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

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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 (*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* Kunze (1 sp.), *Anatropanthus* Schltr. (1 sp.) (Fig. 2), *Clemensiella* Schltr. (2 spp.), *Dischidia* R. Br. (c. 80 spp.) (Fig. 3).
1C, D), Heynella Backer (1 sp.), Madangia P. I. Forst. & al. (1 sp.), Micholiiza 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 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 Absolnsia, Clemensiella, Dischidia, Mandangia or Micholitiza. 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 pellicid margins, anther guide rails without inner edges, and presence of nectaries inside the revolute margins of the outer corona — 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 pellicid 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 “Euhoa”), 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. Anchrostromma Hook. f., H. sect. Crytoperas (Bennett) Hook. f. and H. sect. Pterostelma (Wight) Hook.f.; and Schlechter

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 neotyped (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 pollinia 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 pellicid 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 pollinia of both Dischidia and Hoya generally have well-developed, broad caudicles and the pollinia of Hoya typically have pellicid 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 (Hiepko 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 corolla lobes, erect and attached at the back of the anthers. The pollinia are erect, with a pellicid 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 pollinia (size and shape of corpusculum, pollinia and caudicles, presence of pellicid 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 “Euhoa”), 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. Anchrostromma Hook. f., H. sect. Crytoperas (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.
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(1913, 1915) added another four sections: *H.* sect. *Eriostemma*, *H.* sect. *Oreostemma* Schltr., *H.* sect. *Pelostemma* 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, Wannom & 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 biogeography, 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, *Dischido­opsis* 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-

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Fig. 2. *Anatropanthus borneensis*. – A: inflorescence; B: flower, side view; C: corona, side view. – Drawn by Loh Xiang Yun, based on Somadee s.n. (SING).
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. Ascidiodora* 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 synonomy of *Dischidia* s.l. including *Collyris, Conchophyllum, Dischidiopsis, Leptostemma* and *Oistonema* (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 *Oreoosparte*. We sample *A. borneensis*, *O. celebica* Schltr. and other putative *Oreoosparte* 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 *Oreoosparte* within *Marsdenieae*, we modified the *trnL*-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, Oreoosparte celebica* and three other putative, undescribed *Oreoosparte* 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. urbiflora* (P. I. Forst.) Simonsson & Rodda (*Marsdenia urbiflora* P. I. Forst.) (Simonsson Juhanene & 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 “*Oreoosparte* 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′/*trnHff* (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 (Tabel­let & 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 (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 10000 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 Wannop & 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 Hems., 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 Fockeeae as sister to the rest of the subfamily (BS 100) and the sister-group relationship of Marsdenia 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 Rhyssoleobium 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).

Table 1. Summary statistics of matrices and analyses.

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</tbody>
</table>
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*.
(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. juhonweana 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. pallitima 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. manipuresis 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 Marsdenia, now classified in the recently recognized genus Clerevenia (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. juhonweana 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. pallitima 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. manipuresis 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 parvilifora, and M. urniflora, now Pauahoya urniflora); (2) an Asian/Australian clade outside the Hoya group (M. cornata 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 re-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 things 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 Ceroppegiae 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, Pauahoya 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. 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*), *Dischidopsis* (*D. parasita*), *Leptostemma* (*D. hirsuta*, *D. latifolia*) and *Oistonomia* (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 pollinia 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. carnosa*. 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 Wäldem am Long-Sele, an höher gele-
Rodda & al.: Phylogenetic studies in the Hoya group


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.


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

Description — Epiphytic climber (occasionally semi-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 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 x 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 x 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 x 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 x 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 x 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 x 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 x 70–80 µm; corpusculum ovate, 210–250 x 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 growing tightly attached onto the tree trunk, or climbing on small shrubs, upward toward better-lit areas. 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 NS12-026, N. Simonsson Juhonewe & F. Juhonewe NS0059L (LAE).

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


Description — 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 x c. 1 mm, green, pubescent on both sides; lamina broadly ovate-elliptic, coriaceous, 2–5 x 1–2.5 cm, silky 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 mid-rib at 70–80°. Inflorescence ageotropic, consisting of 1 or 2 flowers; peduncle persistent, terete, 0.2–1 cm x 1–1.5 mm, older peduncles bearing an elongate rachis from previous flowerings, often darker green or purplish, pubescent; pedicels terete, c. 1 cm x 1 mm, green to purplish red, sparsely pubescent. Flower buds valvate, creamy white-yellow, basally flushed pink. Calyx lobes broadly triangular, c. 1 x 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 x 5–7 mm, glabrous outside, pubescent inside with short hairs; lobes narrowly triangular, often fleshy, 8–9 x 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 x 70–100 µm; corpusculum ovate, 200–250 x 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 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, vouchedered at Singapore Botanic Gardens on 23 Apr 2015 from living accession NS13-013, Rodda MR1116 (SING).


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


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


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; pinninerved 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, 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).

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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References

Bruyns P. V., Klak C. & Hanáček P. 2015: Recent radiation of Brachystelma and Ceropogia (Apocynaceae) across the Old World against a background of climatic change. – Molec. Phylogeny Evol. 90: 49–66


Tate J. A. B. & Simpson B. 2003: Paraphyly of Tarasa (Malvaceae) and diverse origins of the polyploid species. – Syst. Bot. 28: 723–737.


White T. J., Bruns T., Lee S. & Taylor J. 1990: Amplification and direct sequencing of fungal ribosomal RNA