



The genus *Phaeanthus* (Annonaceae, Miliuseae) in Thailand: *P. piyae* sp. nov. and resurrection of *P. lucidus*, with molecular phylogenetic analyses

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ABSTRACT: *Phaeanthus piyae*, a new species from southern Thailand, is described and illustrated. It is morphologically most similar to *P. intermedius*, which occurs in Peninsular Malaysia, Singapore, Riau Islands, and Sumatra. The new species can be distinguished from *P. intermedius* by the longer peduncles and pedicels; triangular (vs. filiform-narrowly triangular) sepals; and stigmas that are larger and \pm elongated club-shaped (vs. \pm ellipsoid). The conservation status of *P. piyae* is provisionally assessed. In addition, molecular phylogenetic analyses using up to seven plastid DNA regions (*matK*, *ndhF*, *rbcl* and *ycf1* exons; *trnL* intron; *psbA-trnH* and *trnL-trnF* intergenic spacers) and including, among others, five *Phaeanthus* accessions are carried out. *Phaeanthus piyae* is sister to a clade composed of the remaining accessions of *Phaeanthus*. Furthermore, southern Thailand also harbors a second species of *Phaeanthus*, which appears to be *P. lucidus*, a heterotypic synonym of *P. splendens*. *Phaeanthus lucidus* is herein reinstated; it differs from the sister species *P. splendens* by possessing a lower number of stamens and carpels per flower, as well as dissimilar placentation. A key to the two species of *Phaeanthus* in Thailand is given.

KEY WORDS: Miliuseae, molecular phylogeny, new species, *Phaeanthus*, resurrection, taxonomy, Thailand.

INTRODUCTION

Phaeanthus Hook.f. & Thomson is a small genus of Annonaceae, a large pantropical family of flowering plants comprising 108 genera and approximately 2430 species (Chatrou *et al.*, 2018; Damthongdee *et al.*, 2021; Photikwan *et al.*, 2021). The genus belongs to the tribe Miliuseae of the subfamily Malmeoideae, one of the five recognized subfamilies of Annonaceae (Chatrou *et al.*, 2012; Guo *et al.*, 2017; Chaowasku, 2020), and is composed of eight species, distributed in mainland Southeast Asia (except Cambodia, Laos, and Myanmar), Southeast Asian islands, and New Guinea (Mols and Keßler, 2000). Diagnostic features of *Phaeanthus* include (1) a percurrent tertiary venation, (2) terminal (developing to internodal) inflorescences, (3) sepal-like outer petals, both sepals and outer petals are much smaller than the inner petals, (4) usually a single ovule per ovary, (5) 4-part-lamellate endosperm ruminations, and (6) an atectate exine of pollen (Mols and Keßler, 2000; Mols *et al.*, 2004; Chaowasku *et al.*, 2014). It is noteworthy that the sepaloïd outer-petal character has been inferred to have evolved multiple times in Miliuseae (Chaowasku *et al.*, 2014) and, besides *Phaeanthus*, this trait also occurs in every species of *Miliusa* Lesch. ex A.DC. (e.g. Mols and Keßler, 2003; Chaowasku and Keßler, 2006; Chaowasku *et al.*, 2013) and *Wangia* X.Guo &

R.M.K.Saunders (Guo *et al.*, 2014; Xue *et al.*, 2016). In Piptostigmateae, another tribe belonging to Malmeoideae, every species of *Brieya* De Wild. and *Piptostigma* Oliv. possesses sepal-like outer petals as well (Ghogue *et al.*, 2017). Although *Phaeanthus* is a member of the phaeanthoid clade (consisting of seven genera, the other six genera are *Monoon* Miq., *Neo-uvaria* Airy Shaw, *Sageraea* Dalzell, *Stelechocarpus* Hook.f. & Thomson, *Wangia*, and *Winitia* Chaowasku; e.g. Guo *et al.*, 2014; Xue *et al.*, 2016), the intergeneric relationships in this clade are still partially unresolved as evidenced by the unreliable position of *Phaeanthus* (e.g. Guo *et al.*, 2014; Xue *et al.*, 2016; Chaowasku *et al.*, 2020).

Recent expeditions in Narathiwat Province of southern Thailand yielded collections of *Phaeanthus* that belong to two different species; to a certain extent, one is similar to *P. intermedius* (P.Parm.) I.M.Turner & Veldkamp, while the other is comparable to *P. splendens* Miq. In order to determine the taxonomic status of these gatherings, in this study we perform molecular phylogenetic analyses in combination with detailed morphological investigations and comparisons.

MATERIALS AND METHODS

Phylogenetic analyses

The ingroup consisted of 54 accessions, covering



representatives in the tribes Dendrokingstonieae, Fenerivieae, Maasiae, Malmeeae, Miliuseae, and Monocarpiaceae of the subfamily Malmeoideae; these tribes have been found to constitute a strongly supported clade in previous publications (e.g. Guo *et al.*, 2017). Outgroups were two members of the tribe Piptostigmatheae, which has always been recovered outside a clade composed of the above-mentioned tribes (e.g. Guo *et al.*, 2017). In Miliuseae, representatives of all accepted genera were included, with five accessions of *Phaeanthus*, including one accession of *Phaeanthus* cf. *intermedius* and one accession of *Phaeanthus* cf. *splendens*, both from Narathiwat Province, southern Thailand. The Appendix S1 in supplementary materials indicates voucher information and GenBank accession numbers of all accessions included, with 12 new sequences produced in this study. Up to seven plastid DNA regions (*matK*, *ndhF*, *rbcl*, and *ycf1* exons; *trnL* intron; *psbA-trnH* and *trnL-trnF* intergenic spacers) were included. The methods for DNA extraction, amplification, and sequencing used in the present study, including primer information, followed Chaowasku *et al.* (2018a, 2018b, 2020). Sequences were edited using the Staden package (Staden *et al.*, 2000) and the data matrix was aligned by the Multiple Sequence Comparison by Log-Expectation (MUSCLE; Edgar, 2004) in MEGA7 (Kumar *et al.*, 2016). The aligned data matrix was subsequently manually checked and re-aligned where necessary based on the similarity criterion (Simmons, 2004). In some accessions, there was an inversion of 15-nucleotide stretch in the *psbA-trnH* intergenic spacer and this was complementarily reversed, following Pirie *et al.* (2006). In total, there were 7052 nucleotide plus 13 binary-coded indel characters. Indel coding followed the simple method of Simmons and Ochoterena (2000).

Maximum likelihood analysis was accomplished in IQ-TREE version 1.6.10 (Nguyen *et al.*, 2015) under partition models (Chernomor *et al.*, 2016) implemented with the “-spp” command, whereas Bayesian Markov chain Monte Carlo (MCMC; Yang and Rannala, 1997) phylogenetic analysis was performed in MrBayes version 3.2.6 (Ronquist *et al.*, 2012). Both methods were run via the CIPRES Science Gateway version 3.3 (Miller *et al.*, 2010). The aligned data matrix was divided into six partitions based on identity of DNA regions (the *trnL* intron and adjacent *trnL-trnF* intergenic spacer were united into a single partition). The most suitable model of sequence evolution for each DNA partition was chosen by the Akaike Information Criterion (AIC; Akaike, 1974) scores, using FindModel (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>; Posada and Crandall, 1998). The General Time Reversible (GTR; Tavaré, 1986) nucleotide substitution model with a gamma distribution for among-site rate variation (G) was selected for *matK*, *ndhF*, *rbcl*, and *ycf1* partitions, while the Hasegawa-Kishino-Yano (HKY; Hasegawa *et al.*, 1985) substitution model with G was chosen for the remaining partitions (*psbA-trnH* and *trnLF*

[= *trnL* intron + *trnL-trnF* intergenic spacer]). In the maximum likelihood analysis, the model “JC2+FQ+ASC” was selected by corrected AIC scores for the binary indel partition. Clade support was evaluated by a non-parametric bootstrap resampling (BS; Felsenstein, 1985) with 2000 replicates. A clade with BS \geq 85%, 70–84%, or 50–69% was considered strongly, moderately, or weakly supported, respectively. Incongruence among plastome partitions was evaluated by analyzing each partition individually to see if there was any significant conflict in topology (e.g. Wiens, 1998). In the Bayesian analysis, the setting “coding = variable” was applied for the binary indel partition (employed under a simple F81-like model without G). Four independent runs, each using four MCMC chains, were simultaneously carried out; each run was set for 10 million generations. The default prior settings were used except for the prior parameter of rate multiplier (“ratepr” [=variable]). The temperature parameter was set to 0.08. Trees and all parameter values were sampled every 1000th generation. Convergence was assessed by checking the standard deviation of split frequencies of the runs with values $<$ 0.01 interpreted as indicative of a good convergence and by checking for adequate effective sample sizes (ESS $>$ 200) using Tracer version 1.6 (Rambaut *et al.*, 2013). The first 25 % of all trees sampled were removed as burn-in and the 50 % majority-rule consensus tree was generated from the remaining trees. A clade with posterior probabilities (PP) \geq 0.95, 0.9–0.94, or 0.5–0.89 was considered strongly supported, weakly supported, or unsupported, respectively.

Morphology

Morphological data of *Phaeanthus* spp. for comparisons were from Oliver (1887), Sinclair (1955), and Mols and Keßler (2000). Specimens of *P. intermedius* (Chew & Noor CWL 274 [L]; David 042 [P]; King's collector 3731 [L], 5544 [P]; KMK 79098 [L]; Kochummen FRI 023006 [L]; Maxwell 82-245 [L]; Sinclair s.n. [L: L 0045943]; Stevens *et al.* 35 [L]; T. & P. 824 [KL3424; L]; Whitmore FRI 12307 [L]; Wood 76119 [L]) covering its morphological variation and of *P. splendens* (all L: Hitam SAN 23740; Keßler *et al.* B 1564; Kodoh & Kuntil SAN 81498; Kostermans 4146, 9243; Laman *et al.* TL309; Leopold & Saikeh SAN 82651; Madani SAN 76023; Termiji SAN 75023; van Balgooy & Keßler 5880) at Leiden (L) and Paris (P) herbaria, as well as type specimens at Kew (K: K000574614, K000574615 [*P. lucidus* Oliv., one of the two heterotypic synonyms of *P. splendens*]), L (L 0045058, L 0045059 [*P. splendens*]), and P (P00372671 [*P. crassipetalus* Becc., another heterotypic synonym of *P. splendens*]), P01960440 [*Magnolia intermedia* P.Parm., the basionym of *P. intermedius*], and P00160892 [*P. lucidus*]) herbaria were also consulted. The indumentum terminology of Hewson (1988) was used. The word “circa (ca.)” was added when there was a single measurement/observation.

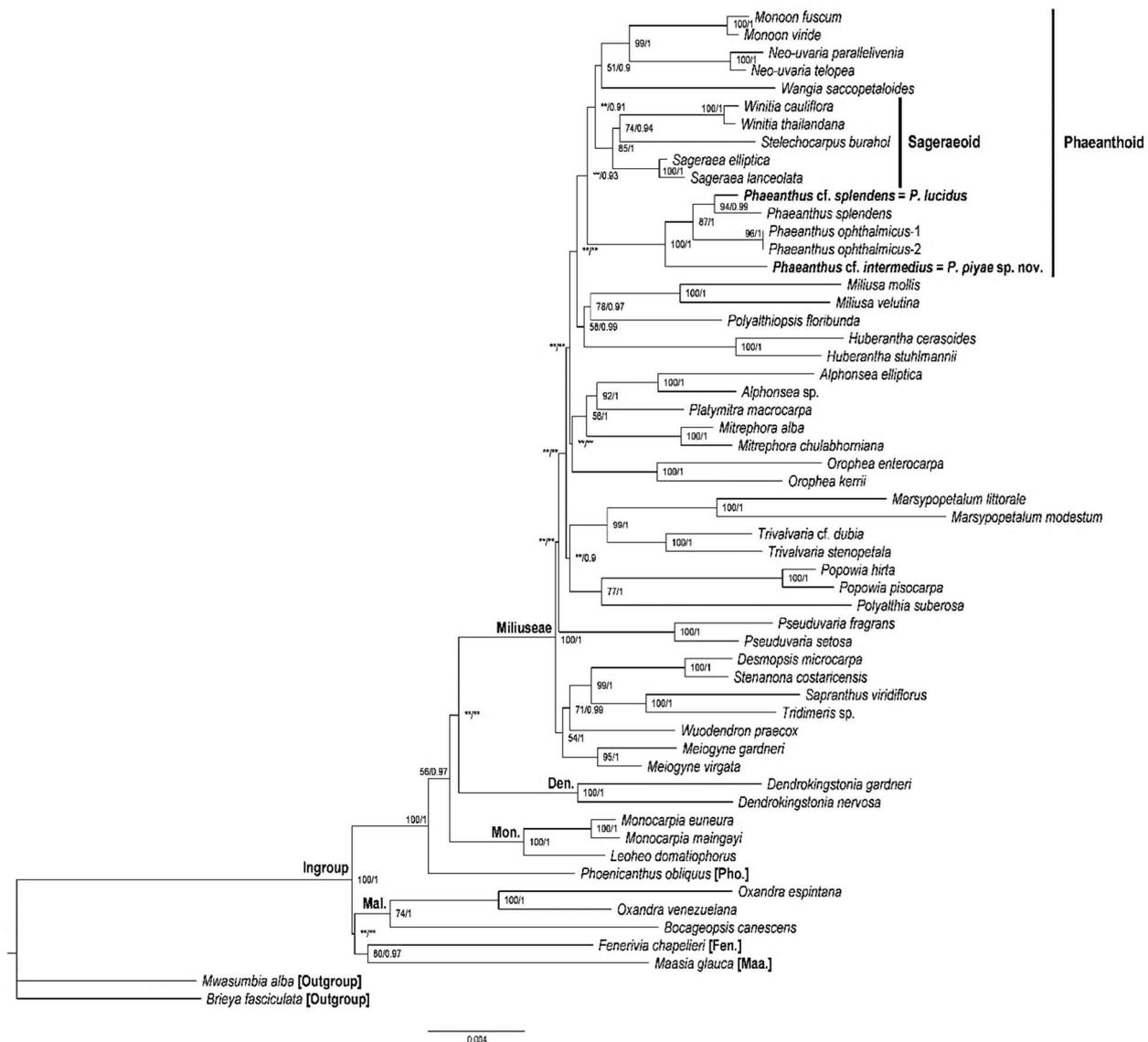


Fig. 1. Phylogram derived from maximum likelihood analysis, with support values indicated: BS (maximum likelihood bootstrap values) / PP (posterior probabilities). ** = BS < 50% and/or PP < 0.9. Scale bar unit: substitutions per site. Den. = Dendrokingstonieae, Fen. = Fenerivieae, Maa. = Maasieae, Mal. = Malmeeae, Mon. = Monocarpieae, Pho. = Phoenicantheae.

RESULTS

There was no strong topological conflict (BS \geq 85%) in the analyses of each plastid DNA partition. As depicted in Fig. 1, the ingroup and tribe Miliuseae received maximum support. In Miliuseae, there was an unsupported to weakly supported phaeanthoid clade (BS < 50%, PP 0.93) comprising *Phaeanthus*, *Sageraea*, *Stelechocarpus*, *Winitia*, *Wangia*, *Neo-uvaria*, and *Monoon*. Accessions of each genus, except one accession of *Stelechocarpus* and of *Wangia*, were recovered in each monophyletic group with maximum support. *Phaeanthus* was the sister group of an unsupported to weakly supported clade (BS < 50%, PP 0.91) comprising the remaining genera in the phaeanthoid clade. In this

unsupported to weakly supported clade, there was a strongly supported sageraeoid clade (BS 85%, PP 1) composed of three genera: *Sageraea*, *Stelechocarpus*, and *Winitia*. The sageraeoid clade was the sister group of a weakly supported clade (BS 51%, PP 0.9) containing *Monoon*, *Neo-uvaria*, and *Wangia*. In *Phaeanthus*, *Phaeanthus* cf. *intermedius* was sister to a strongly supported clade (BS 87%, PP 1) comprising the remaining accessions of *Phaeanthus*. In this strongly supported clade, there were (1) a strongly supported clade (BS 94%, PP 0.99) comprising *Phaeanthus* cf. *splendens* and *P. splendens*, and (2) a strongly supported clade (BS 96%, PP 1) consisting of two accessions of *P. ophthalmicus* (Roxb. ex G. Don) J. Sinclair.

**Table 1.** Morphological differences between *Phaeanthus piyae* sp. nov. [= *Phaeanthus* cf. *intermedius*] and *Phaeanthus intermedius*.

Features	<i>Phaeanthus piyae</i>	<i>Phaeanthus intermedius</i>
Peduncle length (mm)	15–30(–38) [Fig. 3]	2–8(–13) [Fig. S1]
Pedicle length (mm)	52–71 [Fig. 3]	22–45
Sepal shape	triangular [Fig. 2E, 2F]	filiform-narrowly triangular [Fig. S1]
Stigma appearance	± elongated club-shaped, as long as ovaries [Fig. 2G]	± ellipsoid, much shorter than ovaries [Fig. S1]

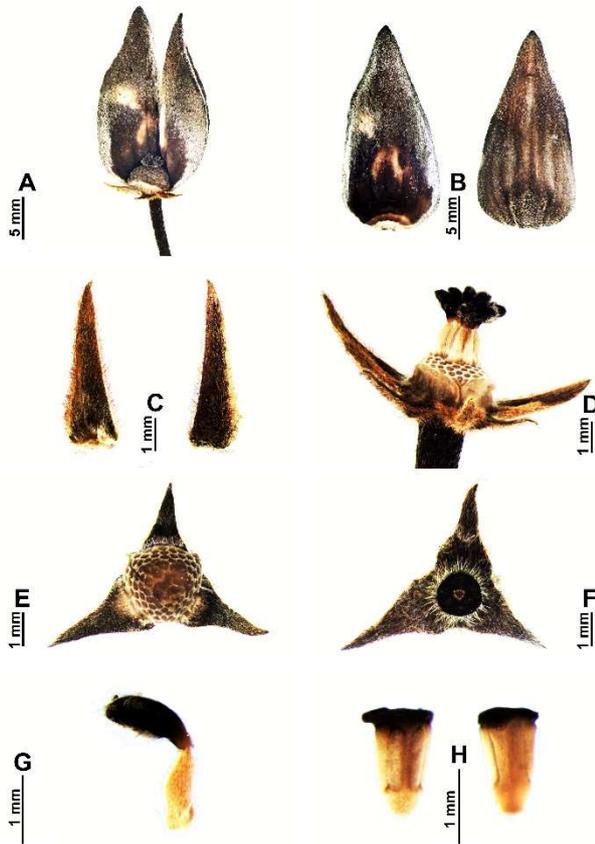


Fig. 2. Flower and floral organs of *Phaeanthus piyae* sp. nov. [= *Phaeanthus* cf. *intermedius*]. **A:** Flower with one inner petal removed. **B:** Inner petal, adaxial (left) and abaxial (right) sides. **C:** Outer petal, adaxial (left) and abaxial (right) sides. **D:** Flower with inner petals and stamens removed. **E:** Flower with petals, stamens, and carpels removed, top view, showing torus and adaxial side of sepals. **F:** Same as (E), but in bottom view, showing abaxial side of sepals. **G:** Carpel. **H:** Stamen, abaxial (left) and adaxial (right) sides. All from Aongyong & Samae 28 (CMUB).

TAXONOMIC TREATMENT

A new species of *Phaeanthus*

Phaeanthus piyae Wiya, Aongyong & Chaowasku, *sp. nov.* **Figs. 2, 3, 4A–C**

Type: THAILAND, Narathiwat Province, Chanee District, elev. of ca. 80 m, May 2021, Aongyong & Baka 39 (holotype CMUB; isotypes BKF, QBG), fl.

Diagnosis: *Phaeanthus piyae* is morphologically most similar to *P. intermedius*. The new species differs by having longer peduncles and pedicels; triangular (vs.

filiform-narrowly triangular) sepals; and stigmas that are larger and ± elongated club-shaped (vs. ± ellipsoid) (Table 1).

Description: *Treelets* to 3 m tall; *young twigs* villous with erect hairs. *Petiole* 5–12 mm long, slightly grooved on upper surface, tomentose-villous with erect hairs on both surfaces; *leaf blade* 12–27.5 × 4.2–9.3 cm, obovate to elliptic, puberulous with erect and appressed hairs on upper surface, villous with mostly erect hairs intermixed with shorter hairs on lower surface, base cuneate to obtuse, apex caudate-acuminate (acumen 1–2.2 cm long), rarely bluntly acute; *midrib* sunken (less so toward apex) on upper surface, villous with erect hairs (hairs shorter toward apex), raised (less so toward apex) on lower surface, villous with mostly erect hairs; *secondary veins* 9–15 per side, angle with midrib 43°–53° (at middle part of blade). *Inflorescences* 2- to 4-flowered, terminal developing to internodal; *peduncle* 15–30(–38) mm long, villous with mostly erect hairs; *rachis* up to 10 mm long when present, bracts present; *pedicel* 52–71 mm long, villous with mostly erect hairs, each bearing a single triangular to narrowly triangular bract, placed at ± midpoint between base and pedicel midpoint; *flowers* dark yellow, brown-purple at base, scented *in vivo*. *Sepals* free, 2.5–4 × 1.5–2.2 mm, triangular, outside and margin tomentose with erect and appressed hairs, inside tomentose with mostly appressed hairs. *Outer petals* 4.5–5.5 × 1.5–1.8 mm, narrowly triangular, indumentum similar to that of sepals; *inner petals* 23–32 × 13–20 mm, ovate, outside and margin tomentose with erect and appressed hairs, inside tomentose with mostly appressed hairs on apical half, almost glabrous on basal half, apex acute, each inner petal with ± 5 prominent veins (best observable on outer side). *Torus* ± depressed hemispherical, ± puberulous with erect hairs on area unoccupied by carpels. *Stamens* 76–88 per flower, 1.5–2 mm long, connective apex truncate, covering thecae. *Carpels* 11–18 per flower, 2.5–3 mm long; *stigmas* ± elongated club-shaped, ± cobwebbed; *ovaries* tomentose-villous with appressed hairs; *ovule* 1 per ovary, almost basal to basal. Each *fruit* consisting of up to 11 monocarps, borne on a pedicel to 60 mm long, seed-bearing portion of *monocarps* 14–15 × 7–8 mm, ellipsoid, bright red *in vivo*, puberulous with erect hairs, apex minutely apiculate, base contracted into a stipe 14–19 mm long, puberulous with erect and appressed hairs. *Seed* 1 per monocarp, ca. 13 × 6 mm, ellipsoid.

Etymology: This species is named in honor of Dr. Piya Chalermglin, whose well-known book of Annonaceae in Thailand (Chalermglin, 2001) has greatly



inspired the last author to chase his dream of becoming a systematic botanist.

Distribution: Southern Thailand (Narathiwat Province).

Habitat and phenology: Occurs in disturbed patches of evergreen forests among rubber and fruit tree plantations; at an elevation of 80–100 m. Flowering material collected in April–August, November; fruiting material collected in June, July, November.

Vernacular name: Lucang-Piyarat (เหลืองปิยะรัตน์; Thai).

Preliminary assessment on conservation status: *Phaeanthus piyae* occurs in disturbed patches of evergreen forests among rubber and fruit tree plantations in Chanai and Sukhirin, two adjacent districts of Narathiwat Province. Only less than 20 individuals have been found and the AOO (area of occupancy) is estimated to be less than 10 km². In combination with the ongoing heavy deforestations in this single unprotected location (Abdulromea Baka and Suhaibukree Samae, pers. comm.), we provisionally assess the conservation status as “critically endangered: CR B2ab(iii)” based on IUCN (2012).

Additional specimens examined (paratypes): THAILAND. Narathiwat Province, Sukhirin District, elev. of ca. 100 m, June 2020, *Aongyong & Samae 26* (CMUB); *ibid.*, July 2020, *Aongyong & Samae 28* (CMUB); *ibid.*, August 2020, *Aongyong & Samae 29* (CMUB); *ibid.*, November 2020, *Aongyong & Samae 30* (CMUB); *ibid.*, April 2021, *Aongyong & Samae 31* (CMUB).



Fig. 3. Holotype of *Phaeanthus piyae* sp. nov. at CMUB [*Aongyong & Baka 39*].

Resurrection of *Phaeanthus lucidus* Oliv.

Phaeanthus lucidus Oliv., Hooker's Icon. Pl. 16: t. 1561. 1887. - *Milusa lucida* (Oliv.) Finet & Gagnep., Bull. Soc. Bot. France 53 (Mém. 4): 96. 1906. Type: Peninsular Malaysia, Penang, Waterfall, May 1866, *Curtis 839* (lectotype K [K000574614], designated by Mols and Keßler, Blumea 45: 223. 2000; isolectotypes K, P, SING).

Fig. 4D–4F

Description: Trees to 8 m tall; young twigs tomentose with mostly appressed hairs. *Petiole* 4–8 mm long, slightly grooved on upper surface, tomentose with mostly appressed hairs on upper surface, puberulous-pilose with appressed hairs on lower surface; *leaf blade* 11.3–16.5 × 3.1–6.2 cm, elliptic, sometimes elliptic-obovate, base cuneate, apex ± caudate-acuminate (acumen 1–1.5 cm long), sometimes acuminate, almost glabrous on upper surface, almost glabrous (but puberulous-tomentose with appressed hairs on secondary veins) on lower surface; *midrib* sunken (less so toward apex) on upper surface, puberulous-tomentose with erect hairs, raised (less so toward apex) on lower surface, puberulous-pilose with appressed hairs; *secondary veins* 10–13 per side, angle with midrib 40°–50° (at middle part of blade). *Inflorescences* 2- to 3-flowered, terminal developing to internodal; *peduncle* 1.5–3 mm long, tomentose with appressed hairs; *rachis* inconspicuous when present, bracts present; *pedicel* 38–52 mm long, puberulous with mostly appressed hairs, each bearing a single ovate-triangular bract, placed a bit below pedicel midpoint; *flowers* pale yellow, yellowish green at base, scented *in vivo*. *Sepals* free, 2–2.5 × 2.5–3 mm, broadly triangular, outside and margin tomentose with appressed hairs, inside almost glabrous. *Outer petals* 1.5–2 × 2–2.5 mm, broadly triangular, indumentum similar to that of sepals; *inner petals* 12–14 × 7.5–8.5 mm, ovate-triangular, outside puberulous-tomentose with appressed hairs, margin tomentose with erect and appressed hairs, inside glabrous except near margin short-tomentose with appressed and erect hairs, apex ± acute, each inner petal without prominent veins. *Torus* ± depressed hemispherical, ± puberulous with erect hairs on area unoccupied by carpels. *Stamens* 38–50 per flower, 1.2–1.7 mm long, connective apex ± truncate, not covering thecae. *Carpels* 15–20 per flower, 2.5–2.8 mm long; *stigmas* ovoid, ellipsoid, to ellipsoid-cylindrical, ± tomentose with erect and appressed hairs; *ovaries* tomentose-villous with appressed hairs; *ovule* 1 per ovary, almost basal to basal. Each *fruit* consisting of up to 4 monocarps, borne on a pedicel to 55 mm long, seed-bearing portion of *monocarps* 18–22 × 9–10 mm, ellipsoid-cylindrical, dark purple *in vivo*, puberulous with appressed hairs, apex minutely apiculate, base contracted into a stipe 15–20 mm long, puberulous with appressed hairs. *Seed* 1 per monocarp, ca. 18 × 8.5 mm, ellipsoid-cylindrical.

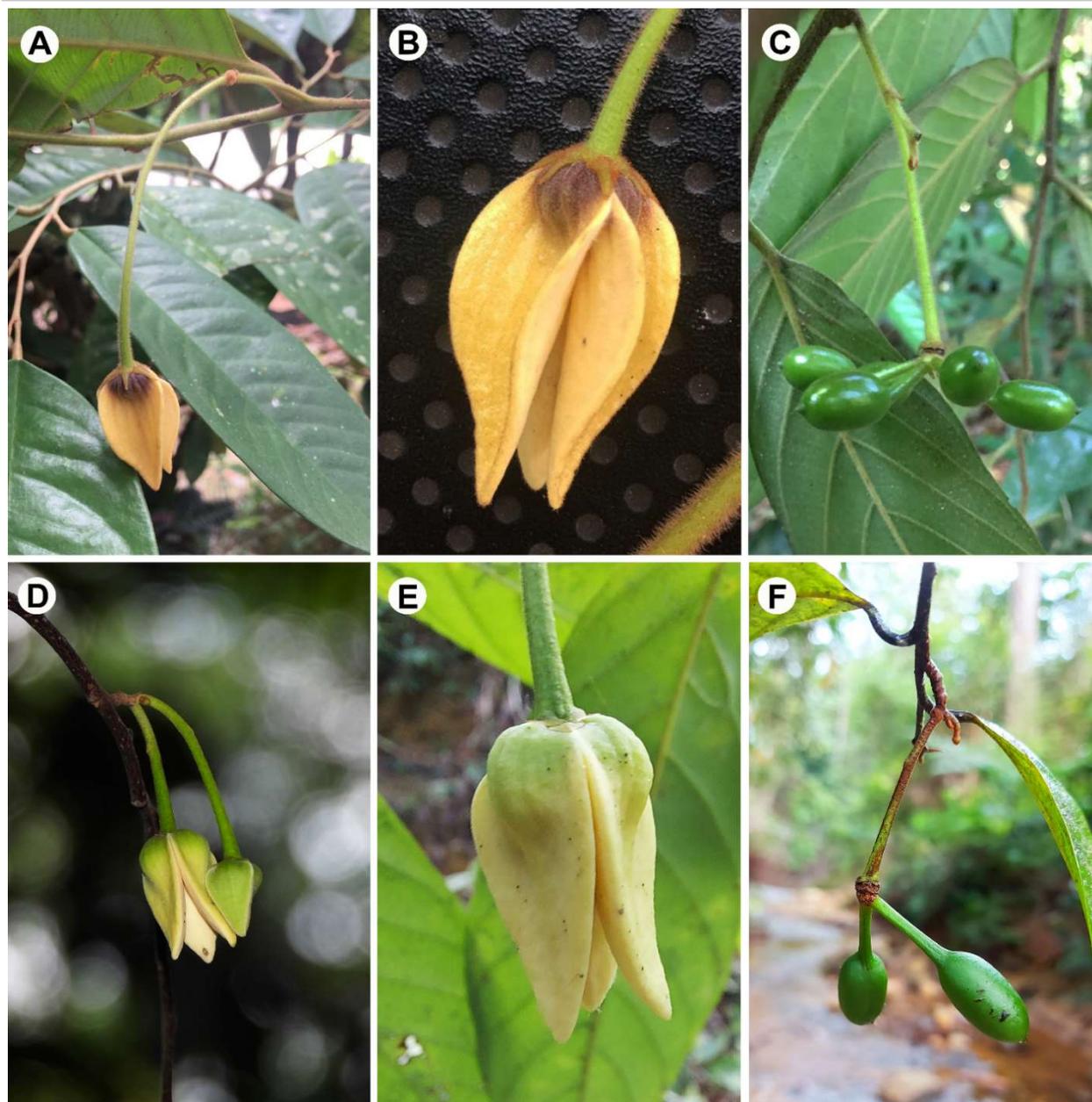


Fig. 4. Inflorescences (with flowers) and infructescences (with fruits) of *Phaeanthus* spp. **A–C:** *Phaeanthus piyae* sp. nov. [= *Phaeanthus* cf. *intermedius*]. **A:** Inflorescence and flower. **B:** Flower enlarged. **C:** Infructescence and fruit (with monocarps). **D–F:** *Phaeanthus lucidus* [= *Phaeanthus* cf. *splendens*]. **D:** Inflorescence and flowers. **E:** Flower enlarged. **F:** Infructescence and fruit (with monocarps). A–C by Suhaibukree Samae, D–F by Abdulromea Baka.

Distribution: Southern Thailand (Narathiwat and Yala Provinces) and Peninsular Malaysia.

Habitat and phenology: Occurs in disturbed patches of evergreen forests among rubber and fruit tree plantations; at an elevation of ca. 80 m. Flowering material collected in May, July, September; fruiting material collected in July, September.

Vernacular name: Hua-Ling (หัวลิง; Thai).

Notes: The description is based only on material from Thailand. The staminal connective apex of this species

does not cover the thecae. *Phaeanthus lucidus* can be distinguished from *P. splendens* by the lower number of stamens (38–50 vs. 60–90) and carpels (15–20 vs. 30–50) per flower, as well as dissimilar placentation (almost basal to basal vs. lateral). In Thailand, *P. lucidus* has been reported earlier from Yala Province (Gardner *et al.*, 2015: 144; as *P. splendens*).

Specimens examined: Thailand. Narathiwat Province, Chanai District, elev. of ca. 80 m, July 2020, *Aongyong & Baka* 27 (CMUB); *ibid.*, May 2021, *Aongyong & Baka* 32 (CMUB); *ibid.*, September 2021, *Aongyong & Baka* 40 (CMUB).



Key to the species of *Phaeanthus* in Thailand

- 1a. Lower leaf surface almost glabrous, with denser hairs on secondary veins (hairs not discernable to the touch); peduncles 1.5–3 mm long; pedicels 38–52 mm long; sepals and outer petals similar in shape, both broadly triangular; inner petals 12–14 × 7.5–8.5 mm, without prominent veins; stamens 38–50 per flower, connective apex not covering thecae; monocarps 18–22 mm long *P. lucidus*
- 1b. Lower leaf surface with dense hairs (hairs discernable to the touch); peduncles 15–30(–38) mm long; pedicels 52–71 mm long; sepals and outer petals dissimilar in shape, sepals triangular, outer petals narrowly triangular; inner petals 23–32 × 13–20 mm, with prominent veins (best observable on abaxial side); stamens 76–88 per flower, connective apex covering thecae; monocarps 14–15 mm long *P. piyae*

DISCUSSION

Based on several morphological differences as shown in Table 1, *Phaeanthus* cf. *intermedius* is described above as *Phaeanthus piyae* sp. nov. Its morphologically most similar species is *P. intermedius* (see holotype of *Magnolia intermedia*, the basionym of *P. intermedius*, in Fig. S1). It is worth noting that, according to Turner and Veldkamp (2011), *P. intermedius* is the correct name for the species generally known as *P. nutans* Hook.f. & Thomson and *P. ophthalmicus*, while *P. ophthalmicus* is the correct name for the species called *P. ebracteolatus* (C.Presl) Merr. The new species *P. piyae* is hitherto known to occur in Narathiwat Province of southern Thailand only, whereas *P. intermedius* has a much wider distribution: Peninsular Malaysia, Singapore, Riau Islands, and Sumatra (Mols and Keßler, 2000). Both species share the inner petals with conspicuous veins (best observable on the abaxial side; Fig. 4A; Sinclair, 1955; Mols and Keßler, 2000).

There are morphological differences between *Phaeanthus* cf. *splendens* and its sister group, *P. splendens* (Mols and Keßler, 2000): number of stamens (38–50 vs. 60–90) and carpels (15–20 vs. 30–50) per flower, and placentation (almost basal to basal vs. lateral), coinciding independently with the phylogenetic branch lengths of each lineage (Fig. 1). Our observations on *Phaeanthus* cf. *splendens* are congruent with the protologue (including a drawing) of *P. lucidus* (Oliver, 1887; the type specimens were collected from Penang), one of the heterotypic synonyms of *P. splendens* (e.g. Mols and Keßler, 2000; Turner, 2018), regarding the number of carpels per flower and placentation. Therefore, *Phaeanthus* cf. *splendens* represents *P. lucidus* and we believe it is appropriate to resurrect *P. lucidus* as a distinct species. Both *P. lucidus* and *P. splendens* (Mols and Keßler, 2000) share the synapomorphic staminal connective apex that does not extend over the thecae. Further research is required to reveal the exact geographic distribution of *P. lucidus*. It is probable that all other collections from Peninsular Malaysia identified as *P. splendens* represent *P. lucidus*.

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