The *Hedyotis-Oldenlandia* complex (Rubiaceae: Spermacoceae) in Asia and the Pacific: Phylogeny revisited with new generic delimitations

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Abstract *Hedyotis* and related genera (here called the *Hedyotis-Oldenlandia* complex) are highly debated groups in the Rubiaceae family with no consensus to date on their generic delimitations. The present study focuses on Asian-Pacific taxa from these groups and aims at resolving taxonomic inconsistencies by describing monophyletic genera within the complex. The generic circumscriptions presented in our study are based on the phylogenetic trees of nuclear (ITS, ETS) and plastid (*petD*, *rps16*) sequence data inferred using Bayesian and maximum likelihood methods. Morphological key features of the group such as habit, fruit type, seed form, and pollen type are studied and compared with the phylogeny to characterize the clades. Based on these results, the Asian-Pacific members are placed in 14 monophyletic groups across the *Hedyotis-Oldenlandia* complex. Of these, we accept and circumscribe 13 monophyletic genera: *Debia*, *Dentella*, *Dimetia, Edrastima*, *Exallage*, *Hedyotis*, *Involucrella*, *Kadua*, *Kohautia*, *Leptopetalum*, *Neanotis*, *Oldenlandia*, and *Scleromitrion*. Two of these, *Debia* and *Involucrella*, are here described as new genera.

Keywords Asia-Pacific; fruit dehiscence pattern; *Hedyotis*; *Oldenlandia*; phylogenetic analysis; pollen; seed; Spermacoceae

Supplementary Material Electronic Supplement (Figs. S1–S2) and alignment are available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/iapt/tax

■ INTRODUCTION

The *Hedyotis-Oldenlandia* complex is one of the most enigmatic groups in Rubiaceae due to a wide range of morphological diversity observed and the long standing taxonomic complexity with conflicting generic delimitations. The group comprises approximately 500–600 species (Groeninckx & al., 2009a; Govaerts & al., 2014), most of which have an herbaceous to suffrutescent habit with a few groups forming small trees. A large number of generic names exist for taxa included in the group, but the most commonly recognized ones are: *Arcytophyllum* Willd ex Schult. & Schult.f., *Exallage* Bremek., *Hedyotis* L., *Houstonia* L., *Kadua* Cham. & Schltdl., *Kohautia* Cham. & Schltdl., *Neanotis* W.H.Lewis, and *Oldenlandia* L. The complex was traditionally assigned to tribe Hedyotideae Cham. & Schltdl. ex DC. but is now part of Spermacoceae Cham. & Schltdl. ex DC. (Bremer, 1996; Andersson & Rova, 1999; Bremer & Manen, 2000). The generic limits within the complex are also not clear-cut due to overlapping morphology in the characters used for delimiting the genera. Furthermore, several genera in the complex were found to be non-monophyletic in recent phylogenetic analyses (Kårehed & al., 2008; Groeninckx & al., 2009a). This necessitates that we either (1) split the complex into smaller natural and monophyletic units or (2) lump all members (>1000 species) of tribe Spermacoceae into a single genus *Spermacoce* L. The former choice (splitting) would result in a large number of genera, sometimes comprising only a few species, and the morphological characterization would be difficult at times. The latter choice (lumping) would result in a morphologically very diverse genus making it almost impractical for any type of identification and botanical inventory.

Following studies at both the morphological (Terrell & Robinson, 2003; Neupane & al., 2009; Groeninckx & al., 2009b, 2010a, b, c) and molecular levels (Kårehed & al., 2008; Groeninckx & al., 2009a; Guo & al., 2013; Wikström & al.,

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2013), there is growing acceptance among taxonomists to recognize morphologically identifiable and monophyletic genera in the complex. The recent studies by Guo & al. (2013) and Wikström & al. (2013) identified several monophyletic groups within the complex. With an extensive sampling from the Asia-Pacific region, the genera *Hedyotis* s.str., and *Neanotis* were confirmed monophyletic by Wikström & al. (2013). Their study also established the monophyly of the clades representing *Dimetia* (Wight & Arn.) Meisn., *Exallage*, *Kadua*, *Leptopetalum* Hook. & Arn., and an "unnamed group" within "clade B". Guo & al. (2013), with a sampling mainly from China, proposed to formally recognize the genera *Dimetia*, *Scleromitrion* (Wight & Arn.) Meis., and *Thecagonum* Babu within the *Hedyotis-Oldenlandia* complex. The results of Guo & al. (2013) and Wikström & al. (2013) were similar but differed with respect to the monophyly of the clades *Dimetia* and *Exallage*. In Guo & al. (2013), species of *Dimetia* and *Exallage* did not form separate clades and the name *Dimetia* was retained to include *Exallage* as a synonym. In Wikström & al. (2013), however, *Dimetia* and *Exallage* were found to be well-supported sister clades in their combined analysis (nuclear and plastid) and the two genera were kept separate. That result is also supported by the morphological differences observed between the two genera: *Dimetia* is characterized by terminal inflorescences, capsules opening septicidally, flattened to winged seeds, and a scandent/climbing habit, whereas *Exallage* has terminal and axillary inflorescences, indehiscent fruits, trigonous seeds, and a herbaceous or suffrutescent habit. The clade recognized as "unnamed group" by Wikström & al. (2013) was also recovered in the study by Guo & al. (2013). It includes morphologically very diverse species, some belonging to *Hedyotis* sect. *Scleromitrion* Wight & Arn. and some to the *Oldenlandia corymbosa–O. diffusa* group (sensu Sivarajan & Biju, 1990). Guo & al. (2013) recognized the generic name *Scleromitrion* for this group primarily based on the presence of homostylous flowers with exserted stamens and styles.

While the studies by Wikström & al. (2013) and Guo & al. (2013) resolved some of the taxonomic issues regarding the clades *Hedyotis* s.str., *Neanotis* and *Scleromitrion*, ambiguity remains with the clades *Dimetia*, *Exallage* and *Leptopetalum*. Similarly, the taxonomic positions of *Hedyotis coronaria* (Kurz) Craib, *Oldenlandia chereevensis* Pierre ex Pit., and *O. ovatifolia* Cav. were unclear in the previous studies. Therefore, this study particularly focused on "clade B" from Wikström & al. (2013), an Asian-Pacific clade that exhibits diverse morphological features where both generic delimitations and circumscriptions are unclear. The members in this clade were historically assigned to either *Hedyotis* or *Oldenlandia* and this tradition continues in many local Floras. But, with the recircumscrption of *Hedyotis* (*Hedyotis* s.str.) and *Oldenlandia* (*Oldenlandia* s.str.) by Guo & al. (2013) and Wikström & al. (2013), the remaining taxa in this clade require new generic circumscriptions and names.

Further, data from pollen, seed, and fruit morphology have been found to be the most consistent traits for taxonomic studies in this group and has been used extensively (e.g., Lewis, 1965a, b; Terrell, 1975, 1996, 2001a, b, c; Terrell & al., 1986; Terrell & Wunderlin, 2002; Terrell & Robinson, 2003; Groeninckx & al., 2010a, b, c). Hence, along with the phylogeny, we also incoprorate these morphological data into our study to further clarify the taxonomy and generic limits within the Asian-Pacific *Hedyotis-Oldenlandia* complex.

■ MATERIALS AND METHODS

Taxon sampling. — A total of 291 accessions were chosen for this study. Of these, 37 accessions were newly sampled, belonging to 27 species. The present study expands on previous work (Wikström & al., 2013) by adding recent collections from China and Thailand. These new samples represent *Dimetia*, *Thecagonum*, and *Scleromitrion* (sensu Guo & al., 2013). Further, due to morphological similarities between some taxa we were also interested in the phylogenetic positions of *Hedyotis coronaria* and *Oldenlandia ovatifolia* in relation to our new additions of *Hedyotis oligocephala* (Pierre ex Pit.) Fukuoka and *Oldenlandia krewanhensis* Pierre ex Pit. from Thailand. Therefore, adding more specices from these groups from our new collections allowed us to test their positions in the *Hedyotis-Oldenlandia* complex phylogeny.

We will not discuss *Kadua* and *Neanotis* in detail in this paper as earlier studies (Guo & al., 2013; Wikström & al., 2013) have already shown them to be monophyletic with their own unique morphological traits. In order to avoid confusion with synonyms and until new generic combinations are provided, the names of the species discussed in the present study follow Govaerts & al. (2014) in all groups except for *Hedyotis* s.str. and *Neanotis*. Names in these two genera follow those given by Wikström & al. (2013).

DNA extraction, amplification, and sequencing. — DNA was extracted from silica-dried and herbarium material with the DNeasy Plant Kit (Qiagen, Valencia, California, U.S.A.). Four DNA regions, two from the nuclear (ITS, ETS), and two from the plastid genome (*petD*, *rpsl6*) were selected for amplification. These regions were selected in order to add our new samples to already existing datasets from an earlier study (Wikström & al., 2013). The primers used for amplification are listed in Table 1. Amplifications were performed in a 25 µl reaction mixture composed of 1 µl of each primer (10 µM), 1 µl of DNA template, 1.25 µl of DMSO, 12.5 µl of GoTaq Green Master Mix (Promega, Madison, Wisconsin, U.S.A.), 8 µl of water and with or without 0.25 µl of BSA (1%). The amplification protocol for nuclear and chloroplast regions follows Kårehed & al. (2008) and Groeninckx & al. (2009a) respectively.

Sequence alignment and phylogenetic reconstruction. — Sequences were aligned using MAFFT v.7 (Katoh & Standley, 2013), followed by manual adjustments for the chloroplast regions. Inversions were identified in the *petD* and *rpsl6* regions and were reverse complemented to align with the dataset. The dataset was partitioned by gene regions (ITS, ETS, *petD*, *rpsl6*) and tested for optimum partition schemes and substitution models (for each partition) using PartitionFinder v.1.1.1 (Lanfear & al., 2012). PartitonFinder was set to use heuristic search algorithm under Bayesian information criterion

Table 1. Primers used for amplification and sequencing.

Region	Primer	Primer sequence from the 5′ end	Reference
ITS	NY183_F	CCTTATCATTTAGAGGAAGGAG	Motley & al. (2005)
	NY43_R2	TATGCTTAAAYTCAGCGGGT	Motley & al. (2005)
ETS	ETS-Erit-F	CTTGTATGGGTTGGTTGGA	Negrón-Ortiz & Watson (2002)
	18S-E	GCAGGATCAACCAGGTAGCA	Baldwin & Markos (1998)
petD	PlpetB1411F	GCCGTMTTTATGTTAATGC	Löhne & Borsch (2005)
	PlpetD738R	AATTTAGCYCTTAATACAGG	Löhne & Borsch (2005)
rps16	rps16_F	GTGGTAGAAAGCAACGTGCGACTT	Oxelman & al. (1997)
	rps16_R2	TCGGGATCGAACATCAATTGCAAC	Oxelman & al. (1997)

(BIC) that resulted in three subsets (ITS, ETS, plastid) as the best-fit partition schemes and GTR+I+Γ as the best model for all three subsets. To infer the phylogeny, Bayesian and maximum likelihood methods were used for the combined (with the identified partitions concatenated) as well as single-gene regions. Bayesian inference was performed using MrBayes v.3.2 (Ronquist & al., 2012) with 15 million MCMC iterations. Maximum likelihood (ML) tree search was performed in Garli v.2.01 (Zwickl, 2006) with 20 independent search replicates where the tree with the best likelihood was chosen for the study. Bootstrap support (BS) for the clades was also obtained using Garli (Zwickl, 2006) with 500 bootstrap replicates. The bootstrap values were calculated from these replicates and placed on the best ML tree using the SumTrees v.3.3.1 program in the DendroPy v.3.12.0 Python package (Sukumaran & Holder, 2010). MrBayes and Garli searches were conducted on CIPRES (Miller & al., 2010) and bioinformatics facility cluster at the University of Connecticut, Storrs.

Habit. — Members of *Hedyotis-Oldenlandia* complex show a wide range of life forms. The coding of these character states was made from herbarium specimens and/or literature data. Accordingly, these life-forms were categorzied into herbs (annual or perennial/suffrutiscent herbs), climbers, shrubs, and small trees.

Fruit and seed morphology. — Fruit dehiscence pattern in various clades was determined from our personal obervation of herbarium and fresh specimens and through literature reviews. Morphological studies of seed shape and seed coat were performed on representative species from all clades from the Asia-Pacific region. Seeds collected from herbarium specimens were mounted on aluminium stubs, coated with gold, and observed under a JEOL 5800 LV Scanning Electron Microscope at the National Botanic Garden of Belgium. Seed shape and seed coat (testa) ornamentations were investigated following the descriptions in Stern (1966) and Dessein (2003).

Pollen morphology. — For the palynological study all samples were obtained from herbarium specimens (Table 2). Pollen grains were acetolyzed following Reitsma's "wetting agent method" (Reitsma, 1969). The acetolyzed samples were studied using both light microscopy (LM) and scanning electron microscopy (SEM). Pollen for SEM were rinsed in ethanol 70% or 96%, pipetted on a stub, and left to dry. Prior to observations under the SEM, the stubs were coated with gold using a SPI-MODULETM sputter coater. Observations and digital images were made under a JEOL 5800 LV Scanning Electron Microscope at the National Botanic Garden of Belgium. Measurement of polar axis length (P) and equatorial diameter (E) were performed on 10 grains of each specimen. Pollen features such as shape, aperture type, number of apertures, and sexine pattern were examined. Terminology for the description of pollen follows Punt & al. (2007).

■ RESULTS

Molecular phylogeny. — The phylogenetic trees obtained from MrBayes and Garli runs showed no major topological incongruence for the clades discussed below. The clades supported in the ML analysis (BS ≥ 60%) were also supported in the Bayesian analysis (Bayesian posterior probability, BPP ≥ 0.95). However, intercladal relationships varied between the analyses. The major clades resolved in the *Hedyotis-Oldenlandia* complex in the phylogeny obtained from the combined nuclear and plastid data (ITS+ETS+*petD*+*rps16*) are: *Edrastima-Agathisanthemum*/*Lelya* (Fig. 1; BS = 100%, BPP = 1), *Arcytophyllum*/*Houstonia* (Fig. 1; BS = 95%, BPP = 1), *Dentella-Pentodon* (Fig. 1; BS = 98%, BPP = 1), *Kohautia* (Fig. 1; BS = 100%, BPP = 1), *Neanotis* (Fig. 1; BS = 100%, BPP = 1), *Pentanopsis* (Fig. 1; BS = 100%, BPP = 1), *Hedyotis* s.str. (Fig. 1 clade A & Fig. 2; BS = 100%, BPP = 1), an Asian-Pacific clade containing *Scleromitrion*/*Kadua*/*Leptopetalum*/*Dimetia*/*Exallage* and two groups (clades I and II) with no available names (Fig. 1 clade C & Fig. 4; BS = 72%, BPP = 1), and a clade containing *Cordylostigma*/*Oldenlandia*/*Spermacoce* (Fig. 1 clade B & Fig. 3; BS = 95%, BPP = 1). The ML tree (Figs. 1–4) obtained from the Garli analysis is used as a basis for the discussion below.

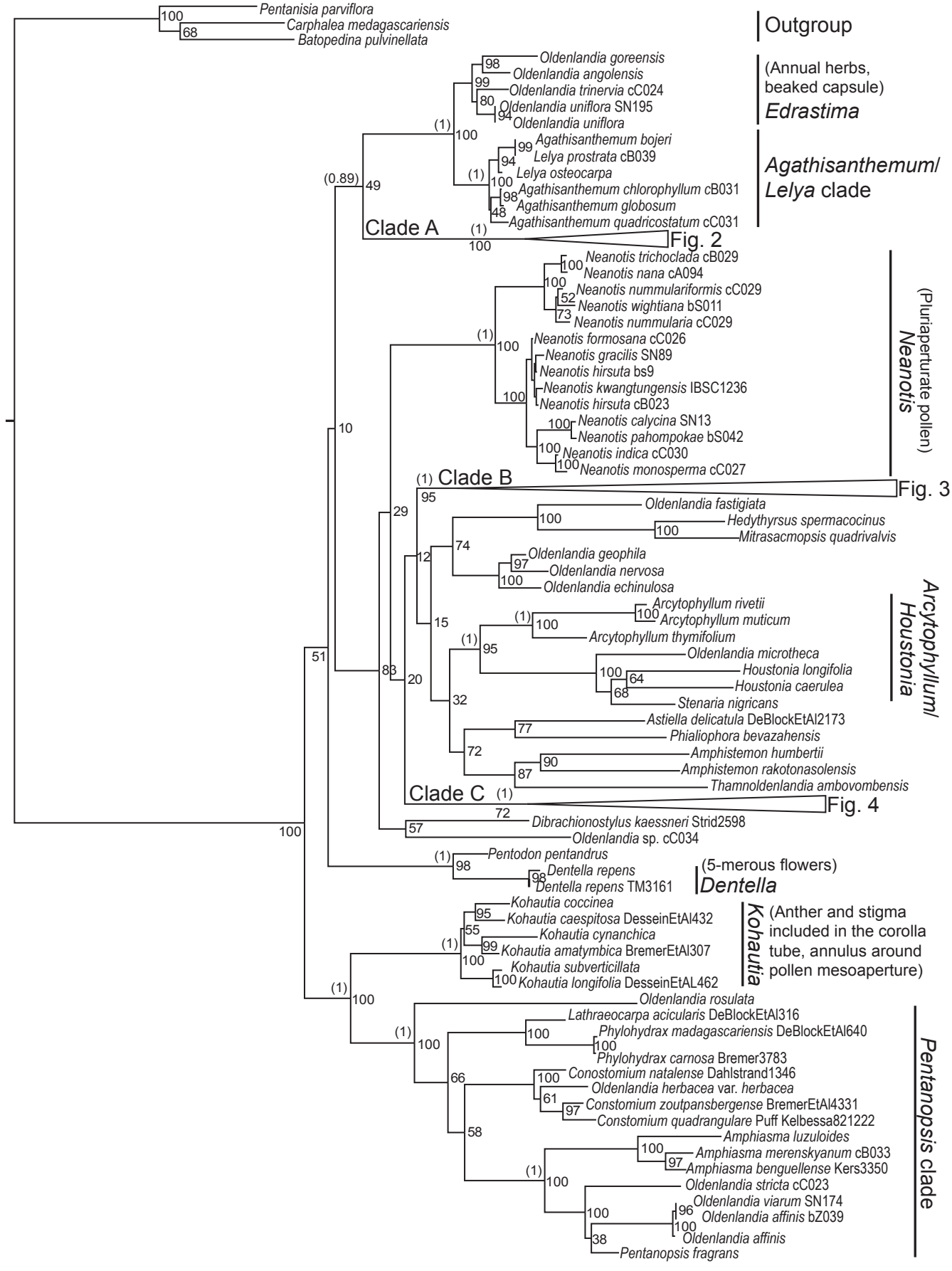
The results from the current analyses confirmed results obtained by Wikström & al. (2013), but also identified additional supported clades. There were no major conflicts between Wikström & al. (2013) and the present study with respect to the monophyly of the clades being discussed. The major groups from Asia-Pacific regions that were well supported in Wikström & al. (2013) and in the present study are: (1) an Asian-Pacific clade (clade C, Fig. 4) that includes *Dimetia* (BS = 82%, BPP = 0.99), *Exallage* (BS = 87%, BPP = 1), *Scleromitrion* (BS = 61%, BPP = 1), *Leptopetalum* (BS = 100%, BPP = 1), and *Kadua* (BS = 100%, BPP = 1); (2) *Hedyotis* s.str.

(BS = 100%, BPP = 1); and (3) *Neanotis* (BS = 100%, BPP = 1). In addition, clades I (BS = 100%, BPP = 1) and II (BS = 100%, BPP = 1) were newly resolved groups comprised of the Southeast Asian *Hedyotis oligocephala*, *Oldenlandia krewanhensis*, *O. ovatifolia* (clade I), and *H. coronaria*, and *O. chereevensis* (clade II). Furthermore, *Leptopetalum* was resolved sister to *Kadua* in the nuclear (ITS+ETS, Electr. Suppl.: Fig. S1), plastid (*petD*+*rpsl6*, Electr. Suppl.: Fig. S2), and combined (ITS+ETS+*petD*+*rpsl6*, Fig. 4) trees whereas *Dimetia* was resolved sister to *Exallage* only in the nuclear and combined trees. Clades I and II were found sister only in the combined nuclear tree (ITS+ETS, Electr. Suppl.: Fig. S1).

Table 2. Specimens used for fruit, seed and pollen study and their voucher information.

Taxon	Voucher information	
Exallage auricularia (L.) Bremek.	*C. Charoenphol, K. Larsen & E. Warncke 4425* (AAU)	Fruit, seed
Exallage lineata (DC.) Bremek.	*S. Neupane 9* (ODU)	Seed
Hedyotis andamanica Kurz	*M.R. Henderson 22294* (NY)	Seed
Hedyotis capitellata Wall. ex G.Don	*J.F. Rock 2029* (A)	Seed
Hedyotis dendroides Alston	*S. Neupane 33* (ODU)	Pollen
Hedyotis fruticosa L.	*S. Neupane 58* (ODU)	Pollen
Hedyotis fruticulosa (Volkens) Merr.	*F.R. Fosberg 46564* (MO)	Seed
Hedyotis marginata (Thwaites ex Trimen) Alston	*S. Neupane 64* (ODU)	Pollen
Hedyotis nodulosa Thwaites	*P.L. Comanor 921* (A)	Pollen
Hedyotis oligocephala (Pierre ex Pit.) Fukuoka	*J.F. Maxwell 93-992* (A)	Seed
Hedyotis scandens Roxb.	*A. Henry 13484* (NY)	Pollen
Hedyotis scandens Roxb.	*A.J.C. Grierson & D.G. Long 4164* (A)	Fruit, seed
Hedyotis trimenii Deb & Ratna Dutta	*S. Neupane 30* (ODU)	Fruit
Hedyotis verticillata (L.) Lam.	*Guang-Wan Hu HGW-00848* (ODU)	Seed
Hedyotis yangchunensis W.C.Ko & Zhang	*W.J. Kress 97-5772* (US)	Pollen
Kohautia gracilis (Wall.) DC.	*W. Koelz 4614* (US)	Pollen
Leptopetalum foetidum (G.Forst.) Neupane & N.Wikstr.	*D. Herbst 7246* (US)	Seed
Neanotis calycina (Wall. ex Hook.f.) W.H.Lewis	*S. Neupane 13* (ODU)	Seed
Neanotis gracilis (Hook.f.) W.H.Lewis	*S. Neupane 12* (ODU)	Seed
Neanotis gracilis (Hook.f.) W.H.Lewis	*S. Neupane 89* (ODU)	Pollen
Oldenlandia chereevensis Pierre ex Pit.	*K. Larsen, T. Smitinand & E. Warncke 790* (AAU)	Pollen
Oldenlandia chereevensis Pierre ex Pit.	*J.F. Maxwell 76-597* (AAU)	Seed
Oldenlandia diffusa (Willd.) Roxb.	*K. Larsen & S. Larsen 34453* (AAU)	Pollen
Oldenlandia hedyotidea (DC.) Hand-Mazz.	*Kuang-Yuh Wang 156* (TNM)	Pollen
Oldenlandia hedyotidea (DC.) Hand-Mazz.	*S.Y. Lau 20070* (NY)	Seed
Oldenlandia krewanhensis Pierre ex Pit.	*J.F. Maxwell 06-814* (A)	Seed
Oldenlandia ovatifolia (Cav.) DC.	*K. Larsen & S. Larsen 34274* (AAU)	Seed
Oldenlandia pinifolia (Wall. ex G.Don) Kuntze	*Norkett 8008* (BM)	Seed
Oldenlandia umbellata L.	*S. Neupane 84* (ODU)	Seed
Thecagonum biflorum (L.) Babu	*W.L. Wagner 6688*(MO)	Seed
Thecagonum strigulosum (Bartl. ex DC.) Terrell & H.Rob.	*F.S. Fosberg 24788* (NY)	Seed

Fig. 1. ML tree showing phylogenetic relationships in tribe Spermacoceae based on the combined nuclear (ITS, ETS) and plastid (*petD*, *rpsl6*) data. Names next to vertical bars are the major clades resolved in the recent molecular phylogenetic studies (Kårehed & al., 2008; Groeninckx & al., 2009a; Guo & al., 2013; Wikström & al., 2013). Asian-Pacific members of the *Hedyotis-Oldenlandia* complex are represented in the *Edrastima-Agathisanthemum/Lelya* clade, clade A (Fig. 2; *Hedyotis*), *Neanotis*, clade B (Fig. 3; *Oldenlandia*), clade C (Fig. 4; clade I, clade II, *Dimetia*, *Exallage*, *Kadua*, *Leptopetalum*, and *Scleromitrion*), *Kohautia* and the *Pentanopsis* clade. The generic limits of *Oldenlandia* subg. *Anotidopsis* (Bremekamp, 1952) were re-evaluated and recognized as a new genus (*Edrastima*) in this study. *Neanotis* is exclusively Asian-Pacific taxa discussed in Wikström & al. (2013). Values at the nodes represent bootstrap support (BS). Values in parenthesis are Bayesian posterior probabilities (BPP) that are shown only for the major clades. ▶


Pentanisia parviflora
Carphalea medagascariensis
Batopedina pulvinellata
Outgroup
Oldenlandia goreensis
Oldenlandia angolensis
Oldenlandia trinervia cC024
Oldenlandia uniflora SN195
Oldenlandia uniflora
(Annual herbs, beaked capsule)
Edrastima
Agathisanthemum bojeri
Lelya prostrata cB039
Lelya osteocarpa
Agathisanthemum chlorophyllum cB031
Agathisanthemum globosum
Agathisanthemum quadricostatum cC031
Agathisanthemum/ Lelya clade
Clade A
Fig. 2
Neanotis trichoclada cB029
Neanotis nana cA094
Neanotis nummulariformis cC029
Neanotis wightiana bS011
Neanotis nummularia cC029
Neanotis formosana cC026
Neanotis gracilis SN89
Neanotis hirsuta bs9
Neanotis kwangtungensis IBSC1236
Neanotis hirsuta cB023
Neanotis calycina SN13
Neanotis pahompokae bS042
Neanotis indica cC030
Neanotis monosperma cC027
(Pluriaperturate pollen) Neanotis
Clade B
Fig. 3
Oldenlandia fastigiata
Hedythyrsus spermacocinus
Mitrasacmopsis quadrivalvis
Oldenlandia geophila
Oldenlandia nervosa
Oldenlandia echinulosa
Arcytophyllum rivetii
Arcytophyllum muticum
Arcytophyllum thymifolium
Oldenlandia microtheca
Houstonia longifolia
Houstonia caerulea
Stenaria nigricans
Arcytophyllum/ Houstonia
Astiella delicatula DeBlockEtAl2173
Phialiophora bevazahensis
Amphistemon humbertii
Amphistemon rakotonasolensis
Thamnoldenlandia ambovombensis
Clade C
Fig. 4
Dibrachionostylus kaessneri Strid2598
Oldenlandia sp. cC034
Pentodon pentandrus
Dentella repens
Dentella repens TM3161
(5-merous flowers)
Dentella
Kohautia coccinea
Kohautia caespitosa DesseinEtAl432
Kohautia cynanchica
Kohautia amatymbica BremerEtAl307
Kohautia subverticillata
Kohautia longifolia DesseinEtAL462
Kohautia
(Anther and stigma included in the corolla tube, annulus around pollen mesoaperture)
Oldenlandia rosulata
Lathraeocarpa acicularis DeBlockEtAl316
Phylohydrax madagascariensis DeBlockEtAl640
Phylohydrax carnosa Bremer3783
Conostomium natalense Dahlstrand1346
Oldenlandia herbacea var. herbacea
Constomium zoutpansbergense BremerEtAl4331
Constomium quadrangulare Puff Kelbessa821222
Amphiasma luzuloides
Amphiasma merenskyanum cB033
Amphiasma benguellense Kers3350
Oldenlandia stricta cC023
Oldenlandia viarum SN174
Oldenlandia affinis bZ039
Oldenlandia affinis
Pentanopsis fragrans
Pentanopsis clade

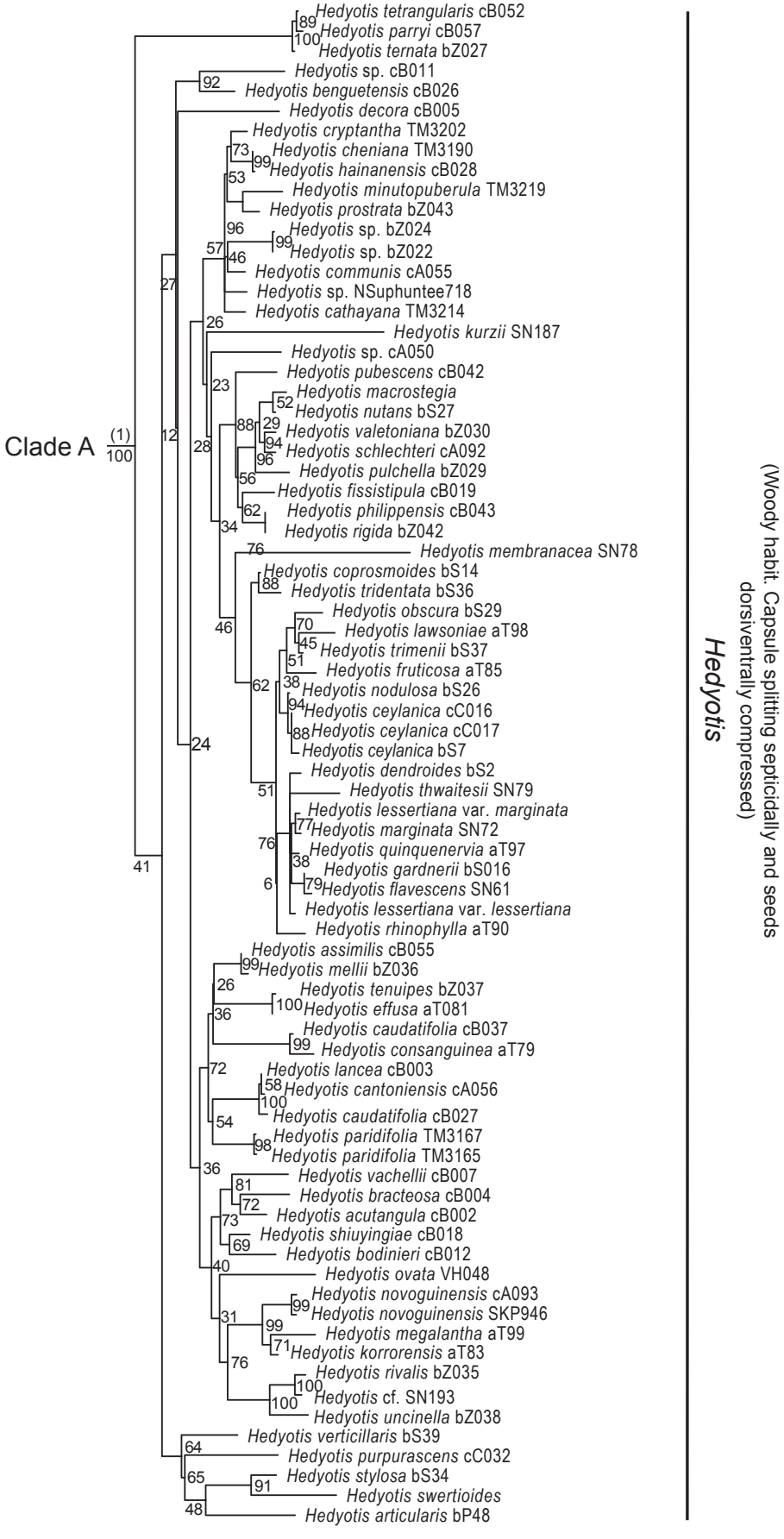


Fig. 2. ML phylogenetic tree representing clade A (from Fig. 1) based on the combined nuclear (ITS, ETS) and plastid (*petD*, *rpsl6*) data. This clade represents *Hedyotis* s.str. Values at the nodes represent bootstrap support (BS). Value in parenthesis is the Bayesian posterior probability (BPP).

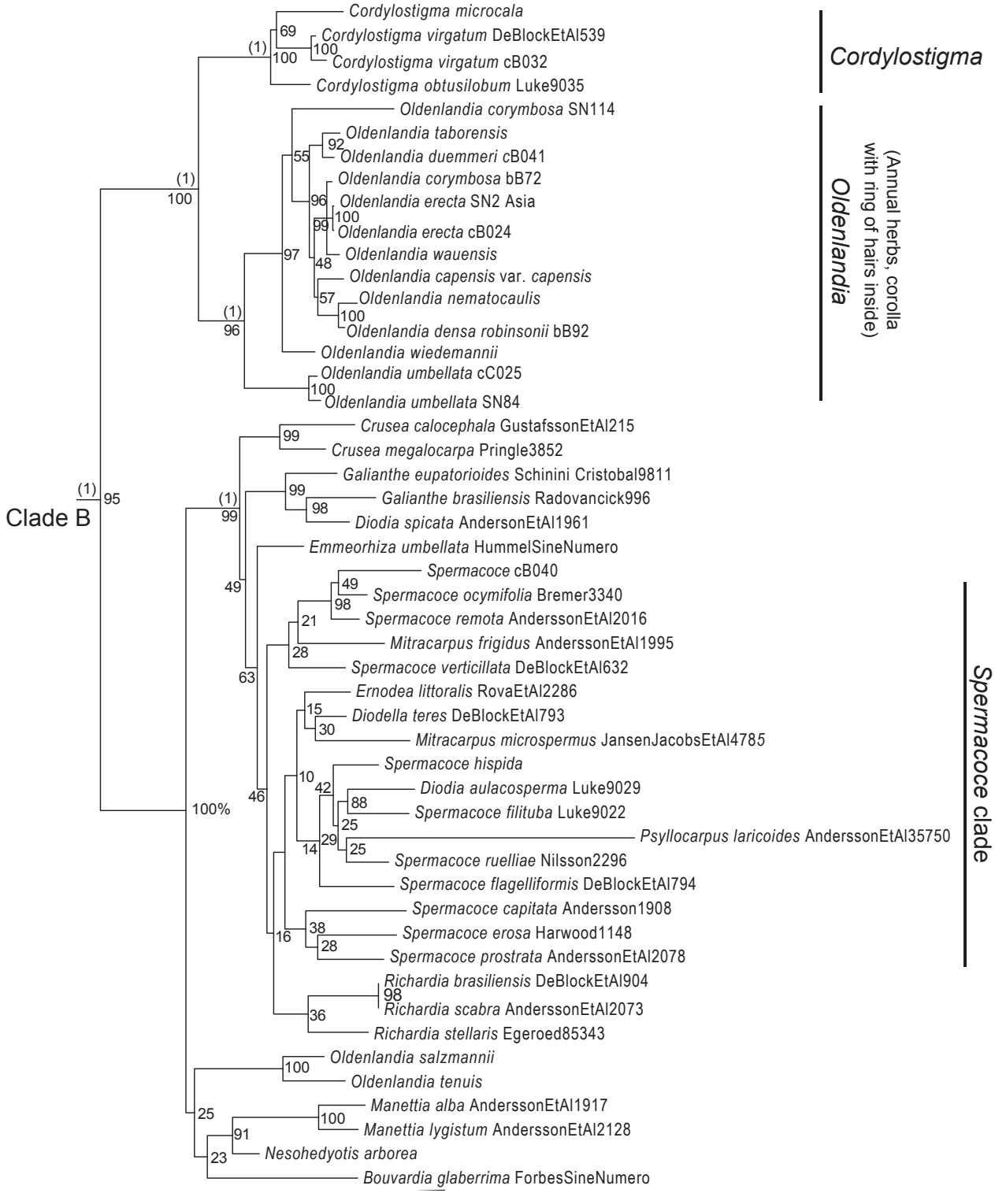


Fig. 3. ML phylogenetic tree representing clade B (from Fig. 1) based on the combined nuclear (ITS, ETS) and plastid (*petD, rps16*) data. This clade includes *Cordylostigma*, *Oldenlandia*, clade *Spermacoce* and a few other species of uncertain affinity. Asia-Pacific members of the *Hedyotis-Oldenlandia* complex are represented by *Oldenlandia*. Values at the nodes represent bootstrap support (BS). Values in parenthesis are Bayesian posterior probabilities (BPP) that are shown only for the major clades.

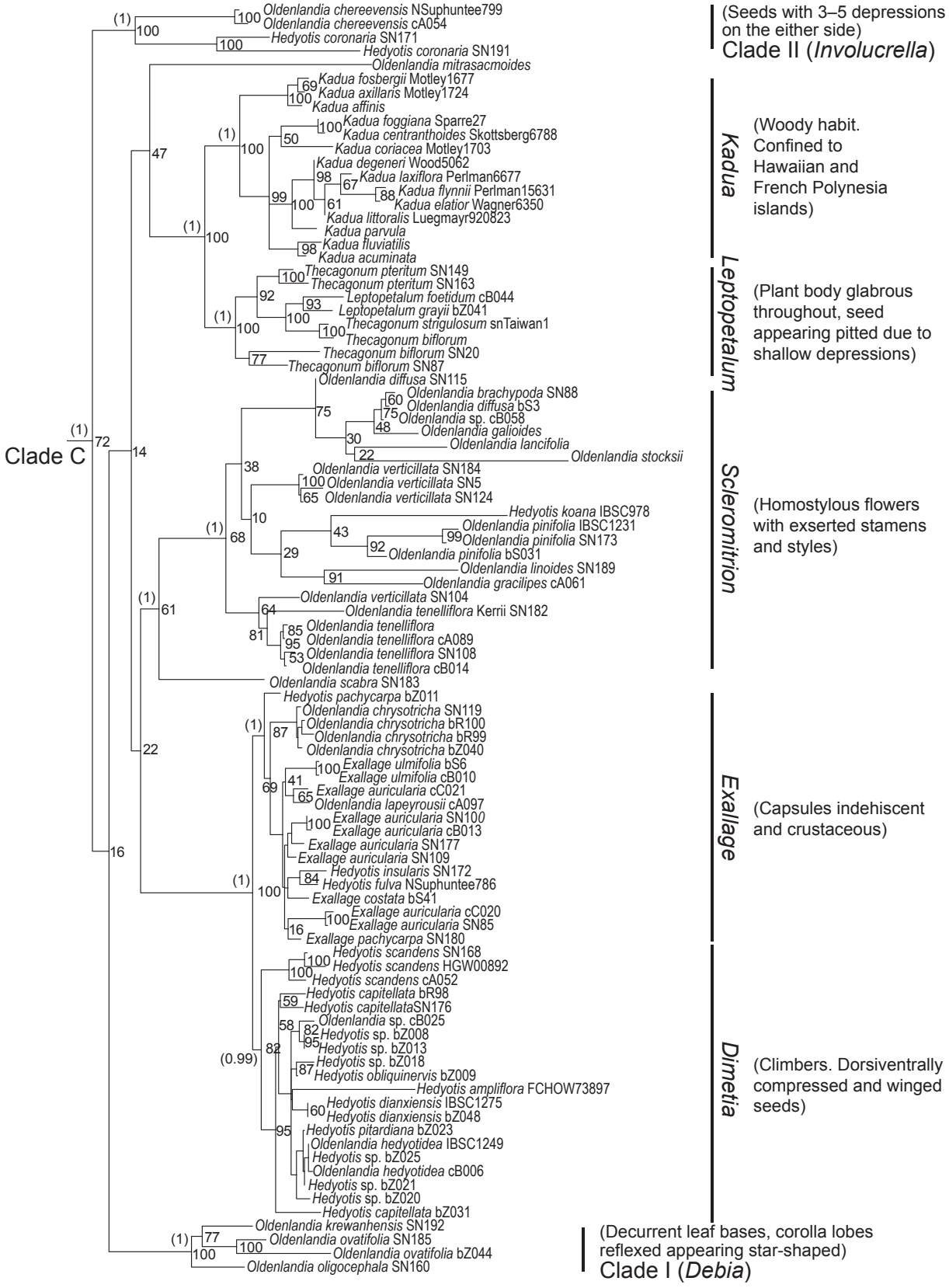


Fig. 4. ML phylogenetic tree representing clade C (from Fig. 1) based on the combined nuclear (ITS, ETS) and plastid (*petD, rps16*) data. The generic limits of several groups from this clade (*Dimetia*, *Exallage*, *Kadua, Leptopetalum*, *Scleromitrion*) were re-evaluated and discussed in the text. Clade I and clade II are described as the new genera *Debia* and *Involucrella* respectively, in this study. Values at the nodes represent bootstrap support (BS). Values in parenthesis are Bayesian posterior probabilities (BPP) that are shown only for the major clades.

Other predominantly African groups, but with representative species from Asia-Pacific are *Edrastima* (Fig. 1; BS = 99%, BPP = 1), *Kohautia* (Fig. 1; BS = 100%, BPP = 1), *Pentanopsis* (Fig. 1; BS = 100%, BPP = 1), and *Oldenlandia* s.str. (Fig. 3; BS = 96%, BPP = 1).

Habit (Table 3). — The *Hedyotis-Oldelandia* complex exhibits a wide diversity of growth forms in the Asia-Pacific region (Table 3; Fig. 5). Members of *Dentella* J.R.Forst. & G.Forst., *Neanotis*, *Oldenlandia*, *Hedyotis coronaria*, *H. oligocephala*, *Oldenlandia krewanhensis*, and *O. ovatifolia* are all annual herbs. *Hedyotis* s.str. and *Kadua* are primarily woody forming shrubs to small trees. The *Exallage*, *Kohautia*, and *Leptopetalum* clades comprise members with annual or perennial herbs. Finally, members of the *Dimetia* clade are characterized by a lianescent habit. This trait is useful in separating *Dimetia* from its sister clade *Exallage*, the latter are either annual or suffrutescent herbs. An illustration of different habits in the Asian-Pacific *Hedyotis-Oldenlandia* complex is shown in Fig. 5.

Fruit morphology (Table 3). — The *Hedyotis-Oldenlandia* complex in Asia-Pacific exhibits a range of diversity in fruit morphology and dehiscence and was categorized into primarily four different types: (Type 1, Fig. 6A) septicidal dehiscence usually followed by partial apical loculicidal dehiscence, typical of *Hedyotis* s.str.; (Type 2, Fig. 6B, C) loculicidally dehiscent from apex followed by partial septicidal dehiscence, found in *Dimetia* and *Kadua*; (Type 3) loculicidally dehiscent from apex, found in the members of clades I and II, *Hedyotis trinervia* (Retz.) Roem. & Schult., *Leptopetalum*, *Kohautia*, *Neanotis*, *Oldenlandia*, and *Scleromitrion*; and (Type 4, Fig. 6D) fruit indehiscent. Indehiscent fruits are found in *Dentella*, *Exallage*, and *Kadua* sect. *Oceanica* (Fosberg) W.L.Wagner & Lorence. In *Hedyotis* s.str., the line of dehiscence clearly develops along the septum often giving rise to a partially closed valve-like structure followed by late dehiscence through locules. Rarely, in some species, including *Hedyotis philippensis* (Willd. ex Spreng.) Merr. ex C.B.Rob. and *H. paridifolia* Dunn, the fruits

Table 3. A morphological summary of the *Hedyotis-Oldenlandia* complex in the Asia-Pacific region.

Genera identified/ proposed	Estimated no. of species	Habit	Other morphological features	Fruit type and dehiscence	Seed shape	Pollen (no. of apertures, endo-aperture type, sexine pattern)	Distribution
Debia Neupane & N.Wikstr. (Fig. 4)	4	Annual herbs	Uppermost leaves appearing whorled, ovate to oblong and with somewhat decurrent leaf base; corolla lobes reflexed and appearing star-shaped	Loculicidally from apex	Bluntly angular or irregular; seed surface ruminate or with undulating cell walls	Not studied	Tropical Asia
Dentella J.R.Forst & G.Forst (Fig. 1)	8	Annual, prostrate herbs	Flowers 5-merous, solitary, terminal or pseudoaxillary	Indehiscent, dry and papery	Trigonous	Not studied	Tropical Asia, tropical Australia, and Pacific
Dimetia (Wight & Arn.) Meisn. (Fig. 4)	7	Herbs or shrubs, lianescent, climbing and scandent	Inflorescence terminal, corolla densely bearded in throat	Capsule apex protruding beyond calyx lobes; dehiscence loculicidally from apex followed by partial septicidal dehiscence	Dorsiventrally compressed, often with winged margin	Type 2, endocingulum, double reticulum	Tropical Asia
Edrastima Raf. (Fig. 1)	5	Annual herbs	Glabrous corolla tube, suglobose stigma	Distinctly beaked capsule, loculicidally from apex	Trigonous	Type 3, endocingulum, double reticulum	Africa, N & S America, Asia
Exallage Bremek. (Fig. 4)	15	Suffrutescent herbs	Inflorescences axillary	Capsules indehiscent and crustaceous	Trigonous	Type 3, endocingulum, double reticulum	Tropical Asia, tropical Australia, and Pacific
Hedyotis L. (Fig. 2)	180	Suffrutescent herbs, shrubs or small tree	Corolla pubescent inside	Capsule apex not protruding beyond calyx lobes; septicidal dehiscence usually followed by partial apical loculicidal dehiscence, usually resulting in two semi-split valves	Dorsiventrally compressed	Type 3, endocingulum, double reticulum	Sri Lanka, India, SE China, Indo-China, Malesia, Papuasia, NW Pacific

Table 3. Continued.

Genera identified/ proposed	Estimated no. of species	Habit	Other morphological features	Fruit type and dehiscence	Seed shape	Pollen (no. of apertures, endo-aperture type, sexine pattern)	Distribution
Involucrella (Benth. & Hook.f.) Neupane & N.Wikstr. (Fig. 4)	2	Annual or perennial herbs	Infloresence terminal or pseudoaxillary; in *Hedyotis coronaria* the flowers are sessile and arranged in capitate structures surrounded by involucre-like leaf bases and stipules	Loculicidally from apex or obscurely dehiscent	Bluntly or irregularly angular 3–5 pits/depressions on either side of seed	Type 3, endocingulum, double reticulum	Southeast Asia
Kadua Cham. & Schltdl. (Fig. 4)	30	Shrubby to small trees	Corolla salverform, fleshy, long-tubed, appendaged	All taxa in subg. *Kadua*, except sect. *Oceanica* (Fosberg) W.L.Wagner & Lorence, have capsules with initial loculicidal dehiscence from the apex followed by septicidal dehiscence at maturity; in subg. *Gouldia* (A.Gray) W.L.Wagner & Lorence and subg. *Kadua* sect. *Oceanica* the fruits are fleshy and indehiscent	Various: fan-shaped, ovoid, flat with broad wing or brick-like	Not studied	Hawaiian Islands and French Polynesia
Kohautia Cham. & Schltdl. (Fig. 1)	27	Annual or perennial herbs	Anther and stigma included in corolla tube; stigma positioned below anthers	Loculicidally from apex	Trigonous	Type 2, lalongate endocolpus; endocolpi have distinct annulus around the meso-aperture	Africa, Arabian Pen. to Indian Subcontinent, Thailand, Australia
Leptopetalum Hook. & Arn. (Fig. 4)	8	Annual herbs or subshrubs	Plants glabrous throughout	Capsules subglobose to winged; dehiscence loculicidal from apex	Ovoid or obtusely angulate seeds appearing pitted due to shallow depressions bordered by thick and sinulate walls	Type 3, endocingulum	Tropical Asia, tropical Australia and Pacific
Neanotis W.H.Lewis (Fig. 1)	31	Annual herbs	Pluriaperturate pollen	Loculicidally from apex	Cymbiform to shallowly cup-shaped	Type 1, endocingulum	Tropical Asia, tropical Australia, and Pacific
Oldenlandia L. (Fig. 3)	unknown	Annual herbs	Corolla often with ring of hairs in throat	Loculicidally from apex	Trigonous	Type 3, lalongate endocolpus	Tropics and subtropical
Scleromitrion (Wight & Arn.) Meisn. (Fig. 4)		Annual herbs or suffrutescent herbs	Homostylous flowers with exserted stamens and styles	Loculicidally from apex	Trigonous	Type 3, lalongate endocolpus	Tropical Asia, tropical Australia, and Pacific

The information was compiled from Fosberg & Sachet (1991), Terrell & Robinson (2003, 2007), Dutta & Deb (2004), Terrell & al. (2005), Neupane & al. (2009), Groeninckx & al. (2010c), Chen & Taylor (2011), Wikström & al. (2013), Govaerts & al. (2014) and from our personal observations. The number of species for each clade was estimated by using the species list in Govaerts & al. (2014) and studying their morphological features described in the literature, and from our personal observations of herbarium specimens and online databases.

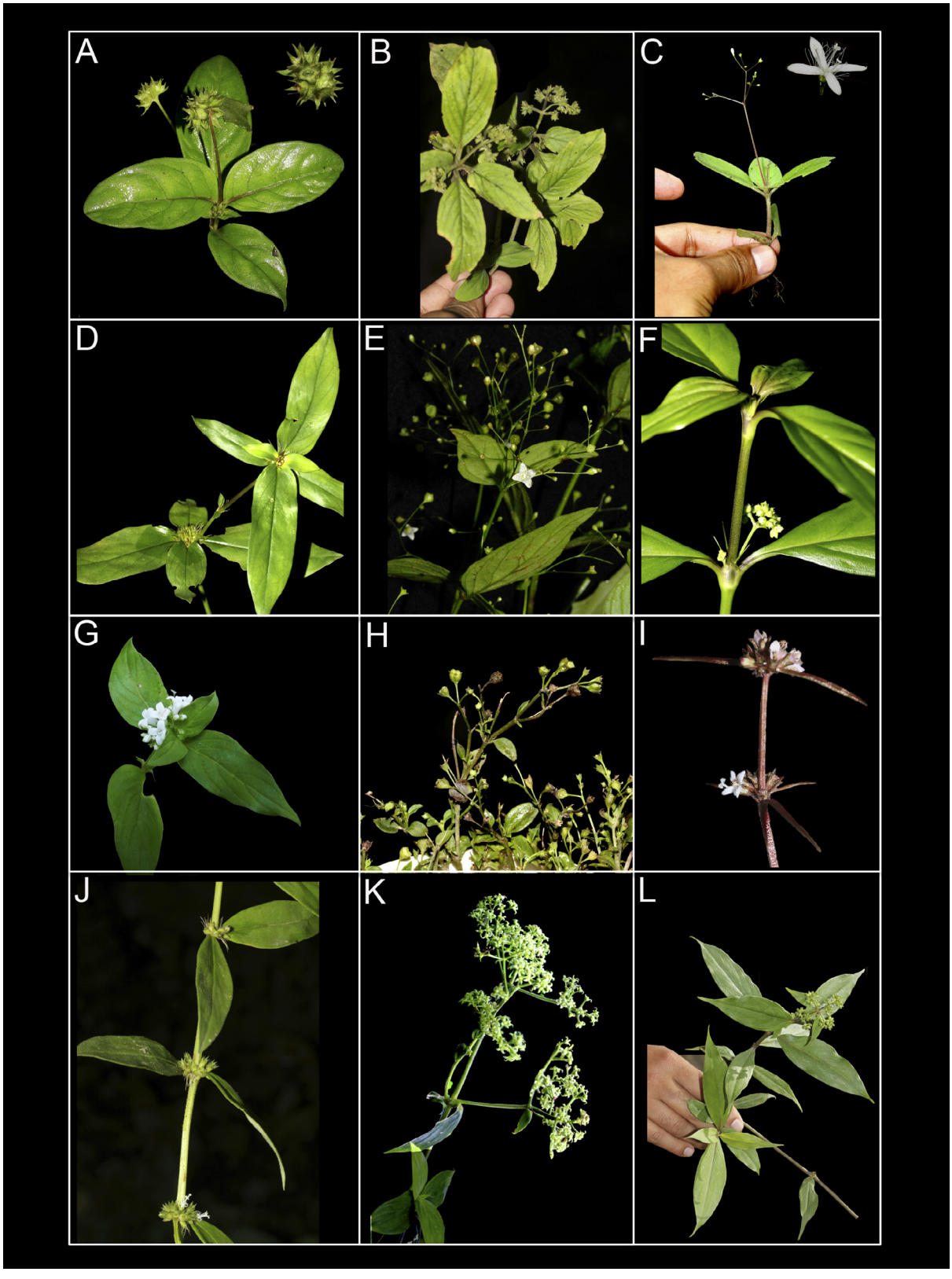


Fig. 5. Habit of different species of the Asian-Pacific *Hedyotis-Oldenlandia* complex. **A,** *Hedyotis oligocephala* (Pierre ex Pit.) Fukuoka; **B,** *Oldenlandia krewanhensis* Pierre ex Pit.; **C,** *Oldenlandia ovatifolia* (Cav.) DC.; **D,** *Hedyotis coronaria* (Kurz) Craib; **E,** *Oldenlandia chereevensis* Pierre ex Pit.; **F,** *Hedyotis insularis* (Spreng.) Deb & Ratna Dutta; **G,** *Neanotis gracilis* (Hook.f.) W.H.Lewis; **H,** *Thecagonum biflorum* (L.) Babu; **I,** *Oldenlandia pinifolia* (Wall. ex G.Don) Kuntze; **J,** *Hedyotis verticillata* (L.) Lam.; **K,** *Oldenlandia hedyotidea* (DC.) Hand.-Mazz.; **L,** *Hedyotis scandens* Roxb.

appear indehiscent, but gentle mechanical pressure separates the capsules into two closed valves as in other members of *Hedyotis* s.str. This feature is different from the indehiscent fruits in the members of *Exallage* where the fruits are hard (cartilaginous) and indehiscent. Similarly, the indehiscent fruits of *Dentella* are papery and dry whereas in *Kadua* sect. *Oceanica* the indehiscent fruits are fleshy. Fruit deshiscence pattern is a useful trait in characterizing clades such as *Dimetia*, *Exallage*, *Hedyotis* s.str., and *Kadua*.

Seed morphology (Table 3). — The Asian Pacific *Hedyotis-Oldenlandia* complex shows diversity in seed shape and seed coat (testa) ornamentation. The seeds in Asian-Pacific *Hedyotis-Oldenlandia* complex were characterized into three basic types based on their shapes: (Type 1) trigonous (Fig. 7J, K, O, P) to bluntly angular appearing conoidal (Fig. 7D, E) or irregular (Fig. 7A–C); (Type 2) dorsiventrally flattened (Fig. 7I), plano-convex (Fig. 7F–H) or cymbiform (Fig. 7Q, R); or (Type 3) globose or sub-globose (Fig. 7L–N). Exotestas are reticulate of various types from simple reticulate to reticulate-areolate, reticulate with polygonal wall, and reticulate-foveolate appearing pitted. Details of seed shape and seed coat ornamentations are summarized in Table 3. Seed morphological features played an important role in characterizing *Debia*, *Dimetia*, *Hedyotis* s.str., *Involucrella*, and *Leptopetalum*.

Pollen morphology (Table 3). — Pollen are all isopolar and radially symmetrical. The pollen shape in the complex ranges from oblate-spheroidal to subprolate (suboblate in few samples of *Neanotis ingrata*) with the majority of species characterized by oblate-spheroidal and/or prolate shapes. Apertures in all species of the complex are zonoaperturate (positioned along the equator) and compound types comprising an external colpus, a mesoporus and an endoaperture. Based on aperture number, three types of pollen were distinguished: (Type 1) pluriaperturate, as in *Neanotis* (Fig. 8D); (Type 2) ectocolpi four to occasionally five, as in members of *Dimetia* (*Hedyotis capitellata* Wall. ex G.Don, *H. scandens* Roxb., *Oldenlandia hedyotideae* (DC.) Hand.-Mazz.) and *Kohautia* (Fig. 8A–C); and (Type 3) ectocolpi in combination of three and four with one of the type being more common than the other in the rest of the clades (Fig. 8E). The endoaperture was an endocingulum in the members of clades II, *Dimetia*, *Exallage*, *Hedyotis* s.str., and *Neanotis* (Fig. 8F) whereas a lalongate endocolpus in the *Kohautia*, *Oldenlandia* and *Scleromitrion* clades (Fig. 8G). The mesoporus in the members of *Kohautia* is unique by having a special thickening (annulus) around it. Sexine patterns vary across the *Hedyotis-Oldenlandia* complex exhibiting perforate (Fig. 8H), microreticulate (Fig. 8I, K) or reticulate types (Fig. 8J) along with intermediate forms. The members of the clades *Hedyotis* s.str., *Dimetia*, *Exallage* and II have predominately double reticulate patterns (Fig. 8H, I, K). The colpus appears sealed in the members of clade II (Fig. 8L). Muri are beset with supratectal elements (which are often granules) in most of the species within the complex particularly in *Dimetia*, *Exallage*, *Hedyotis* s.str., and clade II. In the case of double reticulum, granules are usually found on the infra-reticulum zones. Unique pollen features were found to be taxonomically significant traits in *Neanotis* and *Kohautia*.

■ DISCUSSION

According to the present analysis, members of the *Hedyotis-Oldenlandia* complex from the Asia-Pacific region fall in 14 distinct clades (Figs. 1–4; Table 3). This result is in agreement with Wikström & al. (2013). The generic status of *Dentella*, *Hedyotis*, *Kadua*, *Kohautia*, *Neanotis*, *Oldenlandia*, and *Scleromitrion* has been well treated before (see Terrell & al., 2005; Groeninckx & al., 2010c; Guo & al., 2013; Wikström, 2013) and will not be repeated below. However, nomenclatural changes were made for the new samples that now belong to *Scleromitrion* (sensu Guo & al., 2013). The remaining seven clades will be discussed below. The proposed new genera along with a summary of the morphological traits and geographical distribution for each group is provided in Table 3.

Clade I (Fig. 4). — *Oldenlandia ovatifolia* from this clade has always been associated with *O. biflora* L. (= *Thecagonum biflorum* (L.) Babu), *O. pterita* (Blume) Miq. (= *Thecagonum pteritum* (Blume) Babu), and *O. parishii* Hook.f. (= *Thecagonum parishii* (Hook.f.) Babu), and characterized as a group with a 4-angled capsule and globose or subglobose seeds. Babu (1969) treated this group as the new genus *Thecagonum* Babu, and replaced the illegitimate later homonym *Gonotheca* Blume

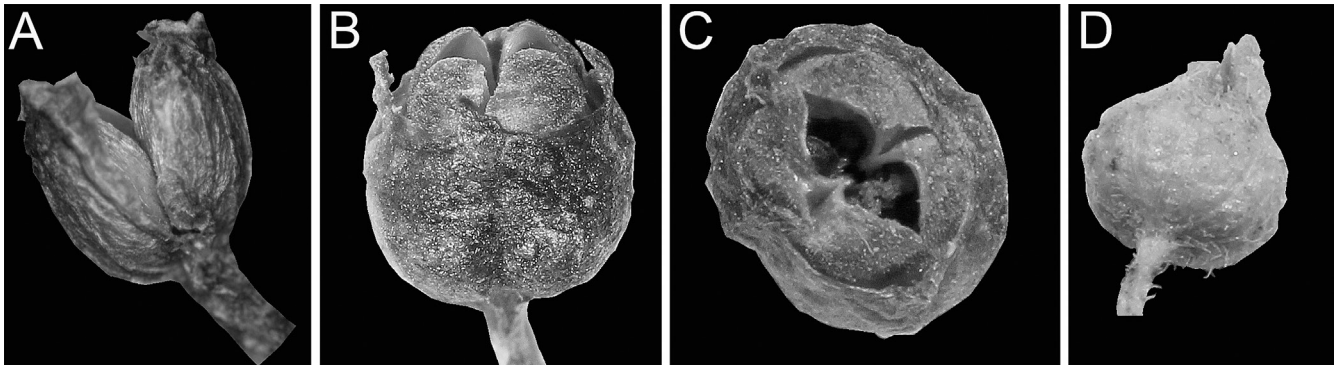


Fig. 6. Fruit types of the *Hedyotis* s.str., *Dimetia*, and *Exallage* clades. **A,** *Hedyotis trimenii* Deb & Ratna Dutta (side view of capsule); **B & C,** *Hedyotis scandens* Roxb. (side and top view of capsule); **D,** *Exallage auricularia* (L.) Bremek. (side view of capsule).

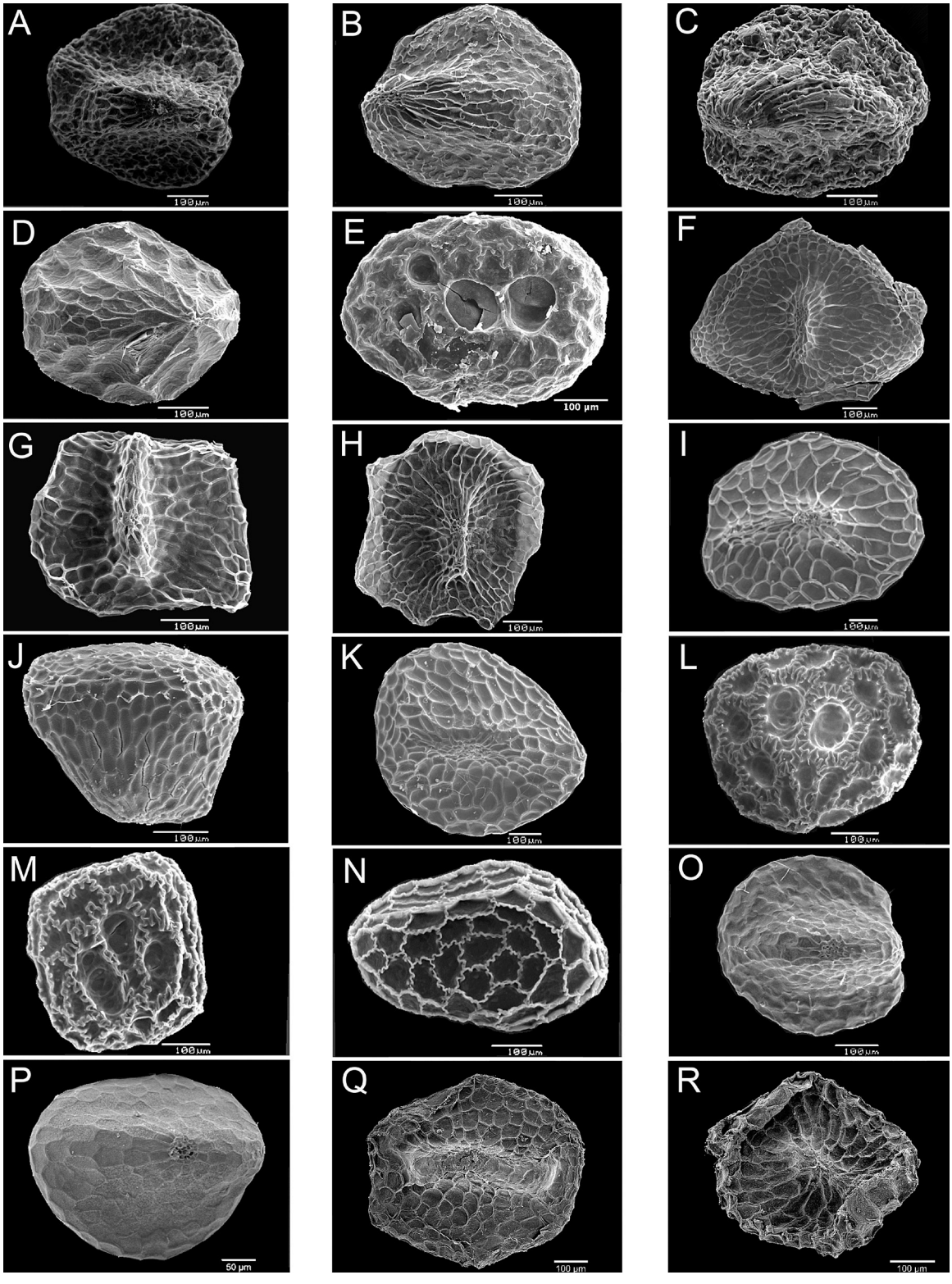


Fig. 7. Seeds of the *Hedyotis-Oldenlandia* complex from the Asian-Pacific region. **A,** *Hedyotis andamanica* Kurz; **B,** *Hedyotis oligocephala* (Pierre ex Pit.) Fukuoka; **C,** *Oldenlandia krewanhensis* Pierre ex Pit.; **D,** *Oldenlandia ovatifolia* (Cav.) DC.; **E,** *Oldenlandia chereevensis* Pierre ex Pit.—note the presence of three depressions/marks on the side of the seed; **F,** *Hedyotis capitellata* Wall. ex G.Don; **G,** *Oldenlandia hedyotidea* (DC.) Hand.-Mazz..; **H,** *Hedyotis scandens* Roxb.; **I,** *Hedyotis fruticulosa* (Volkens) Merr.; **J,** *Exallage auricularia* (L.) Bremek.; **K,** *Exallage lineata* (DC.) Bremek.; **L,** *Thecagonum biflorum* (L.) Babu; **M,** *Thecagonum strigulosum* (Bartl. ex DC.) Terrell & H.Rob.; **N,** *Leptopetalum foetidum* (G.Forst.) Neupane & N.Wikstr.; **O,** *Hedyotis verticillata* (L.) Lam.; **P,** *Oldenlandia pinifolia* (Wall. ex G.Don) Kuntze; **Q,** *Neanotis gracilis* (Hook.f.) W.H.Lewis; **R,** *Neanotis calycina* (Wall. ex Hook.f.) W.H.Lewis..

ex DC. Terrell & Robinson (2007) suggested the exclusion of *Oldenlandia ovatifolia* from the group due to the lack of a depression in the seeds and a different type of capsule. Their suggestion is supported by the molecular phylogenetic studies of Guo & al. (2013), Wikström & al. (2013) and the present study. *Oldenlandia ovatifolia* was resolved sister to the *Exallage*/*Dimetia* clade in Wikström & al. (2013). Clade I is a newly resolved clade of primarily Southeast Asian species that includes *Hedyotis oligocephala*, *Oldenlandia krewanhensis*, and *O. ovatifolia* (Fig. 5A–C). Of these, *Oldenlandia krewanhensis* and *Hedyotis oligocephala* were described by Pitard (1922) from the Indo-China region. *Oldenlandia krewanhensis* is morphologically very similar to another Southeast Asian species, *Hedyotis andamanica* Kurz described from the South

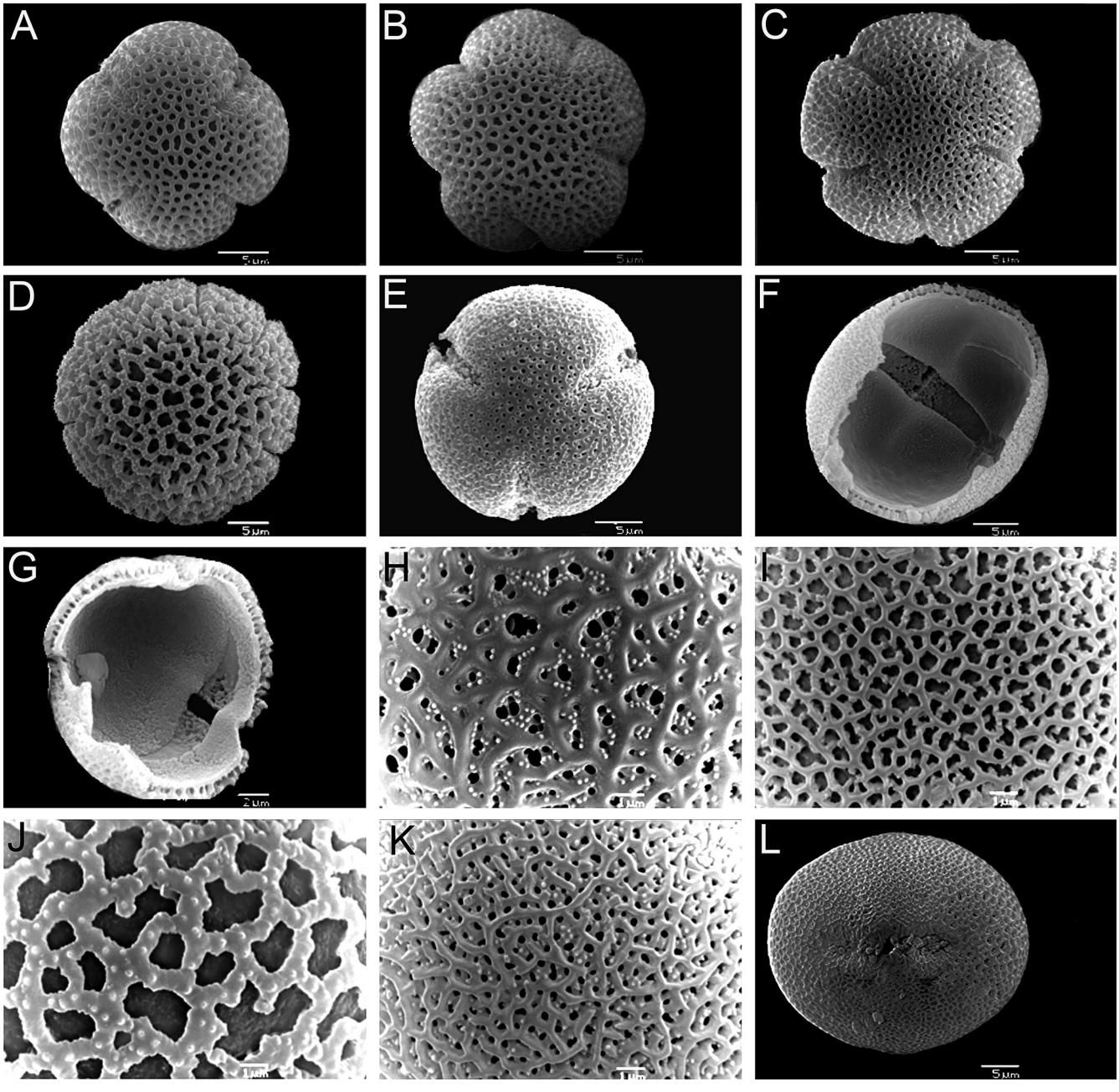


Fig. 8. Pollen of the *Hedyotis-Oldenlandia* complex from the Asian-Pacific region. **A,** *Oldenlandia hedyotidea* (DC.) Hand.-Mazz.; **B,** *Hedyotis scandens* Roxb.; **C,** *Kohautia gracilis* (Wall.) DC; **D,** *Neanotis gracilis* (Hook.f.) W.H.Lewis; **E,** *Hedyotis fruticosa* L.; **F,** *Hedyotis marginata* (Thwaites ex Trimen) Alston; **G,** *Oldenlandia umbellata* L.; **H,** *Hedyotis nodulosa* Thwaites; **I,** *Hedyotis yangchunensis* W.C.Ko & Zhang; **J,** *Oldenlandia diffusa* (Willd.) Roxb.; **K,** *Hedyotis dendroides* Alston; **L,** *Oldenlandia chereevensis* Pierre ex Pit. **A–E,** Polar view showing pollen with 3 **(E),** 4 **(A),** 5 **(B, C)** ecotocolpi and pluriaperture **(D)** pollen; **F & G,** broken pollen grains showing endocingulum **(F)** and an endocolpus **(G);** details of perforate **(H),** microreticulate **(I, K)** and reticulate **(J)** apocolpium.

Andaman Islands (India). We did not include *Hedyotis andamanica* in our study but based on our observation of herbarium specimens, *H. andamanica* and *Oldenlandia krewanhensis* are probably conspecific. Therefore, due to morphological similarity, we choose to recognize clade I at the rank of genus, and the new genus *Debia* Neupane & N.Wikstr. is described including the species of clade I (see below). The genus is named in honour of Debendra Bijoy Deb (1924–2013) who contributed extensively to the taxonomy of Indian *Hedyotis-Oldenlandia* complex.

Clade II (Fig. 4). — This clade includes the morphologically different *Hedyotis coronaria* and *Oldenlandia chereevensis* (Fig. 5D, E). The former was resolved with *Spermacoce hispida* L. in the study by Wikström & al. (2013). However, all *H. coronaria* samples from our recent collections are resolved sister to *Oldenlandia chereevensis*. We rechecked the specimen included in Wikström & al. (2013) and found it to be *Spermacoce* sp., incorrectly determined as *Hedyotis coronaria*. Guo & al. (2013) also found *Hedyotis coronaria* to be related to *Oldenlandia ovatifolia* and *O. chereevensis*. Furthermore, *Hedyotis coronaria* was mentioned as the only species (as *Hedyotis merguensis* Hook.f.; not validly published, see nomenclature editor's note on p. 317) under *H.* sect. *Involucrella* by Bentham & Hooker (1873). *Hedyotis* sect. *Involucrella* was characterized by its terminal and capitate inflorescence having sessile flowers and surrounded by leaf bases and fimbriate stipules. The other species resolved in the clade, *Oldenlandia chereevensis*, has a distinct morphology with an erect and perennial habit up to 50 cm high and with obconical capsules. *Oldenlandia chereevensis* was described by Pitard (1922) from the Indo-China region under "*O.* sect. *Euoldenlandia*" (not validly published; Art. 21.3). Although *Hedyotis coronaria* and *Oldenlandia chereevensis* do not appear similar in their gross morphology, they share a unique seed structure by having 3–5 pits/depressions on either side of the seed (Fig. 7E). In our phylogeny, clade I and clade II were resolved sister in the nuclear trees for both combined (ITS+ETS, Electr. Suppl.: Fig. S1) and separate nuclear genes analysis. However, in the combined nuclear and plastid trees (ITS+ETS+*petD*+*rpsl6*), *Hedyotis coronaria* and *Oldenlandia chereevensis* form a clade separate from clade I. Hence, we elevate Bentham & Hooker's sect. *Involucrella* to the rank of genus and combine *Oldenlandia chereevensis* under this generic name.

***Dimetia* (Fig. 4). —** "*Dimetia*" was first mentioned by Wight & Arnott (1834) as one of the two subgroups of *Hedyotis* (the other being sect. *Macrandria*) closely related to *H.* sect. *Diplophragma* Wight & Arn. that was known to occur outside peninsular India. However, delimitations among *Diplophragma*, *Macrandria*, and *Dimetia* were not clear-cut. *Dimetia* included *Hedyotis capitellata*, *H. polycarpa* R.Br. ex G.Don, *H. scandens*, *H. volubilis* R.Br. ex Wall. (syn. of *H. scandens*), and *H. mollis* Wall. ex G.Don, whereas *Macrandria* included *H. macrostemum* Hook. & Arn. Bentham & Hooker (1873) and Hooker (1880) discussed these groups in detail along with others as sections with the distinction between *Dimetia* and *Diplophragma* being the apex of the capsule protruded between the calyx lobes in the former and absence of such feature in the latter. Despite the lack of good morphological synapomorphies, Guo & al. (2013) merged *Dimetia* with *Exallage* and recognized the group under the generic name *Dimetia*. However, in Wikström & al. (2013) and in the present study, *Dimetia* is clearly a monophyletic group resolved sister to *Exallage*. Furthermore, upon close examination of capsule features of *Dimetia*, it appears that the mode of septicidal dehiscence in the group is different from *Hedyotis* s.str. In *Dimetia*, the capsules divide loculicidally from the apex followed by partly or complete septicidal dehiscence (Fig. 6B, C), whereas in *Hedyotis* s.str. capsules first divide along the septum followed by a split along the locules (Fig. 6A). Seeds of *Dimetia* (Fig. 7F–H) and *Hedyotis* s.str. (Fig. 7I) both have flattened seeds (fruticosa type seeds) with *Dimetia* further characterized by having a narrow ring of wing around the seed. *Dimetia* differs from *Exallage* by having dehiscent fruits, flat and sometimes winged seeds and terminal inflorescences. Whereas in *Exallage* fruits are indehiscent (Fig. 6D), seeds are trigonous and inflorescences are terminal and axillary cymes. Members of *Dimetia* are also unique in the complex by having a lianescent habit (Fig. 5K, L). This provides us with enough confidence to accept *Dimetia* as a genus separate from its sister genus *Exallage*. Following our results, *Dimeti*a should include *Hedyotis ampliflora* Hance, *H. capitellat*a Wall. ex G.Don, *H. dianxiensis* W.C.Ko, *H. obliquinervis* Merr., *H. pitardiana* Craib, *H. scandens* Roxb., and *Oldenlandia hedyotidea* (DC.) Hand.-Mazz. (but see below) (Fig. 5K, L).

***Edrastima* (Fig. 1). —** Bentham & Hooker (1873) described *Hedyotis* sect. *Anotidopsis* to include *H. monocephala* Wall., *H. hirsuta* (L.f.) Sm. (*H. stipulata* R.Br.), *H. lindleyana* Hook. ex Wight & Arn. (*Oldenlandia japonica* Miq.), and *H. trinervia* (Retz.) Roem. & Schult. based on indehiscent membranous fruits and compressed peltate seeds. However, in *Flora of British India*, Hooker (1880) transferred *Hedyotis trinervia* to *Oldenlandia* and included more species in sect. *Anotidopsis* (*H. andamanica*, *H. cyanescens* Thwaites, *H. monocephala*, *H. stipulata*, *H. thomsonii* Hook.f.). Dutta & Deb (2004) circumscribed *Hedyotis* sect. *Anotidopsis* to include only two species (*H. brunonis* Merr., *H. andamanica*). Later, Bremekamp (1952) treated *H.* sect. *Anotidopsis* as a subgenus of *Oldenlandia* to include five African species (with the type *O. trinervia* Retz.). Bremekamp (1952) distinguished *Oldenlandia* subg. *Anotidopsis* based on non-slimy seeds when moistened, subglobose stigmas, distinctly beaked capsules, glabrous corolla tubes, and leaves with bifid or bipartite interpetiolar stipules. Oddly, these African species are morphologically similar to the Asian *Hedyotis trinervia* and the American *Oldenlandia uniflora* L. The recent phylogeny by Wikström & al. (2013) also confirms this relationship and supported *Oldenlandia* subg. *Anotidopsis* as a monophyletic clade sister to *Agathisanthemum* Klotzsch and *Lelya* Bremek. These findings support that *Oldenlandia* subg. *Anotidopsis* is better circumscribed in Bremekamp's (Bremekamp, 1952) sense instead of that of Bentham & Hooker (1873), Hooker (1880) and Pitard (1922). We choose to recognize Bremekamp's *O.* subg.

Anotidopsis at the rank of genus using the earliest available generic name, *Edrastima* Raf. Five species are combined under *Edrastima* (see below).

***Exallage* (Fig. 4). —** The members of this genus are distributed in the entire Asia-Pacific region. However, one of its species, *Exallage auricularia* (L.) Bremek., is also found in tropical Africa and was probably introduced there recently (Bremekamp, 1952). *Exallage auricularia* (as *Hedyotis*) was originally proposed as lectotype of *Hedyotis*, but due to a mismatch between the protologue and fruit type in *Exallage auricularia* (indehiscent fruits) Bremekamp (1939, 1952) dismissed this idea and suggested *Hedyotis fruticosa* L. as the type. Following Bremekamp's suggestion, *Hedyotis fruticosa* has been accepted as the conserved type of the genus (Jarvis, 1992; Barrie, 2006). One character that sets *Exallage* apart from the rest of the *Hedyotis-Oldenlandia* complex is its primarily hard (cartilaginous) and indehiscent fruits (nuts; Fig. 6D). Bremekamp (1952) segregated this group from *Hedyotis* s.l. under his newly defined *Exallage*. Later, Terrell & Robinson (2003) proposed including *Exallage* in *Oldenlandia* as *Oldenlandia* subg. *Exallage* (Bremek.) Terrell & H.Rob. Historically, the group has also been referred to *Hedyotis* sect. *Euhedyotis* by Wight & Arnott (1834) and Hooker (1880). Dutta & Deb (2004) mentioned that some of its members (e.g., *Hedyotis paradoxa* Kurz, *H. fulva* Hook.f., *H. insularis* (Spreng.) Deb & Ratna Dutta, and *H. vestita* R.Br. ex G.Don) have fruits opening with a small slit on the groove. However, upon close examination (by the first author) of the fruits of *Exallage costata* (Roxb.) Bremek. (= *Hedyotis vestita*), *Hedyotis insularis* (Fig. 5F) and *H. paradoxa*, no such slits were apparent. Guo & al. (2013) found this group unresolved in their plastid gene tree. Hence, they expanded the group to include other taxa with dehiscent fruits and described it as an emended *Dimetia*. However, their emended *Dimetia* does not have any usable morphological synapomorphy (comprising species with both dehiscent and indehiscent fruits), and the lack of resolution in their plastid gene trees may simply be due to the lack of phylogenetic signal. The study by Wikström & al. (2013) and the present study provide support for the monophyly of *Exallage* in the nuclear tree (both separate and combined analysis). Accordingly, we accept the generic status of *Exallage* as proposed by Bremekamp (1952). Other morphological features, although not exclusive to this group, are suffrutescent habit, seeds bluntly trigonous with reticulate surface, pollen grains 3–4-colporate with endocingulum as endoaperture, and a double reticulate sexine.

***Leptopetalum* (Fig. 4). —** *Leptopetalum* (sensu Fosberg & Sachet, 1991) comprises a group of five species from the Pacific, broadly redefined by Fosberg & Sachet (1991) under *Hedyotis* subg. *Leptopetalum* (Hook. & Arn.) Fosberg & Sachet (inadvertently referred but validly published as *Hedyotis* subg. *Leptopetalum* (Hook. & Arn.) Hook.f.). *Thecagonum* includes the herbaceous Asian-Pacific members *Oldenlandia biflora* L. (= *Thecagonum biflorum*), *O. pterita* (= *Thecagonum pteritum*), and *O. parishii* Hook.f. (= *Thecagonum parishii*) and is characterized by 4-angular or 4-winged/angled capsules with globose and deeply pitted seeds. *Leptopetalum* and *Thecagonum* were never thought to be related to each other until Wikström & al. (2013) found that two members of *Leptopetalum* were resolved within *Thecagonum*. Corresponding relationships, with *Leptopetalum* nested inside *Thecagonum*, are supported in the present analyses and *Thecagonum* can therefore not be treated as a separate genus, as done by Guo & al. (2013). The different species of *Leptopetalum* are morphologically diverse and differ from *Thecagonum* by their woody habit and corolla shapes. However, upon closer examination of seed features, all members of *Thecagonum* and one of the species of *Leptopetalum* (*L. foetidum* Neupane & N.Wikstr.) are characterized by being glabrous throughout, and ovoid or obtusely angulate seeds appearing pitted due to the shallow depressions bordered by thick and sinulate walls. Based on these features, we choose to recircumscribe *Leptopetalum* Hook. & Arn., by expanding it to also include members of *Thecagonum*. The name *Leptopetalum* must be chosen due to the priority of publication of the name *Leptopetalum* over *Thecagonum*. *Leptopetalum* Hook. & Arn., as recircumscribed here, includes members of *Leptopetalum* (sensu Fosberg & Sachet, 1991) and *Thecagonum* Babu (excluding *O. ovatifolia*).

The *Pentanopsis* clade (Fig. 1). — The members of this clade are primarily distributed in Africa and Madagascar. It includes *Amphiasma* Bremek., *Conostomium* (Stapf) Cufod., *Gomphocalyx* Baker, *Manostachya* Bremek., *Pentanopsis* Rendle, *Phylohydrax* Puff and five other species treated under *Oldenlandia* (Kårehed & al., 2008; Groeninckx & al., 2009a). Three of these *Oldenlandia* species (*O. affinis* (Roem. & Schult.) DC., *O. stricta* L., *O. viarum* Craib) are found in Asia and are resolved with the African *Pentanopsis fragrans* Rendle. This clade is sister to the clade containing *Amphiasma* spp. Two species (*Oldenlandia stricta*, *O. viarum*) sampled in our analysis are strictly Asian and morphologically very similar to *O. affinis*. Furthermore, *Amphiasma*, *Oldenlandia affinis*, and *Pentanopsis* are united by having sessile, linear leaves, indistinctly beaked capsules, and non-punctate testa cells on the seeds (Bremekamp, 1952). Despite the strong molecular support for the *Pentanopsis* clade, the members of this clade are morphologically very diverse and difficult to characterize (Groeninckx & al., 2009a). Due to lack of sufficiently many specimens of *Amphiasma*, *Pentanopsis* and related taxa in the *Pentanopsis* clade, we cannot ascertain and characterize the taxonomic position of three sampled Asian species (*Oldenlandia affinis*, *O. stricta*, *O. viarum*) in relation to *Pentanopsis*. We must wait until more specimens from the *Pentanopsis* clade become available to define generic limits in this group.

■ NOMENCLATURE CHANGES

The following list contains species with their new generic status and basionyms.

Debia Neupane & N.Wikstr., **gen. nov.** – Type: *Debia oligocephala* (Pierre ex Pit.) Neupane & N.Wikstr. (≡ *Oldenlandia oligocephala* Pierre ex Pit.).

Annual herb with uppermost leaves appearing whorled,

ovate to oblong and with somewhat decurrent leaf bases. Inflorescences terminal cymes with somewhat elongated peduncles. Corolla lobes reflexed and star-shaped (stellate; Fig. 5C). Capsules opening loculicidally from apex. Seeds irregularly shaped.

Debia andamanica (Kurz) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis andamanica* Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 41: 311. 1872 – **Lectotype (designated here):** India, Andaman Islands, South Andaman, *Kurz s.n.* (K barcode K000031121 [image!]; isolectotypes: CAL n.v.).

Debia krewanhensis (Pierre ex Pit.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia krewanhensis* Pierre ex Pit. in Lecomte, Fl. Indo-Chine 3: 142. 1922 ≡ *Hedyotis krewanhensis* (Pierre ex Pit.) P.H.Hô in Pham-Hoàng Hô, Cayco Vietnam 3(1): 136. 1993 – **Lectotype (designated here):** Vietnam, Pursath Province, Mt. Krewanh, *Pierre 2002* (P barcode P04959633 [image!]; isolectotype: P barcode P04959635 [image!]).

Debia oligocephala (Pierre ex Pit.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia oligocephala* Pierre ex Pit. in Lecomte, Fl. Indo-Chine 3: 113. 1922 ≡ *Hedyotis oligocephala* (Pierre ex Pit.) Fukuoka in S. E. Asian Stud. 8: 327. 1970 – **Lectotype (designated here):** Vietnam, Baria Province, Mt. Dinh, *Pierre 169* (P barcode P04005566 [image!]; isolectotypes: P barcodes P04004467 [image!], P04004468 [image!] & P04004465 [image!].

Debia ovatifolia (Cav.) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis ovatifolia* Cav., Icon. 6: 52. 1801 ≡ *Oldenlandia ovatifolia* (Cav.) DC., Prodr. 4: 427. 1830 ≡ *Gonotheca ovatifolia* (Cav.) Santapau & Wagh in Bull. Bot. Surv. India 5: 107. 1964 ≡ *Thecagonum ovatifolium* (Cav.) Babu in Bull. Bot. Surv. India 11: 214. 1971 – **Lectotype (designated here):** Manila, *Cavinellus s.n.* (MA [image!]).

Dimetia (Wight & Arn.) Meisn., Pl. Vasc. Gen., Tab. Diagn.: 160. 1838 ≡ *Hedyotis* [unranked] *Dimetia* Wight & Arn., Prodr. Fl. Ind. Orient. 1: 406, adnot. 1834 ≡ *Hedyotis* sect. *Dimetia* (Wight & Arn.) Benth. & Hook.f., Gen. Pl. 2: 57. 1873 – Type (designated by Wang in Molec. Phylogen. Evol. 67: 118. 2013): *Dimetia scandens* (Roxb.) R.J.Wang. (≡ *Hedyotis scandens* Roxb.).

Perennial, lianescent herb or shrubs. Inflorescences terminal compound and capitate cymes. Capsule apex protruding beyond calyx lobes; dehiscence loculicidally from apex followed by partial septicidal dehiscence. Seeds convex or saucer-shaped, narrowly winged with a raised central hilar ridge.

Dimetia ampliflora (Hance) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis ampliflora* Hance in J. Bot. 17: 11. 1879 ≡ *Oldenlandia ampliflora* (Hance) Kuntze, Revis. Gen. Pl. 1: 292. 1891 – **Lectotype (designated here, or perhaps holotype):** China, Hainan, Hoi-Hau, *Bullock s.n.* (BM barcode BM000945086 [image!]).

Dimetia capitellata (Wall. ex G.Don) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis capitellata* Wall. ex G.Don, Gen. Hist. 3: 527. 1834 ≡ *Oldenlandia capitellata* (Wall. ex G.Don) Kuntze, Revis. Gen. Pl. 1: 292. 1891 – Lectotype (designated by Dutta & Deb, Taxon. Revision Hedyotis Indian Subcont.: 48. 2004): 1. *Tavoy, W. Gomez* in Wall. Cat. 837 (K barcode K000031052 [image!]; isolectotypes: CAL n.v., BR barcode BR0000005579402 [image!]).

Dimetia dianxiensis (W.C.Ko) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis dianxiensis* W.C.Ko in J. S. China Agric. Univ. 16(4): 44. 1995 – Holotype: China, Yunnan, Manchiao Xian, thicket near ravine, Apr 1958, *Exped. 57 911* (IBSC n.v.).

Dimetia obliquinervis (Merr.) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis obliquinervis* Merr. in Lingnan Sci. J. 14: 56. 1935 ≡ *Hedyotis hedyotidea* var. *obliquinervis* (Merr.) Fukuoka in S. E. Asian Stud. 8: 326. 1970 – **Lectotype (designated here):** China, Hainan, Fung Leng, Ngai District, *S.K. Lau 452* (A barcode 00097081 [image!]; isolectotypes: B barcode B 10 0279645 [image!], E barcode E00327919 [image!], MO No. 716686 [image!], K barcode K000760291 [image!], US barcode 00997885 [image!], NY barcode 00131745 [image!]).

Dimetia pitardiana (Craib) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis pitardiana* Craib in Bull. Misc. Inform. Kew 1931: 277. 1931 ≡ *Hedyotis hedyotidea* var. *pitardiana* (Craib) Fukuoka in S. E. Asian Stud. 8: 326. 1970 – **Lectotype (designated here, or perhaps holotype):** Thailand, Kaw Chung, Klawng Majom, *A.F.G. Kerr 6870* (K barcode K000760335 [image!]; isolectotype: BK n.v.).

Dimetia scandens (Roxb.) R.J.Wang in Molec. Phylogen. Evol. 67: 118. 2013 ≡ *Hedyotis scandens* Roxb., Fl. Ind. 1: 369. 1820 ≡ *Oldenlandia scandens* (Roxb.) K.Schum. in Engler & Prantl, Nat. Pflanzenfam. 4(4): 26. 1891 – **Lectotype (designated here):** Silhet, *M.R. Smith s.n.* Wall. Cat. 839A EIC (K barcode K000031054 [image!]; isolectotypes: CAL n.v.).

Hedyotis hedyotidea (DC.) Merr. (≡ *Oldenlandia hedyotidea* (DC.) Hand.-Mazz.) also belongs to this group. However, we have failed to locate the correct specimen on which *Hedyotis hedyotidea* could be lectotypified. Although, we suggest recombining the *Hedyotis hedyotidea* under *Dimetia* but the search for the type specimen has to be done first.

Edrastima Raf. in Actes Soc. Linn. Bordeaux 6: 269. 1834 – Type: *Edrastima uniflora* (L.) Raf. (≡ *Oldenlandia uniflora* L.)

= *Hedyotis* sect. *Anotidopsis* Benth. & Hook.f., Gen. Pl. 2: 57. 1873 ≡ *Oldenlandia* sect. *Anotidopsis* (Benth. & Hook.f.) K.Schum. in Engler & Prantl, Nat. Pflanzenfam. 4(4): 25. 1891 ≡ *Oldenlandia* subg. *Anotidopsis* (Benth. & Hook.f.) Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd.

Natuurk., Sect. 2, 48(2): 193–194. 1952 – Type (designated by Bremekamp in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2, 48(2): 194. 1952): *Hedyotis trinervia* (Retz.) Roem. & Schult. (≡ *Oldenlandia trinervia* Retz.).

Annual herbs, often short-lived. Inflorescences terminal and axillary clusters of flowers. Corolla tube glabrous; stigma subglobose. Capsule subglobose with slightly raised beak. Seeds trigonous.

Edrastima angolensis (K.Schum.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia angolensis* K.Schum. in Bot. Jahrb. Syst. 23: 412. 1896 – Lectotype (designated by Bremekamp in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk, Sect. 2, 48(2): 196. 1952): Angola, Malange, *Mechow 379* (K barcode K000414308 [image!]; isolectotype: M barcode M-0106465 [image!]).

Edrastima cephalotes (Hochst.) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis cephalotes* Hochst. in Flora 27: 553. 1844 ≡ *Oldenlandia cephalotes* (Hochst.) Kuntze in Revis. Gen. Pl. 1: 292. 1891 – Lectotype (designated by Bremekamp in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2, 48(2): 194. 1952): South Africa, Port Natal, *Krauss 111* (K barcode K000414277 [image!]; isolectotypes: BM barcode BM000902948 [image!], TUB barcode TUB-004474 [image!]).

Edrastima goreensis (DC.) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis goreensis* DC. in Prodr. 4: 421. 1830 ≡ *Oldenlandia goreensis* (DC.) Summerh. in Bull. Misc. Inform. Kew 1928: 392. 1928 – Lectotype (designated by Bremekamp in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2, 48(2): 197. 1952): Senegal, Cape Verde Peninsula, near Goree Kounoum, *Perrottet 484* (P n.v.; isolectotype: W No. 0008652 [image!]).

Edrastima trinervia (Retz.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia trinervia* Retz. in Observ. Bot. 4: 23. 1786 ≡ *Hedyotis trinervia* (Retz.) Roem. & Schult., Syst. Veg. 3: 197. 1818 – **Lectotype (designated here, or perhaps holotype):** *Koenig s.n.* (LD barcode 1613930 [image!]).

Edrastima uniflora (L.) Raf. in Actes Soc. Linn. Bordeaux 6: 269. 1834 ≡ *Oldenlandia uniflora* L., Sp. Pl.: 119. 1753 ≡ *Hedyotis uniflora* (L.) Lam., Tabl. Encycl. 1: 271. 1792 – Lectotype (designated by Terrell & Robinson in Jarvis, Order Out Of Chaos: 698. 2007): Virginia, *Clayton 587* (LINN 155.3 [image!]; isolectotype: BM barcode 000051625 (BM) [image!]).

Exallage Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2, 48(2): 140. 1952 ≡ *Oldenlandia* subg. *Exallage* (Bremek.) Terrell & H.Rob. in Taxon 52: 776. 2003 – Type: *Exallage auricularia* (L.) Bremek. (≡ *Hedyotis auricularia* L.).

Annual or perennial herbs with woody rootstock, adventitious roots at nodes. Inflorescences axillary cymes. Flowers heterostylous. Capsule crustaceous and indehiscent. Seeds bluntly trigonous.

Exallage chrysotricha (Palib.) Neupane & N.Wikstr., **comb. nov.** ≡ *Anotis chrysotricha* Palib. in Bull. Herb. Boissier, sér. 2, 6: 20. 1906 ≡ *Hedyotis chrysotricha* (Palib.) Merr. in Lingnan Sci. J. 7: 322. 1931 ("1929") ≡ *Oldenlandia chrysotricha* (Palib.) Chun in Sunyatsenia 1: 311. 1934 – Holotype: Foochow, Fokien province, *M. Melnikoff s.n.* (LE [image!]).

Exallage fulva (Hook.f.) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis fulva* Hook.f., Fl. Brit. India 3: 58. 1880 – **Lectotype (designated here, or perhaps holotype):** Khasia, *J.D. Hooker & T. Thomson 60* (K barcode K000031876 [image!]).

Exallage insularis (Spreng.) Neupane & N.Wikstr., **comb. nov.** ≡ *Spermacoce glabra* Roxb., Fl. Ind. 1: 374. 1820 (Hort. Bengal.: 83. 1814, nom. nud.), non Michx. 1803 ≡ *Spermacoce insularis* Spreng., Syst. Veg. 1: 404. 1824 ≡ *Hedyotis glabra* R.Br. ex Wall., Numer. List: No. 848. 1829, nom. superfl. et illeg. ≡ *Knoxia glabra* DC., Prodr. 4: 569. 1830, nom. superfl. et illeg. ≡ *Oldenlandia glabra* Kuntze, Revis. Gen. Pl. 1: 292. 1891, nom. superfl. et illeg. ≡ *Exallage glabra* Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2, 48(2): 142. 1952, nom. superfl. et illeg. ≡ *Hedyotis insularis* (Spreng.) Deb & Ratna Dutta in Taxon 32: 285. 1983 – **Lectotype (designated here):** Penang, *Wall. Cat. 848* (K barcode K000770016 [image!]; isolectotype: CAL n.v.).

Exallage lapeyrousei (DC.) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis lapeyrousei* DC., Prodr. 4: 420. 1830 ("*lapeyrousii*") ≡ *Oldenlandia lapeyrousei* (DC.) Terrell & H.Rob. in Taxon 52: 777. 2003 ("*lapeyrousii*") – **Lectotype (designated here):** Solomon Islands, Vanikoro, *Lapeyrouse s.n.* (P barcode P00698936 [image!]; isolectotypes: P barcodes P00698935 [image!] & P00698937 [image!]).

Involucrella (Benth. & Hook.f.) Neupane & N.Wikstr., **stat. nov.** ≡ *Hedyotis* sect. *Involucrella* Benth. & Hook.f., Gen. Pl. 2: 57. 1873 – **Type (designated here):** *Involucrella coronaria* (Kurz) Neupane & N.Wikstr. (≡ *Scleromitrion coronarium* Kurz; *Hedyotis coronaria* (Kurz) Craib).

Annual or perennial herbs. Leaves oblong, ovate or lanceolate. Inflorescences terminal or pseudoaxillary on short lateral stems, sessile cymes with densely clustered sessile flowers or loose terminal paniculate cymes. Seeds irregularly angular with 3–5 pits/depressions on either side of the seed.

Involucrella chereevensis (Pierre ex Pit.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia chereevensis* Pierre ex Pit. in Lecomte, Fl. Indo-Chine 3: 143. 1922 ≡ *Hedyotis chereevensis* (Pierre ex Pit.) Fukuoka in S. E. Asian Stud. 8: 332. 1970 – **Lectotype (designated here):** Cambodia, province de Samrong-tong, mt. Chéréev, *Pierre 2053* (P!).

Involucrella coronaria (Kurz) Neupane & N.Wikstr., **comb. nov.**[1] ≡ *Scleromitrion coronarium* Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46: 136. 1877 ≡ *Hedyotis connata* Hook.f., Fl. Brit. India 3(7): 62. 1880 ≡ *Oldenlandia connata* (Hook.f.) K.Schum. in Engler & Prantl, Nat. Pflanzenfam. 4(Abt. 4, Lief. 61–62): 25. Jul 1891 (Kuntze, Revis. Gen. Pl. 1: 292. Nov 1891, isonym) ≡ *Hedyotis coronata* Wall. ex B.D.Jacks., Index Kew. 1(2): 1101. 1893, nom. superfl. et illeg. ≡ *Oldenlandia coronata* F.N.Williams in Bull. Herb. Boissier, ser. 2, 5(no. 10): 950. 1905, nom. superfl. et illeg. ≡ *Hedyotis coronaria* (Kurz) Craib, Fl. Siam. 2: 38. 1932 – **Lectotype (designated here for *Scleromitrion coronarium* and *Hedyotis connata*):** Burma [Myanmar]: Amherst, *Wallich s.n.* (K barcode K000031118 [image!]; isolectotypes: K barcode K001110074 [image!], CAL n.v.). – "*Hedyotis merguensis* Hook.f." in Bentham & Hooker, Gen. Pl. 2: 57. 1873, nom. nud.

Leptopetalum Hook. & Arn., Bot. Beechey Voy.: 295. 1838 ≡ *Hedyotis* sect. *Leptopetalum* (Hook. & Arn.) Benth. & Hook.f., Gen. Pl. 2: 57. 1873 ≡ *Hedyotis* subg. *Leptopetalum* (Hook. & Arn.) Fosberg & Sachet – Type: *Leptopetalum mexicanum* Hook. & Arn.

Annual herbs or shrubs. Glabrous throughout. Inflorescences terminal or axillary cymes. Fruit loculicidally dehiscent. Seeds ovoid or obtusely angulate appearing pitted due to shallow depressions bordered by thick and sinulate walls.

Leptopetalum biflorum (L.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia biflora* L., Sp. Pl.: 119. 1753 ≡ *Hedyotis biflora* (L.) Lam., Tabl. Encycl. 1: 272. 1792 ≡ *Gonotheca biflora* (L.) Masam. in Sci. Rep. Kanazawa Univ., Biol. 4: 78. 1955 ≡ *Thecagonum biflorum* (L.) Babu in Bull. Bot. Surv. India 11: 214. 1971 – Lectotype (designated by Biju & al. in Rheedea 2(1): 11–18. 1992): Ceylon, Herb. Hermann 3: 19, No. 68 (BM barcode 000594661(BM) [image!]).

Leptopetalum foetidum (G.Forst.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia foetida* G.Forst., Fl. Ins. Austr.: 10. 1786 ≡ *Hedyotis foetida* (G.Forst.) Sm. in Rees, Cycl. 17: [s.p.]. 1811 – Lectotype (designated by Smith & Darwin in Smith, Fl. Vitiensis Nova 4: 356. 1988): Tonga, Tongatapu, *J.R. & G. Foster s.n.* (BM barcode BM001015811 [image!]).

Leptopetalum pteritum (Blume) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis pterita* Blume in Bjidr. Fl. Ned. Ind.: 972. Oct 1826–Nov 1927 ≡ *Oldenlandia pterita* (Blume) Miq., Fl. Ned. Ind. 2: 193. 1857 ≡ *Thecagonum pteritum* (Blume) Babu in Bull. Bot. Surv. India 11: 214. 1971 – **Lectotype (designated here):** Java, *Blume s.n.* (L barcode L 0057745 [image!]; isolectotype: L barcode L 0057746 [image!]).

Leptopetalum strigulosum (Bartl. ex DC.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia strigulosa* Bartl. ex DC., Prod. 4: 427. 1830 ≡ *Hedyotis strigulosa* (Bartl. ex DC.) Fosberg in Smithsonian Contr. Bot. 45: 28. 1980 ≡ *Thecagonum strigulosum* (Bartl. ex DC.) Terrell & H.Rob. in J. Bot. Res. Inst. Texas 1: 377. 2007 – **Lectotype (designated here):** Marianas Islands, *Haenke*, *s.n.* (G-DC barcode G00208561 [image!]; isotypes: HAL barcode HAL0114272 [image!], GOET barcode GOET010406 [image!]).

■ NOMENCLATURE CHANGES OUTSIDE THE GENERA DISCUSSED ABOVE

Oldenlandia densa Neupane & N.Wikstr., **nom. nov.** ≡ *Oldenlandia robinsonii* Verdc., Fl. Zambes. 5(1): 142. 1989, nom. illeg. – Holotype: Zambia, Mwinilunga, Matonchi, *Robinson 3632* (K barcode K000414287 [image!]).

Scleromitrion gracilipes (Craib) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia gracilipes* Craib in Bull. Misc. Inform. Kew 1931: 441. 1931 ≡ *Hedyotis gracilipes* (Craib) Fukuoka in S. E. Asian Stud. 6: 332. 1970 – **Lectotype (designated here):** Ta Ruang, Chanthaburi, *Kerr 9720* (K barcode K000760521 [image!]; isolectotypes: BK barcode 257356 [image!], BM barcode BM000797125 [image!]).

Scleromitrion linoides (Griff.) Neupane & N.Wikstr., **comb. nov.** ≡ *Oldenlandia linoides* Griff., Not. Pl. Asiat. 4: 265. 1854 ≡ *Hedyotis linoides* (Griff.) Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46(2): 134. 1877 – **Lectotype (designated here):** Burma [Myanmar], Mergui, *Griffith 377* (K barcode K000031275 [image!]; isolectotype: E n.v.).

Scleromitrion scabrum (Wall. ex Hook.f.) Neupane & N.Wikstr., **comb. nov.** ≡ *Hedyotis scabra* Wall. ex Hook.f. in Fl. Brit. Ind. 3: 62. 1880 ≡ *Oldenlandia scabra* (Wall. ex Hook.f.) Kuntze, Revis. Gen. Pl. 1: 293. 1891 – **Lectotype (designated here):** Burma [Myanmar], Martaban and *Tenaserrim*, Lower Burma, Moolmyne, *Wall. Cat. 880* (K-W barcode K000031881 [image!]; isolectotype: CAL n.v.).

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1 Nomenclature Editor's Note: Despite current use to the contrary (e.g., Chen & Taylor, Fl. China: 19: 166. 2011), the currently used "*Hedyotis merguensis* Hook.f." was published only as a nomen nudum by Bentham & Hooker (Gen. Pl. 2: 57. 1873). A review of the literature did not turn up a valid place of publication of "*Hedyotis merguensis*" prior to the valid publication of *Scleromitrion coronarium* Kurz (in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46: 136. 1877). Therefore, *Scleromitrion coronarium* Kurz is the earliest validly published, legitimate name for this species. – G.M.

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Appendix 1. List of taxa from the tribe Spermacoceae investigated for phylogenetic analysis with voucher information (geographic origin, collector, collector number, herbarium) and DNA accession numbers from plastid (*rps16*, *petD*) and nuclear (ITS, ETS) regions. The dataset consists of sequences from Kårehed & al. (2008), Groeninckx & al. (2009a), Wikström & al. (2013), and the newly generated sequences (marked in bold). The taxon names follow Govaerts & al. (2014), except for the names *Leptopetalum foetidum* (G.Forst.) Neupane & N.Wikstr. and *Oldenlandia densa* Neupane & N.Wikstr.

Agathisanthemum chlorophyllum (Hochst.) Bremek., South Africa, *E.E. Galfrin m174* (A), HE649787, HE657551, HE657657, HE681450; ***Agathisanthemum globosum*** (Hochst. ex A.Rich.) Klotzsch, Zambia, *Dessein & al. 201* (BR), EU543019, EU557679, AM939425, –; ***Agathisanthemum quadricostatum*** Bremek., Tanzania, *E. Mboya 606* (S), HE649788, HE657552, HE657658, –; ***Amphiasma benguellense*** (Hiern) Bremek, Angola, *Kers 3350* (S), AF002753, EU557680, AM939426, AM932918; ***Amphiasma luzuloides*** (K.Schum.) Bremek**.,** Zambia, *Dessein & al. 1167* (BR), EU543020, EU557681, AM939428, AM932919; ***Amphiasma merenskyanum*** Bremek., Namibia, *R. Seydel 3118* (A), HE649789, HE657553, HE657659, HE681451; ***Amphistemon humbertii*** Groeninckx, Madagascar, *De Block & al. 2294* (BR), GU475977, GU475973, –, –; ***Amphistemon rakotonasolianus*** Groeninckx, Madagascar, *Groeninckx & al. 147* (BR), GU475978, GU475974, –, –; ***Arcytophyllum muticum*** (Wedd.) Standl., Colombia, *Andersson & al. 2195* (GB), AF002754, EU557682, AM939429, ; ***Arcytophyllum rivetii*** Harling **,** Ecuador, *Harling & Andersson 22232* (GB), –, –, –, –; ***Arcytophyllum thymifolium*** (Ruiz & Pav.) Standl., Ecuador, *Ståhl 4481* (GB), AF333366, EU557683, AM939431, ; ***Astiella delicatula*** Jovet, Madagascar, *De Block & al. 2173* (BR), GU475979, GU475975, –, –; ***Batopedina pulvinellata*** Robbr., Zambia, *Dessein & al. 264* (BR), EU543021, EU557684, –, –; ***Batopedina pulvinellata*** Robbr., D.R. Congo, *Malaisse 7695* (UPS), –, –, AM266989, –; ***Bouvardia glaberrima*** Engelm., cult., *Forbes s.n.* (S), EU543022, EU557685, AM939432, AM932922; ***Carphalea madagascariensis*** Lam., Madagascar, *De Block & al. 578* (BR), EU543023, EU557686, –, –; ***Carphalea madagascariensis*** Lam., Madagascar, *Razafimandimbison 524* (UPS), –, –, AM266995, –; ***Conostomium natalense*** (Hochst.) Bremek., South Africa, *Dahlstrand 1346* (GB), AF002760, EU557687, AM939435, AM932925; ***Conostomium quadrangulare*** (Rendle) Cufod., Ethiopia, *Puff & Kelbessa 821222 2/2* (UPS), EU543024, EU557688, AM939436, AM932926; ***Conostomium zoutpansbergense*** (Bremek.) Bremek., South Africa, *Bremer & al. 4331* (UPS), –, EU557689, AM939437, AM932927; ***Cordylostigma microcala*** (Bremek.) Groeninckx & Dessein, Zambia, *Dessein & al. 1149* (BR), EU543039, EU557725, AM939479, AM932962; ***Cordylostigma obtusilobum*** (Hiern) Groeninckx & Dessein, Kenya, *Luke 9035* (UPS), EU543040, EU557726, AM939481, –; ***Cordylostigma virgatum*** (Willd.) Groeninckx & Dessein, Madagascar, *De Block & al. 539* (BR), –, EU557728, AM939483, AM932965; ***Cordylostigma virgatum*** (Willd.) Groeninckx & Dessein, Namibia, *R. Seydel 2723* (A), HE798557, HE657554, HE657660, HE681452; ***Crusea calocephala*** DC., Guatemala, *Gustafsson & al. 215* (GB), –, EU557690, AM939438, AM932928; ***Crusea megalocarpa*** (A.Gray) S.Watson, Mexico, *Pringle 3852* (S), EU543025, EU557691, AM939439, AM932929; ***Dentella repens*** (L.) J.R.Forst. & G.Forst., Australia, *Andersson 2262* (GB), AF333370, EU557693, AM939440, AM932930; ***Dentella repens*** (L.) J.R.Forst. & G.Forst., China, *Tim Motley 3161* (ODU), –, –, **KP994244,** –; ***Dibrachionostylus kaessneri*** (S.Moore) Bremek., Kenya, *Strid 2598* (GB), AF002761, EU557694, AM939442, AM932932; ***Diodella teres*** (Walter) Small, Madagascar, *De Block & al. 793* (BR), –, –, AM939443, AM932933; ***Diodia aulacosperma*** K.Schum, Kenya, *Luke 9029* (UPS), EU543026, EU557695, AM939444, AM932934; ***Diodia spicata*** Miq., French Guiana, *Anderson & al. 1961* (GB), EU543027, EU557696, AM939535, AM933008; ***Emmeorhiza umbellata*** (Spreng.) K.Schum., Trinidad,

Appendix 1. Continued.

Hummel s.n. (GB), AY764289, EU557697, AM939445, AM932935; ***Ernodea littoralis*** Sw., Cuba, *Rova & al. 2286* (GB), AF002763, EU557698, AM939446, AM932936; ***Exallage auricularia*** (L.) Bremek., China, *Neupane 100* (ODU), **KR005789,** –, **KP994245, KR005760;** ***Exallage auricularia*** (L.) Bremek., China, *Neupane109* (ODU), **KR005790, KR005731, KP994246, KR005761;** ***Exallage auricularia*** (L.) Bremek., China, *Neupane 177* (ODU), **KR005791, KR005732, KP994247, KR005762;** ***Exallage auricularia*** (L.) Bremek., Sri Lanka, *Henni & Hans-Erik Wanntorp 2733* (S), HE649867, HE657617, HE657731, HE681527; ***Exallage auricularia*** (L.) Bremek., China, *Hu & But 21076* (A), HE649866, HE657616, HE657730, HE681526; ***Exallage auricularia*** (L.) Bremek., Fiji, *A.C. Smith 9599* (S), HE649868, HE657618, HE657732, HE681528; ***Exallage costata*** (Roxb.) Bremek., Malaysia, *Christensen & Apu 415* (AAU), HE649805, HE657568, HE657673, HE681468; ***Exallage pachycarpa*** (Ridl.) Bremek., Thailand, *Neupane 180* (ODU), **KR005792, KR005733, KP994249, KR005764;** ***Exallage ulmifolia*** (Wall.) Bremek., Nepal, *Polunin & al. 564* (UPS), HE649889, HE657636, HE657752, HE681547; ***Exallage ulmifolia*** (Wall.) Bremek, Nepal, *M. Suzuki & al. 9470098* (A), HE649890, HE657637, HE657753, HE681548; ***Galianthe brasiliensis*** (Spreng.) E.L.Cabral & Bacigalupo, Argentina, *Vanni & Radovancick 996* (GB), AY764290, EU557699, AM939447, AM932937; ***Galianthe eupatorioides*** (Cham. & Schltdl.) Cabral, Argentina, *Schinini & Cristobal 9811* (GB), EU543028, EU557700, AM939448, AM932938; ***Hedyotis acutangula*** Champ. ex Benth., China, *S.Y. Hu & Y.C. Kong 184* (A), HE649790, HE657555, HE657661, HE681453; ***Hedyotis ampliflora*** Hance, China, *F.C. How 73897* (A), HE649791, HE657556, –, HE681454; ***Hedyotis articularis*** R.Br. ex G.Don, India, *Klackenberg & Lundin 167* (S), HE649793, HE657557, HE657663, HE681456; ***Hedyotis assimilis*** Tutcher, China, *Shiu Ying Hu 10795* (A), HE649865, –, HE657729, –; ***Hedyotis benguetensis*** (Elmer) Elmer, Phillippines, *H.H. Bartlett 13237* (A), HE649869, –, HE657733, HE681529; ***Hedyotis bodinieri*** H.Lév. , China, *Shiu Ying Hu 13816* (A), HE649870, HE657619, HE657734, HE681530; ***Hedyotis bracteosa*** Hance, China, *Shiu Ying Hu 10684* (A), HE649872, HE657621, HE657736, HE681531; ***Hedyotis cantoniensis*** F.C.How ex W.C.Ko, China, *Ruijiang Wang & al. 1250* (IBSC), –, JF700061, JF699912, –; ***Hedyotis cantoniensis*** F.C.How ex W.C.Ko, China, *Li Ming 1193* (MO), HE649794, HE657558, HE657664, HE681457; ***Hedyotis capitellata*** Wall. ex G.Don, Malaysia, *John H. Beaman 8630* (L), HE649796, HE657560, HE657666, HE681459; ***Hedyotis capitellata*** Wall. ex G.Don, Malaysia, *Bremer & Bremer 1825* (UPS), HE649795, HE657559, HE657665, HE681458; ***Hedyotis capitellata*** Wall. ex G.Don, Thailand, *Neupane 176* (ODU), **KR005793, KR005734, KP994250, KR005765;** ***Hedyotis cathayana*** W.C.Ko, China, *Tim Motley 3214* (ODU), HE649798, HE657562, HE657668, HE681461; ***Hedyotis caudatifolia*** Merr. & F.P.Metcalf, China, *W.Y. Chun 6368* (A), HE649799, HE657563, HE657669, HE681462; ***Hedyotis caudatifolia*** Merr. & F.P.Metcalf, China, *Tsang, W T 28727* (A), HE649800, –, –, HE681463; ***Hedyotis ceylanica*** (Thwaites) N.Wikstr. & Neupane, Sri Lanka, *Henni & Hans-Erik Wanntorp 2778* (S), HE649858, HE657609, HE657721, HE681516; ***Hedyotis ceylanica*** (Thwaites) N.Wikstr. & Neupane, Sri Lanka, *Larsson & Pyddoke 14* (S), HE649857, HE657608, HE657722, HE681517; ***Hedyotis cheniana*** R.J.Wang, China, *Tim Motley 3190* (ODU), HE649801, HE657564, –, HE681464; ***Hedyotis communis*** W.C.Ko, China, *Nat. Geogr. Society Hainan Expedition 384* (MO), HE649802, HE657565, HE657670, HE681465; ***Hedyotis consanguinea*** Hance, China, *Shiu Ying Hu 10821* (S), HE649877, EU557701, AM939450, HE681536; ***Hedyotis coprosmoides*** Trimen, Sri Lanka, *Wambeek & al. 2783* (S), HE649803, HE657566, HE657671, HE681466; ***Hedyotis coronaria*** (Kurz) Craib, Thailand, *E.F. Anderson 5464* (A), –, HE657567, HE657672, HE681467; ***Hedyotis coronaria*** (Kurz) Craib, Thailand, *Neupane 191* (ODU), **KR005796,** –, –, **KR005768;** ***Hedyotis coronaria*** (Kurz) Craib, Thailand, *Neupane 171* (ODU), **KR005795, KR005736, KP994252, KR005767;** ***Hedyotis cryptantha*** Dunn, China, *Tim Motley 3202* (ODU), HE649879, HE657627, HE657742, HE681538; ***Hedyotis decora*** Geddes, Thailand, *M. Tagawa & al. 4851* (A), –, –, HE657675, HE681470; ***Hedyotis dendroides*** Alston, Sri Lanka, *Lundqvist 11272* (UPS), HE649807, –, HE657676, HE681471; ***Hedyotis dianxiensis*** W.C.Ko, China, *Tsi Zhanhuo 92-100* (MO), HE649808, HE657570, HE657677, HE681472; ***Hedyotis dianxiensis*** W.C.Ko, China, *IBSC1275-1,* JX111261.1, JX111096.1, JX111210.1, –; ***Hedyotis effusa*** Hance, China, *Tsang 21044* (S), HE649809, –, AM939491, AM932940; ***Hedyotis fissistipula*** Merr., Malaysia (Sabah), *J.B.J. Blewett 17* (A), HE649810, HE657571, HE657678, HE681473; ***Hedyotis flavescens*** Thwaites, Sri Lanka, *Neupane 61* (PDA), HE649811, –, HE657679, HE681474; ***Hedyotis fruticosa*** L., Sri Lanka, *Larsson & Pyddoke 22* (S), HE649812, EU557702, AM939453, AM932941; ***Hedyotis fulva*** Hook.f., Thailand, *Suphuntee 786* (ODU), **KR005797, KR005737, KP994253,** –; ***Hedyotis gardneri*** Thwaites, Sri Lanka, *Fagerlind 5074* (S), –, –, HE657680, HE681475; ***Hedyotis hainanensis*** (Chun) W.C.Ko, China, *F.C. How 72268* (A), HE649884, HE657631, HE657747, HE681543; ***Hedyotis insularis*** (Spreng.) Deb & Ratna Dutta, Thailand, *Neupane 172* (ODU), **KR005798, KR005738, KP994254, KR005769;** ***Hedyotis koana*** R.J.Wang, China, *IBSC978,* JX111267.1, JX111101.1, JX111215.1, –; ***Hedyotis korrorensis*** (Valeton) Hosok., Caroline Islands, *Fosberg 47697* (S), HE649813, EU557703, AM939454, AM932942; ***Hedyotis kurzii*** Merr., Thailand, *Neupane 187* (ODU), **KR005799, KR005739, KP994255, KR005770;** ***Hedyotis lancea*** Thunb. ex Maxim., China, *Xiao Bai-Zhong 3467* (A), HE649887, HE657634, HE657750, HE681545; ***Hedyotis lawsoniae*** Wight & Arn., Sri Lanka, *Wambeek & Wanntorp 2996* (S), HE649815, EU557704, AM939455, AM932943; ***Hedyotis lessertiana*** Thwaites var. ***lessertiana,*** Sri Lanka, *Klackenberg 413* (S), EU543029, EU557705, AM939466, AM932944; ***Hedyotis lessertiana*** var. ***marginata*** Thwaites ex Trimen, Sri Lanka, *Fagerlind 3668* (S), EU543030, EU557706, AM939456, AM932945; ***Hedyotis macrostegia*** Stapf, Malaysia (Sabah), *Wallander 6* (GB), AF002767, –, AM942768, –; ***Hedyotis marginata*** (Thwaites ex Trimen) Alston, Sri Lanka, *Neupane 72* (PDA), HE649817, –, HE657683, HE681478; ***Hedyotis megalantha*** Merr., Marianas (Guam), *Andersson 07* (S), –, –, AM939457, AM932946; ***Hedyotis mellii*** Tutcher, China, *Luo Lin-Bo 0785* (MO), HE649891, HE657638, HE657754, HE681549; ***Hedyotis membranacea*** Thwaites, Sri Lanka, *Neupane 78* (PDA), HE649818, –, HE657684, HE681479; ***Hedyotis minutopuberula*** Merr. & F.P.Metcalf, China, *Tim Motley 3219* (ODU), HE649819, HE657574, HE657685, –; ***Hedyotis nodulosa*** Arn., Sri Lanka, *Bremer & Bremer 1012* (S), HE649821, HE657576, HE657687, HE681481; ***Hedyotis novoguineensis*** Merr. & L.M.Perry, New Guinea, *M.J.S. Sands 2577* (A), HE649822, HE657577, HE657688, HE681482; ***Hedyotis novoguinensis*** Merr. & L.M.Perry, New Guinea, *SKP 946* (ODU), HE649848, HE657600, HE657712, HE681505; ***Hedyotis nutans*** (Valeton) P.Royen, New Guinea, *Bergman s.n. 1949* (S), HE649892, HE657639, –, HE681550; ***Hedyotis obliquinervis*** Merrill, Vietnam, *Razafimandimbison & al. 729* (S), HE649836, HE657588, HE657701, HE681494; ***Hedyotis obscura*** Thwaites, Sri Lanka, *Fagerlind 2733* (S), –, –, HE657689, HE681483; ***Hedyotis ovata*** Thunb. ex Maxim., China, *L. Averyanov & al. VH048* (MO), –, –, HE657690, –; ***Hedyotis paridifolia*** (Dunn) Chun, China, *T. Motley 3167* (ODU), HE649895, HE657641, HE657757, HE681553; ***Hedyotis paridifolia*** (Dunn) Chun, China, *T. Motley 3165* (ODU), HE649894, –, HE657756, HE681552; ***Hedyotis parryi*** Hance, China, *C.O. Levine 1175* (A), HE649824, HE657578, HE657692, HE681485; ***Hedyotis philippensis*** (Willd. ex Spreng.) Merr. ex C.B.Rob., Indonesia, *A.C. Church & al. 1369* (A), HE649825, HE657579, –, –; ***Hedyotis pitardiana*** Craib., Vietnam, *K. Kanulainen & al. 005* (S), HE649843, HE657595, HE657708, HE681501; ***Hedyotis prostrata*** (Blume) Kuntze, China, *National Geographic Society Hainan Expedition 39* (MO), HE649898, HE657644, HE657759, HE681555; ***Hedyotis pubescens*** Valeton, New Guinea, *W. Takeuchi & al. 13326* (A), HE649899, HE657645, HE657760, HE681556; ***Hedyotis pulchella*** Stapf, Malaysia (Sabah), *John H. Beaman 8909* (L), HE649826, HE657580, HE657693, HE681486; ***Hedyotis purpurascens*** Hook.f., India, *Klackenberg & Lundin 546* (S), HE649827, HE657581, HE657694, HE681487; ***Hedyotis quinquinervia*** Thwaites, Sri Lanka, *Bremer & al. 163* (S), HE649828, EU557707, AM939458, AM932947; ***Hedyotis rhinophylla*** Thwaites ex Trimen, Sri Lanka, *Fagerlind 5082* (S), HE649829, EU557708, AM939459, AM932948; ***Hedyotis rigida*** (Blume) Walp., Malaysia (Sabah), *John H. Beaman 10320* (MO), HE649830, HE657582, HE657695, HE681488; ***Hedyotis rivalis*** Ridl., Malaysia, *Nooteboom s.n. 1990* (L), HE649831, HE657583, HE657696, HE681489; ***Hedyotis rugosa*** Blume, Indonesia (Java), *Nyman s.n. 1898* (UPS), HE649859, –, HE657723, HE681518; ***Hedyotis scandens*** Roxb., China, *Gaoligong Shan Biodiversity Survey 25571* (MO), HE649832, HE657584, HE657697, HE681490; ***Hedyotis scandens*** Roxb., China, *Guang-Wan Hu 00892* (ODU), **KR005800, KR005740, KP994256, KR005771;** ***Hedyotis scandens*** Roxb., Nepal, *Neupane 168* (ODU), **KR005801, KR005741, KP994257, KR005772;** ***Hedyotis schlechteri*** Merr. & L.M.Perry, New Guinea, *M.J.S. Sands & al. 1937* (A), HE649833, HE657585, HE657698, HE681491; ***Hedyotis shiuyingiae*** Tao Chen, China, *N.H. Li 204* (A), HE649834, HE657586, HE657699, HE681492; ***Hedyotis* sp.,** Vietnam, *Razafimandimbison & al. 716* (S), HE649835, HE657587, HE657700, HE681493; ***Hedyotis* sp. ,** Vietnam, *Razafimandimbison & al. 735* (S), HE649837, HE657589, HE657702, HE681495; ***Hedyotis* sp.,** Vietnam, *Razafimandimbison & al. 745* (S), HE649838, HE657590, HE657703, HE681496; ***Hedyotis* sp.,** Vietnam, *Razafimandimbison & al. 760* (S), HE649839, HE657591, HE657704, HE681497; ***Hedyotis* sp.,** Vietnam, *Razafimandimbison & al. 785* (S), HE649840, HE657592, HE657705, HE681498; ***Hedyotis* sp.,** Vietnam, *Razafimandimbison & al. 795* (S), HE649841, HE657593, HE657706, HE681499; ***Hedyotis* sp.,** Vietnam, *K. Kanulainen & al. 002* (S), HE649842, HE657594, HE657707, HE681500; ***Hedyotis* sp.,** Vietnam, *K. Kanulainen & al. 012* (S), HE649844, HE657596, HE657709, HE681502; ***Hedyotis* sp.,** Vietnam, *K. Kanulainen & al. 045* (S), HE649845, HE657597, HE657710, HE681503; ***Hedyotis* sp.,** Vietnam, *Averyanov & al. VH2844* (MO), HE649878, HE657626, HE657741, HE681537; ***Hedyotis* sp.,** China, *Li Heng 10588* (GH), HE649797, HE657561,

Appendix 1. Continued.

HE657667, HE681460; ***Hedyotis* sp.,** Thailand, *Suphuntee 718* (ODU), **KR005802, KR005742,** –, –; ***Hedyotis* sp.,** Thailand, *Neupane 193* (ODU), **KR005794, KR005735, KP994251, KR005766; *Hedyotis stylosa*** R.Br. ex G.Don, India, *Klackenberg & Lundin 490* (S), HE649847, HE657599, HE657711, –; ***Hedyotis swertioides*** Hook.f., India, *Klackenberg & Lundin 3* (S), EU543031, EU557709, AM939460, HE681506; ***Hedyotis tenuipes*** Hemsl. ex F.B.Forbes & Hemsl., China, *Hu & Kong 017* (MO), HE649904, HE657649, HE657766, HE681561; ***Hedyotis ternata*** (Pierre ex Pit.) P.H.Ho, Thailand, *M. Greijmans 103* (L), HE649905, HE657650, HE657767, HE681562; ***Hedyotis tetrangularis*** (Korth.) Walp., Thailand, *J.F. Maxwell 84-473* (A), HE649906, HE657651, HE657768, HE681563; ***Hedyotis thwaitesii*** Hook.f., Sri Lanka, *Neupane 79* (PDA), –, –, HE657713, –; ***Hedyotis trichoclada*** Merr. & L.M.Perry, New Guinea, *R. Schodde 2025* (A), HE649849, HE657601, HE657714, HE681507; ***Hedyotis tridentata*** Ridsdale, Sri Lanka, *Fagerlind 3365* (S), –, –, HE657715, HE681508; ***Hedyotis trimenii*** Deb & R.M.Dutta, Sri Lanka, *Bremer & Bremer 1027* (S), HE649850, HE657602, HE657716, HE681509; ***Hedyotis uncinella*** Hook. & Arn., Taiwan, *Huang & al. 531* (MO), HE649851, HE657603, HE657717, HE681510; ***Hedyotis vachellii*** Hook. & Arn., China, *T.W. Lau 057* (A), HE649909, HE657654, HE657771, HE681566; ***Hedyotis valetoniana*** Merr. & L.M.Perry, New Guinea, *R.J. Johns 9869A* (L), HE649852, HE657604, HE657718, HE681511; ***Hedyotis verticillaris*** Wall. ex Wight & Arn., Sri Lanka, *Bremer & al. 37* (S), HE649911, HE657656, HE657773, HE681568; ***Hedythyrsus spermacocinus*** (K.Schum.) Bremek., Zambia, *Dessein & al. 1017* (BR), EU543032, EU557711, AM939461, AM932950; ***Houstonia caerulea*** L., U.S.A., *Vincent & Lammers s.n.* (GB), AF333379, EU557713, AM939464, –; ***Houstonia longifolia*** Gaertn., U.S.A., *Yatskievych 96-49* (MO), AF002766, EU567462, AM939465, –; ***Kadua acuminata*** Cham. & Schltdl., U.S.A. (Hawaii), cult. at BR, –, EU557714, AM939467, AM932952; ***Kadua affinis*** Cham. & Schltdl., U.S.A. (Hawaii), *Motley 1733* (NY), EU642523, –, AM942769, –; ***Kadua axillaris*** (Wawra) W.L.Wagner & Lorence, U.S.A. (Hawaii, Maui), *Motley 1724* (NY), EU642524.1, –, AM942769, –; ***Kadua centranthoides*** Hook. & Arn., U.S.A. (Hawaii), *Skottsberg 6788* (S), EU543033, EU557715, AM939468, –; ***Kadua coriacea*** (J.E.Smith) W.L.Wagner & Lorence, U.S.A. (Hawaii), *Motley 1703* (NY), EU642525.1, –, AM942771, –; ***Kadua degeneri*** (Fosberg) W.L.Wagner & Lorence, U.S.A. (Hawaii), cult. at PTGB, *Wood 5062* (PTGB), AF333371, EU557717, AM939470, AM932953; ***Kadua elatior*** (H.Mann) W.L.Wagner & Lorence, U.S.A. (Hawaii, Kauai), *Wagner 6350* (BISH), EU642526.1, –, AM942772, –; ***Kadua fluviatilis*** C.N.Forbes, U.S.A. (Hawaii), *Motley 1747* (NY), EU642527, –, AM942773, –; ***Kadua flynnii*** (W.L.Wagner & Lorence) W.L.Wagner & Lorence, U.S.A. (Hawaii, Kauai), *Perlman 15631* (BISH), EU642528, –, EU642542, –; ***Kadua foggiana*** (Fosberg) W.L.Wagner & Lorence, U.S.A. (Hawaii), *Sparre 27* (S), –, EU557718, AM939471, –; ***Kadua fosbergii*** (W.L.Wagner & D.R.Herbst) W.L.Wagner & Lorence, U.S.A. (Hawaii, Oahu), *Motley 1677* (NY), EU642529, –, AM942775, –; ***Kadua laxiflora*** H.Mann, U.S.A. (Hawaii, Molokai), *Perlman 6677* (BISH), EU642530, –, AM942776, –; ***Kadua parvula*** A.Gray, U.S.A. (Hawaii), cult. at GB, *Perlman 12783* (GB), AF333375, EU557720, AM939473, –; ***Kohautia amatymbica*** Eckl. & Zeyh., South Africa, *Bremer & al. 4307* (UPS), EU543035, EU557721, AM939484, AM932956; ***Kohautia caespitosa*** Schnizl., Zambia, *Dessein & al. 432* (BR), EU543036, EU557722, AM939474, AM932957; ***Kohautia coccinea*** Royle, Zambia, *Dessein & al. 751* (BR), EU543037, EU557723, AM939476, AM932959; ***Kohautia cynanchica*** DC., Zambia, *Dessein & al. 469* (BR), EU543038, EU557724, AM939477, AM932960; ***Kohautia longifolium*** Klotzsch, Zambia, *Dessein & al. 462* (BR), –, –, AM939478, AM932961; ***Kohautia subverticillata*** (K.Schum.) D.Mantell, Zambia, *Dessein & al. 432* (BR), EU543041, EU557727, AM939482, AM932964; ***Lathraeocarpa acicularis*** Bremek., Madagascar, *De Block & al. 2316* (BR), EU642522, EU642520, –, –; ***Lelya osteocarpa*** Bremek., Tanzania , *Gereau 2513* (BR), –, EU557729, AM939485, –; ***Lelya prostrata*** W.H.Lewis, Zimbabwe, *W.H. Lewis 6119* (GH), HE649854, HE657606, –, HE681513; ***Leptopetalum foetidum*** (G.Forst.) Neupane & N.Wikstr., Marianas Islands, *F.R. Fosberg 59615* (L), HE649855, –, –, HE681514; ***Leptopetalum grayi*** (Hook.f.) Hatus., Japan, *B. Bremer 47001* (S), HE649856, HE657607, HE657720, HE681515; ***Manettia alba*** (Aubl.) Wernh., French Guiana, *Andersson & al. 1917* (GB), AF002768, –, AM939486, AM932966; ***Manettia lygistum*** (L.) Sw., Columbia, *Andersson & al. 2128* (GB), AF002769, EU557730, AM939487, AM932967; ***Mitracarpus frigidus*** (Willd. ex Roem. & Schult.) K.Schum., French Guiana, *Andersson & al. 1995* (GB), AF002770, EU567464, AM939488, –; ***Mitracarpus microspermus*** K.Schum., Guiana, *Jansen- Jacobs & al. 4785* (GB), EU543044, EU557732, AM939489, AM932969; ***Mitrasacmopsis quadrivalvis*** Jovet, Zambia, *Dessein & al. 1273* (BR), EU543045, EU557733, AM939490, AM932970; ***Neanotis calycina*** (Wall. ex Hook.f.) W.H.Lewis, Nepal, *Neupane 13* (ODU), HE649860, HE657610, HE657724, HE681519; ***Neanotis formosana*** (Hayata) Lewis, Taiwan, *C.I. Peng 17402* (S), –, HE657612, HE657725, HE681521; ***Neanotis gracilis*** (Hook.f.) W.H.Lewis, Nepal, *Neupane 89* (ODU), HE649861, HE657611, –, HE681520; ***Neanotis hirsuta*** (L.f.) W.H.Lewis, Nepal, *Polunin & al. 5640* (UPS), HE649846, HE657598, –, HE681504; ***Neanotis hirsuta*** (L.f.) W.H.Lewis, Japan, *K. Deguchi & al. 7859* (A), HE649816, HE657573, HE657682, HE681477; ***Neanotis indica*** (DC.) W.H.Lewis, India, *Klackenberg & Lundin 387* (S), HE649862, HE657613, HE657726, –; ***Neanotis kwangtungensis*** (Merr. & F.P.Metcalf) W.H.Lewis, China, *IBSC1236* (IBSC), JX111293, JX111114, JX111232, –; ***Neanotis monosperma*** (Wight & Arn.) W.H.Lewis, Sri Lanka, *Larsson & Pyddoke 15* (S), HE649863, HE657614, HE657727, HE681522; ***Neanotis nana*** (Merr. & L.M.Perry) N.Wikstr. & Neupane, New Guinea, *W. Vink 16290* (A), HE649820, HE657575, HE657686, HE681480; ***Neanotis nummularia*** (Arn.) W.H.Lewis, Sri Lanka, *Larsson & Pyddoke 16* (S), HE649864, HE657615, HE657728, HE681523; ***Neanotis nummulariformis*** (Arn.) W.H.Lewis, Sri Lanka, *F. Fagerlind 4286* (S), –, –, –, HE681524; ***Neanotis pahompokae*** (Fukuoka) N.Wikstr. & Neupane, Thailand, *Iwatsuki & al. 9562* (AAU), HE649823, –, HE657691, HE681484; ***Neanotis wightiana*** (Wall. ex Wight & Arn.) W.H.Lewis, India, *Hooker & Thomson s.n.* (UPS), –, –, –, HE681525; ***Nesohedyotis arborea*** (Roxb.) Bremek., cult. at K, *Chase 2915* (K), AF003607, –, –, –; ***Oldenlandia affinis*** (Roem. & Schult.) DC., Zambia, *Dessein & al. 627* (BR), EU543046, EU557734, AM939492, AM932971; ***Oldenlandia affinis*** (Roem. & Schult.) DC., Thailand, *Kai Larsen & al. 44192* (MO), HE649814, HE657572, HE657681, HE681476; ***Oldenlandia angolensis*** K.Schum., Zambia, *Dessein & al. 932* (BR), EU543047, EU557735, AM939493, AM932972; ***Oldenlandia brachypoda*** DC., Nepal, *Neupane 88* (ODU), HE649871, HE657620, HE657735, –; ***Oldenlandia capensis*** L.f., Zambia, *Dessein & al. 843* (BR), EU543048, EU557737, AM939496, AM932974; ***Oldenlandia chereevensis*** Pierre ex Pit., Thailand, *K. Larssen & al. 41491* (MO), HE649873, HE657622, HE657737, HE681532; ***Oldenlandia chereevensis*** Pierre ex Pit., Thailand, *Suphuntee 799* (ODU), **KR005803, KR005743, KP994258, KR005773; *Oldenlandia chrysotricha*** (Palib.) Chun, China, *Chow & Wan 79024* (UPS), HE649875, HE657624, HE657739, HE681534; ***Oldenlandia chrysotricha*** (Palib.) Chun, China, *Nie Min-xiang 92393* (UPS), HE649874, HE657623, HE657738, HE681533; ***Oldenlandia chrysotricha*** (Palib.) Chun, China, *Lin Qinzhong 2004180* (MO), HE649876, HE657625, HE657740, HE681535; ***Oldenlandia chrysotricha*** (Palib.) Chun, China, *Neupane 119* (ODU), **KR005804, KR005744, KP994259, KR005774; *Oldenlandia corymbosa*** L., Zambia, *Dessein & al. 487* (BR), EU543050, EU557739, AM939502, AM932979; ***Oldenlandia corymbosa*** L., China, *Neupane 114* (ODU), **KR005805, KR005745,** –, **KR005775; *Oldenlandia densa*** Neupane & N.Wikstr., Zambia, *Dessein & al. 346* (BR), EU543061, EU557751, AM939503, AM932980; ***Oldenlandia diffusa*** (Willd.) Roxb., China, *Tan Ce-ming 95670* (UPS), HE649880, HE657628, HE657743, HE681539; ***Oldenlandia diffusa*** (Willd.) Roxb., China, *Neupane 115* (ODU), **KR005806, KR005746,** –, –; ***Oldenlandia duemmeri*** S.Moore, Uganda, *W.H. Lewis 6018* (GH), HE649881, HE657629, HE657744, HE681540; ***Oldenlandia echinulosa*** K.Schum., Zambia, *Dessein & al. 928* (BR), EU543051, EU557740, AM939504, AM932981; ***Oldenlandia erecta*** (Manilal & Sivar.) R.R.Mill, China, *Li Heng 11298* (A), HE649897, HE657643, HE657758, HE681554; ***Oldenlandia erecta*** (Manilal & Sivar.) R.R.Mill, Nepal, *Neupane 2* (ODU), HE649882, HE657630, HE657745, HE681541; ***Oldenlandia fastigiata*** Bremek., Zambia, *Dessein & al. 1019* (BR), EU543052, EU557742, AM939506, AM932983; ***Oldenlandia galioides*** (F.Muell.) F.Muell., Australia, *Harwood 1511* (BR), EU543053, EU557743, AM939507, –; ***Oldenlandia geophila*** Bremek., Zambia, *Dessein & al. 935* (BR), EU543054, EU557744, AM939508, –; ***Oldenlandia goreensis*** (DC.) Summerh., Zambia, *Dessein & al. 1286* (BR), EU543055, EU557745, AM939510, AM932985; ***Oldenlandia gracilipes*** Craib, Thailand, *J.F. Maxwell 01-591* (L), HE649883, –, HE657746, HE681542; ***Oldenlandia hedyotidea*** (DC.) Hand.-Mazz., Taiwan, *Kuang-Yuh Wang 156* (A), HE649885, HE657632, HE657748, HE681544; ***Oldenlandia hedyotidea*** (DC.) Hand.-Mazz., China, *Ruijiang Wang & al. 1249* (IBSC), JX111265, JX111099, JX111213, –; ***Oldenlandia herbacea*** (L.) Roxb., Zambia, *Dessein & al. 463* (BR), EU543057, EU557747, AM939552, AM932988; ***Oldenlandia krewanhensis*** Pierre ex Pit., Thailand, *Neupane 192* (ODU), **KR005807, KR005747, KP994260, KR005776; *Oldenlandia lancifolia*** (Schumach.) DC., Zambia, *Dessein & al. 1356* (BR), EU543058, –, AM939512, AM932990; ***Oldenlandia lapeyrousii*** (DC.) Terrell & H.Rob., New Guinea, *W. Takeuchi 4727* (A), HE649888, HE657635, HE657751, HE681546; ***Oldenlandia linoides*** Giff., Thailand, *Neupane 189* (ODU), **KR005808,** –, –, –; ***Oldenlandia microtheca*** (Cham. & Schltdl.) DC., Mexico, *Frödeström & Hultén 681* (S), EU543059, EU557749, AM939513, AM932991; ***Oldenlandia mitrasacmoides*** (F.Muell.) F.Muell., Australia, *Harwood 1520* (BR), –, EU557750, AM939515, AM932992; ***Oldenlandia nematocaulis*** Bremek., Zambia, *Dessein & al. 924* (BR), EU543060, –, AM939517, AM932994; ***Oldenlandia nervosa*** Hiern, Gabon, *Andersson & Nilsson 2326* (GB), AF333382, –, AM939518, AM932995; ***Oldenlandia oligocephala*** Pierre ex

Appendix 1. Continued.

Pit., Thailand, *Neupane 160* (ODU), **KR005809, KR005748, KP994261, KR005777; *Oldenlandia ovatifolia*** (Cav.) DC., Thailand, *K. Larssen & al. 43736* (MO), HE649893, HE657640, HE657755, HE681551; ***Oldenlandia ovatifolia*** (Cav.) DC., Thailand, *Neupane 185* (ODU), **KR005810, KR005749, KP994262, KR005778; *Oldenlandia pinifolia*** (Wall. ex G.Don) Kuntze, Indonesia, *Rahmat Si Toroes 2734* (S), HE649896, HE657642, –, –; ***Oldenlandia pinifolia*** (Wall. ex G.Don) Kuntze, China, *Ruijiang Wang 1231* (IBSC), JX111122, JX111122, JX111240, –; ***Oldenlandia pinifolia*** (Wall. ex G.Don) Kuntze, Thailand, *Neupane 173* (ODU), **KR005811, KR005750, KP994263,** –; ***Oldenlandia rosulata*** K.Schum., Zambia, *Dessein & al. 1197* (BR), EU543043, EU567465, AM939519, –; ***Oldenlandia rupicola*** (Sond.) Kuntze, South Africa, *B. Bremer & K. Bremer 3807* (UPS), HE649900, HE657646, HE657762, –; ***Oldenlandia salzmannii*** (DC.) Benth. & Hook.f. ex B.D.Jacks., Brazil, *Harley 15514* (UPS), AY764294, EU557752, AM939520, AM932996; ***Oldenlandia scabra*** (Wall. ex Kurz) Kuntze, Thailand, *Neupane 183* (ODU), **KR005812, KR005751, KP994264, KR005779; *Oldenlandia* sp.,** Thailand, *E.F. Anderson 5559* (A), –, –, HE657761, HE681557; ***Oldenlandia* sp.,** China, *Hu & But 22491* (A), HE649886, HE657633, HE657749, –; ***Oldenlandia stocksii*** Hook.f., India, *Klackenberg & Lundin 326* (S), HE649901, –, HE657763, HE681558; ***Oldenlandia stricta*** L., Sri Lanka, *F. Fagerlind 3027* (S), HE649902, HE657647, HE657764, HE681559; ***Oldenlandia taborensis*** Bremek., Tanzania, *Bidgood & al. 4015* (BR), –, EU557753, AM939522, –; ***Oldenlandia tenelliflora*** (Blume) Kuntze, cult. at BR, EU543062, EU557710, AM939451, AM932949; ***Oldenlandia tenelliflora*** (Blume) Kuntze, China, *Liu Zhengyu 21840* (MO), HE649903, HE657648, HE657765, HE681560; ***Oldenlandia tenelliflora*** (Blume) Kuntze, China, *Shiu Ying Hu 5401* (A), HE649792, –, HE657662, HE681455; ***Oldenlandia tenelliflora*** (Blume) Kuntze, China, *Neupane 108* (ODU), **KR005814, KR005753, KP994266, KR005781; *Oldenlandia tenelliflora*** var. ***kerrii*** Craib, Thailand, *Neupane 182* (ODU), **KR005813, KR005752, KP994265, KR005780; *Oldenlandia tenuis*** K.Schum., Guyana, *Jansen-Jacobs & al. 41* (UPS), AY764293, EU557754, AM939523, –; ***Oldenlandia trinervia*** Retz., Sri Lanka, *F. Fagerlind 4338* (S), HE649907, HE657652, HE657769, HE681564; ***Oldenlandia umbellata*** L., Sri Lanka, *F. Fagerlind 3320* (S), HE649806, HE657569, HE657674, HE681469; ***Oldenlandia umbellata* L.,** India, *Neupane 84* (ODU), HE649908, HE657653, HE657770, HE681565; ***Oldenlandia uniflora*** L., U.S.A., *Godfrey 57268* (GB), AY764295, EU557755, AM939524, –; ***Oldenlandia uniflora* L.,** U.S.A. (Virginia), *Neupane 195* (ODU), **KR005815,** –, –, –; ***Oldenlandia verticillata*** L., China, *Neupane 104* (ODU), **KR005816, KR005754, KP994267, KR005782; *Oldenlandia verticillata*** L., China, *Neupane 124* (ODU), **KR005817,** –, **KP994268,** –; ***Oldenlandia verticillata*** L., Thailand, *Neupane 184* (ODU), **KR005818, KR005755, KP994269,** –; ***Oldenlandia verticillata*** L., Nepal, *Neupane 5* (ODU), HE649910, HE657655, HE657772, HE681567; ***Oldenlandia viarum*** Craib, Thailand, *Neupane 174* (ODU), –, **KR005756, KP994270, KR005783; *Oldenlandia wauensis*** Schweinf. ex Hiern, Ethiopia, *Friis & al. 2560* (UPS), EU543076, EU557774, AM939548, AM933018; ***Oldenlandia wiedemannii*** K.Schum., Kenya, *Luke & Luke 8362* (UPS), EU543063, EU557756, AM939525, AM933001; ***Paraknoxia parviflora*** (Stapf ex Verdc.) Verdc. ex Bremek., Zambia, *Dessein & al. 678* (BR), EU543064, EU557757, –, –; ***Pentanopsis fragrans*** Rendle, Ethiopia, *Gilbert & al. 7458* (UPS), EU543065, EU557758, AM939526, AM933002; ***Pentodon pentandrus*** (Schumach. & Thonn.) Vatke, Zambia, *Dessein & al. 598* (BR), EU543066, EU557759, AM939528, AM933003; ***Phialiphora bevazahensis*** Groeninckx **,** Madagascar, *Briggs Rakotonasolo 297* (K), GU475987, GU475986, –, –; ***Phylohydrax carnosa*** (Hochst.) Puff, South Africa, *Bremer3783* (UPS), EU543067, EU557760, AM939529, –; ***Phylohydrax madagascariensis*** (Willd. ex Roem. & Schult.) Puff , Madagascar, *De Block & al. 640* (BR), AY764292, EU557761, AM939530, –; ***Psyllocarpus laricoides*** Mart. & Zucc., Brazil, *Andersson & al. 35750* (UPS), –, –, AM939531, AM933005; ***Richardia brasiliensis*** Gomes, Madagascar , *De Block & al. 904* (BR), –, –, AM939533, AM933007; ***Richardia scabra*** L., Colombia, *Andersson & al. 2073* (GB), AF003614, EU557762, AM939532, AM933006; ***Richardia stellaris*** L., Australia, *Egeröd 85343* (GB), EU543068, EU557763, AM939534, –; ***Spermacoce capitata*** Ruiz & Pav., French Guiana, *Andersson 1908* (GB), EU543069, EU557764, AM939536, –; ***Spermacoce erosa*** Harwood, Australia, *Harwood 1148* (BR), EU543070, EU557765, AM939537, AM933009; ***Spermacoce filituba*** (K.Schum.) Verdc. **,** Kenya, *Luke 9022* (UPS), EU543071, EU557766, AM939539, AM933011; ***Spermacoce flagelliformis*** Poir., Madagascar, *DeBlock & al. 794* (BR), EU543072, EU557767, –, –; ***Spermacoce hispida*** L., Sri Lanka, *Wanntorp & al. 2667* (S), EU543073, EU557768, AM939540, AM933017; ***Spermacoce ocymifolia*** Willd. ex Roem. & Schult. , Ecuador, *Bremer 3340* (UPS), –, –, AM939462, AM932951; ***Spermacoce prostrata*** Aubl., Colombia, *Andersson & al. 2078* (GB), –, EU557769, AM939541, AM933012; ***Spermacoce remota*** (Lam.) Bacigalupo & Cabral, French Guiana, *Andersson & al. 2016* (GB), –, EU557770, AM939542, AM933013; ***Spermacoce ruelliae*** DC., Gabon, *Andersson & Nilsson 2296* (GB), EU543074, EU557771, AM939543, AM933014; ***Spermacoce verticillata*** L., Madagascar, *De Block & al. 632* (BR), –, –, AM939544, AM933015; ***Stenaria nigricans*** (Lam.) Terrell, U.S.A., *Yatskievych 96-92* (MO), AF333373, EU557772, AM939546, –; ***Thamnoldenlandia ambovombensis*** Groeninckx, Madagascar, *De Block & al. 2328* (BR), GU475980, GU475976, –, –; ***Thecagonum biflorum*** (L.) Babu, cult. at BR, EU567459, EU557736, AM939494, AM932973; ***Thecagonum biflorum*** (L.) Babu, Nepal, *Neupane 20* (ODU), **KR005819, KR005757, KP994271, KR005784; *Thecagonum biflorum*** (L.) Babu, India, *Neupane 87* (ODU), **KR005820,** –, **KP994272, KR005785; *Thecagonum pteritum*** (Blume) Babu, Cambodia, *Neupane 149* (ODU), **KR005821, KR005758, KP994273, KR005786; *Thecagonum pteritum*** (Blume) Babu, Thailand, *Neupane 163* (ODU), **KR005822, KR005759, KP994274, KR005787; *Thecagonum strigulosum*** (Bartl. ex DC.) Terrell & H.Rob., voucher information not available (ODU), –, –, **KP994275, KR005788**