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Phylogeny of Asian *Homalomena* (Araceae) based on the ITS Region Combined with Morphological and Chemical Data

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Abstract—A phylogenetic analysis of the genus *Homalomena* (Araceae: Homalomeneae) based on the nITS region is presented. Eighty-nine taxa are included; representing all Asian supergroups, several Neotropical species currently assigned to *Homalomena*, and selected species of *Philodendron*. Asian *Homalomena* is well supported as monophyletic and excludes Neotropical *Homalomena*. The Cyrtocladon supergroup is monophyletic after transferring the Insignis complex and Havilandii complex into the Punctulata supergroup. The Homalomena and Chamaecladon supergroups are well supported. A reduced phylogeny of 20 accessions representing 15 taxa was used for subsequent morphological and chemical marker optimization. A constricted spathe and four stamens per staminate flower are plesiomorphic for *Homalomena.* Staminodes among the pistillate zone are lost three times independently in Homalomena supergroup, Punctulata supergroup, and *H. vivens*. Chemical markers identified from liquid chromatography-mass spectroscopy profiling provided an independent set of markers that further support the separation of Neotropical species of *Homalomena* from the Asian taxon. Three chemical markers at R_t 2.55 min, 2.69 min, and 2.90 min are shared among the majority of taxa sampled for Asian *Homalomena*, and Neotropical species currently assigned to *Homalomena* show two unique peaks at R_t 3.25 min and 3.54 min. Five chemical markers support the Cyrtocladon supergroup with the exception of *Homalomena vivens*. A chemical marker at R_t 3.60 min is plesiomorphic for the Chamaecladon, Homalomena and Punctulata supergroups. A chemical marker at R_t 2.80 min is apomorphic for the Chamaecladon supergroup, with a separate gain in *H. punctulata*. This study supports removal of the Neotropical species from *Homalomena*, redefines the morphological boundaries of *Homalomena* sensu stricto (i.e. the Asian species), and supports and refines the grouping of Asian species into supergroups.

Keywords—Borneo, character mapping, systematics, taxonomy.

Homalomena Schott is the most species-rich, taxonomically complex, and least well understood aroid genus in tropical Asia. The genus is estimated to comprise more than 500 species, making it the third-largest family after *Anthurium* Schott and *Philodendron* Schott (Boyce et al. 2010; Boyce and Croat 2011). Based on the current circumscription, *Homalomena* is distributed in the Neotropics and Asian tropics, with the overwhelming majority of species and greatest diversity in the tropical forests of South East Asia where there are three centers of diversity: Sumatra, Borneo, and New Guinea (Boyce and Wong 2008). Studies currently focus on Borneo where only 30 accepted names are available to date (P. C. Boyce, pers. obs.), of which 17 are recently described (Boyce and Wong 2008; Baharuddin and Boyce 2010; Boyce et al. 2010; Tung et al. 2010; Hoe et al. 2011a, b; Kurniawan et al. 2011; Wong and Boyce 2011; Wong et al. 2011). Despite the abundance of *Homalomena* specimens in herbaria, the majority of specimens are either undetermined or have incorrect determinations. Much of the material is effectively indeterminable owing to: (1) post-preservation depredation by beetles, and (2) specimens collected post-anthesis by which time critical floral morphologies, notably interpistillar staminodes, have been irreparably damaged during pollination. However, provided concise locality data are available, it is often possible to re-visit key localities, and prepare adequate samples (e.g. images, inflorescences in alcohol) for suspected novelties (Boyce and Wong 2008).

Homalomena has been previously divided into sections based upon the work of Schott (1860) and Engler (1912), with additions by Furtado (1939) and Hotta (1967). Mayo et al. (1997) recognize five sections: *Curmeria* (Linden & André) Engl. & K. Krause (including *Adelonema* Schott) restricted to the Neotropics; *Homalomena* ('*Euhomalomena*' of Engl. & K. Krause); *Cyrtocladon* (Griff.) Furtado; *Chamaecladon* (Miq.) Engl. & K.Krause, and *Geniculatae* M.Hotta. With the exception of *Geniculatae*, all have been recognised as genera at some point in their history. In previous papers (Boyce and Wong 2008; Ng et al. 2011; Wong and Boyce 2011), Asian *Homalomena* was divided into informal morphotaxon units, supergroups and complexes, as useful tools to facilitate taxonomic study until phylogenetic testing is undertaken. This approach has been used in other taxonomically intractable groups (e.g. *Alocasia* G.Don., *Schismatoglottis* Zoll. & Moritzi, *Pothos* L., and *Rhaphidophora* Hassk.; see Boyce 2000a, b, c, 2001a, b; Boyce and Hay 2001; Hay 1998; Hay and Wise 1991; Hay and Yuzammi 2000). The four sections of Asian *Homalomena* were reduced to informal supergroups (SGs): Homalomena, Chamaecladon, Cyrtocladon, and Punctulata (Boyce and Wong 2008; Ng et al. 2011), the last being a replacement name for Hotta's *Geniculatae*.

The Homalomena supergroup (SG) comprises medium to large erect to creeping plants with strongly aromatic tissues, pleionanthic or rarely hapaxanthic shoot modules, and spathes exceeding 1.5 cm long, with no or only a very weak constriction between the lower and upper spathe. Spathe movements during anthesis, where known, comprise simple gaping and closing of the spathe limb, and no spadix movements have been recorded, although in many species the staminate portion of the spadix elongates swiftly at anthesis until it protrudes from the spathe. The ovary is usually three- to four- locular, with the associated staminode equalling the pistil height, exceptionally staminodes are absent (*H. expedita*

A.Hay & Hersc.). Staminate flowers have three to four (rarely five to six) stamens with an expanded connective forming a cap over each stamen; the thecae dehisce laterally.

The Chamaecladon SG comprises minute to small, often creeping, less often erect plants with odorless, very rarely aromatic, vegetative tissues, and as far as is known, only pleionanthic shoot modules. Spathes are mostly less than 1 cm long, very rarely up to 1.5 cm long, with no constriction between the lower and upper spathe. Spathe movement during anthesis, where known, comprises simple gaping and closing of the spathe limb. No spadix movements have been recorded. The ovary is two to three locular, with the associated staminode much shorter than the pistil. Staminate flowers have two (seldom three) stamens, with an unexpanded connective, and thecae dehiscing terminally.

The Cyrtocladon SG comprises medium to very large erect to creeping plants with strongly aromatic tissues, pleionanthic (albeit very few species have been studied) shoot modules, and spathes exceeding 2 cm long (and often much longer), with a weak to pronounced constriction between the lower and upper spathe. All species so far studied undergo a complex series of seemingly coordinated spathe and spadix movements during anthesis. Ovaries are three to four locular, with the associated staminode equal to, or even very slightly exceeded by, the height of the pistil. Staminate flowers have three to four (rarely five to six) stamens and connectives are substantially expanded with thecae dehiscing laterally.

The Punctulata SG (previously known as Geniculata SG; Ng et al. 2011) comprises medium-sized aromatic plants, with pleionanthic shoot modules in which the leaves are frequently sub-distichous or distichous, the spathe more than 2 cm long, with a weak or moderate constriction. Staminate flowers each comprise 3–4 stamens with the connective expanded, and the thecae dehiscing laterally. Pistillate flowers lack associated interpistillar staminodes; the ovary is 4-locular.

Barabé et al. (2002) used the plastid *trnL* intron and *trnL–trnF* intergenic spacer to analyse *Philodendron* and *Homalomena*, with the result that two Neotropical *Homalomena* species were nested within *Philodendron*, rendering *Homalomena* sensu Mayo et al. (1997) polyphyletic. However, a multi-gene analysis by Cabrera et al. (2008) placed *Homalomena* sensu Mayo et al. (1997) as sister to *Philodendron* [based on two taxa, *H. wallisii* 'Harlequin' (a selection of a Neotropical species) and *H. magna* A.Hay (Papua New Guinea)]. Gauthier et al. (2008), focusing on *Philodendron*, resolved Neotropical *Homalomena* as sister to *Philodendron* but Asian *Homalomena* as basal to the entire clade, based on two ribosomal DNA nuclear markers: internal transcribed spacer (ITS), external transcribed spacer (ETS), and the chloroplast intron *rpl16*. However, Gauthier et al. (2008) included only two Asian species of *Homalomena*: *H. cochinchinensis* Engl. and *H. philippinensis* Engl.

Recent phylogenetic work provides compelling evidence that the stem node of Araceae is old (138 million years before present; Janssen and Bremer 2004; Nauheimer et al. 2012b). However, diversification of the extant species only started comparatively recently in *Anthurium* Schott (Carlsen 2011), the Colocasieae (Schott) Brongn. (Nauheimer et al. 2012a), and Schismatoglottideae Nakai (Wong et al. 2010; Low et al. 2011), and then followed rapid radiations. There is very low sequence divergence at the intrageneric level, and relatively short branches characterize the core of the crown clade. At the intergeneric level, the slowly evolving plastic region *matK* is suitable to infer relationships, while at the interspecific level, fast evolving nuclear spacers are more appropriate. So far there are very few phylogenetic studies on Araceae sampling the ITS region for low-level taxonomic to intertribal work. Exceptions are Buzgo et al. (unpubl. data), Gauthier et al. (2008), and Low et al. (2011). Low et al. (2011) showed ITS to be useful at a low taxonomic level in the Hottarum group (Araceae: Schismatoglottideae).

The two published comprehensive accounts of Araceae chemistry (Williams et al. 1981; Hegnauer 1986) sampled only a tiny percentage of the known species. However, overall it seems that aroid secondary metabolites are mainly saponins, phenolic compounds including flavonoids, cyanogenic glucosides, and calcium oxalate raphides (Hegnauer 1997). Some of these compounds are unique to the investigated taxa (e.g. sulphates of esters of sulphuric acid), while others are unique to the family (e.g. procyanidins and C-glycofavones; Williams et al. 1981). Sulphates of esters of caffeic acid are present in subfamilies Monsteroideae (67% of species), Philodendroideae (23%) and Pothoideae (20%) while non-sulphated caffeic acid derivatives with a free carboxylic group are common in subfamilies Colocasioideae (80%), Lasioideae (38%) and Pothoideae (20%). It is highly probable that the two types of acidic caffeic acid derivatives are involved in the irritating properties distinguishing most aroids (Williams et al. 1981). Kite et al. (1997) have shown that the presence of of 2,5-dihydroxymethyl-3,4-dihydroxypyrrolidine (DMDP) and cc-homonojirimycin (HNJ) in leaves of *Nephthytis* Schott, *Anchomanes* Schott, *Pseudohydrosme* Engl. (tribe Nephthytideae), *Aglaonema* Schott and *Aglaodorum* Engl. (tribe Aglaonemateae), which is congruent with the phylogeny of Cabrera et al. (2008). The above illustrates that chemical characters can complement molecular and morphological data in systematic studies.

Published chemistry research on *Homalomena* is somewhat patchy, focused mainly on species with purported medicinal application (e.g. *Homalomena occulta* (Lour.) Schott, *Homalomena aromatica* (Spreng.) Schott), and suffers from problems resulting from poor taxonomic identifications. *Homalomena aromatica* yielded 1.2% essential oil containing mainly monoterpenoids (Hegnauer 1986), with the rhizomes containing an essential oil with up to 80% linalool and several sesquiterpenoids (Sung et al. 1992; Singh et al. 2000). Rhizomes of plants identified as *H. occulta* were reported to yield various compounds of essential oil primarily composed of linalool and lower amounts of other monoterpenoids and sesquiterpenoids (Zhou et al. 1991; Elbandy et al. 2004; Hu et al. 2008; Tian et al. 2010). In the Malesian region, Wong et al. (2006) reported essential oil profiling for an undetermined *Homalomena* (misidentified as '*H. sagittifolia*'). Several pharmacology studies have been carried out on *H. occulta* and *H. aromatica* (Wang et al. 2007; Hu et al. 2008; Tian et al. 2010) that identified anti-microbial and anti-inflammatory activities. However, the name *H. occulta* is to be cautiously applied as the type (probably from Huế in Vietnam) is lost, and the material that Schott annotated as *H. occulta* consists of at least three species (Boyce and Li 2010).

Objectives*—*Homalomena is a large and taxonomically complex group in critical need of rigorous study to define species and resolve their phylogeny. Aside from a need to better understand the most abundant, species-rich and yet least understood mesophytic aroid genus in tropical Asia, an increase of activity in pharmaceutical research requires a basis in sound systematic understanding or risk being futile or even

harmful. This study focuses on resolving the phylogeny of *Homalomena* including verifying its monophyly, focusing on taxa from Malaysian Borneo, one of the main centers of diversity. Representative taxa for all the Asian supergroups are included: Homalomena, Chamaecladon, Cyrtocladon, and Punctulata. Neotropical species are included to test their congeneric status. Species of *Philodendron* are included for the same reason. Other objectives are to produce a testable phylogeny for *Homalomena*, to resolve the veracity of and internal topology of the proposed supergroups (Boyce and Wong 2008; Ng et al. 2011). The second part of the study focuses on the evolutionary patterns of eight morphological characters that are currently used to delimit supergroups. The third part of the study involves liquid chromatography-mass spectroscopy (LCMS) profiling for taxa sampled mainly from Batang Ai, Sri Aman, and Sarawak. The selected species are those highlighted by Christensen (2002) as having moderate to significant importance as medicinal plants among the indigenous Iban people of the area.

Materials and Methods

Taxon Sampling—Eighty-nine taxa were included for the analyses of ITS1, 5.8S, and ITS2 region of the nuclear rRNA genes (Appendix 1). Forty-four sequences were newly generated and deposited into GenBank under Accession numbers JQ955571–JX076808. Forty-five sequences from Gauthier et al. (2008) were obtained from GenBank. Forty-two taxa of Asian *Homalomena*, six of Neotropical *Homalomena*, and 39 of *Philodendron* are represented. Two outgroup taxa (*Philonotion americanum* (A.M.E. Jonker & Jonker) S.Y.Wong & P.C.Boyce and *Schismatoglottis nervosa* Ridl.) were selected from the Schismatoglottid Alliance (Wong et al. 2010). The outgroups were selected based on Cabrera et al. (2008) as ITS sequences from sister tribes of Homalomeneae (Culcasieae, Callopsideae and Anubiadeae) are not available. Voucher information and GenBank accession numbers for all taxa are provided in Appendix 1. The combined data matrix has been deposited to TreeBASE (study number S13375).

Twenty accessions representing 15 taxa were included for the LCMS study (Appendix 1). Except *H. expedita* and *H. wallisii*, all were collected from Nanga Sumpa, Batang Ai, Sarawak between 2009 and 2010. An outgroup, *Schismatoglottis nervosa*, was selected as a representative of tribe Schismatoglottideae with aromatic vegetative tissues.

DNA Extraction, PCR Amplification, and Sequencing—Total DNA was extracted using a modified version of the 2×CTAB protocol (Doyle and Doyle 1987) with the addition of PVP (Polyvinylpyrrolidone; Wong et al. 2010). ITS1, 5.8S subunit and ITS2 were amplified using the primer pairs 1F/1R and 3F/4R, respectively (White et al. 1990). Polymerase chain reactions (PCRs) were conducted in a total reaction volume of 20 µl comprising 1×buffer, 0.1 mM dNTP mix, 0.2 mM of each primer, 2.0 mM $MgCl_2$, 2 units *Taq* DNA polymerase and 2 µl of DNA extract. One to two µl of DMSO was added to each reaction to improve amplification. ITS fragments were amplified using standard cycling conditions. The PCR products were visualized on 1.5% or 2.0% agarose gels, and purified using a PCR purification kit (Fermentas, Vilnius, Lithuania). Purified products were viewed again using a 1% agarose gel, and if a single clear band was present the products were sent for sequencing in forward and reverse directions at First BASE Laboratories Sdn. Bhd., Selangor, Malaysia.

Sequence Alignment and Phylogenetic Analyses—Newly generated sequences of the ITS region were manually trimmed and assembled for each taxon. These sequences were combined with sequences from Gauthier et al. (2008) and Wong et al. (2010). The data matrix was aligned using MUSCLE (Edgar 2004) as implemented in Geneious Pro v5.6.4 (Biomatters Ltd., Auckland, New Zealand; www.geneious.com; Drummond et al. 2012) followed by minor manual adjustment following similarity criterion (Simmons 2004). Indels were treated as missing data. Phylogenetic analyses were performed with PAUP*4.0b10 (Swofford 2002) for maximum parsimony (MP) reconstruction with all characters equally weighted. The most parsimonious trees were obtained with heuristic searches of 1,000 replicates with random stepwise sequences addition, tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, with the multiple-tree option in effect, and saving up to 10,000 trees from each random sequence addition.

The most suitable nucleotide substitution model for each of the gene regions were selected in jModeltest ver. 0.1.1 (Posada 2008) using Akaike information criterion (AIC; Akaike 1974). General time reversible (GTR + I + G) was the nucleotide substitution model selected. Maximum likelihood (ML) analyses were carried out using RAxML 7.2.6 (Stamatakis et al. 2008). ML bootstrap values were obtained by running 10,000 replicates. Bayesian phylogenetic analyses were performed with MrBayes ver. 3.1.2 (Huelsenbeck and Ronquist 2001). Markov chain Monte Carlo (MCMC) was repeated twice to assure parameter convergence. The MCMC algorithm was run for 2,000,000 generations with one cold and three heated chains, starting from random trees and sampling one out of every 100 generations. Convergence was assessed by using the standard deviation of split frequencies as convergence index with values < 0.005 interpreted as indicating good convergence. The first 10% of trees were discarded as burn-in. Remaining trees were used to construct 50% majority-rule consensus trees.

Preparation of Extracts for Chemical Profiling—The petiole and leaf blades were air-dried for ca. 10 d and ground into fine powder. The ground material was extracted by soaking in methanol on an agitator at 110 rpm for 48 hr at ambient room temperature. This procedure was repeated three times to ensure total extraction. The combined methanol extracts were dried in vacuo and the dried crude extracts were kept at 0°C prior to analysis.

Chemical Profiling using Liquid Chromatography-Mass Spectroscopy (LCMS)—LCMS analysis of the crude extracts was performed using an Acquity™ ultra performance liquid chromatography (UPLC)-photo diode array (PDA) system coupled to a Synapt high definition mass spectrometry (HDMS) quadrupole-orthogonal acceleration time-of-flight (oaTOF) detector (Waters Corporation, Milford, MA) equipped with an electrospray ionization (ESI) source. The source capillary voltage and source temperature were set to 2.70 kV and 100°C, respectively. Collision energy was set to 6.0 V and dessolvation gas flow at 700 L/h. Tuning of the MS was carried out using leucine-enkaphaline (500 pg/mL; calculated [M+1]: 556.2771) while calibration of the spectrometer was performed using sodium formate (0.5 M). Accuracy of high resolution mass spectrometry (HRMS) analysis was confirmed with a standard run of caffeine (calculated 195.0882; measured 195.0879, 1.5 ppm). Separation was obtained on an Acquity BEH C18, 2.1×50 mm, 1.7 µm particle size UPLC column, with a constant flow rate of 0.5 mL/min eluting with a binary gradient solvent system of 100% of solution A (water with 0.1% formic acid) to 80% A in 3 min, 80–50% A from 3–4 min, 50–15% A from 4–5 min, 15–0% A from 5–6 min, and then held at 0% A or 100% of solution B (acetonitrile with 0.1% formic acid) for 4 min before conditioning back to 100% A and allowed to equilibrate for 2 min. The analysis was carried out in positive ESI mode. The crude extracts were dissolved in methanol (10 mg/mL), filtered and 3 µL injected onto the UPLC set-up.

Character Mapping—Morphological characters were selected based on those used to delimitate the supergroups of *Homalomena* (Boyce and Wong 2008; Ng et al. 2011). Ancestral morphological character states were reconstructed for one vegetative and seven reproductive characters: (i) Leaf blade posterior lobes: 0 = absence; 1 = presence; (ii) Spathe constriction: 0 = absence; 1 = presence; (iii) Lower/upper spathe length ratio: 0 = < 1; 1 = > 1; (iv) Spadix insertion: 0 = straight; 1 = oblique; (v) Staminodes among the pistillate zone (Interpistillar staminodes): 0 = absence; 1 = presence; (vi) Height of interpistillar staminode in comparison with associated pistil: 0 = equaling or exceeding; 1 = shorter; (vii) Stamen number per staminate flower: 0 = two stamens; 1 = four stamens; (viii) Shape of connective per stamen: 0 = not overtopping; 1 = overtopping. Additionally, twelve chemical markers were identified from the chemical profiling described above, and scored as presence/absence characters. Matrices were comprised of categorical data with all characters treated as binary. All characters are non-ambiguous. Character matrices were analysed in Mesquite ver. 2.7.4 (Maddison and Maddison 2010) using parsimony (unordered; Fitch 1971). The matrices were traced onto the maximum likelihood tree from RAxML analysis based on the ITS region to assess the phylogenetic value of the morphological and chemical characters.

Results and Discussion

Matrix Characteristics—The sequence pherograms for the ITS region provide a clear and unambiguous signal without any indication of polymorphisms; all PCR products were resolved as a single band. The length of ITS1 varied between 264 and 406 bp, and the length of ITS2 varied between

326 and 395 bp, while the length of the 5.8S gene bp was consistent among all the *Homalomena* taxa investigated. A total of 1,517 nucleotide positions (partial ITS1, 5.8S, and partial ITS2) were aligned: 541 characters were constant, 331 variable but parsimony uninformative, and 642 parsimony informative. Tree searches were limited to 100,000 trees of a length of 2,718 steps, Consistency Index (CI) = 0.57 and Retention Index (RI) = 0.78 (50% consensus tree is presented in supplementary data, Fig. S1).

Phylogenetic Analysis—*Homalomena* sensu Mayo et al. (1997) is polyphyletic and sister to the genus *Philodendron* (ML 84%, PP 1.00; Fig. 1). Neotropical *Homalomena* (indicated as clade N.W.H in Fig. 1) is monophyletic and sister to *Philodendron* subgenus *Pteromischum* (ML 61%, PP 0.86) (clade P. Pte.). Neotropical *Homalomena* is separated into two clades: Crinipes and Erythropus. Within the Asian *Homalomena*, Homalomena SG is monophyletic with *H. philippinensis* basal (ML 64%, PP 0.85). *Homalomena* sp. Ar3065 (West Sarawak) is strongly supported in the same clade with *H. curvata*. This is the Selaburensis complex (sensu Ng et al. 2011). *Homalomena* sp. Ar3047 forms a clade with *H. expedita* (ML 79%, PP 0.85). The Chamaecladon SG is poorly supported (ML < 50%, value not shown). Together, the Homalomena and Chamaecladon SGs form a group (ML 84%, PP 1.00). The Punctulata SG is strongly supported as monophyletic (ML 94%, PP 1.00). However, the Havilandii and Insignis complexes, previously placed in Cyrtocladon SG (Ng et al. 2011) fall into the Punctulata SG, a placement supported by the absence of interpistillar staminodes. This clade is moderately supported (ML 76%, PP 1.00).

The Cyrtocladon SG is strongly supported (ML 86%, PP 1.00). Within it, the Hanneae complex (with the inclusion of the single accession of the Rostrata complex and *H. clandestina* (Borneensis complex) is only weakly supported (ML 61%, PP 0.85) although support increased (ML 91%, PP 1.00) with the exclusion of the Rostrata complex. Interestingly, *Homalomena* sp. Ar3051 from the east coast of Peninsular Malaysia is placed together with the Hanneae complex from West Sarawak (ML 96%, PP 1.00), with these taxa separated from the remainder of the Hanneae complex. The Hanneae complex might be relicts from the Riau Pocket (Corner 1960). The Giamensis complex is strongly supported (ML 98%; PP 1.00). However, *H. vivens*, which was initially tentatively placed in the Hanneae complex, is sister to the Giamensis complex (ML 75%, PP 1.00). The Borneensis complex is strongly supported as basal to Cyrtocladon SG (ML 86%, PP 1.00).

Morphological Characters—The supergroup boundaries in *Homalomena* are based upon overall inflorescence shapes and sizes, the morphology of the sterile and fertile flowers, spathe and spadix movements during anthesis, and presence and absence of aromatic tissues. Of these morphological characters, eight morphological characters which delimit the supergroups and complexes in *Homalomena* are presented here (Fig. 2).

1. Leaf Blade Posterior Lobes—Posterior lobe definition follows Mayo et al. (1997, p.8, Fig. 6). The presence of leaf-blade posterior lobes is plesiomorphic in *Homalomena.* Posterior lobes are either independently lost twice in Chamaecladon and Punctulata SGs, or lost once (Chamaecladon SG) and gained once in Homalomena SG. The absence of posterior lobes is plesiomorphic for the Chamaecladon SG (and there maybe adaptive to rheophytism, the primary ecology of species of the Chamaecladon SG) and the Punctulata SG (including Insignis and Havilandii complexes).

2. Spathe Constriction—A constricted portion of the spathe occurring in many genera of *Araceae*; generally occurring at the point corresponding to the junction between the staminate and pistillate zones of the spadix (e.g. *Homalomena*), sometimes situated above the fertile zones (e.g. *Cryptocoryne*). Spathe constriction is plesiomorphic for *Homalomena* and lost once in the Homalomena and Chamaecladon SGs. Spathe constriction is present in Cyrtocladon SG, Punctulata SG and Neotropical *Homalomena*.

3. Lower/upper Spathe Length Ratio—The lower/upper spathe length comparisons are taken from inflorescences at anthesis. Except for the Giamensis and Borneensis complexes (Cyrtocladon SG) the length of the lower spathe is shorter than the upper spathe in *Homalomena*. The significance in this character state needs further investigation; it is possibly linked to accommodating different sizes of pollinators (Y. C. Hoe, pers. obs.).

4. Spadix Insertion—All Asian *Homalomena* have the spadix inserted directly (not obliquely) onto the peduncle; either with or without a naked stipe. By contrast the spadix of Neotropical *Homalomena* is inserted obliquely. Oblique spadix insertion is therefore an apomorphic character state for the Neotropical *Homalomena.*

5. Staminodes Among The Pistillate Zone (Interpistillar Staminodes)—The presence of staminodes among the pistillate zone (one staminode, rarely more, associated with each pistil) is plesiomorphic for the genus *Homalomena*. Staminodes are absent in the Homalomena SG, Punctulata SG, and *H. vivens* (Cyrtocladon SG).

6. Height Of Interpistillar Staminode In Comparison With Associated Pistil—In the Chamaecladon SG, interpistillar staminodes are much shorter (seldom exceeding half the pistil length) than the associated pistils whereas in the Homalomena and Cyrtocladon SGs they equal or slightly exceed the pistil.

7. Stamen Number Per Staminate Flower—Staminate flowers in *Homalomena* are always individually differentiated (although occasionally the differentiation is obscured by close-packing). Each staminate flower has either four or two stamens; flowers with four stamens are plesiomorphic in *Homalomena* with the Chamaecladon SG having two stamens per staminate flower.

8. Shape Of Connective Per Staminate Flower—Except for species of the (where known) fly-pollinated Chamaecladon SG, the connective is expanded and overtops the anthers, forming a rhomboidal plate when viewed from above. The connective in Chamaecladon SG is not at all expanded and the anthers are clearly visible.

Identification of Markers—From the chemical profiles retrieved from LC chromatograms, we analyzed the chromatograms for peaks common or unique to Asian *Homalomena* supergroups. Twelve chemical markers were selected and scored (supplementary data, Table S1). For common peaks, there are two observations worth noting. First, three markers (at R_t 2.55, 2.69, and 2.90 min) are detectable in all the supergroups analyzed (but not detected in several species) (Fig. 3). There is also a region of peaks between 5.90 min and 6.50 min observed in the chromatograms from all samples except *H. expedita* (Homalomena SG) (see supplementary data Fig. S2 for chromatogram). Analysis of UV-visible absorption of the peaks in this region indicated that all eluted peaks are

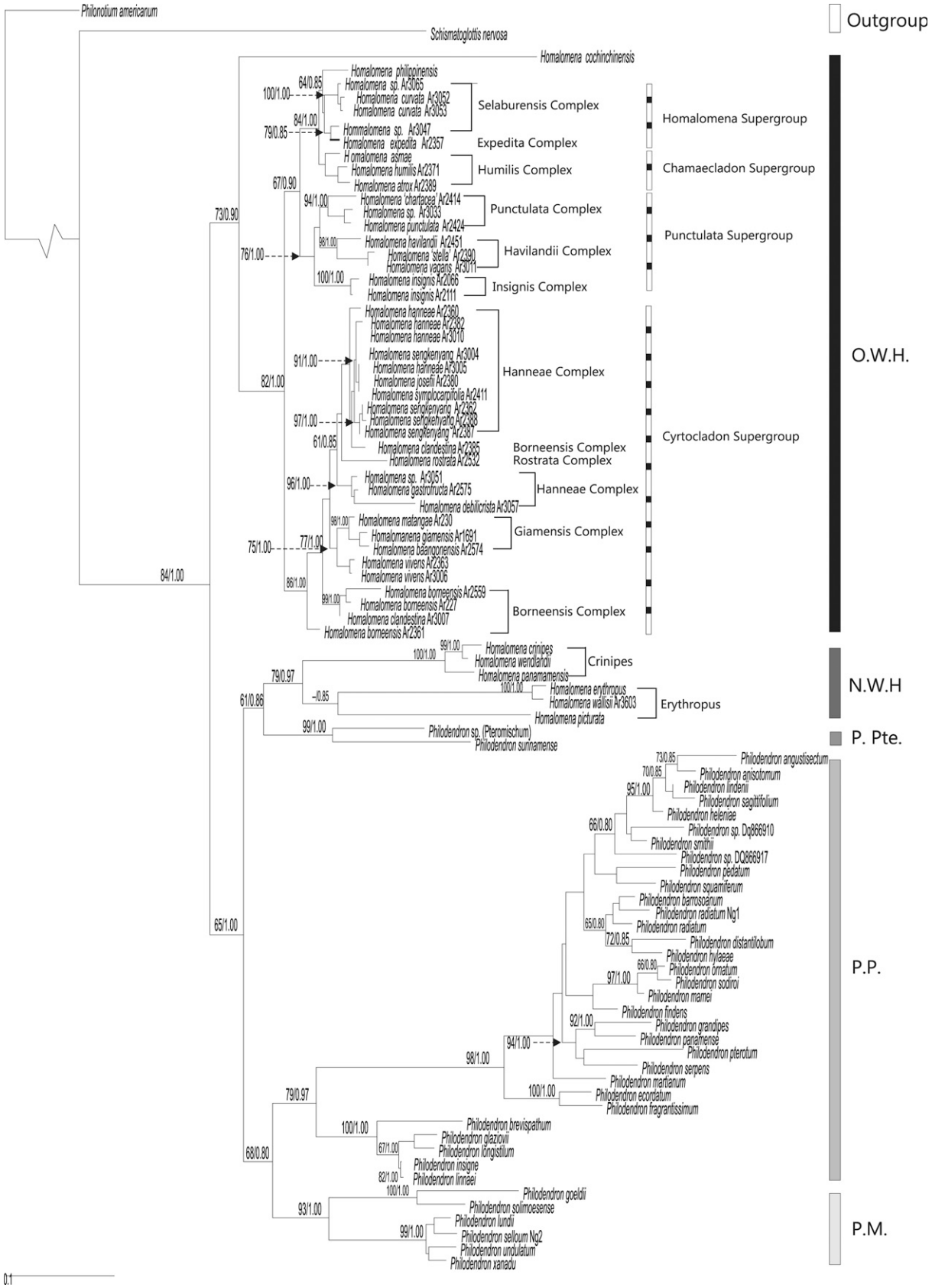

FIG. 1. Maximum likelihood phylogeny of 89 taxa (*Homalomena*, *Philodendron* and outgroups) based on ITS1, ITS2, and the 5.8S region of the nuclear rRNA genes. Clade O.W.H. represents *Homalomena* species from the Old World tropics, N.W.H = New World tropics, P. Pte. = *Philodendron* subgenus *Pteromischum*, P.P = *Philodendron* subgenus *Philodendron*, and P.M. = *Philodendron* subgenus *Meconostigma*. supergroups sensu Boyce and Wong (2008), and Ng et al. (2011) are indicated as black and white boxes. Complexes of the Asian *Homalomena* sensu Boyce and Wong (2008) and Ng et al. (2011), and Crinipes and Erythropus of the Neotropical *Homalomena* are indicated in black lines. Bootstrap (maximum likelihood) and posterior probability values are shown above the branch (bootstrap values < 50% are not shown).

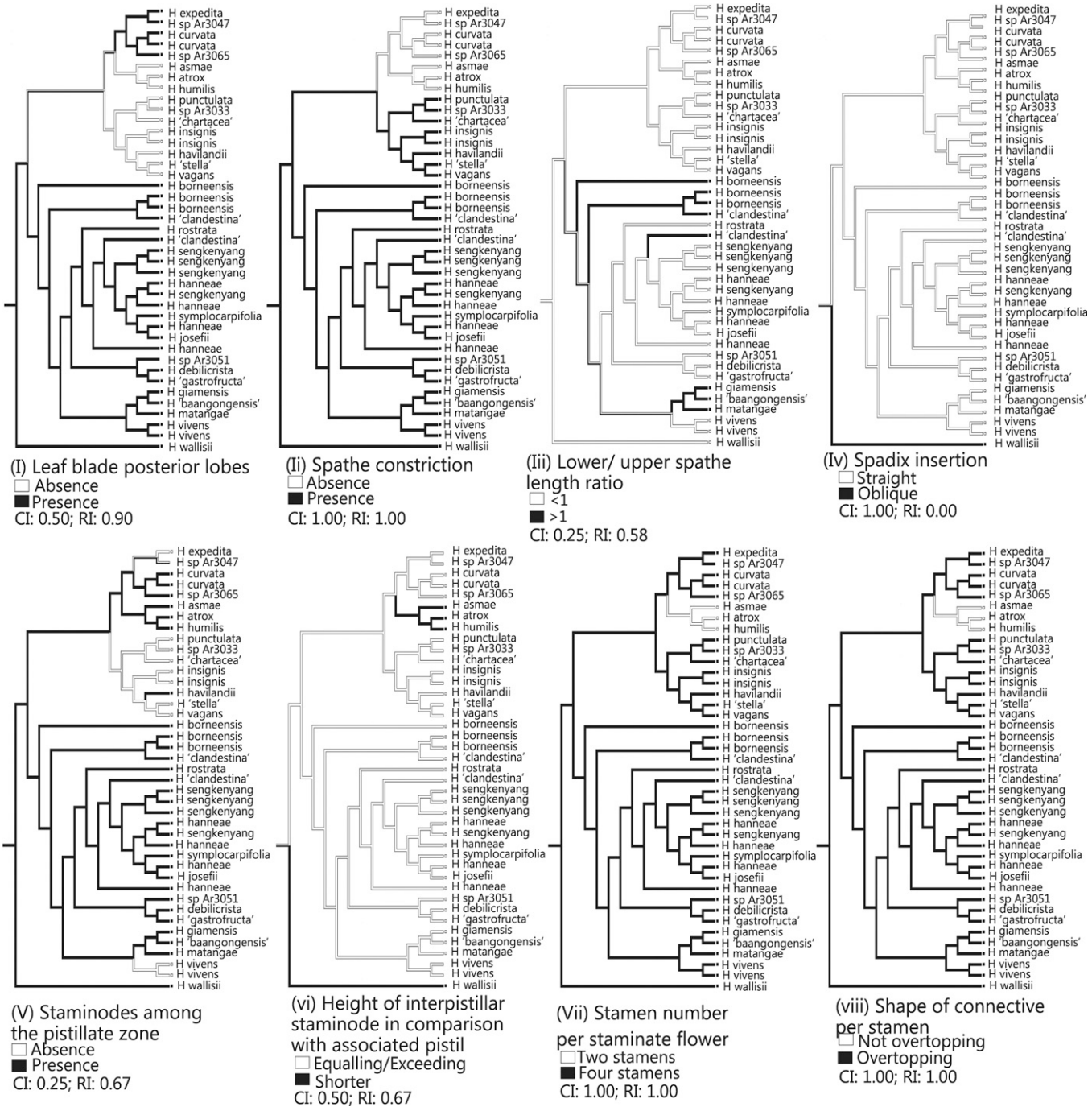

FIG. 2. Eight morphological characters optimized onto a summarized molecular phylogeny from Fig. 1 for *Homalomena*. (i) Leaf blade posterior lobes, (ii) Spathe constriction, (iii) Lower/upper spathe length ratio, (iv) Spadix insertion, (v) Staminodes among the pistillate zone (Interpistillar staminodes), (vi) Height of interpistillar staminode in comparison with associated pistil, (vii) Stamen number per staminate flower, and (viii) Shape of connective per stamen. Consistency index (CI) and retention index (RI) are shown for each morphological characters.

of chlorophyll-type structures with UV-visible absorption maxima at 226, 410, and 660 nm (Kobayashi et al. 2006), and hence not studied further in the character-mapping analysis.

Other than the markers common across many *Homalomena* taxa, there are a number of markers identified as unique to each supergroup. In the Cyrtocladon SG, five markers were found to be present in most of the members (R_t 3.74, 3.81, 3.88, 3.92, and 4.01 min) excluding *H. vivens*. However, these markers showed high homoplasies as the CI values ranged from 0–0.33 and RI, from 0–0.57. Two markers (R_t 2.80 min, CI = 0.50, RI = 0.67, and 3.60 min, CI = 0.50, RI = 0.80) were found to be shared by the Chamaecladon, Punctulata and Homalomena SGs. For Neotropical species (only *H. wallisii* was analyzed in the chemical profiling), two markers (R_t 3.25 and 3.54 min) were identified.

Identity of Markers—To characterize the identity of the twelve markers, all the samples were analyzed by mass spectrometry (MS) with the resultant MS data cross-referenced with a commercial database: Dictionary of Natural Products (Buckingham 2011). It was observed that most of the

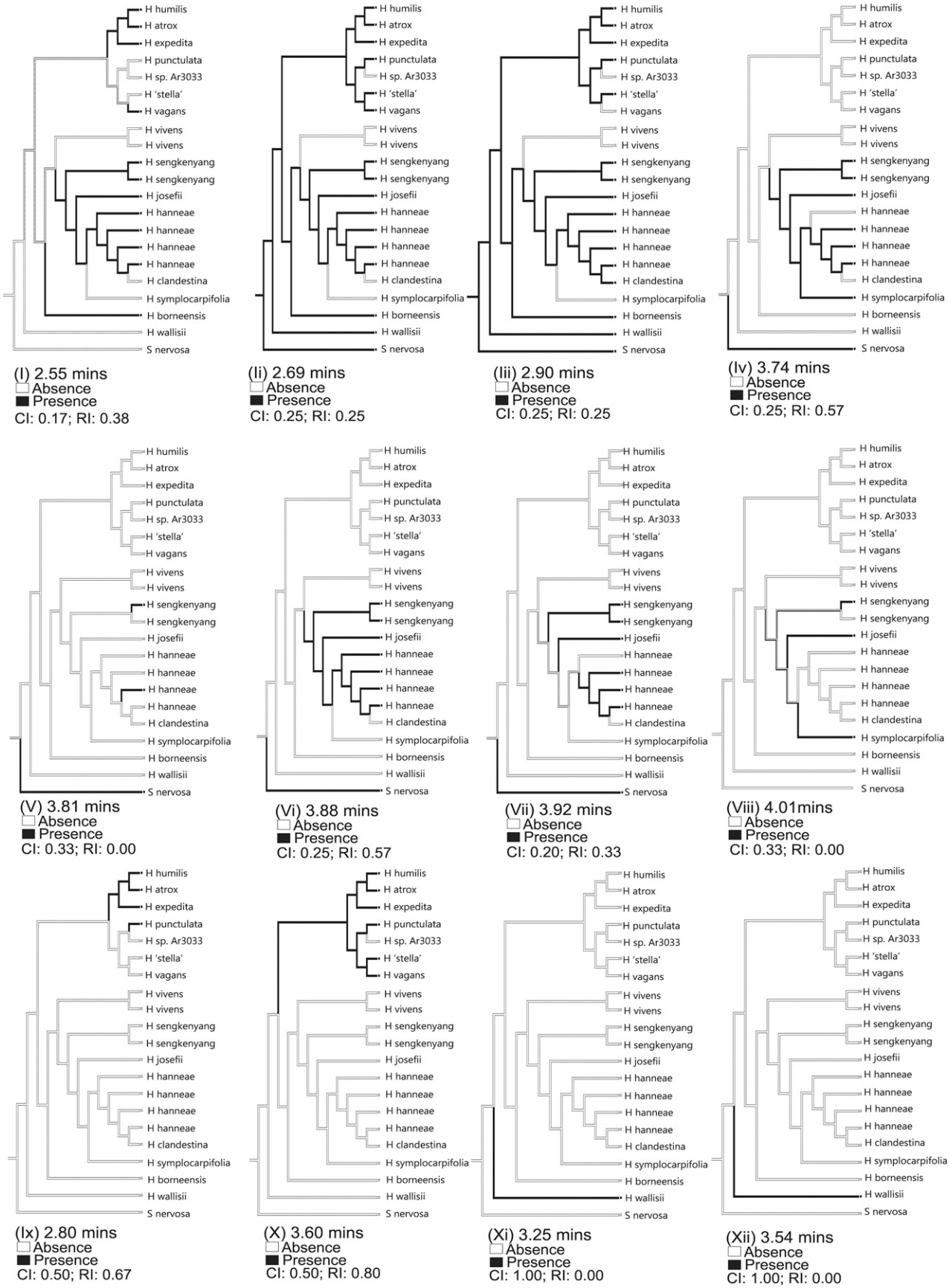

FIG. 3. Twelve chemical markers identified from LCMS profiling, optimized onto a summarized molecular phylogeny shown in Fig. 1 for *Homalomena*. Chemical markers: (i) to (iii) were detected in almost all the taxa analyzed; (iv) to (viii) are unique to the Cyrtocladon supergroup (SG); (ix) were detected in Chamaecladon SG, Homalomena SG and *H. punctulata*; (x) were detected in Chamaecladon, Homalomena and Punctulata SGs; (xi) and (xii) are unique to the Neotropical *Homalomena*. Consistency index (CI) and retention index (RI) are shown for each chemical characters.

identified markers have UV-visible profiles characteristic of flavonoids, which exhibit two major absorption peaks at the range of 300–380 nm and 240–280 nm (Ulubelen et al. 2005). This is in agreement with the chemotaxonomy records by Williams et al. (1981), which reported anthocyanin pigments and flavonoids to be among the common metabolites occurring in Araceae. Of the many types of flavonoids possible, the flavones C-glycosides or C-glycoflavones were found in a high majority (82%) of Araceae species studied (Williams et al. 1981). It is further noteworthy that from the systematic point of view, flavonoids have been qualified by Harborne (1973) as probably the most useful class of plant secondary metabolites. However, as flavonoids are a group of plant secondary metabolites known to be present in many plant families, the markers identified here may not be unique to *Homalomena*. Indeed, some of the markers that we observed in the Cyrtocladon SG were also found to be present in the outgroup, *S. nervosa*.

Homalomena, Currently a Polyphyletic Assemblage—The phylogeny and the associated data presented here strongly support generic separation of Asian *Homalomena* from the Neotropical species, with the generic name retained for the Asian species (the type is Asian). The estimated divergence between these two groups is relatively recent, at least 25 Ma during the Oligocene (Nauheimer et al. 2012b). The Neotropical *Homalomena* clade is supported by one morphological character (refer to Fig. 2): spadix insertion with the spadix of Neotropical *Homalomena* obliquely inserted on the lower spathe/peduncle junction as compared to a straight insertion and often free stipitate insertion in Asian *Homalomena*. Chemical markers are congruent with the phylogeny and morphological characters. Neotropical *Homalomena* form two clades: Crinipes and Erythropus (Fig. 1), with the species in the clades displaying morphological congruity. *Homalomena crinipes*, *H. wendlandii* and *H. panamamensis* share the presence of interpistillar staminodes and indumentose leaves, whereas, *H. erythropus* and *H. wallisii* lack interpistillar staminodes and have glabrous leaves. The specimen of *Homalomena picturata* included from Gauthier et al. (2008) is misidentified, and probably represents a taxonomic novelty; the herbarium specimen is a solitary plant with leaf blades on long, glabrous petioles quite different from the original (Type plant) illustration of *H. picturata* (Linden and André 1873), which is a clumping plant with short, pilose petioles. It is suspected that *H. 'picturata'* sampled here is closer to *H. kvistii* Croat.

Homalomena sensu stricto comprises four supergroups: Cyrtocladon, Chamaecladon, Homalomena, and Punctulata SGs. Cyrtocladon SG is monophyletic after the removal of the Havilandii and Insignis complexes into Punctulata SG. Cyrtocladon SG is sister to the other SGs, and is supported by, among others, having presence of posterior lobes on leaf blades, constricted spathe, and presence of staminodes in the pistillate zone. Five chemical markers were detected to be unique to most of the species of Cyrtocladon SG. Two chemical markers are unique and shared by most species of the Chamaecladon + Homalomena + Punctulata SGs. Among these three SGs, the Chamaecladon SG is morphologically most dissimilar to the other two SGs by having interpistillar staminodes shorter than the associated pistil, and staminate flowers each with two stamens with the connective not overtopping the thecae. Species of the Chamaecladon SG are observed to be visited only by *Colocasiomyia* (Diptera: Drosophilidae), whereas Homalomena and Cyrtocladon SGs are visited by a variety of beetles (Scarabaeidae: Rutelinae, Chrysomelidae, Nitidulidae, Staphylinidae), as well as by *Colocasiomyia*, and based on the damage to staminodes seemingly functioning as food rewards, are most probably beetle pollinated (Tung et al. 2010; Hoe et al. 2011a). The expanded connective in Cyrtocladon SG probably provides protection for the anthers from beetles, which are destructive pollinators. Absence of staminodes among the pistillate zone in the Punctulata SG and *H. expedita* (Homalomena SG) implies an alternative pollination mechanism in these taxa, and observations of *H. expedita* are that only *Colocasiomyia* attend the inflorescences (P.C.Boyce, pers. obs.); further investigations of pollination mechanisms are needed. Although species of Homalomena SG look vegetatively similar to Cyrtocladon SG, they are separated by the absence or only a very weak constriction between the lower and upper spathe, at anthesis the simple gaping and closing of the spathe, and by the absence of spadix movements. *Homalomena vivens* is distinctive in being the only species in Cyrtocladon SG lacking interpistillar staminodes.

All chemical compounds detected were of phenolic origin and suspected to be involved in the much-reported irritating properties that doubtless form part of the plant's chemical arsenal against herbivores. It is interesting to note that in the field vegetative tissues of *Homalomena* were almost never observed to be predated.

Taxonomic Implications—Neotropical *Homalomena* species are sister to *Philodendron* subgenus *Pteromischum*, and together are sister to the rest of *Philodendron*. The separation of the Asian and Neotropical *Homalomena* is at least as well supported as the separation of Neotropical *'Homalomena' + Pteromischum* from the rest of *Philodendron*. Several options exist:

Neotropical *'Homalomena'* (10 described species) may either be combined with *Philodendron* sensu lato, or with *Philodendron* subgenus *Pteromischum* as a genus (*Adelonema*) sister to the remainder of *Philodendron*. This would require recombining all but one Neotropical *'Homalomena'* species and all species of subgenus *Pteromischum* into *Adelonema* (Schott 1860) with *Elopium* (Schott 1865) as a generic synonym. Alternatively, the genera can be maintained as separate taxa, *Adelonema* and *Elopium*, involving moving all *Pteromischum* species into *Elopium*. This will result in *Adelonema + Elopium* being sister to the rest of *Philodendron*. These are patently significant taxonomic changes, and much more comprehensive sampling, especially of *Pteromischum*, is required before these formal changes are undertaken.

While it may seem implausible that a clade of lianas (*Pteromischum*) is more closely related to a clade of terrestrial mesophytes (*Adelonema*) than to an otherwise monophyletic and predominantly lianescent genus (*Philodendron*), closer examination of species of *Pteromischum* reveal striking dissimilarities with subgenera *Philodendron* and *Meconostigma*, and significant similarities to *Adelonema. Pteromischum* exhibits anisophyllous sympodial growth in adult vegetative shoots, with several to many leaves per stem article, while cataphylls are absent (or at least highly inconspicuous), and all expanded leaves have extensively sheathed petioles and lanceolate to elliptical, ovate, or occasionally subcordate blades. Both other subgenera of *Philodendron* (*Philodendron* and *Meconostigma*) undergo diphyllous sympodial growth, with only two leaves produced per article: a (usually) conspicuous cataphyll and a virtually sheathless expanded leaf that may, in some species, be deeply cordate (Grayum

1996). Schott (1860) further characterised *Pteromischum* as having "apically geniculate" petioles with the sheath persistent, and often involute and distally free, and with the spadix ultimately surpassing the spathe. *Adelonema* also has anisophyllous sympodial growth with several to many leaves per stem article, inconspicuous cataphylls (in contrast to the highly developed prophylls and cataphylls of the Asian *Homalomena*), and extensively sheathed petioles. In conclusion, at the very least *Adelonema* should be resurrected and all published species of Neotropical *Homalomena* transferred to *Adelonema*. The status and generic nomenclature of the species currently assigned to *Philodendron* subgenus *Pteromischum* awaits further investigation to include more species of *Adelonema* and a better representation of *Philodendron*.

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Appendix 1. List of specimens investigated: Taxa, collection locality, GPS where available, voucher, and GenBank numbers. An asterisk represents taxa included for LCMS profiling. Taxa are arranged alphabetically according to generic placement.

Homalomena asmae Baharuddin & P. C. Boyce. MALAYSIA. Perak: Hulu Perak, Tasik Banding, *Baharuddin Ar2597* (SAR), JX076771. ****Homalomena atrox*** P.C. Boyce, S.Y. Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2389* (SAR), JQ955571. ***Homalomena 'baangongensis'***. MALAYSIA. Sarawak: Kuching, Padawan, Sikog Village, 01.20 N; 110.20 E, *P. C. Boyce & S. Y. Wong Ar2574* (SAR), JQ955572. ***Homalomena borneensis*** Ridl. MALAYSIA. Sarawak: Kuching, Matang, Maha Mariamman Temple, 01.35 N; 110.13 E, *P. C. Boyce & Jeland Ak Kisai Ar227* (SAR), JQ955578; Sarawak: Kuching, Padawan, Giam Village, 01.19 N; 110.16 E, *P. C. Boyce & S. Y. Wong Ar2559* (SAR), JQ955573. ****Homalomena borneensis*** Ridl. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01°.12 N; 112.03 E, *P. C. Boyce et al. Ar2361* (SAR), JX076772. ***Homalomena 'chartacea'***. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar 2414* (SAR), JX076773. ***Homalomena clandestina*** P.C. Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2385* (SAR), JX076774. ****Homalomena clandestina*** P.C.Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *Ng Kiaw Kiaw & Jipom Ak Tisai Ar3007* (SAR), JX076775. ***Homalomena cochinchinensis*** Engl. VIETNAM. Ninh Binh Province: Cuc Phuong National Park, MBG77907, *Croat 77907* (MO), DQ866877. ***Homalomena crinipes*** Engl.–, MBG81956c, *Croat 81956* (MO), DQ866878. ***Homalomena curvata*** Engl. MALAYSIA. Pahang: Jerantut, Krau Wildlife Centre, 03.50 N; 102.13 E, *P. C. Boyce et al. Ar3052* (SAR), JX076776; Pahang: Jerantut, Krau Wildlife Centre, 03.49 N; 102.13 E, *P. C. Boyce et al. Ar3053* (SAR), JX076777. ***Homalomena debilicrista*** Y.C.Hoe. MALAYSIA. Sarawak: Kuching, Matang, Maha Mariamman Temple, 01.35 N; 110.13 E, *Y. C. Hoe Ar3057* (SAR), JQ955574. ***Homalomena erythropus*** Engl. ssp. ***allenii*** Croat.–, MBG79249, *Croat 79249* MO), DQ866879. ****Homalomena expedita*** A.Hay & Hersc. MALAYSIA. Sarawak: Kuching, Lundu, 01.39 N; 109.52 E, *P. C. Boyce Ar2357* (SAR), JX076778. ***Homalomena 'gastrofructa'***. MALAYSIA. Sarawak: Kuching, Padawan, Sikog Village, 01.20 N; 110. 20 E, *P. C. Boyce & al. Ar2575* (SAR), JQ955575. ***Homalomena giamensis*** L.S.Tung, S.Y.Wong & P.C.Boyce. MALAYSIA. Sarawak: Kuching, Padawan, Giam Village, 01.19 N; 110.16 E, *P. C. Boyce et al. Ar1691* (SAR), JQ929129. ****Homalomena hanneae*** P.C.Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2360* (SAR), JX076801, JX076802. ****Homalomena hanneae*** P.C.Boyce, S.Y.Wong & Fasihuddin. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2382* (SAR), JX076779. ****Homalomena hanneae*** P.C.Boyce, S.Y.Wong & Fasihuddin. Sarawak: Sri Aman, Lubok Antu, Batang Ai, *Ng Kiaw Kiaw & Jipom Ak Tisai Ar3010* (SAR), JX076803, JX076804. ****Homalomena hanneae*** P.C.Boyce, S.Y.Wong & Fasihuddin. Sarawak: Sri Aman, Lubok Antu, Batang Ai, *Ng Kiaw Kiaw & Jipom Ak Tisai Ar3005* (SAR), JX076780. ***Homalomena havilandii*** Ridl. MALAYSIA. Sarawak: Kuching, Bako National Park, *P. C. Boyce & Jeland Ak Kisai Ar2451* (SAR), JX076781. ****Homalomena humilis*** (Jack) Hook.*f*. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P C. Boyce et al. Ar2371* (SAR), JX076805, JX076806. ***Homalomena insignis*** N.E.Br. MALAYSIA. Sarawak: Kuching, Lundu, Gunung Gading National Park, 01.41 N; 109.51 E, *P. C. Boyce et al. Ar2066* (SAR), JX076782. Sarawak: Kuching, Matang National Park, 01.36 N; 110.11 E, *P. C. Boyce et al. Ar2111* (SAR), JX076783. ****Homalomena josefii*** P.C.Boyce & S.Y.Wong. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2380* (SAR), JX076784. ***Homalomena matangae*** Y.C.Hoe, S.Y.Wong & P.C.Boyce. MALAYSIA. Sarawak: Kuching, Matang, Maha Mariamman Temple, 01.35 N; 110.13 E, *P. C. Boyce & Jeland Ak Kisai Ar230* (SAR), JQ955577. ***Homalomena*** aff. ***panamense*** Croat & Marcell.–, MBG90162, *Croat 90162* (MO), DQ866880. ***Homalomena philippinensis*** Engl. PHILIPPINES. MBG52988, *Croat 52988* (MO), DQ866881. ***Homalomena picturata*** Regel.–, MBG90199, *Croat 90199* (MO), DQ866882. ****Homalomena punctulata*** Engl. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2424* (SAR), JX076785. ***Homalomena rostrata*** Griff. INDONESIA. Kalimantan: West Kalimantan: Sekadau, 00.00 N; 111.04 E, *P. C. Boyce & S. Y. Wong Ar2532* (SAR), JX076786. ****Homalomena sengkenyang*** P.C.Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2362* (SAR), JX076787; Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2387* (SAR), JX076788. ****Homalomena sengkenyang*** P.C.Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2388* (SAR), JX076789. ***Homalomena sengkenyang*** P.C.Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, *Ng Kiaw Kiaw & Jipom Ak Tisai Ar3004* (SAR), JX076790. ***Homalomena*** sp. MALAYSIA, Sarawak: Kuching, Padawan, Sikog Village, 01.20 N; 110.21 E, *P. C. Boyce et al.*

Ar3065 (SAR), JX076794. ***Homalomena*** sp. MALAYSIA Melaka: Machap, Hutan Simpan Bukit Sedana, 02.24 N; 102.20 E, *P. C. Boyce et al. Ar3047* (SAR), JX076792. ***Homalomena*** sp. MALAYSIA. Pahang: Jerantut, Krau Wildlife Centre, 02.37 N; 103.21 E, *P. C. Boyce & Ng Kiaw Kiaw Ar3051* (SAR), JX076793. ****Homalomena*** sp. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, *Ng Kiaw Kiaw & Jipom Ak Tisai Ar3033* (SAR), JX076791. ****Homalomena 'stella'***. MALAYSIA. Sarawak: Sarawak, Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2390* (SAR), JX076795. ****Homalomena symplocarpifolia*** P.C.Boyce, S.Y. Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, 01.12 N; 112.03 E, *P. C. Boyce et al. Ar2411* (SAR), JX076807, JX076808. ***Homalomena vagans*** P.C.Boyce. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, *Batang Ai, *Ng Kiaw Kiaw & Jipom Ak Tisai Ar3011* (SAR), JX076809. ****Homalomena vivens*** P.C.Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, *P. C. Boyce et al. Ar2363* (SAR), JX076796. ****Homalomena vivens*** P.C. Boyce, S.Y.Wong & Fasihuddin. MALAYSIA. Sarawak: Sri Aman, Lubok Antu, Batang Ai, *Ng Kiaw Kiaw & Jipom Ak Tisai Ar3006* (SAR), JX076797. ****Homalomena wallisii*** Regel. MALAYSIA. Sarawak: Kuching, cultivated ex Borneo Landscaping Nursery, *Ar3603* (SAR), JX076798. ***Homalomena wendlandii*** Schott.–, MBG85114a, *Croat 85114* (MO), DQ866883. ***Philodendron angustisectum*** Engl.–, JBM 2801–1950, *Gauthier 2* (MT), DQ866884. ***Philodendron anisotomum*** Schott.–, JBM2803–1950, *Gauthier 38* (MT), DQ866885. ***Philodendron barrosoanum*** G.S.Bunting.–, MBG81932a, *Croat 81932* (MO), DQ866886. ***Philodendron brevispathum*** Schott.–, JBM1518–2003,–, DQ866887. ***Philodendron ecordatum*** Schott. JBM145–2003, *Gauthier 1* (MT), DQ866890. ***Philodendron findens*** Croat & Grayum.–, MBG38218, *Croat 38212* (MO), DQ866892. ***Philodendron fragrantissimum*** Kunth.–, FG, *Barabé 77* (MT), DQ866893. ***Philodendron glaziovii*** Hook. *f.*–, BM7014–1998, *Gauthier 26*, DQ866894. ***Philodendron goeldii*** Barroso.–, JBM1699–1996, *Gauthier 27* (MT), DQ866895. ***Philodendron grandipes*** Krause.–, MBG79244, *Croat 79244* (M0), DQ866896. ***Philodendron heleniae*** Croat,–, MBG83278, *Croat 83278* (MO), DQ866897. ***Philodendron hylaeae*** G.S.Bunting.–, MBG84578a, *Croat 84578* (MO), DQ866898. ***Philodendron insigne*** Schott.–, FG, *Barabé 75* (MT), DQ866899. ***Philodendron lindenii*** Wallis.–, JBM7064–1998, *Gauthier 31* (MT), DQ866900. ***Philodendron linnaei*** Kunth.–, *Barabé 76* (MT), DQ866901. ***Philodendron longistilum*** Krause.–, MBG-11–17–78,–, DQ866902. ***Philodendron lundii*** Warm. MBG82932, *Croat 82932* (MO), DQ866903. ***Philodendron mamei*** Andre.–, BM7224–1992, *Gauthier 39* (MT), DQ866904. ***Philodendron martianum*** Engl.–, JBM2424–1946, *Chouteau 6* (MT), DQ866888. ***Philodendron ornatum*** Schott.–, JBM1511–1996, *Gauthier 33* (MT), DQ866891. ***Philodendron panamense*** Krause.–, MBG55184c, *Croat 55184* (MO), DQ866905. ***Philodendron pedatum*** Kunth.–, JBM2043–1997, *Gauthier 44* (MT), DQ866906. ***Philodendron pterotum*** K.Koch & Augustin.–, JBM1840–1955, *Gauthier 42* (MT), DQ866907. ***Philodendron radiatum*** Schott.–, JBM2802–1950, *Gauthier 6* (MT), DQ866908. ***Philodendron radiatum*** Schott. MALAYSIA. Penang: cultivated ex Penang Botanical Garden, *Ng 1* (SAR), JX076799. ***Philodendron sagittifolium*** Liebm.–, JBM3402–1983, *Gauthier 46* (MT), DQ866909. ***Philodendron selloum*** K.Koch. MALAYSIA. cultivated at Penang Botanical Garden, *Ng 2* (SAR), JX089318. ***Philodendron serpens*** Hook.–, MBG 97–100, *Croat 97–100* (MO), DQ866911. ***Philodendron smithii*** Engl.–, MBG64524, *Croat 64524* (MO), DQ866912. ***Philodendron sodiroi*** Hort.–, BM7163–1995, *Gauthier 36* (MT), DQ866913. ***Philodendron solimoense*** A.C.Smith.–, FG, *Barabé 60* (MT), DQ866914. ***Philodendron*** sp. (*pteromischa*).–, MBG84914, *Croat 84914* (MO), DQ866915. ***Philodendron*** sp.–, JBM1130–1952, *Gauthier 20* (MT), DQ866910. ***Philodendron*** sp.,–, JBM1659–1953, *Gauthier 19* (MT), DQ866917. ***Philodendron squamiferum*** Poepp. & Endl.–, JBM7009–1998, *Gauthier 45* (MT), DQ866916. ***Philodendron surinamense*** (Miq. ex Schott) Engl.–, FG, *Haig et al. 14* (KW), DQ866918. ***Philodendron undulatum*** Engl.–, JBM1930–52, *Gauthier 37* (MT), DQ866919. ***Philodendron xanadu*** Croat, Mayo & J. Boos.–, *MBG71897*, DQ866920. ***Philonotion americanum*** (A.M.E. Jonker & Jonker) S.Y.Wong & P.C.Boyce. FRENCH GUIANA. *Bogner 2911* (SAR), JN544445. ****Schismatoglottis nervosa*** Ridl. MALAYSIA. Sarawak: Kuching, Bau, Mount Bidi, 01.23 N; 110.07 E, *P. C. Boyce & Jeland Ak Kisai Ar944* (SAR), JX076800.