be endemic to Borneo and all known populations occur outside national parks and other protected areas. While the extent of occurrence (EOO) of *T. minutissima* is c. 25,700 km^2, its minimal area of occupancy (AOO) is estimated as only 16 km^2. The species is known from five populations representing three locations (sensu IUCN 2012). *Thismia minutissima* is, therefore, assigned a preliminary status of Vulnerable (VU D1+D2) according to the *IUCN Red List Categories and Criteria* (IUCN 2012). However, more localities probably exist in the highlands of central Borneo, with possible occurrences in protected areas. For example, it is likely to be present in the Kayan Mentarang and Betung Kerihun National Parks of Kalimantan, Indonesia.

ETYMOLOGY. The specific epithet reflects the flower size which is probably the smallest in the genus.

NOTES. Based on its external appearance (vermiform roots, developed outer perianth lobes and inner perianth lobes bent upwards and connate to form a mitre with filiform appendages), *Thismia minutissima* superficially resembles species of *Thismia* sect. *Rodwaya*. However, it differs from sect. *Rodwaya* by the perfect dome-like mitre, the presence of a distinct fishtail-shaped lateral appendage of the connectives, rectangular stigmatic lobes, very short outer perianth lobes (<1 mm) without any appendages and by a prominent stem. It is also similar to some species of sect. *Glaziocharis* but they all differ by the complete absence of a lateral appendage of the connectives. In overall appearance, *T. minutissima* shows some affinities to *T. hongkongensis* Mar & R.M.K.Saunders but the latter species does not form a true mitre (the free perianth lobes are just upright and touching each other) and the shape of the lateral appendage of the connectives is rather different. Compared to other *Thismia* species, *T. minutissima* has extraordinarily large seeds (c. 0.9 × 0.4 mm) whose funicle is significantly enlarged (Fig. 3D). To our knowledge, such an enlarged funicle has never been reported in any *Thismia* species and its function is unknown. Thus, no species of *Thismia* shows considerable similarity with *T. minutissima* which makes it a morphologically isolated species. Our five-locus molecular phylogenetic analysis confirms this conclusion as the species forms a separate evolutionary lineage sister to *Thismia* sect. *Thismia* (Fig. 4). Similar results, although with a rather unclear placement of the species in the phylogenetic reconstruction, were also obtained from a three-locus analysis of 42 Old World *Thismia* species (Shepeleva *et al.* 2020). Therefore, we do not propose any placement of *T. minutissima* in the existing infrageneric taxonomy of *Thismia*.

Thismia minutissima, while uniform in morphology of stamens (the trait considered very important in *Thismia* taxonomy; Sochor *et al.* 2018b) and stigma, is remarkably variable in the studied DNA markers. The population from Gunung Penrissen in south-western Sarawak, although only slightly different in external

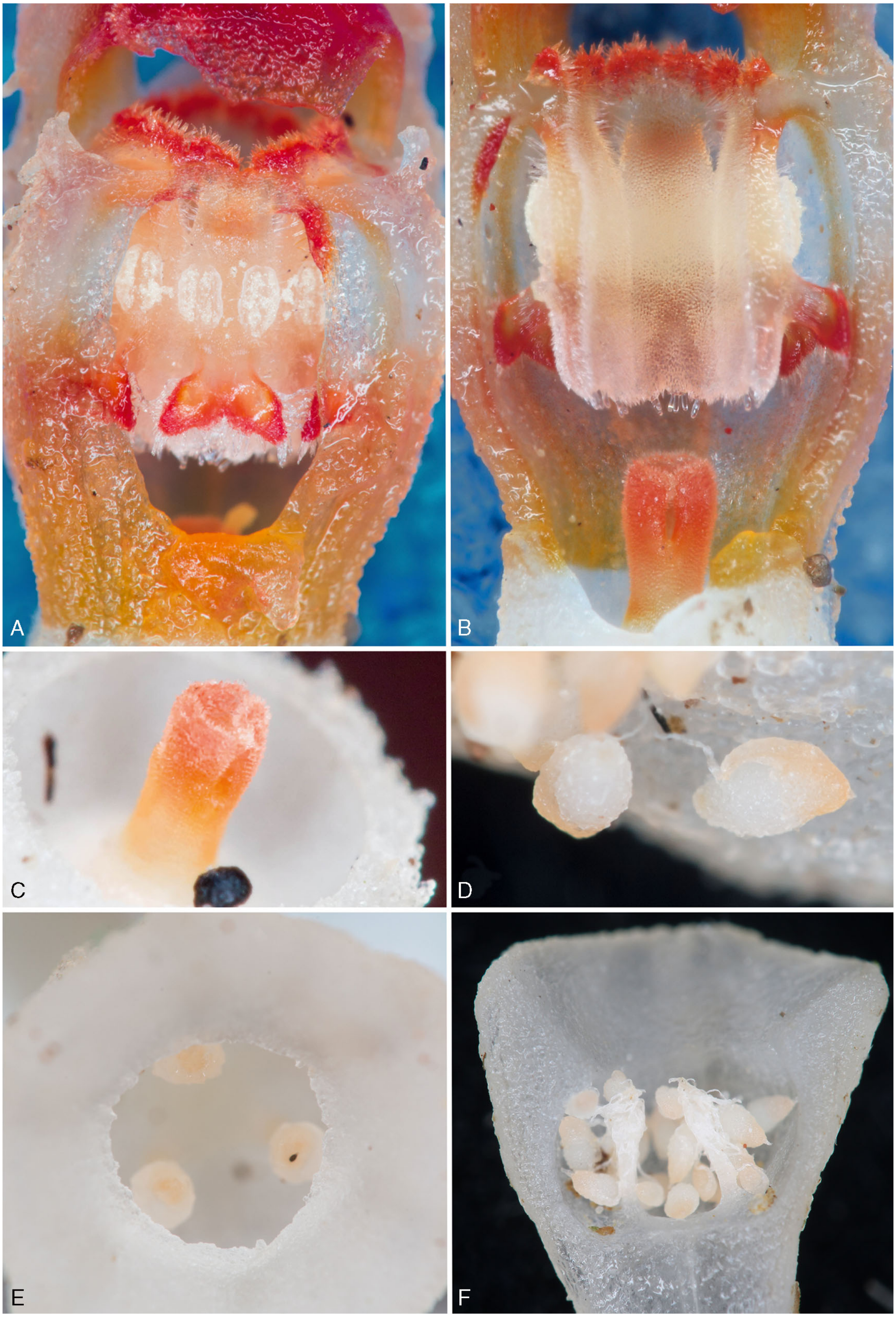


Fig. 3. *Thismia minutissima*. **A** section of floral tube showing stamens; **B** longitudinal section of perianth and connective tube; **C** stigma; **D** seeds; **E** apical view of empty capsule showing three placentae; **F** radial section of capsule with two of the three placentae and attached seeds. **A, B** from *Sochor et al.* BOR5/17; **C** from *Sochor et al.* BOR4/17; **D** from *Sochor et al.* BOR28/*19*; **E** from *Sochor et al.* BOR63/19; **F** from *Sochor et al.* BOR39/19.

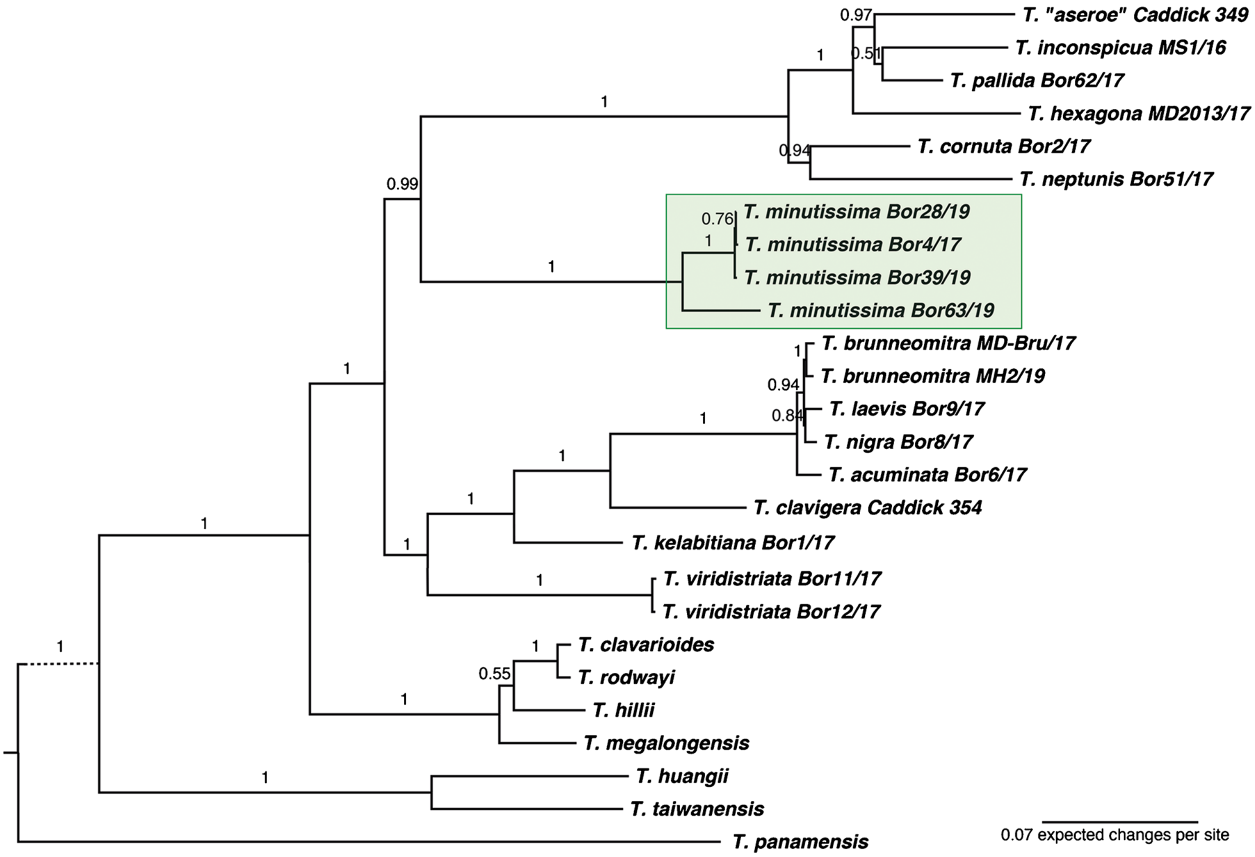


Fig. 4. Bayesian phylogeny inference based on five-loci data set. Posterior probabilities are shown above branches; samples of Caddick and those without collection numbers were downloaded from GenBank and partly compiled from different collections (see Electronic Supplementary Material S1 for Genbank accession numbers). *Thismia* "*aseroe*" *Caddick* 349 was redetermined as *T. ornata* Dančák, Hroneš & Sochor in Dančák *et al*. (2020) shortly before this paper was published.

floral appearance from the type population (Fig. 2C; see also Variability), substantially differs genetically from all populations from north-eastern Sarawak. Surprisingly, the genetic distance of this population from the others is much larger than that commonly found among related, yet phenotypically distinct, species of *Thismia* (especially within sect. *Sarcosiphon*, e.g. *T. brunneomitra* Hroneš, Kobrlová & Dančák, *T. laevis* Sochor, Dančák & Hroneš and *T. acuminata* Hroneš, Dančák & Sochor; Fig. 4). Nevertheless, due to their rather uniform morphology, we prefer to treat all the populations as one species at the present time.

The distribution of *Thismia minutissima*, spanning some 700 km across Borneo, is exceptionally wide compared to most *Thismia* species, which are largely considered to be narrow endemics. For several Old World species, ranges larger than or equal to that of *T. minutissima* are known. These are *T. arachnites* Ridl. (Chantanaorrapint 2018), *T. clandestina* (Blume) Miq. (Chantanaorrapint *et al.* 2015), *T. clavigera* (Becc.) F.Muell. (Chantanaorrapint & Chantanaorrapint 2009), *T. episcopalis* (Becc.) F.Muell., *T. javanica* J.J.Sm., *T. ophiuris* Becc. (Jonker 1938) and *T. tentaculata* (Ho *et al.* 2009). However, for some of these species, serious doubts exist about the identity of the distant populations when compared to their type populations. One such example is a population of *T. clavigera* from Sumatra which has now been described as a distinct species: *T. sumatrana* Suetsugu & Tsukaya (Suetsugu *et al.* 2018b). The strong genetic differentiation in *T. minutissima* suggests that the situation in other *Thismia* species may be even more complex.

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ORIGINAL ARTICLE

New insights into variation, evolution and taxonomy of fairy lanterns (*Thismia,* Thismiaceae) with four new species from Borneo

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Abstract

Fairy lanterns (*Thismia* Griff.) is a genus of poorly known mycoheterotrophic plants with unclear infrageneric classification. Commonly used approaches that utilize just a single or few traits in higher-level taxonomy lead to an apparently artificial system. In this contribution, four new species from Sarawak, northern Borneo, are described and illustrated. *Thismia acuminata*, *T. laevis* and *T. nigra* belong undoubtedly to section *Sarcosiphon*. *Thismia viridistriata* exhibits a high morphological variability with some individuals fitting section *Scaphiophora* based on the presence of a column on the top of the mitre, but otherwise perfectly matching the morphological characteristic of section *Sarcosiphon*. Five-locus (SSU, ITS, LSU, *mat*R, *atp*A) phylogeny inference revealed paraphyly or polyphyly in the studied infrageneric taxa and showed that the importance of some traits traditionally used in *Thismia* taxonomy was overestimated. Most of the markers provide comparable phylogenetic signal; LSU performs best and is highly recommended for further phylogenetic studies. On the other hand, ITS is hypervariable and thus informative only within (sub)sections, as well as on intraspecific level, as proven in *T. viridistriata* with two distinct ITS (and also LSU and *mat*R) alleles and two morphotypes within a small geographic area, which leads to an assumption of strong reproductive isolation even among nearby populations. For delimitation of species, the key trait appears to be the structure of the connective and any of the molecular markers used here.

Keywords Fairy lanterns · Kelabit Highlands · Mycoheterotrophy · Pulong Tau · *Sarcosiphon* · *Thismia*

Introduction

Fairy lanterns (*Thismia* Griff.; Thismiaceae, or Burmanniaceae s.l.) are a genus of small, mycoheterotrophic plants distributed mainly in Southeast Asia, tropical America, Japan, Australia and New Zealand. Around 72 species are currently recognized in the genus, of which more than half is restricted to Southeast Asia, particularly the Malesian floristic region (Hroneš 2016; Cooper 2017; Kumar et al. 2017; Sochor et al. 2017; Sujanapal et al. 2017; Suetsugu et al. 2017; Tsukaya et al. 2017; Chantanaorrapint and Suddee 2018; Suetsugu et al. 2018). As obligate mycoheterotrophs, fairy lanterns are dependent on their fungal symbionts that are further associated with their autotrophic plant symbionts and other organisms (Bidartondo 2005). Fully functional biotic networks may therefore be the crucial factor for *Thismia* occurrence and survival. That is possibly the main reason why these plants are found predominantly in primary tropical rainforests (Merckx et al. 2013b) which are renowned for richness of biotic interactions. Furthermore, the mycorrhizal association is often highly specific and phylogenetically conserved in Thismiaceae and distribution of the fungal symbionts may thus limit occurrence and spread of the plants (Merckx et al. 2012, 2017). On the other hand, the associated fungi are probably widespread and enable relatively rapid expansions of fairy lanterns into

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new areas, as was observed in *T. rodwayi* F.Muell. and *T. hillii* (Cheeseman) N.Pfeiff. (Merckx et al. 2017). Most *Thismia* species are considered extremely rare, though. The underlying reasons may vary from true rarity of the species (resulting from their narrow niche), to our poor ability to detect them. Their ephemeral aboveground growth and inconspicuous appearance in combination with their habitats (mostly difficultly accessible tropical rainforests) and phenology (flowering predominantly during rainy seasons) make them quite a problematic study object.

Besides the difficult detection, several other factors complicate taxonomical studies on fairy lanterns. Obligate mycoheterotrophy resulted in many reductions in vegetative morphology, and only very few characters apart from those on flowers can be used in taxonomy. The systematics of *Thismia* is mostly based on organization of perianth lobes. According to the latest monographic treatment of the genus by Jonker (1938), the Old World species with free perianth lobes are treated in section *Thismia* (*Euthismia* Schlr.) with two subsections—*Odoardoa* Schlr. (with all perianth lobes equal in size and shape) and *Brunonithismia* Jonker (with reduced outer lobes). Sections *Rodwaya* Schltr. and *Glaziocharis* (Taub. ex Warm.) Hatus. include species whose inner tepal lobes are bent inwards but are usually not or only imperfectly connate. Species with inner tepals connate and forming a mitre above the flower opening were included in section *Sarcosiphon* (Blume) Jonker, but only if they lack any filiform appendages on the top of the mitre. If appendages are present, Jonker (1938) treated such species in the separate genera *Scaphiophora* Schltr. and *Geomitra* Becc. (with one or three appendages, respectively), which were recently reduced to sectional status (Kumar et al. 2017). However, such systems based on absolute importance of a single trait may not reflect the true phylogenetic relationships and may thus be artificial.

Species of *Thismia* are traditionally delimited by various traits, from overall habitus to inner flower anatomy (Jonker 1948; Hroneš 2016). Nevertheless, many species are only known from type collections, sometimes very poor (single flowering or even fruiting individual), covering often just a small fragment of true natural variation of the species. Common problem, typical for old plant names but underlined by the limited use of standard (i.e. pressed) herbarium specimens in *Thismia*, is insufficient description with incomplete documentation. Moreover, many species are desperately inaccessible not only for morphological evaluation, but also for DNA analyses due to their rarity and very limited usability of herbarium specimens. Little is known also about population (genetic) structure, reproductive biology, dispersal abilities or population dynamics, among others, despite some recent advances (Mar and Saunders 2015; Merckx et al. 2017). Consequently, making any natural taxonomic system, as well as defining a proper species concept, is problematic. This fact is becoming apparent with increasing number of *Thismia* collections, new taxa descriptions and involvement of molecular methods during the last decade (Merckx et al. 2017).

During our recent expedition to the Kelabit Highlands, Borneo, eight undescribed species of *Thismia* were discovered, some of which exhibited extraordinarily common occurrence as well as extreme variability in outer morphology. In this paper, we aim 1. to describe formally four of these species as new to science; 2. provide data on their morphological and molecular (ribosomal and mitochondrial DNA) variation; and 3. discuss usefulness of different morphological traits and DNA loci for taxonomy and phylogeny inference in fairy lanterns.

Materials and methods

Plant material for this study was collected during a 10-day expedition in the vicinity of Pa'Umor, Pa'Lungan and Bario villages, the Kelabit Highlands, Sarawak, Malaysia. *Thismia* plants were searched systematically in several localities that were mostly selected in advance based on our previous experiences. Each population of each found morphological type (separated by ca > 100 m from the neighbouring population) was studied morphologically in the field camps using hand lenses (20 × – 60 × magnification) and macrophotography. Specimens of whole plants were taken from each population in form of pressed herbarium and/or alcohol (70% ethanol) specimen. Piece of tissue (e.g. pedicel, capsule, part of stem) from one individual per population was silica gel-dried for subsequent DNA extraction. Several fruiting individuals of unknown identity were also added to the molecular analyses, as well as samples of *T. hexagona* Dančák, Hroneš, Kobrlová & Sochor, *T. inconspicua* Sochor & Dančák, *T. brunneomitra* Hroneš, Kobrlová & Dančák, *T. neptunis* Becc. and *T. pallida* Hroneš, Dančák & Rejžek from the type localities in Brunei, western Sarawak and Sabah, respectively.

DNA was extracted by the CTAB method (Doyle and Doyle 1987), and sequence data were generated for three nuclear and two mitochondrial loci. The small subunit of ribosomal DNA (SSU rDNA) and internal transcribed spacers (ITS) were amplified and sequenced with primers NS1, NS6, NS5 and ITS4 (White et al.1990) or 268rev (Kuzoff et al. 1998) and large subunit of ribosomal DNA (LSU rDNA) by primers N-nc26S6 and 2134rev (Kuzoff et al. 1998). Amplification of the LSU region adjacent to ITS2 was attempted by primers N-nc26S1 and 1229rev or 1499rev, but most reactions did not provide specific product and were therefore not analysed further. The mitochondrial *atp*A gene was amplified and sequenced with primers developed by Eyre-Walker and Gaut (1997) and *mat*R gene with primers 26F and 1002R (Meng et al. 2002). All PCRs were performed with Kapa polymerase (Kapa Biosystems) following a standard protocol with 37 to 40 cycles and annealing temperature of 56 °C (rDNA, *atp*A) or 47 °C (*mat*R). The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25 M NaCl in the precipitation mixture) and sequenced in both directions by Sanger method at Macrogene Europe.

Sequences were edited and aligned in Geneious (ver. 7.1.7., Biomatters) and deposited in NCBI GenBank under accession numbers MG008338–MG008393 and MG765543–MG765546. Alleles of each locus were distinguished based on single-nucleotide polymorphisms (sequences differing at least in one mutation were considered different alleles). For characterization of molecular variation at each locus, twelve (morpho)species were selected whose data from all five loci were available (one individual per species); seven from sect. *Sarcosiphon* and five from sect. *Thismia*. Maximum parsimony trees were computed in MEGA (ver. 6.06; Tamura et al. 2011) by subtree-pruning-regrafting method and MP search level of 5 and tested by bootstrapping with 1000 replications. Bayesian phylogeny inference was computed in MrBayes (ver. 3.2.4; Ronquist et al. 2012) with 10^7 generations, sampling every 3000th generation, in two independent runs, each with 4 chains; first 2.5×10^6 generations (25%) were excluded as burn-in. Substitution model for each locus was determined in jModelTest (ver. 2.1.4; Darriba et al. 2012) using Akaike information criterion (AIC). The models used are shown in Table 1. The individual gene trees were subsequently visually compared among loci and analytical methods. Phylogeny inference from concatenated data from the five loci was performed by the same methods as above for the sample set including additional eleven species whose sequences (at least four loci for the ingroup taxa) could be downloaded from NCBI Genbank (Online Resource 1). The substitution models for this analysis were determined in PartitionFinder2 (ver. 2.1.1; Lanfear et al. 2017) using the corrected AIC (AICc) and a greedy search, and partitions were set subsequently according to the loci in MrBayes (ITS1, ITS2 and 5.8S rDNA were treated as separate partitions; see Table 1).

Results

Nine different morphological types (morphotypes) of *Thismia* were discovered in the field. Two of them were later found to belong to the same species; eight species were therefore detected. Six of them were mitriform species with coralliform roots. One of these was morphologically unique species not similar to the rest of the species, and it will be described separately as *Thismia kelabitiana* ined. (Dančák et al. submitted). In another morphospecies, *Thismia* aff. *nigra*, only immature individuals were found, and it cannot be formally described until additional material is collected. The four remaining species of this group are formally described here as *T. acuminata*, *T. laevis*, *T. nigra* and *T. viridistriata*. Based on morphology, three of them belong undoubtedly to section *Sarcosiphon* and the remaining one, *T. viridistriata*, either to this section, or, due to the presence of a column on top of the mitre in some individuals, to the genus *Scaphiophora* sensu Jonker (1938) which is now reduced to *Thismia* (Merckx et al. 2013a; Kumar et al. 2017). The remaining two species were *T. cornuta* Hroneš, Sochor & Dančák (Hroneš et al. 2018) and an undescribed species, which is not treated here and will be described in a separate paper.

Detailed morphological evaluation could be performed in all discovered morphotypes except for the one that was only found with one developing (but not open) flower and possibly represented different species. This was treated as *T.* aff. *nigra* in further analyses (i.e. similar but not identical to *T. nigra*). Intraspecific morphological variability was generally low, except for *T. viridistriata* with two distinct morphotypes

Table 1 Comparison of different loci in terms of total and parsimony-informative variability and usefulness for maximum parsimony (MP) and Bayesian (BI) phylogeny inference; ITS locus covers only the ITS1–5.8S rDNA–ITS2 region

Locus	SSU	ITS	LSU	*atp*A	*mat*R
Alignment length [bp]	1713	691	957	1167	1003
Variable SNPs (% of total)	189 (12%)	492 (71%)	239 (25%)	50 (4%)	155 (15%)
Informative SNPs (% of variable SNPs)	125 (66%)	354 (72%)	179 (75%)	20 (40%)	70 (45%)
# most parsimonious trees	7	1	2	6	6
MP tree length	262	851	395	61	140
# splits with BS $\leq 50\%$	2	1	2	4	3
# splits with PP $< 95\%$	4	5	3	4	5
Substitution model (based on AIC in jModelTest/AICc in PartitionFinder2)	GTR + I + G/GTR + I + G	GTR + I + G/GTR + I + G, SYM + G[a]	TIM3 + G/GTR + G	TVM + I/GTR + I + G	TIM1 + G/GTR + G

SNP single-nucleotide polymorphism, *BS* bootstrap value, *PP* Bayesian posterior probability, *AIC* Akaike informative criterion, *AICc* corrected AIC

[a] For 5.8S rDNA region of the sequence

and several transitional individuals (Table 2). The best character that distinguishes all of the species was revealed to be connective morphology which was very stable within and among populations of the same species. Morphological variation is further discussed in Taxonomic treatment.

All of the five studied genomic loci could be amplified and sequenced easily in most samples. ITS region could not be amplified in *T. hexagona* using primer ITS4 due to two point mutations in the primer complementary sequence in this species. The region was therefore amplified and sequenced with primer 268rev, which anneals further in the LSU region.

In the dataset of twelve studied species from two sections, each locus was clearly able to distinguish between different morphologically defined species, with an exception of *atp*A in *T. nigra* and *T.* aff. *nigra*. The highest variability was observed in the ITS region and most of this variation was parsimony informative (Table 1). It also exhibited the highest intraspecific polymorphism (ten SNPs and one indel in *T. viridistriata* and one SNP in *T. cornuta*; Online Resource 2). Other intraspecific polymorphisms were detected at LSU and *mat*R (two and one SNPs in *T. viridistriata*, respectively, resulting in two alleles at each locus that corresponded to the ITS alleles; Online Resources 1 and 2), and at SSU (three SNPs in *T. cornuta* forming three alleles). Only very few short conserved domains were detected at the ITS locus among species (all in 5.8S rDNA region), and the alignment was therefore very ambiguous, particularly among sections. Each of the remaining loci provided both considerable polymorphism (see Table 1) and multiple conserved motives that allowed for unambiguous alignment.

Ribosomal and mitochondrial DNA markers performed comparably in resolving phylogenetic relationships (Online Resource 3). The best resolving markers according to the number of maximally parsimonious trees and the number of highly supported splits were ITS and LSU (Table 1, Online Resource 3). These were also the only markers that provided a phylogenetic signal (although slightly different from each other) within the "core Sarcosiphon" clade (Online Resource 3). Considering serious ambiguities in alignment of ITS and therefore its limited usability among distant lineages, LSU remains the most suitable marker for whole-genus phylogeny reconstruction, although it has never been used in fairy lanterns until now. Nevertheless, slight incongruencies among loci call for necessity of multilocus phylogenetic inferences.

After inclusion of other species for which at least four of the studied loci were publicly available (Online Resource 1), a well resolved Bayesian multilocus phylogenetic tree with most branches well supported was obtained (Fig. 1). Bootstrap consensus maximum parsimony tree exhibited similar topology, except for a few splits (Online Resource 3). Four lineages were clearly distinguished that correspond to several infrageneric taxa—sect. *Thismia*, sect. *Sarcosiphon*

Table 2 Variation within and among the four new *Thismia* species in selected phenotypic characters

	T. acuminata	*T. laevis*	*T. nigra*	*T. viridistriata*
Height (cm)	3–5	5.5–10.5	2.5–7	2–4.5(–9)
Number of leaves	3–6	4	3–6	2–6
Fruiting pedicel length (cm)	ca 1.5	up to 11	up to 9	up to 6
Number of flowers	1–2(–4)	4	2–5	1–5
Flower size	15–19 mm long, 5–6 mm wide	18 mm long, 7 mm wide	10–12 mm long, 4.5–6 mm wide	13–21 mm long, 4.5–6 mm wide
Perianth tube colour	Greyish or light beige to sometimes brownish orange, with 12 dark brown (to almost blackish) or reddish brown longitudinal stripes	Greyish, with dark brown to blackish apex and ribs and brown stripes between the ribs (together making 12 longitudinal dark stripes)	Dark greenish-grey with 1 transversal and 12 vertical blackish stripes	Greyish to rich brown or reddish brown with darker transversal stripe in the middle and 12 dark brown (to almost blackish) or reddish brown longitudinal stripes
Mitre processes	Absent	3 short obtuse processes	3 short obtuse processes or rarely absent	3 short processes or a single column
Connective apex	Densely hairy with ca 4–5 ± irregular short processes	Glabrous with no processes	2 small lobes with ca 5 long simple hairs	1–2 lobes with ca 5 ca 0.15–0.2 mm long simple hairs
Stigmatic lobes	Deeply divided into 2 triangular lobes or rather shallowly trilobed with the middle lobe smaller	Divided into 2 large and 1 small lobe	Deeply divided into 2 long triangular lobes	Shallowly bilobed

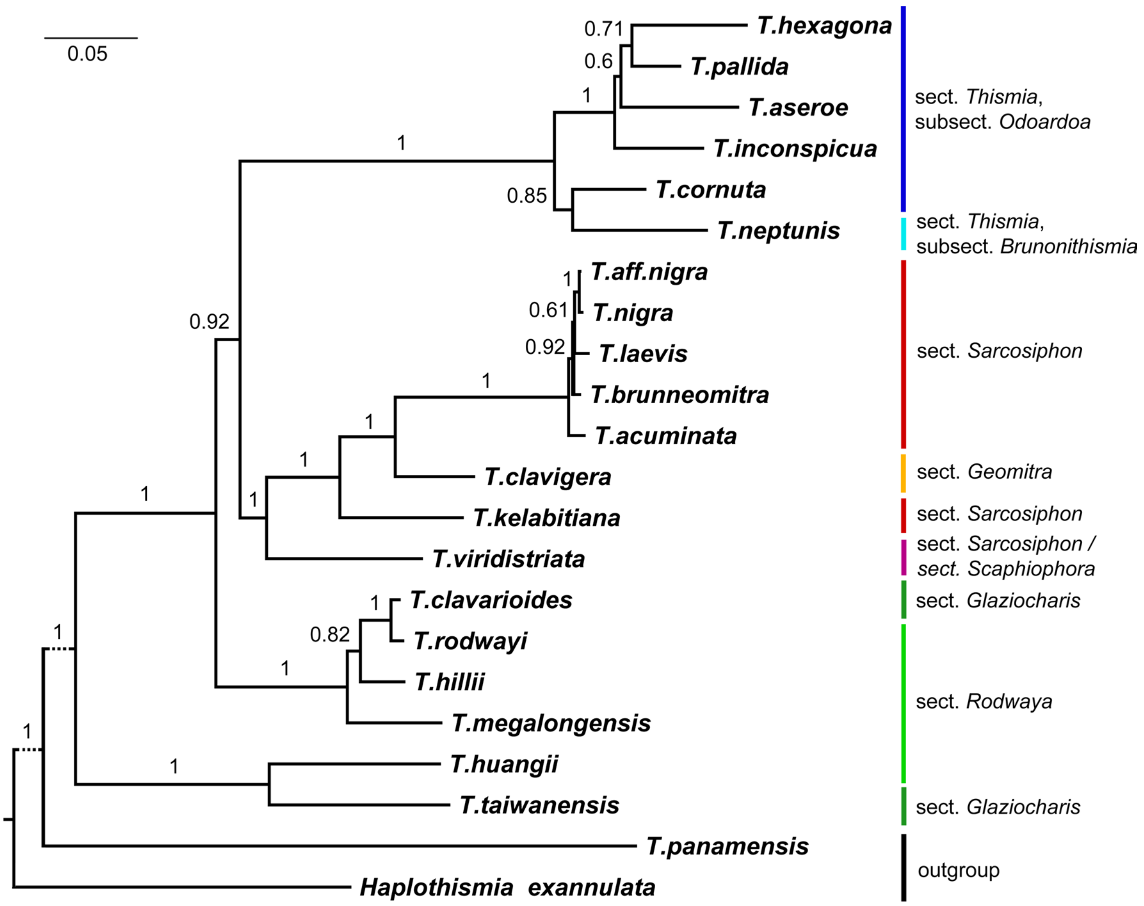

Fig. 1 Bayesian tree inferred from five-locus concatenated alignment; posterior probabilities shown above branches. Infrageneric placement follows the treatment of Kumar et al. 2017, but note that, e.g. *Thismia clavarioides* was originally placed in sect. *Rodwaya*

(including sections *Scaphiophora* and *Geomitra*), and sections *Rodwaya* and *Glaziocharis* (sensu Kumar et al. 2017) sharing two evolutionary lineages. *Thismia clavigera* Becc., assigned to sect. *Geomitra*, groups with species of section *Sarcosiphon*. Three of the four species described here form a well-separated cluster (*T. nigra*, *T. laevis* and *T. acuminata*), whereas *T. viridistriata* forms different, basal lineage within the *Sarcosiphon* clade (Fig. 1; Online Resource 3).

Discussion

Connective morphology is the most appropriate character for species distinction

Despite the recent wave of interest that resulted in description of many new species and some new insights into biology and evolution of fairy lanterns, the genus *Thismia* remains a poorly understood plant genus. For instance, no or only poor and/or indirect data are available on population structure, reproduction systems, clonality, life cycle, dispersal ability, specificity of biotic interactions, etc. Intraspecific variation is also virtually unknown as most species are known only from the type collections. These facts greatly limit the development of taxonomical concepts in the group, including species concept (i.e. definition of species boundaries) and delimitation of higher taxa, particularly sections and subsections. Different approaches are therefore appearing. Whereas some authors treat morphologically atypical populations as infraspecific taxa (e.g. *T. hexagona* var. *grandiflora*; Tsukaya et al. 2014) or conspecific without further taxonomical distinction, e.g. *T. clandestina* Blume (Chantanaorrapint et al. 2015, Suetsugu et al. 2017*), T. crocea* Becc. and *T. versteegii* J.J.Sm. (Jonker 1938), or formerly conspecific *T. rodwayi* and *T. hillii* (Hunt et al. 2014), the common approach is describing new species. The main diagnostic characters for delimitation of species range from external traits (coloration, appendages on perianth lobes, etc.; e.g. Hunt et al. 2014; Chantanaorrapint et al. 2016; Tsukaya et al. 2017) to inner flower structure (e.g. Hroneš et al. 2015), or usually combination of several traits.

During our fieldwork, several populations of two distinct morphotypes were detected that shared inner flower morphology, but differed in outer characters, particularly in colour of flower, presence and length of terminal appendage on top of mitre, shape of perianth tube, flower size, number of stems from one root, number of flowers per stem and stem length (see Taxonomic treatment of *T. viridistriata*). Both morphotypes exhibited only low variation in molecular markers (Online Resources 2 and 3); two related alleles were detected at each of the ITS, LSU and *mat*R loci; one allele was detected in both of the morphotypes and the second allele (rarer) in one of them (Online Resource 1). Moreover, some populations appeared transitional between both morphotypes in their morphology. Therefore, the observed variation could be considered as intraspecific. For delimitation of this species, the main diagnostic traits were inside the flower—mainly structure of connectives. Shape of stigma was also constant in this case, although it can be variable in *Thismia* and may reflect the anthesis phase (Sochor et al. 2017; see also Taxonomic treatment). Connective morphology is crucial also in distinguishing *T. nigra* and *T. brunneomitra*, which are strikingly similar to each other in external appearance, but well differentiated in molecular markers (Fig. 1, Online Resources 1 and 2). Importance of connective appendages morphology in taxonomy on the species level was noticed earlier (e.g. Tsukaya et al. 2014; Hroneš et al. 2015; Chantanaorrapint et al. 2016) and may be critical for comparison of geographically distant populations among which some differentiation can be expected, at least in sect. *Sarcosiphon*. Though, relatively little attention appears to be paid to this feature in some of the new species descriptions (e.g. Jarvie 1996; Kiew 1999; Chiang and Hsieh 2011; Tsukaya and Okada 2012; Dančák et al. 2013; Mar and Saunders 2015; Tsukaya et al. 2017). Another species-diagnostic marker could be any of the conservative genomic regions analyzed here. Unfortunately, herbarium specimens (particularly old and pressed ones) usually do not permit analysis of either of these traits (those on connectives or molecular ones) and the use of old names that are based on insufficient protologues may therefore be very difficult. An illustrative example is *Thismia clandestina* originally described from Java (see, e.g. Smith 1911) and recently reported from Thailand, although slightly differing from the Javan population (Chantanaorrapint et al. 2015; Suetsugu et al. 2017).

Perianth morphology has been overestimated in infrageneric taxonomy

Delimitation of higher infrageneric taxa (mainly sections and subsections) is also very unclear and awaits wider phylogenetic analyses and subsequent thorough revision (Hroneš 2016). The currently accepted concepts (e.g. Govaerts et al. 2007; Kumar et al. 2017) consider mainly modifications of petal lobes, as introduced by Schlechter (1921) and Jonker (1938). Although our preliminary screening covers only six infrageneric taxa (*T.* sect. *Thismia* subsect. *Odoardoa* and *Brunonithismia*, *T.* sect. *Rodwaya, T.* sect. *Glaziocharis, T.* sect. *Sarcosiphon* and *T.* sect. *Geomitra*), four of them (i.e. all with more than one sampled species) appear poly- or paraphyletic. Sect. *Rodwaya* includes at least two unrelated, yet morphologically very similar lineages (Fig. 1; Merckx et al. 2017; Sochor, Dančák, Hroneš, unpublished data). Subsect. *Odoardoa* is only monophyletic if subsect. *Brunonithismia* is included, and sect. *Sarcosiphon* should include sect. *Geomitra*. Interestingly, although very similar in morphology to the "core *Sarcosiphon*" clade (*T. nigra*, *T. laevis*, *T. acuminata,* etc.), *T. viridistriata* clearly forms a basal lineage of the whole *Sarcosiphon–Geomitra* clade (i.e. including *T. clavigera* and morphologically very distinct *T. kelabitiana*; Fig. 1). This position is well supported by every method and marker used (Online Resource 3). Also section *Glaziocharis*, if distinguished by the presence of appendages on outer perianth lobes (Kumar et al. 2017), is clearly polyphyletic (Fig. 1). These contradictions between phylogeny and classical taxonomy may indicate either convergent evolution or limited anagenesis in morphology of perianth in some distantly related lineages. Traits such as the presence of mitre and terminal appendages on perianth lobes therefore appear to have been overestimated in infrageneric taxonomy.

In contrast, root morphology should receive more attention in taxonomy. Root systems of Old World *Thismia* are of two architectural types—vermiform and coralliform (see, e.g. Jonker 1948, Imhof et al. 2013). Already Jonker (1938) pointed out the importance of root system in infrageneric taxonomy of *Thismia* as he used it in characteristics of his sections. He was also aware of coralliform roots of *Scaphiophora* but not *Geomitra*. However, due to scarcity of species with coralloid roots this was generally not emphasized in later research (see, e.g. Merckx et al. 2006). Nevertheless, it seems that root morphology could indeed be a good character of systematic importance as the coralliform roots are exclusively found in one of the four evolutionary lineages studied here (see Fig. 1) that corresponds to section *Sarcosiphon*, including *Geomitra* and *Scaphiophora*. Roots of the other groups are vermiform (or tuberous in neotropical outgroup taxa). Interestingly, the occurrence of coralliform roots is associated with other traits, e.g. species with coralliform roots always have perfect mitre and outer perianth lobes absent, considerably reduced or at least modified. To conclude, proper delimitation of infrageneric taxa and their morphological characterization needs to be critically re-evaluated in Old World fairy lanterns.

Thismia populations may be reproductively isolated at small geographic scale

Thanks to the two morphotypes and two ITS/LSU/*mat*R alleles, as well as to the relatively common occurrence in the studied region, *T. viridistriata* may represent a unique model for further studies on evolution in fairy lanterns. Although the morphotypes were not always clearly separated and transitional forms were observed in some populations, no mixed signal was detected in the ITS or LSU sequences despite the fact that these are multi-copy nuclear markers that are usually able to detect recent, yet not always ancient hybridization (Kovarik et al. 2005; Sochor et al. 2015). *Thismia viridistriata* therefore appears to be a single species with multiple isolated populations (or other evolutionary units) that do not interbreed with each other (or only in an extent that precludes complete homogenization of both molecular and phenotypic traits in the metapopulation). Existence of cryptic species (although in an early stage of speciation) within *T. viridistriata* cannot be ruled out either, but the present data do not allow any finer taxonomical treatment. Interestingly, the studied area was relatively small (ca 10 × 18 km) and both of the morphotypes and genetic lineages were discovered even within one river valley just a few hundred meters apart, mostly not high enough above the water level, so that dispersal of seeds and whole plants by water is, hypothetically, well possible. Isolation by distance, physical barriers, environmental conditions or absence of the fungal symbiont is therefore hardly imaginable. Such a pattern, nevertheless, may be shaped in other ways of reproductive isolation. Based on a characteristic complex inner morphology of the flower and probable (yet tentative) protandry, outcrossing via cross-pollination by flies is generally presumed to be the dominant reproduction mode (see Mar and Saunders 2015 for details). These physical mechanisms preventing selfing, nevertheless, would be insufficient in case of uniclonal population structure or asexual seed development, for instance. Another mechanism leading to the among-population differentiation in both molecular and phenotypic traits could be strong preference of pollinators for particular flower shape and/or colour, which could also explain the differences in outer flower morphology (but see Kay and Sargent 2009). Nevertheless, all of these examples are only speculative at this state of knowledge and need to be systematically studied, before any conclusion can be made.

Taxonomic treatment

Thismia acuminata Hroneš, Dančák & Sochor, **sp. nov.**—HOLOTYPE: Malaysia, Sarawak, Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.0 km N of the village, 1152 m a. s. l., 3°50′14″N, 115°31′08″E, 15 Jan 2017, *Sochor* et al. *BOR6/17* (holotype: SAR [accession number Sochor/BOR-6/17]; isotype: OL [accession number 35271]) (Figs. 2, 3).

Etymology: From the Latin *acuminatus*, reflecting acuminate shape of mitre.

Diagnosis: Similar to *T. laevis* Sochor, Dančák & Hroneš but differing in tall acuminate mitre and by having several small lobes and tomentum of long hairs on connective apex and nose-shaped central lobe of lateral appendage.

Description: Achlorophyllous ground herb, ca 3–5 cm tall. *Roots* short, clustered, coralliform, light beige to brown. *Stem* 14–50(–70) mm long, creeping, ascending to erect, sparsely branched or unbranched, pale to rich brown, pinkish, greyish to almost orange; branching sympodial, with one bud covered in bracts of the flower in anthesis and growing as the main stem after anthesis, pedicels indiscernible during anthesis, elongating during fruit maturing to ca 1.5 cm. *Leaves* 3–6 below the first flower, spirally arranged, scale-like, triangular, acute (to acuminate), entire, sometimes with prominent central rib, 2.2–3.0(–6) × 1.2–1.5(–2.0) mm, of the same colour as stem. *Floral bracts* usually 3, of the same shape and colour as leaves, but slightly larger (4–6 × 1.5–1.7 mm). *Flowers* 1–2 (–4) per stem, actinomorphic, 15–19 mm long, 5–6 mm wide at widest part; perianth tube narrowly urceolate, widest at its upper quarter, often with slight narrowing above the middle; outer surface greyish or light beige to sometimes brownish orange, with 12 dark brown (to almost blackish) or reddish brown longitudinal stripes, with 6 longitudinal ribs; outer perianth lobes absent; inner perianth lobes bent upwards, connate at top and forming mitre with 3 holes; holes elliptic to rounded, 3–4 mm wide, 2–3 mm high; mitre tall and narrow, acuminate, ca 6 mm high, perfectly connate at the tip (without processes), with 3 longitudinal ribs, dark reddish brown to almost blackish with paler base (columns); annulus formed by 12 low crenate lobes, hairy. *Stamens* 6, pendent from the apical margin of the perianth tube; filaments free, short, curved downwards, hairy, light brown-violet to brown-pinkish; connectives broad and flattened, laterally connate to form a tube, densely hairy to tomentose in the apical half, sparsely hairy to glabrous in the basal half, ca 4 mm long, pale violet or pinkish to whitish; interstaminal glands not prominent, oblong, ca 0.5 mm long and 0.25 mm wide, placed between bases of lateral appendages; apical end of individual connective far exceeding lateral appendage, bearing several (ca 4–5) ± irregular short processes (sometimes almost hidden in the tomentum in young flowers); lateral appendage almost glabrous above, dark brown-violet, composed of 3 lobes—central lobe nose-shaped with irregularly dentate and straight to slightly convex margin, lateral lobes straight, with tuft of hairs on the upper margin. Style rather

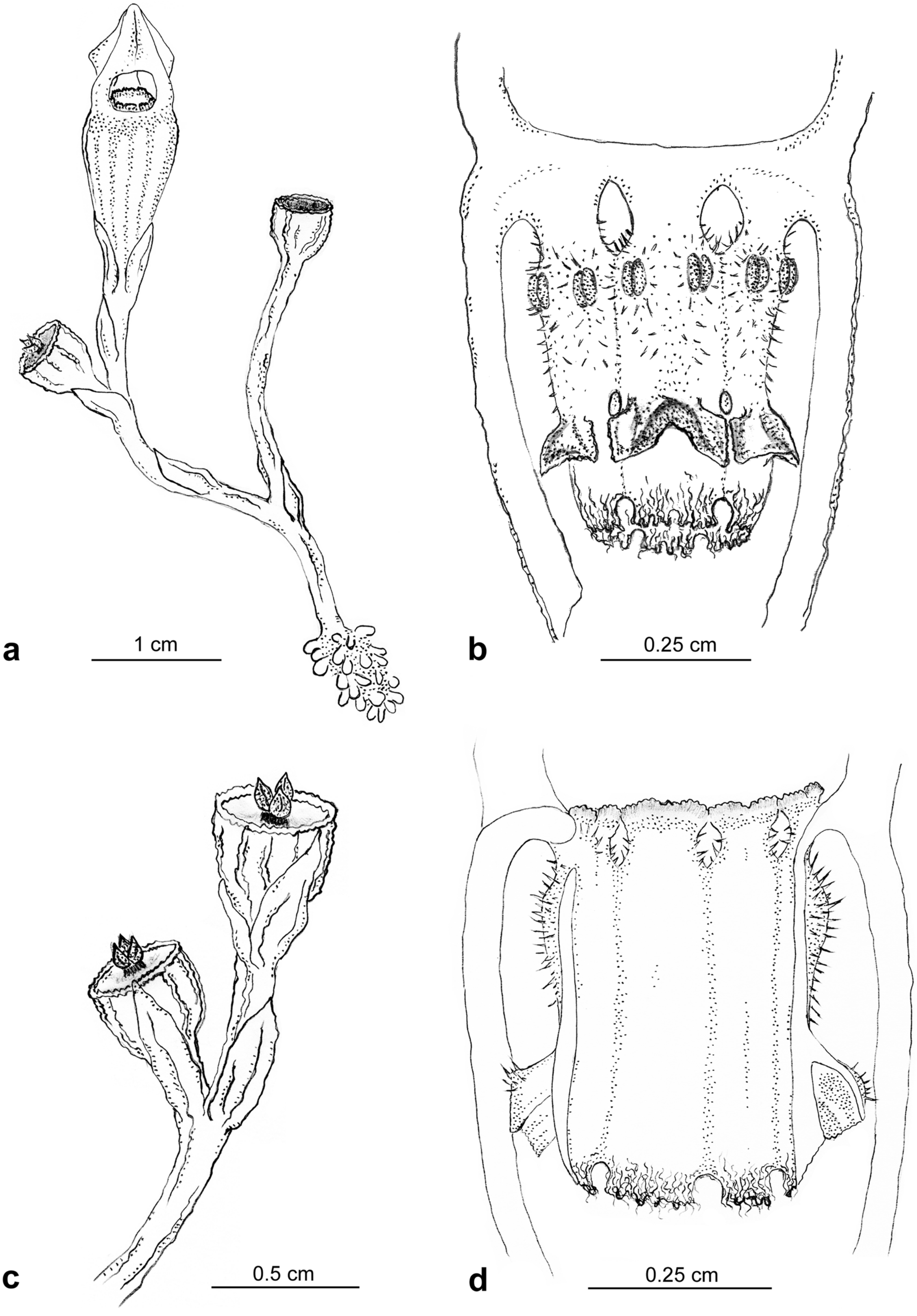

Fig. 2 *Thismia acuminata*: **a** habit; **b** outer view of connective tube; **c** ovaries with stigmas; **d** longitudinal section of connective tube (from *Sochor* et al. *BOR6/17*). Drawn by R. Melichárková

Fig. 3 *Thismia acuminata*: **a, b** habit; **c** outer view of connective tube; **d** longitudinal section of connective tube; **e** detail of appendages on connectives; **f, g** ovaries with two types of stigma; **h** mature capsule with seeds (from *Sochor* et al. *BOR6/17*)

short but distinct (ca 0.3 mm), dark brown; stigma 3-lobed, light beige to whitish, papillose and sometimes with sparse long hairs; each lobe usually deeply divided, forming two triangular lobes or sometimes trilobed (the middle lobe being smaller), laterally adnate to the adjacent stigmatic lobes. *Capsule* cup-shaped, longitudinally ribbed, dark (violet-)brown to almost blackish, ca 5 mm in diameter, on elongated pedicel. *Seeds* light yellow-brown, ellipsoid, ca 0.3–0.4 × 0.16 mm.

Habitats: Thismia acuminata was observed in closed canopy primary lower montane tropical rainforest in humus-rich soil in a river ravine.

Distribution area: The species is known only from the type locality in the Kelabit Highlands, Sarawak, Borneo.

Proposed conservation status: The population of *T. acuminata* is protected against anthropogenic disturbance thanks to its location in the Pulong Tau National Park. Although the inconspicuous appearance and ephemeral growth may contribute to overlooking of the species in the field, the total population size can be estimated to < 50 mature individuals at the present state of knowledge. Therefore, we suggest evaluating the species as critically endangered (CR) based on criterion D of IUCN Red List Categories and Criteria (IUCN 2012).

Notes: Despite the fact that the observed population consisted of 8 individuals with ca three well preserved and two old flowers, quite large variation was observed in flower colour (reddish to dark brown or almost blackish), colour of stem (light brown or greyish to dark reddish brown) and shape of stigmatic lobes (bilobed with deep incision between the lobes to trilobed with middle lobe being smallest). Tomentum on connective apex varied probably due to the age of the flower.

Having coralliform roots, mitre-forming inner perianth lobes and reduced outer perianth lobes, *T. acuminata* clearly belongs to section *Sarcosiphon*. Based on outer morphology, the most similar species is probably *T. laevis* which differs in acute and rather low and wide mitre. From this and other related species (e.g. *T. brunneomitra*, *T. clandestina*, *T. episcopalis* Becc., *T. nigra*), *T. acuminata* also differs in having several small lobes and tomentum of long hairs on connective apex and nose-shaped central lobe of lateral appendage. Lobed and hairy (although described as ciliolate and minutely verrucose) connective apex is present also in the New Guinean *T. versteegii*, which nevertheless has different shape of lateral appendage (described as obtrapeziform with inflexed lateral margins), smaller flowers (7.25 mm long above the ovary and 4.7 mm in diameter), light yellow-orange perianth with red-brown stripes and mitre, small but apparent outer perianth lobes, rather low mitre with obtuse apex and slit-like mitre openings (which, nevertheless, may only reflect an early anthetic phase).

Thismia laevis Sochor, Dančák & Hroneš, **sp. nov.**—HOLOTYPE: Malaysia, Sarawak, Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.0 km N of the village, 1108 m a. s. l., 3°50′13″N, 115°31′11″E, 16 Jan 2017, *M. Sochor* et al. *BOR9/17* (holotype: SAR [accession number Sochor/BOR-9/17]) (Figs. 4, 5).

Etymology: From the Latin *laevis* (smooth) referring to the smooth apex of connectives.

Diagnosis: Similar to *T. episcopalis* Becc., but differing in glabrous, shallowly bilobed apex of connectives, greyish perianth tube with 12 (dark) brown stripes and dark (red-)brown to blackish mitre.

Description: Achlorophyllous ground herb, ca 5.5–10.5 cm tall. *Roots* short, clustered, coralliform, light brown. *Stem* ca 13 cm long (but mostly under ground or in leaf litter), creeping, ascending to erect, sparsely branched, pale brown to pinkish; branching sympodial, with one bud covered in bracts of the flower in anthesis and growing as the main stem afterwards; pedicel very short or almost missing, elongating markedly (to ca 11 cm) after anthesis. *Leaves* around 4 below the first flower, spirally arranged, scale-like, triangular, acute, entire, 4–4.5 mm long and 1.5–2 mm wide at base, of the same colour as stem. *Floral bracts* of the same size and shape as leaves, pinkish, enveloping base of flower and a young bud. *Flowers* around 4 per stem, actinomorphic, 18 mm long, 7 mm wide below top of perianth tube; perianth tube narrowly urceolate with slight constriction above the middle, of 6 fused tepals; outer surface with 6 longitudinal ribs, greyish, with dark brown to blackish apex and ribs and brown stripes between the ribs (together making 12 longitudinal dark stripes); outer perianth lobes absent; inner perianth lobes bent upwards, connate at top and forming mitre with 3 holes; holes elliptic, 5.5 mm wide, 3.5 mm high; mitre with 3 distinct sutures, 3 ribs and short obtuse processes on the top, 6 mm tall, dark (red-)brown to blackish with paler apex and margins of holes; annulus formed by 12 low lobes, each consisting of several small lobes. *Stamens* 6, pendent from the apical margin of the perianth tube, dull orange; filaments free, short, curved downwards; connectives broad and flattened, except for lateral appendage and area around anthers glabrous, laterally connate to form a tube, ca 4 mm long; interstaminal glands not prominent, flat, oblong, ca 0.5 mm long, placed between bases of lateral appendages; apical end of individual connective shallowly bilobed, without any processes, far exceeding lateral appendage; lateral appendage large, (rather sparsely) hairy on margin, box-shaped, composed of 3 lobes—central lobe

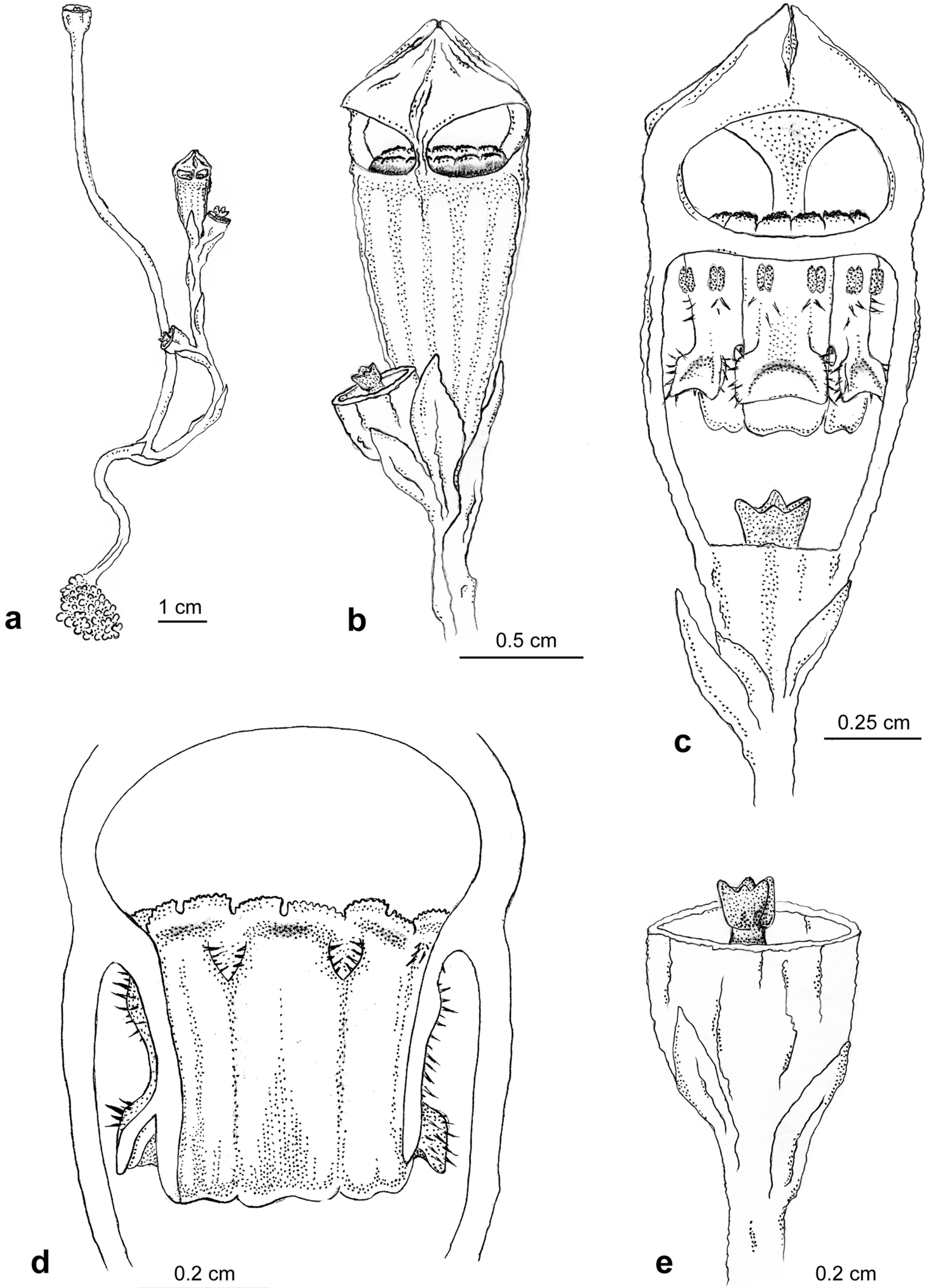

Fig. 4 *Thismia laevis*: **a** habit; **b** detail of flower; **c** section of flower with outer view of stamens; **d** longitudinal section of connective tube; **e** ovary with stigma (from *Sochor* et al. *BOR9/17*). Drawn by R. Melichárková

Fig. 5 *Thismia laevis*: **a** habit; **b** detail of flower; **c** section of flower and outer view of stamens; **d** outer view of stamens; **e** section of connective tube; **f** upper view of mitra; **g** stigma; **h** capsule with seeds (from *Sochor* et al. *BOR9/17*)

convexly down-curved and with slightly concave margin, making acute angles with lateral lobes from outer view. Style short, dark brown, stigma 3-lobed, ± smooth to smoothly papillose, each lobe with 2 large and 1 small lobe on apical margin, curved upwards and together forming triangular cup-like structure. *Capsule* cup-shaped, pinkish-brown, ca 7 mm in diameter, on elongated pedicel (to 11 cm long). *Seeds* beige, ellipsoid, ca 0.4 × 0.16 mm.

Habitats: Thismia laevis was observed in primary lower montane tropical rainforest under closed canopy in humus-rich soil in a river ravine.

Distribution area: The species is known only from two nearby localities in the Kelabit Highlands, Sarawak, Borneo.

Proposed conservation status: Population of *T. laevis* is protected against anthropogenic disturbance thanks to its location in the Pulong Tau National Park. Although wider occurrence of the species can be expected, the total population size can be estimated to < 50 mature individuals due to low population densities. Therefore, we suggest evaluating the species as critically endangered (CR) based on criterion D of IUCN Red List Categories and Criteria (IUCN 2012).

Additional specimens examined: Malaysia. *Sarawak* Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.4 km N of the village, 1224 m a. s. l., 3°50′26″N, 115°30′54″E, 4 Feb 2016, *M. Sochor* and *Z. Egertová BOR-PL/16* (OL [accession number 34700]).

Notes: Based on corraliform roots, inner perianth lobes forming mitre and reduced outer perianth lobes, *T. laevis* can be placed in the sect. *Sarcosiphon*. Morphologically most similar species is *T. clandestina* which was described from West Java in 1850 based on a fruiting individual (Blume 1850). Our current understanding of the species' floral morphology therefore comes from later descriptions of plants from the type area (Smith 1911) and Southern Thailand (Chantanaorrapint et al. 2015, but see Suetsugu et al. 2017). Both of these populations share several characteristic traits with *T. laevis*, such as overall habitus, connective apex far exceeding lateral appendage and 3-lobed stigmatic lobes with the middle lobe smaller (not clear for the Javan plants). Nonetheless, they differ in having 3-lobed, hairy connective apex, straight margin of lateral appendage and acuminate (rather than acute) and rather narrow mitre. While the plants from Java do not differ from *T. laevis* in perianth colour (greyish with dark brown to blackish stripes), Thai plants are orange-brown. Another similar species is *T. episcopalis*. Both species share similar shape o mitre (although more obtuse in *T. episcopalis*), but *T. episcopalis* differs clearly in shape of connective apex (hairy with 3 teeth), flower colour (orange-yellow) and shape of perianth tube (rather short urceolate without constriction above the middle). *T. acuminata* differs mainly in having several small tomentose lobes on connective apex, nose-shaped brown-violet central lobe of lateral appendage and narrow, tall, acuminate mitre. Superficially similar is also recently described Australian *T. lanternatus* W.E.Cooper, particularly in colour of perianth tube, mitre and connectives, and in position and shape of lateral appendage. Nevertheless, it differs, e.g. in underground stem, flattened mitre, connectives with 3- or 4-toothed apices and, importantly, in vermiform roots (Cooper 2017).

Thismia nigra Dančák, Hroneš & Sochor, **sp. nov.**—HOLOTYPE: Malaysia, Sarawak, Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.4 km N of the village, 1224 m a. s. l., 3°50′26″N, 115°30′54″E, 15 Jan 2017, *M. Sochor* et al. *BOR8/17* (holotype: SAR [accession number Sochor/BOR-8/17]; isotype: OL [accession number 35274]) (Figs. 6, 7).

Etymology: From the Latin *nigrum* (black) referring to the colour of the perianth.

Diagnosis: Similar to *T. brunneomitra* Hroneš, Kobrlová & Dančák, but with smaller flowers (10–12 mm long vs. 16–17 mm), apex of connective with two small lobes and one tuft of long simple hairs, and lateral appendage skirt-like with concave curved lower margin.

Description: Achlorophyllous ground herb, ca 2.5–7 cm tall. *Roots* short, clustered, coralliform, light brown to orange-brown. *Stem* 0.9–8 cm tall, usually erect, sometimes basal part creeping in leaf litter, sparsely sympodially branched or unbranched, with 1–4 flowers, glabrous, pale brown to dark reddish brown or greyish; pedicel of the same colour as stem, indiscernible or very short during anthesis, elongating markedly (up to ca 9 cm) after anthesis. *Leaves* 3–6 per branch, spirally arranged, scale-like, triangular, acute, entire, 3–4 mm long, ca 2 mm wide at base, pale brown or greyish-brown to reddish brown. *Floral bracts* 3, similar to leaves but slightly longer (3.5–5 mm), sometimes keeled and sparsely dentate, enveloping base of flower. *Flowers* solitary or usually 2–5 per stem, bisexual, actinomorphic, 10–12 mm long, 4.5–6 mm wide below the top of perianth tube; perianth tube urceolate, of 6 fused tepals; outer surface with 6 (or sometimes more) longitudinal ribs, dark greenish-grey with 1 transversal and 12 vertical blackish stripes; outer tepal lobes absent; inner tepal lobes well developed, bent upwards, connate at top and forming mitre with 3 holes, 3–3.7 mm tall; holes elliptic to almost rounded, 1–2 mm wide, ca 2.5 mm high; mitre dark brown to blackish with greyish base, usually topped by 3 short obtuse processes or rarely rounded on top. Annulus not prominent, blackish, ca 0.9 mm thick and with opening ca 1.3–1.8 mm in diameter, flat with raised inner margin formed by six low rectangular lobes. *Stamens* 6, hanging from top of perianth tube (outer margin of the annulus), blue; filaments flat and

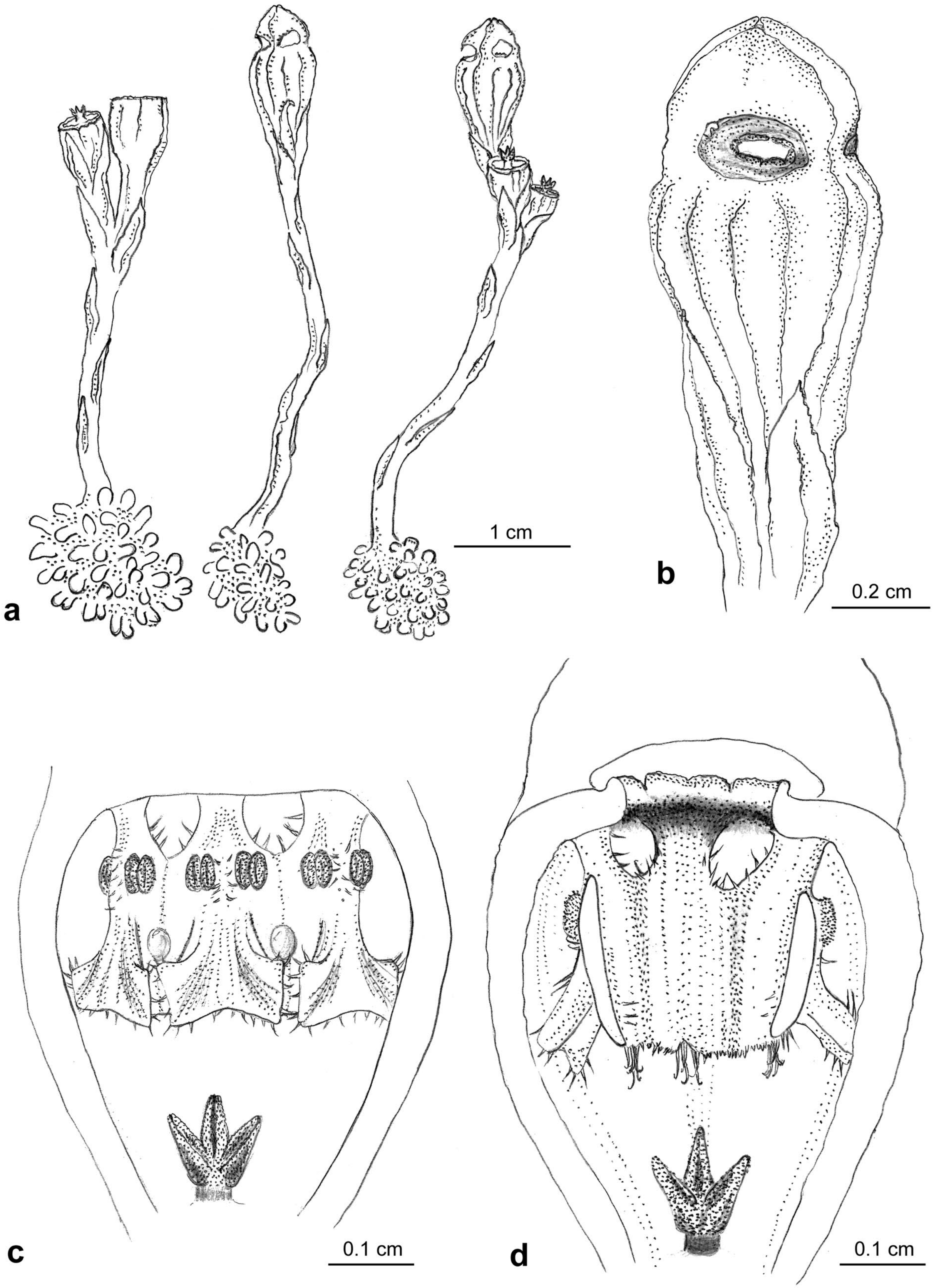

Fig. 6 *Thismia nigra*: **a** habit; **b** detail of flower with annulus; **c** outer view of stamens; **d** section of connective tube (**a** from *Sochor* et al. *BOR14/17* & *BOR15/17*; **b** from *Sochor* et al. *BOR19/*17; **c, d** from *Sochor* et al. *BOR8/17*). Drawn by R. Melichárková

Fig. 7 *Thismia nigra*: **a, b, c** habit; **d** stigma; **e** outer view of stamens; **f** section of connective tube (**a** from *Sochor* et al. *BOR19/17*; **b** from *Sochor* et al. *BOR15*/17; **c–f** from *Sochor* et al. *BOR8/17*)

rather thin (ca 0.6 mm wide, 40–60% of the width of connective), hairy in lower part; connectives flattened, connate to form tube; interstaminal glands flat, circular, ca 0.32 mm in diameter, placed between lateral appendages; individual connectives shortly hairy in the apical quarter, with 2 small lobes (sometimes not prominent) and several (usually around 5) long simple transparent hairs in the middle of the apex; lateral appendage exceeding the connective apex, skirt-like, with concavely curved lower margin and 2 rather small lateral lobes, with long hairs on margins. Ovary inferior, cup-shaped, blackish in upper part and pale otherwise, longitudinally ribbed, often covered in bracts; stigma 3-lobed, each lobe deeply divided into 2 long triangular lobes and laterally adnate to the neighbouring lobes, papillose. *Capsule* cup-shaped to funnel-shaped, ca 6 mm in diameter, pinkish-brown to dark brown.

Habitats: All populations were found in primary lower montane tropical rainforest in elevation above 1200 m a.s.l. near streams or rivers, usually around the line of maximum water level, sometimes also in fresh fluvial sediments, in sandy, clayey and humus-rich soils. All populations were accompanied by other mycoheterotrophic species, such as *Epirixanthes* spp., *Sciaphila* spp., *Thismia viridistriata* and *Thismia laevis*.

Distribution area: The species is known from five nearby localities in the Pulong Tau National Park, Kelabit Highlands, Sarawak.

Additional specimens examined: Malaysia. *Sarawak* Kelabit Highlands, Pa'Lungan village, Arur Dutu, 5.6 km N of the village, 1208 m a. s. l., 3°51′40″N, 115°31′22″E, 19 Jan 2017, *M. Sochor* et al. *BOR14/17* (SAR [accession number Sochor/BOR-14/17]); Kelabit Highlands, Pa'Lungan village, Arur Dutu, 5.7 km N of the village, 1210 m a. s. l., 3°51′43″N, 115°31′24″E, 19 Jan 2017, *M. Sochor* et al. *BOR15/17* (SAR [accession number Sochor/BOR-15/17]); Kelabit Highlands, Pa'Lungan village, Arur Dutu, 5.8 km N of the village, 1210 m a. s. l., N3°51′46″, E115°31′26″, 20 Jan 2017, *M. Sochor* et al. *BOR19/17* (SAR [accession number Sochor/BOR-19/17]); Kelabit Highlands, Pa'Lungan village, Arur Dutu, 5.9 km N of the village, 1210 m a. s. l., 3°51′48″N, 115°31′28″E, 20 Jan 2017, *M. Sochor* et al. *BOR46/17*.

Proposed conservation status: In the studied area, the species seems to occur locally more commonly than is usual in most other *Thismia* species and is under protection of the Pulong Tau National Park. The fact that it is so far known only from this small region, nevertheless, could be attributed to its possible stenoendemism. Considering its low population densities (usually only one or a few individuals), the total population size can be estimated to < 250 mature individuals at the present state of knowledge. Therefore, we suggest evaluating *T. nigra* as endangered (EN) based on criterion D of IUCN Red List Categories and Criteria (IUCN 2012).

Notes: Similarly to the previous species described here, *T. nigra* belongs to section *Sarcosiphon*. Based on the morphology, the closest relative is undoubtedly *T. brunneomitra* which is known from Brunei, less than 90 km from the localities of *T. nigra*. Both species exhibit similar overall appearance (habitus, flower shape and colour), and even colour of connectives. Nevertheless, they differ in shape of connectives, flower size and number and also ecology, among other traits that may vary. Whereas *T. brunneomitra* has three large lobes on connective apex, which are ended by glandular hairs, *T. nigra* has only two small lobes in the centre of connective apex with only one tuft of a few long, simple, straight or hooked hairs. Shape of lateral appendage also differs in the two species (compare Figs. 6c, 7e and Hroneš et al. 2015). Flowers of the former species are in number of 1–2, ca 1.7 × 1 cm long, but those of *T. nigra* are usually 2–5 and smaller (ca 1.1 × 0.5 cm). Also, stigma in *T. brunneomitra* is shallowly notched whereas in *T. nigra* is deeply divided, although this trait may be generally variable within *Thismia* species. And although both species were found always on river banks in primary rain forest, the locality of *T. brunneomitra* is in lowland Dipterocarp forest ca 105 m a.s.l., whereas *T. nigra* grows in lower montane forest > 1200 m a.s.l. Differentiation of both species was further detected in molecular markers, particularly LSU (Fig. 1; Online Resource 2).

Another similar species, *T. brunneomitroides* Suetsugu & Tsukaya, described recently from Thailand, has ivory-coloured perianth, two teeth with glandular hairs on apical margin of the connective and convex margin of lateral appendage. *T. episcopalis*, known from western Sarawak, differs in having more flowers per stem (up to 7), orange-yellow flowers, taller mitre (ca 5 mm), no projections on mitre, 3 teeth on connective apex and lateral appendage not reaching connective apex. Three other similar species, *T. laevis*, *T. acuminata* and *T. clandestina* differ in the connective apex that is of different shape and far exceeding lateral appendage, in trilobed stigmatic lobes with middle lobe being smallest, in the absence of projections on mitre (only in *T. laevis* very small projections are present) and usually in colour and shape of flowers.

Thismia viridistriata Sochor, Hroneš & Dančák, **sp. nov.**—HOLOTYPE: Malaysia, Sarawak, Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.2 km N of the village, 1182 m a. s. l., 3°50′20″N, 115°31′01″E, 16 Jan 2017, *M. Sochor* et al. *BOR11/17* (holotype: SAR [accession number Sochor/BOR-11/17]) (Figs. 8, 9).

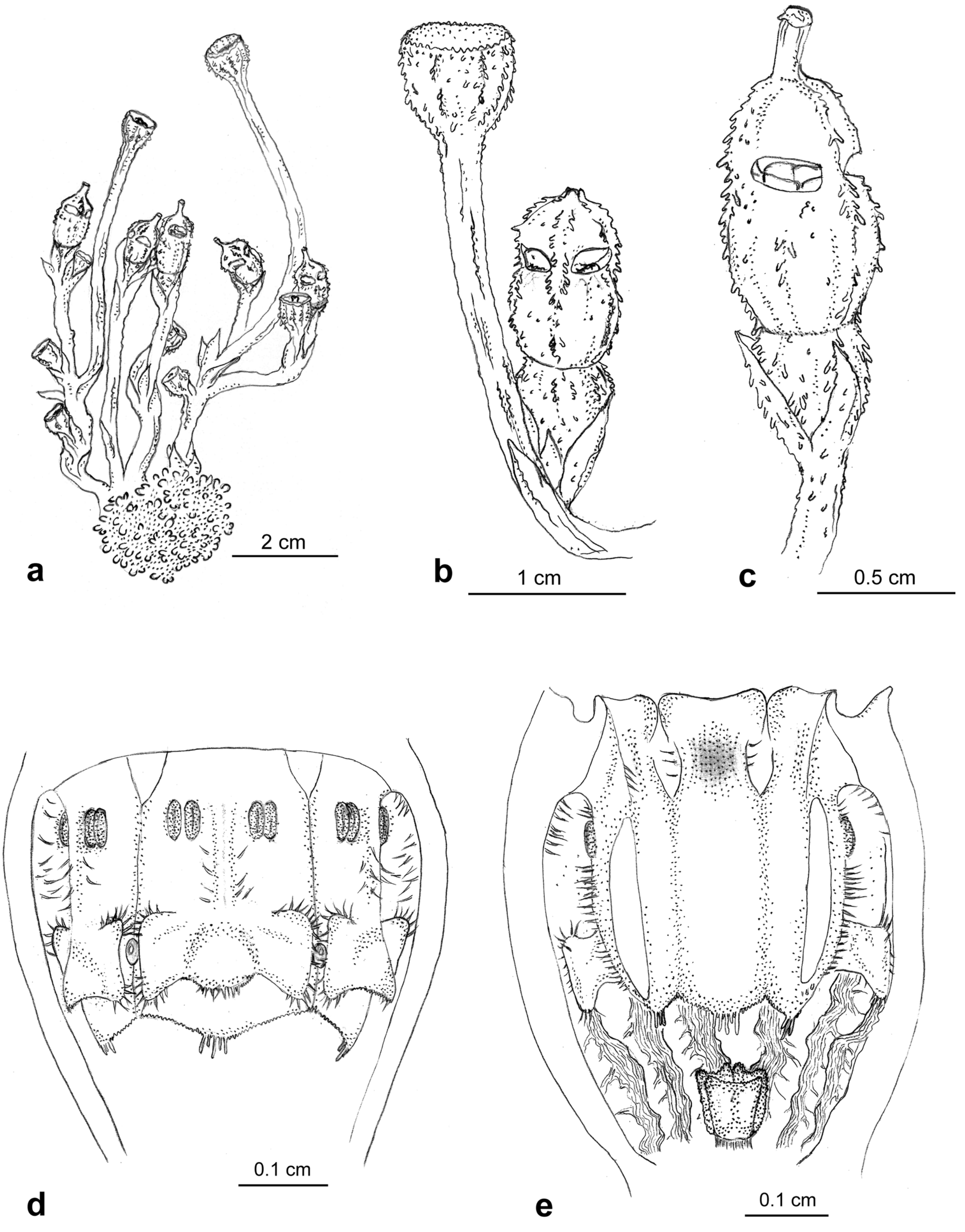

Fig. 8 *Thismia viridistriata:* **a** habit; **b, c** flowers of two different morphotypes; **d** outer view of stamens; **e** section of floral tube (**a** from *Sochor* et al. *BOR11/17*; **b** from *Sochor* et al. *BOR7/*17; **c** from *Sochor* et al. *BOR3/17*; **d** from *Sochor* et al. *BOR13/17*; **e** from *Sochor* et al. *BOR23/17*). Drawn by R. Melichárková


a
b
c
d
e
f
g
h

◂**Fig. 9** *Thismia viridistriata*: **a, b** two different morphotypes; **c** plant with typical green-striped ovary; **d** detail view of floral inner structure—stigma, vertical ribs on perianth tube and longitudinal section of connective tube; **e** outer-bottom view of stamens; **f** section of connective tube; **g** top of mitre; **h** example of the species' habitat diversity—a plant growing on a bare vertical rock (**a, c** from *Sochor* et al. *BOR3/17*; **b, f, g** from *Sochor* et al. *BOR7/*17; **d, h** from *Sochor* et al. *BOR23/17*; **e** from *Sochor* et al. *BOR11/17*)

Etymology: From the Latin *viridis* (green) and *striae* (stripes) referring to the green longitudinal stripes on ovary, sometimes very prominent.

Diagnosis: Thismia viridistriata differs from congeneric species in having the following combination of morphological traits: coralliform roots, inner perianth lobes forming mitre, mitre topped by a single cylindrical column or three short obtuse processes, prickle-like protrusions on ovary and perianth, greenish stripes on ovary, vertical ribs partly detached from inner surface of perianth, and apex of connectives with many short hairs and one tuft of several long hairs.

Description: Achlorophyllous ground herb, ca 2–4.5(–9) cm tall. *Roots* short, densely clustered, coralliform, light beige, forming a dense, spheroidal, tuber-like system, 1–2.5 cm in diameter. *Stem* 0.5–3(–8) cm long, creeping, ascending or erect, simple or sparsely branched, brown to whitish; branching sympodial, branches short (usually < 1 cm); pedicels indiscernible or very short during anthesis, elongating markedly during fruit maturing (up to ca 6 cm). *Leaves* usually 2–6, spirally arranged, scale-like, triangular, acute, entire, 3–6 mm long and 1.5–2 mm wide at base, of the same colour as stem. *Floral bracts* 3, of the same size and appearance as leaves. *Flowers* 1–5 per stem, actinomorphic, 13–21 mm long, 4.5–6 mm wide in the widest point; perianth tube urceolate (widest in the middle or upper third); outer surface with 6 verrucose longitudinal ribs, greyish to rich brown or reddish brown with darker transversal stripe in the middle and 12 dark brown (to almost blackish) or reddish brown longitudinal stripes; perianth inside with 12 transparent vertical ribs partly detached from its surface, most prominent in lower third to half (below connectives); outer perianth lobes usually absent or very short, obtusely triangular; inner perianth lobes bent upwards, connate at top and forming mitre with 3 holes; holes discorectangular or ellipsoid, 1.2–2 × 2–3.5 mm; mitre ± hemispherical, almost smooth, verrucose or covered by short prickle-like protrusions, especially on the 3 central ribs, top of mitre with a single cylindrical, up to ca 6 mm long column (usually dark brown) or with 3 short protrusions (usually dark pink to reddish), basal part of mitre pinkish or light brown to greyish, upper part darker (reddish or dark brown to blackish); annulus thin, often markedly raised, divided into 6 rectangular lobes. *Stamens* 6, pendent from the apical margin of the perianth tube; filaments free, curved downwards, glabrous adaxially, covered by long straight hairs on margins abaxially, dark violet to dark reddish brown; connectives broad and flattened, laterally connate to form a tube, ca 2–2.5 mm long, adaxially, apically and abaxially below lateral appendage densely covered by short transparent hairs, greyish-green (especially in section) or sometimes pinkish; interstaminal glands not prominent, ± flat, slightly oblong, ca 0.45 mm long, placed between lateral appendages and sometimes hidden under their lateral lobes; apical end of individual connective with 1 wide lobe (sometimes divided by notch into 2 short lobes) bearing several (usually 5) transparent, ca 0.15–0.2 mm long hairs; lateral appendage not reaching the connective apex, distinctly 3-lobed (central lobe being smallest), densely hairy on margins. Ovary inferior, cup-shaped, light brown with 12 grey-green to dark green stripes, usually covered by long prickle-like protrusions; stigma 3-lobed, individual lobes shallowly bilobed, curved upwards and together forming triangular cup-like structure. *Capsule* cup-shaped, 5–9 mm in diameter, pinkish, light brown to greyish-brown, usually with darker longitudinal stripes. *Seeds* beige, ellipsoid, ca 0.5–0.75 × 0.2–0.3 mm.

Habitats: Eleven of the twelve known localities are placed in primary lower montane tropical rainforest in elevation of ca 1100 to 1200 m a.s.l. One rich population was found on a borderline between primary forest and old forest clearing (possibly former pastures or fields, now overgrown by *Pteridium aquilinum*). All individuals were discovered near streams or rivers, usually just above the line of maximum water level, but sometimes also in fresh fluvial sediments or on drier slopes up to ca 20 m above the river; in sand, humus-rich soils or even on almost barren rocks. At most localities, it grew together with other mycoheterotrophic taxa, mainly *Epirixanthes kinabaluensis*, *Sciaphila* spp., *Exacum tenue*, *Burmannia lutescens* agg. and other *Thismia* species.

Distribution area: The species is known from 11 localities within an area of ca 10 × 18 km in the Kelabit Highlands, Borneo, Malaysia.

Proposed conservation status: Although *T. viridistriata* seems to be one of the most common *Thismia* species in the Kelabit Highlands, it is known from just a small geographic area (minimal extent of occurrence 121 km^2 and minimal area of occurrence ca 20 km^2). Also, the fact that it had not been detected earlier may imply its limited distribution area or its rare occurrence elsewhere. Four of the detected populations are furthermore unprotected from human activities, and one of them has already probably vanished due to road construction between Bario and Ba'kelalan. The region experienced an extensive logging and development in the last decade, which very likely influenced the total population size and further loss of populations can be expected in the future outside the Pulong Tau National Park. Therefore, we suggest evaluating the species as endangered (EN) based on criterion C2ai of IUCN Red List Categories and Criteria (IUCN 2012).

Additional specimens examined: Malaysia. *Sarawak* Kelabit Highlands, Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village, 1195 m a. s. l., 3°42′1″N, 115°31′28″E, 13 Jan 2017, *M. Sochor* et al. *BOR3/17* (SAR [accession number Sochor/BOR-3/17]); Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.1 km N of the village, 1175 m a. s. l., 3°50′18″N, 115°31′3″E, 15 Jan 2017, *M. Sochor* et al. *BOR7/17* (SAR [accession number Sochor/BOR-7/17]); Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.0 km N of the village, 1164 m a. s. l., 3°50′15″N, 115°31′16″E, 16 Jan 2017, *M.* et al. *BOR12/17* (SAR [accession number Sochor/BOR-12/17]); Kelabit Highlands, Pa'Lungan village, Arur Dutu, 5.5 km N of the village, 1206 m a. s. l., 3°51′38″N, 115°31′21″E, 19 Jan, *M. Sochor* et al. *BOR12/17* (SAR [accession number Sochor/BOR-12/17], OL [accession number 35266]); Kelabit Highlands, Long Rebpun (Rapung), Pa Tabanul, 6.1 km NE of Pa'Lungan village, 1093 m a. s. l., 3°51′6″N, 115°33′26″E, 18 Jan 2017, *M. Sochor* et al. *BOR16/17* (SAR [accession number Sochor/BOR-16/17]); Kelabit Highlands, Pa'Lungan village, Upper Pa'Lungan river, 5.7 km N of the village, 1200 m a. s. l., 3°51′43″N, 115°31′20″E, 20 Jan 2017, *M. Sochor* et al. *BOR17/17* (SAR [accession number Sochor/BOR-17/17]); Kelabit Highlands, Pa'Lungan village, a ridge between Upper Pa'Lungan river and Arur Dutu, 5.8 km N of the village, 1230 m a. s. l., 3°51′45″N, 115°31′23″E, 20 Jan 2017, *M. Sochor* et al. *BOR18/17* (SAR [accession number Sochor/BOR-18/17]); Kelabit Highlands, Bario, Arur Dalan village, 0.9 km WSW of the longhouse, 1120 m a. s. l., 3°45′8″N, 115°26′16″E, 22 Jan 2017, *M. Sochor* and *Z. Egertová BOR23/17* (SAR [accession number Sochor/BOR-23/17]); Kelabit Highlands, Pa'Umor village, Pa'Pidap river catchment, 3.1 km SSE of the village, 1135 m a. s. l., 3°42′41″N, 115°30′57″E, 7 Feb 2016, *M. Dančák* et al. *MD2016/431* (OL [accession number 355512]).

Notes: Compared to other known *Thismia* species, *T. viridistriata* exhibits an extremely high variability in outer macromorphological characters. The greatest variation was observed in colour of flower, particularly mitre (from pink through brown to greyish-brown) and in the presence of cylindrical projection on top of mitre and its length (from absent to ca 6 mm). Outer perianth lobes are sometimes well developed but are frequently lacking with no relation to the presence or absence of the mitre column. Some variation was observed also in shape of perianth tube (widest in the middle or in upper third), flower size (13–21 mm, incl. mitre), number of stems from one root (1–6), number of flowers per stem (1–5) and stem length (0.5–8 cm). Other traits, such as presence and shape of prickle-like processes on flowers, colour of connectives (greyish-green to rather pinkish) or bilobed connective apex, can be partly attributed to flower age and preservation.

As a mitriform species with distinct apical column on the top of the mitre in some individuals, *T. viridistriata* could be placed into the genus *Scaphiophora*, together with *T. appendiculata* Schltr. and *T. gigantea* (Jonker) Hroneš. However, this genus is now generally reduced to *Thismia* (e.g. Maas et al. 1986; Merckx et al. 2013a; Kumar et al. 2017). The example of *Thismia viridistriata* clearly shows that this approach is correct because the main diagnostic trait, i.e. the presence of the apical column, may vary even within the species. This also brings into question the existence of *Scaphiohora* even as a section of *Thismia*. With coralliform roots, inner perianth lobes forming mitre and outer perianth lobes reduced or lacking, *T. viridistriata* (as well as the other species of *Scaphiophora*) can well be placed into section *Sarcosiphon*. *T. viridistriata* differs from members of this section by, e.g. the presence of cylindrical column on top of mitre, prickle-like protrusions on flowers (especially on ovary), vertical ribs partly detached from the inner surface of perianth tube, and shape of connectives. Individuals that lack the mitre column may be superficially similar to *T. brunneomitra, T. nigra* and *T. acuminata* which differ (beside the above mentioned) in having dark brown to blackish flowers, narrowly urceolate perianth tube, narrower mitre and ± smooth outer surface of flower. In our phylogenetic analysis, *T. viridistriata* forms a distinct, basal lineage within the *Sarcosiphon* clade (Fig. 1) and the morphological similarity with the above-mentioned species may therefore reflect either convergent evolution, or limited morphological anagenesis in both lineages.

Identification key of *Thismia* sect. *Sarcosiphon* (incl. *Scaphiophora and Geomitra*, excl. Indochinese species with vermiform roots)

1a. Mitre at its top with 1–3 appendages, at least 2 mm long 2
1b. Mitre at its top without any appendages or with very short, up to 2 mm long processes 8
2a. Mitre at its top with 3 appendages 3
2b. Mitre at its top with 1 appendage (column), sometimes trilobed at its top 4
3a. Perianth yellow-orange to pink-red; connective apex triangular, acute .... ***T. clavigera***
3b. Perianth blue-green; connective apex rounded to slightly emarginate .... ***T. betung-kerihunensis***
4a. Appendage at top of mitre 2–6 mm long 5
4b. Appendage at top of mitre at least 6 mm long 6

5a. Perianth tube verrucose, greyish to rich brown or reddish brown; outer perianth lobes absent or very short, obtusely triangular; connective apex with 1 wide lobe (sometimes divided by a notch into 2 short lobes) bearing several short hairs .... ***T. viridistriata***

5b. Perianth tube smooth, yellowish white; outer perianth lobes small, ear shaped; connective apex with 1 filiform median appendage........................***T. appendiculata***

6a. Mitre appendage dark brown to blackish, apically distinctly trilobed, the lobes acute, mitre black … ***T. hawkesii***

6b. Mitre appendage orange to red, apically clavate to very shallowly trilobed, the lobes obtuse; mitre yellow, orange or pink 7

7a. Mitre fleshy, its margin reflexed and extending downwards over the upper perianth tube, covering their openings; mitre appendage clavate; connective apex without appendages .... ***T. tectipora***

7b. Mitre slender, with large distinct openings; mitre appendage shallowly trilobed at its apex; connective apex with 5 appendages .... ***T. gigantea***

8a. Outer perianth lobes present, distinct 9

8b. Outer perianth lobes absent or indistinct 11

9a. Mitre thick, flashy; connective apex bilobed; mitre purplish brown .... ***T. yorkensis***

9b. Mitre thin, slender; connective apex with one central lobe and two smaller lateral lobes; mitre yellowish or bluish 10

10a. Outer perianth lobes deeply dentate, bright yellow; mitre elevated by three filiform pillars … ***T. kelabitiana* ined.**

10b. Outer perianth lobes smooth with a single central short tooth, blue; mitre not elevated by filiform pillars .... ***T. goodii***

11a. Annulus and stamens sunken inside perianth tube .... ***T. crocea***

11b. Annulus and stamens positioned at the perianth tube opening not sunken inside perianth tube 12

12a. Ovary and perianth tube covered by prickle-like protrusions; vertical ribs elevated and partly detached from inner surface of perianth tube .... ***T. viridistriata***

12b. Ovary and perianth tube verrucose to smooth; vertical ribs not distinctly elevated on inner surface of perianth tube 13

13a. Lateral appendage of connective clearly exceeding connective apex 14

13b. Lateral appendage of connective not exceeding connective apex 15

14a. Flowers 16–17 mm long; connective apex with 2 wide, obtusely triangular lateral lobes and narrowly triangular middle lobe, each lobe with tuft of glandular hairs .... ***T. brunneomitra***

14b. Flowers 10–12 mm long; connective apex with 2 small lobes and several long simple transparent hairs in the middle of the apex .... ***T. nigra***

15a. Connective apex smooth, without any hairs, teeth or processes ....***T. laevis***

15b. Connective apex at least hairy or dentate 16

16a. Mitre apex with 3 short acute processes; ovary densely verrucose; perianth tube ivory … ***T. brunneomitroides***

16b. Mitre apex without any processes; ovary glabrous or sparsely verrucose; perianth tube yellow-orange to brown 17

17a. Connective densely hairy to tomentose, bearing ca 4–5 irregular short processes at apex .... ***T. acuminata***

17b. Connective glabrous to sparsely hairy, bearing at most 3 processes at apex 18

18a. Connective apex shallowly trilobed or obtuse .... ***T. clandestina***

18b. Connective apex with 3 sharp triangular teeth .... ***T. episcopalis***

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Information on Electronic Supplementary Material

Online Resource 1. List of genbank accessions used in phylogeny reconstruction, list of specimens used for molecular analyses with collection data and alleles detected at each locus, and a map of collections.
Online Resource 2. Pairwise genetic distance among alleles detected in the reduced sample set.
Online Resource 3. Phylogenetic trees computed from each locus separately and supplementary trees from multilocus data.
Online Resource 4. Sequence alignments used for the analyses.

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Thismia: the rarest of the rare? Ranges of some Bornean species are much larger than previously believed

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Abstract

Fairy lanterns (*Thismia*; Thismiaceae, Dioscoreales) are believed to be extremely rare and narrowly endemic plants. Despite that, many new *Thismia* populations have been recently discovered in Borneo. These are summarized and discussed here and all twelve Bornean *Thismia* species with multiple localities are reviewed. New localities of *T. brunneomitra*, *T. hexagona*, *T. neptunis*, *T. pallida* and *T. viridistriata* are reported which considerably enlarge ranges of these species. New conservational statuses are proposed for *T. brunneomitra*, *T. goodii, T. hexagona* and *T. neptunis*. New or unpublished localities are also reported for *T. cornuta* and *T. goodii*. Although the known within-species morphological variability is extended only little or not at all by these finds, geographically distant populations often exhibit relatively large genetic differences, in some cases similar to those among distinct species (namely *T. brunneomitra* and *T. minutissima*). The new data show that, at least in some tropical species of *Thismia*, we can expect quite normal type of distribution with multiple localities over relatively large geographical areas.

Keywords: conservation status, Dioscoreales, distribution, Malesia, tropical forest

Introduction

Rare plants have always fascinated biologists and have also been a subject of curiosity for the general public. Today, rarity is a well described and understood biological phenomenon and large numbers of rare organisms are known and studied (Murray *et al.* 2002, Ohlemüller *et al.* 2008). Among plants, such an example could be *Thismia* Griffith (1844: 221; fairy lanterns, Thismiaceae, or Burmanniaceae s.l.), a genus of strange-looking tiny mycoheterotrophic monocot plants which inhabit mostly tropical and subtropical forests. There are around 85 species currently described. At least 55 of them are known only from their type localities and at least 38 species were only seen by their discoverers, in extreme cases as a single individual, e.g. *Thismia bokorensis* Suetsugu & Tsukaya (2018c: 65), *T. kobensis* Suetsugu (2018a: 121)., *T. puberula* Nuraliev (2015: 135) and others.

Thismia are usually very small and inconspicuous plants with highly localized occurrence. Some species are also highly seasonal thus their flowers appear only in certain period of the year, usually during the wet season (Stone 1980). These factors make them very hard to spot in the field, especially if one does not concentrate to find them. This naturally results in the fact that they are easily overlooked. For example, *Thismia neptunis* Beccari (1877: 251), an iconic species described by O. Beccari in 1878 and never seen since until 2017 (Sochor *et al.* 2018a), must have been overlooked for more than 150 years in an area with relatively high level of botanical activity in the Kubah National Park of Sarawak.

In recent years, we have discovered several new species of *Thismia* across Borneo which we originally considered very rare and endemic to their type localities or areas. However, further investigation revealed that some of them

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have much broader distribution and may be even common over large parts of the island. Additionally, we discovered another two new species (*Thismia minutissima* Dančák, Hroneš & Sochor (2020a: 2) and *T. ornata* Dančák, Hroneš & Sochor (2020b: 66)), which also have considerably large ranges with multiple localities. Finally, we found several new localities of the above mentioned previously presumably extinct *Thismia neptunis*. These new distributional data change substantially our understanding of distribution, rarity and endemism of *Thismia* with implications to their conservation strategies and assessments.

In the following text we review all Bornean *Thismia* species with multiple localities and summarize all data related to their distribution.

Material and methods

New localities were discovered during our three expeditions in November 2018, January/February 2019 and January 2020 to Sabah and Sarawak, Borneo. Individuals from newly found populations were studied using hand lens (30–60× magnification), stereo microscope and macro photography. Collected specimens were thoroughly compared with original drawings and descriptions given in protologues of representatives of *Thismia*. Herbarium vouchers of new localities reported in this study are deposited in SAN, SAR and OL. Because *Thismia* populations are sometimes composed by a few or even a single reproductive individual, voucher specimens were not always collected to prevent unnecessary harm to the population. In these cases, plants were documented only by photographs and usually also by DNA sample. Additionally, herbarium material deposited in K, SAN and SAR was studied (herbarium codes according to Thiers 2020) and unpublished records were added as well.

DNA was extracted by the CTAB method (Doyle & Doyle 1987) from a silica gel-dried piece of tissue from one individual per population. Sequence data were generated for three nuclear and two mitochondrial loci. The small subunit of ribosomal DNA (SSU rDNA) was amplified and sequenced with primers NS1, NS6, internal transcribed spacers of ribosomal DNA (ITS) with primers ITS1 and ITS4 (White *et al.* 1990) and large subunit of ribosomal DNA (LSU rDNA) by primers N-nc26S6 and 2134rev (Kuzoff *et al.* 1998). The mitochondrial genes *atp*A and *mat*R were amplified and sequenced with primers developed by Eyre-Walker & Gaut (1997) and primers 26F and 1002R (Meng *et al.* 2002), respectively. All PCRs were performed with Kapa polymerase (Kapa Biosystems) following a standard protocol with 37 to 40 cycles and annealing temperature of 56 °C (rDNA, *atp*A) or 47 °C (*mat*R). The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25 M NaCl in the precipitation mixture) and sequenced in both directions by Sanger method at Macrogene Europe. The most variable locus, ITS, was sequenced in all collections to screen variation, whereas the other loci were only analysed in selected specimens. Reads were assembled, aligned, manually checked, trimmed and analysed in Geneious 8 (Biomatters). Sequences were uploaded to NCBI Genbank under accession numbers MG008340–MG008388, MG765543–MG765546 and MN067225–MN067332.

Protologues and other relevant literature for all known *Thismia* species were thoroughly searched for number of localities and altitudinal distribution of each species. In this work, locality is defined as a place with occurrence of at least one *Thismia* individual distant from another place with occurrence of the same species by at least several hundred metres and usually separated by environment unsuitable for occurrence of this species. It differs from location sensu IUCN (2012) which is defined as “a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the taxon present”. Therefore, in Borneo rainforests, a location usually covers much larger area than a locality and may contain a number of them.

Results

Thismia brunneomitra

Thismia brunneomitra Hroneš, Kobrlová & Dančák, Phytotaxa 234(2): 173. 2015.

Type:—Brunei Darussalam, Temburong distr.: Kuala Belalong, right bank of the stream Sungai Mata Ikan, ca. 150 m NW from the Kuala Belalong Field Studies Centre. WGS 84: N 04°32′51.2″, E 115°09′24.5″; ca. 105 m a. s. l., 3 Feb 2015, *M. Hroneš & L. Kobrlová 402015* (holotype BRUN).

New localities:—Malaysia, Sarawak, Limbang Division, Lawas District, Long Tuyo village: primary forests along a tributary of the Tuyo river, two sites: WGS 84: N 04°27′31″, E 115°29′16″, 550 m a. s. l., 30 Jan 2019, *Sochor, Hroneš & Dančák BOR25/19* (OL), ca. 20 individuals covering an area of ca. 100 m^2; WGS 84: N 04°27′28”, E 115°29′14″, 545 m a. s. l., 30 Jan 2019, *Sochor, Hroneš & Dančák BOR26/19* (OL, SAR), ca. 25 individuals covering an area of ca. 100 m^2; primary forests south of the Tuyo river, two sites: WGS 84: N 04°27′56″, E 115°29′52″, 545 m a. s. l., 31 Jan 2019, *Sochor, Hroneš & Dančák BOR37/19* (OL), five individuals covering an area of ca. 30 m^2; WGS 84: N 04°27′55″, E 115°29′46″, 540 m a. s. l., 31 Jan 2019, *Sochor, Hroneš & Dančák BOR38/19* (OL), ca. 20 individuals covering an area of ca. 500 m^2. – **Malaysia, Sabah, Tawau Division, Tawau District, Tawau Hills National Park:** along trail to sulphur hot springs, primary forest, WGS 84: N 04°24′46″, E 117°53′49″, ca. 330 m a. s. l., 12 Feb 2019, *Hroneš & Dančák 02/2019* (OL, SAN), one flowering and two fruiting individuals covering an area less than 1 m^2.

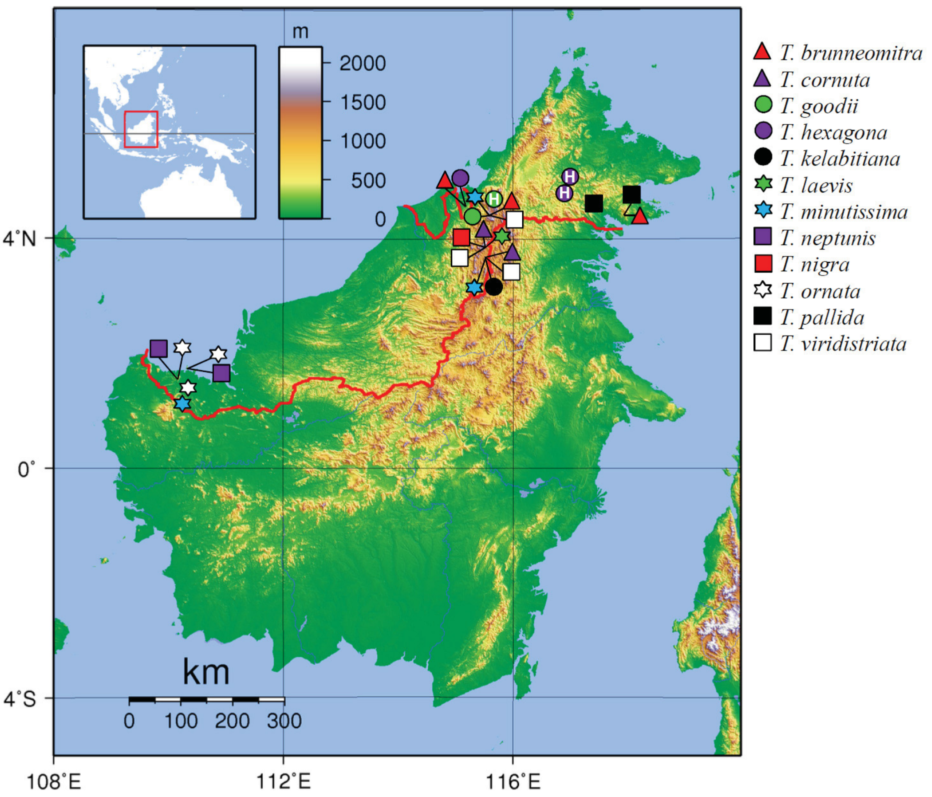


FIGURE 1. Distribution of Bornean *Thismia* species with multiple localities based on our field survey and herbaria revisions. Symbols with H letter inside show localities based on herbaria records, other observations are ours. Multiple localities or locations within 15 km distance are mapped by a single symbol due to the scale of the map. Position of localities with multiple species is indicated by black lines leading from particular symbols.

This species, originally believed to be endemic to Brunei’s Temburong district and known from a single locality (Hroneš *et al.* 2015), has now a range spanning some 300 km across northern Borneo, from Brunei Darussalam through neighbouring Sarawak (Lawas District) as far as Tawau Hills National Park in east Sabah (Fig. 1). With three new localities presented here the number of currently known localities has increased to four (Tab. 2). Compared to the original description (Hroneš *et al.* 2015), the new populations exhibit more flowers per stem (up to six), 1.3–7.5 cm long stem, flowers 13–17 mm long and 5.5–7.5 mm wide, mitre apex obtusely acuminate with or almost without three very small projections, light greyish to very faintly bluish stamens, and rather irregular connective apices with two or three short lobes that can be further divided (Fig. 2A–D). Molecular differentiation was detected mainly for the Tawau population, which was distinct at each of the studied loci, but with differences well comparable with those within other species (Fig. 4, Supplementary material 1). While the population from Tawau hills is genetically somewhat distant to those from Brunei and Sarawak, morphologically are all populations almost identical, though more variable than supposed before. Its elevational maximum is now at 550 m near Long Tuyo village in northern Sarawak.

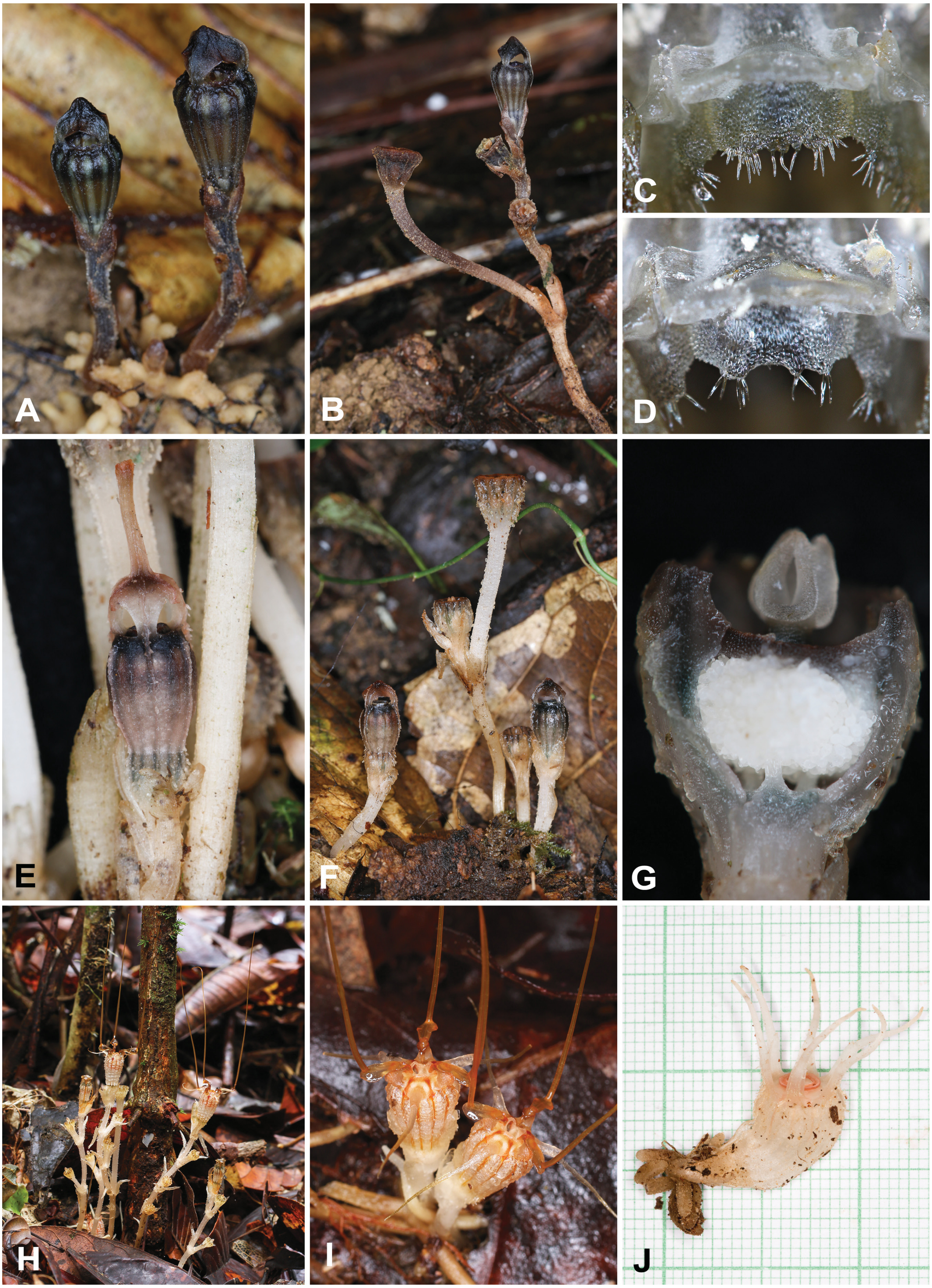


FIGURE 2. *Thismia brunneomitra*: variation in overall appearance (A, B) and connective apices (C, D); *T. viridistriata*: variation in flower morphology (E, F), and section of ovary showing placentae (G); *T. neptunis*: variation in overall appearance (H, I); *T. cornuta* from the Kelabit Highlands (J). From *Sochor et al. BOR26/19* (A, C, D), *BOR25/19* (B), *BOR5/19* (E), *BOR27/19* (F, G), uncollected population from NP Kubah (H), *Sochor et al. BOR52/19* (I), *BOR10/17* (J). (All photos M. Sochor).

Thismia brunneomitra was assigned a preliminary conservation status of critically endangered (CR) based on criterion D (Hroneš *et al.* 2015). As the number of known localities and individuals increased considerably and no longer fulfils the criteria for critically endangered species (IUCN 2012), we propose a new conservation status EN (B2ab(iii)) for this species.

Thismia cornuta

Thismia cornuta Hroneš, Sochor & Dančák, Pl. Ecol. Evol. 151: 111. 2018.

Type:—Borneo, Sarawak (Malaysia), Kelabit Highlands, Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village, N 03°42′1″, E 115°31′28″, 1195 m a. s. l., 13 Jan 2017, *Sochor et al. BOR2/17* (holotype SAR).

New locality:—Malaysia, Sarawak, Miri Division, Bario Subdistrict: Kelabit Highlands, Pa'Umor village, 4.4 km SSE of the village, WGS 84: N 03°42′10″, E 115°31′5″, ca. 1250 m a. s. l., 19 Nov 2018, *M. Dančák* (only photographed, not collected). Two fruiting individuals covering an area less than 1 m^2.

Thismia cornuta (Fig. 2J) has been known from two localities in two valleys in the Kelabit Highlands of Sarawak which are located 15 km apart (Hroneš *et al.* 2018). The new locality is located only ca. 0.8 km from the type locality and is at slightly higher elevation than all previously recorded localities. The new finding brings the number of known localities to three.

Thismia cornuta was assigned (Hroneš *et al.* 2018) a preliminary conservation status of endangered (EN) based on criterion B2ab(iii,v) and this remains unchanged by the new discovery.

Thismia goodii

Thismia goodii Kiew, Gard. Bull. Singapore 51(2): 179. 1999.

Type:—Borneo, Sabah, Sipitang, Ulu Maligan, 19 Mar 1999, *Ruth Kiew RK 4611* (holotype SAN).

New locality:—Malaysia, Sarawak, Limbang Division, Lawas District: Long Tuyo village, Paya Maga mountain plateau, primary forest ca. 200 m NW of camp 2, WGS 84: N 04°27′09″, E 115°33′26″, ca. 1610 m a. s. l., 20 Jan 2020, *Hroneš & Dančák 332020* (OL, SAR). Twelve flowering and fruiting individuals covering an area of 6 m^2.

Due to its bright blue colour (Kiew 1999) this *Thismia* is one of the iconic species of Borneo (Fig. 3A–D). The type locality in Sabah lies within an area heavily affected by deforestation and might no longer exist (R. Kiew, pers. comm.). However, we found another locality of this species some 20 km south of the type one, on Sarawak side of the border in Paya Maga mountain range in Lawas district. Interestingly, this locality is probably identical or is situated nearby the one mentioned in a book on the Paya Maga area (Ampeng *et al.* 2013) where a photograph of the plant appeared but without an exact locality and other details related to the finding. This new locality lies at rather high altitude, around 1610 m, which makes *Thismia goodii* one of the highest growing *Thismia* species (see Tab. 3).

As *Thismia goodii* was not yet assigned any conservation status (IUCN 2012) we propose to evaluate it as CR based on criterion B2ab(ii, iii, iv).

Thismia hexagona

Thismia hexagona Dančák, Hroneš, Kobrlová & Sochor, Phytotaxa 125(1): 34. 2013.

Type:—Brunei Darussalam, Temburong Distr.: Kuala Belalong, eastern ridge of Sungai Belalong, near its confluence with Sungai Temburong. Coordinates WGS 84: N 04° 32.952′; E 115° 09.792′, ca. 320 m a. s. l., 13 Feb 2013, *M. Dančák, M. Hroneš, M. Sochor & L. Kobrlová 2013/17* (holotype BRUN).

New localities:—Malaysia, Sabah: Maliau Basin Conservation Area, on path from Maliau Basin Studies Centre about 100 m along shortcut from the block leading NE down to Maliau river, N 04°44′19″, E 116°59′03″, 16 Aug 2007, *T. Utteridge* (a photograph deposited in K); Tongod, Sungai Imbak, logged-over forest, Pinangah Forest Reserve, 3 Sep 1992, *K. M. Wong WKM2356* (SAN). Both specimens represented *Thismia hexagona* var. *grandiflora*. The labels did not mention size of the populations.

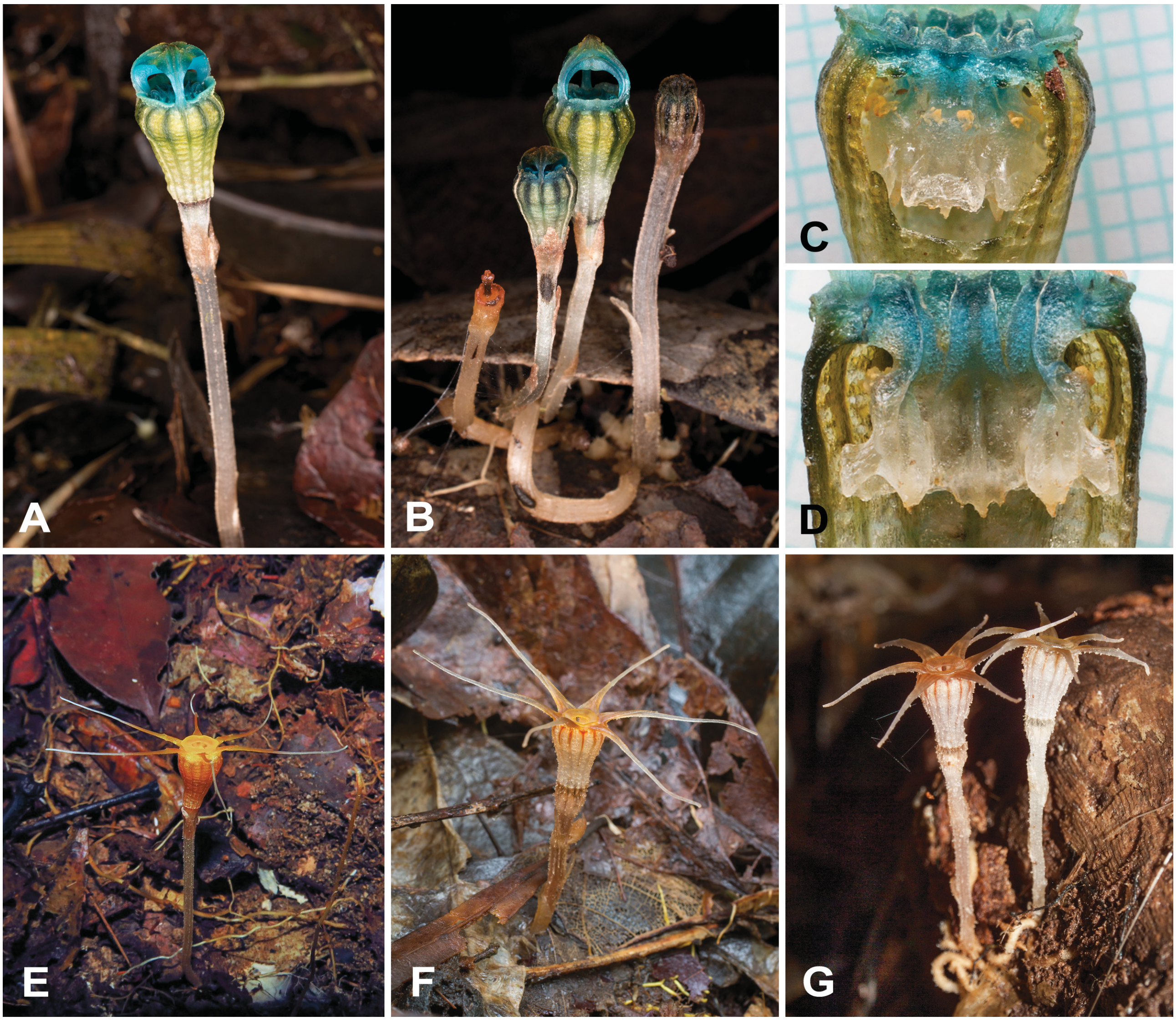
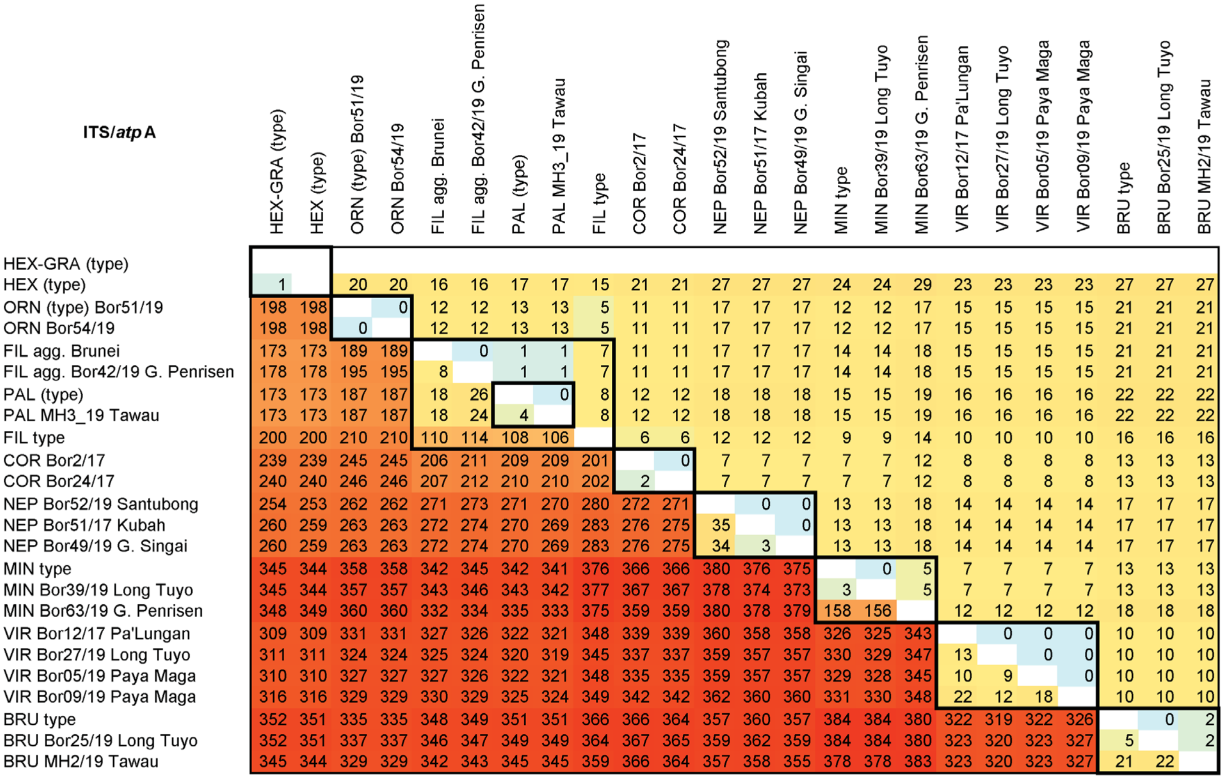


FIGURE 3. *Thismia goodii*: variation in overall appearance (A, B) and inner flower morphology (C, D); *T.* cf. *hexagona*: plant from the Belaga area, Sarawak (E); *T. filiformis* agg.: plant from Gunung Penrisen area, western Sarawak (F); *T. pallida*: plants from Tawau Hills (G). From *Hroneš & Dančák 332020* (A, B, C, D), uncollected population from the Belaga area by Ling Chea Yiing (E), *Sochor et al. BOR42/19* (F), *Hroneš & Dančák 03/2019* (G). (Photos: A, B, C, D, G: Michal Hroneš, E: Ling Chea Yiing, F: Michal Sochor).

This species is known from three considerably distant (ca. 200 km) locations. Apart from the type locality in Temburong district of Brunei Darussalam, it is known from three localities in the Maliau Basin Conservation Area in Sabah (Tsukaya *et al.* 2014), although only two localities are explicitly mentioned in the referred article, and the new locality reported here. Another new locality reported here, Imbak Canyon in Sabah, represent the third location with occurrence of this species. All the known populations outside Brunei belong to a distinct variety, *Thismia hexagona* var. *grandiflora* Tsukaya, Suleiman & H.Okada (2014: 142). Based on photographs we have seen from the Bakun Dam area by Ling Chea Yiing (Fig. 3E), *T. hexagona* var. *grandiflora* occurs very probably also in Sarawak. If the occurrence in the Bakun area is proven, *T. hexagona* would almost equal the size of range of *T. minutissima* (see below).

The population occurring at the type locality is rather unique compared to the other *Thismia* species because plants are regularly observed here since the time of its discovery in 2013, i.e. for eight consecutive years.

Thismia hexagona was assigned a preliminary conservation status of data deficient (DD) by Dančák et al (2013). As we have more data now to evaluate the species we propose conservation status endangered (EN) based on criterion B2ab(iii) (IUCN 2012).



ITS/*atp*A	HEX-GRA (type)	HEX (type)	ORN (type) Bor51/19	ORN Bor54/19	FIL agg. Brunei	FIL agg. Bor42/19 G. Penrisen	PAL (type)	PAL MH3_19 Tawau	FIL type	COR Bor2/17	COR Bor24/17	NEP Bor52/19 Santubong	NEP Bor51/17 Kubah	NEP Bor49/19 G. Singai	MIN type	MIN Bor39/19 Long Tuyo	MIN Bor63/19 G. Penrisen	VIR Bor12/17 Pa'Lungan	VIR Bor27/19 Long Tuyo	VIR Bor05/19 Paya Maga	VIR Bor09/19 Paya Maga	BRU type	BRU Bor25/19 Long Tuyo	BRU MH2/19 Tawau
HEX-GRA (type)																								
HEX (type)	1		20	20	16	16	17	17	15	21	21	27	27	27	24	24	29	23	23	23	23	27	27	27
ORN (type) Bor51/19	198	198		0	12	12	13	13	5	11	11	17	17	17	12	12	17	15	15	15	15	21	21	21
ORN Bor54/19	198	198	0		12	12	13	13	5	11	11	17	17	17	12	12	17	15	15	15	15	21	21	21
FIL agg. Brunei	173	173	189	189		0	1	1	7	11	11	17	17	17	14	14	18	15	15	15	15	21	21	21
FIL agg. Bor42/19 G. Penrisen	178	178	195	195	8		1	1	7	11	11	17	17	17	14	14	18	15	15	15	15	21	21	21
PAL (type)	173	173	187	187	18	26		0	8	12	12	18	18	18	15	15	19	16	16	16	16	22	22	22
PAL MH3_19 Tawau	173	173	187	187	18	24	4		8	12	12	18	18	18	15	15	19	16	16	16	16	22	22	22
FIL type	200	200	210	210	110	114	108	106		6	6	12	12	12	9	9	14	10	10	10	10	16	16	16
COR Bor2/17	239	239	245	245	206	211	209	209	201		0	7	7	7	7	7	12	8	8	8	8	13	13	13
COR Bor24/17	240	240	246	246	207	212	210	210	202	2		7	7	7	7	7	12	8	8	8	8	13	13	13
NEP Bor52/19 Santubong	254	253	262	262	271	273	271	270	280	272	271		0	0	13	13	18	14	14	14	14	17	17	17
NEP Bor51/17 Kubah	260	259	263	263	272	274	270	269	283	276	275	35		0	13	13	18	14	14	14	14	17	17	17
NEP Bor49/19 G. Singai	260	259	263	263	272	274	270	269	283	276	275	34	3		13	13	18	14	14	14	14	17	17	17
MIN type	345	344	358	358	342	345	342	341	376	366	366	380	376	375		0	5	7	7	7	7	13	13	13
MIN Bor39/19 Long Tuyo	345	344	357	357	343	346	343	342	377	367	367	378	374	373	3		5	7	7	7	7	13	13	13
MIN Bor63/19 G. Penrisen	348	349	360	360	332	334	335	333	375	359	359	380	378	379	158	156		12	12	12	12	18	18	18
VIR Bor12/17 Pa'Lungan	309	309	331	331	327	326	322	321	348	339	339	360	358	358	326	325	343		0	0	0	10	10	10
VIR Bor27/19 Long Tuyo	311	311	324	324	325	324	320	319	345	337	337	359	357	357	330	329	347	13		0	0	10	10	10
VIR Bor05/19 Paya Maga	310	310	327	327	327	326	322	321	348	335	335	359	357	357	329	328	345	10	9		0	10	10	10
VIR Bor09/19 Paya Maga	316	316	329	329	330	329	325	324	349	342	342	362	360	360	331	330	348	22	12	18		10	10	10
BRU type	352	351	335	335	348	349	351	351	366	366	364	357	360	357	384	384	380	322	319	322	326		0	2
BRU Bor25/19 Long Tuyo	352	351	337	337	346	347	349	349	364	367	365	359	362	359	384	384	380	323	320	323	327	5		2
BRU MH2/19 Tawau	345	344	329	329	342	343	345	345	359	366	364	357	358	355	378	378	383	323	320	323	327	21	22	

FIGURE 4. Heatmap of pairwise genetic distances (SNP's+indels in bp) between selected populations; species or species aggregates outlined in bold. Abbreviations: HEX-GRA—*T. hexagona* var. *grandiflora*, HEX—*T. hexagona*, ORN—*T. ornata*, FIL—*T. filiformis*, PAL—*T. pallida*, COR—*T. cornuta*, NEP—*T. neptunis*, MIN—*T. minutissima*, VIR—*T. viridistriata*, BRU—*T. brunneomitra*.

Thismia kelabitiana

Thismia kelabitiana Dančák, Hroneš & Sochor, PLoS ONE 13(10): e0203443 (3). 2018.

Type:—Malaysia, Sarawak: Kelabit Highlands, Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village. Coordinates WGS 84: N 03°42′; E 115°31′, 1195 m a. s. l., 13 Jan 2017, *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & J. R. Pasan BOR1/17* (holotype SAR).

This species is actually known from only two very close localities, the type one and the other, ca. 600 m distant locality (Dančák *et al.* 2018) which effectively represent a single location (sensu IUCN 2012).

Thismia laevis

Thismia laevis Sochor, Dančák & Hroneš, Pl. Syst. Evol. 304(5): 708. 2018.

Type:—Malaysia, Sarawak, Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.0 km N of the village, N 03°50′13″, E 115°31′11″, 1108 m a. s. l., 16 Jan 2017, *M. Sochor et al. BOR9/17* (holotype SAR).

As the previous one, this species is also known from only two very close localities, the type one and the other, ca. 650 m distant locality (Sochor *et al.* 2018b).

Thismia minutissima

Thismia minutissima Dančák, Hroneš & Sochor, Kew Bull. 75(2)–29: 2. 2020.

Type:—Malaysia, Sarawak: Kelabit Highlands, Pa'Umor village, Anak Kadi Ridge, 4.4 km SSE of the village. WGS 84: N 03°42′01″; E 115°31′28″, 1195 m a. s. l., 13 Jan 2017, *M. Sochor, M. Hroneš, M. Dančák, Z. Egertová & J.R. Pasan BOR4/17* (holotype SAR).

This recently described species has the largest range of all Bornean *Thismia* species and one of the largest among Old World *Thismia* (Dančák *et al.* 2020a) as it spans nearly 700 km across the central highlands of Borneo. Its elevational range is also quite extensive and spans more than 700 m from upper lowland forests to lower montane belt (540–1260 m). As discussed in the original paper, all the known populations exhibit little morphological differences, but the population from western Sarawak is strikingly divergent in DNA markers, with genetic distance similar to those between distinct species, and possibly belongs to a different, cryptic taxon from the phylogenetic point of view (see Discussion, Fig. 4, Supplementary material 1).

Thismia neptunis

Thismia neptunis Beccari, Malesia 1: 251. 1877.

Type:—Malaysia, Ragiato di Sarawak, Mattang, Apr 1866, *O. Beccari p.b. 1508* (holotype FI-B 013453).

New localities:—Sarawak, Kuching Division, Bau District: Gunung Singai, along the Summit Trail, WGS 84: N 01°30′13″, E 110°09′59″, 417 m a. s. l., 6 Feb 2019, *Sochor & Hroneš BOR49/19* (OL, SAR), three individuals covering an area of less than 1 m^2. **Sarawak, Kuching Division, Lundu District:** Kubah National Park, 0.9 km ENE of Matang Wildlife Centre, WGS 84: N 01°36′48″, E 110°10′02″, 40 m a. s. l., 7 Feb 2019, *Sochor, Hroneš & Dančák BOR50/19* (OL), ca. 15 individuals covering an area of ca. 30 m^2; Kubah National park, 0.5 km ENE of Matang Wildlife Centre, WGS 84: N 01°36′40″, E 110°09′53″, 40 m a. s. l., 9 Feb 2019, only photographed (Fig. 2H), not collected, ca. 40 individuals covering an area of ca. 100 m^2. **Sarawak, Kuching Division, Kuching District**: Gunung Santubong, along the contour trail, WGS 84: N 01°44′24″, E 110°19′32″, 209 m a. s. l., 8 Feb 2019, *Sochor, Hroneš & Dančák BOR52/19* (OL), three individuals covering an area of ca. 1 m^2; Kubah National park, 0.8 km SW of headquarters, WGS 84: N 01°36′24″, E 110°11′30″, 251 m a. s. l., 9 Feb 2019, *Sochor & Hroneš BOR57/19* (OL), five individuals covering an area of ca 30 m^2.

Thismia neptunis was once considered an extinct narrowly endemic species and was rediscovered only recently in its type area within Kubah National park of Sarawak (Sochor *et al.* 2018a). We found three new localities of this species in Kubah National park and two others outside of this area, i.e. Gunung Singai south of Kubah and Gunung Santubong north of Kuching. Compared to the description provided in Sochor *et al.* (2018a), the newly found plants only differed in quantitative traits (considerably shorter or somewhat longer stem and smaller flowers – flower tube 7–8 mm long, 5 mm wide, and up to five flowers per stem, see Fig. 2H, I). Although sequencing of the collection from Santubong was only successful for three loci, it was differentiated at two of them with relatively large distances, yet still small compared to usual interspecific distances (11 SNP's at LSU, 34–35 SNP's at ITS; Fig 4, Supplementary material 1). The extent of occurrence (sensu IUCN 2012) of *Thismia neptunis* is now more than 110 km^2 and minimal area of occupancy 16 km^2 with a total of six populations. Its elevational range is from ca. 40 m to ca 420 m.

Thismia neptunis was assigned the conservation status of critically endangered (CR) based on criteria B2, C2 and D (Sochor *et al.* 2018a). As the number of known localities and individuals increased considerably and no longer fulfils the criteria for critically endangered species (IUCN 2012), we propose a new conservation status endangered (EN) for this species based on criterion B2ab(iii).

Thismia nigra

Thismia nigra Dančák, Hroneš & Sochor, Pl. Syst. Evol. 304(5): 711 (2018).

Type:—Malaysia, Sarawak, Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.4 km N of the village, 3°50′26″N, 115°30′54″E, 1224 m a. s. l., 15 Jan 2017, *M. Sochor et al. BOR8/17* (holotype SAR).

The species is known from five nearby localities in the Pulong Tau National Park, Kelabit Highlands, Sarawak (Sochor *et al.* 2018b). No variation in DNA markers and only negligible variation in morphology were observed. This species is closely related to *Thismia brunneomitra* and is probably an example of geographical vicariance as the two species are, according to the current knowledge, separated by a high mountain range. They are also very closely related as implied by small genetic distances between them (3, 21, 9, 1 and 1 SNP's at SSU, ITS, LSU, *atp*A and *mat*R, respectively; Sochor *et al.* 2018b; compare to Fig. 4 and Supplementary material 1).

Thismia ornata

Thismia ornata Dančák, Hroneš & Sochor, Willdenowia 50(1): 66. 2020.

Type:—Malaysia, Sarawak, Kubah National Park, 0.8 km NE of Matang Wildlife Centre, WGS 84: N 01°36′49″, E 110°09′57″E, 60 m a. s. l., 7 Feb 2019, *Sochor, Hroneš & Dančák BOR51/19* (holotype SAR).

This only recently described species previously misidentified as *Thismia aseroe* Beccari (1877: 252) (see Dančák *et al.* 2020b) was also revealed to have several localities in western Sarawak, which makes it one of the most common species of *Thismia* (see Tab. 1). On the other hand its extent of occurrence is rather small as it is only known from surroundings of the Kuching city. Correspondingly, molecular variation within the species is small (one SNP at each of the SSU and *Mat*R loci; Dančák *et al.* 2020b).

TABLE 1. Species of *Thismia* with more than 10 localities. Bornean species are in bold. EOO = extent of occurrence (sensu IUCN 2012).

Species	Continental distribution	Number of localities	EOO (km^2)
Thismia hillii (Cheeseman) N. Pfeiffer	Australasia	> 25	ca. 680,000*
***Thismia ornata* Dančák, Hroneš & Sochor**	SE Asia	12	270
Thismia panamensis (Standl.) Jonker	C and S America	> 15	ca. 3,348,000
Thismia rodwayi F. Muell.	Australasia	> 30	ca. 67,000**
***Thismia viridistriata* Sochor, Hroneš & Dančák**	SE Asia	17	550

*Including New South Wales site (New Zealand part of range is ca. 60,000 km^2).
**Including Victoria site (Tasmanian part of range is ca. 43,000 km^2).

Thismia pallida

Thismia pallida Hroneš, Dančák & Rejžek, Pl. Ecol. Evol. 151(1): 115. 2018.

Type:—Borneo, Sabah (Malaysia), Kalabakan, SAFE project, plot LFE-10, 4°44′36.41″N, 117°35′16.93″E, c. 485 m a. s. l., 3 Feb 2017, *Nilus & Svátek SAN 158204* (holotype SAN).

New locality:—Sabah, Tawau Division, Tawau District, Tawau Hills National Park: along trail to sulphur hot springs, primary forest, WGS 84: N 04°24′46″N, E 117°53′49″, ca. 330 m a. s. l., 12 Feb 2019, *Hroneš & Dančák 03/2019* (OL, SAN). Five flowering individuals covering an area of ca. 4 m^2.

The newly discovered locality is situated some 50 km apart from the type locality (Hroneš *et al.* 2018) and the plants from the new locality are perfectly identical with those occurring at the type locality (Fig. 3G). Molecular divergence was only observed at the LSU and ITS locus (5 and 4 SNP's, respectively; Fig. 4, Supplementary material 1). The currently known elevational range is from ca. 330 to ca. 485 m.

Despite the discovery of the new locality, we retain its conservation status as CR (Hroneš *et al.* 2018) because the known population size remains extremely small (13 individuals altogether).

Thismia pallida belongs to the group of *Thismia filiformis* Chantanaorr. (2012: 69), a species described from Thailand. This group is represented by several populations across Borneo with some of them morphologically rather distinct, as *Thismia pallida*, yet others hardly morphologically distinguishable from *Thismia filiformis* s. str. (Fig. 3F). Based on photographs we have seen (by Dome Nikong, Edward Entalai and others), the same situation is in Malay Peninsula. The situation is further complicated by the fact that Bornean populations regardless of morphological similarity to *Thismia filiformis* seem to be genetically more related to each other than to *Thismia filiformis* s. str., whose genetic distance to the Bornean populations corresponds to a distance between rather distantly related species (Fig. 4, Supplementary material 1; see also Shepeleva *et al.* 2020).

Thismia viridistriata

Thismia viridistriata Sochor, Hroneš & Dančák, Pl. Syst. Evol. 304(5): 714. 2018.

Type:—Malaysia, Sarawak, Kelabit Highlands, Pa'Lungan village, Arur Bedalawid, 3.2 km N of the village, 3°50′20″N, 115°31′01″E, 1182 m a. s. l., 16 Jan 2017, *M. Sochor et al. BOR11/17* (holotype SAR).

New localities:—Sarawak, Limbang Division, Lawas District, Long Tuyo village: Primary forests south of the Tuyo river, two sites: WGS 84: N 04°27′28″, E 115°29′14″, 545 m a. s. l., 30 Jan 2019, *Sochor, Hroneš & Dančák BOR27/19* (OL), several individuals covering an area of ca 10 m^2; WGS 84: N 04°27′24″, E 115°29′18″, 585 m a. s. l., 30 Jan 2019, *Sochor, Hroneš & Dančák BOR29/19* (OL), several individuals covering an area of ca. 10 m^2. Paya Maga range, primary forest between Camps 1 and 2, three sites: WGS 84: N 04°26′37″, E 115°33′14″, 1375 m a. s. l., 29 Jan 2019, *Sochor, Hroneš & Dančák BOR9/19* (only DNA material, no voucher specimen); WGS 84: N 04°26′36″, E 115°33′09″, 1270 m a. s. l., 29 Jan 2019, *Sochor, Hroneš & Dančák BOR10/19* (only DNA material, no voucher specimen); WGS 84: N 04°26′33″, E 115°33′01″, 1247 m a. s. l., 29 Jan 2019, *Sochor, Hroneš & Dančák BOR14/19* (only DNA material, no voucher specimen), one or two individuals at each site. Paya Maga range, upper part of trail in a primary forest between Camps 1 and 2, WGS 84: N 04°26′48″, E 115°33′23″, 1445 m a. s. l., 27 Jan 2019, *Sochor, Hroneš & Dančák BOR01/19* (only DNA material and photograph taken, no voucher specimen), one fruiting individual. Paya Maga mountain plateau, primary forest ca. 200 m NW of camp 2, WGS 84: 04°27′9″N 115°33′26″E, 1610 m a. s. l., 20. Jan. 2020, *Hroneš & Dančák 332020* (OL), five individuals covering an area of ca. 5 m^2. Paya Maga mountain plateau, waterfall near Camp 2, three sites: at the trail, WGS 84: N 04°27′07″, E 115°33′43″, 1625 m a. s. l. 28 Jan 2019, *Sochor, Hroneš & Dančák BOR04/19* (OL, SAR), ca. 15 individuals covering an area of ca. 30 m^2; left river bank, WGS 84: N 04°27′06″, E 115°33′44″, 1625 m a. s. l. 28 Jan 2019, *Sochor, Hroneš & Dančák BOR05/19* (OL), three individuals covering an area of ca. 1 m^2; at the trail, WGS 84: N 04°27′06″, E 115°33′42″, 1625 m a. s. l., 28 Jan 2019, *Sochor, Hroneš & Dančák BOR06/19* (OL), ca. 10 individuals covering an area of ca. 10 m^2. Paya Maga mountain plateau, primary forest ca. 2 km ENE from Paya Maga summit, WGS 84: N 04°26′30″, E 115°34′47″, 1665 m a. s. l., 20 Jan 2020, *Ľ. Majeský & V. Čermák s. n.* (OL), 15 individuals covering an area of ca 5 m^2.

Thismia viridistriata has been know from 11 localities (Sochor *et al.* 2018b) and we report 6 more here. With 17 localities, it is one of the commonest *Thismia* ever recorded (see Tab. 1), after *T. rodwayi* F. Mueller (1890: 115) which is known from some 30 localities (Threatened Species Section 2019) and *T. hillii* (Cheeseman 1908: 420) N. Pfeiffer (1914: 122) which is known from some 25 localities (New Zealand Plant Conservation Network 2020). However, the known range of *Thismia viridistriata* is not as large and spans some 85 km across the mountains of northern Sarawak. Also, many of its localities lie very close each other, therefore the number of locations is much smaller (5) than the number of localities. Reaching the altitude of 1665 m a. s. l. it is also one of the highest-occurring species of any *Thismia* (see Tab. 3). Its lowest locality was recorded at 545 m a. s. l., thus its elevational range is some 1120 m, the widest in all known *Thismia* species, with only *Thismia hillii* reaching approximately the same elevational range (New Zealand Plant Conservation Network 2020). Phenotypic variation as originally described was not extended by the new finds (Fig. 2E-G), but four genetic lineages, distinguishable by ITS and partly by LSU and *Mat*R (Supplementary material 1), were detected in total, three in the Long Tuyo area, two in the Kelabit Highlands.

Thismia viridistriata was assigned a preliminary conservation status of endangered (EN) based on criterion C2ai (Sochor *et al.* 2018b). Although the number of known localities and individuals increased considerably the species still fulfils the criteria for endangered species (IUCN 2012).

Discussion

The new distributional data for several Bornean species of *Thismia* show that, at least for some species of *Thismia*, we can expect quite normal type of distribution with multiple localities over certain geographical areas rather than unusually narrowly endemic distribution so far expected for this genus (Jonker 1948, Stone 1980). Why *Thismia* species have previously been perceived to be so rare is, however, unclear and multiple factors probably contributed to this. One of the main factors is the scarcity of *Thismia* collections in the past, especially during Jonker's work on the genus (Jonker 1938, 1948). This is closely connected to the intensity of botanical research in the 19th and early 20th century when many areas were inaccessible for collectors. In combination with highly localised occurrence of most *Thismia* populations (a population occupies usually only several m^2), small size of plants and seasonal growth, it resulted in scarcity of collections and the impression that most species are extremely narrow endemics. Even today, when the intensity of botanical research is much higher and rainforest is much more easily accessible, many species are still known from a single locality (see below). We can only speculate that also these species must have more localities as it seems not very likely that a single population covering only several m^2 can survive at a site over a long period of time a in such a dynamic environment as is tropical rain forest. What is the cause of highly localised occurrence of most *Thismia* populations, however, remains unclear as the studies examining the factors influencing this pattern are rare. Among the plausible explanations of patchy occurrence of *Thismia* populations are the mycorrhizal specificity, with distributions constrained by the occurrence of their fungal partners and the tie to specific low-nutrient soil conditions (Gomes *et al.* 2017, 2019).

The assessment of distributional ranges for many *Thismia* species is hampered by taxonomical issues, especially when inadequate material is available for identification. Therefore, in many species the question arises whether populations from distant regions are conspecific with the type area population/populations. A good example can be *Thismia clavigera* (Beccari 1877: 251) F. Mueller (1891: 235), originally described from Borneo but later found in Sumatra and Langkawi Island off the west coast of the Malay Peninsula (Stone 1980) and on the neighbouring island of Tarutao (Chantanaorrapint & Chantanaorrapint 2009). However, recently, two species very similar to *Thismia clavigera* were described from Sumatra and the Malay Peninsula (Siti-Munirah 2018, Suetsugu *et al.* 2018b), which naturally raises a question of taxonomical identity of populations previously classified as *T. clavigera* outside of Borneo. Similarly, another two Bornean species, *Thismia episcopalis* (Beccari 1877: 250) and *Thismia ophiuris* Beccari (1877: 252), were also reported to occur at two localities (Jonker 1938). Both species were described by Beccari (1877) from western Sarawak and Jonker (1938) reported their occurrence also in Sabah, based on specimens collected by Clemens at the foot of Mt. Kinabalu. At the time of Jonker's work on his monograph, a single mitriform species of *Thismia* was known from Borneo (apart from *Thismia clavigera* which he treated in the different genus *Geomitra* Beccari (1877: 250), so one would easily assume that with limited and taxonomically almost useless material available, Jonker had not any other clue than identify the Clemens's gathering as *Thismia episcopalis*. Interestingly, all specimens from Borneo deposited in K herbarium and identified as *Thismia episcopalis* (*Chew et al. 1909*, *Collenette 638*, *Cox 347*) in fact represent another undescribed species from the taxonomical group of *Thismia goodii*, i.e. the group not very similar to *T. episcopalis*. The same actually applies to *Thismia ophiuris* as it was the only *Thismia* subsect. *Odoardoa* Schlechter (1921: 34) known from Borneo at that time. From current perspective it seems improbable that the populations from Kinabalu were conspecific with those from western Sarawak. The crucial task is to rediscover both species at their type localities as *Thismia ophiuris* remains missing since Beccari's times and *Thismia episcopalis* was seen only once at the type locality in 1968 (colour photograph of the whole plant in K by J. Dransfield).

On the other hand, as is obvious from new localities presented here, some species of *Thismia* may occur over relatively large areas. The best known examples are *Thismia rodwayi* and *T. hillii*, both with ranges significantly extending 10,000 km^2 (Tab. 1). Besides, these two species have a relatively large number of localities (over 30 in *T. rodwayi*). These two species are also a good example how morphology-based taxonomy in *Thismia* may lead to wrong classification. Although originally described as two different species, they were merged soon and considered one species until recently when use of molecular markers revealed that they were two clearly distinct species (Merckx *et al.* 2017). Among Bornean taxa we discovered several species with considerably large ranges. These are especially *T. minutissima*, *T. brunneomitra* and *T. hexagona* whose ranges span hundreds of kilometres. Some other species have ranges spanning dozens of kilometres, notably *T. viridistriata*, *T. ornata*, *T. neptunis* and *T. pallida*. The high number of localities for some Bornean species (Tab. 2) is hardly comparable to other species with high number of localities, as *Thismia rodwayi* and *T. hillii*, because the latter have much larger ranges and their localities are usually more distant (have larger extent of occurrence). On the other hand, we probably do not know whole ranges of many Bornean species and we can expect some of them having much broader ranges than we are aware of today. This applies especially for *Thismia viridistriata* and *Thismia minutissima*. Nonetheless, there are still many species known only from the type locality. Among recently described species, this applies to *T. acuminata* Hroneš, Dančák & Sochor (in Sochor *et al.* 2018b: 705), *T. betung-kerihunensis* Tsukaya & H.Okada (2012: 56), *T. bryndonii* Tsukaya, Suetsugu & Suleiman (2017: 135), *T. coronata* Dančák, Hroneš & Sochor (2020b: 71), *T. inconspicua* Sochor & Dančák (2017: 264) and *T. kinabaluensis* T.Nishioka & Suetsugu (2018: 174).

As was mentioned earlier, the use of molecular markers helped considerably to understand the taxonomy and morphological variation in *Thismia*. Interestingly, some of the studied species exhibit considerable genetic variation which is little expressed in their morphology. An example is *T. neptunis* whose population from Gunung Santubong differs considerably genetically from those found in Kubah and Gunung Singai (Supplementary material 1) but morphologically they are totally indistinguishable. In *T. minutissima*, the population from Gunung Penrissen is only slightly morphologically different from those found in northern Sarawak but the genetic distance between them is enormous (Dančák *et al.* 2020a; Supplementary material 1). Also the population of *T. brunneomitra* from eastern Sabah is morphologically only slightly different from the type population but its genetic distance is quite large (Supplementary material 1). This is an interesting phenomenon which may have several explanations. The distant populations may represent a cryptic species geographically isolated for a long time from the parental species. Alternatively, they may represent marginal populations which seem genetically distant because of undersampling of geographically intermediate populations. Either way, isolation by distance appears to play an important role and the populations can be effectively isolated even over a very short distance. This was demonstrated in *Thismia hongkongensis* Mar & R. M. K.Saunders (2015: 23) whose seeds are probably spread by rain-splash over less than 1 m and pollination is carried out by fungus gnats (Guo *et al.* 2019), a short-lived, weak-flying insects. What keeps the different genetic lineages isolated even at a single locality (as in *T. viridistriata*), nevertheless, remains unclear and calls for more data from population genetics and reproductive biology of these plants.

TABLE 2. Number of localities for all Bornean species of *Thismia*. Number in brackets shows number of localities outside of Borneo.

Species	Number of localities	Number of locations sensu IUCN
Thismia acuminata Hroneš, Dančák & Sochor	1	1
Thismia betung-kerihunensis Tsukaya & H. Okada	1	1
Thismia bifida M. Hotta	1	1
Thismia brunneomitra Hroneš, Kobrlová & Dančák	4	3
Thismia bryndonii Tsukaya, Suetsugu & M.Suleiman	1	1
Thismia clavigera (Becc.) F. Muell.	1(3)	4
Thismia cornuta Hroneš, Sochor & Dančák	3	2
Thismia coronata Hroneš, Dančák & Sochor	1	1
Thismia episcopalis (Becc.) F. Muell.	1	1
Thismia goodii Kiew	2	2
Thismia hexagona Dančák, Hroneš, Kobrlová & Sochor	6	3
Thismia inconspicua Sochor & Dančák	1	1
Thismia kelabitiana Dančák, Hroneš & Sochor	2	1
Thismia kinabaluensis T. Nishioka & Suetsugu	1	1
Thismia laevis Sochor, Dančák & Hroneš	2	1
Thismia lauriana Jarvie	1	1
Thismia minutissima Dančák, Hroneš & Sochor	5	3
Thismia mullerensis Tsukaya & H. Okada	1	1
Thismia neptunis Becc.	6	3
Thismia nigra Dančák, Hroneš & Sochor	5	1
Thismia ophiuris Becc.	1	1
Thismia ornata Dančák, Hroneš & Sochor	12	3
Thismia pallida Hroneš, Dančák & Rejžek	2	2
Thismia viridistriata Sochor, Hroneš & Dančák	17	5

TABLE 3. Altitudinal maxima for *Thismia* species occurring above 1200 m. Bornean species are in bold.

Species	Max. altitude (m)
Thismia gongshanensis Hong-Qing Li & Yu-Ke Bi	2275
Thismia taiwanensis Sheng Z., Yang, R. M. K. Saunders & C. J. Hsu	2050
***Thismia viridistriata* Sochor, Hroneš & Dančák**	1665
***Thismia goodii* Kiew**	1610
Thismia huangii P. Y. Jiang & T. H. Hsieh	1500
***Thismia coronata* Hroneš, Dančák & Sochor**	1305
Thismia janeirensis Warm.	1300
***Thismia kelabitiana* Dančák, Hroneš & Sochor**	1300
Thismia submucronata Chant.	1300
***Thismia minutissima* Dančák, Hroneš & Sochor**	1260
Thismia caudata Maas & H. Maas	1250
***Thismia cornuta* Hroneš, Sochor & Dančák**	1250
Thismia fungiformis (Taub. ex Warm.) Maas & H. Maas	1250
Thismia glaziovii Poulsen	1250
Thismia hillii (Cheeseman) N. Pfeiffer	1250
Thismia hyalina (Miers) Benth. & Hook.f. ex F. Muell.	1250
***Thismia laevis* Sochor, Dančák & Hroneš**	1225
***Thismia nigra* Dančák, Hroneš & Sochor**	1225

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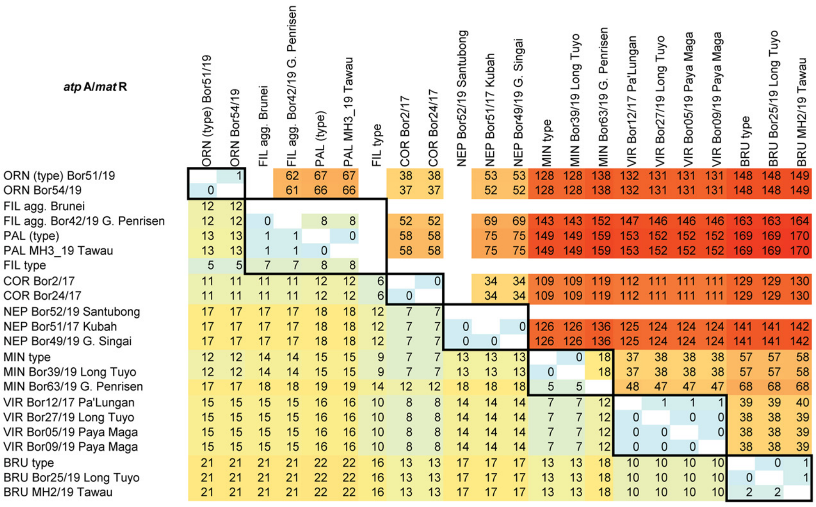
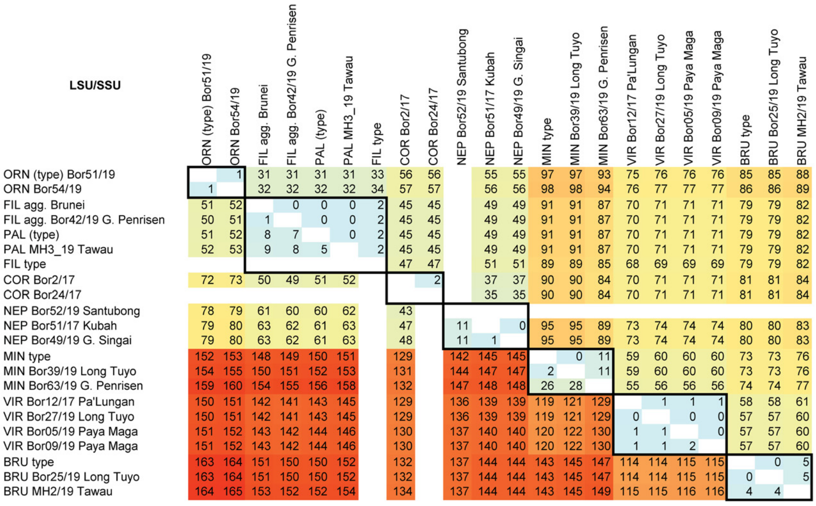
***Thismia*: the rarest of the rare? Ranges of some Bornean species are much larger than previously believed**

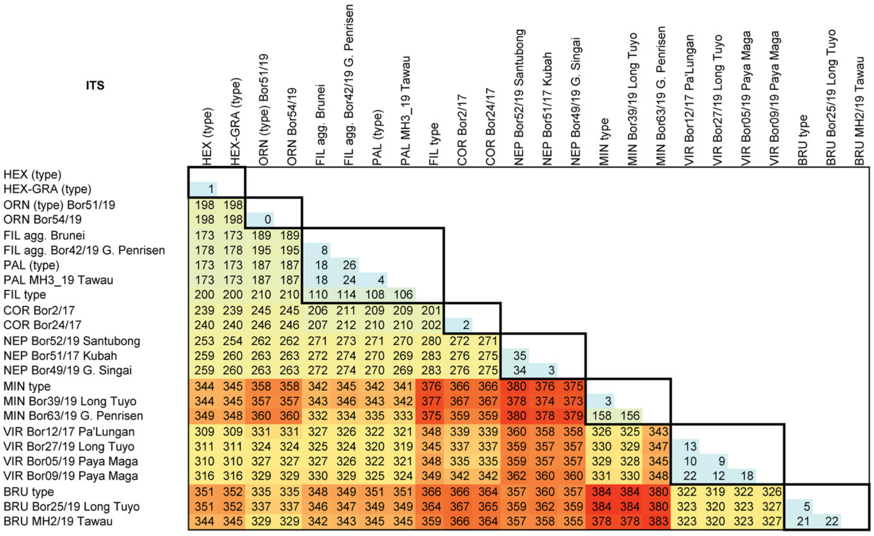
Supplementary material 1



atp A/*mat* R	ORN (type) Bor51/19	ORN Bor54/19	FIL agg. Brunei	FIL agg. Bor42/19 G. Penrisen	PAL (type)	PAL MH3_19 Tawau	FIL type	COR Bor2/17	COR Bor24/17	NEP Bor52/19 Santubong	NEP Bor51/17 Kubah	NEP Bor49/19 G. Singai	MIN type	MIN Bor39/19 Long Tuyo	MIN Bor63/19 G. Penrisen	VIR Bor12/17 Pa'Lungan	VIR Bor27/19 Long Tuyo	VIR Bor05/19 Paya Maga	VIR Bor09/19 Paya Maga	BRU type	BRU Bor25/19 Long Tuyo	BRU MH2/19 Tawau
ORN (type) Bor51/19		1		62	67	67		38	38		53	53	128	128	138	132	131	131	131	148	148	149
ORN Bor54/19	0			61	66	66		37	37		52	52	128	128	138	132	131	131	131	148	148	149
FIL agg. Brunei	12	12																				
FIL agg. Bor42/19 G. Penrisen	12	12	0		8	8		52	52		69	69	143	143	152	147	146	146	146	163	163	164
PAL (type)	13	13	1	1		0		58	58		75	75	149	149	159	153	152	152	152	169	169	170
PAL MH3_19 Tawau	13	13	1	1	0			58	58		75	75	149	149	159	153	152	152	152	169	169	170
FIL type	5	5	7	7	8	8																
COR Bor2/17	11	11	11	11	12	12	6		0		34	34	109	109	119	112	111	111	111	129	129	130
COR Bor24/17	11	11	11	11	12	12	6	0			34	34	109	109	119	112	111	111	111	129	129	130
NEP Bor52/19 Santubong	17	17	17	17	18	18	12	7	7													
NEP Bor51/17 Kubah	17	17	17	17	18	18	12	7	7	0		0	126	126	136	125	124	124	124	141	141	142
NEP Bor49/19 G. Singai	17	17	17	17	18	18	12	7	7	0	0		126	126	136	125	124	124	124	141	141	142
MIN type	12	12	14	14	15	15	9	7	7	13	13	13		0	18	37	38	38	38	57	57	58
MIN Bor39/19 Long Tuyo	12	12	14	14	15	15	9	7	7	13	13	13	0		18	37	38	38	38	57	57	58
MIN Bor63/19 G. Penrisen	17	17	18	18	19	19	14	12	12	18	18	18	5	5		48	47	47	47	68	68	68
VIR Bor12/17 Pa'Lungan	15	15	15	15	16	16	10	8	8	14	14	14	7	7	12		1	1	1	39	39	40
VIR Bor27/19 Long Tuyo	15	15	15	15	16	16	10	8	8	14	14	14	7	7	12	0		0	0	38	38	39
VIR Bor05/19 Paya Maga	15	15	15	15	16	16	10	8	8	14	14	14	7	7	12	0	0		0	38	38	39
VIR Bor09/19 Paya Maga	15	15	15	15	16	16	10	8	8	14	14	14	7	7	12	0	0	0		38	38	39
BRU type	21	21	21	21	22	22	16	13	13	17	17	17	13	13	18	10	10	10	10		0	1
BRU Bor25/19 Long Tuyo	21	21	21	21	22	22	16	13	13	17	17	17	13	13	18	10	10	10	10	0		1
BRU MH2/19 Tawau	21	21	21	21	22	22	16	13	13	17	17	17	13	13	18	10	10	10	10	2	2	



LSU/SSU	ORN (type) Bor51/19	ORN Bor54/19	FIL agg. Brunei	FIL agg. Bor42/19 G. Penrisen	PAL (type)	PAL MH3_19 Tawau	FIL type	COR Bor2/17	COR Bor24/17	NEP Bor52/19 Santubong	NEP Bor51/17 Kubah	NEP Bor49/19 G. Singai	MIN type	MIN Bor39/19 Long Tuyo	MIN Bor63/19 G. Penrisen	VIR Bor12/17 Pa'Lungan	VIR Bor27/19 Long Tuyo	VIR Bor05/19 Paya Maga	VIR Bor09/19 Paya Maga	BRU type	BRU Bor25/19 Long Tuyo	BRU MH2/19 Tawau
ORN (type) Bor51/19		1	31	31	31	31	33	56	56		55	55	97	97	93	75	76	76	76	85	85	88
ORN Bor54/19	1		32	32	32	32	34	57	57		56	56	98	98	94	76	77	77	77	86	86	89
FIL agg. Brunei	51	52		0	0	0	2	45	45		49	49	91	91	87	70	71	71	71	79	79	82
FIL agg. Bor42/19 G. Penrisen	50	51	1		0	0	2	45	45		49	49	91	91	87	70	71	71	71	79	79	82
PAL (type)	51	52	8	7		0	2	45	45		49	49	91	91	87	70	71	71	71	79	79	82
PAL MH3_19 Tawau	52	53	9	8	5		2	45	45		49	49	91	91	87	70	71	71	71	79	79	82
FIL type								47	47		51	51	89	89	85	68	69	69	69	79	79	82
COR Bor2/17	72	73	50	49	51	52			2		37	37	90	90	84	70	71	71	71	81	81	84
COR Bor24/17											35	35	90	90	84	70	71	71	71	81	81	84
NEP Bor52/19 Santubong	78	79	61	60	60	62		43														
NEP Bor51/17 Kubah	79	80	63	62	61	63		47		11		0	95	95	89	73	74	74	74	80	80	83
NEP Bor49/19 G. Singai	79	80	63	62	61	63		48		11	1		95	95	89	73	74	74	74	80	80	83
MIN type	152	153	148	149	150	151		129		142	145	145		0	11	59	60	60	60	73	73	76
MIN Bor39/19 Long Tuyo	154	155	150	151	152	153		131		144	147	147	2		11	59	60	60	60	73	73	76
MIN Bor63/19 G. Penrisen	159	160	154	155	156	158		132		147	148	148	26	28		55	56	56	56	74	74	77
VIR Bor12/17 Pa'Lungan	150	151	142	141	143	145		129		136	139	139	119	121	129		1	1	1	58	58	61
VIR Bor27/19 Long Tuyo	150	151	142	141	143	145		129		136	139	139	119	121	129	0		0	0	57	57	60
VIR Bor05/19 Paya Maga	151	152	143	142	144	146		130		137	140	140	120	122	130	1	1		0	57	57	60
VIR Bor09/19 Paya Maga	151	152	143	142	144	146		130		137	140	140	120	122	130	1	1	2		57	57	60
BRU type	163	164	151	150	150	152		132		137	144	144	143	145	147	114	114	115	115		0	5
BRU Bor25/19 Long Tuyo	163	164	151	150	150	152		132		137	144	144	143	145	147	114	114	115	115	0		5
BRU MH2/19 Tawau	164	165	153	152	152	154		134		137	144	144	143	145	149	115	115	116	116	4	4	



ITS	HEX (type)	HEX-GRA (type)	ORN (type) Bor51/19	ORN Bor54/19	FIL agg. Brunei	FIL agg. Bor42/19 G. Penrisen	PAL (type)	PAL MH3_19 Tawau	FIL type	COR Bor2/17	COR Bor24/17	NEP Bor52/19 Santubong	NEP Bor51/17 Kubah	NEP Bor49/19 G. Singai	MIN type	MIN Bor39/19 Long Tuyo	MIN Bor63/19 G. Penrisen	VIR Bor12/17 Pa'Lungan	VIR Bor27/19 Long Tuyo	VIR Bor05/19 Paya Maga	VIR Bor09/19 Paya Maga	BRU type	BRU Bor25/19 Long Tuyo	BRU MH2/19 Tawau
HEX (type)																								
HEX-GRA (type)	1																							
ORN (type) Bor51/19	198	198																						
ORN Bor54/19	198	198	0																					
FIL agg. Brunei	173	173	189	189																				
FIL agg. Bor42/19 G. Penrisen	178	178	195	195	8																			
PAL (type)	173	173	187	187	18	26																		
PAL MH3_19 Tawau	173	173	187	187	18	24	4																	
FIL type	200	200	210	210	110	114	108	106																
COR Bor2/17	239	239	245	245	206	211	209	209	201															
COR Bor24/17	240	240	246	246	207	212	210	210	202	2														
NEP Bor52/19 Santubong	253	254	262	262	271	273	271	270	280	272	271													
NEP Bor51/17 Kubah	259	260	263	263	272	274	270	269	283	276	275	35												
NEP Bor49/19 G. Singai	259	260	263	263	272	274	270	269	283	276	275	34	3											
MIN type	344	345	358	358	342	345	342	341	376	366	366	380	376	375										
MIN Bor39/19 Long Tuyo	344	345	357	357	343	346	343	342	377	367	367	378	374	373	3									
MIN Bor63/19 G. Penrisen	349	348	360	360	332	334	335	333	375	359	359	380	378	379	158	156								
VIR Bor12/17 Pa'Lungan	309	309	331	331	327	326	322	321	348	339	339	360	358	358	326	325	343							
VIR Bor27/19 Long Tuyo	311	311	324	324	325	324	320	319	345	337	337	359	357	357	330	329	347	13						
VIR Bor05/19 Paya Maga	310	310	327	327	327	326	322	321	348	335	335	359	357	357	329	328	345	10	9					
VIR Bor09/19 Paya Maga	316	316	329	329	330	329	325	324	349	342	342	362	360	360	331	330	348	22	12	18				
BRU type	351	352	335	335	348	349	351	351	366	366	364	357	360	357	384	384	380	322	319	322	326			
BRU Bor25/19 Long Tuyo	351	352	337	337	346	347	349	349	364	367	365	359	362	359	384	384	380	323	320	323	327	5		
BRU MH2/19 Tawau	344	345	329	329	342	343	345	345	359	366	364	357	358	355	378	378	383	323	320	323	327	21	22	

Heatmaps for pairwise genetic distances (SNP's+indels in bp) between selected populations; species or species aggregates outlined in bold. Abbreviations: HEX-GRA - T. hexagona var. grandiflora, HEX - T. hexagona, ORN - T. ornata, FIL - T. filiformis, PAL - T. pallida, COR - T. cornuta, NEP - T. neptunis, MIN - T. minutissima, VIR - T. viridistriata, BRU - T. brunneomitra.

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Article

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Sciaphila atra (Triuridaceae), a new mycoheterotrophic species from Borneo

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Abstract

Sciaphila atra (Triuridaceae) from northern Borneo is described and illustrated. This species is similar to *Sciaphila thaidanica* from northern Thailand, but differs in distinctly darker stem and flowers, lower number of flowers, larger female flowers which usually have more tepals and wider tepals of male flowers. Taxonomy of *Sciaphila secundiflora* species complex is discussed in the paper. Key to currently accepted species of *Sciaphila* in Borneo is included.

Keywords: Malesia, rainforest, Sarawak, *Sciaphila secundiflora* complex, taxonomy

Introduction

Sciaphila Blume (1826: 514) is a genus of small achlorophyllous plants distributed in tropical and subtropical regions of the world (Averyanov 2007). Currently 46 species are accepted (POWO 2019) with another one only recently described (Suetsugu & Kinoshita 2020). Harbouring over 20 species, Malesia is the centre of diversity of this genus (Ohashi *et al.* 2008). Borneo is especially rich in *Sciaphila* with around 15 species reported to occur in the island, five of them described only recently (Tsukaya & Okada 2013, Tsukaya & Suetsugu 2014, Suetsugu 2018).

Taxonomy of *Sciaphila* in Malesia is still hazy mainly due to very broad species concepts adopted in Flora Malesiana treatment (van de Meerendonk 1984) underestimating geographical distributional patterns and morphological differences among populations of superficially similar plants (cf. Suetsugu *et al.* 2019). An excellent example of such a species is *Sciaphila secundiflora* Thwaites ex Bentham (1855: 10) originally described from Ceylon and later expanded by van de Meerendonk (1984) and Ohashi (2000) to include as many as 15 previously described species. More recently, Suetsugu *et al.* (2019) and Suetsugu *et al.* (2020) showed that *S. secundiflora* should be treated as a species complex rather than a single polymorphic species. Two other species that have always been recognized as taxa separate from *S. secundiflora*, e.g. *S. thaidanica* K. Larsen (1961: 48) and *S. alba* Tsukaya & Suetsugu (2014: 284), also clearly belong to this complex.

During our field trips to Sarawak (Malaysian Borneo) in 2017 and 2019, we found two populations of *Sciaphila* with distinctive morphology that obviously belonged to the *S. secundiflora* complex and we describe them as a new species in this paper.

Material and methods

This study is based on material collected in January 2017 and January 2019 in northern Sarawak (Borneo, Malaysia). Morphological characters were studied using hand lens (30–60× magnification), stereo microscope and macro photography. Collected specimens were compared with original drawings and descriptions given in protologues of

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representatives of *Sciaphila* reported from Borneo and neighbouring areas. Herbarium vouchers for this study are deposited in SAR and OL. Additionally, herbarium material deposited in BRUN, K, SAN, SAR and SING was studied (herbarium acronyms according to Thiers 2020).

Results

Sciaphila atra **Dančák, Hroneš & Sochor** ***sp. nov.*** Fig 1

Type:—MALAYSIA. Sarawak, Limbang Distr.: Long Tuyo village, Paya Maga, primary submontane forest between camps 1 and 2, WGS 84: N 04°26’43”; E 115°33’19”, elevation ca. 1420 m a. s. l., 29 Jan 2019, *M. Sochor, M. Hroneš & M. Dančák BOR15/19* (holotype SAR, isotype OL).

Diagnosis:—*Sciaphila atra* differs from the most similar known species, *S. thaidanica*, by female flower diameter (6–7 mm vs 5 mm), number of flowers (3–5 vs 5–7), stem and flower colour (deep purple to blackish vs purple), width of male flower tepals (0.7–0.9 mm vs 0.5 mm) and number of female flower tepals (6–8 vs 6).

Description:—Terrestrial, achlorophyllous herb. Roots wiry, poorly branched. Stem erect mostly straight, grooved throughout, poorly branched or unbranched, 3.5–7 cm tall, blackish purple, glabrous. Leaves 1–4, reduced, scale-like, bowl-shaped, ovate-obovate in outline, obtuse, appressed to stem, reddish-brown, 2.2–2.8 mm long and 1.5–2.0 mm wide. Inflorescence lax secund raceme, usually shorter than 1 cm, with 1–2 female and 2–3 male flowers; lower flowers female, upper male. Floral bracts similar to leaves in shape and size. Pedicels curved, very short, 0.5–2.0 mm, purple. Flowers actinomorphic, unisexual, dark purple to almost blackish in bud, with 6–8 equal ovate-lanceolate, patent tepals. Male flowers ca. 5–6 mm in diameter, tepals 6, 1.5–2.3 mm long, 0.7–0.9 mm wide at base, acute and glabrous at apex; stamens 3, surrounded by densely long-papillose dark purple pistillodes; anthers white, sessile, elliptic, bilobed. Female flowers ca. 6–7 mm in diameter, tepals (6–)7(–8), 1.7–2.5 mm long acute and glabrous at apex; carpels numerous, dark purple, ovary obovoid, covered by dense cylindrical papillae at apex, ca. 0.35 mm long; style inserted laterally; stigma clavate, long papillose, ca. 0.5–0.6 mm long, much exceeding the ovary. Fruits aggregated in globose heads 5–6 mm in diameter, consisting of ca. 50 deep purple, oblique obovoid achenes; each achene ca. 1.7–2.2 mm long, densely covered by numerous cylindrical papillae on upper part, style and stigma much shorter than the fruit. Seeds clavate, ca. 1.7 mm long and 0.5 mm wide, with reticulated coat, brown.

Variability:—*Sciaphila atra* is not noticeably variable. The single plant collected in the Kelabit Highlands is somewhat smaller in all traits than plants from the Paya Maga range. In addition, its colour is lighter than plants from the Paya Maga but still it is very dark coloured.

Habitat and ecology:—*Sciaphila atra* inhabits submontane closed-canopy primary tropical rain forests. Its elevational range is rather narrow and it is known only between ca. 1150 and 1450 m a. s. l.

Distribution:—*Sciaphila atra* is known only from two localities in northern part of central highlands of Borneo. The type locality lies in the Paya Maga mountain range in Limbang district of Sarawak while the other locality is situated in the Kelabit Highlands in Miri district of Sarawak.

Conservation status:—The extent of occurrence (EOO) of *S. atra* has not been estimated but its minimal area of occupancy (AOO) is estimated to be 8 km^2 (within the limits for Critically Endangered status under the criterion B2). *Sciaphila atra* is endemic to Borneo and is known from two specimens. One was collected in a protected forest of Pulong Tau National Park, without immediate threats. Conversely, the second one was collected outside the protected area network, in a patch of primary forest surrounded by a previously logged forests and therefore might be potentially threatened by commercial logging. The species is thus known from two subpopulations which represent two locations (sensu IUCN 2012), falling within the limit for Endangered status. We project that the ongoing loss of its habitat will induce a continuous decline in the number of subpopulations and mature individuals. *Sciaphila atra* is therefore assigned a preliminary status of “Endangered” [EN B2ab(iii,v)] according to the IUCN Red List Categories and Criteria (IUCN 2012).

Etymology:—The species name reflects the colour of plants which are very dark, almost blackish purple.

Additional specimens examined:—MALAYSIA. Sarawak, Miri Distr.: Kelabit Highlands, Pa’Lungan village, Arur Bedalawid, 3.1 km N of the village, WGS 84: 03°50’18”N 115°31’4”E, elevation 1166 m a. s. l., 15 Jan 2017, *M. Sochor, M. Hroneš, M. Dančák & Z. Egertová BOR29/17* (OL).

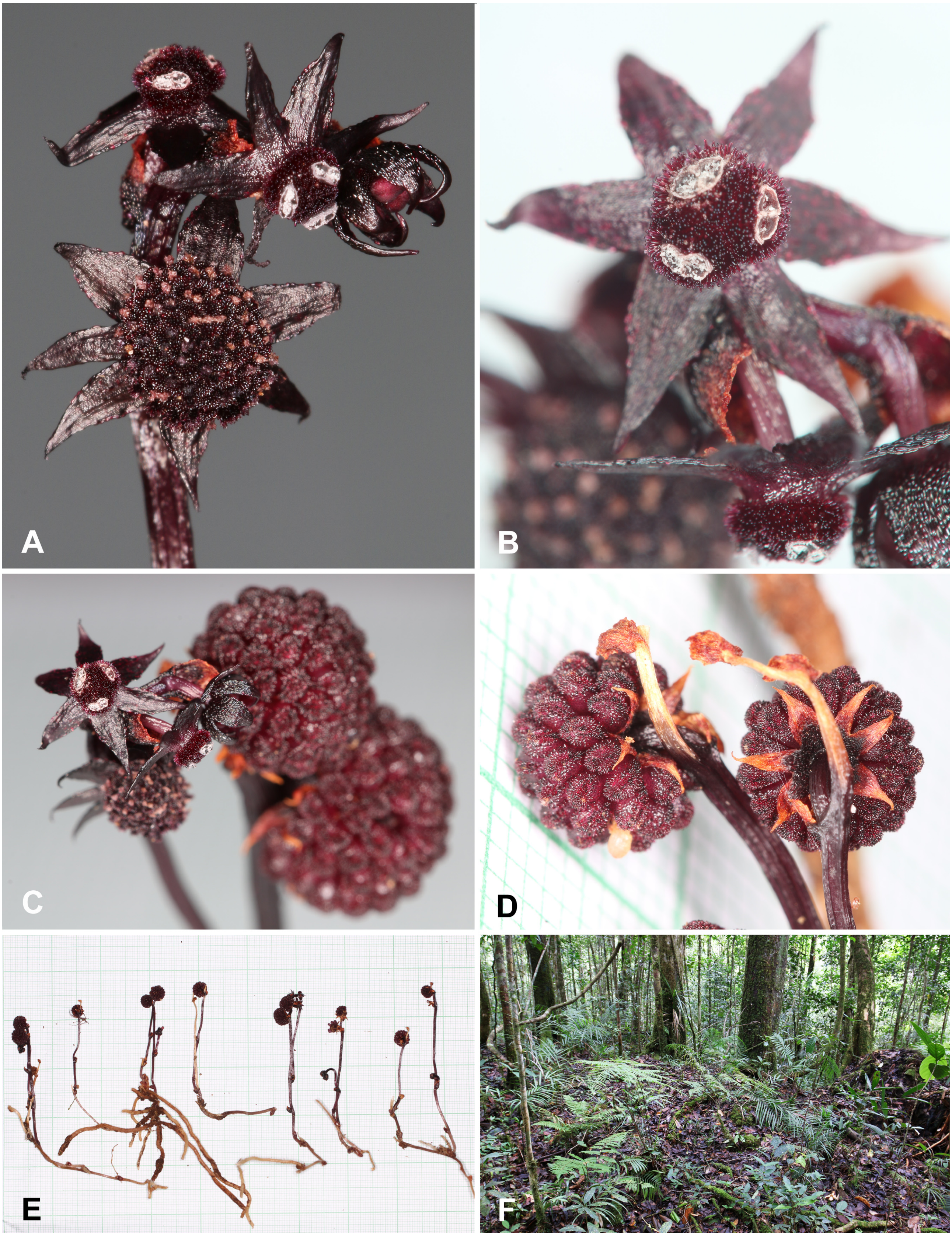

FIGURE 1. *Sciaphila atra*: detail of inflorescence with male and female flowers (A), male flower (B), inflorescence and infructescence (C), mature infructescence with persistent tepals (D), overall appearance (E), habitat (F). From *M. Sochor, M. Hroneš & M. Dančák BOR15/19*. (All photos M. Sochor).

Discussion

Sciaphila atra belongs to the taxonomical complex of *S. secundiflora* defined by large, strictly unisexual flowers with unstable number of tepals, glabrous tepal tips and subgynobasic styles. This group consists of numerous morphotypes described as distinct species in the past but consequently synonymised with *S. secundiflora* by van de Meerendonk (1984). This approach, however, appears untenable (Suetsugu *et al.* 2019). *Sciaphila secundiflora* was described from Ceylon (Bentham 1855) and it is reported to occur from Ceylon to Solomon Island, including Borneo by Flora Malesiana account (van de Meerendonk 1984). Its occurrence in Borneo is probably based only on opinion that *Sciaphila major* Becc. (1890: 332), a species described from Sarawak (Malaysian Borneo), is conspecific with *S. secundiflora*. However, Suetsugu *et al.* (2020) demonstrated that *S. major* is a distinct species and resurrected it from synonymy of *S. secundiflora*. This, consequently, raises a question whether *S. secundiflora* s. str. occurs in Borneo. During our field and herbaria surveys no plants identical with *S. secundiflora* s. str. were found. *Sciaphila secundiflora* is included in Brunei checklist (Coode at al. 1996) but plants labelled by this name are not *S. secundiflora* and are probably identical with plants reported from Kalimantan under the name *S. thaidanica* (Tsukaya & Okada 2013). However, *S. thaidanica* was described from northern Thailand and its occurrence in Borneo would be rather surprising. The photographs published in Tsukaya & Okada (2013) are insufficient to confirm the identity of those plants and because the paper does not contain any morphological description, we prefer to consider occurrence of *S. thaidanica* in Borneo at least as questionable as was previously noted also by Suetsugu (2018). If these plants are a new yet undescribed species or another species not yet known from Borneo remains to be confirmed.

Sciaphila atra is strikingly different from both *Sciaphila secundiflora* s. str. and *S. major* but remarkably similar to abovementioned *S. thaidanica*. Beside the fact that occurrence of this species in two distant and phytogeographically unrelated regions is not very likely, there are also some important morphological differences between the two species. According to the protologue of *S. thaidanica* (description with line drawings; Larsen 1961) it differs from *S. atra* especially in number of flowers per stem, size and colour of female flowers, number of tepals of female flowers and width of male flower tepals. Additionally, plants of *S. thaidanica* are usually richly branched at the base, while plants of *S. atra* are almost unbranched. The main morphological differences among all four discussed species (*S. atra*, *S. major*, *S. secundiflora* s. str. and *S. thaidanica*) are summarised in Table 1. Another Bornean species belonging to the *S. secundiflora* group, *S. alba*, can be easily differentiated from *S. atra* by much taller (usually 15–30 cm) white stems, spirally arranged flowers and absence of pistillodes in male flowers.

TABLE 1. Morphological comparison of *Sciaphila thaidanica*, *S. atra*, *S. major* and *S. secundiflora*. Values for *S. thaidanica* are taken from Larsen (1961), for *S. major* from Suetsugu *et al.* (2020) and for *S. secundiflora* from Suetsugu *et al.* (2019).

species	*S. thaidanica*	*S. atra*	*S. major*	*S. secundiflora*
Height (cm)	ca. 5	3.5–7	(10–)15–25(–35)	(10–)20–33
Stem colour	purple	dark purple	white or pale pinkish	whitish purple
Inflorescence	secund	secund	spirally arranged	secund
Number of flowers	5–7	3–5	8–18(–40)	5–20
Flower pedicel length (mm)	1–2	0.5–2	2.5–4	2–7(–11)
F flower perianth segments	6	(6–)7(–8)	(6–)7–8(–10)	6
M flower diameter	ca. 5	5–6	7-8	7–8
F flower diameter	5	6–7	6-8	7–9
M flower pistillodes	present	present	absent	absent
Tepal length (mm)	2	1.5–2.5	2.9–3.8	3–4
M tepal width (mm)	0.5	0.7–0.9	0.6	0.4–0.6
Tepal colour	purple	blackish	white or pale pinkish	whitish purple?

There are several other species of *S. secundiflora* complex, such as *S. papillosa* Beccari (1890: 334) from New Guinea, *S. tosaensis* Makino (1905: 140) from Japan and Korea, *S. megastyla* Fukuyama & Suzuki (1936: 412) from Japan and Taiwan and *S. kozushimensis* Suetsugu (Suetsugu & Kinoshita 2020: 159) from Japan. All of these species occur outside Borneo, usually in quite distant regions. They also differ in morphology from *S. atra*, e.g. by paler stems and flowers and by absence of pistillodes in male flowers.

Key to the Bornean species of *Sciaphila*

Species with unconfirmed occurrence in Borneo, i.e. *S. secundiflora* and *S. thaidanica* are not included.

1a	Plants with both hermaphrodite and unisexual flowers	2
1b	Plants with only unisexual flowers	4
2a	Perianth segments 4(–5); stamens 2	***S. betung-kerihunensis***
2b	Perianth segments 6; stamens 3–6	3
3a	Male and bisexual flowers with 3 stamens	***S. maculata***
3b	Male flowers with 6 stamens; bisexual flowers with (3–)6 stamens	***S. tenella***
4a	Male flowers with 6 stamens	***S. densiflora***
4b	Male flowers with 2–3 stamens	5
5a	Apex of male flower tepals glabrous	6
5b	Apex of male flower tepals hairy	9
6a	Style subapicaly attached, clearly longer than fruit, male flower tepals knobbed at the tip	***S. arfakiana***
6b	Style basally or laterally attached, clearly shorter than fruit, male flower tepals acute, not knobbed	7
7a	Plants 3.5–7 cm tall, deep purple, flowers almost blackish, male flowers with numerous papillose pistillodes	***S. atra***
7b	Plants mostly 15–30 cm tall, usually white, rarely pale red, male flowers without pistillodes	8
8a	Fully developed inflorescence 8–14 cm long, flowers usually more than 20, usually with 6 tepals	***S. alba***
8b	Fully developed inflorescence 3–6 cm long, flowers usually less than 20, usually with more than 6 tepals	***S. major***
9a	Anthers 4-lobed	***S. micranthera***
9b	Anthers 2-lobed	10
10a	Anthers sessile	11
10b	Anthers on distinct filaments	12
11a	Inflorescence spirally arranged, pedicels short	***S. brevistyla***
11b	Inflorescence secund, pedicels very long	***S. lambirensis***
12a	Tepals obtuse, male flower bed conspicuously thickened	***S. inouei***
12b	Tepals acute, male flower bed not thickened	***S. winkleri***

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Resurrection and emended description of *Sciaphila major* (Triuridaceae)

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Abstract

This paper presents a re-evaluation of the taxonomic identity of *Sciaphila major* described from Sarawak, Borneo, Malaysia which has been considered conspecific with *S. secundiflora.* We revealed that *S. major* is clearly distinguishable from *S. secundiflora s.s.* by the arrangement of flowers on rachis (spirally and subdensely arranged vs. secundly and laxly arranged), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 6–19 cm], tepal length of male flowers (2–2.3 mm vs. 3–4 mm) and the number of perianth segments (more than 6 vs. 6). By spirally-arranged and white flowers, *S. major* is most similar to *S. alba*, but is distinguishable by plant height (15–25 cm vs. 25–35 cm in *S. alba*), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 8–14 cm)], the number of flowers (usually less than 20 vs. usually more than 20), the arrangement of flowers on rachis (subdensely arranged vs. laxly arranged), the number of male perianth segments (usually more than 6 vs. usually 6) and the condition of floral disc (flat vs. bowl-shaped). We also provide an updated key to the species of *Sciaphila* distributed in Borneo.

Keywords: Malesia, Mycoheterotrophy, Sarawak, species revision, taxonomy

Introduction

The family Triuridaceae is a group of fully mycoheterotrophic plants that grow in deep shade understory of ever-wet forests in the tropics and subtropics worldwide, reaching their northernmost limits in temperate region of Japan (van de Meerendonk 1984). The genus *Sciaphila* Blume (1826: 514), which contains more than 40 species, is the largest group within the family (van de Meerendonk 1984, Suetsugu *et al.* 2019).

In taxonomic studies of the genus, species have been primarily discriminated on the basis of the following floral traits: bisexual or unisexual nature of flowers, number and shape of stamens and perianth segments, shape of apical perianth segments, and shape and length of styles (van de Meerendonk 1984; Hsieh *et al.* 2003; Chantanaorrapint & Thaithong 2004; Averyanov 2007; Ohashi *et al.* 2008; Xu *et al.* 2011, Suetsugu *et al.* 2016, 2019; Suetsugu & Nishioka 2017; Suetsugu 2018). However, key characters of male flowers, which are crucial for precise identification, have not been documented for some species, especially if individual specimens were too young at the time of collection (Tsukaya & Okada 2013; Tsukaya & Suetsugu 2014). Given the difficulty of precise identification, the taxonomy of *Sciaphila* remains to be revised.

The taxonomic identity of *Sciaphila secundiflora* Thwaites ex Bentham (1855: 10) has remained particularly unclear (Suetsugu *et al.* 2017, 2019, Suetsugu & Kinoshita 2020). The species was first described from Sri Lanka (Bentham

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1855). Van de Meerendonk (1984) and Ohashi (2000) defined the species in a broad sense, thereby synonymising as many as 15 species with *S. secundiflora* (hereafter called *S. secundiflora s.l.*). Besides Sri Lanka, *Sciaphila secundiflora s.l.* is widely distributed in the Pacific islands, Malesia, Hongkong, Taiwan, Japan, and Korea (van de Meerendonk 1984; Ohashi 2000; Ohashi *et al.* 2008). According to van de Meerendonk (1984) and Ohashi (2000), *S. secundiflora s.l.* can be characterized by unisexual flowers (the female towards the base and the male towards the apex of the inflorescence), 4–8 equal perianth-segments of the male flower without any hair or appendage, 3 stamens, and clavate style and stigma. However, our previous investigations based on the type materials of *S. secundiflora s.l.* showed that gross morphology, floral size and shape of perianth segments often differ among the species that have been considered as synonyms of *S. secundiflora s.s* (Suetsugu *et al.* 2019; Suetsugu & Kinoshita 2020). Therefore, it is highly likely that these treatments are based on the ambiguity of the original species description and that the species complex, in fact, comprises several distinguishable taxa. Suetsugu *et al.* (2019) revealed that both *Sciaphila tosaensis* Makino (1905: 140) and *S. megastyla* Fukuyama & Suzuki (1936: 412) are distinct species rather than synonyms of *S. secundiflora*, based on both molecular and morphological data.

The present study investigated the taxonomic identity of *Sciaphila major* Beccari (1890: 332) that was described from Sarawak, Borneo, Malaysia by examining the detailed morphology of the type specimens and specimens collected around the type locality. A thorough review of relevant literature, herbarium specimens and online digitized plant collections, including JSTOR Global Plants (http://plants.jstor.org/), allowed us to determine that *S. major* is clearly distinguishable from *S. secundiflora s.s.* by the arrangement of flowers on rachis (spirally and subdensely arranged vs. secundly and laxly arranged), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 6–19 cm], tepal length of male flowers (2–2.3 mm vs. 3–4 mm) and the number of perianth segments (more than 6 vs. 6; Figs 1–2). In spirally arranged and white flowers, *S. major* is morphologically similar to *S. alba*, but our detailed comparison of morphological characters between these two species revealed that *S. major* can be distinguishable also from *S. alba.* Here, we provide an emended description of *S. major* based on the type specimen supplemented with newly collected specimens because some important characters were not mentioned in the protologue of the Beccari's original description (1890). We also provide an updated key to *Sciaphila* species distributed in Borneo.

Material and Methods

Plants were studied using hand lens (30–60 × magnification), stereo microscope and macro photography both in the field and in herbaria. We checked the specimens of *S. secundiflora*, *S. major* and *S. alba* kept in the following herbaria: B, BM, BRUN, FI, FR, FU, K, KYO, OL, OSA, P, SAR, SING, TI and TNS. A distribution map was drawn using QGIS 3.10 (2020).

Taxonomic Treatment

***Sciaphila major* Beccari (1890: 332)** Figs. 3–5.

Type:—MALAYSIA. Borneo, Sarawak: Kuching Division, December 1865, *O. Beccari 1210* (syntype, FI, image!), Kuching Division, Sul Monte Mattang, April 1866, *O. Beccari 1507* (syntype, FI and K, image!).

Description:—Monoecious, mycoheterotrophic, perennial herbs. Roots filiform, hairy. Stems erect, underground parts white, aerial parts white to ivory, rarely pale purple, simple or branched at the middle or base, (10–)15–25 cm tall. Scale leaves ovate to lanceolate, ca. 2.5 mm long, apex acute. Inflorescence racemose, rachis (2–)3–6(–7) cm long; flowers 8–18(–30) per inflorescence, spirally and subdensely arranged, male flowers towards the apex of the inflorescence, female flowers towards the base of the inflorescence, internodes 2–6 mm. Bracts appressed to a pedicel, triangular lanceolate, 2 mm long, apex acute. Pedicels 1.5–2 mm long in male flowers and 2–3 mm in female flowers, patent at 90° from rachis, straight. Male flowers: 6–7.2 mm in diam., perianth segments (6–)7–10, white or pale purple, equal in size, narrowly triangular, 2–2.3 mm long, 0.6 mm wide at the base, central parts thick and ridged, fused basally, opening to a flat plane at the base, apex acuminate, smooth, recurved. Floral disc surrounding the stamens, bowl-shaped. Stamens 3, sessile; anthers 2-locular, 0.6 mm long. Female flowers: 6–8 mm in diam., perianth segments (6–)7–11, white or pale purple, equal in size, narrowly triangular, 2.2–2.5 mm long, 0.7 mm wide at the base, fused basally, apex obtuse or acute, smooth, recurved. Carpels more than 30, ellipsoidal, 0.6–0.7 mm long, rounded at apex; style and stigma clavate, 0.7–0.8 mm long, papillate, laterally inserted at the base of ovary.

FIGURE 1. Holotype of *Sciaphila secundiflora* (excluding the upper-left two plants, *G.H.K. Thwaites s.n.* in C.P.2665) deposited in K.

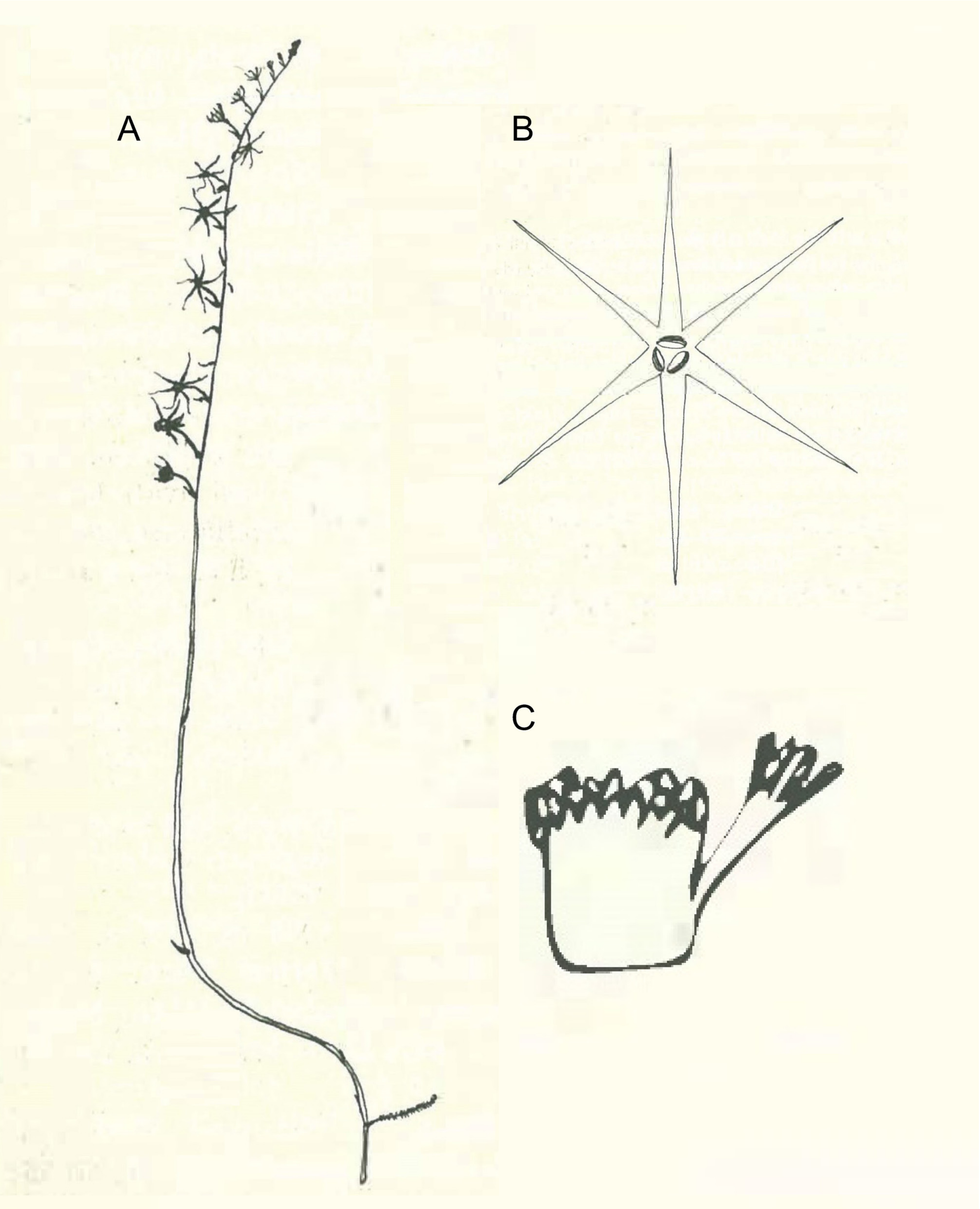

FIGURE 2. Line drawings of *Sciaphila secundiflora*. Reproduced from a monograph by Giesen (1938). A. Habit. B. Male flower. C. Immature carpel with style and stigma.

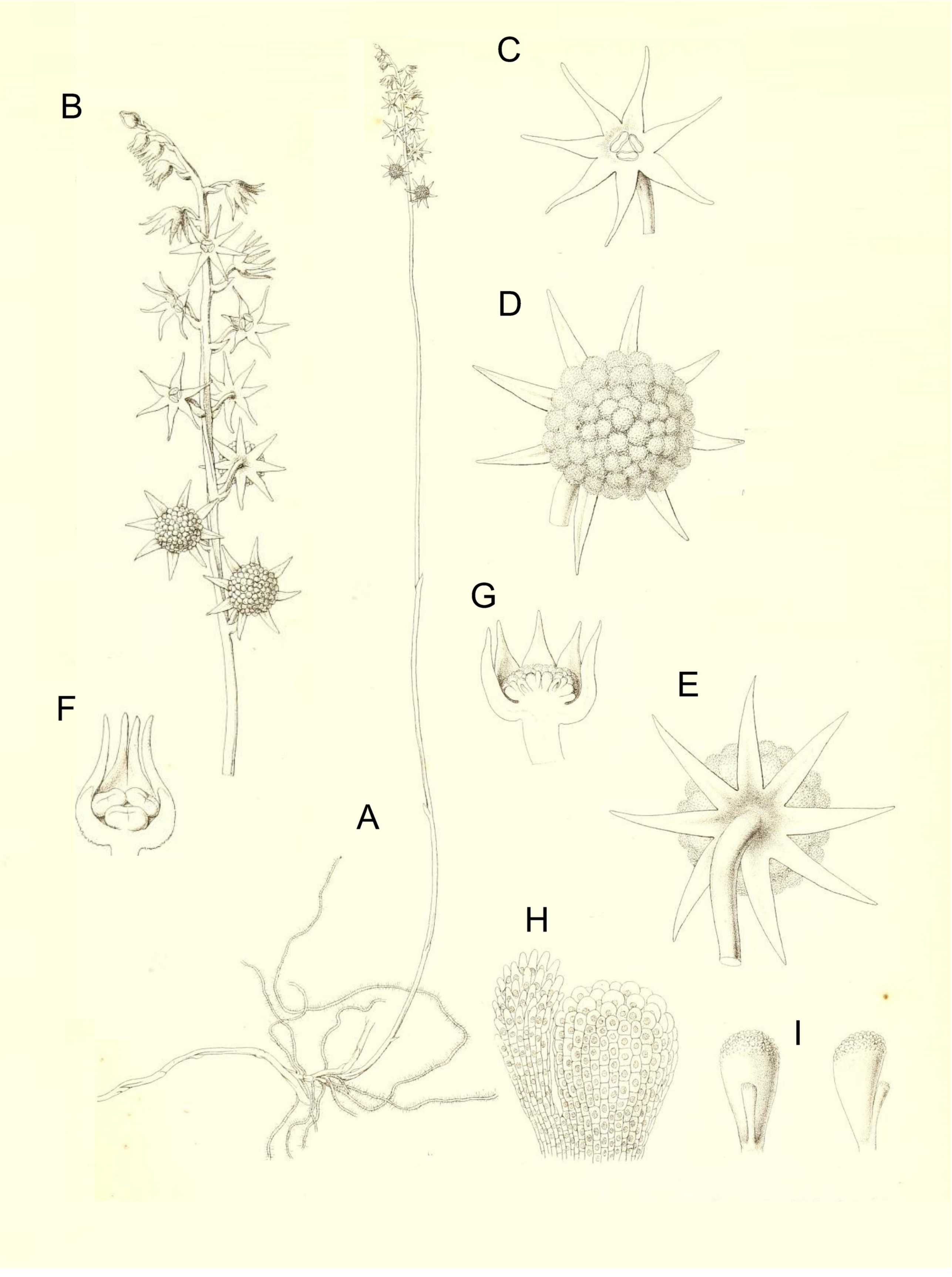

FIGURE 3. Line drawings of *Sciaphila major*. Reproduced from a paper by Beccari (1890) that is the original description. A. Habit. B. Inflorescence. C. Male flower. D–E. Female flowers. F. Immature male flower. G. Immature female flower. H. Immature carpel with style and stigma. I. Immature fruits.

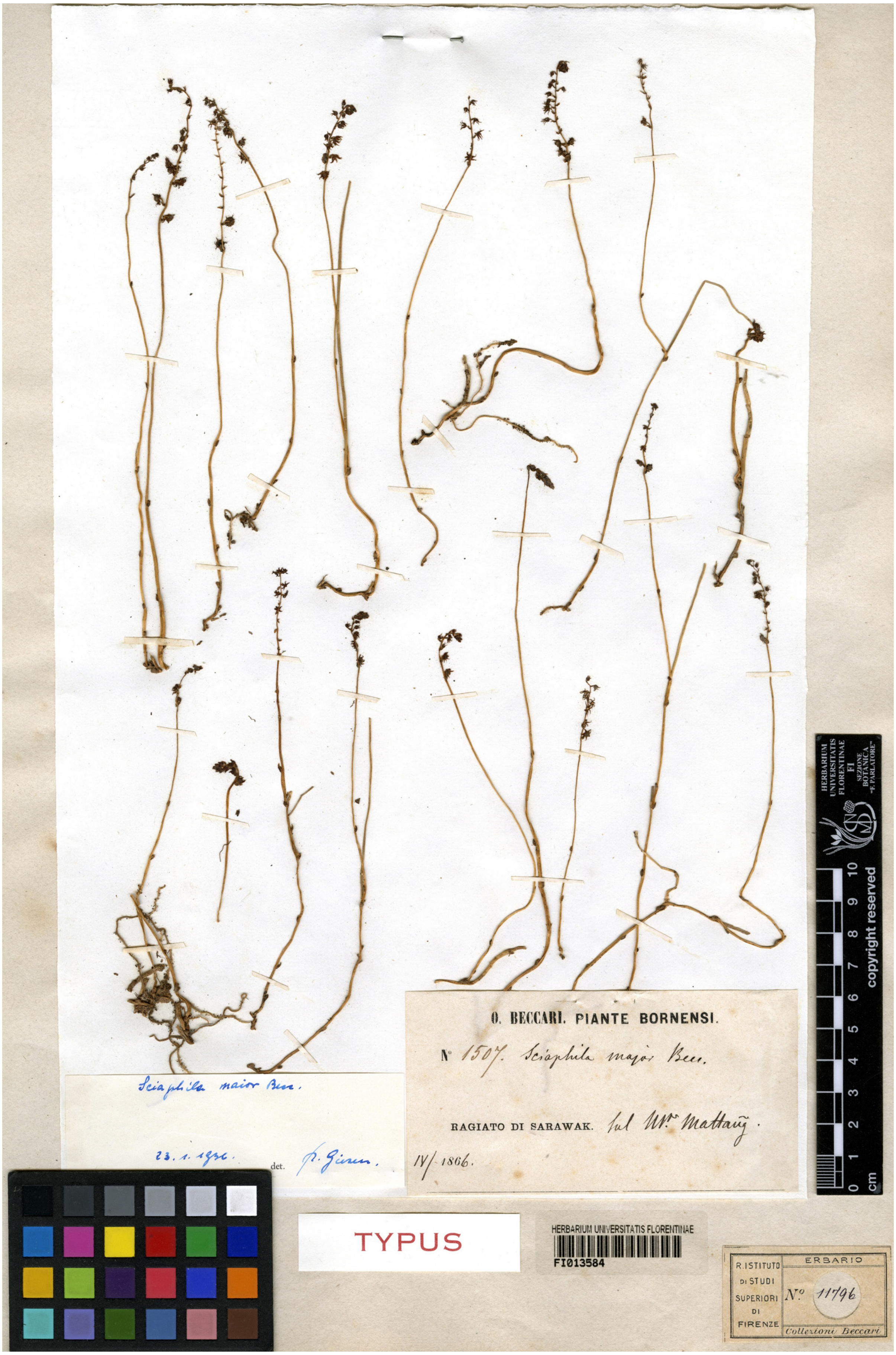

FIGURE 4. Syntype of *Sciaphila major* collected by O. Beccari at the type locality in April 1866 (FI).

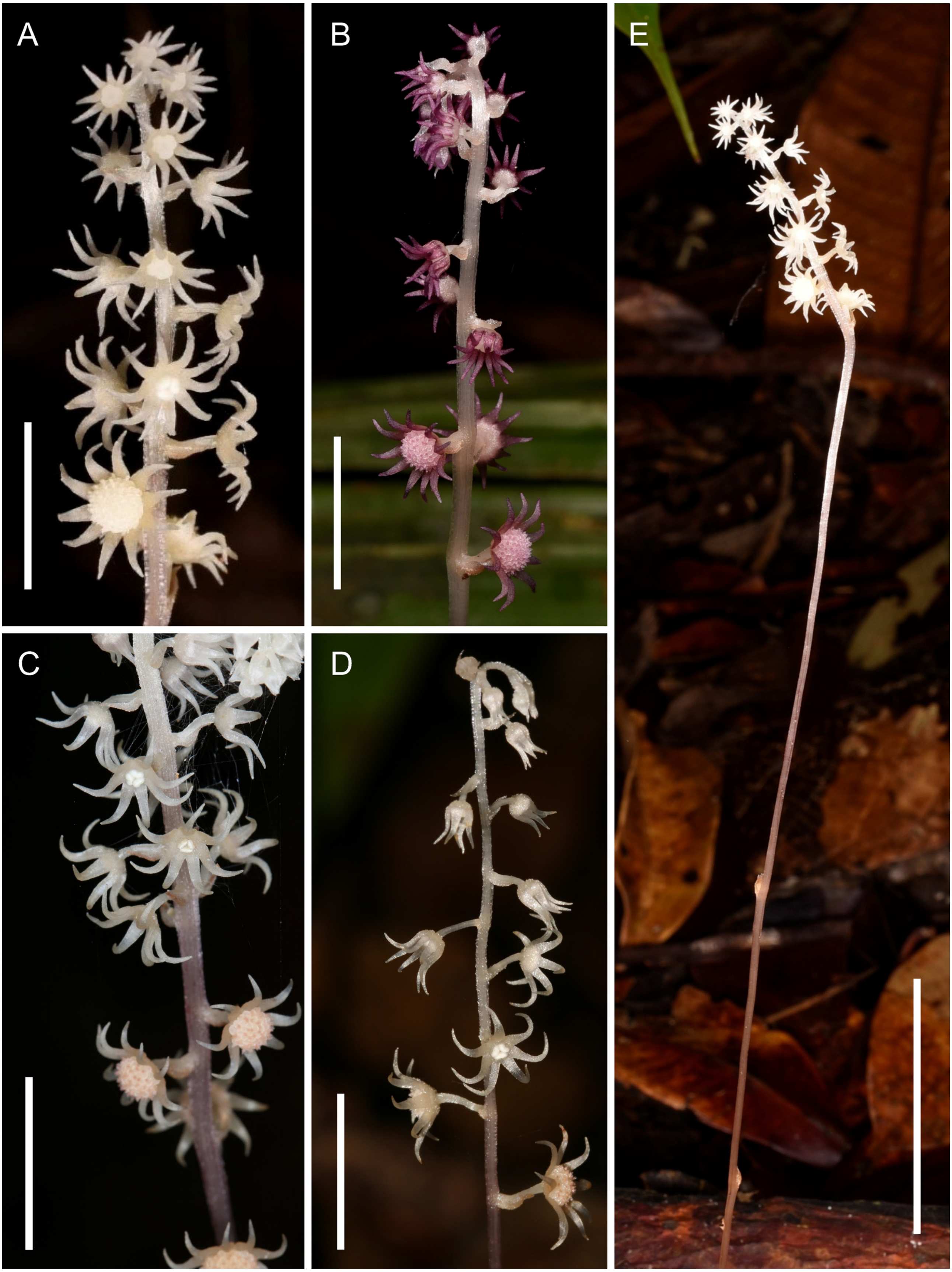

FIGURE 5. *Sciaphila major*. A–B. Inflorescence in Similajau National Park (*Hroneš & Dančák 512020*). C–D. Inflorescence in Kubah National Park (*Sochor, Hroneš & Dančák BOR52/17*). E. Flowering plant in Similajau National Park (*Hroneš & Dančák 512020*). (Photos: A, B, E: Michal Hroneš, C, D: Michal Sochor). Scale bars A–D = 1 cm. E = 3 c m.

Additional specimens examined:—MALAYSIA. Borneo, Sarawak, Kuching Division, Kuching district: Kuching, 6 February 1892, *Haviland s.n.* (SING); Matang, 1903, *Ridley 11707* (SING); Matang, September 1904, *Ridley s.n.* (SING); Kubah National Park, evergreen dipterocarp forest, 01°36′19.91″N, 110°11′23.15″E, alt. 317 m, 4 December 2017, *Tagane, Zhang & Komada SWK4639* (FU, SAR); Kubah National Park, along the Rapids Trail, 01°37′1″N, 110°10′0″E, 7 November 2015, *Mačát s.n.* (OL); Kubah National Park, 0.4 km NE of Matang Wildlife Centre, 01°36′41″N, 110°9′48″E, 26 January 2017, *Sochor, Hroneš & Dančák BOR52/17* (OL); Bako National Park, Telok Asam, 6 Feb 1957, *Purseglove 5584* (SING); Tanjong Dolima, Bako National Park, 7 February 1957, *Purseglove 5584* (SING); Bintulu Division: Bintulu District, Similajau National Park, trail to Batu Anchau, 03°21′44″N, 113°9′55″E, 28 January 2020, *Hroneš & Dančák 512020* (OL, SAR); Tatau District, Tubau, in mixed dipterocarp forest, preserved for water catchment for Rh. Ayaing, 03°16′14.11″N, 113°47′42.73″E, alt. 106 m, 26 January 2017, *A. Naiki, N. Okabe, A. Kawakubo, S. Tagane & Y. Takeuchi SWK4034* (FU, SAR).

Distribution:—Sarawak (Kuching and Bintulu Divisions; Fig. 6). The majority of herbarium specimens for this species was collected from Kubah National Park near Kuching which can be considered as the type locality. Beccari (1890) described the locality simply as Monte Mattang, which is an area now generally known as Matang massif where Kubah National Park is located. This species also occurs in Bako National Park, Sarawak, where field photographs were published on a website [http://angio.bergianska.se/Bilder/monocots/Pandanales/Triuridaceae/Sciaphila/]. Furthermore, it occurs in Bintulu district which is located more than 370 km NE of Kuching (Fig. 4). Further explorations are needed to determine the precise distribution of *S. major*, especially in western Sarawak and adjacent West Kalimantan.

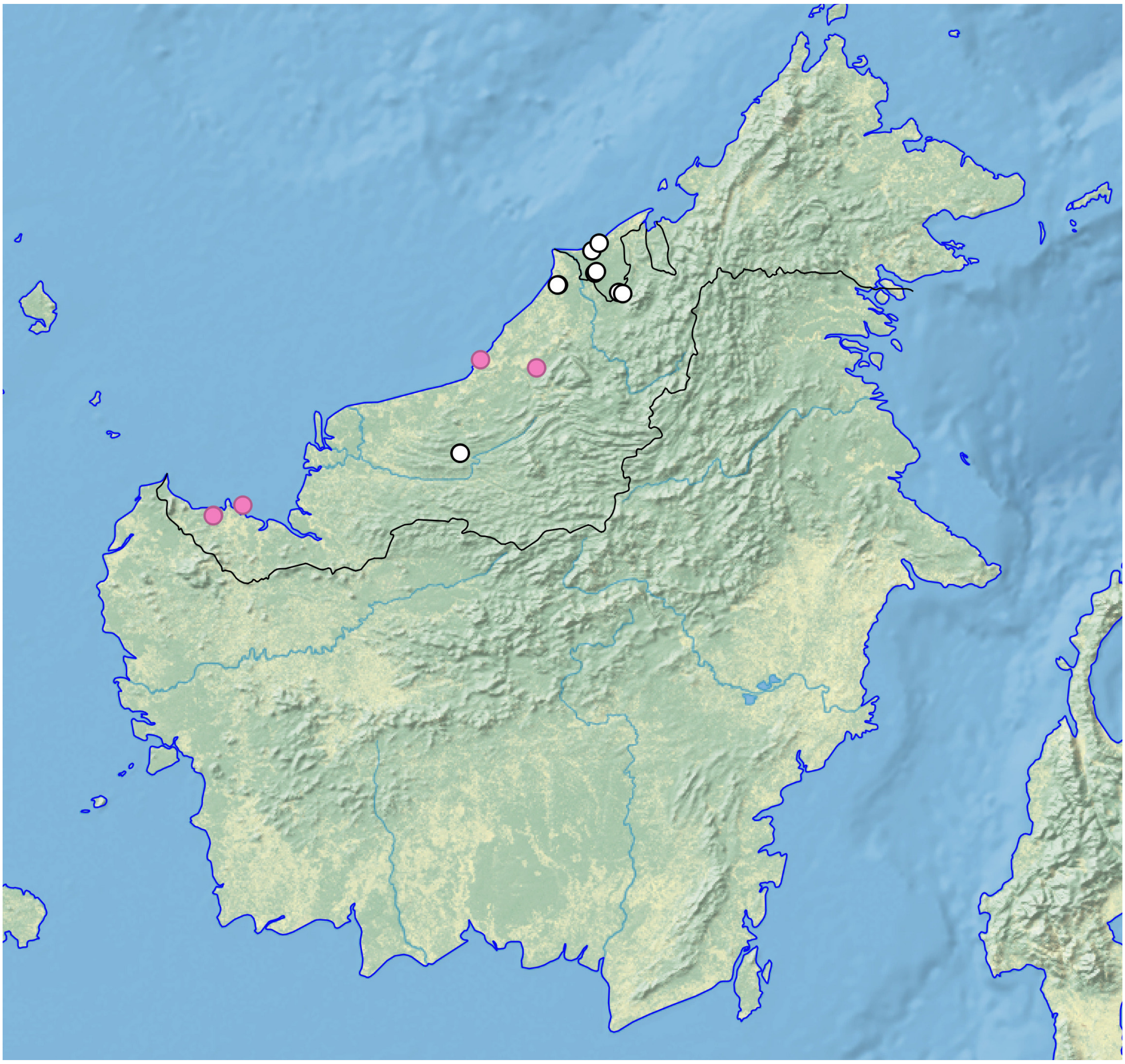

FIGURE 6. Map showing occurrence of *Sciaphila major* and *S. alba*. Pink circles: *S. major* in Borneo. White circles: *S. alba*.

***Sciaphila alba* Tsukaya & Suetsugu (2014: 284)** Figs. 7–8.

Type:—MALAYSIA. Borneo, Sarawak: Miri Division, Miri District, Lambir Hills National Park, along the Lambir Pantu trail, under dipterocarp forest, 3 March 2013, *K. Suetsugu s.n.* (holotype SAR! [spirit coll.], isotype KYO! [spirit coll.]).

Description:—Monoecious, mycoheterotrophic, perennial herbs. Roots filiform, hairy. Stems erect, underground parts white, aerial parts white to pale pinkish white, unbranched, 25–35 cm tall. Scale leaves ovate to lanceolate, ca. 2.5 mm long, apex acute. Inflorescence racemose, rachis 8–14 cm long; flowers (15–)20–40 per inflorescence, spirally and laxly arranged, male flowers towards the apex of the inflorescence, female flowers towards the base of the inflorescence, internodes 3–10 mm. Bracts appressed to a pedicel, triangular lanceolate, 2 mm long, apex acute. Pedicels 2.5–3.5 mm long in male flowers and 3–4 mm in female flowers, patent at 90° from the rachis, straight. Male flowers: 7–8 mm in diam., perianth segments 6(–8), pale pinkish white or rarely reddish purple at the base, fading to pale pinkish white at apex, equal in size, narrowly triangular, 2.9–3.5 mm long, 0.5 mm wide at the base, fused basally, opening to a flat plane at the base, apex obtuse, smooth, recurved. Floral disc surrounding the stamens, flat. Stamens (2–)3, sessile; anthers 2-locular, 0.5–0.7 mm long. Female flowers: 7–8 mm in diam., perianth segments 6–7(–9), pale pinkish white, equal in size, triangular, 3.2–3.8 mm long, 0.7 mm wide at the base, fused basally, apex obtuse or acute, smooth, recurved. Carpels more than 30, ellipsoidal, 0.7–0.8 mm long, rounded at apex; style and stigma clavate, 0.8–0.9 mm long, papillate, laterally inserted a little above the base of ovary.

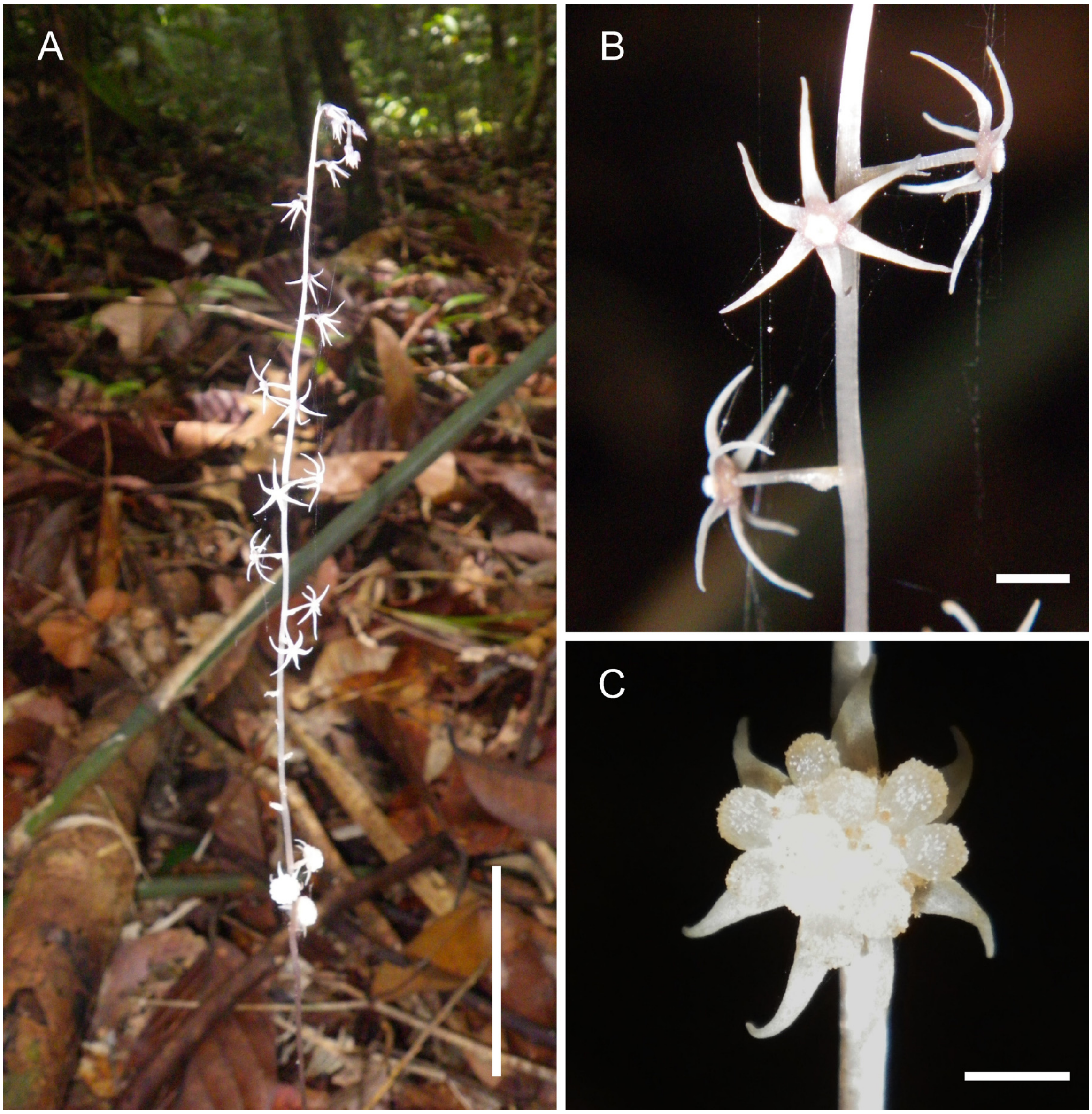

FIGURE 7. *Sciaphila alba* (from the holotype). A. Flowering plant. B. Male flowers. C. Female flower. (Photos: Kenji Suetsugu). Scale bar A = 3 cm. B, C = 2 mm.

FIGURE 8. *Sciaphila alba*. A. Inflorescence in Andulau (*Dančák 2017/56*). B. Inflorescence in Bukit Teraja (*Hroneš & Dančák 192020*). C. Inflorescence in Lambir Hills National Park (*Sochor s.n.*). (Photos: A, B: Michal Hroneš, C: Michal Sochor). Scale bar = 3 cm.

Additional specimens examined:—BRUNEI DARUSSALAM. Belait District: Teraja Forest Reserve, 18 December 1963, *M. Hotta 12710* (KYO); Bukit Teraja, between Wasai Wong Kadir and access road to the summit, 04°19′58″N, 114°26′57″E, 8 July 2019, *Dančák 2019/30* (OL); Bukit Teraja, forest SE Wasai Wong Kadir, 04°20′12 ″N, 114°27′5″E, 13 January 2020, *Hroneš & Dančák 192020* (BRUN); Labi, Sungai Rampayoh, c. 3.5 km above road towards Waterfall no. 2, 04°21′N, 114°28′E, alt. 40 m, 9 January 1994, *Coode 7783* (BRUN); Seria, Badas forest reserve, 04°35′N, 114°25′E, alt. 5–10 m, 24 March 1993, *Coode 7344* (BRUN); Sungai Liang Arboretum, beside the pool, 04°40′N, 114°29′E, alt. 15 m, 14 January 1994, *Dransfield 7345* (BRUN); Sungai Liang, north-western margin of Andulau forest reserve, 04°39′34″N, 114°31′19″E, 23 January 2017, *Dančák 2017/56* (OL); Melilas, Ulu Ingei, W of LP-101A, near Sungai Ingei, 04°07′N, 114°43′E, alt. 30 m, 5 March 1996, *Said BRUN 17313* (BRUN); Batu Melintang to Batu Patau, near Sarawak border, 04°06′N, 114°46′E, alt. 1–180 m, 3 January 1989, *De Vogel 8871* (BRUN). MALAYSIA. Borneo, Sarawak: Miri Division, Miri District, Lambir Hills National Park, ca. 0.4 km NW of the main entrance, in primary forest, 04°12′05″N, 114°02′27″E, alt. 130 m, 8 February 2016, *Sochor s.n.* (OL); Miri Division, Miri District, Lambir Hills National Park, en route to Gn. Pantu, 04°12′00.20″N, 114°01′43.40″E, alt. 170 m, 9 January 2017, *S. Tagane, U. Shimizu-kaya & I. Asano SWK3502* (SAR), Bintulu Division, Tatau District, Tatau, a water catchment forest of Rh. Sayong, a kerangas forest dominated by species of Dipterocarpaceae, 02°18′52.1″N, 112°56′07.4″E, alt. 105 m, 2 February 2016, *A. Naiki et al. SWK1331* (OSA); Bintulu Division, Tatau District, Rh. Sayong, kerangas forest dominated by the species of Dipterocarpaceae, 02°18′47.00″N, 112°56′14.99″E, alt. 109 m, 29 September 2017, *Toyama, Naiki, Lawrence, Sim & Layang SWK5257* (FU).

Distribution:—Brunei Darussalam (Belait District) and Malaysia (Miri and Bintulu Divisions, Sarawak) (Fig. 6).

TABLE 1. Morphological characters of *Sciaphila secundiflora*, *S. major* and *S. alba*.

Characters	***S. secundiflora***	***S. major***	***S. alba***
Plant height	(10–)20–33 cm	(10–)15–25 cm	25–35 cm
Plant coloration	whitish purple	white to ivory, rarely pale purple	white to pale pinkish white
Rachis length	6–19 cm	(2–)3–6(–7) cm	8–14 cm
Arrangement of flowers on rachis	5–20-flowered, secundly and laxly arranged	8–18(–30)-flowered, spirally and subdensely arranged	(15–)20–40-flowered, spirally and laxly arranged
Pedicel length	2–5(–11) mm	1.5–3 mm	2.5–4 mm
Condition of floral disc	flat	bowl-shaped	flat
Number of perianth segments	constantly 6 for both male and female	7–10 for male and 7–11 for female	6(–8) for male and 6–7(–9) for female
Male flower size	7–8 mm in diam.	6–7.2 mm in diam.	7–8 mm in diam.
Shape of male perianth segments	narrowly triangular, 3–4 mm long, 0.4–0.6 mm wide at the base	narrowly triangular, 2–2.3 mm long, 0.6 mm wide at the base	narrowly triangular to acuminate, 2.9–3.5 mm long, 0.5 mm wide at the base
Female flower size	7–9 mm in diam.	6–8 mm in diam.	7–8 mm across
Position of style and stigma	laterally inserted at a little below the middle of ovary	laterally inserted at the base of ovary	laterally inserted a little above the base of ovary
Length of style and stigma	0.8 mm long, as long as ovary in the flowering stage	0.7–0.8 mm long, as long as or slightly exceeds ovary in the flowering stage	0.8–0.9 mm long, as long as or slightly exceeds ovary in the flowering stage

Data of *S. secundiflora* from Giesen (1938) and our own examination of the type specimens deposited in B, BM, FR, K and P.

Discussion

Sciaphila major is similar to *S. secundiflora* in having unisexual flowers (female ones located at the base and male ones at the apex of the inflorescence), equal perianth segments of a male flower without any hair and appendage, 3 stamens, and clavate style and stigmas. However, *S. major* is clearly distinguishable from *S. secundiflora s.s.* by the arrangement of flowers on rachis (spirally and subdensely arranged vs. secundly and laxly arranged), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 6–19 cm], tepal length of male flowers (2–2.3 mm vs. 3–4 mm) and the number of perianth segments (more than 6 vs. 6; Figs 1–2). It is noteworthy that the arrangement of flowers on the rachis is secund in not only *S. secundiflora s.s.* but also most other species that have been considered as the synonyms of *S. secundiflora*. In contrast, *S. major* has spirally arranged flowers. Both types of flower arrangement are steadily recognizable by the position of flowers on the inflorescence rachis even in specimens with only a few flowers. Secund arrangement makes one sided inflorescence (Figs 1 and 2) whereas spiral inflorescences have flowers growing to several sides from the rachis. Even if the inflorescence is lax (Fig. 5B and D), the flowers point to several directions. Therefore, *S. major* is clearly distinguishable from almost all the species of the *S. secundiflora* species complex.

In having spirally arranged flowers and usually white flowers, *S. major* is most similar to *S. alba*, but can be easily distinguished by plant height (15–25 cm in *S. major* vs. 25–35 cm in *S. alba*), rachis length in a fully developed inflorescence (3–6 cm vs. 8–14 cm), the number of flowers (usually less than 20 vs. usually more than 20), the arrangement of flowers on rachis (more densely arranged vs. laxly arranged), the number of male perianth segments (usually more than 6 vs. usually 6), and the condition of floral disc (flat vs. bowl-shaped). On the other hand, Tsukaya & Suetsugu (2014) noted that *S. alba* differs from *S. secundiflora* in having much larger flowers, but further examination of the type specimens of *S. secundiflora* revealed that both *S. secundiflora* and *S. alba* have flowers 7–8 mm in diam. However, *S. alba* can be easily distinguished by the arrangement of flowers on rachis (spirally arranged vs. secundly arranged) and the number of flowers (less than 20 vs. usually more than 20). In addition, these three species can be also distinguished from each other by combination of several morphological characters other than those discussed here. For a detailed comparison of morphological characters among *S. secundiflora*, *S. major* and *S. alba*, see Table 1.

Geographically, *S. alba* and *S. major* seem to have different distribution ranges in Borneo (Fig. 4). According to available records, *S. alba* occurs mostly in Brunei and eastern Sarawak with an isolated occurrence also in central Sarawak, and *S. major* occurs mostly in western Sarawak but reaching the central Sarawak as well.

Key to the Species of *Sciaphila* in Borneo (modified after van de Meerendonk 1984)

1. Plants with bisexual and unisexual flowers 2
  2. Perianth segments 4(or 5) .... *S. betung-kerihunensis*
  2. Perianth segments 6 3
    3. Male and bisexual flowers with 3 stamens .... *S. maculata*
    3. Male flowers with 6 stamens; bisexual flowers with 3–6, but generally 6 stamens .... *S. tenella*
1. Plants with unisexual flowers only 4
  4. Perianth segments equal 5
    5. Flowers secundly arranged 6
      6. Male flowers 1.3–1.4 mm in diam. when flattened; perianth segments bearded at apex .... *S. lambirensis*
      6. Male flowers 7–8 mm in diam.; perianth segments glabrous at apex .... *S. secundiflora*
    5. Flowers spirally arranged 7
      7. Flowers white, rarely pale purple; male flowers more than 5 mm in diam 8
        8. Rachis in a fully developed inflorescence 8–14 cm long; flowers usually more than 20, male perianth segments usually 6, narrowly triangular .... *S. alba*
        8. Rachis in a fully developed inflorescence 3–6 cm long; flowers usually less than 20; male perianth segments usually more than 6, acuminate at apex .... *S. major*
      7. Flowers purple, male flowers less than 5 mm in diam 9
        9. Male flowers ca. 1.2 mm in diam. when flattened; perianth segments with hairs at apex .... *S. brevistyla*
        9. Male flowers 3–4 mm in diam.; perianth segments without hairs at apex .... *S. thaidanica sensu* Tsukaya & Okada (2013)*
  4. Perianth segments unequal (3 larger alternating with 3 smaller ones) 10
    10. Stamens in male flower 3 11
      11. Anthers 2-lobed 12
        12. Apex of perianth segments acute; perianth segments of female flowers 3 longer ones (1.0–1.2 mm long) alternating with 3 shorter ones (0.4–0.6 mm long) .... *S. winkleri*
        12. Apex of perianth segments obtuse; perianth segments of female flowers 3 longer ones (1.4 mm long) alternating with 3 shorter ones (1.1 mm long) .... *S. inouei*
      11. Anthers 3-lobed .... *S. micranthera*
    10. Stamens in male flower 6 .... *S. densiflora*

*As noted by Suetsugu (2018), *Sciaphila* sp. recently recorded as "*S. thaidanica*" by Tsukaya & Okada (2013) from Borneo will be different from *S. thaidanica* Larsen (1961: 48) described from northern Thailand in that flowers are spirally arranged on rachis (vs. secund in *S. thaidanica*; Larsen 1961). Further studies are needed to elucidate the taxonomic identity of *S. thaidanica sensu* Tsukaya & Okada (2013).

Acknowledgement

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