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Thaigardenia (Rubiaceae: Gardenieae), a new genus distributed from Thailand to South China

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ABSTRACT

Identified as *Gardenia* over a century ago, three known species from Thailand to South China differ considerably from typical members of that genus, from which growth habits, aspects of branch architecture and corolla shape set them apart. They form a new genus, here named *Thaigardenia*, the species of which are scrambling to thicket-forming shrubs to sometimes treelets or small trees. They have typically unequal (asymmetric) development of each internode that offsets what began as opposite pairs of axillary buds (and potential axillary branches) from subtending leaf axils at the same level, and small infundibular corollas with insignificant tubular bases. In contrast, typical *Gardenia* are non-scrambling shrubs or trees, often have extra-axillary buds or branches that consistently continue to develop at the same level (i.e., remaining opposite); and showy hypocrateriform (salverform) corollas with elongate tubular bases. The unequal development of different sides of an internode that brings an initially opposite pair of axillary buds (branches) to different levels, so that they do not appear paired subsequently, is, as far as is known, unique and unknown in other Rubiaceae or opposite-leaved plants; this shared feature is a key synapomorphic character for species of the newly recognised genus.

KEYWORDS: Branch architecture, *Gardenia*, hypocrateriform, infundibular.

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INTRODUCTION

A widespread but predominantly tropical family present on all continents, the Rubiaceae are the fourth-largest flowering-plant family in the world (Robbrecht, 1988; Davis *et al.*, 2009). Since the advent of molecular phylogenetic studies in the 1990s, three subfamilies have generally been accepted (Bremer & Eriksson, 2009): Rubioideae, Ixoroideae and Cinchonoideae. The Gardenieae is a tribe within the Ixoroideae, in which phylogenetic relationships are not yet fully resolved (Persson, 2000; Bremer & Eriksson, 2009; Razafimandimbison *et al.*, 2011; Kainulainen *et al.*, 2013; Mouly *et al.*, 2014). The type genus of this tribe is *Gardenia* J.Ellis.

In South-East Asia, *Gardenia* was found to be morphologically heterogeneous, and many species previously placed in that genus are better accommodated in other genera (Wong, 1982, 1984; Wong & Low, 2011; Wong & Pereira, 2016), as also found elsewhere (e.g., Keay, 1958; Tirvengadum, 1978; 1983). More recently, modern accounts of the genus with a stricter circumscription have appeared for Peninsular Malaysia (Wong, 1988) and Singapore (Wong *et al.*, 2019). In this circumscription, *Gardenia* is a genus of unarmed shrubs and small trees, never thicket-forming or scrambling; with resin-covered branch tips, very young twigs and leaves; smooth to often ribbed or keeled calyces with the apex truncate, toothed or lobed; a hypocrateriform

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(or salver-shaped) corolla, the tube of which is especially conspicuous; and pollen grains issued in tetrads.

Elsewhere in SE Asia where the Rubiaceae are largely unrevised, unusual forms are still to be found. In Thailand, one such species, *Gardenia saxatilis* E.T.Geddes (a synonym of *Thaigardenia similis* (Craib) K.M.Wong & L.Neo in the present account), was included by Puff *et al.* (2005) in their guide to the diversity of Rubiaceae in that country. This species develops a shrubby thicket-forming or scrambling habit, with typically asymmetric development of each stem and branch internode that offsets what began as opposite pairs of axillary buds (and potential axillary branches), so that each original pair of axillary branches develops to conspicuously different distances from the axil where they arose. Consequently, these branch pairs are no longer opposite and become, in fact, 'alternate on the same internode'. Also, the corolla is shorter (open corolla span equalling or longer than corolla length) and infundibular, not the longer (open corolla span less than corolla length) hypocrateriform type typical of *Gardenia*.

In studying the material more closely in herbaria as well as the field, and checking the literature, we discovered a cohort of three species with similar characteristics across the region from Thailand to Hainan in South China. These make up an undescribed genus that we can distinguish from *Gardenia* and other allies by a suite of characters, i.e., the subject of the present paper.

MATERIAL AND METHODS

Herbarium specimens were examined at BK, BKF, SING, VNM, US; we also consulted images of specimens from the herbaria of A, AAU, E, IBK, ISBC, K, Naturalis Biodiversity Center (L, WAG), Muséum National d'Histoire Naturelle (P) and TCD herbaria. Herbarium acronyms follow Thiers (2024, continuously updated).

Fieldwork was carried out in Chaiyaphum, Nakhon Ratchasima and Ubon Ratchathani Provinces of Eastern Thailand, as well as Mukdahan Province (North-Eastern Thailand), Suphan Buri Province (Central Thailand) and Phetchaburi Province (South-Western Thailand). Vouchers collected were deposited in BKF, BK and the Natural History Museum of the National Science Museum of Thailand, Pathum Thani Province. A planted specimen of *Gardenia collinsiae* (a synonym of *Thaigardenia collinsiae* (Craib) K.M.Wong, Teerawat. & Sungkaew in the present account) was studied at the Forestry Arboretum of the Faculty of Forestry, Kasetsart University.

Pollen from *Thaigardenia collinsiae* and *T. similis*, compared with that of *Gardenia mutabilis* Reinw. ex Blume, was examined under the light microscope at the BKF and SING herbaria. This was simply to distinguish single grains from tetrads, as the latter had been found in some genera of the Gardenieae but not others.

MORPHOLOGICAL FINDINGS

General habit

Plant sizes for *Thaigardenia cambodiana* (Pit.) K.M.Wong & Chamch. and *T. similis* recorded and seen in the field by us hardly exceed 2–5 m, but *T. collinsiae* can be a little higher (4–8 m) on good soil. The habit in *T. cambodiana* and *T. similis* may be described as shrubby and scrambling or thicket-forming (Fig. 1). That of *T. collinsiae* is similar on soil-deficient rocky areas but frequently comprises treelets or small trees on substrates with better soil development. Poilane, in his collecting notes of a *Thaigardenia* sp. (as '*Gardenia*'), summarised this nicely when he noted "petit arbuste de 1m50 de haut et gros comme un goulot de boutille. . . Arbuste droit mais extrêmement raboteux" (small shrub 1m50 high and as big as the neck of a bottle. . . Straight but extremely rugged shrub) (*E. Poilane 2814*, **VNM**); and "Arbuste fourchu 1m du sol, le tronc depuis la base est couvert de petites branches qui sont aussi raboteuses que les grosses, cet arbuste a un aspect tout à fait particuleir" (Forked shrub 1m from the ground, the trunk from the base is covered with small branches which are as rugged as the large ones, this shrub has a very particular appearance) (*E. Poilane 3082*, **VNM**). The resulting tangled mess of branches in a mature bush of *T. similis* is also nicely shown by Lanorsavanh *et al.* (2014: Fig. 1A). Occasionally, however, very old individuals develop to be low trees of 3–4 m height with very crooked sympodial trunks of around 5 cm diameter or more near the base, such as in *T. similis* (Puff *et al.*, 2005: 42).

Our own observations of *Thaigardenia similis* in the dry rocky savannah with interspersed clusters

of trees of deciduous dipterocarp forest affinity in Ubon Ratchathani (see also Puff *et al.*, 2005: Plate 3.1.6 J, K), as well as *T. collinsiae* on soil-deficient limestone at Chaiyaphum, Eastern Thailand and Suphan Buri in Central Thailand) attest to the xerophytic characteristics of these species. These plants develop relatively few leaves that are generally small, somewhat thick and not long-lived. Instead, tissue investment favours vegetative axis development and new stem and branch internodes elongate rather quickly, and the bark of older internodes turn grey or brown and do not remain tender and green for long. At most, only one or two distal leaf-bearing nodes and internodes remain green. For the *Thaigardenia* ('*Gardenia*') from Nhatrang in Vietnam, *E. Poilane 2814* had noted "récolté sur une petite eminence (rochers aride sans terre végétale)" (collected on a small hill (arid rocks without topsoil)), and *E. Poilane 3082*: "sol argile rocheux" (rocky clay soil). In the case of the Hainan collections of *T. collinsiae* (recorded as *Gardenia reflexisepala* N.H.Xia & X.E.Ye), the habitat was stated as "Forests or thickets along stream banks, in valleys or jungles on exposed slopes" (Ye & Xia, 2016).

Figure 1. *Thaigardenia similis* (Craib) K.M.Wong & L.Neo: A. The shrubby and scrambling or thicket-forming habit, B. A tangle of basal shoots and branches, with their characteristic alternate axillary branches. Photos: K.M. Wong.

In contrast, typical *Gardenia* spp. are either shrubs or trees with distinct stems or trunks without a proliferation of branches that could contribute to a thicket-forming habit. They may be adapted to exposed conditions or forest shade but typically occur where there is a reasonable amount of moist topsoil development.

Vegetative branching and supernumerary axillary buds.

It is characteristic of opposite-leaved plants that they have paired axillary buds that give rise to similarly paired axillary axes along the main stem and branches. These branches sometimes develop unequal or just one of a pair of higher-order branches that contribute to sympodial branch system extension (Wong, 1988; Zahid & Wong, 2004; Wong *et al.*, 2019). It is rare that along the main stem, axillary branches are solitary rather than paired, such as in *Lasianthus* Jack (Wong, 1988; Puff *et al.*, 2005; Wong *et al.*, 2019). Even more unusual is the occurrence of 'extra-axillary branching' such as is typical in *Gardenia*, although it is more conspicuous in some species than others (Wong, 1988: 67). This term describes the condition when axillary branches are raised above the actual axils of the leaves that subtend them, and must come about because the internodal space between subtending leaf and axillary bud (or axillary branch) and just above a node increases due to tissue elongation. In all *Gardenia* spp. as so far known, these extra-axillary buds or branches along the stem or trunk consistently continue to develop at the same level (i.e., remaining visibly opposite).

In contrast, although *Thaigardenia* spp. also develop extra-axillary buds and branches, there is typically unequal (asymmetric) development of each internode that offsets what began as opposite pairs of axillary buds (and potentially axillary branches) from subtending leaf axils at the same level (Fig. 2). The unequal development of different sides of an internode then brings an initially opposite pair of axillary buds (or branches) to different levels above the node, so that they do not appear paired subsequently. Occasionally, as might be expected, the unequal development of opposite sides of the internode renders a noticeable slight curvature but the commonness of relatively straight internodes suggests that later internodal extension balances out between opposite sides. This is, as far as is known, unique and unknown in other Rubiaceae or other opposite-leaved plants. The detailed studies of shoot development in the related but heterogeneous *Randia s.l.* complex by Fagerlind (1943), for example, do not document this developmental mode. Such growth renders the impression of a *Thaigardenia* plant from some distance as having "spirally arranged, solitary (rather than paired) side branches" (Puff *et al.*, 2005: Plate 3.1.6. K and caption), which departs significantly from that of a typical woody Rubiaceae plant. This feature of the morphology is also well captured by the illustration of *Gardenia reflexisepala* in Ye & Xia (2016), which is here considered the same as *T. collinsiae*, as well as a photograph of shoot sequences in *G. saxatilis* (here *T. similis*) by Lanorsavanh *et al.* (2014: Fig. 1B).

The only exception to extra-axillary branching in both *Gardenia s.s.* and *Thaigardenia* is to be found on the lateral branches where flowers terminate shoot segments immediately after a leaf-pair. At such points, one or a pair of axillary branches could develop that enable continuing branch elongation (Fig. 3A).

An additional difference from typical *Gardenia* spp. is the frequent development of more than one axillary bud per leaf axil in *Thaigardenia* (Fig. 4). The number of supernumerary or 'serial' buds at opposite leaf axils is not necessarily the same. It can be just one or two on one side, and as many as 2–4 on another. Again, this contrasts greatly with typical *Gardenia* spp., in which we have not observed supernumerary axillary buds. In genera from other tribes, such as *Stichianthus* Valeton or *Urophyllum* Wall., such buds are indeed common (Wong, 1988; van Balgooy *et al.*, 2015; Wong *et al.*, 2019).

Plant architecture

Shrubby species of *Gardenia* typically have leaves in whorls of threes, and so commonly develop three branches at the terminal whorl when shoot growth is terminated by flowering; in this way these shrubs continue to branch sequentially to higher orders (with all vegetative axes equivalent) and build up a generally obpyramidal structure (Fig. 3A). Branches from a node are always at the same level. The resulting habit is a bush of neatly regular architectural modules (Hallé *et al.*, 1978: Leeuwenberg's model), certainly not an untidy thicket. Tree species of *Gardenia*, on the other hand, and as far as has

been observed, have monopodial rhythmically growing stems or trunks, at clear intervals producing orthotropic branches that are laterally extending sympodial complexes, and conform to the architectural model of Scarrone (Hallé *et al.*, 1978).

In a *Thaigardenia* plant, all lateral shoots have opposite and decussate leaves (i.e., are orthotropic as in the main stems) and by terminal flowering are limited in growth and therefore modular-like. However, the main stem appears to be continuous in growth and flowering is usually found on side branches. Its adaptation to a seasonal climate does not appear to constrain it to rhythmic growth, but instead, each season is characterised by 1–few internodes of subequal length developing both at the stem and branch tips, so in this sense growth is continuous as there is no spatial rhythmicity that creates tiers of branches (in fact, every internode develops branches or at least visible primordia).

Figure 2. *Thaigardenia collinsiae* (Craib) K.M.Wong, Teerawat. & Sungkaew: A. Unequal (asymmetric) development of each internode that offsets what began as opposite pairs of axillary buds (and potentially axillary branches) from subtending leaf axils at the same level; *Thaigardenia similis* (Craib) K.M.Wong & L.Neo: B. The current growth still with green internodes, C. Old stem and branches still show the 'offset' axillary branches but only with faint traces of nodes, D. Two axillary branches (AB1, AB2) at different levels above the node (N, originally with a leaf-pair), indicating differential growth rates between node and developing axillary bud, thus resulting in a slight curvature of the internode; this is eventually 'straightened out' by continuing internode growth. Photos: A. Teerawatananon (A) and K.M. Wong (B–D).

The architecture of the plants therefore seems to conform to the model of Stone (Hallé *et al.*, 1978), apparently rare among dicots.

Stipules and terminal bud resin

The stipules in *Thaigardenia* are broad-triangular structures fused along part or most of their edges (Fig. 5). The short, thin stipular sheath remains for a time around the internode base in *T. collinsiae*. In the case of *T. similis*, when the terminal bud develops, it ruptures this stipular 'cone' and the ruptured margins rapidly turn brown (necrotic) with the main stipular structure remaining only as a green collar around the node for a short time. In contrast, typical *Gardenia* spp. have stipules fused into a cylindric sheath split slightly on one side (Fig. 3B), and parts of the detached stipular sheaths can remain as 'cicatrices' around the internode base well into the next one or two growing seasons.

Generally, very slight resin exudation lightly coats the young leaves in *Thaigardenia*, but on occasion in well-shaded *T. collinsiae*, copious amounts of resin can accumulate as a yellow blob at the terminal bud (frequently dissipated in oven-dried specimens). This is much as is typical for *Gardenia*, and the resin can remain as a visibly waxy coating over stipules, young internodes and leaves.

Inflorescences

The inflorescence in *Thaigardenia*, as also in typical *Gardenia* (Fig. 3C), is one-flowered and terminal to the shoot, the sole flower either subsessile

Figure 3. Some attributes of *Gardenia s.s.*, *G. mutabilis* Reinw. ex Blume: A. Plant development, in which shoots are determinate in growth or terminated by flowering after a few internodes, the final node typically producing a whorl of (2–)3 branches, so that an essentially 'obpyramidal' structure builds up, B. Sheathing stipules, C. Typically hypocrateriform corolla; *Gardenia jasminoides* J.Ellis: D. Top view down on open flower, showing characteristic curvatures of the corolla lobes. Photos: K.M. Wong.

(*T. similis*) or short-pedicellate (*T. cambodiana*, *T. collinsiae* and *T. similis*). Also, as in *Gardenia*, (occasionally one, sometimes two) axillary shoots rapidly develop from the axils of the leaf pair subtending the terminal flower.

Corolla and other floral attributes

All three species of *Thaigardenia* have short infundibular corollas with insignificant tubular bases much shorter than the flared upper portion (Fig. 6; Puff *et al.*, 2005: Plate 3.1.6 H). In contrast, typical *Gardenia* flowers have showy hypocrateriform (salverform) corollas with very long tubes and a hardly widened upper portion near the throat (Fig. 3C).

Additionally, in the open flowers of typical *Gardenia*, the corolla lobes have their basal margins strongly recurved, often giving the impression of an abruptly narrowed proximal portion. The distal portion, however, is spread out with one margin (the right margin when viewed from above) strongly upcurved, and the other somewhat down-curved (Fig. 3C, D). *Thaigardenia* spp. do not have these consistent folds or curvatures in their corolla lobes.

The pollen of typical *Gardenia* spp. is issued as tetrads (a comparatively rare condition in the tribe: Robbrecht & Puff, 1986; Robbrecht, 1988; Persson, 1993). Those of *Thaigardenia*, likewise, are also issued as tetrads, possibly implying a close relationship.

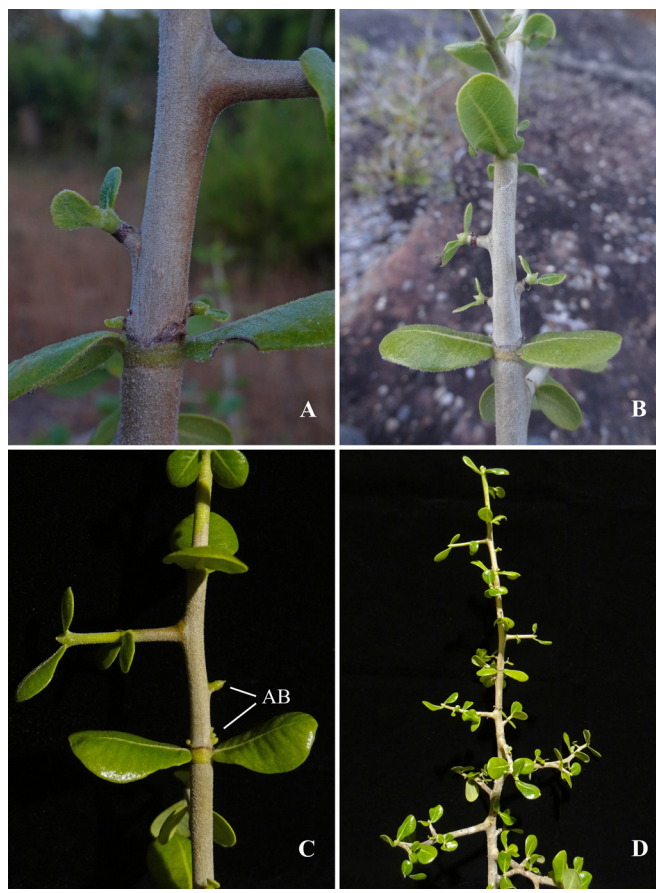

Figure 4. Supernumerary (more than one) axillary buds in *Thaigardenia similis* (Craib) K.M.Wong & L.Neo: A. Two from each leaf axil developing into branches, at different levels, B. Two axillary buds on the left, and one on the right, C. Two on the left (the upper one already a branch), and four axillary buds (AB) on the right, D. Shoot sequence, the distal part (with intact leaf-pairs at nodes) the current season's growth, below that of the previous season; all shoots sprouting new leaves from their tips or newly developing axillary buds. Photos: K.M. Wong.

Fruits

Fruits of typical *Gardenia* are variously ornamented, sometimes by prolongation of the calyx tube (e.g., *G. griffithii* Hook.f.) or longitudinal ribs or keels running down the calyx tube, and sometimes even to the fruit base (Wong *et al.*, 2019), and also by elaboration of the calyx limb including lobes (Wong, 1982). Very seldom is the calyx tube sub-truncate, as in *G. elata* Ridl., or sheath-like with a slanted opening (*G. mutabilis* Reinw. ex Blume) (Wong & Low, 2011).

On the other hand, all three *Thaigardenia* spp. have fruits with very narrowly triangular (*T. similis*) to linear (*T. collinsiae*, *T. similis*) or narrowly obovate (*T. cambodiana*) calyx lobes, without further elaboration (Figs. 5–9). Fruits can be smooth on the outside, or sometimes faintly ribbed, each rib (which is a major vascular trace) corresponding to a calyx lobe in position.

TAXONOMY

Robbrecht (1988) listed the main morphological attributes of the Gardenieae A.Rich. ex DC. to include woodiness, interpetiolar and entire stipules, absence of raphides in the tissues, contorted corolla lobes, and presence of 'stylar pollen presentation' (= secondary pollen presentation). Wong (1988) added anthers included within the corolla as one of the characters. Both these circumscriptions accepted that inflorescences could be terminal (Gardeniinae DC.)

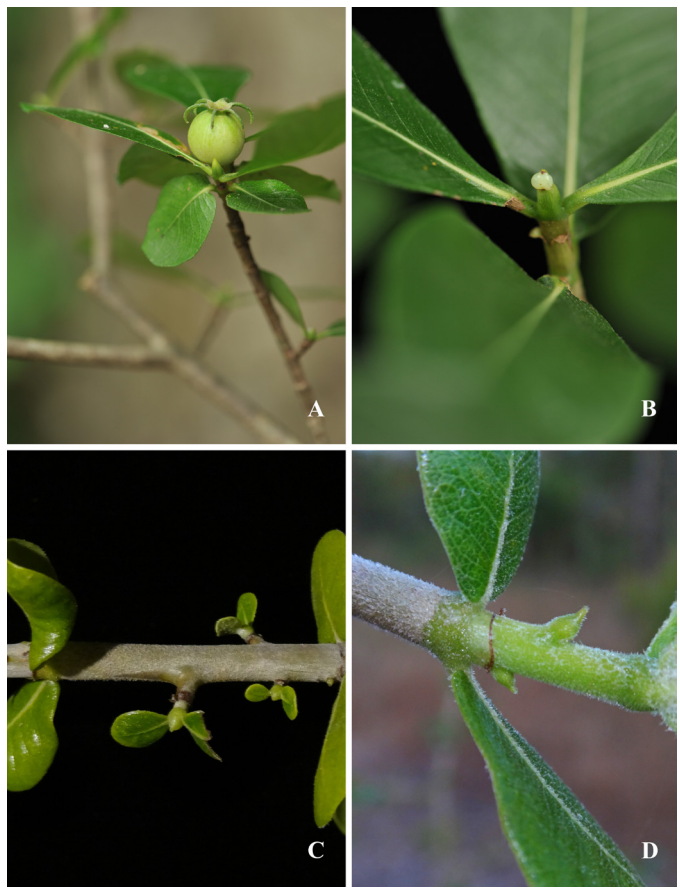

Figure 5. Stipules in *Thaigardenia* are broad-triangular structures fused along part (e.g., in *T. collinsiae* (Craib) K.M.Wong, Teerawat. & Sungkaew: A, B) or most (*T. similis* (Craib) K.M.Wong & L.Neo: C, D) of their edges, A. Young shoot apex next to fruiting branch, B. Young shoot apex, showing resin blob exuded from shoot-tip stipules; C. Young shoot tips with stipules from a single internode, D. Older leafy node with stipular remains (as a leathery 'band' on which the brown senescent margin shows where most of the original tissue has fallen away). Photos: A. Teerawatananon (A, B) and K.M. Wong (C, D).

or axillary and opposite, the latter accommodating the Diplosporinae Miq. Later, the genera of the latter subtribe were shown to belong to different tribes, Vanguerieae A.Rich. ex Dumort. (*Diplospora* auct. non DC. in SE Asia = *Dibridsonia* K.M.Wong) (Wong *et al.*, 2019), or Coffeeae DC. (*Diplospora* DC. and *Discospermum* Dalzell) (Bremer, 2009; Turner in Wong *et al.*, 2019). The classical Gardenieae gradually came to be remodelled without the Diplosporinae by Robbrecht & Puff (1986), with these general characteristics: woody plants (including climbers), inflorescences terminal (rarely pseudo-axillary), sometimes leaf-opposed, flowers mostly large, (4–5–)pleiomerous, ovaries 2(–9)-carpellate, placentas axile or parietal, mostly with many ovules; fruits mostly large, often with dry, woody or leathery wall, placenta in fruit well-developed, fleshy to pulpy, mostly completely embedding the seeds; seeds many, lenticular, endosperm entire; pollen grains in tetrads or monads. *Thaigardenia* therefore conforms to the most recent interpretation of this tribe.

The concept of *Gardenia* has had a checquered history (see Wong, 1982; 1984). In SE Asia, it also included taxa with non-salverform corolla, such as what was later isolated as *Kailarsenia* Tirveng. and *Catunaregam* Wolf, which had campanulate corollas (Wong, 1982, 1984, 1988). As such, it is not surprising that taxonomic designations of the older period (including Craib, 1914; Pitard, 1923) did not recognise the distinctiveness of *Thaigardenia* spp. in spite of their infundibular, not salverform, corollas.

Figure 6. *Thaigardenia* species have small infundibular corollas with insignificant tubular bases much shorter than the flared upper portion (A, *Pooma et al. 2916* (**BKF**): *T. similis*; B, *Smithinand 8508* (**BKF**) & C, *Winit 1796* (**BKF**): *T. collinsiae*) and calyx lobes vary from triangular (A) to linear (B, C) to elliptic-oblanceolate (D, *Larsen et al. 31730* (**BKF**): *T. cambodiana*). Photos: K.M. Wong.

The two genera, as we understand from the current distinguishing characters of *Gardenia* (Wong, 1988; Wong *et al.*, 2019), are rather different. As discussed above, the differences range from habit, the development of axillary buds and branches arising from a nodal leaf-pair to different levels along the internode in *Thaigardenia*, presence of supernumerary or 'serial' buds in the leaf axils, stipule form, corolla shape, and elaboration and ornamentation of the fruit calyx.

Thaigardenia Sungkaew, Teerawat., Chamch. & K.M.Wong, **gen. nov.**

Thaigardenia is a new genus of the Rubiaceae, allied to *Gardenia* J.Ellis, differing in the species being shrubs with a scrambling to thicket-forming habit or small trees with crooked sympodial trunks (vs *Gardenia s.s.* which are mostly trees with monopodial trunks or non-thicket forming bushes), developing extra-axillary buds and branches at different distances from a leaf-pair at the same node on stems and branches (sometimes these extra-axillary buds more than one per leaf axil) (vs with extra-axillary buds and branches always at the same level, and solitary buds in *Gardenia*), broad-triangular stipules fused along their edges (vs typical *Gardenia* spp. with stipules fused into a cylindric sheath split slightly on one side), infundibular corolla with insignificant tubular bases much shorter than the inflated upper portion (vs hypocrateriform corollas with relatively long basal tubes with a hardly widened uppermost portion in *Gardenia*), and pollen issued as tetrads. Type: *Thaigardenia collinsiae* (Craib) K.M.Wong, Teerawat. & Sungkaew.

Shrubs or small crooked trees. *Resinous exudate* coating branch tips, twigs and other young parts of the plant. *Stipules* broad-triangular, fused along part or most of their edges, the bases later remaining for a short time as subtruncate rings around the node, these also caducous. *Leaves* opposite and decussate on all axes, with short to subobsolete petioles, blade elliptic to obovate, sometimes panduriform, thinly coriaceous to coriaceous; axillary buds sometimes more than one per axil, mostly paired but rapidly positioned at different levels of the same internode due to differential intercalary growth, axillary branches typically remaining short and ending in a series of abbreviated internodes, the whole somewhat indurated and aiding entanglement with other shoots or branches (contributing to the growth thicket). *Flowers* solitary, mostly terminal to side branches; calyx with 5–7 linear to narrowly lanceolate to obovate lobes; lobes erect to spreading or sometimes recurved; corolla infundibular with a very short inconspicuous tubular base (typically hardly 1.5 cm long) that is much shorter than the inflated upper part, lobes 5–7, obovate, contorted in bud, spreading in the open flower, the distal half sometimes slightly recurved; stamens 5–7, attached to the upper part of the corolla throat, filaments very short, anthers linear, medifixed, with apical half or at least apices exserted in the open flower, splitting longitudinally, pollen in tetrads; ovary 1-locular, pubescent, style slender, stigma clavate, 2-lobed, reaching the throat in the open flower, placentation parietal, ovules numerous. *Fruits* globose to ellipsoid, smooth, crowned by calyx remains; seeds many.

KEY TO *THAIGARDENIA* SPECIES

1. Leaf apices obtuse and often minutely cuspidate. Calyx lobes elliptic to oblanceolate, 1.5–4 mm wide **1. T. cambodiana**
1. Leaf apices various, not cuspidate. Calyx lobes triangular to linear, not exceeding 1.5 mm width
  2. Leaf secondary veins (5–)7–10(–13) pairs, fading towards the margin without conspicuous loops; tertiary veins lax or dense, immersed or prominent on the lower leaf surface. Fruiting calyx lobes triangular or linear
    3. Young twigs and leaves glabrous or subglabrous on both surfaces, at most with scattered caducous minute pale trichomes much shorter than 0.5 mm. Leaf blades with fine veins forming lax reticulations immersed in the upper surface when dry, apices most often acute, occasionally obtuse or subcaudate, very unusually retuse, with domatia in secondary vein axils on the lower surface. Petioles (1–)3–5 mm long. Calyx lobes linear, spreading to recurved including at fruit stage; more than twice the length of the calyx tube (i.e., the tubular part of the hypanthium limb), not exceeding 1 mm wide throughout **2. T. collinsiae**
    3. Young twigs and leaves densely covered with caducous pale short erect trichomes 0.5–1 mm long. Leaf blades with prominent tertiary veins in a dense subscalariform-reticulate formation on the upper surface when dry, apices typically rounded to obtuse, without domatia in secondary vein axils on the lower surface. Petioles subobsolete to 1(–2) mm long. Calyx lobes broadly to narrowly triangular (sub-linear), erect even to fruit stage; shorter than or (rarely) to twice as long as the calyx tube, 0.5–1.5 mm wide at the base **3. T. similis**
  2. Leaf secondary veins 4–6 pairs, conspicuously looping near the margin; tertiary veins lax, immersed in the lower leaf surface. Fruiting calyx lobes linear **Thaigardenia 'Nhatrang'** (possibly unnamed taxon requiring better material to diagnose)

Distribution.— A genus of three known species. Thailand, Laos, Cambodia, Vietnam, China (Hainan).

Etymology.— The name *Thaigardenia* refers to Thailand, where studies into the taxonomy of this group were initiated, and where the generic type can be abundantly found, as well as *Gardenia*, the genus in which its species were earlier placed. Thailand has been eponymously included in the nomenclature of two other plant genera: *Thaia* Seidenf. (Orchidaceae) (Seidenfaden, 1975) and *Thailentadopsis* Kosterm. (Leguminosae) (Kostermans, 1977), both of which continue to be in use (Lewis & Schrire, 2003; Xiang *et al.*, 2012).

1. Thaigardenia cambodiana (Pit.) K.M.Wong & Chamch., **comb. nov.** (Fig. 7).— *Gardenia cambodiana* Pit. in Lecomte, Fl. Indo-Chine 3: 250, figs. 19 (13–15), 20 (1). 1923. Type: Cambodia, Kampong Speu Province: Samrong-tong, Mt Chéreer (now Samraong Tong District, Phnum Chreav), Apr. 1870, *L. Pierre 540a* (lectotype **P** [P0083646] photo seen, designated by Ye & Xia, 2016; isolectotypes **P** [P00836465, P00836466] photos seen).

Image of lectotype and isolectotypes available at https://science.mnhn.fr/institution/mnhn/collection/p/item/list?full_text=Gardenia+cambodiana&recordedBy=Pierre&genus=Gardenia

Figure 7. *Thaigardenia cambodiana* (Pit.) K.M.Wong & Chamch. A. Typical habit in several individuals, at Ta Phraya District, Sakaew Province near the border with Cambodia. B. Fruit showing erect calyx lobes. C. Branch sequences with ripe orange-coloured fruits, many already dehisced or damaged by birds. Photos: S. Sawangsawat.

— *Gardenia magnifica* E.T.Geddes, Bull. Misc. Inform. Kew 1928: 243. 1928. Type: Thailand, Prachuap Khiri Khan, Sam Roi Yawt, *A.F.G. Kerr 10894* (holotype **K** [K000763033], isotypes **BK**, **BM** [BM000945314]).

Shrubs or small trees, 2–5 m high; twigs glabrate. *Stipules* fused around the twig, apex obtuse to round, 2–5 mm long, pubescent. *Leaves* opposite and decussate, usually clustered at the branch ends; petioles 1–7 mm long, minutely pubescent to glabrescent; blade thin-coriaceous, (elliptic to) obovate to panduriform, 4–7 × 2–4.5 cm, base cuneate, apex obtuse and shortly acuminate, pubescent especially on veins; secondary veins (5–)8–10(–13) pairs, intercostals faint, with ciliate pit-domatia in secondary vein axils on the lower surface; axillary buds sometimes more than one per axil, mostly paired but rapidly positioned at different levels of the same internode due to differential intercalary growth, axillary branches typically remaining short and ending in a series of abbreviated internodes, the whole somewhat indurated and aiding entanglement with other shoots or branches (contributing to the thicket habit). *Flowers* solitary, terminal to side branches; calyx obconical, up to 13 mm long, lobes 5–7, elliptic to obovate or oblanceolate, 10–15 × 3–4 mm, erect to spreading; corolla infundibular, tube up to 17 mm long, lobes 5–7, obovate, up to 13 mm long; stamens 5–7, attached to the upper part of the corolla throat, filaments very short, anthers up to 12 mm long. *Fruits* subglobose, 10–15 mm diameter, with weak longitudinal ridges, apex with spreading obconical calyx.

Thailand.— EASTERN: Chaiyaphum [15°48′ N 102°02′ E, 200–300 m, 12 Aug. 1972, *Larsen et al. 31730* (**BKF**)]; Nakhon Ratchasima [Sung Nern, *Suvatabhandhu s.n.* (**BK**); 24 Mar. 1958, *Sørensen et al. 2504* (**BKF**, **L**)]; CENTRAL: Saraburi [Aug. 1927, *Put 1094* (**E**); Mueang Saraburi, 100 m, 29 Mar. 1975, *Maxwell 75-334* (**BK**, **L**); ibid., 13 June 1975, *Maxwell 75-589* (**BK**, **L**)].

Distribution.— Cambodia, Laos.

Ecology.— Mixed deciduous forest; about 100 m alt.

Vernacular names.— Phut (พุด), phut khamen (พุดเขมร)(Proposed here).

Additional specimens studied.— CAMBODIA: Koh Kong [route de Sre Ambel, 2 June 1930, *Poilane 17411* (**WAG**)]; Kratie [Sambour, 30 m, 11 Aug. 2007, *Maxwell 07-603* (**L**)]; Pursat [June 1870, *Pierre 540b* (**P**); 1–31 July 1965, *Martin 67* (**L**, **P**)]; Siem Reap [Banteay Spey, ca 6 km north of Khna Rongvas village, 125 m, 29 July 2009, *Maxwell 09-239* (**L**, **P**)]. LAOS: Champasak [Khong, Khong Island, 75 m, 8 Feb. 1997, *Maxwell 97-1056* (**L**)].

2. Thaigardenia collinsiae (Craib) K.M.Wong, Teerawat. & Sungkaew, **comb. nov.** (Fig. 8A).— *Gardenia collinsiae* Craib, Bull. Misc. Inform. Kew 1914: 127. 1914 (‘*collinsae*’). Type: Thailand, Chonburi Province, Sriracha, near beach, Mar. 1913, *E.E.*(*‘Mrs’*) *Collins 110* (lectotype **K** [K000763034] photo seen, designated here; isolectotypes **BM** [BM000945315] photo seen, **E** [E00661602] photo seen).

Image of holotype and isotypes available at https://www.gbif.org/occurrence/912584055, https://data.nhm.ac.uk/media/06263f00-1a8a-4160-b7e1-bba6f3f235a6 and https://data.rbge.org.uk/herb/E00661602

— *Gardenia reflexisepala* N.H.Xia & X.E.Ye, Phytotaxa 257: 194. 2016. Type: China. Hainan Province: Ya County, Baochi Village [now Ledong County, Liguo Town, Baoqu Village], 12 Sept. 1933, *H.Y. Liang 63049* (holotype **IBSC**; isotypes **A**, **IBK**).

Small trees, up to 8 m high; twigs glabrous. *Stipules* fused around the twig, apex obtuse, up to 10 mm long, glabrous to sparsely pubescent, especially at base. *Leaves* opposite and decussate; petioles (1–)3–4(–7) mm long, pubescent to glabrous; blade chartaceous to thin coriaceous, obovate, elliptic to panduriform, 2–10 × 1.5–6 cm, base cuneate to occasionally rounded, apex acute to occasionally obtuse, glabrous to scattered short-hairy on both surfaces; secondary veins (6–)10–13 pairs, intercostals faint, with ciliate pit-domatia in secondary vein axils on the lower surface; axillary buds sometimes more than one per axil, mostly paired but rapidly positioned at different levels of the same internode due to differential intercalary growth, axillary branches typically remaining short and ending in a series of abbreviated internodes, the whole somewhat indurated and aiding entanglement with other shoots or

branches (contributing to the thicket habit). *Flowers* solitary, terminal to side branches; calyx lobes (6–)7, linear, 10–15(–17) × ca 1 mm, typically becoming strongly recurved; corolla infundibular, tube up to 20(–25) mm long, lobes 6, obovate, up to 24 mm long; stamens 6, attached to the upper part of the corolla throat, filaments very short, anthers up to 10 mm long. *Fruits* subglobose, up to 15 mm diameter, with weak longitudinal ridges, apex with reflexed linear calyx lobes.

Thailand.— NORTHERN: Nakhon Sawan [Banphot Phisai, 135 m, 2 Sept. 2016, *Pooma & Pattharahirantricin 7950* (**BKF**); Takli, 220 m, 22 Feb. 2004, *van de Bult 757* (**BKF**, **L**); ibid., 15°18′20″ N, 100°23′46″ E, 132 m, 10 Apr. 2015, *Poopath et al. 1039* (**BKF**); ibid., 100 m, 27 Sept. 2003, *Phonsena et al., 4017* (**BKF**)]; EASTERN: Nakhon Ratchasima [Pak Chong, 14°30′34.42″ N, 101°22′39.10″ E, 28 July 2018, *Sungkaew & Teerawatananon 1575*, *1576*, *1577* (Thailand Natural History Museum); Sikhio, 727 m, 28 Apr. 1942, *Promphubaet 11* (**BKF**)]; SOUTH-WESTERN: Kanchanaburi [Mueang Kanchanaburi, 100 m, 4 Mar. 2009, *Maxwell 09-73* (**L**, **P**); Nong Hoi, ca 250 m, 10 July 1978, *Phengklai et al. 4275* (**BKF**, **L**); Sadong (Sadawng), ca 80 m, 4 Feb. 1965, *Smitinand 8639* (**L**); Sai Yok, Loom Soom, 50 m, 14 Mar. 2006, *Maxwell 06-159* (**L**); ibid., 200 m, 14 May 2006, *Chongko 506* (**L**); Salag Prah Wildlife Sanctuary, 14°15′ N, 99°12′ E, 100 m, 30 Nov. 1971, *van Beusekom et al. 4057* (**L**, **P**); Wang Kanai, ca 300 m, 15 May 1927, *Kerr 12863* (**BK**)]; Ratchaburi [Ban Kao, 20 Nov. 1961, *Larsen 8354* (**BKF**)]; Phetchaburi [Cha-am, ca 5 m, Mar. 1926, *Winit 1796* (**BK**, **BKF**); Huai Sai, 300 m, 25 Aug. 1999, *Niyomdham & Pudjaa 5889* (**BKF**); Khao Yoi, 13°14′6.52″ N, 99°49′39.07″ E, 41 m, 8 Aug. 2023, *Sungkaew & Teerawatananon 1798* (Thailand Natural History Museum); ibid., 13°14′5.75″ N, 99°49′39.78″ E, 31 m, 8 Aug. 2023, *Sungkaew & Teerawatananon 1799* (Thailand Natural History Museum)]; Prachuap Khiri Khan [13 Sept. 1926, *Put 238* (**BK**, **E**); 40 m, 2 July 1920, *Winit 577* (**BK**); Ban Nawng Kang, ca 100 m, 10 July 1926, *Kerr 10914* (**BK**, **E**, **L**, **TCD**); Hua Hin, ca 60 m, 29 June 1996, *Santisuk s.n.* (**BKF**); ibid., 100 m, 1 Aug. 1976, *Maxwell 76-472* (**BK**, **L**); Khao Ngon Payawm, ca 200 m, 5 July 1924, *Kerr s.n.* (**BK**); Mueang Prachuap Khiri Khan, 11°50′14′′ N, 99°49′51″ E, 20 m, 8 Jan. 2002, *Chayamarit et al. 3046* (**BKF**); Pran Buri, 10–70 m, 4 Dec. 1979,

Figure 8. Fruits of *Thaigardenia collinsiae* (Craib) K.M.Wong, Teerawat. & Sungkaew (A), showing a very short calyx tube with linear-tentacular calyx lobes and *T. similis* (Craib) K.M.Wong & L.Neo (B), showing a very short calyx tube with very narrowly triangular calyx lobes. Photos: A. Teerawatananon.

Shimizu et al. T-26103 (**BKF**); ibid., 100–150 m, 14 Aug. 1992, *Niyomdham 2987* (**BKF**); ibid., 12°32′ N, 99°28′ E, 40 m, 1 July, 2000, *Newman et al. 1164* (**AAU**, **E**); ibid., 12°8′ N, 99°58′ E, 17 Aug. 2002, *Middleton et al. 1157* (**BKF**, **L**, **E**, **P**); Sam Roy Yot, 12°25′ N, 99°55′ E, 100–250 m, 6 May 1974, *Larsen & Larsen 33673* (**BKF**, **L**); Thap Sakae, 11°38′ N, 99°37′ E, 150 m, 28 Jan. 2004, *Middleton et al. 2643* (**BKF**)]; CENTRAL: Lop Buri [Chai Badan, 15°14′21″ N, 101°16′ 38″ E, 170 m, 29 Aug. 2001, *Pooma et al. 1228* (**BKF**); Phatthana Nikhom, 170 m, 30 Aug. 2001, *Pooma et al. 3020* (**BKF**, **SING**)]; Suphan Buri [U-Thong, 14°22′29″ N, 99°51′43″ E, 145 m, 25 May 2017, *Pooma & Pattharahirantricin 8004* (**BKF**)]; Saraburi [near Pukae Botanic Garden, 14°29′ N, 100°56′ E, ca 140 m, 20 Nov. 1984, *Murata et al., T51050* (**BKF**); ca 150 m, 5 Mar. 1965, *Smitinand & Phengklai 8650* (**BKF**)]; SOUTH-EASTERN: Sa Kaeo [Khao Aaang Ruenai, 18 Jan. 1997, *Santisuk et al. s.n.* (**BKF**)]; Chonburi [Bahng La Moong, Lahn Island, 125 m, 5 Sept. 2004, *Maxwell 04-459* (**BKF**, **L**); Khao Khiao, under 50 m, 5 Feb. 1969, *Phengklai 1994* (**BKF**); Phattaya, Ko Phai, m.s.l., 11 July 1998, *Wongprasert et al. s.n.* (**BKF**); Sattahip, Ko Samaesan, 0–150 m, 30 May 1998, *Phengklai et al. 15117* (**BKF**); Ko Changkluea, 0–30 m, 13 Feb. 1999, *Phengklai et al. 11466* (**BKF**); Ko Ira, close to sea level, 7 Sept. 1975, *Maxwell 75-999* (**BK**, **L**); Ko Jan, m.s.l., 13 June 1998, *Wongprasert et al. s.n.* (**BKF**); Ko Juang, m.s.l., 10 July 1998, *Wongprasert et al. s.n.* (**BKF**); ibid., m.s.l., 8 Aug. 1998, *Wongprasert et al. s.n.* (**BKF**); Ko Khram, 0–40 m, 14 Aug. 1999, *Phengklai et al. 11917* (**BKF**); ibid, 0–10 m, 3 Aug. 1999, *Phengklai et al. 11960* (**BKF**); Ko Maravichai, 0–70 m, 24 June 2000, *Phengklai et al. 12488* (**BKF**); Ko Phai, 0–50 m, 26 Aug. 2000, *Phengklai et al. 12828* (**BKF**); Si Chang Island, 50 m, 14 Feb. 1993, *Maxwell 93-163* (**BKF**, **L**); ibid., 75 m, 24 July 1993, *Maxwell 93-823* (**BKF**, **L**); Sriracha, 2.4 m, Mar. 1913, *Collins 231* (**BM**, **E**, **K**, **P**); ibid., 16 Mar. 1923, *Collins 778* (**BK**, **US**); ibid., 29 Mar. 1927, *Collins 1504* (**BK**, **US**)]; PENINSULAR: Surat Thani [Ko Mae-Koh, 0–100 m, 25 Apr. 2009, *Phengklai et al. 15937* (**BKF**); Ko Tao, ca 10 m, 10 Apr. 1927, *Kerr 12811* (**BK**)]; Without locality: *Smitinand 8508* (**BKF**).

Distribution.— South China (Hainan).

Ecology.— Scrub forest, mixed deciduous forest to dry evergreen forest on limestone: sea level–300 m.

Additional specimens studied.— CHINA: Hainan [Gan′en County, Mt. Haobiling (now Dongfang City, Tianan Village), 11 Aug. 1936, *Lau 27656* (**A**, **IBSC**); Ledong, Jiusuo Town, 12 Sept. 1954, *Liang 68341* (**IBSC**); Sanya, Tianya Town, 21 Aug. 1976, *Chung 60210* (**IBSC**)].

Vernacular names.— Phut (พุด), phut pha (พุดผา), khoi dan (ข่อยด่าน), khoi hin (ข่อยหิน)(General).

Uses.— Ornamental.

Nomenclatural notes.— The collection *Collins 110* was mentioned as the ‘type′ of *Gardenia collinsiae* in the protologue by Craib (1914). Three duplicates (Art. 9.3 of ICN, Turland *et al.*, 2018) matching the detailed description in the protologue in BM, E, K were available. We select the **K** specimen (K000763034) as the lectotype since it is the specimen in best condition and the other specimens in **BM** (BM000945315) and **E** (E00661602) are then isolectotypes.

3. Thaigardenia similis (Craib) K.M.Wong & L.Neo, **comb. nov.** (Figs. 8B, 9).— *Randia similis* Craib, Bull. Misc. Inform. Kew 1911: 391. 1911. — *Gardenia similis* (Craib) Craib, Fl. Siam. 2: 122. 1932. Type: Thailand, Lower Siam, Paknampo, dry deciduous jungle, *D.O. Witt 22* (holotype K [K000763031]).

— *Gardenia angkorensis* Pierre ex Pit. in Lecomte, Fl. Indo-Chine 3: 252. 1923. Type: Cambodia, Kampong Thom Province: Dai kla, 29 May 1909, *Magnen, J.-E. Gourgand & V.L. Châtillon s.n.* (lectotype **P** [P00836460] photo seen, designated by Ye & Xia, 2016; isolectotype **P** [P04001729] photo seen).

— *Gardenia saxatilis* E.T.Geddes, Bull. Misc. Inform. Kew 1928: 243. 1928. Type: Thailand, Nakawn Panom Province, Muk Tahan (now in Mukdahan Province), 100 m, 6 Feb. 1924, *A.F.G. Kerr 8049* (lectotype **BM** [BM000945313] photo seen, designated here; isolectotypes **BK** [BK257343!], **K** [K000763032] photo seen, **P** [P00836487] photo seen, **TCD** [TCD0017634] photo seen).

Images of types available at https://data.nhm.ac.uk/media/c7b9ff02-0d14-4a6a-83d3-8b6c6a6dcb63, https://plants.jstor.org/stable/10.5555/al.ap.specimen.bk257343, https://www.kew.org/herbcatimg/340619.jpg, http://coldb.mnhn.fr/catalognumber/mnhn/p/p00836487 and http://plants.jstor.org/stable/10.5555/al.ap.specimen.tcd0017634

Shrubs or small crooked trees, 2–4 m high; young twigs with short pale trichomes. *Stipules* fused around the twig, apex acute to round, 2–3(–5) mm long, pubescent. *Leaves* opposite and decussate, usually clustered at the branch ends; petioles 1–4 mm long, pubescent; blade coriaceous, obovate, not infrequently panduriform, elliptic to sub-orbicular, 1.5–4.5 × 1–2.5 cm, base cuneate to obtuse, apex acute, rounded to obtuse or sub-emarginate, densely pale pubescent on both surfaces but sometimes trichomes caducous; secondary veins (5–)6–10(–12) pairs, intercostal veins densely sub-scalariform to reticulate, prominent on upper surface when dry, without domatia in secondary vein axils on the lower surface; axillary buds sometimes more than one per axil, mostly paired but rapidly positioned at different levels of the same internode due to differential intercalary growth, axillary branches typically remaining short and ending in a series of abbreviated internodes, the whole somewhat indurated and aiding entanglement with other shoots or branches (contributing to the thicket habit). *Flowers* solitary, terminal to side branches; calyx lobes 6, deltoid-lanceolate, 2–4 × 0.5 mm, erect; corolla infundibular, tube up to 25 mm long, lobes (5–)6(–7), obovate, up to 35 mm long; stamens 6, attached to the upper part of the corolla throat, filaments very short, anthers 10–15 mm long. *Fruits* ovoid, ellipsoid to subglobose, 10–15 mm diameter, smooth, apex with erect to slightly spreading deltoid-lanceolate calyx.

Thailand.— NORTH-EASTERN: Udon Thani [Non Sang, 23 May 1968, *Bunchuai 1652* (**BKF**, **L**, **P**)]; Nong Khai [Phu Wua Wildlife Sanctuary, 250–350 m, 6–7 May 1997, *Puff 970505-1/10* (**BKF**)]; Bueng Kan [Bung Khla, 21 June 1997, *Niyomdham 5095* (**BKF**)]; Sakon Nakhon [Phu Phan National Park, *Chantaranothai et al. 462* (**BKF**)]; Mukdahan [Mueang Mukdahan, 16°26′01″ N, 104°48′33″ E, ca 180 m, 23 Aug. 2001, *Pooma et al. 2433* (**BKF**); Mukdahan National Park, 16°30′ N, 104°43′ E, 285–290 m, 5 Aug. 2004, *Nielsen et al. 1501* (**BKF**); Nikom-Khamsoi, Phu Moo Forest Park, 280 m, 11 Dec. 1982, *Koyama et al. T-30844* (**P**); Phu Pha Thoep National Park, ca 150 m, 27 Oct. 1998, *Wongprasert s.n.* (**BKF**)]; Khon Kaen [Mancha Khiri, 16°04′54″ N, 102°20′31″ E, 200 m, 28 Aug. 2001, *Pooma et al. 2916* (**BKF**)]; EASTERN: Chaiyaphum [Mueang Chaiyaphum, Tat Ton National Park, 15°58′55.32″ N, 102°2′20.11″ E, 262

Figure 9. Open flower (inset) and fruiting twig of *Thaigardenia similis* (Craib) K.M.Wong & L.Neo, showing narrowly triangular lobes on a short calyx tube. Photos: D. Prathumthong (flower) and A. Teerawatananon.

m, 29 July 2018, *Sungkaew & Teerawatananon 1578* (Thailand Natural History Museum); Nong Bua Deng, 15°10′ N, 101°30′ E, 300–400 m, 15 Aug. 1972, *Larsen et al. 31893* (**BKF**, **L**, **US**)], Ubon Ratchatani [Khong Chiam, 19 Oct. 1998, *Niyomdham 5588* (**BKF**); ibid., 150 m, 16 Sept. 2001, *Maxwell 01-451* (**BKF**, **L**); ibid., 8 July 2004, *Wongprasert 047-5* (**BKF**); ibid., 1 Mar. 2007, *Suddee et al. 3089* (**BKF**); ibid., 15°24′4.78″ N, 105°30′5.61″ E, 171 m, 27 Oct. 2021, *Sungkaew & Teerawatananon 1630* (Thailand Natural History Museum); Nam Yuen, 26 May 2004, *Virapongse AV79* (**BKF**); ibid., 1 May 2005, *Virapongse AV261* (**BKF**); Phibun Mangsahan, 15°17′29″ N 105°20′5″ E, 124 m, 2 July 2014, *Meeboonya et al. RM323* (**AAU**, **BKF**); Pho Sai, 15°45′18.46″N, 105°29′48.64″E, 156 m, 17 Nov. 2017, *Sungkaew 1572* (Thailand Natural History Museum)]; CENTRAL: Lop Buri [Lam Narai, 50 m, 5 Apr. 1975, *Smitinand 12093* (**BKF**)]; Without locality: [1931, *Kerr 19958* (**TCD**)]; [May 1932, *Kerr 21422* (**TCD**)].

Distribution.— Cambodia, Laos.

Ecology.— Mainly in open areas on exposed sandstone bedrock in deciduous dipterocarp and mixed deciduous forests.

Additional specimens studied.— CAMBODIA: Angkor-thom [7 Aug. 1873, *Harmand 940* (**P**)]; Dangrek [14 Aug. 1928, *Poilane 14938* (**VNM**)]. LAOS: [21 Oct. 1938, *Poilane 28219* (**P**)].

Vernacular names.— Pat hin (ปัดหิน), khoi (ข่อย), khoi khok (ข่อยโคก), khoi dan (ข่อยดาน), khoi hin (ข่อยหิน), sam phan ta (สามพันตา), phut pha (พุดผา), phut (พุด), phut pae (พุดป่า), phut hin (พุดหิน).

Uses.— Ornamental: the crooked forms especially favoured for ‘bonsai’ culture.

Nomenclatural notes.— The collection *A.F.G. Kerr 8049* was mentioned as ‘type’ of *Gardenia saxatilis* in the protologue by Geddes (1928), but he did not specify a holotype. We found five duplicates which are syntypes (Art. 9.3 of ICN, Turland *et al.*, 2018) matching the detailed description and specimen label information included in the protologue “Nakawn Panom, Muk Tahan (now in Mukdahan Province), 100 m., rocky ground, *A.F.G. Kerr 8409*” in five herbaria (BK, BM, K, P, TCD). We select the **BM** specimen (BM000945313) as the lectotype since it is the specimen in best condition, the other specimens in **BK** (BK257343), **K** (K000763032), **P** (P00836487), and **TCD** (TCD0017634) are isolectotypes.

Incompletely understood taxon:

Thaigardenia ‘Nhatrang’

The fourth entity is an incompletely understood taxon from Vietnam (*Thaigardenia* ‘*Nhatrang*’), reflected in the Key. The few specimens studied for this are from the VNM Herbarium in Saigon, as well as a duplicate at WAG (now in Leiden).

Specimens studied.— VIETNAM: Annam [Nhatrang, S Vietnam, 10 Sept. 1922, *Poilane 4532* (**P** [P04001481], **WAG** [WAG.1322170]); 24 Mar. 1922, *Poilane 2814* (**P** [P04001736], **VNM** [VNM00011923]), 6 Apr. 1922, *Poilane 2912* (**P** [P04001479]); 14 Apr. 1922, *Poilane 3017* (**P** [P04001480, P04001737], **VNM** [VNM00011925]); 21 Apr. 1922, *Poilane 3082* (**P** [P04001482], **VNM** [VNM00011926])].

Reproductive ecology and phenological aspects

Little is known regarding pollination or reproductive ecology. One of us (VC) has observed bulbuls feeding on exposed seeds of ripe *Thaigardenia similis* fruits. We can infer that birds could be habitual dispersers (Fig. 7C).

We examined the dates of flowering and fruiting on all available specimens, with respect to very broadly circumscribed latitudinal zones; N, NE and E Thailand as the northernmost latitudinal zone; SW, C and SE Thailand; and Peninsular Thailand as the southernmost. No clear seasons for flowering and fruiting in terms of collecting months were discerned within and between zones, although it is possible that *Thaigardenia similis* may have two discrete seasons for flowering (around April–May and August) within the northern zone. *Thaigardenia collinsiae*, the most widespread species, also did not display any immediately obvious difference between the northern and central zones, at least from the limited collections available.

Notwithstanding the sporadic flowering encountered in the field in our experience, there are suggestions of gregarious flowering documented by others (see https://www.banmuang.co.th/news/region/271531). This could be due to local variation in climate, to which small populations respond.

It is possible that taken as a whole, the latitudinal span of Thailand does not allow easy distinction of seasonality effects simply by the months of specimen

collections. Also, there may be more-or-less specific zones of climatic adaptations displayed by different plant taxa.

The past and the future: some biogeographic postulates

It is admittedly difficult to draw firm biogeographic conclusions without any well-sampled phylogeny and divergence time estimation of the genus and its close allies, so the ideas presently discussed are still at best speculative rather than demonstrable. They serve as possible directions in the continuing investigation into this highly interesting group of plants.

Based on the morphological affinities of *Thaigardenia* to *Gardenia s.s.*, as well as the appearance of a consistent and unique morphological trait (axillary buds and branches not in strictly opposite pairs) in the former, we may expect the much more geographically widespread *Gardenia* to be ancestral with respect to *Thaigardenia*. It is naturally tempting to also suggest that the apparent commonness of *Thaigardenia* species on xerophytic, soil-deficient substrates, (such as in the drier sandstone-derived rocky landscapes of east Thailand and Laos, the thin skeletal soils on limestone outcrops elsewhere in Thailand, or similarly exposed slopes in Hainan island) could represent the emergence of a lineage adapted to such environment as this region of the mainland SE Asian region was shaped through a period of geographical and climatic evolution since the Miocene collision of the Indian plate with south Asia.

Horticultural potential and conservation aspects

There appears to be quite a lot of interest in *Thaigardenia collinsiae* and *T. similis* because individual plants can be rather floriferous (at the right season) and the numerous white blooms adorning a multiple-stemmed plant can be a sight to behold. In some areas, the populations flower gregariously.

https://www.kasettambon.com/ข่อยหิน-หรือ-พุดผา-ลำต้น/

https://www.banmuang.co.th/news/region/271531

https://apps.phar.ubu.ac.th/phargarden/main.php?action=viewpage&pid=83

Among the horticultural community in Thailand, another aspect has gained popularity. Plants of *Thaigardenia collinsiae* and *T. similis* especially are grown as bonsai because of their slow growth, unusual branching and crooked, sometimes gnarled stem bases in very old individuals. Also, at times that these plants are seasonally semi-deciduous, or when they are maintained so as to simulate this, the restriction of leaves to only scattered shoots seems to enhance their appearance for this genre of horticulture.

https://web.facebook.com/watch/live/?ref=watch_permalink&v=468981437808054

https://www.youtube.com/watch?v=BAlciBrgb7w

We were concerned that this value may have led to destructive harvesting of mature plants in the wild. Also, we considered that, in view of the naming of these plants as the new genus *Thaigardenia*, their popularity would only increase in Thailand, and there could be a surge in pressure on populations in the wild. With these in mind, we visited an Ordovician limestone outcrop at the grounds of the Khao Thamsua Temple, U-Thong, in Suphan Buri Province, and found a thriving population of *T. collinsiae*. We also visited a nursery not far away that had some stock of *T. collinsiae* and *T. similis* 'bonsai'.

Our conclusions in this context were as follows:

(1) *Thaigardenia collinsiae* is somewhat widespread in Thailand and there is no indication of wild populations being ravaged. Bonsai nurseries test a very wide range of species for their specific growth responses and value and there is no special selection for *T. collinsiae*, there being many candidates for ornamental 'bonsai'.

(2) *Thaigardenia* spp. are slow-growing, and so many other faster-growing 'bonsai' candidate taxa are preferred by nurseries.

(3) There is a provision for an IUCN conservation category called 'Other effective area-based conservation measures' (OECMs), which are areas that achieve the long term and effective in-situ conservation of biodiversity outside of protected areas. This category is feasible in Thailand (VC, this authorship) and would seem to apply to this circumstance.

https://www.iucn.org/our-union/commissions/group/iucn-wcpa-other-effective-area-based-conservation-measures-specialist

In our present view, the populations of *Thaigardenia* would seem reasonably safe from a conservation perspective.

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