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

Wong Sin Yeng,[1,4] Tan Pei Jean,[2] Ng Kiaw Kiaw,[3] Ahmad S. Othman,[3] Lee Hong Boon,[2] Fasihuddin B. Ahmad,[1] and Peter C. Boyce[3]

[1]Department of Plant Science and Environmental Ecology, Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, 94300 Samarahan, Sarawak, Malaysia.
[2]Drug Discovery Laboratory, Cancer Research Initiatives Foundation, 12A Jalan TP 5, Taman Perindustrian UEP, 47600 Subang Jaya, Selangor, Malaysia.
[3]School Of Biological Sciences, Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Malaysia.
[4]Author for correspondence (sywong@frst.unimas.my)

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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*