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RESEARCH ARTICLE

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Taxonomic notes on *Sophora phulangkaensis*, a new species of *Sophora* (*Fabaceae – Sophoreae*) from Thailand based on morphological and molecular evidence

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Key words

Fabaceae
lectotypification
Leguminosae
molecular phylogeny
Nakhon Phanom
Phulangka
Sophora

Abstract *Sophora phulangkaensis* is illustrated and newly described here. The species shows similarities with its congener, *S. exigua*, by having an obovate terminal leaflet and up to 15 leaflets but differs in the floral parts. A morphological comparison between the two species is provided along with a discussion. The phylogenetic placement of the new species is presented and discussed based on molecular evidence by nuclear (ITS) and chloroplast markers (*matK*). The results suggest that the new species is nested into sect. *Rubriflorae*, which includes *S. exigua* and *S. huamotensis*. The circumscription of sect. *Rubriflorae* is expanded after being redefined by our findings. In addition, the updated key to species of the genus *Sophora* for the Flora of Thailand is given based on recent specimen observations. Additionally, lectotypes for *S. exigua, S. tonkinensis*, and *S. violacea* var. *pilosa* are designated.

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INTRODUCTION

Sophora L. (Linnaeus 1753) belongs to the tribe *Sophoreae* of the family *Fabaceae*. It is distributed in temperate to tropical regions, ranging from Eurasia, through Malesia to Australasia and the Pacific. Asia, particularly China, is considered to be one of the centres of diversity (Pennington et al. 2005, POWO 2022), harbouring appropriately 50 – 70 species (Pennington et al. 2005, Bojian & Vincent 2010, Niyomdham & Mattapha 2018). The genus *Sophora* as currently circumscribed is characterised by imparipinnate leaves, the absence of bracteoles, free or basally fused stamens (10 + 0), and indehiscent or dehiscent moniliform pods, the latter are rarely flattened or winged (Pennington et al. 2005). The most comprehensive taxonomic work of the genus *Sophora* was by Tsoong & Ma (1981) and Ma (1990), who subdivided it into two subgenera with seven sections and 20 series. Although the classifications in these works are based on leaf, fruit, and colour traits, the speciation in the genus was heavily influenced by environmental conditions, such as a declined global temperature and decreased sea levels, volcanism, glacial and interglacial cycles, and mountain formation (Liao et al. 2021). The new sectional classification divided *Sophora* s.lat. into nine sections based on nuclear and chloroplast markers (Liao et al. 2021) with strong statistical support.

Recent floristic enumerations recorded five *Sophora* species in Indo-China (Thuân et al. 1987) and six in Thailand (Niyomdham 1980, Niyomdham & Mattapha 2018). However, these taxonomic investigations were mostly based on specimens stored in herbaria, with just a few collected samples for each species.

The phylogenetic relationships of species in *Sophora*, a genus belonging to the core Genistoid clade, appeared to be ambiguous based on the integration of morphological features and the seed alkaloid composition (Pena & Cassels 1996) and molecular data (Crisp et al. 2000, Kajita et al. 2001, Pennington et al. 2001, Wojciechowski et al. 2004, Cardoso et al. 2012, 2013, 2015). The results mainly agreed with prior molecular studies with additional markers, such as by Duan et al. (2019) and Liao et al. (2023), which showed that the genus is polyphyletic based on nuclear internal transcribed spacers (ITS) and three plastid markers (*matK*, *psbA-trnH*, and *trnL-F*). Molecular studies (Duan et al. 2019, Mitchell & Heenan 2002) have also shown that several species of *Sophora* fail to resolve at the sectional level, like the relationships amongst sections *Disamaea* P.C.Tsoong, *Edwardsia* (Salisb.) Seem., and *Sophora* Yakovlev. In a more recent study, Liao et al. (2021) also showed that the intersectional relationships are poorly understood, which was based on whole chloroplast genome and protein-coding sequence data of representative species of sections; their and Duan et al. (2019) results are in agreement with Pena & Cassels (1996), but incongruent with the taxonomic classifications of Tsoong & Ma (1981) and Ma (1990).

According to the classifications of Tsoong & Ma (1981) and Ma (1990), sect. *Sophora* was previously subdivided into nine series, one of which ser. *Rubriflorae* P.C.Tsoong was defined by the following characteristics: absence of stipules; violet flowers; standard petal with a long claw; wing petals sagittate or hastate and keel petals with appendage; and stamens shortly jointed at base, distally free.

Recently, Liao et al. (2023), using three nuclear and four plastid markers, showed that *Sophora* s.str., with *Ammodendron* Fisch.

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ex DC., *Ammothamnus* Bunge, and *Echinosophora* Nakai embedded in it, was comprised of nine well-supported clades. In their study, they raised the rank of *Sophora* ser. *Rubriflorae* to sectional level, *Sophora* sect. *Rubriflorae* (P.C.Tsoong) M.Liao & B.Xu. Nonetheless, they suggested that the relationships in this section still need to be confirmed, thus further additional species and molecular data are needed. This means, that deriving at a new classification for the tribe *Sophoreae*, necessitates a comprehensive sampling of *Sophora* with closely related taxa, including *Euchresta* Benn., as well as increasing the number of informative molecular markers.

Section *Rubriflorae* comprises five species, one of which is indigenous to China (*Sophora praetorulosa* P.T.Li), one to Sri Lanka (*S. rubriflora* P.C.Tsoong, now *S. violacea* Thwaites), and one to the Indo-Chinese region including Thailand (*S. exigua* Craib), *S. oblongata* P.C.Tsoong is confined to Vanuatu and *S. longipes* Merr. is widespread, ranging from the Philippines to the Lesser Sunda Islands and the Northern Territory of Australia.

Phu Langka National Park is situated in Nakhon Phanom Province, north-eastern Thailand, near the Mekong River, which is the border between Thailand and Laos. With several range-restricted species, the National Park is one of the areas that is regarded to be botanically isolated (Suddee et al. 2019). Several species were recently described, such as *Bauhinia nakhonphanomensis* Chatan (*Fabaceae*; now *Phanera nakhonphanomensis* (Chatan) Mackinder & R.Clark) (Chatan 2013); *Argyreia pseudosolanum* Traiperm & Suddee (*Convolvulaceae*) (Traiperm & Suddee 2020; *Convolvulaceae*), and *Thunbergia amphaii* Suwanph., K.Khamm., D.J.Middleton & Suddee (*Acanthaceae*) (Suwanphakdee et al. 2021).

We describe a new species of *Sophora*, *S. phulangkaensis*, discovered on a sandstone plateau in Phu Langka National Park. The new species appeared to be related with *S. exigua* and *S. huamotensis* Mattapha, Suddee & Rueangr. based on evidence from nuclear ITS and plastid *matK* markers. This discovery brings the total number of *Sophora* species to eight in Thailand. We also construct a key to the *Sophora* species for the Flora of Thailand. Furthermore, after careful examination of type specimens, we additionally assign lectotypes for *S. exigua, S. tonkinensis* Gagnep. and *S. violacea* Thwaites var. *pilosa* Gagnep.

MATERIALS AND METHODS

Molecular work

DNA extraction, *PCR amplification*, *and sequencing*

To study the phylogenetic position of the new species in *Sophora*, sequences of *Sophora* and related genera were used to construct a phylogeny based on 54 nuclear ribosomal ITS sequences and 46 *matK* chloroplast-marker sequences. We analysed each marker independently with a comparison the phylogenetic topologies and a concatenated dataset. We selected as outgroup taxa that represent the main lineages, which are closely related to the *Sophoreae*, namely, *Dalbergia cultrata* T.S.Ralph, representing the *Dalbergioid* s.lat. clade, *Bowringia callicarpa* Champ. ex Benth. from the baphioid clade and taxa from the core genistoids clade in subfamily *Fabaceae-Papilionoideae* (Cardoso et al. 2012, 2013, Duan et al. 2019, Liao et al. 2021). The sequences of *Sophora* and other genera were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/). Data on all taxa used in this study are provided in the Appendix. Silica-dried leaf samples were collected in the field, and corresponding voucher specimens were deposited in BKF, KKU, and QBG (for abbreviations of herbaria see Thiers continuously updated). See the Appendix for information on the specimens studied. Three *Sophora* species, including the putative new species, were sampled: *Sophora exigua* (two collections), *S. huamotensis* Mattapha, Suddee & Rueangr., and *S. phulangkaensis*, sp. nov.

Total genomic DNA was extracted from silica-dried leaf fragments by QIAGEN (Germany) and from fresh leaves using Thermo Scientific direct PCR solutions following the manufacturer's protocol. The nuclear ribosomal ITS regions (ITS1, ITS2, and 5.8S) were amplified using the primers ITS1 (forward) and ITS4 (reverse) (Taberlet et al. 1991). PCR amplifications were carried out in 25 µL reactions containing 12.5 µL of 2× Phire Plant Direct PCR Master Mix (Thermo Scientific, Lithuania), 0.9 µL of each primer, 0.5–1 µL bovine serum albumin (BSA), and 0.5–1 µL DMSO; the volume was adjusted with nuclease-free water. One to two microlitres of gDNA template were used in each reaction. The thermal cycling conditions were 94 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, 48 °C for 40 s, and 72 °C for 1 min, and a final extension at 72 °C for 10 min. For *matK*, we used the primers trnK685F (forward) and trnK2R (reverse) (Hu et al. 2000, Wojciechowski et al. 2004, Cardoso et al. 2012). Amplification was performed at 95 °C for 4 min, followed by 40 cycles of 95 °C for 30 s, 50 °C for 40 s, and 72 °C for 50 min, with a final extension at 72 °C for 2 min. The primers are listed in Table 1. The amplicons were resolved by electrophoresis on 1.5 % agarose gels and stained with ethidium bromide. The PCR products were sequenced via barcode-tagged sequencing at Celemics Inc., Korea, based on next-generation sequencing technology. The sequences generated have been deposited in GenBank.

Sequence alignment and analyses

Multiple alignments of all sequences from GenBank and those generated in this study were conducted using Muscle in MEGA v. 11 (Tamura et al. 2021). Manual adjustment for alignment mistakes was performed in Bioedit v. 7.0.5.3 (Hall 1999). Ambiguous nucleotide base assignments were removed. Individual ITS and *matK* markers, and the combined dataset were phylogenetically analysed using Maximum Parsimony (MP), Maximum-likelihood (ML), and Bayesian interference (BI).

MP cladograms were calculated in MEGA v. 11 (Tamura et al. 2021), with 10 times a heuristic search with a random starting tree and Tree-Bisection-Reconnection (TBR) branch swapping; the results were tested with 1 000 times bootstrapping with the same settings.

ML analysis was performed using RAxML-HPC2 on XSEDE v. 8.2.12 (Stamatakis 2014) on the CIPRES Gateway v. 3.3 (https://www.phylo.org; Miller et al. 2010) with also 1 000 bootstraps. For Bayesian analysis, best-fit evolutionary models were selected under the Bayesian information criterion (BIC) using jModelTest2 on XSEDE on the CIPRES Gateway (Guindon &

Table 1 Primers used for PCR amplification and sequencing of this study.

Primer name	Sequence (5'-3')	Direction	References
ITS1	TCC GTA GGT GAA CCT GCG G	forward	Taberlet et al. 1991
ITS 4	TCC TCC GCT TAT TGA TAT GC	reverse	Taberlet et al. 1991
trnK685F	GTA TCG CAC TAT GTA TCA TTT GA	forward	Hu et al. 2000, Wojciechowski et al. 2004, Cardoso et al. 2012
trnK2R	CCC GGA ACT AGT CGG ATGG	reverse	Hu et al. 2000, Wojciechowski et al. 2004, Cardoso et al. 2012

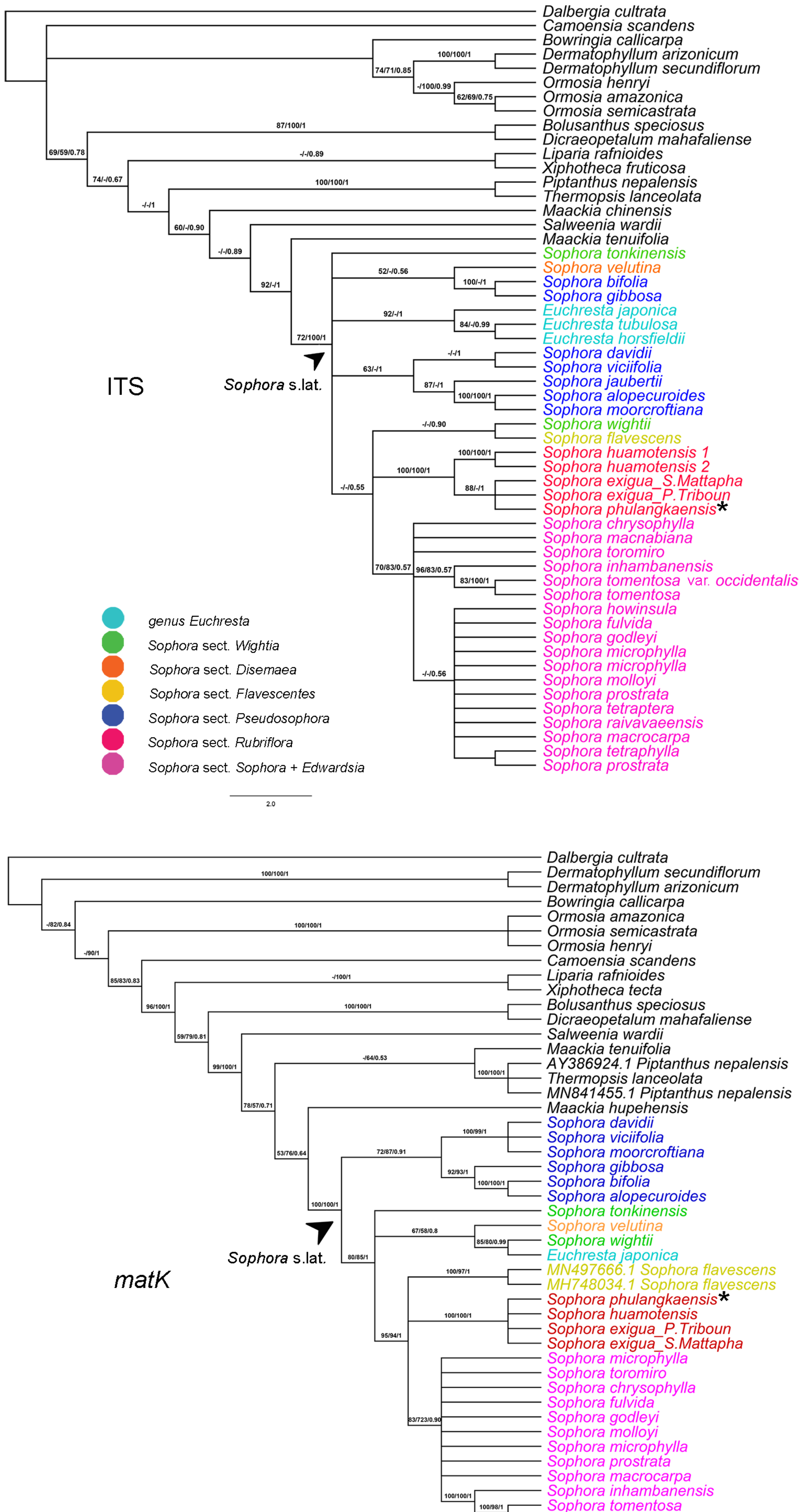

Fig. 1 Bayesian 50 % majority-rule consensus topologies of the individual analysis of ITS/5.8S (above) and *matK* (below). The new species, *Sophora phulangkaensis*, marked with an asterisk (*), is placed in sect. *Rubriflorae* highlighted in red. Numbers above branches are bootstrap support values of the MP and ML analyses and the posterior probabilities of the BI analysis, respectively. Bootstrap support values < 50 % and posterior probabilities < 0.5 are not shown, they are represented by dashes.

Gascuel 2003, Darriba et al. 2012). The best-fit models for BI analyses were TIM2+G for ITS, TVM+I for *matK*, and GTR+I+G for the concatenated data. Bayesian analysis was then independently run using MrBayes on XSEDE (v. 3.2.7a) (Ronquist et al. 2012) embedded on CIPRES Science Gateway v. 3.3 (https://www.phylo.org; Miller et al. 2010). BI analysis was performed with two simultaneous runs of four Markov Chain Monte Carlo (MCMC) chains, running for 120 000 000 generations with sampling every 1 000 generations. The initial 10 % of the sampled data were discarded as burn-in prior to calculating a 50 % majority-rule consensus tree annotated with Bayesian posterior probabilities (PP). Mixing and focussing of the chains was verified using Tracer v. 1.7.2 (http://tree.bio.ed.ac.uk/software/tracer/; Rambaut et al. 2018), and all the ESS (Effective Sample Size) values > 200. The 50 % majority rule consensus tree with branch lengths, bootstrap (BS), and posterior probability (PP) values were viewed and manipulated in FigTree software v. 14.0 (Rambaut & Drummond 2012). Ultimately, the phylogenetic trees of all analyses were compared for congruence.

Morphological observations, identifications and nomenclature

Specimens of the putative new species were checked against keys and descriptions of known species (Thuân et al. 1987, Niyomdham 2014, Niyomdham & Mattapha 2018) and consulted in the herbaria BK, BKF, BM, CMUB, K, KKU, P, and QBG (herbarium abbreviations follow Thiers continuously updated). For online comparisons with the type specimens of closely related species the websites of Kew (https://apps.kew.org/herbcat/navigator.do) and the Paris herbarium (https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US) were consulted. Morphological analysis of the new species was based on living material, and photographs and detailed illustrations were generated. The conservation status of the new species was assessed following the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022).

RESULTS AND DISCUSSION

Phylogenetic analyses

We presented the phylogenetic trees of both individual and the concatenated datasets resulting from MP, ML, and BI analyses (Fig. 1, 2) based on the Bayesian 50 % majority-rule consensus topologies. The MP, ML, and BI analyses of the three datasets showed slight differences in the well-supported nodes, but all generated trees were strongly congruent.

The analyses show that *Sophora* s.str. is paraphyletic and should include the genus *Euchresta* to form *Sophora* s.lat. The latter has high ML and BI support in all three analyses. In the analyses of the individual markers *Euchresta* is part of basal polytomy within *Sophora* s.lat. (Fig. 1), but in the combined analysis the basal polytomy is resolved and *Euchresta* groups with *S. velutina* Lindl. and *S. wightii* Baker as a separate clade with not too high support (Fig. 2). The sections *Sophora* and *Edwardsia* (Fig. 1, 2) are a non-resolved monophyletic group in all analyses with modest (Fig. 1) to high ML and BI support (Fig. 2).

In all analyses, the new species, *S. phulangkaensis* (marked with an asterisk (*) in Fig. 1, 2) groups in the highly supported sect. *Rubiflorae*, forming a polytomy with the two specimens of *S. exigua* (relatively high support) and *S. huamotensis* as sister to this group.

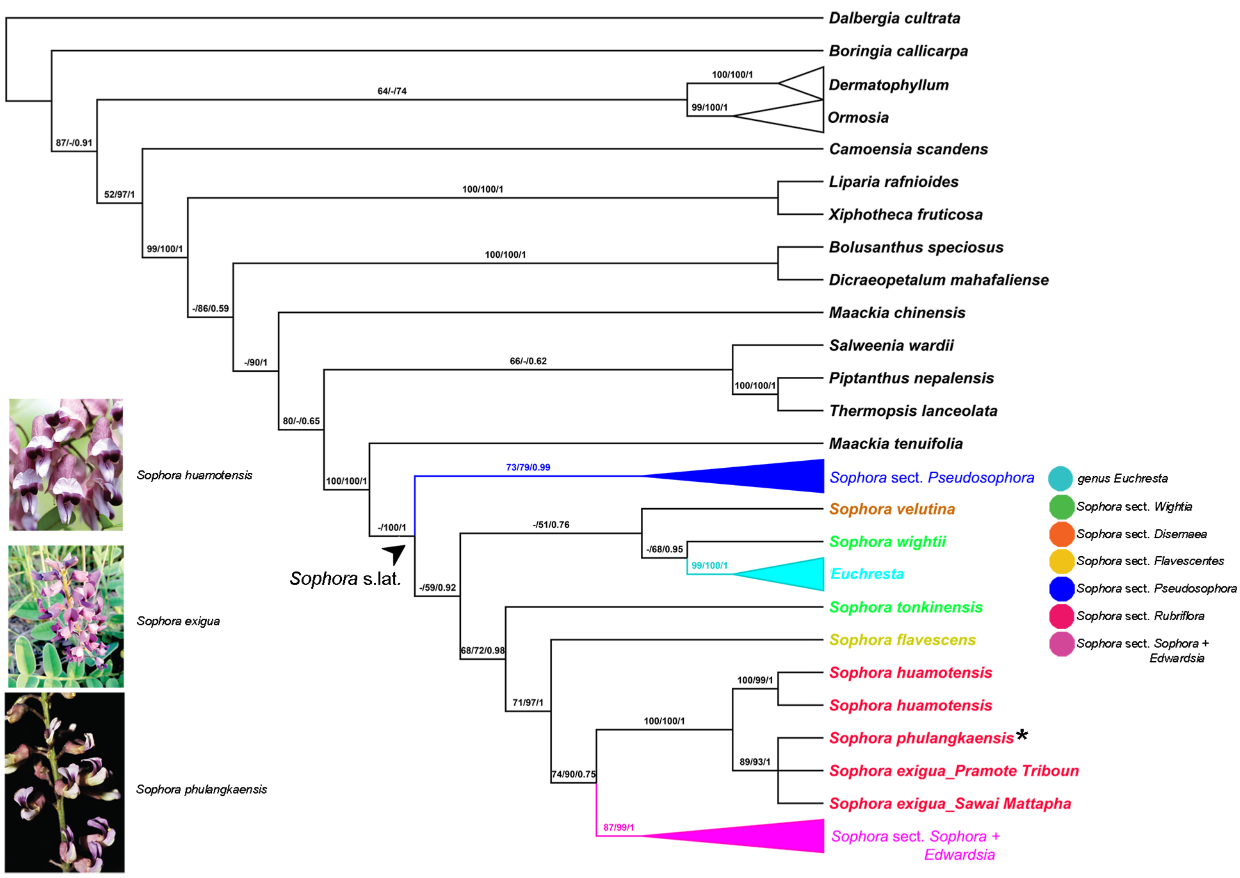

Fig. 2 Bayesian 50 % majority-rule consensus topology of the concatenated analysis of the ITS/5.8S and *matK* datasets. The new species, *Sophora phulangkaensis*, marked with an asterisk (*), is placed in sect. *Rubiflorae* highlighted in red. Numbers above branches are bootstrap support values of the MP and ML analyses and the posterior probabilities of the BI analysis, respectively. Bootstrap support values < 50 % and posterior probabilities < 0.5 are not shown, they are represented by dashes.

The analyses of our selection of sequences, taken mainly from GenBank, do (unsurprisingly) support the results of Pena & Cassels (1996), Mitchell & Heenan (2002), Duan et al. (2019), and Liao et al. (2023). The new species, *S. phulangkaensis,* is classified in the monophyletic sect. *Rubriflorae*.

Section *Rubriflorae* is expanded here and is now characterised by the following characters: violet flowers, articulated pedicels, prominent calyx lobes, spathulate standard petal with a long claw and strongly curved upwards, wing petals with a hook-like auricle, sagittate or hastate at base and stamens shortly jointed at base but distally free. Likely, this circumscription will have to be adapted, as two other species, so far not included, but belonging to the section, are classified in it as indicated by Liao et al. (2023).

TAXONOMY

A detailed description of the new species is provided and the key to the *Sophora* species for the Flora of Thailand is revised. To facilitate identification of the new species, a colour plate and line drawings of micromorphology are provided.

EMENDED KEY TO THE SOPHORA SPECIES FOR THE FLORA OF THAILAND

1. Calyx campanulate, teeth inconspicuous 2
1. Calyx tubular, teeth conspicuous 3

2. Corolla creamy white. — Plant in main land *S. flavescens*
2. Corolla yellow. — Plant coastal . . . . *S. tomentosa*

3. Leaflets 7–15 4
3. Leaflets 19–39. 6

4. Undershrub, up to 0.5 m tall, standard 18–20 mm long . . . . *S. exigua*
4. Small shrub to small tree, 0.5–6 m tall; standard 5–10 mm long 5

5. Small shrub, 0.5–2 m tall; inflorescence erect . . . . *S. phulangkaensis*
5. Shrub or small tree, 4–6 m tall; inflorescence pendulous . . . . *S. wightii*

6. Pedicels 8–10.5 mm long; auricles of wing petals absent . . . . *S. huamotensis*
6. Pedicels 2–3 mm long; auricles of wing petals present . . . . *S. velutina*

Sophora phulangkaensis Mattapha, K.Khamm. & Suddee, *sp. nov.* — Fig. 3, 4

Closely related to *S. exigua* Craib, from which it differs by being a small shrub 0.5–2 m tall (vs undershrub up to 0.5 m tall in *S. exigua*), with sparse to dense hairs on midrib and margins of leaf blade (vs densely tomentose in *S. exigua*, particularly when young), presence of bracteoles (absent in *S. exigua*), the standard 15–16 mm long (18–20 mm long in *S. exigua*), filaments hairy at base with hairy anthers (glabrous in *S. exigua*), ovary densely strigose (tomentose in *S. exigua*) and longer pods (7–13 cm long vs 5–7 cm long in *S. exigua*). — Type: *Khammongkol 211* (holo BKF; iso BKF!), Thailand, Nakhon Phanom, Ban Phaeng district, Phu Langka National Park, summit plateau, near golden stupa, N17°58'12" E104°07'02", 550 m, 24 Mar. 2020, fl. For paratypes see below.

Etymology. The specific epithet refers to the name of Phu Langka National Park, where the species was discovered.

Small shrub, 0.5–2 m tall; young twigs densely hairy with strigose hairs. *Leaves* imparipinnate; petioles 4–8 cm long, densely strigose, grooved above; stipules lanceolate, c. 1 by 0.5 mm, outside densely strigose, early caducous; rachis 10–18.5 cm long; ultrajugal part up to 2.5 cm long. *Leaflets* 7–15; petiolules 1–2 mm long, densely strigose; lamina elliptic or elliptic-oblong, terminal leaflet sometimes obovate, 1–3 by 0.8–1.8 cm in flower, 5–8 by 2.5–3.5 cm in fruit, apex retuse, acute or obtuse, base obtuse of broadly cuneate, margins entire, upper surface glabrous, lower surface sparsely to densely hairy on midrib and margins, otherwise glabrous or with a few sparse hairs; secondary veins 5–10 on each side of midrib, raised on both sides, anastomosing near margin distinct; stipels absent. *Inflorescences* racemose, terminal, 12–20 cm long, leaf-opposed, with strigose hairs throughout. *Flowers* pale purplish white to purplish pink, standard with a dark purple blotch at base above claw on the dorsal face, glabrous; bracts and bracteoles triangular, very minute, early caducous. *Pedicels* including the articulate section 4–8 mm long, articulated near apex, hairy. *Calyx* tubular, pale pinkish purple; tube 5–8 mm long; lobes 5, broad, 1–1.5 by 2.5–3 mm, apex acute to rounded, margin hairy, hairy outside, glabrous inside. *Corolla*: standard petal spathulate, 15–16 mm long, blade obovate, curved upwards, 5–6 by 6–7 mm, apex emarginate, base without callosities, tapering attenuately into the claw, glabrous on both sides, claw 9–10 mm long; wing petals suboblong, 11–13.5 mm long, blade 8.5–9 by 2.5–3 mm, slightly constricted below the middle, base auriculate, with a hook-like auricle of c. 1 mm long on each side, apex rounded, outside with lunate sculpturing on the lower half, glabrous on both sides, claw 4–4.5 mm long, flattened; keel petals oblique oblong, 11–13 mm long, blade 6.5–7 by 2.5–3 mm, apex rounded to subtruncate, glabrous on both sides, claw 4.5–5 mm long, flattened. *Stamens* 10, shortly joined at base, distally free; filaments 10–12 mm long, flattened, hairy at base; anthers oblong, c. 0.5 by 0.2 mm, hairy. *Ovary* densely strigose, 8–9 mm long; stipe c. 2 mm long; style c. 3 mm long, glabrous. *Pods* submoniliform, constricted between seeds or slightly septate, 7–13 by 0.5–0.7 cm, densely and shortly adpressed hairy, apex often pointed. *Seeds* (1–)2–5 per pod, ellipsoid or oblong, 7–7.5 by 3–4 mm.

Distribution — Endemic to Thailand, only known from the type locality.

Ecology — Grassland on sandstone plateau. Flowering: March; fruiting: April, May.

Vernacular name — Phit sanat phu langka (พิษนาศน์ภูลังกา), the name is given by the authors.

Conservation status — According to the IUCN threatened criteria (IUCN 2022), the species has a small population size with few individuals found, but in a protected area. We assess it here as Data Deficient (DD) due to the inadequacy of the distribution information.

Additional specimens examined (paratypes). Northern, *Mattapha s.n.* (BKF, KKU), Nakhon Phanom [Ban Phaeng district, Phu Langka National Park, c. 200 m, 14 July 2012, fr.; *Kerr 8427* (BK [SN212294]!, K [K000759742!]), Nakhon Phanom, precise locality not known, c. 200 m, 11 Feb. 1924, fl.

Notes — *Sophora phulangkaensis* is characterised by being a small shrub up to 2 m tall, leaves with 7–15 leaflets, racemes up to 20 cm long, leaf-opposed, tubular calyx with hairs outside, obovate standard without basal callosities and glabrous on both sides, wing petals with a hook-like auricle c. 1 mm long on each side at base, submoniliform fruits with densely and shortly adpressed hairs.

The morphological characters support placement of the species in sect. *Rubriflorae*: flowers violet, pedicels articulated, standard with a long claw, wing petals at base sagittate or hastate and at base with a hook-like auricle; and stamens shortly joined at base, distally free. Moreover, the calyx has prominent lobes and the spathulate standard petal curves strongly upwards (as in sect. *Rubriflorae*). In addition, *S. phulangkaensis* has stipules that are early caducous; by contrast, Tsoong & Ma (1981) and Ma (1990) reported that sect. *Rubriflorae* lacks stipules.

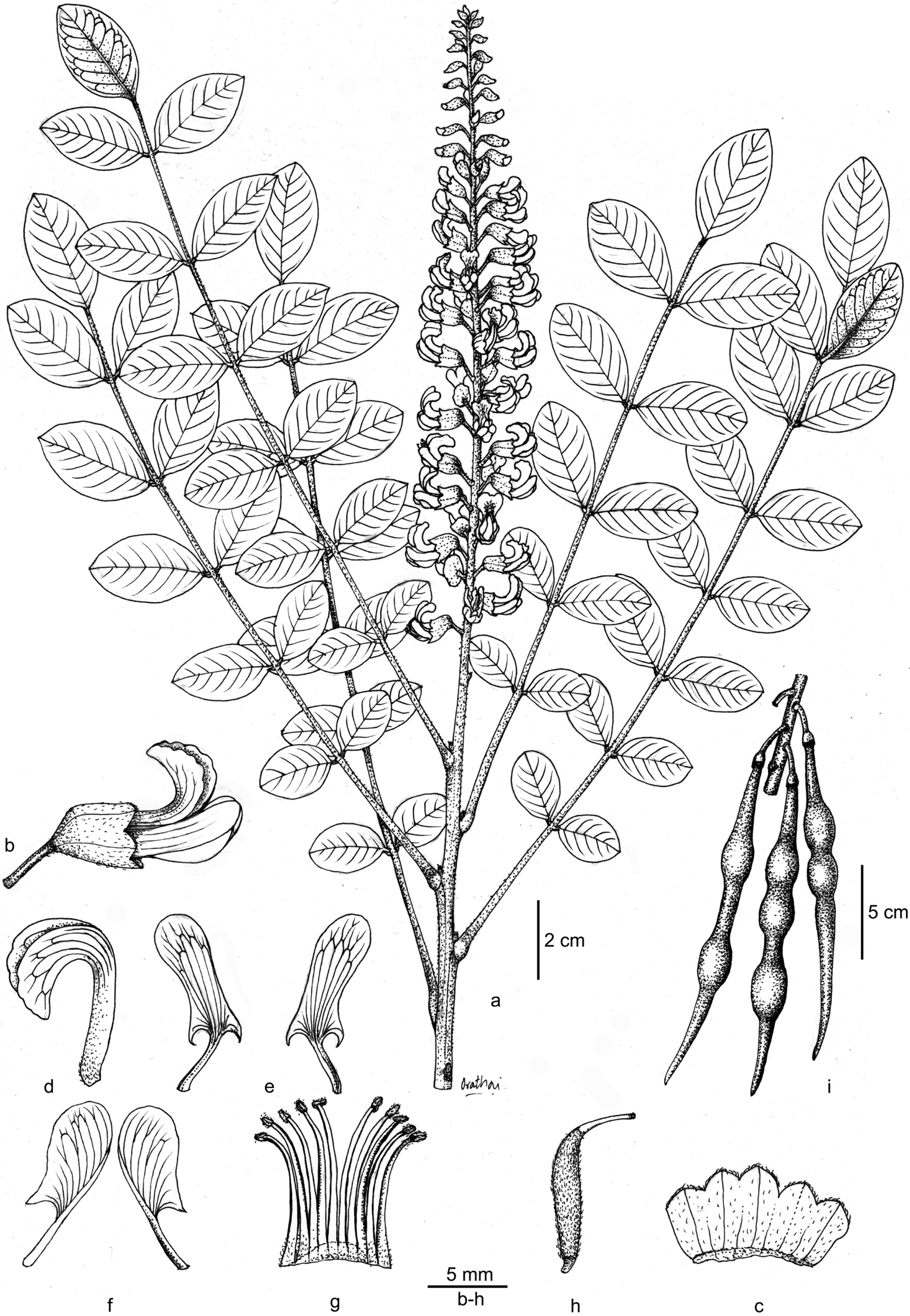

Fig. 3 *Sophora phulangkaensis* Mattapha, K.Khamm. & Suddee. a. Leaves at the flowering stage and inflorescence; b. flower; c. opened calyx showing outer surface; d. standard (side view); e. wing petals; f. keel petals; g. stamens; h. ovary; i. fruits (a–h: *K. Khammongkol 211*, BKF; i: *S. Mattapha s.n.*, BKF, KKU). — Drawing by Orathai Kerdkaew.

Fig. 4 *Sophora phulangkaensis* Mattapha, K.Khamm. & Suddee. a. Leaves and inflorescence; b. part of inflorescence; c. opened calyx; d. standard petals; e. wing petals; f. keel petals; g. stamens; h. ovary; i. infructescence and mature leaves. — Photographs by a. K. Khammongkol, b–h. W. Kiewbang, i. S. Mattapha.

LECTOTYPIFICATIONS

Sophora exigua Craib

Sophora exigua Craib (1927) 71; (1928) 496; Niyomdham (1980) 17, f. 7; Thuân, Phon & Niyomdham (1987) 16; Niyomdham & Mattapha (2018) 237. — Lectotype (designated here): *Kerr 8427A* (lecto K [K000759743]!; isolecto BK [SN258034]!, SN212293]!, BM [BM000958785]!, P [P01817806]!, Thailand, Prov. Nong Bua Lamphu, c. 200 m, 5 Mar. 1924, fl.

Sophora violacea Thwaites var. *pilosa* Gagnep. (1920) 505. — *Sophora violacea* subsp. *pilosa* (Gagnep.) Yakovlev (1976) 173. — Lectotype (designated here): *Pierre 563* (lecto P [P02931613]!; isolecto P [P02931611, P02931615, P02931616]!); Cambodia, Prov. Kampong Speu, Samraong Tong distr., Apr. 1870.

Distribution — Cambodia, Thailand.

Habitat & Ecology — In open deciduous forest, mostly growing in the sandy soil areas. Altitude: up to 1 300 m. Flowering and fruiting: March to April.

Notes — 1. The *A.F.G. Kerr 8427A* collection consists of five sheets. The sheet K000759743 is the most suitable to serve as a lectotype since it contains more leaflets and an inflorescence with dissected flowers, as opposed to the remaining sheets which have fewer leaflets and flowers.

2. Two collections of *A.F.G. Kerr 8427* at BK [SN212294] and K [K000759742], lacking a precise locality other than Nakhon Phanom Province, were formerly identified as *S. exigua*, but morphological examination showed that they conform with *S. phulangkaensis*, despite lacking a fruit.

3. Four syntypes of *S. violacea* var. *pilosa* at P, of which the sheet P02931613 bears numerous leaflets and flowers, designated here as a lectotype of the variety of the species.

Sophora tonkinensis Gagnep.

Sophora tonkinensis Gagnep. (1914) 18; (1916) 502; Thuân, Phon & Niyomdham (1987) 18. — *Cephalostigmaton tonkinensis* (Gagnep.) Yakovlev (1967) 47. — Lectotype (designated here): *B. Balansa 1297* (lecto P [P01817818]!; isolecto: P [P01817819]!, P01817820]!), Vietnam, Tonkin, 3 July 1885. Other syntypes: *H.F. Bon 755* (P [P02755343!, P02755344!]), Vietnam, Hao Nho, in monte Trui, 10 Sept. 1881; *6040* (P [P02755341!, P02755345!]), Vietnam, Tonkin, without collection date; *J. Cavalerie* 3684 (P [P02755339!, P02755340!]), China, Kouy-tchéou, Tin-fan, June 1909.

Sophora subprostrata Chun & T.C.Chen in Chun & How (1958) 30. — Syntypes: *S.P. Ko 55680* (fr.) (herbarium not known), China, Kwangsi, Tsinghsi Hsien, Piaolin Hsiang, Luangshan, 1 Sept. 1935; *C. Wang 40917* (fl.) (herbarium not known), China Kwangsi, Nantan Hsien, Lihu Hsiang, 26 June 1937.

Note — In the protologue of *S. tonkinensis*, three syntypes of *B. Balansa 1297* at P were traced. The first sheet [P01817818] has numerous leaflets, two inflorescences with flowers and dissected flowers, but no fruits. The latter two sheets [P01817819, P01817820] bear leaflets and inflorescences with young fruits. Therefore, we designate the first sheet as the lectotype. Since we are unable to trace the types of *S. subprostrata,* we refrain from a lectotypification.

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REFERENCES

Bojian B, Vincent MA. 2010. Sophora Linnaeus. In: Wu Z, Raven PH, Hong D (eds), Flora of China 10: 85–93, Fabaceae. Beijing, Science Press; St. Louis, Missouri Botanical Garden Press.

Cardoso D, De Queiroz LP, Pennington RT, et al. 2012. Revisiting the phylogeny of papilionoid legumes: New insights from comprehensively sampled early-branching lineages. American Journal of Botany 99(12): 1991–2013. https://doi.org/10.3732/ajb.1200380.

Cardoso D, Pennington RT, De Queiroz LP, et al. 2013. Reconstructing the deep-branching relationships of the papilionoid legumes. South African Journal of Botany 89: 58–75. https://doi.org/10.1016/j.sajb.2013.05.001.

Cardoso D, São-Mateus WMB, Da Cruz DT, et al. 2015. Filling in the gaps of the papilionoid legume phylogeny: the enigmatic Amazonian genus Petaladenium is a new branch of the early-diverging Amburaneae clade. Molecular Phylogenetics and Evolution 84: 112–124. https://doi.org/10.1016/j.ympev.2014.12.015.

Chatan W. 2013. A new species of Bauhinia L. (Caesalpinioideae, Leguminosae) from Nakhon Phanom Province, Thailand. PhytoKeys 26: 1–5. https://doi.org/10.3897/phytokeys.26.6008.

Chun W-Y, How F.-C. 1958. Contributions to the Flora of South China (I). Acta Phytotaxonomica Sinica 7(1): 1–90.

Craib WG. 1927. Contributions to the Flora of Siam. Additamentum XX. Bulletin of Miscellaneous Information, Royal Gardens, Kew. Additional Series. Kew 1927(2): 71.

Craib WG. 1928. Florae Siamensis Enumeratio 1(3). The Siam Society, Bangkok.

Crisp MD, Gilmore S, Van Wyk BE. 2000. Molecular phylogeny of the genistoid tribes of papilionoid legumes. In: Herendeen PS, Bruneae A, Pollard PS (eds), Advances in Legume Systematics 9: 249–276. Royal Botanic Gardens, Kew.

Darriba D, Taboada GL, Doallo R, et al. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9(8): 772.

Duan L, Harris AJ, Ye W, et al. 2019. Untangling the taxonomy of the Cladrastis clade (Leguminosae: Papilionoideae) by integrating phylogenetics and ecological evidence. Taxon 68(6): 1189–1203. https://doi.org/10.1002/tax.12155.

Gagnepain F. 1914. Notulae Systematicae. Herbier du Museum de Paris. Phanerogramie. Paris 3: 18–19.

Gagnepain F. 1916. Léguminseuses-Papilionoïdées. In: Lecomte H (ed), Flore Générale de l'Indo-Chine 2: 361–504. Paris, Masson & Cie.

Gagnepan F. 1920. Léguminseuses-Papilionoïdées. In: Lecomte H (ed), Flore Générale de l'Indo-Chine 2: 505–680. Paris, Masson & Cie.

Guindon S, Gascuel O. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52: 696–704.

Hall T. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium 41: 95–98.

Hu JM, Lavin M, Wojciechowski MF, et al. 2000. Phylogenetic systematics of the tribe Millettieae (Leguminosae) based on chloroplast trnK/matK sequences and its implications for evolutionary patterns in Papilionoideae. American Journal of Botany 87(3): 418–430. https://doi.org/10.2307/2656638.

IUCN Standards and Petitions Committee. 2022. Guidelines for using the IUCN Red List Categories and Criteria. Version 15.1. Prepared by the Standards and Petitions Committee. Downloadable from https://www.iucnredlist.org/documents/RedListGuidelines.pdf [accessed 5 Aug. 2022].

Kajita T, Ohashi H, Tateishi Y, et al. 2001. rbcL and legume phylogeny, with particular reference to Phaseoleae, Millettieae, and allies. Systematic Botany 26(3): 515–536. https://doi.org/10.1043/0363-6445-26.3.515.

Liao M, Gao XF, Zhang JY, et al. 2021. Comparative chloroplast genomics of Sophora species: evolution and phylogenetic relationships in the early-diverging legume subfamily Papilionoideae (Fabaceae). Frontiers in Plant Science 12: 778933. https://doi.org/10.3389/fpls.2021.778933.

Liao M, Shepherd LD, Zhang JY, et al. 2023. Phylogeny, biogeography, and character evolution of the genus Sophora s.l. (Fabaceae, Papilionoideae). Molecular Phylogenetics and Evolution 181: 107713. https://doi.org/10.1016/j.ympev.2023.107713.

Linnaeus C. 1753. Species Plantarum, Stockholm.

Ma CY. 1990. Review of the classifical system on the genus Sophora. Bulletin of Botanical Research 10(4): 77–86.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE): 1–8.

Mitchell AD, Heenan PB. 2002. Sophora sect. Edwardsia (Fabaceae): further evidence from nrDNA sequence data of a recent and rapid radiation around the Southern Oceans. Botanical Journal of the Linnean Society 140(4): 435–441. https://doi.org/10.1046/j.1095-8339.2002.00101.x.

Niyomdham C. 1980. Preliminary revision of tribe Sophoreae (Leguminosae-Faboideae) in Thailand: Ormosia Jacks. and Sophora Linn. Thai Forest Bulletin (Botany) 13: 1–22. https://li01.tci-thaijo.org/index.php/ThaiForestBulletin/article/view/25110.

Niyomdham C, Mattapha S. 2018. Sophora. In: Balslev H, Chantaranothai P (eds), Flora of Thailand 4: 236–240. The Forest Herbarium, Bangkok.
Pena RC, Cassels BK. 1996. Phylogenetic relationships among Chilean Sophora species. Biochemical Systematics and Ecology 24(7/8): 725–733.
Pennington RT, Lavin M, Ireland H, et al. 2001. Phylogenetic relationships of basal papilionoid legumes based upon sequences of the chloroplast trnL intron. Systematic Botany 26: 537–556.
Pennington RT, Stirton CH, Schrire BD. 2005. Tribe Sophoreae. In: Lewis GP, Schrire BD, Mackinder BA (eds), Legumes of the World: 227–249. Royal Botanic Gardens, Kew.
POWO 2022. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the internet http://www.plantsoftheworldonline.org/ [accessed 12 June 2022].
Rambaut A, Drummond AJ. 2012. FigTree version 1.4.0. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. http://tree.bio.ed.ac.uk/software/figtree/.
Rambaut A, Drummond AJ, Xie D, et al. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67: 901–904. https://doi.org/10.1093/sysbio/syy032.
Ronquist F, Teslenko M, Van der Mark P, et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029.
Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033.
Suddee S, Paton A, Parnell J, et al. 2019. Five new species of Platostoma (Lamiaceae) from North-Eastern Thailand. Thai Forest Bulletin (Botany) 47(2): 226–240. https://doi.org/10.20531/tfb.2019.47.2.13.
Suwanphakdee C, Khammonkol K, Middleton D, et al. 2021. Thunbergia amphaii (Acanthaceae) a new species from Thailand. Thai Forest Bulletin (Botany) 49(1): 57–62. https://doi.org/10.20531/tfb.2021.49.1.06.
Taberlet P, Gielly L, Pautou G, et al. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Molecular Biology 17(5): 1105–1109. https://doi.org/10.1007/BF00037152.
Tamura K, Stecher G, Kumar S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis version 11. Molecular Biology and Evolution 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120.
Thiers B. Continuously updated. Index Herbariorum. A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available from: https://sweetgum.nybg.org/science/ih [accessed 20 August 2022].
Thuân NV, Phon PD, Niyomdham C. 1987. Léguminseuses-Papilionoïdées. In: Morat PH (ed), Flore du Cambodge, du Laos et du Viêt-nam 23: 14–20. Muséum National d'Histoire Naturelle, Paris.
Traiperm P, Suddee S. 2020. A new species of Argyreia (Convolvulaceae) from Thailand. PhytoKeys 149: 109–115. https://doi.org/10.3897/phytokeys.149.50379.
Tsoong PC, Ma CY. 1981. A study on the genus Sophora Linn. (cont.). Acta Phytotaxonomica Sinica 19(1): 143–167.
Wojciechowski MF, Lavin M, Sanderson MJ. 2004. A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. American Journal of Botany 91(11): 1846–1862. https://doi.org/10.3732/ajb.91.11.1846.
Wojciechowski MF, Sanderson MJ, Baldwin BG, et al. 1993. Monophyly of aneuploid Astragalus (Fabaceae): evidence from nuclear ribosomal DNA internal transcribed spacer sequences. American Journal of Botany 80(6): 711–722. https://doi.org/10.1002/j.1537-2197.1993.tb15241.x.
Yakovlev GP. 1967. Notes on the systematics and geography of the genus Sophora and related genera. Proceedings of the Leningrad Chem.-Pharm. Institute 21: 42–62. [In Russian.]
Yakovlev GP. 1976. Conspectus tribus Sophoreae (Spreng.) DC. s.l. familiae Fabaceae in floris Vietnamensi et Cambodzhiensi. Novosti Sistematiki Vysshikh Rastenii 13: 168–174.

Appendix List of species, voucher information and GenBank accession numbers of taxa and genera used in this study.

SEQUENCE: ***Species***, voucher information of ITS (specimen and herbarium), NCBI accession number, voucher information of *matK* (specimen and herbarium), NCBI accession number, respectively. – = absent; newly sequenced species are identified with an *. In case there is no specimen voucher indication, the species is replaced by the Taxonomy ID as indicated in the Genbank (as *taxon:*).

Bolusanthus speciosus (Bolus) Harms, *P. Poilecot 7721* (K), KX595230.1, Lavin 6227 (herbarium not indicated), AF142685.1; ***Bowringia callicarpa*** Champ. ex Benth., *H.F.Chen 2012006* (IBSC), MN496316.1 *SCBGP227_2* (herbarium not indicated), KP093643.1; ***Camoensia scandens*** (Welw.) J.B.Gillett, *Compere 459* (herbarium not indicated), KT718821.1, *D.Cardoso 2356* (HUEFS), JX295919.1; ***Dalbergia cultrata*** T.S.Ralph, *HJL2601* (herbarium not indicated), MW044352.1, *taxon:862910*, MT644128.1; ***Dermatophyllum arizonicum*** (S.Watson) Vincent, *M.Johnson et al. 406* (K), MN496350.1, *M.Johnson et al. 406* (K), MN497661.1; ***D. secundiflorum*** (Ortega) Gandhi & Reveal, *J.L.Reveal 2619* (US), MN496358.1, *P.Tenorio 19995* (MO), NC_047349.1; ***Dicraeopetalum mahafaliense*** (M.Peltier) Yakovlev, *J.-N. Lablat et al. 3627* (K), KX595233.1, *J.-N. Lablat et al. 3627* (K), KX595203.1; ***Euchresta horsfieldii*** (Lesch.) Benn., *KTCN1* (herbarium not indicated), MH842697.1, –; ***E. japonica*** Hook.f. ex Regel, *SCB2* (herbarium not indicated), MH842694.1, *NA-seedling* (herbarium not indicated), NC_047352.1; ***E. tubulosa*** Dunn, *SCHU3* (herbarium not indicated), MH842696.1, –, –; ***Liparia rafnioides*** A.L.Schutte, *M. Johns s.n.* (JRAU), AM261489.1, *JWB033* (herbarium not indicated), JX517668.1; ***Maackia hupehensis*** Takeda, *taxon:449085*, EF457721.1, *HZ407* (herbarium not indicated), MH659426.1; ***M. tenuifolia*** (Hemsl.) Hand.-Mazz., *CB08827* (CSH), MN496338.1, CB08827 (CSH), MN497647.1; ***Ormosia amazonica*** Ducke, *T.Plowman et al.* 6594 (US), MN496339.1, *T.Plowman et al. 6594* (US), MN497649.1; ***O. henryi*** Prain, *1763* (herbarium not indicated), MH844591.1, *GL219* (herbarium indicated), MN583072.1; ***O. semicastrata*** Hance, *H.F.Chen 2012001* (IBSC), MN496343.1, W. Y. Chun 6478 (A), KY079071.1; ***Piptanthus nepalensis*** (Hook.) Sweet, –, *Hodgson 10787* (ASU), AY386924.1; ***P. nepalensis*** (Hook.) Sweet, *taxon:70606*, AF215922.1, *Hodgson 10787* (ASU), AY386924.1; ***Salweenia wardii*** Baker f., *SunH-07zx-1772* (US), MN496347.1, SunH-07zx-1772 (US), MN497658.1; ***Sophora alopecuroides*** L., *TianXH188* (herbarium not indicated), MH808474.1, *Duan 2016010* (IBSC); MN497659.1; ***S. bifolia*** Pall. (*Ammodendron bifolium* (Pallas) Yakovlev, *Duan 2016008* (TURP), MN496315.1, *Duan 2016008* (TURP), MN497625.1; ***S. chrysophylla*** (Salisb.) Seem., *N.Kona & T.Flynn 3165* (US), MN496351.1, *N.Kona & T.Flynn 3165* (US), MN497662.1; ***S. davidi*** (Franch.) Skeels, *taxon:49839*, JX495413.1, *T.T. Tian 21* (herbarium not indicated), MN722144.1; ***S. davidi*** (Franch.) Skeels, *BOP010272* (herbarium not indicated), MT227706.1, –, –; ***S. exigua*** Craib, *S.Mattapha s.n.* (BKF), OP537916*, *S.Mattapha s.n.* (BKF), OP787197*; ***S. exigua*** Craib, *P.Triboun s.n.* (BKF), OP537919*, *P.Triboun s.n.* (BKF), OP795677*; ***S. flavescens*** Aiton, *taxon:49840,* AF123452.1, *Duan 2012204* (WUK), MN497666.1; ***S. flavescens*** Aiton, –, –, *taxon:49840*, MH748034.1; ***S. fulvida*** (Allan) Heenan & de Lange, *taxon:171563*, AY056072.1, *CHR599386* (herbarium not indicated), MW191852.1; ***S. gibbosa*** (DC.) Yakovlev (*Ammothamnus gibbosus* DC.), *H.Al-Hassan 322* (K), KX595229.1, *H.Al-Hassan 322* (K), KX595217.1; ***S. godleyi*** Heenan & de Lange, *taxon:171564*, AY056073.1, *CHR517172* (herbarium not indicated), MW191853.1; ***S. howinsula*** (W.R.B.Oliv.) P.S.Green, *taxon:171242*, AY046514.1, –, –; ***S. huamotensis*** Mattapha, Suddee & Rueangr., *Thananthaisong et al 642* (BKF), OP537920*, *Thananthaisong et al 642* (BKF), OP745446*; ***S. inhambanensis*** Klotzsch, *JRAU:van Wyk 3574* (herbarium not indicated), FN813570.1, OM4026 (herbarium not indicated), KM896910.1; ***S. jaubertii*** Spach, *taxon:49841*, Z72342.1, –, –; ***S. longicarinata*** G.Simpson & J.S. Thomson (*Sophora microphylla* var. *longicarinata* (G.Simpson) Allan), *taxon:171565*, AY056074.1, –, –; ***S. macrocarpa*** Sm., *Ruiz 344* (CONC), AY616486.1, *taxon: 76397*, NC_057683.1; ***S. microphylla*** Aiton (*Sophora microphylla* subsp. *Macnabiana* (Graham) Yakovlev), *MF Gardner & SG Knees 4703* (K), AJ409923.1, *CHR617032* (herbarium not indicated), MW191854.1; ***S. microphylla*** Aiton, *taxon:70607*, AY056075.1, *L.R.Landrum 7622* (ASU), JQ619976.1; ***S. molloyi*** Heenan & de Lange, *taxon:171566*, AY056076.1, *CHR524704* (herbarium not indicated), MW191855.1; ***S. moorcroftiana*** (Benth.) Benth. ex Baker, *taxon:1323965*, MT893341.1, *2019Smcp* (herbarium not indicated), NC_056151.1; ***S. phulangaensis*** Mattapha, Khamm. & Suddee, *Khammongkol 212* (BKF), OP537922*, *Khammongkol 212* (BKF), OP787198*; ***S. prostrata*** Buchanan, *RBG, Kew, 1988-2824* (K), AJ409922.1, *CHR617035* (herbarium not indicated), MW191856.1; ***S. prostrata*** Buchanan, *taxon:76398*, AY056077.1, –, –; ***S. raivavaeensis*** H.St. John, *taxon:171568*, AY056080.1, –, –; ***S. tetraptera*** J.S.Muell., *RBG, Kew, 1977-1212* (K), AJ310734.1, –, –; ***S. tetraptera*** J.S.Muell., *taxon:171567*, AY056078.1, –, –; ***S. tomentosa*** L., –, –, *TuTY2668xs* (herbarium not indicated), MH767997.1; ***S. tomentosa*** L., *TuTY2668xs* (herbarium not indicated), MH768292.1, –, –; ***S. tomentosa*** L. var. ***occidentalis*** (L.) Isely (*Sophora occidentalis* L.), *J.Deaw 289* (US), MN496356.1, *J.Deaw 289* (US), MN497667.1; ***S. tonkinensis*** Gagnep., *YC0104MT0* (herbarium not indicated), KC902516.1, *taxon:714503*, MH779853.1; ***S. toromiro*** (Phil.) Skottsb., *RBG, Kew, 1994-2331* (K), AJ409921.1, *Maunder M. 6993* (herbarium not indicated), GQ248201.1; ***S. velutina*** Lindl., *JRAU:van Wyk 4229* (herbarium not indicated), FN813569.1, *taxon:149669*, MW940398.1; ***S. wightii*** Baker (*Sophora prazeri* Prain), *Guizhoudui 333* (WUK), MN496357.1, *taxon:1323966*, MW940396.1; ***Thermopsis lanceolata*** R.Br., *2011458* (herbarium not indicated), MZ198556.1, –, –; ***Xiphotheca fruticosa*** (L.) A.L.Schutte & B.-E. van Wyk, *Schutte 673-675* (RAU), AJ310726.1, –, –.