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

Authors: Rodda, Michele, Simonsson, Nadhanielle, Ercole, Enrico, Khew, Gillian, Niissalo, Matti, et al.

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

**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 (mDNA 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* Kunze (1 sp.), *Anatropanthus* Schltr. (1 sp.) (Fig. 2), *Clemensiella* Schltr. (2 spp.), *Dischidia* R. Br. (c. 80 spp.) (Fig.
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 pollinia (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 Miqel (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. Plcostenema (Blume) Miq. and H. sect. Splringlea (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.
(1913, 1915) added another four sections: \textit{H.} sect. \textit{Eriostemma}, \textit{H.} sect. \textit{Oreostemma} Schltr., \textit{H.} sect. \textit{Pelostemma} Schltr. and \textit{H.} sect. \textit{Physostelma} (Wight) Schltr. The sectional classification of \textit{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 \textit{Hoya} has never been published. While sections such as \textit{H.} sect. \textit{Eriostemma} are supported as monophyletic in molecular analyses, others such as \textit{H.} sect. \textit{Cyrtoceras} and \textit{H.} sect. \textit{Plocostemma} are not (Wanntorp & al. 2011). In the most recent phylogeny, Wanntorp & al. (2014) divided \textit{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 biogeography, but only two of these can be readily aligned with previously published sections: \textit{H.} sect. \textit{Acanthostemma} (Blume) Kloppenburg and \textit{H.} sect. \textit{Eriostemma}.

\textit{Dischidia} R. Br. — Like \textit{Hoya} s.l., the circumscription of \textit{Dischidia} has been expanded to include eight segregate genera: \textit{Collyris} Vahl, \textit{Conchophyllum} Blume, \textit{Dischidopsis} Schltr., \textit{Dolichostegia} Schltr. (monotypic), \textit{Hoyella} Ridl. (monotypic), \textit{Leptostemma} Blume, \textit{Olistonema} Schltr. (monotypic) and \textit{Spathidolepis} Schltr. (monotypic) (Omlor 1998; Forster 2000; Livshultz 2003a, 2003b). Combinations in \textit{Dischidia} exist for species of all of these genera. Typical of the taxonomic history of other genera within \textit{Asclepiadaceae}, 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 Oistomena (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. Ascididiophora 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. Ascididiophora 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; Wann torp & 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 trnL-F 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 (Asclepiadaceae). 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 Wann torp & 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 main gayi (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 infrageneric 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′-trnH (Sang & al. 1997; Tate & Simpson 2003) for psbA-trnH, trnTUGU(a) trnLUA(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.
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 (Taberla & 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.

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 Wannertorp & 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.
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 Fockeae as sister to the rest of the subfamily (BS 100) and the sister-group relationship of Marsdenieae (BS 93). The position of Eustegieae as sister to 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, Ruehsia 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 clade names of Wanntorp & al. (2014: fig. 3, 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. laetifolia (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).

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 – trnT-trnL | 1338                         | 774                              | 162                           |
| 3             | 110 – trnL-trnF | 1093                         | 860                              | 134                           |
| 4             | 54 – combined nu + cp | N/A                          | 3900                             | 512                           |
| 5             | 54 – cp | N/A                           | 2869                             | 241                           |
| 6             | 54 – trnT-trnL | 1338                         | 774                              | 58                            |
| 7             | 54 – trnL-trnF | 1093                         | 860                              | 37                            |
| 8             | 54 – psbA-trnH | 820                          | 314                              | 76                            |
| 9             | 54 – matK | 921                           | 921                              | 70                            |
| 10            | 54 – nu | N/A                           | 1031                             | 271                           |
| 11            | 54 – ETS | 388                           | 369                              | 111                           |
| 12            | 54 – ITS | 700                           | 662                              | 160                           |
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.
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 Wanntorp & 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. Wanntorp & Meve and *H. omlorii* Oreosparte II (*Papuahoya*).

**Fig. 4.** Maximum likelihood tree of the combined chloroplast and nuclear 54-taxon matrix. Clade and group names follow Wanntorp & al. (2014) except “clade X”, which corresponds to clade 8 of Rodda & al. (2013) and the novel *Clemensiella* clade. Species sampled by Wanntorp & 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.
(Livsh. & Meve) L. Wanntorp & Meve, formerly classified in the segregate genus Clemensiella. Group I 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. juhoneveana* 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 *Micholitia* (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 polyphylly 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 resurrected *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 Simonsen & 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. retrosa; 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), Dischidopsis (D. parasita), Leptostemma (D. hirsuta, D. latifolia) and Ostonomema (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 epiphytically 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.

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 phylogenetic 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-
**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** lanate 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 glbose 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-
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 easily distinguished from similar species 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 NS12-026, N. Simonsson & Rodda, sp. nov. — Fig. 7. Holotype: Papua New Guinea, Morobe Province, Laba-vex, exposed. — Fig. 7.

Papuahoya neoguineensis Simonsson & Rodda, sp. nov. — Slender creeping climber. Stems cylin-dric, 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 neuguineensis*. – 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 μm. – Voucher 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]; isoelectotypes: 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 cylindric, 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; pinnerved 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. Polliina 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*) 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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