



## *Hoya papaschonii* (Apocynaceae: Asclepiadoideae), a new species from southern Thailand with a peculiar corona

MICHELE RODDA<sup>1</sup> & ENRICO ERCOLE<sup>2</sup>

<sup>1</sup>The Herbarium, Singapore Botanic Gardens, 1 Cluny Road, 259569, Singapore; e-mail: [rodda.michele@gmail.com](mailto:rodda.michele@gmail.com)

<sup>2</sup>Dipartimento di Scienze della Vita e Biologia dei Sistemi, Viale PA Mattioli 25, 10125, Torino, Italy

### Abstract

The new *Hoya* species, here described and fully illustrated, is an epiphytic shrub with white-cream coloured flowers superficially similar to those of *Hoya telosmoides*. Its gynostegial corona includes five staminal and five interstaminal lobes, the latter never before observed in *Hoya*. The placement of the new species within *Hoya* was confirmed by a phylogenetic analysis based on nuclear ribosomal ITS and 5'-ETS regions, and chloroplast *psbA-trnH* and *trnT-trnL* intergenic spacers. It belongs to a group of species including *Hoya multiflora* and *Hoya praetorii*, characterised together with *H. papaschonii* by non-climbing habit, thin leaves lacking basal colleters, and short-lived peduncles.

**Keywords:** *Hoya* sect. *Centrostemma*, *Hoya* sect. *Cystidianthus*, *Hoya* sect. *Plocostemma*, ITS, 5'-ETS, *psbA-trnH*, *trnT-trnL*.

### Introduction

The flowers of Apocynaceae subfamilies Asclepiadoideae and Periplocoideae are characterised by an extreme diversification in the morphology of the corona (Endress & Bruyns 2000, Fishbein 2001, Kunze 2005). A general system to describe the corona devised by Liede & Kunze (1993) defined basic corona types and subdivided them as corolline and gynostegial. Corolline coronas (Cc) are situated primarily in the petal sinuses or form a continuous ring around the base of the gynostegium (Ca), while gynostegial coronas are connate with the stamens. These can be staminal (Cs), attached at the back of the stamens, or interstaminal (Cis), originating at the base of the filament tube in the interstaminal sections. Liede & Kunze (1993) suggested that complex corona morphologies arise from the combination and fusion of these basic corona types. In contrast, Fishbein (2001) postulated that staminal and interstaminal coronas may be treated as homologous, differing simply in the varied elaboration of different segments of the flower, as observed in *Sarcostemma* Brown (1810: 463) (now *Cynanchum* Linnaeus [1753: 212]) by Endress & Bruyns (2000).

The most common corona type in *Hoya* Brown (1810: 459) (Apocynaceae-Asclepiadoideae-Marsdenieae [Endress *et al.* 2014]) is staminal and its lobes are typically inrolled on the outer edge (Forster & Liddle 1991, Forster *et al.* 1998). In a recent study on corona morphology of *Hoya* by Kunze & Wanntorp (2008a), the staminal corona was described as the combination of two non-homologous elements: (1) the staminal lobe, formed by an inner and an outer process (Rintz 1978), and (2) two latero-basal lobes of the anther that can form two homologous structures, the revolute margins and the anther skirt. The lobes of the anther skirt originating from adjoining staminal corona lobes are usually separated by the guide rails. However, in *Hoya spartioides* Kloppenburg (2001: 8), in contrast, the anther skirts are fused in the interstaminal sector (Kunze & Wanntorp 2008b). In addition, a few *Hoya* species, e.g. *Hoya multiflora* Blume (1823: 49), and *Hoya curtisii* King & Gamble (1908: 563), exhibit an annular corona (Ca) situated below the gynostegium, connate to the pollen tube (Kunze & Wanntorp 2008a). Annular corolline coronas are rare in other Marsdenieae but instead commonly observed in Gonolobinae and Ceropegieae (Liede & Kunze 1993, Fishbein 2001, Krings 2008).

Based on phylogenetic analyses (Wanntorp *et al.* 2006a,b), a reassessment of morphological synapomorphies for *Hoya* was undertaken by Wanntorp & Kunze (2009). However, the recently described *Hoya ignorata* Trần *et al.*

(2011: 509) and *Hoya corymbosa* Rodda *et al.* (2013: 1126) bear very atypical corona morphologies not included in Wanntorp & Kunze (2009). The former exhibits a globular corona without distinct lobes and the latter anvil-shaped corona lobes without inrolled edges. Similarly, species formerly in the genus *Clemensiella* Schlechter (1915: 566) have been transferred to *Hoya* based on phylogeny, but not on morphology (Wanntorp & Meve 2011). In addition, although most species of *Hoya* are epiphytic or hemi-epiphytic climbers or display a pendulous habit, several recently described species exhibit a shrubby epiphytic habit otherwise rare for the genus (e.g. *Hoya ignorata*, *H. corymbosa*, *Hoya medinillifolia* Rodda & Simonsson [2011: 149], *Hoya lockii* Pham & Averyanov [2011: 49], and *Hoya platycaulis* Simonsson & Rodda [2009: 15]). This further confirms that the genus still requires extensive field investigations and accurate documentation of new species before a satisfactory, comprehensive revision can be compiled.

We here report a new epiphytic shrubby species from Yala province in Thailand that exhibits five staminal corona lobes, as well as five interstaminal lobes. In light of the atypical morphology, the objectives of this study are to: (1) ascertain the position of the new species in *Hoya* by including it in the most recent molecular phylogenetic analysis of the genus (i.e., Wanntorp *et al.* 2014), (2) examine the phylogenetic relationships of the new species with regard to other shrubby *Hoya* species, and (3) describe the new taxon and discuss its sectional placement.

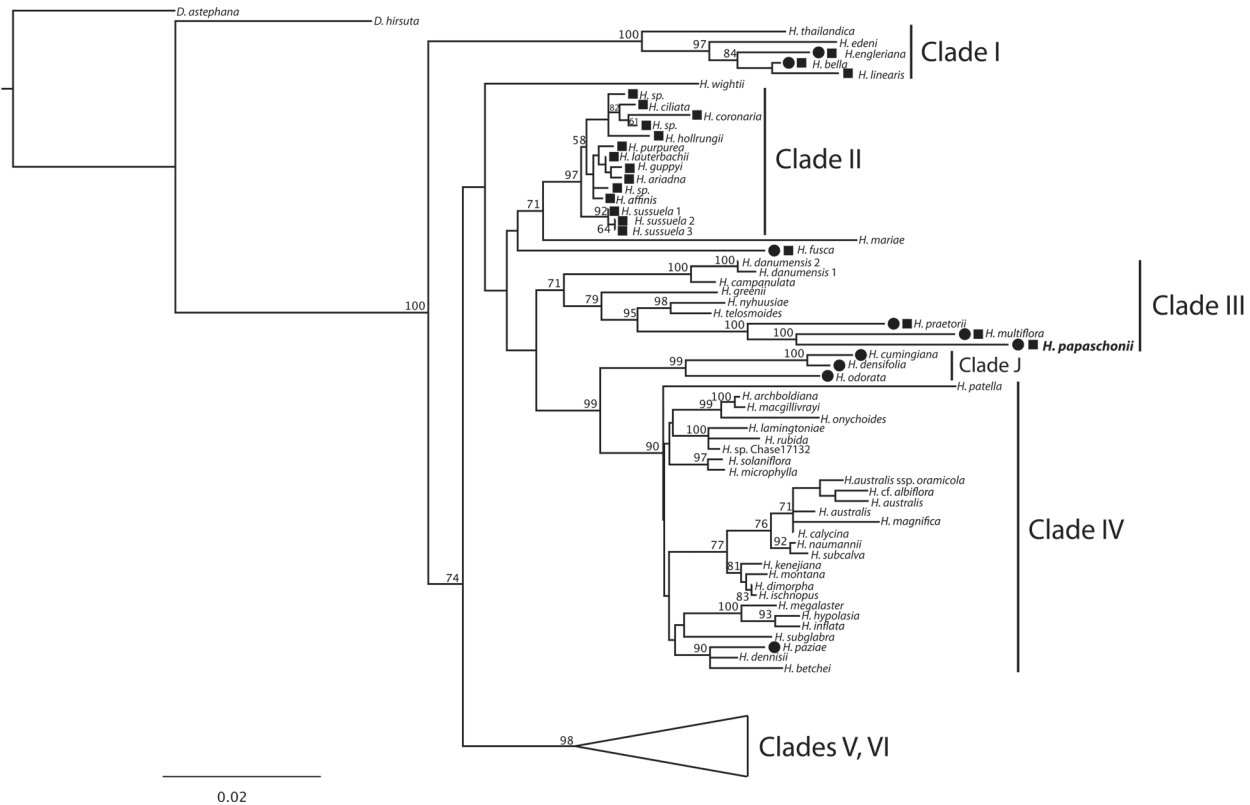
## Materials and methods

**Morphological observation:**—The description of the new species is based on the observation of living specimens cultivated at the Singapore Botanic Gardens (SBG living collection acc. no. 20132440) and herbarium specimens preserved at SING and BKF herbaria. Inflorescence and fruit ontogeny was observed throughout development in living plants. Dissected flowers were examined with the aid of a light microscope. Pollinaria were extracted and mounted on glass slides prior to microscopic observation. For the morphological examination of the corona, we follow Liede & Kunze (1993) and Kunze & Wanntorp (2008a), however our use of ‘interstaminal lobe’ only refers to the position of the lobe in flowers at anthesis and not to its ontogenetic derivation (see Discussion).

**Phylogenetic analysis:**—To confirm the position of the new species within *Hoya*, we included one accession of *Hoya papaschonii* Rodda (Voucher: *KEW2012-011*, SING) in the phylogenetic analysis of *Hoya* based on combined nuclear ribosomal internal transcribed spacer (ITS), external transcribed spacer (5'-ETS), and chloroplast *psbA-trnH* and *trnT-trnL* intergeneric spacers published by Wanntorp *et al.* (2014). DNA of *H. papaschonii* was extracted using DNeasy® Plant Mini Kit (Qiagen Inc., Valencia, CA, USA). PCR amplification and sequencing was carried out using the primer pairs ITS1 and ITS4 for the ITS spacer (White *et al.* 1990), AsETS-F and AsETS-R for 5'-ETS (Yamashiro *et al.* 2004), *psbA3'f/trnHf* (Sang *et al.* 1997, Tate & Simpson 2003) for *psbA-trnH*, and *trnT*<sup>UGU</sup>(a) and *trnL*<sup>UAA</sup>(b) (Taberlet *et al.* 1991) for *trnT-trnL*. PCR amplification was carried out using GoTaq® Green Master Mix (Promega Corporation, Madison, Wisconsin, USA) in 25 µl reactions, containing a concentration of 0.4 µM each primer and approximately 50 ng of total DNA. PCR followed a three-step cycle with initial denaturation at 95°C for 2 min, 35 cycles of denaturation at 95°C for 30", primer annealing at 52°C for 30", and primer extension at 72°C for 1 min, with a final extension at 72°C for 5 min. The PCR products were purified using Wizard® PCR and gel clean-up system (Promega Corporation, Madison, Wisconsin, USA), according to the manufacturer's recommendations. AITBiotech Pte Ltd, Singapore, performed sequencing. The sequences from *H. papaschonii* were deposited in GenBank (ITS: KJ881405; 5'-ETS: KJ881406; *psbA-trnH*: KJ881407; *trnT-trnL*: KJ881408). For the phylogenetic analysis, our sequences were aligned with 155 reference samples, including 153 *Hoya* (ingroup) and two *Dischidia* Brown (1810: 461) (outgroup taxa) corresponding to Matrix 3 in Wanntorp *et al.* (2014). The complete dataset was downloaded from TreeBase (<http://www.treebase.org>, accession no. S13728). Phylogenetic analysis was performed by maximum likelihood using RAxML-HPC v.7.2.6 (Stamatakis 2006, Stamatakis *et al.* 2008), which can rapidly estimate a Maximum Likelihood-based tree, generate a sufficient number of bootstrap pseudo-replicates to determine branch support (Felsenstein 1985, Pattengale *et al.* 2009), and implement multiple model estimates for multi-gene alignments. Set-up details follow Wanntorp *et al.* (2014), with the only difference being the use of GTRGAMMA instead of GTRCAT to find a “best-known tree”. Following Wanntorp *et al.* (2014), bootstrap support values (BS) of 60–79 were considered as moderate support and of 80–100 as high support. Alignment and tree files can be retrieved from TreeBase (<http://www.treebase.org>, accession no. 16078).

## Results

**Phylogenetic analysis:**—The tree generated (Figs. 1 & 2) is in accordance with recent phylogenetic investigations of *Hoya* (Wanntorp *et al.* 2014). All major clades (Clades I to VI) and minor clades (Clades J, M & P) described in Wanntorp *et al.* (2014) are maintained, however, clades III and VI are moderately supported ( $BS_{ML} = 71$  and 65 respectively). *Hoya papaschonii* is nested within the clade identified as Indomalayan Clade III (= *Hoya multiflora* clade sensu Wanntorp *et al.* 2011) (Fig. 1) and is sister to *H. multiflora*.



**FIGURE 1.** Best-known ML tree obtained from the combined nuclear ribosomal regions ITS and 5'-ETS and *psbA-trnH* and *trnT-trnL* intergenic spacers data set. The tree is rooted under the assumption that *Dischidia* and *Hoya* are mutually monophyletic. The part of the tree including clades V and VI, here contracted, is presented in Fig. 2. Bootstrap support values >60 (based on 100 replicates) are indicated at branches. Voucher information and GenBank accession numbers for *H. papaschonii* can be found in the Materials and Methods section. For voucher information and GenBank accession numbers of all other sequences see Wanntorp *et al.* (2014, electronic supplement S1). Species with a shrubby habit are marked by a round symbol; species with short-lived peduncles are marked by a square symbol. In the case names have been updated, the original name is indicated in brackets.

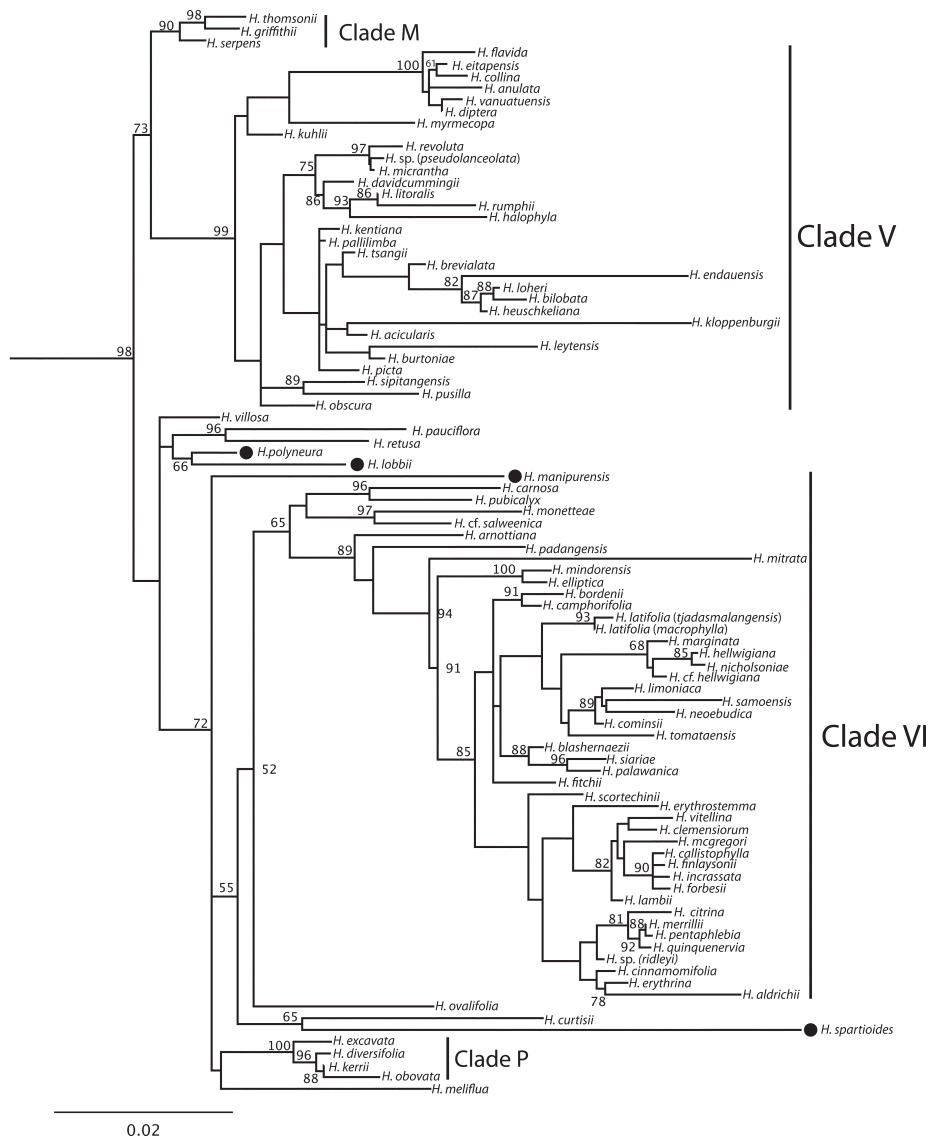
## Discussion

The results of the phylogenetic analysis (Figs. 1 & 2) demonstrate that the new species, despite the atypical corona, is a species of *Hoya* closely related to *Hoya multiflora*. The clade to which it belongs (Clade III) was described by Wanntorp *et al.* (2014) as being, together with Clade II, 'non epiphytic', and 'including eleven shrubby species'. However, the description of the taxa belonging to the clade is inaccurate as none are strictly terrestrial. *Hoya campanulata* Blume (1826: 1064), *H. danumensis* Rodda & Nyhuus (2009: 164), *H. greenii* Kloppenburg (1995: 12), *H. nyhuusiae* Kloppenburg (2003: 1) and *H. telosmoides* Omlor (1996: 290) are generally epiphytic climbers, while *H. multiflora* and *H. praetorii* Miquel (1861: 526) are the only shrubby species but are, once again, generally epiphytic.

Clade III includes the type species of *Hoya* sect. *Cyrtoceras* (*Hoya multiflora*), the type species of *Hoya* sect. *Cystidianthus* (*H. campanulata*), and *H. praetorii*, a species very similar to and easily confused with the type species of *Hoya* sect. *Plocostemma* (*Hoya lasiantha* Blume [1849: 30]). This suggests that the sectional subdivision may need to be revised and redefined. However, as *H. lasiantha*, as well as additional taxa that may belong to the clade have not been so far included in the molecular analysis, we do not formally revise the sectional subdivision of the group yet. The

only clear morphological similarity between all eight taxa in Clade III is to be found in the lack of colleters at the lamina base (otherwise commonly observed in *Hoya*). We have not examined leaves of all taxa included in the phylogeny and therefore are presently unable to assess whether the lack of colleters at the lamina base is a synapomorphy of Clade III. The subclade containing *H. multiflora*, *H. papaschonii*, and *H. praetorii* (BS<sub>ML</sub> 100) is characterised by non-climbing habit, thin leaves, and short-lived peduncles. Numerous species with a shrubby habit are also present in Clade I (*Hoya bella* Hooker [1848: t. 4402], *Hoya engleriana* Hosseus [1907: 315]), Clade IV (*Hoya paziae* Kloppenburg [1990: VI]), Clade J (*Hoya cumingiana* Decaisne [1844: 636], *Hoya densifolia* Turczaninow [1848: 261] and *Hoya odorata* Schlechter [1906: 303]), or are not included in any major or minor clade (*Hoya fusca* Wallich [1830: 68], *Hoya lobbii* Hooker [1883: 54], *Hoya manipurensis* Deb [1955: 50], *Hoya polyneura* Hooker [1883: 54] and *H. spartioides*). Short-lived peduncles are also typical of *H. bella*, *H. engleriana* and *Hoya linearis* Wallich in Wight (1834: 36) (Clade I), and all taxa included in Clade II, *H. fusca*, *H. lobbii*, *H. manipurensis* and *H. polyneura*. It is therefore apparent that shrubby habit evolved independently multiple times in *Hoya*, and is often present in species that have short-lived peduncles. The two characters are mapped in Figs. 1 & 2.

Ontogenetic studies will be required to assess the homologies between the various coronal elements in *H. papaschonii*, as the conspicuous interstaminal lobes might be formed (i) by the fusion of the anther skirts of adjoining staminal corona lobes as observed in *H. spartioides*, (ii) by the fusion of the basal part of adjoining staminal lobes, or (iii) by tissues originating in the interstaminal sector.



**FIGURE 2.** Clades V, VI, M and P of the best-known ML tree obtained from the combined nuclear ribosomal regions ITS and 5'-ETS and *psbA-trnH* and *trnT-trnL* intergenic spacers data set (see Fig. 1 for remainder of tree). Rooted as in Fig. 1

## Taxonomy

### *Hoya papaschonii* Rodda, *spec. nov.* (Figs. 3 & 4)

Similar in habit to *Hoya multiflora*, and in corolla morphology to *Hoya telosmoides* but the gynostegial corona presents a unique combination of both staminal and interstaminal lobes.

Type:—THAILAND. Original collection in Yala: Betong, cultivated in Thailand, Ratchaburi Province, Ratchaburi, November 2012, *Papaschon Chamwong* KEW2012-011 (holotype BKF, isotypes BCU, K, SING).

*Epiphytic* shrub, with white latex in all vegetative parts. *Roots* only basal, no adventitious roots observed. *Stems* slender, 2–4 mm diam., bright green, sparsely pubescent; older stems grey, glabrous; internodes (1.5)4–8 cm. *Leaf blades* thin, not succulent, chartaceous when dry, lanceolate, base acute, apex acuminate, 7–12 × 2–4 cm, dark green on adaxial surface, lighter green on abaxial surface, glabrous, venation pinnate, midrib slightly depressed on adaxial surface, convex on abaxial surface, secondary veins 5–7 pairs, basal collectors absent; *petioles* terete channelled above, (5)10–15(20) × (1.5)2–3 mm in diam., green, sparsely pubescent. *Inflorescences* umbelliform, convex, of 4–10(15) flowers, *peduncles* extra-axillary, negatively geotropic or rarely horizontal, unbranched, 1 or rarely 2 at each node, producing flowers only once, terete, 2–25 mm × 1–1.5 mm, green, sparsely pubescent just below the rachis, otherwise glabrous; *rachis* with membranaceous bracts at the base of each pedicel, triangular, ca. 1 × 1 mm, glabrous. *Flowers* with terete *pedicels* 4–10 mm × ca. 1 mm in diam, light green, glabrous. *Calyx lobes* ovate- broadly triangular, apex round, 1.8–2.2 × 1–2 mm, light green, glabrous, basal collectors absent. *Corolla* tube basally bulbous, tightly enveloping the corona, with a contracted throat, a short almost straight tube and free, lanceolate, spreading lobes, white-cream coloured; basal bulbous part 1.8–2.2 mm tall, 3–4 mm diam., tube ca. 2.5 mm long, ca. 2 mm wide at the base, ca. 3 mm at the apex, free lobes triangular, valvate in bud, laterally recurved outward, 2.5–3.5 × 1.5–2 mm, tube sparsely pubescent inside, lobes glabrous. *Corona* gynostegial, stiff and waxy-looking with staminal (Cs) and interstaminal C(is) elements, 2–2.5 mm high, 3–4 mm in diam., ivory white; Cs inner lobes erect, recurved inward, oblong, alternating with the pollinaria, ca. 1.5 × 0.5 mm, Cs outer lobes missing; C(is) forming 5 globose lobes with an umbonate tip. *Guide rail* terminating in the umbo. *Anthers* broadly triangular, ca. 1 × 0.7 mm, with apical round membranaceous appendage just shorter than the style-head apex. *Pollinia* oblong, narrowing towards the base with a round base and apex, 380–420 × 80–110 µm; pellucid margin apical, short, limited to the upper outer half of the pollinium; *caudicles* much reduced, 60–70 µm long; *retinaculum* ovoid, 120–140 × 50–60 µm; *style-head* 5 angled in cross section, with 5 spreading lobes alternating with the stamens, *style-head apex* conical, 1–1.5 mm long, 0.8–1 mm broad at the base, apex acute; *ovary* bi-carpellate, ovoid, apex narrowed, truncate, 1.5–2 mm high. *Fruits* single or paired fusiform follicles, held at ca. 90° to each other when paired, 7–9 cm × 3–5 mm, light green when immature, light brown at maturity, glabrous. *Seeds* 15–30 in each follicle, slightly flattened, without differentiated margins, 4–5 × ca. 1 mm, long-comose, coma 3–4 cm long.

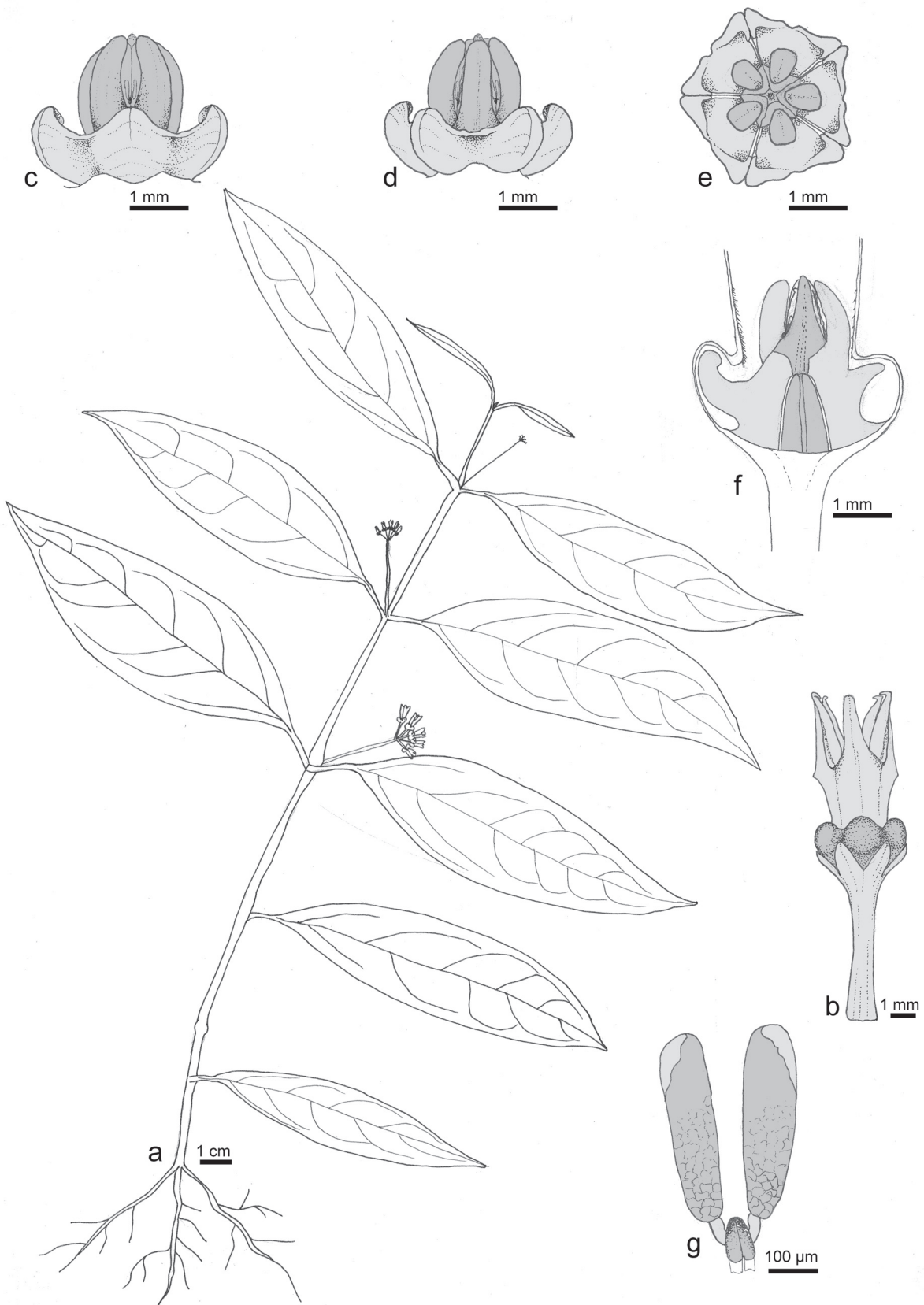
**Etymology:**—The new species is named after the collector and *Hoya* enthusiast Mr. Papaschon Chamwong who, in 2012, sent a specimen of the new species to Singapore Botanic Gardens for identification.

**Distribution and ecology:**—*Hoya papaschonii* is only known from two collections in Betong District, Yala Province in southern Thailand. It was collected in evergreen forest, where it was growing epiphytically.

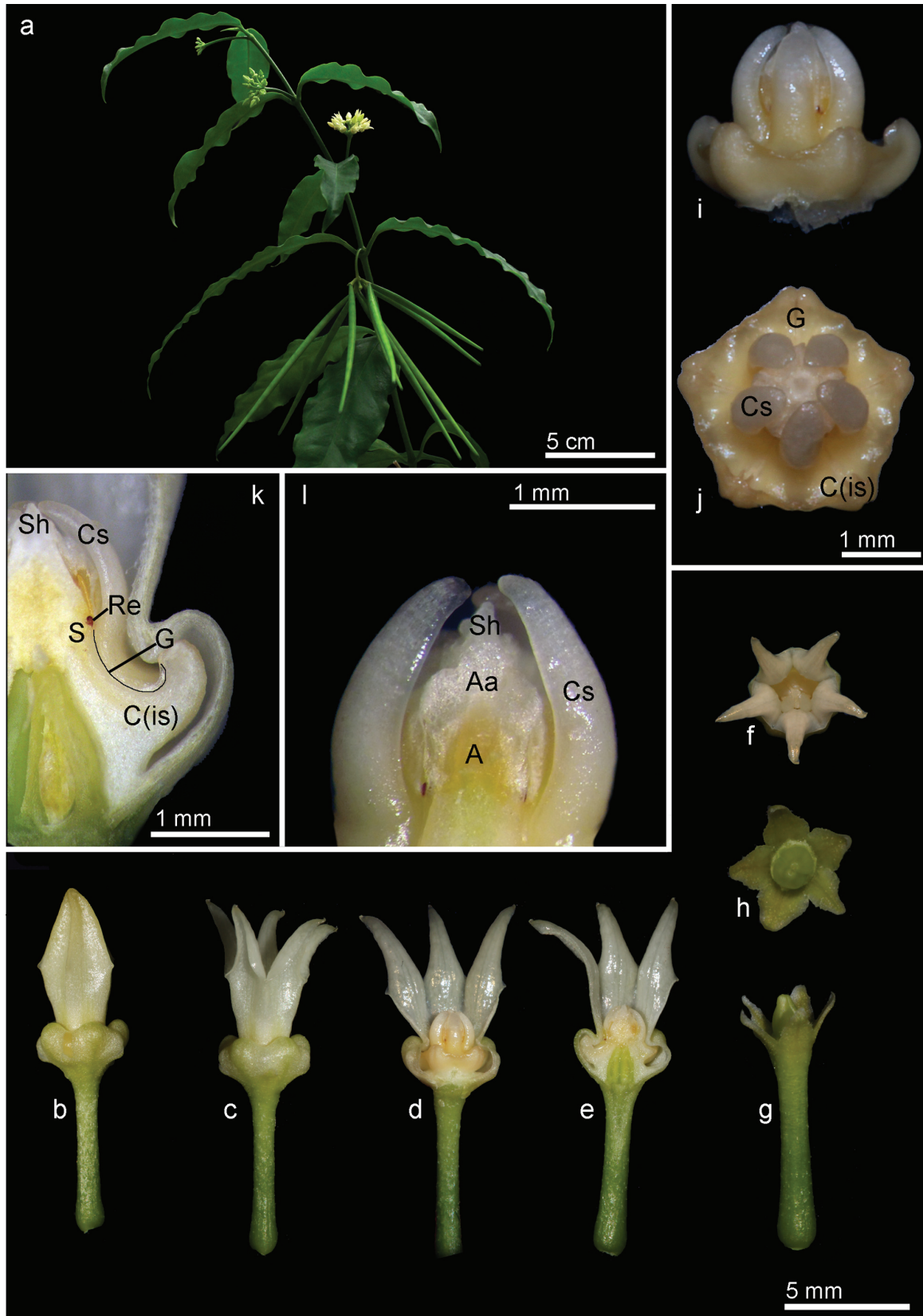
**Conservation status:**—Known only from two collections from Yala Province in Thailand. The distribution area, the population size and the possible threats to the habitat are unknown. We therefore consider *H. papaschonii* as Data Deficient (DD) (IUCN 2014).

**Notes:**—*Hoya papaschonii* exhibits a pellucid margin along the outer portion of the pollinium, a character typical of *Hoya* (Wanntorp & Kunze 2009).

Among species of *Hoya*, the tubular corolla with free spreading lobes of *H. papaschonii*, is only similar to that of *H. telosmoides*, a species from the highlands of Borneo. The two taxa are closely related and belong to Clade III (Fig. 1). However, in *H. telosmoides* the base of the corolla is inflated and does not tightly envelop the corona, the corona is staminal and the corona lobes present the *Hoya*-typical inrolled anther skirt. Among genera closely related to *Hoya*, similar corollas are also encountered in *Oreosparte celebica* Schlechter (1916: 16) (Rodda & Omlor 2014), in *Dischidia* and in unpublished taxa of *Oreosparte* and *Hoya*.



**FIGURE 3.** *Hoya papaschonii*: a. Whole plant; b. Flower, lateral view; c & d. Corona, lateral view; e. Corona, top view; f. Flower, longitudinal section; g. Pollinarium. Drawn by M. Rodda, based on *Papaschon Chamwong KEW2012-011* (SING)



**FIGURE 4.** Photographs of a living plant of *Hoya papaschonii* cultivated at the Singapore Botanic Gardens (acc. no. 20132440): a. Flowering branch and paired fruits; b. Bud; c. Flower, lateral view; d. Flower with two corolla lobes removed, showing the position of the corona basally enveloped by the corolla lobes; e. Flower, longitudinal section; f. Flower, viewed from above; g. Calyx lateral view; h. Calyx and ovaries, viewed from above; i. Corona, lateral view; j. Corona, top view; k. Flower, longitudinal section with the position of the guide rail highlighted in black; l. Anther and anther appendages (after removal of one staminal corona lobe). Photographs by M. Rodda. The parts of the gynostegium are labelled as: A = Anther; Aa = Anther appendage; C(is) = interstaminal corona lobe; Cs = Staminal corona lobe; G = Guide rail; Re = Retinaculum; S = Stigma; Sh = Stigma head.

The general morphology of the corona of *H. papaschonii* is dissimilar from all known species belonging to the genus, but instead superficially resembles the corona of a group of species of *Cynanchum* formerly included in *Sarcostemma* (Meve & Liede-Schumann 2012), in which the corona exhibits 5 distinct erect staminal lobes and a continuous basal ring of staminal and interstaminal elements. However, in *Cynanchum* the guide rails are linear and terminate shortly below the pollinaria, while in *H. papaschonii* they are very long and terminate at the umbonate tip of the interstaminal lobe. A separation of guide rail and nectar tube as suggested by Kunze & Wanntorp (2008a) is not evident in *H. papaschonii*.

**Additional specimens examined:**—THAILAND. Yala, Betong, Hala-Bala, 22 June 1999, *C. Niyomdham 5715* (BKF!)

## Acknowledgements

This study is part of an on-going research project on the systematics of Marsdenieae. Financial support was received from the National Parks Board (Singapore). We would like to thank the curators of BCU, BK, BKF, BM, BRUN, FI, K, KEP, L, LAE, P, SAN, SAR, SNP, and SING herbaria for allowing access and/or for providing high quality images of herbarium specimens, Dr. Obchant Thaitong and Dr. Manit Kidyoo for the fruitful discussion in preparation for the manuscript and for examining specimens at BCU herbarium; Antone Jones for the fruitful discussion on the morphology of the new taxon. A special thanks goes to Dr. Gillian Khew who has been providing essential advice and allowed access to the facilities in the molecular laboratory at the Singapore Botanic Gardens. Finally we would like to thank Dr. Tanya Livschultz and two anonymous reviewers for their valuable comments on the manuscript.

## References

- Blume, C.L. (1923) *Catalogus van eenige der Merkwaardigste Zoo in- als Uitheemse Gewassen te Vinden in 's Lands Plantentuin te Buitenzorg Opgemaakt Door C. L. Blume, M.D., Directeur van Voorz.* Tuin s.l. n.d. Batavia [Jakarta], 112 pp.
- Blume, C.L. (1826) *Bijdragen tot de flora van Nederlandsch Indië 16*, Ter Lands Drukkerij, Batavia [Jakarta], 1169 pp.
- Blume, C.L. (1849) *Rumphia: sive, Commentationes botanicæ imprimis de plantis Indiæ Orientalis, tum penitus incognitis tum quæ in libris Rheodii Rumphii, Roxburghii, Wallichii aliorum recensentur* (Vol. 4).  
<http://dx.doi.org/10.5962/bhl.title.51502>
- Brown, R. (1810) *Prodromus floræ Novæ Hollandiæ et insulæ Van Diemen, etc.* Richard Taylor et al., London, 590 pp.  
<http://dx.doi.org/10.5962/bhl.title.3633>
- Deb, D.B. (1955) A new species of *Hoya* from Manipur. *Journal of the Indian Botanical Society* 34: 50–52.
- Decaisne, J. (1844) *Hoya*. In: De Candolle, A.P. (Ed.) *Prodromus* 8, Fortin, Masson & Co, Paris, pp. 634–640.
- Endress, M.E. & Bruyns, P.V. (2000) A revised classification of the Apocynaceae s.l. *The Botanical Review* 66: 1–56.  
<http://dx.doi.org/10.1007/bf02857781>
- Endress, M.E., Liede-Schumann, S. & Meve, U. (2014) An updated classification for Apocynaceae. *Phytotaxa* 159: 175–194.  
<http://dx.doi.org/10.11646/phytotaxa.159.3.2>
- Felsenstein, J. (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.  
<http://dx.doi.org/10.2307/2408678>
- Fishbein, M. (2001) Evolutionary innovation and diversification in the flowers of Asclepiadaceae. *Annals of the Missouri Botanical Garden* 88: 603–623.  
<http://dx.doi.org/10.2307/3298636>
- Forster, P.I. & Liddle, D.J. (1991) Variation in *Hoya australis* R.Br. ex Traill (Asclepiadaceae). *Austrobaileya* 3: 503–521
- Forster, P.I., Liddle, D.J. & Liddle, I.M. (1998) Diversity in the genus *Hoya* (Asclepiadaceae-Marsdenieae). *Aloe* 35: 44–48.
- Hooker, W.J. (1848) *Hoya bella*. *Botanical Magazine* 74: t. 4402.
- Hooker, J.D. (1883) *The flora of British India*, vol. 4. London: L. Reeve & Co.
- Hosseus, C.C. (1907) Zwei interessante Neuheiten aus Siam im Kgl. Bot. Garten zu Dahlem. *Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin*. 4: 314–318.  
<http://dx.doi.org/10.2307/3994123>
- IUCN Standards and Petitions Subcommittee. (2014) *Guidelines for using the IUCN Red List categories and criteria*. Version 11. Prepared by the Standards and Petitions Subcommittee. Downloadable from <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>



(accessed: 12 June 2014).

- King, G. & Gamble, J.S. (1908) *Hoya*. In: Materials for a flora of the Malayan Peninsula. *Journal of the Asiatic Society of Bengal. Part 2. Natural History* 74: 559–580.
- Kloppenburger, R.D. (1990) New Philippine *Hoya* species. *Fraterna* 3 supplement: I–VII.
- Kloppenburger, R.D. (1995) *Hoya greenii* Kloppenburger sp. nova. *Fraterna* 8(2): 12
- Kloppenburger, R.D. (2001) Change of genus. *Fraterna* 14(2): 8–10.
- Kloppenburger, R.D. (2003) *Hoya nyhuusiae*. *Fraterna* 16(3): 1–6.
- Krings, A. (2008) Revision of *Gonolobus* s.s. (Apocynaceae: Asclepiadoideae) in the West Indies. *Journal of the Botanical Research Institute of Texas* 2: 95–138.
- Kunze, H. (2005) Morphology and evolution of the corolla and corona in the Apocynaceae s.l. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 126: 347–383.
- Kunze, H. & Wanntorp, L. (2008a) Corona and anther skirt in *Hoya* (Apocynaceae, Marsdenieae). *Plant Systematics and Evolution* 271: 9–17.  
<http://dx.doi.org/10.1007/s00606-007-0602-6>
- Kunze, H. & Wanntorp, L. (2008b) The gynostegium of *Hoya spartioides* (Apocynaceae-Asclepiadoideae): A striking case of incongruence between molecular and phenotypic evolution. *Organisms Diversity and Evolution* 8: 346–357.  
<http://dx.doi.org/10.1016/j.ode.2008.06.002>
- Liede, S. & Kunze, H. (1993) A descriptive system for corona analysis in the Asclepiadaceae. *Plant Systematics and Evolution* 185: 99–284.
- Linnaeus, K. (1753) *Species Plantarum* 1. Laurentius Salvius, Stockholm, 560 pp.
- Meve, U. & Liede-Schumann, S. (2012). Taxonomic dissolution of *Sarcostemma* (Apocynaceae: Asclepiadoideae). *Kew Bulletin* 67: 751–758.  
<http://dx.doi.org/10.1007/s12225-012-9384-2>
- Miquel, F.A.W (1861) *Flora van Nederlandsch Indie* 2. Fried Fleischer, Leipzig, 1103 pp.
- Omlor, R. (1996) Notes on Marsdenieae (Asclepiadaceae): A new, unusual species of *Hoya* from Northern Borneo. *Novon* 6: 288–294.  
<http://dx.doi.org/10.2307/3392096>
- Pattengale, N.D., Masoud, A., Bininda-Emonds, O.R.P., Moret, B.M.E. & Stamatakis, A. (2009) How many bootstrap replicates are necessary? In: Batzoglou, S. (Ed.) *Research in computational molecular biology 13th annual international conference; Proceedings*, Springer, Berlin, Heidelberg, pp. 184–200.
- Pham, V.T., & Averyanov, L.V. (2011) New species from Vietnam – *Hoya lockii* (Apocynaceae, Asclepiadoideae). *Taiwania* 57: 49–54.
- Rintz, R.E. (1978) The peninsular Malaysian species of *Hoya* (Asclepiadaceae). *Malayan Nature Journal* 30: 467–522.
- Rodda, M & Nyhuus, T. (2009) *Hoya danumensis*, a new species of *Hoya* (Apocynaceae, Asclepiadoideae) from Borneo. *Webbia* 64: 163–167.  
<http://dx.doi.org/10.1080/00837792.2009.10670856>
- Rodda, M. & Simonsson, N. (2011) *Hoya medinillifolia* (Apocynaceae Asclepiadoideae), a new species from lowland forests of Sarawak, Borneo. *Webbia* 66: 149–154.  
<http://dx.doi.org/10.1080/00837792.2011.10670893>
- Rodda, M., Simonsson Juhonewe, N. & Ercole, E. (2013) *Hoya corymbosa* (Apocynaceae, Asclepiadoideae), a new unusual species from Sabah, Borneo, and its systematic position based on phylogenetic analysis. *Systematic Botany* 38: 1125–1131.
- Rodda, M. & Omlor, R. (2014) The taxonomy of *Oreosparte* (Apocynaceae: Asclepiadoideae). *Webbia* 68: 91–95.  
<http://dx.doi.org/10.1080/00837792.2013.850898>
- Sang, T., Crawford, D.J. & Stuessy, T.F. (1997) Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany* 84: 1120–1136.  
<http://dx.doi.org/10.2307/2446155>
- Schlechter, R. (1906) New Philippine Asclepiadaceae. *Philippine Journal of Science* 1(Suppl. 4): 295–303.
- Schlechter, R. (1915) Asclepiadaceae Philippinenses I *Repertorium specierum novarum regni vegetabilis* 13: 537–544.  
<http://dx.doi.org/10.1002/fedr.19150133310>
- Schlechter, R. (1916) Neue Asclepiadaceen von Sumatra und Celebes. *Beihefte zum Botanischen Centralblatt* 34: 1–18.
- Simonsson, N. & Rodda, M. (2009) *Hoya platycaulis* Simonsson and Rodda sp. nov., an attractive new *Hoya* (Apocynaceae-Asclepiadoideae) from the Philippines. *Asklepios* 106: 13–18.
- Stamatakis, A. (2006) RAxML-VI-HPC: Maximum-likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.  
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57:

758–771.

<http://dx.doi.org/10.1080/10635150802429642>

- Taberlet, P.L., Gielly, L., Patou, G. & Bouvet, J. (1991) Universal primers for amplification of three noncoding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.  
<http://dx.doi.org/10.1007/BF00037152>
- Tate, J.A. & Simpson, B.B. (2003) Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. *Systematic Botany* 28: 723–737.
- Trần, T.B., Kim, J.H., Kim, D.K., Lee, J., Bui, T.H., Simonsson Juhonewe, N. & Rodda, M. (2011) *Hoya ignorata* (Apocynaceae, Asclepiadoideae): An overlooked species widely distributed across South East Asia. *Novon* 21: 508–514.  
<http://dx.doi.org/10.3417/2010068>
- Turczaninow, N.S. (1848) Asclepiadeae aliquae indesscriptae. *Bulletin de la Société Imperiale des Naturalistes de Moscou* 21: 252–262.
- Wallich, N. (1830) *Hoya fusca*. *Plantae Asiaticae Rariores* 1: 68.
- Wanntorp, L., Kocyan, A. & Renner, S.S. (2006a) Wax plants disentangled: a phylogeny of *Hoya* (Marsdenieae, Apocynaceae) inferred from nuclear and chloroplast DNA sequences. *Molecular Phylogenetics and Evolution* 39: 722–733.  
<http://dx.doi.org/10.1016/j.ympev.2006.01.022>
- Wanntorp, L., Kocyan, A., van Donkelaar, R. & Renner, S.S. (2006b) Towards a monophyletic *Hoya* (Marsdenieae, Apocynaceae): inferences from the chloroplast *trnL* region and the *rbcL-atpB* spacer. *Systematic Botany* 31: 586–596.  
<http://dx.doi.org/10.1600/036364406778388593>
- Wanntorp, L. & Kunze, H. (2009) Identifying synapomorphies in the flowers of *Hoya* and *Dischidia* – towards phylogenetic understanding. *International Journal of Plant Sciences* 170: 331–342.  
<http://dx.doi.org/10.1086/596329>
- Wanntorp, L. & Meve, U. (2011) New combinations in *Hoya* for the species of *Clemensiella* (Marsdenieae, Apocynaceae). *Willdenowia* 41: 97–99.  
<http://dx.doi.org/10.3372/wi.41.41110>
- Wanntorp, L., Gotthardt, K. & Muellner, A.N. (2011) Revisiting the wax plants (*Hoya*, Marsdenieae, Apocynaceae): Phylogenetic tree using the *matK* gene and *psbA-trnH* intergenic spacer. *Taxon* 60: 4–14.
- Wanntorp, L., Grudinski, M., Forster, P.I., Muellner-Riehl, A.N. & Grimm, G.W. (2014) Wax plants (*Hoya*, Apocynaceae) evolution: Epiphytism drives successful radiation. *Taxon* 63: 89–102.  
<http://dx.doi.org/10.12705/631.3>
- White, T.J., Bruns, T., Lee, S. & Taylor, J.W. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (eds.) *PCR protocols: A guide to methods and applications*, Academic Press Inc., New York, pp. 315–322.
- Wight, R. (1834) Contributions to the botany of India, Parbury, Allen & Co., London, 136 pp.
- Yamashiro, T., Fukuda, T., Yokoyama, J. & Maki, M. (2004) Molecular phylogeny of *Vincetoxicum* (Apocynaceae-Asclepiadoideae) based on the nucleotide sequences of cpDNA and nrDNA. *Molecular Phylogenetics and Evolution* 31: 689–700.  
<http://dx.doi.org/10.1016/j.ympev.2003.08.016>