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Phylogenetic studies in the *Hoya* group (*Apocynaceae*, *Marsdenieae*): the position of *Anatropanthus* and *Oreosparte*

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Abstract: Recent molecular phylogenetic studies have shown that *Hoya* is paraphyletic without *Absolmsia*, *Clemensiella*, *Madangia*, and *Micholitzia*. These genera have been placed in synonymy with *Hoya*, but the monophyly of *Hoya* sensu lato relative to other genera of the broader *Hoya* group (*Dischidia*, *Anatropanthus* and *Oreosparte*, the latter two never included in a molecular phylogenetic analysis) remained unclear. Furthermore, no analysis has included both a significant sample of the *Hoya* group and outgroup genera of *Marsdenieae* to test the monophyly of the *Hoya* group and its position within the tribe. To address these gaps, we assembled two data sets: (1) the chloroplast *trnT-trnL-trnF* locus from 110 species and (2) three chloroplast loci (*trnT-trnL-trnF*, *atpB-psbA* spacer and *matK*) and two nuclear loci (nrDNA ITS and ETS) from 54 species. The *Hoya* group is monophyletic and nested in an Asian/Australian clade of *Marsdenia* s.l. The genus *Hoya* is paraphyletic unless *Anatropanthus*, *Dischidia* and *Oreosparte* are included. However, current evidence is not sufficient to synonymize *Dischidia* and *Oreosparte* with *Hoya*. Support for synonymy of *Anatropanthus* with *Hoya* is strong and the new name *H. insularis* is proposed. A clade of three new species with *Oreosparte*-like morphology is sister to the rest of the *Hoya* group and is described as the new genus *Papuahoya*.

Key words: *Anatropanthus*, *Apocynaceae*, *Dischidia*, epiphyte, *Hoya*, *Marsdenia*, *Marsdenieae*, molecular phylogeny, new genus, new species, *Oreosparte*, *Papuahoya*, systematics

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Introduction

Hoya R. Br. (Fig. 1A, B) (*Marsdenieae*, *Asclepiadoideae*) is the largest genus in *Apocynaceae*, comprising 350–450 species of Asian and Australasian succulent epiphytic and terrestrial vines and shrubs (Rodda 2015) that are highly prized horticulturally for their showy “wax” flowers. The flowers of *Hoya* are characterized by the presence of a staminal corona with the proximal (apical) part of the lobe entire, distal (basal) part

of the lobe with an “anther skirt” and revolute margins containing nectaries. The anther guide rails lack inner edges and the pollinia have a pellucid margin along the outer edge (Wanntorp & Kunze 2009; Endress & al. 2019).

The Hoya group — *Hoya* has been associated with a number of smaller genera including *Absolmsia* Kuntze (1 sp.), *Anatropanthus* Schltr. (1 sp.) (Fig. 2), *Clemensiella* Schltr. (2 spp.), *Dischidia* R. Br. (c. 80 spp.) (Fig.

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1C, D), *Heynella* Backer (1 sp.), *Madangia* P. I. Forst. & al. (1 sp.), *Micholitzia* N. E. Br. (1 sp.) and *Oreosparte* Schltr. (1 sp.) (Fig. 1E, F) in what has come to be termed the “*Hoya* group” (Omlor 1996, 1998; Wanntorp & Forster, 2007; Meve & al. 2009). A combination of characters separate these genera from the rest of *Marsdenieae* including succulent and epiphytic growth form (vs. woody and terrestrial), highly condensed, persistent inflorescences that re-flower multiple times before they senesce (vs. expanded, once-flowering deciduous inflorescences), valvate corolla lobes in bud (vs. contorted), and narrow, spindle-shaped seeds (vs. flattened, ovate seeds) (Omlor 1998). However, many of these diagnostic characters are variable within the *Hoya* group (e.g. *H. coronaria* Blume is a terrestrial vine; *H. lanceolata* Wall. ex D. Don has ephemeral inflorescences).

The *Hoya* group has always received strong support as monophyletic in molecular phylogenetic analyses that have sampled at least two of the included genera along with other *Marsdenieae* genera (Potgieter & Albert 2001; Verhoeven & al. 2003; Meve & Liede 2004; Wanntorp & al. 2006a, 2006b, 2011; Surveswaran & al. 2014). However, the studies with the best sampling of *Hoya* group taxa have had the sparsest sampling of other *Marsdenieae* genera (Wanntorp & al. 2011) and vice versa (Verhoeven & al. 2003; Meve & Liede 2004).

In the most comprehensive analysis of the *Hoya* group to date (Wanntorp & al. 2014), *Hoya* was not supported as monophyletic relative to *Absolmsia*, *Clemensiella*, *Dischidia*, *Madangia* or *Micholitzia*. The larger infrageneric sampling of *Hoya* sensu stricto in Wanntorp & al. (2014: fig. 3, 4) does not allow evaluation of the monophyly of *Hoya* relative to *Dischidia* because the latter was designated as the outgroup. In a taxonomically reduced dataset (their fig. 5A), *Dischidia* is nested within *Hoya* but with minimal bootstrap support. All of these genera except *Dischidia* have been synonymized with *Hoya* (Wanntorp & Forster 2007; Wanntorp & Meve 2011). Floral characters including pollinia with pellucid margins, anther guide rails without inner edges, and presence of nectaries inside the revolute margins of the outer processes of the staminal corona lobes, i.e. the “anther skirt”, support the inclusion of *Absolmsia*, *Madangia* and *Micholitzia* in *Hoya* s.l. (Wanntorp & Forster 2007; Wanntorp & Kunze 2009). *Clemensiella* lacks these traits but shares similarities of terrestrial growth form and pollinium morphology with species of the atypical *H.* sect. *Eriostemma* Schltr. (Wanntorp & Meve 2011). With the inclusion of *Clemensiella*, *Hoya* s.l. becomes very heterogeneous, with a circumscription that includes most of the morphological variation within the larger *Hoya* group. This extension of *Hoya* mirrors a trend toward expansion of generic boundaries consequent to molecular phylogenetic analyses of other large *Apocynaceae* genera including *Ceropegia* L. (Bruyns & al. 2015), *Cynanchum* L. (Khanum & al. 2016) and *Vincetoxicum* Wolf (Liede-Schumann & al. 2012).

Anatropanthus Schltr. and *Oreosparte* Schltr. — *Anatropanthus*, *Heynella* and *Oreosparte* are the most poorly known genera of the *Hoya* group (Omlor 1998). No authentic material of these three genera was available for study until *O. celebica* Schltr. was neotypified (Rodda & Omlor 2013) and a detailed description and illustrations were provided. *Oreosparte* shares all the diagnostic characters of the *Hoya* group, but its corona and pollinaria are distinct from both those of *Dischidia* and *Hoya*. *Oreosparte celebica* has erect staminal corona lobes with bifid apices and without revolute margins; the pollinarium has very narrow caudicles and pollinia without pellucid margins. In contrast, *Hoya* has corona lobes with entire apices and generally revolute margins, while *Dischidia* typically has inverted anchor-shaped staminal corona lobes. The pollinaria of both *Dischidia* and *Hoya* generally have well-developed, broad caudicles and the pollinia of *Hoya* typically have pellucid margins. Other undescribed species with the “*Oreosparte* floral phenotype”, i.e. presence of urceolate corollas and stipitate gynostegium with erect corona lobes, have been discovered in herbaria or collected in the field and are also sampled. *Anatropanthus borneensis* Schltr. was known only from its type specimen collected in 1901 in Sarawak, Malaysia, and destroyed during the fire of the Berlin Herbarium in 1943 (Hiepkko 1978; Nicholas 1992). It was recently collected in Kalimantan, Indonesia. Its flowers have a peculiar, curved pedicel that is similar to that of *H. retrorsa* Gavrus & al. The corolla is unique in the *Hoya* group: tubular, apically inflexed and terminating in erect, lanceolate lobes (Fig. 2). The gynostegium has oblong, concave corona lobes, erect and attached at the back of the anthers. The pollinia are erect, with a pellucid margin all along the outer margin as generally seen in *Hoya*. Given the morphological heterogeneity of *Hoya*, a molecular phylogenetic analysis is necessary to ascertain whether *Anatropanthus* and *Oreosparte* should be maintained as separate genera from *Hoya*.

Hoya sections — In addition to the difficulty of drawing the generic boundaries of *Hoya*, no complete infrageneric system has been published to date. Infrageneric groups in *Hoya* are circumscribed based on the shape of the corolla (campanulate, urceolate, rotate, revolute), the corona (size and shape of the staminal corona lobes and their inner and outer processes) and the pollinaria (size and shape of corpusculum, pollinia and caudicles, presence of pellucid margin of the pollinia). The first infrageneric classification of *Hoya* s.l. was published by Miquel (1856), who recognized six sections: *H.* sect. *Cathetostemma* (Blume) Miq., *H.* sect. *Hoya* (published as “*Euhoya*”), *H.* sect. *Otostemma* (Blume) Miq., *H.* sect. *Physostemma* (Blume) Miq., *H.* sect. *Plocostemma* (Blume) Miq. and *H.* sect. *Sperlingia* (Vahl) Miq. Subsequently, Hooker (1885) added three more sections: *H.* sect. *Ancistrostemma* Hook. f., *H.* sect. *Cyrtoceras* (Bennett) Hook. f. and *H.* sect. *Pterostelma* (Wight) Hook.f.; and Schlechter

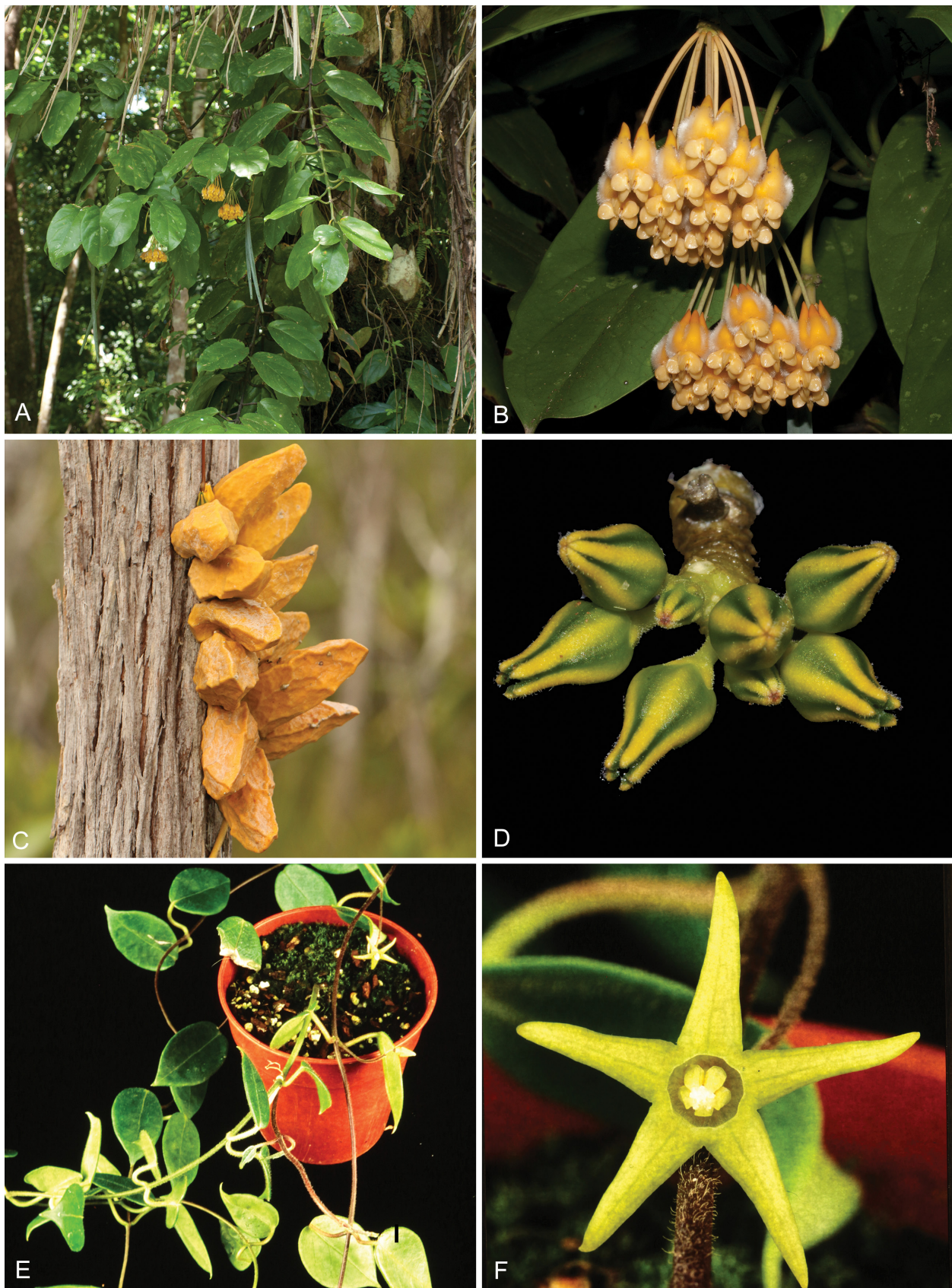


Fig. 1. Morphological diversity within the *Hoya* group. – A: *Hoya lasiantha*, epiphytic shrub growth form; B: *H. lasiantha*, flowers with reflexed corollas and prominent coronas; C: *Dischidia major*, ant-house leaves; D: *D. major*, flowers with closed, urceolate corollas; E: *Oreosparte celebica*, cultivated plant; F: *O. celebica*, flower with urceolate corolla. – Photographs: A–D by M. Rodda; E, F by D. White.

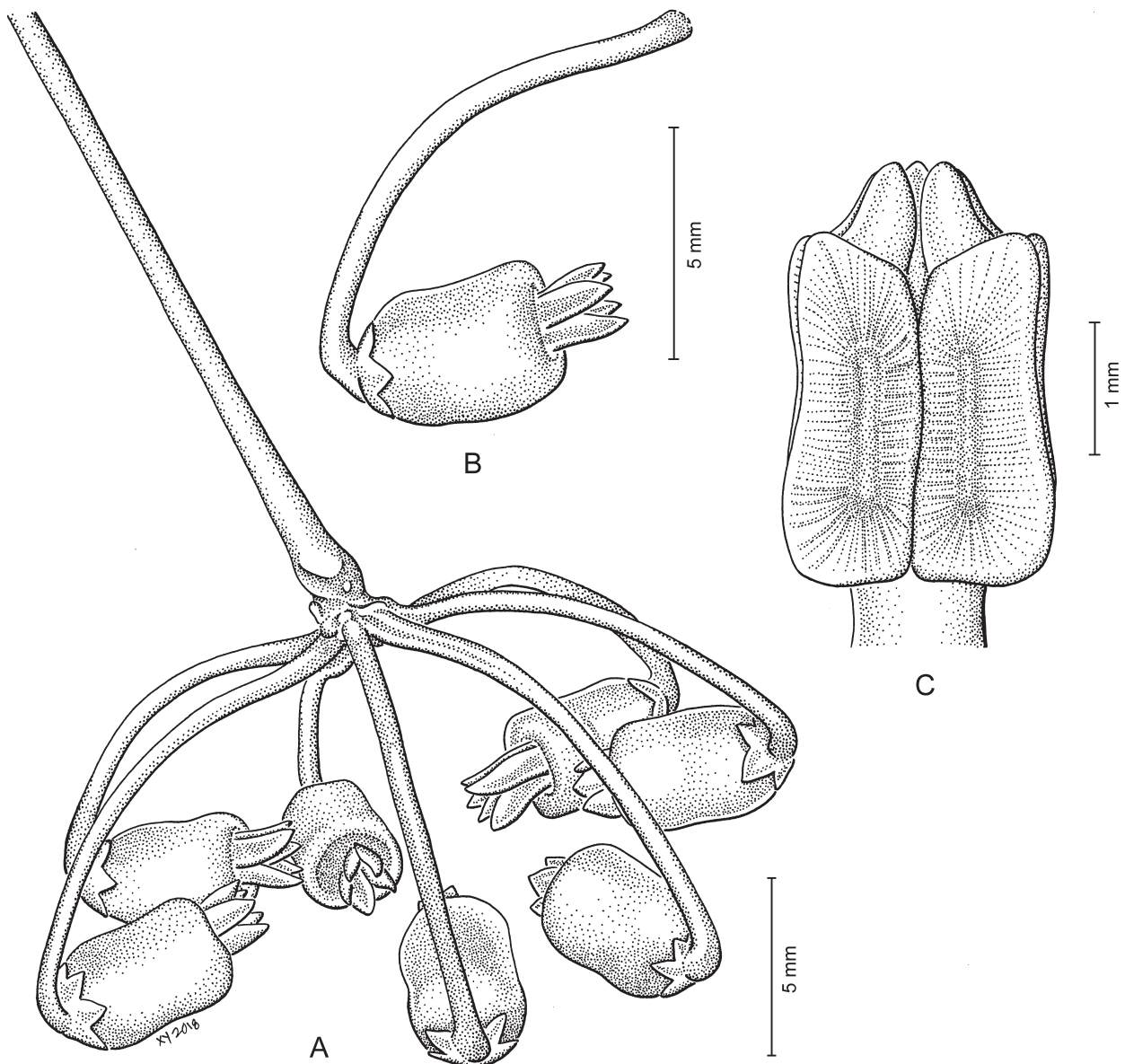


Fig. 2. *Anatropanthus borneensis*. – A: inflorescence; B: flower, side view; C: corona, side view. – Drawn by Loh Xiang Yun, based on *Somadée s.n.* (SING).

(1913, 1915) added another four sections: *H.* sect. *Eriostemma*, *H.* sect. *Oreostemma* Schltr., *H.* sect. *Peltostemma* Schltr. and *H.* sect. *Physostelma* (Wight) Schltr. The sectional classification of *Hoya* was further developed by Burton (1985, 1995, 1996a, 1996b, 1996c) and Kloppenburg (1993, 1994), who used up to 21 sections. A critical revision of the infrageneric classification of *Hoya* has never been published. While sections such as *H.* sect. *Eriostemma* are supported as monophyletic in molecular analyses, others such as *H.* sect. *Cyrtoceras* and *H.* sect. *Plocostemma* are not (Wanntorp & al. 2011). In the most recent phylogeny, Wanntorp & al. (2014) divided *Hoya* s.l. into six unnamed clades, some of which are diagnosable by morphology (e.g. growth form, pollinium and corona structure, nectar colour) and/or biogeogra-

phy, but only two of these can be readily aligned with previously published sections: *H.* sect. *Acanthostemma* (Blume) Kloppenburg and *H.* sect. *Eriostemma*.

Dischidia R. Br. — Like *Hoya* s.l., the circumscription of *Dischidia* has been expanded to include eight segregate genera: *Collyris* Vahl, *Conchophyllum* Blume, *Dischidiopsis* Schltr., *Dolichostegia* Schltr. (monotypic), *Hoyella* Ridl. (monotypic), *Leptostemma* Blume, *Oistonema* Schltr. (monotypic) and *Spathidolepis* Schltr. (monotypic) (Omlor 1998; Forster 2000; Livshultz 2003a, 2003b). Combinations in *Dischidia* exist for species of all of these genera. Typical of the taxonomic history of other genera within *Asclepiadoideae*, most of these segregates were diagnosed by the divergent structure of the stami-

nal corona relative to the membranous, inverted-anchor-shaped lobes characteristic of *Dischidia* s.s. However, later taxonomists, again consistent with trends across the subfamily, recognized a diversity of corona morphologies within *Dischidia* s.l. (Rintz 1980; Livshultz & al. 2005). In a molecular phylogenetic analysis of 46 ingroup species and eight outgroup *Marsdenieae* species (including *Hoya*, *Marsdenia* R. Br. and *Telosma* Coville) based on the second intron of the nuclear gene *Leafy*, there was strong support for monophyly of *Dischidia* s.l. including *Collyris*, *Conchophyllum*, *Dischidiopsis*, *Leptostemma* and *Oistonema* (Livshultz 2003b).

The most frequently used infrageneric classification of *Dischidia* divides it into three sections based on leaf morphology: *D.* sect. *Dischidia* with unmodified, laminar leaves; *D.* sect. *Conchophyllum* (Blume) K. Schum. with concavo-convex, shell-shaped, ant-house leaves; and *D.* sect. *Asciophora* K. Schum. with dimorphic leaves, producing both unmodified, laminar leaves and pouch-shaped, ant-house leaves (Livshultz 2003b). Molecular phylogenetic evidence indicated that *D.* sect. *Dischidia* is paraphyletic to a clade that includes all sampled species of *D.* sect. *Asciophora* and *D.* sect. *Conchophyllum*, while relationships between the latter two taxa were unresolved (Livshultz 2003b).

In this study, we test (1) the monophyly and phylogenetic position of the *Hoya* group in an analysis that includes both a representative sample of *Hoya* group taxa and other *Marsdenieae* genera, and (2) the current circumscription of *Hoya*, specifically asking if there is sufficient evidence for expanding the synonymy of *Hoya* to include *Anatropanthus*, *Dischidia* and *Oreosparte*. We sample *A. borneensis*, *O. celebica* Schltr. and other putative *Oreosparte* species for the first time. We include a substantially expanded sample of *Dischidia*, including its type species *D. nummularia* R. Br., and of *Marsdenia* species relative to previous analyses (Wanntorp & al. 2011; Wanntorp & al. 2014).

Material and methods

Sampling Matrix 1 (110 taxa) — To test the position of the *Hoya* group and *Oreosparte* within *Marsdenieae*, we modified the *trnT-L* spacer, *trnL* intron, *trnL-F* spacer dataset of Meve & Liede (2004), which includes the largest generic sample of *Marsdenieae* published to date (9 of 27 currently recognized genera; Endress & al. 2019; Espírito Santo & al. 2019). We excluded the species of *Periplocoideae*, which are only distantly related to *Asclepiadoideae* (Straub & al. 2014), the single unidentified *Marsdenia* species, and the *Hoya* group species, and then added 54 species of *Marsdenieae*, primarily of the *Hoya* group, and a sample of *Vincetoxicum flexuosum* (R. Br.) Kuntze (*Asclepiadoideae*). We included 12 *Dischidia* species, representing the morphological diversity of the genus including morphologies diagnostic of the synonymized genera

Conchophyllum, *Dischidiopsis* and *Leptostemma*, *Anatropanthus borneensis*, *Oreosparte celebica* and three other putative, undescribed *Oreosparte* species. We sampled 33 *Hoya* species including all synonymized genera and representatives of all major clades identified in the latest phylogeny of the genus (Wanntorp & al. 2014), including *H. urniflora* (P. I. Forst.) Simonsson & Rodda (*Marsdenia urniflora* P. I. Forst.) (Simonsson Juhonewe & Rodda 2017). We included all *Hoya* group species sampled by Wanntorp & al. (2014) where the complete six-locus dataset was available and where the identity of the species could be verified by examining the voucher specimen. Early-diverging lineages of *Hoya* were more densely sampled than highly nested ones. For other *Marsdenieae*, we added one species of *Jasminanthes*, namely *J. maingayi* (Hook. f.) Rodda [*Marsdenia maingayi* (Hook. f.) P. I. Forst.] and four additional species of *Marsdenia*, including *M. ridleyi* P. I. Forst, a species that displays “*Oreosparte* floral phenotype”, to increase sampling of this morphologically heterogeneous genus.

Sampling Matrix 2 (54 taxa) — In a second analysis, we reduced outgroup sampling and increased sequence sampling to investigate inter- and intrageneric relationships with the *Hoya* group. We limited the taxon sample to the 54 *Marsdenieae* species used in Matrix 1 and used *Jasminanthes maingayi*, *Marsdenia flavescens* A. Cunn. and *M. rostrata* R. Br. to root the tree. We added the chloroplast *trnH-psbA* spacer and part of the *matK* gene as well as the nuclear 5'-ETS and ITS loci to all samples.

The new specimens for the present study were obtained during fieldwork in Papua New Guinea, from the extensive living research collections at Singapore Botanic Gardens (Singapore) and Nong Nooch Tropical Botanical Garden (Thailand) and from herbarium specimens at E and SNP (herbarium codes according to *Index herbariorum*; <http://sweetgum.nybg.org/science/ih/>). Identification of specimens was carried out by consulting the relevant taxonomic literature including all protologues and comparing our collections with reference herbarium materials at the herbaria A, BISH, BK, BKF, BM, BRUN, FI, G, HBG, IBSC, K, KEP, KUN, L, M, MO, P, SAN, SAR, SING, SNP, TO, UC, US, W and WRSL. Vouchers are listed in Appendix 1 (in Supplemental Content online).

DNA extraction, PCR amplification and sequencing — Silica-dried or fresh leaf samples were extracted using DNeasy® Plant Mini Kit (Qiagen Inc., Valencia, California, U.S.A.). PCR amplification and sequencing were carried out using the primer pairs ITS5 and ITS4 for the ITS spacer (White & al. 1990), AsETS-F and AsETS-R for 5'-ETS (Yamashiro & al. 2004), psbA3'f/trnHf (Sang & al. 1997; Tate & Simpson 2003) for *psbA-trnH*, trnTUGU(a) and trnLUAA(b) for *trnT-trnL* and trnL(c)-trnF(f) for the *trnL* intron amplified together with the *trnF* gene (Taberlet & al. 1991), and 390F and 1326R for the *matK* gene

(Cuénoud & al. 2002). Internal primers were designed for the *trnT-trnL* locus of *Oreosparte* based on *Oreosparte* sp. 1 *trnT-LfOre* TCACAAATCAATACAATTTACAA and *trnT-LrOre* TGAATGGAATGAAAGCGGAGG. PCR amplification was carried out using Phusion Green High-Fidelity DNA Polymerase (Thermo Scientific) in 25 µl reactions, containing a concentration of 0.4 µM of each primer and approximately 50 ng of total DNA. PCR followed a three-step cycle with initial denaturation at 98°C for 30 seconds, 35 cycles of denaturation at 98°C for 10 seconds, primer annealing at 50°C (*matK*, ITS, *psbA-trnH*), 52°C (*trnT-L*, *trnL-F*) or 50°C (ETS) for 15 seconds, and primer extension at 72°C for 30 seconds, with a final extension at 72°C for 10 minutes.

The PCR products were purified using Wizard® PCR and gel clean-up system (Promega Corporation, Madison, Wisconsin, U.S.A.), according to the manufacturer's recommendations. AITBiotech Pte Ltd, Singapore, performed sequencing. Forward and reverse reads were assembled with Geneious Version 8.0 (Biomatters LLC) and the new sequences deposited in GenBank (Appendix 1 in Supplemental Content online).

Alignment and matrix construction — Sequences of each locus were aligned with the ClustalW (Larkin & al. 2007) plugin in Geneious prime 2019.0.4 (<https://www.geneious.com/>) using default parameters and adjusted by eye to correct obvious mis-alignments. Regions of ambiguous alignment were removed with GBLOCKS (Talavera & Castresana 2007) run on the GBLOCKS server version 0.91b (http://molevol.cmima.csic.es/castresana/Gblocks_server.html). For the *trnT-trnL* and *trnL-F* matrices, GBLOCKS was accessed on 5 May 2019 and sites selected using the following criteria: minimum number of sequences for a conserved position: 56; minimum number of sequences for a flanking position: 56; maximum number of contiguous non-conserved positions: 8; minimum length of a block: 5; allowed gap positions: with half. For ITS, ETS, *psbA-trnH* and *matK*, GBLOCKS was accessed on 5 May 2019 using the following selection criteria: minimum number of sequences for a conserved position: 28; minimum number of sequences for a flanking position: 28; maximum number of contiguous non-conserved positions: 8; minimum length of a block: 5; allowed gap positions: with half. Indels were not coded as characters because they are not modelled by the GTR family of models.

Incongruence — Each of the six loci was analysed independently, then concatenated into a nuclear matrix and a chloroplast matrix, and finally into a combined nuclear plus chloroplast matrix. Incongruence between the nuclear and chloroplast matrices and parsimony and ML analyses was assessed by identifying contradictory clades with moderate to high bootstrap support (BS > 75).

Parsimony tree searches, consensus tree calculation and bootstrap — Analyses were conducted with PAUP 4.0a

(Swofford 2002). To find most parsimonious trees, a heuristic search with TBR branch swapping of 1000 random starting trees was conducted, saving up to 10 equally parsimonious trees per iteration, followed by swapping to completion on all equally parsimonious trees, or until 10 000 trees were saved. The resulting trees were used to construct a strict consensus. The bootstrap analysis consisted of 1000 resampled replicates, with TBR swapping on one random starting tree, saving a maximum of 20 equally parsimonious trees per replicate and calculating the strict consensus tree from each replicate.

Maximum likelihood tree searches and bootstrap — Analyses were conducted with RAxML 8.2.11 (Stamatakis 2014) as implemented on Geneious prime 2019.0.4 (<https://www.geneious.com/>). The GTR plus GAMMA model of nucleotide substitution was applied in all steps of the analysis. The search for maximum likelihood trees combined the tree search and the rapid bootstrap analysis (-f a) using 10 000 rapid bootstrap iterations followed by a tree search through ML. Datasets were not partitioned.

Results

Sequencing — In total 227 new sequences were generated for this study (Appendix 1 in Supplemental Content online), including 15 from species previously sampled by Wanntorp & al. (2014), two from *Hoya corymbosa* Rodda & Simonsson, previously sampled in Rodda & al. (2013), two from *H. papaschonii* Rodda, previously sampled in Rodda & Ercole (2014), and 209 from 34 newly sampled species.

Matrices — Summary statistics are shown in Table 1. Taxon sampling was complete for each locus. As judged from the number of aligned positions removed by GBLOCKS, the alignment of the *psbA-trnH* locus had by far the most gaps and alignment ambiguity (only 314 of 820 aligned positions retained for analysis, Table 1). For Matrix 2 (54 taxa), the ITS locus contributed the largest number of PICs (160) and the *trnL-F* locus the fewest (37) (Table 1).

Incongruence — There were no moderately to strongly supported (BS > 75) incongruences between parsimony and ML analyses of any data matrix (data not shown). The only moderately to strongly supported incongruence between chloroplast and nuclear loci concerns the position of *Dischidia milnei* Hemsl., which was supported as sister to *D. major* (Vahl) Merr. by the cp loci (ML BS 90) versus sister to the rest of the ant-house-leaved *Dischidia* species by the nuclear loci (ML BS 97). In the combined analysis, *D. milnei* is placed in the position favoured by the nuclear loci but with poor support (ML BS 57) (Fig. 4). Support for the sister-group relationship of *D. milnei* and *D. major* appears to come primarily from the *trnT-trnL* locus, which has two unambiguous synapomorphies

Table 1. Summary statistics of matrices and analyses.

Matrix number	Matrix	Alignment length (base pairs)	Alignment length (after GBLOCKS)	Number of PICs (after GBLOCKS)
1	110 – cp	N/A	1634	296
2	110 – <i>trnT-trnL</i>	1338	774	162
3	110 – <i>trnL-trnF</i>	1093	860	134
4	54 – combined nu + cp	N/A	3900	512
5	54 – cp	N/A	2869	241
6	54 – <i>trnT-trnL</i>	1338	774	58
7	54 – <i>trnL-trnF</i>	1093	860	37
8	54 – <i>psbA-trnH</i>	820	314	76
9	54 – <i>matK</i>	921	921	70
10	54 – nu	N/A	1031	271
11	54 – ETS	388	369	111
12	54 – ITS	700	662	160

that favour this relationship. There are no unambiguous synapomorphies for this relationship in parsimony analyses of any of the other three chloroplast loci (data not shown).

Topology — ML topologies are shown in Fig. 3 and 4 with BS support (ML/parsimony) indicated at each node. Nodes absent from the parsimony strict consensus tree are indicated with “–”. Only the ML BS support will be mentioned in the descriptions below.

Analysis 1: 110-taxon matrix (Fig. 3) — The monophyly of each tribe of *Asclepiadoideae* is strongly supported (BS 90–100), as are the position of tribe *Fockeeae* as sister to the rest of the subfamily (BS 100) and the sister-group relationship of *Ceropegieae* and *Marsdenieae* (BS 93). The position of *Eustegieae* as sister to *Ceropegieae* plus *Marsdenieae* is moderately supported (BS 75). Within *Marsdenieae*, there is a polytomy among three well-supported clades: (1) an African and Madagascan clade of two taxa, *Marsdenia verrucosa* Decne. and *Rhyssolobium dumosum* E. Mey (BS 97); (2) a miscellaneous clade of African, Asian and American taxa including species of *Cionura* Griseb., *Gymnema* R. Br., *Marsdenia*, *Ruehssia* H. Karst. and *Telosma* (BS 93); and (3) an Asian and Australasian clade including species of *Gongronema* (Endl.) Decne., *Marsdenia* and the *Hoya* group (BS 97). The *Hoya* group clade is strongly supported (BS 99) as including all accessions of *Dischidia*, *Hoya* and *Oreosparte*, as well as one species of *Marsdenia*, *M. ridleyi*, sister to *Oreosparte* sp. 3 (BS 100).

Analysis 2: 54-taxon matrix (Fig. 4) — The inclusion of four additional loci resulted in greater resolution and support for relationships within the *Hoya* group than in the 110-taxon matrix (compare Fig. 3 and 4), and the topology of the *Hoya* group will be discussed based on the

combined chloroplast and nuclear analysis (Fig. 4). To facilitate comparison, for the *Hoya* clades, we used the clade names of Wanntorp & al. (2014: fig. 3, 4) and highlighted the species that they sampled in bold italics in our Fig. 4.

Three taxa, including *Hoya urniflora* and two putative *Oreosparte* species form a strongly supported, monophyletic (BS 100) clade (*Oreosparte* I), sister to the rest of the taxa in the *Hoya* group that form a moderately supported clade (BS 79). Within this clade, four strongly to moderately supported clades can be recognized. The first (*Oreosparte* II, BS 100) includes the type of *Oreosparte* as well as *Marsdenia ridleyi* and another putative *Oreosparte* sp. 3.

Oreosparte II is sister, but without support, to *Dischidia* s.l., which is strongly supported as monophyletic (BS 100). The *Dischidia* clade includes species originally described in the segregate genera *Dischidiopsis* [*Dischidia parasita* (Blanco) Arshed & al., the type of *Dischidiopsis*] and *Leptostemma* [*D. hirsuta* (Blume) Steud. and *D. latifolia* (Blume) Decne.], and species with morphology diagnostic of the segregate genus *Conchophyllum* [*D. astephana* Scort. ex King & Gamble (= *C. angulatum* Schltr.) and *D. milnei*]. Within *Dischidia*, there is strong support for the monophyly of all ant-house-leaved species (*D.* sect. *Ascidophora* and *D.* sect. *Conchophyllum*) (BS 97) and for a clade that includes all ant-house-leaved species plus the Bornean endemic *D. antennifera* Becc. and the widespread *D. nummularia* R. Br. (the type of *Dischidia*) (BS 100). The latter two species have small, ovate to orbicular leaves, resulting in a paraphyletic *D.* sect. *Dischidia*. The two pitcher-leaved species, *D. major* and *D. vidalii* Becc. (*D.* sect. *Ascidophora*), are weakly supported as sister taxa (BS 55). The widespread *D. acutifolia* Maingay ex Hook. f. and *D. tomentella* Ridl. (a limestone endemic from Thailand and N peninsular Malaysia) are strongly supported as sister taxa (BS 99).

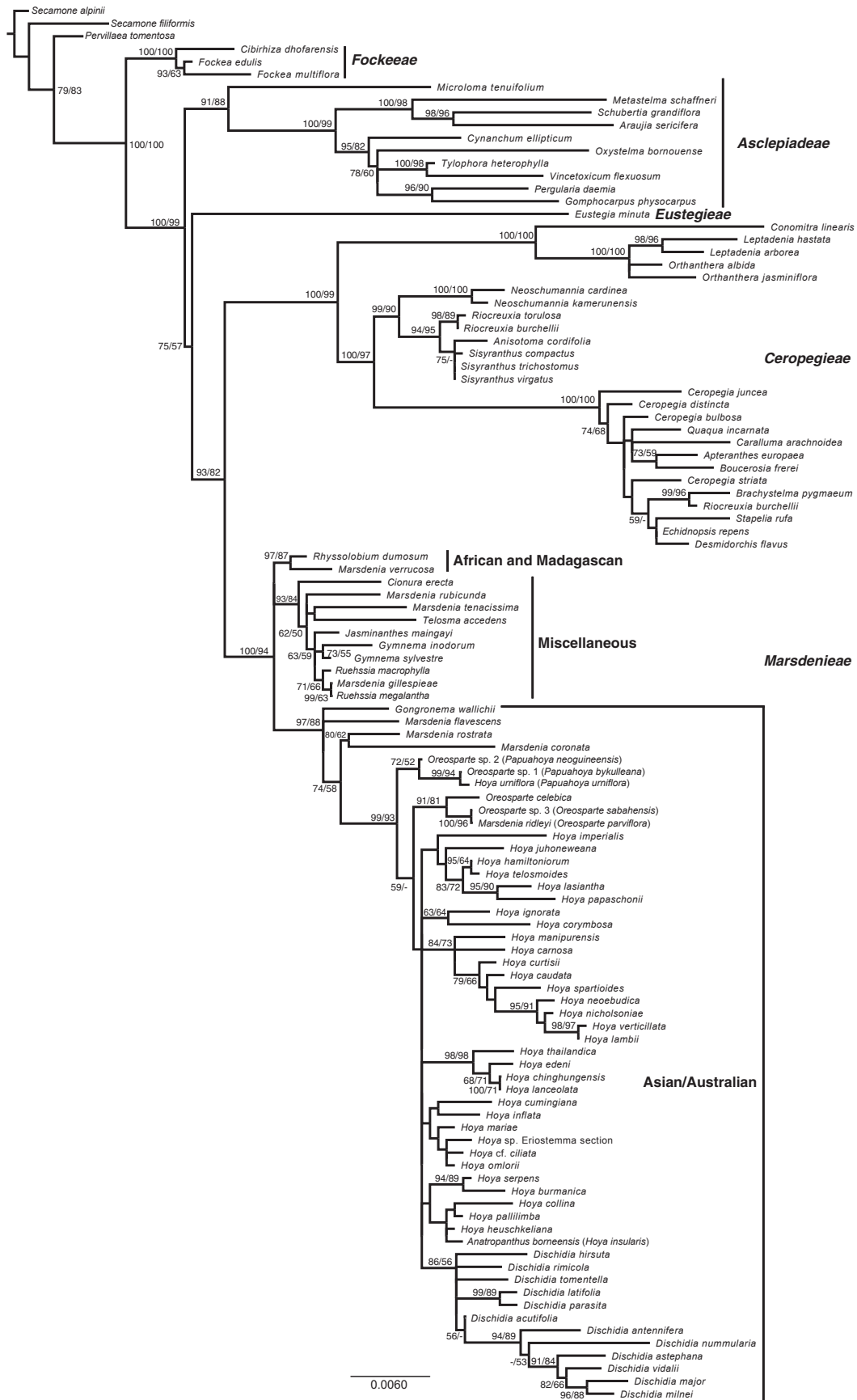


Fig. 3. Maximum likelihood tree of the 110-taxon matrix of *trnT-trnL-trnF* sequences. Bootstrap support below the branches is shown as ML/parsimony; “-” indicates that the clade does not occur in the strict consensus of most parsimonious trees.

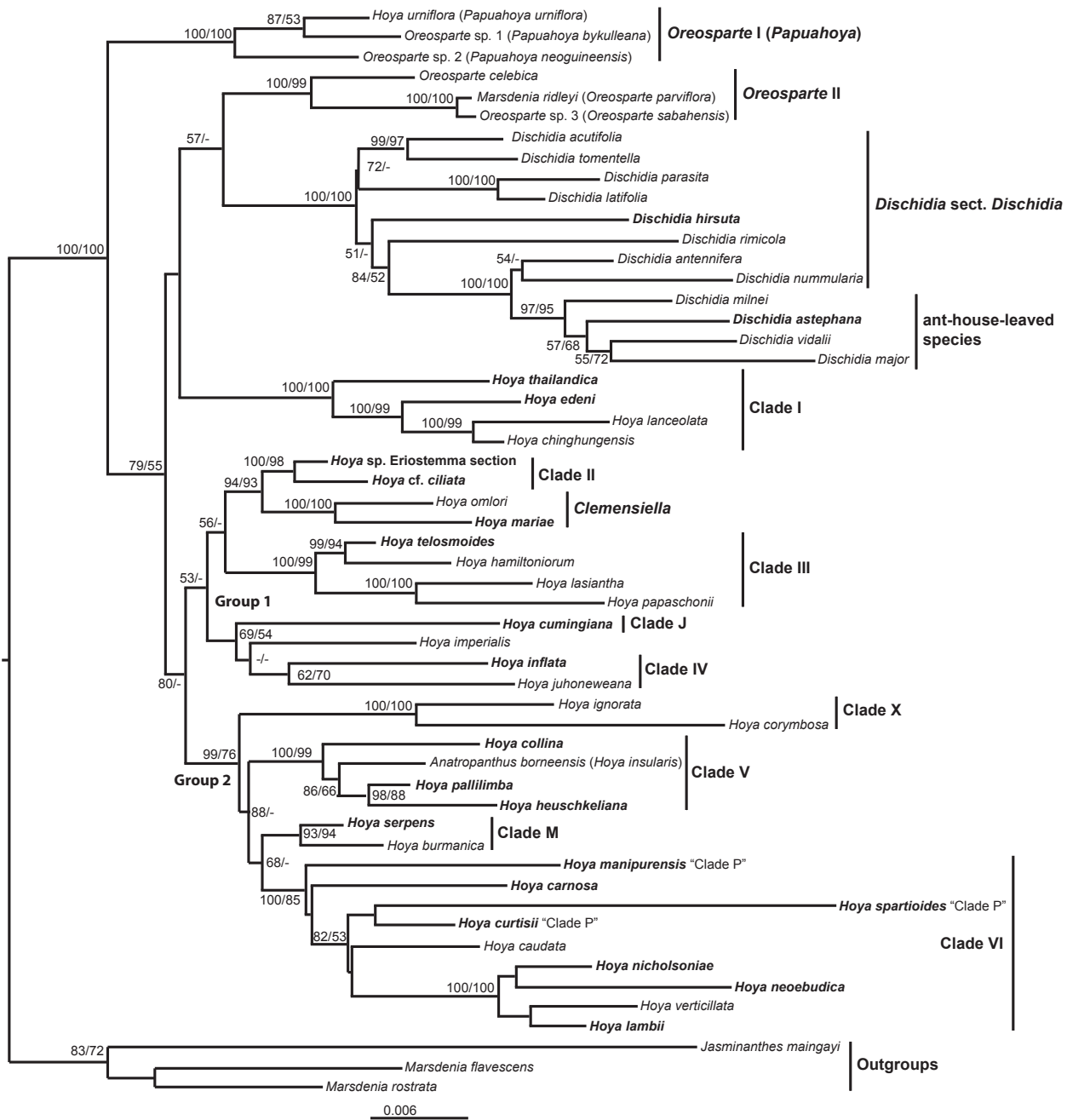


Fig. 4. Maximum likelihood tree of the combined chloroplast and nuclear 54-taxon matrix. Clade and group names follow Wannrtorp & al. (2014) except “clade X”, which corresponds to clade 8 of Rodda & al. (2013) and the novel *Clemensiella* clade. Species sampled by Wannrtorp & al. (2014) are in bold italics. Bootstrap support below the branches is shown as ML/parsimony; “-” indicates that the clade does not occur in the strict consensus of most parsimonious trees.

Dischidia parasita, endemic to the Philippines, is sister to *D. latifolia* (BS 100), distributed in Borneo and Java. Other relationships are weakly to moderately supported.

Dischidia and *Oreosparte* II are sister, but without support, to a clade (clade 1, BS 100) including *Hoya* species from continental Asia that, with the exception of *H. thailandica* Thaitong, are non-climbing pendulous shrubs.

The rest of *Hoya* forms a moderately supported clade (BS 80) where eight of the subclades identified by Rodda & al. (2013) and Wannrtorp & al. (2014) can be delimited. However, clade J has only one species, *H. cumingiana*

Decne, and *H. imperialis* Lindl. is not included in any clade. All but clade IV are moderately to strongly supported.

Two main subclades can be recognized: the unsupported group 1 (BS 53) and the well-supported group 2 (BS 99). Group 1 includes clades II, III, and IV plus clade J and *Clemensiella*. Clade II (BS 100) comprises terrestrial climbers from Sundaland, Papua and the Philippines classified in *Hoya* sect. *Eriostemma*. Clade II is sister to the *Clemensiella* clade (BS 100) and includes two species, *H. mariae* (Schltr.) L. Wannrtorp & Meve and *H. omlorii*

(Livsh. & Meve) L. Wanntorp & Meve, formerly classified in the segregate genus *Clemensiella*. Group 1 also includes clade III (BS 100) with two Borneo endemics, *H. hamiltoniorum* A. L. Lamb & al. and *H. telosmoides* Omlor, as well as two shrubby species, *H. lasiantha* (Korth. ex Blume) Miq. and *H. papaschonii*, all distributed in W Malesia. A moderately supported clade consisting of species placed in clades IV and J by Wanntorp & al. (2014) (BS 69) includes two Sundaland species and two Papua endemics, *H. inflata* (P. I. Forst. & al.) L. Wanntorp & P. I. Forst. (originally described in the synonymized genus *Madangia*) and *H. juhoneweana* Simonsson & Rodda. Group 2 includes four subclades: clade X (clade 8 of Rodda & al. 2013) and clades V, M and VI. The Borneo endemic *H. corymbosa* and the widespread *H. ignorata* T. B. Tran & al. form clade X (BS 100), not sampled by Wanntorp & al. (2014). Forming clade V (BS 100) are *H. heuschkeliana* Kloppenb. and *H. pallilimba* Kleijn & Donkelaar, both classified in *H.* sect. *Acanthostemma*, the former endemic to the Philippines, the latter endemic to Sulawesi, plus *H. collina* Schltr. from Papua and *Anatropanthus borneensis*. Clade M (BS 93) includes two montane species from continental Asia and is sister to clade VI (BS 100), which includes two very widely distributed species, *H. nicholsoniae* F. Muell. and *H. verticillata* (Vahl) G. Don, plus species described in the segregate genera *Absolmsia* (*H. spartioides* (Benth.) Kloppenb.) and *Micholitzia* (*H. manipurensis* Deb). “Clade” (actually grade) P of Wanntorp & al. (2014) falls within clade VI in the present analysis (Fig. 4) rather than clade VI being nested in grade P as in Wanntorp & al. (2014).

Discussion

This study is the best-sampled analysis of the morphological and taxonomic diversity of the *Hoya* group conducted to date, including for the first time the enigmatic *Anatropanthus* and *Oreosparte*. The 110-taxon analysis (Fig. 3) is completely congruent with the tribal-level topology published by Meve & Liede (2004) and clearly shows that the *Hoya* group clade (BS 99), including *Anatropanthus*, *Dischidia* s.l., *Hoya* s.l. and *Oreosparte*, is nested within *Marsdenieae* in a clade with other Asian and Australasian species. The *Hoya* group is paraphyletic unless one *Marsdenia* species (*M. ridleyi*) is included. By increasing sampling of *Marsdenia* s.l. from six to 11 species, our result also highlights the polyphyly of the current concept of *Marsdenia* s.l. (Forster 1995). *Marsdenia* species are placed within: (1) the *Hoya* group (*M. ridleyi*, now *Oreosparte parviflora*, and *M. urniflora*, now *Papuahoya urniflora*); (2) an Asian/Australian clade outside the *Hoya* group (*M. coronata* Benth, *M. flavescens* and *M. rostrata*); (3) an African and Madagascan clade (*M. verrucosa*); and (4) a miscellaneous clade (two *Marsdenia* species from tropical Asia and *M. gillespieae* Morillo, which will have to be moved to the recently resur-

rected *Ruehssia*; Espírito Santo & al. 2019). We have not sampled the type of *Marsdenia*, *M. tinctoria* R. Br., and will not discuss the taxonomic implications at this time except for the obvious necessity to transfer *M. ridleyi* to a genus within the *Hoya* group. This species is epiphytic with persistent inflorescences and valvate corolla lobes, all synapomorphies of the *Hoya* group.

Hoya group phylogeny and taxonomy — Generic delimitation within the *Hoya* group (Fig. 4) remains problematic. Our analysis shows much the same topology, with the exception of “clade P” sensu Wanntorp & al. (2014) nesting within clade VI (Fig. 4), and the same ambiguities, evident in the studies previously published using the same loci (Wanntorp & al. 2006; Wanntorp & al. 2011; Rodda & al. 2013; Rodda & Ercole 2014; Wanntorp & al. 2014). *Dischidia* s.l. is strongly supported as monophyletic (BS 100), but *Hoya* s.l. is unsupported. To complicate matters further, *Oreosparte celebica* and the species with “*Oreosparte* floral phenotype” sampled do not form a monophyletic clade but are subdivided into two clades. Clade *Oreosparte* I is sister to the rest of the *Hoya* group and includes *H. urniflora* and two new species from Papua New Guinea. Clade *Oreosparte* II is sister to *Dischidia* (Fig. 4) and includes the type of the genus as well as *M. ridleyi* and a new species from Borneo. Our analysis provides strong evidence that the “*Oreosparte* floral phenotype” has also evolved independently in *H. hamiltoniorum* within clade III of *Hoya* s.l. The floral morphology of the former *Clemensiella* species is also very similar (Meve & al. 2009). While this lack of resolution among the primary branches of the *Hoya* group clade has been interpreted as evidence of a rapid radiation (Wanntorp & al. 2014), it may also be a matter of insufficient character sampling. For example, the position of *Eustegieae* had been controversial based on molecular matrices of few loci such as this one (sister to *Ceropegieae* plus *Marsdenieae*, BS 75, Fig. 3) or sister to *Asclepiadeae* (BS 76) (Surveswaran & al. 2014), but was resolved with high support as sister to *Asclepiadeae* in a plastome analysis (Straub & al. 2013). Taxonomic undersampling may also contribute to the lack of support (Zwickl & Hillis 2002). While we have sampled the geographic and morphological diversity of *Hoya* s.s., we still may not have sampled all early-diverging lineages, and we have not sampled *Heynella*.

Oreosparte I and *Oreosparte* II are separated geographically, the first from Papua New Guinea, the second from West Malesia. Additionally, species of *Oreosparte* II have bifid corona lobe apices, whereas species of *Oreosparte* I have entire corona lobe apices. We therefore recognize *Oreosparte* I as the new genus, *Papuahoya* Rodda & Simonsson.

Because of the lack of support for relationships among *Oreosparte* I and the *Dischidia* and *Hoya* clades, we consider the evidence insufficient for placing *Oreosparte* and *Dischidia* in synonymy with *Hoya* s.l. (Fig. 4).

Anatropanthus borneensis is nested within *Hoya* clade V with high support (Fig. 4). Its tubular corolla is very unusual, but corollas in *Hoya* can be particularly diverse and new species with unusual corollas are still being discovered, e.g. *H. versteegii* Simonsson & Rodda from New Guinea is the first species in the genus with an infundibuliform corolla with a long, narrow tube. Other characters of *Anatropanthus* are already found among *Hoya* species. The long, linear leaves of *A. borneensis* are similar to those of *H. acicularis* T. Green & Kloppenb., also from Borneo; the recurved pedicels are similar to those of *H. retrorsa*; and the pollinia have an evident pellucid margin, as commonly observed in the majority of *Hoya* species. *Anatropanthus borneensis* is therefore transferred here to *Hoya*.

Dischidia phylogeny and taxonomy — Phylogenetic relationships within *Dischidia* are congruent with those found by Livshultz (2003b) in an analysis of the nuclear second *Leafy* intron. Aside from the relationships of the ant-house-leaved species, discussed above, the phylogeny supports the recognition of *Dischidia* s.l., including the synonymized genera *Conchophyllum* (*D. astephana*, morphology similar to *D. milnei*), *Dischidiopsis* (*D. parasita*), *Leptostemma* (*D. hirsuta*, *D. latifolia*) and *Oistonema* (morphology similar to *D. latifolia*), erected on the basis of atypical corona morphologies. The division into three sections based on leaf morphology is also not supported because both *D. sect. Conchophyllum* and *D. sect. Dischidia* are paraphyletic (Fig. 4). The sister-group relationship of two laminar-leaved species, *D. antennifera* and *D. nummularia*, with the ant-house-leaved clade (BS 100) is supported by a potential vegetative synapomorphy: presence of prominent wax chimneys around the stomata, particularly evident on the abaxial leaf surfaces, and a diagnostic floral character: absence of papillate epidermal cells on the adaxial surface of the corolla lobes. The sister-group relationship of *D. latifolia* and *D. parasita* is congruent with a number of morphological characters. Both species are relatively robust vines with larger leaves (compared to most other *Dischidia* species) with both opposite and alternate phyllotaxis; other potential synapomorphies include fleshy corona lobes with abaxial sulci and pollinaria with very short caudicles. While the larger clade that includes these two species plus *D. acutifolia* and *D. tomentella* is weakly supported (BS 72), it is consistent with the presence of alternate phyllotaxy in seedlings of *D. acutifolia*. *Dischidia acutifolia* and *D. tomentella* have similar floral and inflorescence morphology. *Dischidia tomentella* is endemic to karst in N Malaysia and S Thailand (Rintz 1980), often growing epilithically on exposed rock surfaces rather than epiphytically (Livshultz, pers. obs.). It may have evolved from isolated populations of the widespread, lowland species *D. acutifolia* that adapted to the more challenging edaphic conditions on karst via evolution of smaller, more succulent leaves, greater pubescence and slower growth.

Hoya s.l. phylogeny and taxonomy — Eight of the nine clades recognized in *Hoya* (Fig. 4) were also identified by Wanntorp & al. (2014). *Hoya corymbosa* and *H. ignorata*, forming clade X, were not sampled by Wanntorp & al. (2014). Our sampling of *Hoya* species is insufficient to provide a strong basis for an updated subgeneric classification of the genus, but five already recognized sections can be identified. Clade I corresponds to *H. sect. Ancistrostemma* and includes its type, *H. edeni* King ex Hook. f. Clade II corresponds to *H. sect. Eriostemma*. Clade III corresponds to *H. sect. Plocostemma* and includes its type, *H. lasiantha*. Clade V corresponds to *H. sect. Acanthostemma*. The morphologically diverse clade VI includes the type of *H. sect. Hoya*, *H. carnososa*. Four clades do not represent any of the currently recognized sections: (1) the *Clemensiella* clade, including the two species formerly included in that genus; (2) clade IV, including three Papuan species; (3) clade X with the shrubby *H. corymbosa* and *H. ignorata*; and (4) clade M, with two Asian representatives. A much more comprehensive sampling including the type species of all the sections and subsections described so far would be necessary to verify whether any of these four clades represent a published infrageneric entity.

Conclusions

Our analysis is the first to include a comprehensive sampling of *Anatropanthus*, *Dischidia*, *Hoya* and *Oreosparte* without a significant amount of missing data, as well as numerous outgroups, in a comprehensive phylogenetic analysis. *Anatropanthus* is strongly supported as nested in *Hoya* within clade V (Fig. 4) and is here transferred to *Hoya* as *H. insularis*.

The available data show once again that *Hoya* is paraphyletic unless *Dischidia* and *Oreosparte* are synonymized (Fig. 4). However, the relationships among *Hoya* and *Oreosparte* clade II and *Dischidia* s.l. are not supported. Current evidence is not sufficient to synonymize *Dischidia* and *Oreosparte* with *Hoya*. A phylogenomic approach is needed to clarify relationships among these taxa.

Oreosparte is strongly supported as belonging to the *Hoya* group (Fig. 3), but its species are separated into two clades, one of which is described as a new genus, *Papuahoya*. The *Hoya* group is placed within a grade of Asian and Australasian *Marsdenieae* (Fig. 3). Our results underline the polyphyly of the current concept of *Marsdenia* (Fig. 3).

Taxonomy

Hoya insularis Rodda & S. Rahayu, **nom. nov.** (Fig. 2) ≡ *Anatropanthus borneensis* Schltr. in Bot. Jahrb. Syst. 40(Beibl. 92): 18. 1908 [non *Hoya borneensis* Kloppenb. in *Hoya* New 8(3): 10. 2018]. – Type: Borneo, auf Bäumen in den Wäldern am Long-Sele, an höher gele-

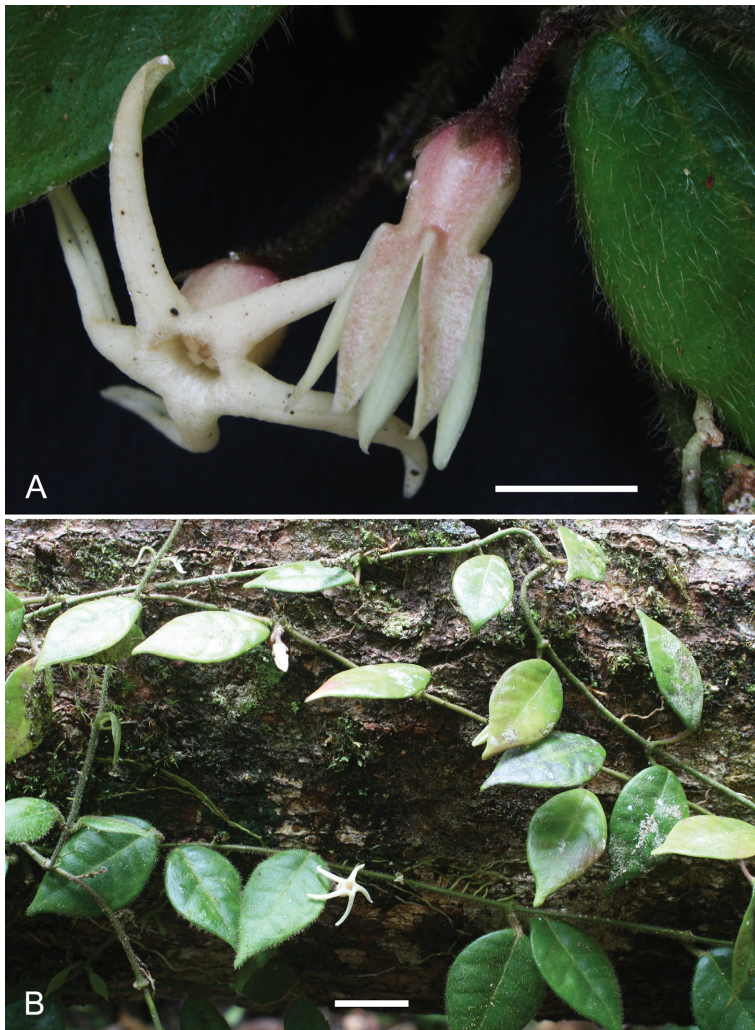


Fig. 5. *Papuahoya bykulleana*. – A: inflorescence with an opening bud and a fully open flower; B: habit. – Scale bars: A = 5 mm; B = 2 cm. – Vouchered by Simonsson Juhonewe & Juhonewe NS0029B. – Photographs by N. Simonsson.

genen Orten, Aug 1901, R. Schlechter 13483 (B [destroyed]). – **Lectotype (designated here):** [icon] “Fig. 2. *Anatropanthus borneensis* Schltr. n. sp.” in Bot. Jahrb. Syst. 40(Beibl. 92): t. 2 ad p. 18. 1908.

Remarks — The type specimen of *Anatropanthus borneensis* was lost in the fire that destroyed the Berlin Herbarium in 1943 (Omlor 1998). No duplicates have been traced and it is likely that only a single specimen was made—Schlechter (1908) stated “I found very little material in bloom”. The illustration in the protologue (Schlechter 1908: t. 2) is therefore designated as the lectotype.

Specimens examined — THAILAND: cultivated, 2018, *Somadee s.n.* (SING). — INDONESIA: originally collected in West Kalimantan by Sulaiman Hasim, cultivated in Bogor Botanic Garden, 2017, *Rahayu 877* (BO).

***Papuahoya* Rodda & Simonsson, gen. nov.**

Type: *Papuahoya bykulleana* Simonsson & Rodda – Fig. 5, 6.

Description — Epiphytic climber (occasionally hemi-epiphytic in mossy forest), with white latex in all vegetative parts. *Roots* basal and adventitious. *Stems* pubescent. *Stipular colleters* present, 1 at each side of base of petiole. *Lamina* lanceolate to ovate, stiff and chartaceous, pubescent turning glabrescent on old leaves, basal colleters present; venation pinnate. *Inflorescences* 1 per node, extra-axillary, convex, consisting of (1 or)2–10 flowers, *peduncle* perennial, pubescent, older inflorescences with an elongated rachis. *Pedicels* all of same length within an inflorescence. *Calyx* lobes oblong, free; colleters present in calyx lobe sinus. *Corolla* campanulate to urceolate, terminating in free, spreading lobes; *lobes* triangular-lanceolate, valvate in bud. *Gynostegium* shortly stipitate. *Corona* staminal; lobes erect, almost completely fused to back of anthers, basal part of corona lobe globose or indistinct, without revolute basal margins, apical part of corona lobe acute with a rounded tip. *Style-head* conic, hidden by apical anther appendages. *Pollinia* oblong, without pellucid margin; *corpusculum* ovoid; *caudicles* attached at base of corpusculum. *Ovary* conic. *Fruit and seeds* not observed.

Remarks — The “*Oreosparte* floral phenotype”, i.e. presence of urceolate corollas and stipitate gynostegia with erect corona lobes, is present in the *Clemensiella* clade and clade III of *Hoya*, *Oreosparte* and *Papuahoya*. Both *Oreosparte* and *Papuahoya* are epiphytic climbers and the only reliable morphological character for the separation of the two genera is the different morphology of the corona lobe apices, which are bifid in *Oreosparte* and simple in *Papuahoya*. The species in the *Clemensiella* clade also have simple corona lobe apices, but they are terrestrial climbers.

***Papuahoya bykulleana* Simonsson & Rodda, sp. nov.** – Fig. 5, 6.

Holotype: Papua New Guinea, Morobe Province, Faseu, 1574 m, 23 Feb 2011, N. Simonsson Juhonewe & F. Juhonewe NS0029B (SING [incl. spirit]; isotype: LAE).

Description — Slender, creeping climber. *Stems* cylindrical, 1–3 mm in diam., mid-green, pubescent; older stems glabrescent, internodes 2–10(–20) cm long; *adventitious roots* sparsely present along stem. *Leaves: petiole* terete, 1.5–4 × c. 1 mm, bright green, pubescent; *lamina* coriaceous, broadly ovate-elliptic, 2–5 × 1–2.5 cm, pale green on abaxial surface, bright green on adaxial sur-

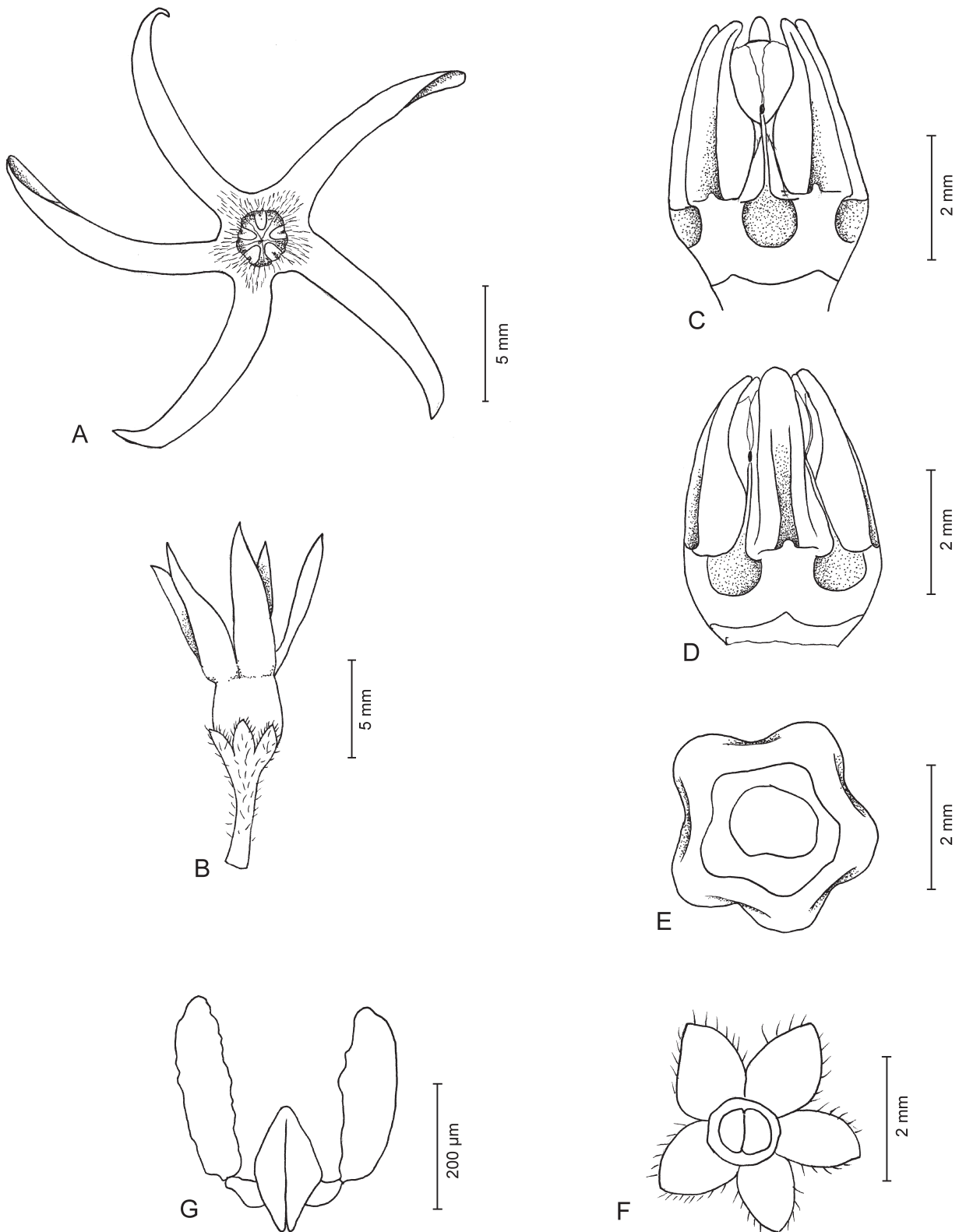


Fig. 6. *Papuahoya bykulleana*. – A: fully open flower, top view; B: opening bud, side view; C, D: gynostegium, side view; E: gynostegium, from below; F: calyx and ovary; G: pollinarium. – Drawn by M. Rodda, based on *Simonsson Juhonewe & Juhonewe NS0029B*.

face, pubescent on both surfaces, base rounded to acute, margin recurved, apex broadly acute to caudate; midrib depressed on adaxial surface, secondary veins 2–6 on

each side, branching from midrib at 70–80°, slightly depressed, creating a bullate surface. *Inflorescence* ageotropic, consisting of 1 or 2 flowers; *peduncle* persistent,

terete, 0.5–2 cm × 1–1.5 mm, older peduncles bearing an elongate rachis from previous flowerings, often darker green or purplish, pubescent; *pedicels* terete, 0.5–1.5 cm × c. 1 mm, dark green to purplish red, slightly pubescent. *Flower buds* valvate, snow-white, often flushed pink near calyx if exposed to strong light. *Calyx* lobes lanceolate, c. 2 × 1 mm, outside sparsely pubescent, inside glabrous, apex rounded to acute. *Corolla* narrowly campanulate with free, spreading lobes, 1.5–2 cm in diam.; *tube* 4–5 × 3–4 mm, snow-white, flushed pink on outside near calyx, outside glabrous, inside pubescent, with longer hairs around mouth; *lobes* lanceolate, often twisted, 6–9 × 2–3 mm, outside glabrous, inside pubescent only basally, margin recurved to revolute, apex acute. *Corona* staminal, ovoid, c. 5 mm high, 3–4 mm in diam., fleshy, white; *lobes* erect, oblong, c. 3 mm × 1 mm, with 1 deep, central groove along entire length, basal part of corona lobe deeply grooved, without appendages, apical part of corona lobe acute with a rounded tip. *Style-head* convex, exposed. *Pollinia* oblong, 300–350 × 70–80 µm; *corpusculum* ovate, 210–250 × 110–140 µm; *caudicles* c. 50 µm. *Ovary* 2-carpellate, broadly conic, c. 1.5 mm long; each carpel c. 1 mm wide at base, light green, glabrous. *Fruit* and *seeds* not observed.

Distribution — Known only from the type locality in Morobe Province of Papua New Guinea.

Ecology — Recorded at 1500–1700 m on two ridges in primary mossy forests, where it grows on mossy ground, at the base of tree trunks near the ground or as an epiphyte. *Papuahoya bykulleana* is often hemi-epiphytic as it starts growing in mossy areas, at the base of a tree or on moss-covered shrubs and continues growing tightly attached onto the tree trunk, or climbing on small shrubs, upward toward better-lit areas. It is absent either further up or down the mountain, even on the same slope.

Etymology — Named after Gunilla Bykulle of Sweden, who contributes to N. Simonsson's work in Papua New Guinea.

Remarks — Similar to *Papuahoya neoguineensis* in being a slender, pubescent climber with campanulate flowers with lanceolate corolla lobes. It is easily distinguished because its corona is ovoid with erect, oblong lobes without a distinct basal process, whereas *P. neoguineensis* has a conic corona with lobes with a rounded and spreading basal process. Both taxa were found in Morobe Province but on separate mountain ranges c. 110 km apart and at different altitudes, 1500–1700 m for *P. bykulleana* and c. 800 m for *P. neoguineensis*.

Additional specimens examined — PAPUA NEW GUINEA: MOROBE PROVINCE: Faseu, c. 1700 m, vouchered at Ukarumpa on 13 Nov 2012 from living accession NS12-

018, *N. Simonsson Juhonewe & F. Juhonewe NS0058L* (LAE); Faseu, c. 1700 m, vouchered at Ukarumpa on 13 Nov 2012 from living accession NS12-026, *N. Simonsson Juhonewe & F. Juhonewe NS0059L* (LAE).

Papuahoya neoguineensis Simonsson & Rodda, **sp. nov.** — Fig. 7.

Holotype: Papua New Guinea, Morobe Province, Lababia, Kamiali Wildlife Management Area, on ridge trail to Blue Mountain, mossy forest on ultrabasic soil, c. 800 m, 15 Jul 2011, S. A. James & O. Paul s.n., vouchered at Ukarumpa on 26 Apr 2015 from living accession NS13-013, *N. Simonsson Juhonewe & F. Juhonewe NS0103L* (SING; isotype: LAE).

Description — Slender creeping climber. *Stems* cylindrical, 1–2 mm in diam., green, pubescent; older stems glabrescent, lignified, up to 4 mm in diam., internodes 2–10(–20) cm long; *adventitious roots* produced along stem when in contact with substrate. *Leaves*: *petiole* terete, 1.5–10 × c. 1 mm, green, pubescent on both sides; *lamina* broadly ovate-elliptic, coriaceous, 2–5 × 1–2.5 cm, silvery to pale green on abaxial surface, bright to dull green on adaxial surface, often with purplish hue in bright light, pubescent on both surfaces, turning glabrescent, base rounded to acute, margin sometimes recurved, apex broadly acute to cuspidate; midrib depressed on adaxial surface, often brighter coloured, secondary veins 2–6 on each side, branching from midrib at 70–80°. *Inflorescence* ageotropic, consisting of 1 or 2 flowers; *peduncle* persistent, terete, 0.2–1 cm × 1–1.5 mm, older peduncles bearing an elongate rachis from previous flowerings, often darker green or purplish, pubescent; *pedicels* terete, c. 1 cm × 1 mm, green to purplish red, sparsely pubescent. *Flower buds* valvate, creamy white-yellow, basally flushed pink. *Calyx* lobes broadly triangular, c. 1 × 1.5 mm, apex rounded, glabrous to sparsely pubescent outside, with a hump at base of each lobe on outside. *Corolla* campanulate, 2–2.4 cm in diam., creamy white-yellow, flushed pink on outside near calyx if under bright light; *tube* c. 4 × 5–7 mm, glabrous outside, pubescent inside with short hairs; *lobes* narrowly triangular, often fleshy, 8–9 × c. 5 mm, outside glabrous, inside pubescent, margin recurved, apex acute. *Corona* staminal, c. 5 mm high, c. 5 mm in diam., fleshy, yellow; *lobes* 4–5 mm long, with 1 deep, central groove along entire length, basal part of corona lobe spreading, rounded, apical part of corona lobe erect, acute. *Style-head* convex, exposed, c. 1 mm in diam. *Pollinia* oblong, 300–350 × 70–100 µm; *corpusculum* ovate, 200–250 × 180–220 µm; *caudicles* 70–90 µm long. *Ovary* 2-carpellate, conic, c. 2 mm long; each carpel c. 0.7 mm wide at base, light green, glabrous. *Fruit* and *seeds* not observed.

Distribution — Known only from the type locality in Morobe Province of Papua New Guinea.

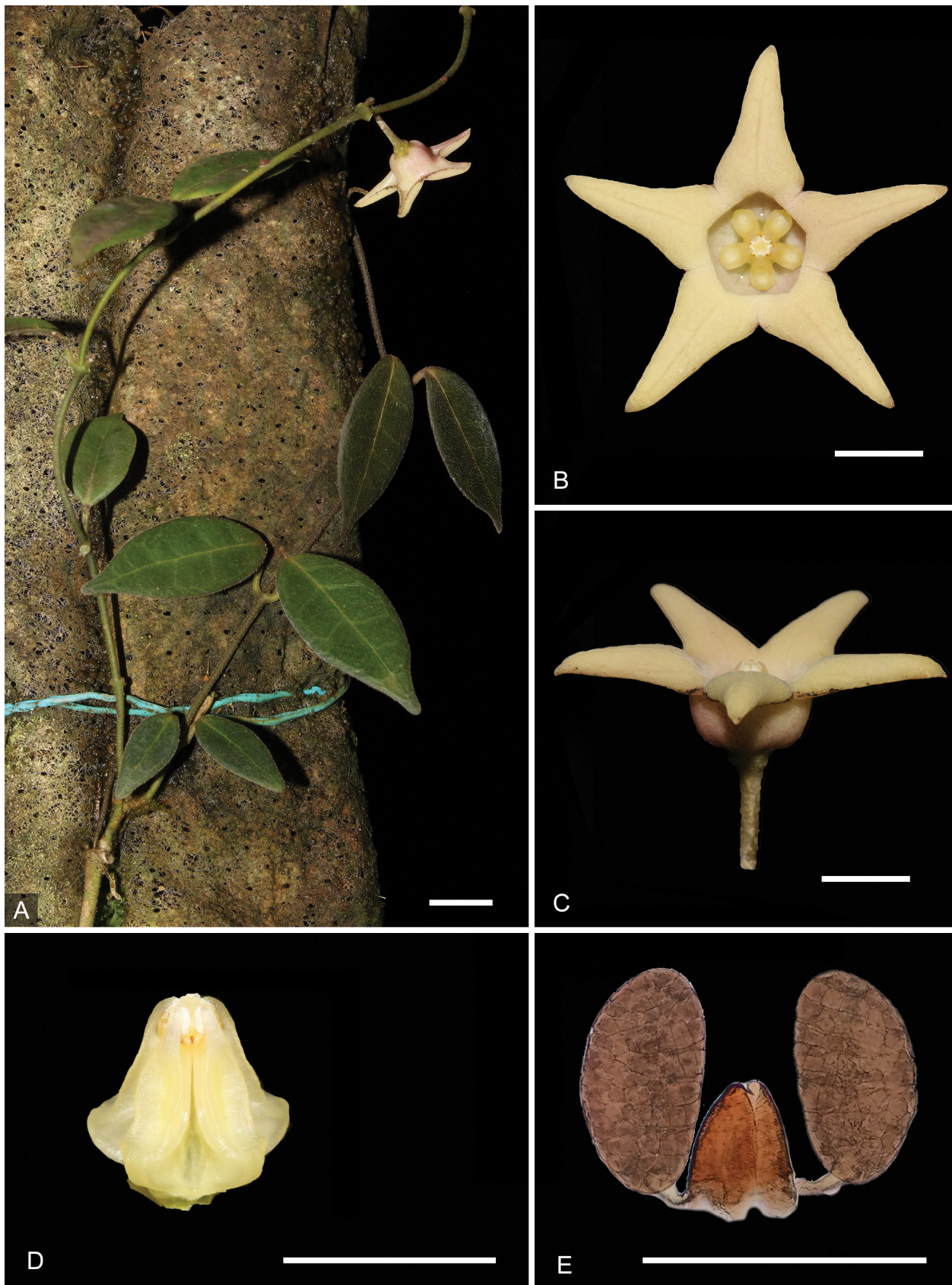


Fig. 7. *Papuahoya neoguineensis*. – A: habit, in cultivation; B: fully open flower, top view; C: fully open flower, side view; D: gynostegium, side view; E: pollinarium. – Scale bars: A = 1 cm; B–D = 5 mm; E = 500 μ m. – Vouchered by *Simonsson Juhonewe & Juhonewe NS0103L*. – Photographs: A–D by N. Simonsson; E by M. Rodda.

Ecology — *Papuahoya neoguineensis* was collected as a sterile cutting in primary mossy forest along a ridge on ultrabasic soil, at about 800 m.

Etymology — Named after the island of New Guinea, where the genus *Papuahoya* is endemic.

Additional specimen examined — PAPUA NEW GUINEA: MOROBE PROVINCE: Lababia, c. 800 m, vouchered at Singapore Botanic Gardens on 23 Apr 2015 from living accession NS13-013, Rodda MR1116 (SING).

Papuahoya urniflora (P. I. Forst.) Rodda & Simonsson, **comb. nov.** ≡ *Marsdenia urniflora* P. I. Forst. in Austral. Syst. Bot. 8: 752. 1995 ≡ *Hoya urniflora* (P. I. Forst.) Simonsson & Rodda in Gard. Bull. Singapore 69: 137. 2017. — Lectotype (designated by Rodda & Simonsson Juhonewe 2017: 137): Papua New Guinea, Oro Province, Lala River, c. 5500 ft. [c. 1675 m], 28 Dec 1935, C. E. Carr 14065 (SING [SING0122003]; isolectotypes: BM [BM001014154], K, L, SING [SING122001, SING122002]).

Remarks — *Papuahoya urniflora* is fully described and illustrated in Rodda & Simonsson Juhonewe (2017).

Oreosparte parviflora (Ridl.) Rodda & Simonsson, **comb. nov.** ≡ *Stephanotis parviflora* Ridl. in J. Straits Branch Roy. Asiat. Soc. 57: 69. 1911 ≡ *Marsdenia ridleyi* P. I. Forst. in Austral. Syst. Bot. 8: 700. 1995, nom. illeg. superfl. — Lectotype (designated by Forster 1995: 700): Malaysia, Perak, Tapah, Tenok road, 1908, H. N. Ridley s.n. (SING [SING0072733]).

Additional specimens examined — MALAYSIA: Perak, Ulu Temango, Jul 1909, H. N. Ridley s.n. (SING [SING007274]); Terengganu, Kemaman, Bukit Kajang, 26 Nov 1936, Corner 30564 (SING). — SINGAPORE: cultivated plant vouchered at Singapore Botanic Gardens, 16 Aug 2016, Rodda MR1786 (SING).

Oreosparte sabahensis Rodda & Simonsson, **sp. nov.** — Fig. 8.

Holotype: Malaysia, Sabah, Tawau, Hoya River, Merotai Kanan, 18 Feb 2002, S. Dolois, J. Yabainus, G. Masius & J. Gusili SNP16224 (SNP; isotype: SNP).

Description — Climber with white latex in vegetative parts. *Roots* unknown, no evidence of adventitious roots. *Stems* cylindrical, 4–6 mm in diam., sparsely pubescent, older parts glabrous, internodes 10–25 cm long. *Leaves*: *petiole* terete, channelled adaxially, 1.5–2(–2.5) cm × 2–3 mm, pubescent turning glabrescent; *lamina* broadly elliptic to ovate, coriaceous when dry, 4–8 × 3–5 cm, pubescent or sparsely pubescent on young leaves only, older leaves glabrescent, with sparse hairs along abaxial midrib, base rounded and slightly peltate, margin

slightly recurved, apex acute; penninerved but with 2 prominent, basal secondary veins, midrib depressed on adaxial surface, secondary veins 2 or 3 per side, branching from midrib at 30–45°. *Inflorescences* consisting of 1 or 2 flowers, often with only 1 flower open at a time; *peduncle* terete, persistent, extra-axillary, (0.7–)6–8 cm × 3–5 mm, pubescent on young peduncles only; *rachis* unbranched, thicker than peduncle, 5–6 mm in diam.; *pedicels* terete, 3–5 × c. 2 mm, sparsely pubescent. *Calyx* lobes ovate or triangular, c. 4 × 2 mm, sparsely puberulent outside, with 2 or 3 basal colleters at each lobe sinus, apex rounded or acute, ciliate. *Corolla* campanulate, with a contracted throat and free, spreading lobes, white or yellow, (2–)3–3.5 cm in diam.; *tube* 5–6 × 6–7 mm, outside glabrous, inside minutely pubescent at throat; *lobes* triangular to ovate, (7–)11–15 × 5–7 mm, glabrous, apex acute, laterally reflexed. *Gynostegium* stipitate; *stipe* 1.5–2 mm high. *Corona* staminal, conic, just exceeding corolla tube, 3.5–4.5 × 3–4 mm, corona lobes erect, triangular, c. 4 × 2 mm, basal part of corona lobe truncate, with a spreading margin, apical part of corona lobe bifid, slightly exceeding style-head. *Style-head* radially 5-lobed, apically bilobed, papillate. *Pollinia* erect, clavate, 1100–1200 × 350–500 µm; *corpusculum* ovate, c. 1000 × 550 µm, brown; *caudicles* simple, attached at base of corpusculum, 400–450 × 100–110 µm. *Fruit follicles* (unripe) paired, each follicle held at a c. 45° angle from pedicel, recurved, c. 2.5 × 0.6–0.7 cm, densely pubescent; *seeds* (unripe) flattened, ciliate from mid-portion to chalazal end, long comose at micropylar end.

Distribution — Known only from two collections in Sabah, Malaysia. The species was also seen in Kalimantan (Indonesia) (Rahayu, pers. obs.), but no specimens were obtained.

Ecology — The only available habitat information gathered from the type specimen is that the species was found growing along a river bank, likely as an epiphytic climber. The other specimen known (*Aban & al.* SAN86905, SAN) was collected in lowland dipterocarp forest.

Etymology — Named after the Malaysian state of Sabah, where the type specimen was collected.

Remarks — *Oreosparte sabahensis* is vegetatively similar to *O. parviflora* because both species have broadly elliptic to ovate leaves and rather stout peduncles. The two species can be separated by *O. parviflora* having a very pubescent corolla throat (vs. minutely pubescent in *O. sabahensis*) and a divergent apical part of the corona lobe (vs. convergent in *O. sabahensis*).

Additional specimen examined — MALAYSIA: Sabah, Sandakan, Sepilok Forest Reserve, 18 Aug 1977, *Aban, Henry & J. Nasip* SAN86905 (SAN).

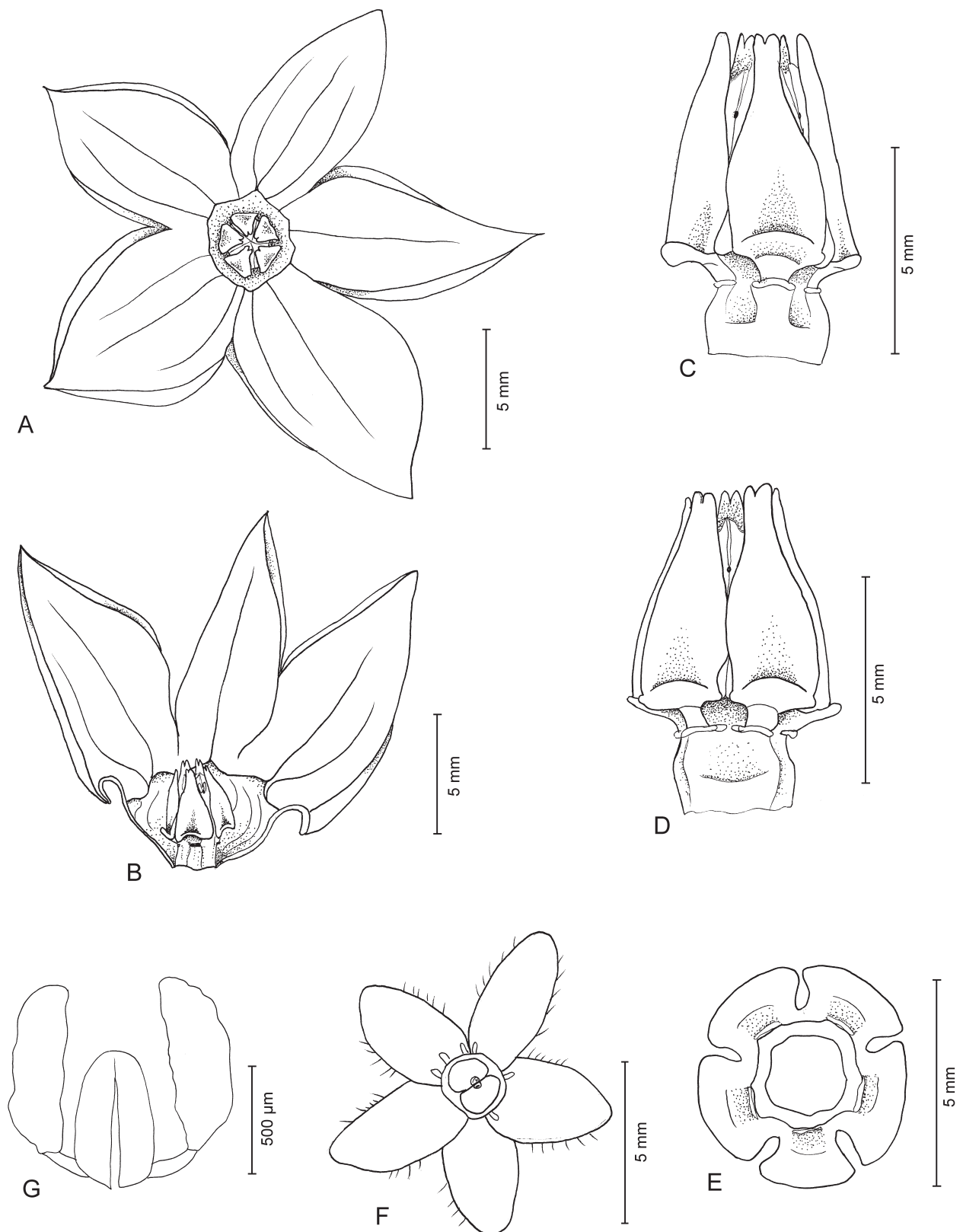


Fig. 8. *Oreosparte sabahensis*. – A: fully open flower, top view; B: flower, side view, with part of corolla removed exposing gynostegium; C, D: gynostegium, side view; E: gynostegium, from below; F: calyx and ovary; G: pollinarium. – Drawn by M. Rodda, based on *Dolois & al. SNP16224*.

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