Goniothalamus roseipetalus and G. sukhirinensis (Annonaceae): Two new species from Peninsular Thailand

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Abstract

Two new Goniothalamus species (Annonaceae), G. roseipetalus sp. nov. and G. sukhirinensis sp. nov., are described from the southern limits of Peninsular Thailand (Narathiwat and Yala Provinces). Both new species resemble G. macrophyllus, G. scortechinii and G. uvarioides. The addition of these two new species brings the total number of Goniothalamus species in Thailand to 27. Separate identification keys are provided for flowering and fruiting specimens of the Thai species.

Keywords

Annonaceae, Goniothalamus roseipetalus, Goniothalamus sukhirinensis, new species, Thailand

Introduction

The genus Goniothalamus (Blume) Hook.f. & Thomson (Annonaceae subfam. Annonoideae tribe Annoneae: Chatrou et al. 2012; Guo et al. 2017) is widely distributed in lowland and submontane tropical forests across Southeast Asia (Thomas et al. 2017). It is characterised by pendent, protogynous flowers with two trimerous petal whorls, with the inner whorl forming a mitriform dome over the reproductive organs (a ‘type
III’ chamber sensu Saunders 2010). The outer petals are typically larger than the inner and periodically block the apertures between the inner petals, thereby controlling pollinator access and enabling the flower to temporarily trap the pollinating beetles (Lau et al. 2016). The timing of the petal movements that regulate pollinator trapping and release are synchronised with the circadian rhythms of the beetles (Lau et al. 2017; Sanders 2020); this allows the plant to utilise beetles with diverse circadian activities, and also allows the staminate floral phase to be extended to promote pollen deposition and enhance interfloral movement of beetles. These floral characteristics provide a possible biotic explanation for the statistically significant increase in the evolutionary diversification rate recently reported for the genus (Xue et al. 2020).

Goniothalamus fruits are apocarpous, with distinct fleshy ‘monocarps’ that develop from individual carpels after fertilisation. Two contrasting seed dispersal systems have been inferred, correlated with differences in fruit and seed morphology (Tang et al. 2015a): the species that are dispersed by non-volant mammals typically have ramiflorous or cauliflorous fruits with large (often sessile) monocarps and hairy seeds; whereas the species that are bird-dispersed have fruits that are borne on young growth and have small stipitate monocarps with glabrous seeds.

Goniothalamus is comparatively species-rich, with over 130 species. Although the genus has never been comprehensively revised, there are several recent regional taxonomic studies, including Thailand (Saunders and Chalermglin 2008), Peninsular Malaysia (Saunders 2003), Sumatra (Saunders 2002) and Borneo (Turner 2014). Twenty-five Goniothalamus species have been recorded from Thailand (Saunders and Chalermglin 2008), with the majority (14 species) occurring in Peninsular Thailand, viz. G. expansus Craib, G. giganteus (Wall. ex) Hook.f. & Thomson, G. latestigma C.E.C.Fisch., G. macrophyllus (Blume) Hook.f. & Thomson, G. malayanus Hook.f. & Thomson, G. ridleyi King, G. rotundisepalus M.R.Hend., G. scortechinii King, G. tapis Miq., G. tavoensis Chatterjee, G. tenuifolius King, G. tortilipetalus M.R.Hend., G. undulatus Ridl. and G. uvarioides King. Several other Goniothalamus species are recorded from Peninsular Malaysia, close to the Thai border (Saunders 2003), viz. G. curtisii King, G. montanus J.Sinclair and G. subevenius King. Recent fieldwork in Narathiwat and Yala Provinces of Peninsular Thailand has resulted in collections of two new species that are described here as G. roseipetalus and G. sukhirinensis. The species descriptions provided here are based on observations and measurements from living material.

New species descriptions

Goniothalamus roseipetalus Leerat., Chalermglin & R.M.K.Saunders, sp. nov.
urn:lsid:ipni.org:names:77221293-1
Figs 1–3

Diagnosis. Goniothalamus roseipetalus resembles G. scortechinii and G. uvarioides but is distinguished by its leaves with generally fewer secondary veins (15–22 pairs), wider sepals (24–35 mm), and wider inner petals (8–11 mm). It is also distinguished
Two new Goniothalamus species from Thailand

Figure 1. Goniothalamus roseipetalus sp. nov. A flowering branch B flower C calyx of fused sepals (abaxial) D calyx of fused sepals (adaxial) E outer petal (abaxial) F outer petals (adaxial) G inner petal (abaxial) H inner petal (adaxial) I stamen (abaxial) J stamen (adaxial) K carpel (abaxial) L carpel (adaxial) M fruit, composed of separate monocarps. N–P seeds (different orientations). Drawn by A. Somphrom A–L from C. Leeratiwong 21–1708 (PSU) M–P from C. Leeratiwong 21–1707 (PSU).
from *G. scortechinii* by its wider outer petals (14–25 mm), and is distinguished from *G. uvarioides* by its smaller, single-seeded monocarps (8–15 by 7–9 mm), borne on shorter stipes (3–5 mm).

**Types. Thailand:** Narathiwat: Cha Nae, Du Son Yo subdistrict, 400 m alt., 15 April 2021, C. Leeratiwong 211706 (holotype PSU; isotypes BKF, KKU).

**Description.** Shrubs to small trees, to 4 m. Young branches glabrous. Leaf laminas 15–40 by 3–13 cm, length/width ratio 2.8–5, elliptic to oblanceolate, apex generally acuminate (rarely acute to obtuse), acumen 3–10 mm long, base broadly cuneate, chartaceous, glabrous ab- and adaxially (sometimes sparsely pubescent over midrib); midrib strongly prominent abaxially, sunken adaxially; secondary veins 15–22 pairs, plane adaxially; tertiary veins percurrent, slightly distinct, lacking a ‘granular’ appearance abaxially; petioles 12–22 mm by 1.5–2.5 mm, glabrous to sparsely pubescent. Flowers solitary, of-
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Ten on main trunk (cauliflorous), rarely on older branches (ramiflorous), pendent; flowering pedicels 10–17 mm long, sparsely hairy; pedicel bracts ovate to broadly lanceolate, 2–4 by 2–3 mm. Sepals (violet-)pink, broadly ovate, 20–30 by 24–35 mm, basally connate (10–17 mm from base), apex rounded, glabrous ab- and adaxially, with sparsely hairy margins, venation distinct, 5–7-veined. Outer petals greenish-pink when young, (violet-)pink (green at claw) when mature, 25–45 by 14–25 mm with 4–10 mm-long claw, length/width ratio 1.7–2.2, fleshy, (lanceolate-)ovate, apex obtuse to mucronate, reflexed, sparsely hairy abaxially (more densely along margins basally), sparsely hairy (more densely apically) adaxially with velutinous basal region facing apertures between inner petals, midrib and venation indistinct ab- and adaxially. Inner petals 12–20 by 8–11 mm with 2–5 mm-long claw, length/width ratio 1.5–1.8, oblanceolate, densely hairy ab- and adaxially, greenish-pink when young, pale pink when mature, apex acute, lacking

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**Figure 3.** *Goniothalamus roseipetalus* sp. nov. **A, B** flowers, **C, D** fruits showing persistent calyx. Photos by P. Chalermglin.
a glabrous lasteral flange on the inner petal claws. Stamens numerous, narrowly oblong, 3–4 mm long; connectives apiculate, papillate. Carpels 20–35 per flower, ovary oblong, 2–2.5 mm long, with white hairs; stigma and pseudostyle 2–3 mm long, stigma subulate, glabrous. Fruits with persistent calyx, immature fruits greenish-pink, mature fruits (pinkish-)red; fruiting pedicels 10–20 by 2–2.5 mm, sparsely hairy to glabrous. Monocarps 5–20 per fruit, 1–2-seeded, 8–17 by 7–10 mm, length/width ratio 1.1–1.7, ellipsoid to ovoid, apex apiculate, apicule 0.5–1.5 mm long, smooth, sparsely hairy, glossy, pericarp 1–2 mm thick, stipes 3–6 by 1.5–2 mm, moderately hairy. Seeds with mucilage, 9–11 by 8–9 mm, length/width ratio 1.1–1.6, ovoid, testa sparsely pubescent, rugose.

**Phenology.** Flowering in March and April; fruiting in August (based on limited data).

**Distribution and habitat.** Endemic to Peninsular Thailand, where it occurs in Narathiwat and Yala Provinces (Fig. 4). Growing in shady and moist areas of tropical rainforests and forest margins between para-rubber plantations and remnant rainforests; 100–400 m alt.
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**Etymology.** In reference to the red pigmentation of the petals.

**Local name.** Panan klip muang (ปาหนันกลีบม่วง) (general).

**Additional specimens examined (paratypes).** Thailand: Yala Province, Bannang Sata, 350 m alt., 1 August 2020, C. Leeratiwong 20–1684 (PSU); Narathiwat Province: Cha Nae District, Du Son Yo subdistrict, 100 m alt., 6 March 2021, C. Leeratiwong 21–1705 (PSU).

**Discussion.** Although *G. roseipetalus* is yet to be included in a molecular phylogenetic analysis, it shares several morphological similarities with species in a clade (nested within clade ‘A1a’ sensu Tang et al. 2015a, b) that comprises *G. loerzingii* R.M.K.Saunders, *G. macrophyllus*, *G. scortechinii*, *G. uvarioides* and *G. wrayi* King. These species were previously classified by Bân (1974) within *Goniothalamus* subgen. *Goniothalamus*, and are characterised by their essentially glabrous vegetative shoots and petioles, percurrent tertiary leaf venation, generally fused sepals with distinct venation, short inner petals, apiculate staminal connectives, relatively few carpels per flower, thick-cylindrical pseudostyles with a broad, hairy stigma, and seeds with a hairy testa. Although *G. roseipetalus* shares most of these diagnostic characters, its stigmas are glabrous.

*Goniothalamus roseipetalus* is morphologically most similar to *G. scortechinii* and *G. uvarioides*. It differs from these species, however, as it generally has fewer secondary veins in its leaves (15–22 pairs, vs [18–]21–26[–32] in *G. scortechinii* and 24–35 in *G. uvarioides*), larger sepals (20–30 by 24–35 mm, vs 8–24 by 8–23 mm in *G. scortechinii* and 12–16 by 5–13 mm in *G. uvarioides*), and wider inner petals (8–11 mm, vs 5–8 mm in *G. scortechinii* and 7–8.5 mm in *G. uvarioides*). It also has wider outer petals (14–25 mm) than *G. scortechinii* (8–14 mm), and can be distinguished from *G. uvarioides* by reference to its smaller monocarps (8–15 by 7–9 mm, vs 31–44 by 15–18 mm) with a single seed (vs four or five seeds per monocarp) and shorter stipes (3–5 mm, vs 12.5–17.5 mm). *Goniothalamus roseipetalus* also resembles the widespread species *G. macrophyllus*, although the latter species has creamy-white petals.

*Goniothalamus sukhirinensis* Leen., Chalermglin & R.M.K.Saunders, sp. nov.

**Figs 5, 6**

**Diagnosis.** *Goniothalamus sukhirinensis* resembles *G. macrophyllus* and *G. scortechinii*, but is distinguished by its densely hairy shoots, numerous secondary veins (32–40 pairs per leaf), generally longer pedicels (flowering: 12–18 mm; fruiting: 20–25 mm), larger outer petals (34–37 by 18–22 mm), larger monocarps (20–27 by 9–13 mm) that are densely hairy, and longer seeds (13–17 mm).
Types. Thailand: Narathiwat: Sukhirin, Ban Yade village, Ma Mong subdistrict, 167 m alt., 6 March 2021, C. Leeratiwong 21–1708 (holotype PSU; isotypes BKF, KKU).

Description. Shrubs to small trees, to 4 m. Young branches densely appressed-pubescent. Leaf laminas 28–50 by 7–16 cm, length/width ratio 3.1–4, (lanceolate-)oblong, apex generally acuminate to caudate (rarely acute to obtuse), acumen 7–20 mm long, base broadly cuneate, subcoriaceous, glabrous abaxially (sparingly hairy over midrib), sparsely pubescent adaxially (densely hairy over veins); midrib strongly prominent abaxially, sunken adaxially; secondary veins 32–40 pairs, plane adaxially; tertiary veins percurrent, distinct, lacking a ‘granular’ appearance abaxially; petioles 20–30 mm by 4–6 mm, densely pubescent. Flowers solitary or paired, often on main trunk (cauliflorous), rarely on older branches (ramiflorous), pendent; flowering pedicels 12–18 mm long, densely hairy; pedicel bracts ovate-triangular, 2.5–3 by 1–1.5 mm. Sepals greenish-pink, broadly ovate, 7–9.5 by 7.5–10 mm, basally connate (2.5–3 mm from base), apex acute, moderately hairy abaxially, sparsely hairy adaxially, venation indistinct. Outer petals greenish-yellow when young, whitish-yellow (green at claw) when mature, 34–37 by 18–22 mm with 3–5 mm-long claw, length/width ratio 1.6–1.9, fleshy, (lanceolate-)ovate, apex acuminate, densely hairy abaxially, moderately hairy adaxially with velutinous basal region facing apertures between inner petals, midrib raised adaxially, venation indistinct ab- and adaxially. Inner petals 13–15 by 7–8 mm with 2–3 mm long claw, length/width ratio 1.8–1.9, ovate-lanceolate, densely hairy abaxially, sparsely hairy distally adaxially, yellowish-green when young, pinkish-orange to reddish-brown when mature, apex acuminate, lacking a glabrous lateral flange on the inner petal claws. Stamens numerous, oblong, 2.5–3.7 mm long; connectives apiculate, papillate. Carpels 11–20 per flower, ovary oblong, 2–3 mm long, with white hairs; stigma and pseudostyle 2–2.5 mm long, stigma funnel-shaped, hairy. Fruits sometimes with persistent calyx, immature fruits brownish-green, mature fruits not seen; fruiting pedicels 20–25 by 2–3.5 mm, sparsely hairy. Monocarps 5–14 per fruit, single-seeded, 20–27 by 9–13 mm, length/width ratio 2–2.7, (ovoid-)ellipsoid, apex apiculate, apicule 5–8 mm long, smooth, densely hairy, glossy, pericarp 1–2 mm thick, stipes 7–15 by 2–3 mm, densely hairy. Seeds 13–17 by 8–10 mm, length/width ratio 1.6–1.7, ellipsoid, testa densely villose, slightly rugose.

Phenology. Flowering and fruiting in February and March (based on limited data).

Distribution and habitat. Endemic to Narathiwat Province, Peninsular Thailand (Fig. 4). Growing in shady and moist areas of tropical rainforests; 167–200 m alt.

Etymology. From the name Sukhirin, Narathiwat Province.

Local name. Ratchakhru khao (ราชครูขาว) (Narathiwat).

Additional specimen examined (paratype). Thailand: Narathiwat Province: Sukhirin District, Ban Yade village, Ma Mong subdistrict, 200 m alt., 28 February 2021, C. Leeratiwong 21–1707 (PSU).

Discussion. As with the previous species, G. sukhirinensis is yet to be included in a molecular phylogenetic analysis but has strong morphological affiliations with a clade that comprises G. loerzingii R.M.K.Saunders, G. macrophyllus, G. scortechinii, G. uvarioides and G. wrayi King (nested within clade ‘A1a’ sensu Tang et al. 2015a, b). The morphological characteristics of this clade are detailed under G. roseipetalus, above.
Two new *Goniothalamus* species from Thailand

Figure 5. *Goniothalamus sukhirinensis* sp. nov. **A** vegetative branch **B** petiole, showing base of leaf lamina **C** flowers **D** sepal (abaxial) **E** sepal (adaxial) **F** outer petal (abaxial) **G** outer petals (adaxial) **H** inner petal (abaxial) **I** inner petal (adaxial) **J** stamen (abaxial) **K** stamen (adaxial) **L** carpel (abaxial) **M** carpel (adaxial) **N** fruit, composed of separate monocarps **O** seed with hairy surface. Drawn by A. Somphrom from C. Leeratiwong 21–1708 (PSU).
Goniothalamus sukhirinensis resembles G. macrophyllus and G. scortechinii, but differs in several key characters: densely hairy shoots (vs glabrous to medium-hairy); numerous secondary veins (32–40 pairs per leaf, vs 12–23 in G. macrophyllus and [18–]21–26[–32] in G. scortechinii); generally longer flowering pedicels (12–18 mm, vs 5–11.5 mm in G. macrophyllus and 8–13 mm in G. scortechinii); larger outer petals (34–37 by 18–22 mm, vs 10–28 by 4.5–11.5 mm in G. macrophyllus and 20–33 by 8–14 mm in G. scortechinii); longer fruiting pedicels (20–25 mm, vs 7–19 in G. macrophyllus and 8–20 mm in G. scortechinii); larger monocarps (20–27 by 9–13 mm, vs 8–15 by 7.5–10 mm in G. macrophyllus and 9–18 by 6–10 mm in G. scortechinii) that are densely hairy (vs subglabrous to medium-hairy); and longer seeds (13–17 mm, vs 8.5–12 mm in G. macrophyllus and 8–11 mm in G. scortechinii). Goniothalamus

Figure 6. Goniothalamus sukhirinensis sp. nov. A leaf (abaxial) B, C flowers D fruit. Photos by P. Chalermglin.
Two new Goniothalamus species from Thailand also differ from *G. macrophyllus* as its leaves lack the fine ‘granular’ appearance of the latter species (due to the immersion of tertiary and higher-order veins: Saunders, 2002), and has longer monocarp stipes (7–15 mm, vs up to 1.8 mm in *G. macrophyllus*).

**Key to Goniothalamus species in Thailand (flowering specimens)**

| 1a | Stamen connective apex apiculate ................................................. | 2 |
| 2a | Young branches densely hairy to velutinous .................................. | 3 |
| 3a | Leaf laminas 28–50 cm long, with 32–40 pairs of secondary veins; sepals 7–9.5 by 7.5–10 mm; outer petals 34–37 by 18–22 mm; inner petals 13–15 by 7–8 mm .............................................................. | *G. sukhirinensis* sp. nov. |
| 3b | Leaf laminas 50–76 cm long, with 24–32 pairs of secondary veins; sepals 30–40 by 28–30 mm; outer petals 60–80 by 30–40 mm; inner petals ca. 35 by ca. 17 mm .............................................................. | *G. cheliensis* H.H.Hu |
| 2b | Young branches glabrous to hairy ................................................ | 4 |
| 4a | Flowers in large fascicles, exclusively from woody tubercles at base of trunk........ | *G. ridleyi* King |
| 4b | Flowers solitary or in pairs, not exclusively from base of trunk .......... | 5 |
| 5a | Adaxial surface of outer petals with glabrous or sparsely hairy region facing apertures between inner petals .............................................................. | 6 |
| 6a | Leaves with 24–35 pairs of secondary veins ................................ | *G. uvarioides* King |
| 6b | Leaves with 11–22 pairs of secondary veins .................................. | *G. tapis* Miq. |
| 5b | Adaxial surface of outer petals with velutinous region facing apertures between inner petals .............................................................. | 7 |
| 7a | Flowering pedicels 20–37 mm long; carpels 50–100 per flower ............. | *G. tortilipetalus* M.R.Hend. |
| 7b | Flowering pedicels 5–19 mm long; carpels 8–50 per flower ................ | 8 |
| 8a | Leaves with 9–12 pairs of secondary veins; stamen connective apex distinctly tapered; carpels 8–10 per flower .............................................................. | *G. tavoyensis* Chatterjee |
| 8b | Leaves with 12–26(–32) pairs of secondary veins; stamen connective apex not distinctly tapered; carpels 11–50 per flower .............................................................. | 9 |
| 9a | Tertiary venation reticulate .......................................................... | 10 |
| 10a | Sepals 11–18.5 mm long, 8–15.5 mm wide; outer petals 21–46 mm long, 4.5–18 mm wide, yellow; inner petal length/width ratio 3–6.5; stamens 95–120 per flower .............................................................. | *G. calvicarpus* Craib |
| 10b | Sepals 14–29 mm long, 12–26 mm wide; outer petals 36–104 mm long, 14–24 mm wide, green; inner petals length/width ratio 1.8–3.6; stamens 100–200 per flower .............................................................. | *G. griffithii* Hook.f. & Thomson |
| 9b | Tertiary venation percurrent ....................................................... | 11 |
| 11a | Sepals 24–35 mm wide; outer petals 14–25 mm wide ...................... | *G. rosiipedalus* sp. nov. |
| 11b | Sepals 4–23 mm wide; outer petals 4.5–14 mm wide ........................ | 12 |
12a Leaf laminas (sub-)coriaceous, with fine “granular” texture abaxially (due to immersion of tertiary and lower order veins); leaves with 12–23 pairs of secondary veins ...........................................G. macrophyllus (Blume) Hook.f. & Thomson

12b Leaf laminas papyraceous, without fine ‘granular’ texture abaxially; leaves with (18–)21–26(–32) pairs of secondary veins.................................G. scortechinii King

1b Stamen connective apex truncate ..................................................13

13a Inner petal claws with distinct glabrous lateral flange .........................14

14a Flowering pedicels 7–23 mm long; stigma subulate..............................15

15a Outer petals 23–43 mm long, 12–23 mm wide; carpels 40–100 per flower ..... ..............................................................................................................G. sawtehii C.E.C.Fisch.

15b Outer petals 10.5–32 mm long, 5.5–17.5 mm wide; carpels 10–54 per flower . ..............................................................................................................G. undulatus Ridl.

14b Flowering pedicels 2–11.5 mm long; stigma fusiform or funnel-shaped.......16

16a Young branches densely hairy to velutinous ........................................G. tamirensis Pierre ex Finet & Gagnep.

16b Young branches glabrous to hairy........................................................17

17a Flowering pedicels 5–11.5 mm long; sepal venation generally indistinct; outer petals 12.5–73 mm long; stigma fusiform....G. laoticus (Finet & Gagnep.) Bân

17b Flowering pedicels 2–6 mm long; sepal venation distinct; outer petals 8.5–39 mm long; stigma funnel-shaped ......................................................18

18a Leaf laminas 8–14 cm long, 1.5–4 cm wide; petioles 3.5–7 mm long; sepals 3–9 mm long, 3.5–6 mm wide; outer petals 8.5–15 mm long, 3.5–8 mm wide, very densely hairy ab- and adaxially; inner petals 6.5–10 mm long, 3–4.5 mm wide; ovary glabrous ............................................................................G. elegans Ast

18b Leaf laminas 12.5–24.5 cm long, 4–8.5 cm wide; petioles 5–15 mm long; sepals 7.5–12.5 mm long, 5.5–11 mm wide; outer petals 23–39 mm long, 7–15 mm wide, glabrous to hairy ab- and adaxially; inner petals 10–16 mm long, 5.5–9 mm wide; ovary sparsely hairy ........................................G. latestigma C.E.C.Fisch.

19a Tertiary leaf venation generally reticulate; outer petals with velutinous region at base of adaxial surface (facing aperture between inner petals); inner petals velutinous adaxially .........................................................................................19

20a Sepals 2.5–3.5 mm long, basally connate, venation indistinct; outer petal venation distinct; stigma fusiform ..............G. repevensis Pierre ex Finet & Gagnep.

20b Sepals 4.5–19 mm long, free, venation indistinct; outer petal venation indistinct; stigma subulate or funnel-shaped .................................................................21

21a Young branches glabrous; outer petal length/width ratio 3.4–5.2.................................G. expansus Craib

21b Young branches very sparsely to densely hairy; outer petal length/width ratio 1.6–3.8 .........................................................22

22a Leaves with fine “granular” texture abaxially (due to immersion of tertiary and lower order veins); flowers slightly supra-axillary...G. rotundisepalus M.R.Hend.

22b Leaves without fine “granular” texture abaxially; flowers axillary .................................................................G. tenuifolius King
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19b Tertiary leaf venation percurrent; outer petals with glabrous or sparsely hairy region at base of adaxial surface (facing aperture between inner petals); inner petals glabrous to densely hairy adaxially..................................................23

23a Flowering pedicels 20–48 mm long; sepals 7–15 mm long; outer petals 68–113 mm long, 28–63 mm wide ........G. giganteus (Wall. ex) Hook.f. & Thomson

23b Flowering pedicels 8–16(–21) mm long; sepals 2–8 mm long; outer petals 16–50(–62) mm long, 7–22(–32) mm wide ........................................................................24

24a Inner petals glabrous adaxially; ovaries densely hairy.........................................................G. malayanus Hook.f. & Thomson

24b Inner petals (densely) hairy adaxially (sometimes glabrous towards base); ovaries glabrous to sparsely hairy .................................................................

25a Leaf laminas 23–32 cm long, with 14–21 pairs of secondary veins; stamens 50–160 per flower; carpels 4–11 per flower.................................................................G. aurantiacus R.M.K.Saunders & Chalermglin

25b Leaf laminas 17–25.5 cm long, with 13–16 pairs of secondary veins; stamens ca. 180–200 per flower; carpels ca. 18–20 per flower........................................26

26a Flowering pedicels densely hairy; outer petals densely hairy abaxially, very densely hairy adaxially, venation indistinct; inner petals very densely hairy abaxially..

...............................................................G. maewongensis R.M.K.Saunders & Chalermglin

26b Flowering pedicels very sparsely hairy; outer petals subglabrous abaxially, glabrous adaxially, venation distinct; inner petals sparsely hairy abaxially..........

...............................................................G. rongklanus R.M.K.Saunders & Chalermglin

Key to Goniothalamus species in Thailand (fruiting specimens)

1a Adaxial surface of leaves with very prominent secondary veins ....................2

2a Leaf laminas 50–76 cm long, 13–22 cm wide, with 24–32 pairs of secondary veins; leaf midrib densely hairy to velutinous; petioles 17–30 mm long, velutinous; monocarps densely hairy..........................G. cheliensis H.H.Hu

2b Leaf laminas 12.5–39.5 cm long, 3.5–9.5(–11.5) cm wide, with 10–22 pairs of secondary veins; leaf midrib glabrous to sparsely hairy; petioles 4–16 mm long, glabrous to hairy; monocarps glabrous to hairy .........................3

3a Monocarps distinctly warty.........G. giganteus (Wall. ex) Hook.f. & Thomson

3b Monocarps smooth or finely rugulose ........................................................................4

4a Fruits restricted to trunk; fruiting pedicels 19–36 mm long.................................G. tortilipetalus M.R.Hend.

4b Fruits not restricted to trunk; fruiting pedicels 10–19 mm long...............5

5a Tertiary leaf venation percurrent; fruits without persistent calyx; monocarps 16–40 mm long, 8–13(–17) mm wide; seeds 13–20 mm long, with (sparsely) hairy testa ................................G. malayanus Hook.f. & Thomson

5b Tertiary leaf venation reticulate; fruits with persistent calyx; monocarps 10–14 mm long, 7–8 mm wide; seeds 10–12 mm long, with glabrous testa........6

6a Monocarps red; seeds slightly rugose...............................G. calvicarpus Craib

6b Monocarps yellow-brown; seeds smooth ......G. griffithii Hook.f. & Thomson
1b Adaxial surface of leaves with impressed or only slightly prominent secondary veins 

7a Tertiary leaf venation percurrent ................................................................. 8
8a Monocarps apiculate..................................................................................... 9
9a Young branches densely hairy; leaves with 32–40 pairs of secondary veins; fruiting pedicels 20–25 mm long; monocarp stipes 7–15 mm long. .................................................. G. sukhirinensis sp. nov.
9b Young branches glabrous to hairy; leaves with 12–23 pairs of secondary veins; fruiting pedicels 7–20 mm long; monocarps 8–15 mm long (very) sparsely hairy; monocarp stipes up to 5 mm long................................. 10
10a Fruits without persistent calyx .................................................................

.................................................. G. macrophyllus (Blume) Hook.f. & Thomson
10b Fruits with persistent calyx................................................................. G. roseipetalus sp. nov.
8b Monocarps not apiculate.........................................................................
11a Monocarps 7–18 mm long, 6–10 mm wide ................................................... 12
12a Leaf laminas 22–40(–50) cm long, 5.5–12(–19.5) cm wide, with (18–)21–26(–32) pairs of secondary veins ................................................. G. scortechinii King
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14a Fruits restricted to base of trunk; fruiting pedicels 30–130 mm long ........

.................................................. G. ridleyi King
14b Fruits not restricted to base of trunk; fruiting pedicels 10–22 mm long..... 15
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15b Monocarp stipes 2–8 mm long; seeds 13–17 mm wide; smooth to slightly rugulose ................................................................. 16
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20b Leaf laminas matt adaxially; monocarp stipes 3–6 mm long; seeds 11–14 mm long ................................................................. G. sawtehii C.E.C. Fisch.

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21a Leaf lamina tertiary venation (clearly) distinct .............................................. G. expansus Craib

21b Leaf lamina tertiary venation indistinct to ± distinct ..................................... 22

22a Leaf laminas with 9–12 pairs of secondary veins; monocarps greenish-yellow, ca. 19 mm long; seeds 17–18 mm long ......................... G. tavoyensis Chatterjee

22b Leaf laminas with 11–16 pairs of secondary veins; monocarps (dark) red, 10–14 mm long; seeds 9–12 mm long .................................. G. tapis Miq.

18b Fruiting pedicels 4–8 mm long ....................................................................... 23

23a Monocarps greenish-yellow ........................................................................ 24

24a Young branches hairy; leaf laminas 12.5–24.5 cm long, 4–8.5 cm wide; monocarps smooth; seeds ca. 17.5 mm long ......................... G. latestigma C.E.C. Fisch.

24b Young branches (very) sparsely hairy; leaf laminas 10.5–13.5(–16) cm long, 3–5 cm wide; monocarps very finely rugulose; seeds ca. 9.5 mm long ................................................................. G. repevensis Pierre ex Finet & Gagnep.

23b Monocarps red .................................................................................................. 25

25a Fruits without persistent calyx; seeds subglabrous to hairy ....................... G. tapis Miq.

25b Fruits with persistent calyx; seeds glabrous ................................................ 26

26a Leaf laminas 1.5–4 cm wide, ± glossy adaxially ........................................... G. elegans Ast

26b Leaf laminas 3.5–8.5 cm wide, (±) matt adaxially ........................................ 27

27a Monocarps glabrous; monocarp stipes 4.5–13 mm long .......................... G. tamirensis Pierre ex Finet & Gagnep.

27b Monocarps very sparsely hairy; monocarp stipes 2–3 mm long ................. G. rotundisepalus M.R. Hend.

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References

Bân NT (1974) On the taxonomy of the genus Goniothalamus (Blume) J.D. Hook. & Thomson (Annonaceae). 2. Botaničeskij Žurnal 59: 660–672.

Chatrou LW, Pirie MD, Erkens RHJ, Couvreur TLP, Neubig KM, Abbott JR, Mols JB, Maas JW, Saunders RMK, Chase MW (2012) A new subfamilial and tribal classification of
the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. Botanical Journal of the Linnean Society 169(1): 5–40. https://doi.org/10.1111/j.1095-8339.2012.01235.x

Guo X, Tang CC, Thomas DC, Couvreur TLP, Saunders RMK (2017) A mega-phylogeny of the Annonaceae: Taxonomic placement of five enigmatic genera and recognition of a new tribe, Phoenicantheae. Scientific Reports 7(1): e7323. https://doi.org/10.1038/s41598-017-07252-2

Lau JYY, Pang C-C, Ramsden L, Saunders RMK (2016) Reproductive resource partitioning in two sympatric *Goniothalamus* species (Annonaceae) from Borneo: Floral biology, pollinator trapping and plant breeding system. Scientific Reports 6(1): e35674. https://doi.org/10.1038/srep35674

Lau JYY, Guo X, Pang C-C, Tang CC, Thomas DC, Saunders RMK (2017) Time-dependent trapping of pollinators driven by the alignment of floral phenology with insect circadian rhythms. Frontiers in Plant Science 8: e1119. https://doi.org/10.3389/fpls.2017.01119

Saunders RMK (2002) The genus *Goniothalamus* (Annonaceae) in Sumatra. Botanical Journal of the Linnean Society 139(3): 225–254. https://doi.org/10.1046/j.1095-8339.2002.00061.x

Saunders RMK (2003) A synopsis of *Goniothalamus* species (Annonaceae) in Peninsular Malaysia, with a description of a new species. Botanical Journal of the Linnean Society 142(3): 321–339. https://doi.org/10.1046/j.1095-8339.2003.00177.x

Saunders RMK (2010) Floral evolution in the Annonaceae: Hypotheses of homeotic mutations and functional convergence. Biological Reviews of the Cambridge Philosophical Society 85: 571–591. https://doi.org/10.1111/j.1469-185X.2009.00116.x

Saunders RMK (2020) The evolution of key functional floral traits in the early divergent angiosperm family Annonaceae. Journal of Systematics and Evolution 58(4): 369–392. https://doi.org/10.1111/jse.12645

Saunders RMK, Chalermglin P (2008) A synopsis of *Goniothalamus* species (Annonaceae) in Thailand, with descriptions of three new species. Botanical Journal of the Linnean Society 156(3): 355–384. https://doi.org/10.1111/j.1095-8339.2007.00762.x

Tang CC, Thomas DC, Saunders RMK (2015a) Molecular phylogenetics of the species-rich angiosperm genus *Goniothalamus* (Annonaceae) inferred from nine chloroplast regions: Synapomorphies and putative correlated evolutionary changes in fruit and seed morphology. Molecular Phylogenetics and Evolution 92: 124–139. https://doi.org/10.1016/j.ympev.2015.06.016

Tang CC, Thomas DC, Saunders RMK (2015b) Molecular and morphological data supporting phylogenetic reconstruction of the genus *Goniothalamus* (Annonaceae), including a reassessment of previous infragenetic classifications. Data in Brief 4: 410–421. https://doi.org/10.1016/j.dib.2015.06.021

Thomas DC, Tang CC, Saunders RMK (2017) Historical biogeography of *Goniothalamus* and Annonaceae tribe Annoneae: Dispersal-vicariance patterns in tropical Asia and intercontinental tropical disjunctions revisited. Journal of Biogeography 44(12): 2862–2876. https://doi.org/10.1111/jbi.13086
Turner IM [Ed.] (2014) Annonaceae. In: Soepadmo E, Saw LG, Chung RCK, Kiew R (Eds) Tree Flora of Sabah and Sarawak. Vol. 8. Forest Research Institute Malaysia/Sabah Forestry Department/Sarawak Forestry Department, Kuala Lumpur, 92–104.

Xue B, Guo X, Landis JB, Sun M, Tang CC, Soltis PS, Soltis DE, Saunders RMK (2020) Accelerated diversification correlated with functional traits shapes extant diversity of the early divergent angiosperm family Annonaceae. Molecular Phylogenetics and Evolution 142: e106659. https://doi.org/10.1016/j.ympev.2019.106659